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Quantifying the influence of wood carbon fractions on tree- and forest ecosystem-scale carbon estimation in a temperate forest

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Abstract. Accurate forest carbon (C) accounting is critical for understanding the role forests play in the global C cycle. Forest C accounting relies on wood carbon fractions (CF) in order to convert estimates of tree biomass into C stock estimates, which are then upscaled to estimate forest C stocks at larger spatial scales. Generic wood CFs are often used in C accounting frameworks, despite evidence suggesting this trait varies widely across species, and that this variability influences our understanding of C stocks in trees and forests. Here, we couple data from over 39,000 trees in a 13.5-ha forest dynamics plot in central Ontario, Canada, with open-access wood CF databases, to quantify how wood CFs influence C stock estimates at individual tree- through to 400 m^2 and 1-ha forest ecosystem scales. In comparison to generalized wood CF assumptions (e.g., assuming a 50% CF or using wood CFs from the Intergovernmental Panel on Climate Change), species-specific wood CFs significantly influence C estimates at multiple scales. In comparison to species-specific wood CF data, tree-level estimates derived from other wood CF assumptions were biased by 0.8-3.9 kg of C per tree on average, with differences ranging up to >500 kg of C in large trees. While relatively small, these tree-level differences compound at larger spatial scales, with C stocks estimated using generalized wood CFs differing by 1.3-3.2 Mg of C ha^{-1} on average vs. those generated using species-specific wood CFs. These forest-scale discrepancies in C estimates increase in forest stands with high amounts of aboveground biomass in large trees and greater proportions of gymnosperms, in some instances exceeding 23.5 Mg of C ha^{-1} in especially biomass-dense gymnosperm-dominated forest stands. When extrapolated to the temperate forest biome, our results indicate that a 50% wood CF assumption—historically and presently one of the most common methodological assumptions in forest C research—overestimates global C stocks by 2.2-2.5 Pg of C. Our study is among the first to examine how wood CF assumptions influence tree- and forest-scale C accounting. We specifically demonstrate that species-specific wood CF data—especially for species that comprise the largest trees—are critical to ensuring accurate C stock estimates derived from forest and tree inventory data.

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1 Introduction

Forests play a critical role in the global carbon (C) cycle and in mitigating climate change, with estimates from 2020 indicating that forest biomes store ~870±61 Pg of C globally, of which ~135.78 Pg (~15%) originate in the temperate forest biome (Pan et al., 2024). Between 1990-2010, forests across the globe sequestered ~3.6±0.4 Pg C year^{-1} (Pan et al., 2024). While global forest C sequestration has remained stable at this rate over the past three decades, the differential impacts of biotic and abiotic environmental change drivers on forest structure and composition across space and time (e.g., Anderegg et al., 2015; Hartmann et al., 2022; Simler-Williamson et al., 2019; Hogan et al., 2024; Weed et al., 2013) have led to distinct changes in sink strength across and within biomes (Yang et al., 2023; Harris et al., 2021; Xu et al., 2021).

Specifically, the C sinks in both boreal and tropical intact forests have declined by an estimated 36% and 31%, respectively, while temperate forest C sinks have increased by an estimated 30% since 1990, from 0.53±0.04 Pg C year^{-1} in the 1990s to 0.69±0.05 Pg C year^{-1} in the 2010s. Increasing C sink strength among temperate forests was largely driven by afforestation in China, which offset reductions in temperate forest C sink strength in the United States and Europe (Pan et al., 2024). Standing carbon stock densities in temperate forests have followed similar trends, increasing from 157.03 Mg C ha^{-1} in the 1990s to 171.00 Mg C ha^{-1} through the 2010s (Pan et al., 2024).

Within temperate forests, ~38% of C stocks persist as living aboveground biomass (AGB)—the focus of our research here—while 54% is present in soils: values that closely approximate global estimates where 43% of C stocks exist within living AGB and ~45% in soils (with ~8% in deadwood and ~4% in leaf litter) (Pan et al., 2024). Carbon stocks and fluxes in living AGB in temperate forests, especially in North America, therefore represent a vitally important component of current and future global forest C cycles (Domke et al., 2020; Yang et al., 2023). In turn, accurate estimates of temperate tree and forest C stocks are critical for understanding the role forests play in mitigating the climate forcing potential of anthropogenic greenhouse gas emissions.

Obtaining tree- and forest-level C estimates entails first determining AGB, generally done through field-based forest surveys (e.g., Davies et al., 2021) or remote sensing methods (e.g., Coops et al., 2021), and then converting AGB to C stocks by multiplying AGB by a wood carbon fraction (CF) that represents the proportion of biomass comprised of elemental carbon (Martin and Thomas, 2011; Thomas and Martin, 2012). In forest C estimation studies and models, researchers commonly assume generic wood CFs, with 50% being the most common assumption or other generic wood CF values (reviewed by Martin et al., 2018). However, recent studies have demonstrated that a single wood CF conversion factor may overlook ecologically meaningful variability in wood chemistry across species, ultimately leading to inaccurate estimates of tree- and forest-scale C stocks.

Meta-analyses have shown that wood CFs vary across all tree species and forested biomes, ranging from 28-65% (Doraisami et al., 2022 and references therein). Databases of wood CFs indicate that temperate tree species have CFs ranging from 40.5-55.6%, with angiosperms (46.5±0.3% [s.e.]) typically having lower average CFs than gymnosperms (50.1±0.4% [s.e.]). These trends are hypothesized to reflect a larger contribution of C-rich lignin to wood chemical composition in gymnosperms, and generally lower lignin/holocellulose ratios in angiosperm wood (Doraisami et al., 2024; Martin et al., 2018; Lamlom and Savidge, 2003). Furthermore, the published literature suggests that using a 50% wood CF assumption, or other CFs recommended by the Intergovernmental Panel on

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Climate Change (IPCC), systematically overestimate temperate forest C stocks (cf. Table 1 in Martin et al., 2018). However, we lack a precise understanding of how this error at the tree level (in terms of kg of C tree^{-1}) scales up to the ecosystem level (in terms of Mg C ha^{-1} of forest), since mean CF values across tree species do not correspond to mean values representative of whole ecosystems.

The literature documenting variability in wood chemical traits suggests C accounting errors associated with generic wood CF assumptions (especially a 50% assumption) may be lower in certain forest communities compared to others, due to varying species composition and the proportion of angiosperms and gymnosperms. Specifically, in forests dominated by gymnosperms, one might expect lower C accounting errors, since gymnosperm CFs are closer to 50% or existing IPCC recommendations, as compared to angiosperms (Doraisami et al., 2024; Martin et al., 2018; Lamlom and Savidge, 2003). Conversely, C accounting in angiosperm-dominated forests would be expected to be overestimated by generic wood CF assumptions. To our knowledge, no study has integrated forest inventory data with wood CF data to test this hypothesis or quantify the magnitude of large-scale biases.

Recently published frameworks exist for selecting appropriate wood CFs for forest C accounting studies and models under different data availability scenarios (Doraisami et al., 2024). Specifically, recent work suggests that there exist different options for wood CF values that can be applied to C accounting methods and models. Generally, among the levels of wood CF determination, species-specific wood CFs—derived from wood chemical trait data (Lamlom and Savidge, 2003) or trait databases (Doraisami et al., 2022)—should produce tree- and ultimately forest-level C estimates that account for species differences in wood C chemistry. The level of species-specificity in wood CFs is considered the most data-informed trait option, relative to other wood CFs that are A) generalized for gymnosperms and angiosperms at varying levels of biome-specificity, or B) reflect a generic 50% wood CF assumption (Doraisami et al., 2024). Explicitly comparing how estimates of C differ across these approaches, across tree- to forest ecosystem scales, would provide a more detailed understanding of the degree to which wood CF assumptions influence our understanding of temperate (and global) forest C dynamics.

In this study, we paired forest inventory data from a large-scale temperate research plot (Davies et al., 2021; Kish et al., 2022) with CFs obtained from open-access wood CF databases (Doraisami et al., 2022) and recently developed decision matrices for integrating wood CFs into C accounting protocols (Doraisami et al., 2024), to characterize the role that wood CF variation plays in forest C accounting. We integrated these to address the following research questions: 1) What is the magnitude of error in tree-level C stocks associated with generic wood CF assumptions? 2) How does this error scale up from the tree level to the forest ecosystem level? 3) Does the magnitude of this error vary according to forest attributes, including tree species composition and/ or forest biomass?

2 Materials and Methods

2.1 Study site

Our study was conducted in the Haliburton Forest Dynamics Plot (HFDP), in the Haliburton Forest & Wild Life Reserve Ltd., in Ontario, Canada (43° 130′ N, 78° 350′ W) (Fig. 1). The HFDP is among a network of forest inventory plots of the Forest Global Earth Observatory (ForestGEO): a network comprised of 71 forest inventory plots located across all forested biomes and ranging in size from 4-50 ha (Davies et al., 2021). Across all ForestGEO plots,

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every tree ≥1 cm diameter at breast height (DBH) has its DBH measured, is identified to species, and is mapped every five years (Davies et al., 2021). The HFDP is located in the temperate forest biome and is representative of the Great Lakes–St. Lawrence forest region of eastern Canada and the United States (Kish et al., 2022).

The HFDP is a 13.5 ha forest inventory plot situated on the margins of a freshwater lake and has an average elevation of 434 m a.s.l. across a gradient ranging from 413-454 m a.s.l (Fig. 1). The HFDP consists of trees belonging to 30 species, with *Acer saccharum* (L.), *Abies balsamea* ([L.] Mill.), *Fagus grandifolia* (Ehrh.), and *Tsuga canadensis* (L.) being among the most common and dominant canopy species. Within the HFDP, other common angiosperm species include *Acer rubrum* (L.), *Betula allegheniensis* (Britt.), *Betula cordifolia* (Regel), *Prunus serotina* (Ehrh.), and *Quercus rubra* (L.), while other common gymnosperms include *Picea glauca* ([Moench] Voss), *Pinus strobus* (L.), and *Thuja occidentalis* (L.) (Kish et al., 2022). Shrubs that reach ≥1 cm DBH in the HFDP are also included in the census and our analysis here. In recent years, forest structure and C dynamics have been especially influenced by the presence and spread of beech bark disease, which is currently among the most important drivers of biomass and C dynamics in the HFDP (Kish et al., 2022).

2.2 Tree-level aboveground biomass and carbon estimation

Based on the ForestGEO sampling protocols (Davies et al., 2021), we used stem DBH values taken from the 2014 HFDP recensus to quantify aboveground biomass (AGB) and C stocks for n=39,064 trees ≥1 cm DBH, while assuming five different wood CF scenarios. To do so, we first used DBH measurements in conjunction with published species-specific allometric equations to derive tree-level AGB estimates. Specifically, we employed allometric equations published by Lambert et al. (2005), which estimates AGB (in kg) for three separate tree compartments—stems, branches, and bark—as:

$$y_{wood} = \beta_{wood1}\mathrm{DBH}^{\beta wood2} \quad \text{(Equation 1)}$$

$$y_{branches} = \beta_{branches1}\mathrm{DBH}^{\beta branches2} \quad \text{(Equation 2)}$$

$$y_{bark} = \beta_{bark1}\mathrm{DBH}^{\beta bark2} \quad \text{(Equation 3)}$$

where tree DBH is measured in cm, β_{wood1} and β_{wood2} represent species-specific model coefficients for estimating AGB in stem wood, $\beta_{brachnes1}$ and $\beta_{branches2}$ represent species-specific model coefficients for estimating AGB in branches, and β_{bark1} and β_{bark2} represent species-specific model coefficients for estimating AGB in bark (Lambert et al., 2011). Based on these values, we then estimated total AGB for each tree (y_{total}) as:

$$y_{total} = y_{wood} + y_{branches} + y_{bark} \quad \text{(Equation 4)}$$

Tree-level C estimates were then calculated based on AGB data (from Equation 4), using varying degrees of wood CF specificity: low degrees of specificity entail wood CFs that are more general in nature (i.e., a 50% wood CF assumption for all trees), whereas a high degree of specificity entails (for example) wood CFs that are informed by species-specific trait data. The wood CFs employed in our study broadly correspond to Tiers 1-3 forest C stock estimation methods employed by the IPCC, which incorporate wood CFs at five different levels based on the framework published by Doraisami et al. (2024).

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Tree-level C estimates at Level 1 (C_{tree1}) entail the use of species-specific wood CFs based on stem tissue. The use of wood CFs of stem tissue is due to its close correlation with wood C concentrations from all plant tissues within a given species (Martin et al., 2018; Thomas and Martin, 2012), especially with respect to species in the HFDP (Martin et al., 2015). Level 2 (C_{tree2}) presents a lower degree of species-specificity, whereby wood CFs are specific to angiosperms (46.5%) and gymnosperms (50.1%) from temperate forested biomes. Level 3 (C_{tree3}) uses taxonomic divisions; however, the values for angiosperms (46.8%) and gymnosperms (48.5%) are more generalized as they are derived from data for trees across all forested biomes. Wood CFs employed to generate values of C_{tree2} and C_{tree3} are based on global analyses of wood CF data (Martin et al., 2018) from open-access databases (Doraisami et al., 2022), which have specifically been proposed as alternatives to existing IPCC-based forest C accounting protocols (Doraisami et al., 2024). The most generalized two levels, Levels 4 and 5, both apply a single conversion factor when converting AGB to carbon. Specifically, Level 4 (C_{tree4}) is based on IPCC forest C accounting guidelines (Ipcc, 2006), which employs a single default wood CF of 0.47 for all trees. Lastly, Level 5 (C_{tree5}) entails the use of the coarsest (and most common) wood CF assumption, employing a default wood CF of 50% for all trees. In summary, for each of the n=39,064 individual trees within the HDFP, we generated five different tree-level C values denoted as C_{tree1} through C_{tree5}, with decreasing species-specificity in their wood CFs used to convert all values of y_{total} into C_{tree} values.

2.3 Statistical analysis—the influence of wood CFs on tree-level C estimates

All analyses were performed using R v. 4.2.2 statistical software (R Foundation for Statistical Computing, Vienna, Austria). First, we performed paired t-tests to assess differences in $\log_{10}$-transformed C_{tree} values across different wood CF assumptions (n=39,064 trees in all paired t-tests, implemented using the 't.test' function). Here, C_{tree1}, which represents our most species-specific wood CF assumption, was taken as a reference point such that only the following contrasts were assessed: C_{tree1} vs. Ct_{ree2}; C_{tree1} vs. C_{tree3}; C_{tree1} vs. C_{tree4}; and C_{tree1} vs. C_{tree5}. We refined our analysis to these contrasts only because we were explicitly interested in understanding how species-specific wood CFs refined our understanding of tree- and forest-level C stocks compared to more generalized wood CF assumptions.

We then conducted more detailed analyses of differences in C estimates (measured in kg C $tree^{-1}$) across the same wood CF contrasts (i.e., C_{tree1} vs. C_{tree2}-C_{tree5}) for all n=39,064 trees in our dataset. Differences in tree-level C estimates (measured in kg C $tree^{-1}$) were calculated as C_{tree1} minus C_{tree2}-C_{tree5}, such that negative values denote instances where more generalized wood CFs overestimate tree-level C estimates (compared to species-specific wood CFs) and positive differences denote instances where generic wood CFs underestimate tree-level C estimates (compared to species-specific wood CFs assumptions).

Lastly, we used analysis of covariance (ANCOVA) to test if differences in tree-level C estimates owing to wood CF assumptions differ across taxonomic divisions and/or scale with tree DBH. These models were fit for each of the four sets of differences (i.e., C_{tree1} minus C_{tree2}-C_{tree5}), where differences in tree-level C estimates were predicted as a function of an intercept term (corresponding to an average C stock difference between C_{tree1} vs. the

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other four C_{tree} estimates), taxonomic division (as a categorical factor), DBH, a second-order polynomial DBH term (DBH^2), as well as division-by-DBH and division-by-DBH^2 interaction terms.

2.4 Statistical analysis—the influence of wood CFs on forest-level C estimates

To assess how wood CF assumptions scale from trees to forests, we used our data to scale all five C_{tree} values to two area-based estimates: 1) a 20-by-20 m subplot level ($C_{subplot}$) and 2) a per ha level (C_{ha}) (Fig. 1). At both scales, we again derived five distinct values of $C_{subplot}$ and C_{ha} for each wood CF assumption (also denoted as $C_{subplot1}$ through $C_{subplot5}$, and C_{ha1} through C_{ha5}). In the HFDP, there are n=369 distinct subplots, which were then aggregated into n=10 ha of forest following previous analyses of deadwood C dynamics in the HFDP (Doraisami et al, unpublished). Due to the irregular shape of the HFDP, all $C_{subplot}$ values derived from subplots situated on the lake margin were scaled to their respective area (Fig. 1), with a number of subplots omitted from analyses of C_{ha} data.

At both scales, we again calculated differences in $C_{subplot}$ and C_{ha} values, specifically comparing values underpinned by species-specific wood CF data ($C_{subplot1}$ and C_{ha1}, respectively) vs. values derived from more general wood CFs ($C_{subplot2}$ through $C_{subplot4}$, and C_{ha1} through C_{ha4}, respectively). We then used ANCOVA models to evaluate how tree biomass and species composition at the subplot or ha scale influenced differences in $C_{subplot}$ or C_{ha} values. Here, we were especially interested in understanding the role that large trees play in C estimate differences (akin to our DBH terms in the tree-level ANCOVA models above), and the role that species composition may play in driving differences (akin to the taxonomic division model terms in the ANCOVAs described above). Therefore, in these models, differences in $C_{subplot}$ or C_{ha} values between any two estimates were predicted as a function of large tree biomass (defined as the total kg of biomass in trees ≥10 cm DBH in a subplot or per ha), small tree (1-10 cm DBH) biomass, and the proportion of biomass represented by gymnosperms in a subplot or per ha. To allow for non-linearity in relationships between biomass and discrepancies in C estimates (as informed by our tree-level analysis described below), we also included 2^{nd}-order polynomial terms in these models for large tree biomass and small tree biomass. The sample sizes for these models were n=368 subplots and n=10 ha; so, we interpret the per ha analysis cautiously. Finally, these models did not include any biomass-by-composition interaction terms to simplify the interpretation of our results and avoid model over-fitting (especially at the per ha scale of analysis).

3. Results

3.1 The influence of wood CF assumptions on tree-level C estimates

Wood CF assumptions influenced tree-level C stock estimates, with estimates of C_{tree1} generated using species-specific wood CFs differing significantly from all other C_{tree} estimates (paired t-test on $\log_{10}$-transformed data, $p<0.001$, absolute $t_{39,063}\geq255.9$ in all four comparisons; Tables 1 and 2). In all but the instance of a 50% wood CF assumption (C_{tree5}), species-specific wood CFs (C_{tree1}) resulted in significantly higher average tree-level C estimates (mean=69.7 kg, median=2.35 kg, range=0.045-7783.82 kg) vs. those generated using: A) wood CFs for temperate biome trees specific to gymnosperms and angiosperms (C_{tree2}, mean=68.9 kg, median=2.28 kg, range=0.044-7,799.39 kg); B) non-biome-specific wood CFs for gymnosperms and angiosperms (C_{tree3}, mean=67.59 kg, median=2.3 kg,

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range=0.044-7,550.31 kg); and C) the IPCC default wood CF assumption (C_{tree4}, mean=65.9 kg, median=2.27 kg, range=0.044-7,270.09 kg). A 50% wood CF assumption (C_{tree5}) resulted in considerably higher tree-level C values (mean=70.56 kg, median=2.43 kg, range=0.047-7,783.82 kg) (Table 1).

Differences in C_{tree1} vs. other C_{tree} estimates varied significantly as a function of taxonomic division and DBH (ANCOVA model r^2=0.266-0.971, p<0.01 in all cases; Fig. 2, Table A1). The ANCOVA also returned statistically significant terms for DBH^2, and the division-by-DBH and division-by-DBH^2 interaction terms (p<0.01 in all but one case where p=0.048): differences between C_{tree1} and other C_{tree} estimates were larger in gymnosperms vs. angiosperms (p<0.01 for the taxonomic division and division-by-DBH interaction terms) and scaled non-linearly with tree size (p<0.01 for the taxonomic division and division-by-DBH^2 interaction terms; Fig. 2, Table A1). Non-linear increases in the absolute differences between C_{tree1} vs. $C_{tree2-5}$ largely tracked allometric relationships associated with different tree species, such that these differences in C_{tree} increased with tree-level AGB (i.e., y_{total} values). The rate at which C_{tree} differences increased with DBH depended on species identities (Fig. 2), reflecting differences in allometric relationships between y_{total} and DBH. The strong influence of DBH on tree-level C estimates is also evidenced by our results showing that the lower 5% of tree-level C estimates was largely consistent across C_{tree1} through C_{tree5} (range of lower 5% confidence intervals [CI]=0.11-0.119 kg C), though differences were more pronounced at the upper 90% CI (C_{tree1}=169.69 kg C vs. $C_{tree2-Ctree5}$=160.08-171.37 kg C) and upper 95% CI (C_{tree1}=370.58 kg C vs. $C_{tree2-Ctree5}$=352.59-377.508) (Fig. 2, Table 2).

3.2 The influence of wood CF assumptions on forest-level C estimates at small spatial scales

Differences in tree-level C estimates (C_{tree1}-C_{tree5}) scaled up to influence forest-level C stocks at both the 400-m^2 subplot ($C_{subplot1}$-$C_{subplot5}$) and ha (C_{ha1}-C_{ha5}) scales. At the subplot level, C stock estimates derived from species-specific wood CFs ($C_{subplot1}$) differed significantly from all other C stock estimates (paired t-test p<0.001, absolute $t_{39,063}$≥24.1 in all four comparisons; Fig. 3, Table 2, Fig. A1). Mean $C_{subplot}$ values owing to different wood CF assumptions ranged from 6,995-7,489 kg C 400 m^{-2} (median range of $C_{subplot}$ values=4,278-4,580 Mg C 400 m^{-2}). At this scale of analysis, the most generalized wood CF assumptions led to the widest range of average $C_{subplot}$ values, with the IPCC-recommended wood CF ($C_{subplot4}$) resulting in the lowest mean/median $C_{subplot}$ estimates, and a 50% wood CF ($C_{subplot5}$) resulting the highest mean/median estimates (Table 2).

Consistent with the previous findings of variability in C_{tree} estimates being especially pronounced in large trees, statistically significant differences in $C_{subplot1}$ vs. all other $C_{subplot}$ estimates were also driven by high-biomass subplots. Specifically, the lower 5th percentile of $C_{subplot}$ ranged by 87 kg of C, and the higher 95th percentile of $C_{subplot}$ values across all estimates ranged by over 468 kg of C (Table 2). An ANCOVA model predicting differences in $C_{subplot}$ as a function of subplot-level characteristics corroborated this trend, indicating that differences in $C_{subplot1}$ values vs. $C_{subplot2}$-$C_{subplot5}$ values were statistically correlated with the amount of subplot biomass contained in large trees (p<0.01, partial r^2=0.221-0.961 for the large tree biomass term; Fig. 3, Table A2). However, the wide range of partial r^2 values for the large tree biomass term indicates that these relationships were idiosyncratic.

Differences between $C_{subplot1}$ vs. $C_{subplot3}$ (taxonomic division-specific wood CFs) and $C_{subplot4}$ (IPCC-recommended wood CFs) were consistently positive, with differences ranging from 0.6-2,927.7 kg of C per subplot

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(mean difference=223.9 and 402.9 kg of C per subplot, respectively), indicating that these assumptions consistently underestimate $C_{subplot}$ values compared to species-specific wood CF data (Fig. 3). Differences in $C_{subplot1}$ vs. $C_{subplot3}$ and $C_{subplot4}$ became larger as the amount of total biomass contained in large trees increased (ANCOVA model parameter $p<0.01$, partial $r^2=0.932$ and 0.961, respectively, Table A2). This trend indicates that underestimates in $C_{subplot3}$ and $C_{subplot4}$ values (compared to $C_{subplot1}$ estimates) increase with greater subplot-level biomass. In these comparisons, we also found a statistically significant contribution of gymnosperm biomass proportion explaining these differences (ANCOVA model parameter $p<0.01$, partial $r^2=0.087$ and 0.635, respectively, Table A2).

Comparatively, differences in $C_{subplot1}$ vs. $C_{subplot2}$ (i.e., biome-specific wood CFs for angiosperms and gymnosperms) were smaller (mean difference=85.5 kg C subplot^{-1}, range=-29.7 to 225.9 kg C subplot^{-1}) and were both positive and negative, indicating that the wood CF assumptions embedded in $C_{subplot2}$ led to both over- and underestimates of $C_{subplot}$ compared to estimates using species-specific data. Here, differences in $C_{subplot}$ estimates were more strongly dictated by species composition, such that gymnosperm biomass proportion was the strongest correlate of these $C_{subplot1}$ vs. $C_{subplot2}$ differences (ANCOVA model parameter $p<0.01$, partial $r^2=0.654$ and 0.635, respectively, Table A2). Large tree biomass played a secondary, albeit statistically significant, role in governing $C_{subplot}$ estimation differences (ANCOVA model parameter $p<0.01$, partial $r^2=0.087$ and 0.635, respectively), and these relationships were non-linear (Fig. 3).

Differences between $C_{subplot1}$ and $C_{subplot5}$ (a 50% wood CF fraction) were unique in that these differences were the only negative average values (mean difference=-91.5 kg C subplot^{-1}), indicating that a 50% assumption overestimates $C_{subplot}$ values. However, individual differences calculated for $C_{subplot1}$ vs. $C_{subplot5}$ did indicate that a 50% wood CF assumption resulted in both over- and underestimates compared to species-specific wood CF data. The 50% wood CF overestimated $C_{subplot}$ values in 342 of 368 subplots, with these overestimates being much larger than the few underestimates (Fig. A1). Again, in these comparisons, species composition was the strongest correlate of these differences: as gymnosperm proportions increased, the differences between $C_{subplot}$ values generated using species-specific data vs. a 50% assumption generally grew closer to 0 (ANCOVA model parameter $p<0.01$, partial $r^2=0.635$, respectively; Table A2). The amount of biomass in large trees also influenced this relationship, albeit in a non-linear manner (Fig. 3). Here, trends indicated that as large gymnosperm biomass increased, differences in $C_{subplot1}$ vs. $C_{subplot5}$ became less negative; conversely, differences in $C_{subplot1}$ vs. $C_{subplot5}$ values were largest in subplots with high angiosperm proportions (Fig. 3).

3.3 The influence of wood CF assumptions on forest-level C estimates at larger spatial scales

Species-specific wood CFs led to higher forest C stocks on a per ha scale (C_{ha1}) and resulted in statistically higher estimates than those based on more generalized wood CFs (namely, C_{ha2}-C_{ha4}; $t_9 \geq 5.8$, $p<0.01$ in all three paired *t*-tests; Fig. 4, Fig. A2, Tables 1 and 2). Specifically, in these comparisons, C_{ha1} averaged 83.3 Mg C ha^{-1}, vs. 80.1-80.6 Mg C ha^{-1} on average under C_{ha2}-C_{ha4} assumptions (Table 1). Similar to our tree- or subplot-level analyses, statistically significant differences across C_{ha1} vs. other estimates were most pronounced at the higher range of C_{ha} values (Table 2). Furthermore, across these comparisons (C_{ha1} vs. C_{ha2}-C_{ha4}), species-specific wood CF data increased C_{ha} estimates by 2.6-9.0 Mg C ha^{-1} on average, with differences ranging from 1.3-23.5 Mg C ha^{-1} (Fig. 4). Differences

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in C_{ha} values mostly increased as wood CF assumptions became more generalized, being most pronounced when comparing C_{ha1} to estimates generated using the IPCC's default value (C_{ha4}; Fig. 4, Table 2).

Consistent with subplot-scale analyses, differences in C_{ha1} vs. C_{ha2}, C_{ha3}, and C_{ha4} were statistically correlated with the quantity of large tree biomass in each hectare of forest, although at this scale, species composition played a clearer role in driving C estimate differences (Fig. 4, Table A3). Specifically, differences between C_{ha1} and C_{ha2} were largest in areas of the forest dominated by angiosperms, suggesting wood CF data for angiosperm species differ most strongly from the wood CF values assumed in these estimates. Alternatively, differences in C_{ha1} vs. C_{ha3} and C_{ha4} values were largest in forests with the highest gymnosperm values (Fig. 4), suggesting the wood CF values assumed in these estimates (i.e., those of the IPCC) differ strongly from actual wood CF values.

At the per ha scale, the 50% wood CF assumption was the only assumption leading to systematic overestimates of C_{ha} values compared to estimates underpinned by species-specific wood CF data (paired *t*-test t_9=-6.6, p<0.01). Specifically, in comparison to species-specific wood CF data, the 50% assumption overestimated forest C stocks by 2.8 Mg of C ha^{-1} on average, with overestimates occurring in all 10 hectares of forest analyzed here, ranging from 1.9-3.2 Mg C ha^{-1} (Fig. 4, Fig. A2). These overestimates were largest in forests dominated by angiosperms, with differences declining with greater gymnosperm biomass (especially large gymnosperms), indicating that the 50% wood CF differs most widely from wood CFs in angiosperms (Fig. 4).

4. Discussion

Studies documenting variability in wood CFs among trees have expanded over the past decade (Doraisami et al., 2022), leading to a considerably greater amount of wood CF data now available for integration with forest C accounting frameworks (Doraisami et al., 2024). Documentation of high variability in wood CFs among co-occurring tree species (e.g., Lamlom and Savidge, 2003; Thomas and Malczewski, 2007) or across forests globally (Martin et al., 2018) implies that this variability systematically influences forest C stocks from individual trees through to global scales. Moreover, much of the literature on wood CF variation makes this case in the context of comparing species-specific wood CF data to a 50% wood CF assumption. Here, studies commonly point to overestimates in C stocks, especially in angiosperm-dominated forests (Martin and Thomas, 2011; Lamlom and Savidge, 2003). To our knowledge, the present study is the first to integrate multiple wood CF assumptions into detailed inventory-based C assessments. In doing so, we find that although certain assertions in the wood CF/forest C accounting literature are supported by our C estimation analysis, there exists considerable nuance surrounding how wood CF variation influences tree- to forest-level C stocks.

Our clearest finding is that a 50% wood CF assumption—historically the value most commonly employed in large-scale studies and national-scale models of forest C stocks and fluxes—consistently overestimates C stocks in comparison to estimates generated using species-specific wood CF data, and that this systematic error compounds across individual trees (C_{tree}; 0.86 kg of C $tree^{-1}$ on average), to small spatial scales ($C_{subplot}$; 91.5 kg of C 400 m^{-2} on average), and ultimately to larger forest ecosystem scales (C_{ha}; 2.8 Mg of C ha^{-1} on average) (Figs. 2-4). Consistent with angiosperms expressing lower wood CFs compared to gymnosperms (Martin et al., 2018), these overestimates are especially prominent in angiosperm trees and angiosperm-dominated forests (Figs. 3, 4).

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A novel contribution of our study is evidence that while the 50% wood CF assumption systematically overestimates C across all scales, the size of this error—in absolute C_{tree}, $C_{subplot}$, and C_{ha} terms—is actually smaller than the error associated with other wood CF assumptions. Our analysis finds that a 50% CF assumption leads to A) the smallest absolute errors, but simultaneously, B) errors that consistently overestimate C stocks in nearly all trees and forest stands. To illustrate, a 50% wood CF results in a total estimate of 2,756.2 Mg of C across our 13.5-ha forest dynamics plot: a value that is 33.7 Mg of C larger than the estimate using species-specific CFs (i.e., 2,722.5 Mg of C). At larger scales, even if our minimum observed difference between C_{ha1} and C_{ha5} (1.9 Mg C ha^{-1}) is scaled to the temperate forest biome—estimated at 794,072,373 ha in recent analyses (Pan et al., 2024)—the 50% wood CF overestimates temperate forest C stocks by 1.5 Pg of C (equivalent to 1,508,737,509 Mg of C). However, if our average or maximum discrepancy between C_{ha1} and C_{ha5} (2.8 and 3.2 Mg C ha^{-1}, respectively) is scaled in a similar manner, this overestimate would be equivalent to 2.2-2.5 Pg of C. This value is lower than coarse estimates of similar errors discussed for tropical forests (Martin and Thomas, 2011), which suggests that the dominance of angiosperms would lead to differences between our C_{ha1} and C_{ha5} terms that are much larger. Nonetheless, our findings here provide among the most detailed analyses demonstrating that a 50% wood CF assumption systematically overestimates C stock estimates at tree, forest ecosystem, and ultimately biome scales.

Our analyses of other wood CF assumptions contribute the novel finding that alternative generic CF values—for example, those recommended by the IPCC (C_{tree4})—generally underestimate C compared to estimates based on species-specific wood CF data. Here, the influence of wood CF assumptions on C estimation is more nuanced, but certain trends emerged. First, the magnitude of underestimates depends on tree species identity and DBH at the individual tree scale (Fig. 2), as well as forest composition and the amount of forest biomass contained in large (≥10 cm DBH) trees at the forest scale (Fig. 3, 3). Second, the overall magnitude of these underestimates generally increases as wood CF assumptions become more generalized from i) temperate biome-specific wood CFs for angiosperms and gymnosperms (C_{tree2}), to ii) wood CFs for angiosperms and gymnosperms that are not biome-specific (C_{tree3}), and finally, iii) the IPCC's default wood CF of 0.47 for all trees (C_{tree4}). We therefore suggest the current IPCC values recommended for C estimation should be replaced by existing published values, specifically wood CF data for angiosperms and gymnosperms that are biome-specific (e.g., as presented most recently in (Doraisami et al., 2024)]).

As expected following previous studies, our analysis found that generalized wood CF assumptions used to estimate our C_{tree2}-C_{tree5} data approximate the empirically-derived wood CFs (i.e., those used to estimate C_{tree1}) better for some tree species than others (Fig. 2). This has been well-described by existing studies on wood CF variation among trees globally (Martin et al., 2018; Thomas and Martin, 2012). Here, we show that the precise wood CF data are especially important for tree- and forest C stock estimates for large trees (≥10 cm DBH) that contribute large proportions of forest biomass (Fig. 3, Fig. 4). In our study site, large trees represent 87.0-90.0% of total live aboveground biomass at the 400 m^2 subplot and per ha scales. In turn, four species, namely balsam fir (*A. balsamea*), sugar maple (*A. saccharum*), eastern hemlock (*T. canadensis*), and American beech (*F. grandifolia*), represent ~76% of the large trees in our dataset, with differences in their wood CFs vs. generalized assumptions therefore having a major influence on C stock estimate discrepancies among methods.

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Stem wood CFs extracted from open-access databases (Doraisami et al., 2022) and used in our C_{tree1} calculations for *A. balsamea* and *T. canadensis* were 50.0% and 50.1%, respectively. This likely suggests that forest-scale overestimates owing to a 50% wood CF assumption (Fig. 4, Fig. A2) may be more constrained in our study site vs. others where dominant trees differ more widely from a 50% wood CF. Empirically derived wood CFs for these two gymnosperm species become progressively more different vs. wood CF assumptions embedded in estimates of C_{tree2} (50.1%), C_{tree3} (48.5%), and C_{tree4} (46.7%). These two species-specific patterns therefore contribute substantially to our findings that differences in tree- and forest-scale C accounting between $C_{subplot}$ and C_{ha1} values vs. all other estimates (except those based on a 50% assumption) both A) increase with greater wood CF generality and B) are correlated with large gymnosperm biomass.

The most common angiosperms in our datasets, *A. saccharum* and *F. grandifolia*, had empirically derived wood CF values of 48.4% and 47.9%, respectively (Doraisami et al., 2024). Differences between these species-specific wood CF values vs. wood CFs embedded in C_{tree2} (46.5%), C_{tree3} (46.8%), and C_{tree4} (46.7%) estimates did not increase systematically with greater generality of wood CF assumptions. Therefore, except for a 50% wood CF assumption, C_{tree} values associated with these dominant angiosperms did not necessarily increase or decrease systematically with more generalized wood CFs (i.e., those used to calculate C_{tree2}, C_{tree3}, and C_{tree4}; Fig. 2). In turn, our analysis indicates that while species-specific wood CF data correct for underestimates in angiosperm C stocks compared to all general wood CF assumptions (except a 50% value), ultimately, discrepancies in C estimates for angiosperm-dominated forests do not become larger as more general wood CFs are employed in C estimation.

One important question raised by our analysis is whether or not the majority of variation in wood CFs exists among vs. within tree species: a critical question that underpins much of the ecological theory surrounding how plant diversity influences ecosystem functioning (e.g., Albert et al., 2011; Siefert et al., 2015). If wood CFs vary more widely among than within tree species, then one might infer that species-specific wood CF values are a "gold standard" in forest C accounting protocols. This follows logically if, in fact, wood CFs do not vary across factors associated with intraspecific trait variation, such as environmental conditions or tree age/ size. Meta-analyses have shown that species identity is the most important factor explaining wood CF differences in the dataset employed in our analysis here, with intraspecific variation owing to tissue type being less important (Doraisami et al., 2024; Martin et al., 2018). However, other studies have pointed to variability that exists in wood CFs across tissue types (e.g., Ma et al., 2018), spatial/ edaphic factors (e.g., Dong et al., 2025), climate gradients (e.g., Paroshy et al., 2021), and tree age/ size (e.g., Martin and Thomas, 2013). Nonetheless, these studies aiming to understand how such factors influence wood CFs, either individually or collectively, are not necessarily definitive. For example, the meta-analysis by Ma et al. (2020) found that tree DBH or age explained 1-2% of the variability in wood CFs, compared to >85% of the variability explained by spatial location (a source of intraspecific variability) and species identity (a source of interspecific variation). We would therefore argue that despite much recent research on the topic, the relative contribution of inter- vs. intraspecific variability in wood CFs remains only loosely disentangled. Many studies, including our own (Martin et al., 2013), commonly and in some circumstances unavoidably conflate these different sources of variation. In relation to our findings here (Figs. 2-4), we suggest that studies isolating the "structure" of intraspecific variation in wood CFs (sensu Albert et al., 2010) within individual tree species, especially across continuous ranges of tree sizes

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(e.g., Martin and Thomas, 2013), remains important to better understand how wood chemical trait variation scales up to influence tree and forest C accounting.

From an applied perspective, our findings are applicable towards the assessment, monitoring, and potential enhancement of forest C stocks across several management-relevant contexts, frameworks, and scales. At the national scale, our results suggest that the adoption of more species-specific wood CFs into forest C estimation protocols leads to marked changes in C stock estimates, which scale up from the tree-, to forest ecosystem-, and ultimately to biome scales. Our findings suggest that species-specific wood CFs should be employed when estimating forest C stocks and fluxes, though when not available, alternative wood CFs other than a 50% wood CF are likely to provide a more conservative estimate of forest C stocks and fluxes. Additionally, and consistent with research on the critical role that large trees play in forest ecosystem functioning (e.g., Lutz et al., 2018), our results suggest that careful consideration of wood CFs among common trees that contribute the most to large stem biomass is especially important in accurately accounting for C stocks and fluxes in trees and forests.

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Table 1. Summary statistics of carbon stock estimates at tree^{-1} (kg of C), 400 m^{-2} subplot (kg of C), and ha^{-1} (Mg of C) scales, generated using five different wood carbon fraction (CF) assumptions. Descriptive statistics presented here are based on n=39,064 trees (for C_{tree}), n=368 subplots (for $C_{subplot}$), and n=10 ha (for C_{ha}).

Carbon estimators and wood CF assumptions			Central tendency			Range		Distributions				
Scale	**Estimate**	**Description of estimate**	**Mean**	**Median**	**S.D.**	**Min.**	**Max.**	**0.05**	**0.1**	**0.9**	**0.95**	**IQR**
Tree-level (kg C tree^{-1})	C_{tree1}	Species-specific wood CF	69.695	2.353	263.206	0.045	7,783.824	0.113	0.173	167.685	370.583	16.654
	C_{tree2}	Division- and biome wood CF	68.889	2.283	262.654	0.043	7,799.391	0.110	0.170	163.370	363.311	16.515
	C_{tree3}	Division-specific wood CF	67.586	2.298	255.325	0.044	7,550.309	0.111	0.169	162.654	359.401	16.131
	C_{tree4}	IPCC C conversion factor	65.900	2.267	246.859	0.044	7,270.091	0.111	0.168	160.081	352.593	15.845
	C_{tree5}	50% C conversion factor	70.557	2.428	264.303	0.047	7,783.824	0.119	0.180	171.393	377.508	16.965
Subplot (kg C 400m^{-2})	$C_{subplot1}$	Species-specific wood CF	7,398.1	4,443.00	7,620.25	10.36	45,387.39	1,318.61	2,350.09	16,886.63	22,791.41	5,470.102
	$C_{subplot2}$	Division- and biome wood CF	7,312.6	4,313.36	7,640.96	9.47	45,397.22	1,303.79	2,269.55	16,857.13	22,705.73	5,520.831
	$C_{subplot3}$	Division-specific wood CF	7,174.3	4,319.16	7,392.15	9.50	44,023.68	1,269.56	2,272.43	16,377.18	22,103.26	5,308.894
	$C_{subplot4}$	IPCC C conversion factor	6,995.3	4,278.03	7,113.72	9.45	42,459.75	1,254.71	2,245.66	15,869.13	21,395.42	5,053.282
	$C_{subplot5}$	50% C conversion factor	7,489.6	4,580.33	7,616.40	10.12	45,460.12	1,343.37	2,404.35	16,990.50	22,907.31	5,410.367
Hectare (Mg C ha^{-1})	C_{ha1}	Species-specific wood CF	175.7	137.4	110.4	83.3	383.8	87.3	91.3	375.8	379.8	48.6
	C_{ha2}	Division- and biome wood CF	173.1	134.4	111.1	80.1	382.5	84.2	88.2	374.4	378.5	48.4
	C_{ha3}	Division-specific wood CF	170.5	133.2	107.1	80.6	372.3	84.6	88.6	364.5	368.4	47.1
	C_{ha4}	IPCC C conversion factor	166.8	131.2	102.5	80.5	360.4	84.4	88.2	352.8	356.6	45.5
	C_{ha5}	50% C conversion factor	178.5	140.4	110.0	86.1	385.8	90.3	94.5	377.7	381.8	48.7

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Table 2. Summary statistics of carbon stock differences calculated at tree^{-1} (kg of C), 400 m^{-2} subplot (kg of C), and ha^{-1} (Mg of C) scales, generated using five different wood carbon fraction (CF) assumptions. In these calculations, C estimates at all scales are generated by converting tree-level biomass to C with species-specific wood CF data (C_{tree1}, $C_{subplot1}$, and C_{ha1}, as described in Table 1). Therefore, positive differences denote instances where more generalized wood CF assumptions underestimate tree-, subplot-, and per ha C stock estimates (i.e., C_{tree2}-C_{tree4}, $C_{subplot2}$-$C_{subplot4}$, C_{ha2}-C_{ha4}), while negative values denote instances where generalized wood CF assumptions overestimate tree-, subplot-, and per ha C stock estimates (i.e., C_{tree5}, $C_{subplot5}$, C_{ha5}). Also shown are paired *t*-tests evaluating statistical differences in all estimate comparisons, where n= 39,064 trees (C_{tree}), n=368 subplots ($C_{subplot}$), and n=10 ha (C_{ha}). Summary statistics and raw values are presented visually in Fig. 2 (for C_{tree} comparisons), Fig. 3 (for $C_{subplot}$ comparisons), and Fig. 4 (for C_{ha} comparisons).

Scale	Carbon estimate comparison	Mean difference	Min. difference	Max. difference	*t*-value (*p*-value)
Tree-level (kg C tree^{-1})	C_{tree1} - C_{tree2}	0.803	-15.568	83.627	$t_{39,063}$=255.9 (p<0.01)
	C_{tree1} - C_{tree3}	2.109	-0.149	233.515	$t_{39,063}$=526.0 (p<0.01)
	C_{tree1} - C_{tree4}	3.795	-0.099	513.732	$t_{39,063}$=385.3 (p<0.01)
	C_{tree1} - C_{tree5}	-0.862	-88.328	11.482	$t_{39,063}$=-263.8 (p<0.01)
Subplot (kg C 400m^{-2})	$C_{subplot1}$ - $C_{subplot2}$	85.5	-29.7	225.9	t_{367}=25.2 (p<0.01)
	$C_{subplot1}$ - $C_{subplot3}$	223.9	0.6	1363.7	t_{367}=92.8 (p<0.01)
	$C_{subplot1}$ - $C_{subplot4}$	402.9	0.9	2,927.7	t_{367}=62.0 (p<0.01)
	$C_{subplot1}$ - $C_{subplot5}$	-91.5	-267.3	16.4	t_{367}=-24.1 (p<0.01)
Hectare (Mg C ha^{-1})	C_{ha1} - C_{ha2}	2.6	1.3	3.3	t_{9}=5.8 (p<0.01)
	C_{ha1} - C_{ha3}	5.3	2.6	11.5	t_{9}=108.1 (p<0.01)
	C_{ha1} - C_{ha4}	9.0	2.8	23.5	t_{9}=15.0 (p<0.01)
	C_{ha1} - C_{ha5}	-2.8	-3.2	-1.9	t_{9}=-6.7 (p<0.01)

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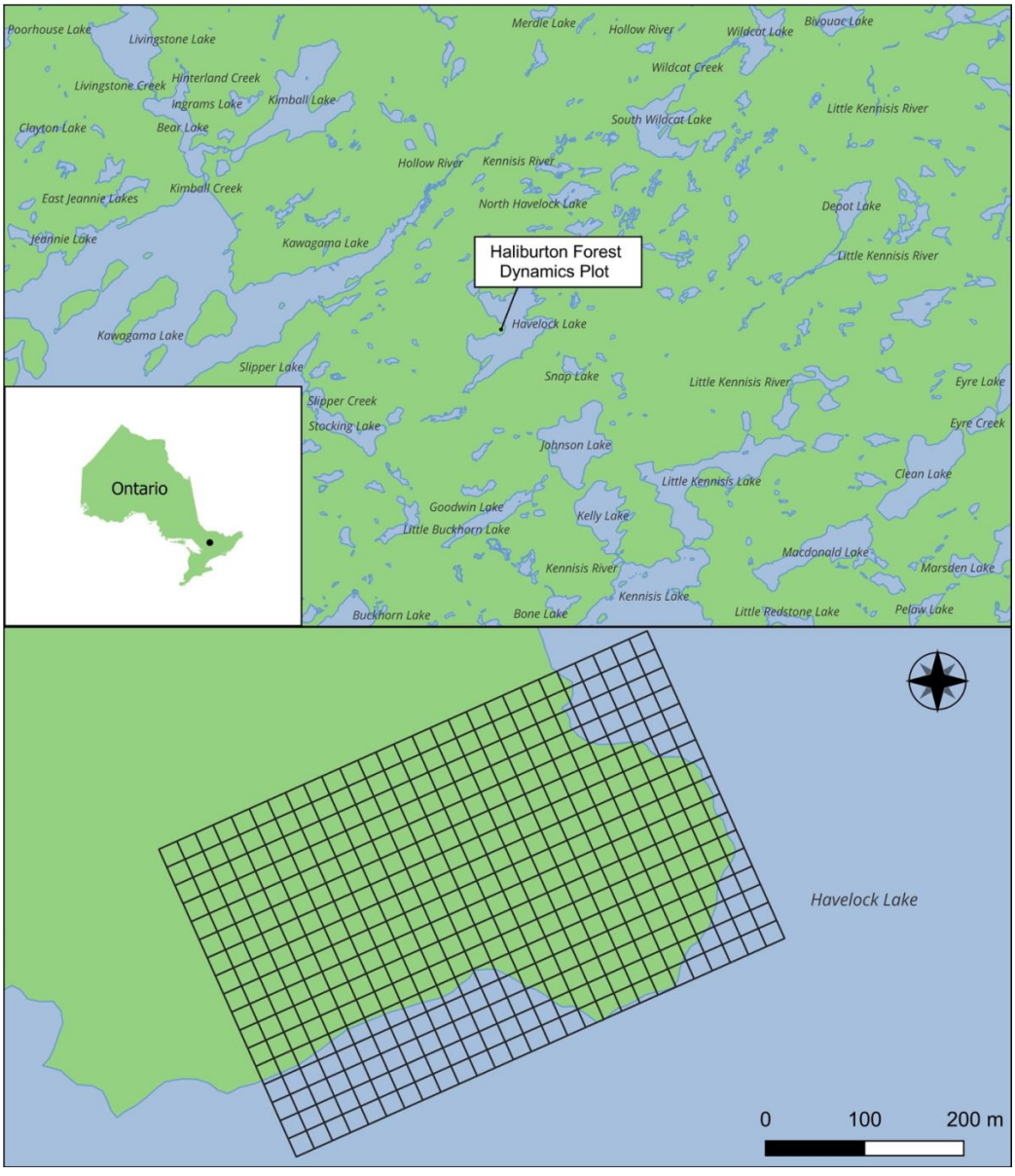

Fig. 1. Geogrpahical location of the Haliburton Forest Dynamics Plot (HFDP) situated in Haliburton County, Ontario, Canada. Panels A and B represent the location of the HFDP within provincial and regional contets, respectively, while Panel C represents the extent of the 13.5-ha HFDP as subdivided into n=368 subplots of 400 m^2 (20-by-20 m) in size.

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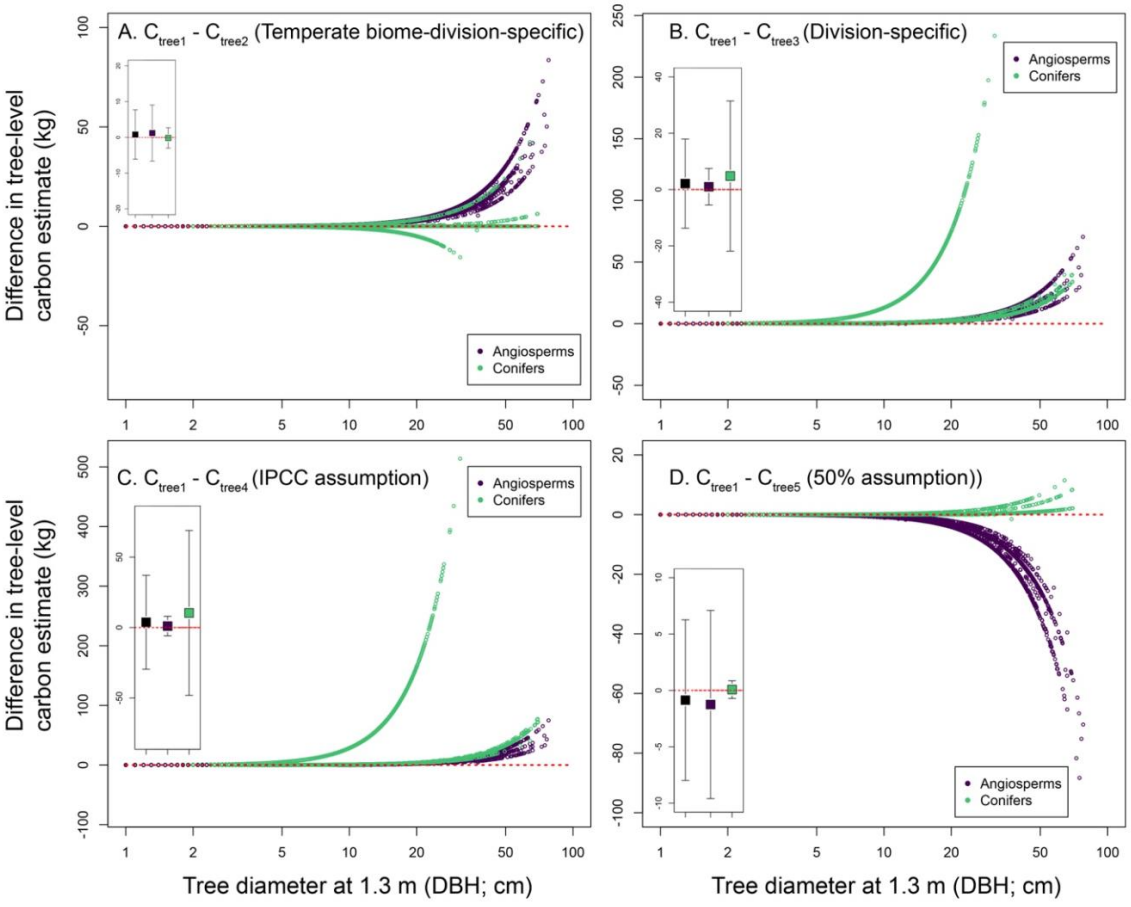

Fig. 2. Differences in tree-level carbon (C) stocks (measured in kg C $tree^{-1}$) estimated using different wood carbon fraction (CF) assumptions. Main panels show differences in tree-level C stocks for *n*=39,064 trees distributed across angiosperms (*n*=27,589; purple open points) and gymnosperms (*n*=11,475; green open points), calculated as the difference between C_{tree1} (generated using species-specific wood CF data) and C_{tree2} (Panel A; generated assuming wood CFs for temperate biome trees specific to gymnosperms and angiosperms); C_{tree3} (Panel B; generated assuming non-biome-specific wood CFs for gymnosperms and angiosperms); C_{tree4} (Panel C; generated assuming a single IPCC default wood CF assumption); and C_{tree5} (Panel D; generated assuming a single 50% wood CF assumption). Red dotted lines denote 0 differences in tree-level C stock estimates, such that i) all values above 0 indicate instances where species-specific wood CFs (C_{tree1}) are higher compared to estimates generated using generalized wood CF assumptions (C_{tree2}-C_{tree5}), and ii) all values below 0 indicate instances where species-specific wood CFs (C_{tree1}) are lower compared to estimates generated using generalized wood CF assumptions (C_{tree2}-C_{tree5}). Inset graphs in each panel represent mean differences in C_{tree} estimates (calculated as in the main panels) across all

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453 trees (black symbols), angiosperms (purple filled symbols), and gymnosperms (green filled symbols), with error bars
454 denoting 2 standard deviations about the mean.

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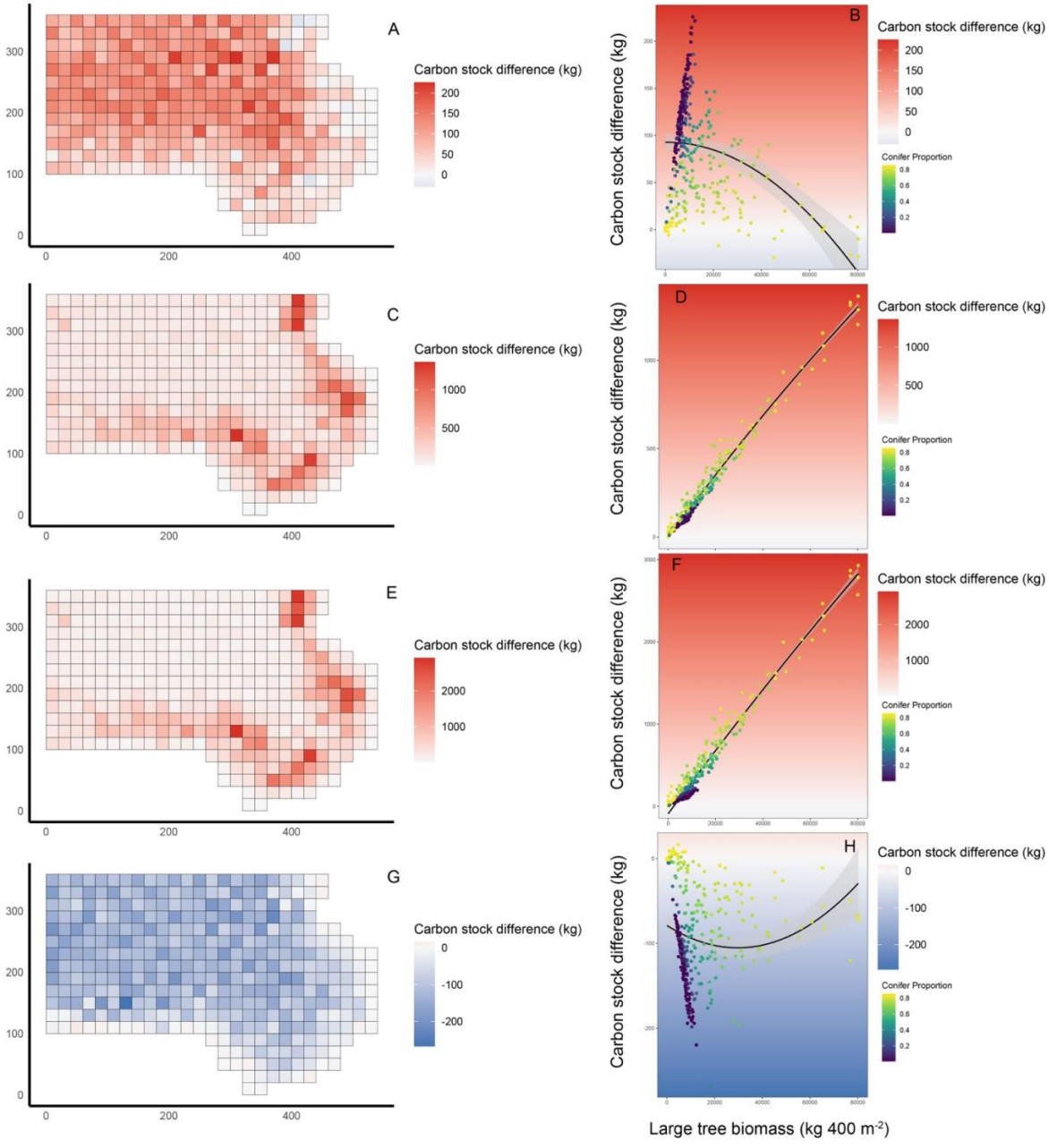

Fig. 3. Differences in 400-m^2 subplot-level carbon ($C_{subplot}$) stocks (measured in kg C subplot^{-1}) estimated using different wood carbon fraction (CF) assumptions. Subplot-level differences are calculated as the difference between $C_{subplot1}$ (generated using species-specific wood CF data) and $C_{subplot2}$ (Panels A-B; generated assuming wood CFs for

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459 temperate biome trees specific to gymnosperms and angiosperms); $C_{subplot3}$ (Panels C-D; generated assuming non-
460 biome-specific wood CFs for gymnosperms and angiosperms); $C_{subplot4}$ (Panels E-F; generated assuming a single
461 IPCC default wood CF assumption); and $C_{subplot5}$ (Panel G-H; generated assuming a single 50% wood CF
462 assumption). Therefore in all maps and graphs, i) all values above 0 and in red shading indicate instances where
463 species-specific wood CFs ($C_{subplot1}$) are higher compared to estimates generated using generalized wood CF
464 assumptions ($C_{subplot2}$-$C_{subplot5}$), and ii) all values below 0 and in blue shading indicate instances where species-
465 specific wood CFs ($C_{subplot1}$) are lower compared to estimates generated using generalized wood CF assumptions
466 ($C_{subplot2}$-$C_{subplot5}$). Left-side panels show spatial variability in differences between subplot-level C stocks for n=368
467 subplots distributed across a 13.5-ha forest dynamics plot in Haliburton, Ontario, Canada. Right-hand panels shows
468 statistically significant relationships between differences in C stock estimates (as described above) modeled as a
469 function of large tree biomass (≥10 cm diameter at 1.3 m aboveground) in each subplot, and a second-order
470 polynomial term for large tree biomass. Error bars represent 95% confidence limits surrounding model fits, and
471 point colors correspond to the proportion of biomass represented by gymnosperms in each subplot (a full analysis of
472 covariance model parameters for each fit is presented in Table A2).

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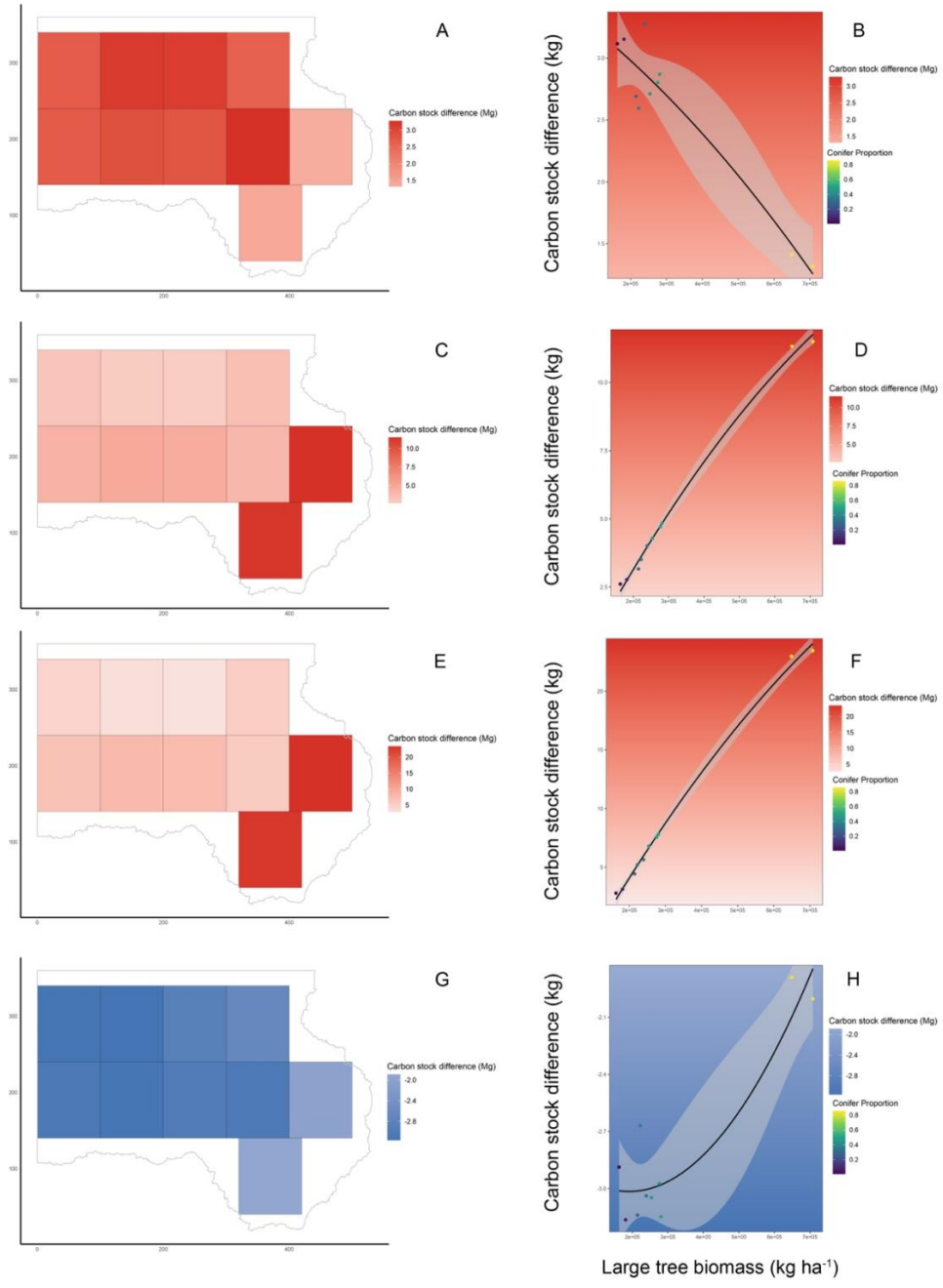

Fig. 4. Differences in ha-scale carbon (C_{ha}) stocks (measured in Mg C ha^{-1}) estimated using different wood carbon fraction (CF) assumptions. Per ha-level differences are calculated as the difference between C_{ha1} (generated using

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476 species-specific wood CF data) and C_{ha2} (Panels A-B; generated assuming wood CFs for temperate biome trees
477 specific to gymnosperms and angiosperms); C_{ha3} (Panels C-D; generated assuming non-biome-specific wood CFs
478 for gymnosperms and angiosperms); C_{ha4} (Panels E-F; generated assuming a single IPCC default wood CF
479 assumption); and C_{ha5} (Panel G-H; generated assuming a single 50% wood CF assumption). Therefore in all maps
480 and graphs, i) all values above 0 and in red shading indicate instances where species-specific wood CFs (C_{ha1}) are
481 higher compared to estimates generated using generalized wood CF assumptions (C_{ha2}-C_{ha5}), and ii) all values below
482 0 and in blue shading indicate instances where species-specific wood CFs (C_{ha1}) are lower compared to estimates
483 generated using generalized wood CF assumptions (C_{ha2}-C_{ha5}). Left-side panels show spatial variability in
484 differences in subplot-level C stocks for n=10 ha designations distributed across a 13.5-ha forest dynamics plot in
485 Haliburton, Ontario, Canada. Right-hand panels shows statistically significant relationships between differences in C
486 stock estimates (as described above) modeled as a function of large tree biomass (≥10 cm diameter at 1.3 m
487 aboveground) in each ha of forest, and a second-order polynomial term for large tree biomass. In these graphs, error
488 bars represent 95% confidence limits surrounding model fits, and point colors correspond to the proportion of
489 biomass represented by gymnosperms in each ha of forest (a full analysis of covariance model parameters for each
490 fit is presented in Table A3).

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Code availability

No custom code were used in the analysis presented here, though code is available upon request to the corresponding author.

Availability of data

Data for this research are available through the Forest Global Earth Observatory Network data portal.

Author contributions

Data collection: A.R.M., M.D., M.G., R.M., L.S., S.C.T.

Data analysis: A.R.M., D.M., M.D.

Manuscript writing: A.R.M., D.M.

Manuscript editing: M.D., M.G., A.G., D.O., A.B.P., B.T., R.O.M., L.S., S.C.T.

Funding acquisition and logistics: A.R.M., A.G., D.O., A.B.P., B.T., S.C.T.

Competing interests

The authors declare no competing interests.

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Appendices

Appendix A

Table A1. Parameters from an Analysis of covariance (ANCOVA) model predicting differences in tree-level carbon (C) estimates (measured in kg C $tree^{-1}$) as a function of an intercept term (corresponding to an average C stock difference among C_{tree} estimates), taxonomic division (as a categorical factor), DBH, a second-order polynomial DBH term (DBH^2), as well as division-by-DBH and division-by-DBH^2 interaction terms. Differences in tree-level C estimates were calculated based on five separate tree-level C estimates, denoted as C_{tree} as follows: C_{tree1}) generated using species-specific wood CF data; C_{tree2}) generated assuming wood CFs for temperate biome trees specific to conifers and angiosperms; C_{tree3}) generated assuming non-biome-specific wood CFs for conifers and angiosperms; C_{tree4}) generated assuming a single IPCC default wood CF assumption; C_{tree5}) generated assuming a single 50% wood CF assumption. The taxonomic division term is based on a categorical variable with two values (angiosperm and conifer), such that angiosperms are the reference group in ANCOVA models. Sample sizes for all four ANCOVA models was n=39,064 trees distributed across angiosperms (n=27,589) and conifers (n=11,475).

C estimation difference	Parameter	Estimate	Std. Error	t (p-value)	Partial r^2	Model p	Model r^2
C_{tree1} - C_{tree2}	Intercept	0.101	0.01	10.4 (<0.001)	0.003	<0.001	0.9151
	Conifer	0.127	0.02	6.3 (<0.001)	0.001		
	DBH	-0.063	0.002	-34.3 (<0.001)	0.029		
	DBH^2	0.011	0.00004	257.5 (<0.001)	0.629		
	Conifer * DBH	-0.026	0.003	-8.2 (<0.001)	0.002		
	Conifer * DBH^2	-0.009	0.0001	-119.6 (<0.001)	0.268		
C_{tree1} - C_{tree3}	Intercept	0.064	0.063	1.0 (0.311)	0.000	<0.001	0.3257
	Conifer	-3.947	0.13	-30.3 (<0.001)	0.023		
	DBH	-0.046	0.012	-3.9 (<0.001)	0.000		
	DBH^2	0.009	0.0003	32.2 (<0.001)	0.026		
	Conifer * DBH	1.385	0.021	66.0 (<0.001)	0.100		
	Conifer * DBH^2	-0.028	0.001	-57.2 (<0.001)	0.077		
C_{tree1} - C_{tree4}	Intercept	0.076	0.138	0.6 (0.583)	0.000	<0.001	0.2656
	Conifer	-8.591	0.287	-30.0 (<0.001)	0.022		
	DBH	-0.051	0.026	-2.0 (0.048)	0.000		
	DBH^2	0.01	0.001	15.8 (<0.001)	0.006		
	Conifer * DBH	3.0	0.046	65.0 (<0.001)	0.097		
	Conifer * DBH^2	-0.052	0.001	-48.7 (<0.001)	0.057		
C_{tree1} - C_{tree5}	Intercept	-0.33	0.006	-56.5 (<0.001)	0.076	<0.001	0.9714
	Conifer	0.36	0.012	29.6 (<0.001)	0.022		

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	DBH	0.133	0.001	120.7 (<0.001)	0.272		
	DBH^2	-0.014	0.00003	-513.3 (<0.001)	0.871		
	Conifer * DBH	-0.143	0.002	-73.6 (<0.001)	0.122		
	Conifer * DBH^2	0.015	0.00004	325.1 (<0.001)	0.730		

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Table A2. Parameters from linear models predicting differences in 400-m^2 subplot-level carbon (C) estimates (measured in kg C $subplot^{-1}$) as a function of an intercept term (corresponding to an average C stock difference among $C_{subplot}$ estimates), as well as the following subplot-scale variables: large tree (i.e., ≥10 cm DBH) biomass, small tree (1-10 cm DBH) biomass, second-order polynomial terms of large and small tree, and the proportion of total biomass represented by conifer tree species. Differences in subplot-level C estimates were calculated based on five separate tree-level C estimates, denoted as C_{tree} as follows: $C_{subplot1}$) generated using species-specific wood CF data; $C_{subplot2}$) generated assuming wood CFs for temperate biome trees specific to conifers and angiosperms; $C_{subplot3}$) generated assuming non-biome-specific wood CFs for conifers and angiosperms; $C_{subplot4}$) generated assuming a single IPCC default wood CF assumption; $C_{subplot5}$) generated assuming a single 50% wood CF assumption. Sample sizes for all four linear models was n=368 400-m^2 subplots (presented visually in Fig. 3).

C estimation difference	Parameter	Estimate	Std. Error	*t* (*p*-value)	Partial r^2	Model r^2	Model *p*
$C_{subplot1}$ - $C_{subplot2}$	Intercept	111.3	2.859	39.0 (<0.01)	0.81	0.7648	<0.001
	Large tree biomass	0.004	0.0004	10.5 (<0.01)	0.221		
	Large tree biomass^2	0.0001	0.0001	-10.4 (<0.01)	0.235		
	Small tree biomass	0.001	0.002	0.3 (0.776)	0.0002		
	Small tree biomass^2	0.0001	0.0001	-1.2 (0.237)	0.004		
	Conifer proportion	-120.4	4.652	-25.9 (<0.01)	0.654		
$C_{subplot1}$ - $C_{subplot3}$	Intercept	0.37	1.246	0.295 (0.769)	0.0002		
	Large tree biomass	0.0143	0.0002	93.0 (<0.01)	0.961	0.9975	<0.001
	Large tree biomass^2	0.0001	0.0001	3.2 (0.002)	0.027		
	Small tree biomass	0.02	0.002	18.3 (<0.01)	0.487		
	Small tree biomass^2	0.0001	0.0001	1.1 (0.258)	0.004		
	Conifer proportion	11.85	2.03	5.8 (<0.01)	0.088		
$C_{subplot1}$ - $C_{subplot4}$	Intercept	-98.91	3.22	-30.8 (<0.01)	0.727		
	Large tree biomass	0.03	0.001	69.6 (<0.01)	0.932	0.9967	<0.001
	Large tree biomass^2	0.0001	0.0001	10.6 (<0.01)	0.241		
	Small tree biomass	0.03	0.002	15.0 (<0.01)	0.389		
	Small tree biomass^2	0.0001	0.0001	1.8 (<0.01)	0.009		
	Conifer proportion	130.2	5.24	24.9 (<0.01)	0.635		
$C_{subplot1}$ - $C_{subplot5}$	Intercept	-98.91	3.22	-30.8 (<0.01)	0.727		
	Large tree biomass	-0.01	0.001	-13.4 (<0.01)	0.335	0.7166	<0.001
	Large tree biomass^2	0.0001	0.0001	10.6 (<0.01)	0.241		
	Small tree biomass	-0.002	0.002	-1.1 (0.292)	0.003		
	Small tree biomass^2	0.0001	0.0001	1.8 (0.077)	0.009		
	Conifer proportion	130.2	5.24	24.9 (<0.01)	0.635		

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Table A3. Parameters from linear models predicting differences in per ha carbon (C) estimates (measured in Mg C subplot^{-1}) predicted as a function of an intercept term (corresponding to an average C stock difference), as well as the following per ha-scale variables: large tree (i.e., ≥10 cm DBH) biomass, small tree (1-10 cm DBH) biomass, second-order polynomial terms of large and small tree, and the proportion of total biomass represented by conifer tree species. Differences in per ha C estimates were calculated based on five separate tree-level C estimates, denoted as C_{tree} as follows: C_{ha1}) generated using species-specific wood CF data; C_{ha2}) generated assuming wood CFs for temperate biome trees specific to conifers and angiosperms; C_{ha3}) generated assuming non-biome-specific wood CFs for conifers and angiosperms; C_{ha4}) generated assuming a single IPCC default wood CF assumption; C_{ha5}) generated assuming a single 50% wood CF assumption. Sample sizes for all four linear models was n=10 has (presented visually in Fig. 4).

C estimation difference	Parameter	Estimate	Std. Error	*t* (*p*-value)	Partial r^2	Model r^2	Model *p*
C_{ha1} - C_{ha2}	Intercept	-1487.0	1440.0	-1.0 (0.36)	0.211	0.966	<0.001
	Large tree biomass	0.033	0.01	3.2 (0.034)	0.716		
	Large tree biomass^2	0.0001	0.0001	-3.4 (0.028)	0.741		
	Small tree biomass	0.007	0.01	0.7 (0.538)	0.102		
	Small tree biomass^2	0.0001	0.0001	-2.0 (0.112)	0.509		
	Conifer proportion	-4998.0	1157.0	-4.3 (0.012)	0.824		
C_{ha1} - C_{ha3}	Intercept	-904.5	1517.0	-0.6 (0.583)	0.082	0.998	<0.01
	Large tree biomass	0.021	0.011	1.9 (0.124)	0.486		
	Large tree biomass^2	0.0001	0.0001	-0.5 (0.621)	0.0667		
	Small tree biomass	0.012	0.011	1.1 (0.337)	0.229		
	Small tree biomass^2	0.0001	0.0001	0.3 (0.757)	0.027		
	Conifer proportion	-945.3	1219.0	-0.8 (0.481)	0.131		
C_{ha1} - C_{ha4}	Intercept	-383.4	1795.0	-0.2 (0.841)	0.011	0.999	<0.01
	Large tree biomass	0.015	0.013	1.1 (0.325)	0.239		
	Large tree biomass^2	0.0001	0.0001	1.6 (0.191)	0.382		
	Small tree biomass	0.02	0.013	1.6 (0.197)	0.375		
	Small tree biomass^2	0.0001	0.0001	2.0 (0.117)	0.498		
	Conifer proportion	2681.0	1442.0	1.9 (0.137)	0.463		
C_{ha1} - C_{ha5}	Intercept	-383.4	1795.0	-0.2 (0.841)	0.011	0.889	0.01
	Large tree biomass	-0.019	0.013	-1.4 (0.227)	0.337		
	Large tree biomass^2	0.0001	0.0001	1.6 (0.191)	0.382		
	Small tree biomass	-0.013	0.013	-1.0 (0.369)	0.204		
	Small tree biomass^2	0.0001	0.0001	2.0 (0.117)	0.498		
	Conifer proportion	2681.0	1442.0	1.9 (0.137)	0.463		

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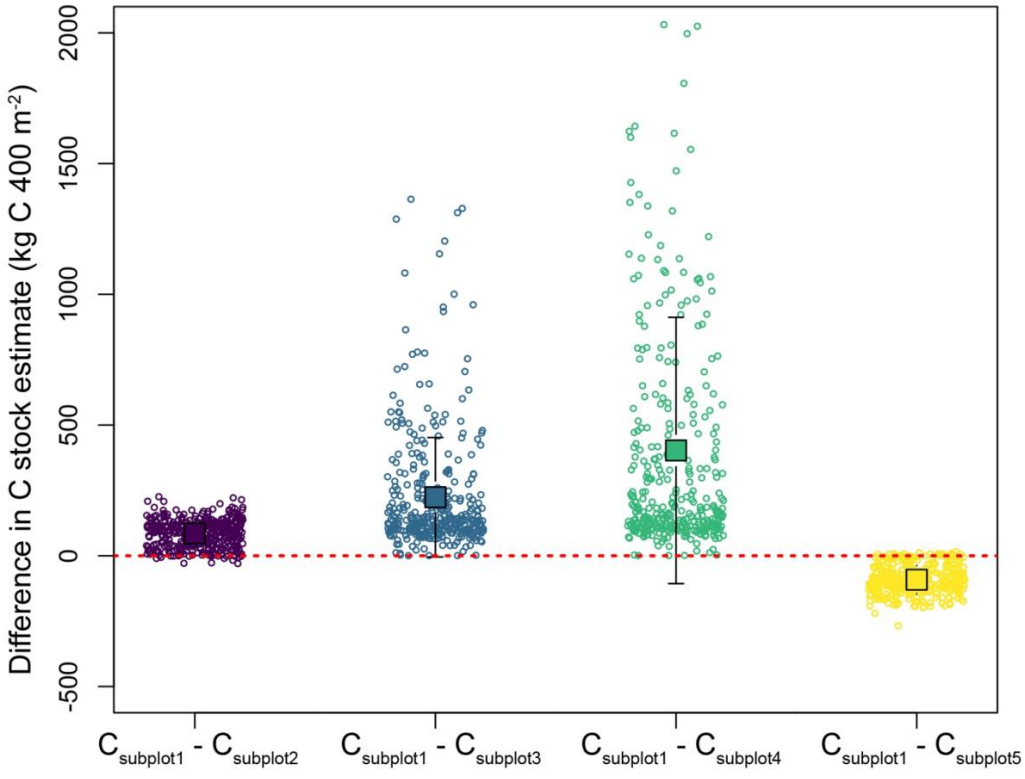

Fig. A1. Differences in 400-m^2 subplot-level carbon ($C_{subplot}$) stocks (measured in kg C subplot^{-1}) estimated using different wood carbon fraction (CF) assumptions. Subplot-level differences are calculated as the difference between $C_{subplot1}$ (generated using species-specific wood CF data) vs. $C_{subplot2}$ (generated assuming wood CFs for temperate biome trees specific to conifers and angiosperms); $C_{subplot3}$ (generated assuming non-biome-specific wood CFs for conifers and angiosperms); $C_{subplot4}$ (generated assuming a single IPCC default wood CF assumption); and $C_{subplot5}$ (generated assuming a single 50% wood CF assumption). Red dotted line denotes differences between the two C estimation values of 0. Therefore i) all values above 0 indicate instances where species-specific wood CFs ($C_{subplot1}$) are higher compared to estimates generated using generalized wood CF assumptions ($C_{subplot2}$-$C_{subplot5}$), and ii) all values below 0 indicate instances where species-specific wood CFs ($C_{subplot1}$) are lower compared to estimates generated using generalized wood CF assumptions ($C_{subplot2}$-$C_{subplot5}$). Open circles denote individual subplots (n=368 subplots total) and closed symbols denote mean differences for a given comparison (± 1 s.d.). Values here are presented visually in Fig. 3 and summarized in Table 2 in the main text.

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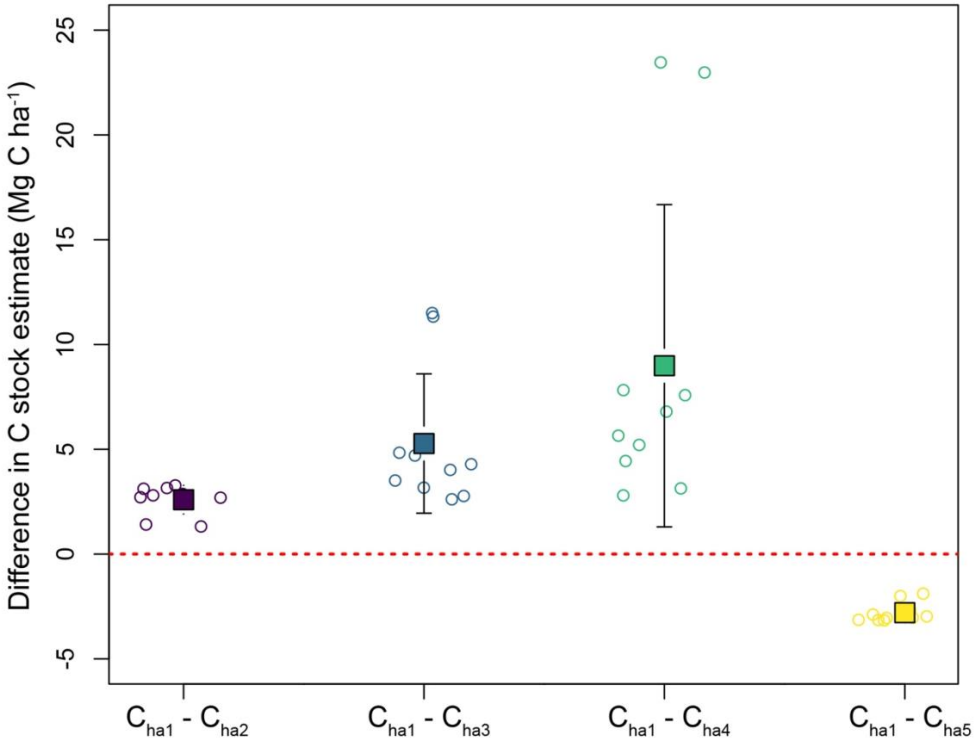

Fig. A2. Differences in per ha subplot-level carbon (C_{ha}) stocks (measured in Mg C ha^{-1}) estimated using different wood carbon fraction (CF) assumptions. Per ha-level differences are calculated as the difference between C_{ha1} (generated using species-specific wood CF data) vs. C_{ha2} (generated assuming wood CFs for temperate biome trees specific to conifers and angiosperms); C_{ha3} (generated assuming non-biome-specific wood CFs for conifers and angiosperms); C_{ha4} (generated assuming a single IPCC default wood CF assumption); and C_{ha5} (generated assuming a single 50% wood CF assumption). Red dotted line denotes differences between the two C estimation values of 0. Therefore i) all values above 0 indicate instances where species-specific wood CFs (C_{ha1}) are higher compared to estimates generated using generalized wood CF assumptions (C_{ha2}-C_{ha5}), and ii) all values below 0 indicate instances where species-specific wood CFs (C_{ha1}) are lower compared to estimates generated using generalized wood CF assumptions (C_{ha2}-C_{ha5}). Open circles denote individual ha of forest (n=10 individual ha total) and closed symbols denote mean differences for a given comparison (±1 s.d.). Values here are presented visually in Fig. 4 and summarized in Table 2 in the main text.