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Chao, K-J, Chen, Y-S, Song, G-ZM et al. (4 more authors) (2017) Carbon concentration declines with decay class in tropical forest woody debris. Forest Ecology and Management, 391. pp. 75-85. ISSN 0378-1127

https://doi.org/10.1016/j.foreco.2017.01.020

Carbon concentration declines with decay class in tropical forest woody debris

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Abstract

Carbon stored in woody debris is a key carbon pool in forest ecosystems. The most widely-used method to convert woody debris volume to carbon is by first multiplying field-measured volume with wood density to obtain necromass, and then assuming that a fixed proportion (often 50%) of the necromass is carbon. However, this crucial assumption is rarely tested directly, especially in the tropics. The aim of this study is to verify the field carbon concentration values of living trees and woody debris in two distinct tropical forests in Taiwan. Wood from living trees and woody debris across all five decay classes was sampled to measure density and carbon concentrations. We found that both wood density and carbon concentration (carbon mass / total mass) declined significantly with the decay class of the wood. Mean (± SE) carbon concentration values for living trees were 44.6 ± 0.1%, while for decay classes one to five they were respectively 41.1 ± 1.4%, 41.4 ± 1.0%, 37.7 ± 1.3%, 30.5 ± 2.0%, and 19.6 ± 2.2%. Total necromass carbon stock was low, only 3.33 ± 0.55 Mg C ha^{-1} in the windward forest (Lanjenchi) and 4.65 ± 1.63 Mg C ha^{-1} in the lowland forest (Nanjenshan). Applying the conventional 50% necromass carbon fraction value would cause a substantial overestimate of the carbon stocks in woody debris of between 17% and 36%, or about 1 Mg of carbon per hectare. The decline in carbon concentration and the increase of variances in the heavily decayed class suggest that in high-diversity tropical forests there are diverse decomposition trajectories and that assuming a fixed carbon fraction across woody pieces is not justified. Our work reveals the need to consider site-specific and decay class-specific carbon concentrations in order to accurately estimate carbon stocks and fluxes in forest ecosystems. If the marked decline in carbon content with necromass decay is typical of tropical forests, the dead wood carbon pool in the biome needs revision and is likely to be overestimated.

Keywords: Carbon content, Decomposition, Necromass, Woody debris, Specific gravity, Tropical forest

1 Introduction

Natural forest ecosystems may help mitigate the increasing atmospheric carbon concentration caused by human activities (Malhi et al., 1999). Therefore, many studies have tried to estimate the carbon stocks and fluxes in forest ecosystems to evaluate their dynamics and carbon balance (e.g., Brienen et al., 2015; Rice et al., 2004; Saner et al., 2012; Wilcke et al., 2005). The major carbon pools in forest ecosystems include biomass (living trees), necromass (woody debris), and soil organic matter (Saner et al., 2012). Although necromass accounts for a smaller proportion (6% to 25%) of the vegetative mass pools than biomass, neglecting the carbon store and fluxes associated with woody debris can lead to inaccuracies and greater uncertainty when attempting to estimate the whole carbon balance in forest ecosystems (Chao et al., 2009; Nascimento and Laurance, 2002; Rice et al., 2004).

Many woody debris studies inventoried volumes and mass of woody debris, but not carbon concentration (Russell et al., 2015). Carbon concentration (also known as carbon fraction or carbon content; the proportion of carbon per unit dry mass) is in fact a rarely studied variable both for living trees (Martin and Thomas, 2011; Thomas and Martin, 2012) and woody debris (Russell et al., 2015). When no field data are available, the conventional approach is assuming that a fixed value, often 50%, of dry mass is carbon for living trees (e.g. Brienen et al., 2015; Houghton, 2005), woody debris (e.g. Chao et al., 2009; Coomes et al., 2002), or for both living and dead mass (e.g. Latte et al., 2013; Rice et al., 2004).

Some field-based studies have shown that carbon concentration can vary significantly for living trees (Elias and Potvin, 2003). For example, a recent review showed that carbon concentration of living trees can range from 41.9 to 51.6% in tropical species, 45.7 to 60.7% in subtropical and Mediterranean, and 43.4 to 55.6% in temperate and boreal species (Thomas and Martin, 2012). The Intergovernmental Panel on Climate Change (IPCC) also recommended that when forest-type-specific carbon concentration are not available, the value 47% as carbon should be used for tropical rainforests, in order to estimate national carbon storage and carbon emissions (IPCC, 2006). Therefore, the use of 50% as carbon concentration may be inappropriate, and may introduce errors of more than 10% into tropical forest biomass carbon estimates (Elias and Potvin, 2003). Thus, precise and large-scale estimates of forest carbon content cannot be achieved without fine-scaled and forest-type-specific carbon concentration values (IPCC, 2006).

The carbon concentration of woody debris also needs to be inventoried (Harmon et al., 2013; Russell et al., 2015; Weggler et al., 2012). There is yet no consensus about the relationships between carbon concentration and decay classes of woody debris for at least two reasons. First, decay classes of woody debris vary study-to-study. Classes are subjectively defined by researchers in the field, generally based on morphological traits and hardness of samples (Harmon et al., 1986; Russell et al., 2015). The commonly used number of decay class is a five-class system, but it can range from two to eight classes, depending on the researcher interest (Harmon et al., 1986; Russell et al., 2015). The general rule is that the less the structural integrity of woody debris, the higher the decay classes of the samples. Second, based on the few studies which have reported carbon concentration among decay classes in woody debris, their results are inconsistent, and have variable sample size. For example, in temperate and boreal forest studies, some found that the concentration barely changes with decay classes (Mäkinen et al., 2006; Weggler et al., 2012). However, one study did find that carbon concentration per unit dry mass can be low for the highly decomposed samples (Carmona et al., 2002). In contrast, another found a significant increase in carbon concentration for gymnosperms with increasing decay class (Harmon et al., 2013). Based on our review, only four studies have attempted to examine the carbon concentration of woody debris in tropical forests (Clark et al., 2002; Iwashita et al., 2013; Meriem et al., 2016; Wilcke et al., 2005). These suggest either similar carbon concentrations among decay classes, ranging from 40.0 to 47.9% (Iwashita et al., 2013; Meriem et al., 2016; Wilcke et al., 2005), or slight declines with decay class (Clark et al., 2002). The sample sizes of these tropical studies ranged from 16 (Wilcke et al., 2005) to 261 (Meriem et al., 2016) per study plot. As necromass is one of the important carbon pools in tropical forests (Chao et al., 2009), and one which may potentially be increasing as mortality rates increase with drought frequency (Brienen et al., 2015), it is critical to quantify and understand variations in carbon concentration both for living trees and woody debris in tropical forests.

Here, we investigate the wood density and carbon concentration values of woody debris among decay classes in tropical forests in Taiwan, as a contribution to improve the accuracy of carbon stocks and flux estimation in tropical forest ecosystems. Total necromass of two distinct forest types was measured in order to estimate the carbon stocks in these forests. We aimed to uncover patterns of carbon concentration change along the woody decomposition spectrum, by evaluating wood density and carbon concentration among living trees and woody debris within the same forests. We also aimed to sample at sufficient intensity to make robust conclusions about the direction of relationship, if any, between carbon fraction and woody decay. Other elements, e.g. nitrogen and hydrogen, were also measured in order to have an overview of chemical components in our samples.

2 Methods

2.1 Study sites

The study sites are located in the Nanjenshan Reserve, Kenting National Park, Taiwan. The mean temperature is 22.7 °C and mean annual rainfall ranges from 3252 mm in the lowland forests to 3989 mm on windward mountain summit in the reserve (Chao et al., 2010b). Soils are classified as Typic Paleudults, characterised by highly weathering pedogenesis and relatively low cation concentration in the slopes facing the northeast monsoon wind (Chen et al., 1997). Several Forest Dynamics Plots were established since 1989 in order to monitor the ecology of the forest ecosystems in this reserve (Chao et al., 2007; Chao et al., 2010b). We collected samples of living trees and woody debris in two forest types: one is a tropical lowland windswept evergreen dwarf forest (Lanjenchi Plot; 5.88 ha), and the other is a tropical lowland evergreen broad-leaved forests (Nanjenshan Plot I and Nanjenshan Plot II; 2.1 ha and 0.64 ha, respectively) (Chao et al., 2010b). The definition of forest types followed Taiwan Forestry Bureau (2011). Lanjenchi Plot suffers from wind of northeast monsoon in winters and its dominant species are Illicium arborescens, Castanopsis cuspidate var. carlesii, and Schefflera octophylla (Chao et al., 2010b). The forest canopy height varied from 3 m at the windward summit to 15 m in valley (Chao et al., 2010b). Both Nanjenshan Plots I and II are in a northeast monsoon-sheltered valley about 3 km away from the Lanjenchi

Plot, and their dominant species are Ficus benjamina, Psychotria rubra, and Dysoxylum hongkongense (Chao et al., 2010b). The forest canopy height is 15 to 20 m (Chao et al., 2010b). Samples collected from Nanjenshan Plots I and II were treated from the same forest as the plots were floristically and structurally similar to each other (Chao et al., 2010a; Chao et al., 2010b). Therefore, hereafter we denote the samples collected in Nanjenshan Plots I and II simply as Nanjenshan Plots. Typhoons in summer are the dominant disturbance type for both forests. For detailed vegetation composition please refer to Chao et al. (2010b).

2.2 Wood sample collection and property measurements

Wood cores of living trees were taken in January to February 2015 for wood density and carbon concentration measurements. Ten out of the top 15 dominant tree species of the Lanjenchi Plot (Chao et al., 2007) and of the Nanjenshan Plots (Chao et al., 2010a) were selected (Appendix 1). The ranks of species dominance were based on their basal area within each forest (as listed in Chao et al., 2010a; Chao et al., 2007). For each selected species, one to three living individuals were chosen for wood coring. For each sampled individual, one core was taken by an increment borer (number of sampled wood cores n = 30 in the Lanjenchi Plot; n = 27 in the Nanjenshan Plots; Appendix 1). The individuals were randomly selected from outside the study plots (within 500 m) in order to prevent damage to the tagged living individuals within the Forest Dynamics Plots. We only sampled individuals with DBH (diameter at 1.3 m height) ≥ 7 cm, in order to reduce the risk of mortality caused by wood core sampling. We assumed that these samples from dominant species represent plot-level averages of living trees.

Woody debris is defined here as all dead, woody material of trees with diameter larger than 1 cm. We walked along the four border lines of each plot, and collected woody debris samples outside the plots for wood density measurement. These samples were collected in July 2012 outside the Lanjenchi Plot (woody debris, n = 378) and in July 2009 outside the Nanjenshan Plots I and II (woody debris, n = 357). Carbon concentration samples were collected in February 2013 within the plots (Lanjenchi Plot, n = 95 and the Nanjenshan Plots, n = 95), avoiding those woody debris crossed by the volume transect lines. As it is very difficult to identify the species of woody debris in species-rich tropical forests, we intended to collect a plot-level representative sample pool. This meant that samples were collected throughout the plots to represent dominant species and microhabitats in our plots.

We used the five decay class system to classify the woody debris samples, based on morphology and hardness observed in the field (modified from Harmon et al., 1986) (Table 1). Living trees were designated as having decay class 0 in our study. To evaluate whether necromass decay class classification depended subjectively on individual investigators or not, we performed a simple analysis by comparing decay class classification among two main investigators (YSC and CML) with 455 woody debris samples, each scored independently. We found that 83.3% of the samples were classified in the same decay class. For 6.8% of samples YSC scored 1 decay class lower than CML, for 9.7% of samples that YSC scored 1 decay class higher than CML, and for 0.2% of the samples (one sample) YSC scored 2 decay classes higher than CML. The findings suggested that there is some small between-researcher variation in the subjective classification (uncertainty), but that there was no systematic difference either low or high (paired two-tailed t-test, $p = 0.092$). The penetrometer method for determining the decay class (Larjavaara and Muller-Landau, 2010) is not suitable for our study sites since the majority of woody debris pieces in the field are smaller than 20 cm in diameter.

Table 1. Description of woody debris decay classes (modified from Harmon et al., 1986).

Decay Class	Description	Characteristics
0	Living tree	Alive
1	Intact	With intact bark or fingers cannot press into the wood at all
2	Slightly decayed	With some signs of decay on the surface but still relatively hard
3	Intermediate	Without bark or nails can press into the woods; hardness intermediate
4	Slightly rotten	Can become fragments when pressed hard
5	Rotten	Easily become fragments when pressed lightly

The majority of samples (living trees and woody debris) were taken back to the laboratory, in the form of wood cores, wood disks or chunks. For wood density (dry weight/volume) measurements, fresh volumes were measured by the water displacement method (Chave et al., 2006). Some samples in the decay class five (59 out of 73 samples) were too fragile to be measured by the water displacement method. These samples were collected in the field by a fixed-volume cup (volume = 33.07 ml). The fixed-volume cup can assist wood density measurement and avoid seriously fresh volume compaction when taking those samples back to the laboratory. All samples for wood density measurement were oven dried (65 ºC for living woods and 70 ºC for woody debris) until the weight of samples was relatively constant. Wood density (ρ; g cm^{-3}) was calculated as the ratio of oven-dry weight (g) to fresh volume (cm^3) (total n = 792, including living trees (n = 57) and woody debris (n = 735)).

For woody debris carbon concentration measurements, samples were collected in the field in the form of woody disks or chunks. As there is no need to take fixed volume samples for carbon concentration measurement, fragile samples were collected and placed into envelopes. Although Harmon et al. (2013) have demonstrated that bark could have higher carbon concentration than heartwood and sapwood in temperate and boreal forests, we did not separate our woody debris samples into tissue types. This is because bark can-not be reliably distinguished from other tissues types in heavily decayed samples in our sites. All collected samples were oven-dried at 65 ºC for one week. Once the weight was constant, a cross section of each sample was sawed to collect a set of well mixed sawdust, representing its proportion of tissue types. Each set of sawdust was ground into powder using a mortar and pestle. Wood cores from living trees were similarly ground from bark to heartwood. The equipment (saw, mortar, and pestle) was cleaned with a gas gun to prevent any between sample contamination. For each sample, the finely ground powders were collected and well-mixed. A fine subsample of these powders (1.3 to 3.9 mg) was put into a tin capsule for weight measurement. For each piece of wood two powder samples were used to derive each piece's average carbon concentration and nitrogen concentration values. Acetanilid (71.09% carbon (C), 10.36% nitrogen (N), and 6.71% hydrogen (H)) was used as a standard for analysing the C, N and H elements in the samples. Total sample size of element concentration analyses (C, N and H) was 247, including 57 living trees and 190 woody debris. The measurements were conducted using Elemental analyzers in National University of Tainan (2400 Series II CHNS/O Analyzer, Perkin Elmer, California, USA; n = 43) and in National Chung Hsing University (vario EL III CHNS/O Analyzer, Elementar Analysensysteme GmbH, Hanau, Germany; n = 204).

Six samples at the decay class five (three samples from the Lanjenchi Plot and three from the Nanjenshan Plots) were subjectively selected based on their carbon concentrations for further chemical element analysis in oxygen (O), sulphur (S) and wood ash percentages. The vario EL III CHNS/O Analyzer in National Chung Hsing University (Elementar Analysensysteme GmbH, Hanau, Germany) was used for the oxygen and sulphur analyses. The standard for analysing the oxygen is Benzoic acid (26.20% oxygen), and for analysing the sulphur is Sulfanilic acid (18.50% sulphur). Wood ash percentage was determined in an ashing furnace (Carbolite CWF 13/5 Laboratory Chamber Furnace, 5 Liters, Carbolite, UK) by heating to 550 to 600 °C for 24 h. After the weights of samples have become relatively constant, the remaining ash samples were weighted for calculating ash percentages.

In the literature, the temperature required to dry the carbon concentration samples ranges from freeze-drying conditions (Martin and Thomas, 2011), 55 ºC (Harmon et al., 2013), 65 ºC (Weggler et al., 2012), 80 ºC (Clark et al., 2002), and 110 ºC (Martin and Thomas, 2011). We chose to use 65 ºC as a trade-off between the loss of both water and of volatile carbon at high temperatures. This is because wood dried at 105 ºC can increase about 0.8% to 1% carbon content (due to additional dehydration) (Weggler et al., 2012) but can also cause loss of volatile carbon (about 2.48%) (Martin and Thomas, 2011).

2.3 Necromass estimation

Necromass is estimated as the product of volume and wood density. We measured the volumes of two types of above-ground woody debris (fallen and standing) in the Lanjenchi and Nanjenshan plots annually since 2012. Necromass in the Lanjenchi Plot has been inventoried four times (2012, 2013, 2014, and 2015), and in the Nanjenshan Plots three times (2013, 2014, and 2015). We used the line-intersect method for quantifying fallen woody debris (van Wagner, 1968) and the plot-based method for standing woody debris, such that standing woody debris on either side (5 m) of the line-intersect transects (i.e. 10 m width in total) were recorded. Fallen woody debris was defined as those fragmented woody branches or trunks either lying on the ground or stuck above-ground level. All fallen woody debris with intercepted diameter ≥ 1 cm was measured, and its diameter, void proportion, decay class and locality were recorded. Standing woody debris was defined as those dead trunks still upright and rooted to the soil. Void proportion is defined as the proportion of hollow space observable from the cross section at the ends of woody debris pieces. Dead re-sprouts were also considered as standing woody debris. All standing woody debris with diameter ≥ 1 cm at base (close to ground) and ≥ 0.02 m in length within the sampled quadrats was measured. The measurements made included base diameter, void proportion, decay class, top diameter (where ≥ 1 cm or equal to 1 cm), and height. The top diameters and height of the main trunk of standing dead wood were all visually estimated, using the hands-raised height of researchers (ca. 2 to 2.2 m) as a scale. Any remaining fine branches on top of standing woody debris were ignored, as the volume is small and visual estimates of this fraction would lack accuracy; we focused on the main trunk of standing woody debris and it is therefore likely we very slightly underestimated total woody debris volume.

Five transects were established in Lanjenchi, five in Nanjenshan Plot I, and three in Nanjenshan Plot II. These were oriented a priori along two perpendicular directions, east to west and north to south, in order to reduce the possibility of systematic bias affecting the necromass estimates (Bell et al., 1996). In the Lanjenchi Plot, three of the transects were oriented from east to west, with total lengths of 198, 200, and 280 m, respectively, and two oriented from north to south with total lengths of 194 and 198 m. In Nanjenshan Plot I, two transects were oriented east to west with total lengths of 100 and 105 m, and three from north to south with total lengths of 105, 105 and 111 m. In Nanjenshan Plot II, one transect was oriented from east to west, with total length of 60 m, and two from north to south with total lengths of 60 and 64 m.

Volumes of fallen woody debris were estimated using the method proposed by van Wagner (1968):

$$V = (\pi^2 \sum d^2) / 8 L, \qquad \text{eqn 1}$$

where V is the volume at unit area (m^3 ha^{-1}), d is the intercepted diameter (cm) for each fallen woody debris, and L in the total length (m) of each transect. If void proportion was recorded in the field, the d^2 of each sample was further multiplied by (100 % − void proportion (%)) to exclude void space. The averages of the plot-level volumes of fallen woody debris were weighted by transect length.

Volumes of standing woody debris were estimated using the Smalian's formula (Phillip, 1994):

$$v = (\pi/8) \times L_S \times (d_b^2 + d_t^2), \qquad \text{eqn 2}$$

where v is the volume (m^3) of the target standing woody debris, d_b and d_t (m) are the diameters at base and top, respectively, and L_S (m) is the length of the target standing woody debris. If void proportion was recorded in the field, v was further multiplied by (100 % − void proportion (%)). The averages of the plot-level volumes of standing woody debris were weighted by transect length.

Plot-level variance (σ^2) values were also weighted by transect length as suggested by (Keller et al., 2004).

$$\sigma_i^2 = \frac{\left[\sum L_j (V_{ij} - \bar{V}_i)^2\right]}{\left[(n-1)\sum L_j\right]}, \qquad \text{eqn 3}$$

where L_j is the length of each transect; V_{ij} is the measured volume of each transect j (m^3 ha^{-1}) at the decay class i; $\bar{V}_i$ is the weighted average of each plot at the decay class i; n is the number of sampled transects. Standard error of the mean (SE) was calculated as $\sigma/\sqrt{n}$. Plot-level SE is the sum of each SE at each decay class.

Necromass of each decay class is calculated by $M_i = \rho_i \times V_i$, where M_i is necromass at decay class i, ρ_i is average wood density at decay class i and V_i is volume at decay class

i. Carbon stock of each decay class is calculated by $CS_i = c_i \times M_i$, where CS_i is carbon stock at decay class i, c_i is carbon concentration at decay class i and M_i is necromass at decay class i.

The standard error of M_i is

$$SE_{M_i} = SE_{\rho i} \times V_i + SE_{V_i} \times \rho_i, \qquad \text{eqn 4}$$

where $SE_{\rho i}$ and SE_{V_i} are the standard errors in density and volume at decay class i, respectively (Keller et al., 2004). The same function was applied for the standard error of carbon concentration.

2.4 Statistical analysis

Weighted and unweighted linear regressions were used to find the relationships between dependent and independent variables. When a dependent variable y (e.g. wood density, carbon concentration, or nitrogen concentration) had homogeneous variances (σ^2) for different values of an independent variable x (e.g. decay class), then unweighted linear regressions were applied. We tested whether residuals varied with the fitted values of independent variables (Appendix 2), indicating that y did not have homogeneous σ^2 with decay class, and in these cases a weighted regression was used (James et al., 2013). The weights for each independent variable value, x, were the inverse of an estimated variance function ($\frac{1}{\widehat{\sigma}^2(x)}$), where $\widehat{\sigma}^2(x)$ is the estimated variance function (Appendix 3). Weighted and unweighted linear regressions were performed with the lm() function in the program R, version 3.3.0 (R Core Team, 2016). Other statistical analyses were carried out by IBM SPSS Statistics v. 20 (IBM Corporation, New York, USA).

3 Results

3.1 Wood density and carbon concentration of living trees

For living trees, carbon concentration (% carbon per unit mass; C_{alive}) had a significant relationship with the wood density (g cm^{-3}) of living trees (ρ_{alive}) (Fig. 1a), whereas nitrogen concentration (%) did not (Fig. 1b). The results showed that for living trees, species with high wood density are likely to also have high carbon concentration (Fig. 1a).

3.2 Wood properties among decay classes

Wood density and carbon concentration of living trees and woody debris decreased with decay class in the study plots (Table 2), whereas nitrogen concentration has an increasing trend (Table 3). There was a significant difference between plots in wood density values and nitrogen concentration, such that wood in the Lanjenchi Plot had higher wood density and lower nitrogen concentration than in the Nanjenshan Plots (Mann-Whitney U tests, both p values < 0.001; Table 2; Table 3). However, there was no significant difference between plots in carbon concentration values (Mann-Whitney U test, $p = 0.627$) (Table 2).

As preliminary tests found that neither dependent variable had constant variance (Appendix 2), weighted regressions were used to find the best-fitted mean functions and variance functions (Fig. 2). Notably, the mean function of carbon concentration declined with decay classes. Moreover, the conventional value 50% was significantly higher than carbon concentration of both living and woody debris samples (one sample t-test, $p < 0.001$; Fig. 2b). The variances of wood density, carbon concentration, and nitrogen concentration all increased with decay classes, indicating that the higher the decay classes, the higher the variability (Fig. 2).

Nitrogen concentration (%) in both plots increased slightly with decay classes (Table 3; Fig. 2c). In contrast, the patterns of C:N ratio decreased significantly from living trees to heavily decayed woody debris (decay class 5) (two-way ANOVA, ln transformed C:N ratio, decay class $F_{[5, 247]} = 14.264$, $p = 0.006$; plot $F_{[1, 247]} = 9.345$, $p = 0.028$; Table 3). There is no significant relationship between carbon concentration and nitrogen concentration (Fig 3a), but the relationship between carbon concentration and hydrogen concentration is significantly positive for all the living trees and woody debris samples (Fig. 3b).

To better understand the chemical properties of decayed wood, we further examined the proportion of oxygen, hydrogen, sulphur, and ash of six pieces in the decay class five (Fig. 4). The six pieces were subsampled from the decay class five pool (three samples from the Lanjenchi Plot and three samples from Nanjenshan Plots). The samples were subjectively selected in order to represent a wide range of carbon concentration (ranging from 5.63% to 44.33%). Examining the six samples, we found a significant negative relationship between ash (%) and carbon (%), suggesting an accumulation of inorganic elements with the decay of carbon. Ash concentration can reach values as high as 87%. Other elements had positive or no relationships with carbon (%) (Fig. 4).

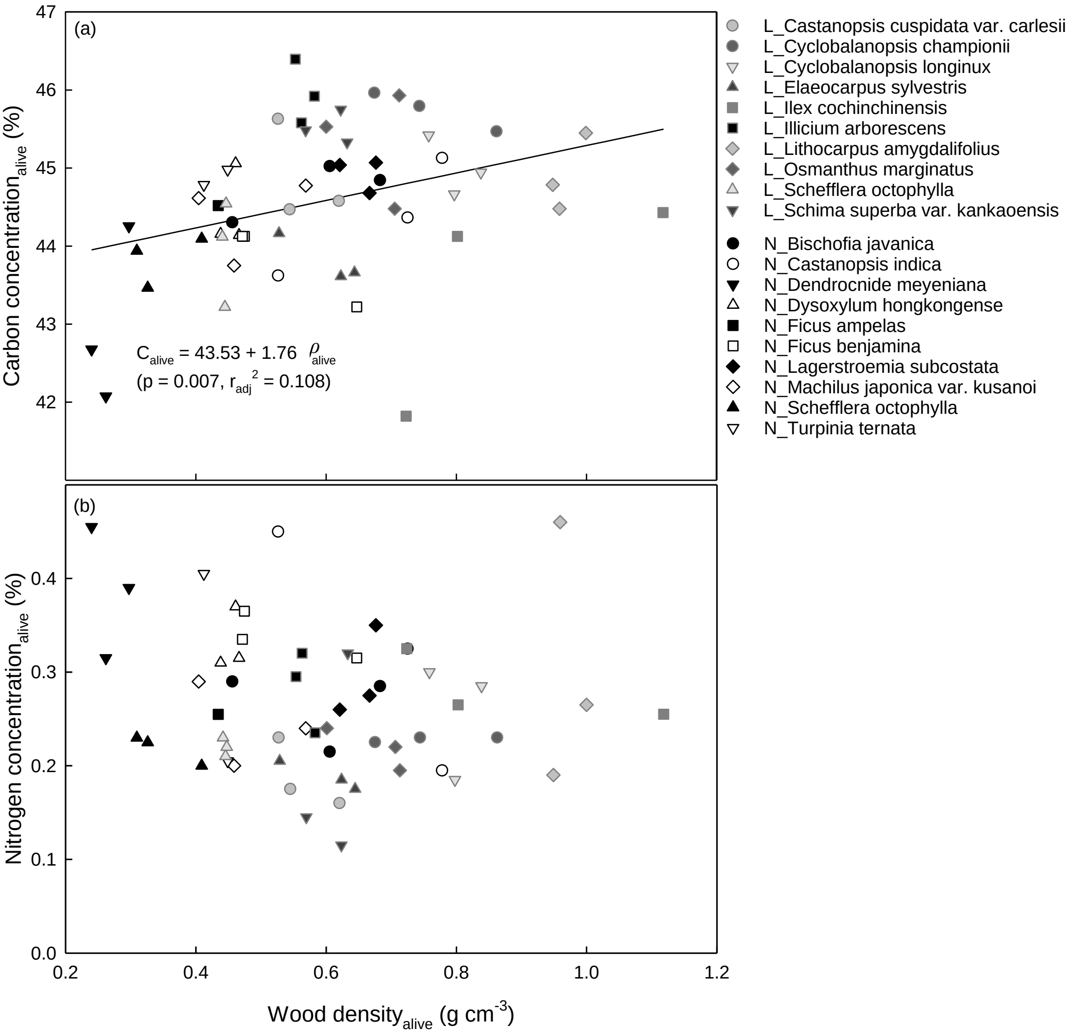
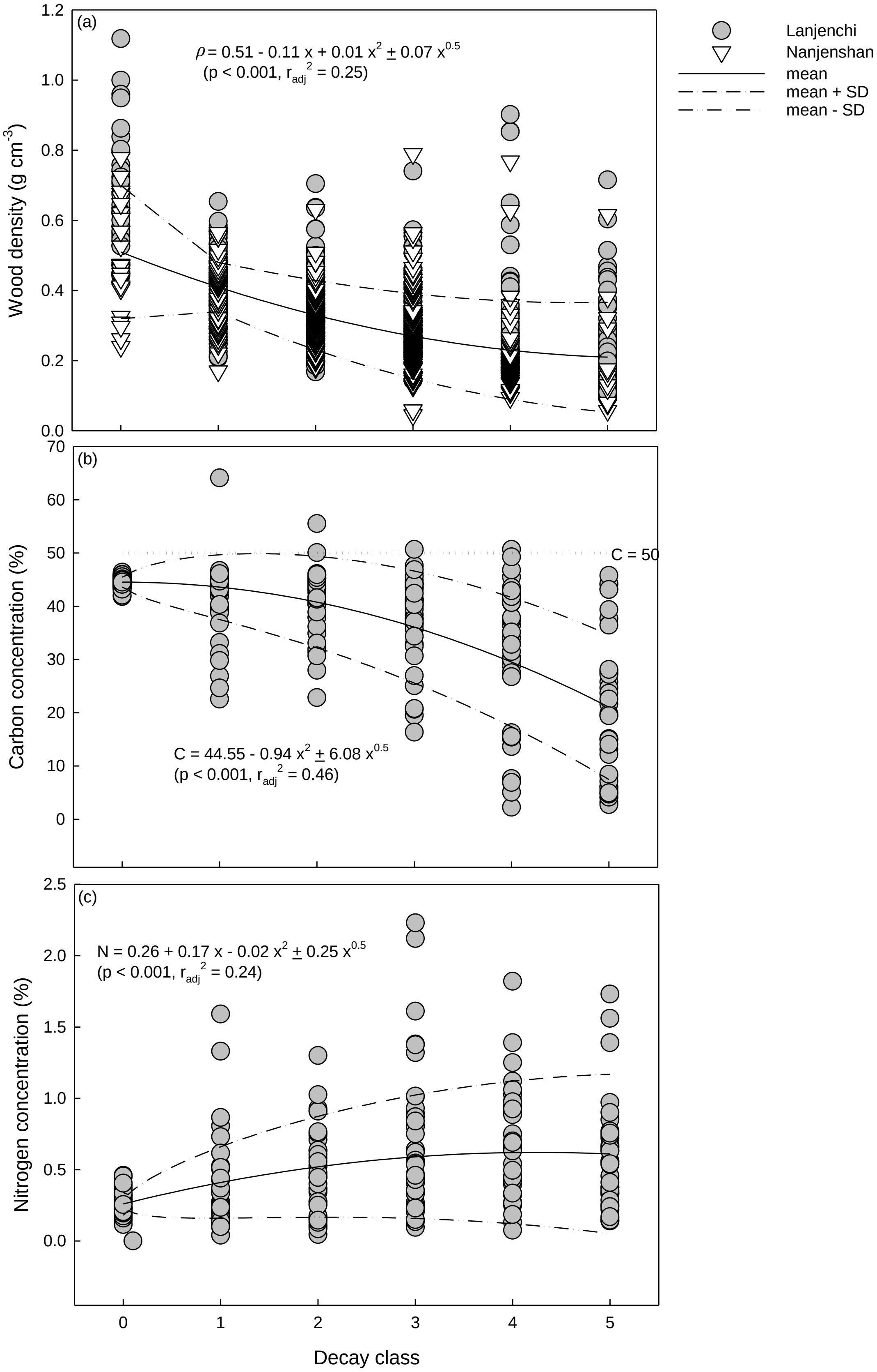


Fig. 1 Relationships between wood density and other elements of living trees. (a) Carbon concentration of living trees (C_{alive}; %) has significant relationship with wood density (ρ_{alive}; g cm^{-3}) of the same individual (unweighted regression; p = 0.007, r_{adj}^2 = 0.108, n = 57). (b) Relationship between wood density and nitrogen concentration (N_{alive}; %) of living trees is not significant (unweighted regression; p = 0.242, n = 57). L_: samples from the Lanjenchi Plot; N_: samples from the Nanjenshan Plots. Detailed species information please refer to Appendix 1.

Table 2. Wood density and carbon concentration of living trees and woody debris in Lanjenchi and Nanjenshan Forest Dynamics Plots, Taiwan. (mean ± SE (n); n = sample size)

Decay class*	Wood density (g cm^{-3})			Carbon concentration (%)		
	Lanjenchi	Nanjenshan	Overall	Lanjenchi	Nanjenshan	Overall
0	0.69 ± 0.03 (30)	0.49 ± 0.03 (27)	0.59 ± 0.02 (57)	44.9 ± 0.2 (30)	44.3 ± 0.1 (27)	44.6 ± 0.1 (57)
1	0.41 ± 0.01 (91)	0.37 ± 0.01 (50)	0.40 ± 0.01 (141)	37.6 ± 2.0 (17)	45.0 ± 1.4 (16)	41.1 ± 1.4 (33)
2	0.36 ± 0.01 (97)	0.32 ± 0.01 (105)	0.34 ± 0.01 (202)	41.1 ± 1.9 (19)	41.7 ± 0.9 (20)	41.4 ± 1.0 (39)
3	0.33 ± 0.01 (65)	0.27 ± 0.01 (131)	0.29 ± 0.01 (196)	36.6 ± 2.2 (19)	38.8 ± 1.5 (20)	37.7 ± 1.3 (39)
4	0.31 ± 0.02 (65)	0.22 ± 0.02 (58)	0.27 ± 0.01 (123)	28.7 ± 3.5 (20)	32.2 ± 2.1 (20)	30.5 ± 2.0 (40)
5	0.24 ± 0.02 (60)	0.20 ± 0.04 (13)	0.23 ± 0.02 (73)	15.8 ± 2.7 (20)	23.7 ± 3.5 (19)	19.6 ± 2.2 (39)

*Decay class 0 refers to living trees



(a)
ρ = 0.51 - 0.11 x + 0.01 x2 ± 0.07 x0.5
(p < 0.001, radj2 = 0.25)
Wood density (g cm-3)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Lanjenchi
Nanjenshan
mean
mean + SD
mean - SD
(b)
Carbon concentration (%)
70
60
50
40
30
20
10
0
C = 50
C = 44.55 - 0.94 x2 ± 6.08 x0.5
(p < 0.001, radj2 = 0.46)
(c)
Nitrogen concentration (%)
2.5
2.0
1.5
1.0
0.5
0.0
N = 0.26 + 0.17 x - 0.02 x2 ± 0.25 x0.5
(p < 0.001, radj2 = 0.24)
0
1
2
3
4
5
Decay class

Fig. 2 (a) Wood density, (b) carbon concentration, and (c) nitrogen concentration among decay classes in the Lanjenchi and Nanjenshan Forest Dynamics Plots, Taiwan. Solid lines are weighted regressions (mean functions) for all the samples and dash-dotted lines were the mean functions ± standard deviation ($\sqrt{\sigma^2(x)}$) functions. The dotted line in (b) is the reference line for C = 50. The mean function ± standard deviation function at each figures are (a) $\rho = 0.51 - 0.11\ x + 0.01\ x^2 \pm 0.07\ x^{0.5}$ (weighted regression; $p < 0.001$, $r_{adj}^2 = 0.25$, $n = 792$; ρ is wood density ($g\ cm^{-3}$) and x is the decay class). (b) $C = 44.55 – 0.94\ x^2 \pm 6.08\ x^{0.5}$ (weighted regression; $p < 0.001$, $r_{adj}^2 = 0.46$, $n = 247$; C is carbon concentration (%)). (c) $N = 0.26 + 0.17\ x - 0.02\ x^2 \pm 0.25\ x^{0.5}$ (weighted regression; $p < 0.001$, $r_{adj}^2 = 0.24$, $n = 247$; N is nitrogen concentration (%)). Decay class 0 refers to samples from living trees.

Table 3. Nitrogen concentration (%) and C:N ratio of living trees and woody debris in Lanjenchi and Nanjenshan Forest Dynamics Plots, Taiwan. (mean ± SE (n); n = sample size)

Decay Class*	Nitrogen concentration (%)			C:N ratio		
	Lanjenchi	Nanjenshan	Overall	Lanjenchi	Nanjenshan	Overall
0	0.24 ± 0.01 (30)	0.30 ± 0.01 (27)	0.27 ± 0.01 (57)	204.4 ± 10.7 (30)	157.5 ± 7.7 (27)	182.2 ± 7.4 (57)
1	0.33 ± 0.08 (17)	0.46 ± 0.09 (16)	0.39 ± 0.06 (33)	193.0 ± 32.3 (17)	171.1 ± 34.6 (16)	182.4 ± 23.3 (33)
2	0.31 ± 0.06 (19)	0.62 ± 0.06 (20)	0.47 ± 0.05 (39)	233.7 ± 39.8 (19)	78.1 ± 6.7 (20)	153.9 ± 23.1 (39)
3	0.39 ± 0.05 (19)	1.02 ± 0.12 (20)	0.71 ± 0.08 (39)	123.2 ± 16.9 (19)	47.5 ± 5.5 (20)	84.4 ± 10.6 (39)
4	0.47 ± 0.06 (20)	0.81 ± 0.09 (20)	0.64 ± 0.06 (40)	65.2 ± 7.1 (20)	48.7 ± 5.8 (20)	56.9 ± 4.7 (40)
5	0.40 ± 0.05 (20)	0.72 ± 0.10 (19)	0.56 ± 0.06 (39)	35.9 ± 3.1 (20)	34.1 ± 4.2 (19)	35.0 ± 2.5 (39)

*Decay class 0 refers to living trees

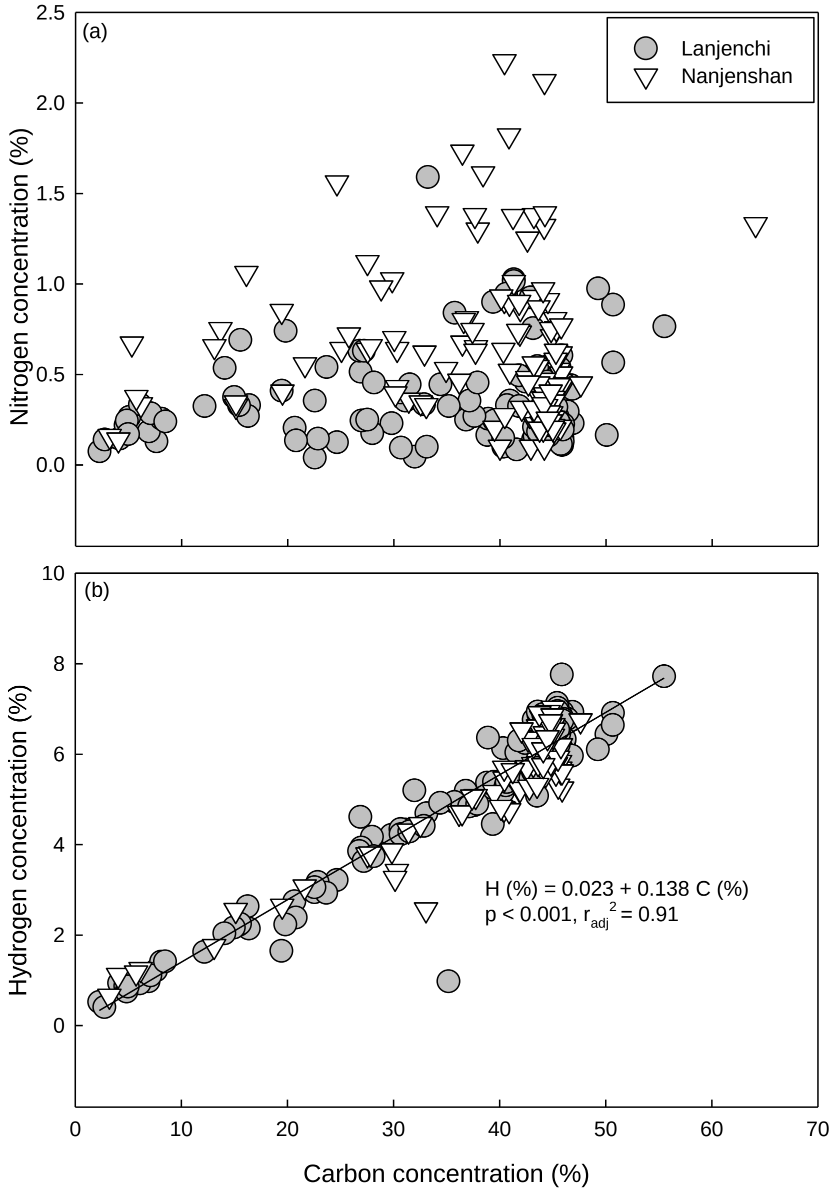


Fig. 3 Relationships between carbon concentration and other elements.

Both living trees and woody debris were included in the figures. (a) No significant relationship between carbon concentration (C; %) and nitrogen concentration (N; %) (unweighted regression, $p = 0.105$, $n = 247$). (b) The relationship between carbon concentration and hydrogen concentration (H; %) was significant (unweighted regression, $H = 0.023 + 0.138\ C$, $p < 0.001$, $r_{adj}^2 = 0.91$, $n = 204$).

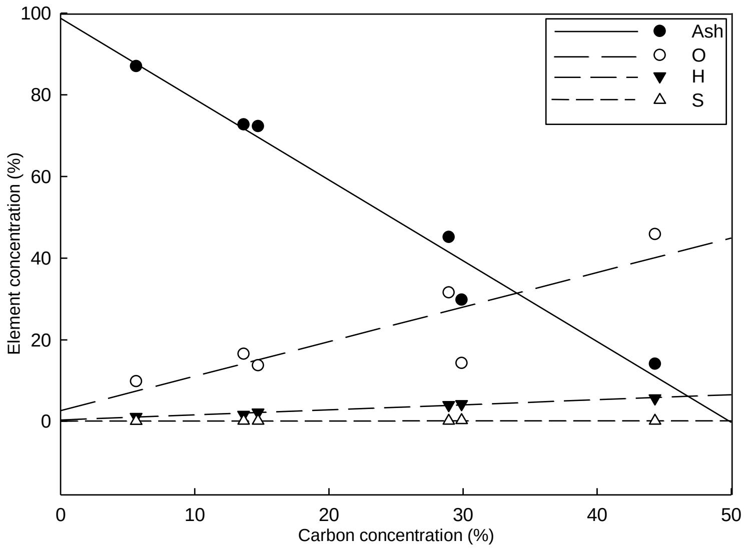


Fig. 4 Relationships between carbon (C) and other chemical elements of woody debris at decay class five. Oxygen (O), hydrogen (H), sulphur (S) and ash concentrations were plotted against carbon concentration (n = 6). The lower the carbon concentration the higher the ash concentration (unweighted regression, ash = 98.8 - 2.0 C, $p < 0.001$, $r_{adj}^2 = 0.96$, n = 6), suggesting that inorganic components accumulate as woody debris becomes de-carbonised. Other elements (H and O) were positively related to the carbon concentration in the decay class five (unweighted regression, $p < 0.001$ and $p = 0.028$), but sulphur did not ($p = 0.414$).

3.3 Necromass and carbon stocks

The total above-ground necromass was 8.99 ± 1.24 Mg ha^{-1} (mean ± SE) in Lanjenchi and 10.81 ± 3.58 Mg ha^{-1} in Nanjenshan (Table 4). The Lanjenchi plot in general had more fine necromass (32.3% of total necromass) then the Nanjenshan plots (20.6% of total necromass) (Table 4). Average ratios of standing to fallen woody debris varied between 0.26 and 0.68 (Table 4). Applying our measured carbon concentration (%) to necromass at each decay class, we estimated a woody debris carbon stock of 3.33 ±

0.55 Mg ha^{-1} in Lanjenchi and 4.65 ± 1.63 Mg ha^{-1} in Nanjenshan plots (Table 5). If we had simply assumed that carbon is 50% of the necromass, then the carbon stocks in the forests would have been overestimated by from 16.8% to 35.6% (Table 5).

Table 4. Necromass (mean ± SE), fine necromass proportion (diameter smaller than 10 cm), and standing to fallen woody debris mass ratio (S/F) in Lanjenchi and Nanjenshan Forest Dynamics Plots, Taiwan.

	Necromass total (Mg ha^{-1})		Fine necromass proportion (%)*		S/F	
Census year	Lanjenchi	Nanjenshan	Lanjenchi	Nanjenshan	Lanjenchi	Nanjenshan
Feb 2012	7.71 ± 1.98	…	28.6	…	0.57	…
Feb 2013	8.37 ± 1.01	8.29 ± 1.93	30.6	22.2	0.58	0.56
Feb 2014	9.30 ± 1.41	14.90 ± 3.37	34.5	16.4	0.31	0.29
Feb 2015	10.56 ± 2.09	9.23 ± 1.99	35.5	23.3	0.26	0.68
Mean	8.99 ± 1.24	10.81 ± 3.58	32.3	20.6	0.43	0.51

* proportion of mass

Table 5. Carbon stock (mean ± SE) in Lanjenchi and Nanjenshan Forest Dynamics Plots, Taiwan.

	Carbon stock (CS)* (Mg ha^{-1} of carbon)		Carbon stock if assume 50% as carbon (CS_{50}) (Mg ha^{-1} of carbon)		$(CS-CS_{50})/CS_{50}$ (%)	
Census year	Lanjenchi	Nanjenshan	Lanjenchi	Nanjenshan	Lanjenchi	Nanjenshan
Feb 2012	2.69 ± 0.88	…	3.85	…	43.5	…
Feb 2013	3.13 ± 0.53	3.44 ± 0.91	4.19	4.15	33.7	20.5
Feb 2014	3.51 ± 0.72	6.50 ± 1.67	4.65	7.45	32.5	14.6
Feb 2015	3.99 ± 0.99	4.00 ± 0.99	5.28	4.61	32.5	15.2
Mean	3.33 ± 0.55	4.65 ± 1.63	4.49	5.40	35.6	16.8

* Apply measured carbon concentration (%) at each decay class in Table 2 to convert necromass to carbon stock

4 Discussion

There has been surprisingly little attention paid to determining the carbon concentration of tropical forest woody debris, with no tropical study having simultaneously compared carbon concentration among living trees and woody debris within the same plots (Table 6). Our study showed that in our studied tropical forests the carbon concentration of necromass can decrease significantly with the decay of wood (Fig. 2). Moreover, regardless of level of decay, carbon concentration is substantially below the value (50% of dry mass; one sample t-test, $p < 0.001$) that has been applied as an approximation of carbon concentration for carbon stored in biomass (Houghton et al., 2001; Rice et al., 2004) and woody debris (Chao et al., 2009; Ngo et al., 2013). This demonstrates that a finer scale and forest-type-specific carbon concentration values may be needed for accurate estimate of necromass carbon stock, and by extension total ecosystem carbon stocks.

Table 6 Carbon concentration (%) of woody debris in tropical forestry literature.

Forest type	Country	Decay class 0 (%)	Decay class 1 (%)	Decay class 2 (%)	Decay class 3 (%)	Decay class 4 (%)	Decay class 5 (%)	Sample size	Criteria	Sample description	Reference
Lowland windswept forest	Taiwan	44.9	37.6	41.1	36.6	28.7	15.8	125	≥ 1 cm	Five decay classes and 10 living species	This study
Lowland rainforest	Taiwan	44.3	45.0	41.7	38.8	32.2	23.7	122	≥ 1 cm	Five decay classes and 10 living species	This study
Lowland rainforest	Indonesia	…	43.0	…	41.5	…	40.0	261	≥ 10 cm	Three decay classes	Meriem et al. (2016)
Montane wet forest	Hawaii	…	46.3	46.8	…	47.6	47.9	48	≥ 2 cm	Four decay classes	Iwashita et al. (2013)
Wet forest	Costa Rica	…	48.3	…	47.2	…	46.4	21	≥ 10 cm	Three decay classes	Clark et al. (2002)
Lower montane forest	Ecuador	…	46.8	…	…	…	47.2	16	≥ 10 cm	Two decay classes	Wilcke et al. (2005)

4.1 Wood density and carbon concentration of living trees

Carbon concentration of living trees in tropical forests ranges from 41.9 to 51.6% (Thomas and Martin, 2012). In our studied forests, the carbon concentrations of living trees are relatively low (Appendix 1). Nonetheless, our results do support the suggestion in Elias and Potvin (2003) that the proportion of carbon of living trees is related to the wood density (Fig. 1a). For those forests lacking any measurement of carbon concentration, it is therefore possible to apply species wood density to estimate the carbon concentration of living trees. This will be an attractive practical choice for many researchers because the measurement of wood density is a much easier and cheaper undertaking than the measurement of carbon concentration (Elias and Potvin, 2003). Moreover, applying the available global wood density databases (e.g. Zanne et al., 2009) can help to better estimate carbon concentration of tropical trees.

Our recommendations for carbon concentration estimation of living trees are as follows. At a lowest-level of certainty (e.g. IPCC Tier 1), researchers can apply a fixed value of carbon concentration from a similar ecosystem (e.g. Table 4.3 in IPCC, 2006). At an intermediate-level of certainty, researchers can apply equations developed from a similar ecosystem to convert wood density to carbon concentration (such as Fig. 1a for Southeast Asian tropical forests). At a more specific level, researchers should apply species-specific carbon concentration values based on in situ field measurements.

4.2 Wood density and carbon concentration among decay classes

Converting volume to carbon requires knowing both wood density and carbon concentration (IPCC, 2006; Latte et al., 2013; Weggler et al., 2012). Our study found that both wood density and carbon concentration decline significantly with the class of decay (Fig. 2). The decline of wood density with decay classes is a common finding among studies and ecosystems (e.g.: Chao et al., 2008; Clark et al., 2002; Mackensen and Bauhus, 2003). It underlines the importance of measuring the density of woody debris to help achieve greater accuracy in estimates of necromass. Simply assuming woody debris has the same wood density as living trees would result in overestimating the necromass (Weggler et al., 2012).

As for the carbon concentration, many studies have for convenience used a fixed value (e.g. 50%) of mass as carbon in both biomass and necromass (Brienen et al., 2015; Chao et al., 2009; Coomes et al., 2002; Latte et al., 2013). We found that carbon concentration decreased markedly with decay classes (Table 2; Fig. 2). Our findings contradict with previous studies which found that carbon concentration seems relatively constant among decay classes in tropical forests (Iwashita et al., 2013; Meriem et al., 2016; Wilcke et al., 2005) (Table 6). Only a single study from Costa Rica (Clark et al., 2002) suggested that the carbon concentration by mass might slightly decrease with advancing decay class. By contrast, a direct measurement of woody debris decomposition (which is not based on decay classes) in tropical China found that there was a significant decrease of carbon concentration after 9 years of observation (Yang et al., 2010). The apparent divergence between these studies merits further investigation, especially because it suggests that the underlying mechanisms involved may differ.

Besides the patterns of mean values, our study also found that the variances of carbon increased with decay class (Fig. 2b). This is a common pattern among tropical, temperate, and boreal studies (Carmona et al., 2002; Harmon et al., 2013; Meriem et al., 2016). This suggests that element concentration can vary greatly for heavily decayed pieces which is due to the complicated decomposition trajectories. Thus, it is important to acquire adequate sample sizes to achieve reliable conclusions. As decomposition trajectory involves the interactions between woody substrates, decomposer organisms, and climatic characteristics (Berbeco et al., 2012; Harmon et al., 1986; Weedon et al., 2009; Yang et al., 2010), we hypothesise that a fixed carbon fraction (i.e. steady carbon release) across woody pieces may not be typical for high-biodiversity tropical forests.

Several mechanisms may contribute to the high variation of carbon content of woody pieces among and within decay classes. For substrate characteristics, we suspect that the chemical properties of wood and tissue type proportions are crucial factors. Decomposition can be simplified into two major processes: fragmentation (physical and biological fragmentation) and mineralisation (leaching and respiration) (Harmon et al., 1986). The decrease of carbon concentration for any piece of wood is likely due to leaching of soluble carbohydrates and respiration of labile carbon compounds (Fujisaki and Perrin, 2015). For example, soluble carbohydrates would decrease with the increase of lignin concentration during decomposition, as lignin is relatively recalcitrant (Ganjegunte et al., 2004). Therefore, the original proportion of these carbohydrate compounds of wood pieces may influence the carbon concentration in woody debris with decay classes, and result in the high variability in carbon concentration among heavily decayed pieces (Fig. 2b).

Differences in tissue type proportions among wood may also contribute to the variation. For example, working in temperate and boreal forests, Harmon et al. (2013) found that bark samples can have slightly greater (about 1.0%) carbon concentrations than the interior woody parts. Although we did not separate the tissue types, field observation showed that majority of the woody debris at decay class four and five were lacking bark, or their bark barely distinguishable from other tissue types. This can be due to in tropical rainforests where fire or temperature seasonality is not an issue for plant survival, trees usually have thinner outer barks (Rosell, 2016). In contrast, some woody pieces at decay class four and five in our study plots only have outer bark and hollow interiors. Thus, the high variances in carbon concentration in heavily decayed wood are likely due to divergent decomposition trajectories, including potentially differing susceptibility of bark. The overall decline in carbon concentration with decay class in our forests may also be, to some extent, associated with the lack of bark tissue in the more decayed woody debris pieces.

Other mechanisms related to decomposer organisms and climatic characteristics also are worth further investigation. For example, Schilling et al. (2015) have demonstrated that the decomposer community (e.g. fungi) has significant influence on the declining patterns of woody debris properties, especially on lignin and wood density. Microsite moisture and temperature also can significantly influence wood decomposition (e.g. Berbeco et al., 2012; Jomura et al., 2015), although the effects on carbon concentration are not clear yet. Thus, further studies should focus on comparing the variation in substrate quality (chemical properties and tissue types), decomposer communities, and climatic characteristics across regions and forest types. These variations may be responsible for the large variance and the potential declining or increasing patterns of carbon concentration in decayed woods.

4.3 Woody debris characters between forests

Species composition has been suggested to be an issue in affecting elemental concentrations of necromass, at least in some temperate and boreal forests (Harmon et al., 2013). Ideally, if species-specific measurements on woody debris are available, it can help to disentangle the varied patterns between studies. However, in species-rich tropical forests identifying woody debris at the species level is always difficult, and often impossible. For this reason we used a plot-level carbon concentration for woody debris. For living trees, species identification is relatively easy. Thus, we selected dominant species in the plots and assumed that these represent the plot-level values in living woods. Overall, the challenges with producing taxa-based woody debris carbon concentrations estimates for tropical forests limit exploration of the potential role of community floristic composition in explaining between-site differences in tropical necromass decay.

Forest structure could be another factor affecting carbon concentration values between forests, especially the diameter size of fragments. Chambers et al. (2000) showed that diameter of trees is negatively related to decomposition rate. Heilmann-Clausen and Christensen (2004) argue that diameter size (i.e. surface area per volume) can influence decomposer community which in turn results in the divergence of decayed wood property (Schilling et al., 2015). We also observed that small pieces of wood had more similar outer and inner decomposition status than those of large woods. In our study forests, trees are generally small in diameter due to the influences of northeast monsoon wind (Chao et al., 2010b). Thus, our small forests may have faster decomposition rate, differed decomposer community, and more consistent outer and inner decayed woody material, comparing with other forests dominated by large diameter trees. On the contrary, for forests dominated by large woody pieces, a rotten woody debris piece may include some less decayed (and high carbon concentration) interior.

The subjective classification of decay class, and the underlying assumption that the appearance and/or hardness of woody debris represents the decomposition processes can introduce uncertainty in chemical properties between studies. We suspect that the application of the subjective classification may differ among forest types, especially for large and heavily decayed pieces, which could potentially complicate the determination of carbon concentration. Thus, there is a need to verify the actual physical (e.g. wood density) and chemical (e.g. carbon concentration) indications of the decay class classification scheme between forests.

4.4 Concentration of other elements among decay classes

What remains behind the marked decline of carbon concentration in decayed woods? In general, dry mass of living wood is composed of 50% carbon, 6% hydrogen, 44% oxygen, and other trace amounts of inorganics (Rowell, 2012). A minor proportion, 0.2 to 3.4%, is ash (Fengel and Wegener, 1989). Examining the six subsamples from decay class five, we found a significant increase of ash (%) with the decrease of carbon (%), but other elements, in general, increased with carbon (%) (Fig. 4). Fengel and Wegener (1989) suggest that the main components of ash are inorganic components, such as potassium, calcium, magnesium, and silicon. Therefore, our finding of increasing ash contents in heavily decayed wood demonstrates that inorganic components tend to accumulate as carbon declines over time. This is likely due to cumulative impact of leaching and heterotrophic respiration of organics during wood decay (Foudyl-Bey et al., 2016; Morris et al., 2015).

The average nitrogen concentration values in wood of living trees in our study plots (0.24% to 0.30%; Table 3) are similar to those from other tropical trees (average 0.24%; Martin et al., 2014). Therefore, any differences in mineralisation rates appear unlikely due to the differences in the nitrogen concentration in our study plots. We also found that nitrogen concentration increased with decay classes, supporting the accumulation of nitrogen during decomposition of woods found in other temperate (Harmon et al., 1986), subtropical (Ricker et al., 2016), and tropical (Clark et al., 2002; Wilcke et al., 2005) studies. The consistency between studies further emphasises the N retention role of wood debris among sites. This accumulation of nitrogen is due to nitrogen fixation and inhabitation of wood by other heterotrophs which can translocate nitrogen to the decaying wood (Foudyl-Bey et al., 2016; Harmon et al., 1986).

The increase of nitrogen and decrease of carbon with the decay classes of wood resulted in declining patterns of C:N ratio in our study sites (Table 3). The declining pattern is also consistent with other tropical and subtropical studies (Clark et al., 2002; Meriem et al., 2016; Wilcke et al., 2005; Yang et al., 2010). However, ratios were relatively low in our sites (47.5 to 204.4), compared with other studies (32.4 to 365) (Clark et al., 2002; Fujisaki and Perrin, 2015; Meriem et al., 2016; Wilcke et al., 2005; Yang et al., 2010). The low C:N ratio of wood indicates potential for high respiration rate and fast decay (Mackensen and Bauhus, 2003).

Oxygen and hydrogen percentages are highly correlated with carbon concentration (Fig. 3 and Fig. 4), suggesting that they are parts of the carbohydrate components. Thus, their decomposition patterns should be correlated with that of carbons and decrease with decay classes. Other compounds and elements which did not measured in our study, such as P and Mg (Wilcke et al., 2005) and decay-resistant phenol-based extractives (Harmon et al., 2013), may also accumulate with decomposition. These suggest that woody debris can accumulate nutrients in the process of decomposition while losing mass and carbon. In our forests at least, although the overall quantity of necromass is generally low in the fully decayed class, such heavily decayed woody debris is rich in inorganic nutrients.

4.5 Conclusions

The "carbon conversion factor" (wood density × carbon concentration) has been suggested by the IPCC (2006) as a required parameter to be able to estimate forest carbon stocks and emissions. As the classification of decay class is subjective and simply based on the appearance of wood pieces (e.g. Table 1), there is a need to verify the actual physical (e.g. wood density) and chemical (e.g. carbon concentration) indications of the decay class classification scheme. Our study reveals a pattern of decreasing carbon concentration with decay status of wood within tropical forests in Taiwan and also a pattern of increasing variance in the heavily decayed class. We hypothesise that a fixed carbon fraction (i.e. steady carbon release) across woody pieces is unlikely to be typical for high-biodiversity tropical forests due to diverse decomposition trajectories involving variable woody substrate quality, decomposer organism activities, and climatic conditions. Applying the conventional 50% carbon concentration would substantially overestimate the carbon stores in woody debris, potentially by more than a third. We therefore identify here a clear need to move beyond applying blanket assumptions about carbon concentration in necromass, and instead to evaluate it at the individual site-level, especially for tropical forests. Further, although our study plots are rather small, if the marked decline in carbon fraction with necromass decay turns out to be a widespread phenomenon across tropical forests, then the size of the dead wood carbon pool in the biome is likely to be somewhat less than simple mass-based calculations would suggest.

5 Acknowledgements

We sincerely appreciate the great assistance in fieldwork from Yen-Chen Chao, Chia-Min Lin, Hui-Ru Lin, Chia-Wen Chen, Chien-Hui Liao and numerous volunteers. We also thank Dr. Peter Chesson for the critical statistical help and Dr. Sheng-Yang Wang for comments and supports on the chemical analyses. This study was funded by grants to Kuo-Jung Chao from the Ministry of Science and Technology, Taiwan (NSC 101 - 2313 - B - 005 - 024 - MY3 and MOST 104 - 2313 - B - 005 - 032 - MY3). Oliver L. Phillips is supported by an ERC Advanced Grant (T-Forces) and is a Royal Society-Wolfson Research Merit Award holder.

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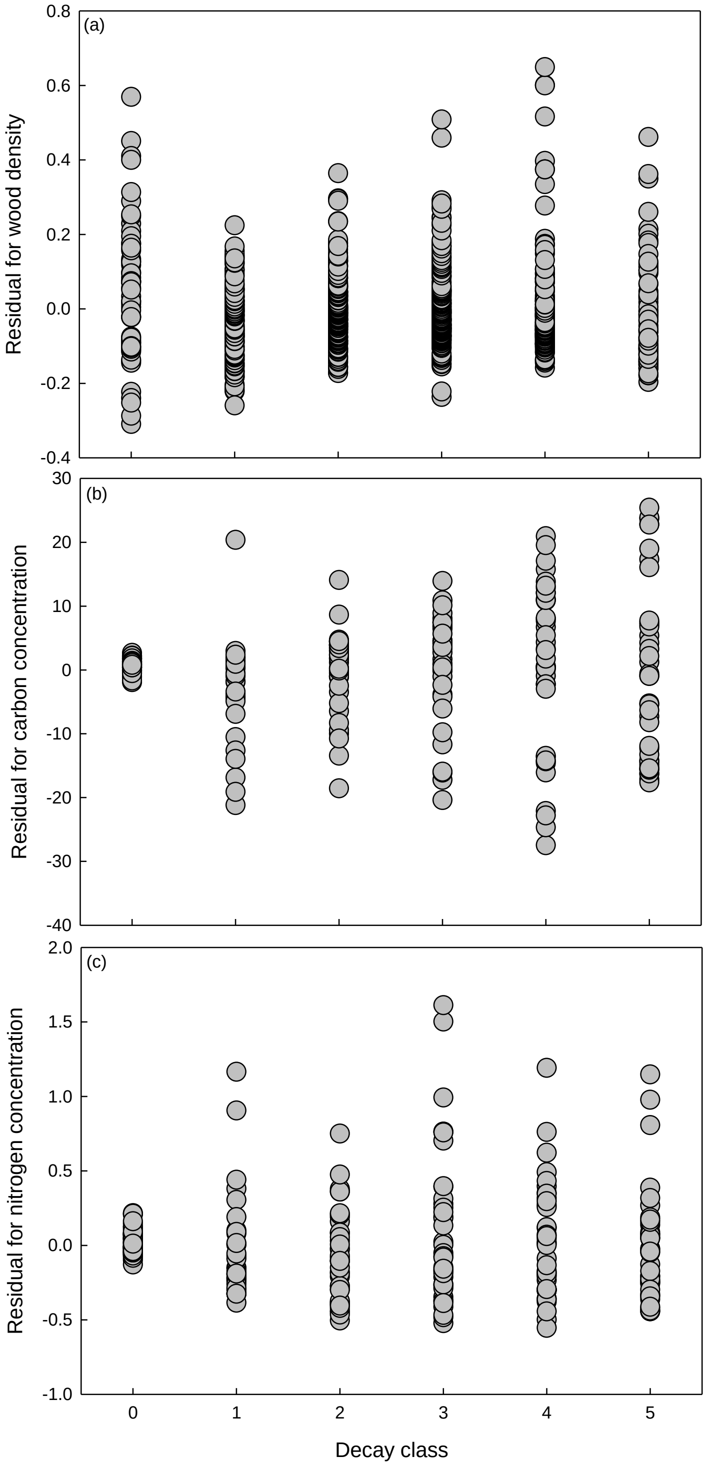
Appendix 1 Living tree samples in Lanjenchi and Nanjenshan Forest Dynamics Plots, Taiwan.

Species code	Plot	Family	Species	Dominance rank*	Wood density ($g\ cm^{-3}$) (mean ± SE)	Carbon concentration (%) (mean ± SE)	Nitrogen concentration (%) (mean ± SE)	n	Sampled diameter (mean ± SD)
LCAC	Lanjenchi	Fagaceae	Castanopsis cuspidata var. carlesii	1	0.56 ± 0.03	44.9 ± 0.4	0.19 ± 0.02	3	19.9 ± 3.5
LCL	Lanjenchi	Fagaceae	Cyclobalanopsis longinux	4	0.80 ± 0.02	45.0 ± 0.2	0.26 ± 0.04	3	14.8 ± 3.8
LCYC	Lanjenchi	Fagaceae	Cyclobalanopsis championii	6	0.76 ± 0.05	45.7 ± 0.1	0.23 ± 0.00	3	26.4 ± 8.0
LES	Lanjenchi	Elaeocarpaceae	Elaeocarpus sylvestris	12	0.60 ± 0.04	43.8 ± 0.2	0.19 ± 0.01	3	21.3 ± 5.0
LIA	Lanjenchi	Illiciaceae	Illicium arborescens	3	0.57 ± 0.01	46.0 ± 0.2	0.28 ± 0.03	3	10.4 ± 1.9
LIC	Lanjenchi	Aquifoliaceae	Ilex cochinchinensis	8	0.88 ± 0.12	43.5 ± 0.8	0.28 ± 0.02	3	12.2 ± 4.0
LLA	Lanjenchi	Fagaceae	Lithocarpus amygdalifolius	10	0.97 ± 0.02	44.9 ± 0.3	0.31 ± 0.08	3	13.8 ± 6.0
LOM	Lanjenchi	Oleaceae	Osmanthus marginatus	9	0.67 ± 0.04	45.3 ± 0.4	0.22 ± 0.01	3	11.2 ± 3.9
LSO	Lanjenchi	Araliaceae	Schefflera octophylla	2	0.44 ± 0.00	44.0 ± 0.4	0.22 ± 0.01	3	37.5 ± 17.
LSS	Lanjenchi	Theaceae	Schima superba var. kankaoensis	5	0.61 ± 0.02	45.5 ± 0.1	0.19 ± 0.06	3	17.5 ± 5.1
NBJ	Nanjenshan	Euphorbiaceae	Bischofia javanica	1	0.58 ± 0.07	44.7 ± 0.2	0.26 ± 0.02	3	40.8 ± 15.
NCI	Nanjenshan	Fagaceae	Castanopsis indica	8	0.68 ± 0.08	44.4 ± 0.4	0.32 ± 0.07	3	44.6 ± 6.4
NDH	Nanjenshan	Meliaceae	Dysoxylum hongkongense	3	0.46 ± 0.01	44.5 ± 0.3	0.33 ± 0.02	3	16.1 ± 5.0
NDM	Nanjenshan	Urticaceae	Dendrocnide meyeniana	4	0.27 ± 0.02	43.0 ± 0.7	0.39 ± 0.04	3	9.5 ± 1.6
NFA	Nanjenshan	Moraceae	Ficus ampelas	15	0.43	44.5	0.26	1	18.0
NFB	Nanjenshan	Moraceae	Ficus benjamina	2	0.53 ± 0.06	43.8 ± 0.3	0.34 ± 0.01	3	16.6 ± 2.2
NLS	Nanjenshan	Lythraceae	Lagerstroemia subcostata	9	0.65 ± 0.02	44.9 ± 0.1	0.30 ± 0.03	3	23.6 ± 7.7
NMJ	Nanjenshan	Lauraceae	Machilus japonica var. kusanoi	10	0.48 ± 0.05	44.4 ± 0.3	0.24 ± 0.03	3	25.0 ± 20.
NSO	Nanjenshan	Araliaceae	Schefflera octophylla	6	0.35 ± 0.03	43.8 ± 0.2	0.22 ± 0.01	3	37.5 ± 17.
NTT	Nanjenshan	Staphyleaceae	Turpinia ternata	11	0.43	44.9	0.31	2	13.5 ± 4.9
Total					0.59 ± 0.02	44.6 ± 0.1	0.27 ± 0.01	57	20.9 ± 12.3

n = number of individuals; * based on basal area ($m^2\ ha^{-1}$) within each forest (Chao et al., 2010a; Chao et al., 2007)

Appendix 2 Diagnostic plots of residuals against decay class in preliminary fitted quadratic regressions. (a) Wood density (g cm^{-3}), (b) carbon concentration (%), and (c) nitrogen concentration (%).



Appendix 3 Statistical supplementary.

One of the assumptions of regression is that there is constant variation (homogeneity) in y for all values of x (James et al., 2013). This means that for $y = \mu(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_{p-1} x_{p-1} + \epsilon$, ϵ (error) has a constant variance σ^2 (where x_1, x_2,… and x_{p-1} are the independent variables and β_0, β_1, … and β_{p-1} are the parameters). When variances of the dependent variable y were not homogeneous for different values of the independent x variable, we used weighted regression (James et al., 2013). The statistical model is $y = \mu(x) + \sigma(x)\epsilon$, where $\mu(x)$ is the mean function for y against x, $\sigma(x)$ is the standard deviation of y as a function of x, and $\epsilon \sim N(0,1)$. First, we fitted a preliminary linear regression $\mu_r(x)$ without weight. Visual inspection of the residuals suggested that the variance function, $\sigma^2(x)$, is approximately linear in x, i.e. $\sigma^2(x) = \sigma_0^2 + \delta^2 x$, where σ_0^2 and δ^2 are constants. However, as $\sigma^2(0) = \sigma_0^2$ was found to be very small or did not follow the general trend with $x > 0$, we used a variation on this model. When $x > 0$, $\sigma^2(x) = \delta^2 x$, which was relatively easy to fit to the data using maximum likelihood.

The maximum likelihood estimate, $\hat{\delta}^2$, of δ^2 (please see the proof listed at the end of this appendix) was found to be

$$\hat{\delta}^2 = \frac{1}{n-p} \sum_{i=1}^{k} \sum_{j=1}^{m} \frac{(y_{ij} - \mu_r(x_i))^2}{x_i}, \qquad \text{eqn A.1}$$

where y is the dependent variable, n is the total sample size of y, p is the number of fitted parameters for $\mu_r(x)$, i is the index of the decay class x, which is given the numerical value x_i in general but here $x_i = i$ (from 1 to k), m is the subsample size of y at each decay class x_i, y_{ij} is the sampled values of y at decay class i. In equation A.1 $\mu_r(x_i)$ is the preliminary unweighted fit of the linear regression at decay class i. The variance for the decay class 0, σ_0^2, was estimated as simply the sample variance about the mean of y for decay class 0. These estimates gave us the maximum likelihood estimates: for x > 0, $\widehat{\sigma}^2(x) = \widehat{\delta}^2\, x$; for x = 0, $\widehat{\sigma}^2(0) = \widehat{\sigma}_0^2$.

For the weighted regression, the weights of woody debris at each decay class i were the inverse of the estimated variances ($\frac{1}{\widehat{\sigma}^2(x)}$). Finally, we re-fitted the μ (x) with weights estimated above. The statistical tests for the weighted regression coefficients in the main text are based on these weighted coefficients. The sample variance of y at each decay class i can also be estimated using the following equation

$$s^2(x_i) = \frac{1}{m}\sum_{j=1}^{m}\left(y_{ij} - \hat{\mu}_r(x_i)\right)^2, \qquad \text{eqn A.2,}$$

where y is the independent variable, m is the subsample size of y at decay class i, $\hat{\mu}_r(x_i)$ is its value fitted from the weighted regression.

The variance estimated as $s^2(x_i)$ (eqn A.2) and as $\widehat{\sigma}^2(x)$ were plotted in the following Fig. A.1a, b and c. We did not find systematic changes between these two types of variance estimates.

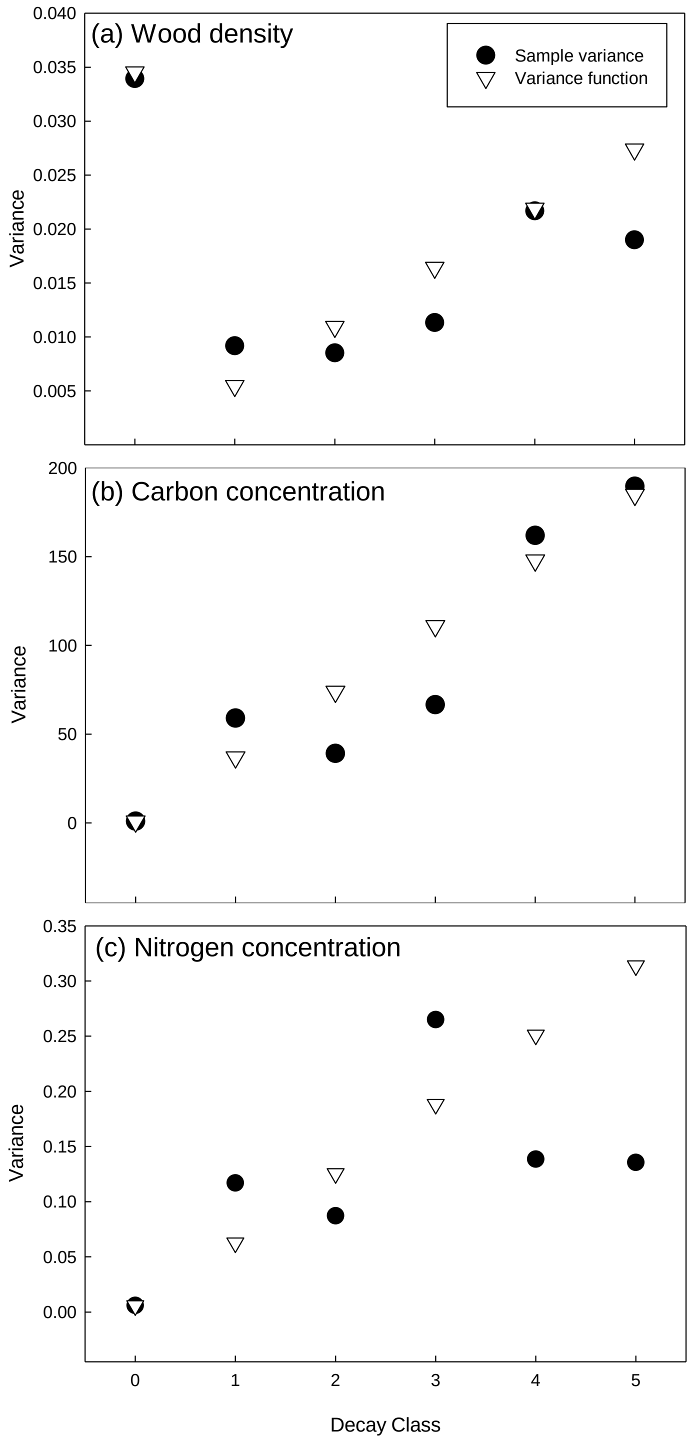


Fig. A.1 Variance estimates based on sample variance ($s^2(x_i)$ in eqn A.2) and variance function ($\hat{\sigma}^2(x)$; df = n-3). (a) Wood density, (b) carbon concentration, and (c) nitrogen concentration.

Statistical proof of the variance model

This is the proof of the maximum likelihood estimate, $\hat{\delta}^2$, of δ^2

x = decay class

$y = \mu(x) + \sigma^2(x)\ \epsilon$

$\epsilon \sim N(0,1)$

Likelihood function is the product of the probability density function for the normal distribution:

$$L\big(\mu\,(x), \sigma^2(x)|x_{1,}\, \dots \dots, x_n\big) = \prod_{i=1}^{n} \frac{1}{\sqrt{2\pi\sigma^2(x_i)}} e^{-\frac{1}{2}\frac{(y_i-\mu(x_i))^2}{\sigma^2(x_i)}}$$

$$= \left(\prod_{i=1}^{n} 2\pi\sigma^2(x_i)\right)^{-\frac{1}{2}} \times \exp\left(-\frac{1}{2}\sum_{i=1}^{n}\frac{(y_i-\mu(x_i))^2}{\sigma^2(x_i)}\right),$$

where $\mu(x)$ is the mean function and $\sigma^2(x)$ is the variance function, given the data x_1 to x_n.

To estimate $\sigma^2(x_i)$, we assumed that $\sigma^2(x_i)$ is a function of parameters p. The log likelihood is

$$l\big(\mu\,(x), \sigma^2(x)|x_{1,}\, \dots \dots, x_n\big)$$

$$= \ln\left(\prod_{i=1}^{n} 2\pi\sigma^2(x_i)\right)^{-\frac{1}{2}} \times \exp\left(-\frac{1}{2}\sum_{i=1}^{n}\frac{(y_i-\mu(x_i))^2}{\sigma^2(x_i)}\right)$$

$$= -\frac{n}{2}\ln 2\pi - \sum_{i=1}^{n}\frac{1}{2}\ln\sigma^2(x_i) - \frac{1}{2}\sum_{i=1}^{n}\frac{\big(y_i-\mu(x_i)\big)^2}{\sigma^2(x_i)}$$

The maximum likelihood estimates of any parameter p of the variance function are found by equating the derivative of the log likelihood to 0. Here the gives

$$\frac{d}{dp}\, l\big(\mu\,(x), \sigma^2(x)|x_{1,}\, \dots \dots, x_n\big) = \frac{d}{dp}\Big(-\frac{n}{2}\ln 2\pi - \sum_{i=1}^{n}\frac{1}{2}\ln\sigma^2(x_i) - \frac{1}{2}\sum_{i=1}^{n}\frac{\big(y_i-\mu(x_i)\big)^2}{\sigma^2(x_i)}\Big) = \sum_{i=1}^{n}\left(-\frac{1}{2\sigma^2(x_i)} + \frac{1}{2}\frac{\big(y_i-\mu(x_i)\big)^2}{(\sigma^2(x_i))^2}\right)\frac{d\sigma^2(x_i)}{dp} = 0,$$

assuming that μ (x) does not depend on p.

If $\sigma^2(x_i) \equiv \sigma^2$ then $\frac{d\sigma^2(x_i)}{dp} = 1$ (i.e. variance is not a function of x as in unweighted regression). Thus

$$\sum_{i=1}^{n}\left(-\frac{1}{2\sigma^2} + \frac{1}{2}\frac{\left(y_i-\mu(x_i)\right)^2}{(\sigma^2)^2}\right) = 0$$

$$\sum_{i=1}^{n}\left(-\frac{1}{\sigma^2} + \frac{\left(y_i-\mu(x_i)\right)^2}{\sigma^4}\right) = 0$$

$$\sum_{i=1}^{n}\left(-\sigma^2 + \left(y_i - \mu(x_i)\right)^2\right) = 0$$

$$\mathrm{n}\sigma^2 = \sum_{i=1}^{n}\left(y_i - \mu(x_i)\right)^2$$

$$\sigma^2 = \frac{\sum_{i=1}^{n}\left(y_i-\mu(x_i)\right)^2}{\mathrm{n}}$$

This is the usual maximum likelihood estimate for population homogeneous variance using unweighted regression. If we fit p parameters for μ, then the divider n is replaced by n-p (the degree of freedom) to make it unbiased.

As Appendix 2 has showed that the variances of the independent variables are likely to be linear in x for x > 0, we propose that $\sigma^2(x) = \delta^2 x$.

Then p = δ^2, $\frac{d\sigma^2(x_i)}{dp} = x_i$ and the equations to solve are:

$$\sum_{i=1}^{n}\left(-\frac{1}{\delta^2 x_i} + \frac{\left(y_i-\mu(x_i)\right)^2}{(\delta^2 x_i)^2}\right)x_i = 0$$

$$\sum_{i=1}^{n}\left(-\frac{x_i}{\delta^2 x_i} + \frac{\left(y_i-\mu(x_i)\right)^2 x_i}{(\delta^2 x_i)^2}\right) = 0$$

$$\sum_{i=1}^{n}\left(-\frac{x_i}{\delta^2 x_i} + \frac{\left(y_i-\mu(x_i)\right)^2 x_i}{\delta^4 x_i^2}\right) = 0$$

$$\sum_{i=1}^{n}\left(-\delta^2 + \frac{\left(y_i-\mu(x_i)\right)^2}{x_i}\right) = 0$$

$$\delta^2 = \frac{1}{n}\sum_{i=1}^{n}\frac{\left(y_i-\mu(x_i)\right)^2}{x_i}$$

If we fit p parameters for μ, then the divider n have become n-p to account for the degree of freedom.

$$\hat{\delta}^2 = \frac{1}{n-p}\sum_{i=1}^{n}\frac{\left(y_i-\mu(x_i)\right)^2}{x_i}$$

Accounting the m observations at each decay class, we get

$$\hat{\delta}^2 = \frac{1}{n-p}\sum_{i=1}^{k}\sum_{j=1}^{m}\frac{(y_{ij}-\mu_r(x_i))^2}{x_i}$$

Thus, the variance model for this fit is $\hat{\sigma}^2(x) = \hat{\delta}^2\, x$.