INTRODUCTION

Tropical forests play an important global ecological role accounting for one-third of land-surface productivity and evapotranspiration (Malhi, 2012), and hosting over half of all global terrestrial biodiversity (Pimm & Raven, 2000). Humans have been interacting with and modifying tropical forests for tens of thousands of years, but the intensity of this interaction has been increasing substantially in a new human-dominated geological epoch—the Anthropocene (Lewis & Maslin, 2015; Malhi et al., 2014).

Understanding the global C cycle is impossible without estimates of carbon stocks in tropical ecosystems. Moreover, the largest errors

Coarse woody debris density and carbon concentration by decay classes in mixed montane wet tropical forests

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Abstract

The role of coarse woody debris (CWD) in the global carbon (C) cycle is growing under increasing tree mortality driven by climate variability and disturbances. Quantifying C in CWD critically depends on accurate estimates of CWD density and C concentration in CWD. This study considered the main decomposition pathways (the proportions of CWD decomposed by fungi vs. invertebrates; fungal decay types) and the relationships between decay class, wood density, moisture, and C content of CWD in old-growth mixed monsoon montane tropical forests in Vietnam based on the inventory of 359 CWD pieces. The bulk density of wood of the 1st, 2nd, 3rd, 4th, and 5th decay classes averaged 0.56, 0.49, 0.37, 0.28, and 0.15 g cm⁻³, respectively. The density reduction across decay classes did not significantly differ for snags, stumps, branches, leaning, and lying logs. Wood density was negatively related to wood moisture. The wood mass loss averaged 0%, 20%, 37%, 54%, and 74% in the CWD of the 1st, 2nd, 3rd, 4th, and 5th decay classes, respectively. Signs of invertebrate activity were recorded on 3% of CWD pieces. Among CWD samples with identifiable decay type, 88% were decomposed by white-rot, 8% were decomposed as brown-rot, and 4% of pieces contained both white- and brown-rot patches. The mean C concentration in wood was 46.5%. It did not change with decay class. Our research provides an empirical basis for future inventories of CWD carbon stocks in Asian montane tropical mixed forests.

KEYWORDS
biomass, deadwood, decomposition, downed logs, necromass, old growth forest, snags, Vietnam
in estimates of the terrestrial carbon balance are believed to result from uncertain rates of tropical deforestation (Houghton, 2005). The emissions of carbon from tropical deforestation are determined by two factors: rates of land-use change including harvest of wood and other forms of management, and per hectare changes in carbon stocks following deforestation or harvest. However, detailed quantifications of total C stocks in live and dead biomass in tropical forests are still limited (Clark, 2004; Houghton, 2005; Pfeifer et al., 2015).

The impact of increasing disturbances (windthrows, fires, insects and diseases) on the forest carbon (C) cycle encompasses additional input of coarse woody debris (CWD) through tree mortality (Giardina, 2019). Monitoring forest ecosystem carbon fluxes, characterizing respiration and combustion losses, as well as validating simulation models projecting future carbon dynamics depends on the knowledge of CWD C stocks. Quantifying C in CWD critically depends on accurate estimates of CWD density and C concentration in CWD to convert volume into biomass and C (Harmon et al., 2013; Maas et al., 2020).

The data on wood density, mass reduction, and C concentration by decay classes in tropical forests are fragmentary (Martin et al., 2021). First of all, great uncertainties are related to the CWD characteristics prior to decomposition (Harmon, 2021). There is a wide variation in reported estimates of wood densities of tropical tree species across studies (Zanne et al., 2009). For some species, the information is completely missing. On a tree level, wood density is a phylogenetically conserved trait (Chave et al., 2006) and closely tied to growth rate and mortality patterns (Lawton, 1984; Sungpalee et al., 2009; Swenson & Enquist, 2007). Community-wide wood density varies along climatic, environmental, and disturbance gradients (Lawton, 1984; Slik et al., 2010; Swenson & Enquist, 2007) and successional status of communities (McCulloh et al., 2011). Generally, there is a strong abiotic filtering of wood density values in forest communities (Swenson & Enquist, 2007). According to the Weiher and Keddy’s model (1995), the mean and variance of values for local community wood density decrease in more stressful locations along gradients (i.e., elevation and latitude). In montane tropical forests, the abiotic environment is expected to be the primary determinant of mean trait values and variances (Swenson & Enquist, 2007). Furthermore, tropical tree community wood density indicates the stage of ecological succession, regulated by dry season intensity influencing the start and trajectory of succession, resulting in convergence of community trait mean over time as vegetation cover builds up (Poorter et al., 2019). In wet tropical forests, succession proceeds from low- to high-community wood density (acquisitive toward conservative trait values), in line with standard successional theory. In dry forest, however, succession proceeds from high- to low-community wood density (conservative toward acquisitive trait values) (Poorter et al., 2019). In tropical montane forests, community-level wood bulk density has been reported only in a small number of studies (Culmsee et al., 2010; Sungpalee et al., 2009). Not all sources of variability and radial or vertical variation in trunk wood density and branch densities in tropical trees are understood (Sarmiento et al., 2011).

The wood density reduction and mass loss across decay classes may vary depending on region, tree species identity, prevailing decomposition pathways (respiration vs combustion by invertebrates, decay type) and position (standing vs. downed wood and branches vs. stems) (Harmon, 2021; Harmon et al., 2011, 2013, 2020). The density dynamics in tropical CWD were examined only for few tree species without covering all tropical ecosystem and species diversity (Harmon et al., 2020; Iwashita et al., 2013; Martin et al., 2021; Schilling et al., 2015; Shorohova et al., 2021). Regionally, identifying the role of invertebrates in tropical dead wood decomposition is essential to better predict the wood vs soil and void proportion in CWD of different decay classes (Shorohova et al., 2021). Distinguishing wood decay type is important for predicting density and other physiochemical characteristics of wood (Fukasawa, 2021).

Wood decay types are determined by wood-decaying fungi and are traditionally categorized into three types—white-rot, brown-rot, and soft-rot—based on their species-specific ability to decompose lignin, cellulose, and hemicellulose (Eaton & Hale, 1993). The presence of white- or brown-rot is used among indicators to identify decay classes for standing and downed dead trees and predict CWD density (Harmon et al., 2011). Since decay classes are largely based on exterior appearances, it is likely that in the drier conditions the exterior of standing dead wood will continue to degrade whereas the interior will remain relatively sound. Thus, for a given decay class, density reduction factors for downed woody debris are typically less than those for snags given differences in decomposition agents for downed versus standing debris (Harmon et al., 2011). Wood moisture is one of the main factors influencing microbial respiration rates during decomposition of CWD in tropical forests. The CWD respiration rates increase with increasing moisture, although this relationship appears to be ultimately controlled by the relationship between wood moisture and wood density (Chambers et al., 2001). As wood decays, density decreases, cell wall polymers are hydrolyzed, and the matrix potential at a given water content rises, increasing the availability of moisture to microbial communities (Dix, 1985). Fungi can also actively regulate wood moisture content, creating a more favorable decay environment (Rayner & Boddy, 1988). Quantifying the relationships between wood density and moisture of CWD provides empirical data for predictive modeling of C release during decomposition of CWD in given conditions under given air temperature gradients. To the best of our knowledge, possible differences in density reduction by decay classes among tropical CWD of different position and decay type related to wood moisture content have not been examined.

Mechanisms underlying variation in patterns of dead wood C change through decomposition are largely related to decay type (Fukasawa, 2021; Martin et al., 2021). Lignin has a considerably higher C concentration than cellulose and hemicellulose. Thus, carbon concentration would be expected to increase in brown-rot, where cellulose and hemicellulose are decayed, but lignin remains relatively unchanged. In white-rot, where lignin is decayed selectively or simultaneously with cellulose and hemicellulose, the C concentration would be expected to decrease or remain stable.
Our objective was to reveal the main decomposition pathways (the proportions of CWD decomposed by fungi vs. invertebrates; fungal decay types) and determine CWD decay-class specific density and C concentrations in old-growth mixed monsoon montane tropical forests. Specifically, we aimed to (1) identify mean wood densities of live trees and non-decomposed CWD, (2) identify the relative proportions of CWD pieces decomposed by fungi vs. invertebrates and by white- versus brown-rot fungi, (3) estimate wood density, mass loss and C concentration in wood of CWD of different position, or type (snags, stumps, lying logs, leaning logs, and branches) by decay classes, and (4) examine the relationship between wood density and moisture. We tested the following hypotheses: (1) wood density reduction and mass loss across 5 classes increase in the order: snags, leaning logs, stumps, lying logs and branches, (2) wood moisture is negatively related to its density and advance in decay, and (3) C concentration in wood remains stable during decomposition.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in 2018–2019 in November-December in Central Highlands in the Bi Doup - Nui Ba (Vườn quốc gia Bi Doup - Núi Bà) national park (N12° 10.885°–11.235°; E108° 40.469°–41.406°). With a total area of 70,038 ha, the park ranks as one of five largest national parks in Vietnam. In our study area, the altitude varies from 1446 to 1892 m a.s.l. Mean annual temperature is 18.2°C. Monthly variation in temperature is from 5 to 28 (mean 13) °C in January and from 14 to 26 (mean 19) °C in June. Mean monthly air humidity exceeds 93% (Gorbunov et al., 2018). The region is characterized by a monsoon climate with two separate seasons—a cool, dry season from December to April and a warm, wet monsoon season from May to November. The mean annual rainfall is ca. 1860 mm, with <50 mm per month from December to March. The onset of monsoon rains is in May–June. Montane cloud forests are frequently covered with fog (Kuznetsova et al., 2006, 2011).

The territory of the national park is composed by Jurassic and Cretaceous volcanic rocks of various lithological composition covered with a thick weathering crust. The geomorphologic landforms are structural denudational and fluvial (Gorbunov et al., 2018). Ferralsols of various texture (sandy loamy or loamy) is the dominated soil type in the study area. Covering the mountain hills, they are formed on clayey weathering crust of dacites or rubble-stone dacite deluvium. There are Fluvisols in the river valleys, which are formed on the pebble-boulder alluvium of dacites, andesites, tufts, and sandstone (Gorbunov et al., 2018).

In the studied forest stands, one to five tree layers are distinguished in the vertical forest structure. The tree height varies from 2 to 40 m, and tree diameter reaches up to more than 100 cm. The forest stands are composed of the angiosperm trees from the families Fabaceae, Elaeocarpaceae, Magnoliaceae, Theaceae, Myrtaceae, Sapindaceae, Euphorbiaceae, Betulaceae, Annonaceae, Juglandaceae, Hamamelidaceae, Sapotaceae, Altingiaceae, Fabaceae, Schisandraceae, Styracaceae, Cornaceae, Ebenaceae, Pentaphylacaceae, Proteaceae, Malvaceae, Rubiaceae, Palmae, and gymnosperm trees from Pinaceae, Podocarpaceae, and Cupressaceae (Table 1). Vegetation communities vary along the altitudinal gradient. Middle montane broadleaved deciduous poly-dominant forests are located at 850–1600 m above sea level (a.s.l.) Mixed broadleaf-coniferous forests are situated at 1500–1700 m a.s.l. on ridges, expansions, and upper slopes of granite ridges. Middle montane fire-driven coniferous (Pinus kesiya) forests are found at 1500–1700 m a.s.l. High montane cloud forests occur at 1700–2000 m a.s.l. (Kuznetsova & Kuznetsova, 2013; Kuznetsova et al., 2006, 2011). Based on the morphological description and chemical analyses (Gorbunov et al., 2018), the soils of the studied plots are identified as Haplic (or Umbric) Ferralsols (Arenic or Loamic). The thickness of litter layer varies from 1 to 20 cm. The humus horizon of Haplic Ferralsols is acidic (pH [KCl] = 3.2–3.7) and contains 5.5%–8.3% of organic C. The C/N ratio ranges from 24 to 27.

2.2 | Sampling and analyses

Tree stand and vegetation inventories included identifying trees with more than 6 cm in diameter at genus or, when possible, species levels on the 3–4 500 m² sized plots per site. Altogether, 14 sites were characterized (Shorohova et al., 2021). The forest types were mixed deciduous forests with Pinus dalatensis, Dacrycarpus imbricatus, Dacrydium elatum, and Pinus krempfii (5), the above with Fokienia hodginsii (2), pure Pinus kesiya forests (2), riparian deciduous forests (3), and cloud forests (2).

Coarse woody debris inventories with line intercept sampling for downed CWD and strip survey for standing CWD were conducted on 41 (3–4 per site) 50 m long and 4 m wide transects. All CWD pieces of more than 6 cm in diameter were inventoried. They were distributed by position as follows: stumps and standing dead trees (snags) (N = 136), lying logs (N = 109), leaning logs (N = 72), and branches (N = 42). In total, 359 CWD pieces of different position were sampled (Table 2). The diameter at 1.3 m from the stem base averaged 20 cm. Presence of bark, branches, sporocarps of wood-inhabiting fungi and epiphytic or epixylic vegetation was recorded. Percentage of wood consumed by invertebrates was visually estimated on the saw-made cross cuts. The cross-cuts about half CWD diameter were made at 1–3 location per CWD piece.

We assigned each sampled CWD individual to a decay class using five decay classes that span a spectrum from fresh mortality to nearly complete decay with collapsed bole shape (Table 3). Decay classes were defined based on the physical appearance and structural integrity of individual CWD pieces.

Density sampling for CWD wood was performed using a hand saw and a knife at 1–3 locations per CWD piece, including the sides of logs. The decay type was identified, when possible, based on visual characteristics, mainly color and structure (cubes vs. fibers), of residual
An adjustment for volume losses during decomposition was made (Fraver et al., 2013); the initial shape of highly decomposed samples was reconstructed. Small samples of regular shape up to 100 cm³ in size were taken. Their length, width, and thickness were measured in the field. In 2019, 248 samples were weighed in order to determine relative wood moisture by decay classes (Table S1). The samples were collected during the dry season, that is, in relatively dry conditions.

In the laboratory, the samples were oven-dried at 103°C for 48 h and weighed. The bulk density of a wood sample (\( \rho, \text{g cm}^{-3} \)) was calculated by dividing the dry mass by the fresh volume of a sample. The total bulk density of a CWD item was calculated taking into account the proportion of wood consumed by invertebrates (void). The mass loss was calculated based on the loss of total density, that is, it included all decomposition processes: respiration, consumption by invertebrates, fragmentation, and leaching.

The initial bulk density of wood was estimated for the tree species (genera) dominating in the studied forest stands based on the global wood density database (Zanne et al., 2009) for tropical monsoon montane tropical forests of Bi Doup - Nui Ba national park, Vietnam. The data were extracted from the global wood density database (Zanne et al., 2009); the measurements from this study are given in parentheses.

| Family       | Tree genera or species                                                                 | Range        | Mean    | # of records |
|--------------|----------------------------------------------------------------------------------------|--------------|---------|--------------|
| Angiosperms  |                                                                                        | 0.26–0.88    | 0.53    | 96           |
| Sapindaceae  | Acer sp. (A. decandrum, A. laurinum)                                                   | 0.43–0.75    | 0.61    | 6            |
| Pentaphylacaceae | Adinandra sp. (A. hainanensis, A. integerrima)                                          | 0.47–0.56    | 0.52    | 2            |
| Burseraceae  | Canarium sp. (C. littorale, C. pimela)                                                  | 0.45–0.56    | 0.52    | 4            |
| Fagaceae     | Castanopsis sp. (C. acuminatissima, C. echinocarpa, C. fissa, C. indica, C. tribuloides) | 0.42–0.68    | 0.54    | 13           |
| Lauraceae    | Cinnamomum sp. (C. tamala, C. verum)                                                   |              |         |              |
|             | C. zeylanicum                                                                          | 0.43–0.51    | 0.48    | 4            |
| Elaeocarpaceae | Elaeocarpus sp. (E. apiculatus, E. chinensis, E. dubius, E. lanceaeolius, E. stipularis, E. subglobosus, E. sylvestris) | 0.37–0.57    | 0.49    | 16           |
| Euphorbiaceae | Endospermum sp. (E. chinense)                                                           | 0.34–0.36    | 0.35    | 2            |
| Juglandaceae | Engelhardia spicata                                                                     | 0.37–0.49    | 0.44    | 3            |
| Hamamelidaceae | Exbucklandia populnea                                                                  | 0.55–0.68    | 0.62    | 4            |
| Fagaceae     | Lithocarpus sp. (L. corneus, L. dealbata, L. elegans, L. scortechini, L. vestitus)      | 0.70–0.88    | 0.72    | 7            |
| Lauraceae    | Litsea sp. (L. baviensis, L. cubeba, L. monopetala, L. vang)                           | 0.31–0.46    | 0.42    | 12           |
| Hamamelidaceae | Rhodoleia championii                                                                  | 0.60         | 0.60    | 1            |
| Theaceae     | Schima wallichii                                                                       | 0.50–0.62    | 0.56    | 8            |
|             | Second and third tree layers                                                           | 0.26–0.67    | 0.51    | 14           |
| Fabaceae     | Archidendron sp. (A. clypearia)                                                        | 0.26–0.37    | 0.32    | 3            |
| Symplocaceae | Symplocos sp. (S. adenophylla, S. anomala, S. cochinchinensis)                         | 0.47–0.67    | 0.55    | 9            |
| Myrtaceae    | Syzygium sp. (S. cuminii)                                                               | 0.60–0.65    | 0.63    | 2            |
|             | Gymnosperms                                                                            | 0.37–0.53    | 0.49    | 20           |
| Podocarpaceae | Dacrycarpus imbricatus                                                                | 0.37–0.45    | 0.41    | 3            |
| Podocarpaceae | Dacrydium elatum                                                                      | 0.46–0.51    | 0.49    | 2            |
| Cupressaceae | Fokienia hodginsii                                                                     | 0.39 (0.46–0.83) | 0.39 (0.61) | (3)     |
| Podocarpaceae | Nageia fleuryi                                                                        | Na           | Na      |              |
| Pinaceae     | Pinus dalatensis                                                                       | Na           | Na      |              |
| Pinaceae     | Pinus keymia                                                                            | 0.42–0.51 (0.44–0.93) | 0.47 (0.69) | (2)     |
| Pinaceae     | Pinus krempfii                                                                          | 0.48 (0.49–0.93) | 0.48 (0.59) | (4)     |
| Podocarpaceae | Podocarpus neriifolius                                                                 | 0.44–0.53    | 0.49    | 6            |
| Tree community |                                                                                        | 0.26–1.10    | 0.52    | 116          |
TABLE 2 Number and size of CWD pieces sampled in Bi Doup - Nui Ba national park, Vietnam

| Variable                  | Decay class |
|----------------------------|-------------|
|                            | I | II | III | IV | V  |
| Position                   |   |    |     |    |    |
| Stumps                     | 1 | 27 | 35  | 28 | 24 |
| Snags                      | 7 | 5  | 7   | 2  | 0  |
| Lying logs                 | 8 | 25 | 39  | 25 | 12 |
| Leaning logs               | 15| 33 | 20  | 4  | 0  |
| Lying branches             | 2 | 4  | 7   | 5  | 1  |
| Leaning branches           | 3 | 13 | 3   | 4  | 0  |
| Total                      | 36| 107| 111 | 68 | 37 |
| Mean diameter, cm          | 19| 19 | 19  | 23 | 23 |
| Samples taken for moisture | 17| 81 | 77  | 47 | 26 |
| Samples taken for C concen. |28| 83 | 77  | 47 | 24 |

South-East Asia (Table 1). The tree community-level mean density was calculated as a weighted mean.

Chemical analysis of 259 wood samples (Table S1) was conducted in the Analytical Laboratory of Forest Research Institute KarRC RAS (Petrozavodsk, Russia). In the laboratory, the samples were liophilically dried at -30°C. Mechanical trituration of the samples by laboratory mill using liquid nitrogen was used to fix tissues. The C mass concentrations were measured for freeze-dried material (1.5–2.5 mg) using a Perkin Elmer 2400 Series II CHNS/O Analyzer, calibrated with the organic analytical standard acetanilide (Perkin-Elmer №0204-1121).

The effects of decay class on the wood bulk density, moisture, and C concentration were examined with generalized linear models (glm) (Table S1). In each decay class, the effects of tree component (stem vs. branch), position (snags, stumps, leaning logs, lying logs), and decay type (white- vs. brown- rot) on wood bulk density were tested. The effects of CWD position on C concentration in wood were also examined separately for each decay class (Table S1). Additionally possible effects of forest type on the variation in initial wood density (decay classes one and two, separately) were explored with glm (Table S1). The relationship between the bulk density and moisture of wood was investigated with glm (Table S1). The best glm models were chosen based on the likelihood-ratio tests and Akaike's information criteria (AIC). All graphs and the analyses were performed in R software (R Core Team, 2013).

3 RESULTS

The tree community-level wood density averaged 0.52 g cm$^{-3}$ (Table 1). Angiosperms had denser wood than gymnosperms (Table 1). The mean density of living trees was lower than the mean density of CWD wood in the first decay class (Tables 1 and 3).

The CWD wood density decreased through decomposition with the highest variation in the first decay class (Table 3, Figure 1) and was negatively related to wood moisture (Figure 2). The density reduction across decay classes did not differ significantly among snags, stumps, leaning and lying logs and branches (Table S1). Among CWD samples with identifiable type of rot, 88% of decomposed by white-rot, 8% were decomposed as brown-rot, and 4% of pieces contained both white and brown rot patches. The signs of invertebrate activity were recorded on the 3% of CWD pieces. The mean proportion of wood volume consumed by invertebrates was 8%. Decay type did not influence the wood density by decay classes (Table S1). Wood moisture of CWD in advanced decay classes was significantly higher compared with that in earlier decay classes (Figure 1b). The C concentration in wood averaged 46.5%. It varied greatly, from 27.2% to 60.2%, but independently of decay class and CWD position (Table S1). The wood mass loss averaged 0%, 20%, 37%, 54%, and 74% in the CWD of the 1st, 2nd, 3rd, 4th, and 5th decay classes, respectively.

4 DISCUSSION

In our study, mean wood density of CWD in the 1st decay class varied from 0.30 to 1.19 g cm$^{-3}$ and averaged 0.56 g cm$^{-3}$, which is close to the mean tree wood density in tropical Asia (0.57 g cm$^{-3}$; Reyes et al., 1992) and in Thai tropical montane forest (0.55 g cm$^{-3}$; Sungpalee et al., 2009). The mean tree community density calculated based on the data derived from global wood density database (0.52 g cm$^{-3}$) could be underestimated because the wood densities of many tree species present in our study area belonging to the genera with high wood density (e.g., Acer erythranthum, A. flabellatum, A. laurinum, Lithocarpus echinatus, L. lemeeanus, L. congtrien-sis, L. yersini, Quercus braianensis, Q. langbianensis; Ternstroemia sp.; Nagahama et al., 2019) are unknown and thus were not included in the calculations. Wood density also increases with tree aging. In our old-growth forests, wood densities of the same tree species could be higher compared to earlier reported values from younger forests. Similarly, higher wood density values measured in our study compared to those from other studies for the same trees’ species (Fokienia hodginsii, Pinus krempfii, P. kesiya) (Table 1) can be explained by a high age of the sampled trees.
To provide accurate, unbiased estimates of the biomass and C stocks of tropical CWD, it is necessary to have estimates of community-level wood density. Given very high variation of wood density reflecting high tree species diversity in the studied forests and a negligibly small reduction of density from fresh wood to decay class 1, wood density sampling from fresh CWD instead of destructive sampling from living trees can be recommended in montane tropical forests of high conservation value.

In our study, the densities of non-decomposed branch wood and stem wood did not differ. Branches were reported to have lower density than stems in Central Amazonian (Nogueira et al., 2005), French Guinea (Sarmiento et al., 2011), and Colombian (Pulido-Rodríguez et al., 2020) tropical forests. In other study from Colombian forest, the relationship between stem and branch wood density was almost linear (Duque et al., 2017). In general, the relationship between branch xylem and trunk xylem densities varies considerably among families and sites (Duque et al., 2017; Pulido-Rodríguez et al., 2020; Sarmiento et al., 2011). The densities of branch and stem wood recorded in our study do not necessarily reflect the inter-tree density variations. In tropical forests, CWD is formed either through mortality of single trees or tree groups or through branch-fall. The type of tree mortality may be tree species specific and related to tree size and age (van der Meer & Bongers, 1996).

The decrease in wood density with increasing decay class coincides with other studies (Russell et al., 2015) including tropical forests (Chao et al., 2017; Iwashita et al., 2013; Meriem et al., 2016; Moreira et al., 2019). In contrast to our hypothesis, the density by decay classes did not differ for different CWD types. This suggests an independence of decomposition from proximity to ground and moisture conditions because of generally high air humidity in the study sites (Gorbunov et al., 2018). In humid environments, downed and standing dead wood both may retain moisture and hence the decomposition pathway and the density of snags and downed logs of similar decay class might remain similar (Harmon et al., 2011).

In our study, wood moisture is, most likely, underestimated, since the samples were collected only during dry season. However, even during a dry season, for the most severely decayed samples, the values of wood moisture exceeded 500%. The negative relationship between wood density and moisture along decomposition of CWD was observed in many studies (Mackensen & Bauhus, 2003; Přívětivý & Šamonil, 2021; Rinne-Garmston et al., 2019). The wood moisture may increase up to 400% (Přívětivý & Šamonil, 2021). These patterns can be explained by the increase in water holding capacity related to the increase in air versus solid wood volume and by active fungal decay processes in wood. Fungi can significantly increase the moisture of wood substrate during the decay process (Boddy, 1983). The dominance of white-rot found in CWD in our study supports the importance of white-rot fungi to lignin degradation in tropical forests (Fujii, 2014; Schilling et al., 2015). Most brown-rot fungi are generalists or gymnosperm specialists, whereas most white-rot fungi are angiosperm specialists (Krah et al., 2018). Angiosperm CWD dominates in our sites.
The relatively low percentage of signs of invertebrate activity in the inventoried CWD pieces indicates predominantly microbial-driven decomposition processes. In tropical forests, insects, mainly termites, can play a very important role in consuming and fragmenting CWD (Shorohova et al., 2021; Ulyshen, 2016). However, their relative contribution to wood decomposition in different regions and types of tropical forests requires further research (Ulyshen, 2016).

Our estimate of the mean C concentration of CWD (46.5%) corresponds to the recently published compilation of existing data for C concentration in tropical trees 47.2% (Martin et al., 2021). It did not depend either on decay class or on position. The dominance of white-rot predisposed preferential decay of lignin selectively or simultaneously with cellulose and hemicellulose and thus stable C concentration in CWD across decay classes. In tropical forest woody debris, the C concentration in CWD may decrease (Chao et al., 2017; Clark et al., 2002) or not change (Iwashita et al., 2016; Meriem et al., 2016; Moreira et al., 2019) during decomposition. These differences can be attributed to initial variation in C concentration among tree species, methodological differences across studies (Harmon et al., 2013), as well as varying decomposer communities and CWD decomposition pathways (Martin et al., 2021).

Limitations of our study include unknown tree species identity of sampled CWD, unbalanced dataset for different CWD types by decay classes and overlooked effect of bark on CWD density. The dataset encompassed CWD of a wide range of tree species with varying initial density and C concentration. Hence, tree species specific patterns of density and C dynamics during decomposition could not be recognized. Studied forests were characterized by varying proportions of downed and standing dead wood in different decay classes. Therefore, our results on the density reduction factors and C dynamics across decay classes by dead wood types should be interpreted with caution. There is limited evidence on differences in chemistry between bark and wood in tropical tree species (Dossa et al., 2016). In boreal and temperate tree species, C concentration in bark is generally higher than in wood (Harmon et al., 2013; Martin et al., 2021). In four of the five studied tropical tree species, the opposite pattern was observed (Dossa et al., 2016). Bark cover and bark traits influence the wood decomposition process (Dossa et al., 2018) and consequently bulk density and C dynamics. In our study, CWD sampling was restricted to wood; and therefore, we could not either track density and C dynamics of bark during decomposition or account for bark effect on wood density across decay classes.

Despite these limitations, to our knowledge, this study is the first attempt to track the dynamics of C concentration across decay classes in tropical mixed montane forest CWD. Thus, more research is needed to understand possible sources of variation in the effects of decay on C concentration in CWD in such forests. Particularly, possible differences in the patterns of C dynamics during decomposition of gymnosperms and angiosperms should be tested (Harmon et al., 2013).
5 | CONCLUSIONS

The data-driven decay class-specific estimates of density and mass loss provide an empirical basis for future C inventories in CWD in Asian montane tropical mixed forests. Our research indicates that using a carbon concentration of 50% would overestimate the store of carbon in CWD. Observed variable patterns in density, mass loss, and C dynamics through decomposition of CWD highlight the need for further research into better understanding decomposition mechanisms and pathways in montane tropical mixed forests. Narrowing the uncertainties in the estimates of C concentration in tropical dead wood is critical for refining global C budgets and quantifying dead wood fluxes under global change.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.4mw6m90bb (Shorohova et al., 2022).

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