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Level and pattern of overstory retention influence rates and forms of tree mortality in mature, coniferous forests of the Pacific Northwest, USA

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ABSTRACT

Mortality of retained trees can compromise the ecological objectives of variable-retention harvest. We used a large-scale experiment replicated at six locations in western Washington and Oregon to examine the influences of retention level (40% vs. 15% of original basal area) and its spatial pattern (aggregated vs. dispersed) on the rate and form of tree mortality for 11–12 years following harvest. Cumulative mortality of conifers was greater at lower levels of retention and in dispersed treatments—a result common to most seral groups and canopy strata. The greatest losses, averaging 18% of stems, occurred at low levels of dispersed retention. Mortality peaked in the first year in dispersed treatments and at low levels of aggregated retention, then rates declined to levels comparable to the controls (~0.8% of stems/year). Harvest-related bole damage—common in the dispersed treatments—did not increase risk of mortality. Standing dead accounted for most mortality at greater levels of retention, but uprooting was nearly as common at lower retention—particularly in dispersed treatments. Forest aggregates (1 ha in size) did not exhibit greater overall mortality than controls. In fact, at 40% retention, mortality rates were reduced in the aggregates due to greater survival of late-seral and suppressed stems, presumably a response to edge creation and increased resource supply. Although cumulative mortality was no higher at 15% retention, larger harvest-unit openings and greater exposure of aggregates resulted in greater uprooting among dead trees. Current standards and guidelines for retention harvests on federal lands in the Pacific Northwest require a minimum of 15% retention within each harvest unit, with 70% of this distributed in aggregates of $\geqslant$0.2 ha. Our results suggest that these minimum standards lead to greater risk of tree mortality in dispersed settings and to elevated rates of uprooting regardless of pattern, potentially compromising the objectives of live-tree retention. However, with larger (1-ha) aggregates and moderate levels of retention, managers have considerable flexibility in implementing variable retention without risk of excessive mortality.

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1. Introduction

Variable-retention harvest (VRH) is a key component of ecological forestry worldwide (Lindenmayer et al., 2012). VRH involves the retention of forest structural elements—live trees, snags, and logs—through harvest to emulate the outcomes of natural disturbance. Retention of overstory trees is intended to provide microclimatic amelioration and structural enhancement within regenerating stands and to ensure "lifeboating" of species through disturbance (Franklin et al., 1997; Rosenvald and Lõhmus, 2008). Loss of residual trees to mortality can compromise these functions and thus is a critical concern in VRH systems (Coates, 1997; Moore et al., 2003; Bladon et al., 2008). On the other hand, modest levels of mortality can provide ecological benefits in the form of snags and logs that enrich the regenerating forest (Franklin et al., 1987, 2002). The timing, rate, species composition, canopy distribution, and form(s) of mortality (standing, broken, or uprooted) can have important consequences for the ecological functioning and future development of forests (Harmon et al., 1986; Maser et al., 1988; Schaetzl et al., 1989; Franklin et al., 2002). For example, snags provide high habitat value for arboreal wildlife (Rose et al., 2001), whereas uprooted stems create micro-topographic heterogeneity (pits and mounds; Peterson et al., 1990); mediate soil moisture, organic matter, and nutrient pools (Harmon et al., 1986); and serve as important substrates for conifer regeneration (Christy and Mack, 1984; Harmon and Franklin, 1989) or wood-dependent bryophytes (Rambo and Muir, 1998; Rambo, 2001; Turner and Pharo, 2005). How each of these components of mortality is influenced by the level (amount) and pattern (spatial arrangement) of retention is not well understood in many forest ecosystems.

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Elevated rates of post-harvest mortality have been observed in previous studies of VRH (Coates, 1997; Hautala et al., 2004; Caspersen, 2006; Thorpe et al., 2008; Rollerson et al., 2009). Mechanical agents, directly or indirectly related to wind, are among the primary causes of tree death when stand density is reduced or distinct edges are created (Huggard et al., 1999; Arnott and Beese, 1997; Buermeyer and Harrington, 2002; Moore et al., 2003; Martínez Pastur et al., 2009; Rollerson et al., 2009). Increased exposure to light and wind can also impose physiological stresses that increase susceptibility to other agents of mortality (Franklin et al., 1997; Moore et al., 2003; Palik et al., 2005; Busby et al., 2006; Bladon et al., 2008). Finally, bole wounding during harvest can increase risk of windthrow in the short term or decay-induced mortality in the longer term (Moore et al., 2002; Bladon et al., 2008; Thorpe et al., 2008). Conversely, partial harvest of the overstory can increase resource availability and reduce competition-induced mortality—particularly for smaller, suppressed individuals (Boucher et al., 2007; Powers et al., 2010; Boyden et al., 2012; Prévost and Dumais, 2013).

The timing or duration of elevated mortality has implications for the longer-term stability of forests. Yet, long-term assessments of mortality are uncommon and yield varying results (see review in Thorpe and Thomas, 2007). Some studies suggest an initial elevated risk of windthrow, then a decline (Busby et al., 2006; Roberts et al., 2007; Thorpe et al., 2008); others indicate that mortality can remain elevated for more than a decade after harvest (Ruel et al., 2001; Solarik et al., 2012).

In this paper, we examine 11- to 12-year trends in tree mortality as part of a regional-scale VRH experiment in mature, coniferous forests of the Pacific Northwest, The Demonstration of Ecosystem Management Options (DEMO) Study (Aubry et al., 1999, 2009). Federal standards and guidelines for regeneration harvests in this region require a minimum of 15% overstory retention in each harvest unit, with 70% of this distributed as large (0.2–1.0 ha) aggregates (USDA and USDI, 1994). The DEMO Study provides a critical test of these standards. The factorial design—unique among VRH experiments—allows for clear separation of the effects of retention level (40% and 15% of original basal area) and pattern (dispersed vs. 1-ha aggregates) in shaping ecological responses to harvest. Here, we examine how both factors influence the timing and amount of mortality; its distribution among principal species, seral groups, and canopy strata; and the physical forms in which it occurs (as standing, broken, or uprooted stems). We also explore whether logging damage to tree boles (Moore et al., 2002) increases risk of mortality. We view mortality from two distinct perspectives: loss of stems and loss of basal area, which may be driven by different processes (e.g., suppression vs. mechanical damage; Lutz and Halpern, 2006) and have different silvicultural or ecological implications (e.g., future productivity and inputs of dead wood). This study builds on an earlier, cursory analysis of stem loss as part of a broader assessment of post-harvest stand dynamics (Maguire et al., 2006). We address the following hypotheses:

Hypothesis 1 (H1). Mortality among species and seral groups: Cumulative mortality will be proportionately greater at lower levels of retention and in dispersed treatments for both *Pseudotsuga menziesii* (the principal early-seral species) and late-seral (shade-tolerant) conifers.

Hypothesis 2 (H2). Mortality among canopy classes: Taller canopy classes (dominant, co-dominant, and intermediate stems) will exhibit greater mortality at lower levels of retention and in dispersed treatments. Suppressed (sub-canopy) stems will respond similarly, but indirectly, due to damage from taller canopy classes. Alternatively, mortality of suppressed stems may be reduced if losses to mechanical damage are outweighed by decreased competition-induced mortality in response to increases in resource supply.

Hypothesis 3 (H3). Physical forms of mortality: Mechanical forms (stem breakage or uprooting) will comprise a greater proportion of mortality in dispersed treatments and at lower levels of retention. Conversely, standing dead will comprise a greater proportion of mortality in aggregated treatments and at higher levels of retention.

Hypothesis 4 (H4). Stability of aggregates: (a) Mortality will be greater in aggregates than in controls, particularly at lower levels of retention where aggregates are more exposed to wind. (b) Mechanical forms of mortality (stem breakage and uprooting) will be more frequent in aggregates than in controls. (c) Mortality will be more frequent in the outer portions of aggregates than at the centers, particularly at lower levels of retention.

Hypothesis 5 (H5). Consequence of bole damage: Trees damaged during logging operations will have greater mortality rates than undamaged trees.

2. Methods

2.1. Study areas

The experiment was replicated at six sites (blocks) in western Washington and Oregon. Sites were chosen to represent a diversity of physical environments and mature forest types at low to moderate elevations (Table 1). Five blocks are in the western Cascade Range, including three in the Gifford Pinchot National Forest, Washington (BU, LWS, and PH) and two in the Umpqua National Forest, Oregon (WF and DP). The sixth block (CF) is in the Black Hills near Olympia, Washington on state lands (Washington Department of Natural Resources). Sites were chosen to minimize variation of experimental units within blocks (Aubry et al., 1999), but this was difficult to achieve at some sites due to varying topography, presence of perennial streams, and past management (harvest units and roads). As a result, environmental and stand conditions varied markedly within some blocks (Table 1; Maguire et al., 2007).

The climate of the region is maritime. Summers are warm and dry and winters are cool and wet with most precipitation falling between October and April (Franklin and Dyrness, 1988). Winter storms are episodic, characterized by strong southwesterly winds and heavy rains. Storm events sufficient to cause windthrow occurred in nearly every year of the study period (Office of the Washington State Climatologist, 2013).

Soils vary in depth and texture; most are moderately deep and well-drained loams to loamy sands derived from andesite, breccia, or basalt, or from pumice deposits (Radtke and Edwards, 1976; Pringle, 1990; Wade et al., 1992). *P. menziesii* was the dominant canopy species in all blocks, although forest age, structure, composition, and past management varied considerably (Table 1; for details see Halpern and McKenzie, 2001; Maguire et al., 2007).

2.2. Experimental design

The full experiment, a randomized complete block design, consists of six 13-ha (operational-scale) treatments including a control (Fig. 1), replicated at each of six locations (blocks) (Aubry et al., 1999). In this paper, we consider five of these treatments: the control (100% retention) and four that form a balanced, two-factor design with two levels of retention (40% or 15% of original basal area) in one of two spatial patterns (trees aggregated or dispersed). The four harvest treatments were implemented as follows:

(1) *15% Aggregated retention (15%A)*: two 1-ha circular aggregates were retained in diagonally opposite quarters of the 13-ha experimental unit (separated by ~115 m); all merchantable stems (>18 cm dbh) in the intervening harvest matrix were felled.

Table 1
Physical environments and pre-treatment structural characteristics of forests comprising the six experimental blocks.

Block	Elevation (m)	Slope (%)	Aspect	Stand age (year)	Tree density (no./ha)	Basal area (m^2/ha)	Canopy height (m)	Minor canopy species
Watson Falls (WF)	945–1310	4–7	Flat	110–130	310–500	36–52	42–45	Ac, Th, Pp, Pm
Dog Prairie (DP)	1460–1710	34–62	SW	165	258–475	72–106	45–47	Ac, Am, Cd
Butte (BU)	975–1280	40–53	E–SE	70–80	759–1781	48–65	30–33	Th, Tp
Little White Salmon (LWS)	825–975	40–66	NW–NE	140–170	182–335	61–77	53–55	Ag
Paradise Hills (PH)	850–1035	9–33	Varied	110–140	512–1005	59–87	32–37	Th, Tp, Aa
Capitol Forest	210–275	28–52	Varied	65	221–562	54–73	45–47	Th, Tp

Minimum and maximum values are experimental unit means. Minor canopy species are Ac = *Abies concolor*, Ag = *Abies grandis*, Am = *Abies magnifica* var. *shastensis*, Cd = *Calocedrus decurrens*, Pm = *Pinus monticola*, Pp = *Pinus ponderosa*, Th = *Tsuga heterophylla*, Tp = *Thuja plicata*; nomenclature follows Hitchcock and Cronquist (1973). Canopy heights are mean heights of trees within the 75th to 95th percentiles of the height distribution.

(2) *40% Aggregated retention (40%A)*: five 1-ha circular aggregates were retained at ~30 m distance from each other; all merchantable stems in the intervening matrix were felled.
(3) *15% Dispersed retention (15%D)*: a proportion of the dominant and co-dominant trees were retained in a relatively even distribution throughout the 13-ha experimental unit; the basal area retained was equivalent to that of the corresponding aggregated-retention treatment (15%A).
(4) *40% Dispersed retention (40%D)*: a proportion of the dominant and co-dominant trees were retained as above; the basal area retained was equivalent to that of the corresponding aggregated-retention treatment (40%A).

2.3. Treatment implementation

Felling and yarding were completed in 1997 or 1998. Yarding methods varied among blocks: where terrain was steep, helicopters (DP, BU, LWS) or suspension cables (CF) were used. On more gentle slopes, ground-based equipment was used (WF, PH). At four blocks (DP, BU, LWS, PH), tree canopies were left attached to the uppermost log and yarded to off-site landings, thus reducing the accumulation of slash. Slash was not treated, except at WF, where fuel loadings were deemed excessive and reduced by machine piling and burning on temporary skid roads. Sub-merchantable stems (<18 cm dbh) were left standing in the harvested portions of most blocks. However, at PH they were uniformly felled and at WF they were felled if damaged (for details on harvest treatments, see Halpern and McKenzie, 2001).

2.4. Sampling

Prior to harvest, a sampling grid (7 × 9 or 8 × 8, slope-corrected spacing of 40-m) was established in each experimental unit. Permanent tree plots (0.04 ha, 11.28 m radius) were established at a subset of grid points. In control and dispersed treatments, plots were established at alternate points ($n = 32$); however, the sampling intensity of dispersed treatments was increased after harvest to include all grid points ($n = 63$ or 64) due to the reduced densities of trees. In aggregated treatments, characterized by two distinct post-harvest environments, plots were established at 32–37 grid points: all non-edge points in each aggregate ($n = 24$–25 in 40%A, $n = 10$ in 15%A) and a subset of points in the harvested matrix (the latter are not considered here). Plots in the aggregates represent either "center" or "outer" positions. The boundaries of "outer" plots extend to within ~5 m of the aggregate edge.

During the first growing season after treatment (1998 or 1999), all trees ⩾5 cm dbh in each plot were individually tagged; identified by species; measured for dbh, assigned a canopy class (dominant [emergent], co-dominant, intermediate, or suppressed) based on relative position in the pre-treatment forest; and rated for harvest-related disturbance (presence of bole scars caused by felling or yarding; Moore et al., 2002). Trees were censused annually for mortality in each of the next 2–3 years (1999–2001 or 2000–2001 depending on timing of treatment), and again after 5–6 (2003) and 11–12 years (2009). At each census, dead trees were measured for dbh, but live trees were measured only at 5–6 and 11–12 years. Each dead tree was also assigned one of four physical forms of mortality: (i) "standing" (standing with an intact crown), (ii) "broken" (standing with main stem broken or snapped), (iii) "uprooted" (down, characterized by a tip-up mound), or (iv) "crushed" (down but buried under another tree or trees).

2.5. Analyses

2.5.1. Data manipulation

We express mortality with two metrics: (i) proportion of stems and (ii) proportion of basal area lost from the initial post-harvest population of trees. For the latter, we accounted for the diameter growth of trees for sampling dates when the mortality census was accompanied by a remeasurement of live-tree diameters (the last two measurements, 2003 and 2009). Neither metric, however, considered post-harvest recruitment of regeneration into the overstory (⩾5 cm dbh) (Urgenson et al., 2013).

2.5.2. Temporal trends in mortality

To characterize temporal trends in mortality over the study period, we generated a mean ($n = 6$) cumulative mortality curve for each treatment from measurements made 1, 2.5, 5.5, and 11.5 years after harvest ("half-years" represent average times for blocks harvested in different years). For each time interval we also computed a simple, annualized rate of mortality that accounted for the number of years between measurements.

2.5.3. Treatment effects on the composition and physical form of mortality (H1–H3)

For most analyses, data were aggregated as cumulative mortality over the study period at the scale of the experimental units (13 ha). However, we first generated frequency histograms (percentage of total mortality attributable to individual plots) to determine whether mortality was broadly distributed or concentrated in relatively few plots within harvest units. Histograms were averaged for replicates of each treatment ($n = 6$) and treatments were compared in pairwise fashion using a bootstrap version of the Kolmogorov–Smirnov (K–S) test (Abadie, 2002).

We used a set of general linear mixed models (GLMMs, binomial distribution, logit link; McCulloch et al., 2008) to compare cumulative mortality among treatments (*H1–H3*). In each model, treatment was considered a fixed effect and block, a random effect; experimental unit was included as an individual-level random effect to account for overdispersion (Browne et al., 2005). Attempts to incorporate potentially important site-specific predictors of mortality including topography (slope, aspect) and stand structural conditions (density, basal area, or height-to-diameter ratios), led to non-significant relationships. Our models are thus limited to the

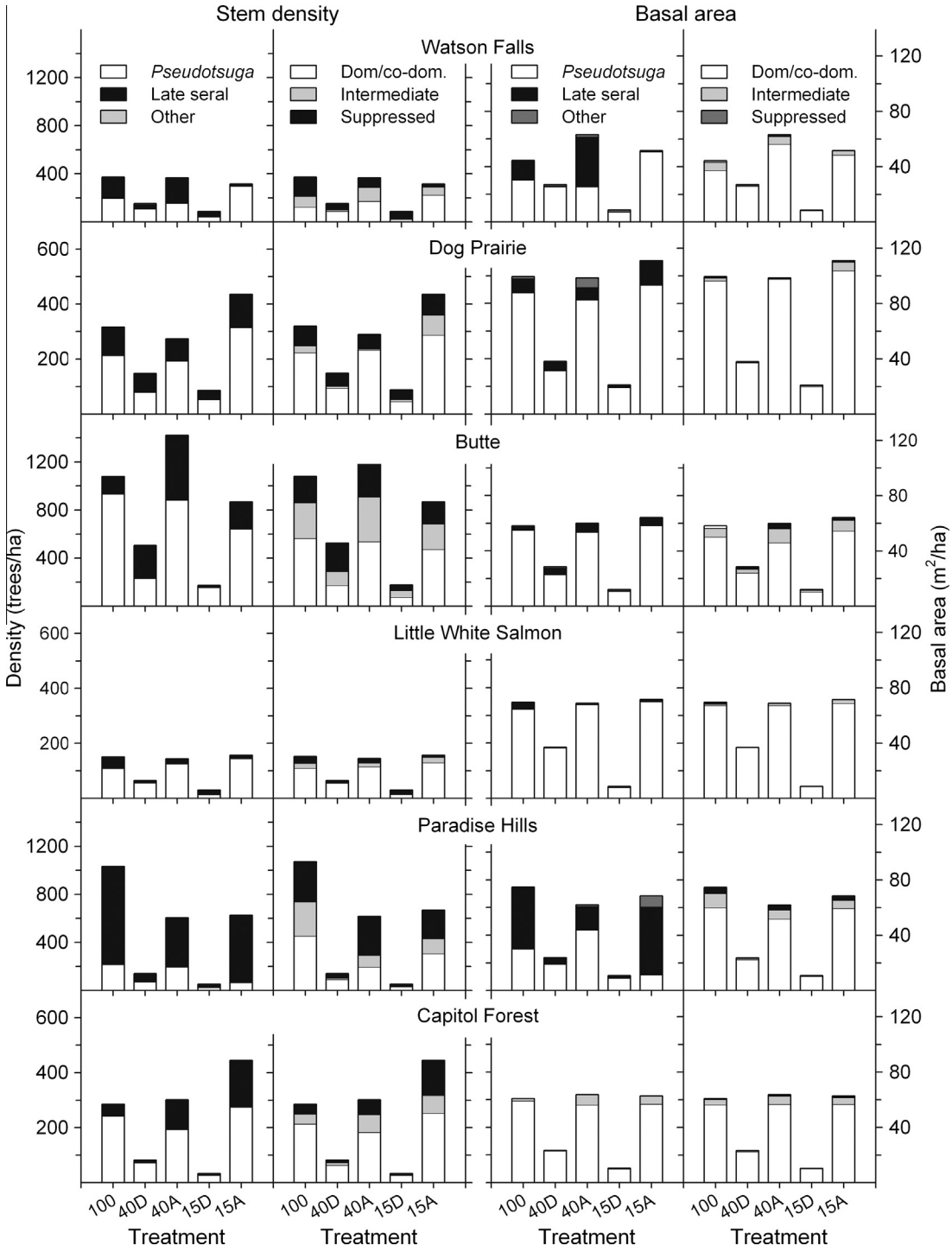

Fig. 1. Post-harvest density (left pair of columns) and basal area (right pair of columns) of overstory trees in the five treatments at each site (experimental block). Values for aggregated treatments are based on plots within the aggregates only. Values are shown for the primary species/seral groups (left column of each pair) and canopy classes (right column of each pair). Late-seral species include one or more of the following: *Abies amabilis*, *A. concolor*, *A. grandis*, *A. lasiocarpa*, *Calocedrus decurrens*, *Chamaecyparis nootkatensis*, *Picea engelmannii*, *Taxus brevifolia*, *Thuja plicata*, *Tsuga heterophylla* and *Tsuga mertensiana*. "Other" species include one or more of the following: *Abies magnifica* var. *shastensis*, *A. procera*, *Pinus contorta*, *P. monticola*, and *P. ponderosa*.

principal design elements of the study, level and pattern of retention.

Models were run on conifers as a group (all conifers), and on different subsets of the initial post-harvest population of live trees (i.e., individual species, seral groups or canopy classes), or on the proportion of dead trees comprising each form of mortality (standing, broken, or uprooted). Because temporal trends suggested a transient peak in mortality in the first year, we reran the cumulative, all-conifers model excluding first-year losses to test whether subsequent mortality varied among treatments.

For each subset of the data, separate models were run for loss of stems and loss of basal area. The division by species or seral groups was limited to *P. menziesii* (the predominant early-seral species) and late-seral (shade-tolerant) conifers, whose composition varied among blocks (Table 1). Other early-seral conifers and broadleaved species were uncommon or restricted to individual blocks and

were either omitted from all analyses (broadleaved species) or from seral-group analyses (early-seral conifers). For analyses of canopy classes, the relatively few occurrences of dominant stems were combined with co-dominant stems; for simplicity, we refer to the combined group as co-dominant. Analyses of forms of mortality did not include the relatively few instances of crushed stems. Significant models were followed by orthogonal contrasts to assess effects of retention level (40% vs. 15%), pattern (aggregated vs. dispersed), and their interaction (*H1–H3*).

2.5.4. Stability of aggregates (H4)

A second set of GLMMs (binomial distribution, logit link) was used to assess the stability (*H4a*) and forms of mortality (*H4b*) in aggregates relative to controls. As above, treatment (100%, 40%A, or 15%A) was considered a fixed effect and block, a random effect; experimental unit was included as an individual-level random effect to account for overdispersion. Significant models were followed by Tukey (pairwise) contrasts of means. We then assessed the spatial distribution of mortality within aggregates (*H4c*). Data were modeled as a randomized block, split-plot design with aggregated treatment (40%A or 15%A) as the whole-plot and position (center or outer plot) as the split-plot (fixed effects); position within experimental unit was included as a random effect to account for overdispersion.

2.5.5. Consequence of bole damage (H5)

A final GLMM (binomial distribution, logit link) was used to test whether logging damage (limited to dispersed treatments) resulted in greater mortality than in undamaged trees (*H5*). A single model was run with cumulative mortality of stems as the response variable, dispersed treatment (40%D or 15%D) and damage condition (present/absent) as fixed effects, and block as a random effect. Damage condition within experimental unit was treated as an individual-level random effect to account for overdispersion.

All analyses were conducted in R v.2.14.2 (R Development Core Team, 2012).

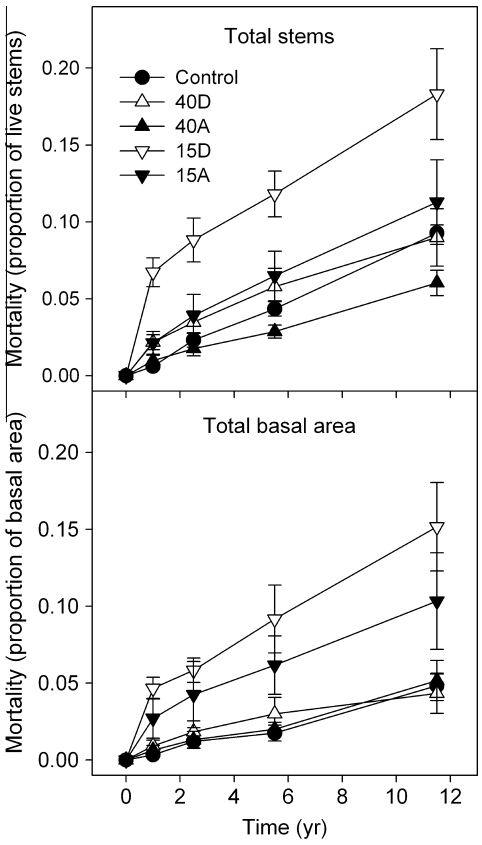

Fig. 2. Cumulative mortality of conifers (mean ± 1 SE) among treatments over the study period. Mortality is expressed as the proportion of stems (top) and basal area (bottom) lost from the initial, post-harvest population of trees (⩾5 cm dbh). Sampling dates after the second year represent average times since harvest among blocks (a difference of 1 year).

3. Results

Retention harvests imposed on forests of varying structure (Table 1) created substantial among-treatment and among-block variation in the post-harvest density, basal area, and canopy-class distribution of trees (Fig. 1). Not only were density and basal area reduced in dispersed treatments, but so was the representation of late-seral and intermediate-class stems. Several-fold differences in initial density among blocks yielded large differences in post-harvest density among replicates of the same treatment.

3.1. Temporal trends in mortality

Temporal trends in mortality varied among treatments (Fig. 2). In the controls (100%) annual rates of stem mortality remained fairly constant over the study period (mean of 0.8%, range of 0.6–1.1% among sampling intervals). Rates were also fairly constant (0.5–1.0%/year) at higher levels of aggregated retention (40%A). In contrast, mortality peaked in the first year in dispersed treatments (6.7% and 2.2% in 15%D and 40%D, respectively) and at low levels of aggregated retention (2.1% in 15%A), then declined to lower, relatively constant rates (means of 0.7–1.2%/year among treatments).

3.2. Treatment effects on the composition and physical form of mortality (H1–H3)

On average, the distribution of mortality among plots did not differ among treatments ($P > 0.05$ for all pairwise K–S tests; Fig. 3). A large percentage of plots experienced either no mortality (35–60% of plots) or <5% of total experimental-unit mortality (13–42% of plots). Relatively few plots accounted for >20% of total mortality.

Cumulative stem mortality in all groups—conifers, *Pseudotsuga*, and late-seral species—was greater at lower levels of retention and in dispersed treatments, as predicted (*H1*) (Fig. 4). Conifer mortality was greatest in 15%D, averaging 18% of stems (with a maximum of 28% at PH). In a model that excluded first-year losses, mortality varied with level (15% > 40%), but not pattern of retention. However, in post hoc comparisons for this time period, mortality at 15 and 40% retention did not differ from that of controls. Over the full study period, cumulative losses of basal area varied with level, but not pattern of retention, paralleling trends in *Pseudotsuga*, the dominant species (Fig. 4).

Stem mortality was greater at lower levels of retention for all canopy classes (as predicted; *H2*), and greater in dispersed treatments for intermediate and suppressed (but not co-dominant) stems (Fig. 5). Loss of intermediate stems was particularly high in 15%D (mean of 28%, maximum of 35% at DP). In contrast, loss of basal area varied with retention level, but not pattern (Fig. 5).

Standing dead was the most common form of mortality accounting for 55–80% of dead trees except at low levels of dispersed retention (34%; Fig. 6). As predicted (*H3*), the proportion of mortality attributable to uprooting was greater at lower levels of retention (for stems and basal area) and in dispersed treatments (for stems only) (Fig. 6); however, at low levels of retention, the proportion varied widely among blocks (1–67% of stems). There were no effects of treatments on stem breakage. Standing dead accounted for an increasing proportion of mortality at higher

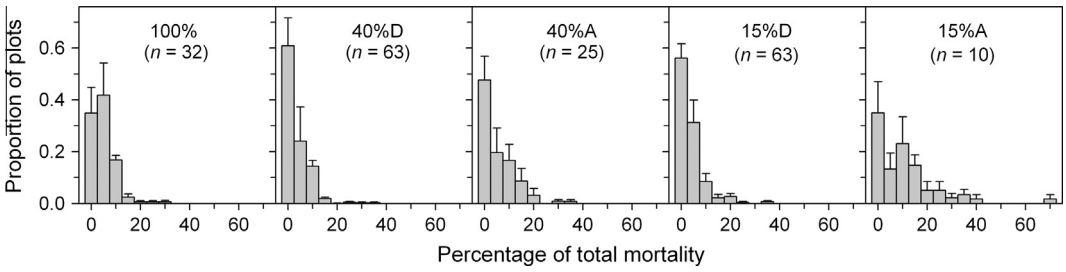

Fig. 3. Frequency distribution of cumulative mortality among plots within 15% and 40% dispersed (*D*) and aggregated (*A*) treatments at the end of the study period (11–12 years). Numbers of plots per treatment are shown in parentheses. Values are treatment means + 1 SE ($n = 6$). Bins are in 5% units, with an initial bin for 0% (i.e., 0%, 0.1–5%, 5.1–10%, etc.).

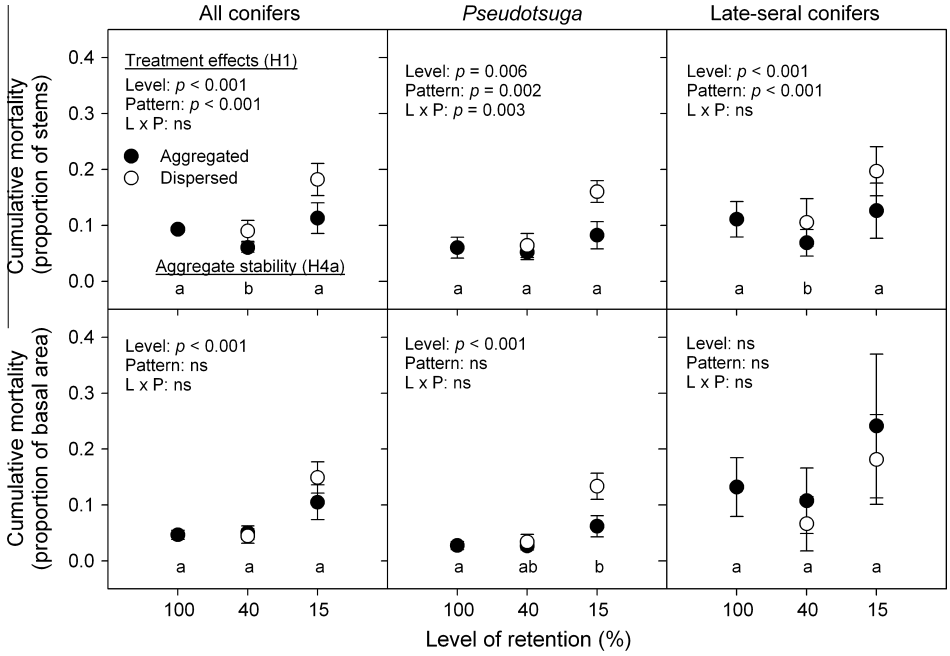

Fig. 4. Effects of level and pattern of retention on cumulative mortality of all conifers; the principal early-seral species, *Pseudotsuga menziesii*; and late-seral conifers (hypothesis 1) (see Fig. 1 caption for a full list of late-seral species). Values are the mean proportions (±1 SE) of initially tagged stems (top row) or basal area (bottom row). GLMMs were used to compare cumulative mortality among treatments. Orthogonal contrasts were used to test for the significance ($P \leqslant 0.05$) of retention level (40% vs. 15%), pattern (aggregated vs. dispersed), and their interaction (L × P) (hypothesis 1). A second set of GLMMs was used to assess the stability of aggregates (40%A, 15%A) relative to controls (100%) (hypothesis 4a). Lower-case letters represent the results of Tukey contrasts among these three treatments; different letters indicate significant differences ($P \leqslant 0.05$) among means.

retention (as expected), but not in the aggregated treatments (counter to expectation).

3.3. Stability of aggregates (H4)

Cumulative mortality was no greater in the aggregates than the controls, counter to expectation (*H4a*). In fact, in the aggregates of 40%A, late-seral and suppressed stems showed increased survival (Figs. 4 and 5). The only instance of elevated mortality among aggregates was in 15%A, where loss of *Pseudotsuga* basal area was greater than in the controls (6% vs. 3%, respectively; Fig. 4).

Consistent with expectation (*H4b*), uprooting accounted for a greater proportion of dead stems in 15%A (28%) than in the controls (7%). Standing dead accounted for the greatest proportion of dead stems and basal area in the controls (71–80%, Fig. 6).

Counter to expectation (*H4c*), mortality rates were no greater in the outer plots than in the center plots of aggregates (Fig. 7). In fact, intermediate and suppressed stems had significantly lower mortality in the outer plots.

3.4. Consequence of bole damage (H5)

Counter to expectation, bole damage associated with felling or yarding (limited to dispersed treatments) did not lead to significantly greater mortality. Cumulative mortality of damaged trees was 11% and 19% (40%D and 15%D, respectively) and in undamaged trees, 8% and 17% (40%D and 15%D, respectively).

4. Discussion

The DEMO experiment is unique in its explicit consideration of both level and pattern of retention in shaping ecological responses to timber harvest. Our results illustrate that both elements of residual forest structure contribute to the amount and physical form of post-harvest mortality. We observed greater mortality and greater losses to mechanical processes at lower levels of retention, consistent with previous research (Beese and Bryant, 1999; Scott and Mitchell, 2005; Busby et al., 2006; Solarik et al., 2012). However, our results also highlight the importance of pattern, with

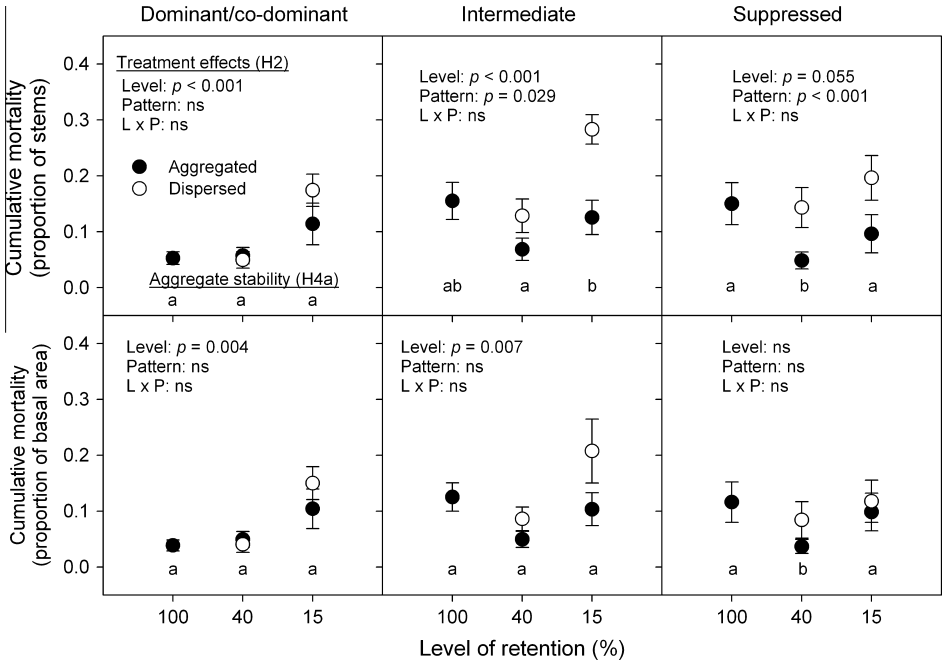

Fig. 5. Effects of level and pattern of retention on cumulative mortality of canopy classes (hypothesis 2). See Fig. 4 for other details.

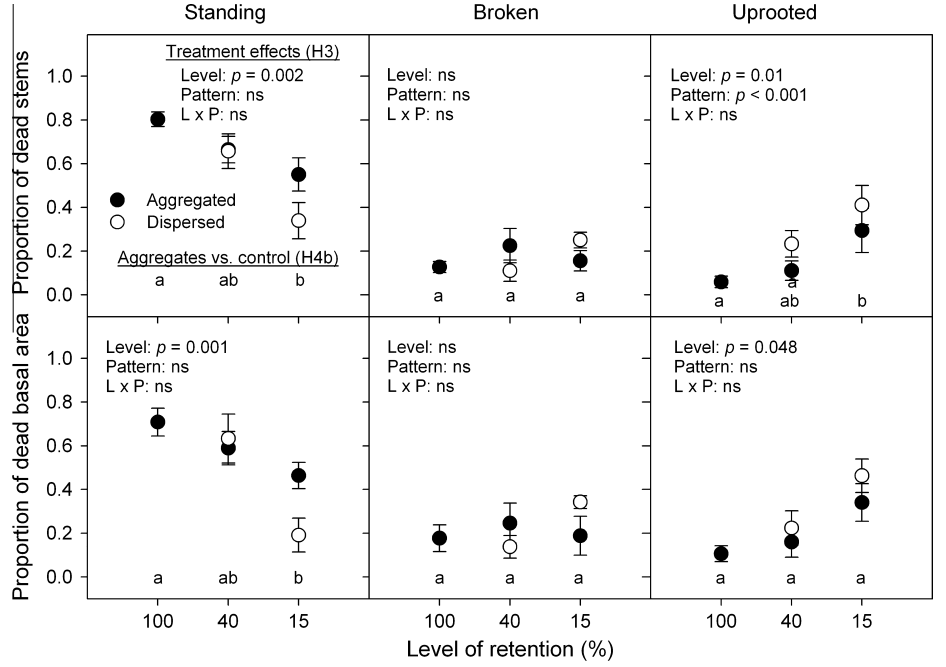

Fig. 6. Effects of level and pattern of retention on the contributions of different physical forms to cumulative mortality (hypothesis 3). Values are the mean proportions (±1 SE) of all dead stems (top row) or dead basal area (bottom row). See Fig. 4 for other details.

mortality reduced in aggregated relative to dispersed treatments at comparable levels of retention—an effect that has been difficult to infer from previous studies. That both elements of residual forest structure can influence mortality across a wide range of forest ages, structures, and physical environments, has important implications for the design of VRH systems and for current retention standards in the Pacific Northwest.

4.1. Effects of level and pattern of retention on the timing, composition, and form of mortality

Plot-scale frequency histograms suggest that mortality is a fine-scale spatial phenomenon in this system. Regardless of level or pattern of retention, mortality was irregularly concentrated, with a large proportion of plots with either no or only moderate amounts of mortality and a small proportion with much higher rates of loss. Temporal patterns suggest that differences among treatments were driven, in large part, by initial responses to harvest. Mortality peaked in the first year at lower levels of retention—notably in dispersed settings (15%D) in which ~7% of stems were lost. Thereafter, cumulative mortality did not differ from controls. This transient peak is consistent with previous studies that have reported short-term increases in mortality after harvest (Jönsson et al., 2007; Bladon et al., 2008; Thorpe et al., 2008; Martínez Pastur et al., 2009). Susceptible trees (due to form, exposure, or damage) may succumb to wind or other harvest-related damage,

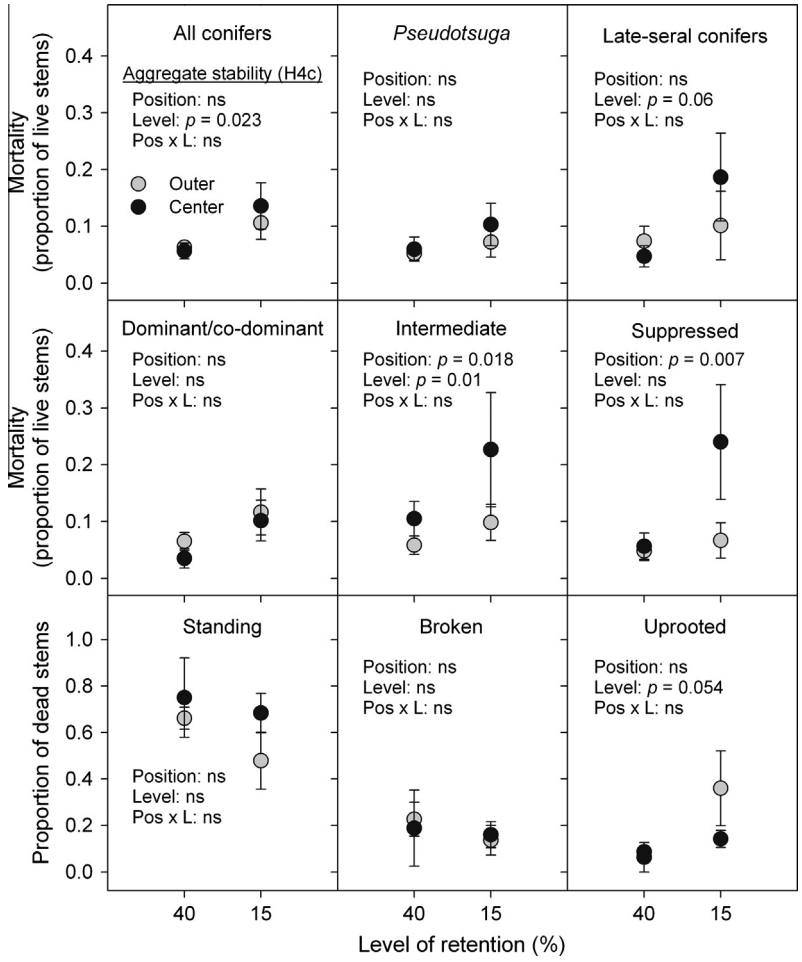

Fig. 7. Cumulative mortality of stems in the outer and center plots of aggregates (hypothesis 5). Values are the mean proportions (±1 SE) of initially tagged stems (for species/seral groups and canopy classes) or mean proportions (±1 SE) of dead stems (for forms of mortality). GLMMs were used to compare mortality with respect to position (center or outer plot), level of aggregated retention (40% or 15%), and their interaction.

leaving more stable survivors. Over time, trees may also adjust radial growth, canopy architecture, or root systems to resist mechanical stresses (Urban et al., 1994; Coutts et al., 1999; Brüchert and Gardiner, 2006). However, our results contrasts with other studies in which mortality remained elevated for more than a decade (Ruel et al., 2001; Solarik et al., 2012). Reconciling this variation may be difficult given that timing of mortality may hinge not only on factors that are intrinsic to a system (species' rooting habits or bole strength, soil stability, or topography), but to extrinsic factors that are less predictable (e.g., landscape context or timing of storm events relative to harvest) (Schaetzl et al., 1989; Ruel, 1995; Thorpe and Thomas, 2007; Xi and Peet, 2011; Mitchell, 2013).

Cumulative mortality among retention treatments was comparable to, or lower than, that reported in other VRH studies. Decadal-scale losses averaged 6–11% of stems (0.5–1.0%/year) among all but the 15%D treatment (18% of stems; 1.6%/year). Moreover, mortality rates closely bounded those of the controls (9%; 0.8%/year) and are very similar to those documented in mature and old-growth forests of this region (Franklin et al., 1987; Larson and Franklin, 2010). By comparison, in a survey of variable-retention units in western Oregon, Busby et al. (2006) estimated mortality rates approaching ~9%/year for the first 3–6 years after harvest, although they declined subsequently to <2%/year. Rates more comparable to the current study have been reported from *Picea–Populus* forests of northwestern Alberta (1.7–2.4%/year; Solarik et al., 2012) and *Picea* forests of northern Ontario (10.5% over 10 years; Thorpe et al., 2008). Working in the interior cedar-hemlock biogeoclimatic zone of BC, Coates (1997) reported that mortality in excess of 10–20% would be viewed as an operational failure or warrant further intervention. Indeed, losses exceeding this threshold have been observed in many VRH contexts (Beese and Bryant, 1999; Scott and Mitchell, 2005; Hautala and Vanha-Majamaa, 2007; Jönsson et al., 2007). However, thresholds for acceptable rates of mortality are likely to differ among regions and forest types and to reflect the specific goals of management. A more objective basis for comparing "success" may lie in the extent to which mortality departs from natural, background levels (i.e., in untreated controls; Bladon et al., 2008; Thorpe et al., 2008). From this perspective, our results indicate highly successful outcomes except at low levels of dispersed retention, where losses averaged twice those of controls or, in the extreme (PH), nearly three times.

We predicted greater mortality of the dominant, early-seral species, *Pseudotsuga*, at lower levels of retention and in dispersed treatments. Mechanistically, we expected reduced densities to result in greater uprooting or breakage of large-diameter stems whose larger canopy surface areas increase susceptibility to wind (Canham et al., 2001; Rich et al., 2007; Steil et al., 2009). Rates of stem loss were consistent with these predictions. However, loss of basal area was unaffected by pattern. This suggests that although greater numbers of *Pseudotsuga* were lost in dispersed treatments, they tended to be smaller in size. Mortality rates in strata dominated by *Pseudotsuga* support this interpretation: pattern had a strong effect on intermediate, but not co-dominant

stems (Fig. 5). This effect was especially pronounced at lower levels of retention, where more than twice as many intermediates were lost in dispersed as in aggregated treatments (28% vs. 13% of stems), a large proportion of these to uprooting. Greater mechanical failure following harvest is likely to reflect the greater height-to-diameter ratios of intermediates than co-dominants (85–89 vs. 67–75, respectively; P. D. Anderson, unpublished data) (Peltola et al., 1999; Wonn and O'Hara, 2001; Martínez Pastur et al., 2009; Solarik et al., 2012). At low levels of retention, loss of these sub-canopy stems had two principal outcomes: reducing an already-low stand density and shifting the height distribution toward even greater representation of co-dominants, further simplifying canopy structure.

As expected, late-seral species also suffered greater stem loss at lower retention and in dispersed treatments. However, losses were not attributable to "crushing", a natural form of mortality in the lower strata of older forests in this region (Franklin et al., 1987; Larson and Franklin, 2010). In fact, crushing was rarely recorded in the field. Instead, elevated rates of mortality were attributable to uprooting and, to lesser extent, stem breakage. Susceptibility to uprooting of these largely sub-canopy species does not appear related to tree form: height-to-diameter ratios were smaller in late-seral species than in *Pseudotsuga* (72.4 vs. 79.7). Similarly, uprooting does not appear related to bole damage during logging, as observed in other systems (Gullison and Hardner, 1993; Gea-Izquierdo et al., 2004; Thorpe et al., 2008). Although bole scarring was common in the dispersed treatments of this experiment (Moore et al., 2002), damaged and undamaged trees died at comparable rates. It is possible that mortality is better predicted by severity of bole damage, which was not assessed in this study. Alternatively, damage-induced mortality may be manifested over longer timeframes, particularly if it is mediated through introduction of fungal pathogens (Whitney et al., 2002). It is also possible that the propensity for uprooting in late-seral conifers reflects the relatively shallow rooting depths of the principal species, *Tsuga heterophylla* and *Abies amabilis* (Crawford and Oliver, 1990; Packee, 1990).

The forms in which trees die determine the physical characteristics and vertical distribution of dead wood, factors that are critical to the ecological functioning of forests (Harmon et al., 1986; Franklin et al., 1987; Stevens, 1997; Rose et al., 2001; Lutz and Halpern, 2006). Except at low levels of retention, most trees that died remained standing and intact, as snags. Rates of stem breakage were considerably less common and unrelated to treatment. Only at low levels of retention was uprooting common (although it was highly variable among blocks), and only at low-levels of dispersed retention did it dominate inputs to dead-wood pools. These differences in the physical form of mortality produced striking contrasts among treatments in the vertical distribution of dead wood: primarily as intact snags at higher levels of retention, but displaced to the forest floor (as logs) at lower levels of dispersed retention. Mortality that leads directly to downed wood circumvents a post-harvest period that can last decades, during which snags serve as critical habitat for wildlife (Rose et al., 2001) and contribute wood gradually to the forest floor through fragmentation or uprooting (Cline et al., 1980). On the other hand, large inputs of downed wood can also provide benefits, e.g., as long-term sources of organic matter and nutrients, and as sites for asymbiotic fixation of nitrogen (Harmon et al., 1986). This may be desirable in forest ecosystems in which coarse woody debris has been reduced by past management (Hautala and Vanha-Majamaa, 2007; Gustafsson et al., 2010). However, other benefits of downed wood, e.g., as substrate for epixylic bryophytes, may not accrue until microclimatic conditions become more conducive to re-colonization (Dovčiak et al., 2006).

4.2. Stability of aggregates

To what extent does the significance of retention pattern reflect the inherent stability of the 1-ha aggregates? Comparisons among aggregated treatments and controls offer several insights. Counter to expectation, cumulative mortality was no greater in the 1-ha aggregates than the controls. In fact, mortality was significantly reduced in the aggregates of 40%A due to greater survival of late-seral and suppressed stems. This result suggests an easing of competition-induced mortality (Palik et al., 2003, 2005), consistent with an increase in resource supply along the edges of aggregates. Previous studies of microclimatic gradients in the aggregated treatments indicate that understory light can be elevated to a distance of 15–20 m from the edge or further along southwestern exposures (Nelson and Halpern, 2005; Heithecker and Halpern, 2007). Additional evidence for the easing of competition lies in the greater survival of intermediate and suppressed stems in the outer relative to center plots of aggregates. These are the canopy classes most likely to show positive responses to increases in light.

Similar effects were not observed in aggregates at lower levels of retention (15%A). Although cumulative mortality was comparable to the controls, these more exposed aggregates (greater inter-aggregate distances) suffered greater loss of *Pseudotsuga* basal area, and among dead trees, a greater proportion of uprooting. The latter underscores the importance of opening size or edge exposure for risk of windthrow (Rollerson et al., 2009; Scott and Mitchell, 2005). With increasing exposure or isolation of forest fragments, forest-dependent species may become increasingly susceptible to edge effects (e.g., increased solar radiation, reduced humidity, increased wind speed) and to environmental or demographic stochasticity (Gilpin and Soulé, 1986; Lande, 1993). Indeed, in companion studies of the understory, bryophytes and late-seral herbs have shown progressively greater (albeit non-significant) declines with increasing exposure of aggregates (Halpern et al., 2012). Increasing rates of uprooting at lower levels of retention is likely to exacerbate these effects, reducing the intended functions of these forest remnants as refugia and sources for dispersal into adjacent harvest areas (Baker et al., 2013). Although we did not manipulate the size of aggregates, this result nevertheless has indirect implications for aggregate size. At similar levels of retention and in similar physiographic settings, smaller, more isolated, forest fragments, permitted under federal retention standards, are more likely to suffer wind damage (Esseen, 1994; Jönsson et al., 2007). However, we also observed considerable site-to-site variation in mortality, suggesting that managers may be able to situate aggregates in topographic settings that reduce vulnerability to wind (Mason, 2002; Roberts et al., 2007; Wood et al., 2008; Rollerson et al., 2009). Indeed, there are numerous reasons for subjective placement of aggregates within harvest units (e.g., minimizing disturbance to important habitat features or hotspots of biological diversity). This was not possible in the context of this highly structured experiment.

4.3. Conclusions and management implications

This large-scale, 11–12 year experiment demonstrates that rates of conifer mortality and the forms in which trees die after harvest are influenced both by the level (amount) of retention and its spatial distribution. Greater retention reduces mortality; comparisons with undisturbed controls suggest a threshold, rather than linear response, with substantially greater risk of mortality associated with lower levels of retention (15%). At these lower retention levels, mortality increasingly takes the form of uprooting. Otherwise trees primarily die standing and intact (as snags). Temporal trends indicate that risk of elevated mortality is transient, limited to the first year after harvest, despite

frequent storm events sufficient to cause wind damage. At comparable levels of retention, aggregation reduces mortality, although its benefits do not extend to reducing loss of dominant/co-dominant stems or stand basal area. Level and pattern can also interact to accentuate effects of pattern at lower levels of retention (e.g., on mortality of *Pseudotsuga*). Large (1-ha) aggregates are structurally stable, although increasing exposure leads to higher risk of uprooting.

Current standards and guidelines for retention harvests on federal lands in the Pacific Northwest require a minimum of 15% retention of live trees and allow for aggregates as small as 0.2 ha. The results of this study suggest that these minimum retention standards can lead to high risk of mortality in dispersed settings (approaching 30% in some sites) and to elevated rates of uprooting, even in aggregated settings, potentially negating the intended benefits of retaining live trees. Companion studies demonstrate that low levels of dispersed retention offer little microclimatic amelioration (Heithecker and Halpern, 2006) and low potential to maintain forest-dependent species (Luoma et al., 2004; Dovčiak et al., 2006; Halaj et al., 2008; Halpern et al., 2012). Susceptibility to mortality can only exacerbate these effects. On the other hand, low levels of dispersed retention can facilitate rapid re-establishment of *Pseudotsuga* and enhanced growth of planted seedlings (Urgenson et al., 2013). Managers may thus be faced with a trade-off between loss of retained trees and recruitment and growth of the regenerating cohort. Alternatively, a two-stage regeneration system consisting of a partial, preparatory cut to facilitate canopy development and wind firming prior to a final reduction to low residual density may meet the objectives of variable-retention systems where low densities of dispersed trees are desirable. For example the general public—whether informed of ecological benefits or not—tends to prefer the aesthetics of dispersed retention over patchy or aggregated retention (Ribe, 2005, 2009). Regardless of harvest regimen, forest managers have the ability to mitigate mortality risk through strategic placement of treatments, or components of treatments (e.g., aggregates), in more stable landscape or topographic settings (Mitchell, 2013). Although this experiment does not allow us to identify critical thresholds to minimize risk of mortality—either with respect to retention level or aggregate size—it does suggest that in using larger (1-ha) aggregates and moderate levels of retention, managers have wide latitude in designing variable-retention harvests to meet multiple objectives, avoiding risk of excessive mortality.

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