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Level and pattern of overstory retention interact to shape long-term responses of understories to timber harvest

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Abstract. In many regions of the world, variable retention has replaced clear-cutlogging as the principal method of regeneration harvest. Partial retention of the overstory is thought to ensure greater continuity of the species and ecological processes that characterize older forests. Level (amount) and spatial pattern of overstory retention are two basic elements of forest structure that can be manipulated to achieve specific ecological or silvicultural objectives. However, experiments that elucidate the relative importance of retention level and pattern (or their interaction) are rare. Here we assess long-term (>10 yr) responses of forest understories to experimental harvests of mature coniferous forests replicated at five sites in the Pacific Northwest (PNW). Treatments contrast both the level of retention (40% vs. 15% of original basal area) and its spatial distribution (dispersed vs. aggregated in 1-ha patches). For most vascular plant groups (early seral, forest generalist, and late seral), postharvest changes in cover and richness were reduced at higher levels of retention and in dispersed relative to aggregated treatments. Although retained forest patches were stable, changes in adjacent harvested (cleared) areas were significantly greater than in dispersed treatments. Late-seral herbs were highly sensitive to level and pattern of retention, with extirpations most frequent in the cleared areas of aggregated treatments and at low levels of dispersed retention. In contrast, early-seral species were most abundant in these environments. Forest-floor bryophytes exhibited large and persistent declines regardless of treatment, suggesting that threshold levels of disturbance or stress were exceeded. Our results indicate that 15% retention (the minimum standard on federal forestlands in the PNW) is insufficient to retain the abundance or diversity of species characteristic of late-seral forests. Although 1-ha aggregates provide refugia, they are susceptible to edge effects or stochastic processes; thus, smaller aggregates are unlikely to serve this function. The ability to achieve multiple ecological or silvicultural objectives with variable retention will require the spatial partitioning of habitats to include dispersed retention and larger undisturbed aggregates along with cleared areas.

Key words: early-seral species; *forest management*; *green-tree retention*; *late-seral herbs*; *Pacific Northwest, USA*; *species diversity*; *structural retention*; *understory dynamics*; *variable retention.*

Introduction

In many regions of the world, variable-retention harvest has replaced clear-cutlogging (Vanha-Majamaa and Jalonen 2001, Beese et al. 2003, Gustafsson et al. 2010, 2012). A fundamental goal of variable retention is to enhance the ecological values of forests managed for wood production, including maintenance or recovery of late-seral species (Franklin et al. 1997, Lindenmayer and Franklin 2002). A principal strategy for achieving this goal is to retain live trees, snags, or logs that serve important ecological functions in postharvest stands: moderating microclimate, providing habitats or refugia, and enhancing landscape connectivity (Franklin et al. 1997). Variable retention thus provides regenerating stands with some of the "biological legacies" that are characteristic of naturally disturbed forests, but are lacking or greatly reduced by clear-cutting (Bergeron et al. 2002, Lindenmayer and Franklin 2002, Palik et al. 2002, Keeton 2006). To what extent and by what means variable retention enhances the ecological values of managed forests remain questions of global interest and inquiry (Rosenvald and Lõhmus 2008, Gustafsson et al. 2010, 2012).

In their seminal paper on variable-retention systems, Franklin et al. (1997) identify level (amount) and spatial pattern of overstory retention as two fundamental elements of forest structure that can be manipulated to target specific ecological objectives. Greater retention is expected to favor closed-canopy species that depend on stable, shaded understories and to inhibit early-seral species that benefit from canopy removal or disturbance.

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Similarly, pattern of retention can be varied to influence microclimatic and ecological responses. Dispersed retention can serve multiple functions, reducing microclimatic extremes (Childs and Flint 1987, Heithecker and Halpern 2006), providing substrates for epiphytic species (Hedenås and Hedström 2007, Lõhmus and Lõhmus 2010), or ensuring continuity of ectomycorrhizal communities (Luoma et al. 2006). However, it may be ineffective for species that are sensitive to ground disturbance or to changes in light, temperature, or humidity. These species may require undisturbed forest patches, or aggregates, that serve as refugia until conditions in the harvested matrix become conducive to establishment (Franklin et al. 1997).

Level and pattern of retention can also interact to shape responses to harvest. For example, aggregates that are too small or exposed could be compromised by edge effects, physical disturbance (windthrow), or stochastic processes (Murcia 1995, Moen and Jonsson 2003, Perhans et al. 2009), yielding no ecological advantage over similar levels of dispersed retention. Similarly, low levels of dispersed retention may be insufficient to moderate understory microclimate, resulting in temperature regimes that are no different from those of clearcuts (Heithecker and Halpern 2006). The ability to manage for multiple ecological or silvicultural objectives thus requires an understanding of the individual and interactive effects of level and pattern of retention, knowledge that is lacking in most forest ecosystems (Rosenvald and Lõhmus 2008, Gustafsson et al. 2010).

Here, we present the results of a novel experiment designed to test responses to contrasting levels and patterns of overstory retention in mature coniferous forests of the Pacific Northwest, USA (Aubry et al. 1999, 2009). The DEMO (Demonstration of Ecosystem Management Options) experiment was initiated in 1994 as a regional-scale study to evaluate newly implemented standards for regeneration harvests on federal forests within the range of the Northern Spotted Owl, as part of a broader plan for ecosystem management, the Northwest Forest Plan (USDA and USDI 1994, Tuchmann et al. 1996). These included a minimum level of retention (15% of each harvest unit) with most retention (70%) in undisturbed aggregates of 0.2–1.0 ha. Although the experiment addresses these specific standards, it was designed more generally to determine how level and pattern of retention shape the responses of a diversity of forest organisms (Aubry et al. 2009).

In this paper, we explore changes in the composition, abundance, and diversity of understory bryophytes and vascular plants 6–11 yr after treatment, building on our initial assessment of disturbance, microclimatic variation, and vegetation change (Halpern and McKenzie 2001, Halpern et al. 2005, Heithecker and Halpern 2006, 2007). Among vascular plants, we focus on species with differing functional traits and seral roles (early seral, forest generalist, and late seral) for which we anticipated contrasting responses to harvest. Although our primary emphasis is on forest-dependent species, we also assess trade-offs for other ecosystem values, including the quality and longevity of early-seral habitats, which are of increasing concern in some managed landscapes (Swanson et al. 2011). We pose the following hypotheses.

Hypothesis 1: Treatment-scale responses to level and pattern of retention.—Changes in species composition, abundance, and diversity will be moderated by greater levels of retention and by aggregated (vs. dispersed) retention. Early- and late-seral species will exhibit contrasting responses to level of retention consistent with their life histories and physiological requirements. Bryophytes and late-seral herbs will be highly sensitive to pattern of retention.

Hypothesis 2: Moderating influences of dispersed trees in harvested areas.—Dispersed trees will have a moderating influence on changes in species composition, abundance, and diversity relative to changes in the cleared areas of aggregated treatments. Early-seral species will respond negatively but bryophytes and late-seral herbs will respond positively to the presence of dispersed trees.

Hypothesis 3: Forest aggregates as refugia.—Forest aggregates (1-ha patches) will show small changes in composition, abundance, and diversity relative to controls and thus provide refugia for bryophytes and late-seral herbs.

Methods

Study sites

The DEMO (Demonstration of Ecosystem Management Options) experiment is replicated at six sites (blocks) in western Oregon and Washington, USA (Aubry et al. 1999, 2009). Long-term sampling of the vegetation has occurred at five of these: three on the Gifford Pinchot National Forest, Washington (BU, LWS, and PH) and two on the Umpqua National Forest, Oregon (WF and DP). Elevations range from 800 to 1700 m. Climate 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). Soils are moderately deep, well-drained loams to loamy sands derived from andesite, breccia, basalt, or pumice deposits (Radtke and Edwards 1976, Wade et al. 1992).

Experimental blocks encompass upland communities in four vegetation zones (*Tsuga heterophylla*, *Abies grandis*, *A. concolor*, and *A. amabilis*; Franklin and Dyrness 1988). However, *Pseudotsuga menziesii* was the dominant canopy species at all blocks. Stand age (70–170 yr), forest structure, and understory composition varied markedly among blocks, as did disturbance history. Three supported undisturbed forests, but two had been thinned or salvage logged several decades before the experiment (Halpern et al. 2005, Maguire et al. 2007).

TABLE 1. Treatment descriptions and numbers of plots sampled per treatment or within-treatment environment in the DEMO (Demonstration of Ecosystem Management Options) experiment in western Oregon and Washington, USA.

Treatment	Code	Description	Number of plots		
			Uncut	Harvested	Total
Control	100%	no harvest	32		32
40% aggregated	40%A	retention in five 1-ha (56 m radius) circular forest patches (40%A-p); all merchantable trees (>18 cm dbh) in adjacent cleared areas (40%A-c) cut and removed	24–25	12	36–37
40% dispersed	40%D	retention of dominant and codominant trees evenly dispersed through the treatment area; retained basal area equivalent to that in 40%A		32	32
15% aggregated	15%A	retention in two 1-ha (56 m radius) circular forest patches (15%A-p); all merchantable trees (>18 cm dbh) in adjacent cleared areas (15%A-c) cut and removed	9–10	21–22	31–32
15% dispersed	15%D	retention of dominant and codominant trees evenly dispersed through the treatment area; retained basal area equivalent to that in 15%A		31–32	31–32

Experimental design and treatment implementation

Treatments were randomly assigned to 13-ha experimental units within each block. These included a control (100% retention) and four comprising one of two levels of retention (40% or 15% of original basal area) and one of two spatial patterns (trees uniformly dispersed or aggregated in circular, 1-ha [56 m radius] patches; Table 1, Fig. 1). Tree boles were yarded by helicopter or suspension cables in blocks with steep slopes and with ground-based equipment elsewhere. Non-merchantable stems (<18 cm dbh) were felled (PH), felled if damaged (WF), or left standing (remaining blocks). Logging slash was not treated, except at WF, where fuels were partially reduced by machine piling and burning on temporary skid roads. Logging was completed in each block in fall 1997 or 1998. Conifer seedlings were planted at low densities in the harvested areas of all experimental units in spring/early summer 1998 or 1999; species and planting density varied among blocks (Halpern et al. 2005). Details on treatment implementation can be found in Halpern and McKenzie (2001) and Halpern et al. (2005).

Sampling design and data collection

Prior to harvest we established a sampling grid (7×9 or 8×8; 40-m spacing) in each experimental unit (Aubry

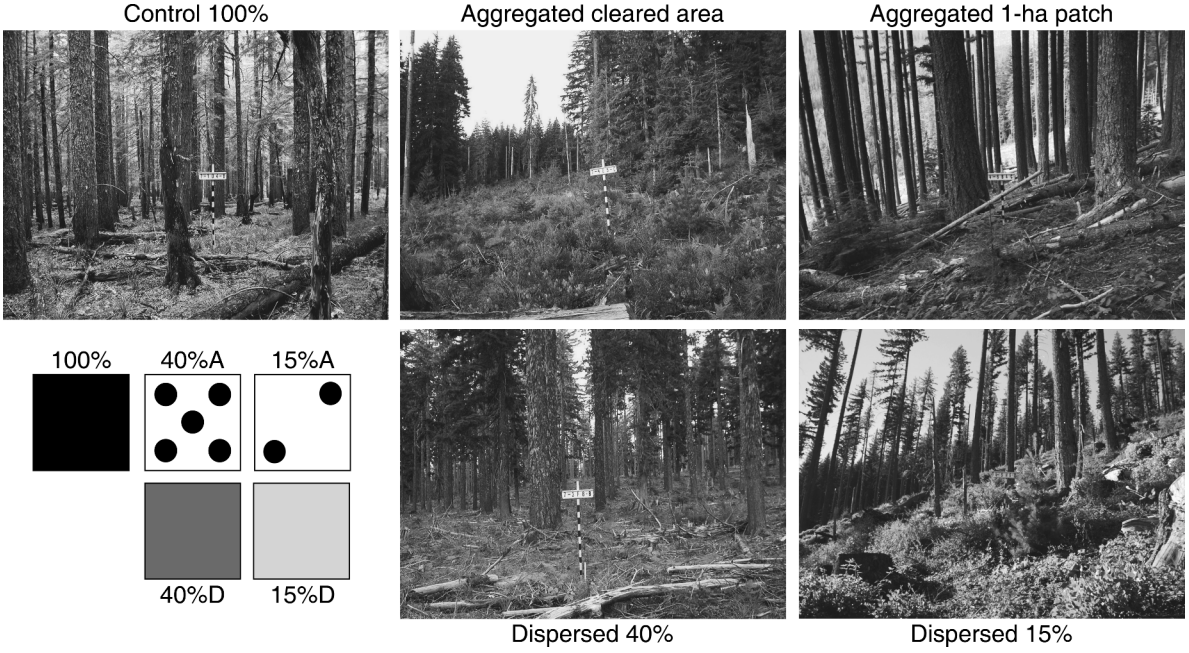

FIG. 1. Experimental design with photos of treatments representing varying retention levels (100%, 40%, and 15%) and patterns (D, dispersed; A, aggregated) in the DEMO (Demonstration of Ecosystem Management Options) experiment in western Oregon and Washington, USA. For aggregated treatments, separate photos illustrate a cleared area (40%A, top center photo) with the edges of two forest patches visible in the upper left and upper right, and a 1-ha forest patch (15%A, top right photo) with the cleared area visible in the background.

TABLE 2. Pretreatment means (with SD in parentheses) of understory response variables among the five experimental units in each block.

Response variable	Watson Falls (WF)	Dog Prairie (DP)	Butte (BU)	Little White Salmon (LWS)	Paradise Hills (PH)
Cover (%)					
Bryophytes			6.2 (2.0)	10.2 (2.9)	22.6 (4.4)
Total herbs	60.6 (10.2)	22.1 (8.4)	29.4 (6.7)	52.7 (9.2)	16.3 (11.9)
Early-seral herbs	1.7 (0.7)	2.1 (1.6)	5.1 (2.5)	0.1 (0.2)	0.9 (1.3)
Forest herbs	29.8 (5.5)	11.1 (2.8)	16.5 (3.7)	9.6 (2.3)	9.6 (5.7)
Late-seral herbs	28.9 (6.0)	8.7 (5.7)	7.6 (1.6)	43.0 (7.6)	5.7 (6.4)
Total shrubs	6.4 (3.4)	1.9 (1.1)	21.9 (10.0)	82.3 (15.7)	10.0 (10.1)
Early-seral shrubs	0.3 (0.2)	0.5 (0.7)	0.3 (0.2)	0.5 (0.2)	<0.1 (0.0)
Forest shrubs	3.0 (1.8)	1.3 (0.8)	21.2 (10.6)	81.5 (15.7)	9.9 (10.0)
Species richness (species/plot)					
Total herbs	25.2 (3.1)	18.5 (4.7)	14.0 (1.3)	16.9 (1.8)	10.1 (4.0)
Early-seral herbs	1.7 (0.5)	2.1 (1.0)	0.9 (0.2)	0.1 (0.1)	0.4 (0.5)
Forest herbs	13.8 (2.0)	9.9 (2.6)	7.2 (0.9)	8.1 (0.9)	4.3 (1.6)
Late-seral herbs	9.3 (0.7)	5.8 (1.8)	5.7 (0.8)	8.6 (1.1)	5.3 (2.2)
Height (m)					
Total shrubs	0.7 (0.5)	0.3 (0.1)	1.7 (1.0)	3.3 (0.4)	0.5 (0.2)

Note: Bryophyte cover was low in the Oregon blocks and not analyzed.

et al. 1999). Permanent vegetation plots were established at a subset of grid points ($n = 32$–37; Table 1). In control and dispersed treatments, plots were placed at alternate points. In aggregated treatments, they were placed at a subset of points in cleared areas (henceforth, 40%A-c and 15%A-c) and in each circular forest patch (40%A-p and 15%A-p): one at patch center and four along perpendicular radii, 40 m from the center. Patch edges were not sampled (but see Nelson and Halpern 2005*a*, *b* for studies of edge gradients).

Within each permanent plot, understory vegetation was sampled along four perpendicular transects (6 m), each with six evenly spaced quadrats (0.2×0.5 m; 24 quadrats in total). Total cover of bryophytes (Washington blocks only) and cover of herbaceous and low-growing woody species (<1 m tall at maturity) were estimated in each quadrat. For quadrats that fell on coarse woody debris or the bases of shrubs or trees, sampling of bryophytes was limited to a height of 1 m from the forest floor. Cover of tall shrubs (woody species typically >1 m tall at maturity) and understory trees (<5 cm dbh) was estimated along each transect using the line-intercept method. Maximum shrub height was estimated in each of six, 1-m intervals per transect (maximum of 24 heights per plot). Pretreatment sampling occurred in 1994–1995 (1996 at DP), and posttreatment sampling in 1998–2000 (years 1–2), 2004 (years 6–7), and 2008–2009 (years 10–11). The initial posttreatment data were reported in an earlier paper (Halpern et al. 2005) and are not included here. Plant nomenclature follows Hitchcock and Cronquist (1973) and Hickman (1993).

Response variables and data aggregation

Our analyses focus on groups of species defined by growth form and seral role. Species were assigned to one of four growth forms: bryophytes (mosses and liverworts), herbs (including ferns and low-growing woody species), tall shrubs (henceforth, shrubs), and trees (Appendix A). Herb and shrub species were also assigned to seral groups (early seral, forest generalist, or late seral), reflecting differences in life history (longevity, reproductive mode), tolerance of disturbance, and sensitivity to abiotic stress. Species' assignments follow previous classifications (Halpern 1989, Halpern and Spies 1995, Halpern et al. 2005, Dovčiak and Halpern 2010). Early-seral species ($n = 65$ herbs and 20 shrubs) respond positively to disturbance or increased resource availability. Post-disturbance establishment is typically from seed (soil seed bank or long-distance dispersal; Kellman 1974, Halpern 1989, Halpern et al. 1999). Forest generalists (henceforth, forest species; $n = 66$ herbs and 14 shrubs) are tolerant of disturbance and present in all stages of forest development (Halpern 1989, Halpern and Spies 1995). Responses to overstory removal can vary from positive (release) to initially negative, followed by gradual recovery, typically by vegetative means (Halpern 1989). Late-seral species (herbs only; $n = 40$) are most abundant in older stands (Halpern and Spies 1995, Jules et al. 1999). They are shade-tolerant and often sensitive to disturbance or sudden exposure to sun (Halpern and Spies 1995, Lindh and Muir 2004, Nelson et al. 2007). If extirpated by logging disturbance, recovery is slow (Halpern 1989). Understory trees ($n = 25$) and species that could not be classified ($n = 74$ herbs and 8 shrubs) were excluded from seral group analyses; however, the latter were infrequent and contributed minimally to vegetation cover.

For each growth form and growth form × seral group, we considered one or more measures of response: summed (total) cover of species, number of species per plot (herb groups only), and mean maximum height (shrubs only) (Table 2). Plot values (computed from quadrat or transect values) were averaged for each control or dispersed treatment and for the two environments within each aggregated treatment (cleared

areas and forest patches). Postharvest means for aggregated treatments were computed as weighted averages of cleared areas and forest patches. To account for significant variation among experimental units prior to treatment, we computed the difference between pre- and posttreatment values (post- minus pretreatment), i.e., change over time, as our measure of response.

We also quantified changes in species composition, computed as percentage dissimilarity (PD or Bray Curtis dissimilarity) between pre- and posttreatment samples. PD can range from 0 (no change in cover of any species) to 100 (no species in common). For each plot, PD was computed for each time interval (pretreatment to years 6–7 and 10–11). Treatment means were then computed as described for seral groups. All species were included in this measure.

Analyses

We used nonmetric multidimensional scaling (NMS; Kruskal 1964) to visually illustrate compositional changes among and within treatments. A separate ordination was run for each block to prevent regional variation in the flora from masking responses to treatment. Each ordination was run on a sample × time × species matrix representing the average species composition of seven environments: control (100%), dispersed retention (40%D and 15%D), and cleared areas (40%A-c and 15%A-c) and forest patches (40%A-p and 15%A-p) of aggregated treatments. Three times were included: preharvest and 6–7 and 10–11 yr after treatment. All species were included, and Bray-Curtis was used as the distance measure. Each ordination was initiated from a random configuration for a maximum of 500 iterations and rerun up to 50 times or until an instability criterion of 0.00001 was met (McCune and Grace 2002). Final solutions were two dimensional for all but one block (PH), with stress values of 4.0–10.6. Final scores were rotated to maximize the variation explained by the first axis (McCune and Grace 2002). NMS was performed in PC-Ord version 4.41 (McCune and Mefford 1999).

We analyzed compositional change (PD) and growth form and seral group responses with a series of randomized-block, split-plot ANOVA models. Block was treated as a random factor, treatment (or within-treatment environment) as the whole plot (fixed factor), and time since disturbance (time) as the split plot (fixed factor). We used three variants of this model, each with different sets of treatments or environments within treatments to address the three hypotheses. The first model compared mean responses to level and pattern of retention at the treatment scale (hypothesis 1). All treatments were used, with postharvest means in aggregated treatments computed as weighted averages of responses in cleared areas and forest patches (see *Methods: Response variables and data aggregation*). Treatment effects were then decomposed into four orthogonal contrasts (Sokal and Rohlf 1981): control vs. harvest (i.e., all harvested treatments), level of retention (40% vs. 15%), pattern of retention (dispersed vs. aggregated), and the interaction of level and pattern. For significant time × treatment interactions, contrasts were conducted separately for each time period. The second model compared responses within the harvested portions of treatments, testing the influences of dispersed trees (40%D and 15%D) relative to cleared areas (40%A-c and 15%A-c) (hypothesis 2). For this model, controls (100%) and plots from forest patches were excluded. Treatment effects were decomposed into three orthogonal contrasts (level, pattern, and their interaction). The third model tested whether forest patches served as refugia (hypothesis 3), comparing patches at both high and low retention (40%A-p and 15%A-p) and controls (100%). Dispersed treatments and plots from the cleared areas of aggregated treatments were excluded. For this hypothesis, we tested a reduced set of variables (primarily groups in the herb layer). For all response variables, diagnostic plots were used to assess homogeneity of variance and normality of residuals; transformations (log, square root, or reciprocal) were applied when necessary. Main effects and interactions were judged to be significant at an $\alpha \leq 0.05$. Alpha levels, which were typically <0.001, were not adjusted for multiple comparisons. Analyses were conducted in SPSS version 12.0 (SPSS 2003).

A final set of analyses explored patterns of decline and extirpation of late-seral herb species based on presence prior to treatment and at final sampling. For each treatment unit or within-treatment environment (aggregated treatments), we calculated the change in frequency of occurrence of each species (proportion of plots in which a species was present). We then computed three measures of decline: (1) ubiquity of species' decline—the percentage of species that declined in frequency; (2) average rate of decline—average change in frequency among species; and (3) rate of extirpation—percentage of species lost from all plots.

Results

Compositional changes among and within treatments

Patterns of compositional change were generally consistent with our hypotheses (Fig. 2). The magnitude of compositional change (movement in NMS space) was tempered by greater retention (hypothesis 1) and by the presence of dispersed trees in harvested areas (hypothesis 2). In addition, forest patches showed little change, although in some blocks (LWS, PH) patches at lower retention (15%A-p) showed greater change than at higher retention (40%A-p) (Fig. 2d, e).

Treatment-scale responses to level and pattern of retention

Herb-layer richness and total cover increased in all treated units (Fig. 3; for results of ANOVAs see Appendix B: Table B1). Richness was enhanced at lower retention and in dispersed treatments (Fig. 3c), but increases in cover were comparable among treat-

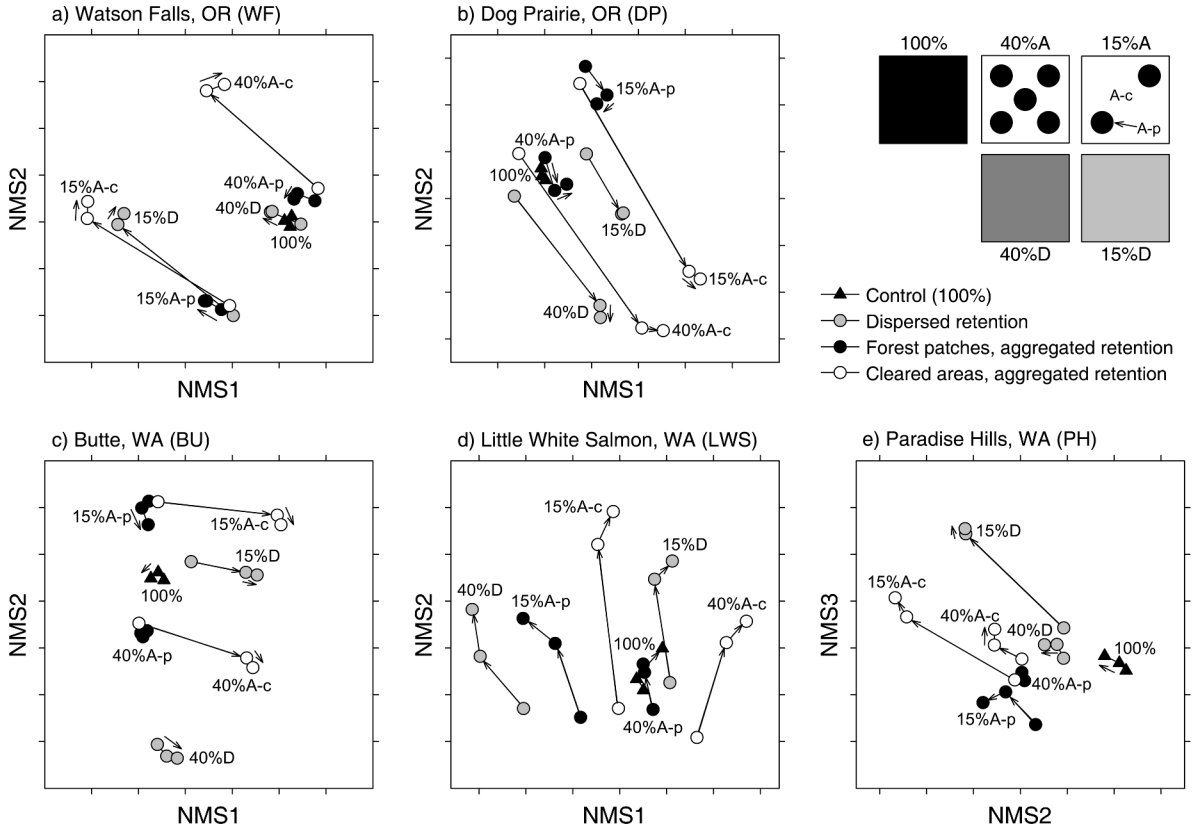

FIG. 2. Nonmetric multidimensional scaling (NMS) ordination of species compositional changes among treatments and within-treatment environments in each experimental block. Points represent the average species composition of plots in controls (100%), dispersed retention (40%D and 15%D), and for aggregated treatments, forest patches (40%A-p and 15%A-p) or cleared areas (40%A-c and 15%A-c). Lines connect pre- and postharvest samples (6–7 and 10–11 yr); arrows indicate the direction of change. Abbreviations are: OR, Oregon; WA, Washington.

ments (Fig. 3g). In contrast, total shrub cover was unchanged by harvest (Fig. 3k) and although shrub height was reduced, the effect was transient (significant treatment × time interaction; Fig. 3n).

Changes in species composition (PD; Fig. 3b), and in the abundance and richness of seral groups were tempered by greater levels of retention, consistent with hypothesis 1. These effects included reduced colonization by early-seral herbs (Fig. 3d, h) and shrubs (Fig. 3l), smaller increases in forest herbs (Fig. 3e, i), and smaller declines in late-seral herbs (Fig. 3f, j) and forest shrubs (Fig. 3m). In contrast, for bryophytes (Fig. 3a), greater retention had no effect on loss of cover, which was significantly reduced in all treatments (by 20–60% of initial cover; Table 2).

Responses to pattern of retention, however, were not consistent with our hypothesis. For species composition (Fig. 3b) and all seral groups except forest herbs (Fig. 3e, i), changes were more, not less, pronounced in aggregated than in dispersed treatments. For early-seral herbs, this effect was reduced at lower retention (significant level × pattern interaction; Fig. 3d, h). For bryophytes (Fig. 3a), pattern of retention had no effect on loss of cover.

Moderating influences of dispersed trees in harvested areas

Within harvested areas, herb-layer richness was enhanced at lower retention and in dispersed treatments (Fig. 4c), but increases in total cover were comparable in all treatments (Fig. 4g; for results of ANOVAs see Appendix B: Table B2). Shrub cover increased significantly between sampling dates, but increases were comparable among treatments (Fig. 4k). Shrub height was consistently reduced, with greater loss at lower retention and in the cleared areas of aggregated treatments (Fig. 4n).

Changes in species composition and in the abundance and diversity of seral groups were largely tempered by the presence of dispersed trees, consistent with hypothesis 2 (Fig. 4). Only forest-herb richness showed a greater increase in dispersed treatments (Fig. 4e). In addition, for numerous measures of response (PD, richness or cover of early-seral herbs and shrubs, and richness of late-seral herbs) the moderating effect of dispersed trees was stronger at higher retention (significant level × pattern interactions; Fig. 4).

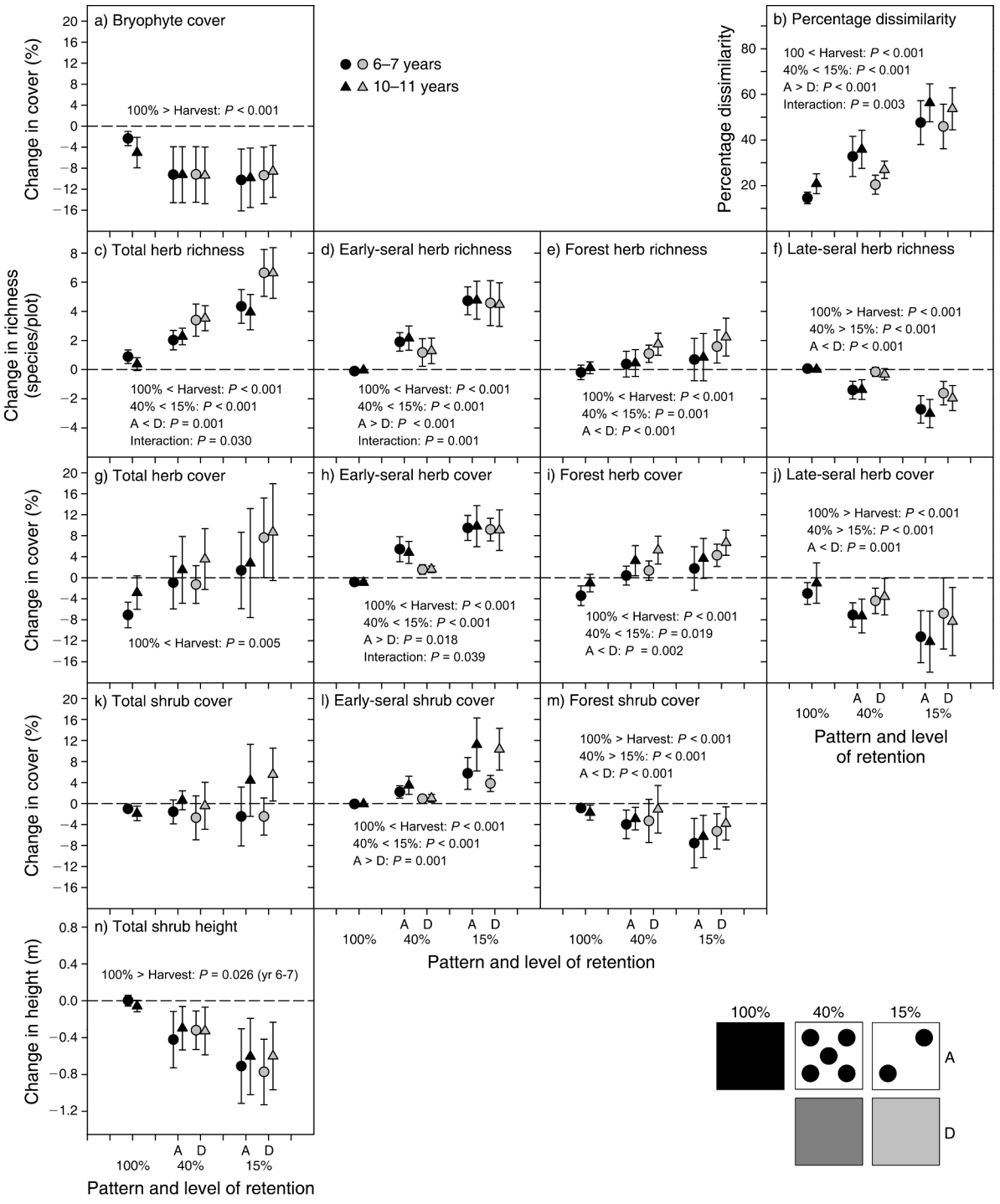

FIG. 3. Treatment-scale responses to level and pattern of retention including changes in species composition (percentage dissimilarity), richness (number of species per plot), cover, and height. Values are differences (mean ± SE) between pre- and posttreatment samples after 6–7 yr (circles) and 10–11 yr (triangles). Cover is the summed cover of species within a group. *P* values represent the results of orthogonal contrasts testing effects of harvest (100% vs. all other treatments), retention level (40% vs. 15%), pattern of retention (aggregated [A] vs. dispersed [D]), and level × pattern interaction (Interaction); only significant ($P \leq 0.05$) results are reported. See Appendix B (Table B1) for *F* and *P* values for main effects and interactions from randomized-block, split-plot ANOVAs.

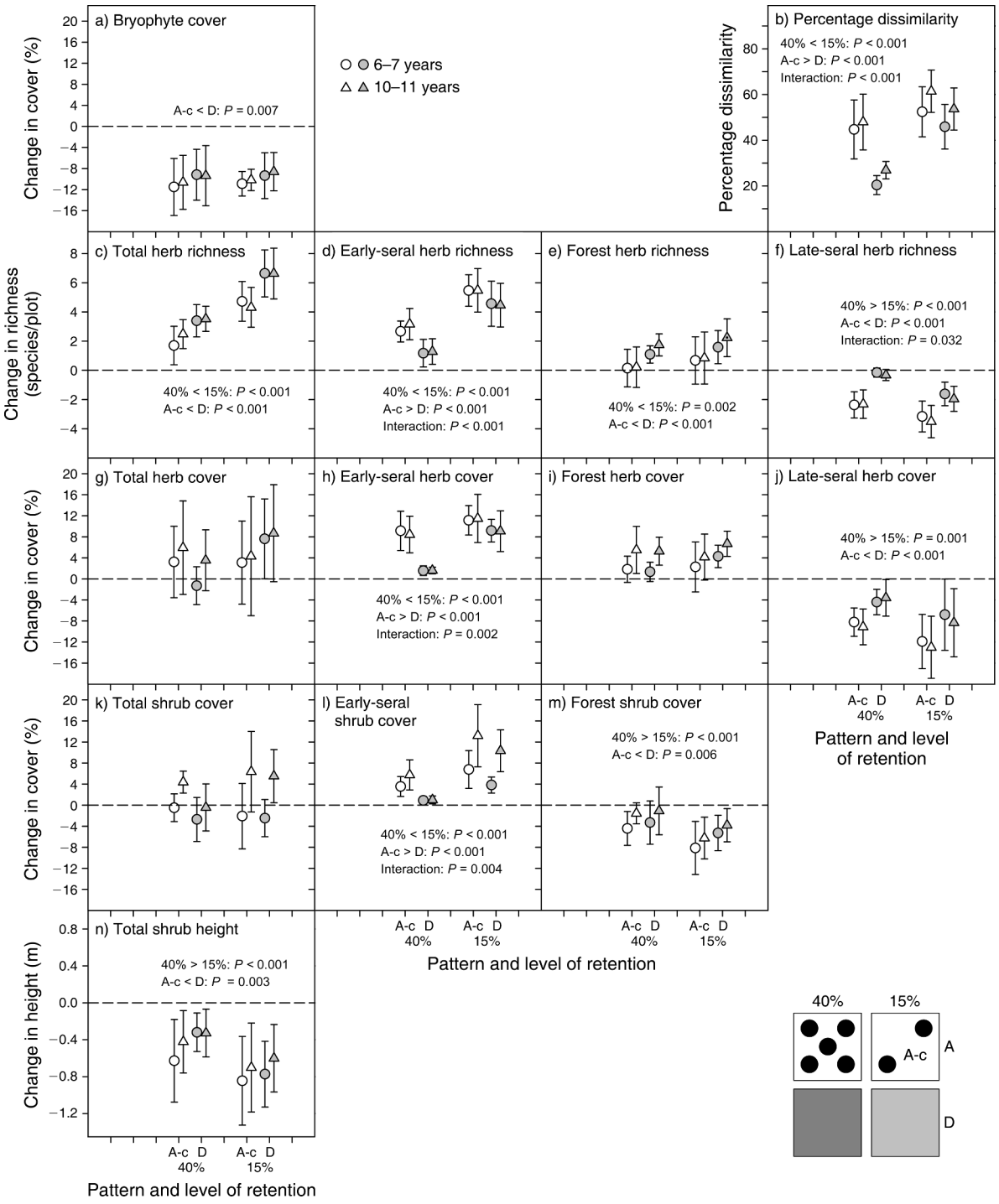

FIG. 4. Responses (mean ± SE) within the harvested areas of aggregated and dispersed treatments including changes in species composition (percentage dissimilarity), richness (number of species per plot), cover, and height. *P* values represent the results of orthogonal contrasts testing effects of retention level (15% vs. 40%), cleared areas vs. dispersed retention (A-c vs. D), and their interaction (Interaction); only significant ($P \leq 0.05$) results are reported. For other details see Fig. 3. See Appendix B (Table B2) for *F* and *P* values for main effects and interactions from randomized-block, split-plot ANOVAs.

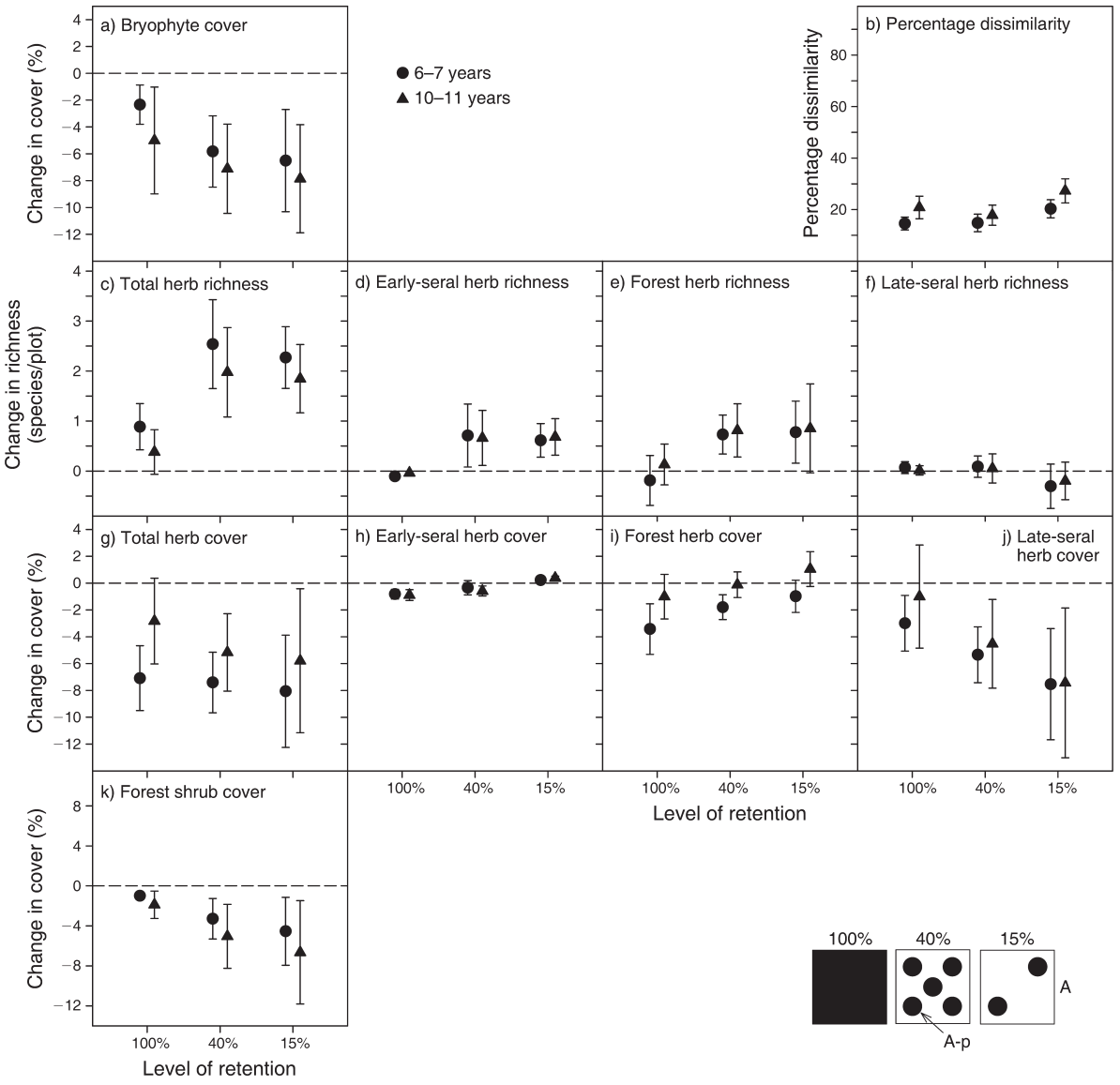

FIG. 5. Responses (mean ± SE) within the aggregates (40%A-p and 15%A-p) and controls (100%) including changes in species composition (percentage dissimilarity), richness (number of species per plot), and cover. For other details see Fig. 3. See Appendix B (Table B3) for *F* and *P* values for significant main effects (time only) from randomized-block, split-plot ANOVAs.

Forest aggregates as refugia

Changes in species composition, abundance, and richness did not differ significantly among residual forest patches and controls (Fig. 5; Appendix B: Table B3), consistent with hypothesis 3. Yet, for most measures of response, changes tended to be greater with increasing isolation or exposure of patches (100% < 40%A-p < 15%A-p). These included greater changes in species composition (Fig. 5b) and greater declines in bryophytes (Fig. 5a) and late-seral herbs (Fig. 5f, j).

Declines and extirpations of late-seral herb species

Patterns of decline and extirpation of late-seral herb species were consistent with expectation (hypotheses 1–3). On average, fewer than half of late-seral herbs declined in frequency in controls (38%), forest patches (40–42%), or higher levels of dispersed retention (44%) (Table 3a). In contrast, most species declined in frequency in the cleared areas of aggregated treatments (66–86%) and at lower levels of dispersed retention (72%). Similarly, the average decline in species' frequency was low in forest patches (<4%) and at higher levels of dispersed retention (<8%), but was much higher in cleared areas (38–64%) and at lower levels of dispersed retention (35%) (Table 3b). Rates of extirpation (percentage of species lost from all plots) ranged from 9% to 14% in controls, forest patches, and higher levels of dispersed retention, but were 2–4× higher in cleared

TABLE 3. Rates of decline and extirpation of late-seral herbs among treatments and within-treatment environments.

Experimental block	Response, by treatment						
	100% 32 plots	40%A-p 24–25 plots	40%A-c 12 plots	40%D 32 plots	15%A-p 9–10 plots	15%A-c 21–22 plots	15%D 31–32 plots
a) Ubiquity of species' decline: percentage of (*n*) species that declined in frequency							
Watson Falls	27.8 (18)	43.8 (16)	93.8 (16)	44.4 (18)	38.9 (18)	100.0 (19)	85.7 (21)
Dog Prairie	50.0 (20)	40.0 (15)	100.0 (14)	72.2 (18)	68.4 (19)	100.0 (20)	75.0 (16)
Butte	36.8 (19)	38.9 (18)	41.2 (17)	25.0 (16)	13.3 (15)	88.9 (18)	73.3 (15)
Little White Salmon	38.9 (18)	35.3 (17)	46.7 (15)	38.1 (21)	38.5 (13)	69.2 (13)	61.1 (18)
Paradise Hills	38.5 (13)	50.0 (18)	50.0 (16)	42.9 (14)	40.0 (15)	72.2 (17)	63.6 (22)
Average among blocks	38.4 (18)	41.6 (17)	66.3 (16)	44.5 (17)	39.7 (16)	86.1 (17)	71.8 (18)
b) Average rate of decline: average change in frequency (%) among species							
Watson Falls	24.9	−18.1	−77.7	−16.8	−4.7	−79.8	−68.4
Dog Prairie	−15.6	−12.0	−76.7	−23.1	−15.9	−82.9	−42.7
Butte	0.0	42.8	−20.9	13.6	18.0	−66.6	−46.0
Little White Salmon	7.2	−3.4	0.9	5.9	−20.1	−41.7	−3.8
Paradise Hills	14.0	−27.7	−16.7	−17.1	7.5	−50.9	−12.4
Average among blocks	6.1	−3.7	−38.2	−7.5	−3.0	−64.4	−34.7
c) Rate of extirpation: percentage of species lost from all plots							
Watson Falls	0.0	12.5	56.3	16.7	11.1	36.8	28.6
Dog Prairie	15.0	6.7	50.0	16.7	15.8	50.0	31.3
Butte	15.8	5.6	11.8	6.3	6.7	44.4	26.7
Little White Salmon	5.6	5.9	13.3	4.8	15.4	30.8	11.1
Paradise Hills	7.7	16.7	12.5	14.3	20.0	29.4	31.8
Average among blocks	8.8	9.5	28.8	11.7	13.8	38.3	25.9

areas (29–38%) and at lower levels of dispersed retention (26%) (Table 3c). Among the species most frequently lost from these environments were orchids (*Corallorhiza maculata*, *Goodyera oblongifolia*, and *Listera caurina*) and ericads (*Chimaphila menziesii*, *Pyrola chlorantha*, *P. picta*, and *P. secunda*).

DISCUSSION

Ours is one of the few experiments in variable retention to illustrate how the amount and spatial distribution of retained trees contribute to the postharvest dynamics of the understory. In these forests, both factors appear critical. Variation in one or both elements of overstory structure had significant effects on the abundance and diversity of species with differing sensitivities to disturbance and environmental stress. For some groups, responses to pattern were contingent on level of retention, indicative of thresholds beyond which retained trees exerted minimal influence on the understory. That pattern had minimal short-term effect (Halpern et al. 2005), but significant influence in the current study, illustrates the potential for lagged responses to disturbance or the cumulative effects of residual forest structure. It underscores the dynamic nature of the postharvest vegetation and the necessity for longer-term measurements.

General responses to structural-retention harvests

Despite large initial declines in plant abundance and diversity (Halpern et al. 2005), revegetation was rapid, with most growth forms attaining or exceeding preharvest cover or height within 6–10 yr after treatment. This rapid regrowth occurred through a combination of recruitment by early-seral species and vegetative recovery and expansion of disturbance-tolerant forest herbs (Halpern 1989). Forest shrubs were slower to recover due to the greater propensity for damage to woody stems and their inherently slower growth rates (Halpern 1989, Lindh and Muir 2004, Wilson et al. 2009). Trends in the cover of forest-floor bryophytes were a notable exception to the general pattern of growth-form recovery. Bryophyte cover remained greatly reduced, at the same levels observed one year after harvest (~40–80% of pretreatment values; Dovčiak et al. 2006). Similar postharvest losses have been observed in other temperate and boreal forests (Hannerz and Hånell 1997, Vanha-Majamaa and Jalonen 2001, Fenton et al. 2003, Perhans et al. 2009), although the persistence of this effect has not been well documented through long-term studies (but see Hylander 2009, Baldwin and Bradfield 2010).

Responses to level and pattern of retention

We hypothesized that increasing levels of retention would temper treatment-scale responses to harvest (hypothesis 1). In the short term, we expected residual trees to moderate the extent or intensity of mechanical damage or burial (Halpern and McKenzie 2001, Roberts 2007) and, in the longer term, to reduce environmental extremes both in the dispersed treatments and more locally in aggregated treatments (Barg and Edmonds 1999, Heithecker and Halpern 2006, 2007). For most components of the understory, responses to level of retention were consistent with these expectations (see synthesis in Fig. 6). In contrast, responses to pattern ran counter to expectation (hypothesis 1); for most plant

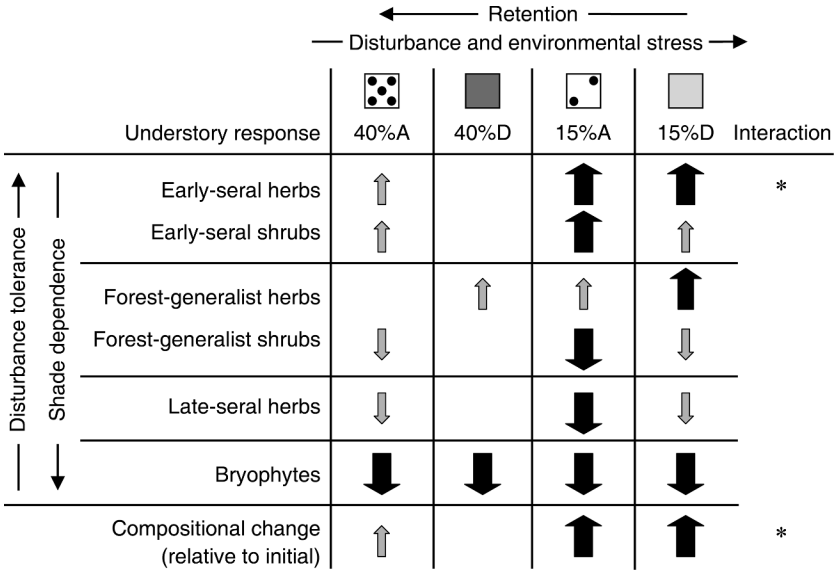

FIG. 6. Summary of treatment-scale responses of seral groups, bryophytes, and community composition (degree of change) to level and pattern of overstory retention. Upward arrows indicate positive responses; downward arrows indicate negative responses. Arrow size and shading are proportional to the magnitude of effect. In the interaction column an asterisk indicates $P \leq 0.05$.

groups we observed greater change in aggregated than in dispersed treatments, although for some groups, effects of pattern were contingent on level (Fig. 6). Two factors contributed to this result: changes were greater in cleared areas than in dispersed treatments and forest patches that changed minimally comprised only 15–40% of the harvest unit. Thus, responses in aggregated treatments were dominated by changes in the cleared areas. Effects of pattern were uncommon in our initial assessment of the vegetation (Halpern et al. 2005), indeed for most components of the biota (see review in Aubry et al. 2009).

Seral groups contributed in contrasting, but predictable ways to variation in the level and pattern of retention (Fig. 6). Early-seral species showed strong responses to retention level, consistent with observations in other systems (e.g., Craig and Macdonald 2009). However, effects of pattern were evident only at higher retention. Although these ruderal species benefit from exposure of mineral soil (Halpern 1989, McGee and Feller 1993, Newmaster et al. 2007, Bescond et al. 2011), ground disturbance was uniformly low in all treatments (mean of 5–7% cover; Halpern and McKenzie 2001) and is unlikely to explain this strong treatment interaction. Instead, it is likely to reflect differences in resource availability, notably light. Light transmission was markedly lower in 40%D than in 15%D or 15%A-c (13.6 vs. 24.8 and 33.9 $mol \cdot m^{-2} \cdot d^{-1}$, respectively; Heithecker and Halpern 2006). Although competition for belowground resources can also vary with tree density, there was little support for this mechanism; soil moisture availability was comparable among treatments (Heithecker and Halpern 2006).

Temporal trends in early-seral herbs suggest that cover and diversity peaked within a decade, similar to the timing of peak development after more intensive forms of disturbance (clear-cutting and burning; Schoonmaker and McKee 1988, Halpern and Franklin 1990). In contrast, temporal trends for early-seral shrubs—mostly seed-banking taxa in the genera *Arctostaphylos*, *Ceanothus*, *Ribes*, and *Rubus* (Appendix A)—indicate strong potential for further increase, particularly at lower levels of retention. These species are likely to persist until they are overtopped by forest shrubs or regenerating conifers (Wittinger et al. 1977, Conard et al. 1985, Halpern 1989, Donato et al. 2012).

Among forest generalists, responses to level and pattern of retention differed markedly for herbaceous and woody growth forms (Fig. 6). Forest herbs, which included an array of disturbance- and stress-tolerant species, responded positively to reduced levels of retention and to dispersed (relative to aggregated) retention. Individual species exhibited varying rates of recovery and release, including significant vegetative expansion of initially subordinate subshrubs (e.g., *Rubus ursinus* and *Symphoricarpos mollis*), taxa known to respond positively to increases in light (Halpern 1989, Lindh 2005, Ares et al. 2009). The apparent benefit of dispersed retention for forest generalists can be explained by the tempering effect of forest patches, the only environment in which these subshrubs did not show release. In contrast to generalist herbs, cover of forest shrubs (mainly *Acer circinatum*) remained depressed (Fig. 6). Recovery was slower at lower levels of retention and in aggregated treatments where woody stems likely suffered greater logging damage and burial (Thomas et al. 1999, Lindh and Muir 2004). For both herbaceous

and woody generalists, however, temporal trends suggest continued release or recovery—patterns that are unlikely to change until understory light is reduced, either by crown expansion of residual trees (40%D) or by shading from regenerating conifers.

Late-seral herbs displayed strong and predictable responses to level of retention, but not to spatial pattern. Although species showed significant declines in cleared areas, survival was not limited to forest aggregates, as anticipated. Rather, the presence of a dispersed canopy had a tempering effect (Fig. 6). This was surprisingly strong at higher levels of retention, where rates of species' loss were comparable to those in the aggregates and controls (9–14%). Although responses to harvest may reflect variation in ground disturbance or burial (Halpern and McKenzie 2001), the strong contrasts among treatments are more consistent with differences in light regime and resulting physiological stress. Estimates of understory light in 40%D did not differ from controls (13.6 vs. 7.0 $mol \cdot m^{-2} \cdot d^{-1}$) but were significantly higher in 15%D and 15%A-c (24.8 and 33.9 $mol \cdot m^{-2} \cdot d^{-1}$) (Heithecker and Halpern 2006). Shade-adapted species that are unable to acclimate to sudden increases in radiation can experience light, temperature, or water-deficit stress, compromising photosynthetic function (Powles 1984, Pearcy et al. 1989). In addition, for some late-seral herbs, declines may reflect loss of mycorrhizal symbionts in these postharvest environments (Read 1983, Alexander and Hadley 1985). Long-term successional studies suggest that once these species are lost, recolonization is slow (Halpern 1989).

As a group, bryophytes displayed greater sensitivity to harvest than did late-seral herbs (Fig. 6). Declines were large, even at 40% retention. The small stature and slow rates of growth of bryophytes make them susceptible to damage or burial by logging slash (Dovčiak et al. 2006, Schmalholz and Hylander 2011, but see Bråkenhielm and Liu 1998, Åström et al. 2005, Fenton and Frego 2005). In addition, forest bryophytes are shade plants, adapted to cool, moist, and low-light environments (Proctor and Tuba 2002, Marschall and Proctor 2004). Although they are poikilohydric (surviving periodic desiccation through dormancy; Alpert 2000), prolonged stasis can limit the ability to regain photosynthetic function or to maintain a positive carbon balance (Proctor et al. 2007). Even at 40% retention, light, temperature, or humidity may exceed critical thresholds for survival or recolonization (but see Caners et al. 2010). Although we did not assess species-specific responses (as in our initial assessment; Dovčiak et al. 2006), declines among rarer or more sensitive taxa may have been more dramatic, particularly for liverworts that are sensitive to humidity (Söderström 1988, Fenton et al. 2003, Nelson and Halpern 2005*b*).

Decade-scale responses offer little evidence of bryophyte recovery. Similar to late-seral herbs, the combined effects of physiological stress and dispersal limitation (Ross-Davis and Frego 2004) pose barriers to bryophyte recovery across the full range of harvested environments. Until microclimatic conditions become more conducive to establishment, these may leave forest aggregates as the primary environments capable of supporting these shade-dependent species (Nelson and Halpern 2005*b*, Dovčiak et al. 2006, Baldwin and Bradfield 2007).

Forest aggregates as refugia

As predicted (hypothesis 3), changes in species composition, abundance, and diversity were no greater in the 1-ha retention patches than in the unmanipulated controls. Patches remained highly resistant to colonization by early-seral species. Although forest-edge vegetation may inhibit dispersal (Cadenasso and Pickett 2001), limited establishment is more likely to reflect insufficient soil disturbance or light for germination (Brothers and Spingarn 1992, Honnay et al. 2002, Nelson and Halpern 2005*a*). For other plant groups we observed greater (but nonsignificant) changes with decreasing retention (100% $<$ 40%A-p $<$ 15%-p). For forest-floor bryophytes and late-seral herbs, these trends suggest increasing susceptibility to edge effects with greater exposure of aggregates. Elevated levels of light, air, and soil temperature may extend $>$40 m into these patches depending on edge orientation and canopy structure (Heithecker and Halpern 2007). Advective heating can be an important influence, as wind moves warmer air masses from adjacent cleared areas into these tree islands (Chen et al. 1995), and this process is likely to be enhanced by larger-sized openings. Effects on humidity may be especially detrimental to bryophytes that have limited ability to regulate water loss (Proctor 1981). With greater exposure, forest fragments are also more susceptible to wind damage, potentially exacerbating these effects (Esseen 1994, Hautala and Vanha-Majamaa 2006, Jönsson et al. 2007). Indeed, rates of tree mortality have been slightly greater in the more exposed patches of 15%A (Maguire et al. 2006; C. B. Halpern, *unpublished data*). Finally, small, isolated populations of bryophytes or late-seral herbs are more susceptible to extirpations arising from demographic or environmental stochasticity (Gilpin and Soulé 1986, Saunders et al. 1991, Lande 1993), although these effects are likely to be manifested over longer periods of time.

To what extent patches will serve as propagule sources for adjacent harvested areas (sinks) is unclear. This function requires that patches remain structurally stable and plant populations viable and reproductive until sink areas become more hospitable to colonization (Dynesius and Hylander 2007, Perhans et al. 2009, Roberge et al. 2011). Although trends suggest the potential for longer-term stability, companion studies of aggregate-edge environments offer little evidence to date that there has been dispersal-aided recovery of adjacent disturbed areas (Nelson and Halpern 2005*a*, *b*; C. R. Nelson, *unpublished data*).

Ecological and management implications

Our results have important implications for current policy and future implementation of variable-retention harvests in these and other forest ecosystems. That responses were consistent among stands of diverse age, overstory structure, and physical environment, suggests broad applicability of our findings to west-side forests of the Pacific Northwest. Decadal responses support our initial conclusions that current minimum standards for retention (15% of the harvest unit) yield marginal, if any, benefit for most forest-dependent species (Halpern et al. 2005, Aubry et al. 2009). Although low-level dispersed retention may offer other ecological benefits (e.g., substrate or habitat features associated with structural enrichment; Franklin et al. 1997, Rosenvald and Lõhmus 2008), tree densities are insufficient to maintain the light, temperature, and humidity regimes that are critical to maintaining many shade-dependent taxa. At low densities, residual trees are also highly susceptible to windthrow (Scott and Mitchell 2005, Maguire et al. 2006), potentially negating even the structural-enrichment function of dispersed retention.

In contrast, we illustrate that large (1-ha) aggregates are capable of retaining most (but not all) forest-dependent plant species in the short term. Even at this size, however, they are susceptible to edge effects that may compromise their function as dispersal sources. This suggests that smaller aggregates are less suitable for maintaining the diversity of species found in mature, undisturbed forests. Forest-floor bryophytes may be particularly sensitive to effects of forest fragmentation (Baldwin and Bradfield 2007), requiring undisturbed patches that are considerably larger than those retained in most temperate and boreal forests.

Responses to level of retention were strong and predictable, consistent with theory (Franklin et al. 1997) and with observations from the vast majority of studies to date (Rosenvald and Lõhmus 2008). Effects of pattern were more complex, slower to emerge, and often contingent on retention level. These interactions have important implications for management because they require explicit consideration of both elements of structure. For example, dispersed canopies offer little benefit to late-seral herbs at low retention, but greatly moderate species' loss at higher retention. Thus, for these species, the life-boating function of forest aggregates appears context dependent—critical at lower, but not higher retention levels. Similarly, the ability to maintain early-seral habitat—viewed as increasingly important in forests traditionally managed for rapid reforestation (Swanson et al. 2011, Donato et al. 2012)—is contingent on both elements of structure. Establishment of early-seral species was limited under higher levels of dispersed retention, but not in the cleared areas of aggregated treatments. Even so, cleared areas supported only modest cover of these species. Greater development of the early-seral component of these forests likely requires fire (broadcast burning) in addition to overstory removal to meet the germination requirements of these species (exposure of mineral soil or heating). Although more costly to implement, low-severity fire can be introduced into larger openings with limited risk to retained forest patches (Franklin et al. 1997, Hickey et al. 2001).

Our results also highlight the differing sensitivities of seral groups to variation in forest structure. Some are highly sensitive to one or both elements of structure; others are largely insensitive. Managers thus have the ability to manipulate structure to target particular groups (e.g., early- and late-seral herbs and bryophytes), but at the same time, "ignore" others (forest generalists). Ultimately, however, the ability to achieve multiple ecological objectives may require spatial partitioning of postharvest habitats to meet these objectives: areas of dispersed retention or large undisturbed patches (for bryophytes and late-seral herbs) separated by cleared areas (early-seral habitat). Ideally, habitat boundaries would exploit existing variation in topography, forest structure, or other habitat values (e.g., natural openings or "biodiversity hotspots"; Neitlich and McCune 1997). This approach would emulate natural disturbance processes, creating habitat diversity through heterogeneity in the extent and intensity of disturbance and associated forest structures. Disturbance-based approaches to forest management, including variable retention, remain in their infancy—widely applied but not fully tested. The DEMO experiment offers novel and evolving insights into the ecological benefits of retention harvests and how they are shaped by the level and spatial pattern of retained trees.

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Supplemental Material

Appendix A

List of vascular plant species observed in the five experimental blocks before or after treatment (years 6–7 or 11–12) (*Ecological Archives* A022-111-A1).

Appendix B

Results of randomized-block, split-plot ANOVA models for responses at the treatment-scale, in harvested areas, and in residual forest patches and controls (*Ecological Archives* A022-111-A2).