Direct estimates of downslope deadwood movement over 30 years in a temperature forest illustrate impacts of treefall on forest ecosystem dynamics

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Abstract: Deadwood plays important roles in forest ecosystems by storing carbon, influencing hydrology, and provisioning countless organisms. Models for these processes often assume that deadwood does not move and ignore redistribution that occurs when trees fall. To evaluate the effects of treefall, we provide the first direct estimates for the magnitude, direction, and drivers of deadwood movement in a long-term oak–hickory forest dynamics plot in Missouri, USA. Among 1871 total pieces of deadwood, logs today pointed downslope more often than branches and occurred at lower elevation than snags. Of these, 477 logs retained tags from which we reconstructed movement using new formulae for reconciling survey coordinates and calculating log shape. Relocated logs occurred at lower elevation than their original rooting location, with the magnitude of the drop dependent on log size, degree of decay, and slope. Although changes in elevation were modest, the log centroids moved up to several meters horizontally. Consequently, as large trees fall, they predictably redistribute deadwood downhill, suggesting that models of deadwood dynamics in small inventory plots may gain accuracy by incorporating import and export along with recruitment and decay. We highlight implications of small-scale deadwood movement for forest inventories, carbon dynamics, and biodiversity.

Key words: carbon inventory, deadwood, geomorphology, log volume, oak–hickory forest.

Introduction

Deadwood plays critical roles in many terrestrial ecosystems. In forests, it represents a large carbon pool (Harmon et al. 1986; Russell et al. 2015). In some western North American forests, where climate change and beetle outbreaks have decimated living trees, deadwood currently stores even more carbon than soils (Wilson et al. 2013). Deadwood also strongly influences forest hydrology and geomorphology by controlling water infiltration, stream channel development, and hillslope processes (Pyper et al. 2011). Along with these ecosystem functions, deadwood represents a keystone resource for forest organisms from microbes to endangered birds (Stokland 2012).

Mechanistic understanding of how deadwood influences forest ecosystems often depends on knowing its spatial distribution. Log density, aggregation, and orientation influence the accuracy of standard deadwood carbon estimates (Woldendorp et al. 2004). Likewise, the effects of deadwood on geomorphic processes depend on its topographic position and orientation (Raíka 2012). Logs that are perpendicular to hillslopes and stream channels slow flow rates and limit sediment run out more than parallel logs.
Finally, the abundance and dynamics of saproxylic organisms depend on the spatial distribution and quality of this key resource (Schiegg 2000). Despite the importance of location data, most forest inventories estimate deadwood abundance in a spatially implicit fashion, if at all (Woodall et al. 2013).

With limited data on deadwood spatial distributions, models for related processes often make the innocuous assumption that deadwood recruits and decays without moving (Westfall et al. 2013). However, different processes may drive deadwood movement across a range of spatial scales (Harmon et al. 1986). At the broadest scales, floods transport deadwood up to several kilometers (May and Gresswell 2003). At a much finer scale, deadwood moves downhill when a tree falls. When a tree falls, its center of mass rotates from above its base onto the forest floor, suddenly redistributing biomass in both the vertical and horizontal dimensions (Fig. 1). Once on the ground, gradual processes can move deadwood further still. Surface flow may translate logs across the landscape, whereas decay may shift the position of the center of mass depending on how the decay rate varies with log geometry (Raška 2012). These movements may seem trivial but their magnitude is likely to scale with log length, which can vary from a few meters to more than 100 m. This range is comparable with the size of many inventory plots and the distances moved by many organisms that depend on deadwood (Stokland 2012).

Even though deadwood movement may impact important forest processes, estimates are rare because they require tracking deadwood through time. Existing landscape-scale analyses tend to estimate movement indirectly by comparing the contemporary distribution of deadwood with other features of the landscape. For instance, Rentch (2010) evaluated the current orientations of logs in several temperate forests and found weak evidence that either slope–aspect or prevailing wind explained the direction of treefall. In a Colorado forest, logs point away from prevailing winds as the legacy of unusually destructive blowdowns (Kulakowski and Yeblen 2003). Likewise, Rubino and McCarthy (2003) compared the abundance of deadwood with that of living trees along topographic gradients and found that topography did not influence the strong relationship between the abundance of living trees and the abundance of dead trees. Although these studies are among the best to evaluate deadwood movement at the landscape scale, the unexpected conclusion that deadwood does not fall downhill may reflect the limitations of estimating deadwood movement indirectly from contemporary location data.

We estimated the magnitude and drivers of deadwood movement by applying new methods to long-term data in a stem-mapped temperate forest-dynamics plot. We first compared the distribution and orientation of different kinds of deadwood (i.e., branches, logs, and snags) across the landscape today. We predicted that if treefall drives deadwood movement, logs should occur at lower elevation than snags, and their orientations should be concentrated in the direction of slope aspect, whereas orientations of fallen branches that began with variable positions in the canopy should have directions that are less concentrated. Then, we reconstructed deadwood movement in a subset of logs using location data associated with retained inventory tags. We evaluated three main predictions for the magnitude and direction of deadwood movement. First, we predicted that the bases of larger, less decayed logs will occur closer to their original location due to greater inertia and less time for movement but that their centroids will occur further away because of greater displacement with rotation from their original standing positions (Fig. 1). Second, we predicted that movement relative to both the base and centroid would be greater on steeper slopes regardless of the size of the log. Finally, we predicted that the direction of movement at the centroid, which integrates movement due to translation and rotation, to be more strongly correlated with slope–aspect than the direction of movement at the base. We discuss potential implications of our results for forest inventory, models of forest carbon dynamics, and biodiversity.

Materials and methods

Study site

We conducted our study at the Tyson Research Center Forest Dynamics Plot (TRCP), a 25 ha stem-mapped forest plot located at Washington University’s Tyson Research Center near St. Louis, Missouri. The plot is typical of the northern Ozark Highlands ecoregion of east central North America, with steep limestone ridges that are dominated by oak (Quercus) and hickory (Carya) species. The TRCP is part of a global network of forest–ecology plots monitored through the Smithsonian Forest Global Earth Observatory (Anderson-Teixeira et al. 2015). For this study, we used long-term data from the original 4 ha (200 m × 200 m) section of the plot established in 1981 (Hampe 1984). All free-standing stems of woody species ≥ 2 cm diameter at breast height (DBH, 1.4 m) in the 4 ha plot were identified, tagged, and mapped in 1981–1982 (N = 5931 stems) and in 1989 (N = 5538 stems). All stems ≥ 1 cm DBH were censused in 2011–2012 using ForestGEO protocols (Anderson-Teixeira et al. 2015). During each census, new stems were tagged with unique identification numbers. Like many forests in the region, the site was selectively logged and grazed until the beginning of the 20th century when the US government purchased the site and restricted access; then, natural vegetation began recovering (Zimmerman and Wagner 1979). Because no major wind-throw event has occurred in the surveyed history of the site, tree mortality may depend more on self-thinning and periodic drought. We expect that snag formation and downhill failure under gravity dominate log recruitment. Additional information about the study site is available in Spasojevic et al. (2014).

To characterize the terrain of the plot, we analyzed a publicly available high-resolution (1.4 m) LiDAR-based digital elevation model (DEM) produced by St. Louis Metropolitan Sewer District. Because the DEM data are provided in UTM15 NAD83 projection and the TRCP coordinate system is based on the MOPS east NAD83 projection, we reprojected the DEM data using the “project-Raster” function in the package “raster” version 2.2–12 (Hijmans and van Etten 2010) in R version 3.0.2 (R Development Core Team).
Deadwood inclusion and classification

Within the original 4 ha section of the plot, we mapped and measured all pieces of deadwood that met at least one of three criteria: (i) downed wood ≥ 7 cm in diameter for 1 m with its large end located within the plot boundary, (ii) snags ≥ 2 cm DBH, or (iii) pieces with attached identification tags regardless of size. We recorded the tag number if the tag was physically attached to the deadwood or if we could unambiguously associate nearby tagged stumps with logs. We classified each piece of deadwood into one of the following eight categories based on vertical position, length, and apparent origin: (i) stumps – suspended deadwood with an intact base and a total length < 2 m; (ii) snags – suspended deadwood leaning less than 45° from vertical and ≥ 2 m long; (iii) suspended logs – deadwood leaning more than 45° from vertical with no ground contact for the majority of its total length; (iv) logs – main boles of a stem with ground contact along the majority of its length; (v) branches – distinguished from logs by irregular shape and the absence of a base; (vi) suspended branches – branches leaning more than 45° from vertical; (vii) vines – portions of dead lianas; (viii) deadwood – any sample that we could not positively assign to other categories. In addition to type, we classified each deadwood piece using standard criteria for temperate hardwood forests (Pyle and Brown 1998). Decay class (DC) 1 included the least decayed specimens that still retained fine branches or leaves. DC2 included more decayed specimens that had lost fine branches but still retained most of their bark. DC3 included specimens that had lost most of their bark but had mostly intact exposed wood. DC4 included specimens with major surface deformities but that otherwise supported their own weight. DC5 specimens were the most decayed and had lost structural integrity.

Deadwood shape and location

For each piece of deadwood, we estimated its shape from several dimensional measurements. We measured total log length from the most basal point where the horizontal diameter was ≥ 7 cm and measured along the largest diameter branch as far as the horizontal diameter of the piece remained ≥ 7 cm. If a bole had broken, we measured each piece independently if the break was longer than 20 cm or if it shifted the orientation of the main bole by more than 10°. We measured the cross-sectional dimensions of logs and branches at both the large and small ends. If either location was suspended above the ground, we measured a single diameter using a diameter tape. If the location was in contact with the ground, we measured the horizontal and vertical diameters (i.e., parallel to and perpendicular to the ground, Appendix A, Fig. A1) using calipers. In cases where the cross-section at the terminus was not representative of the cross-sectional shape of the bole (e.g., root flare and asymmetrical breakage), we measured a representative shape and noted the distance from the measurement location to the terminus. For pieces that were longer than 2 m, we made additional cross-sectional measurements at 1.4 m from the large end of the object. In some cases, we could not measure diameters due to burial or local deformities. Rather than exclude these samples, we took advantage of predictable relationships between height and width in our dataset. To identify the best-fit model relating height to width, we compared a series of models for the height to width ratio as a function of measurement location (base, 1.4 m, apex) and different sets of decay classes. The best-fit model, based on the Akaike information criterion (AIC, Akaike 1973), explained the vertical to horizontal ratio as a function of measurement position and advanced decay classes (i.e., DC4 and DC5; Supplementary Table S1). We then used the parameter estimates from the best-fit model for the vertical to horizontal ratio to impute missing values of either height or width from the complementary measurement. Although our goal was simply to reconstruct log volume, our approach parallels methods for estimating volume reduction of deadwood from collapse ratios (Fraver et al. 2013).

For log location, we mapped the large end of each piece in relation to the surveyed coordinates of 20 m × 20 m quadrat boundary poles based on the distance from the reference quadrat pole to the midpoint of the large end, as measured with a meter tape, and the azimuth, as measured with a sighting compass. We measured the orientation of each piece as the azimuth from the midpoint of the large end to the opposite terminus. From these data, we calculated the x, y coordinates for the large end of each piece using trigonometric identities (Supplementary Fig. S2). We also calculated the position of the geometric centroid of each piece using new formulae that we derived for the volume and centroid location of volumes of revolution bounded by parallel ellipses (Appendix A). Standard formulae for other shapes applied to deadwood, including the elliptical cone, cylinder, and frustra, thereof are special cases of this formula.

Statistical analyses

To evaluate indirect evidence for downhill movement in the contemporary distribution of deadwood, we compared the elevations and orientations of logs with those of snags and branches, respectively. We measured differences in elevation between logs and snags by extracting the elevation at the x, y coordinates for every snag, log base, and log centroid. Because orientation is a circular response variable, we analyzed differences in the orientations of logs and branches using circular statistics. To test for differences in the orientations of logs and branches, we conducted an equal k test, which evaluates the homogeneity of concentration parameters drawn from von Mises distributed populations (Jammalamadaka and Sengupta 2001). To test whether variation in the surrounding terrain explained deadwood orientation, we conducted circular regressions (Jammalamadaka and Sengupta 2001). We implemented circular tests using package “circular” version 0.4–7 (Agostinelli and Lund 2013) in R.

To directly quantify movement, we estimated the position of each tree while alive using a projective transformation of the mapped coordinates from the living tree census. This projective
transformation corrected for the distortion in the original mapping grid observed today (Appendix B). We computed the distance between the position of the tree while alive and its current position as a log relative to two locations. First, we computed the distance between the original location of the living tree and the mapped location of the base of the log. This value represents the minimum displacement of the log due to translation (Fig. 1). We then computed the distance between the original location of the tree and the current estimated position of the centroid. This value represents the displacement of the terrestrial projection of the estimated center of mass incorporating movement with translation and rotation. We computed these distances using estimated displacement in the vertical dimension and the natural logarithm of the Euclidean distance in the horizontal dimension.

Using these estimates, we evaluated the magnitude, direction, and drivers of deadwood movement both vertically and horizontally (Fig. 1). To evaluate the direction of vertical movement, we used paired t-tests to compare the elevation at the rooting location of the living tree with the elevations at both the log base and centroid. To identify drivers of vertical and horizontal movement, we compared linear models with different log- and landscape-level predictors. For log-level predictors, we compared models including decay class as a continuous predictor and one of two metrics for log size, i.e., large end diameter and the natural logarithm of log length. Our landscape-level predictors included slope and the natural logarithm total catchment area. Based on our mapping procedure, errors may increase with distance from the reference grid poles, so we included mapping distance as a fixed effect covariate in our model selection. We evaluated the effects of drivers based on whether associated predictors occurred in the best-fit linear model as assessed by AIC. For each best-fit model, we examined the normal quantile plot of residuals for violations of regression assumptions.

Because our data are spatial and errors may be autocorrelated, we modeled the spatial error structure in each best-fit model using an intrinsic Gaussian conditional autoregressive (CAR) effect. The intrinsic Gaussian CAR effect represents the first-order conditional dependency of residuals over those in a fixed neighborhood of adjacent areas (Besag et al. 1991). We defined neighborhoods based on a 25 m x 25 m square grid to balance precision in our estimates with power of a relatively high number (6.8) of observations per grid cell. We estimated our intrinsic Gaussian CAR models in a Bayesian framework with an improper flat prior on the overall intercept, diffuse normal priors (e.g., mean of zero variance of 1000) over the regression parameters, a wide uniform prior (e.g., minimum of zero and maximum of 100) over the residual standard deviation, and a gamma prior (e.g., shape = 0.5 and rate = 2) over the Gaussian CAR precision. For fitting the models, we used the software OpenBUGS version 3.2.1 (Lunn et al. 2009) to run three independent MCMC chains for 3000 iterations each, discarding the first 1000 steps as burn-in. Following burn-in, we assessed convergence by visually inspecting the trace plots and confirming that the Brooks Gelman Rubin statistic (Brooks and Gelman 1998) was less than 1.05. In every case, the posterior parameter estimates for regression parameters from the spatially explicit models agreed in direction and relative magnitude with estimates from the nonspatial models, so we report only the estimated posterior standard deviation of the spatial effect, noting when the 95% credible intervals for the regression parameter estimates included zero.

Finally, we examined the effects of aspect and hydrological-flow direction on the direction of movement using circular regressions. Because likelihood methods are not well-characterized for circular regressions, we assessed statistical significance using p values.

![Fig. 2. Log centroids occur at lower elevation than snag bases in a 4 ha forest plot. Curves represent kernel-based densities, and vertical lines represent means for all deadwood > 7 cm diameter for at least 1 m.](image)

### Results

**Contemporary distributions of deadwood**

Of the 1871 total deadwood observations in the 4 ha plot, 1359 were at least 7 cm in diameter at the large end. Of these 727 were logs, 273 were branches, and 229 were snags, with the other categories of deadwood (e.g., suspended logs, suspended branches, stumps, vines, and unidentified) accounting for the remaining 130 observations. Most large deadwood was classified into an intermediate stage of decay, with DC3 being the most frequent (496), followed by DC4 (367), DC2 (272), DC5 (115), and DC1 (109).

Differences in position between large snags, logs, and branches were consistent with downhill deadwood movement as trees fall. Based on the projected, smoothed DEM, the average elevation in the plot was 204.0 m, and the average elevation of snag bases was slightly lower at 202.7 m. Log bases tended to occur lower than snags, with an average elevation of 201.8 m, and log centroids occurred lower still, with an average elevation of 201.5 m (Fig. 2). Consistent with expectations, the horizontal diameter at the base of tagged logs ranged from 2 to 50.3 cm, with an average value of 10.41 cm. Although individual logs pointed in many directions, their average orientation was significantly associated with slope-aspect (Fig. 3A; circular regression: n = 726, \( \rho = 0.374, \kappa = 0.809, p < 0.001 \)). However, branch orientations differed from logs (equal \( \kappa \) test: degrees of freedom (df) = 1, \( \chi^2 = 10.41, p < 0.001 \)) and was not associated with slope-aspect (Fig. 3B; circular regression: n = 273, \( \rho = 0.135, \kappa = 0.809, p = 0.77 \)).

**Movement of tagged logs**

We relocated 784 dead stems, including 477 logs that retained tags from previous censuses. The horizontal diameter at the base of tagged logs ranged from 2 to 50.3 cm, with an average value of 9.7 cm. Tagged log length ranged from 0.34 to 23 m, with an average length of 3.9 m. The distribution of decay classes among tagged logs was more concentrated in intermediate decay stages. The majority of tagged logs were classified as DC3 (264), followed by DC4 (109), DC2 (69), DC5 (27), and DC1 (8).
Just as the contemporary difference in elevation between snags and logs implied downhill movement, the current elevation of log bases and centroids was consistently lower than the original rooting location of the corresponding living trees (Fig. 4A). The average elevation of log bases was more than 19 cm below that of the original rooting location (one-sample t test: n = 477, t = –8.56, p < 0.001), with a range spanning from a 1.3 m gain in elevation to a 3.6 m drop in elevation. The average elevation of log centroids was 45 cm lower in elevation (one-sample t test: n = 477, t = –14.65, p < 0.001), with an even wider range from 1.8 m gain in elevation to a 3.7 m drop in elevation.

The magnitude of the drop in elevation depended on both log and landscape factors (Supplementary Table S21). Log length was an important predictor of vertical movement, such that bases of longer logs were closer in elevation to the original rooting location, whereas their centroids occurred much further downhill (Figs. 4B and 4C). For logs at the mean decay class and slope, a doubling of log length reduced the drop in elevation at the base by 8 cm (linear regression: t = 2.64, p = 0.009). At the same time, a doubling of log length increased the drop in elevation at the centroid by 21 cm (linear regression: t = –5.28, p < 0.001). The change in elevation at the log centroid also depended on slope and decay class, with larger drops among logs in more advanced stages of decay (Fig. 5A; linear regression: t = –2.10, p = 0.037) and larger and more variable drops on steeper slopes (Fig. 5B; linear regression: t = –7.95, p < 0.001). Spatially explicit models for drivers of horizontal movement attributed more variation to nonspatial errors than spatial errors relative to the log base (horizontal movement at base Gaussian CAR: spatial error, standard deviation = 0.961, nonspatial error, standard deviation = 1.406) but similar amounts of variation in horizontal movement at the centroid (centroid horizontal movement Gaussian CAR: σ = 0.578, nonspatial σ = 0.599).

The effect of terrain on the direction of log movement depended on the reference location along the log. Just as all logs on the landscape today tended to point downhill, the direction of movement from the living tree to the log centroid showed a weak but significant correlation with slope aspect (Fig. 6A; circular regression: κ = 1.21, p = 0.03). However, the direction of movement to the log base was not correlated (Fig. 6B; circular regression: κ = 0.71, p = 0.19).

Discussion

Our results support the hypothesis that deadwood is predictably redistributed downhill as large trees fall. Previous studies of deadwood movement have largely estimated movement indirectly from contemporary location data (e.g., Kulakowski and Veblen 2003; Rubino and McCarthy 2003; Rentch 2010). In contrast, direct estimates of movement are rare, because they require tracking deadwood through time. By quantifying long-term movement from remapped trees, our study provides some of the first direct estimates for the magnitude, direction, and drivers of deadwood redistribution at the landscape scale. Logs occurred at lower average elevations than snags and pointed more consistently downhill than branches. Both log bases and centroids occurred at lower elevations than the elevation of the same tree while it was living. Estimated downhill movement was modest, typically less than 1 m. However, depending on the shape of the log and the surrounding topography, the log centroid moved as much as several meters from its original location since living trees were mapped 30 years ago. Deadwood movement at these small scales may have important implications for forest carbon dynamics in small inventory plots (Russell et al. 2015), nutrient fluxes...
Fig. 4. Deadwood movement in (A–C) vertical and (D–F) horizontal dimensions. The bases of long logs occur closer to the location of the living tree, but their centroids occur further away downhill. Log centroids tend to be located further than log bases in both (A) vertical and (B) horizontal dimensions. Curves in (A) and (D) represent kernel-based densities. Solid lines in (B), (C), (E), and (F) represent best-fit marginal linear regressions and dashed curves represent 95% credible intervals for the slopes.
The relationships between log movement, shape, and topography suggest that downhill rotation during treefall drives most of the deadwood redistribution across our study site. Consistent with our expectations, the centroids of longer logs dropped further on steeper slopes, and the horizontal direction of movement from original rooting location to current log centroid was correlated with slope–aspect, as were the overall orientations of all logs on the landscape today. Similarly, an analysis of deadwood recruitment into small streams in conifer-dominated forests of the Pacific Northwest found that large trees were more likely to fall into streams where side slopes were steeper (Sobota et al. 2006). These consistent results from very different systems suggest that the magnitude of deadwood movement with downhill treefall is often proportional to the size of the tree and the steepness of the slope.

The prominent role for downhill treefall at our site may reflect its recent history. In contrast to some mature forests where wind throw is both the major agent of tree mortality and log recruitment (e.g., Kulakowski and Veblen 2003), the forest at our study site is in an intermediate stage of succession and has experienced recent extreme drought (Spasojevic et al. 2014). Related self-thinning and water stress tend to form snags that ultimately recruit as logs when mechanical stress exceeds structural resistance (Russell et al. 2015). Both contemporary log orientations and reconstructed movement suggest that downhill failure under gravity felled most snags in this forest up to now. Although this mode of log recruitment may not be universal, it may become more important with expected changes to forests in the region. Many hardwood forests in the central United States are recovering from disturbance 80–90 years ago at which point deadwood density tends to increase as canopy trees senesce (Spetich et al. 1999). Senescing trees may be especially vulnerable to mortality with drought, which may become more frequent and intense with expected climate change (Bennett et al. 2015). For both of these reasons, we expect that snag formation and treefall will remain an important driver of deadwood dynamics in this forest and in other forests.

Fig. 5. Log bases were mapped at a relatively lower elevation when (A) logs were in an advanced decay class and when (B) living trees grew on steep slopes. Solid lines represent best-fit marginal linear regressions, and the dashed curves represent 95% credible intervals for the slopes.

Fig. 6. (A) The direction of movement from the location of the living tree base to the location of the log centroid is associated with slope–aspect, whereas (B) the direction of movement to the log base is random. Outer curves represent kernel-based density, and arrows represent the estimated concentration parameters for the horizontal direction of movement (black arrow) and landscape (gray arrow).
logs, which could reflect both modest cumulative movement with intermittent surface flow for stems that have been on the ground longer or apparent movement of the log base as it gradually decomposes (Raška 2012).

Predictable downhill movement during treefall has important implications for the accuracy of deadwood inventories. Several inventories use fixed area plots with varying rules for including deadwood that crosses plot boundaries (Russell et al. 2015). For instance, logs with large ends inside the plot may be included under the assumption that their large end corresponds to their original rooting location (Gove and Van Deusen 2011). Our results show that large ends of logs often move more than 1 m from their original rooting location after falling downhill. Another common method samples deadwood using line intercept sampling along short transects (e.g., Böhl and Brändli 2007; Ritter and Saborowski 2014). For instance, the U.S. Forest Inventory and Analysis (FIA) program samples deadwood in 0.232 ha plots using a regular array of 12 transects, each of which is approximately 7 m long (Woodall et al. 2013). This transect length corresponds to the 90th percentile of centroid movement in our plot, suggesting that these plots inventory deadwood at a scale comparable with the distance deadwood moves when trees fall. For this reason, factors that influence the distance a tree falls may strongly influence deadwood abundance in these plots. Furthermore, the line intercept method assumes random log orientations and samples logs proportional to their length (Van Wagner 1982). We found that log orientations were correlated with slope aspect and log movement correlated with log length. Although most inventories, including FIA, limit bias from nonrandom log orientations by using transects that face different directions, they do not account for longer logs moving further along steep slopes. Further studies are necessary to evaluate whether deadwood inventory methods are robust to potential bias associated with predictable downslope treefall.

Deadwood movement may also complicate efforts to estimate carbon flux from local deadwood pools. Spatially explicit forest models generally assume that deadwood does not move (Harmon et al. 1986; Russell et al. 2015). Under this assumption, the size of the local deadwood pool depends solely on the balance of wood senescence and decay in the steady state. Our results suggest that local deadwood pools may also depend on rates of import and export along the hillslope, especially in forests with tall trees and complex terrain. All else being equal, sampling locations that are at the top of hillslopes are likely to be net exporters with relatively smaller pools, whereas those near the bottom of hillslopes are likely to be net importers with relatively larger pools (Kennedy et al. 2008). Not only does deadwood movement complicate the accounting of deadwood dynamics in small inventory plots, but it also predictably changes the environment for wood decay across heterogeneous landscapes. A recent experimental study at our site found that wood decay rates in valleys were 50% faster than wood decay rates on ridgetops (Zanne et al. 2015). Assuming that differences in the decay rate scale with elevation (Meier et al. 2010), downhill treefall at our site would reduce the residence time of the coarse deadwood pool by over 1% compared with an alternative where logs decay at the same elevation as snags. Although this difference in residence time appears small, it applies to the entire deadwood pool across the landscape. Moreover, our results imply that the acceleration of wood decay with downslope movement could be even larger in forests with taller trees and steeper slopes such as forests of the Pacific Northwest where logs can represent over 40% of all biomass and the lion’s share of net primary productivity (Grier and Logan 1977). Future forest carbon modeling efforts may gain accuracy by incorporating downslope treefall and accelerated decay. In the meantime, estimates of local carbon flux based on variation in pool size across plots that are small relative to terrain features may be more accurate if stratified by topographic position.

Beyond implications for forest carbon inventory and modeling, downslope deadwood movement could influence geomorphology and forest hydrology. Creep, or gradual downhill shifts of the hill slope under gravity, tends to tip trees downhill, explaining why canopy gaps form more frequently on slopes and why logs often align with slope-aspect (Sobota et al. 2006). On slopes where creep drops trees, logs point downhill and open canopies increase the velocity of surface flow and the potential for erosion (Raška 2012). The feedback between creep and erosion, two processes that destabilize slopes, mediated by gap formation and downhill treefall could link slope development with stand structure across landscapes (Marston 2010). In addition to impacting upland processes, deadwood movement also influences streams and sedimentation. High rates of downslope failure influence stream channel morphology and sediment output (May and Gresswell 2003). In simulations of an Oregon watershed, deadwood slowed debris flows, reduced velocity in stream channels, and decreased sediment run-out length by an order of magnitude (Lancaster et al. 2003). Likewise, deadwood was more likely to recruit into small streams in coastal Washington where surrounding slopes were steeper (Jackson and Sturm 2002). The effects of deadwood movement on hillslope failure and sediment run out could be different in other sites with more recent history of major wind throw. Where strong winds blow across slopes, windthrown trees may impede surface flow (Rentch 2010). Our results suggest that comparing these drivers of deadwood movement may help improve risk assessments of hillslope failure.

Deadwood movement at this scale also has implications for conserving deadwood biodiversity. In forests, deadwood is a keystone structure that supports a diverse range of organisms (Tews et al. 2004). In boreal and temperate forests, deadwood abundance correlates with species richness of many groups (Lassauce et al. 2011). The effect of deadwood on richness often depends on spatial scale and landscape context (Sverdrup-Thygeson et al. 2014). For example, the diversity of flies increased with deadwood connectivity at scales of 150 m (Schiegg 2000). Similarly, rare polypore fungi showed higher diversity in patches with higher snag connectivity in Scandinavian forests (Hottola and Siitonen 2008). Our results suggest that habitats at the bottoms of hillslopes, which may form relatively contiguous zones of high deadwood abundance, may represent landscape-level hotspots for saproxylic species diversity. At the opposite end of this topographic gradient, upslope habitats can have different microclimates that affect the physical quality of deadwood (Oberle et al. 2014). Because these habitats may tend to export deadwood downslope, tree removal along ridges may disproportionally affect upslope habitat specialists.

Although individual falling snags move only a few meters, the collective tendency for deadwood to move downhill may impact forest carbon cycling, hydrology, and biodiversity across heterogeneous landscapes. As more forest inventories map and measure deadwood, it may soon be possible to estimate characteristic spatial scales at which deadwood movement influences various forest dynamics. In the meantime, inventory methods, process models, and management strategies that assume that deadwood is stationary may gain accuracy by considering how deadwood moves further as trees get taller and slopes get steeper.

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Oberle et al. 359

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Appendix A: derivations for volume and centroid position formulae

To estimate the volume and centroid position of from dimensional measurements of deadwood, we considered the geometry of an object of arbitrary length \( L \) with measurements in the vertical \( V \) and horizontal \( H \) directions at both its base and apex \((V_b, H_b, V_a, H_a)\) respectively. The volume of such an object equals the integral over the area of every elliptical cross section at each position \( z \) along the central axis \( L \).

\[
\text{(A1)} \quad \text{Volume} = \pi \int_0^L \left[ H_b \left( \frac{z(V_a - V_b)}{L} \right) + \frac{z(V_b - V_a)}{L} \right] dz
\]

\[
\text{(A2)} \quad \text{Volume} = \frac{\pi L}{3} \left[ H_b V_a + H_b V_b + \frac{1}{2} (H_a V_b + H_b V_a) \right]
\]

We note that this formula represents a weighted average for the volumes of four elliptical cylinders: one formed from by ellipse at the base, one formed from by ellipse at the top, and two ellipses formed from the opposing major and minor axes of the ellipses at the top and bottom, respectively. The distance from the base of the object to the position of its centroid is given by the integral

\[
\text{(A3)} \quad \text{Centroid} = \int_0^L \frac{z(\text{volume}) dz}{\text{volume}}
\]

\[
\text{(A4)} \quad \text{Centroid} = \frac{1}{2} \left[ H_b (V_a + V_b) + H_a (V_b + 3V_a) \right] / \left[ 2(H_b (2V_a + V_b) + H_a (V_b + 2V_a)) \right]
\]

The standard formulae for the volume and centroid positions of other volumes of revolution including the cylinder, ellipsoid cylinder, cone, and frustrum of a cone are special cases of eqs. A2 and A4. We further note that this formula and Smalian’s formula, which estimates log volume as a frustrum of a paraboloid, provide identical values for cones and conical frustra, but they diverge for other shapes. We took advantage of the generality of our formula to include measurements made using a diameter tape. Diameter tape measurements assume that the log cross section is circular. To incorporate these data, we input the diameter tape measurement for both the vertical and horizontal axis lengths.

For logs that we measured at multiple distances, we calculated the cumulative volume as the sum of the volumes of each segment. We also calculated the overall centroid position as the average centroid position of each segment weighted by the proportion of the total log volume contributed by that segment.

Appendix B: coordinate system projective transformation and validation

The research team that established the Tyson Research Center Plot (TRCP) in 1981 deployed a 20 m × 20 m reference grid and calculated tree coordinates assuming that the grid vertices were perfectly rectilinear. The research team that re-established the TRCP in 2009 relocated and mapped the original poles using modern survey equipment. The current positions of the original grid poles do not form a rectilinear grid. If this distortion was present when the plot was established, then the original tree coordinates would be inaccurate. To correct for this source of mapping error, we defined a series of transformations to project the original coordinate system onto the current surveyed coordinate system grid cell by grid cell. Consider a quadrilateral grid cell \( G \) with vertices in the original space located at \((x_1, y_1), (x_2, y_2), (x_3, y_3), \) and \((x_4, y_4)\). The corresponding coordinates in the new space are \(n_1, n_2, n_3, n_4\), respectively. The projective transformation from the original onto the new subspace is defined by a series of eight linear equations that can be represented in matrix notation as a product of a matrix of the original coordinates \( O \), a projection matrix \( P \), and a matrix of the new coordinates \( N \)

\[
\begin{bmatrix}
  x_1 & x_1 y_1 & 1 & a & c \\
  x_2 & x_2 y_2 & 1 & b & f \\
  x_3 & x_3 y_3 & 1 & c & g \\
  x_4 & x_4 y_4 & 1 & d & h
\end{bmatrix}
= \begin{bmatrix}
  n_1 & m_1 \\
  n_2 & m_2 \\
  n_3 & m_3 \\
  n_4 & m_4
\end{bmatrix}
\]

Solving this equation for \( P \) allows the projection of arbitrary points in the original subspace onto the new subspace using the following formula:
For each grid cell, we used the four pairs of coordinates for relocated quadrat boundary poles in the original and surveyed coordinate system to solve for the projection matrix in eq. B1 and then projected the original tree coordinates onto the new space using eq. B2. We validated our approach by comparing the both the unprojected original tree coordinates and the projected original tree coordinates against the surveyed current coordinates of relocated living trees based on retained tags. The average Euclidean distance between the unprojected original coordinates and the surveyed current coordinates of relocated tagged trees was greater than 7.4 m, whereas the average Euclidean distance between the projected original coordinates and the surveyed current coordinates was only 1.7 m (Appendix A, Fig. A2). We interpreted the dramatic reduction in positional error as evidence that the original grid was distorted and used the projected original coordinates for all estimates of original stem location and subsequent movement in the plot.