

Relationships of dead wood patterns with biophysical characteristics and ownership according to scale in Coastal Oregon, USA

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Abstract Dead wood patterns and dynamics vary with biophysical factors, disturbance history, ownership, and management practices; the relative importance of these factors is poorly understood, especially at landscape to regional scales. This study examined current dead wood amounts in the Coastal Province of Oregon, USA, at multiple spatial scales. Objectives were to: (1) describe current regional amounts of several characteristics of dead wood; (2) compare dead wood amounts across ownerships; (3) determine the relative importance, according to spatial scale, of biophysical and ownership characteristics, to regional dead wood abundance. Dead wood plot data were evaluated with respect to explanatory variables at four spatial scales of resolution: plots, subwatersheds, watersheds and subbasins. The relationships of dead wood characteristics with biophysical attributes and ownership were diverse and scale-specific. Region-wide dead wood abundance and types varied among ownerships, with public lands typically having higher amounts of dead wood and more large dead wood than private lands. Regression analysis of total dead wood

volume indicated that ownership was important at the subbasin scale. Growing season moisture stress was important at plot, subwatershed, and watershed scales. Topography was important at the two coarser scales. Multivariate analysis of dead wood gradients showed that ownership was important at all scales, topography at the subbasin scale, historical vegetation at watershed and subbasin scales, and current vegetation at plot and subwatershed scales. Management for dead wood and related biodiversity at watershed to landscape scales should consider the distinct dynamics of snags and logs, the importance of historical effects, and the relevance of ownership patterns.

Keywords Coarse woody debris · Snags · Logs · Legacy · Forest management · Landscape ecology · Topography · Forest history · Climate · Coast range

Introduction

Dead wood is an important component of forest ecosystems, through its influences on biodiversity, long-term forest productivity and carbon sequestration, and the structure and dynamics of riparian ecosystems (Harmon et al. 1986; Lindenmayer and Franklin 2002; Maser et al. 1988). However, because dead wood is difficult to quantify over large areas using satellite imagery or other remote sensing technologies such as laser altimetry (Lidar) (Lefsky et al. 2002; Wulder and Franklin 2003), relatively

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few studies have addressed dead wood patterns and related processes at landscape to regional scales (Butler and Schlaepfer 2004; Ohmann et al. 2007; Poulos et al. 2007). Furthermore, whereas the ecological importance of specific dead wood attributes (e.g., individual large, tall snags, or large logs) has been widely noted, these dead wood attributes are not accounted for by the broader land cover or fuels classifications typically used in landscape ecology research, except by inference (Wimberly and Ohmann 2004). We took advantage of a large, spatially referenced forest inventory to assess dead wood patterns and relationships with biophysical variables at multiple spatial scales from mid-sized watersheds to a physiographic region.

Understanding patterns and processes related to dead wood abundance may be aided by examining multiple spatial and temporal scales, because factors related to vegetation patterns and biodiversity may differ according to scale (Levin 2000; Wu 2004). For example, infrequent large stand replacement fires may produce high amounts of dead wood, whereas frequently recurring, small, low-severity fires may reduce dead wood amounts at finer temporal and spatial scales (Skinner 2002). Post-fire live vegetation patterns also influence subsequent dead wood production potential. In managed forests, harvest frequency and intensity may be related to dead wood amounts and types; regional vegetation patterns have been found to be associated with ownership-specific management (Ohmann et al. 2007). Landslides and floods contribute to dead wood production, migration, and repositioning, especially near streams or on steep slopes (Maser et al. 1988). Upper slope positions may be source areas and riparian areas and streams sinks for dead wood (Kennedy and Spies 2007), and site productivity and species composition are linked to topography (Pabst and Spies 1999). Soils and regional climate gradients are also related to site productivity, influencing large tree and subsequent dead wood production potential. Microclimate conditions also influence decomposition rates of dead wood (Harmon et al. 1986).

The comparative importance of these factors to dead wood abundance at different scales remains unclear, but is relevant for several reasons. First, landscapes are often managed both for long-term and broad spatial scale ecological goals such as older forest conditions, and individual structures such as

snags and logs, to support biodiversity goals (U.S.D.A. Forest Service and U.S.D.I. Bureau of Land Management 1994). Managers need frameworks for developing objectives and expected trends for dead wood across large diverse areas. Second, species and ecological processes may cross ownership lines, and elucidating ownership-specific patterns can assist habitat assessment. Third, present-day dead wood patterns may not reflect current management because they were generated by past events and the decomposition time of large dead wood may exceed the duration of management plans (Sollins 1982); hence, effects of management on long-term dead wood abundance may be masked if the relative contribution of legacy (from the previous stand) dead wood is unknown. Fourth, the efficacy of forest management to achieve goals related to dead wood retention or production may be limited without an understanding of the controls on patterns of dead wood and how they vary by scale.

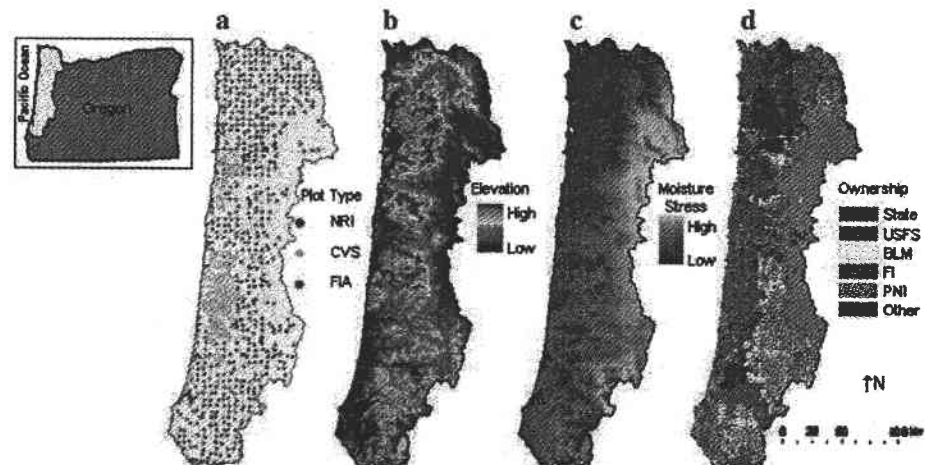
This study evaluated current patterns of dead wood and related patterns and processes in the Coastal Province of Oregon, USA, at multiple spatial scales, from plots to subbasins. The study had three objectives: (1) describe current regional amounts of several characteristics of dead wood; (2) compare dead wood amounts across ownerships; (3) determine the relationship of dead wood abundance to current and past vegetation conditions, ownership, climate, topography, and soils, and characterize how these relationships vary with spatial scale.

Methods

Study area

The study area was the Coastal Province of Oregon, a mountainous region of approximately 30,000 km², in the Pacific Northwestern USA (Fig. 1). Elevation ranges from sea level to 1,247 m and there is a dense stream network. The maritime climate has warm, dry summers and cool, wet winters; high levels of precipitation (2500–3000 mm yr⁻¹) occur primarily as winter rains or snow. Growing-season moisture stress increases with ocean distance as temperature increases and precipitation decreases. Soils are derived mainly from marine sandstones and basaltic volcanics (Franklin and Dyrness 1988).

Fig. 1 Attributes of coastal Oregon, USA: (a) plot locations, (b) elevation, (c) moisture stress index, and (d) ownership. See text for description of plot types



The Coastal Province is in the western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) vegetation zones (Franklin and Dyrness 1988). Dominant tree species include Douglas-fir (*Pseudotsuga menziesii*), western hemlock, western redcedar (*Thuja plicata*), and Sitka spruce, the latter prevalent near the coast. Hardwood trees, especially red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*), occur in patches in the coniferous matrix, often near streams or on recently disturbed sites (Franklin and Dyrness 1988; Kennedy and Spies 2005).

Land ownership is mainly public (Forest Service, Bureau of Land Management, State of Oregon) or forest industry, and is not strongly differentiated by topography; non-industrial private land ownership tends to occur in the valleys. Bureau of Land Management holdings tend to be interspersed with forest industry lands, whereas Forest Service, forest industry, and State lands tend to occur in larger blocks (Fig. 1). Forest age is typically up to 150 years on public lands and up to 60 years on private lands. Land ownership changes in the past several decades have occurred primarily within and not between the three main ownerships (federal, forest industry, non-industrial private).

Prior to Euro-American settlement and more recent (mid-1900s) fire suppression, forest patterns in the Coastal Province were mainly influenced by large, high severity fires with a mean fire return interval of 200–300 years (Agee 1993). Large fires in the past two centuries occurred on lands currently owned by the State (1868; 1929–1951), and the Forest Service (1850s–1880s). Windstorms also felled many trees. Historically, frequent burning at

the forest margins was conducted by native Americans. Euro-American settlement and timber harvest selectively removed large trees, and forests were cleared for grazing and farming in the latter 1800s to mid-1900s. In the early 1900s, railroad-based logging was prevalent. Thereafter, most coastal forests were intensively managed for timber production until the early 1990s, when large areas of the federal lands were designated as reserves for the northern spotted owl (*Strix occidentalis*) and marbled murrelet (*Brachyramphus marmoratus*).

Data sources

Dead and live vegetation data were obtained from field plot samples established for regional forest inventories: Current Vegetation Survey (CVS) (Siuslaw National Forest, $n = 317$, measured 1993–1996), Forest Inventory and Analysis (FIA) (nonfederal lands, $n = 497$, measured 1997), Natural Resources Inventory (NRI) (Bureau of Land Management, $n = 116$, measured 1997) (Fig. 1). All plots were regularly spaced at 5.5 km apart excepting CVS plots (2.75 km apart), were about 1 ha in size, and were forested. Data were combined into a consistent format and summary variables calculated for live vegetation and dead wood attributes, on a units per hectare basis for uniform land cover condition classes in each plot. Because plot sampling densities were non-uniform across component datasets, weighted mean values were calculated for area-based measures of plot data; e.g., CVS plot mean values had one-fourth the weight of other plot mean values. The minimum piece sizes

considered were 12.5 cm diameter at breast height (dbh) and 2 m tall for snags, and 12.5 cm large-end diameter (led) and 1 m long for logs; this was the minimum uniform size across the three datasets. Summary statistics were calculated for each plot for the number and volume of snags ($\text{m}^3 \text{ha}^{-1}$) of various sizes, snag biomass (Mg ha^{-1}), snag carbon (Mg C ha^{-1}), number and volume of legacy snags, and percent of all snags that are legacy. Summary statistics for logs included the volume of logs for various sizes of logs, log biomass, log carbon, volume of legacy logs, and percent of all logs that are legacy. Legacy dead wood was defined as that which was produced by a previous forest stand, as determined by comparison of diameters and decay classes with characteristics of the present-day stand, after field data collection. Dead wood was considered as legacy if either (1) plot has <40% cover and snag or log is ≥ 50 cm dbh; or (2) plot has $\geq 40\%$ cover, plot quadratic mean diameter (QMD) is <50 cm, and snag or log dbh is at least 50 cm greater than the plot QMD. Plot-level summarized dead wood data were converted into a point coverage in a GIS using geographic coordinates obtained for each plot.

A suite of 98 potential explanatory variables were evaluated based on hypothesized relationships with dead wood and on mapped data availability. Some of the variables are associated with patterns of live vegetation in the region (Ohmann and Spies 1998). To obtain mean (for continuous variables) or maximum (for categorical variables) plot values for each mapped explanatory variable, plot locations, defined as a window of 13, 30 m pixels arranged in a diamond pattern and centered by the plot's X and Y coordinates, were superimposed on 30-m-resolution GIS grids of each variable as described in Ohmann et al. (2007). This shape approximates the plot's layout on the ground (Ohmann et al. 2007). Climate variables were obtained from Daymet (Thornton et al. 1997) rasters at 1 km resolution based on 18 years of weather station data. Topography-related variables were derived from a digital elevation model having 30 m resolution, excepting potential relative radiation (Pierce et al. 2005) and topographic position index (calculated as the difference between a cell's elevation and the mean elevation of cells within a 300 m radius window). Land ownership data originated from a GIS coverage based on many data sources including fire protection district maps and

county assessor plats; it was considered current for 1990–1996. Geologic types were obtained from a digitized geologic map of Oregon (Walker and MacLeod 1991). Ecoregions originated from a digitized map of Pacific Northwest Ecoregions. Historical vegetation information was obtained for 1936 from a digitized forest vegetation map (minimum mapping unit of about 16 ha) developed by the Pacific Northwest Research Station from surveys conducted between 1933 and 1936 (Andrews and Cowlin 1940). Historical vegetation data for 1900 was from a digitized Oregon map of timber resources surveyed by township between 1898 and 1902 obtained from the BLM.

Data analysis

Statistical analyses were conducted at four scales across the Coastal Province region. From the finest to coarsest grain size, these scales were: plots ($n = 930$), subwatersheds (6th code hydrologic units (HUs), $n = 345$), watersheds (5th code HUs, $n = 84$), and subbasins (4th code HUs; $n = 18$). Subwatersheds had a maximum size of about 225 km^2 , watersheds $1,265 \text{ km}^2$, and subbasins $3,260 \text{ km}^2$. The hydrologic units-level analyses were conducted by summarizing plot-level data for each hydrologic unit, as follows: for continuous variables, mean per hydrologic unit; for categorical variables, percent of hydrologic unit in each class. Subwatersheds were nested within watersheds, and watersheds within subbasins. We used hydrologic units because they provided a means of linking plot data to riparian and in-stream processes, which have been strongly associated with dead wood patterns (Bisson et al. 1986; Fetherston et al. 1995).

Median values were calculated for each plot for each dead wood variable, and for each ownership type. To test for differences among ownership groups, two-sided Wilcoxon rank-sum tests were performed on the medians, because dead wood data are commonly skewed and would not meet normality assumptions (Ohmann and Waddell 2002). Weighted mean values are reported (Appendix A) for each plot for each dead wood variable, province-wide and for ownership groups, to facilitate comparison with other studies (Ohmann and Waddell 2002; Spies and Cline 1988).

Stepwise multiple linear regression was conducted for total dead wood volume on a suite of biophysical factors and forest management at plot, subwatershed, watershed, and subbasin scales. Univariate statistical analyses were carried out using SAS (SAS Institute Inc. 2004). Twelve candidate explanatory variables were considered (Table 1) at all scales, after the following selection process: (1) we omitted those that were highly correlated ($|r| > 0.8$) with any other candidate variable at a given scale; (2) we transformed skewed variables; (3) we developed an up-to-6-variable stepwise multiple linear regression model for each single dead wood variable at each scale; (4) we evaluated variables that appeared in a range of univariate models and scales, to ensure inclusion of variables with relatively high R^2 values for at least one univariate model at each scale; and (5) we retained two variables from each of six subsets of factors (climate, topography, current vegetation, ownership, historical vegetation, ecoregion/geology) (Table 1). Regression models were developed such that each explanatory variable must have a partial R^2 value of at least 0.05 to remain in the model. We carried out statistical tests using a permutation test under the reduced model, following the procedure and rationale described by Wimberly and Ohmann (2004).

The multivariate relationships of dead wood gradients to potentially related factors were

assessed for multiple scales using Canonical Correspondence Analysis (CCA) (ter Braak 1986). Seventeen dead wood variables were included, to span the variety of dead wood attributes (Table 2). The analysis included all sample units containing dead wood; 27 plots and eight subwatersheds with no dead wood were omitted. Because CCA is sensitive to the number of explanatory variables considered in relation to the number of sample units, the 96 explanatory variables were reduced to the same 12 variables used for multiple linear regression of dead wood volume. The contribution of explanatory variable sets to explained variation in dead wood gradients was calculated. For each CCA model, all significant explanatory variables ($P < 0.05$) were included. A Monte Carlo permutation test on the reduced model with 999 permutations (H_0 : no relationship between matrices) was used to test for significance. To determine the percentage of total inertia contributed by each subset of explanatory variables and avoid confounding correlation among variables from different subsets, subset-CCAs were conducted. The relative contribution to explained variation was reported by subsets of variables summarized for Axes 1 and 2. Multivariate analyses were conducted using the computer programs PC-ORD (McCune and Mefford 1999). and CANOCO (ter Braak and Smilauer 1997).

Table 1 Mapped explanatory variables included in scale-related analyses of dead wood in Coastal Oregon after reduction from a 96-variable set of candidate variables

Variable code	Class-Definition
ANNGDD	Climate-Total annual growing degree days
SMRTP	Climate-Moisture stress during the growing season, calculated as $SMRTMP/SMRPRE$, where SMRTMP is the mean temperature in May–September ($^{\circ}C(mm)^{-1}$) and SMRPRE is mean precipitation from May to September(mm)
RIVBUF100	Topography-Within 100 m of streams
SLPPCT	Topography-Slope(percent), from 30-m DEM
USFS	Land Ownership-USDA Forest Service
NIP	Land Ownership-Non-industrial private
QMDAALL	Current Vegetation-Quadratic Mean Diameter(cm) of all live trees
BAA4	Current Vegetation-Total basal area of all trees in size class 75–100 cm dbh
00NONFOR	1900 Vegetation-Nonforest
36CONOG	1936 Vegetation-Douglas-fir, old-growth, >56 cm dbh
ECOVOL	Ecoregion-Volcanics
ECOSD	Ecoregion-Mid-coastal sedimentary

Table 2 Median amount per hectare of dead wood characteristics, for the Coastal Province of Oregon (CP), and by ownership group, using plot-scale data

Variable <i>n</i> :	CP 694	Public 282	Private 412	<i>P</i> -value	USFS 81	BLM 117	State 84	FI 271	NIP 141
Total dead wood volume >12.5 cm	121.1	192.1	92.6	<0.001	204.0 ^a	136.6 ^{ab}	233.4 ^a	128.8 ^b	45.5 ^c
Total dead wood volume >50.0 cm	63.9	116.6	43.4	<0.001	118.6 ^a	80.1 ^{ab}	169.0 ^a	67.9 ^b	12.6 ^c
<i>Snags</i>									
Number of snags >12.5 cm*(STPH12)	8.2	22.7	0	<0.001	32.3 ^a	20.8 ^b	18.0 ^b	2.2 ^c	0 ^c
Number of snags >50 cm*(STPH50)	0	2.7	0	<0.001	9.9 ^a	2.6 ^b	2.2 ^b	0 ^c	0 ^c
Number of snags >50 cm, >15 m tall	0	0	0	<0.001	0 ^a	0 ^b	0 ^c	0 ^d	0 ^{cd}
Volume of snags >12.5 cm	7.3	16.4	0	<0.001	40.9 ^a	11.8 ^b	13.2 ^b	2.6 ^c	0 ^{cd}
Volume of snags >50 cm	0	8.2	0	<0.001	31.6 ^a	6.7 ^{bc}	2.8 ^c	0 ^d	0 ^c
Volume of snags 12.5–25.0 cm*(SVPH1)	0	0	0	<0.001	0.5 ^a	0.7 ^a	0 ^{ab}	0 ^b	0 ^c
Volume of snags 25.0–50.0 cm*(SVPH2)	0	1.0	0	<0.001	3.5 ^a	0 ^b	0 ^b	0 ^c	0 ^c
Volume of snags 50.0–75.0 cm*(SVPH3)	0	0	0	<0.001	3.8 ^a	0 ^b	0 ^b	0 ^c	0 ^c
Volume of snags 75.0–100.0 cm*(SVPH4)	0	0	0	<0.001	0.0 ^a	0 ^b	0 ^c	0 ^c	0 ^c
Volume of snags >100.0 cm*(SVPH5)	0	0	0	<0.001	16.2 ^a	0 ^b	0 ^b	0 ^c	0 ^c
Snag biomass (Mg)	1.9	5.2	0	<0.001	10.4 ^a	4.6 ^b	4.5 ^b	0.5 ^c	0 ^c
Snag carbon (Mg C)	1.0	2.7	0	<0.001	5.4 ^a	2.4 ^b	2.3 ^b	0.3 ^c	0 ^c
Number of legacy snags*(TPHREMS)	0	0	0	0.03	0 ^{abc}	0 ^{ab}	0 ^a	0 ^b	0 ^c
Volume of legacy snags >12.5 cm*(VPHREMS)	0	0	0	0.03	0 ^{abc}	0 ^{ab}	0 ^a	0 ^b	0 ^c
% of all >12.5 cm snags, legacy*(REMPCTS)	0	0	0	n.s.	0 ^{ab}	0 ^{ab}	0 ^a	0 ^{ab}	0 ^b
<i>Logs</i>									
Volume of logs >12.5 cm	103.8	149.4	78.1	<0.001	135.3 ^{ac}	115.2 ^{ac}	201.5 ^b	114.5 ^c	33.7 ^d
Volume of logs >25 cm	91.6	138.3	66.7	<0.001	125.5 ^{ac}	100.2 ^{ac}	188.3 ^b	101.9 ^c	25.1 ^d
Volume of logs >50 cm	53.1	96.7	37.2	<0.001	63.9 ^{ac}	62.0 ^{ac}	146.7 ^b	65.2 ^c	9.9 ^d
Volume of logs 12.5–25.0 cm*(DVPH1)	8.1	7.3	8.7	0.04	11.6 ^{ac}	6.2 ^{bd}	7.1 ^{bd}	10.5 ^{bc}	5.8 ^d
Volume of logs 25.0–50.0 cm*(DVPH2)	25.7	32.4	23.8	0.001	27.1 ^a	27.1 ^a	34.8 ^a	29.1 ^a	11.6 ^b
Volume of logs 50.0–75.0 cm*(DVPH3)	20.1	26.2	17.2	0.02	26.2 ^a	0 ^a	39.4 ^b	24.7 ^a	0 ^c
Volume of logs 75.0–100.0 cm*(DVPH4)	0	0	0	0.001	0 ^{ac}	0 ^{ac}	33.0 ^b	0 ^c	0 ^d
Volume of logs >100.0 cm*(DVPH5)	0	0	0	n.s.	0 ^a	0 ^{ac}	42.2 ^b	0 ^c	0 ^a
Log biomass (Mg)	28.1	39.0	24.3	<0.001	33.4 ^a	30.4 ^a	59.3 ^b	34.6 ^a	10.2 ^c
Log carbon (Mg C)	14.5	20.3	12.4	<0.001	17.3 ^a	15.8 ^a	30.9 ^b	17.9 ^a	5.2 ^c
Volume of legacy logs >12.5 cm*(VPHREMD)	0	0	0	n.s.	0 ^a	0 ^b	79.0 ^c	22.1 ^d	0 ^a
Legacy logs, % of all >12.5 cm logs*(REMPCTD)	0	0	0	n.s.	0 ^{ad}	0 ^{bd}	33.8 ^c	20.5 ^c	0 ^d

Only plots occurring on the 5.5 km spacing grid were used. *P*-values indicate difference in dead wood amount between public and private ownerships; for the five ownership classes, different superscript letters indicate significant difference ($P < 0.05$) between classes in dead wood amount, from two-sided Wilcoxon rank-sum tests. Asterisks indicate dead wood attributes used in canonical correspondence analysis (CCA), and abbreviations are codes used in CCA biplots. FI is forest industry. NIP is non-industrial private. Snag size is dbh; log is led; volume units is m³. Weighted means are available in Appendix A

Results

Regional patterns

Much of the dead wood present in the Coastal Province was in the form of logs: about 85% of the biomass and 70% of the volume of dead wood

occurred as logs (Appendix A). Very large logs (>100 cm led) comprised about 65% of total log volume, and very large snags (>100 cm dbh) comprised about half of total snag volume. The volumes of moderate-sized logs and snags (25–50 dbh or led) were about the same as the volume of large logs and snags (75–100 cm dbh or led), indicating there were

probably fewer larger-sized pieces. Legacy snags and logs were each about 20% of the total volume of snags and logs. About 70% of total dead wood volume was >50 cm dbh or led.

Relationships with ownership

Snag amounts differed according to ownership (Table 2). The volume of snags was much higher on public than private lands (mean 44.3 vs. 13.0 m³ ha⁻¹), as was the number of large snags (mean 7.9 vs. 2.3 snags ha⁻¹); in fact, federal ownerships had higher snag amounts than private ownerships for all the snag metrics considered (Table 2). Among public owners (USFS, BLM, and State), the USFS had about twice the mean amounts of the other public ownerships for all snags (67.7 (s.e. 4.2) vs. 37.9 (7.1) and 29.7 (4.4), respectively), and for large snags (55.8 (3.7) vs. 32.0 (7.0) and 19.7 (4.0), respectively). State lands were similar to private ownerships for some snag metrics, such as the volume of 75–100 cm dbh snags (Table 2). In general, the number and volume of small snags per hectare on private ownerships was about 50–70% of that of public ownerships, whereas the number and volume of large snags was only about 20–30% (Appendix A).

Public ownerships had higher log volumes than did private ownerships for nearly all sizes of logs (Table 2). The exception to this was very small logs

(12.5–25.0 cm led), which occurred at slightly higher volumes on private lands. In general, the volume of small logs on private lands was about 60–80% that of public lands, whereas the volume of large logs was about 45–70% that of public lands. Log volumes for all sizes of logs were much lower on non-industrial private than on forest industry lands. Neither legacy log nor snag amounts as a proportion of the total differed significantly between the generalized public-private ownership groups (Table 2).

Total volume of dead wood and scale

The total volume of dead wood varied at fairly fine scales. Variability among subwatersheds was high and apparently clustered (Fig. 2a). At watershed and subbasin scales, the variation decreased. For example, total dead wood volume in the interior forested watersheds and subbasins of the Coastal Province tended to be consistently low relative to the more coastal watersheds and subbasins, regardless of scale (Figs. 2b, c).

The factors most strongly associated with variation in the total volume of dead wood differed by scale (Table 3). Climate was the most important at all but the subbasin scale: lower dead wood volume occurred where growing season moisture stress was greater at the other scales. Current vegetation (basal area of large trees) was also positively associated with total dead wood volume at all but the coarsest scales.

Fig. 2 Total volume of dead wood (m³ ha⁻¹) in coastal Oregon, USA, summarized by (a) subwatershed, (b) watershed, (c) subbasin. Twelve subwatersheds, outlined in black, contained plots but no dead wood. Thirty subwatersheds, colored white, were non-forested (not sampled). Two central interior watersheds contained only two plots (primarily non-forested)

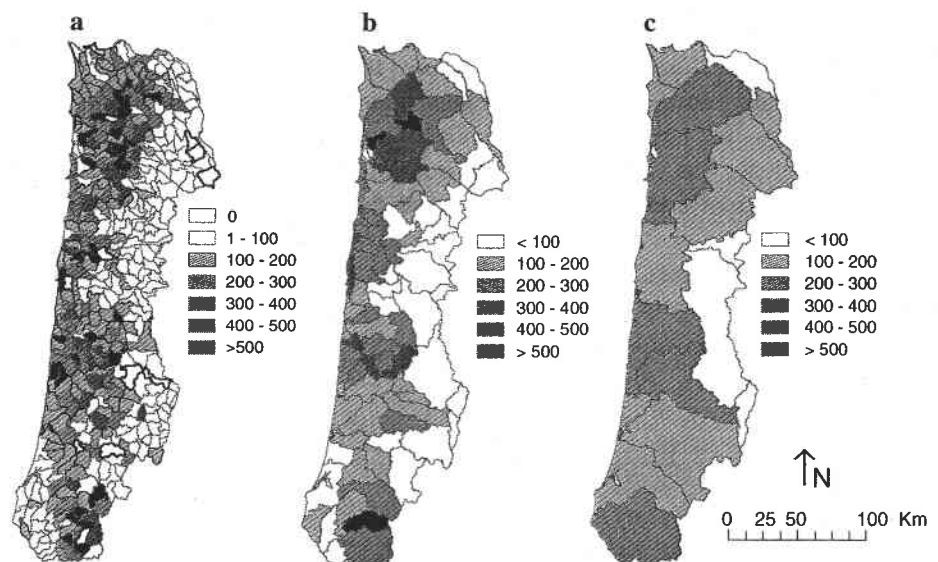


Table 3 Stepwise regression models used to predict total dead wood volume at four spatial scales in coastal Oregon, USA

Model	Variable	Coefficient	F	P-value ^a	Partial R ^{b, c}	Cumulative R ^b
Plot	SMRTP	-10.09	157.11	<0.001	0.14	0.14
	BAA4 (ln)	1.71	99.66	<0.001	0.08	0.23
Subwatershed	SMRTP	-12.50	162.56	<0.001	0.32	0.32
	BAA4(ln)	1.77	46.31	<0.001	0.08	0.40
	36CONOG	4.70	44.55	<0.001	0.07	0.47
Watershed	SMRTP	-233.50	46.34	<0.001	0.36	0.36
	SLPPCT	3.18	22.05	<0.001	0.14	0.50
	BAA4 (ln)	41.40	10.35	<0.001	0.06	0.56
Subbasin	NIP	-292.32	22.37	0.028	0.58	0.58
	RIVBUF100	218.59	5.90	<0.001	0.12	0.70

^a Plot and subwatershed dead wood volume square-root-transformed to meet normality assumptions

^b Derived from a randomization test based on permutations under the reduced model

^c Value of 0.05 required for inclusion in model

Current and historical vegetation patterns (basal area of large trees and 1936 conifer old growth) were significant at the subwatershed scale. Topography was significant at coarser scales, with dead wood volume increasing with % slope at the watershed scale, and increasing with proximity to streams at the subbasin scale. Ownership was most important at the coarsest scale, with a strong negative association between the amount of non-industrial private land ownership and total dead wood volume. Total dead wood volume was most predictable at the subbasin scale (Table 3).

Total dead wood volume was most highly correlated with total log volume at all scales (Pearson correlation coefficient 0.97 at the plot scale and higher for other scales). Thus, these regression models tend to describe dead wood-environmental pattern-process relationships for logs more than snags, and since most of total log volume comes from large logs, for large logs in particular. Therefore, to evaluate the influence of environmental patterns in terms of a more complete suite of dead wood characteristics, we also characterized multivariate dead wood gradients and their relationships to environment according to scale.

Multivariate gradients of explanatory variables and dead wood

The gradients of explanatory and dead wood variables were generally similar among the scales but the

relative dominance of gradients and importance of some variables shifted among scales (Fig. 3; Table 4). At both plot and subwatershed scales, the full set of explanatory variables explained 17% of the cumulative variation in dead wood gradients (Axes 1 and 2); at the watershed, 32%; and at the subbasin, 56%. At plot and subwatershed scales, the dominant gradient of explanatory variables was associated with large diameter trees, high basal area stands and USFS land. Dead wood variables scoring low on this axis were related to legacy logs and snags, whereas high-scoring variables were related to snag volume. The second axis differed between the two scales. At the plot scale, it ranged from USFS lands, steeper slopes, or volcanic sites, to sites with high amounts of old forest in 1936, high amounts of nonforest in 1900, or high growing season moisture stress. Dead wood characteristics scoring low on this axis were legacy snags, while volume of large logs scored higher. The second axis at the subwatershed scale showed a stronger influence of percent slope and area of nonforest in 1900. Dead wood characteristics scoring low included volume of large snags and those scoring high included volume of small diameter snags and logs.

At the watershed scale, the dominant gradient ranged from steep slopes, old forest in 1936, high percent area within 100 m of streams, and volcanic soils, to area of nonforest in 1900, many annual growing degree days, and high growing season moisture stress. Dead wood variables scoring low on this axis included legacy log volume and those

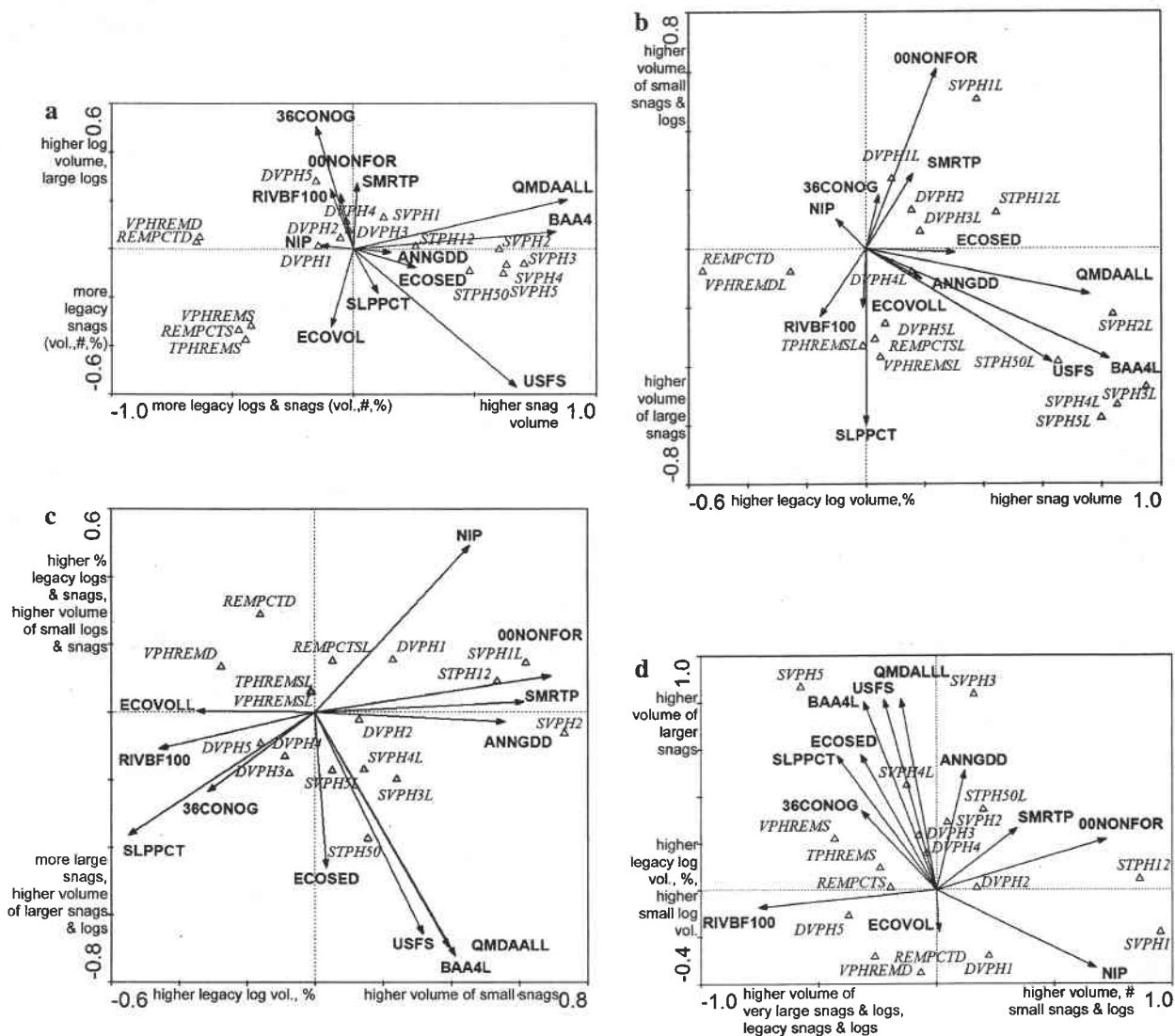


Fig. 3 Biplots from CCAs of dead wood attributes at four scales: (a) plot, (b) subwatershed, (c) watershed, and (d) subbasin in coastal Oregon, USA. Vectors show important explanatory variables; line length indicates magnitude of contribution to explained variation in dead wood variables. Triangle locations indicate relationship of each dead wood

variable to the explanatory variables. Dead wood variable codes (triangle labels) are defined in Table 2. Explanatory variables are listed in Table 1. An 'L' variable name suffix indicates logarithmic transformation. Axes are labeled with dead wood attributes based on dead wood variable scores in biplot scaling

scoring high included volume of small snags. The second axis ranged from sites with large diameter trees, high basal area stands, and occurrence of USFS land, to NIP lands. Dead wood variables scoring low on this gradient included density and volume of large snags; variables scoring high included percent of legacy logs and snags and volume of small logs and snags. Ownership and historical vegetation variables were of greater

relative importance at watershed and subbasin scales than at plot and subwatershed scales.

At the subbasin scale, the dominant gradient was from high percent area within 100 m of streams to high percent area of non-forest and NIP ownership. Dead wood variables scoring low on this axis ranged from volume of very large snags and logs to volume of small snags and logs. The second axis at the subbasin scale ranged from NIP land to USFS land, high basal

Table 4 Relative contribution to explained variation (Axes 1 and 2) in dead wood gradients by subsets of factors in coastal Oregon, from CCA, at four scales

Subset of explanatory variable	Percentage of total inertia			
	Scale of Model			
	Plot <i>n</i> = 903	Subwatershed <i>n</i> = 337	Watershed <i>n</i> = 84	Subbasin <i>n</i> = 18
Climate(ANNGDD, SMRTP)	2.0	2.4	12.2	15.4
Topography(RIVBF100, SLPPCT)	1.0	1.8	11.0	32.9
Current Veg.(QMDAALL, BAA4)	14.3	11.8	10.6	20.8
Ownership(USFS, NIP)	7.7	6.7	15.0	32.9
Historical Veg.(36CONOG, 00NONFOR)	1.4	2.8	16.5	33.1
Ecoregion/Geology(ECOVOL, ECOSD)	1.9	2.6	9.0	16.1

Seventeen dead wood variables were included (see Table 2). Percentage of total inertia is from a CCA on each subset; thus correlations among variables between subsets may result in totals of greater than 100%. Percentages should be compared among subsets at each scale, not among scales

area stands, and large diameter live trees. Dead wood variables scoring low on this axis included legacy log volume and small log volume; variables scoring high included volume of large snags.

Discussion

This study illustrates that dead wood patterns are spatially complex and highly variable depending on the type of dead wood assessed. Relative to our original objectives, dead wood volume varied highly across the region, and coarser resolutions decreased the variation in dead wood volume among spatial units. Our evaluation of the relative importance of biophysical and ownership characteristics to regional dead wood abundance indicated two main attributes of these relationships in coastal Oregon forests. First, the importance of biophysical characteristics and ownership patterns to dead wood differs according to scale. Second, their relative importance also changes depending on which dead wood attributes are considered (e.g., snags vs. logs). These general patterns lead to a great deal of complexity in dead wood relationships with biophysical and ownership factors. However, the root of this complexity is the specificity of the relationships, not a lack of relationships between dead wood patterns and the processes considered.

This study illustrates the importance of being specific about which components of dead wood are being evaluated, with regard to size, type, and origin. Univariate analysis of individual log and snag variables at the plot level (multiple linear regression; results not shown) showed strong relationships of snags with current vegetation and USFS ownership, and logs with historical vegetation; this is consistent with the results of the plot-level multivariate analysis (Fig. 3a). The dead wood volume regression analysis primarily reflects the volume of large logs, where most of the volume is concentrated. Volume-based measures are useful because they are related to carbon sequestration and wildlife concerns, and an overall measure of dead wood volume may be easier to obtain than one parsed by size or type of structure. The multivariate analysis, with snag characteristics more evenly weighted against logs, brought forward other important biophysical and ownership relationships, such as the importance at multiple scales of current vegetation and ownership to snags, that would be missed in an evaluation of dead wood volume alone. These relationships are important because (1) the processes creating and decaying these two types (snags and logs) are different, and (2) wildlife habitat and piece longevity varies by dead wood type. The persistence time of an individual snag may be quite short—on the order of 10–20 years, whereas a large log may take centuries to decompose (Harmon et al. 1986).

Relationships with ownership

Ownership was especially important in this study at the scales of watersheds and subbasins. Its relevance at these scales reflects in part the scale of ownership patterns in the Coastal Province. A single ownership dominates in many subwatersheds, especially for Forest Service, State, and forest industry ownerships. However, BLM parcels may be as small as 2.25 km², interspersed by forest industry lands. Non-industrial private lands tend toward a more linear configuration, reflecting their location near larger streams. Management varies according to the size and spatial and temporal distribution of land allocation types within each land unit: e.g., on private lands, clearcuts are typically located in upslope areas in patches as large as 49 ha and industrial forestry rotation lengths may be ~30–50 years, whereas thinning or no-action areas are typically located along narrow, riparian corridors. Forest Service, State, and forest industry are the major landowners, so larger blocks predominate and ownership is mainly patterned at larger patch sizes. Private non-industrial lands historically tended to be cleared, whereas forest industry lands historically contained older, higher productivity forests, and public lands were sites of recent historical fires.

Research in other regions has also found that dead wood varies with management history and disturbance (Grove 2001; Sturtevant et al. 1997; Tinker and Knight 2000). In research evaluating unmanaged and managed stands with varying levels of management intensity (Green and Peterken 1997; Krankina et al. 2002), older or less-intensively managed stands had dead wood amounts more similar to those of natural stands, and disturbance history was important. In the Coastal Province, Wimberly and Ohmann (2004) found that ownership was always the most important predictor related to change in the amount of large conifer forest cover over 60 years at similar scales and with similar potential explanatory variables to this study. The results of the present study, with biophysical and historical factors also important to dead wood volume patterns, imply that there may be more intricate influences on dead wood patterns than those affecting change in large conifer forests as indicated by Wimberly and Ohmann (2004). This probably reflects the diversity of disturbance types that can create dead wood, and the long persistence

time for dead wood, during which it is subject to numerous influences on decomposition.

Current and historical vegetation

The importance of historical vegetation is highlighted by legacy logs comprising over one-third of log volume. Although the area that was coniferous old-growth in 1936 in coastal Oregon has declined to about 44% of prior amounts through conversion to younger forest (Wimberly and Ohmann 2004), dead wood from past older forests contributes much to today's dead wood pools at broader scales. The inverse relationship of historically (1900) nonforested (but presently forested) areas with large dead wood abundance at subwatershed, watershed, and subbasin scales (Fig. 3), indicates that aforestation may not yet be producing high quantities of large dead wood, and that land use effects remain for long time periods. The difference in the explanatory variables between logs and snags (i.e. historical vegetation and climate vs. current vegetation) reflects the differences in the processes and longevities of snags and logs. Snags are typically the first stage of dead wood after trees die, hence are more proximal to live trees than are logs, and fall to become logs in relatively short time periods. Logs tend to persist longer and would more likely be related to historical disturbance and longer-term vegetation patterns and broader climatic trends.

Relationships with climate

Climate was of some importance in the watershed scale multivariate analysis. This may reflect a complex of influences including productivity and decay rates. Sites with lower summer moisture stress in the Coastal Province are more productive and have the capacity to generate larger pieces of dead wood (Franklin and Dyrness 1988). Dead wood on these sites may also have lower decomposition rates, resulting in longer retention times (Harmon et al. 1986). The importance of climate at intermediate scales may be a function of the pattern of climate resulting from the combination of elevation, orographic and maritime gradients that divide the province into smaller climatic subregions. Further work is needed to determine how much climate

within this region influences processes that affect dead wood abundance.

Topographic effects

The potential importance of topography to amounts of dead wood has been widely noted. Higher topographic positions have been shown to have higher potential for tree death and higher mass and volume of dead wood (Gale 2000; Muller 2003), but steep slopes and high landslide and debris flow potential in areas of great topographic relief and dense stream networks may result in high amounts of down wood accumulating in areas near streams (Kennedy and Spies 2007; May and Gresswell 2003). This was reflected in the present study by the importance of topography, in particular the characteristics of proximity to streams and percent slope, to dead wood patterns at the broadest scale (subbasin) we evaluated.

Implications for regional biodiversity and future dead wood patterns

Management for dead wood on lands currently depauperate in dead wood would increase habitat for dead wood associates and promote regional biodiversity. Non-industrial private lands, with their low dead wood amounts, probably provide a small contribution to dead-wood-associated biodiversity, though they may provide other components of biodiversity, such as hardwoods in the coniferous landscape (Kennedy and Spies 2005). If other habitat requirements are met, biodiversity of dead wood-associated species might be highest on State and Forest Service ownerships, because they had more large log volume and snag volume, respectively.

Some Coastal Province management practices have only been in effect for a few decades, so future dead wood patterns may differ. For example, federal land management for late successional and old-growth forests began in the mid-1990s. Likewise, the long-term effect of intensive management on forest productivity and dead wood is poorly understood (Harmon et al. 1996), but simulation modeling indicates that future live vegetation patterns will more strongly follow ownership patterns (Spies et al. 2007).

Conclusions

This study illustrates the importance of a multi-factor, multi-scale perspective in understanding dead wood characteristics and patterns. Snags and logs should be considered separately if snags are of concern. Forest history is important, especially to large log abundance. Scale relationships are not straightforward; climate's proposed influence at broadest scales was overridden by disturbance and mid-scale dynamics (ownership and current vegetation). This leads to a management challenge in setting dead wood targets because of the dynamic nature of dead wood, and the importance of historical effects. Because ownership now drives much of the pattern of dead wood, efforts to manage and develop policies for dead wood at watershed and landscape scales should take ownership into account.

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Appendix A

Weighted mean amount ha^{-1} and standard error (s.e.) of attributes of dead wood in coastal Oregon and by public and private ownership classes, using plot-scale data. Snag size is dbh, log is led; volume units is m^3

Variable	Coastal Province (<i>n</i> = 930) Mean(s.e.)	All Public (<i>n</i> = 511) Mean(s.e.)	All Private (<i>n</i> = 419) Mean(s.e.)
Total dead wood volume >12.5 cm	186.5(6.4)	249.6(10.4)	140.2(7.0)
Total dead wood volume >50.0 cm	132.8(5.8)	188.9(9.8)	91.7(6.0)
<i>Snags</i>			
Number of snags >12.5 cm	34.1(2.0)	43.8(2.7)	26.9(3.0)
Number of snags >50 cm	4.7(0.3)	7.9(0.5)	2.3(0.2)
Number of snags >50 cm and >15 m tall	0.6(0.1)	1.2(0.1)	0.2(0.1)
Volume of snags >12.5 cm	26.3(1.7)	44.3(3.0)	13.0(1.5)

Appendix A continued

Variable	Coastal Province (<i>n</i> = 930) Mean(s.e.)	All Public (<i>n</i> = 511) Mean(s.e.)	All Private (<i>n</i> = 419) Mean(s.e.)
Volume of snags >50 cm	19.6(1.6)	35.5(2.9)	8.0(1.3)
Volume of snags 12.5–25.0 cm	2.6(0.2)	3.2(0.3)	2.2(0.3)
Volume of snags 25.0–50.0 cm	4.0(0.3)	5.7(0.5)	2.8(0.4)
Volume of snags 50.0–75.0 cm	3.0(0.3)	5.4(0.5)	1.2(0.2)
Volume of snags 75.0–100.0 cm	4.2(0.4)	7.3(0.7)	2.0(0.4)
Volume of snags >100.0 cm	12.4(1.3)	22.8(2.4)	4.8(1.0)
Snag biomass (Mg)	7.4(0.5)	12.5(0.9)	3.7(0.5)
Snag carbon (Mg C)	3.9(0.3)	6.5(0.5)	1.9(0.2)
Number of legacy snags >12.5 cm	1.4(0.1)	1.9(0.2)	1.0(0.1)
Volume of legacy snags >12.5 cm	7.1(0.8)	10.0(1.3)	5.1(1.0)
% of all snags >12.5 cm, legacy	19.9(1.4)	22.0(2.2)	18.3(1.8)
<i>Logs</i>			
Volume of logs >12.5 cm	160.2(5.7)	205.2(9.2)	127.2(6.5)
Volume of logs >25 cm	149.0(5.6)	194.8(9.1)	115.3(6.3)
Volume of logs >50 cm	113.2(5.1)	153.4(8.5)	83.7(5.6)
Volume of logs 12.5–25.0 cm	11.3(0.4)	10.4(0.6)	11.8(0.5)
Volume of logs 25.0–50.0 cm	35.8(1.1)	41.4(1.7)	31.6(1.4)
Volume of logs 50.0–75.0 cm	40.1(1.7)	49.1(2.7)	33.5(2.2)
Volume of logs 75.0–100.0 cm	34.2(2.1)	50.3(3.8)	22.4(2.0)
Volume of logs >100.0 cm	38.9(3.2)	54.0(5.5)	27.8(3.3)
Log biomass(Mg)	44.2(1.6)	54.4(2.4)	36.8(1.9)
Log carbon(Mg C)	23.0(0.8)	28.3(1.3)	19.1(1.0)
Volume of legacy logs >12.5 cm	55.2(3.3)	63.4(5.0)	49.2(4.3)
Legacy logs, % of all >12.5 cm logs	21.9(1.0)	20.2(1.3)	23.1(1.4)

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