Environmental, Structural, and Disturbance Influences over Forest Floor Components in Interior Douglas-Fir Forests of the Intermountain West, USA

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Abstract: Downed woody material (DWM) is a key component in forest ecosystems with age, structure, and disturbance described as primary factors that influence DWM dynamics. In particular, much emphasis is placed on large coarse woody debris (CWD). Fine woody debris (FWD) (less than 7.62 cm diameter), duff, and litter also contribute to carbon stocks, provide habitat, add to nutrient cycling, and are often the most available fuels for fire, yet are regularly overlooked in studies describing the forest floor. Throughout the middle montane zone within the Intermountain West region USA, interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* Mirb. Franco) is a predominant forest type, yet little is known about the forest floor complex in these forests. We used a chronosequence approach to compare DWM patterns over the course of stand development among stands with different disturbance histories. Using classification and regression trees, we also evaluated an assemblage of environmental, structural, and disturbance variables to determine factors of most importance for estimating loading for DWM, duff, and litter. We found CWD resembled a U-shaped pattern of buildup while FWD components remained stable over the course of stand development regardless of disturbance history. Our results indicate that large DWM components are most closely associated with the amount of standing dead material in a stand, primarily the density and basal area of snags. Fine woody material was more aligned with live stand components, while duff and litter were more influenced by disturbance.

Keywords: coarse woody debris; fine woody debris; interior Douglas-fir; forest inventory analysis; intermountain west; fire; insects

1. Introduction

Downed woody material (DWM) is an integral structural component within forest ecosystems [1,2] which includes any dead wood from large tree boles [3,4] to small branches and twigs [5]. These forest floor components are often stratified by a diameter size threshold into two types: coarse woody debris (CWD) and fine woody debris (FWD). Throughout the literature, CWD has been defined by a minimal diameter class ranging from as low as 2.5 cm diameter [6] to the more common 7.62 cm and greater [7], while FWD often consists of pieces less than 7.62 cm diameter. Collectively these structural elements serve a variety of important ecosystem functions.

Coarse woody debris provides a critical habitat for wildlife [8–10], substrate for plant regeneration [11,12], and shading and protection of seedlings [1,7]; stabilizes soils and acts as erosion control [13]; and is also intrinsically tied to forest nutrient cycling processes [14,15]. It is important in forest carbon budgets acting as both a source and a sink [16], and when incorporated into riparian habitats, provides nutrients for aquatic life and refuge for fish [17]. The importance of FWD is

highlighted as a key input in wildfire behavior modeling programs [18,19], and has been used as a species indicator for forest cryptogams [20].

Aside from DWM, litter and duff are two additional important forest floor components that have impacts on the ecological functioning of forests. Litter influences the rates of soil nutrient cycling through decomposition, shades seeds and emerging seedlings, and affects soil temperatures [21]. Litter is also an important fuel and primary carrier of surface fire. Duff, the partially decomposed material below the litter layer, contributes to reducing soil erosion and increasing water retention [22,23]. During wildfires the long residual time frame of smoldering duff can elevate soil temperatures to become lethal to soil biota and destroy rhizomes and seeds, and can create extensive smoke hazards impacting air quality and public health [24,25].

Through efforts set forth by Harmon et al. (1986) and Maser and Trappe (1984) [2,26], the importance of CWD in forest ecosystems has gained traction with focuses on understanding the patterns and availability of CWD in relation to disturbance and stand dynamics [27]. Specifically, stand age, structure, environmental site conditions, and disturbance history have been identified as important factors that influence deadwood patterns.

Most studies addressing the importance and dynamics of DWM have been directed at old-growth forests [27], and to a lesser extent towards forests of younger age classes and those affected by disturbances at different stand development periods. For example, old-growth coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) forests have received great interest in relation to CWD [3,14,28]. However, limited information is available regarding deadwood dynamics within interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco) forests. The few studies that have looked at deadwood components were primarily focused on the accumulation of DWM following insect outbreaks, specifically Douglas-fir beetle (DFB; *Dendroctonus pseudotsugae* Hopkins Curculionidae: Scolytinae), [29–31], western spruce budworm (WSBW; *Choristoneura occidentalis* Freeman, Lepidoptera: Tortricidae) [32], and their relationships with fuel loading and fire behavior in a narrow 0–30 year window. One study that did examine DWM trends in interior Douglas-fir forests was limited to the first 150 years of stand development [33]. Furthermore, the majority of studies concentrated on DWM are focused on large (>7.62 cm) CWD pieces with little research investigating the buildup of FWD material [34].

For this study we used a U.S. Forest Service, Forest Inventory and Analysis (FIA) dataset to assess patterns of deadwood distribution, duff, and litter loads in interior Douglas-fir forests across its broad geographic range. In the Intermountain West, USA, interior Douglas-fir is one of the most widely distributed conifer species and is a prevalent forest type across the middle montane zone that commonly ranges between 900 and 1500 m above mean sea level (amsl) [35,36]. These forests sustain a rich diversity in composition and structure primarily determined by biogeoclimatic, genetic, and disturbance factors [37], and which is highly adaptive to an array of site conditions that extend across xeric to mesic gradients [29,36].

As in other western Rocky Mountain forest types (e.g., lodgepole pine (*Pinus contorta* var. *latifolia* Dougl.), and spruce/fir (*Picea engelmannii* Parry ex Engelm./*Abies lasiocarpa* (Hook.) Nutt.)), disturbance processes exert strong influences over forest development trajectories [38]. In interior Douglas-fir forests, fire and insects are two of the most important disturbance agents affecting species composition, nutrient cycling, stand structure, and other ecological processes [30,39].

The purpose of this study is to quantify and asses DWM, duff, and litter loads over the course of stand development in interior Douglas-fir stands with different disturbance histories. These include stands with no evidence of major disturbance (NMD), stands affected by wildfire, and stands that were classified as having been infested by insects. Furthermore, we sought to identify the important factors that influence the loading of different DWM size classes in these forests. These factors include stand structural components such as live and dead basal area, live and dead stand density index, and mean quadratic mean diameter (QMD). We took into account environmental variables including

mean maximum and minimum annual temperature, mean precipitation, mean elevation, and solar radiation index, and also stand development factor of stand age. Specific objectives are as follows:

(1) Compare the estimates of DWM (CWD, FWD), duff, and litter loading among stands with different disturbance histories;

(2) Evaluate DWM (CWD, FWD), duff, and litter loading response for each disturbance type at different stand development stages (stand initiation, stem exclusion, and mature);

(3) Identify factors including environmental and stand structural in nature that dictate DWM, duff, and litter loading in interior Douglas-fir forests of the Intermountain West, USA region.

We hypothesize mean annual total precipitation will be a key factor in regard to DWM loading and stands with more precipitation will be more productive (e.g., higher basal areas and higher number of trees per hectare) and therefore have greater mean DWM loads. We also hypothesize large disturbances will be a key factor in affecting DWM patterns and lead to higher levels of DWM loading compared with stands that have no prior major disturbance such as fire, disease, and/or insect infestations. We expect stands with NMD will display a U-shaped pattern of DWM loading as observed in other Douglas-fir forest types [3]. Stands affected by fire will likely have a higher input of CWD associated with greater snag densities during the stand initiation phase, while mature insect-affected stands will display higher litter loads compared with young stands. This is because older mature forests are often more susceptible to insect attack which is linked to changing DWM and litter loading following infestations [29]. Assessing changes in DWM, litter, and duff among a variety of interior Douglas-fir forested sites can lead to a better understanding of surface fuel conditions as well as carbon levels in this prominent yet often overlooked forest ecosystem.

2. Materials and Methods

2.1. Sampling Design

The data for this project were derived from United States Department of Agriculture USDA Forest Service FIA annual surveys completed between 2004 and 2015 in the states of Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming, USA. The FIA program is the lead government organization responsible for collecting forest inventory data across all land ownership categories (private, public, commercial) within the United States [40]. These surveys are based on a two-phase sampling design scheme. In Phase 1, aerial photography, satellite imagery, and other remote sensing data are used to classify land cover into forest and non-forest categories across the U.S. [41]. During Phase 2, a nationally standardized mapped plot design is employed where one permanent sample plot is established approximately every 2400 ha in a forested cover land class [42]. For each plot, a condition class is assigned based on species types, stand types, ages, or presence of forest and non-forest cover over a site area. Since plots are preassigned to a random geographical location along a grid network, multiple condition classes can be present on a sample plot for a given site [33]. All FIA plots are now on a remeasurement cycle of five years for eastern states and ten years for western states. A detailed explanation of FIA plot establishment procedures is described in O'Connell et al. [43]. All FIA data are freely available to the public and are deposited in the FIA database located at https://apps.fs.usda.gov/fia/datamart/.

2.2. Data Collection

A standard FIA plot consists of four 7.3 m fixed-radius subplots (approximately 0.017 hectares in size) spaced 36.6 m apart in a triangular pattern around a central Subplot 1. Subplots 2, 3, and 4 are located at angles of 120°, 240°, and 360° from Subplot 1 center (see Figure 1). On each subplot the overstory consisting of living and standing dead trees 12.7 cm and greater in diameter is measured. Tree characteristics including height, diameter at breast height (DBH) (measured at 1.37 m from base of tree), uncompacted and compacted crown ratios, species, decay class (for standing dead), and evidence

of damage (fire, insect, disease, mechanical, animal, or other) are collected for each tree within each subplot. These attributes are used to compute variables such as volume, biomass, and carbon estimates. Within each individual subplot is a nested 2.07 m fixed-radius microplot located at 90° azimuth and 3.66 m from subplot center on which saplings (≥2.54 and <12.7 cm diameter) and seedlings (<2.54 cm diameter) are measured. Height, DBH, crown ratio, and species type data are collected for saplings, while for seedlings, species type and a count of individuals per species are recorded. Stand age is derived from the mean age of all live trees from the dominant size class, or seedlings and saplings using ages derived by other means from all four subplots. For trees and saplings (>7.62 cm diameter), a minimum of two trees per species and size class are selected and bored at DBH using an increment corer. Tree ring counts between the outside edges of the core and the pith are counted in the field to determine individual tree age at breast height. Tree core samples that are difficult to count in the field are collected, brought back to the lab, sanded, mounted, and counted under a microscope. Seedling age is determined from mean whorl count per species for all four subplots in which seedlings occur.

Downed woody material and other forest floor variables measured in the field include coarse wood (>7.62 cm diameter), fine wood (<7.62 cm diameter), duff, and litter. Fine wood is further categorized into three size classes: small (0–0.61 cm), medium (0.62–2.4 cm), and large (2.54–7.5 cm). All DWM components are counted using a line intercept method (Figure 1). On each subplot, two transects established from the subplot center extend out a horizontal distance of 7.3 m to the subplot edge. Transect directions are defined as Subplot 1, 90° + 270°; Subplot 2, 180° + 360°; Subplot 3, 135° + 315°; and Subplot 4, 45° + 225° (Figure 1). Coarse woody debris is tallied along the entire length of each 7.3 m transect and only pieces where the central longitudinal axis intersects a transect are counted; this includes pieces that are suspended above the ground but still cross the intersect. For each tally piece, its species, diameter at intersection, decay class (1–5, with 1 being sound freshly fallen wood to 5 being almost completely decayed), and large-end diameter are recorded. Small and medium fine woody pieces are tallied by size class along the 4.2–6.1 m section of a transect, while large fine woody pieces are tallied along the 4.2–7.3 m section of each transect.

Litter is defined as the forest floor layer consisting of leaves, needles, twigs, bark flakes, cones, dead moss, lichens, dead herbaceous material, and small pieces of decayed wood. Duff is defined as the layer below litter consisting of decomposed organic material that is no longer distinguishable as litter down to the top of the mineral soil layer [44]. Duff and litter depths are measured using a ruler at the 7.3 m mark at the end of each transect.

Carbon content for coarse woody pieces is calculated using volume, specific gravity for the species, and a deduction for decay class [45,46]. When the species is not identifiable, hardwood vs softwood class is used. Fine wood carbon is calculated similarly, except that only hardwood and softwood classes are used. Litter and duff carbon is calculated using depth measurements to determine volume per unit area and bulk density factors. Species-specific and pool-specific factors can be found in documentation supporting FIA computation procedures [46].
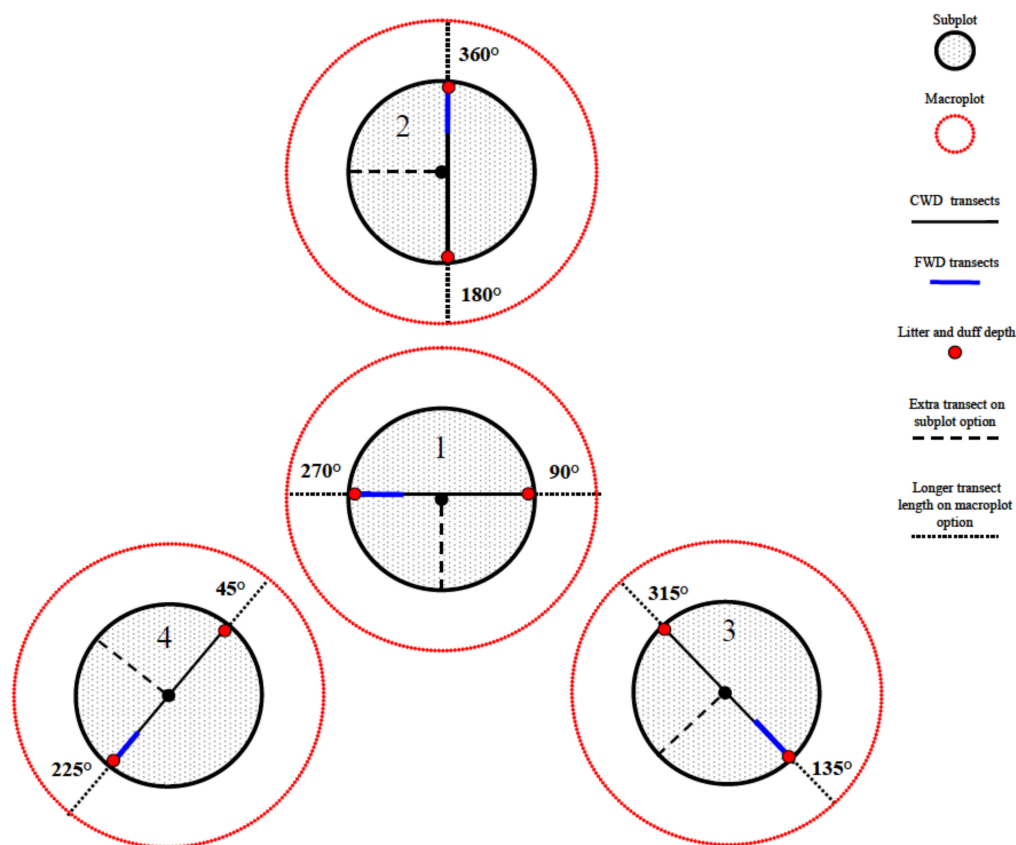
Figure 1. Downed woody material (DWM), duff, and litter transect sampling layout for Interior West Forest Inventory and Analysis (FIA) Phase 2 plots covering a single condition class. Each individual subplot (1–4) has a fixed radius of 7.3 m and each DWM transect is 7.3 m in length. Diagram reproduced from FIA National Core Field Manual v.7.1.

2.3. Dataset Assembly

The initial dataset created for this project consisted of 7228 single conditions that contained interior Douglas-fir as a component of stand composition. For our purposes, the terms condition, plot, and stand are synonymous. Hereafter the term "stand" will be used to refer to the sampled area at a given location. From this grouping we eliminated 1725 stands that contained no DWM measurements. We then filtered the dataset to include only stands where interior Douglas-fir represented >50 percent of total stand basal area, leaving 1994 stands for analysis. From this selection, we stratified stands into three disturbance categories with the first being stands classified has having no major disturbance (NMD) (1420). Major disturbance is coded by field crews when there is evidence of insects, fire, disease, wind, animal damage, landslides, and or avalanches affecting a greater than 0.40 ha area of a stand. If this threshold is not met then stands are categorized as having no major disturbance. We recognize that some form of disturbance is almost always present in a stand creating deadwood; however, for the purposes of our study and based on our field protocols, both the size threshold and evidence of a disturbance agent within the last 10 years of a stand visit must be met before a stand is coded as having a disturbance. The second disturbance category was stands affected by wildfire (333), and the third disturbance category was stands infested by insects (241). Stands affected by fire were determined by field verification from evidence of bole charring, crown scorch, and burned vegetation affecting a minimum of 0.40 ha of the area of a stand. In addition, Monitoring Trends in Burn Severity (MTBS) [47] data were overlaid on our stand locations to determine which stands had been burned. Insect-infested stands were determined through stand visits and verification of the physical presence of an actual insect damage agent, larval galleries, frass, topkill, and or

defoliation affecting at least a 0.40 ha area of the stand. Insects of concern were those that primarily utilize Douglas-fir as a host and can cause tree mortality (e.g., DFB, WSBW, Douglas-fir tussock moth *Orgyia pseudotsugata* (McDunnough)). Disturbance types for this study were chosen based on the two most prominent disturbance agents—fire and insects—which characteristically affect interior Douglas-fir [48,49]. We recognize that all stands have some level of disturbance present be it endemic insect infestations, disease pockets, and/or wind damage, but for our purposes, stands with less than 0.40 ha affected by a disturbance agent were not considered to have a major disturbance.

Stands were further stratified based on their development stage using stand age classes. Since disturbances exert strong influences over stand development across various temporal and spatial scales [50,51], no specific age cutoff exists for each stage in interior Douglas-fir forests. We utilized Oliver and Larson's [52] stand development model as a guide to classify stands into stand age class categories as follows: stand initiation (0–30 years old), stem exclusion (31–120 years old), and mature (>120 years old).

We consider the sample of 1994 stands included for analysis as primarily representing natural conditions and processes found in interior Douglas-fir stands throughout the Intermountain West, USA. Although human use of interior Douglas-fir stands has been and is still evident, primarily for commercial logging uses [53,54], this activity exerts a small footprint in the context of the Intermountain West landscape [33]. None of the stands utilized for this study had any recent evidence of harvesting.

Overall, stands in the dataset covered the broad geographic distribution of interior Douglas-fir and ranged from 31.7° to 48.9° N latitude, from −110° to −117° W longitude (Figure 2), and along an elevation gradient of 473 to 3244 m. Additional environmental metrics are displayed (Table 1).
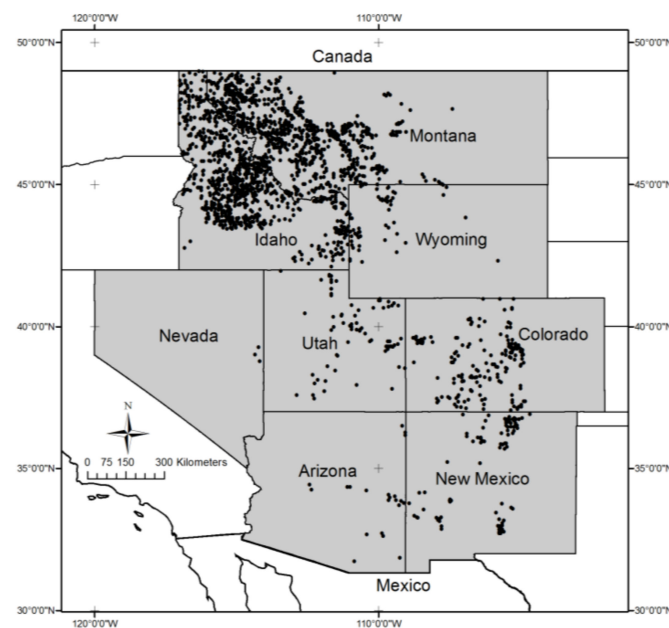

Figure 2. Locations of Forest Inventory and Analysis stands representing interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forest type used in this study from across the Interior West, USA.

Table 1. Mean and standard error of stand environmental characteristics for each disturbance type and development stage.

Stand Type	Age Class	N	Elevation (m)	Relative * Elevation (m)	Slope (%)	Aspect (°)	PPT [†] (mm)	Tmax [†] (°C)	Tmin [†] (°C)
NMD	0–30	219	1723 ± 36	71 ± 21	39.1 ± 1.5	177.6 ± 6.8	704 ± 16.6	11.6 ± 0.1	−1.1 ± 0.1
	31–120	801	1748 ± 19	87 ± 11	43.5 ± 0.7	181.6 ± 3.8	719.5 ± 8.9	11.5 ± 0.07	−1.2 ± 0.1
	>120	400	2115 ± 26	−120 ± 14	46.8 ± 1.0	195.2 ± 5.4	674.7 ± 10.5	10.8 ± 0.1	−2.3 ± 0.1
Fire	0–30	207	1971 ± 28	31 ± 22	48.7 ± 1.4	184.4 ± 7.5	734.8 ± 14.6	11.4 ± 0.2	−2.1 ± 0.1

Table 1. *Cont.*

Stand Type	Age Class	N	Elevation (m)	Relative * Elevation (m)	Slope (%)	Aspect (°)	PPT [†] (mm)	Tmax [†] (°C)	Tmin [†] (°C)
	31–120	62	1852 ± 57	93 ± 46	51.5 ± 2.8	179.1 ± 12.8	768.8 ± 26.8	11.8 ± 0.3	−1.5 ± 0.3
	>120	64	1996 ± 55	−26 ± 36	54.8 ± 2.1	211.7 ± 11.2	766.1 ± 25.9	11.1 ± 0.2	−2.3 ± 0.2
	0–30	11	2207 ± 117	−162 ± 48	47.6 ± 4.6	163.8 ± 1.9	697.9 ± 76.7	10.4 ± 0.5	−3.0 ± 0.3
Insect	31–120	108	2105 ± 41	−154 ± 20	38.7 ± 1.6	159 ± 11.1	604.6 ± 17.3	10.8 ± 0.2	−2.5 ± 0.1
	>120	122	2288 ± 38	−232 ± 16	41.5 ± 1.6	183.7 ± 10.3	629.0 ± 13.1	10.2 ± 0.1	−2.9 ± 0.1

NMD = no major disturbance, PPT = annual precipitation total, Tmax = maximum annual temperature, Tmin = minimum annual temperature. * Relative elevation is the deviation from mean elevation based on a stand's latitudinal location. [†] Climatic variables computed from PRISM dataset [55].

2.4. Data Analyses

We relied on a chronosequence approach to approximate the relative abundance of live and dead wood components over the course of stand development. The chronosequence method is often employed for DWM studies due to the slow rate of change over a stand's advancement [33]. In addition, the Intermountain West FIA program has only recently begun their second round of annual state visits so there is a lack of repeated stand measures in the dataset. In many past studies, DWM has been modeled as a function of stand age [2,3,56]. Quantitative descriptive comparisons were made to compare DWM, duff, and litter loading estimates among stand development stages and disturbance types.

The original intent of this study was to use stand age as a predictor to estimate loading of each DWM, litter, and duff variable through a mixed-model regression approach. Initial investigation of the dataset through examination of scatterplots and correlation coefficients revealed no linear patterns between stand factors (structural, environmental, developmental) among each disturbance type. Oftentimes, "ecological data are highly dimensional with nonlinear and complex interactions among variables" [57] (p. 2738). To better assess influences on DWM loading, we used Random Forests (RF) statistical modeling to identify and rank important variables related to loading for each DWM size, duff, and litter category. Random forests is a nonparametric technique that utilizes classification and regression trees (CART). This process involves constructing a combination of many trees where each individual tree is built from bootstrap samples and leaves out approximately a third of the dataset for validation, known as out-of-bag predictions. Each split of a tree is determined using a randomized subset of the predictors at each node and the best split is performed. This process continues until a tree reaches the largest possible size and is left unpruned (i.e., no more splitting occurs). The final outcome is the average of the results of all the trees [58,59]. An RF approach enables one to examine complex multi-order interactions and identify important predictor variables, while gaining high-classification-accuracy output [57].

Due to the large latitudinal gradient of the stands in the dataset and in order to better compare the influence of the variable elevation on DWM loads among stands, we fitted a polynomial regression equation ($Y = -10.242x^2 + 742.83x - 10747$ where x = latitude) to calculate the relative elevation for each stand. The variable aspect was converted from field-measured degrees to radians with sine and cosine functions applied to calculate a transformed (folded) aspect and used in the RF model runs. When different slope aspects are compared in ecological data and aspect is to be used in quantitative analysis, untransformed aspects are an inadequate representation of the data since, e.g., 1° is far from 360°, where the numbers are different but the aspect is similar [60]. For models to determine if stand age was an important variable, all stand ages were included and not grouped by stand development stage. All predictor variables were continuous in nature aside from disturbance type which was classified as a categorical variable. A description of independent variables utilized for this portion of the analysis are in Supplementary File S1. Individual DWM size classes, duff, and litter loading were the dependent variables. Models were built utilizing a training dataset with test proportion set to 0.2. Independent tenfold cross validation was built into model runs and the accuracy of predictors was assessed using an independent model test set for each dependent variable and based on the

percentage increase of the mean squared error. This measure corresponds to the difference between the misclassification rate for the original and the permuted out-of-bag samples, averaged over all the trees and divided by the standard deviation of the differences [58]. Overall model fit was assessed through Pearson's correlation coefficients. All RF models were run using the package Model Map [59] in R v.3.3.3 [61].

3. Results

3.1. Stand Characterization

The majority of interior Douglas-fir stands sampled had no evidence of major disturbance associated with stand history (71%), followed by stands affected by fire (17%) and insects (12%). In terms of live volume, mature (>120 years) NMD stands had the greatest mean live total basal area as well as the greatest mean live Douglas-fir basal area followed by mature insect-infested stands (Table 2). Fire-affected stands had the lowest live volume of trees regardless of stand development stage. The greatest live tree densities were found in young (0–30 years) insect-infested stands which also contained the greatest mean live density (1008.0 trees ha^{-1}) of interior Douglas-fir. Mature NMD stands had the greatest live stand density index which is a proxy for indicating stand competition based on tree size–density relationships [62]. Young fire-affected stands had the greatest mean basal area of standing snags and interior Douglas-fir snags. These stands coincidently had the highest mean density of total standing snags with the greatest amount of dead interior Douglas-fir (195 trees ha^{-1}), followed by mature fire-affected stands (Figure 3). Overall, NMD and insect-infested stands had similar stand structure characteristics based on basal area, tree density, and stand density index, whereas fire-affected stands regardless of stand development stage had fewer live trees and more dead trees.

Table 2. Mean and standard error of stand characteristics for each disturbance type and development stage. Total live and total dead refer to the cumulative amount of interior Douglas-fir and other species within the stand composition for each stand characteristic in the table.

Stand Characteristics	SAC	Disturbance Type					
		NMD		Fire		Insect	
		N	Mean/SE	*N*	Mean/SE	*N*	Mean/SE
Total Live BA (m^2 ha^{-1})	0–30	219	6.0 ± 0.4	207	1.5 ± 0.2	11	8.5 ± 1.8
	31–120	801	23.8 ± 0.4	62	14.7 ± 1.0	108	23.7 ± 1.3
	>120	400	29.0 ± 0.7	64	19.2 ± 1.5	122	26.8 ± 1.2
Total Dead BA (m^2 ha^{-1})	0–30	219	1.9 ± 0.3	207	14.5 ± 0.8	11	3.8 ± 1.2
	31–120	801	3.0 ± 0.2	62	7.9 ± 0.9	108	4.9 ± 0.7
	>120	400	5.2 ± 0.3	64	10.4 ± 1.0	122	8.1 ± 0.9
Total Live trees (ha^{-1})	0–30	219	585.1 ± 55.5	207	82.1 ± 15.4	11	1332.4 ± 498.3
	31–120	801	895.1 ± 31.4	62	268.8 ± 31.7	108	944.5 ± 108.3
	>120	400	834.4 ± 32.8	64	412.3 ± 60.6	122	731.3 ± 60.8
Total Dead trees (ha^{-1})	0–30	219	24.8 ± 3.3	207	195.5 ± 10.7	11	57.2 ± 18.8
	31–120	801	46.4 ± 2.1	62	113.9 ± 16.7	108	94.9 ± 11.2
	>120	400	68.2 ± 3.6	64	126.9 ± 14.2	122	123.7 ± 12.4
QMD (cm)	0–30	219	17.3 ± 0.7	207	3.9 ± 0.4	11	6.7 ± 1.1
	31–120	801	22.8 ± 0.3	62	12.0 ± 0.5	108	8.5 ± 0.3
	>120	400	24.7 ± 0.5	64	12.5 ± 0.6	122	10.2 ± 0.3
SDI Live	0–30	219	54.3 ± 3.6	207	11.1 ± 1.4	11	83.6 ± 19.7
	31–120	801	182.3 ± 3.3	62	103.7 ± 6.9	108	184.7 ± 8.5
	>120	400	210.6 ± 4.6	64	130.7 ± 9.9	122	194.9 ± 8.3
SDI Dead	0–30	219	12.7 ± 1.6	207	99.1 ± 5.1	11	27.5 ± 8.7
	31–120	801	21.0 ± 1.1	62	53.7 ± 5.6	108	35.9 ± 4.6
	>120	400	35.4 ± 1.9	64	69.9 ± 6.7	122	56.2 ± 5.9

BA = basal area, NMD = no major disturbance, QMD = quadratic mean diameter, SAC = stand age class, SDI = stand density index, SE = standard error, Trees ha^{-1} = trees per hectare.
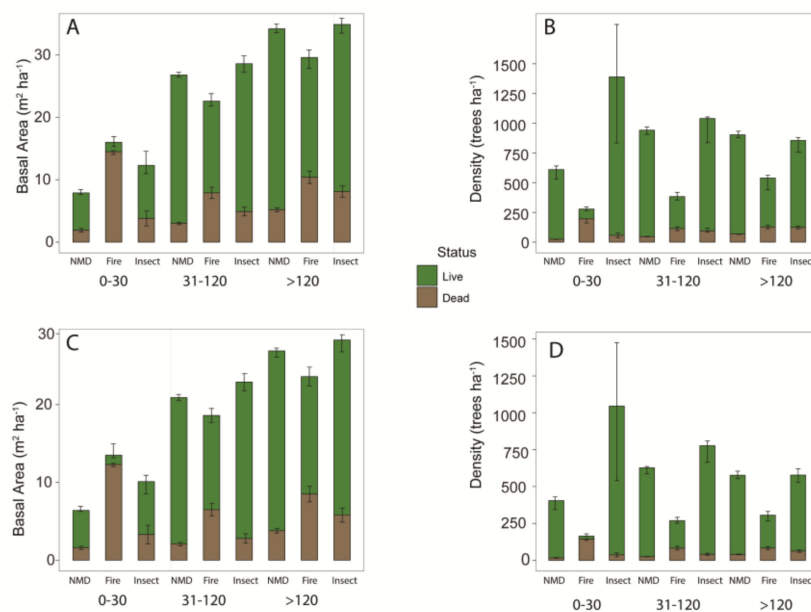
Figure 3. (**A**) Mean total basal area (m^2 ha^{-1}) for live and dead standing trees; (**B**) mean density for the total number of live and dead trees (trees ha^{-1}); (**C**) mean basal area for live and dead Douglas-fir (m^2 ha^{-1}); (**D**) mean density of live and dead Douglas-fir trees (trees ha^{-1}) grouped by disturbance type and stand development stage. Error bars are one standard error above and below the mean.

3.2. DWM, Duff, and Litter Patterns

For NMD stands, average initial inputs of CWD into newly established stands were around 40 m^3 ha^{-1}, reflecting the remains of downed trees from previous stand legacies comprising the bulk of CWD material (Figure 4). The first twenty years of stand development showed a slight increase in CWD buildup before declining by half as stands progressed into the stem exclusion stage. After the onset of the stem exclusion stage, CWD gradually increased over time through the mature stage following a lack of disturbance-related inputs, reaching a peak mean loading of approximately 90 m^3 ha^{-1}. The overall CWD pattern resembled the "U-shaped" trajectory as described by Harmon et al. (1986) [2]. Fine woody debris components of all size classes remained fairly constant regardless of stand development stage.

Insect-infested stands displayed a similar pattern of DWM over the course of stand development as found in stands with NMD, although a slight buildup of CWD material during the end period of the stand initiation stage (20–30 years) was not detected. Overall peak loading of CWD in insect-infested stands during the mature stage (65 m^3 ha^{-1}) was lower compared with peak loading in mature NMD stands. The general CWD pattern in insect-infested stands also displayed a "U"-shaped form. A gradual buildup of large fine woody debris was detected as insect-infested stands progressed through the stem exclusion stage before leveling off in mature stands. This pattern was not seen in large fine woody debris in NMD stands.

Stands with a history of fire disturbance displayed a markedly different DWM trajectory. Mean loading of CWD in young fire-affected stands was much higher compared with stands with other disturbance histories, with an initial mean loading of approximately 80 m^3 ha^{-1}. A sharper decline in CWD was observed compared with in NMD and insect-infested stands over a similar time period during the transition from the stand initiation to the stem exclusion stage. Two prominent peak buildups of CWD not observed in stands with insect or NMD disturbance histories were seen in fire-affected stands. The first peak occurred during the end of the stem exclusion stage (~100 years), and a second peak during the middle of the mature stage (~160 years). It is likely these peaks coincide with fire events during these periods of stand development where stand densities and volume of trees

are at their highest, making stands more susceptible to fire in conjunction with favorable weather conditions conducive to fire initiation and spread. Fire disturbance provides an avenue for creating a large buildup of dead material as snag fall rates increase with time since fire. Large fine woody debris loading and, to a lesser extent, medium fine woody debris loading also displayed a bimodal pattern with peak loading at the onset of the stem exclusion stage and the onset of the mature stage.

Duff and litter patterns were examined in terms of carbon loading. The amount of duff and litter loading in NMD stands followed similar patterns to that of DWM with initial large loading of 4000 kg of duff at the onset of stand initiation followed by a peak decline in the stem exclusion stage followed by a gradual buildup as stands progress into the mature stage (Figure 5). Carbon litter loads remained fairly constant throughout the course of stand development. In fire-affected stands, two prominent peaks in both duff and litter carbon loading were detected but at different stand development stages. The first peak of mean duff carbon loading occurred in the early part of the stem exclusion stage (~60 years), whereas peak litter carbon loading occurred at the end of the stand initiation stage (~30 years). The second peak loading periods for both duff and litter carbon coincided with the onset of the mature stage (~120 years). In insect-infested stands, it was found that there was a decrease in carbon loading throughout the stand initiation stage while carbon litter loading increased during this time. Build ups of duff carbon occurred during both stem exclusion and maturation stages whereas a buildup of carbon litter did not occur until the mature stage.
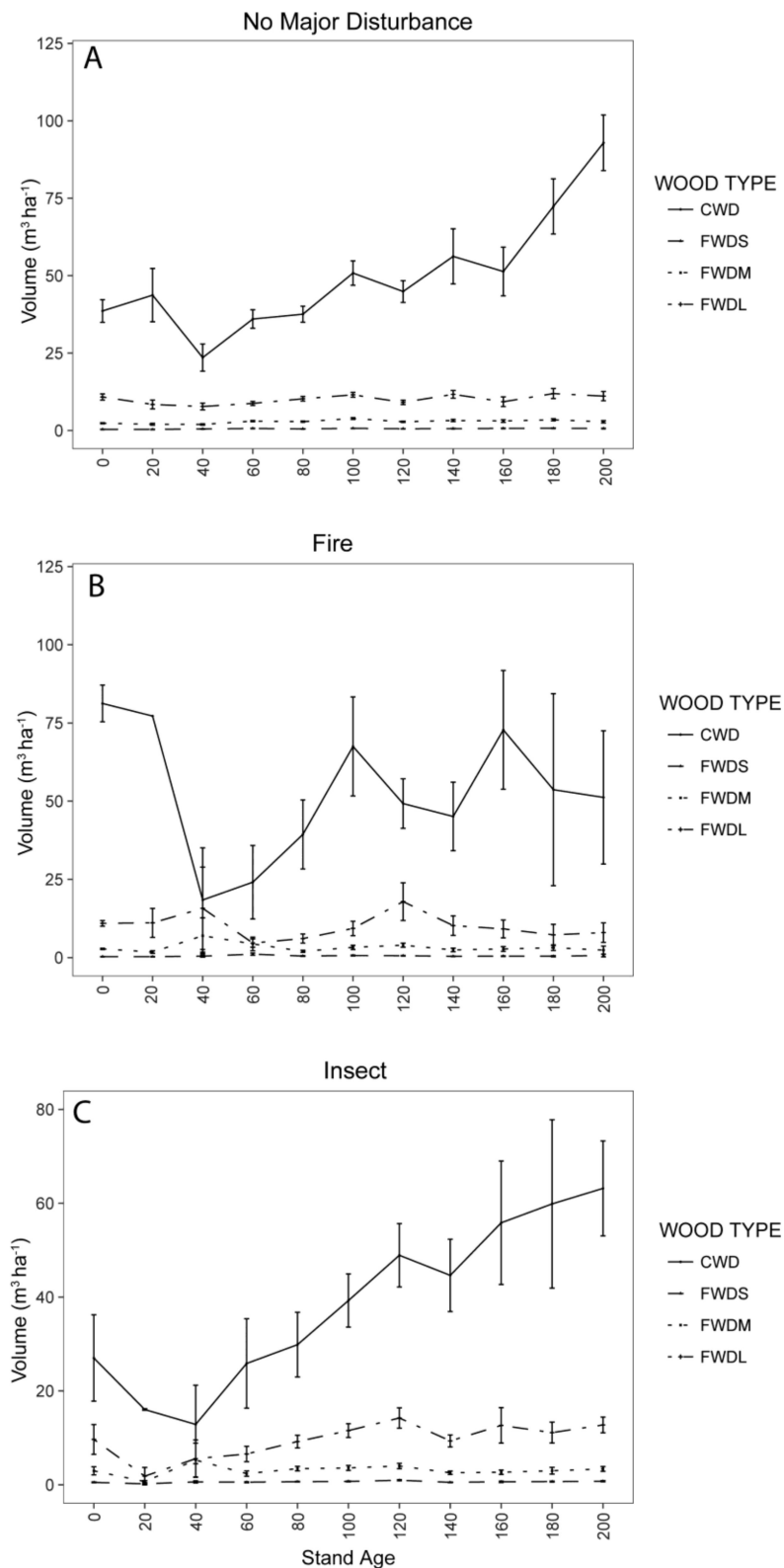
Figure 4. Mean and standard error of volume (m^3 ha^{-1}) for downed woody material (DWM) components including coarse woody debris (CWD), fine woody debris small (FWDS), medium (FWDM), and large (FWDL) across a range of stand ages for interior Douglas-fir forests with stand histories of (**A**) NMD, (**B**) fire, and (**C**) insect.
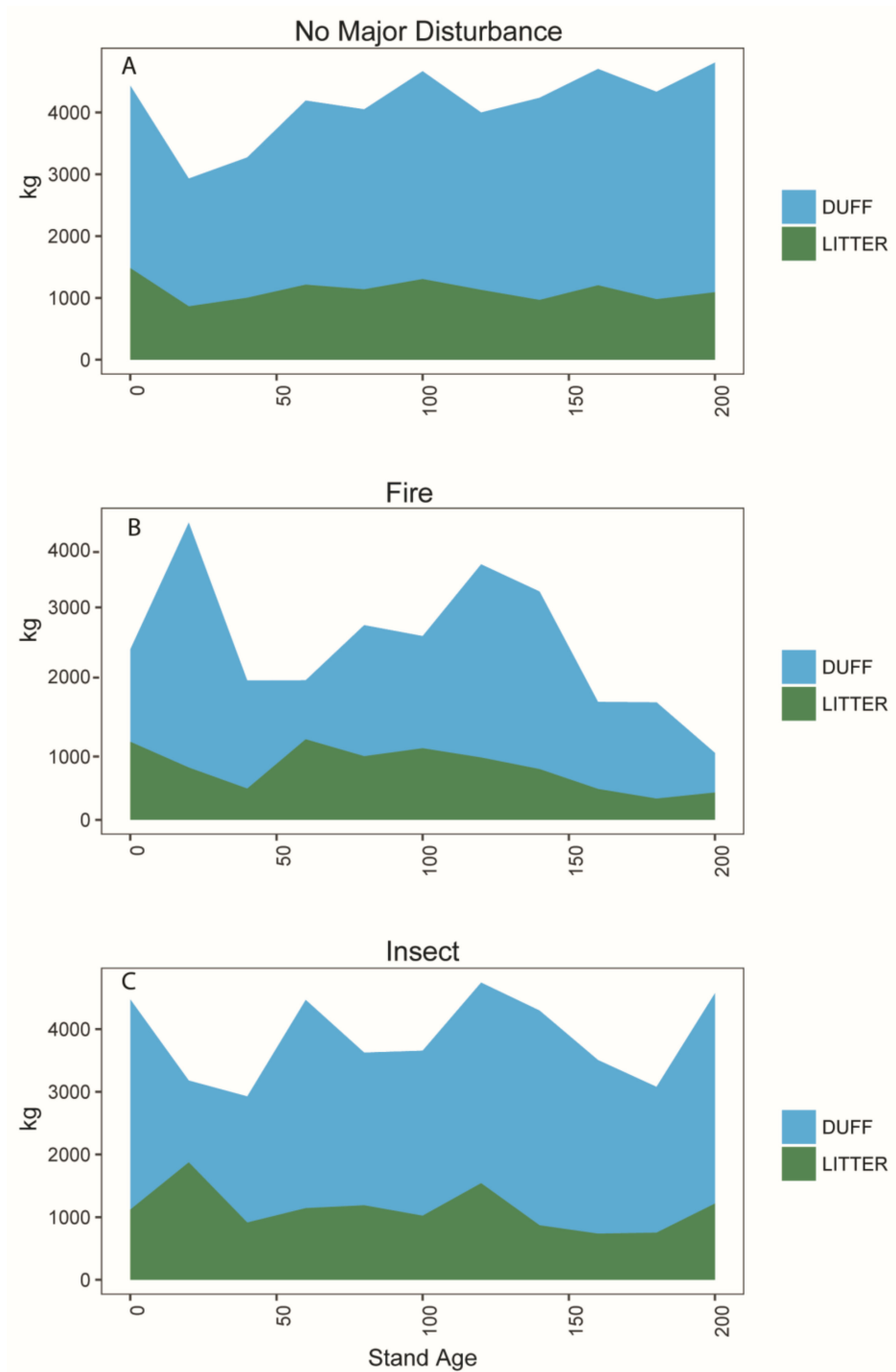
Figure 5. Stacked line graphs representing mean duff and litter carbon loading (kg) across a range of stand age classes for (**A**) stands with no major disturbance, (**B**) fire-affected stands, and (**C**) insect-infested stands.

3.3. DWM Comparisons

3.3.1. CWD

Young stands with past evidence of fire had the overall highest mean CWD loading compared with all other stands regardless of disturbance history or stand development stage (Figure 6). In looking at only fire-affected stands, stands in both the stem exclusion and mature stages had similar amounts

of CWD. Young insect-infested stands had the lowest CWD loading out of all stands. Among only insect stands, mature-stage stands had the highest mean levels of CWD loading. The highest mean loading of CWD in NMD stands was found during the mature stage with similar loading amounts between stand initiation and stem exclusion stages.
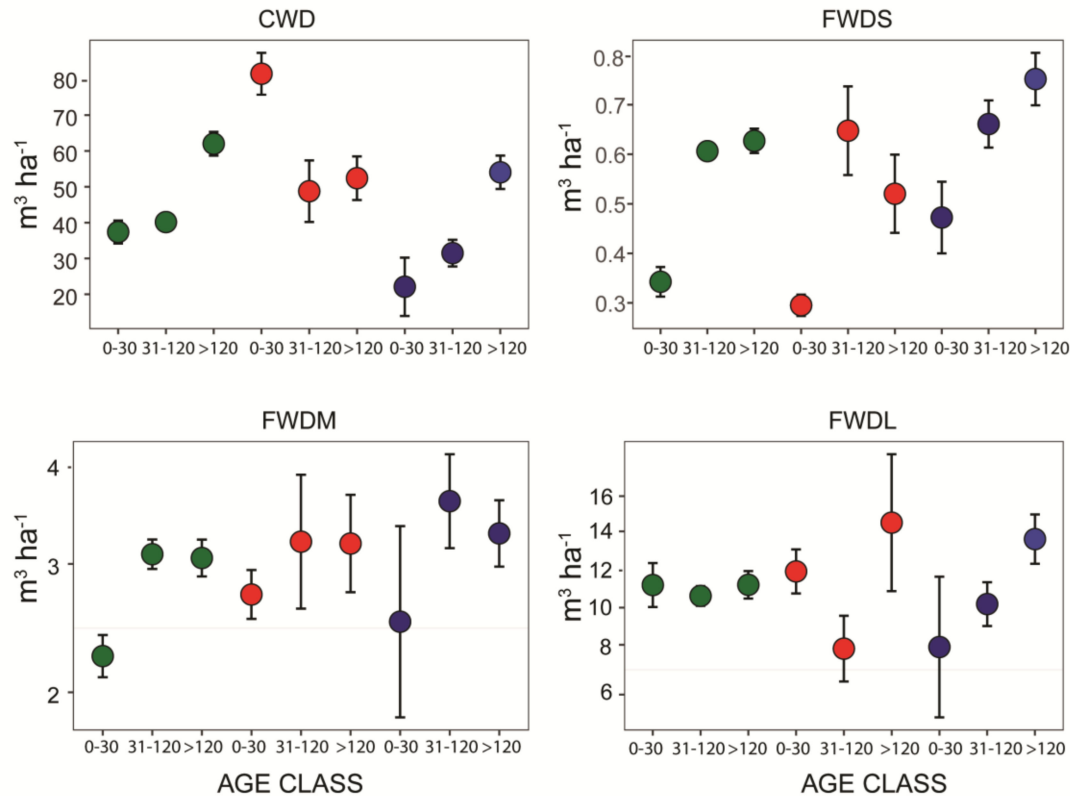
Figure 6. Mean volume and standard error values of coarse woody debris (CWD), fine woody debris size classes small (FWDS), medium (FWDM), and large (FWDL), for stand disturbance types no major disturbance (NMD) (green dots), fire (red dots), and insects (blue dots), separated by stand development age classes for each disturbance type.

3.3.2. FWD

Mature insect-infested stands had the greatest mean FWDS loading whereas young fire-affected stands had the least mean FWDS loading. In insect-infested stands, FWDS loading gradually increased over the course of stand development from a low of 0.45 m^3 ha^{-1} to a high of 0.8 m^3 ha^{-1} (Figure 6). In fire-affected stands, mean loading of FWDS peaked in the stem exclusion stage and decreased in the mature stage. The smallest amount of FWDM loading was observed in young NMD stands (2.5 m^3 ha^{-1}) (Figure 6), though overall, little variability in FWDM loading was detected among disturbance types and stand development stages with mean FWDM loading between 2 and 4 m^3 ha^{-1} (Figure 6). Mature fire-affected stands had the greatest mean loading of FWDL while little variation in FWDL was detected in NMD stands among different stand development stages. Only in insect-infested stands did mean loading of FWDL continually increase throughout stand development. As expected based on its size, coarse woody debris accounted for the majority of the deadwood volume found in interior Douglas-fir stands regardless of stand disturbance history and stand development stage.

3.4. Duff and Litter

In all cases, regardless of stand disturbance history, mean duff depths increased with the progression of stand development (Figure 7). The overall mean highest duff depths were found

in mature stands with NMD (2.5 cm) followed closely by mature insect-infested stands (2.0 cm). Young fire-affected stands had the mean lowest duff depths and fire-affected stands had the mean lowest duff depths at each stand development stage compared with non-fire-affected stands. Fire-affected stands coincidently had the lowest mean litter depths for all stand development stages compared with insect and NMD stands. Both stem exclusion and mature stage stands with NMD and insect disturbance had higher mean litter depths compared with stands in the stem initiation stage. Overall, mean duff and mean litter depths did not deviate substantially from one another among stand development stages or among stands with different disturbance histories.
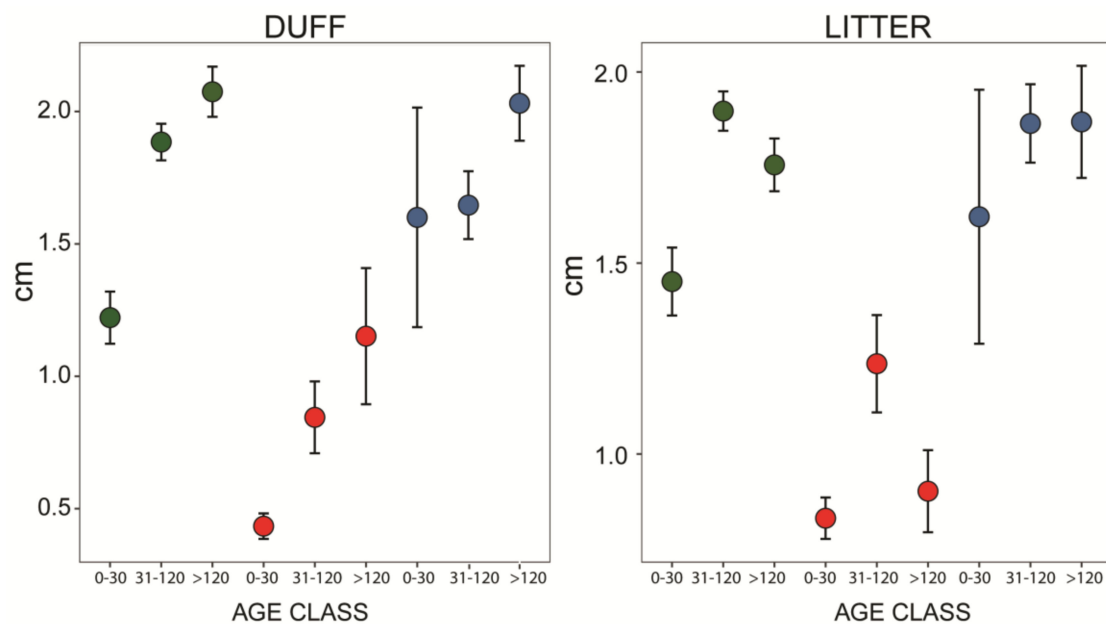
Figure 7. Mean depth (cm) of duff and litter for interior Douglas-fir stands stratified by disturbance types no major disturbance (NMD) (green dots), fire (red dots), and insects (blue dots) across stand development age classes for each disturbance type.

3.5. Variables of Importance Influencing DWM, Litter, and Duff

The top three variables of importance predicated by the RF model for CWD loading were stand age (STDAGE), stand density index dead (SDI_dead), and total density of dead trees per hectare (TPHSNAGTOT) (Figure 8). The Pearson's correlation coefficient for model fit was 0.44 (Table 3) suggesting a modest overall fit. For the top predictor stand age, this result was consistent with what was observed when CWD loading was averaged over stand development stages. Aside from fire-disturbed stands, the amount of CWD increased on average in both stands with NMD and insect-infested stands as stands developed over time (Figure 6). Young fire-affected stands, which had the highest dead stand density index, also had the highest mean CWD loading. A three-dimensional interaction plot revealed the relationships between the top two predictors of importance and CWD loading (Figure 9). Both stand age and SDI_dead had a slight negative relationship with CWD loading up to approximately stand age 50 and SDI_dead index of 100. Above these levels, there appears to be little to no relationship between these predictors on CWD loading. Similar to the results for CWD, stand age and total live trees per hectare were also found to be of most importance for FWDL with live Douglas-fir basal area being the second most important predictor variable. For the smaller DWM components FWDM and FWDS, stand density index live and density of live Douglas-fir were found to be most important for both DWM categories, though the FWDS had a stronger model fit ($R^2 = 0.45$) compared with FWDM ($R^2 = 0.29$).
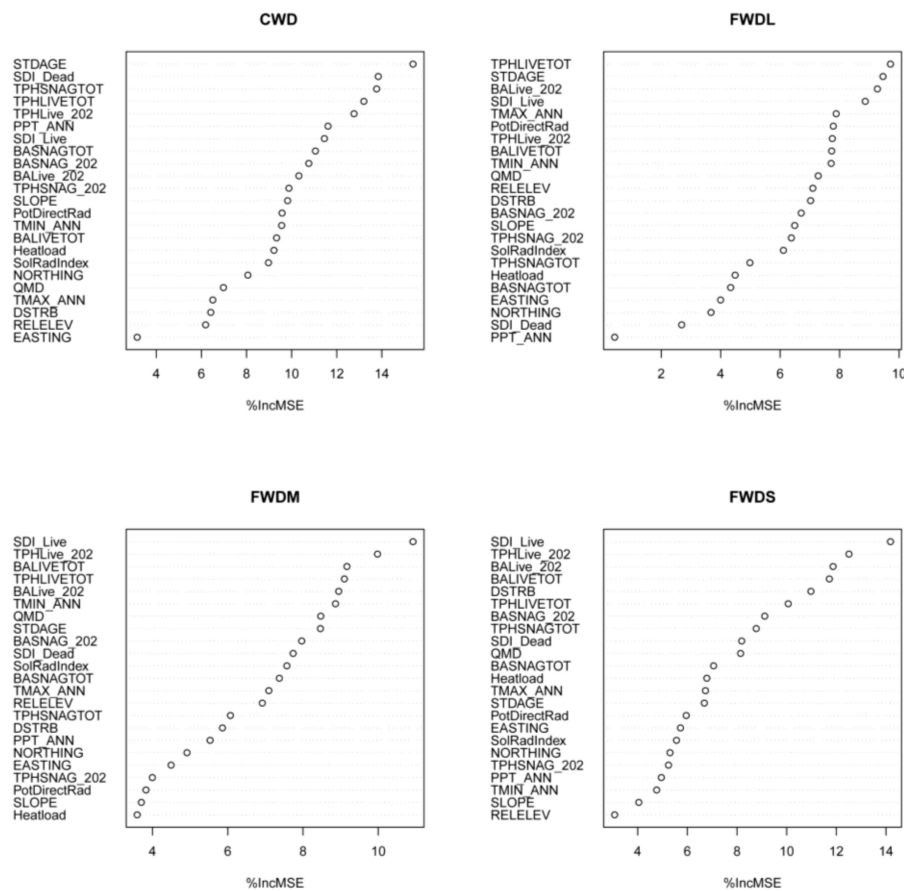
Figure 8. Variable of importance plot displaying ranked importance of predictor variables from random forest classifications used to predict each DWM response category for interior Douglas-fir stands throughout the Intermountain West, USA. Due to the continuous nature of the response variables, model ranking of the importance of predictor variables is delineated by the percent increase in mean square error (%MSE). Higher percent MSE values indicate variables that are more important to the classification. Variable codes are defined in Supplementary File S1.

Table 3. Random forest model validation results including regression equations for each DWM, duff, and litter response variable of interest.

Variable	RMSD	Pearson's Correlation Coefficient	Model Regression Equation
CWD	53.5	0.44	Y = 1.02(x) + −3.86
FWDS	0.46	0.45	Y =1.12(x) + −0.06
FWDM	2.72	0.29	Y = 1.15(x) + −0.53
FWDL	12.04	0.27	Y = 1.22(x) + −1.99
Duff Depth	1.43	0.43	Y = 0.92(x) + 0.01
Litter Depth	1.27	0.31	Y = 0.85(x) + 0.23
Duff Loading	5463	0.35	Y = 0.88(x) + 308.8
Litter Loading	2140.91	0.29	Y = 0.81(x) + 465.6

CWD = coarse woody debris, FWDS = fine woody debris size small, FWDM = fine woody debris size medium, FWDL = fine woody debris size large, RMSD = root-mean-square deviation. Model regression equation: Y = response variable, x = predictor variable. Note: duff and litter loading reported as carbon estimates as opposed to direct volume estimates.
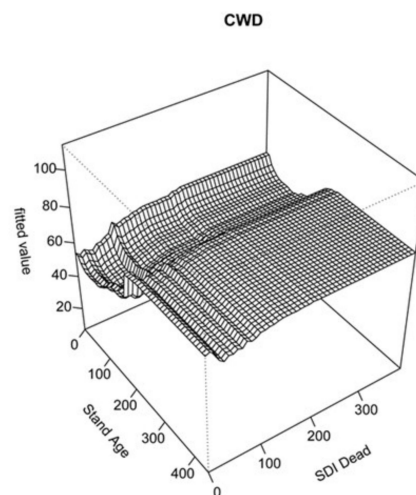
Figure 9. Three-dimensional interaction plot showing the relationship between the top two predictors from random forest model stand age and stand density index dead (SDI_dead) on CWD loading. The vertical axis is the fitted values for CWD loading.

Disturbance was recognized as a top predictor variable for duff depth with stand structure components quadratic mean diameter and density of live Douglas-fir also identified as important (Figure 10). Both quadratic mean diameter and total live tree density were also identified as strong predictor variables for duff carbon loading. For litter depth and litter carbon loading, live Douglas-fir basal area and stand age were recognized as the top two predictors.
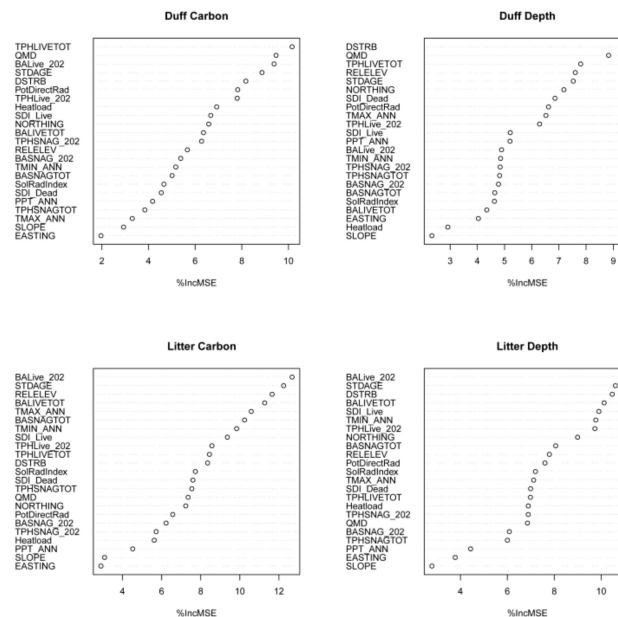
Figure 10. Variable of importance plot displaying ranked importance of predictor variables from random forests classifications used to predict each duff and litter response category for interior Douglas-fir stands throughout the Intermountain West, USA. Due to the continuous nature of the response variables, model ranking of the importance of predictor variables is delineated by the percent increase in mean square error (%MSE). Higher percent MSE values indicate variables that are more important to the classification. Both duff and litter carbon were based on loading estimates. Variable codes are defined in Supplementary File S1.

4. Discussion

The impetus for carrying out this project was to continue novel explorations of the relatively new national FIA DWM dataset as encouraged by previous researchers [63]. As mentioned earlier, a great deal of work has been focused on CWD dynamics in coastal Douglas-fir forests which tend to have higher productivity and stand longevity, and growth rates that are influenced by a moister climate regime. To our knowledge, this is one of the first studies to take a detailed look at not only CWD but FWD, duff, and litter trends in interior Douglas-fir forests, as well as the important factors that govern DWM in these forests. The results from our study support the framework that DWM and CWD in particular have an initial residual loading following disturbance, then a reduction as stand development is reinitiated, before accumulating over time as stands mature which has been observed in other forest chronosequence studies [3,33,64]. However, the peaks and timings of the development of CWD are markedly different among stands affected by fire and stands with NMD or insect disturbance.

4.1. Stand Development

The RF model approach enabled us to compare a suite of environmental, structural, developmental, and disturbance attributes to determine which factors were most likely important for influencing DWM, duff, and litter loading in interior Douglas-fir forests. Stand age was recognized as the most important variable for determining CWD. Stand age can be considered a proxy for stand development stage. A conceptual framework for CWD patterns over the course of stand development, described in [2,61,65], has been widely accepted. In the early period of stand development, the amount of DWM and, in particular, CWD is dictated by individual stand histories [3] and driven in large part by the preceding stand's senescence and ultimately stand-replacing disturbance event. Pre-disturbance debris, disturbance-generated CWD, and residual standing trees contribute to an initial loading of CWD into a newly formed stand [66], with the amounts of CWD generated related to the disturbance type (e.g., fire, insect, disease) and intensity [66,67]. Looking at the temporal trends in our dataset separated by disturbance type, young stands following fire had a CWD load almost twice that of young stands with no major disturbance or young stands that were infested by insects. Fire creates a large number of standing snags that are key inputs to the initial CWD reservoir in newly established stands [33]. As stands progress from stand initiation towards the stem exclusion stage, decay dynamics and lack of standing dead trees limit the availability of DWM inputs. This leads to a net decline in CWD as stands move through the stem exclusion and into the mature stage of development as measured in coastal Douglas-fir [3], Douglas-fir-western-hemlock (*Tsuga heterophylla* (Raf.) Sarg.) [64], and other forest types [65]. In the absence of disturbance, stand density and self-thinning rates regulate tree mortality [68,69] which dictates future deposits of CWD. In coastal Douglas-fir forests of Washington and Oregon, USA, Spies and Cline (1988) [70] reported the mean volume of deadwood to be 423 m^3 ha^{-1} for young stands (age 65), 250 m^3 ha^{-1} for mature stands (age 120), and 534 m^3 ha^{-1} for old growth stands (age 404). Although our stand development stage cutoffs were slightly different, and we did not have any comparative old growth stands (i.e., stands 400 years or greater), the mean loading of CWD in interior Douglas-fir stands was much lower. The mean highest CWD load for our study was only 80 m^3 ha^{-1}. Others have found that in the coniferous forests of Northwest USA, the volume of logs ranges from 77 to 346 m^3 ha^{-1} [3], which is greater than that in interior Douglas-fir forests. Our results for CWD, FWDM, duff, and litter were more aligned with the work in [33] where it was found that the minimum total live and dead volume appears to occur by age 30–40, after which there appears to be a steadily increasing volume of the standing and downed CWD. In their study they found that peak mean CWD loading was approximately 60 m^3 ha^{-1}, similar to our results when averaged among all disturbance types.

Fine woody material loading remained relatively constant throughout stand development for all disturbance types with input and output rates based on chronosequences fairly equal. Stand age was not identified through RF models as an important variable related to any fine woody debris category

aside from FWL. The larger fine woody debris fuels are often related to branches that become detached during snag fall or wind events and are found distributed in close proximity to standing dead trees or fallen snags. The one notable change in fine woody material was with FWDS where we found this material to be in mean lowest abundance in young stands. In young fire-affected stands, FWDS loading was twice as low compared with the other stand development stages. This material is typically more susceptible to burning compared with larger size classes due to its larger surface-area-to-volume ratios which can increase surface fire rates of spread [71]. Furthermore, young trees have yet to reach the point where canopy closure results in the shading of neighboring branches which can lead to self-pruning of lower branches that do not receive sufficient light to maintain photosynthesis [52]. During the stand initiation stage, the lack of canopy competition precludes self-thinning which can be an important source of FWM in a stand. As expected, duff and litter depths were found to be lowest in young stands regardless of past stand history. The lack of a developed canopy leads to reduced inputs of litter that in turn create less accumulation of litter which eventually becomes incorporated into the duff layer as needles decompose over time.

4.2. Stand Structure

A consistent variable type that was identified through RF model runs as important for DWM loading of all size classes, duff, and litter components was structure (e.g., basal area, density, stand density index). For the largest size classes CWD and FWDL, dead structural components including stand density index dead and total snag basal area were ranked as the top most important variables in determining estimates of loading. Although RF models cannot definitively state that the variables of most importance are the most correct factors for determining CWD loading, the RF results do relate logically to ecological processes observed in forests concerning deadwood. The majority of CWD pieces encountered on the forest floor are tree boles, large branches, and broken tops related to decreased structural integrity of standing deadwood. Wind, ice, root rot pockets, and other events increase snag fall rates in which snags become incorporated into the DWM fuel complex.

For smaller-diameter DWM, live structural features were found to be of most importance (e.g., live Douglas-fir basal area, live Douglas-fir density). Fine woody material comprising mostly twigs and small branches results from other sources aside from dead trees such as self-thinning, crown lift, and inter-tree competition associated with stand development. The highest mean FWDS and FWDM loads were detected in stands in the stem exclusion or mature stage where tree competition is most evident.

4.3. Disturbance

Contrary to our hypotheses, large disturbance events were not identified as an important factor influencing DWM dynamics and were found to be the top influential variable only for estimating litter and duff depths. Based on our data it is implied that frequent smaller-scale disturbance within a stand regulates structure over time compared to large stand-replacing events. In terms of litter depths, litter is the smallest fuel size class that was included for analysis and is often the primary carrier of surface fire. Litter depth was found to be lowest in fire-affected stands across all stand development stages compared with stands with no disturbance and insect-infested stands. Duff depths were also lowest in young stands with past fire history. It has been found that smoldering combustion is a major cause of duff depletion following fire [72]. In the more arid Intermountain West forests, duff accumulation can be slow to build up over time due to slower decomposition rates compared to more mesic types of forests and this is reflected in the low duff depths found in young interior Douglas-fir stands. Mature insect-infested stands are often most susceptible to DFB, a primary pest in Douglas-fir. It has been shown there is a 1–5 year window after successful beetle infestations where litter buildup proceeds following a period of needle release [29,30]. Mature insect stands had some of the highest mean litter depths. Only young fire-affected stands which had the mean highest amount of CWD material out of all stand disturbance types and age classes showed an effect of disturbance

in regard to increased DWM loading. NMD stands had on average more CWD compared with plots infested by insects, and mature NMD stands had on average more CWD compared with mature stands with fire. Disturbance was ranked low as a predictor for DWM aside from FWDS where it was still ranked below live stand structural components including stand density index, basal area, and tree density, and was identified to be influential for only litter and duff depths. These results suggest stand structure and development have stronger influences over DWM loading in interior Douglas-fir stands than disturbance.

The majority of stands used for analysis were not classified with disturbance at the time of sampling. As our stands represent a broad range of interior Douglas-fir across the Intermountain West, USA, it can be inferred that most stands at the present time are following the NMD DWM trajectory. Oftentimes, disturbances are patchy in nature and only affect a portion of a stand [2]. Fire is a dominant disturbance where interior Douglas-fir forests are characterized as having a mixed-severity fire regime, experiencing natural fires across severity levels that range from low to medium to high [29,36], and with variable fire return intervals that span 30–100 years or more [73]. Across the landscape, even-age forest structures are most common where stand-replacing fires are prevalent, and interspersed between these even-age patches are uneven-aged stands where frequent surface fires are dominant [74,75]. Where high-severity fires are prevalent, a buildup of CWD is expected and becomes legacy components of newly established stands. Low-severity fires are mostly confined to the forest floor, consuming dead branches, twigs, needles, cones, grasses, herbaceous vegetation, and with little to no mortality of live standing vegetation limiting the amount of CWD inputs through snag fall [76].

In the Intermountain West, USA, interior Douglas-fir ordinarily does not experience high rates of mortality due to insects or disease [33]. However, during the past decade, insects have become increasingly active in Douglas-fir forests, with an area disturbed by insects currently estimated at 0.9 million hectares [77]. DFB is the most prominent bark beetle that utilizes interior Douglas-fir exclusively [78,79]. Where Douglas-fir are the uniform dominant overstory component, past logging and fire history often create mosaics in which Douglas-fir oscillates in age and density [80]. Consequently, the varied age and size classes do not necessarily meet conditions that warrant epidemic outbreaks, and mortality centers become confined to small groups of trees to a few hectares infested [30,81]. However, under certain conditions, drought coupled with a supply of recently downed trees can facilitate the development of DFB populations from endemic into epidemic levels where upwards of hundreds of hectares can become infested [82]. Following a bark beetle infestation, there is often a delayed DWM response compared to fire. With fire, and especially high-severity crown fires, an instant reduction in fine fuel volume is observed through direct combustion of needles, twigs within tree crowns, and litter on the forest floor. With bark-beetle-infested stands, a lag period of 3–5 years in litter accumulation and as well as FWDS material typically coincides with the time it takes for infested trees to shed their needles following tree mortality [81]. Even in infested stands, the buildup of DWM is not necessarily to be greater than levels in non-infested stands. In a study comparing DWM in non-infested and DFB-killed forests in the Greater Yellowstone Ecosystem, USA, significant changes to surface fuels were few aside from an increase in CWD fuels during the silver stage (25–30 years) post infestation [29]. Where stands are affected by disturbance, the individual stands may see an increase in DWM as these stands continue to develop, but the overall mean loading of the deadwood may not necessarily be any greater compared to similar stands without disturbance.

4.4. Environmental Metrics

Environmental variables were found to not be important, which did not support our hypothesis that precipitation would be an important factor for estimating DWM. It has been shown by others [33,83] that environmental site characteristics such as temperature and precipitation strongly regulate site productivity which influences stand structure and, ultimately, deadwood dynamics. This type of study looks at range of forest types over large elevational and latitudinal ranges. Although interior Douglas-fir encompasses a large geographic distribution, when evaluated in terms of elevation

and latitude, specific precipitation and temperature gradients were quite similar. At the lowest latitudes, interior Douglas-fir occupies cool, moist, high-elevation, north-facing slopes, for example, in the Santa Catalina Mountains of Arizona, USA, Douglas-fir is the dominant conifer species above 2450 m [84] and their distribution is limited by precipitation. The climate at these locales will be more similar to that for stands at higher latitudes which occupy lower-elevation warmer sites where distribution is limited by temperature [85]. Stands utilized for this analysis had a narrow mean max temperature range (10.2–11.6 °C) and a precipitation regime that varied by 100 mm.

One important process intrinsically tied to DWM and litter dynamics is decay. Environment plays a role in decay dynamics where temperature, moisture, and aeration along with substrate quality affect the rates of wood decay [67]. In cold or dry environments typical of the Intermountain West, biological decay is limited, which allows for the accumulation of plant debris [7]. Numerous past studies have explored the relationship of different species and conditions that regulate decay and the release of carbon and nutrients back into forests. To our knowledge, no study to date has tracked the decay rates of interior Douglas-fir, but studies have looked at decay rates of coastal Douglas-fir where it was found to be 0.10/year (k decay constant) [14]. These coastal Douglas-fir forests are much wetter compared with interior Douglas-fir forests. It is likely that CWD of a similar size class in drier interior Douglas-fir forests could have twice the decay time as their counterparts towards the coast. We recognize that individual stand histories i.e., disturbance as well as local site factors such as climate, slope position, and stand composition collectively influence DWM dynamics in a stand. Furthermore, direct assessments of deposition and depletion of DWM, litter, and duff material can only accurately be gained from repeated measurements in each sampled stand. At this current time, there is a lack of repeated site visits (FIA interior West program has recently just begun stand re-measurements); with future repeated measurements of DWM material, the FIA data records could seemingly be used as a surrogate for determining future DWD populations [85] and can be a tool for gaining better insight into decay, depletion, and accretion rates in these drier Douglas-fir forests. The intent of this study was not to define decay rates but to assess the general patterns of DWM, duff, and litter that currently exist across the interior Douglas-fir landscape. We feel the use of a chronosequence approach was most appropriate for estimating DWM patterns in interior Douglas-fir across the landscape based on our large sample size representing a geographically diverse area of this species.

4.5. Future Research Needs

We have identified research gaps which could further contribute to our understanding of DWM dynamics in interior Douglas-fir forests. Below is a list of proposed future research needs.

- Calculate carbon source and sinks in relation to DWM inputs and depletion in interior Douglas-fir stands;
- Utilize repeated data measurements from future inventory collections to see how individual stands are changing over time;
- Initiate long-term decay studies of CWD in cooler, drier interior Douglas-fir stands to see how they relate to coastal Douglas-fir decay dynamics.

5. Conclusions/Management Implications

This study demonstrates that the primary drivers of DWM loading in interior Douglas-fir forests are more related to minor disturbance such as tree mortality, endemic insect infestations, and individual blowdowns, as well as competition during stand development which influences stand structure, than to large episodic disturbance events. Large deadwood components were found to be most closely associated with the amount of dead material in the stand, primarily the dead stand density and basal area of snags. Fine woody fuels were more aligned with live stand components, while duff and litter were more affected by disturbance. While large disturbances were not found to be an important contributor to DWM estimates, we were able to demonstrate that different disturbance histories can

affect DWM, duff, and litter patterns over the course of stand development. Although disturbance can lead to elevated levels of DWM, especially CWD and particularly in young stands following fire disturbance, levels of DWM might actually be greater in stands with no major disturbance. Due to its significance for ecosystem health and functioning, increasing efforts have been made to manage DWM as an important habitat and carbon storage component of forest ecosystems [86].

The results from our project are useful for forest managers to determine where their current interior Douglas-fir stands are in terms of DWM loading, and what to expect under different disturbance scenarios for the future DWM states of their forests. This information is helpful for a variety of forest planning processes from assessing wildlife habitat suitability, to identifying carbon source and sinks, as well as making hazardous fuels assessments. We acknowledge that the results from our work are most applicable to the Intermountain West, USA, yet the broad implications from our findings could be useful for Douglas-fir systems in other regions.

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