An assessment of dead wood patterns and their relationships with biophysical characteristics in two landscapes with different disturbance histories in coastal Oregon, USA

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Abstract: Understanding the relative importance of landscape history, topography, vegetation, and climate to dead wood patterns is important for assessing pattern–process relationships related to dead wood and associated biodiversity. We sampled dead wood at four topographic positions in two landscapes (1400–2100 km^2) that experienced different wildfire and salvage histories in coastal Oregon. Study objectives were to (*i*) determine whether and how the landscapes differed in dead wood amounts and characteristics and (*ii*) evaluate relationships between dead wood characteristics and potentially related biophysical variables associated with historical and current vegetation, topography, climate, soils, and ecoregion. Despite differences in history, the two landscapes differed little in total dead wood volume; however, they differed in dead wood volume by structural type, decay class, and source (legacy/nonlegacy). Dead wood varied by topographic position, and topography was of greatest importance compared with other factors. In this mountainous region, upper topographic positions may be source areas for dead wood and riparian areas and streams sinks for dead wood. Climate explained more variance in dead wood in the landscape that burned earlier and was not salvaged. Landscape-scale patterns of dead wood are evident in landscapes with different disturbance histories and despite finer-scale variation in topography, vegetation, and other biophysical attributes.

Résumé : Il est important de comprendre l'importance relative de l'impact de l'historique du paysage, de la topographie, de la végétation et du climat sur les caractéristiques du bois mort pour évaluer les relations entre les patrons et les processus reliés au bois mort et à la biodiversité qui y est associée. Nous avons échantillonné le bois mort dans quatre positions topographiques dans deux paysages (1 400–2 100 km^2) avec différents historiques de feux et de récupération dans la zone côtière de l'Oregon. L'étude avait pour but (*i*) de déterminer si les paysages diffèrent par les caractéristiques et la quantité de bois mort et de quelle façon et (*ii*) d'évaluer les relations entre les caractéristiques du bois mort et les variables biophysiques particulièrement reliées à la nature passée et présente de la végétation, de la topographie, du climat, des sols et de l'écorégion. Malgré un historique différent, les deux paysages différaient peu en volume total de bois mort. Cependant, ils différaient en volume de bois mort par type de structure, classe de décomposition et source (legs ou non). Le bois mort variait selon la position topographique et la topographie avait une très grande importance comparativement aux autres facteurs. Dans cette région montagneuse, les positions topographiques plus élevées peuvent être des sources de bois mort et les zones riveraines ainsi que les cours d'eau des puits. Le climat expliquait une plus forte proportion de la variance du bois mort dans le paysage qui avait déjà brûlé et où il n'y avait pas eu de récupération. À l'échelle du paysage, les patrons du bois mort sont évidents dans les paysages qui ont différents historiques de perturbation et cela malgré les variations de la topographie, de la végétation et des autres attributs biophysiques à des échelles plus fines.

[Traduit par la Rédaction]

Introduction

Understanding landscape history is important for assessing pattern–process relationships in ecosystems and may be important for maintaining biodiversity (Eriksson et al. 2002; Schrott et al. 2005) and developing successful landscape plans (Marcucci 2000; Hellberg et al. 2003). Past changes in land use, such as the conversion of forest to agriculture and subsequent regrowth of forests, have been widely studied as drivers of current vegetation patterns in forested landscapes (Stover and Marks 1998; Burgi 1999; Aragon and Morales 2003). In forest landscapes that have not undergone such transformations, the influence of landscape history may be more subtle. For example, abundance patterns of dead wood, which is a product of forest disturbances (Spies et al. 1988) and may take centuries to decay (Harmon et al. 1986), may reflect landscape history more than current forest conditions (Lohmus and Lohmus 2005). However, the relative importance of forest history and other potentially important biophysical factors such as current vegetation, topography, and climate is poorly understood at the landscape scale (Muller 2003).

The combination of limited information about historical

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management and complex natural disturbance patterns makes it difficult to characterize forest history. In forest landscapes such as the coastal forests of the Pacific northwestern United States, large-scale, infrequent, stand replacement wildfires were a dominant influence on historical vegetation patterns (Agee 1993). In many landscapes, fires occurred after Euro-American settlement but before the fire suppression period, and the most recent stand replacement wildfires are still reflected in the age and structure of current vegetation. These landscapes may generally be identified by a combination of the record of these events in the cultural lore and present-day vegetation patterns. Landscapes at different stages of development may be evaluated for differences with respect to time since disturbance, if other potential related factors such as climate and topography are similar. Landscape vegetation also reflects idiosyncratic past events such as windthrow and salvage logging, the knowledge of which informs the interpretation of ecological pattern–process relationships. The chronosequence approach to the study of landscapes can yield insights about ecological pattern–process relationships and how they might shift over time in relation to past events. The temporal sequence is important because the relative influence of processes related to vegetation patterns, such as those of dead wood, may change over time (Muller 2003).

Understanding what influences dead wood patterns at the landscape scale adds to the scientific knowledge base and can contribute to more effective forest management practices. Dead wood increases the structural diversity of forests (Hansen et al. 1991), serves as habitat for sensitive species (Jonsson and Kruys 2001), and contributes to long-term nutrient stores (Harmon et al. 1986; Maser et al. 1988). Many types of dead wood-related wildlife such as cavity-nesting birds and dead-wood-related ecosystem processes such as stream and river system dynamics function at the scale of landscapes (Maser et al. 1988; McComb and Lindenmayer 1999), but our information about landscape-scale dead wood pattern–process relationships is limited. In addition, the scale of the dominant form of disturbance affecting the production and spatial distribution of dead wood may be larger than a stand but smaller than a region (e.g., fire, windstorm). A landscape is a land area where local ecosystems and land uses are repeated in similar form (Forman and Godron 1986). Therefore, taking a landscape view can add key insights to our understanding of these related entities. Furthermore, management plans are also increasingly developed for entire landscapes, and these plans must often incorporate provisions addressing wildlife and aquatic habitat including snags and logs (USDA Forest Service and USDI Bureau of Land Management 1994).

In the Pacific northwestern United States, terrestrial dead wood patterns and related factors have been evaluated at stand and regional scales (Spies et al. 1988; Ohmann and Waddell 2002) but terrestrial landscape-scale patterns have not been the subject of much study (Muller 2003); see Maser et al. (1988) for a description of landscape-scale patterns in aquatic systems. Stand-scale patterns of dead wood amounts have been shown to follow a rough U-shaped pattern over time, increasing immediately after natural disturbance, decreasing as disturbance-created mortality decomposes, and increasing again as the stand develops after disturbance (Harmon et al. 1986; Spies et al. 1988). Studies of topographic effects on dead wood patterns at the stand scale in Pacific Northwest forests indicate that dead wood amounts may decline with increases in elevation (Spies et al. 1988), but in other regions, conflicting relationships have been reported (Gale 2000; Rubino and McCarthy 2003). In numerous regional-scale biomes, dead wood abundance and characteristics have been shown to vary across habitat types, disturbance types, and climatic gradients (Brown and Schroeder 1999; Krankina et al. 2002).

Because landscapes are comprised by stands and occur in a regional context, landscape-scale dead wood patterns likely are influenced by a combination of the processes that are important at stand and regional scales. Fire, floods, windthrow, landslides, insects, disease, and forest management affect dead wood patterns at multiple spatial scales. Current live vegetation may influence the kinds and pattern of recent dead wood produced and subsequent decomposition rates. Past vegetation patterns within landscapes may be more closely associated with variability in dead wood than present-day vegetation patterns because of long decay times (Sollins et al. 1987). Topographic factors may influence productivity, species composition, and microclimate and affect the likelihood of movement of dead wood. Climatic variability at broader spatial scales within landscapes may be related to variability in finer- and coarser-scale dead wood production and decomposition rates. However, the relative influence of various potential factors on dead wood at the landscape scale and over several decades of post-disturbance development remains unclear.

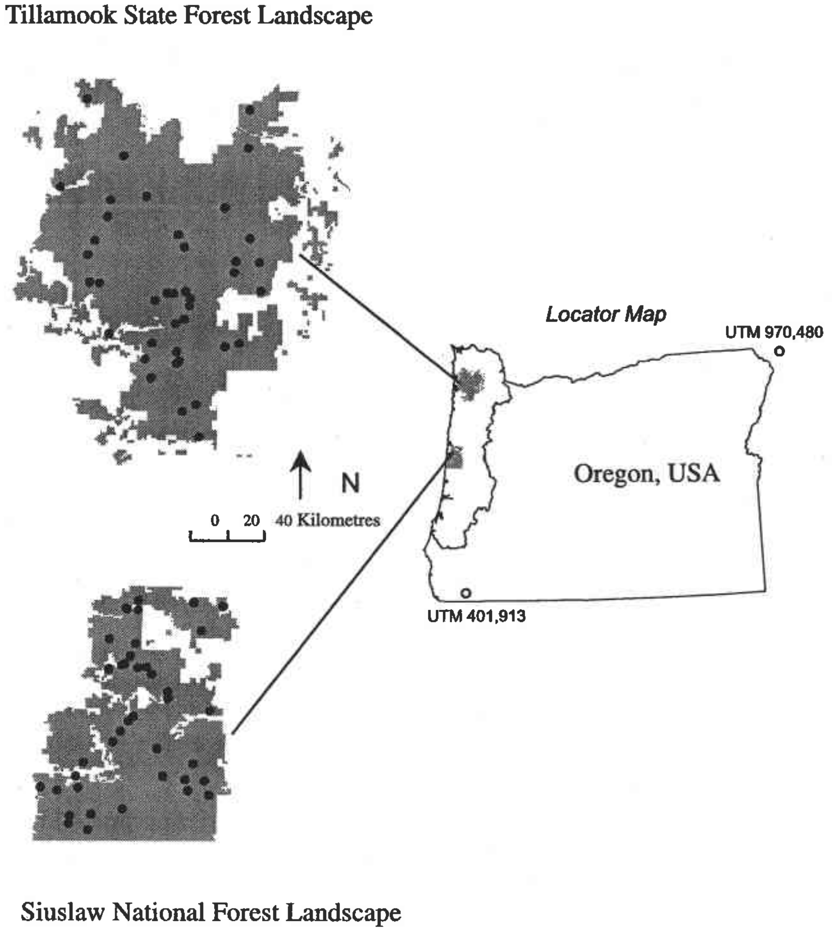
This study assessed patterns of dead wood abundance in two landscapes in the Coastal Province of Oregon, USA, to address these issues. The two landscapes differed in the time since high severity fire and in the subsequent type of post-fire management activities. These two landscapes were selected because much of the Coastal Province has been converted to young plantations and these two landscapes represented two remaining large, relatively contiguous areas in which potential landscape-scale historical effects on dead wood patterns could be evaluated.

The two specific objectives of the study were to (*i*) determine whether the two landscapes differed in the abundance and characteristics of dead wood and (*ii*) evaluate relationships of the dead wood characteristics in each landscape to potentially important biophysical features. In each landscape, we characterized the landscape history and evaluated relationships among dead wood attributes such as size and type (snag or log) and potentially related patterns and processes including live vegetation, topography, climate, historical vegetation, geology, ecoregion, and geographic location. We also focused on the potential effects of topography because topography is likely to have a strong effect on dead wood patterns in high-relief landscapes such as the mountainous terrain characteristic of the Coastal Province. We also evaluated whether some topographic positions exhibited patterns of accumulation that might result from source–sink redistribution of dead wood.

Study area

The Coast Range mountains run north–south in the

Fig. 1. Location of two landscapes in the Coastal Province of Oregon, USA. Points indicate locations of sample plots in each landscape. UTM (zone 10, datum NAD27) coordinates (km) are shown for the points located in the lower left and upper right corners of the locator map.

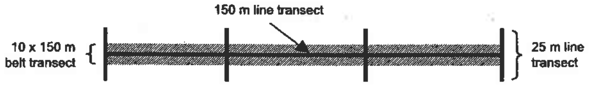


Coastal Province of Oregon, USA, and are characterized by steep and rugged terrain that is dissected by a dense network of intermittent and perennial streams. Elevations range from sea level to 1249 m over an east–west span of about 40 km. The climate is maritime, with mild wet winters and cool dry summers. Forest vegetation in the bulk of the area lies within the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) vegetation zone, while the westernmost extremes adjacent to the Pacific Ocean are in the Sitka spruce (*Picea sitchensis* (Bong.) Carrière) zone (Franklin and Dyrness 1988). Vegetation is dominated by conifers including Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock, and western redcedar (*Thuja plicata* Donn ex D. Don) with Sitka spruce along the coastal margin. Broadleaf trees (primarily red alder (*Alnus rubra* Bong.) and bigleaf maple (*Acer macrophyllum* Pursh)) occur in patches within the conifer matrix. Past disturbance in the Coast Range was characterized by stand replacement wildfire, which occurred with a mean fire frequency of about 200–300 years (Agee 1993), before the mid-1900s when fire suppression became effective. Other, finer-scale (<1 ha, years to decades) disturbances related to dead wood recruitment and transport include windthrow related to storms in the 1950s and 1960s, large floods in the 1960s and 1990s, periodic landslides and debris flows, and chronic mortality of Douglas-fir and western redcedar from laminated root rot fungus.

We studied two landscapes, parts of the Siuslaw National Forest and the Tillamook State Forest, that differed in the time since disturbance and management actions taken thereafter. The Siuslaw National Forest landscape, an area of about 1400 km^2 located in the central portion of the Coastal Province (Fig. 1), most recently underwent stand replacement fires between 1850 and 1880. Unmanaged stands were about 120–150 years old at the time of study based on analysis of increment cores of dominant site trees. Sampling in the Siuslaw was stratified to include only unmanaged mature and older forests because some parts of the Siuslaw have been converted to conifer plantations in recent decades.

The Tillamook State Forest landscape, an area of about 2100 km^2 located in the northwestern portion of the Coastal Province (Fig. 1), underwent a series of stand replacement fires between 1929 and 1951. Most of the landscape burned two to four times during this period (Chen 1997). Prior to these fires, much of the landscape consisted of old-growth forest, as determined by stand reconstruction research (R.S.H. Kennedy, unpublished data) and historical accounts (Levesque 1985; Fick and Martin 1992). Salvage logging after the fires resulted in fairly uniform removal of moderate

Fig. 2. Layout of transects used to sample logs, snags, and legacy stumps in forests of the Coastal Province of Oregon. Black lines indicate the 250 m line transect (logs); the grey area indicates the 1500 m^2 belt transect (snags and stumps). Transects followed the slope contour and were slope-corrected to obtain horizontal distance. The transect pictured is not to scale.



to high amounts of dead wood, as indicated by analysis of historical aerial photograph series (R.S.H. Kennedy, unpublished data) and Oregon Department of Forestry harvest records (Fick and Martin 1992). Approximately 7.5 billion board feet (roughly equivalent to 1.5 billion ft^3 or 42.5 million m^3) of timber were removed from the Tillamook between 1934 and 1955 (Oregon Department of Forestry 1997). Additional salvage of high-value, slow-decaying species, such as western redcedar, continued up to recent decades (Fick and Martin 1992). To prevent the spread of potential fires, several miles of roads were established along ridgelines and snags were felled in these zones (Fick and Martin 1992). The burned area was planted and aerially seeded after the fires, resulting in a fairly uniform, even-aged conifer forest of approximately 60–70 years of age at the time of study.

Methods

To address the objectives, dead wood was sampled throughout the two landscapes in plots located randomly at each of four topographic positions. Abundance patterns of dead wood were evaluated by size and type between the two landscapes. A suite of statistical models was developed describing the potential association of various sizes and types of dead wood with a suite of factors for each landscape.

Sampling design

Forty plots were sampled in each of the two landscapes using a stratified random sampling design. In each landscape, 10 plots were sampled at each of four topographic positions, stream lower, middle, and upper slopes, by locating the topographic zone nearest a randomly placed point in a GIS and establishing a transect in the field along the contour of the slope at each location. Selection of stream plots was further stratified to span the range of stream orders present in each landscape. For stream plots, transects followed the length of the stream (along stream centers for smaller streams and along the stream edge for larger streams). Lower slope plots were located within the lower third of the slope, outside the riparian zone to avoid direct fluvial influences, midslope plots within the center third of the slope, and upper slope plots within the upper third of the slope.

Data collection and preparation

To measure logs, snags, and legacy stumps (stumps from trees that originated in the previous stand) at each plot location, we established two slope-corrected (to obtain horizontal distance) transects originating at the same GPS-located point (Fig. 2). A 250 m line transect, comprised by one 150 m long transect and four 25 m transects located at 0, 50, 100, and 150 m along the long transect that were at right angles to and were bisected by the longer transect, was sampled for logs. All logs >1 m in length and >30 cm large-end diameter were measured and the following characteristics recorded: species, decay class, legacy status, distance along the transect, large-end diameter, small-end diameter, transect intercept diameter, length, whether the log was cut, presence of char (evidence of fire), and whether a root wad was attached, and for stream plots, the source (adjacent to stream (local) or transported from outside the immediate area), whether the log was in a jam, and if so, the number of pieces in the log jam. A 10 m × 150 m (1500 m^2) belt transect, centered on the line transect and running its length, was sampled for snags and legacy stumps. All snags >30 cm diameter at breast height (DBH) and all legacy stumps were measured and the following characteristics recorded: species, decay class, legacy status, distance along the transect (measured along the central line transect), height, DBH (where applicable), and whether bark was present. Where legacy stumps were shorter than breast height (1.3 m), species was identified, the stump height measured from the base, and DBH estimated by comparison with field observations of taper–DBH relationships in snags of the same species. Legacy stumps were measured to develop a more complete estimate of the basal area of the predisturbance stand than by snags alone where both snags and stumps were present and to establish a baseline, in combination with snag data, for the evaluation of potential source areas for dead wood, according to topographic position. For all dead wood pieces measured, it was noted whether the piece was from the current stand or from a legacy (previous) stand by evaluating the decay status and size in comparison with the age of the dominant trees present in the live stand. Decay classes 1–5 for dead wood pieces were identified in the field following standard protocols (Spies et al. 1988). Class 1 logs and snags are intact, not decayed, whereas class 5 logs and snags are most decayed, as indicated by characteristics of branches, limbs, bark remaining, sapwood and heartwood condition, and height (snags). Several characteristics of the live stand were also recorded, including the two dominant overstory species, the two dominant understory species, the species, DBH, and age of one representative dominant tree, the species and DBH of one representative smaller tree, and the basal area of the stand at 0, 50, 100, and 150 m along the transect.

Several characteristics related to the size and abundance of dead wood were calculated. These included the number of logs, log volume ($m^3 \cdot ha^{-1}$), log biomass ($Mg \cdot ha^{-1}$), log carbon ($Mg\ C \cdot ha^{-1}$), the number of snags (ha^{-1}), snag basal area ($m^2 \cdot ha^{-1}$), snag volume ($m^3 \cdot ha^{-1}$), snag biomass ($Mg \cdot ha^{-1}$), snag carbon ($Mg\ C \cdot ha^{-1}$), the number of legacy stumps (ha^{-1}), legacy stump basal area ($m^2 \cdot ha^{-1}$), and total dead wood volume ($m^3 \cdot ha^{-1}$). To calculate the volume of logs, we used the Smalian formula $V = ((A_1 + A_2)/2) \times L$, where V is the volume of the log (m^3), A_1 is the area of the small end (m^2), A_2 is the area of the large end (m^2), and L is the length of the log (m) (Avery and Burkhart 1994). We summarized the volume (m^3) per hectare that each log represented on the plot using the following equation (modified from DeVries 1973): LOGVOLPH = (3.1416/(2 × PLOTLEN) × (LOGVOL/LOGLEN)) × 10 000, where LOGVOLPH is the log volume (m^3) per hectare, PLOTLEN is the length of the plot transect (m), LOGVOL is the volume of the log (m^3), and LOGLEN is the length of the log (m). To calculate log biomass, we used the following equation: LOGBIOMKGH = LOGVOLPH × 1000 × SPGRAV × DCR, where LOGBIOMKGH is the biomass of logs ($kg \cdot ha^{-1}$), LOGVOLPH is the log volume (m^3) per hectare, and SPGRAV and DCR are specific gravity and decay reduction factors that vary by tree species (Waddell 2002). To calculate log carbon, we multiplied LOGBIOMKGH by the proportion of wood biomass that is carbon for the type of species (softwood or hardwood). We used the same types of equations to calculate the biomass and carbon of snags. To calculate the volume of snags, we used the Kozak equation, which is a polynomial equation that incorporates species-specific taper coefficients (Garman et al. 1995) and is based on height–DBH relationships. The Kozak equation is $V = 0.0000785 \times \mathrm{DBH}^2 \times X$, where V is the volume of the snag (m^3) and $X = \beta_0 \times h_1 + (\beta_1/2) \times (h_1^2/h) + (\beta_2/3) \times (h_1^3/h^2)$. In calculating X, the betas (β) are the species-specific taper coefficients, h_1 is the actual height, and h is the potential full height of the snag. The Kozak equation is considered to be more accurate than the Smalian equation, which may over- or under-estimate log volumes depending on the degree of taper of the bole and from where along the bole the log originates (Ministry of Forests of the Province of British Columbia 2005). However, we did not know from where along the bole of the tree each field-sampled log had originated. We therefore determined that using the Kozak equation under these circumstances would be questionable for logs. We summarized the results for logs by size for the size classes <50 and >50 cm large-end diameter because distinguishing between small and large logs provides important information to managers of wildlife in western forests (Laudenslayer et al. 2002). For parametric statistical tests, the number of logs, log volume, number of snags, snag volume, snag basal area, and total dead wood volume required the logarithmic transformation to meet assumptions of normality.

We obtained information about a suite of factors that could potentially assist in explaining observed patterns of dead wood in landscapes from a GIS and from field sampling. All GIS analyses were performed in ArcInfo (Environmental Systems Research Institute, Inc. 2002). Digital data layers were converted to grids for subsequent analysis. Factors related to topography included elevation (m), slope (%), slope position (relativized, from 0 (bottom of drainage) to 100 (ridgetop)), aspect, and topographic position class (stream, lower, middle, or upper slope) and were derived from a 30 m digital elevation model, with the exception of topographic position class, which was obtained during field sampling and through evaluation of digital raster graphics of US Geological Survey standard series topographic maps. Slope position was calculated using a published Arc Macro Language (AML) (Environmental Systems Research Institute, Inc. 2002) using default parameters for all arguments. Aspect was transformed using the Beers transformation ASPTR = COS(45 – ASP) + 1 (Beers et al. 1966) so that for the most exposed plots (southwest), aspect = 0.0, and for the least exposed plots (northeast), aspect = 2.0. We determined whether plot locations were inside or outside 50 and 100 m buffers from streams. Climate-related variables included several variables for precipitation, solar radiation, temperature, and humidity and were obtained from DAYMET (Thornton et al. 1997). We also obtained data for geologic substrate (Walker and MacLeod 1991) and ecoregions. Information about historical vegetation was obtained from a digital version of the 1936 Forest Survey Type Map (Andrews and Cowlin 1940).

We acquired current vegetation data and related factors through field sampling and from LANDSAT Thematic Mapper (TM) satellite imagery from 1996. We considered two remote sensing based variables, tasseled cap wetness and tasseled cap greenness (Kauth and Thomas 1976), that have demonstrated relationships with forest vegetation in the Pacific Northwest region (Cohen et al. 2001). Greenness has been associated with total vegetation cover and percent broadleaf cover and wetness with vegetation structure (stand age and crown diameter). We also considered the Landsat TM band ratio 5:7, filtered twice in succession using a 3 pixel × 3 pixel window to reduce fine-scale heterogeneity. This has been shown to be a significant variable in the predictive mapping of forest composition and structure (including attributes of dead wood) research (Ohmann and Gregory 2002).

To reduce the set of variables related to environmental and site factors for statistical model development (see Data analysis section below), we examined a correlation matrix for all variables. Variables were retained that were not highly correlated ($|r| < 0.8$). If two variables were highly correlated, we kept the one that had the lowest correlation with other variables and included it. In this way, for each landscape, we developed a final, reduced set of variables to consider in statistical modeling (Table 1) with the goal that the selected variables would represent unique attributes of each landscape. However, we also considered these variables in the context of grouped sets, such as topography, climate, current vegetation, historical vegetation, geology, and location, in assessing general relationships among variables and dead wood patterns. We did this because typically the variables in each set were related, and because they tended to be characteristic of a scale of pattern or process.

Data analysis

Weighted mean and median values for each plot for each dead wood variable for each landscape were calculated. Weights were based on the proportional area of each topographic position in the landscape, based on GIS analysis. For Tillamook State Forest, the proportional areas used were as follows: upper, 0.209; middle, 0.255; lower, 0.469; streams, 0.067. For Siuslaw National Forest, the proportional areas used were as follows: upper, 0.263; middle, 0.266; lower, 0.409; streams, 0.062. The area of streams was estimated by applying a 25 m buffer (12.5 m per side) to the linear streams coverage. To test for differences among landscapes, we performed two-sided Wilcoxon rank sum tests on the medians because dead wood data are commonly skewed and therefore tests of difference between means would not

Table 1. Mapped explanatory variables considered in stepwise regression models and CCA.

Variable code	Definition
Topography	
ELEV	Elevation (m), from 30 m digital elevation model (DEM)
ASPTR	Cosine transformation of aspect (degrees) (Beers et al. 1966), 0.0 (southwest) to 2.0 (northeast), from 30 m DEM
SLPPCT	Slope (percent), from 30 m DEM
SLPPOS	Slope position, from 0 (bottom of drainage) to 100 (ridgetop), from 30 m DEM
STREAM	In-stream plot
LOWER	Lower slope plot
MIDDLE	Midslope plot
UPPER	Upper slope plot
STRMBUF50	Within 50 m of streams
STRMBUF100	Within 100 m of streams
Climate	
ANNFROST	Total number of days, annually, where the daily minimum air temperature is ≤0.0 °C (ln for Tillamook)
ANNSW	Total annual shortwave radiation ($MJ \cdot m^{-2} \cdot day^{-1}$)
ANNHDD	Total annual heating degree-days, the summation of the difference between 18.3 °C and the daily average air temperature, for days when the average air temperature is <18.3 °C (ln)[a]
ANNPRE	Mean annual precipitation (ln, mm)[a]
AUGMAXT	Mean maximum temperature in August (°C)
CONTPRE	Percentage of mean annual precipitation falling in June–August
DIFTMP	Difference between August maximum temperature and December minimum temperature (°C)[b]
SMRPRE	Mean precipitation from May to September (ln, mm)[a]
SMRTP	Moisture stress during the growing season, calculated as SMRTMP/SMRPRE, where SMRTMP is the mean temperature in May–September ($°C \cdot (ln, mm)^{-1}$) (ln)[b]
Current vegetation	
LIVEBA	Basal area of live trees ($m^2 \cdot ha^{-1}$)
Landsat TM	
WET	Wetness axis from tasseled cap transformation, twice median filtered
GRN	Greenness axis from tasseled cap transformation, twice median filtered (ln for Siuslaw)
R57	Ratio of band 5 to band 7, twice median filtered (ln for Tillamook)
Historical vegetation	
HVDFOG	Historical vegetation (1936) was Douglas-fir old growth; forest was over 60% Douglas-fir, old-growth >55.9 cm DBH
HVDFLSG	Historical vegetation was Douglas-fir large second growth; forest was over 60% Douglas-fir, second-growth >55.9 cm DBH
HVDFSSG	Historical vegetation was Douglas-fir small second growth; forest was over 60% Douglas-fir, between 15.2 and 50.8 cm DBH
HVAAM	Historical vegetation was hardwood type of alder–ash–maple; a timberland type with alder, ash, and (or) maple predominating
HVRC	Historical vegetation was recent cutover
HVNF	Historical vegetation was nonforest land other than agriculture
Ecoregion	
UPL	Coastal uplands[c]
VOL	Volcanics[c]
Geology	
VOLC	Volcanic and intrusive rocks[d]
MAFO	Mafic rocks (basalt, basaltic andesite, andesite, gabbro); Miocene and older[d]
SEDR	Sedimentary rocks (siltstones, sandstones, mudstones, conglomerates)[d]
Location	
X	Latitude (m, UTM zone 10)
Y	Longitude (m, UTM zone 10)

[a] Regression, Siuslaw only.

[b] Regression, Tillamook only.

[c] CCA, Siuslaw only.

[d] CCA, Tillamook only.

meet normality assumptions (Ohmann and Waddell 2002). However, reporting of means for dead wood amounts is commonplace (Spies et al. 1988; Ohmann and Waddell 2002), so some mean values are reported here as well to ease comparison with other studies.

Several statistical tests were employed to evaluate relationships between patterns of dead wood and potential explanatory factors. We used stepwise regression to relate individual dead wood attributes, such as the volume of logs, to environmental and site variables. We used nonparametric statistics including the Wilcoxon rank sum and Kruskal–Wallis tests (Conover 1998) to determine whether there were differences in the observed patterns of dead wood between landscapes and between topographic positions within landscapes. We used canonical correspondence analysis (CCA) (ter Braak 1986) to describe the dominant factors associated with overall gradients of dead wood. CCA has been shown to perform well with skewed distributions of response variables and with highly intercorrelated environmental variables (Palmer 1993). In CCA, we included the following dead wood attributes in the set of response variables: dead wood volume, number of logs, log volume, number of snags, snag basal area, snag volume, and snag plus stump basal area, log-transforming these response variables when necessary to meet the required normality assumptions. We omitted variables related to ecoregion in the CCA in the Tillamook landscape and geology from consideration in the CCA in the Siuslaw landscape because there was inadequate between-plot variation in these factors for CCA, but included all other variables from the set of potential explanatory factors in CCA (Table 1). We conducted a preliminary CCA on the full set of potential explanatory factors to determine how much of the variability in dead wood patterns is explained by these factors and then conducted individual CCAs on each subset of factors (i.e., inclusion of only the variables in the topography group, etc.) to determine the relative contribution to explained variation in the response variables by each explanatory variable subset. This approach presumes that there is some association among variables between explanatory variable subsets and allows for the description of the strength of relationships of the factors within each subset (i.e., topography) to the variation in the set of response variables (i.e., the suite of dead wood-related variables).

Results

Amount and characteristics of dead wood

Total dead wood volume was not significantly different between the Tillamook and Siuslaw landscapes, but there were several differences in other characteristics of dead wood between the two landscapes, including the relative abundance of snags and logs to the total amount and the contribution of legacy wood (Table 2). The Tillamook had a higher volume of logs, comprised mainly by very large logs (>100 cm large-end diameter) (Table 3). Snags of all sizes were far more common in the Siuslaw (Table 3), resulting in higher volumes of snags there, with the exception of large tall snags (>50 cm DBH, >15 m height), amounts of which were low and did not differ between the two landscapes (Table 3). The Siuslaw had a large number of >100 cm DBH snags (ha^{-1}), and these large-diameter snags were about 60% of the total volume of snags. Median volume of legacy logs was greater in the Tillamook, whereas median volumes of nonlegacy logs and nonlegacy snags were greater in the Siuslaw, as was the volume of legacy snags (Table 2). Most of the snags present in the Tillamook were legacy snags >50 cm DBH (Tables 2 and 3). These legacy wood differences offset each other such that total dead wood volume (legacy and nonlegacy combined) did not differ between the two landscapes. Biomass and carbon patterns were similar to those of volume for both landscapes (Table 2). The Tillamook had a higher combined basal area of legacy snags and stumps than the Siuslaw.

Much of the volume and biomass of dead wood in both landscapes was in the form of large pieces (Table 3) and were of decay classes 3 and 4 (Fig. 3). For example, about 45% of the total volume of dead wood in the Tillamook was of logs and snags >100 cm large-end diameter or DBH, and almost 70% of this was of large logs. In the Siuslaw, 32% was in pieces >100 cm. The Tillamook had higher mean volume and mass of decay class 3 logs and snags than the Siuslaw (logs: $p < 0.0001$, snags: $p = 0.01$; paired t tests), whereas the Siuslaw had higher mean volume and mass of decay class 2 and 5 logs and decay class 2 snags than the Tillamook (Fig. 3). Measured amounts of decay class 5 logs and snags were very low in both landscapes.

Factors related to dead wood abundance

In the Tillamook State Forest, the regression models with the highest R^2 values were for nonlegacy dead wood (Table 4). Independent variables related to topography were of greatest importance in these models, with lower elevations associated with the highest nonlegacy dead wood and log volumes and lower slope positions with higher nonlegacy dead wood biomass and numbers of logs. For nonlegacy logs, climate-related factors were also important, with a positive association between log volume and annual frost. The historical hardwood vegetation type was positively associated with nonlegacy snag volume and basal area, as was riparian location (Table 4). Numbers and basal areas of legacy snags and legacy stumps were positively associated with higher elevations.

In the Siuslaw National Forest, the regression models with the highest R^2 values were related to snags (Table 4). Current vegetation, historical vegetation, and distance to streams were the most important independent variables in these models. Total number of snags and number, volume, and basal area of nonlegacy snags were positively associated with live tree basal area. Volume, number, and basal area of legacy and total snags were negatively associated with areas of hardwoods (i.e., higher greenness). Snags tended to be found outside near-stream areas: nearly all models describing snag characteristics indicated a negative relationship of snag abundance with stream topographic locations and (or) the 50 m stream buffer. Legacy snag volume and biomass were positively associated with historical hardwoods, whereas nonlegacy snag volume and basal area were positively associated with the occurrence of historical small second-growth Douglas-fir. Climate was also of some importance: total snag biomass and legacy snag and stump

Table 2. Weighted mean, SE, and median dead wood amounts (ha^{-1}) for two landscapes with different histories located in the Coastal Province of Oregon.

	Tillamook State Forest			Siuslaw National Forest			
Dead wood variable	Mean	SE	Median	Mean	SE	Median	p
Total dead wood							
Dead wood volume (m^3)	275.7	31.9	218.7	282.6	32.1	251.4	ns
Legacy dead wood volume (m^3)	265.3	31.6	190.2	192.7	25.6	124.8	0.02
Nonlegacy dead wood volume (m^3)	10.4	3.0	0.0	90.0	14.2	70.0	<0.0001
Dead wood biomass (Mg)	73.0	9.2	54.6	73.9	8.5	61.0	ns
Legacy dead wood biomass (Mg)	69.7	9.1	53.8	45.4	6.3	30.0	0.009
Nonlegacy dead wood biomass (Mg)	3.4	1.0	0.0	28.5	4.6	20.4	<0.0001
Dead wood carbon (Mg)	38.0	4.8	28.3	38.4	4.4	31.8	ns
Legacy dead wood carbon (Mg)	36.3	4.7	28.0	23.6	3.3	15.7	0.009
Nonlegacy dead wood carbon (Mg)	1.7	0.5	0.0	14.8	2.4	10.6	<0.0001
Logs							
Number of logs	168.6	18.4	154.8	163.4	20.7	117.6	ns
Number of legacy logs	159.1	18.5	125.2	89.9	11.5	70.6	0.0007
Number of nonlegacy logs	9.5	2.8	0.0	73.6	13.3	40.3	<0.0001
Log volume (m^3)	226.7	27.6	190.2	176.1	23.2	130.2	0.04
Legacy log volume (m^3)	216.8	27.9	160.0	109.3	16.8	69.4	0.0003
Nonlegacy log volume (m^3)	9.8	2.9	0.0	66.8	11.3	42.8	<0.0001
Log biomass (Mg)	60.4	8.1	51.0	46.6	6.6	36.1	0.07
Legacy log biomass (Mg)	57.2	8.2	40.7	26.3	4.4	16.2	0.0003
Nonlegacy log biomass (Mg)	3.2	0.9	0.0	20.3	3.5	11.4	<0.0001
Log carbon (Mg)	31.5	4.2	26.6	24.2	3.4	18.8	0.07
Legacy log carbon (Mg)	29.8	4.3	21.2	13.7	2.3	8.5	0.0004
Nonlegacy log carbon (Mg)	1.6	0.5	0.0	10.5	1.8	6.0	<0.0001
Snags							
Number of snags	11.9	2.1	6.7	47.8	5.8	40.0	<0.0001
Number of legacy snags	11.0	2.0	6.7	32.2	4.8	20.0	0.002
Number of nonlegacy snags	0.9	0.5	0.0	15.6	3.1	6.7	<0.0001
Snag volume (m^3)	49.0	15.8	6.4	106.6	15.1	95.1	0.0006
Legacy snag volume (m^3)	48.5	15.8	6.4	83.4	14.4	46.4	0.01
Nonlegacy snag volume (m^3)	0.5	0.3	0.0	23.2	5.7	5.4	<0.0001
Snag biomass (Mg)	12.6	4.6	1.2	27.3	3.8	24.3	0.0003
Legacy snag biomass (Mg)	12.5	4.6	1.2	19.1	3.4	9.1	0.01
Nonlegacy snag biomass (Mg)	0.2	0.1	0.0	4.3	1.1	0.6	<0.0001
Snag carbon (Mg)	6.6	2.4	0.6	14.2	2.0	12.7	0.0003
Legacy snag carbon (Mg)	6.5	2.4	0.6	10.0	1.8	4.7	0.01
Nonlegacy snag carbon (Mg)	0.1	0.1	0.0	4.3	1.1	0.6	<0.0001
Snag basal area (m^2)	8.8	2.1	3.3	25.9	3.6	21.2	0.0005
Legacy snag basal area (m^2)	8.6	2.1	3.3	21.8	3.5	14.6	0.005
Nonlegacy snag basal area (m^2)	0.2	0.1	0.0	4.1	0.9	1.3	<0.0001
Number of legacy stumps	49.8	5.5	33.3	17.4	6.3	6.7	<0.0001
Legacy stump basal area (m^2)	49.5	4.2	49.8	10.9	4.3	2.0	<0.0001
Legacy snag plus stump basal area (m^2)	58.1	5.1	59.2	32.7	4.7	26.5	0.0004

Note: p values from Wilcoxon rank sum tests of differences between medians (ns, not significant).

basal area were negatively associated with lower August maximum temperature, and the number of nonlegacy snags was positively associated with higher annual precipitation. Likewise, the abundance, volume, and biomass of nonlegacy logs and the total volume of nonlegacy dead wood were positively associated with sites with higher summer precipitation and more frost-free days per year (Table 4).

In both landscapes, CCA indicated that overall gradients in dead wood were most strongly associated with topography followed by climate and current vegetation, in that order (Table 5). In the Siuslaw, climate and location were somewhat more important than in the Tillamook. Biplots of axes 1 and 2 indicated that in the Tillamook, snag variables grouped with higher slope positions and high-elevation streams, and log volume and number grouped with lower slope positions. In the Siuslaw, snag variables grouped away from stream plots in areas with more summer rains, and log volume and number and dead wood volume variables grouped near stream plots and in areas with higher August maximum temperatures. In the Tillamook, the full model explained 63% of the total explained variation and in the Siuslaw explained 79%.