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Level and pattern of overstory retention shape the abundance and long-term dynamics of natural and created snags

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ARTICLE INFO

Keywords:

Aggregated retention
Dispersed retention
Regeneration harvest
Snag decay
Snag longevity
Snag recruitment

ABSTRACT

Standing dead trees, or snags, serve myriad functions in natural forests, but are often scarce in forests managed for timber production. Variable retention (VR), the retention of live and dead trees through harvest, has been adopted globally as a less intensive form of regeneration harvest. In this study, we explore how two key elements of VR systems — level (amount) and spatial pattern of live-tree retention — affect the carryover and post-harvest dynamics of natural and artificially created snags. We present nearly two decades of data from the DEMO Study, a regional-scale experiment in VR harvests of Douglas-fir-dominated forests in the Pacific Northwest. Snag losses to harvest were greater at 15 than at 40% retention (67 vs. 47% declines in density) and greater in dispersed than in aggregated treatments (64 vs. 50% declines). Densities of hard and tall (≥ 5 m) snags were particularly sensitive to low-level dispersed retention, declining by 76 and 81%, respectively. Despite these losses, post-harvest densities correlated with pre-harvest densities for most snag size and decay classes. In contrast to initial harvest effects, snag densities changed minimally over the post-harvest period (years 1 to 18 or 19), with low rates of recruitment offsetting low rates of loss. Post-harvest survival of snags was greater at 15 than at 40% retention (79 vs. 69%), as were rates of decay (68 vs. 52% of hard snags transitioned to soft). However, pattern had no effect on either process. Snag recruitment did not vary with retention level or pattern at the scale of the 13-ha harvest unit, but was several-fold greater in the 1-ha aggregates (14.3–27.8 snags ha^{-1}) than in the corresponding dispersed treatments (4.2–5.3 snags ha^{-1}). Snag size (diameter) distributions showed greater change in dispersed than in aggregated treatments, reflecting greater loss of smaller snags and recruitment biased toward larger snags. Created snags showed uniformly high survival (97%), irrespective of treatment, but rates of decay were greater at lower retention. If a goal of VR is to sustain snag abundance and diversity through harvest, emphasis should be placed on minimizing initial losses, either by reducing the intensity of felling in areas of dispersed retention or locating forest aggregates in areas of greater initial snag density, diversity, or incipient decay.

1. Introduction

Standing dead trees, or snags, provide myriad functions in natural forests. They contribute to the storage and cycling of carbon, nutrients, and water (Harmon et al., 1986; Oberle et al., 2018; Woodall et al., 2012); serve as habitat, substrate, and food for wood-dependent arthropods, cryptogams (lichens, bryophytes), and fungi (Berg et al., 1994; Löhms and Löhms, 2001; Siitonen, 2001; Spribille et al., 2008; Svensson et al., 2016; Ulyshen, 2018); and provide foraging, nesting, and roosting sites for birds and small mammals (Arnett and Hayes, 2009; Carey et al., 1997; Erickson and West, 2003; Neitro et al., 1985; Raphael

and White, 1984). The ecological functions of snags also vary in time as the physical, chemical, and biological properties of dead wood change (Bunnell et al., 2002; Harmon et al., 1986; Saint-Germain et al., 2007; Siitonen, 2001; Svensson et al., 2005). For example, as snags decay, the composition of arthropods shifts from primarily bark-dwelling to fungivorous species (Brunet and Isacson, 2009; Furniss and Carolin, 1977; Harmon et al., 1986; Jacobs et al., 2007; Spribille et al., 2008; Svensson et al., 2016). Similarly, changes in wood quality coupled with slow rates of dispersal and colonization lead to changes in the composition of epixylic lichens (Löhms and Löhms 2001, 2011; Runnel et al., 2013).

The abundance and physical characteristics of snags are critical to

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Table 1

Range of physical environments, pre-harvest structures, and treatment histories among the five study sites. Ranges represent experimental unit variation.

	Watson Falls, OR (WF)	Dog Prairie, OR (DP)	Butte, WA (B)	Little White Salmon, WA (LW)	Paradise Hills, WA (PH)
Latitude, longitude (deg)	43.27 N, 122.34 W	43.20 N, 122.20 W	46.37 N, 121.59 W	45.86 N, 121.69 W	46.01 N, 121.99 W
Elevation (m)	945–1310	1460–1710	975–1280	825–975	959–1018
Slope (%)	0–4	20–28	14–42	40–66	3–15
Aspect	flat	SW	E–SE	NW–NE	S–SE
Annual precipitation (mm) ¹	1443	1683	1860	1968	2968
Minimum, maximum mean monthly temperature (°C) ¹	–3.7, 26.2	–6.4, 22.3	–5.5, 21.5	–4.3, 24.0	–4.0, 22.1
Forest zone ^{2,3}	Abco	Abco	Tshe	Abgr	Abam
Minor tree species ³	Abco, Tshe, Pipo, Pimo	Abco, Abmas, Cade	Tshe, Thpl	Abgr	Tshe, Thpl, Abam
Stand age at harvest (years)	110–130	165	70–80	140–170	110–140
Density (trees ha ⁻¹ , ≥5 cm dbh)	310–500	258–475	759–1781	182–335	512–1005
Basal area (m ² /ha ⁻¹)	36–52	72–106	48–65	61–77	59–87
Canopy height (m) ⁴	42–45	45–47	30–33	53–55	32–37
Prior management	salvage logged, 1970–1978	thinned, 1986	none	none	none
Harvest date	Jun–Oct 1998	Jul–Sep 1998	May–Sep 1997	Mar–Sep 1998	Jun–Oct 1997
Yarding method	shovel loader	helicopter	helicopter	helicopter	shovel loader, skidder
Treatment of non-merchantable stems (<18 cm dbh)	felled if damaged	retained (but uncommon)	retained	retained (but uncommon)	felled
Method of snag creation	girdled	girdled	topped	girdled	topped

¹ Estimated means are from DAYMET (1980–1987; Thornton et al., 1997).² Forest zone, named for the climax tree species (Franklin and Dyrness, 1988).³ Tree species codes and full names: Abam = *Abies amabilis*, Abco = *Abies concolor*, Abgr = *Abies grandis*, Abmas = *Abies magnifica* var. *shastensis*, Cade = *Calocedrus decurrens*, Pimo = *Pinus monticola*, Pipo = *Pinus ponderosa*, Thpl = *Thuja plicata*, Tshe = *Tsuga heterophylla*.⁴ Mean height of trees in the 75th–95th percentile of the height distribution.

the persistence and reproduction of cavity-nesting birds and small mammals. For example, in western coniferous forests, snag density predicts the abundance of primary cavity nesters (Carey et al., 1991; Raphael and White, 1984; Zarnowitz and Manuwal, 1985). The size and decay state of snags determine their suitability as nesting or foraging sites (Bunnell et al., 2002; Lundquist and Mariani, 1991; Mannan et al., 1980; Raphael and White, 1984; Thomas et al., 1979). Although species' requirements vary, most cavity-nesting birds select decaying snags of larger diameter — a characteristic that affords greater protection and facilitates excavation (Bunnell, 2013; Miller and Miller, 1980; Thomas et al., 1979). As a result, large snags contribute disproportionately to biodiversity over their lifespans (Bunnell, 2013; Lindenmayer et al., 2012; Thomas et al., 1979) — supporting primary excavators (e.g., woodpeckers) which, in turn, provide for diverse communities of secondary cavity nesters, including birds and mammals. The availability of large snags can also be a limiting factor for bats (including several species of conservation concern; Rodhouse et al., 2015), which use them as day, night, or maternity roosts, and for mammals (including Pacific fisher, *Pekania pennanti*, and Pacific marten, *Martes caurina*), which use them for denning (Delheimer et al., 2019; Lofroth et al., 2011). On the other hand, small snags serve as the primary foraging sites for many secondary cavity nesters (Bunnell, 2013).

In unmanaged forests, the abundance and physical characteristics of snags vary with forest age and physical environment — factors that shape rates of production and loss to fragmentation or decay (Cline et al., 1980; Harmon et al., 1986; Ohmann and Waddell, 2002; Spies et al., 1988). In the Douglas-fir region of the western U.S., the density, size, or mass of snags can vary by as much as two orders of magnitude over the course of succession: initially high following stand-replacing disturbance (Cline et al., 1980; Spies et al., 1988); declining over the next century as losses to stem failure, fragmentation, and decay exceed inputs; then increasing as forests develop the characteristics of old-growth (Cline et al., 1980; Franklin et al., 2002; Spies and Cline, 1988). The pace and magnitude of these changes can vary with the severity of stand-initiating disturbance, site productivity, or environmental conditions.

For example, wood decays more rapidly in warmer or more humid and stable environments — conditions that promote heterotrophic activity (Chambers et al., 2000; Harmon et al., 1986; Oberle et al., 2018). In contrast, colder temperatures or changes in forest structure that reduce humidity (e.g., silvicultural thinning or gap creation), can limit the activity of fungi, slowing the decay process (Angers et al., 2011; Mielke, 1950; Rayner and Todd, 1980; Shorohova and Kapitsa, 2014).

The abundance of natural snags is greatly reduced in forests managed for timber production, where safety concerns and economic objectives conflict with the ecological benefits of standing dead wood (Hayes et al., 2005; Kroll et al., 2012b; Spies et al., 1988; Wilhere, 2003). Short-rotation, even-aged management results in little carryover or production of snags of a size or quality that benefit wildlife (Hagar, 2007; Rose et al., 2001). Where intensive management occurs at a landscape scale, the implications for snag-dependent organisms can be dramatic (Siitonen, 2001; Thorn et al., 2020). Efforts to mitigate these effects include snag creation by topping, girdling, or other means (Lewis, 1998). Although created snags can support some wood-dependent species in the short term (Brandeis et al., 2002; Chambers et al., 1997; Hane et al., 2019; Shea et al., 2002), their functional longevity may be limited (Barry et al., 2018; Hallett et al., 2001).

Variable retention (VR), posed as an alternative to more intensive forms of regeneration harvest, seeks greater balance between the production and ecological values of managed forests, including the functions provided by dead wood. By retaining live (or 'green') trees and snags within harvest units, VR seeks to emulate the outcomes of natural disturbance processes (e.g., wildfire or windstorms; Franklin et al., 1997; Gustafsson et al., 2012; Lindenmayer and Franklin, 2002). By definition, VR can take multiple forms, but is typically defined by the level of live-tree retention (e.g., proportion of original basal area) and the spatial pattern in which trees are retained (dispersed or aggregated; Franklin et al., 1997). A considerable body of research has been devoted to how level and pattern of retention sustain or enhance the recovery of biodiversity (Fedrowitz et al., 2014; Gustafsson et al., 2010; Rosenwald and Löhms, 2008), but few studies have considered how they shape the

abundance and long-term dynamics of snags, on which many forest species depend.

Level and pattern of live-tree retention may shape the abundance and physical characteristics of snags through the intensity or spatial distribution of logging disturbance or through effects on post-harvest processes (i.e., snag survival, decay, and recruitment). For example, retaining trees in undisturbed patches or aggregates should facilitate greater, albeit localized, carryover of snags from the original forest (Franklin et al., 1997). Although dispersed retention may limit carryover due to safety concerns during felling (Hayes et al., 2005; Myers and Fosbroke, 1995; Wilhere, 2003), it should foster greater spatial dispersion of snags in the future (Franklin et al., 1997). Level of retention may produce similar tradeoffs. For example, although greater retention may enhance snag production, it may also promote decay, reducing snag longevity. Conversely, low-level retention may reduce rates of decay, but limit recruitment.

We explore these relationships with residual forest structure using two decades of data on the dynamics of snags from the Demonstration of Ecosystem Management Options (DEMO) Study, a large-scale experiment in VR in mature, Douglas-fir-dominated forests of the Pacific Northwest (Aubry et al., 1999, 2009; Aubry and Halpern, 2020). Initiated in 1994, DEMO was designed to evaluate newly established standards for regeneration harvests on federal forests within the range of the Northern Spotted Owl — standards adopted as part of a broader regional plan for ecosystem management, the Northwest Forest Plan (NWFP; Tuchmann et al., 1996; USDA and USDI, 1994). The experiment includes factorial combinations of level of retention (15 or 40% of original basal area) and spatial pattern (trees dispersed through the harvest unit or aggregated in 1-ha patches), as well as a control, replicated across forests of varying age, structure, and physical environment. Although specific elements of the design were chosen to test the efficacy of newly adopted standards (i.e., a minimum of 15% retention and the use of large aggregates), the broader intent was to elucidate the roles of level and pattern more generally (Aubry et al., 1999, 2009; Aubry and Halpern, 2020). The objectives of the current paper are two-fold: (1) to quantify two decades of change in snag frequency, density, and physical characteristics (decay, height, and diameter) as they relate to level and pattern of retention; and (2) to elucidate how logging disturbance and post-harvest processes (snag fall, decay, breakage, and recruitment) contribute to these changes. We focus on the dynamics of natural snags, but also assess the fates of created snags, established at low density in the harvested areas of treatments to meet requirements of the Northwest Forest Plan.

2. Methods

2.1. Study sites

The experiment is replicated at five sites representing a wide range of biophysical environments at low to moderate elevation (825 to 1710 m) in the western Cascade Range of Oregon and Washington (Table 1). Sites occur on federal ‘matrix’ lands, i.e., those managed for timber production under the NWFP (USDA and USDI, 1994). The climate is maritime, characterized by warm, dry summers and cool, wet winters. Most precipitation falls between October and April leading to frequent summer drought (Franklin and Dyrness, 1988). Soils are moderately deep, well-drained loams to loamy sands originating from andesite, breccia, or basalt parent material or pumice deposits (Radtke and Edwards, 1976; Wade et al., 1992). Topography ranges from flat to fairly steep (0 to 66% slope; Table 1).

Sites encompass four forest zones defined by the climate and climax trees species (Franklin and Dyrness 1988): warm/dry *Abies concolor* (Watson Falls [WF] and Dog Prairie [DP]) and *Abies grandis* zones (Little White Salmon [LW]); warm/moist *Tsuga heterophylla* zone (Butte [B]); and cool/moist *Abies amabilis* zone (Paradise Hills [PH]). *Pseudotsuga menziesii* (Douglas-fir) was the dominant tree species at all sites but

species composition and stand structure varied markedly (Table 1). At the time of harvest, stand ages ranged from ~ 70 to 170 years among sites. Sites in Washington had no prior history of management, but sites in Oregon had been partially thinned (DP) or salvage logged (WF) several decades earlier. Within sites, harvest-unit locations were chosen to minimize variation in physical environment and forest structure, within the constraints imposed by topography and past management. Additional details about site characteristics can be found in Aubry and Halpern (2020).

2.2. Experimental design and treatment implementation

The experiment is a randomized complete-block design with six treatments applied to 13-ha (square or slightly rectangular) experimental units (Aubry et al., 1999; Aubry and Halpern, 2020). For this study we sampled five of the treatments: a no-harvest control (100% retention) and four that comprise a balanced, two-factor design with two levels of retention — 15 or 40% of original basal area — and two spatial patterns — trees evenly dispersed (D) or aggregated (A) in 1-ha (56-m radius) circular forest patches (Ap). In dispersed treatments (15D and 40D), dominant and co-dominant trees were retained uniformly, using as the retention target, the cumulative basal area of trees in the corresponding aggregated treatment (15A or 40A). All other merchantable trees (≥ 18 cm dbh; mostly suppressed, intermediate, and some co-dominant stems) were felled and removed. Aggregated treatments differed in the number of patches: two in 15A, retained in opposite corners of the harvest unit (~115 m apart), and five in 40A, retained in the four corners and center of the unit (~30 m apart). All merchantable stems in the adjacent harvest area (15Ah and 40Ah) were felled, except those to be converted to snags, as described below. Treatment of non-merchantable stems (<18 cm dbh) varied among sites: stems were retained at DP, B, and LW; cut at PH; and cut if damaged at WF (Table 1).

At each site, trees were felled and yarded over a 3- to 7-month period in 1997 or 1998 (Table 1). Methods of yarding varied among sites: helicopters were used on steep terrain (DP, B, and LW) and ground-based machinery was used on gentle topography (WF and PH). Tree limbs were left attached to the bole to reduce slash accumulation. Snags were felled where they posed a safety hazard. However, to meet snag-density requirements of the NWFP (USDA and USDI, 1994), an additional 6.5 live trees ha^{-1} were retained in the harvested portions of each unit (D or Ah), to be topped (B and PH) or girdled (WF, DP, and LW) within the first post-harvest year (Table 1). Trees targeted for snag creation were typically large, decadent or broken-topped *P. menziesii* (mean and range of diameters of 69 and 43–164 cm). Additional details on treatment implementation can be found in previous publications (Aubry et al., 1999; Aubry and Halpern, 2020; Halpern and McKenzie, 2001).

2.3. Tree and snag measurements

In each harvest-unit sampling was distributed across a systematic grid of 63 or 64 sample points (40 m spacing). Grid points served as the centers of a nested pair of tree and snag plots (0.04 ha and 0.08 ha, respectively). In the control (100), we sampled alternate points on the grid ($n = 32$). In the aggregated treatments (15A and 40A), we sampled all grid points in the aggregates ($n = 10$ in 15Ap; $n = 24$ – 25 in 40Ap) and a subset of points in the harvested area ($n = 22$ in 15Ah; $n = 12$ in 40Ah). In the dispersed treatments (15D and 40D), sampling intensity varied among sites and sampling dates. Prior to harvest, we sampled all ($n = 2$ sites) or alternate points ($n = 3$ sites). However, after harvest, we sampled all points in each dispersed treatment to account for the reduced density of trees and snags. In total, 756 plots were sampled prior to harvest and 974 plots afterwards. Pre-harvest sampling occurred between 1994 and 1996 and post-harvest sampling occurred in 1998/1999 (year 1), 2003 (year 5 or 6), 2009 (year 11 or 12), and 2016 (year 18 or 19).

Prior to harvest, all live trees ≥ 5 cm diameter at breast height (dbh)

were identified to species and measured for diameter. All snags (dead trees ≥ 0.5 m tall and ≥ 25 cm dbh) were identified to species (if possible), measured for diameter at breast height (or at 0.5 m if shorter than 1.37 m), and assessed for decay state and height class. Decay states (1–5) follow the classification of [Cline et al. \(1980\)](#) based on presence/absence of fine branches, sloughing of bark, and degree of decomposition of sapwood and heartwood. Height classes (1–4) were as follows: 0.5–1.5 m, >1.5–5 m, >5–15 m, and > 15 m.

Following harvest, all live trees and snags were identified to species (if possible), measured for diameter, and tagged to provide individual-based demographic data. Snag origin was noted to separate natural from created snags. At each post-harvest sampling date, all live trees were measured for diameter and assigned a status: surviving, ingrowth (reaching 5 cm dbh), dead/standing, or dead/fallen. All residual (surviving) and created snags were reassessed for status (standing or fallen), decay state, and height class, but diameter was not remeasured. Any new snags (recruitment) were tagged as needed, identified to species, measured for diameter, and assessed for decay state and height class. At final sampling (2016), all surviving snags were measured for height to the nearest 0.1 m using a Haglof Vertex IV hypsometer.

2.4. Data reduction and measures of response

We focused our analyses on data from the pre-harvest, immediate post-harvest (year 1), and final sampling dates (year 18–19). To simplify analyses related to decay, we reduced the five decay states to two: ‘hard’ and ‘soft’ (decay classes 1–2 and 3–5, respectively), following the classification system of [Thomas et al. \(1976\)](#). Similarly, we reduced the four height classes to two: ‘tall’ (≥ 5 m) and ‘short’ (< 5 m). Given the preference of many cavity-nesting species for snags with larger diameters (typically > 50 cm dbh; [Bunnell, 2013](#)), we also grouped snags as ‘small’ (< 50 cm dbh) and ‘large’ (≥ 50 cm dbh).

Analyses were conducted at the scale of the harvest unit ($n = 20$ units among the five sites). For each harvest unit \times sampling date, we computed the frequency (proportion of plots) and mean density of snags (number ha^{-1}) for each decay, height, and diameter class, as well the total frequency and density of snags. For aggregated treatments, frequency and density were computed as area-based weighted means of the patch (Ap) and harvest-area (Ah) environments.

We used post-harvest demographic data (survival, recruitment, and transitions in physical state) to interpret long-term changes in the density of decay, height, and diameter classes. For each experimental unit, survival of residual snags was computed as the proportion of post-harvest (year 1) residuals standing at final sampling (year 18–19), irrespective of any change in decay state or height class. Survival was also computed for each post-harvest decay, height, and diameter class. Survival of recruitment was computed similarly, but was limited to snags that had recruited prior to final sampling.

Transitions in physical state were computed separately for residuals and recruits in each experimental unit. For each group, we computed the proportion of initially hard snags that remained hard at final sampling and the proportion that had transitioned to soft (the sum of the two proportions was equivalent to survival of hard snags). The same proportions were computed for initially tall snags (i.e., remained tall or transitioned to short). Transitions in physical state were not computed for soft or short snags, because they either survived or fell. For recruitment, transitions in physical state were limited to snags that had recruited prior to final sampling. Survival and transitions in physical state were assessed similarly for created snags.

2.5. Models of treatment effects on frequency, density, survival, and transitions in physical state

We used general linear models (GLMs) to test effects of retention level and pattern on each measure of response (frequency, density, survival, and transitions in physical state). Data from the controls were

not included in models but are presented for comparison in all figures. To distinguish effects of logging from post-harvest processes, we ran separate models on post-harvest (year 1) and final (year 18–19) frequency and density. For the latter, residuals and recruits were modeled separately. In addition, because recruitment was limited to areas with residual trees (D or Ap environments), we modeled recruitment in two ways: for the harvest-unit as whole (weighted means of Ap and Ah environments in the aggregated treatments) and for the subset of plots with retained trees (D or Ap environments). Finally, we modeled cumulative responses to treatments (pre-harvest to final sampling) at the scale of the harvest unit, combining the densities of residuals and recruits.

In all models, predictors included site, level (15 vs. 40), pattern (D vs. A), and the level \times pattern interaction. Frequency and density models also included a covariate to account for prior (pre- or post-harvest) variation among harvest units. Pre-harvest values were used as covariates in models of post-harvest or cumulative response. Post-harvest values were used as covariates in models of final response (assessing post-harvest processes). Models of survival and transitions in physical state did not require a covariate because the response variables implicitly account for prior conditions.

Models of created-snag survival and transitions in physical state were limited to four sites because few created snags fell within the sample plots at the Butte (B) site. In these models, pattern contrasts the response in dispersed (D) vs. harvested areas of aggregated treatments (Ah).

For all models, standard diagnostics were used to assess homogeneity of variance and normality of residuals (Levene’s and Shapiro-Wilk tests, respectively). Data were log transformed as needed. Main effects and interactions were judged as significant at an α of 0.05 and as marginally significant at an α of 0.05 to 0.1. All GLMs and diagnostic tests were conducted in JMP Pro 15.2.0 software ([SAS, 2019](#)).

2.6. Effects of treatments on diameter distributions

We used a series of two-sample Kolmogorov-Smirnov (KS) tests to assess the effects of treatments on the diameter distributions of snags, independent of changes in density. Analyses were conducted separately for residuals and recruits. Because tests are conducted as pairwise comparisons, and diameter distributions varied widely among harvest units prior to treatment, we focused on temporal changes within each unit, from pre- to post-harvest and post-harvest to final sampling (residuals only). From these multiple comparisons we summarized when, how often, and in which treatment contexts, distributions changed significantly, as well as the nature of those changes (e.g., a shift toward larger diameters). Tests were run for each decay class and for snags in total. For recruitment, diameter distributions were compared at final sampling between harvest units within each site. Here, we tested the effect of level for each pattern (15A vs. 40A, 15D vs. 40D) and the effect of pattern for each level (15A vs. 15D, 40A vs. 40D). Tests were limited to recruitment totals due to the small number of recruits in some decay classes at some sites. Finally, to assess the cumulative effects of treatments, we compared pre-harvest to final diameter distributions for each harvest unit, combining residuals and recruits in the final sample.

Prior to running KS tests, we adjusted the sample of snags from the aggregated treatments to account for the disproportionate sampling of patch (Ap) relative to harvest-area (Ah) environments (see [Section 2.3](#)). To achieve comparable sampling intensity, we retained all snags from plots in 15Ah and 40Ah, and randomly selected 17.7% and 66.7% of snags from plots in 15Ap and 40Ap, respectively. Two-sample KS tests and graphical representations of diameter distributions were made using JMP Pro 15.2.0 software ([SAS, 2019](#)).

3. Results

3.1. Snag characteristics prior to harvest

Prior to harvest there were 14 species of snags, but the vast majority

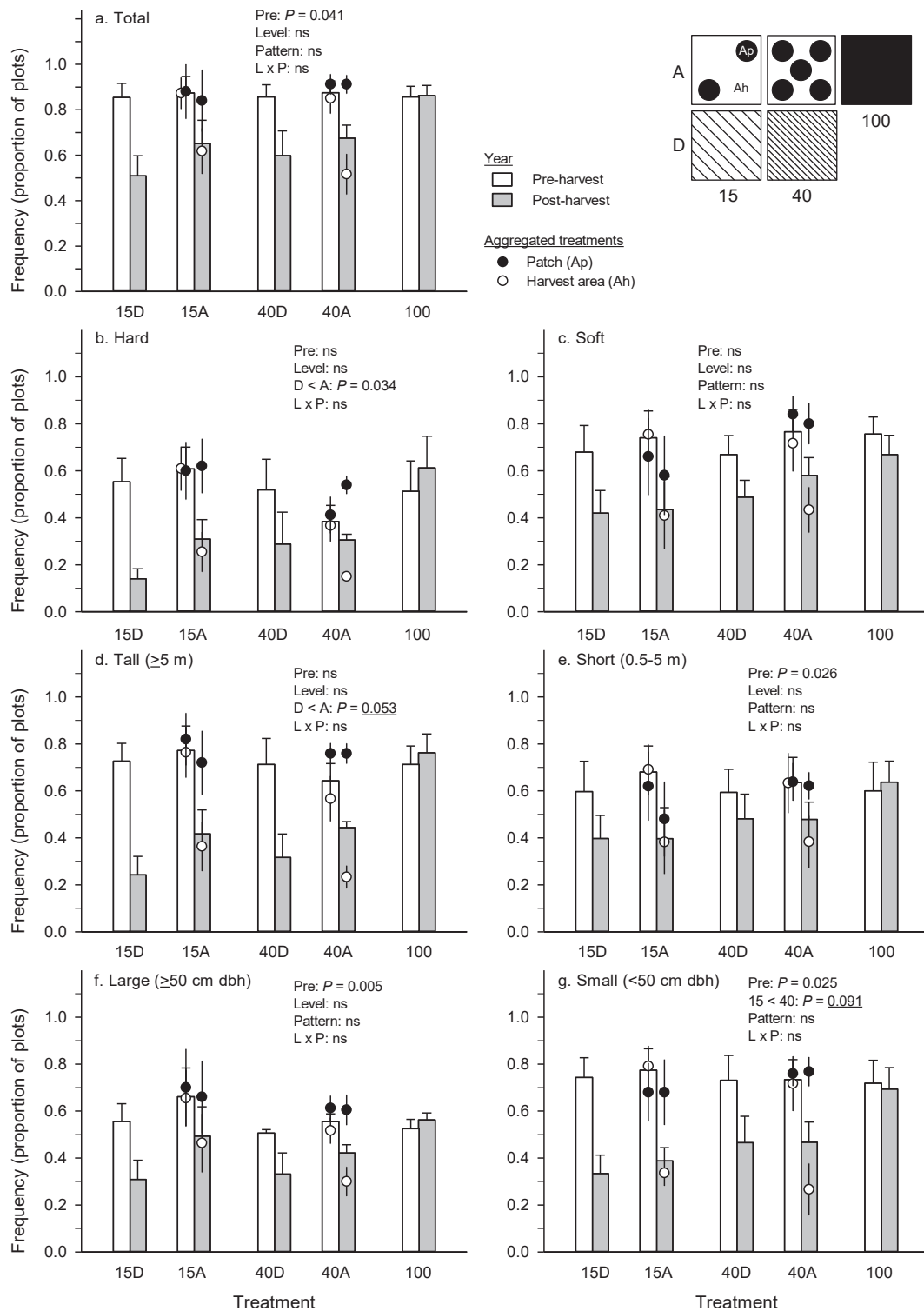


Fig. 1. Snag frequency by decay, height, and diameter class at pre- and post-harvest (year 1) sampling (white and grey bars, respectively). Values are treatment means with SEs ($n = 5$ sites). Values for aggregated treatments (15A, 40A) are weighted means of forest patches (Ap, closed circles) and harvest areas (Ah, open circles); see harvest-design schematic in the upper right. P values are shown for significant ($P \leq 0.05$) or marginally significant ($0.05 < P \leq 0.1$; underlined) terms from general linear models of post-harvest frequency as a function of pre-harvest frequency (Pre), level (15 vs. 40), pattern (A vs. D), and the level \times pattern ($L \times P$) interaction. Controls (100) are shown for reference.

were *Pseudotsuga menziesii* and *Abies concolor*. Of 1,930 snags identified to species ($n = 756$ plots), 66.5% were *P. menziesii* (present at all five sites) and 18.1% were *A. concolor* (present at two sites).

Snag frequency (proportion of plots with snags) and density varied widely among harvest units prior to treatment (Fig. A1, Appendix A).

Across all harvest units, 86% of plots had snags (Fig. 1a, white bars); among individual units, frequencies ranging from 64 to 100%. Soft snags were more frequent than hard snags (means of 71 vs. 52% of plots; Fig. 1b and c), tall snags were more frequent than short snags (71 vs. 63% of plots; Fig. 1d and e), and small-diameter snags were more

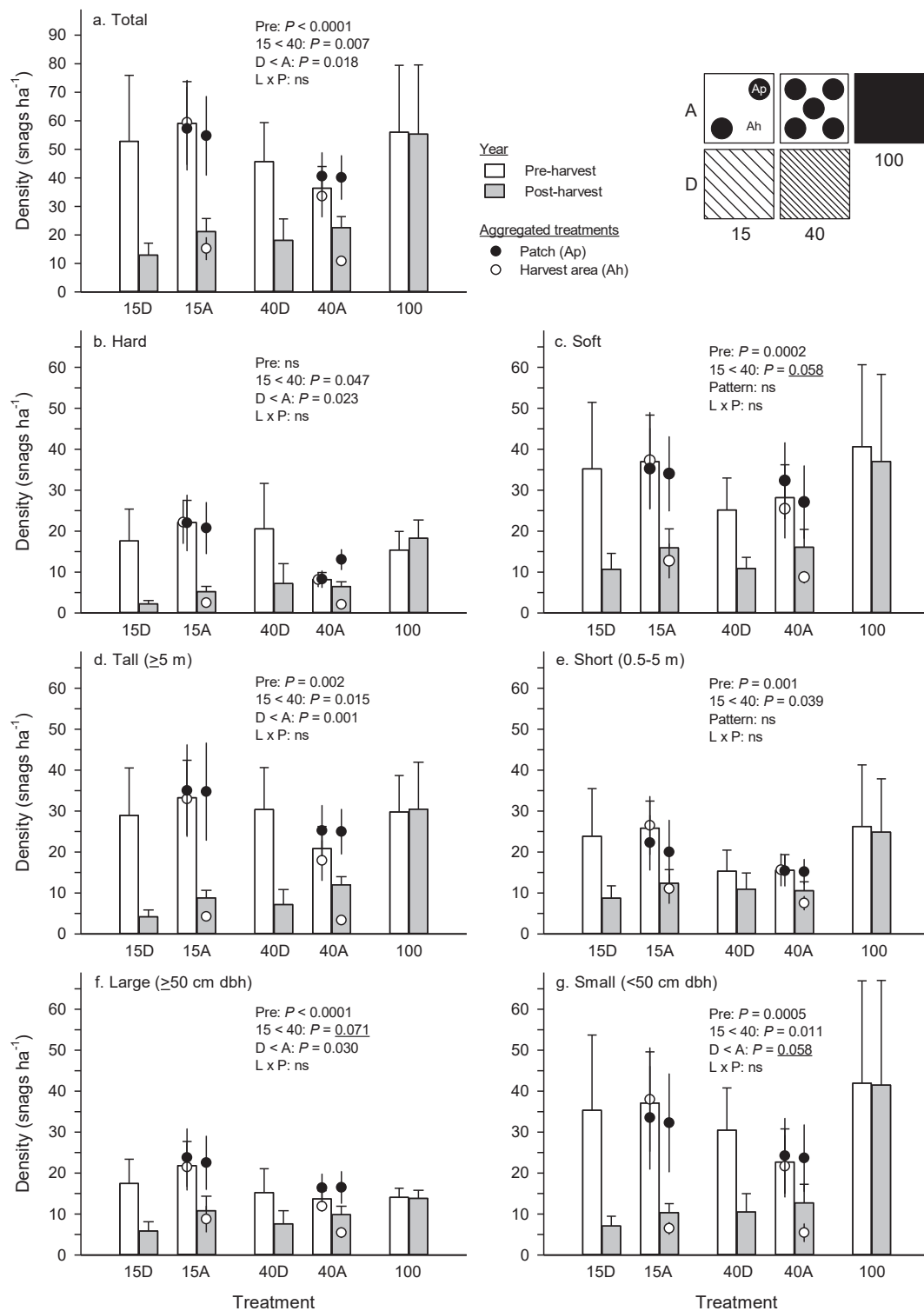


Fig. 2. Snag density by decay, height, and diameter class at pre- and post-harvest (year 1) sampling (white and grey bars, respectively). Values are treatment means with SEs ($n = 5$). Values for aggregated treatments (15A, 40A) are weighted means of forest patches (Ap, closed circles) and harvest areas (Ah, open circles); see harvest-design schematic. P values are shown for significant ($P \leq 0.05$) or marginally significant ($0.05 < P \leq 0.1$; underlined) terms from general linear models of post-harvest density as a function of pre-harvest density (Pre), level (15 vs. 40), pattern (A vs. D), and the level \times pattern (L \times P) interaction. Controls (100) are shown for reference.

frequent than large-diameter snags (75 vs. 57% of plots; Fig. 1f and g).

Pre-harvest density averaged $48.5 \text{ snags ha}^{-1}$ (Fig. 2a, white bars) but ranged from 12.9 to $141.8 \text{ snags ha}^{-1}$ among individual harvest units (Fig. A1, Appendix A). Soft snags were more numerous than hard snags (mean densities of 31.4 vs. 17.1 ha^{-1} ; Fig. 2b and c), tall snags

were more numerous than short snags (28.4 vs. 20.1 ha^{-1} ; Fig. 2d and e), and small-diameter snags were more numerous than large-diameter snags (31.4 vs. 17.1 ha^{-1} ; Fig. 2f and g). Pre-harvest diameter distributions were typically reverse-J shaped, but occasionally hump-shaped (e.g., LW site; Fig. A2, Appendix A).

3.2. Snag carryover through harvest

3.2.1. Snag frequency

Of 1,131 snags identified to species in the post-harvest (year 1) sample, 75.8% were *P. menziesii* and 14.5% were *A. concolor*. Total frequency changed minimally (<1%) in the controls, but was reduced in all harvested treatments (mean of 60.9%, a 30% reduction from the pre-harvest mean; Fig. 1a). However, neither level nor pattern of retention affected the magnitude of decline (Fig. 1a). Soft snags remained more frequent than hard snags (means of 48 vs. 26% of plots; Fig. 1b and c), tall snags became less frequent than short snags (36 vs. 44% of plots; Fig. 1d and e), and small-diameter snags were no longer more frequent than large-diameter snags (39 vs. 41% of plots). Pre-harvest frequency was a significant predictor of post-harvest frequency for short, large-diameter, and small-diameter snags (Fig. 1e-g), but not for tall snags (Fig. 1d) or either decay class (Fig. 1b and c). Level and pattern of retention had little effect on the frequency of most snag groups. Exceptions included a tempering of the decline in hard and tall snags in aggregated treatments ($A > D$; Fig. 1b and d), attributable to their stability in the patches (Ap).

3.2.2. Snag density

Snag densities were reduced in all harvested treatments to an average of 18.7 ha^{-1} (37% of the pre-harvest mean; Fig. 2a). For comparison, densities changed minimally (~2%) in the controls. Among individual harvest units, post-harvest densities ranged from 4.5 to $48.0 \text{ snags ha}^{-1}$ (Fig. A1, Appendix A). Soft snags remained more numerous than hard snags (means of 13.4 vs. 5.3 ha^{-1} ; Fig. 2b and c), but tall and small-diameter snags were reduced to levels comparable to those of short- and large-diameter snags (means of ~8.0 to 10.6 ha^{-1} ; Fig. 2d-g). For all classes of snags, post-harvest density correlated with pre-harvest density, but losses to harvest were reduced by greater retention (Fig. 2). As with snag frequency, stability within the aggregates tempered declines in the density of hard and tall snags (Fig. 2b and d) and in the density of large- and small-diameter snags (Fig. 2f and g).

3.2.3. Diameter distributions

Diameter distributions were altered by harvest in 9 of the 20 harvest units (significant or marginally significant effects) and more often at lower retention (Fig. A2, Appendix A). Soft snags were more susceptible to change than were hard snags (significant or marginally significant effects in 7 vs. 3 units, respectively), particularly in dispersed treatments. In nearly all instances, distributions shifted toward larger-diameter snags, with median diameters increasing by 6–24 cm from pre- to post-harvest sampling.

3.3. Long-term changes in snag abundance, diameter distribution, and height

3.3.1. Frequency of residuals and recruits

After harvest, residual snag frequency declined from an average of 60.9% in year 1 to an average of 52.5% in year 18–19 (Fig. 3a). Frequencies of hard and tall snags declined substantially (by an average of 79 and 37%, respectively), although aggregated retention tempered the decline in hard snags ($A > D$; Fig. 3b). The remaining groups showed smaller changes in frequency, with greater declines at 40 than at 15% retention (soft, short, and small-diameter snags; Fig. 3c, e, and g) and greater declines in dispersed than in aggregated treatments (short and small-diameter snags; Fig. 3e and g). Despite this turnover, final frequency was correlated with post-harvest frequency for all but hard snags (Fig. 3).

By final sampling, snags had recruited into an average of 22% of plots. Of recruits identified to species (91% of the total), 53% were

P. menziesii (present at all sites) and 31% were *A. concolor* (present at two sites). At final sampling, soft recruits were 70% more frequent than hard recruits (Fig. 3b and c), tall recruits were more than twice as frequent as short recruits (Fig. 3d and e), and large-diameter recruits were 60% more frequent than small-diameter recruits (Fig. 3f and g). Level of retention had no effect on frequency of recruitment of any class of snags. Effects of pattern were limited to marginally greater frequency of recruitment of large-diameter snags in D than in A (Fig. 3f). However, when analyses were limited to the subset of plots with potential source trees, nearly all groups showed significantly greater frequency of recruitment in the patches of aggregated treatments than in dispersed treatments ($Ap > D$; Fig. 3).

3.3.2. Density of residuals and recruits

Total snag density was largely unchanged through final sampling (mean of $18.6 \text{ snags ha}^{-1}$, Fig. 4a; harvest-unit range of 4.8 to $32.7 \text{ snags ha}^{-1}$, Fig. A1, Appendix A). Loss of residuals was largely offset by recruitment. Densities of residual hard, tall, and small-diameter snags declined by an average of 85, 46, and 36%, respectively (Fig. 4b, d, and g), but densities of residual soft, short, and large-diameter snags declined by less than 20% (Fig. 4c, e, and f). For most groups, final density was correlated with post-harvest density but unaffected by level or pattern (Fig. 4). Hard snags were an exception: final density was marginally greater in aggregated than in dispersed treatments but unrelated to post-harvest density (Fig. 4b).

Trends in the density of recruitment mirrored those of frequency. At final sampling, soft recruits were ~50% more numerous than hard recruits (Fig. 4b and c), tall recruits were 2.5 times as numerous as short recruits (Fig. 4d and e), and large-diameter recruits were 67% more numerous than small-diameter recruits (Fig. 4f and g). Neither level nor pattern of retention affected recruitment density at the scale of the harvest unit (mean of 5.1 ha^{-1} , range of 0.6– 13.7 ha^{-1}). However, recruitment densities were significantly higher in Ap than in D for all but large-diameter snags (Fig. 4). Total recruitment densities averaged 27.8 and 14.4 ha^{-1} in 15Ap and 40Ap, but only 4.2 and 5.4 ha^{-1} in 15D and 40D (Fig. 4a). In the controls, recruitment density averaged 18.4 ha^{-1} .

3.3.3. Diameter distributions of residuals and recruits

The diameter distributions of residual snags did not change significantly between post-harvest (year 1) and final sampling (year 18–19) in any of the harvest units ($P > 0.1$ in all KS tests; data not shown). However, the distributions of recruited snags frequently differed among treatments at final sampling (Fig. A3, Appendix A). Differences were most apparent at low levels of retention where recruits were typically larger in D than in Ap (difference in median diameters of 9–28 cm).

3.3.4. Snag heights at final sampling

At final sampling, recruits were typically taller than residuals of the same decay or diameter class (mean heights of 18.1 and 5.1 m, respectively; Fig. 5). We did not detect an effect of level or pattern on final height for most classes of snags. Small-diameter recruits were an exception: final heights were significantly greater in the patches of aggregated than in dispersed treatments (means of 12.0 and 7.2 m, respectively Fig. 5e).

3.4. Post-harvest survival and transitions in physical state

3.4.1. Survival of residuals and recruits

At final sampling, survival of residual snags averaged 74.3% among harvest units — comparable to rates in the controls (72.4%). Survival was marginally greater at 15 than at 40% retention (means of 79.3% vs. 69.2%; Fig. 6a), but it was unaffected by pattern. For *P. menziesii*, the primary species, survival averaged 88.8% and was invariant to

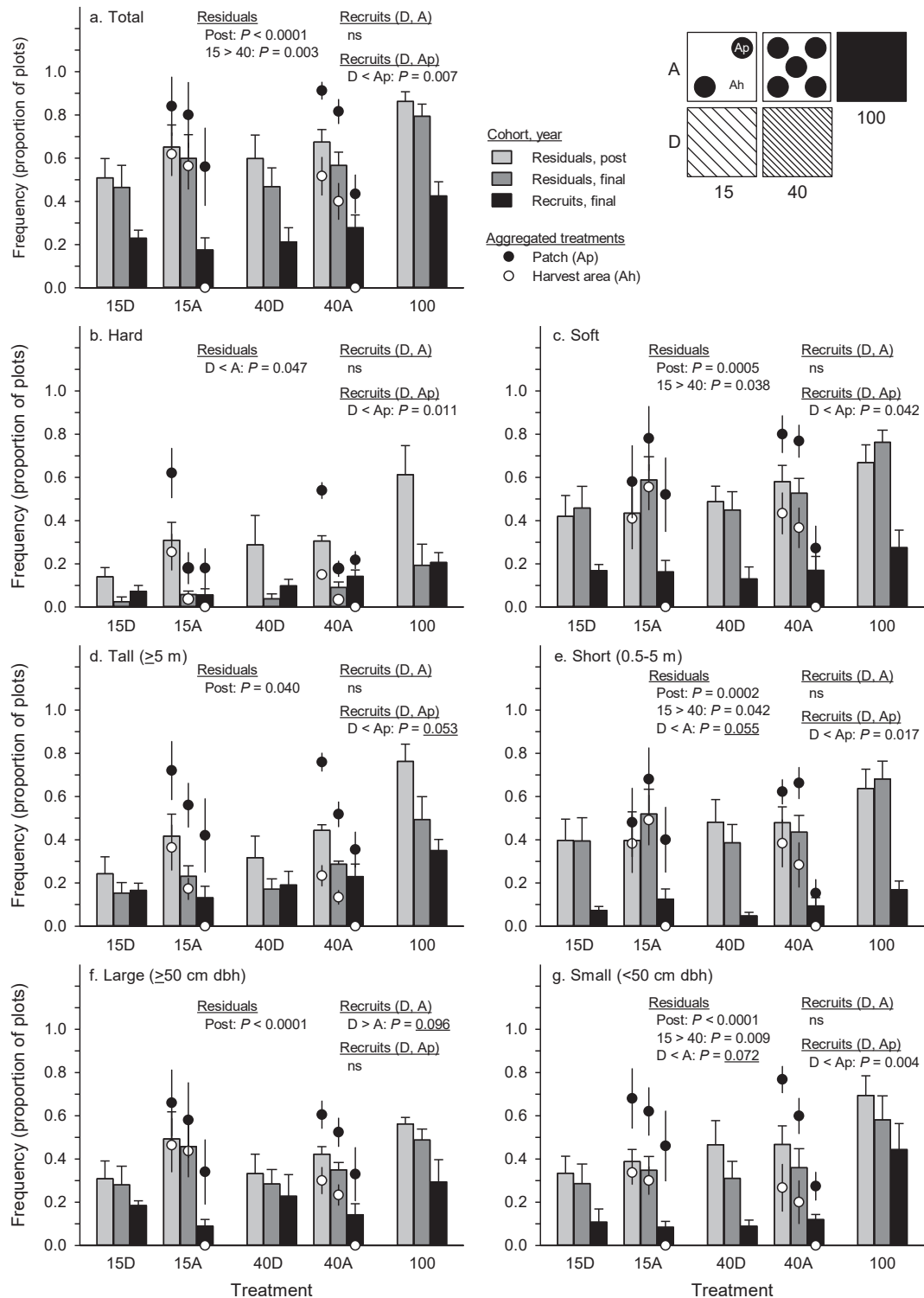


Fig. 3. Snag frequency by decay, height, and diameter class at post-harvest (year 1) and final sampling (year 18–19) for residuals (grey and dark grey bars) and recruits (black bars, final sampling only). Values are treatment means with SEs ($n = 5$). Values for aggregated treatments (15A, 40A) are weighted means of forest patches (Ap, closed circles) and harvest areas (Ah, open circles); see harvest-design schematic. P values are shown for significant ($P \leq 0.05$) or marginally significant ($0.05 < P \leq 0.1$; underlined) terms from general linear models of final frequency as a function of post-harvest frequency (Post), level (15 vs. 40), pattern (A vs. D), and the level \times pattern ($L \times P$) interaction. ns = all terms non-significant. For recruits, two models were run to test D vs. A and D vs. Ap (in addition to Post, level, and the $L \times P$ interaction). Controls (100) are shown for reference.

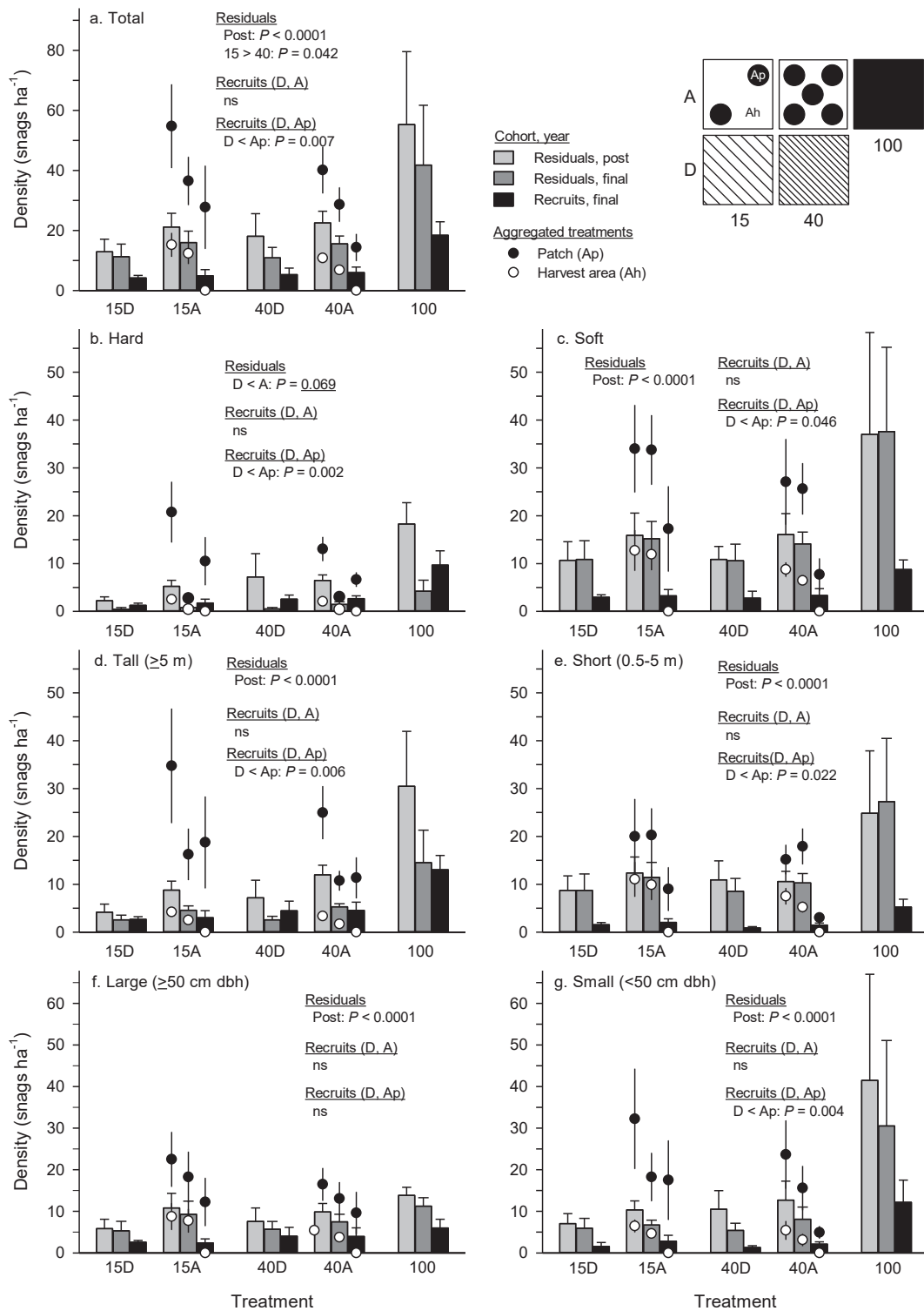


Fig. 4. Snag density by decay, height, and diameter class at post-harvest (year 1) and final sampling (year 18–19) for residuals (grey and dark grey bars) and recruits (black bars, final sampling only). Values are treatment means with SEs ($n = 5$). Values for aggregated treatments (15A, 40A) are weighted means of forest patches (Ap, closed circles) and harvest areas (Ah, open circles); see harvest-design schematic. P values are shown for significant ($P \leq 0.05$) or marginally significant ($0.05 < P \leq 0.1$; underlined) terms from general linear models of final density as a function of post-harvest density (Post), level (15 vs. 40), pattern (A vs. D), and the level \times pattern ($L \times P$) interaction. ns = all terms non-significant. For recruits, two models were run to test D vs. A and D vs. Ap (in addition to Post, level, and the $L \times P$ interaction). Controls (100) are shown for reference.

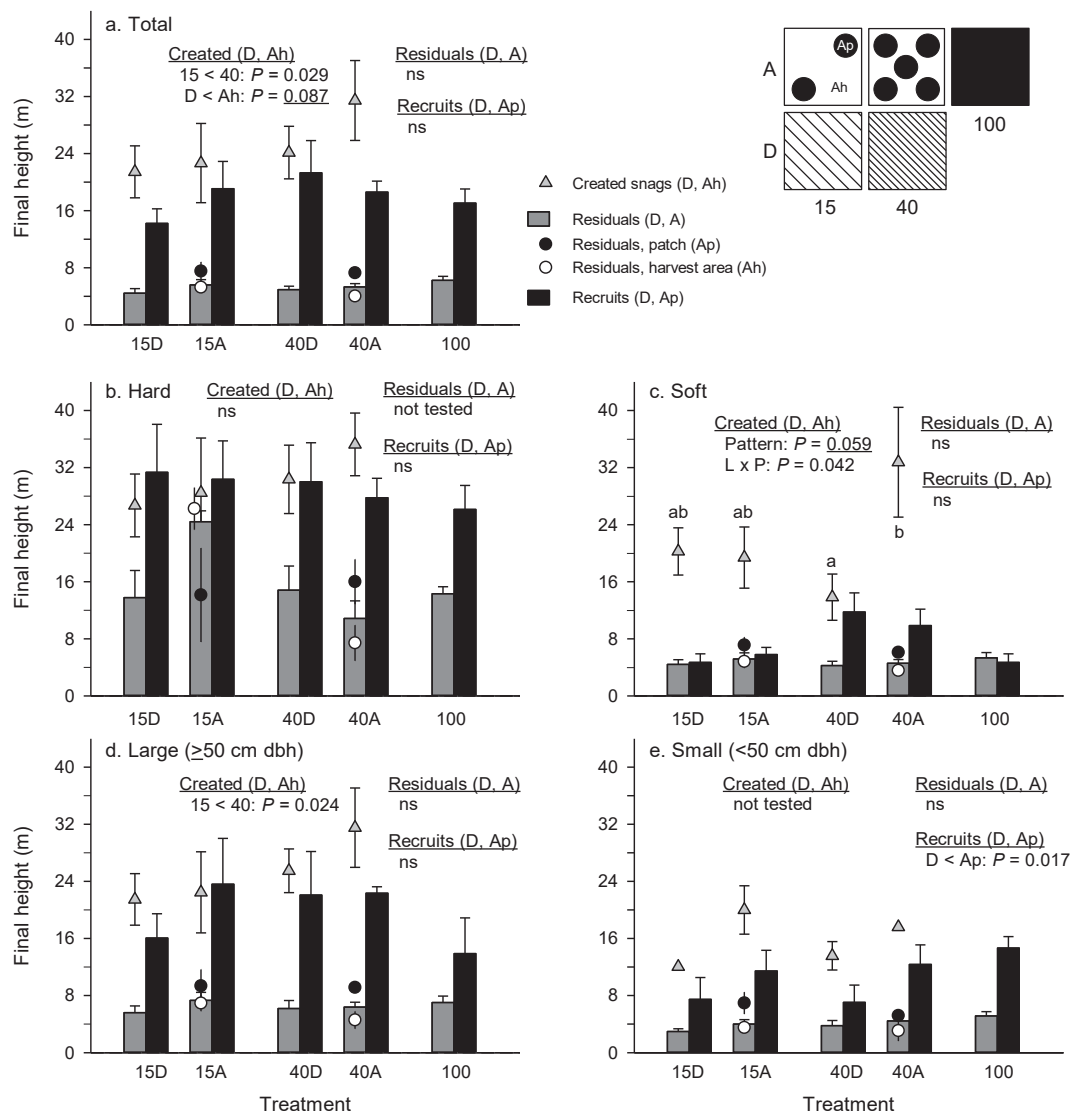


Fig. 5. Snag heights at final sampling (years 18–19) by decay and diameter class for residuals (dark grey bars), recruits (black bars), and created snags (triangles). Values are treatment means with SEs ($n = 5$). Values for aggregated treatments (15A, 40A) represent weighted means of patch (Ap) and harvest area (Ah) plots for residuals, Ap plots for recruits, and Ah plots for created snags (see harvest-design schematic). P values are from general linear models of final height as a function of level (15 vs. 40), pattern (A vs. D), and the level \times pattern (L \times P) interaction. ns = all terms non-significant. Hard residuals and small-diameter created snags were too infrequent to model. Controls (100) are shown for reference.

treatments (treatment means of 87.9 to 90.2%). Among decay, height, and diameter classes, survival was greater in hard than in soft snags (means of 79.9 vs. 71.0%; Fig. 6b and c), greater in tall than in short snags (means of 77.1 vs. 72.8%; Fig. 6d and e), and greater in large- than in small-diameter snags (81.6 vs. 66.8%; Fig. 6f and g). Neither treatment affected survival of hard, tall, or large-diameter snags (Fig. 6b, d, and f), but soft, short, and small-diameter snags showed greater survival at lower retention (Fig. 6c, e, and g).

Among snags recruiting prior to final sampling, survival averaged 94.2% (vs. 88.8% in the controls; Fig. A4a, Appendix A). Survival of hard and tall recruits tended to be greater in D than in Ap, although for hard recruits, the effect was limited to lower levels of retention (significant level \times pattern interaction; Fig. A4b, Appendix A). Among height and diameter classes, survival of recruits was unaffected by level or pattern (Fig. A4d-g, Appendix A).

3.4.2. Transitions in physical state among residuals and recruits

A majority (59.9%) of hard residual snags transitioned to the soft

class by final sampling (Fig. 6b). Rates of transition were significantly greater at 15 than at 40% retention (67.8 vs. 51.9%), but unaffected by pattern (Fig. 6b). Slightly fewer than one-fourth (24.1%) of tall residual snags transitioned to the short class by final sampling, and rates were unaffected by level or pattern (Fig. 6d).

Similar to residuals, more than half (54%) of hard recruits transitioned to the soft class by final sampling. However, transition rates were only marginally greater at 15 than at 40% retention (63.9 vs. 44.1%; Fig. A4b, Appendix A). Few recruits (17.8%) transitioned from tall to short by final sampling, and rates were unaffected by either treatment (Fig. A4d, Appendix A).

3.5. Cumulative responses to treatments

3.5.1. Combined final density of residuals and recruits

Mirroring its significance in models of carryover, pre-harvest density was a significant predictor of final density in nearly all models of cumulative response (combined density of residuals and recruits; Fig. 7).

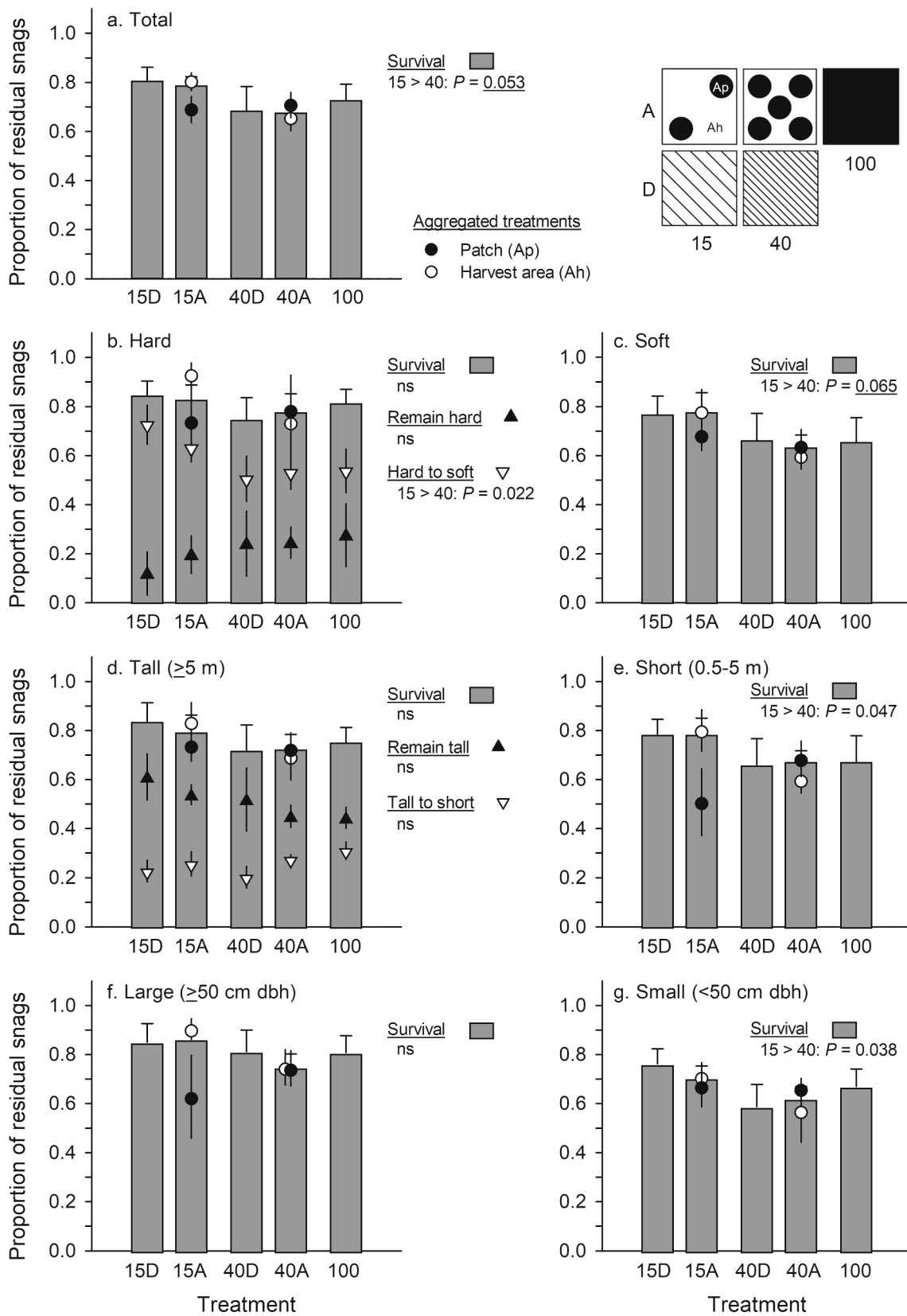


Fig. 6. Residual snag survival (vertical bars and circles) and transitions in physical state (up and down triangles) by decay, height, and diameter class. Values are treatment means with SEs ($n = 5$). For aggregated treatments (15A, 40A), values are weighted means of forest patches (Ap, closed circles) and harvest areas (Ah, open circles); see harvest-design schematic. Transition proportions, i.e., remain hard (or tall) and transition to soft (or short), sum to the proportions of hard (or tall) snags surviving. P values are shown for significant ($P \leq 0.05$) or marginally significant ($0.05 < P \leq 0.1$; underlined) terms from general linear models of survival or transitions in physical state as a function of level (15 vs. 40), pattern (D vs. A), and the level \times pattern interaction. ns = all terms non-significant. Controls (100) are shown for reference.

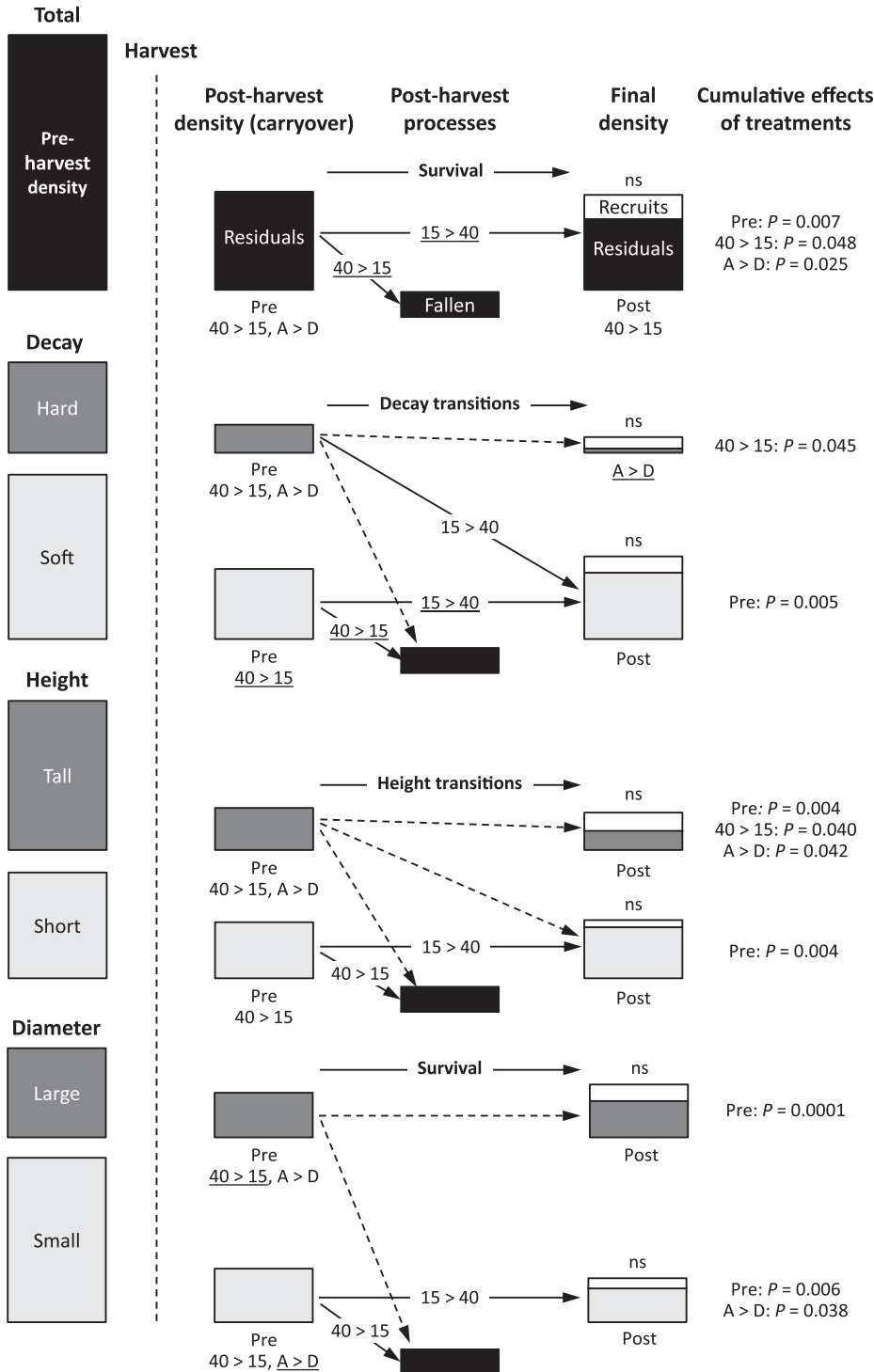


Fig. 7. Summary of natural snag responses to treatments. Box sizes are proportional to snag-class density at each point in time. Density of residuals and recruits (shaded and open boxes) are shown separately at final sampling. Significant and marginally significant (underlined) effects of prior density (Pre or Post), level, or pattern are shown below each residual snag class or above recruitment (all terms non-significant, ns). Arrows represent post-harvest fall rates and transitions in physical state. Solid arrows denote significant effects; dashed arrows denote non-significant effects (underline indicates marginal significance). The last column summarizes the cumulative effects of treatments on the combined density of residuals and recruits while accounting for pre-harvest density (Pre).

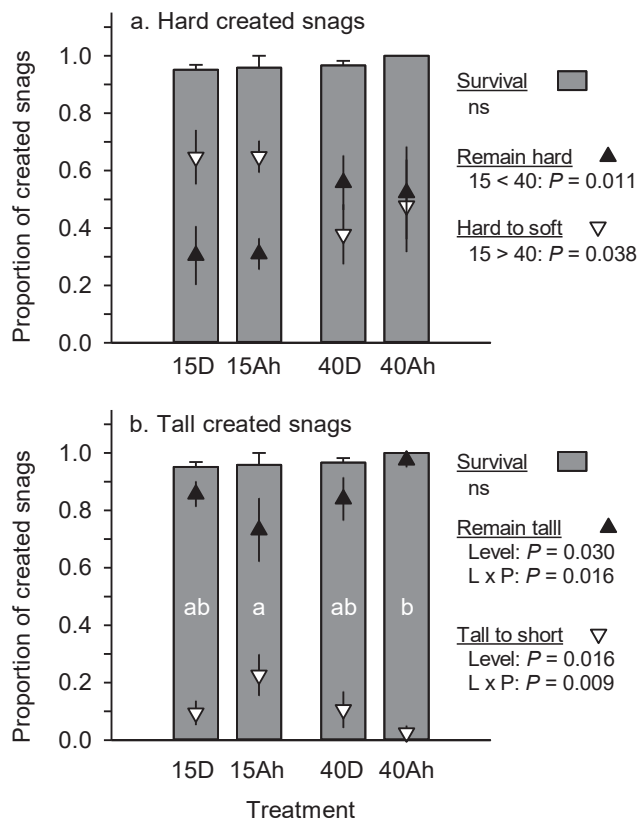


Fig. 8. Created-s snag survival (bars) and transitions in physical state (up and down triangles). Only hard and tall snags are shown (few snags began as soft or short). Values are treatment means with SEs ($n = 4$); the B site was dropped due to low sample size. Values for aggregated treatments represent harvest areas (15Ah, 40Ah). Transition proportions, i.e., remain hard (or tall) and transition to soft (or short) sum to the proportions of hard (or tall) snags surviving. P values are shown for significant ($P < 0.05$) terms from general linear models of proportion surviving or transitioning in state as a function of level (15 vs. 40), pattern (D vs. Ah), and the level \times pattern ($L \times P$) interaction. ns = all terms non-significant. For tall-s snag transitions, treatment means sharing the same lower-case letter did not differ based on a Tukey HSD test.

Hard snags were the exception. As in models of carryover, level and/or pattern of retention were significant predictors in models of cumulative response for total, hard, tall, and small-diameter snags. For the remaining groups (soft, short, and large-diameter snags), pre-harvest density was the sole predictor of final density (Fig. 7).

3.5.2. Pre-harvest vs. final diameter distributions

Comparisons of pre-harvest to final diameter distributions for total, hard, and soft snags yielded significant results in 30 of 60 tests (Fig. A5, Appendix A). In all instances, distributions shifted toward greater representation of larger snags, with median diameters increasing by 6–40 cm. For hard snags, the effect was more common with dispersed (D) than with aggregated (A) retention (significance or marginal significance in 7 of 10 vs. 1 of 10 tests, respectively). For soft snags, the effect was equally common in D and A (significance or marginal significance in 5 of 10 tests each). Distributions shifted in nearly all harvest units at WF and DP, but in few units at B or LW (Fig. A5, Appendix A).

3.6. Created snags: survival, transitions in physical state, and final height

All but three of 298 created snags were rated as hard and tall at the time of creation and $> 90\%$ had diameters ≥ 50 cm. Long-term survival was high (96.9%) and unaffected by level or pattern of retention (Fig. 8). Rate of decay (proportion of snags transitioning from hard to soft) was

significantly greater at 15 than at 40% retention (means of 64.8 vs. 42.3%; Fig. 8a). Fewer snags transitioned from tall to short, but rates varied among treatments (significant level \times pattern interaction; Fig. 8b). Height loss was greatest in 15Ah (22.6%), intermediate in dispersed treatments ($\sim 10\%$), and least in 40Ah (2.5%) (Fig. 8b).

At final sampling, heights of created snags averaged 24.9 m — 36% taller than the average heights of recruits (Fig. 5a). Heights of created snags were significantly greater at higher retention and marginally greater in the harvested areas of aggregated (Ah) than in dispersed treatments (D) (Fig. 5a). Snags rated as hard at final sampling were considerably taller than those rated as soft (means of 30.4 m and 21.5 m; Fig. 5b and c). Heights of hard snags were unaffected by level or pattern (Fig. 5b) but heights of soft snags were greater in 40Ah than in 40D (significant level \times pattern interaction; Fig. 5c).

4. Discussion

It has been shown that retaining live trees through harvest sustains biodiversity, and that these benefits vary predictably with level and pattern of retention (Baker et al., 2016; Beese et al., 2019; Fedrowitz et al., 2014; Gustafsson et al., 2010; Halpern et al., 2012; Rosenvald and Löhmuus, 2008). What roles snags play in these relationships is less clear (but see Halaj et al., 2009; Jacobs et al., 2007; Langor et al., 2008; Linden et al., 2012; Runnel et al., 2013). Determining how level and pattern of retention affect the abundance and post-harvest dynamics of snags represents a first critical step toward addressing this problem. In this study we document strong effects of level and pattern on snag carryover through harvest, but more subtle effects on two subsequent decades of survival, changes in physical state, and recruitment (summarized in Fig. 7).

4.1. Snag carryover through harvest

Level and pattern of retention had strong and predictable effects on snag carryover through harvest (Fig. 7). Declines in frequency were modest and less sensitive to level and pattern than were declines in density. Snags were eliminated from $\sim 30\%$ of plots (hard, tall, and large-diameter snags to a greater extent), but rarely from the patches of aggregated treatments. However, reductions in density were larger and more sensitive to treatments, with greater loss at lower levels of retention (all classes of snags) and in dispersed treatments (hard, tall, and large-diameter snags). The combined effects of level and pattern were dramatic, reducing pre-harvest densities by 75% in 15D, but by half of that in 40A.

Harvest-related reductions in snag density arise from intentional felling for hazard reduction (Myers and Fosbrooke, 1995; Wilhere, 2003), inadvertent uprooting or breakage during logging, and, to some extent, natural failure during the carryover period. We were unable to distinguish between intentional and inadvertent uprooting of snags, but data from the controls suggest that rates of natural failure were low. Treatment effects are consistent with the greater physical damage caused by more intensive and spatially extensive removal of trees (Garber et al., 2005; Graves et al., 2000). They are also consistent with observed patterns of bole damage during harvest: scarring of live trees (≥ 25 cm dbh) was more frequent in dispersed than in aggregated treatments and most frequent in 15D, where 30% of stems were affected (Moore et al., 2002).

Snag densities were reduced across the range of diameters, however snags with smaller diameters tended to be lost at a greater rate — particularly soft and tall snags. Snags in a more advanced state of decay or with a larger height-to-diameter ratio are more susceptible to physical damage during harvest (Ganey and Vojta, 2005; Graham, 1981; Parish et al., 2010). Interestingly, in dispersed treatments, diameter distributions were more often altered at higher than at lower levels of retention. With reduced felling intensity, larger snags are less likely to be damaged, shifting the size structure of residuals; with more intense felling snag loss may be simply a function of density. Conversely, in aggregated

treatments, diameter distributions were more often altered at lower levels of retention. This counterintuitive result suggests that harvesting uncovered spatial variation in the pre-harvest diameter distribution of snags, a natural feature of many forests (Cline et al., 1980; Ohmann and Waddell, 2002). In sum, level and pattern of retention imposed strong effects on the post-harvest density of snags and on their decay and size structure: density was reduced in proportion to the intensity or spatial extent of felling; losses were minimal within the aggregates; and composition shifted toward dominance by soft, short, and larger-diameter snags, particularly at lower levels of dispersed retention.

4.2. Long-term dynamics of residual snags

Post-harvest changes in snag frequency and density were small compared to the initial effects of harvest (Fig. 7). Snag survival averaged 74% after 18–19 years, but was considerably higher (89%) for the primary species, *P. menziesii*. Among western conifers, *P. menziesii* typically shows a greater lag time between tree death and snag fall — a pattern attributed to its higher ratio of decay-resistant heartwood to sapwood (Harmon et al., 1986; Kimmey and Furniss, 1943). Rates of survival in the current study are similar to previous reports, although direct comparisons with other studies are made difficult by differences in height or diameter thresholds, disturbance history, physical environment, or other factors (Harmon et al., 1986; Ohmann and Waddell, 2002). Studies of snag longevity in *P. menziesii* suggest a half-life of 15–16 years for stems < 50 cm in diameter, but > 35–60 years for larger stems (Cline et al., 1980; Everett et al., 1999; Parish et al., 2010; Russell et al., 2006).

Among decay, height, and diameter classes, we observed greater survival of hard, tall, and large-diameter snags than of soft, short, or small-diameter snags. Differences in snag age or other attributes that affect physical stability likely account for these differences in longevity. Soft and short snags are likely to be older than hard and tall snags, thus more likely to fail in the post-harvest period. Cline et al. (1980) provide estimates of snag age based on the decay characteristics of *P. menziesii* in mature (80- to 200-year-old) forest. For smaller snags (<50 cm dbh), maximum ages range from 5, 15, and 30 years for classes 1, 2 and 3 (hard) snags, respectively, to 60 or more years for class 4 and 5 (soft) snags. Height also declines with age, although rates of fragmentation and breakage can be highly erratic, leading to a less predictable relationship (Graham, 1981; Harmon et al., 1986). Finally, rates of fragmentation and fall decrease with diameter (Bull et al., 1997; Garber et al., 2005; Parish et al., 2010) and remnants of snags taller than 0.5 m (our threshold for survival) can persist for one to two centuries (Cline et al., 1980).

In contrast to patterns of snag fall, we found mixed evidence for the more rapid decay expected under conditions of greater and more stable humidity (Harmon et al., 1986; Oberle et al., 2018). Soft, short, and small-diameter snags showed reduced survival under higher retention, consistent with this expectation. However, hard snags showed no response to pattern and slower rates of decay under higher retention. Several factors may contribute to these inconsistencies. First, smaller snags with a larger sapwood-to-heartwood ratio, and soft (older) snags in a more advanced state of decay, may be more sensitive to changes in microclimate than harder (younger) snags. Second, decay ratings in the field may be biased toward bark characteristics in more open stands, where desiccation from sun and wind can cause bark shrinkage, separation from sapwood, and sloughing (Dossa et al., 2018; Maser and Trappe, 1984). This would suggest more advanced decay, despite the greater exposure of sapwood to sun and wind, which slows decay (Mielke, 1950; Rayner and Todd, 1980). Finally, incursion of radiation, warm air, and wind into the aggregates may reduce the microclimatic contrast with dispersed treatments, particularly at lower levels of retention (Heithecker and Halpern, 2006, 2007). In combination, our results suggest that snag longevity and changes in physical state appear more sensitive to conditions at the time of harvest (e.g., snag age, decay state, and height) than to variation in post-harvest structure or

microclimate.

4.3. Snag recruitment

Snag recruitment was continuous but sparse, averaging 0.3 snags $\text{ha}^{-1} \text{year}^{-1}$ over the 17- to 18-year post-harvest period. Nevertheless, recruitment was sufficient to offset loss of residuals, resulting in little net change in density (Fig. 7). At the scale of the harvest unit, recruitment frequency and density were surprisingly insensitive to level and pattern of retention. However, for pattern, this reflected the absence of trees over large portions (60 to 85%) of the aggregated-retention units. When harvest-area plots were dropped from the analyses, pattern was highly significant, with three to six times greater recruitment density in the aggregates than in the corresponding dispersed treatments.

Despite comparable rates of snag recruitment among treatments, we observed marked variation in tree mortality rates and in the proportion of dead trees that remained standing. Probability of recruitment, expressed as a percentage of ‘source’ trees, varied from as low as 6% in 40D to as high as 14% in 15D, where tree density was nearly three times lower. Companion studies of tree mortality offer insights into this variation (Halpern and Urgenson, 2021; Urgenson et al., 2013a). Among trees large enough to produce snags, annualized rates of mortality varied from as low as 0.4% at 40% retention to 0.8% in 15Ap and 1.3% in 15D. Yet, not all trees died standing. Where mortality rates were highest (15D), ~50% of dead trees remained standing, whereas the remainder were windthrown. Where mortality rates were lower (40% retention), >80% died standing — a result of suppression, fungal infection, or wind snap. In sum, different sets of constraints led to comparable densities of snag recruitment. Where the density of, or area with, live trees was greater (40D, 40Ap), snag recruitment was limited by low rates of mortality. Where rates of mortality were higher, recruitment was limited by source area (15Ap) or by the combined effects of low tree density and higher rates of windthrow (15D).

4.4. Models of cumulative response to treatments (pre-harvest to final sampling)

Comparisons of cumulative-response models to those of carryover highlight the importance of legacy and disturbance effects (Fig. 7). First, as in carryover models, pre-harvest density was a significant predictor in all but the hard-snag model of cumulative response. Second, level and/or pattern were significant in both carryover and cumulative-response models for total, hard, tall, and small-diameter snags, underscoring the persistence of initial disturbance effects. Together, these outcomes suggest strong potential to design retention harvests around the pre-harvest distributions of standing dead wood to enhance both the carryover and long-term survival of legacy snags.

Comparisons among carryover, final-density, and cumulative-response models also illustrate more subtle, temporally offsetting or amplifying effects of treatments. For example, at higher retention, greater carryover of soft, short, and small-diameter snags was offset by reduced post-harvest survival, leaving pattern and/or pre-harvest density as predictors of final snag density (Fig. 7). In contrast, in dispersed treatments, the shift in snag size structure was driven by greater loss of smaller snags during harvest and greater recruitment of larger snags post-harvest.

4.5. Long-term dynamics of created snags

We found that nearly all (97%) of snags created by topping or girdling remained standing at final sampling. These high rates of survival clearly reflect the selection of large-diameter *P. menziesii*, which have among the longest lag times between death and snag fall (Harmon et al., 1986). Both the species and size contribute to greater bark thickness (thus persistence) and to a greater ratio of decay-resistant heartwood to sapwood (Graham, 1981; Harmon et al., 1986).

Although girdling can leave smaller-diameter trees susceptible to breakage at the location of cambial damage (Hallett et al., 2001; Parks et al., 1996), the large sizes of our snags likely prevented such failure. Barry et al. (2017) reported similarly high rates of survival (91% over 25 years) for topped *P. menziesii* in settings similar to ours, including clearcuts (akin to the harvested areas of 15A), and low-level (25%) dispersed retention. In younger plantations with smaller trees, Hane et al. (2019) reported poorer survival after topping — an average of only 60% after 19 years.

Although the fall rates of created snags did not vary among treatments in this study, rates of decay and height loss did. Decay was more rapid at lower retention, as with residual and recruited snags, although this runs counter to the expectation of more rapid decay under higher retention. Nevertheless, it parallels the results of Barry et al. (2017), who reported more rapid decay — based on peeling or loss of bark — in clearcut and dispersed-retention units than in denser, group-selection stands. Although they attributed these differences to greater extremes in temperature and desiccation in the more open stands, it is not clear whether other aspects of decay were affected similarly (e.g., fungal infection of sapwood or heartwood). Similarly, it is difficult to explain patterns of height loss in our study, i.e., the distinctly greater proportion of tall snags transitioning to short in 15A. Although the vast majority of created snags remained in the tall class, comparisons with live canopy dominants suggests considerable height loss over the study period — on the order 10–20 m. In one of few studies of comparable duration, Barry et al. (2017) reported much lower rates of height loss, averaging 1.1 m over 25 years. These differences likely reflect the methods by which snags were created: topping by removing a large portion of the less-stable upper bole (study of Barry et al., 2017) vs. stem girdling (three of four sites in our study). Given limited replication of topping in our study, we did not attempt to compare height loss or decay between topped and girdled stems. Although topping may slow rates of height loss, past work suggests that it leads to more rapid fungal infection and decay of the heartwood, thus a shorter functional lifespan (Brandeis et al., 2002; Bull and Partridge, 1986; Hallett et al., 2001; Miller and Miller, 1980).

5. Management implications and conclusions

5.1. Retention and future production of snags

Large, regional-scale experiments such as DEMO make it possible to generalize to a wide range of mature, coniferous forest types. Despite marked variation in the age, structure, and physical environments of these forests, level and pattern of live-tree retention emerged as strong predictors of snag abundance and composition in the post-harvest stand. Moreover, despite felling of snags for hazard reduction, final densities remained correlated with pre-harvest densities for nearly all classes of snags. This suggests that in operational settings, where managers have greater latitude in the design of harvest prescriptions, retention strategies can be tailored to site conditions to preserve natural variation in the distribution, size structure, and abundance of standing dead wood, for example, by reducing the intensity of felling, or by siting aggregates in areas of greater snag abundance, diversity, or incipient decay (Rose et al., 2001).

Although our experiment was designed to test for level \times pattern interactions indicative of contingent or synergistic effects, these interactions were rare, ensuring greater predictability of treatment outcomes. Responses to level were invariant to pattern and responses to pattern, albeit weaker, were similar at low and high levels of retention. That said, the additive effects of level and pattern were strong, reducing hard- and tall-snag densities by $> 85\%$ in 15D. Our results highlight the challenge of sustaining snag abundance and diversity under the current, 15% minimum-retention standard for regeneration harvests in this region (USDA and USDI, 1994), reinforcing the conclusions of companion studies of biological response (Dovčiak et al., 2006; Halaj et al., 2008;

Halpern et al., 2005, 2012; Luoma et al., 2004), microclimate (Heithecker and Halpern, 2006), and public perceptions of retention harvests (Ribe, 2005).

Our long-term assessments of snag density, diversity, and demography contrast the strong legacy of initial disturbance effects with the more subtle contributions of post-harvest processes (survival, transitions in physical states, and recruitment). The implications for management are clear: if sustaining the abundance, variety, and spatial distribution of dead wood is an objective of retention harvests (Franklin et al., 1997; Gustafsson et al., 2012), prescriptions should focus on minimizing snag loss at the outset.

Where management objectives dictate lower levels of retention, losses can be mitigated, in the short term, by creating snags (Bull and Partridge, 1986; Hope and McComb, 1994; Walter and Maguire, 2005). Although snags created from large-diameter *P. menziesii* will likely outlast most legacy snags, their functional lifespans are still limited (Hayes and Hagar, 2002; Hagar, 2007; Barry et al., 2018). Thus, it seems prudent to stagger snag creation over time to provide greater continuity of structure and function (Barry et al., 2018; Hallett et al., 2001; Schreiber and deCalesta, 1992). Delaying the conversion of live trees to snags (thus increasing residual tree density) offers additional benefits: reducing rates of windthrow in the early years after harvest (Thorpe et al., 2008; Urgenson et al., 2013a); ameliorating microclimatic stress (Barg and Edmonds, 1999; Heithecker and Halpern, 2006); enhancing seed rain early in stand development (Halpern and Urgenson, 2021; Urgenson et al., 2013b), and maintaining ectomycorrhizal networks that support seedling establishment and growth (Cline et al., 2005; Luoma et al., 2006; Simard et al., 2021).

Although our findings are most relevant to mature, previously unmanaged forests, they should also apply to younger, second-growth stands, which constitute a large proportion of the managed forest landscape in this region. Here, histories of past management present additional challenges: snags densities are greatly reduced and live trees are smaller, with a thinner bark and a lower ratio of decay-resistant heartwood to sapwood. In these stands, the retention of aggregates will be critical to producing the characteristics of snags that develop under natural conditions. To mitigate for the paucity of standing dead wood, some snag creation may also be needed in these patches. Finally, it may also be necessary to retain a greater density of live trees in the harvest area to be converted to snags — either initially or over an extended period of time. In sum, as the context of stand management shifts from mature to younger forests, the emphasis will need to shift from sustaining dead wood through harvest to the immediate and longer-term production of snags.

5.2. Implications for snag-associated species

Current guidelines for snag retention and creation in managed stands reflect the importance of dead wood as substrates, habitats, and food resources for diverse groups of forest organisms (Jonsson et al., 2005; Neitro et al., 1985; Siitonen, 2001; Thomas et al., 1979). Given the variety of life histories and habitat requirements of species, decisions on how much to retain and in what spatial pattern will invariably lead to tradeoffs, favoring some taxa at the expense of others (Bunnell, 2013). Among the taxa most likely to suffer from reductions in snag abundance or quality are those with narrow habitat requirements and poor dispersal, including some species of epixylic lichens and saproxylic beetles (Humphrey et al., 2002; Jacobs et al., 2007; Jonsell et al., 1998; Löhmus and Löhmus, 2011; Nascimbene et al., 2013; Nordén et al., 2014). Our results suggest that large, closed-canopy aggregates, which maintain a stable distribution of snag sizes and decay states, and a relatively tempered microclimate, should provide the habitat continuity required by these species (Hjältén et al., 2012; Sverdrup-Thygeson et al., 2014). Whether aggregates serve as source populations for the harvest area will depend on their longer-term stability, the rates at which comparable snag habitats develop in the harvest area, and the ability of

species to disperse to those habitats (Nordén et al., 2014; Sverdrup-Thygeson et al., 2014).

Predicting the responses of more vagile, snag-associated species (e.g., cavity-nesting birds and small mammals) is more challenging. Responses are often context- or scale-dependent, varying with the abundance, size structure, or diversity of decay states prior to harvest; with harvest-related changes in stand structure (Basile et al., 2019; Bunnell, 2013; Hansen et al., 1995); and with the abundance of snags in the broader landscape (Bunnell, 2013; Kroll et al., 2012a; Lawler and Edwards, 2002). For example, the abundance of cavity-nesting species may decline steeply if snag densities fall below species' threshold requirements (typically 3–10 large snags ha⁻¹), but abundance may change little if snag densities exceed those thresholds (Bunnell, 2013; Gunn and Hagan, 2000). Depending on snag densities prior to harvest, managing for these species may require a shift in emphasis, from maximizing carryover to future provisioning of hard and tall snags, which may be limiting to cavity nesters in the longer term. Similarly, wildlife use of created snags may vary with the availability of natural snags in the surrounding forests: if natural snags are abundant, there may be little benefit of snag creation. Landscape-scale considerations are also important for wide-ranging mammals that utilize standing dead wood but are sensitive to forest fragmentation (e.g., Pacific fisher and Pacific marten; Fisher and Wilkinson, 2005; Sauder and Rachlow, 2014). In addition to serving as undisturbed reserves, stands with naturally high densities of large snags could be managed at higher levels of aggregated retention to facilitate movement and dispersal of these species in the managed forest landscape (Bunnell, 2013).

Notwithstanding these complexities of context and scale, the results of our long-term experiment suggest that higher levels of retention and the retention of large, undisturbed aggregates will benefit the vast majority of species that utilize standing dead wood. In the short term, both strategies foster greater carryover of the range of snag sizes and decay states required to sustain a diversity of snag-dependent organisms, including fungi, arthropods, birds, and small mammals. Aggregates, in particular, mitigate the loss of large, tall, and hard snags that contribute disproportionately to biodiversity — as cavity-nesting and foraging sites for primary excavators (e.g., woodpeckers), as nest sites for secondary users (including birds and mammals; Bunnell, 2013; Bunnell et al., 2002; Lundquist and Mariani, 1991; Mannan et al., 1980), and as resting or roosting sites for forest bats (including species of conservation concern; Bondo et al., 2019; Humes et al., 1999; Rodhouse et al., 2015). Aggregates also preserve the small scale of clumping of snags that enhances the foraging efficiency of primary excavators (Bunnell, 2013; Chambers and Mast, 2005; Lundquist and Mariani, 1991; Raphael and White, 1984). Finally, aggregates provide for the carryover and continuous recruitment of smaller snags, which serve as foraging sites for both primary and secondary cavity nesters (Bunnell, 2013). These processes and functions may be diminished or delayed by dispersed retention.

Although many species are likely to benefit from aggregated retention, others, including cavity-nesting aerial insectivores (e.g., purple martin), may be less sensitive to snag density than to the coincidence of nesting and foraging opportunities (e.g., availability of nest sites in more open and productive early-seral habitat; Bunnell, 2013; Hagar et al., 2004; Halaj et al., 2009; Sherman and Hagar, 2021). The habitat needs of these species will be better met by low levels of dispersed retention, which support greater abundance of arthropod prey (Halaj et al., 2009; Hansen et al., 1995). However, in these settings, provisioning of cavity-nesting sites will likely require the creation of snags to mitigate loss of natural snags during harvest.

Managing for snag-associated species in the long term will require the sustained provisioning of standing dead wood. Our results suggest that snag recruitment after harvest, averaging ~ 0.3 snags ha⁻¹ yr⁻¹, is sufficient to offset the loss of residuals for at least two decades,

irrespective of level or pattern of retention (Fig. 7). However, sustaining these rates of recruitment in the longer term may be a challenge at low levels of dispersed retention. Here, long-term provisioning of standing dead wood may require somewhat higher levels of retention, allowing for a staggered approach to snag creation (Barry et al., 2018; Hallett et al., 2001). Although aggregated retention offers greater potential for sustaining a diversity of snag sizes and decay states, it clearly limits their spatial distributions well into the future.

Ultimately, managing forests for deadwood-associated species will require multiple strategies of retention, applied at a range of spatial scales, as decisions on how much to retain, and in what pattern, will invariably lead to tradeoffs for species with differing habitat or resource requirements. In addition, we suggest that harvest prescriptions account for the initial density and size structure of snags and live trees: both will contribute to the carryover and longer-term production of standing dead wood. Strategies aimed at sustaining the broader community of wood-associated species will be most successful if they target a diversity of post-harvest structures — intact patches of forest, areas of reduced tree density, and clearings of sufficient size to benefit open-canopy species — mimicking the heterogeneity of live and dead structure created by natural disturbance. Although tree felling invariably reduces snag density, strong carryover effects and high rates of post-harvest survival suggest that it is possible to achieve an important objective of variable retention — enriching the post-harvest stand with standing dead wood from the original forest.

CRedit authorship contribution statement

Charles B. Halpern: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization, Project administration, Funding acquisition. **Allison K. Rossman:** Conceptualization, Methodology, Investigation, Writing – review & editing. **Joan C. Hagar:** Conceptualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available in the HJ Andrews LTER archive: Pre-treatment: <https://andlter.forestry.oregonstate.edu//data/Abstract.aspx?dbcode=TP104> Post-treatment: <https://andlter.forestry.oregonstate.edu//data/Abstract.aspx?dbcode=TP108>

Acknowledgments

Jerry Franklin deserves special recognition for his early efforts in conceptualizing and planning this large-scale experiment. We thank our many field assistants and federal collaborators from the Gifford Pinchot and Umpqua National Forests (GPNF, UNF). Special thanks to Shelley Evans (University of Washington) for coordinating field efforts. Logistical support was provided by Jon Nakae (GPNF), Jim White (GPNF), Rick Abbott (UNF), and Russell Oakes (UNF). Joe Antos, Jerry Franklin, Annette Olson, and an anonymous reviewer provided constructive feedback on earlier drafts of the manuscript. Funding was provided by the USDA Forest Service, PNW Research Station (agreements 13-CR-11261992-053 and 14-CR-11261992-023). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A

(See Figs. A1-A5)

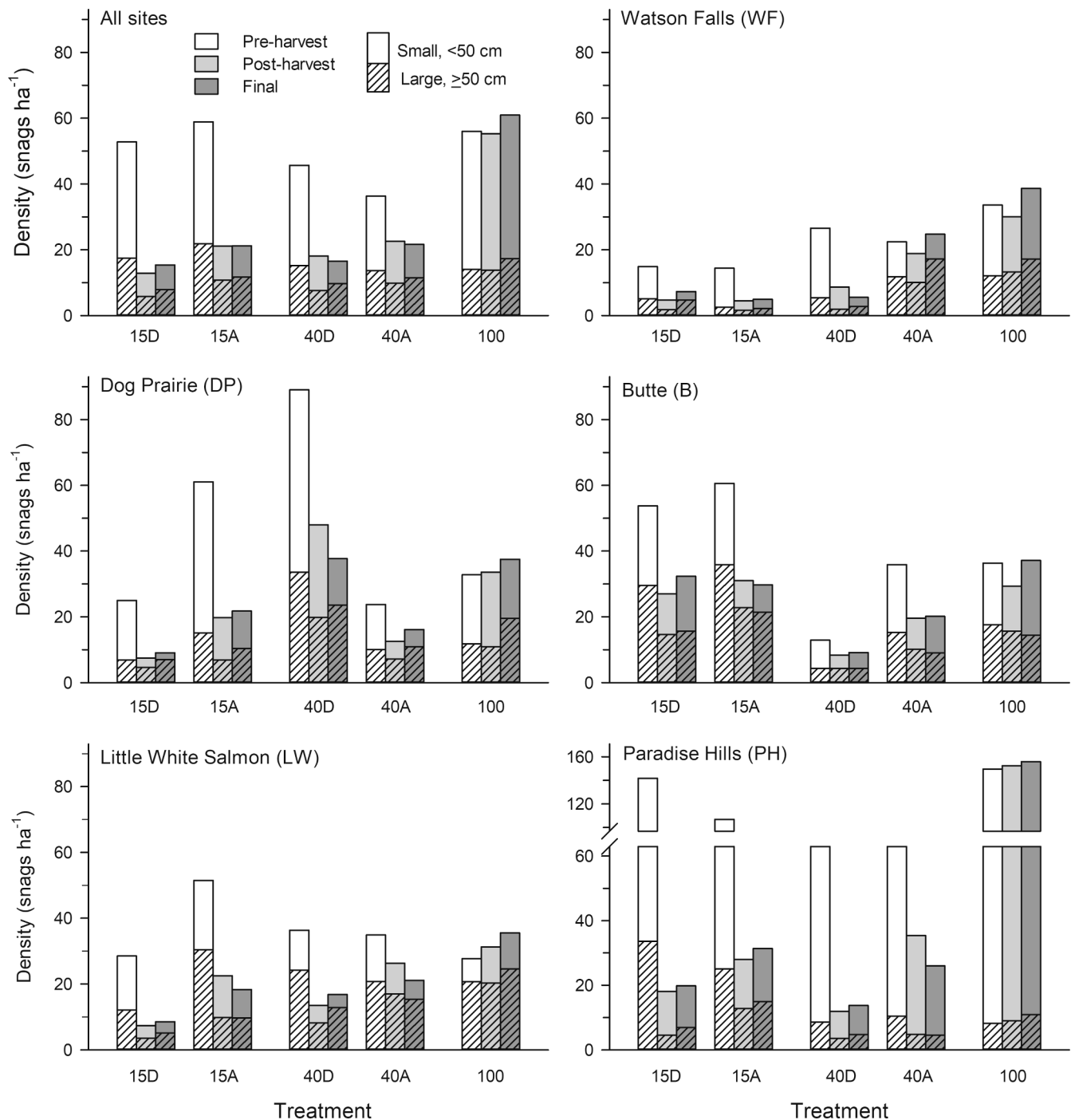


Fig. A1. Variation in snag density among sites and harvest units over time, illustrating the contributions of small- (<50 cm dbh) and large-diameter (≥50 cm dbh) snags. Pre-harvest, post-harvest (year 1), and final (year 18–19) densities are shown as triplets for each treatment combination. Values for aggregated treatments (15A, 40A) are weighted means of forest patches (Ap) and harvest areas (Ah).

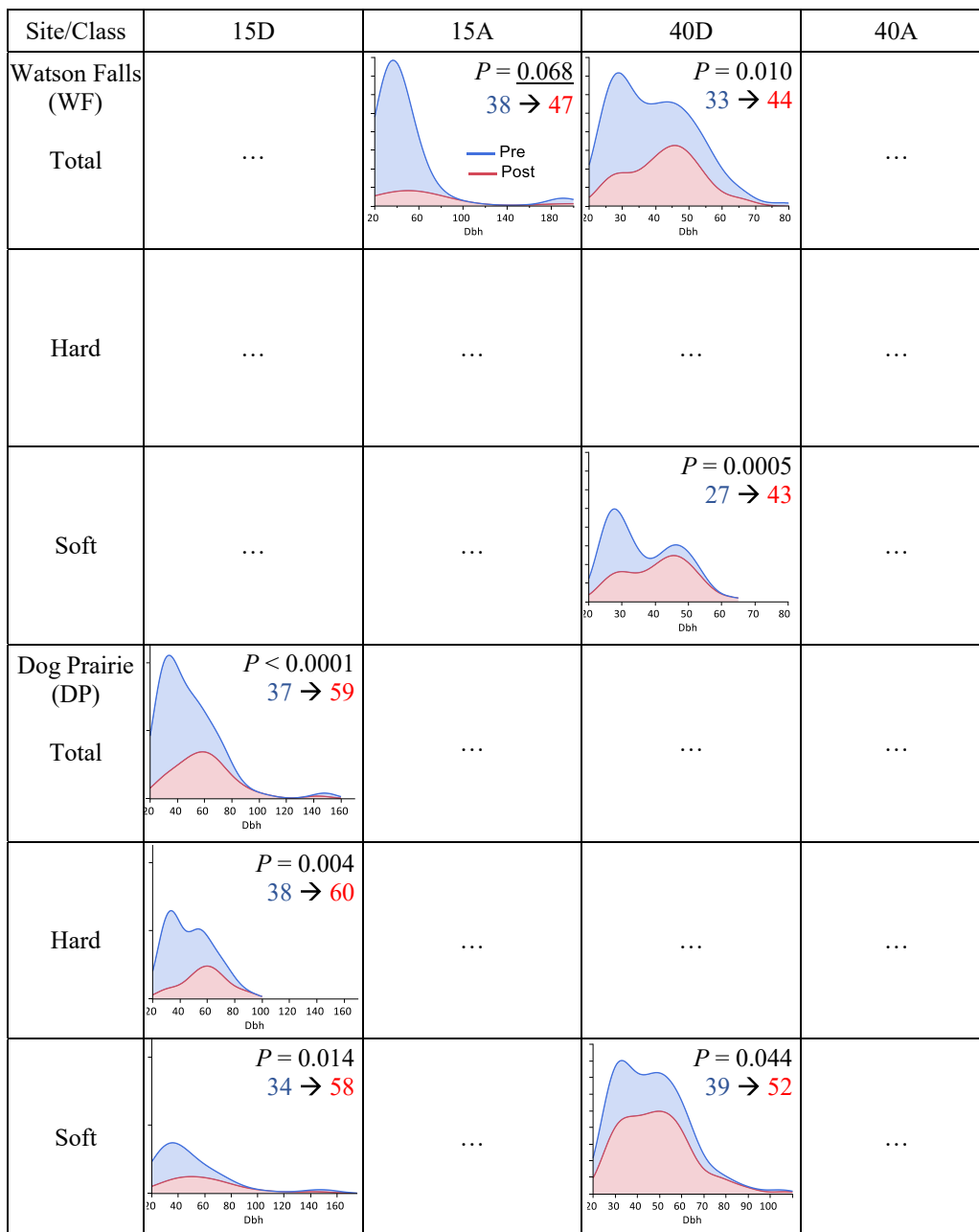


Fig. A2. Harvest units in which pre- (blue) and post-harvest (red) diameter distributions differed significantly ($P \leq 0.05$) or marginally ($0.05 < P \leq 0.1$, underlined) based on a two-sample KS test. Separate tests were run for snag totals and each decay class (hard and soft). Values are relativized densities; scales of the Y axes vary. Median pre-and post-harvest diameters are reported below P values.

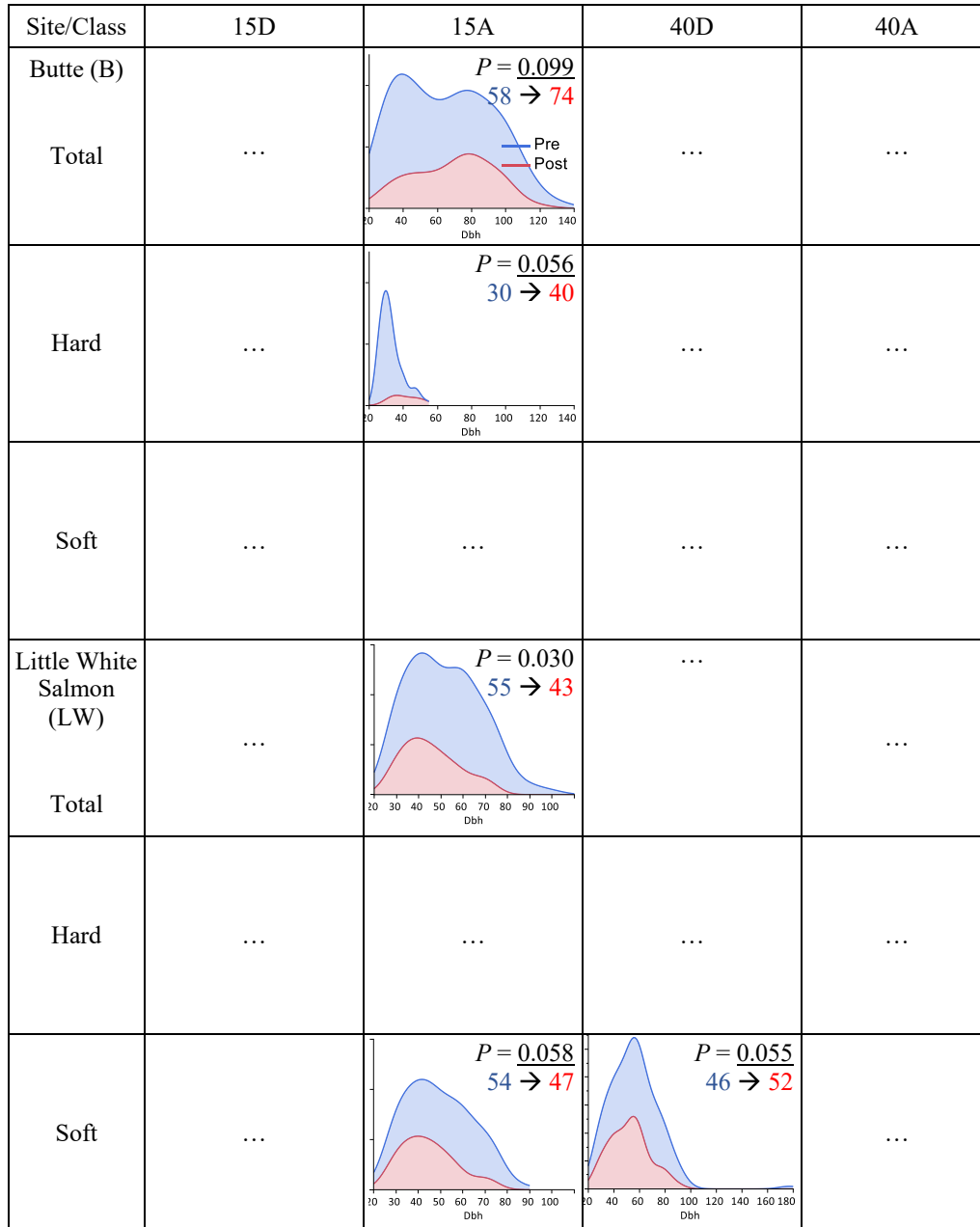


Fig. A2. (continued).

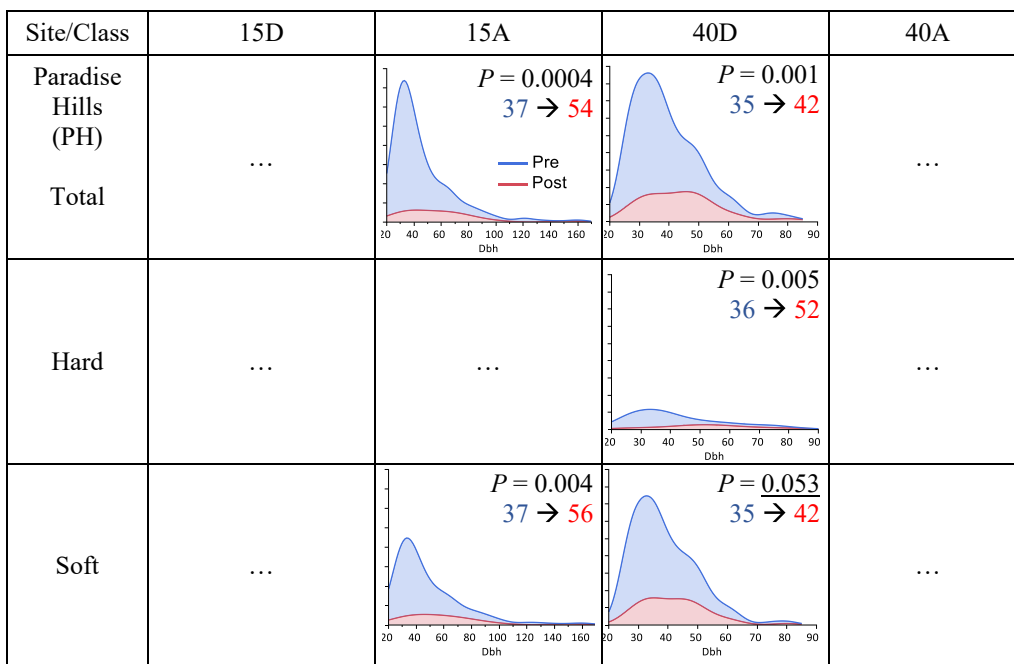


Fig. A2. (continued).

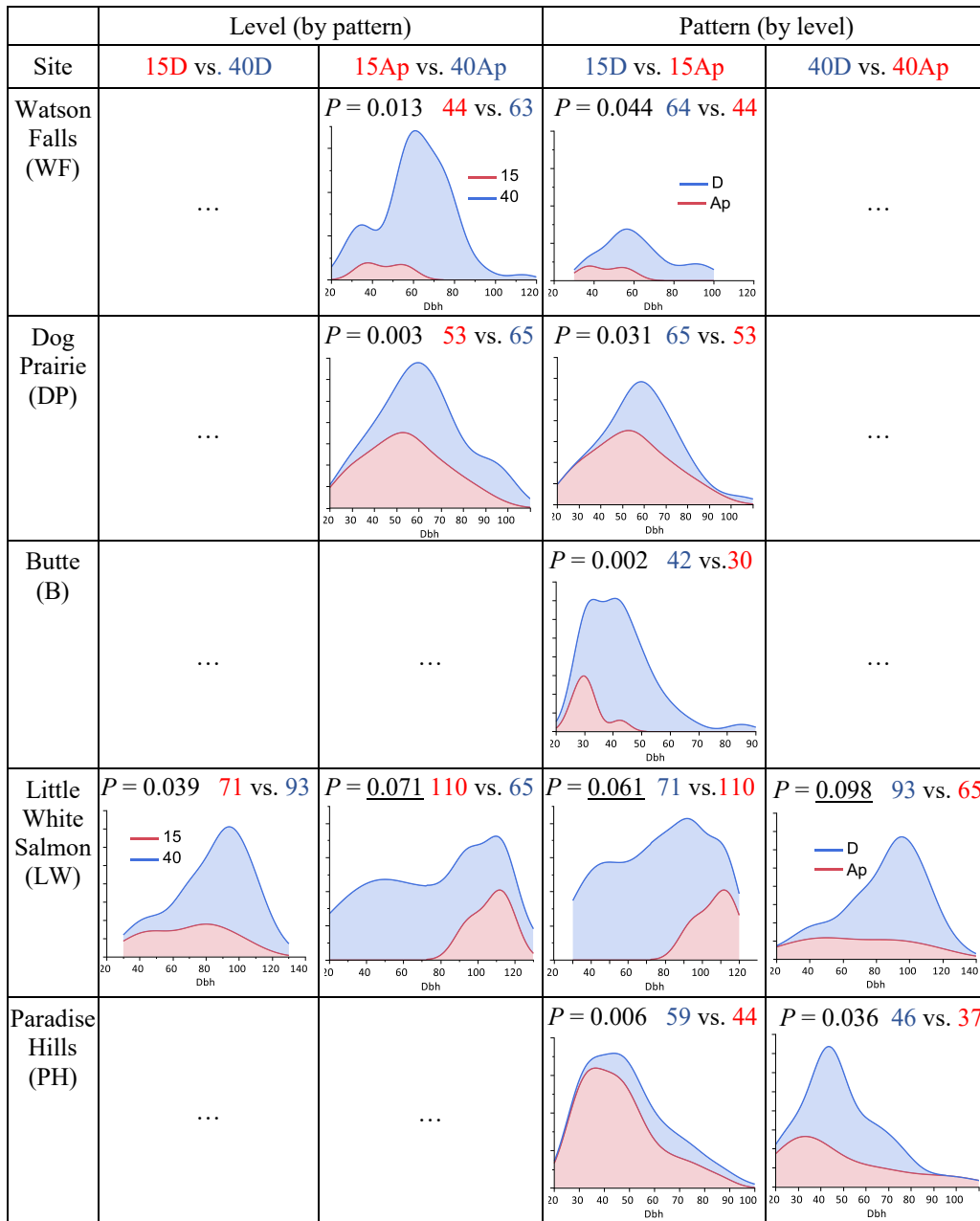


Fig. A3. Pairs of treatment combinations for which diameter distributions of recruitment differed significantly ($P \leq 0.05$) or marginally ($0.05 < P \leq 0.1$, underlined) at final sampling, based on a two-sample KS test. For each site, we compared level of retention (15 vs. 40) for each pattern (D or Ap) and pattern for each level of retention. Values are relativized densities; scales of the Y axes vary. Median diameters are reported to the right of P values.

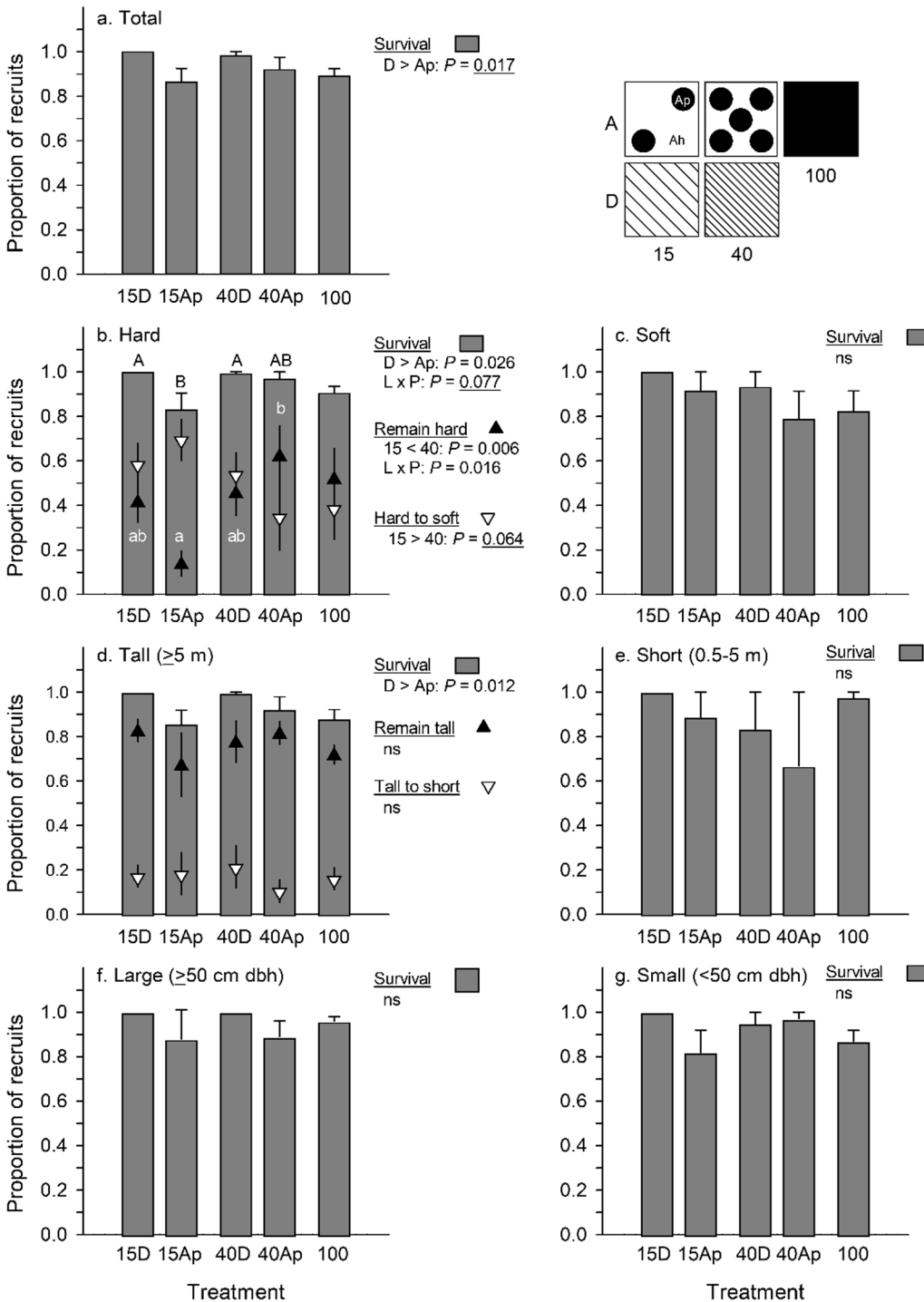


Fig. A4. Recruitment survival (bars) and transitions in physical state (up and down triangles) for (a) total snags, (b, c), decay classes, (d, e) height classes, and (f, g) diameter classes based on physical state at the time of recruitment. Values are means with SEs ($n = 5$). Values for aggregated treatments represent the patches (15p, 40Ap). Transition proportions (e.g., remain hard, transition from hard to soft) sum to the proportion surviving. P values are shown for significant ($P \leq 0.05$) or marginally significant ($0.05 < P \leq 0.1$; underlined) terms from general linear models of transition rate as a function of level (15 vs. 40), pattern (D vs. Ap), and the level \times pattern (L \times P) interaction. ns = all terms non-significant. For hard snags, treatment means sharing the same upper- or lower-case letter did not differ for survival or for proportion remaining hard, respectively, based on a Tukey HSD test.

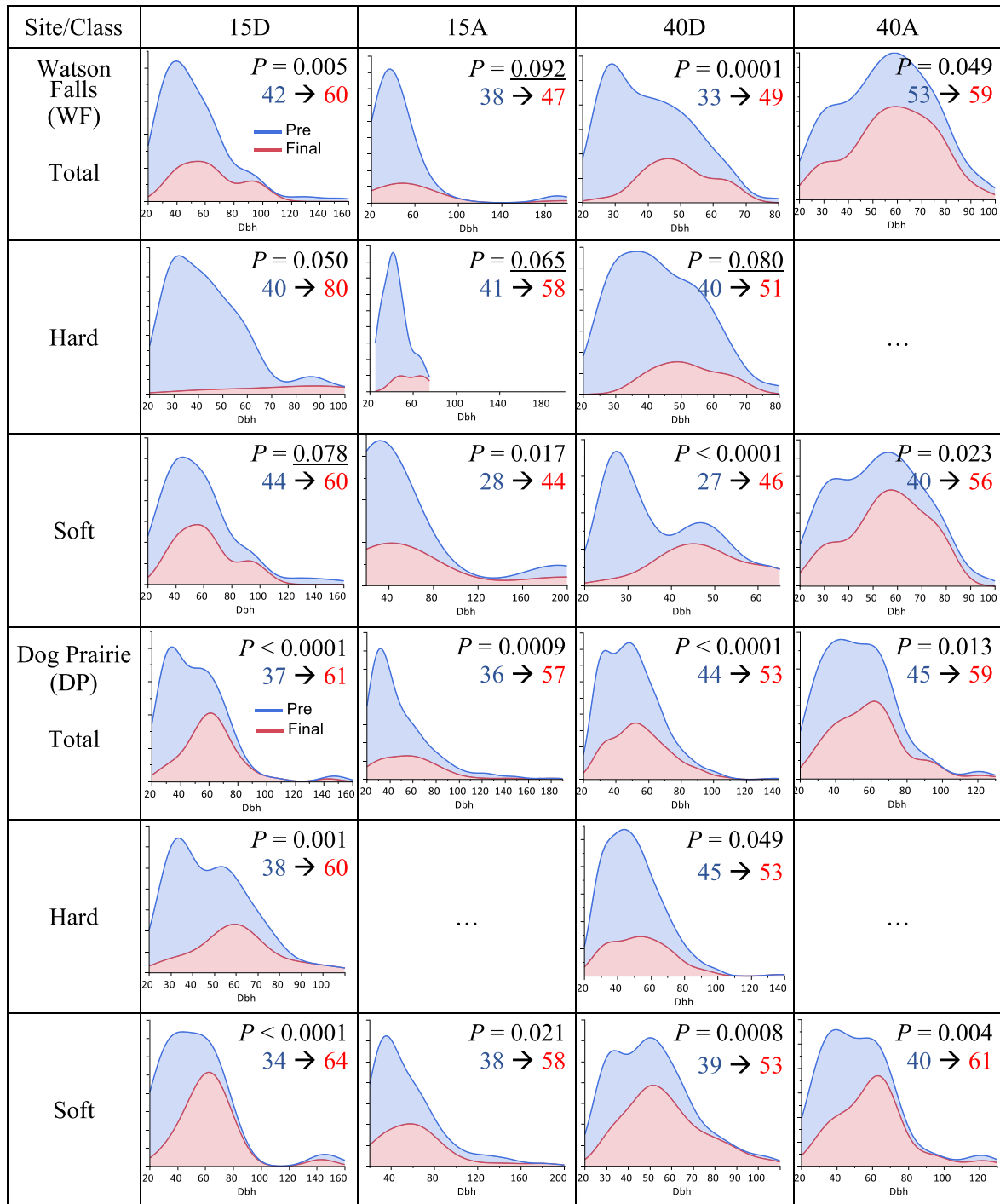


Fig. A5. Harvest units in which pre-harvest (blue) and final (red) diameter distributions differed significantly ($P \leq 0.05$) or marginally ($0.05 < P \leq 0.1$; underlined) based on a two-sample KS test. Final distributions include residuals and recruits. Separate tests were run for snag totals and each decay class (hard and soft). Values are relativized densities; scales of the Y axes vary. Median pre-harvest and final diameters are reported below P values.

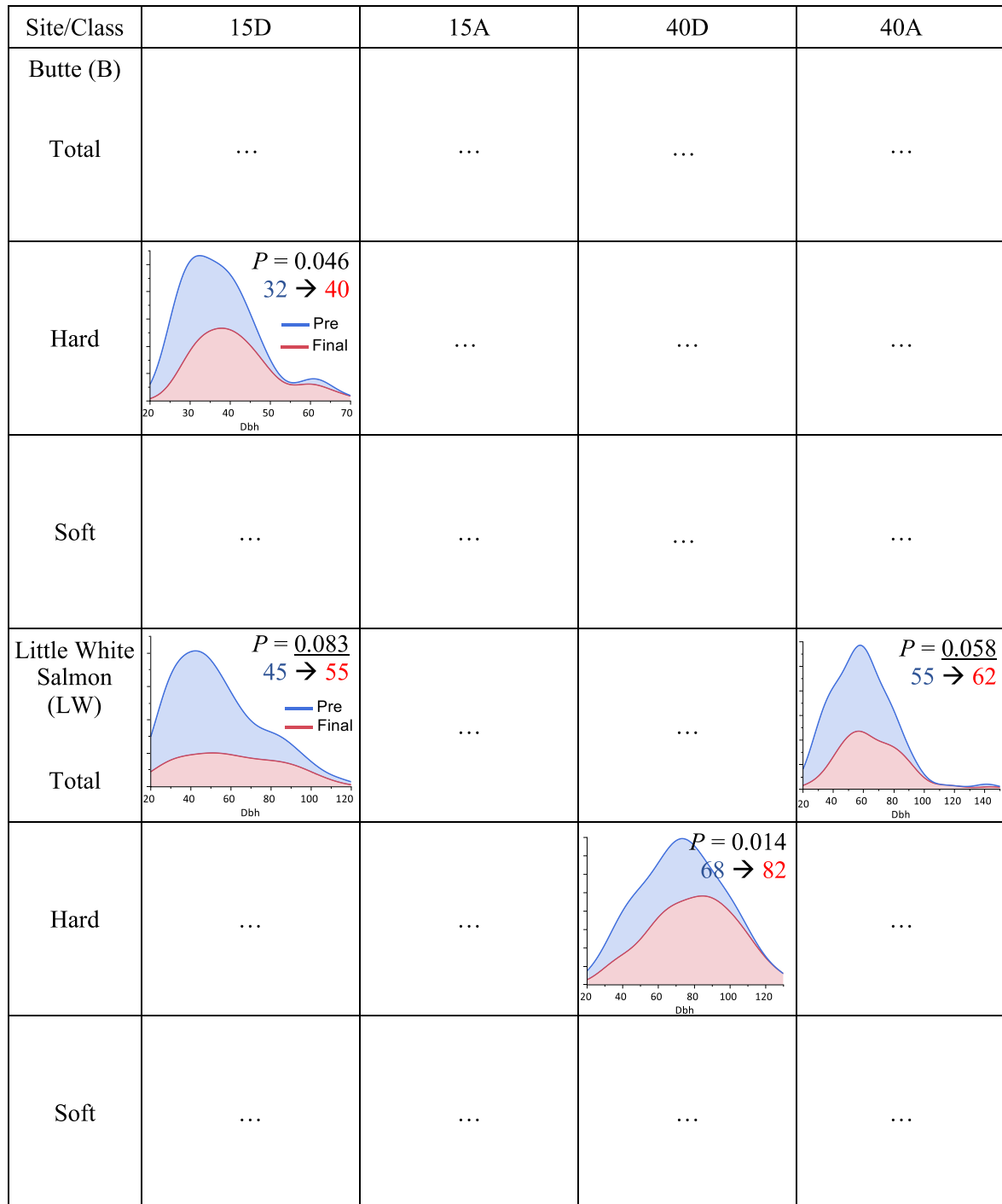


Fig. A5. (continued).

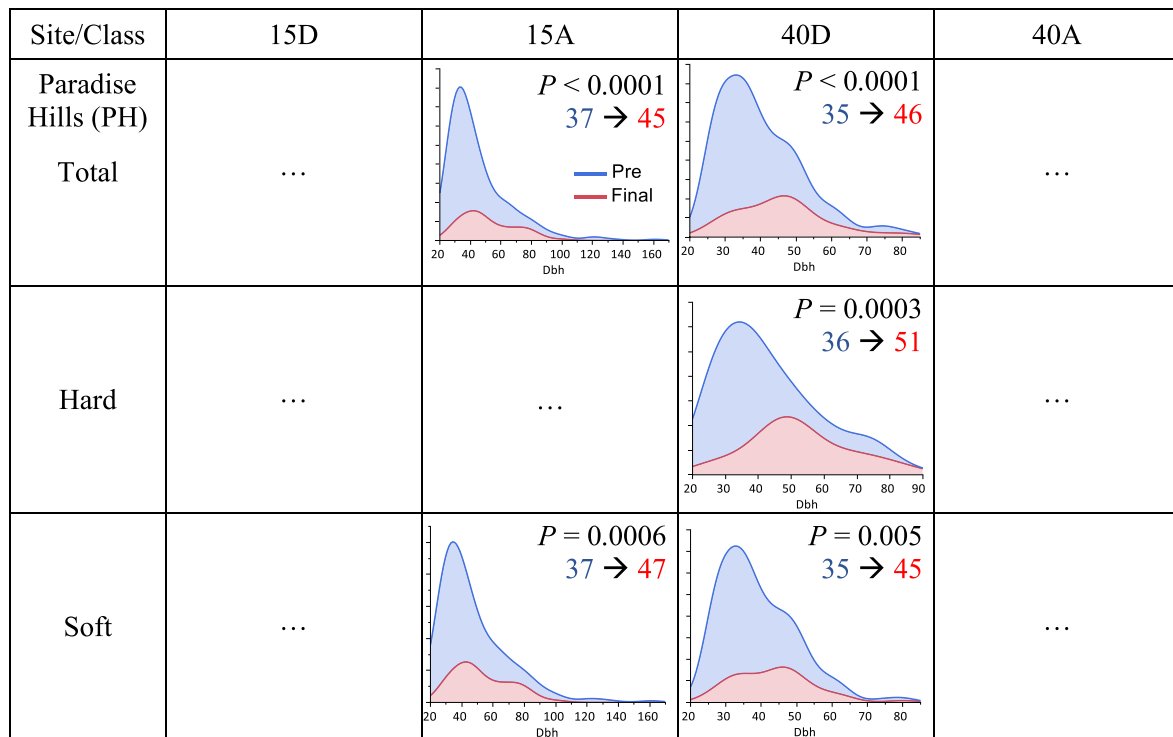


Fig. A5. (continued).

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