INTERSPECIFIC WOOD TRAIT VARIATION PREDICTS DECREASED CARBON RESIDENCE TIME IN CHANGING FORESTS

BY

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THESIS

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ABSTRACT

1. Increasing disturbance will result in a significant flux in aboveground carbon (C) from live trees to deadwood, concurrent with compositional shifts. While interspecific decay variation is widely reported, the implications of forest compositional change on ecosystem-level deadwood decay and consequently, the future of a globally significant C pool have not been previously explored.

2. Leveraging a 25-year treefall record for two eastern hardwood forests in central Illinois, USA, we used a chronosequence approach to estimate downed deadwood decay rates for eight common tree taxa. We hypothesized the increasing dominance of *Acer* spp. in eastern forests, due to disturbance regime changes, is driving a decrease in the mean species-weighted deadwood decay rate, decreasing the total C storage capacity of regional forests.

3. We observed significantly greater interspecific variation in deadwood decay rates than short-term studies, with a thirteen-fold difference in half-lives between *Aesculus glabra* ($T_{1/2}$ = 6.4 years) and *Quercus* spp. ($T_{1/2}$ = 77.8) logs. The canopy-dominant *Acer saccharum* ($T_{1/2}$ = 17.8) decayed significantly faster than other historically dominant eastern taxa, *Quercus* spp. and *Fraxinus* spp. ($T_{1/2}$ = 47.4). At multi-decadal timescales, wood traits, notably taxon initial wood C:N ratio and Mn concentration, outweighed environmental factors in explaining variation in decay rates. A significant interaction between soil pH and wood Mn, which co-regulate microbial lignin degradation, suggests a similar importance of Mn in modulating woody debris decay rates as has been previously described for litter decay.

4. *Synthesis*. Our decay estimates highlight the importance of long-term studies for accurately assessing decay of recalcitrant species (high C:N ratio), as short-term decay studies are prone to

underestimating their decay rates. Our results suggest that current and future forest compositional changes will have direct consequences on the residence time of the deadwood C pool due to interspecific wood trait variation.

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CHAPTER 1: INTERSPECIFIC WOOD TRAIT VARIATION PREDICTS DECREASED CARBON RESIDENCE TIME IN CHANGING FORESTS

INTRODUCTION

Downed deadwood plays a number of important roles in forest ecosystem processes, including influencing forest hydrology (Pypker, Levia, Staelens, & Van Stan, 2011), providing habitat and resources for both macro- and microorganisms (Stokland, Siitonen, & Jonsson, 2012), serving as a rooting substrate for seedlings (Harmon & Franklin, 1989), and contributing to a considerable portion of the nitrogen (N) and phosphorus (P) stored aboveground (Harmon et al., 1986). Perhaps most significantly, downed deadwood can account for up to 20% of total ecosystem carbon (C) storage in forests (Russell et al., 2014).

Deadwood is lost from forest systems through several mechanisms: microbially-mediated decomposition, fragmentation, consumption by invertebrates, leaching, and combustion (Cornwell et al., 2009; Harmon et al., 1986). As the rate at which deadwood is affected by these processes is controlled by its environmental context and species traits, the relative importance of each mechanism varies across ecosystems and forest communities (Cornwell et al., 2009). While past efforts to model the effect of climate change on wood decomposition generally assumed that regional climate was the best predictor of decay, there is a growing appreciation of the influence of local-scale environmental factors and species traits on decay (Bradford et al., 2014; Zanne et al., 2015). However, the influence of decay drivers has been shown to change throughout the decay process, and most decay studies occur on short time scales relative to the residence time of deadwood (Oberle et al., 2019). Therefore, uncertainty remains in our understanding of the

relative importance of decay controls at longer time scales that better characterize decomposition of individual logs.

Teasing apart the influence of decay factors is necessary to determine if deadwood positively influences C storage in forests (Magnússon, Tietema, Cornelissen, Hefting, & Kalbitz, 2016) and to predict if forests will serve as C sinks or sources in the future (Yu et al., 2019). Presently, the majority of aboveground C in eastern US forests is sequestered in live trees, and with minimal deadwood recruitment (i.e., mortality), C loss from deadwood generally outweighs deadwood C sequestration (Woodall, 2010). Climate and anthropogenic land use change are forecasted to impact forests through increased frequency and severity of fire, disease, pests, species invasion, drought, and other disturbances (Allen et al., 2010; Clark et al., 2016; Dale et al., 2001; Dukes et al., 2009; McDowell et al., 2020). Into the future, we can expect that the cumulative effect of these disturbances will result in a significant flux in forest aboveground C from live trees and recruitment to the deadwood pool (Harmon et al., 2020). Therefore, parsing the effects and relative importance of controls on deadwood loss, which determine its fate and residency time, is critical for earth system models to effectively assess future C storage (Yu et al., 2019) and to anticipate changes to other deadwood ecosystem services.

Increased disturbance not only affects the fate of C in forests, but also impacts forest composition, which likely has consequences for the C storage capacity of forests. Over the past century in US eastern deciduous forests maples (*Acer* spp.) have become increasingly dominant through the process of mesophication, driven primarily by fire suppression, which has limited recruitment of historical canopy-dominant species (Abrams, 1998; Nowacki & Abrams, 2008). This process has been augmented by disease- and pest-driven mortality, such as the recent impacts of the emerald ash borer and gypsy moth, creating recruitment opportunities for *Acer*

individuals (Flower, Knight, & Gonzalez-Meler, 2013; Gandhi & Herms, 2010). Currently, maples account for approximately 20% of trees in eastern forests and timberland (USDA Forest Service, 2020). Our observations of decay in naturally recruited deadwood suggested that maples, specifically *Acer saccharum*, decay faster than other dominant taxa in regional forests. Therefore, we predicted that eastern deciduous forest compositional changes are driving a decrease in the mean species-weighted deadwood decay rate, reducing the C storage capacity of these forests. Interspecific variation in deadwood decay rates has been widely reported to be a function of wood traits (Cornwell et al., 2009; Freschet, Weedon, Aerts, van Hal, & Cornelissen, 2012; van Geffen, Poorter, Sass-Klaassen, van Logtestijn, & Cornelissen, 2010; Vrška et al., 2015; Weedon et al., 2009; Zanne et al., 2015). However, few studies have explicitly compared decay rates between hardwood species in eastern forests, and those that have report considerable variation in the degree of differences in decay rates between common tree species in the region (MacMillan, 1988; Mattson, Swank, & Waide, 1987; Oberle et al., 2018; Russell et al., 2014; Zanne et al., 2015).

To quantify decay rates and controls, two broad approaches are generally employed. Deadwood loss may be examined experimentally, using wood blocks or homogenous log sections, an approach which is particularly suitable for evaluating biotic and abiotic drivers of decay rate. Yet, long-term decay experiments are often logistically prohibitive and short-term experimental studies may be uninformative for modeling long-term decay processes (Freschet et al., 2012). Alternatively, a chronosequence approach may be used to assess decay rates of naturally recruited deadwood by sampling logs of varying ages to reconstruct decay curves for a given species (Harmon et al., 1986). To this end, time elapsed is commonly estimated by assigning decay classes, determined primarily qualitatively based on deadwood's visual

characteristics (Larjavaara & Muller-Landau, 2010). For example, Russell and colleagues (2014) estimated wood decomposition rates for 36 eastern US tree species by modeling transitions between decay classes using US Forest Service Forest Inventory and Analysis (FIA) data. This approach for age estimation is inherently subjective as the distinctions between decay classes fail to capture inevitable variation in deadwood decay modes (Creed, Webster, & Morrison, 2004). Deadwood ages in chronosequence methods may also be estimated through historical records, known dates of disturbances (e.g., natural disaster, logging), or radiocarbon dating, to name a few (Freschet et al., 2012; Harmon et al., 1986). Unlike experimental methods, chronosequences capture decay over long time scales, but typically have coarse resolution due to the uncertainty associated with time sequence reconstruction and lack of information on the initial condition of logs.

Here, we assess the controls on deadwood decay over decadal timescales by leveraging a long-term treefall record, spanning 25 years, for two old-growth mixed mesophytic hardwood forests in central Illinois. This dataset uniquely provided precise fall dates as well as information on the initial condition of logs, which allowed us to reconstruct decay curves for eight common eastern US tree taxa. From this, we evaluated over multi-decadal scales if species traits or abiotic factors most strongly regulate decay rates. Ultimately, we explore how shifting forest composition in this system impacts ecosystem-level deadwood decay and consequently, the size of a globally significant C storage pool.

METHODS

Study sites

Sampling was conducted at Trelease and Brownfield Woods (24.5 ha and 26.1 ha, respectively), two old-growth deciduous mixed mesophytic forests located 8 km northeast of Urbana, Illinois, USA (40°09′ N, 88°10′ W). The sites are remnants of a 26 km^2 pre-settlement prairie grove, known as the "Big Woods", and have been managed with minimal disturbance by the University of Illinois since the early 1900s (Lin & Augspurger, 2008). The canopies at both sites are dominated by *A. saccharum*, with *Celtis occidentalis*, *Fraxinus americana*, *Tilia americana*, *Juglans nigra*, and *Aesculus glabra* being other significant species (Lin & Augspurger, 2008). Although *Quercus* species are not abundant at either site, they account for a significant fraction of total basal area. While the sites are compositionally similar, they vary in their edaphic conditions; Trelease is flat and poorly-drained, and Brownfield has approximately 8 m in elevation variation across the site and is well-drained. Local mean annual temperature is 10.5 °C and mean annual precipitation is 1010 mm.

Dead and live wood sampling

An ongoing census of large treefalls (≥ 30 cm diameter at breast height (DBH; breast height = 130 cm)) in Trelease and Brownfield Woods began in 1994. We selected logs from the treefall record belonging to 11 canopy species: *A. saccharum*, *C. occidentalis*, *F. americana*, *T. americana*, *J. nigra*, *A. glabra*, *Quercus macrocarpa*, *Quercus rubra*, *Ulmus rubra*, *Fraxinus quadrangulata*, and *Ulmus americana*. Cumulatively, these species constituted 94% of the basal area at Trelease Woods in 2005 (Edington, unpublished). For species for which sampling was limited by the number of logs in the treefall record, samples herein are grouped by genus

(*Fraxinus*, *Quercus*, and *Ulmus* spp.). For each taxon, when a sufficient number of samples permitted, we randomly selected five logs for sampling from five age groups each spanning five years between 1994 and 2018, for a total of 25 logs across the sites (Figure 1). The fast decay rates of buckeye and basswood prevented us from sampling across the entirety of this 25-year time period. Initial DBH of the sampled logs varied between taxa (Figure 1). The treefall record included information on pre-fall condition of logs (e.g., fall type, heart rot, hollowed, ant damage, unhealthy), and we selected only logs that died due to windthrow (i.e., trees recorded as alive prior to treefall). In our analyses, we included five logs from the treefall record that we were able to confidently locate, but had completely decayed at 130 cm. There were an additional 34 logs we were unable to relocate with confidence and were assumed to be either fully decomposed or represented erroneous location records.

In June and July 2019, we removed radial samples from the selected logs by chainsawing perpendicular to their bole at 130 cm from the base of uprooted trees. For logs that snapped off from a main stem, samples were collected approximately 5–10 cm from their end to ensure that only intact, unexposed wood was collected. Current log diameter at the sampling point and distance from the ground were recorded. To determine initial wood density and nutrients for each species, in November 2019 we cored four randomly selected live trees of each species in Trelease Woods (for *U. americana*, only three trees were cored). All cored trees were ≥ 30 cm DBH. We removed the bark of each live tree to the cambium at a sampling point at breast height and cored trees to a depth of 6 cm with a Haglöf increment borer.

Wood specific gravity and traits

To quantify wood specific gravity of fresh and decayed wood samples, we measured sample volume following the water displacement method (Williamson & Wiemann, 2010). For deadwood, the center wedge of chainsawed samples was removed, and if samples had variable degrees of decay, we took subsamples across the sample's radius (Figure 2). We soaked wood samples in water for 24 h to fill void spaces (Fortunel, Ruelle, Beauchêne, Fine, & Baraloto, 2014) and then submerged each saturated sample with an insect pin in a beaker of water on a top-loading balance. The mass of water displaced by a sample was equivalent to its volume. Samples were then dried at 105 °C for 72 h, after which we measured dry sample mass. We calculated wood specific gravity (SG; herein referred to as density) as the dried mass of each sample divided by its saturated volume. A weighted mean density was calculated based on the relative proportion of each subsample's length (l) across the sample's radius (r): $SG_{FINAL} = (SG_1 * (l_1 / r)) + (SG_2 * (l_2 / r)) + \ldots + (SG_n * (l_n / r))$ (Figure 2). We imputed the initial wood density ($SG_{INITIAL}$) of each sampled log based on the average live tree density for each taxon.

To assess the influence of species wood traits on decay, we analyzed live tree cores for wood nutrient concentrations. For each species we ground dried wood cores from four live tree individuals (except *U. americana*, for which three individuals were sampled) using a ball mill grinder. We analyzed 10 mg (± 1 mg) of the ground samples for total C and N using a Costech 4010 CHNSO (Valencia, CA, USA). Samples were additionally analyzed for P, potassium (K), magnesium (Mg), aluminum (Al), manganese (Mn), and calcium (Ca) concentrations by ashing 30 mg (± 1 mg) of ground sample at 550 °C for 3 h, then dissolving samples in 5.1 mL of 1 M nitric acid, diluted to a concentration of 2% nitric acid. Samples were analyzed on a Thermo Scientific iCAP Q ICP-MS (Waltham, MA, USA).

Environmental covariates

To assess the influence of soil conditions on decay, we collected composite soil samples (0–10 cm depth, 2 cm diam.) at the base of each sampled log at Trelease and Brownfield in May 2019. After removing the organic horizon, we collected three cores from the mineral soil, and a minimum of three cores were pooled for each sample. We resampled soils in August 2019 to capture the maximum (May) and minimum (August) soil moisture conditions. At both sites, samples were analyzed for gravimetric soil moisture content (105 °C for 48 hr) and for pH (1:3 ratio of dry soil to deionized H_2O).

To quantify inorganic N availability, which influences microbial decomposer activity, we performed KCl extractions on field and lab-incubated (stored in sealed plastic bag at room temperature for one week) soils. Approximately ~2 g of soil were added to 20 mL of 2 M KCl, thoroughly shaken and frozen (–20 °C), and prior to analysis, solutions were thawed and filtered through 0.7 μm Whatman glass microfiber filters. Ammonium (phenolate method), and NO_3^--N and NO_2^--N (cadmium column reduction) concentrations for all samples were determined using flow injection analysis (Lachat QuikChem 8000, Hach Company, Loveland, CO, USA). Data were corrected for gravimetric soil moisture content and with KCl blanks. Net N mineralization was estimated as the difference in nitrate and ammonium between incubated and field soil.

We collected the locations of logs using a Trimble GeoExplorer GXH6000 and performed post-hoc differential correction in Trimble GPS Pathfinder Office. To determine the influence of topographic variation on decay, we calculated the slope at each log using a LiDAR-derived digital terrain model for Champaign County, IL (Illinois State Geological Survey, 2008) and ArcMap 10.7.1 (ESRI, Redlands, CA, USA). As decay has been shown to be influenced by

edge effects (Crockatt & Bebber, 2015), the distance from each log to the perimeter of forest sites was also determined.

Statistical analysis

For all analyses, if a deadwood sample had a density that was greater than the taxon initial mean live-tree density ($SG_F > SG_I$), it was assumed that no decomposition had occurred ($SG_F = SG_I$). This was observed in fifteen percent of deadwood samples. Of these samples, 54% of their SG_F's were within 1 standard deviation of SG_I, 29% were within 2 standard deviations, and the remaining 17% were within 3 standard deviations (Figure 3).

We determined taxon-specific best fit decay models based on the fraction of initial density (SG_F / SG_I) as a function of time using the 'litterfitter' function (Cornwell & Weedon, 2014; Cornwell, Weedon, & Guofang, 2014). This and all other analyses were performed in the R statistical environment (R Core Team, 2020). Half-life values for each taxon and standard errors were then estimated using the jackknife method based on the results of 'litterfitter' analysis. To account for uncertainty in our reconstructive sampling approach, we additionally ran our decay rate models for each taxon including the 34 logs that we could not relocate during our sampling.

We used a general linear model with generalized least squares (GLS) to quantify the effects of abiotic and biotic factors on decay rate (k), where $k = \Delta SG / t = (SG_I - SG_F) / t$. To meet distribution assumptions, decay rates were square root-transformed. As heteroscedasticity persisted in the decay data, a GLS error structure was added, specifying variance by sampling site with the 'gls' function in the package 'nlme' (Pinherio, Bates, DebRoy, Deepayan, & R Development Core Team, 2020). We used Moran's Index to confirm that decay rates were not

spatially autocorrelated ('Moran.I' function in 'nlme'). We evaluated the effects of wood traits (taxon initial wood density, Mg, Al, P, K, Mn, and Ca concentrations and C:N ratio), soil conditions (pH, N mineralization rate, soil moisture, P concentration), spatial conditions (distance to edge, slope), and log-specific characteristics (sample distance to ground (distance from ground to underside of log + current log radius), fall type, initial diameter, pre-fall damage (heart rot, hollowed, or ant damage)). All non-significant explanatory variables were ultimately dropped from the models reported here. Model best fit was determined based on the comparison of AIC values and the absence of multicollinearity between variables ('vif' function in 'car' package). The variation explained by the final model was estimated using a pseudo-R^2 approach ('R2.lik' function in 'rr2' package). The significance of model terms was determined based on type III sum of squares ('Anova' function in 'car'). To determine the effect size of explanatory variables on decay rates, we rescaled the variables by centering observations around the variable's mean and then scaling by the variable's standard deviation ('scale' function). All regression coefficients were back-transformed from the square root scale with the sign (direction of the effect) reintroduced post-transformation. To explore the effect of other decay controls, which were excluded from the final regression model due to multicollinearity, we additionally performed simple regression analyses on these variables using the same general linear model with GLS, described above.

RESULTS

Decay rates

Mean live wood density for most taxa was consistent with published values (Zanne et al., 2009) (Figure 3). *Acer saccharum* and *Ulmus* wood densities from Trelease were slightly higher than

previously reported values. This intraspecific variation in wood densities may be a result of tree age, diameter, sampling location along bole, or environmental or genotypic variation influencing growth rate (Chave et al., 2009).

Decay rates were highly variable among species, with time to 50% loss of initial wood density ($T_{1/2}$) varying from six to 78 years (Table 1). Of the tree species considered here, *A. glabra* decayed the fastest ($T_{1/2}$ = 6.4 years). *Tilia americana*, *Ulmus*, and *C. occidentalis* deadwood all exhibited similar rates of deadwood loss ($T_{1/2}$ = 13.1, 13.6, and 13.8, respectively; Table 1, Figure 4). *Acer saccharum* logs had intermediate rates of decay ($T_{1/2}$ = 17.8), followed by *Fraxinus* and *J. nigra* ($T_{1/2}$ = 47.4 and 57.9, respectively), which decayed considerably slower. *Juglans nigra* had the greatest variation in predicted decay rates of all taxa due to limited sampling of this species (n = 10) and greater model uncertainty associated with its slow decay rate. *Quercus* was the slowest decaying taxa ($T_{1/2}$ = 77.8). When we re-ran our decay models to include the 34 missing logs (samples that could not be confidently relocated and were excluded from the original model), assuming for these samples that $SG_F = 0$, we found that our estimate for *T. americana* decreased significantly, and under this alternate model, *T. americana* was the fastest decaying species ($T_{1/2}$ = 5.0; Figure 5).

Decay drivers

Principle component analysis (PCA) of wood traits and examination of a covariance matrix revealed that several significant predictors of decay covaried (Table 2, Figure 6); specifically, initial wood C:N ratio negatively covaried with initial wood Mg and P concentrations. The PCA additionally showed that initial wood Mn exhibited high variance from other wood nutrients. From our multiple regression analysis, we found that 33% of the variation in decay rates was

explained by taxon-specific wood traits and soil conditions ($R^2 = 0.33$). Specifically, decay rates varied with taxon initial wood C:N ($P < 0.001$), Mn concentration ($P < 0.001$), and soil pH ($P < 0.001$). An interaction between wood Mn and soil pH ($P = 0.001$) explained additional variation in decay rates. Wood C:N had the strongest effect on decay rates (standardized $\beta = –0.021$; Figure 7), although this effect was not significantly greater than the effect of soil pH (std. $\beta = –0.020$) or the interaction between wood Mn and soil pH (std. $\beta = –0.018$). Wood Mn was the only factor in the model with a positive effect on decay and it explained the least variation in decay rates (std. $\beta = 0.009$).

From our simple regression analyses, we found that log fall type (uproot vs. snapoff) ($P = 0.04$) and taxon initial wood Al ($P = 0.009$), Fe ($P < 0.001$), Mg ($P = 0.003$), and P ($P = 0.006$) were also significant predictors of deadwood decay rates (Figure 8). Fall type had the greatest effect on decay rates (std. $\beta = –0.024$); yet, the effect of this variable was not significantly greater than the effect of wood C:N (std. $\beta = –0.019$), wood Fe (std. $\beta = –0.019$), soil pH (std. $\beta = –0.016$), or wood Al (std. $\beta = –0.015$). In addition to wood Mn, wood P (std. $\beta = 0.009$) and Mg (std. $\beta = 0.008$) were both positively correlated with decay rates. While we initially found that wood density had no effect decay, when we excluded *A. saccharum*, which have a high decay rate relative to initial wood density, initial density was negatively associated with decay rates ($P = 0.007$, std. $\beta = –0.014$). We found no significant effect of initial wood K or Ca, soil N mineralization rate, soil moisture, soil P, distance to edge, slope, sample distance to ground, initial DBH, or pre-fall damage on decay rates.

DISCUSSION

At long timescales, species wood traits drive decay variation

We observed significant variation in decay rates across tree taxa, consistent with previous work on decomposition in temperate woody species (Freschet et al., 2012; Zanne et al., 2015). We attribute this interspecific variation in part to taxon initial wood C:N ratio, which was one of the strongest predictors of deadwood decay rate variation in our deadwood samples. Generally, fast-decaying taxa were associated with low wood C:N, while recalcitrant taxa had high C:N (Table 3). This result is consistent with the N-limitation model, which posits that there is a tradeoff between allocating resources to C-targeting versus nutrient-targeting enzymes, such that under low N more resources are invested in N-targeting enzymes at the cost of producing lignolytic enzymes (Sinsabaugh & Moorhead, 1994). Nitrogen limitation may also reduce microbial growth and biomass, potentially resulting in an additional negative feedback to decomposition. Thus, under N-limited conditions, decay rates are expected to be slower (Cornwell et al., 2009; Sinsabaugh & Moorhead, 1994; Weedon et al., 2009). However, previous long-term, temperate decay studies have found no effect of C:N on decay rates of wood (Freschet et al., 2012; Oberle et al., 2019), with authors hypothesizing that the effect of initial wood C:N on decay is minimal provided that C:N ratios do not exceed ~40–400 (van Geffen et al., 2010), the critical range for saprophytic fungal N-limitation. Our findings largely contradict this hypothesis (here, taxon mean C:N ratio range: 135–504). The difference between our findings and others may be because these studies examined decay in both angiosperms and gymnosperms. In angiosperms, wood C:N is associated with decay rates, while this effect is not seen in gymnosperm species, potentially due to the latter having higher C:N concentrations (Weedon et al., 2009).

Decay rates were also associated with an interaction between taxon initial wood Mn concentrations and soil pH. White-rot fungi use several peroxidases to degrade lignin, including lignin peroxidase (LiP) and manganese peroxidase (MnP). While MnP, the only peroxidase produced by all white-rot fungi, is Mn-dependent, concentrations of Mn^{2+} also regulate LiP production (Hofrichter, 2002; ten Have & Teunissen, 2001). The importance of Mn availability as a rate-limiting control has been demonstrated in litter decay (Keiluweit et al., 2015), and our results suggest a similar importance of Mn in the breakdown of deadwood. As the reduction of MnP Compound II, a Fe^{4+} oxo-porphyrin complex, in the MnP catalytic cycle is pH-dependent, with optimum rates at pH 5.0–5.4, the interaction between pH and wood Mn may be a function of basic conditions inhibiting MnP lignin degradation (Kishi, Wariishi, Marquez, Dunford, & Gold, 1994). Thus, we would expect lower decay rates at both low Mn concentrations and at high pH, due to limitations on enzymatic activity, consistent with our observations. Additionally, a negative relationship between soil pH and decay rates has been previously demonstrated, which is attributed to both direct effects on the rate of microbial activity and indirect effects due to shifts in microbial community composition under varying edaphic conditions (Fravolini et al., 2016; Heineman et al., 2015).

From our simple regression analyses, we found that in addition to taxon initial wood C:N and Mn concentrations, decay rates were correlated with initial concentrations of wood Fe, Al, Mg, and P. Previous studies have similarly demonstrated the importance of macro- and micronutrients as rate-limiting decay controls by influencing microbial activity (Cornwell et al., 2009; Zanne et al., 2015). However, we found that initial wood Mg and P concentrations negatively covaried with wood C:N in our samples (Table 2, Figure 8) and as a result, it is

difficult to conclude if the influence of these wood traits on decay is directly a function of one of these factors alone or an interaction between them.

Diameter effects on decay have previously been reported in deadwood decay studies (Oberle et al., 2018; van Geffen et al., 2010) and arise for several reasons. As log diameter increases, the surface-area-to-volume ratio decreases and the heartwood-to-sapwood ratio increases, resulting in dampened rates of nutrient leaching and mass loss, and an increased relative proportion of recalcitrant wood (Harmon et al., 1986). Larger diameter logs are also often elevated farther above the substrate, limiting fungal dispersal and access to resources essential to microbial activity, which are in greater abundance in soils and litter (Oberle et al., 2018; Stenlid & Gustafsson, 2001). Here, we found no effect of sample distance from the ground; yet, we were only able to explore the effect of the current distance, which may not reflect a log's initial condition post-fall. As decay controls are temporally variable (Oberle et al., 2019), substrate distance may be only important during the beginning stages of decay, when microbial colonization and external nutrient sources are most essential. In spite of considerable variation in the diameters of sampled logs (25–137 cm), we found no effect of initial DBH on decay rates. Albeit, we were only able to examine this is uprooted samples, these results indicate that initial DBH may have only a small effect on decay rate for large-diameter, naturally recruited deadwood. However, we did find that uprooted logs decayed significantly slower than snapped off logs. As uprooted samples (boles sampled at 130 cm from their base) in general had a larger diameter than snapoffs (broken crowns or branches), this result may be due to an uncaptured diameter effect on decay rate.

Finally, our analyses showed that taxon initial mean wood density was a good decay predictor, if *A. saccharum* data were excluded from the analysis. This is consistent with the

previously described relationship between decay rates and wood density in angiosperms (Chave et al., 2009). *Acer* logs had a high decay rate relative to their initial wood density, and our results point to the species being anomalous due to their notably higher initial concentration of Mn than other taxa (Table 3).

Capturing decay rates and controls requires appropriate method selection

While our method allowed us to directly evaluate decay processes over longer timescales than previous studies, chronosequence approaches underestimate the decay rates of rapidly decomposing species. When we included the 34 missing logs in our decay models, there was a significant difference between the original and alternate models predicting decay rate for basswood. The sample size of missing *T. americana* samples (n = 21) and that this species has the lowest initial wood density (Figure 3), together suggest that *T. americana* decay rates are likely closer to our second model's estimate. In fact, this latter model may still be an underestimation of decay rates because our approach assumed that complete decomposition ($SG_F = 0$) was reached in 2019, while it may have occurred earlier. This suggests that the variation in decay rates between taxa may be even more pronounced than we observed.

When we compared our half-life estimates to those of previous downed deadwood decay studies conducted in eastern deciduous forests, we found that our results showed considerably higher variation in decay rates among taxa than previously reported (Figure 9). While our predicted half-lives were consistent with these studies for fast-decaying species, for recalcitrant species our half-live estimates were significantly higher. This is likely due to study duration; short-term studies may be prone to underestimating decay rates for slow-decaying species by only examining the initial decay stages, when decay is the fastest. Yet, as we addressed above,

there are potential shortcomings of long-term studies for fast-decaying species. We propose a framework for evaluating methodological selection based on initial wood C:N. In low C:N relative to high C:N species, microbial N demand is more readily met and other factors may be relatively more influential on microbial activity and in turn, decomposition. In comparing the influence of decay controls between recalcitrant taxa (generally, high C:N) and fast-decaying taxa (low C:N), we found that the effect sizes of decay controls were significantly greater for rapidly decaying taxa relative to slowly decaying taxa (Figure 10). We suggest that short-term studies, therefore, are more suitable for revealing decay controls, as they have higher temporal resolution than long-term approaches, whereas long-term decay studies provide more robust estimates of decay rates for slow-decaying woody taxa. Further, studies using small diameter logs may be unrepresentative of the decay dynamics of naturally recruited deadwood; small deadwood generally decays more rapidly than larger logs, and such studies may therefore fail to capture decay variation between species that is only evident at protracted timescales.

Decreased downed deadwood C storage capacity in future forests

Here, we demonstrated that over multi-decadal timescales, common eastern US tree species exhibit considerable variation in decay rates, due to interspecific wood nutrient variation. Under global change, disturbance events are increasing in both frequency and severity, resulting in a significant flux in aboveground C in forests from live trees to deadwood and subsequent shifts in forest composition (Harmon et al., 2020). Our results suggest that these coupled effects of aboveground C flux and compositional changes will have consequences for the C storage capacity of regional forests. Specifically, as *Quercus*, *Fraxinus*, and other historically-dominant, recalcitrant species continue to be replaced by *Acer* and other fast-growing, labile species in

eastern forests (Abrams, 1998; Nowacki & Abrams, 2008), we can expect to see the species-weighted mean deadwood decay rate increase into the future. Further, as increased disturbance will inhibit progression to later stages of succession, which in temperate forests are characterized by slower-growing, dense-wood species (Wilfahrt, Collins, & White, 2014), this pattern of decreased deadwood C storage is likely not limited to eastern hardwood forests.

FIGURES AND TABLES

Figure 1

a) Distribution of sample ages for all samples, and b) distribution of samples' initial diameter at breast height (DBH) for uprooted logs and live trees. The initial diameter of snapoff samples is unknown.

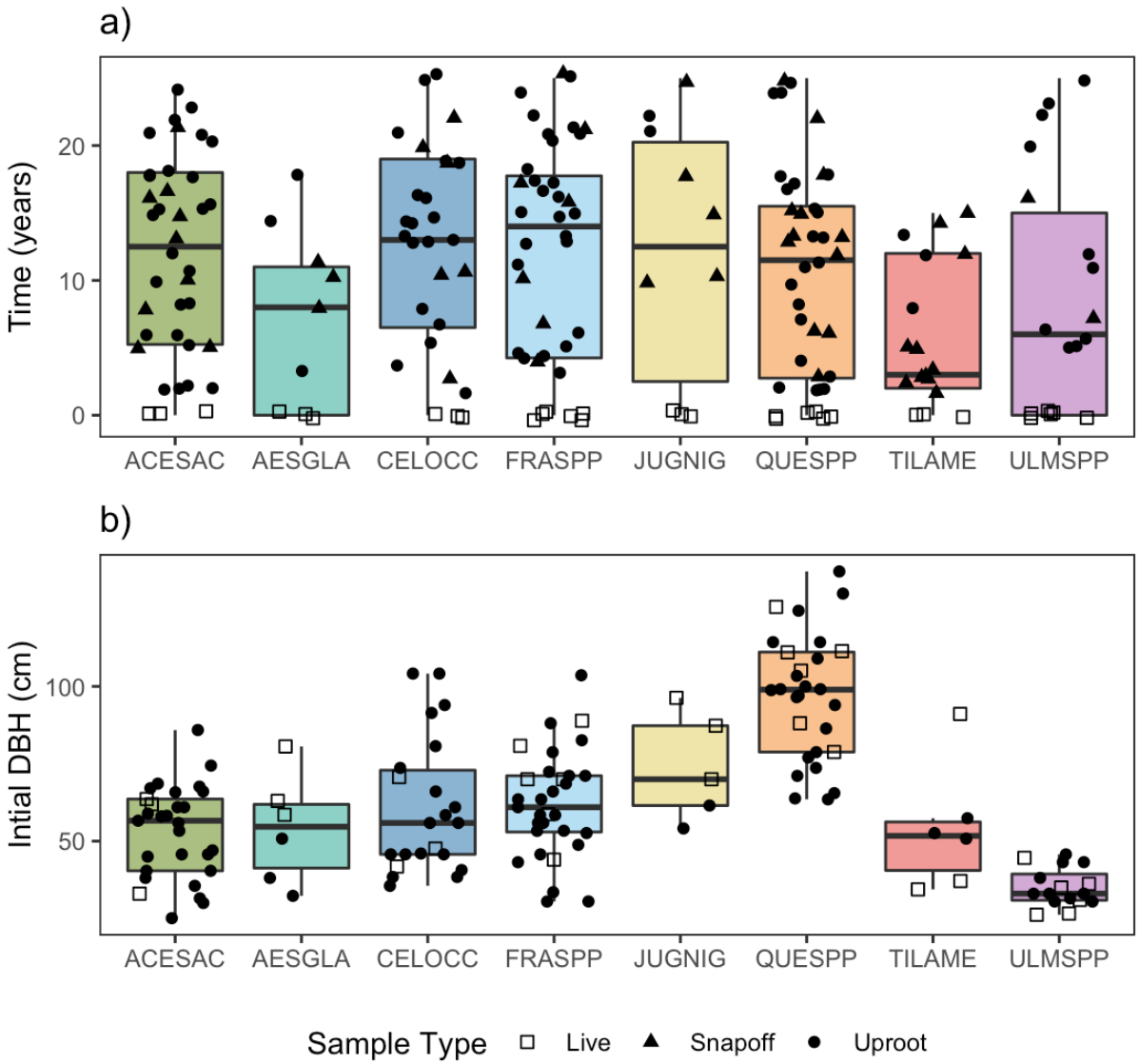


Figure 2

Sampling approach for deadwood. Samples were taken 130 cm from the base of uprooted logs and perpendicular to the bole (red shaded region). The wedge indicates the location on the sample used for wood density analysis.

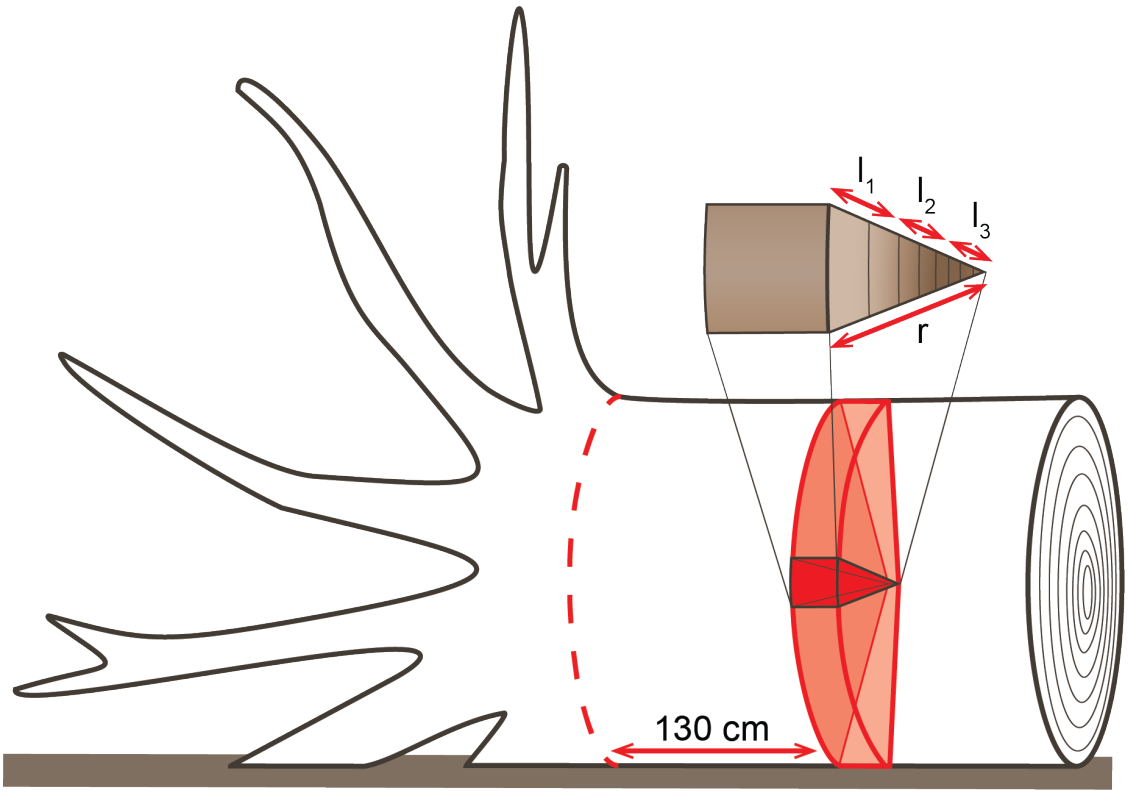


Figure 3

Wood specific gravity (oven-dried mass/fresh volume) of live trees sampled at Trelease Woods compared to values reported in the Global Wood Density Database (Zanne et al., 2009). Mean and standard deviation for each taxon from our dataset are reported in bold.

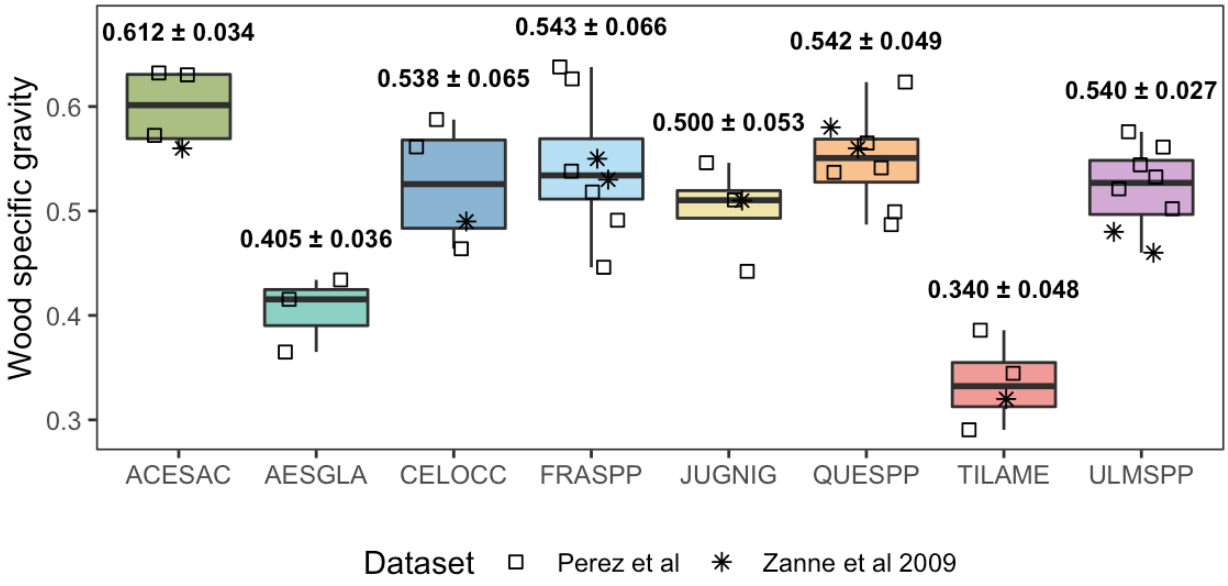


Figure 4

Estimated change in relative wood density over time for each taxon. Shaded bands represent 95% confidence intervals around estimated density. Dots indicate the measured wood density of logs. See Table 1 for species name codes.

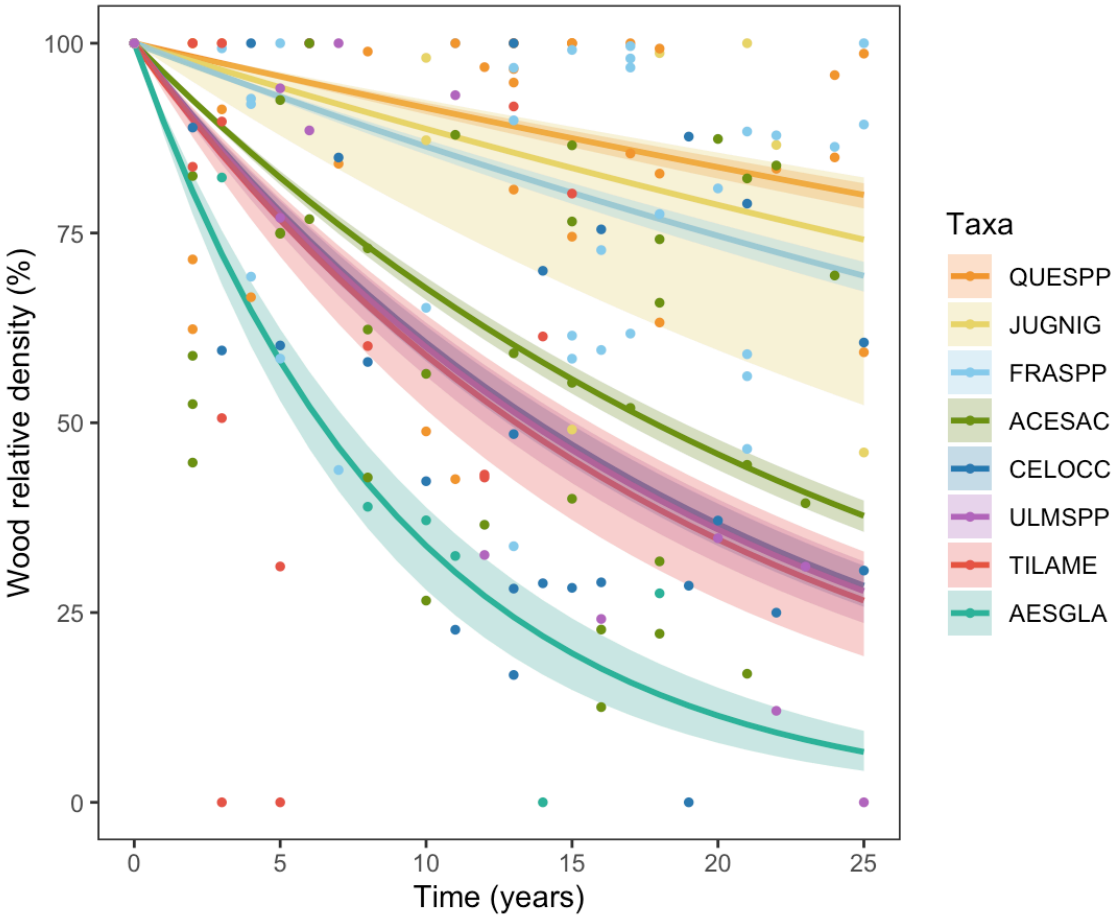


Figure 5

Estimated change in relative wood density over time for each taxon, including missing logs. Shaded bars represent 95% confidence intervals around estimated density. Dots indicate the measured wood density of logs.

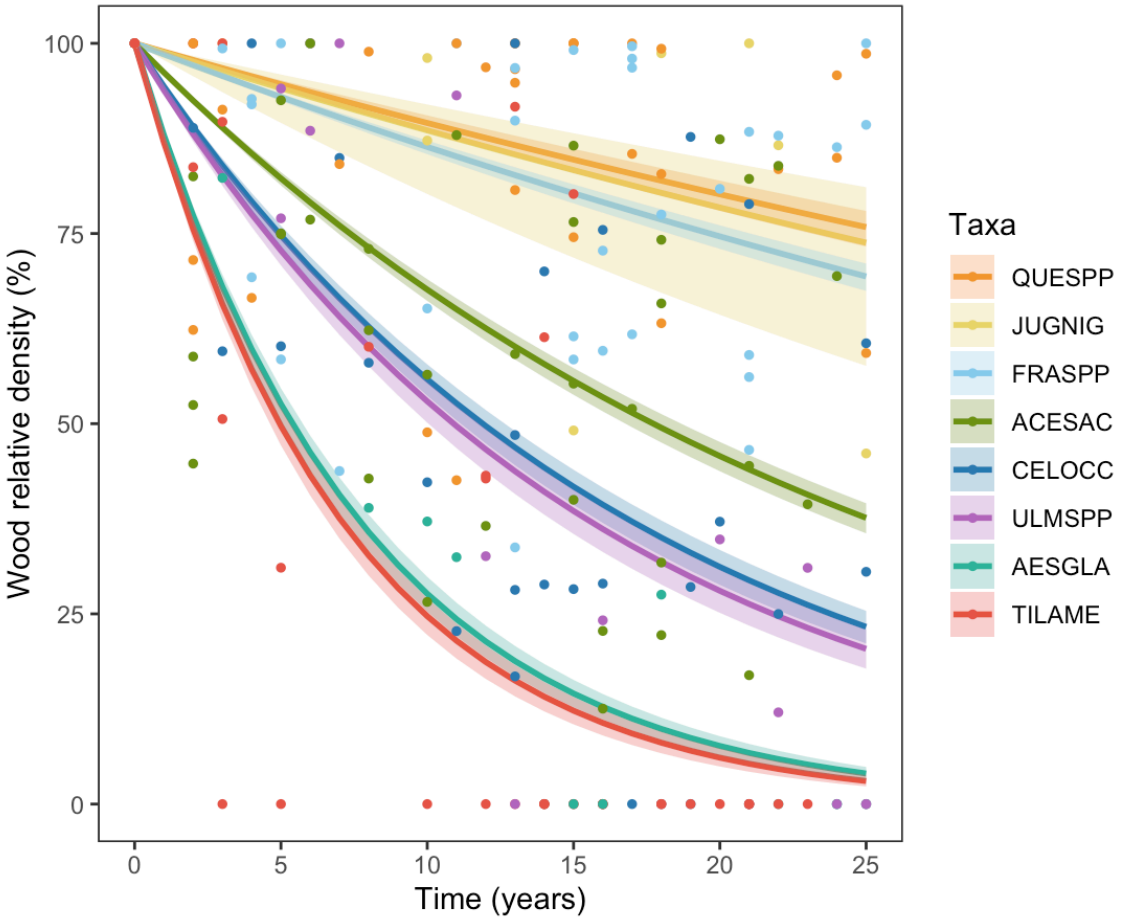


Figure 6

Principle component analysis (PCA) plot of initial (live tree) wood nutrient traits and mean decay rates by taxon. Wood density was imputed from taxa means for samples where density was not measured (n = 24; total n = 43).

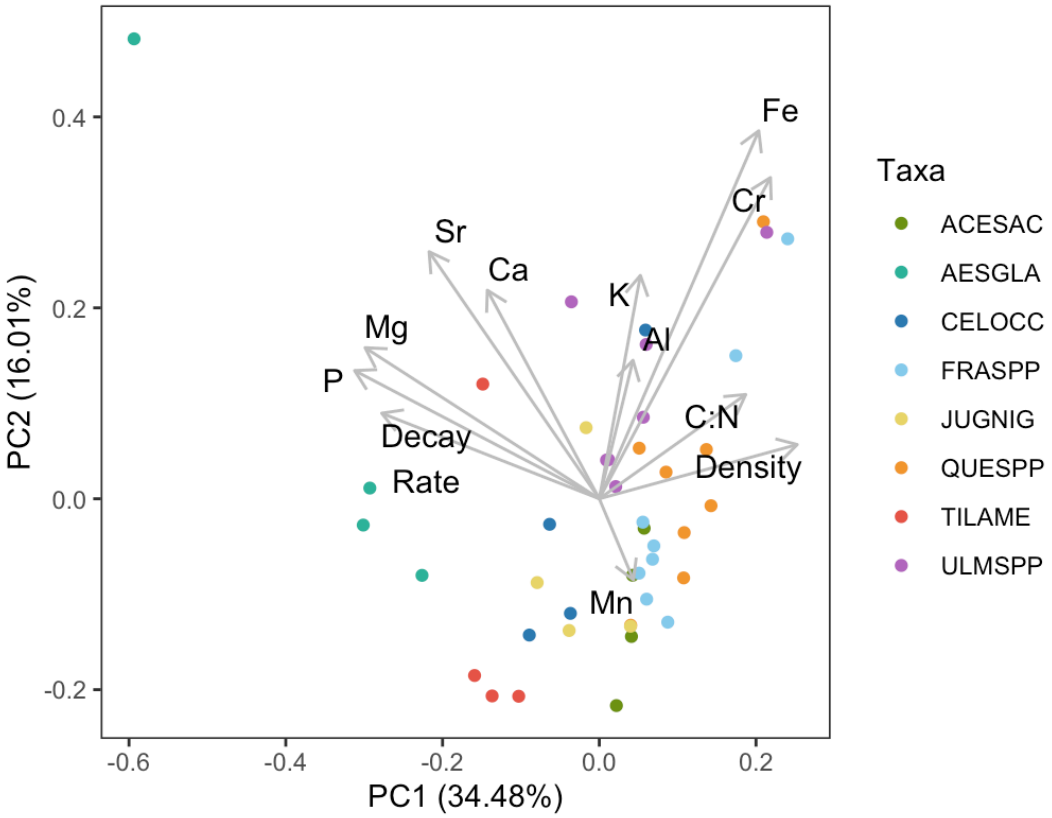


Figure 7

a) Effect size (standardized regression coefficients (β)) of wood traits and soil conditions on decay rates from multiple linear regression model. Error bars indicate 95% confidence intervals around estimated effect size, and asterisks indicate the significance level of decay predictors ($P <$ 0.001 = ***; $P < 0.01$ = **; $P < 0.05$ = *). b) Estimated decay rates under varying wood and soil nutrient conditions. Shaded bands represent 95% confidence intervals around decay rate estimations. Decay rates for wood Mn and soil pH were estimated at the mean concentration of the other factor in the interaction.

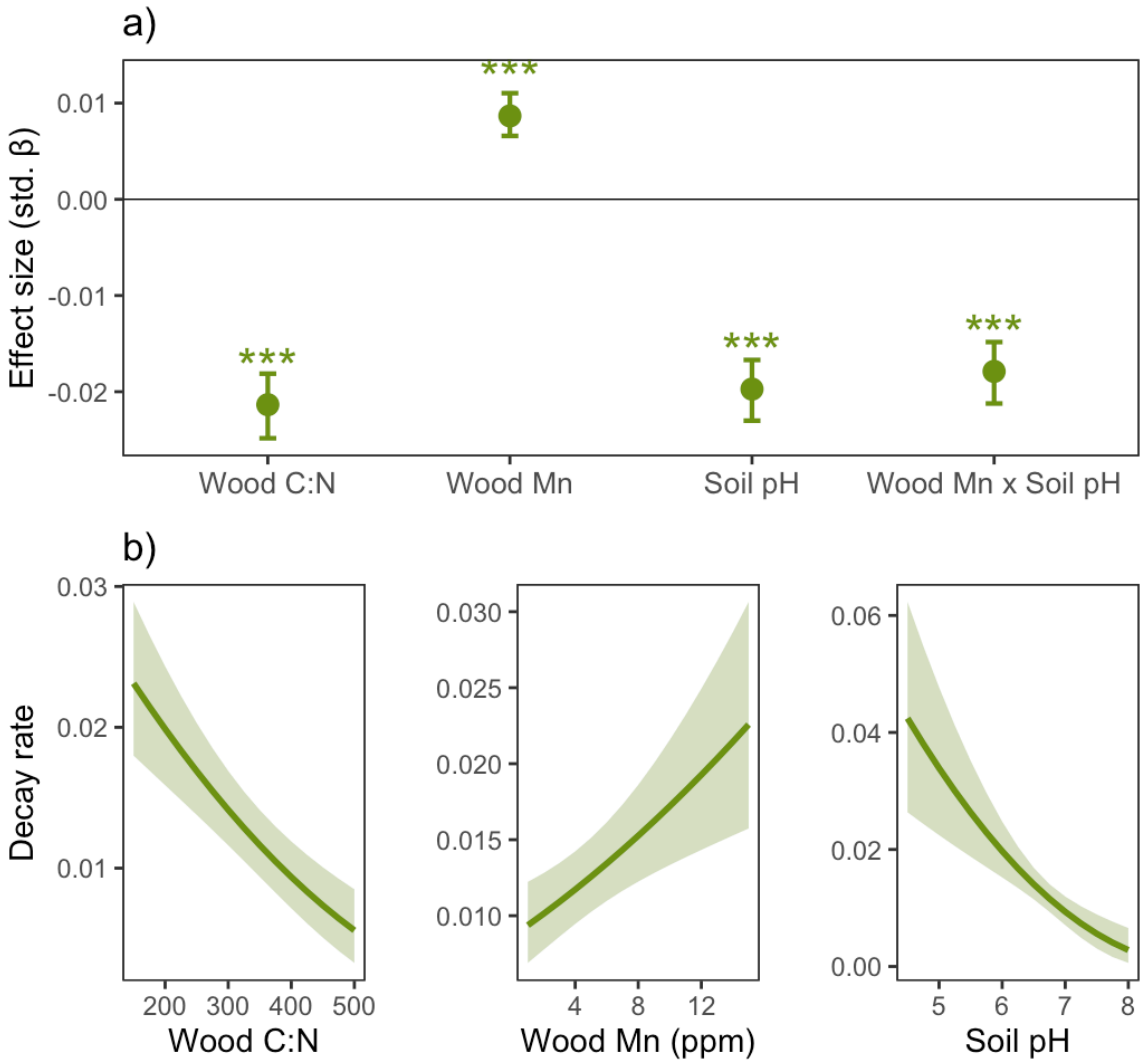


Figure 8

Effect size (standardized regression coefficients (β)) of wood traits and soil conditions on decay rates from bivariate linear models. Error bars indicate 95% confidence intervals around estimated effect size, and asterisks indicate the significance level of decay predictors ($P < 0.001$ = ***; $P < 0.01$ = **; $P < 0.05$ = *).

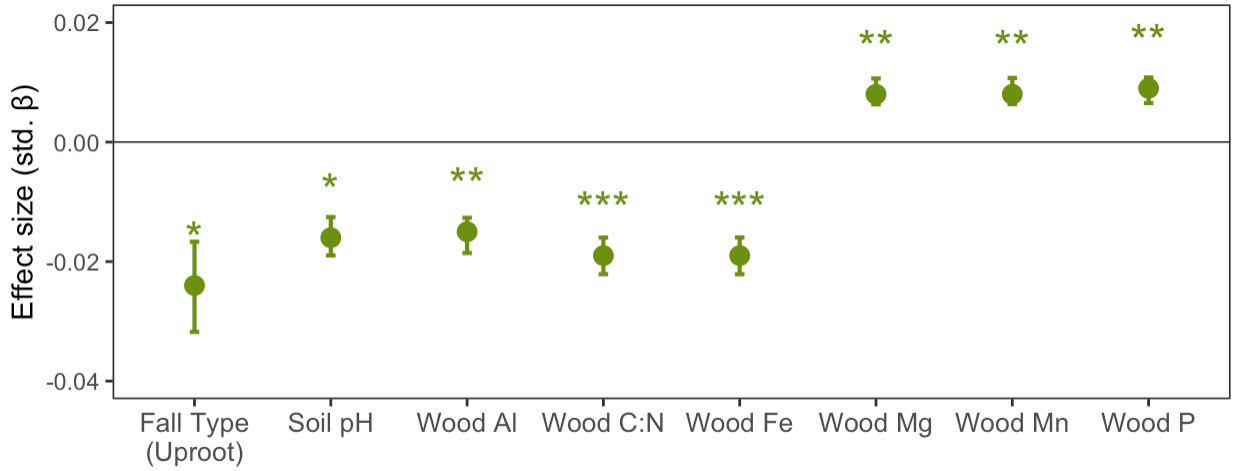
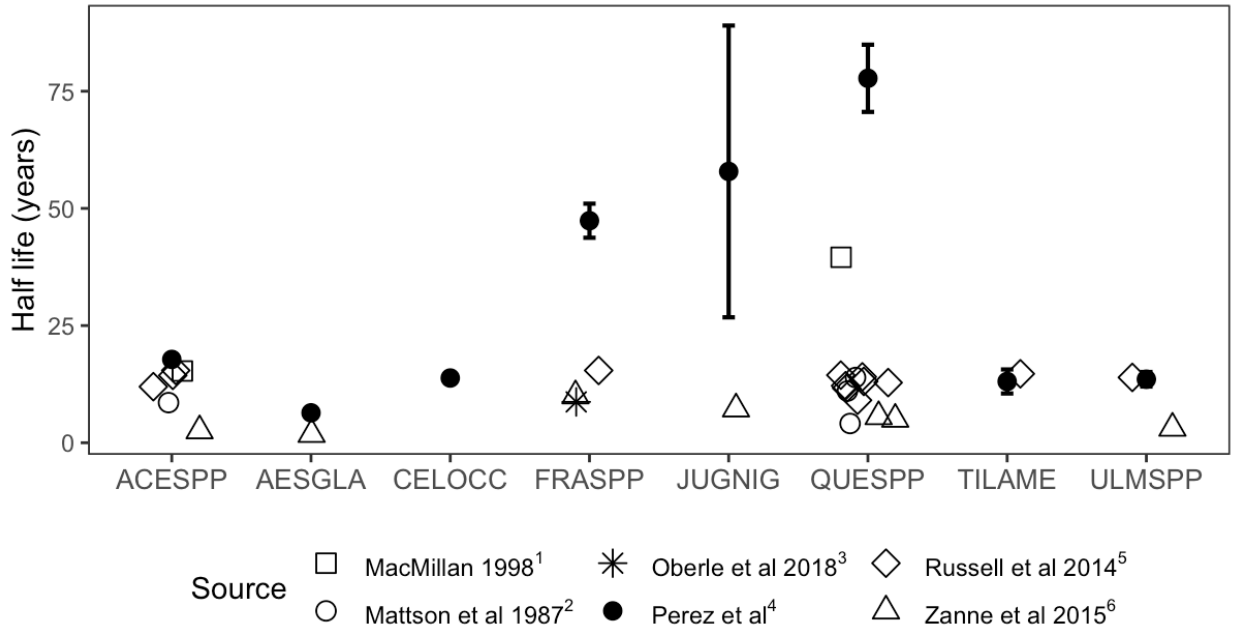


Figure 9

Comparison of half-life by taxon between downed deadwood decay studies conducted in the eastern US. For other studies, half-life values were estimated from reported decay rates, assuming negative exponential decay. Error bars around half-life estimates from this study represent 95% confidence intervals.



[1] Location: IN, USA; duration: 25 years; mean sample diameter: 31 cm; species: *Acer* spp., *Quercus* spp.
[2] NC, USA; 6 years; 12 cm; *Acer rubrum*, *Quercus alba*, *Q. coccinea*, *Q. montana*
[3] MO, USA; 3 years; 16 cm; *Fraxinus americana*
[4] IL, USA; 25 years; 63 cm; *Acer saccharum*, *Aesculus glabra*, *Celtis occidentalis*, *Fraxinus* spp., *Juglans nigra*, *Quercus* spp., *Tilia americana*, *Ulmus* spp.
[5] Eastern USA; 200 years; 18 cm; *Acer rubrum*, *A. saccharium*, *A. saccharum*, *Fraxinus nigra*, *Quercus alba*, *Q. falcata*, *Q. nigra*, *Q. prinus*, *Q. rubra*, *Q. stellata*, *Q. velutina*, *Tilia americana*, *Ulmus americana*
[6] MO, USA; 1 year; 7 cm; *Acer rubrum*, *Aesculus glabra*, *Fraxinus americana*, *Juglans nigra*, *Quercus alba*, *Q. velutina*, *Q. rubra*

Figure 10

Comparison of effect size (standardized regression coefficients (β)) of wood traits and soil conditions on decay rates from multiple linear regression model for fast-decaying (*A. saccharum*, *A. glabra*, *C. occidentalis*, *T. americana*, *Ulmus* spp.) and slow-decaying taxa (*Fraxinus* spp., *J. nigra*, *Quercus* spp.). Error bars indicate 95% confidence intervals around estimated effect size, and asterisks indicate the significance level of decay predictors ($P < 0.001$ = ***; $P < 0.01$ = **; $P < 0.05$ = *).

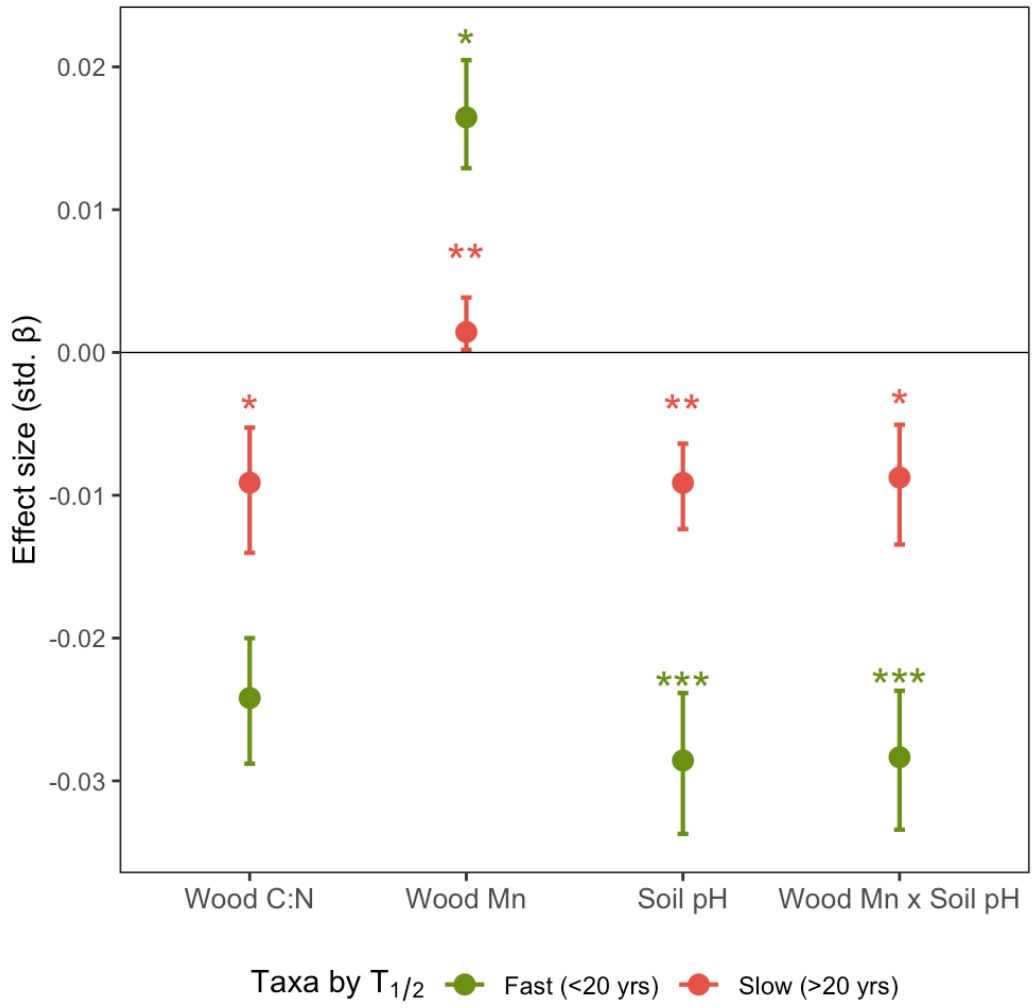


Table 1

Deadwood half-life ($T_{1/2}$) and decay rates (k) by taxon estimated with negative exponential decay model.

Taxa	Code	*n*	$T_{1/2}$ (95% CI)	*k*
Acer saccharum	ACESAC	38	17.8 (± 1.0)	0.0390
Aesculus glabra	AESGLA	9	6.4 (± 0.9)	0.1085
Celtis occidentalis	CELOCC	28	13.8 (± 1.0)	0.0502
Fraxinus spp.	FRASPP	38	47.4 (± 3.6)	0.0146
F. americana		18		
F. quadrangulata		20		
Juglans nigra	JUGNIG	10	57.9 (± 31.1)	0.0120
Quercus spp.	QUESPP	40	77.8 (± 7.2)	0.0089
Q. macrocarpa		14		
Q. rubra		26		
Tilia americana	TILAME	17	13.1 (± 2.6)	0.0523
Ulmus spp.	ULMSPP	18	13.6 (± 1.5)	0.0512
U. americana		5		
U. rubra		13		

Table 2

Covariance matrix of initial (live tree) wood nutrient traits by taxa. Wood density was imputed from taxa means for samples where density was not measured. Bold values highlight correlations >50% between wood traits.

	Mg	Al	P	K	Ca	Cr	Mn	Fe	Sr	C:N	SG_I
Mg	1										
Al	-0.039	1									
P	**0.576**	-0.055	1								
K	-0.011	0.201	-0.164	1							
Ca	0.267	0.085	0.066	-0.033	1						
Cr	-0.235	0.289	**-0.528**	**0.604**	0.027	1					
Mn	-0.027	0.359	-0.052	0.431	-0.276	0.357	1				
Fe	-0.241	0.390	-0.469	**0.632**	0.005	**0.864**	0.381	1			
Sr	0.320	0.087	0.197	0.045	**0.920**	0.016	-0.200	-0.005	1		
C:N	**-0.575**	0.046	**-0.768**	0.126	-0.298	0.381	0.038	0.432	-0.387	1	
SG_I	-0.239	0.240	**-0.528**	0.256	-0.279	0.477	0.424	0.341	-0.277	**0.536**	1

Table 3

Taxon initial wood nutrient mean concentrations (above) and standard deviations (below).

Concentrations are all reported in dry mass-corrected ppm.

	ACESAC	AESGLA	CELOCC	FRASPP	JUGNIG	QUESPP	TILAME	ULMAME
C:N	232.2	134.6	163.5	443.9	254.3	504.0	147.0	473.3
	14.6	69.3	17.3	140.4	154.2	183.7	41.2	533.0
Mg	292.7	1019.7	235.4	206.2	387.5	94.9	293.0	313.8
	51.4	317.5	63.2	59.3	92.6	107.3	107.0	73.6
Al	16.6	15.3	15.2	15.2	10.9	23.1	7.8	16.1
	6.1	6.7	14.8	7.1	5.0	25.9	3.7	16.0
P	65.7	340.0	109.6	73.0	127.3	36.4	191.5	42.5
	16.3	176.6	23.4	18.5	74.2	33.5	90.9	32.6
K	749.9	342.1	777.5	1124.9	394.2	821.0	996.5	2421.7
	628.5	268.8	214.3	500.7	244.9	595.7	1568.4	1525.0
Ca	1136.9	2293.5	2190.7	844.0	1749.7	1838.2	1356.4	1946.0
	232.8	1081.0	287.7	209.5	328.1	1304.6	361.7	744.9
Cr	18.3	6.1	24.0	31.8	20.0	27.3	11.2	34.4
	9.7	1.6	21.4	28.5	17.5	15.4	11.6	13.9
Mn	15.8	2.0	2.1	3.0	1.2	2.7	2.1	2.4
	7.6	0.5	0.8	1.4	0.5	1.1	1.7	1.2
Fe	97.6	85.5	97.0	175.2	99.6	193.6	66.6	180.6
	38.1	40.8	80.7	87.9	51.9	101.5	57.6	80.1
Sr	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0
	0.0	4.5	0.0	0.0	0.0	0.0	0.0	0.0

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