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Estimates of downed woody debris decay class transitions for forests across the eastern United States

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ABSTRACT

Large-scale inventories of downed woody debris (DWD; downed dead wood of a minimum size) often record decay status by assigning pieces to classes of decay according to their visual/structural attributes (e.g., presence of branches, log shape, and texture and color of wood). DWD decay classes are not only essential for estimating current DWD biomass and carbon stocks, but may also facilitate the prediction of future DWD attributes. Estimating temporal transitions between decay classes may provide a mechanism for projecting DWD attributes in forest ecosystems. To date, modeling decay class transitions for individual DWD pieces has not been fully explored in this context. The goal of this study was to use a repeated DWD inventory across the eastern US to estimate decay class transitions to inform DWD dynamics across this broad geographic region.

Using matched and non-matched DWD from the repeated inventory, ordinal regression techniques were used to estimate the five-year probability of a DWD piece remaining in the same decay class or moving into more advanced decay classes. Models indicated that these transitions were largely related to DWD piece length and climatic regime, as transitions occurred more slowly for longer DWD pieces located in regions with a low number of degree days (a climatic variable serving as a proxy for decomposition potential). Cumulative link mixed models allowed the estimation of forest type-specific effects (i.e., random effects) on the DWD transition process. Hardwood species transitioned into subsequent decay classes more rapidly than softwoods. Model assessments indicated that the correct decay class observed after five years was correctly predicted for approximately 50–70% of observations, but was dependent on forest type and initial decay class.

Results differed depending on the models under examination. For example, using the matched data, the average number of classes moved per five years was 1.28 ± 0.07 (mean $\pm$ SE) classes for decay class 1 logs found in spruce-fir forests, however, using the matched plus non-matched data, the average number of classes moved per five years was 3.51 ± 0.19 for these same logs. These two model sets (matched and matched plus non-matched DWD pieces) may denote upper and lower bounds for DWD decay class transition rates. Analyses presented herein provide an initial assessment of DWD decay across eastern US forests and thus provide quantitative tools that apply to emerging bioenergy questions and associated DWD dynamics research. Developed models, coupled with traditional forest productivity simulation tools, may be used in the future to determine accurate estimates of future forest C stocks.

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1. Introduction

Forest ecosystems and their management have become a central focus of global strategies aimed at reducing greenhouse gas (GHG) emissions and possibly mitigating future climate change effects (Ryan et al., 2010; Malmsheimer et al., 2011; McKinley et al., 2011). Forests may reduce GHG emissions by sequestrating carbon (C) through afforestation, wood substitution in building materials, and substitution of forest-derived bioenergy for fossil fuels (Malmsheimer et al., 2008; Malmsheimer et al., 2011). In contrast, forests may contribute to GHG emissions through deforestation and/or management activities that inadvertently promote reduced C storage (Ryan et al., 2010). Given the complex pathways of C emissions/sequestration associated with forest ecosystems, there are substantial knowledge gaps regarding C implications of forest management activities (Malmsheimer et al., 2011; McKinley et al., 2011).

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In particular, the fate of downed woody debris (DWD; downed dead wood of a minimum size) has emerged as a knowledge gap hampering our ability to fully evaluate temporal changes in forest C pools (Birdsey et al., 2006) and implications of expanded bioenergy production from harvest residues (MCCS, 2010; Lippke et al., 2011). Since DWD C stocks represent a balance between accretion (e.g., tree mortality) and depletion (e.g., combustion; decay), the DWD C pool may appear relatively stable over long time periods. Examples here might include forests with no disturbances and contain slowly decaying DWD pieces. In contrast, some forests may experience dramatic changes in DWD stocks over very short periods of time. Examples here include forests that see rapid DWD inputs (e.g., combustion; harvest) or losses (e.g., biomass harvest; DWD undergoing rapid decay). Residence time, defined as the duration that a DWD piece remains in a given decay class, is an important aspect of forest C stock dynamics as it reflects respiration and C flux rates from DWD and measures losses from the DWD biomass and C pools. Despite its importance, limited information exists on DWD dynamics for most forest types (Harmon et al., 2011a). As a result, quantifying the fate of these DWD pieces through time has emerged as a substantial knowledge gap associated with deadwood ecology and C accounting.

A decay class matrix model, also termed the "stage-based" model, has been used to estimate the time it takes for a DWD piece to transition into subsequent decay classes or to leave the DWD pool (Kruys et al., 2002; Aakala, 2010, 2011). However, there are two limitations of using the stage-based approach for quantifying DWD residence at large spatial scales. First, time since death for DWD pieces is often obtained through detailed dendrochronological analyses. Although this provides a comprehensive assessment of individual log dynamics, substantial time and effort would be required to collect such detailed information as part of large-scale forest inventories or in ecosystems in which accurate dendrochronological data across tree species cannot be obtained. This challenge is reflected in the nature of previous studies that have modeled individual log dynamics, as they have been based on data collected from a limited number of sites and a few select species. As examples, Aakala (2010) collected data on DWD pieces of a single species at three locations, while Kruys et al. (2002) sampled from 21 stands, but collected data only from one species found in a specific stand type. Second, these models often rely on site- and species-specific mean residence times of DWD in each decay class. These variables are likely absent from large-scale DWD assessments, such as national forest inventories, which favor field protocols covering a wide range of species, ecosystems, and geographic scales.

Ordinal regression techniques have become an attractive method for modeling deadwood dynamics through their ability to incorporate the ordered nature of deadwood in various stages of decay (Bater et al., 2009; Eskelson et al., 2012; Russell et al., 2012). To be effective for integration into life cycle assessments and quantifying forest C dynamics across wide geographic regions, models of DWD dynamics would gain from incorporation of large-scale forest inventory data from remeasured permanent sample plots that employ a hierarchy of information related to DWD decay. This hierarchy might range from the forest type and climate conditions (i.e., forest-level), to the DWD piece attributes (log-level).

As the monitoring of downed deadwood across the US has been conducted for over a decade (Woodall and Monleon, 2008), a DWD piece matching algorithm (individual DWD pieces from a subsequent inventory were matched with a previous inventory) was recently developed to utilize data collected from a national forest inventory to inform DWD dynamics (Woodall et al., 2012). This algorithm resulted in remeasurement of a series of permanent sample plots across the eastern US, presenting a unique dataset to quantify DWD decay class transitions. Aside from the traditional years since death and residence time variables (e.g., Kruys et al., 2002; Aakala, 2010), DWD decay rates have been modeled in relation to climate and/or geographic locale (Yin, 1999; Mackensen et al., 2003; Radtke et al., 2009; Zell et al., 2009), DWD size (Mackensen et al., 2003), and species (Zell et al., 2009). The question of which of these and other variables influence DWD decay class transitions for forests across the eastern US remains unanswered.

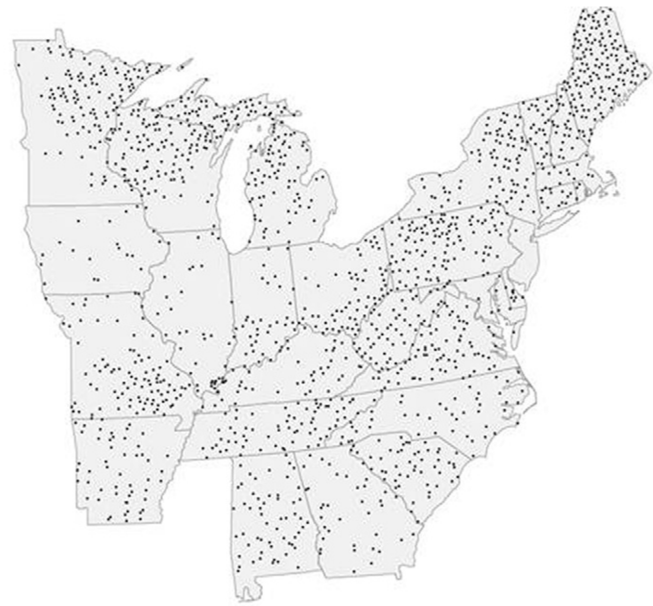

Fig. 1. Approximate locations of inventory plots across eastern US where downed woody debris pieces were assessed, 2002–2010.

The primary goal of this study was to quantify DWD decay class transitions across forests in the eastern US for the purpose of projecting future DWD biomass and C dynamics. Specific objectives were to: (1) analyze a dataset of matched and non-matched DWD pieces from a repeated DWD inventory to determine the variability in DWD attributes across eastern US forests, (2) develop and assess a DWD decay class transition model that can be applied to varying climatic conditions, forest types, and species groups, and (3) apply the transition model to estimate DWD residence times in eastern US forests.

2. Methods

2.1. Study area

Forests of the eastern US are diverse, ranging from hemlock-white pine-northern hardwood (north), oak-hickory (west), and southern pine forests (south and east) (Braun, 1950). The study area ranged eastward from the state of Minnesota to Maine in the north to Louisiana and Georgia in the south, spanning 18° of latitude and 29° of longitude (Fig. 1). Mean annual temperatures range from 1.4 to 19.8 °C and precipitation from 55 to 201 cm (Table 1). Assignment of forest types in the USDA Forest Service's Forest Inventory and Analysis (FIA) program was developed using historical FIA data, forest type lists obtained from the Society of American Foresters, and FIA typing algorithms (Woudenberg et al., 2010). Seventy-five forest types were identified that represented 14 broader forest type groups. Forest types with the largest number of DWD observations were observed in the sugar maple-yellow birch-beech, white oak-red oak-hickory, and aspen types (n = 691, 502, and 212, respectively).

Table 1
Summary statistics for climatic conditions of inventory plots across eastern US where downed woody debris pieces were assessed.

Scale	Variable[a]	Mean	SD	Min	Max
Hardwoods					
Forest type			$n = 68$		
Plot[b]			$n = 1261$		
	MAT (°C)	8.6	3.9	1.4	19.8
	MAP (cm)	104.4	21.0	55.4	200.5
	DD5 (>5 °C)	2491.6	797.4	1104.0	5415.0
Softwoods					
Forest type			$n = 62$		
Plot[b]			$n = 592$		
	MAT (°C)	7.4	4.9	1.4	19.8
	MAP (cm)	105.3	22.1	62.4	185.1
	DD5 (>5 °C)	2304.3	1018.9	1104.0	5415.0

[a] Variables are mean annual temperature (MAT), mean annual precipitation (MAP), and number of degree days (DD5).
[b] Climate data obtained from USDA Forest Service (2012).

2.2. Data

The FIA program is responsible for inventorying forests of the US, including both standing trees and dead wood on permanent sample plots established across the US using a three phase inventory (Bechtold and Patterson, 2005). During the inventory's first phase, sample plot locations are established at an intensity of approximately 1 plot per 2400 ha. If the plot lies partially or wholly within a forested area, field personnel visit the site and establish a second phase inventory plot. These plots consist of four 7.32-m (24.0-ft) fixed radius subplots for a total plot area of approximately 0.07 ha where standing tree and site attributes are measured (Fig. 2).

During FIA's third phase, a subset of plots (approximately one of every 16 phase two plots in this study) is sampled for downed woody materials including DWD. Downed woody pieces are defined as downed woody debris in forested conditions with a diameter greater than 7.62 cm (3.0 in.) along a length of at least 0.91 m (3.0 ft) and a lean angle greater than 45° from vertical (Woodall and Monleon, 2008). Dead woody pieces with a lean angle less than 45° from vertical are considered standing dead trees (i.e., snags) and were not included in this study. DWD pieces are sampled on each of three 7.32-m horizontal distance transects radiating from each FIA subplot center at azimuths of 30, 150, and 270°, totaling 87.8 m for a fully forested inventory plot. Data collected for every DWD piece include location information (i.e., plot, subplot, and transect number; horizontal distance along a sampling transect from subplot center to DWD location) and individual piece attributes (transect diameter, small-end diameter, large-end diameter, decay class [DC], length, and species). Transect diameter is the diameter of a DWD piece measured perpendicular to its center longitudinal axis at the point of intersection with a sampling transect. Length is defined as the total length of the DWD piece between the small- and large-end diameter measurements. Decay class is a subjective determination of the amount of decay present in an individual DWD piece summarized across its entirety. A DC of one is the least decayed (freshly fallen log), while a DC of five is an extremely decayed log (Sollins, 1982; Waddell, 2002; Harmon et al., 2008) (Table 2). The species of each fallen log is identified through determination of species-specific bark, branching, bud, and wood composition attributes. For DC5 pieces, species is not identified and

Table 2
Downed woody debris decay class definitions.

Decay class	Observed in	Structural integrity/description	Texture of rotten portions	Color of wood	Invading roots	Branches and twigs
1	Field	Sound, freshly fallen, intact logs	Intact, no rot; conks of stem decay absent	Original	Absent	If branches are present, fine twigs are still attached and have tight bark
2	Field	Sound	Mostly intact; sapwood partly soft (starting to decay) but cannot be pulled apart by hand	Original	Absent	If branches are present, many fine twigs are gone and remaining fine twigs have peeling bark
3	Field	Heartwood sound; piece supports its own weight	Hard, large pieces; sapwood can be pulled apart by hand or sapwood absent	Reddish-brown or original	Sapwood only	Branch stubs will not pull out
4	Field	Heartwood rotten; piece does not support its own weight, but maintains its shape	Soft, small blocky pieces; a metal pin can be pushed into heartwood	Reddish or light brown	Throughout	Branch stubs pull out
5	Field	None, piece no longer maintains its shape, it spreads out on ground	Soft; powdery when dry	Red-brown to dark brown	Throughout	Branch stubs and pitch pockets have usually rotted down
5+	Office	Piece is non-matched OR non-detectable, IF it was observed at an initial measurement	–	–	–	–

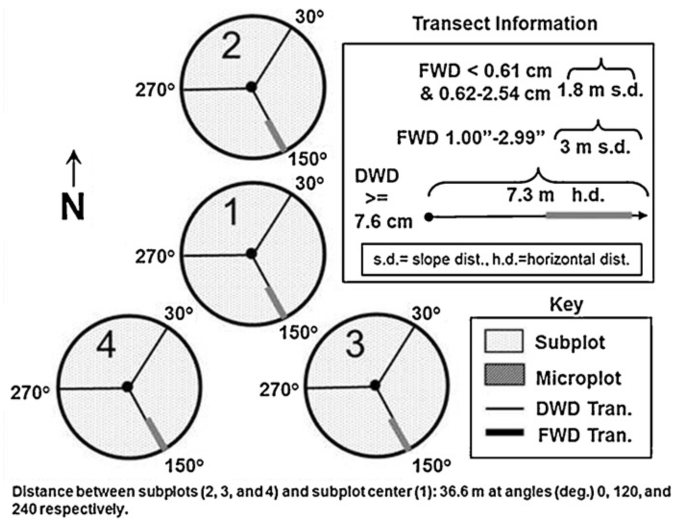

Fig. 2. Plot-level sample design for the USDA Forest Service Forest Inventory and Analysis monitoring of downed woody debris, 2002–2010.

end diameters are not measured to gain field efficiency. All remeasured FIA plots in the eastern US where DWD was measured were included in this study (Fig. 1). Plots were initially measured in 2002 or soon thereafter, then were remeasured on an average of 5 years later (Woodall et al., 2012). The final remeasurements occurred in 2010. Nearly 10,700 DWD pieces were measured at time one (T_1) and over 11,000 DWD pieces measured at time two (T_2). For further details regarding FIA's inventory, see Woodall and Monleon (2008) and Woodall et al. (2010).

2.3. Estimating matched DWD pieces

A matching algorithm was used in this study to match DWD pieces sampled along FIA transects at T_1 with probable DWD pieces sampled along the same transect at T_2 (Woodall et al., 2012). In short, the algorithm consisted of three steps. First, the plot, subplot, and transect number were aligned in an attempt to relocate pieces measured at T_1 and T_2. Second, individual piece metrics (e.g., large-end diameter and decay class) were ranked on a scale from ideal- to no-match. In this approach, ideal matches were defined as DWD pieces at T_2 that were not only in the same spatial location as T_1, but also ideally matched the individual metrics of T_1 pieces. Third, a scoring index of DWD attributes was developed that acknowledged inherent decay class and measurement errors intrinsic with such a large-scale inventory (Westfall and Woodall, 2007). This index ranked individual DWD piece metrics as ideal (score = 1), potential (score = 0.5), or non-matched (score = 0). The product of these scores resulted in the scoring index. For most forest type groups, this study's algorithm matched between 20% and 40% of DWD pieces between inventories. In addition, the matching index provided an objective method for selecting one match from a list of "one to many" DWD matches.

Hereafter, we define the collection of the matched DWD pieces as the "matched data" (M), the collection of DWD pieces measured initially which failed to be matched with remeasured pieces as the "non-matched data" (NM), and both datasets combined as the "matched plus non-matched data" (M + NM). Datasets were comprised of 3579 M and 10,837 M + NM pieces. The proportion of hardwood species was 0.65 and 0.60 for the M and M + NM data respectively. For hardwood species observed at T_1 for the M + NM data, mean large-end diameter and length for DWD pieces was 18.3 ± 8.8 cm (mean ± SD) and 5.7 ± 5.1 m, respectively. For softwoods these same values were 18.5 ± 8.8 cm and 6.3 ± 5.5 m, respectively. Modeling efforts employed data from 1095 and 1516 FIA plots for the M and M + NM datasets, respectively.

2.4. Modeling DWD decay class transitions

Stage-based matrix models developed by Kruys et al. (2002) predict the five-year probability of deadwood advancing from one decay class to another. Using this approach, DWD pieces in DC i can either (1) remain in the same class i, (2) move to DC $i+1$, or (3) move to DC $i+2$. In analyses that use either known (e.g., Kruys et al., 2002; Aakala, 2011) or estimated time since death (e.g., Russell and Weiskittel, 2012), calculation of the mean residence time that a DWD piece remains in a given DC is a key attribute of the stage-based model. Hence, calculation of mean residence time is straightforward in these approaches because the number of years since death is known. In the FIA data, however, year of death for DWD pieces is not determined. Hence, we sought a modeling approach that estimates DWD DC transition independent of residence time.

Cumulative link models (CLMs) are a type of ordinal regression model in which response variables are considered categorical or ordered (Agresti, 2007). First, we considered the M dataset, where the DC was noted in any of the $k = 5$ decay class codes for each DWD piece i. In the cumulative link model, the probability of DWD_i moving through each of the successive k decay classes (DC1, DC2, DC3, DC4, DC5, respectively) was modeled as cumulative probabilities (γ_k), such that:

$$\begin{aligned}
&P(k=\text{DC1}) = \pi_{\text{DC1}} = \gamma_1\\
&P(k=\text{DC1 or DC2}) = \pi_{\text{DC1}} + \pi_{\text{DC2}} = \gamma_2\\
&P(k=\text{DC1 or DC2 or DC3}) = \pi_{\text{DC1}} + \pi_{\text{DC2}} + \pi_{\text{DC3}} = \gamma_3\\
&P(k=\text{DC1 or DC2 or DC3 or DC4}) = \pi_{\text{DC1}} + \pi_{\text{DC2}} + \pi_{\text{DC3}} + \pi_{\text{DC4}} = \gamma_4\\
&P(k=\text{DC1 or DC2 or DC3 or DC4 or DC5}) = \pi_{\text{DC1}} + \pi_{\text{DC2}} + \pi_{\text{DC3}} + \pi_{\text{DC4}} + \pi_{\text{DC5}} = \gamma_5
\end{aligned} \tag{1}$$

Cumulative probabilities were then estimated by:

$$\text{logit}(\gamma_{ik}) = \theta_k - \mathbf{x}_i^T \boldsymbol{\beta} + \varepsilon_i \tag{2}$$

where θ_k is the intercept term for DC k (also termed a threshold or cut-point), $\mathbf{x}_i$ is a vector of independent variables for the ith DWD observation, $\boldsymbol{\beta}$ is the corresponding set of parameters to be estimated, and $\varepsilon_i \sim N(0,\sigma^2)$ is the random parameter.

To examine the extent to which decay class transitions were influenced by a host of variables, thirty-year (1961–1990) climate data were obtained by specifying latitude, longitude, and elevation of each FIA plot location to a spline surface model developed from climate station data across forests of North America (Rehfeldt, 2006; USFS, 2012). As a measure of decomposition potential across the study plots, the number of degree days greater than 5 °C (DD5), coupled with the length of the DWD piece (LEN; m) and DC as measured at T_1, were used to estimate the DWD DC transitions for the M data. Incorporating additional climate variables into the modeling framework (e.g., growing season precipitation, length of frost-free period, mean annual temperature/precipitation) and various measures of DWD piece size (e.g., large-end diameter, combined variable of large-end diameter squared multiplied by length) did not reduce Akaike's information criteria and log-likelihood values. The mixed CLM model was parameterized to incorporate variability that may be attributed to the FIA forest type (ForType) in which the DWD piece resides. Hence, the final model fitted to the M data was:

$$\text{logit}(\gamma_{ikj}) = \theta_k - \beta_1\text{DD5} - \beta_2\text{LEN} - u(\text{ForType}_j) \tag{3}$$

where parameters were fitted using maximum likelihood with the Laplace approximation (Azevedo-Filho and Shachter, 1994). The random effect $u(\text{ForType}_j)$ was specified to represent forest type-specific effects on the transition process and is assumed to be random and independent and identically distributed such that $u(\text{ForType}_j) \sim N(0, \sigma_j^2)$. Likelihood ratio tests concluded that incorporating forest type as a random effect was significant and thus appropriate to use in the model built from the M data. To lend some specificity to species groups, model parameters for hardwoods and softwoods were estimated separately. Estimated random effects were graphed against key physiographic variables such as latitude, longitude, elevation, slope and aspect (each of which was computed as the mean value within each forest type) to identify factors determining DC transitions.

For the M + NM data, alternative strategies were needed to model DWD DC transition. Of considerable importance was the fate of the NM pieces, which made up a considerable amount of observations depending on forest type group (e.g., 84% for the oak/gum/cypress forest type group; Woodall et al., 2012). For DWD pieces that were not matched via the algorithm, we employed an office-assigned DC for the T_2 measurement that followed DC5. This class, termed DC5$^+$, was defined as a DWD piece that was measured at T_1, but was either non-matched or non-detectable when the FIA plot was revisited at T_2 (Table 2). Although a piece assigned a DC5$^+$ may have undergone a multitude of pathways, including (1) complete decomposition, (2) fragmenting in length and now being below the minimum FIA size threshold, or (3) being measured with error such that they did not pass through the matching algorithm, the NM data likely provide insight into DWD DC transitions that may not be observed when analyzing the M data solely.

For modeling the M + NM data, the introduction of DC5$^+$ warranted a sixth categorical variable into which a DWD piece could transition. Hence, Eq. (1) resulted in:

$$P(k = \text{DC1} \;\text{ or }\; \text{DC2} \;\text{ or} \ldots \text{or }\; \text{DC5}^+)$$
$$= \pi_{\text{DC1}} + \pi_{\text{DC2}} + \cdots + \pi_{\text{DC5+}} = \tau_{5+} \tag{4}$$

to reflect the additional DC5$^+$ category. The M + NM data also required a change in how species groups were handled. As the FIA program does not identify the species for DC5 pieces and such pieces were more common in the M + NM data (14% of all observations) compared to the M data (2%), an indicator variable I was used to represent a species group:

$$\begin{aligned} I_{\text{HW}} &= 1 \quad \text{if hardwood}, \quad 0 \quad \text{otherwise}; \\ I_{\text{SW}} &= 1 \quad \text{if softwood}, \quad 0 \quad \text{otherwise}; \\ I_{\text{NO-ID}} &= 1 \quad \text{if non-identified}, \quad 0 \quad \text{otherwise} \end{aligned} \tag{5}$$

A mixed CLM model was initially parameterized to the M + NM data (similar to Eq. (3)), however, likelihood ratio tests concluded that incorporating forest type as a random effect was insignificant and thus, we excluded it from the final model, expressed as:

$$\text{logit}(\tau_{ik}) = \phi_k - \varphi_1\text{DD5} - \varphi_2\text{LEN} - \varphi_3 I_{\text{HW}} - \varphi_4 I_{\text{SW}} \tag{6}$$

where ϕ_k is the intercept term for DC k (k = 1, 2, 3, 4, 5, 5+), φ_1–φ_4 are parameters estimated with the CLM model, and all other variables are as previously defined.

We present models built on the M and M + NM data to represent lower and upper bound estimates, respectively, of DWD DC transition. Models built with the M + NM data as opposed to the M data alone likely provide a more rapid transition of DC due to the large amount of DWD pieces that were coded as DC5+. As mentioned above, the NM pieces may have decomposed completely or to the point their size attributes fell below measurement thresholds. In contrast, DC predicted using models designed with the M data are likely to occur at slower transition rates due to (1) the reliability in matching subsequent measurements of individual pieces, (2) the supposition that these DWD pieces were not fully decomposed, and (3) the absence of DC5+ pieces. The 'ordinal' package in R (Christensen, 2012) was used for fitting the models described here.

2.5. Analyzing model performance

To examine the performance of the developed models, Eqs. (3) and (6) were applied to the M and M + NM datasets, respectively. In this approach, the five-year probability of a DWD piece remaining in the same DC or advancing into subsequent DCs was predicted using each respective model. We considered the most likely DC that a DWD piece would be observed in at T_2 as the DC displaying the highest predicted probability. The proportion of predictions in which the model correctly predicted the DC at T_2 was computed, as well as the proportion of predictions in which the model correctly predicted transitions to within one DC.

To determine the transition rates of DWD pieces, a random number (0,1) from a uniform distribution was drawn for each DWD piece. If the random number was less than or equal to the predicted probability of remaining in the same DC, it remained in the same class (i.e., the number of decay classes moved per five years was 0). If the random number fell between the predicted probability of remaining in the same DC and the cumulative probability of remaining in the same DC or advancing one DC, it moved one class. This process was applied iteratively through all classes to calculate a five-year probability of a DWD piece moving to each stage of decay. The mean number of classes moved per five years was calculated by DC for each species group, length size class, and forest type.

3. Results

3.1. Factors influencing DWD decay class transition

Model results suggest that DWD in climates with a greater number of degree days transition more rapidly than their low degree day counterparts (Table 3). To illustrate this effect, consider a hardwood DWD piece in two different climates: the 10th and 90th quantiles of degree days observed in the M data. At these respective quantiles, the cumulative probability that a DC1 piece would remain in DC1 or transition to DC2 in five years was 0.364 and 0.250, respectively (Table 4). Softwoods were predicted to transition at a slightly lower rate than hardwoods for a fixed DWD piece length (e.g., at a low number of degree days, softwoods would remain in DC1 with a 0.053 probability compared to a 0.017 probability for hardwoods). Longer DWD pieces would transition into subsequent decay classes at a lower rate than shorter pieces, as indicated by the significant negative term in Eqs. (3) and (6). Random effects from the mixed models (Eq. (3)) exhibited no correlation with key physiographic features of the inventory plot including latitude, longitude, slope, aspect, or elevation.

Table 3
Parameter estimates (standard errors in parentheses) for ordinal regression models predicting downed woody debris decay class transitions for forests in the eastern US, separated by hardwoods and softwoods.

	Parameter[a]	Estimate	Threshold	Estimate
		Hardwoods		
Matched data[b]	θ_2	0.346 (0.157)	1|2	−3.739 (0.361)
	θ_3	1.887 (0.156)	2|3	−0.213 (0.243)
	θ_4	5.132 (0.253)	3|4	3.213 (0.258)
	DD5	2.995e−4 (7.40e−5)	4|5	7.607 (0.338)
	LEN	−2.464e−2 (8.62e−3)		
		Softwoods		
	θ_2	1.583 (0.295)	1|2	−2.637 (0.532)
	θ_3	3.733 (0.313)	2|3	1.008 (0.445)
	θ_4	7.793 (0.452)	3|4	4.940 (0.465)
	DD5	2.928e−4 (1.34e−4)	4|5	10.075 (0.583)
	LEN	−2.696e−2 (1.18e−2)		
		All species		
Matched + non-matched data[c]	ϕ_2	0.0520 (0.0855)	1|2	−7.376 (0.272)
	ϕ_3	0.329 (0.0809)	2|3	−4.189 (0.175)
	ϕ_4	1.547 (0.0933)	3|4	−2.206 (0.170)
	ϕ_5	2.042 (0.345)	4|5	−1.635 (0.169)
	DD5	3.122e−4 (2.58e−5)	5|5+	−1.593 (0.169)
	LEN	−6.289e−2 (4.17e−3)		
	I_{HW}	−1.896 (0.135)		
	I_{SW}	−1.212 (0.138)		

[a] Variables: Number of growing degree days > 5 °C (DD5); length of DWD piece in m (LEN); indicator variable for hardwood (I_{HW}) or softwood (I_{SW}) species.
[b] Model: $\text{logit}(\gamma_{ikj}) = \theta_k - \beta_1 \text{DD}_5 - \beta_2 \text{LEN} - u(\text{ForType}_j)$; see supplementary material for predicted random effects for u_j term for forest type.
[c] Model: $\text{logit}(\tau_{ik}) = \phi_k - \varphi_1 \text{DD}_5 - \varphi_2 \text{LEN} - \varphi_3 I_{HW} - \varphi_4 I_{SW}$.

3.2. DWD model performance

Model performance depended on the forest type group of interest and initial decay class. Averaged across all forest types, the proportion of softwood observations in which the model correctly predicted the DC at T_2 was 0.54 and 0.62 for the M and M + NM models, respectively. The performance of the models for hardwood observations was slightly better, as this proportion was 0.61 and 0.65 for the M and M + NM models, respectively. For the M data, nearly all observations were predicted to within ±1 DC (≥0.96 of all observations), however, for the M + NM data, predictions were only improved by 4 and 1% for hardwoods and softwoods, respectively, after comparing predictions that correctly predicted the DC at T_2 to those that predicted DC to within ±1 DC. When analyzed within initial DCs, the proportion of observations that correctly predicted DC at T_2 ranged from 0.42 to 0.64 and from 0.53 to 0.65 for the M and M + NM models, respectively (Table 5).

For DC1 pieces in the M data, the average number of classes moved per five years was as low as 1.28 ± 0.07 (mean ± SE) classes for spruce-fir forests and as high as 1.95 ± 0.11 classes for loblolly-shortleaf pine forests. In contrast, for DC1 pieces in the M + NM data, the average number of classes moved per five years was as low as 3.37 ± 0.17 classes for aspen-birch forests and as high as 4.31 ± 0.19 classes for white-red-jack pine forests. For the M data, similar minimum and maximum values observed by forest type were predicted for DC3 pieces. However, for the M + NM data, the average number of classes moved per five years for DC3 pieces was as low as 1.62 ± 0.07 classes for aspen-birch forests and as high as 2.44 ± 0.09 classes for loblolly-shortleaf pine forests (Fig. 3). For both the M and M + NM data, there was little difference between the average

Table 4
Example of downed woody debris decay class transitions using the average piece length and the 10th and 90th percentile degree days for the matched dataset, separated by hardwoods and softwoods.

Hardwoods													
Degree days = 1638; length = 5.8 m							Degree days = 3438; length = 5.8 m						
		To class							To class				
		1	2	3	4	5			1	2	3	4	5
From class	1	0.017	0.347	0.583	0.053	0.001	From class	1	0.010	0.240	0.661	0.088	0.001
	2		0.288	0.638	0.074	0.001		2		0.191	0.688	0.120	0.002
	3			0.727	0.269	0.005		3			0.608	0.384	0.008
	4				0.894	0.106		4				0.830	0.170
	5					1		5					1
Softwoods													
Degree days = 1423; length = 6.1 m							Degree days = 3520; length = 6.1 m						
		To class							To class				
		1	2	3	4	5			1	2	3	4	5
From class	1	0.053	0.628	0.311	0.009	0	From class	1	0.029	0.506	0.448	0.017	0
	2		0.304	0.653	0.043	0		2		0.191	0.732	0.076	0
	3			0.722	0.276	0.002		3			0.584	0.411	0.004
	4				0.884	0.116		4				0.805	0.195
	5					1		5					1

Table 5
Evaluations of decay class transition models by forest type group and initial decay class for downed woody debris pieces eastern US forests (n is the number of observations, DC is the proportion of observations for which the model predicted the correct decay class, and DC ± 1 is the proportion of observations for which the model predicted the correct decay class to within one class).

	Matched						Matched + non-matched					
	Hardwoods			Softwoods			Hardwoods			Softwoods		
	n	DC	DC ± 1	n	DC	DC ± 1	n	DC	DC ± 1	n	DC	DC ± 1
Forest type												
Aspen/birch	211	0.58	0.99	119	0.58	0.98	583	0.57	0.61	317	0.61	0.62
Elm/ash/cottonwood	112	0.61	1.00	24	0.67	0.96	366	0.67	0.70	60	0.60	0.62
Loblolly/shortleaf pine	8	0.88	1.00	58	0.60	0.97	61	0.87	0.87	228	0.71	0.75
Maple/birch/beech	723	0.56	0.98	209	0.56	0.99	1893	0.57	0.61	447	0.51	0.52
Oak/gum/cypress	23	0.65	1.00	10	0.30	1.00	123	0.82	0.82	57	0.82	0.82
Oak/hickory	1066	0.57	0.98	149	0.52	0.99	2869	0.61	0.64	385	0.62	0.63
Oak/pine	59	0.53	0.97	101	0.52	0.96	207	0.67	0.69	255	0.60	0.62
Spruce/fir	55	0.40	0.98	379	0.54	0.99	154	0.47	0.56	855	0.53	0.53
White/red/jack pine	31	0.68	1.00	83	0.53	1.00	84	0.64	0.68	187	0.55	0.55
Initial decay class												
1	66	0.56	0.98	64	0.55	0.97	598	0.55	0.57	154	0.57	0.57
2	284	0.57	0.98	277	0.56	0.98	1603	0.62	0.64	599	0.53	0.53
3	500	0.59	0.98	495	0.64	0.99	2735	0.60	0.62	1189	0.57	0.58
4	310	0.52	1.00	309	0.42	1.00	1507	0.64	0.71	908	0.65	0.67
5	–	–	–	–	–	–	13	0.00	0.62	26	0.00	0.08

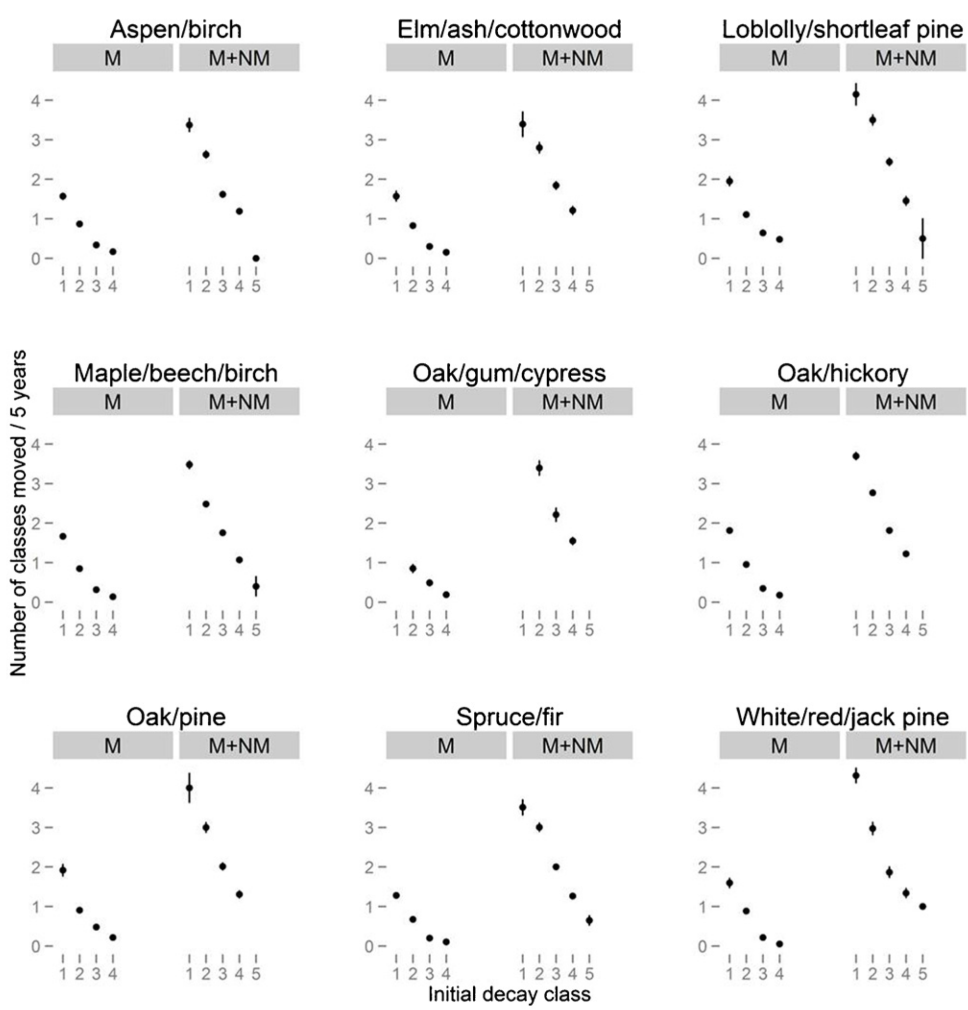

Fig. 3. Mean number of decay class moved per 5 years (with standard errors) by initial decay class for matched (M) and matched plus non-matched (M + NM) models predicting downed woody debris decay class transitions by forest type group.

number of classes moved per five years between long (DWD piece length ≥ mean DWD length) and short (DWD piece length < mean DWD length) DWD pieces when separated by species group.

4. Discussion

Our DC transition models can be used to quantify the degree to which DWD transitions from one class to successive classes. Given the importance that DC plays in estimating the biomass and C content of deadwood (Harmon et al., 2011b), understanding the probabilities of transition between successive decay classes is crucial for modeling temporal changes in DWD biomass and C stocks. Using a dataset compiled from a large-scale repeated (five-year time step) DWD inventory of matched and non-matched DWD pieces, DC transition models were developed that can be applied across eastern US forests. As the selection of matched DWD pieces provided some level of subjectivity and not all pieces were matched (up to 40% depending on forest type group; Woodall et al., 2012), the M model (Eq. (3)) may provide a lower-bound (e.g., "conservative" estimate) of DWD DC transition. Conversely, as non-matched pieces may have decayed after five years to the point that they were non-detectable, or may have degraded to the point that they fell below the sampling thresholds (e.g., diameter < 7.62 cm; length < 0.91 m), the M + NM model (Eq. (6)) could provide an upper-bound (e.g., "liberal" estimate) of DWD DC transition. Methodologies developed here could be used to inform DWD dynamics in areas such as life cycle assessments, forest fuel-load reductions through time, and ecological simulation models. Which of these estimates (i.e., upper and lower bound) is used for examining DWD dynamics will depend largely on the questions being asked. For example, estimates derived from the M model may be more suitable for informing questions related to DWD decay and residence time given their reliance on resampled pieces, whereas M + NM models may better describe changes in the abundance of DWD in different decay classes given their linkage to processes including fragmentation and rapid decay. The modeling tools developed here would benefit from a comparison to complementary studies, particularly those that monitor individual DWD pieces through time and employ methods that ensure relocation of DWD pieces.

As discussed by Radtke et al. (2004), there may be a large number of factors influencing DWD decay in forests, hence, parsimonious DWD modeling efforts (as displayed here) might be required. This analysis indicates that the five-year probability of a DWD piece advancing to subsequent decay classes is related to forest type (i.e., general species composition), degree days, DWD piece length, and the piece's initial decay class. This hierarchy of information permits quantification of decay class transitions for any DWD piece across a wide geographic range. Similar to other studies (Yin, 1999; Mackensen et al., 2003; Radtke et al., 2009; Zell et al., 2009), this analysis found climate variables (i.e., degree days) to be useful in predicting DWD decay. Traditional stage-based methods (e.g., Kruys et al., 2002; Aakala, 2010) have not tested climate as a predictor of DWD decay class transitions, perhaps because those studies were conducted in a limited geographical area. Random effects allowed for specificity of differences in DC transitions across the various forest types found throughout the eastern US; however, these values were not correlated with key physiographic features of plot locations and were not needed in modeling the M + NM dataset. Attractively, this finding lends support to using the developed models throughout the physiographic regions studied. Conversely, a more thorough investigation of this random variation might be attributed to more site-specific factors not examined here, such as the resident wood-decay fungal community, silvicultural regime or disturbance patterns common to a given forest type.

The number of growing degree days reflects the accumulation of heat energy and has seen widespread use throughout the agricultural sciences (McMaster and Wilhelm, 1997). There has been some use of degree days throughout the forest science literature, but most analyses have focused on its relationship with forest site productivity (e.g., Monserud et al., 2006; Crookston et al., 2010; Weiskittel et al., 2011). To our knowledge, degree days have yet to be used for as a surrogate for decomposition potential in ecological simulation tools. The advantages for including degree days in these kinds of models are that it displays wide variability when examining large spatial scales and can serve as a proxy for both growth and decomposition potential.

Although several studies have found that log diameter influences the decay rate of DWD (Mackensen et al., 2003; Zell et al., 2009), our findings are consistent with previous work that indicated a lack of relationship between decay rate and log diameter (e.g., Harmon et al., 1987; Radtke et al., 2009). The finding that models were more sensitive to DWD piece length (a measure of the extent of nonfragmentation and intactness of DWD logs) as opposed to large-end diameter may be due to the line intercept sampling (LIS) design used in this study (i.e., probability proportional to length). It should be noted that if modeling efforts employ data collected from national forest inventories (and whether DWD pieces are tagged or not), a thorough understanding of the field protocols and sampling design should be noted. Most national forest inventories employ either LIS or fixed-area plots for sampling DWD (Woodall et al., 2009), yet the protocols of these surveys are often not clear and not necessarily made publicly available (Woodall et al., 2009; Gove and Van Deusen, 2011). Comprehensive documentation of inventory protocols will have tremendous implications when individual DWD pieces are scaled to represent plot- and stand-level summaries of deadwood biomass and C.

The matching algorithm used to generate the M dataset contained no "observed data" for comparing the accurateness of the matches, but it did match 70% of remeasured DWD pieces when two measurements were conducted over a span of a few weeks (Woodall et al., 2012). An obvious method to improve the reliability of remeasurements from identical DWD pieces is to individually tag and number them. However, after tagging standing deadwood in managed *Pinus taeda* L. plantations, Radtke et al. (2009) estimated that there was an approximately 0.50 probability that individually tagged standing dead trees would be identifiable ten years following tree death for trees located in western locales of the natural *P. taeda* range. This highlights the fact that although DWD could be tagged in permanent sample plots, factors such as rapid decomposition rates in forest types and water disturbance on plots could impede "100% matching" if DWD pieces are tagged. As opposed to monitoring individual DWD pieces through time, an expensive and arduous task for any forest inventory of considerable scope, inventory planners may instead pursue well-documented quality assurance/quality control (QA/QC) measures. As measurement error could remove approximately a third of all matched DWD observations (Woodall et al., 2012), proper QA/QC procedures may help to distinguish non-matched pieces that result from either measurement error or from effects of the DWD decay process.

The transition of DWD through decay classes was shown to be heavily dependent on whether the M or M + NM models are used. For example, in the loblolly-shortleaf pine forest type group, model assessments indicated that DC1 pieces would move 1.95 ± 0.11 and 4.15 ± 0.27 classes in five years for the M and M + NM data, respectively. Although the true decay pathways of non-matched DWD pieces remain unknown, the NM data likely provide insight into DWD DC transitions that may not be observed when analyzing the M data alone. Although there are few studies that have quantified DWD decay class transitions across the eastern US, there are studies available from specific forest types that can be used for comparing general patterns of DWD decay. Alban and Pastor (1993) found *Populus tremuloides* Michx. logs to decay at a faster rate than *Picea glauca* (Moench) Voss. logs at two sites in Minnesota: we similarly observed that DWD found in aspen-birch forest types would transition more rapidly into subsequent decay classes than DWD found in spruce-fir forest types (1.57 versus 1.28 decay classes moved per five years for each forest type, respectively). Radtke et al. (2009) reported DWD half-lives (time to lose 50% of initial biomass) for *P. taeda* to range between six and seven years, which corresponds to the largest number of DCs moved per five years that we observed in the loblolly-shortleaf pine forest type. Lambert et al. (1980) reported that *Abies balsamea* (L.) Mill. DWD found at high elevations in New Hampshire would remain on the forest floor for 154 years, and Foster and Lang (1982) observed similar times of 159 and 140 years for *A. balsamea* and *Picea rubens* Sarg. DWD, respectively, in New Hampshire. Comparisons of the results obtained here are challenging to make with these experiments which estimate DWD residence time; however, results here showed that spruce-fir forest types contained the slowest estimates of DC transitions for all forest types examined. Future work could focus on using the DC transition models developed here to examine the temporal aspects of DWD dynamics across the study region. Only then can such comparisons of DWD residence time be made to studies such as Lambert et al. (1980) and Foster and Lang (1982). By analyzing and modeling the M and M + NM data separately, we strive to place lower and upper bounds on DWD DC transitions, which perhaps could be considered “conservative” and “liberal” estimates of DC transition for eastern US forests. The true rate of DWD transition should be bounded between these two estimates.

Models indicated the average number of classes moved per five years within a given DC was dependent on forest type and species group. Softwood species were predicted to transition slower than hardwoods, a finding that has been similarly shown using nonlinear decay functions (Zell et al., 2009) and a global meta-analysis compiled from field studies that employed either traditional chronosequence or direct measurements of DWD dynamics (Weedon et al., 2009). Differences in decay class transitions observed between softwoods and hardwoods may correspond to the distribution of toxic phenolic compounds formed in heartwood (Scheffer and Cowling, 1966). The presence of these decay-resistant extractives may ultimately result in different decay resistance for softwood and hardwood species. Although not necessarily specified as a parameter in the cumulative link model investigated here, this finding could relate to a more apparent lag time in decay class transition for softwood species. Specifying forest type as a random effect was a similar approach used by Zell et al. (2009) who used species as a random effect in a meta-analysis approach to estimate DWD decay. For the M and M + NM data, forest type groups located at northern climes (e.g., spruce-fir and aspen-birch) generally displayed a lower number of decay class transitions per five years across all decay classes than those occurring in more southern climes (e.g., loblolly-shortleaf pine and oak-pine). Results for the M data show an apparent trend that forest type, reflective of the general species composition of a site, influences DC transitions above climate and DWD piece observations alone. Although the manner in which a forest type is classified by the FIA program contains some subjectivity, results can begin to answer current questions surrounding the ecological sustainability of forest-derived bioenergy and can improve life cycle assessments of forest products.

The models developed herein could subsequently be used to investigate the temporal dynamics of DWD mass loss, and hence C reduction. Two such metrics that are important from a bioenergy perspective are the half-life (time to 50% initial biomass loss) and residence time of DWD (time to 90% biomass loss; e.g., Hérault et al., 2010). As a case study, consider the DWD examples presented in Table 4 using the M model (Eq. (3)). Using these conditions, a 25.4 cm nondecayed balsam fir (*A. balsamea* [L.] Mill.) log found in a spruce-fir forest would likely transition one DC over a five-year span if one considers the most probable transition (i.e., the mode). In contrast, a loblolly pine (*P. taeda* L.) log of the same size but found in a loblolly pine forest would likely transition two classes. Upon estimating the conic-paraboloid volume of the two logs (Fraver et al., 2007) and taking into account species-specific bulk density, initial (e.g., nondecayed) biomass would be 52.9 and 73.2 kg for the balsam fir and loblolly pine logs, respectively. After applying decay class reduction factors (Harmon et al., 2011b), remaining biomass calculated after the five-year span was 46.1 and 51.2 kg for these same logs. This equates to the balsam fir log, a species likely to be found in much cooler climates across the study area, losing 13% of its biomass over five years. In contrast the loblolly pine tree (a species whose natural range is found in warm climates across eastern US forests) would lose 30% of its biomass over five years. This example illustrates an analytical approach that could be applied using the tools developed through this work to estimate DWD C flux across eastern US forests by relating these models to forest type, climatic conditions, and DWD piece attributes.

Given that ecologically plausible estimates of DWD transitions across forests in the eastern US are proposed here, results from this study could inform efforts to project future forest DWD C stocks. In particular, this analysis offers quantitative tools that can inform bioenergy policy decisions and DWD dynamics. Developed models, coupled with traditional forest productivity simulation tools, could be used to determine accurate estimates of present and future forest C stocks.

5. Conclusions

Cumulative link models that quantify the ordinal response of DWD moving into subsequent DCs offer substantial advantages over traditional approaches that rely on difficult to obtain time since death and mean residence time variables. By using the model coupled with climate and DWD piece size attributes, the five-year probability of a DWD piece moving into subsequent decay classes can be estimated for forest types across the eastern US. Methodologies presented herein can inform DWD dynamics research and improve predictions of future DWD biomass and C stocks, as well as determining impacts of bioenergy policy throughout contrasting forest types. Models from matched and non-matched DWD pieces may provide a set of bounds for DWD decay class transition rates. Specifically, future work that quantifies deadwood longevity, as measured by DWD biomass or C reduction through time, and relating this longevity to attributes collected as part of deadwood inventories, will be crucial for further refining these models and our ability to predict DWD dynamics.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.12.012.

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