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Direct estimates of downslope deadwood movement over 30 years in a temperate 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 down slope 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. While 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 (Pypker 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 (Raška 2012). Logs that are perpendicular to hillslopes and stream channels slow flow rates and limit sediment run out more than parallel logs (Raška 2012). 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 every time 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 (Figure 1). Once on the ground, gradual processes can move deadwood further still. Surface flow may translate logs across the landscape while 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 to over 100 meters. This range is comparable to 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 to other features of the landscape. For instance, Rentsch (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 tree fall. In a Colorado forest, logs point away from prevailing winds as the legacy of unusually destructive blowdowns (Kulakowski and Veblen, 2003). Likewise, Rubino and McCarthy (2003) compared the abundance of deadwood to that of living trees along topographic gradients and found that topography did not influence the strong relationship between the abundance of living and dead trees. While 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 tree fall 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 which 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 (Figure 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 x 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) in the 4-ha plot were identified, tagged and mapped in 1981–1982 (N = 5931 stems) and 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; 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 MOSP east NAD83 projection, we reprojected the DEM data using the “projectRaster” function in the package “raster” v 2.2-12 (Hijmans and van Etten 2010) in R v. 3.0.2 (R Development Core Team 2010) using the proj4 reference, “EPSG:26996” for the plot coordinate system. Initial topographic analyses of the projected DEM data were highly sensitive to fine-scale features. Because our focus was on landscape-level terrain, we smoothed the DEM by applying a 5x5 pixel square Gaussian filter with a sigma value of 1.1 using the function “focalWeight” in the R package “raster”. To validate the accuracy of the smoothed, projected DEM data, we compared the surveyed elevation of 797

reference posts to the estimated elevations at the same locations in the DEM. Surveyed and DEM-derived elevations and were highly correlated (slope = 1.0003 ± 0.0009 [s.e.]; adjusted $R^2 > 0.99$), indicating a highly accurate relationship (Figure S1).

Based on the projected and smoothed DEM, we calculated several terrain indices using WhiteBox GAT v 3.2.0 (Lindsay 2014). We calculated slope and aspect using Horn's 3rd order finite difference method with slope in degrees and aspect as clockwise azimuth with zero at north (Horn 1981). In addition to these basic terrain indices, we also calculated two hydrological indices, total catchment area and flow direction, using the D-infinity method (Tarboton 1997). This method identifies the direction of flow from each cell to one or more downslope neighbors as well as the total upslope catchment area. We computed these indices after removing apparent depressions (Lindsay 2014).

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: (1) down wood ≥ 7 cm in diameter for 1 m with its large end located within the plot boundary, (2) snags ≥ 2 cm DBH, or (3) 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 eight categories based on vertical position, length and apparent origin: (1) *stumps* – suspended deadwood with an intact base and a total length < 2 m; (2) *snags* – suspended deadwood leaning less than 45° from vertical and > 2 m long; (3) *suspended logs* – deadwood leaning more than 45° from vertical with no ground contact for the majority of its total length; (4) *logs* – main boles of a stem with ground contact along the majority of its length; (5) *branches* – distinguished from logs by irregular shape and the absence of a base; (6) *suspended branches* – branches leaning

more than 45° from vertical; (7) *vines* – portions of dead lianas; (8) *deadwood* – any sample that we could not positively assign to other categories. In addition to type, we classified the degree of decay for each 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, Figure 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, asymmetrical breakage), we measured horizontal and vertical diameters at the most basal location with 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 meters, 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. DC 4 & 5, 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. While our goal was simply to reconstruct log volume, our approach parallels methods for estimating volume reduction of dead wood 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 20x20 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 XY coordinates for the large end of each piece using trigonometric identities (Figure 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 1). 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 to

those of snags and branches, respectively. We measured differences in elevation between logs and snags by extracting the elevation at the XY 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 κ 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” v. 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 2). 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 (Figure 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 to 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—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 25x25 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 equal 0.5 and rate equal 2) over the Gaussian-CAR precision. For fitting the models, we used the software OpenBUGS v. 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 non-spatial 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.

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 DC 4 (367), DC 2 (272), DC 5 (115) and DC 1 (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; log centroids occurred lower still with an average elevation of 201.5 m (Fig. 2). Consistent with expectations, logs tended to point downhill (Fig. 3A). While 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 κ test, $df = 1$, $\chi^2 = 10.41$, $p < 0.001$) 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. 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.

The magnitude of the drop in elevation depended on both log and landscape factors (Table S2). Log length was an important predictor of vertical movement, such that bases of longer logs were closer in elevation to the original rooting location, while their centroids occurred much further downhill (Fig. 4 B, C). 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 (Figure 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 vertical movement attributed similar variation to both non-spatial and spatially structured errors (vertical movement at base Gaussian CAR $\sigma = 0.572$, non-spatial $\sigma = 0.426$; vertical movement at centroid Gaussian CAR $\sigma = 0.586$, non-spatial $\sigma = 0.593$).

Compared to vertical movement, horizontal movement was greater in magnitude with a more highly skewed distribution. Bases of logs were relocated between 7 cm and 15.4 m from their coordinates as living trees, with an average horizontal movement of 1.5 meters (Fig. 4D). The centroids of dead trees moved even further, ranging from 9 cm to 14.9 m with an average of 2.5 meters (Fig. 4D). As with vertical movement, the effect of log length on the magnitude of horizontal movement to the base differed from its effect on movement to the centroid. The bases of longer logs occurred closer to the position of the living tree (Fig. 4E), with a doubling of log length corresponding to a 23% decrease in the horizontal movement of the tree base (linear regression, $t = -4.92$, $p < 0.001$). In contrast, the centroids of longer logs occurred further away from the original living tree location (Fig. 4F) with a doubling of log length increasing the horizontal distance to the log centroid by 44% (linear regression, $t = 10.914$, $p < 0.001$) at locations with average slope. Decay class was not among the predictors in the best-fit models for horizontal movement to either the log base or its centroid (Table S2). Spatially explicit models for drivers of horizontal movement attributed more variation to non-spatial errors than spatial errors relative to the log base (horizontal movement at base Gaussian CAR spatial error standard deviation = 0.961, non-spatial error standard deviation = 1.406) but similar amounts of

1 variation in horizontal movement at the centroid (centroid horizontal movement Gaussian CAR σ
2 = 0.578, non-spatial $\sigma = 0.599$).

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

8 Discussion

9 Our results support the hypothesis that deadwood is predictably redistributed downhill as
10 large trees fall. Previous studies of deadwood movement have largely estimated movement
11 indirectly from contemporary location data (e.g. Kulakowski and Veblen 2003, Rubino and
12 McCarthy, Rentsch 2010). In contrast, direct estimates of movement are rare because they
13 require tracking deadwood through time. By quantifying long-term movement from remapped
14 trees, our study provides some of the first direct estimates for the magnitude, direction and
15 drivers of deadwood redistribution at the landscape scale. Logs occurred at lower average
16 elevations than snags and pointed more consistently downhill than branches. Both log bases and
17 centroids occurred at lower elevations than the elevation of the same tree while it was living.
18 Estimated downhill movement was modest, typically less than a meter. However, depending on
19 the shape of the log and the surrounding topography the log centroid moved as much as several
20 meters from its original location since living trees were mapped 30 years ago. Deadwood
21 movement at these small scales may have important implications for forest carbon dynamics in
22 small inventory plots (Russell et al. 2015), nutrient fluxes (Spetich et al. 1999), and biodiversity
23 of organisms that utilize deadwood (Stokland et al. 2012).

1 The relationships between log movement, shape and topography suggest that downhill
2 rotation during tree fall drives most deadwood redistribution across our study site. Consistent
3 with our expectations, the centroids of longer logs dropped further on steeper slopes and the
4 horizontal direction of movement from original rooting location to current log centroid was
5 correlated with slope-aspect as were the overall orientations of all logs on the landscape today.
6 Similarly, an analysis of deadwood recruitment into small streams in conifer-dominated forests
7 of the Pacific Northwest found that large trees were more likely to fall into streams where side
8 slopes were steeper (Sobota et al. 2006). These consistent results from very different systems
9 suggest that the magnitude of deadwood movement with downhill tree fall is often proportional
10 to the size of the tree and the steepness of the slope.

11 The prominent role for downhill treefall at our site may reflect its recent history. In
12 contrast to some mature forests where wind throw is both the major agent of tree mortality and
13 log recruitment (e.g. Kulakowski and Veblen 2003), the forest at our study site is in an
14 intermediate stage of succession and has experienced recent extreme drought (Spasojevic et al.
15 2014). Related self-thinning and water stress tend to form snags that ultimately recruit as logs
16 when mechanical stress exceeds structural resistance (Russel et al. 2015). Both contemporary
17 log orientations and reconstructed movement suggest that downhill failure under gravity felled
18 most snags in this forest up to now. While this mode of log recruitment may not be universal, it
19 may become more important with expected changes to forests in the region. Many hardwood
20 forests in the central United States are recovering from disturbance 80-90 years ago at which
21 point deadwood density tends to increase as canopy trees senesce (Spetich et al., 1999).
22 Senescing trees may be especially vulnerable to mortality with drought which may become more
23 frequent and intense with expected climate change (Bennett et al. 2015). For both of these

reasons, we expect that snag formation and fall will remain an important driver of deadwood dynamics in this and other forests.

In contrast to consistent downhill movement to the log centroid, movement at the base of the tree exhibited different patterns. The bases of longer logs occurred closer to the rooting location of the corresponding living tree, suggesting that inertia may limit translation of large logs. Furthermore, the direction of movement from rooting location to log base was not correlated with slope aspect, much like the orientation of fallen branches, indicating that forces which drive deadwood translation do not always follow the local path of steepest descent on the landscape. However, the bases of logs in more advanced stages of decay occurred at even lower elevations than the bases of less decayed 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 tree fall 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 over one meter from their original rooting locations, calling this assumption into question. 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 program (FIA) samples deadwood in 0.232-ha plots using a regular array of 12 transects, each of which is approximately 7 meters 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 to 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. While most inventories, including FIA, limit bias from non-random 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 tree fall.

Deadwood movement may also complicate efforts to estimate carbon flux from local deadwood pools. Spatially explicit forest carbon 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 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, 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 was 50% faster than on ridgetops (Zanne et al. 2015). Assuming that differences in 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 to 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 tree fall 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 downward 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 tree fall 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, wind thrown 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 density 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 disproportionately 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 which 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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1 **Figure captions**

2 **Figure 1:** Schematic representation of log movement on a hill slope. Log rotation refers to
3 angular movement while translation refers to changes in position without changes in orientation.

4 **Figure 2:** Log centroids occur at lower elevation than snag bases in a 4-ha forest plot. Curves
5 represent kernel-based densities and vertical lines represent means for all deadwood >7-cm
6 diameter for at least one meter.

7 **Figure 3:** Log orientations are concentrated in the downhill direction while branches have
8 random orientations. Circular histograms represent the measured log (panel A) and branch
9 (panel B) orientations. Curves represent kernel-based density and arrows represent concentration
10 parameters for deadwood (black arrow) and landscape (gray arrow).

11 **Figure 4:** Deadwood movement in vertical (panels A-C) and horizontal (panels D-F)
12 dimensions. The bases of long logs occur closer to the location of the living tree, but their
13 centroids occur further away downhill. Log centroids tend to be located further than log bases in
14 both vertical (panel A) and horizontal (panel D) dimensions. Curves in panels A and D represent
15 kernel-based densities. Solid lines in panels B, C, E and F represent best-fit marginal linear
16 regressions and dashed curves represent 95% CIs for the slopes.

17 **Figure 5:** Log bases were mapped at relatively lower elevation when logs were in advanced
18 decay class (panel A) and when living trees grew on steep slopes (panel B). Solid lines represent
19 best-fit marginal linear regressions and the dashed curves represent 95% CIs for the slopes.

20 **Figure 6:** The direction of movement from the location of the living tree base to the location of
21 the log centroid is associated with slope-aspect (panel A) while the direction of movement to the
22 log base is random (panel B). Curves represent kernel-based density and arrows represent the

estimated concentration parameters for the horizontal direction of movement (black arrow) and landscape (gray arrow).

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Appendix 1: Derivations for volume and centroid position formulae

Figure A1: Geometry of a log segment measured with perpendicular diameters (V, H) at two locations (b,a) along its length (L).

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 and horizontal directions at both its base and apex (V_b, H_b, V_a, H_a). 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 :

$$Volume = \pi \int_0^L \left(H_b + \frac{z * (H_a - H_b)}{L} \right) * \left(V_b + \frac{z * (V_a - V_b)}{L} \right) dz \quad (1)$$

$$Volume = \frac{\pi L}{3} \left(H_a V_a + H_b V_b + \frac{1}{2} (H_a V_b + H_b V_a) \right) \quad 13 \quad (2)$$

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:

$$Centroid = \frac{\int_0^L z * (Volume) dz}{Volume} \tag{3}$$

$$Centroid = \frac{L(H_b(V_b + V_a) + H_a(V_b + 3V_a))}{2(H_b(2V_b + V_a) + H_a(V_b + 2V_a))} \tag{4}$$

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 equations (2) and (4). 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 tapes. 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 length.

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 2: coordinate system projective transformation and validation

The research team that established the Tyson Research Center Plot (TRCP) in 1981 deployed a 20 x 20 meter reference grid and calculated tree coordinates assuming that the grid vertices were perfectly rectilinear. The research team that reestablished 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_i with vertices in the original space located at x_1y_1 , x_2y_2 , x_3y_3 and x_4y_4 . The corresponding coordinates in the new space are n_1m_1 , n_2m_2 , n_3m_3 and n_4m_4 . 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]:

$$\begin{bmatrix} x_1 & y_1 & x_1y_1 & 1 \\ x_2 & y_1 & x_2y_2 & 1 \\ x_3 & y_3 & x_3y_3 & 1 \\ x_4 & y_4 & x_4y_4 & 1 \end{bmatrix} * \begin{bmatrix} a & e \\ b & f \\ c & g \\ d & h \end{bmatrix} = \begin{bmatrix} n_1 & m_1 \\ n_2 & m_2 \\ n_3 & m_3 \\ n_4 & m_4 \end{bmatrix} \quad (1)$$

Solving this equation for the transformation matrix [P] allows the projection of arbitrary points in the original subspace onto the new subspace using the formula:

$$\begin{bmatrix} a & b & c & d \\ e & f & g & h \end{bmatrix} * \begin{bmatrix} x_j \\ y_j \\ x_jy_j \\ 1 \end{bmatrix} = \begin{bmatrix} n_j \\ m_j \end{bmatrix} \quad (2)$$

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 eqn (1) and then projected the original tree coordinates onto the new space using eqn (2). 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 over 7.4 meters, while the average Euclidean distance between the projected original coordinates and the surveyed current coordinates was only 1.7 meters (Figure 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.

1 **Figure A2:** The distance between the original coordinates and current coordinates of relocated
2 living stems using the original coordinate system (A) is much greater than the distance using a
3 projection of the original coordinate system that accounts for the observed distortion of the
4 mapping grid observed today (B).

Figure 1:

C Centroid
B Base

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1 Figure 4:

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Figure 5

Figure 6:

Table S1: Model selection statistics for imputing missing dimensional measurements

Model	df	AIC	ΔAIC	rel.lik	Weight
null	2	-1430.01	194.35	0.00	0.00
POS	4	-1452.76	171.60	0.00	0.00
DC[1:5]	6	-1600.85	23.51	0.00	0.00
POS + DC[5]	5	-1611.94	12.42	0.00	0.00
POS + DC[4,5]	5	-1514.51	109.84	0.00	0.00
POS + DC[3,4,5]	5	-1474.24	150.12	0.00	0.00
POS + DC[4:5]	6	-1624.36	0.00	1.00	0.84
POS + DC[1:5]	8	-1621.03	3.32	0.19	0.16

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Table S2: Model selection statistics for factors explaining deadwood movement in the vertical and horizontal dimension. The null model includes only an intercept. DIA represents the horizontal diameter at the log base, LEN represents log length, DC represents Decay Class, TCA represents the natural logarithm of Total Catchment Area, SLO represents slope and dist represents the distance from the base of the log to the reference mapping pole included as a covariate for mapping error

model	df	VERTICAL				HORIZONTAL			
		BASE		CENTROID		BASE		CENTROID	
		AIC	ΔAIC	Weight	AIC	ΔAIC	Weight	AIC	ΔAIC
Null	2	646.15	26.15	0.00	978.50	92.89	0.00	1110.6	36.18
DIA	3	647.45	27.44	0.00	967.92	82.30	0.00	1104.7	30.31
log(LEN)	3	636.36	16.35	0.00	966.03	80.42	0.00	1090	15.61
DC	3	643.77	23.76	0.00	979.76	94.15	0.00	1111.8	37.38
TCA	3	646.33	26.32	0.00	978.24	92.63	0.00	1112.6	38.18
SLO	3	625.70	5.69	0.03	920.45	34.83	0.00	1109.6	35.14
dist	3	648.15	28.15	0.00	979.50	93.88	0.00	1096.2	21.79
DIA + dist	4	649.45	29.44	0.00	968.98	83.36	0.00	1090.4	15.94
log(LEN) + dist	4	638.36	18.35	0.00	966.92	81.31	0.00	1074.4	0.00
DC + dist	4	645.77	25.76	0.00	980.78	95.17	0.00	1097.3	22.87
TCA + dist	4	648.33	28.32	0.00	979.15	93.54	0.00	1098.2	23.76
SLO + dist	4	627.69	7.68	0.01	921.70	36.09	0.00	1094.7	20.26
SLO x log(LEN)	5	620.39	0.39	0.36	885.61	0.00	0.69	1092.7	18.24
DC + log(LEN) + SLO	5	620.01	0.00	0.43	896.33	10.71	0.00	1092.7	18.22
DC + log(LEN) + SLO + dist	6	621.99	1.98	0.16	897.49	11.87	0.00	1076.8	2.32

Figure S1: Validation of DEM-based elevations using independently surveyed elevation at 797 reference grid poles in the 25-ha Tyson Research Center Forest Dynamics Plot. Red line is 1:1.

Figure S2: Map of the distribution of coarse woody debris in the 4-ha Tyson Forest Dynamics plot. Hill shade represents slope aspect as calculated from a LiDAR-based DEM with north as white and south as black. Logs are represented as line segments with perpendicular bars at their bases. Snags are represented by filled circles.