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forest ecology

Spatiotemporal Dynamics of Coarse Woody Debris in an Old-Growth Temperate Deciduous Forest

Jessica G. Davis, Julia I. Chapman, Shuang-Ye Wu, and Ryan W. McEwan

Forest ecosystems are an important component in the global carbon cycle. Coarse woody debris (CWD), which is a substantial portion of the aboveground forest biomass, can be an indicator of historical disturbance events and is a key variable for estimating carbon storage in forests. This study focused on identifying spatial and temporal dynamics in CWD pools within an old-growth temperate deciduous forest. The CWD in the study site was measured three times (1989, 1999, and 2012) following identical methods. Volumes of CWD were relatively stable over the measurement intervals, with the only significant difference being a higher CWD load in the midslope (mesophytic) community in 1989. The spatial arrangement of CWD across the topographically complex landscape was assessed using a geographical information systems (GIS) model that tested for physiographic predictors of CWD volume. Topographic patterns were not discovered, suggesting that CWD deposition was spatially stochastic. The relative temporal and spatial uniformity in CWD matches expectations for old-growth temperate forests; however, oncoming pests and pathogens as well as climate effects have the potential to drive future shifts in CWD loads.

Keywords: biomass, carbon sequestration, CWD, GIS, primary forest

Forest ecosystems are an important element of the global carbon cycle and can serve as a carbon dioxide sink. Terrestrial ecosystems sequester almost 3 billion tons of atmospheric carbon each year, amounting to roughly 30% of all carbon dioxide emissions resulting from the burning of fossil fuels (Canadell and Raupach 2008, Fahey et al. 2010). The nearly 4 billion ha of forest across the globe store more than double the amount of carbon in the atmosphere (Canadell and Raupach 2008, Fahey et al. 2010). By removing carbon dioxide from the atmosphere and storing it within the woody tissue of trees, forests provide a buffering effect for the ongoing, long-term increase in atmospheric carbon dioxide from fossil fuel combustion (Luyssaert et al. 2008, Stocker et al. 2013). Downed woody material including coarse woody debris (CWD) plays an important role in the terrestrial carbon cycle and is a substantial portion of the carbon stock in mature forests (Creed et al. 2004, Ganjegunte et al. 2004, Kueppers et al. 2004, Webster and Jenkins 2005, Beets et al. 2008). In fact, CWD can account for 20% of the aboveground forest biomass (Harmon et al. 1986, Fraver et al. 2013) and has residence times on the forest floor ranging from ca. 46 to 124 years depending on various factors (Russell et al. 2014a, Russell et al. 2014b). Due to this extended residence time on the forest floor, CWD is a proxy measure for disturbance, and con-

temporary CWD pools may be strongly influenced by earlier anthropogenic or natural disturbances (Webster and Jenkins 2005).

Forests of eastern North America are increasingly buffeted by myriad tree-mortality factors with the potential for driving alterations in carbon dynamics. There is evidence of altered mortality rates and distribution shifts of forest tree species in response to climate change (Chmielewski and Rötzer 2001, Parmesan 2006, Pearson 2006, Allen et al. 2010), and some of these changes could result in alterations in forest carbon storage. Waves of insects and pathogens have pulsed through the forests of eastern North America over the last several decades, causing tree mortality and thus potentially altering CWD pools. Large-scale mortality factors have included insect pests such as gypsy moth (*Lymantria dispar dispar*) and emerald ash borer (*Agrilus planipennis*) and pathogens such as dogwood anthracnose (*Discula destructiva*) and armillaria root disease (*Armillaria*) (Beedlow et al. 2004, Cobb et al. 2012). Ongoing dynamics in tree species composition may also be driven by changes in the historical climate conditions and disturbance regime. For instance, climatic events including changes in drought frequency and widespread frost damage may be linked to long-term shifts in species composition in the eastern deciduous forest (Pederson et al. 2014). Shifts in climatic conditions likely interact with a range of

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other disturbance factors to drive shifts in species composition across a large geographic area of eastern North America (Nowacki and Abrams 2008, McEwan et al. 2011). In the face of these alterations in forest composition and patterns of mortality, understanding dynamics in forest carbon storage is an increasingly pressing scientific goal. Old-growth forests, defined here as those forest systems that were never subjected to widespread clearing/timber harvesting by humans, offer a unique opportunity to study spatial patterns and long-term dynamics of CWD.

In the absence of large-scale disturbance, tree mortality and gap creation, and therefore the incumbent deposition of CWD on the forest floor, is thought to be a stochastic process (e.g., Runkle 1982, Franklin et al. 1987, Runkle et al. 2000). Previously, old-growth forests were thought to exhibit no net gain or loss of carbon over the long term (Kira and Shidei 1967, Gower et al. 1996, Murty and McMurtrie 2000, Binkley et al. 2002). More recent studies have found that old-growth forests continue to increase in carbon gain up to 800 years of age and sequester approximately 1.3 ± 0.5 gigatons of carbon per year (Luyssaert et al. 2008). Tree mortality events involving more than just individual trees (or small patches) could create pulses of CWD, which then cycle through decomposition processes. For example, Keller et al. (2004) and Woodall and Nagel (2007) found that large amounts of CWD were deposited on the forest floor during severe storms. Dynamics in old-growth forests, including those that may influence carbon storage, unfold over long time frames, thus, emphasizing the need for long-term assessments. Though exceedingly rare, old-growth stands in the deciduous forests of eastern North America have served as an important study system for analysis of forest ecosystem dynamics (Goebel and Hix 1996, Foster 1998, Gunn et al. 2014).

This study focused on spatial and temporal patterns of CWD within an old-growth temperate deciduous forest in eastern North America. This study is unique in that it encompasses three samplings of the same plots, following identical methodologies, that occurred across a ca. 20-year time frame. Steep topography in the site allowed for assessing CWD patterns in relation to physiographic features, while the diversity of ecological communities present represented much broader areas of the eastern deciduous forest. Data were interpreted in relation to three ecologically relevant null hypotheses. First, because of the old-growth nature of the study site and the fact that we knew of no major disturbance processes occurring in the recent past, we hypothesized (H_1) that CWD mass would not deviate over the ca. 20-year time frame of this study. Second, although the study area where this work was conducted consists of highly dissected terrain, we did not anticipate that CWD would be spatially congregated and thus hypothesized (H_2) no discernible spatial pattern. Finally, the analyses included a model-building and testing procedure using a suite of potential explanatory variables; given that tree mortality is thought to be a stochastic process, we hypothesized that (H_3) neither biotic nor abiotic factors would be good predictors of CWD biomass across the landscape.

Methods

Study Site

The field location for this study is a 52 ha watershed named Big Everidge Hollow (BEH) that is located within the Lilley Cornett Woods Appalachian Ecological Research Station (LCW) on the Cumberland Plateau of eastern Kentucky, USA (Muller 1982, Muller and Liu 1991, Muller 2003). Slope generally ranges from 35 to 80%, and elevation ranges from 320 to 600 m above sea level

Table 1. Descriptive statistics for overstory stems in an old-growth temperate forest in southeastern Kentucky.

Year	Live stems		Dead standing stems	
	Density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)
1989	1,247.8 ± 43.2	31.5 ± 0.9	145.3 ± 13.4	2.7 ± 0.4
1999	1,376.9 ± 46.7	35.2 ± 1.2	119.0 ± 10.2	2.4 ± 0.3
2010	1,343.0 ± 49.1	36.6 ± 1.3	185.8 ± 14.1	2.2 ± 0.3

Sampling dates were 1989, 1999, and 2010. All values are mean ± SE (standard error).

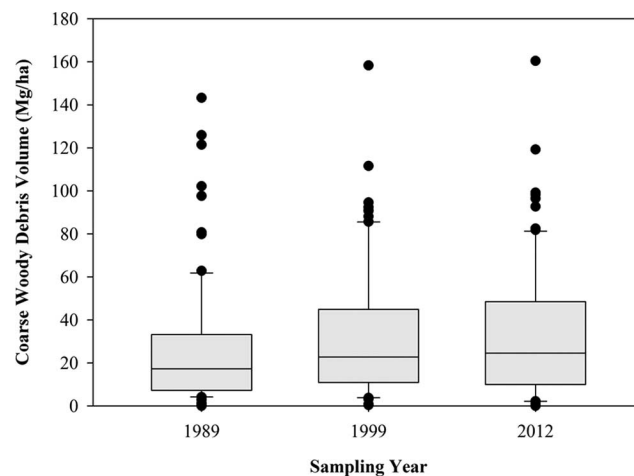


Figure 1. Mean (± SE) CWD biomass (Mg ha⁻¹) per plot (n = 80) in an old-growth temperate forest in southeastern Kentucky. Sampling years were 1989, 1999, and 2012.

(a.s.l.) (Muller 1982). The climate of this region is humid continental with warm summers, cool winters, and no distinct dry season (Trewartha 1968). Mean annual temperature is 13° C with a mean annual precipitation of 133 cm (Hill 1976).

The study watershed contains old-growth mixed mesophytic forest (Braun 1950; stand summary statistics given in Table 1). Muller (1982) characterized three overstory community types within BEH: chestnut oak ($n = 32$ plots) on upper slopes, comprised of xerophytic species; beech ($n = 31$) on lower slopes, dominated by American beech (*Fagus grandifolia* Ehrh.) and hemlock (*Tsuga canadensis* (L.) Carr.); and mixed mesophytic ($n = 17$) on midslopes, dominated by a diverse mix of overstory species including sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.), and cucumber magnolia (*Magnolia acuminata* (L.) L.) (community designations are indicated in black points in Figures 4 and 5). Due to its protected nature, disturbance has been limited within the study site. In the distant past, dead trees have been removed from the location, and livestock may have been allowed to forage, but no cutting of living trees is believed to have occurred (Martin 1975). In the spring of 2010, a wildfire burned sections of the upper south- and east-facing slopes of the watershed and may have enabled the first introduction of invasive plant species to BEH (Chapman et al. 2012).

Data Collection Methods

Muller (1982) established the 80 plots used for this study in 1979. These permanent plots are 0.04 ha and circular and were installed throughout the study area using a stratified random sampling scheme (Muller 1982). In the plot establishment process, the

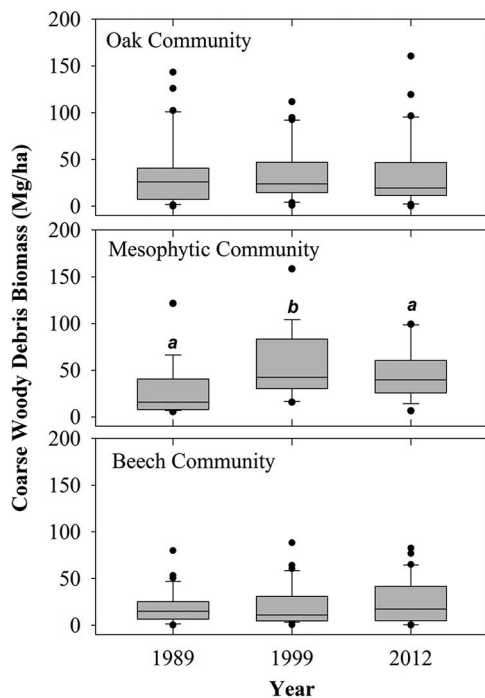


Figure 2. Mean (\pm SE) CWD biomass (Mg ha^{-1}) by overstory community type in an old-growth temperate forest. Sampling years were 1989, 1999, and 2012. Community types are oak ($n = 32$ plots), mesophytic ($n = 17$), and beech ($n = 31$).

watershed was divided into three elevational strata (upper, middle, and lower) and three slope aspect directions (north-, south-, and east-facing), and 10 plots were randomly established within each aspect-elevation combination. The topography of the watershed could not accommodate a set of plots on the east-facing lower slope, thus leaving the site with 8 aspect-elevation combinations and 80 total plots (plots can be seen as black points in Figures 4 and 5). Coarse woody debris, defined by Muller and Liu (1991) as woody material greater than 20 cm in diameter, was measured within each plot in 1989 by Muller and Liu (1991), in 1999 by Muller (2003), and again in 2012 (this study) following identical methodologies. Each sample of CWD was assigned to one of three CWD categories: log, branch, or snag. For branch and log fragments, the direction of fall and length were measured using a compass and logging tape, respectively. The diameters at both ends and middle of each log or branch were measured with a caliper. The volume (V) of each branch or log was calculated by treating each section (as delimited by adjacent diameter measurement points) as a truncated cone, where h is the length of the section, R is the radius of the larger diameter, and r is the radius of the smaller diameter

$$V = \pi \times h \times (R^2 + r^2 + Rr) \times (1/3)$$

The volumes of the sections were then added together to obtain the total volume of the branch or log. Snag height was determined with a laser distance meter, and the basal diameter was measured with a caliper just above the basal swell. Snags were treated as cones and volumes were calculated accordingly ($V = \pi \times r^2 \times h/3$), where r is the radius of the basal diameter and h is the height of the snag.

All samples were identified to species when possible and assigned to a decomposition class based on the visual appearance of decay depth and bark slippage (Muller and Liu 1991, Muller 2003). The biomass for each sample was estimated using wood density (specific

gravity) estimates from Harmon et al. (2008), multiplying volume by density. Some samples could only be identified to genus (e.g., *Acer* sp., *Carya* sp.), and the wood density values used for these genera were averages of the most common species in the watershed. Some *Quercus* samples could only be identified to subgroup *Leucobalanus* or *Erythrobalanus*. The *Leucobalanus* wood density values were averages of *Q. alba* and *Q. prinus*, while the *Erythrobalanus* wood density values were averages of *Q. rubra*, *Q. coccinea*, and *Q. velutina*. The 2012 sampling included some unidentified species, for which average wood density values were generated using values from species with ≥ 5 CWD samples present in the sampling area in 2012 (*C. glabra*, *F. grandifolia*, *Q. alba*, *Q. prinus*, *A. rubrum*, *A. saccharum*, *T. americana*, *F. americana*, *Q. rubra*, *Q. velutina*, *L. tulipifera*, and *T. canadensis*). Finally, for each sampling interval (1989–1999 and 1999–2012), the change in biomass was calculated by subtracting the biomass in the latter year from the biomass value in the former year.

Data Analysis

A Scheirer–Ray–Hare test was used to examine the effects of community type (regardless of year), year, and the interaction of community and year on CWD (Scheirer et al. 1976) when the assumption of normality could not be met for parametric analysis. The Scheirer–Ray–Hare test is a nonparametric alternative to traditional two-way analysis of variance (ANOVA) and is based on data ranks and a comparison of sums of square error over mean square error (MS) total to yield an H statistic examined on a chi-square distribution analogous to a traditional ANOVA F statistic (Sokal and Rohlf 1995). We calculated type III sums of squares to accommodate the study's unbalanced design to avoid unwanted priority effects of model term entry (Herr 1986). We obtained the mean squares our analysis is based on using ranked observation data and the “Anova” function in the R package “car” that allows for the proper type of sum of square (SS) calculation. Significance values were determined using the “pchisq” function in the base R stats package at the appropriate degrees of freedom for the term. Individual means were subsequently compared at $\alpha = 0.05$ using a Kruskal multiple comparison if the SRH-test indicated significant group-wise differences (Siegel and Castellan 1988) implemented using the “kruskalmc” function in the R-package “pgirmess” (Giraudeau 2014). Estimates of CWD biomass were compared across years within community types using a Kruskal–Wallis nonparametric ANOVA followed by Tukey multiple comparison tests where a significant overall effect was found.

Linear regression was used to assess the bivariate relationship between CWD biomass and both slope and elevation. Multiple linear regression was performed to test for relationships between CWD measures (biomass and change in biomass) and topography (slope, aspect, and elevation). A backwards selection process was used where nonsignificant variables were removed to achieve the best-fit model. These statistical analyses were conducted within GraphPad Prism version 5.0 (GraphPad Software, San Diego, CA, USA¹), SigmaPlot (Systat Software, Inc., San Jose, CA, USA), and R statistical software version 3.1.1 (R Foundation for Statistical Computing, Vienna, Austria²).

Spatial patterns of CWD biomass and decadal changes were visualized using inverse distance weighted (IDW) interpolation in ArcMap Geographical Information Systems (GIS) 10.1 (ESRI 2012). The IDW method was chosen for its simplicity as these maps

Table 2. CWD biomass (Mg ha⁻¹) distribution among decomposition classes in an old-growth temperate forest.

Decomposition class	1989		1999		2012	
	Mean ± SE (Mg ha ⁻¹)	% of total	Mean ± SE (Mg ha ⁻¹)	% of total	Mean ± SE (Mg ha ⁻¹)	% of total
I	10.8 ± 2.7	39.9	7.8 ± 1.9	23.1	8.1 ± 2.7	24.3
II	8.1 ± 1.5	30.0	5.6 ± 1.6	16.7	8.9 ± 2.0	26.9
III	2.4 ± 0.6	8.9	7.6 ± 1.7	22.5	7.5 ± 1.4	22.6
IV	5.8 ± 0.8	21.2	12.7 ± 1.3	37.7	8.7 ± 1.1	26.3
Total	27.1 ± 3.3	100.0	33.8 ± 3.5	100.0	33.2 ± 3.5	100.0

Mean ± SE per plot (n = 80) is presented for each decomposition class as well as total CWD for the site.

Table 3. Distribution of CWD biomass (Mg ha⁻¹) among species within an old-growth temperate forest.

Species	1989		1999		2012	
	Mean ± SE (Mg ha ⁻¹)	% of total	Mean ± SE (Mg ha ⁻¹)	% of total	Mean ± SE (Mg ha ⁻¹)	% of total
<i>Quercus prinus</i>	7.78 ± 2.4	28.9	6.07 ± 1.3	18.0	5.35 ± 1.5	16.1
<i>Fagus grandifolia</i>	3.94 ± 1.2	14.6	4.43 ± 1.2	13.1	4.24 ± 1.4	12.7
<i>Quercus alba</i>	3.16 ± 0.8	11.7	1.86 ± 1.1	5.5	1.20 ± 0.5	3.6
<i>Castanea dentata</i>	3.01 ± 0.7	11.1	3.46 ± 0.8	10.3	0.09 ± 0.1	0.3
<i>Quercus velutina</i>	2.14 ± 1.2	7.9	1.66 ± 1.1	4.9	0.32 ± 0.2	1.0
<i>Quercus rubra</i>	1.44 ± 0.7	5.3	1.13 ± 0.6	3.4	4.88 ± 2.5	14.7
<i>Carya glabra</i>	1.41 ± 0.8	5.2	2.36 ± 1.4	7.0	0.51 ± 0.3	1.5
<i>Acer saccharum</i>	0.76 ± 0.8	2.8	1.91 ± 0.9	5.7	2.09 ± 0.9	6.3
<i>Tilia heterophylla</i>	0.48 ± 0.7	1.8	2.08 ± 1.2	6.2	0.58 ± 0.5	1.8
<i>Tsuga canadensis</i>	0.45 ± 0.2	1.7	0.20 ± 0.1	0.6	0.18 ± 0.1	0.5
<i>Liriodendron tulipifera</i>	0.26 ± 0.4	1.0	1.41 ± 0.7	4.2	1.53 ± 1.0	4.6
<i>Fraxinus americana</i>	0.02 ± 0.9	0.1	0.54 ± 0.3	1.6	0.53 ± 0.3	1.6
Other ^a	2.22 ± 0.7	8.2	6.65 ± 1.0	19.7	11.73 ± 1.8	35.3

Sampling years were 1989, 1999, and 2012. The 12 most important species are shown and species are rank-ordered by % of total in 1989. ^aOther 1989: *Carya ovata*, *Juglans nigra*, *Betula lenta*, *Quercus coccinea*, *Morus rubra*, *Magnolia acuminata*, *Sassafras albidum*, *Robinia pseudoacacia*, *Acer rubrum*, *Aesculus flava*, *Nyssa sylvatica*; Other 1999: *Pinus virginiana*, *Carya cordiformis*, *Carya tomentosa*, *Juglans nigra*, *Betula lenta*, *Quercus coccinea*, *Magnolia acuminata*, *Sassafras albidum*, *Amelanchier arborea*, *Robinia pseudoacacia*, *Acer rubrum*, *Aesculus flava*, *Nyssa sylvatica*, *Cornus florida*, *Oxydendrum arboreum*, *Leucobalanus*, *Erythrobalanus*, *Carya* sp., *Acer* sp.; Other 2012: *Pinus echinata*, *Carya cordiformis*, *Carya ovata*, *Carya tomentosa*, *Juglans nigra*, *Betula lenta*, *Quercus coccinea*, *Robinia pseudoacacia*, *Acer rubrum*, *Aesculus flava*, *Oxydendrum arboreum*, *Leucobalanus*, *Erythrobalanus*, *Carya* sp., *Acer* sp., *Quercus* sp., Unknown.

were for visual reference only, and the interpolated values (i.e., estimated map values generated via interpolation) were not used in subsequent analyses. Global Moran’s I (Moran 1950) was used to test for spatial autocorrelation among measured plot values of CWD biomass and biomass change. High/low clustering analysis (Getis–Ord General G; Getis and Ord 1992, Ord and Getis 1995) was used to test for significant clustering of measured CWD biomass and biomass change values. Biomass change values included negative values, which are not permitted in these spatial analyses, thus a constant was added to all values for each sampling interval (80 for 1989–1999 and 122 for 1999–2012) to make all values positive. A fixed distance band of 150.23 m was used for conceptualization of spatial relationships (determined using the Calculate Distance Band from Neighbor Count tool), which ensured a minimum of four neighbors for each feature. This particular distance band was chosen as a balance between the reliability of the Z score (more than two neighbors recommended, with eight being ideal) and environmental heterogeneity of the site due to its diverse topography (marked differences in microenvironment can occur over short distances).

Results

Biomass of CWD across the forest did not exhibit a statistically discernible change over the three samplings ($H = 5.88$, $df = 2$, $P = 0.053$) with values (plot mean ± standard error) of 27.1 ± 3.3 Mg ha⁻¹ in 1989, 33.8 ± 3.5 in 1999, and 33.2 ± 3.5 in 2012. Variation among the plots was also relatively consistent with minimum values near zero and maximum values reasonably similar across the

years (143.3, 158.3, and 160.5 Mg ha⁻¹; Figure 1). Differences were minimal among CWD decomposition categories as well, with the potential exception that in 1989, category III had lower levels than the other 2 years (Table 2). *Q. prinus* was the most important species in the CWD pool in all three samplings (Table 3). *F. grandifolia* was the second most important species in both 1989 and 1999; however, in 2012, *Q. rubra* was the second most important species. *Castanea dentata* was an important species in the 1989 and 1999 samples but had slipped markedly in importance in the final sampling (Table 3).

Across all three samplings, the beech community had significantly lower biomass than the oak and mesophytic communities (Table 4; Figure 2), but there was no difference between the oak and mesophytic communities. The mass of CWD did not differ among years in the oak community; in fact, the range of variation was quite similar across years (Figure 2), and the average change in biomass between years in each sampling interval was close to zero (-0.61 ± 6.69 for 1989–1999, and -0.42 ± 8.18 for 1999–2012). In the mesophytic community, there was a statistically significant effect of time ($P = 0.006$; Table 4) and posttests revealed that the year 1999 had more biomass (56.98 ± 8.95 Mg ha⁻¹) than the other 2 years in the sampling (27.19 ± 7.07 Mg ha⁻¹ in 1989, and 46.08 ± 6.52 Mg ha⁻¹ in 2012). This might be a reflection of an increase in *Tilia americana* in 1999, which was apparent in the individual species values (Table 3). The mesophytic community biomass generally increased from 1989 to 1999 (29.79 ± 11.78 Mg ha⁻¹) but had a slight average decrease from 1999 to 2012 (-10.9 ± 10.4 Mg ha⁻¹).

Table 4. Results of the Schierer–Ray–Hare test for differences in CWD biomass (Mg ha^{-1}) between years, between communities (using all 3 years of data combined), and for an interaction between the two factors in an old-growth temperate forest.

Schierer–Ray–Hare test				
Factor	SS	H	df	P
Community	107,396	22.04	2	0.000016
Year	28,629	5.88	2	0.053
Community year	33,686	6.91	4	0.14
Residuals	994,731		231	
Kruskal–Wallis				
	Chi-squared	df	P	
Community biomass by year				
Oak	0.43	2	0.81	
Mesophytic	10.13	2	0.0063	
Beech	0.65	2	0.72	
Change in mass by community				
1989–1999	9.02	2	0.011	
1999–2012	3.34	2	0.19	

Results of Kruskal–Wallis tests for differences in CWD biomass between years within each community type in the study watershed.

No statistically discernible differences were found between years in the beech community, and the range of values largely overlaps (Figure 2). Biomass change in the beech community was generally close to zero for both sampling intervals ($1.54 \pm 4.12 \text{ Mg ha}^{-1}$ for 1989–1999, and $5.06 \pm 5.64 \text{ Mg ha}^{-1}$ for 1999–2012).

Topographic variables failed to predict CWD mass during any of the three sampling regimes (Figure 3; Table 5). Slope steepness exhibited a slightly positive relationship with CWD in 1999 and 2012; however, the line was not statistically different from zero in either case ($P = 0.5$ in 1999 and $P = 0.2$ in 2012). Elevation, similarly, exhibited nonsignificant though slightly positive results (Figure 3). Interpolation maps of CWD biomass did not visually

suggest any strong spatial patterns in relation to topography (Figure 4)—a conclusion supported by a lack of significant models obtained from multiple regression analysis (Table 5).

Global Moran’s I indicated no significant spatial autocorrelation of CWD biomass values within the watershed in 1989 ($I = 0.006$, $Z = 0.49$, $P = 0.62$) or 2012 ($I = 0.021$, $Z = 0.86$, $P = 0.39$); that is, the distribution of CWD at those time points was not distinguishably different from random. In 1999, however, there was significant positive spatial autocorrelation of CWD biomass ($I = 0.086$, $Z = 2.52$, $P = 0.012$), indicating that values have neighbors of similar values more often than would be expected for a random spatial distribution (clustering). A similar trend was seen in high/low clustering analysis, as there was no significant clustering of high nor low values in 1989 ($G = 0.16$, $Z = 0.065$, $P = 0.95$) or 2012 ($G = 0.17$, $Z = 0.98$, $P = 0.33$), but high values were significantly clustered in 1999 ($G = 0.23$, $Z = 3.20$, $P = 0.0014$).

The spatial patterns of change in biomass were visually different between the two sampling intervals (1989–1999 and 1999–2012; Figure 5). Interestingly, between 1989 and 1999 the north- and east-facing slopes experienced a slight average increase in CWD biomass (12.14 ± 7.86 and 11.74 ± 7.87 , respectively), but were generally unchanged from 1999 to 2012 (-3.34 ± 8.24 and -1.14 ± 6.70 , respectively). The south-facing slope had generally constant biomass from 1989–1999 (-2.14 ± 5.73) and 1999–2012 (1.98 ± 7.7). Statistical analysis revealed, however, that these patterns were not explained by topographic variation within the site (Table 5). Change in biomass did not exhibit significant global spatial autocorrelation (Moran’s I) for either time interval ($I = -0.027$, $Z = -0.35$, $P = 0.72$ for 1989–1999, and $I = 0.018$, $Z = 0.78$, $P = 0.43$ for 1999–2012), indicating that changes in total plot biomass occurred randomly throughout the watershed. Similarly, high/low clustering analysis (Getis–Ord General G)

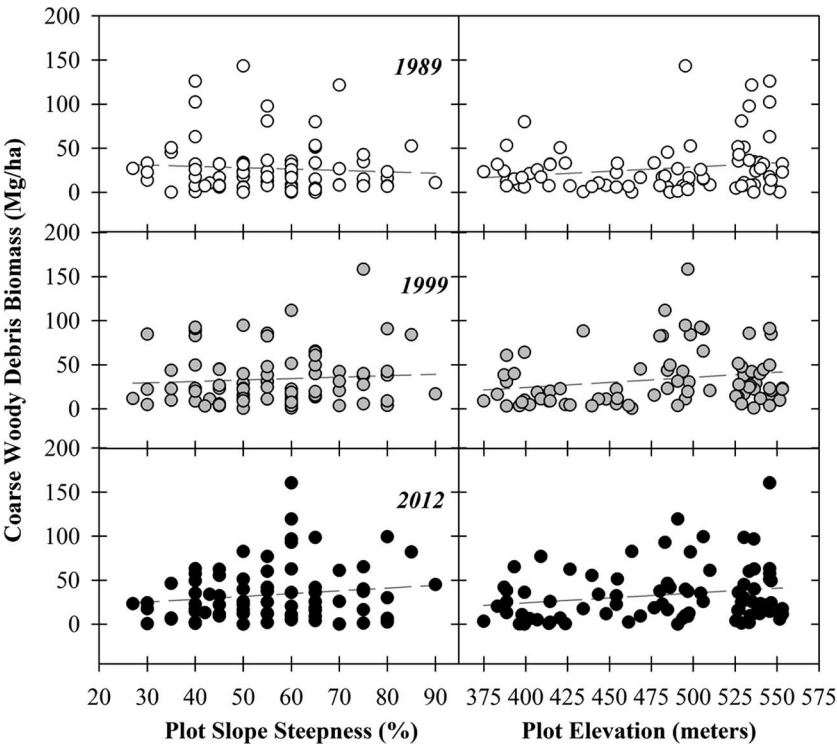


Figure 3. CWD biomass (Mg ha^{-1}) in relation to two topographic variables within an old-growth temperate forest.

Table 5. Results of ordinary least squares (OLS) multiple regression models testing for relationships between CWD mass and topographic variables within an old-growth temperate forest.

Model	Predictor coefficients			Test statistics	
	Aspect	Elevation	Slope	r^2	P
Mass (Mg ha^{-1})					
1989	-2.97	0.030	-0.12	0.0055	0.34
1999	5.33	0.034	0.14	0.028	0.16
2012	2.97	0.034	0.31	0.030	0.15
Change in mass					
1989–1999	8.30	0.0044	0.26	0.0071	0.32
1999–2012	-2.36	-0.00052	0.17	-0.034	0.95

showed no significant clustering of values ($G = 0.16$, $Z = -0.16$, $P = 0.88$ for 1989–1999, and $G = 0.0022$, $Z = 0.59$, $P = 0.55$ for 1999–2012).

Discussion

CWD dynamics within a forest are greatly influenced by the nature and timing of disturbances (Spies et al. 1988, Siitonen et al. 2000), and across large spatial scales, latitude and moisture regimes are important factors in CWD accumulation (Harmon et al. 1986). Runkle (2000) found that forest age and size structures impact the amount of CWD, with younger forests typically accumulating less CWD than older forests; however, Parker and Hart (2014) reported no differences in woody debris across a riparian chronosequence.

Forest harvesting activities strongly influence CWD pools and Jenkins et al. (2004) noted that even in mature managed forests CWD volumes are less than those in old-growth forests. Previous studies of CWD dynamics in old-growth deciduous forests have found larger CWD biomass accumulation in cool, temperate forests ($34\text{--}49 \text{ Mg ha}^{-1}$) and lower accumulations ($22\text{--}32 \text{ Mg ha}^{-1}$) in warm, temperate forests like those of our study site (Tritton 1980, Muller and Liu 1991). The CWD biomass accumulation across all three sampling points in this study falls near the upper part of the range ($22\text{--}32 \text{ Mg ha}^{-1}$) suggested by Tritton (1980) for old-growth forests in warm, temperate regions. One important caveat is that the definition of CWD has changed through time, making it difficult to compare our results to previous studies. Minimum diameters of CWD have varied in the literature from 1 to 25 cm (most utilizing either 7.6 or 10 cm as a minimum diameter), thus creating a need for adopting a standardized definition of CWD having a minimum diameter of 10 cm (Woldendorp and Keenan 2005). For continuity in the long-term study, our methodology followed the Muller definition of 20 cm and therefore likely provides an underestimate of CWD biomass relative to other studies (Muller and Liu 1991).

Old-growth deciduous forest has standardly served as a forest development endpoint where dynamics are thought to be driven by individual tree mortality events (Bormann and Likens 1979, Oliver and Larson 1996). In the absence of large-scale disturbance, theory suggests that tree mortality events, which are associated with a variety of factors (Franklin et al. 1987), become temporally and spatially

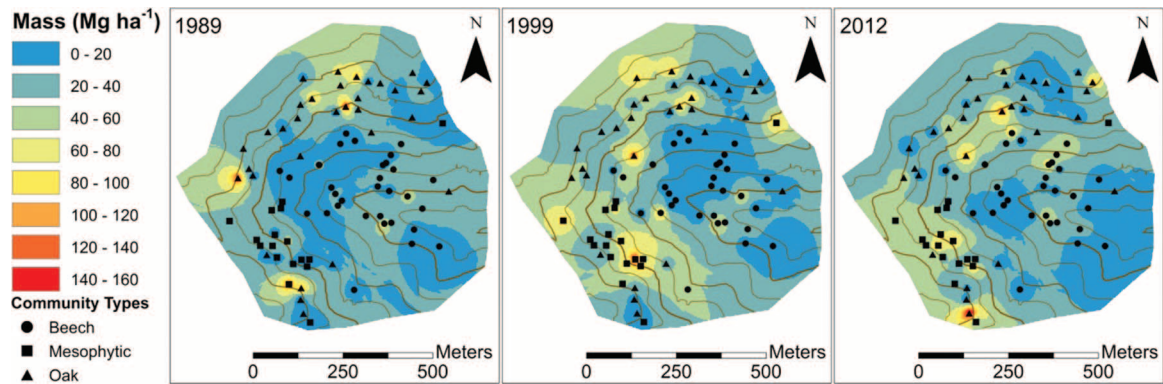


Figure 4. Inverse distance weighted interpolation maps representing total CWD biomass (Mg ha^{-1}) across an old-growth temperate forest. Sampling years were 1989, 1999, and 2012. Plot locations are denoted by points, and community type is indicated by point shape.

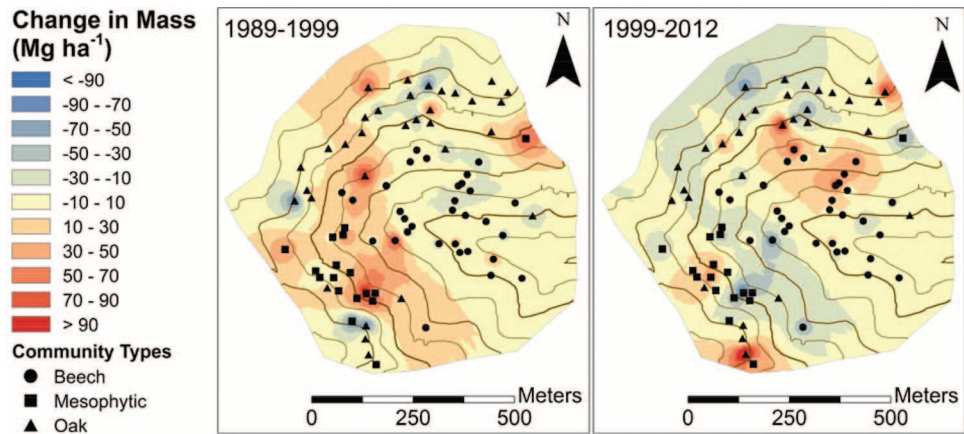


Figure 5. Inverse distance weighted interpolation maps representing change in total CWD biomass (Mg ha^{-1}) between 1989–1999 and 1999–2012 in an old-growth temperate forest. Plot locations are denoted by points, and community type is indicated by point shape.

stochastic (Runkle and Yetter 1987). Mass of CWD should be indicative of long-term mortality patterns, and we hypothesized (H_1) that CWD mass would not deviate over the time frame of this study. In fact, there was no detectable change in CWD biomass across the watershed over the time course of the study, and the only variation we discovered was within the mesophytic community, where mass was higher in 1999 than other years. This pulse of CWD is vaguely represented in our spatial analysis as higher biomass in 1999 on the north-facing midslope sites (Figure 4) and greater change in the same areas from 1989 to 1999 (Figure 5). The source of this mild variation is unknown, and, overall, we interpret CWD volumes as relatively stable over the time course of this study. This stability may support gap dynamics as an important driver of disturbance in this watershed. McEwan et al. (2014) found that 94% of sampled trees in this same watershed had experienced at least one release event indicating a canopy gap, and found an overall return interval of *ca.* 5 years (over a time span of *ca.* 300 years).

Despite the rich research history on the relationship between vegetation and topography, little information exists regarding the spatial distribution of CWD in topographically-complex areas like eastern North American and LCW (Rubino and McCarthy 2003). Our project was guided by the null hypothesis (H_2) of no discernible spatial pattern in CWD. Rubino and McCarthy (2003) found no significant relationship between slope aspect and CWD biomass in an old-growth Ohio forest; however, they did point out that distribution patterns of CWD are thought to fluctuate with environmental parameters as these features are important in configuring arrangements of live vegetation. Large CWD biomass deposition has historically been found on northeasterly slopes due to such environmental parameters, particularly increased moisture and fertility (Spies et al. 1988, Robertson and Bowser 1999, McCarthy et al. 2001). Our analyses revealed no statistical relationship between elevation or slope steepness, and our broader spatial analysis revealed no discernible pattern. Model building (H_3) ultimately was ineffective for discerning biotic or abiotic predictors of CWD, leading to the conclusion that woody debris accumulation is, indeed, a stochastic process within this watershed and is likely linked with gap dynamics or localized disturbance events.

Long-term carbon storage dynamics as linked to CWD are likely to change through time in response to ongoing pest and pathogen loads and climate warming. For instance, the watershed is currently undergoing an infestation of the hemlock wooly adelgid (Orwig and Foster 1998) that will likely drive a pulse of *T. canadensis* CWD on lower slopes in the coming decade. Emerald ash borer is an increasingly important mortality agent for members of the genus *Fraxinus* and has the potential for initiating dynamics in CWD (Flower et al. 2013). Across broad areas of eastern North America, there is evidence of oaks (*Quercus*) being replaced by more mesophytic species including maples (*Acer*) (McEwan et al. 2011). In the BEH watershed, this pattern was apparent in the living oak community overstory (McEwan and Muller 2006), which may lead, over the long term, to a shift in CWD pools on upper slopes in the watershed. Additionally, climate change could alter the terrestrial carbon balance by influencing productivity rates, and CWD carbon storage has been found to decrease as mean annual temperature increases, presumably due to acceleration of decomposition rates (Iwashita et al. 2013, Russell et al. 2014b). Work in our study watershed that addresses decomposition rates could be illuminating (e.g., Fraver et al. 2013), and continued long-term monitoring is needed to assess

both climatic pressures on CWD pools and also the potential for impacts associated with pests and pathogens.

In summary, this work demonstrated relative stability in CWD pools across the topographically complex landscape represented by our old-growth study site. Estimates of CWD were statistically indistinguishable except for one time point in the mesophytic community (1999). This supports the notion that, in the absence of large-scale disturbance, old-growth temperate forests are relatively stable in terms of tree mortality and deposition of woody material to the forest floor. Topographic variables were poor predictors of CWD biomass, and our data suggest CWD deposition to the forest floor is a spatially stochastic process over the time frame of this study. Long-term monitoring of temperate forests is particularly pressing given threats from outbreaks of forest pests and pathogens and the potential for climate change to influence CWD pools, especially over decadal time scales.

Endnotes

1. For more information, please visit www.graphpad.com.
2. For more information, please visit www.R-project.org.

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