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Variable-retention harvests in the Pacific Northwest:

a review of short-term findings from the DEMO study

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Abstract

In the Pacific Northwest (PNW) region of the contiguous United States, retention of live (green) trees in harvest units is an integral part of forest management practices on federal lands, yet the ecological benefits that result from various levels or patterns of retained trees remain speculative. The Demonstration of Ecosystem Management Options (DEMO) study was established to address these informational gaps. The experimental design consists of six treatments, each 13 ha in size, replicated at six locations (blocks) in western Washington and Oregon. Treatments represent strong contrasts in retention level (15-100% of original basal area) and pattern (trees dispersed vs. aggregated in 1-ha patches) in mature Douglas-fir (*Pseudotsuga menziesii*) forests. A wide variety of ecological responses and public perceptions of visual quality have been examined; this paper provides a comprehensive review of the short-term (1-7 years) results of these studies. Level of retention had a strong effect on many responses. At 15% retention, regardless of pattern, microclimate, ecological responses, and public perceptions of visual quality did not differ from those measured in the "clearcut" areas of aggregated treatments. In contrast to level of retention, pattern of retention had limited effect on most measures of biological response. Small changes within forest aggregates were balanced by large changes in adjacent harvested areas, thus on average, responses within aggregated treatments were comparable to those in dispersed treatments. Nevertheless, retaining trees in 1-ha aggregates provided several benefits over dispersed retention. Aggregates greatly reduced damage to and mortality of residual trees (particularly at lower levels of retention) and provided short-term refugia for forest organisms sensitive to disturbance or environmental stress (e.g., bryophytes and late-seral herbs). However, aggregates were susceptible to edge effects (e.g., elevated light and temperature), which may compromise their ability to serve as sources for recolonization of adjacent harvested areas. Collectively, our findings suggest that retention levels >15% are needed to effectively retain sensitive plants and animals, ameliorate harsh microclimatic conditions, and gain public acceptance of retention harvests in these forests. A combination of relatively large (≥1 ha) aggregates and dispersed trees at levels considerably greater than current minimum standards in the PNW may be the most effective strategy for sustaining a broad array of forest values in managed stands.

Keywords: aggregated retention; biological responses; dispersed retention; forest structure; variable-retention harvest; refugia; public perceptions

1. Introduction

During much of the 20th century, the perceived value of forests in the Pacific Northwest (PNW) region of the contiguous United States was to provide wood, water, grazing, recreation, and other commodities; there was little concern about potential loss of biological diversity from harvest of old-growth forests. In recent decades, however, even-aged management designed to maximize wood production has largely been replaced by silvicultural strategies designed for sustainable production of a broader array of forest values (Curtis et al., 1998). Similar changes in forest management have occurred globally (e.g., Fries et al., 1997; Vanha-Majamaa and Jalonen, 2001; Deal et al., 2002; Beese et al., 2003). On federal lands allocated to timber harvest ("matrix" lands) in the PNW, clearcutting is no longer permitted; instead, variable-retention is now required (USDA and USDI, 1994). These harvests are directed primarily at mature, rather than old-growth forests. Current standards and guidelines specify (1) retention of green (live) trees in ≥15% of the area in each harvest unit; (2) of this, 70% must be in aggregates 0.2-1.0 ha or larger, with the remainder dispersed either as single trees or in small clumps ≤0.2 ha in size;

(3) to the extent possible, retention should include the largest and oldest live trees, decadent or leaning trees, and hard snags; and (4) aggregates should be retained indefinitely. However, these prescriptions rely largely on professional judgments that have not been tested experimentally.

A fundamental goal of variable-retention harvests is to maintain or accelerate the recovery of species and ecological processes characteristic of older forests (Franklin et al., 1997; Franklin et al., 2002; Lindenmayer and Franklin, 2002; Beese et al., 2003). Trees retained in harvest units are thought to provide critical ecological functions during the regeneration phase of forest development, including moderation of microclimatic conditions, subsidies for mycorrhizal fungi, and habitat or substrate for arboreal or epiphytic species, among other functions (see Franklin et al., 1997). However, it is not clear how effective different levels or spatial patterns of retention are for achieving these goals, nor how they affect public perceptions of variable-retention harvests. In response to these uncertainties, a regional, operational-scale experiment in variable-retention harvests—the Demonstration of Ecosystem Management Options (DEMO) study—was initiated in the PNW during the mid-1990s (Aubry et al., 1999, Halpern and Raphael, 1999).

The DEMO experiment tests the importance of level (amount) and pattern (spatial distribution) of retained trees in structuring ecological responses and shaping public perceptions of a broad array of harvest options (Aubry et al., 1999). Level and pattern of retention are two basic elements of forest structure that can be manipulated to achieve particular silvicultural, ecological, or visual objectives. For example, higher levels of retention are expected to yield correspondingly greater survival of forest-dependent species. Pattern of retention may also influence the fate of forest organisms. Dispersed retention provides for more uniform moderation of microclimatic stress and broader dispersion of habitat elements across a harvest unit, whereas aggregated retention provides patches of undisturbed forest that may serve as refugia (i.e., “lifeboats”; Franklin et al., 1997) and subsequent sources of dispersal for organisms sensitive to disturbance or environmental stress. To provide these functions, however, aggregates must be resistant to physical disturbance (e.g., windthrow) and uncompromised by edge effects (e.g., elevated light or temperature).

The DEMO experiment is unique in several ways. First, it evaluates a broad range of retention levels: 15% (the minimum standard in the Northwest Forest Plan; USDA and USDI, 1994), 40%, and 75%, as well as an unharvested control (100%). In addition, at 15 and 40% retention, trees are retained in either dispersed or aggregated patterns. This facilitates clear separation of the effects of level and pattern of retention, and an ability to identify interactions (e.g., effects of pattern at lower, but not higher levels of retention); similar inferences are not possible in most other large-scale silvicultural experiments. Although DEMO does not include a clearcut treatment (0% retention), the harvested portions of aggregated treatments (60-85% of the total area) offer such a reference point for some variables of interest. Finally, treatments are replicated among a diversity of forest types and physical environments in this region, providing a broad basis for inference. This design allows us to investigate fundamental questions about variable-retention harvests in these forests: (1) Do physical changes, biological responses, and public perceptions of visual quality vary with level of retention? (2) At a given level of retention, do responses vary with pattern of retention? (3) Do 1-ha forest aggregates serve as refugia for organisms sensitive to disturbance or environmental stress?

In this paper, we compare and contrast results from the many studies that comprise the DEMO experiment. We limit our review to papers published in the primary literature; these address physical factors (ground disturbance, slash accumulation, and microclimate), biological responses (overstory and understory vegetation, ectomycorrhizal fungi, arthropods, amphibians, and small mammals), and public perceptions of variable-retention harvests. Although we consider many forest attributes, we focus on the responses of organisms associated with late-seral forests (e.g., Ruggiero et al., 1991; Halpern and Spies, 1995), as their persistence has been the primary objective of variable-retention harvests in the PNW (USDA and USDI, 1994; Beese et al., 2003). For studies in which these taxa were too rare or infrequently detected to analyze statistically, we examine other groups for which we expected strong responses to treatments (e.g., forest-dependent or early seral taxa). Our objectives are threefold: (1) to assemble and briefly review results from studies that address the importance of level or pattern of retention, or the efficacy of forest aggregates as refugia; (2) to identify commonalities and differences among these results; and (3) to discuss the implications of our findings for implementing variable-retention harvests in the PNW. Because these are stand-scale studies, we cannot assess the efficacy of treatments for enhancing connectivity within the broader forest landscape (Franklin et al., 1997). Moreover, we have limited ability to identify landscape-scale factors that moderate or enhance responses to treatments, although we identify organisms and processes that show significant variation among experimental blocks. We draw upon research from other regions and forest types, but do not attempt to synthesize this broader literature. For a comprehensive review of the biodiversity aspects of green-tree retention, see Rosenvald and Lõhmus (2008).

2. Study Areas and Experimental Design

We selected six study areas (blocks) to represent a diversity of physical environments and forest types at low to moderate elevations (210-1,700 m) in western Washington and Oregon (Fig. 1). Three are in the Cascade Range and one is in the Black Hills of southwestern Washington; two are in the Cascade Range of southwestern Oregon. Blocks represent several forest zones (defined by different climax species), but Douglas-fir (*Pseudotsuga menziesii*) is the dominant tree species throughout (see Maguire et al., 2007). We established 13-ha experimental units on moderate slopes (4-66%) in upland areas of relatively homogeneous mature forest. Perennial streams, wetlands, roads, and existing harvest units were avoided. Past management activities varied among blocks: three had no previous activity, one was salvage-logged, one was thinned, and one regenerated naturally after clearcut logging ~65 years earlier.

The experiment is a randomized complete block design, containing six treatments (Fig. 1): (1) **Unharvested control**—a reference for assessing responses to harvest and natural temporal variation; (2) **75% aggregated retention**—all merchantable trees (>18 cm dbh) were harvested from three 1-ha circular gaps (56.4 m radius; 25% of the treatment unit); (3) **40% aggregated retention**—five circular 1-ha aggregates were retained (40% of the treatment unit); all merchantable trees in the surrounding matrix ("clearcut areas") were harvested; (4) **40% dispersed retention**—dominant and co-dominant trees were retained in an even distribution throughout the treatment unit; in each block, the basal area retained was equal to that retained in the corresponding 40% aggregated treatment; (5) **15% aggregated retention**—two circular 1-ha aggregates were retained (15% of the treatment unit); all merchantable trees in the surrounding matrix were harvested; (6) **15% dispersed retention**—dominant and co-dominant trees were retained in an even distribution throughout the treatment unit; in each block, the basal area retained was equal to that retained in the corresponding 15% aggregated treatment.

Because we defined treatments by proportional reductions in basal area, variation in initial forest structure among blocks resulted in substantial variation in residual structure among replicates of each treatment (Maguire et al., 2007). Details on yarding methods and post-harvest activities (e.g., treatment of non-merchantable trees and slash, snag creation, and planting) are presented elsewhere (Aubry et al., 1999; Halpern and McKenzie, 2001; Halpern et al., 2005).

We established a permanent grid (8 x 8 or 7 x 9, with 40-m spacing) in each experimental unit to systematically sample most biological responses (Aubry et al., 1999). For some studies, additional transect- or gradient-based designs were established in a subset of forest aggregates to test for the presence, depth, or magnitude of edge effects that could affect their ability to serve as refugia for organisms sensitive to disturbance or environmental stress. Details on field and analytical methods, timing and duration of sampling, and subsampling of blocks or treatments are available in the primary publications referenced below.

3. Results

In the following sections, we summarize the results of component studies that elucidate the importance of level or pattern of retention (Questions 1 and 2), the role of forest aggregates as refugia, and whether this function may be compromised by edge effects (Question 3). References to statistical significance reflect an alpha level of 0.05.

3.1. Effects of level and pattern of retention on soil disturbance, slash accumulation, and understory microclimate

Soil disturbance was generally low and did not vary with level or pattern of retention. In contrast, cover and depth of slash and additions of coarse woody debris were greater at 15 than at 40% retention (Halpern and McKenzie, 2001; Table 1). Deposition of logging slash varied with pattern of retention: cover was greater in the harvested areas of aggregated treatments than in dispersed treatments. For most measures of disturbance and slash accumulation, however, there was substantially greater variation among blocks than among treatments.

Transmitted light and summer air and soil temperatures measured 6-7 years after harvest generally declined with level of retention (Heithecker and Halpern, 2006; Fig. 2; Table 1).

Reductions in light were steep and highly significant across the retention gradient (Fig. 2a). However, differences in temperature were small and often non-significant (Figs. 2b-c). Notably, maximum air temperature and mean and maximum soil temperature did not differ between 40% dispersed retention and the clearcut areas of aggregated treatments. Soil moisture at the end of the growing season did not vary with level of retention, but was more sensitive to local ground conditions and vegetation cover (Fig. 2d).

3.2. Effects of level and pattern of retention on biological attributes

3.2.1. Overstory trees

Logging damage to tree boles did not vary with level of retention (Moore et al., 2002; Table 1). However, it was dramatically higher in dispersed (17-27% of trees) than in aggregated treatments (~2% of trees), reflecting minimal disturbance to stems in the 1-ha aggregates. Frequency of bole damage was comparable between Douglas-fir and western hemlock (*Tsuga heterophylla*), the most common species, but was more frequent for suppressed (8% of trees, mean among all experimental units) than for intermediate, co-dominant, or dominant individuals (3.5-6% of trees). Subsequent (5-6 year) mortality of canopy dominants (Douglas-fir) reflected an interaction between level and pattern of retention (Maguire et al., 2006; Table 1). At 40% retention, mortality was low in both aggregated and dispersed treatments; however, at 15% retention it was significantly higher in dispersed treatments (~7% of trees), reflecting greater exposure of stems to windthrow and stem breakage. In contrast, mortality within the aggregates was consistently low and comparable to rates in unharvested controls (<1.5%). Volume growth (per unit initial volume) did not vary with level of retention, but did vary with pattern: trees in dispersed treatments showed significantly greater diameter growth than those in aggregated treatments (Maguire et al., 2006; Table 1).

3.2.2. Mortality of planted conifers

Patterns of mortality for planted tree seedlings varied among species. Over a period of 5 years, true fir (*Abies magnifica* and *A. procera*) showed significant responses to pattern of retention, with greater mortality in the clearcut areas of aggregated treatments than in dispersed treatments (means of ~11-14% vs. 8-9% of seedlings, respectively; Maguire et al., 2006; Table 1). Ponderosa pine (*Pinus ponderosa*), which is less tolerant of shade, showed a significant response to level of retention, with greater mortality at 40 than at 15% retention (~6% vs. ~3% of seedlings, respectively). Mortality of Douglas-fir seedlings did not vary with either factor.

3.2.3. Forest-floor bryophytes

Forest-floor bryophytes (liverworts and mosses) were highly sensitive to harvest (Dovčiak et al., 2006; Fig. 3, Table 1). First-year declines in cover (Fig. 3a) and species presence (Fig. 3b) were comparably large at 15 and 40% retention. Declines in richness (Fig. 3c) tended to be greater in aggregated than in dispersed treatments, but differences were not statistically significant (Table 1). Cover and/or richness were negatively correlated with level of soil disturbance and logging slash, but positively correlated with cover of residual herbs and shrubs.

3.2.4. Vascular plants

Initial (first- and second-year) changes in the composition of understory plant communities were greater at 15 than at 40% retention, but were comparable in aggregated and dispersed treatments (Halpern et al., 2005; Table 1). Despite substantial changes in overstory structure, early seral species contributed minimally to vegetation cover and diversity (consistent with low levels of soil disturbance and abundant slash). Level of retention had a significant and predictable effect on height of the shrub layer, and on loss of diversity among forest generalist and late-seral plant species (Table 1). However, pattern of retention had little effect on most measures of understory response. Changes were small within forest aggregates, but large in adjacent harvested areas; declines in dispersed treatments were intermediate to these. Late-seral herbs experienced more frequent extirpation from the harvested portions of aggregated treatments than from dispersed treatments (Fig. 4).

3.2.5. Ectomycorrhizal fungi

Production and diversity of fungal sporocarps (mushrooms and truffles) showed high annual and seasonal (fall and spring) variation within the unharvested controls, complicating interpretation of treatment effects (Luoma et al., 2004). Among harvest treatments, declines in diversity and production over 3 years were correlated with intensity of overstory removal, with the greatest reductions at 15% retention (Table 1); responses to pattern of retention were highly variable among retention levels and seasons of sampling.

3.2.6. Canopy and litter-dwelling arthropods

Among a broad diversity of functional groups, canopy arthropods on overstory Douglas-fir and understory vine maple (*Acer circinatum*) showed minimal responses to level or pattern of retention after 2 years (Schowalter et al., 2005; Table 1). Considerably greater variation was observed among blocks and over time in both harvested treatments and controls.

Litter-dwelling predatory arthropods (spiders and carabid beetles) exhibited strong responses to harvest at all levels of retention 5-7 years after treatment (Halaj et al., 2008; Table 1). Spiders associated with open habitats (Lycosidae and Gnaphosidae) were 6-7 times more abundant in harvest treatments than in unharvested controls. In contrast, forest-dependent spiders (Linyphiidae, Hahniidae, and Opiliones) declined by >50% relative to controls. Richness and abundance of carabid beetles were 40-60% lower in harvested treatments than in controls. Responses to level of retention were more subtle: among more than a dozen groups, only three—

all forest-dependent taxa—showed greater reductions at 15 than at 40% retention. Pattern of retention had no effect on any of the arthropod groups considered (Table 1).

3.2.7. Amphibians

Captures of amphibians over a 4-year period (two before and two after harvest) consisted mainly of salamanders (Maguire et al., 2005). Analyses were limited to three species with sufficiently high captures and adequate representation among experimental blocks: ensatina (*Ensatina eschscholtzii*), northwestern salamander (*Ambystoma gracile*), and roughskin newt (*Taricha granulosa*). However, neither level nor pattern of retention influenced their post-harvest abundance (Table 1).

3.2.8. Forest-floor small mammals

Twelve species of small mammals had adequate captures and representation among blocks for statistical analyses; these included early successional species, habitat generalists, and closed-canopy species. For some species, abundance varied significantly with level of retention, but no species responded to pattern of retention (Table 1). The western red-backed vole (*Myodes californicus*), an obligate fungivore of mature forests, responded negatively to overstory removal, decreasing in abundance as harvest intensity increased (Gitzen et al., 2007; Fig. 5, Table 1). In contrast, two open-habitat species, the deer mouse (*Peromyscus maniculatus*) and long-tailed vole (*Microtus longicaudus*), increased with harvest intensity. Other small mammals showed mixed responses, reflecting regional variation in habitat conditions, climate, and community composition. Demographic traits (e.g., sex ratios, age-class distributions, proportion of adult females with evidence of reproduction) did not vary significantly among treatments.

3.3. Effects of level and pattern of retention on public perceptions of variable-retention harvests

Public perceptions of the visual qualities of variable-retention harvests were examined with opinion surveys in which respondents rated the "scenic beauty" of photographs or simulated images of vista views (Ribe, 2005). Responses to level and pattern of retention were complex. Responses to 15% retention were strongly negative, regardless of pattern (Table 1). However, responses to 40 and 75% retention were contingent on pattern. At both levels, ratings of scenic beauty were significantly higher for dispersed than for aggregated treatments (Table 1; Fig. 6).

When photos were accompanied by information on management objectives and expected resource values, perceptions of the "overall acceptability" of different treatments were influenced by several factors (Ribe, 2006). These included value to wildlife and scenic beauty (positively correlated with acceptability), economic/safety-based values (positive, but non-linear relationship), and level of retention (non-linear, but downward-trending at high retention levels). Wildlife value explained most variation in acceptability (47%); the remaining factors each accounted for only 2-7% of the variation. Surveys suggested widespread and passionate opposition to clearcutting, less passionate opposition to 15% retention, and broad acceptability of moderate levels of retention (40-50%), regardless of pattern.

3.4. Ecological integrity of forest aggregates: role as refugia and susceptibility to edge effects

3.4.1. Gradients in soil disturbance, slash accumulation, and microclimate

Harvest-related impacts to forest aggregates were generally small (Nelson and Halpern, 2005a). Exposure of mineral soil was minimal and occurred only within 5 m of the edge. Inputs of logging slash were more frequent, but limited to a distance of 10-15 m from the edge.

Aggregates were characterized by strong gradients in microclimate. Light was elevated at the edge, but declined steeply with distance, particularly along north- and east-facing edges (Heithecker and Halpern, 2007; Table 1, Fig. 7a). The steepest declines occurred within 20 m of the edge; beyond this distance, light levels were generally comparable to those in the unharvested controls. Elevated temperatures (air and soil) extended further into the aggregates than did light, with similarly strong contrasts between NE and SW exposures (Figs. 7b-d). Temperatures within aggregates also tended to be higher than in controls. For all microclimatic variables, the magnitude and depth of edge effects were strongly influenced by forest structure. Where stand density and canopy cover were low, light and temperature remained elevated to the centers of the aggregates and aspect-related differences were small.

3.4.2. Forest-floor bryophytes

Initial (first-year) changes in the abundance or species richness of bryophytes (mosses and liverworts) were generally small within aggregates, but dependent on level of retention. Relative to unharvested controls, richness declined within aggregates at 15% retention (two patches), but not at 40% (five patches; Dovčiak et al., 2006; Table 1). Mosses, as a group, did not show a response to edge (Nelson and Halpern, 2005b; Table 1). However, the richness and cover of liverworts and frequency of *Scapania bolanderi* (one of two common liverwort species), declined significantly with proximity to edge. Declines were correlated with increases in light and cover of logging slash. Edge orientation did not influence the magnitude of decline.

3.4.3. Vascular plants

Initial (first- and second-year) changes in the frequency or cover of forest herbs and shrubs were generally small within aggregates (Halpern et al., 2005; Nelson and Halpern, 2005a; Table 1). Aggregates were also resistant to invasion by early seral species (Nelson and Halpern, 2005a). However, changes in species composition and richness were highly correlated with proximity to edge. The strength of these relationships increased over time: of 23 herbaceous species with sufficient abundance for analysis, 13% in year 1 and 35% in year 2 showed significant declines in cover with proximity to edge (Table 1). Declines were correlated with increases in light and cover of logging slash. In contrast, shrubs showed little sensitivity to edge.

3.4.4. Canopy and litter-dwelling arthropods

None of the primary functional groups of canopy arthropods, either on Douglas-fir or vine maple, showed a consistent response to edge (i.e., difference in abundance between edge and interior trees within forest aggregates; Schowalter et al., 2005; Table 1). Several individual taxa were more common at edge or interior positions, although these positional effects were sometimes dependent on season of sampling or treatment context (i.e., level of retention).

Aggregates retained the full suite of forest-associated, litter-dwelling arthropods, but their abundance and richness were significantly reduced relative to unharvested controls (Halaj et al., 2008; Table 1). Declines reflected strong responses to edge among forest-dependent spiders (Linyphiidae, Hahniidae, and Opiliones; Fig. 8a) and carabid beetles (Fig. 8b) (Table 1). Edge effects were also indicated by the incursion of spiders associated with open or xeric conditions (Gnaphosidae and Lycosidae, Figs. 8c-d).

4. Discussion

A unique and important feature of the DEMO experiment is that it permits clear separation of the effects of level and pattern of retention in shaping biological responses to changes in forest structure. These effects are often confounded in comparative or experimental studies of green-tree retention, or of more conventional regeneration harvests, making it difficult to isolate the elements of forest structure to which organisms are responding. In a meta-analysis of 34 studies, Rosenvald and Lõhmus (2008) were unable to identify consistent relationships between level or pattern of retention and relative changes in species richness or abundance. In contrast, the

DEMO experiment allows for strong inferences about the effects of retention level and pattern, the efficacy of 1-ha aggregates as refugia for forest-dependent taxa, and the elements of forest structure and changes in the physical environment that underlie biological responses.

4.1. Effects of level and pattern of retention on ecological responses

In the short term, biological responses to most silvicultural treatments are shaped by the severity of disturbance and resulting changes in the physical environment (e.g., Hungerford and Babbitt, 1987; Roberts and Gilliam, 1995; Fleming and Baldwin, 2008; Sullivan et al., 2008). For ground-dwelling organisms, responses to level of retention are unlikely to have been driven by variation in soil disturbance, given the uniformly low levels of disturbed soil among treatments. However, greater accumulations of slash at lower retention may have contributed to declines of some taxa, particular those susceptible to burial (bryophytes and late-seral herbs). At the same time, relatively deep slash accumulations are likely to have limited the establishment of early seral plant species (Halpern et al., 2005). In situations where slash loadings are excessive and require subsequent treatment with fire (e.g., broadcast or under-burning), initial responses to retention harvest may differ for taxa that are strongly influenced by fire.

A primary motivation for retaining live trees within harvest units is to reduce extremes in light, temperature, and associated stresses (Franklin et al., 1997; Vanha-Majamaa and Jalonen, 2001), yet surprisingly few studies have explicitly quantified these effects in the context of retention harvests (but see Barg and Edmonds, 1999; Chen et al., 1999, Zheng et al., 2000; Drever and Lertzman, 2003). Measurements of summer microclimate suggest surprisingly small variation among the levels of dispersed retention tested. Although residual trees significantly reduced penetration of solar radiation, even moderate levels of retention (40%) had relatively small effects on air and soil temperatures (and none on soil moisture). Moreover, at 15%

retention, the minimum standard on federal forests in the PNW, microclimatic conditions were no different from those in the clearcut areas of aggregated treatments. Although low densities of dispersed trees may provide direct benefits to species that require them for nesting, foraging, or dispersal (e.g., Hansen et al., 1995), their role in moderation of the physical environment is likely to be very limited. For taxa that are particularly sensitive to changes in temperature or humidity, even high levels of dispersed retention may be inadequate, and persistence within harvest units may be limited to the centers of relatively large (≥1.0 ha), intact forest patches.

As expected, for many (but not all) taxa considered to be sensitive to disturbance or environmental stress, all levels of timber harvest resulted in large declines in abundance, diversity, or performance. However, responses to the retention gradient varied markedly among groups. For some taxa (e.g., ectomycorrhizal fungi and late-seral herbs), declines were proportional to the level of overstory removal. This may reflect the role of trees as carbon sources for mycorrhizal fungi, or in providing shade for species sensitive to large increases in solar radiation (e.g., shade-dependent forest herbs; Pearcy and Sims, 1994; Nelson et al., 2007). For more sensitive forest organisms (e.g., forest-floor bryophytes, predatory litter-dwelling arthropods, western red-backed vole), reductions in abundance or diversity were comparably large at both low and moderate levels of retention. For these taxa, physical conditions (e.g., excessive accumulations of slash), physiological stresses (e.g., extremes in temperature or humidity), or reductions in substrate quality (e.g., of decayed wood) may exceed thresholds for persistence even at moderate levels of retention (e.g., Söderström, 1988; Hannerz and Hånell, 1997; Jalonen and Vanha-Majamaa, 2001; Fenton et al., 2003; Newmaster et al., 2003).

For some taxa, including canopy arthropods, most forest-associated small mammals, and salamanders, responses to harvest were not detected, regardless of retention level. Several factors may explain the absence of treatment effects. Canopy arthropods may be more sensitive to regional gradients in environmental conditions (Progar and Schowalter, 2002) or temporal variation in weather than to disturbance or changes in forest structure (Schowalter et al., 2005). For some species of small mammals, retention levels as low as or lower than 15% may be sufficient to maintain populations (e.g., Sullivan and Sullivan, 2001; Moses and Boutin, 2001). Alternatively, small mammals can exhibit strong annual fluctuations in abundance (Ostfeld, 1988) that mask more subtle treatment effects. Declines can also be delayed if disturbance results in short-term increases in food resources (inputs of seeds or invertebrates) or enhancement of habitat elements (e.g., accumulations of slash and CWD) that compensate for overstory removal (Kirkland, 1990; Gitzen et al., 2007). For salamanders, which are relatively long-lived, sedentary, and occupy forest-floor and below-ground microhabitats that are buffered from environmental stresses, the effects of varying levels of retention may become apparent only after initial populations turn over (Lehmkuhl et al., 1999; Maguire et al., 2005).

Contrary to initial expectations (Halpern and Raphael, 1999), pattern of retention had little effect on the treatment-level responses of most groups of forest organisms. This counterintuitive result may be due to the heterogeneous nature of aggregated treatments. Although changes within the forest patches were minimal, changes in adjacent clearcut areas were greater than those in corresponding dispersed treatments (e.g., Halpern et al., 2005; Dovčiak et al., 2006). Thus, on average, treatment-scale responses were similar. Pattern of retention did, however, have a significant effect on several aspects of structure and dynamics in the overstory. Bole damage was considerably greater in dispersed than in aggregated treatments, reflecting the greater intensity and wider dispersion of felling and yarding activities. This may have longer term consequences for growth, wood quality, and risk of mortality (Moore et al., 2002; Thorpe et al., 2008). However, negative effects on wood volume were not readily apparent—growth rates were significantly higher for trees in dispersed settings. Greater volume growth in dispersed treatments may reflect the greater representation of dominant and co-dominant crown classes and the more uniform distribution of stems with greater access to light and soil resources.

One of the more striking and ecologically significant effects of retention pattern was seen in the post-harvest mortality of remnant trees. Rates of mortality were consistently low in aggregated treatments and at moderate levels of dispersed retention (comparable to background levels in the controls), but were highly elevated at low levels of dispersed retention. Many factors (both extrinsic and intrinsic) can contribute to accelerated rates of mortality following partial canopy removal, and these increases have been observed when trees are retained as dispersed individuals or in clumps (e.g., Esseen, 1994; Coates, 1997; Scott and Mitchell, 2005; Thorpe et al., 2008). Although stem breakage and uprooting tend to increase with harvest intensity and dispersion of residual trees, mortality rates are also affected by initial structure, topography, and species composition (e.g., Thorpe and Thomas, 2007). Our short-term results are consistent with previous observations, but provide clear evidence of the interaction between level and pattern of retention in these forests. At moderate levels of retention (e.g., 40%), stands are resistant to wind damage regardless of the spatial arrangement of stems; however, below a certain threshold level (15% or possibly higher), the potential for wind damage can be unacceptably high in dispersed settings.

4.2. Effects of level and pattern of retention on public perceptions

Public perceptions of retention harvests were also influenced by level and pattern of retention, but responses to residual forest structure were complex. Aggregated treatments were consistently perceived as “ugly.” Negative responses to clearcut areas in aggregated treatments offset potential increases in perceived scenic beauty associated with greater levels of retention and intact forest patches. Dispersed treatments were viewed more favorably, but only if retention was sufficiently high (40%). These results are consistent with studies of public perceptions in British Columbia: harvests with 20-25% dispersed retention had a 50-67% chance of achieving visual-quality objectives (British Columbia Ministry of Forests, 1997).

Although consideration of scenic beauty strongly influenced public perceptions of variable-retention harvests, it was not the only factor, nor the most important one. Wildlife habitat value emerged as the strongest predictor of overall acceptability—scenic beauty, economic and safety considerations, and level of retention contributing to a lesser degree. This result is supported by previous studies suggesting that public perceptions of alternative approaches to forest management are influenced by both the visual qualities of residual stand structures and knowledge of their ecological benefits (Shindler et al., 1996; Burchfield et al., 2003). These findings underscore the importance of educating the public about the ecological benefits and tradeoffs of different levels and patterns of green-tree retention.

4.3. Efficacy of 1-ha forest aggregates as refugia for forest-dependent organisms

For forest aggregates to serve as refugia for taxa sensitive to timber harvest or associated changes in environment, species' habitat and microclimatic requirements must not be compromised by edge effects. Because aggregates were intentionally avoided during felling and yarding, disturbance was minimized and most forest attributes were left intact, including soil and litter layers, woody debris, and herb, shrub, and tree strata. Although air and soil temperatures were elevated 20-40 m from the forest edge, aggregates were sufficiently large (56.4 m radius) in some experimental blocks (those with higher tree densities) to support core areas with microclimates comparable to those of undisturbed controls—an unanticipated result given the general assumption that edge effects are more intrusive (e.g., Chen et al., 1995). In contrast, where forests were characterized by a more open canopy structure, light and temperature were elevated throughout the patch, indicating that forest structure plays an important role in moderating edge effects (e.g., Canham et al., 1990; Matlack 1993; Denyer et al., 2006).

To varying degrees, biological responses were consistent with these changes in microclimate. Although extinctions were uncommon, some groups (e.g., forest-dependent litter-dwelling arthropods and forest-floor liverworts) showed significant reductions in abundance or local richness—patterns driven, in large part, by edge-related declines. However, declines were often limited to a relatively narrow (5-10 m) zone at the forest edge, considerably less than the distances to which temperature remained elevated. These results should be interpreted cautiously, however, as temporal trends for some taxa (e.g., forest herbs) suggest that edge effects may become more pronounced over time, affecting greater numbers of taxa or extending more deeply into forest aggregates (e.g., Baldwin and Bradfield, 2005).

The DEMO experiment does not explicitly address the role of patch size in mitigating effects on forest-dependent taxa. However, edge-related declines within 1-ha aggregates suggest that current retention standards in the PNW which allow for aggregates $\leq$0.2 ha (USDA and USDI, 1994), may be inadequate to maintain the diversity or abundance of some taxa that are sensitive to changes in light, temperature, or humidity. Although small forest fragments can have high conservation value in some landscape contexts (e.g., Shafer, 1995), smaller patches are clearly more vulnerable to edge effects (e.g., Moen and Jonsson, 2003), more prone to wind damage (e.g., Esseen, 1994), and more susceptible to demographic or environmental stochasticity (e.g., Diamond, 1984; Gilpin and Soule, 1986; Hanski and Ovaskainen, 2002). In a variety of forest ecosystems, remnant patches smaller than 1 ha consistently showed declines in the richness or abundance of species dependent on forest-interior environments (e.g., Jalonen and Vanha-Majamaa, 2001; Fenton and Frego, 2005; Baker et al., 2007). Clearly, the potential to retain sensitive species through harvest can be enhanced by increasing the relative size, number, or area of undisturbed forest patches within a harvest unit.

5. Management Implications

Short-term results from the DEMO experiment have important implications for variable-retention practices in the PNW. The current federal standard, which requires retaining live trees in 15% of each harvest unit, does little to achieve the intended goal of microclimatic amelioration; considerably greater levels of retention are needed to effectively reduce solar radiation and air or soil temperatures. Similarly, at minimum levels of dispersed retention, trees are highly susceptible to logging damage and post-harvest windthrow or stem breakage. In contrast, retention of large ($\geq$1 ha) aggregates or at greater densities of dispersion (e.g., 40%), reduces the potential for damage and subsequent mortality, at least in the short term. However, smaller aggregates permitted under the Northwest Forest Plan ($\leq$0.2 ha) may be less stable, given their greater edge-to-area ratios.

For many groups of forest organisms, increasing levels of retention result in greater persistence, abundance, or diversity. However, some taxa, including bryophytes, late-seral herbs, litter arthropods, and the western red-backed vole, are particularly sensitive to microclimatic stress, burial, or other habitat changes, and even moderate levels of retention appear insufficient to prevent declines. Relatively large ($\geq$1 ha) forest aggregates may provide short-term refugia for some of these sensitive taxa, but they are susceptible to edge effects; thus, smaller aggregates are unlikely to provide this function. Within harvest units, pattern of retention had little effect on responses by most forest organisms, but strongly influenced public perceptions of the visual qualities of variable-retention harvests.

The specific objectives of retention harvests in this region, and elsewhere, will vary with local forest structure, species composition, and landscape context. Nevertheless, our results suggest a general strategy for ensuring short-term persistence (and, presumably, long-term recovery) of the vast majority of forest-dependent species, and for gaining public acceptance of green-tree retention for sustaining both the ecological and commodity values of managed forests. This strategy includes a combination of aggregates ≥1 ha in size and dispersed retention at levels considerably greater than current minimum standards. A commitment to monitoring future changes in these stands will be needed to evaluate the long-term contributions of level and pattern of retention to the structural enrichment and biological recovery of regenerating forests.

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Figure captions

Fig. 1. Locations of the six experimental blocks in the DEMO study (CF = Capitol Forest, BU = Butte, PH = Paradise Hills, LW = Little White Salmon, WF = Watson Falls, DP = Dog Prairie), and a schematic representation of the six treatments (retention level vs. pattern) implemented in each block. In the schematic, dark areas represent uncut forest (100 and 75% retention treatments) or 1-ha forest aggregates (15 and 40% retention treatments).

Fig. 2. Mean values (±1 S.E.) of (a) transmitted light (PPFD), (b) air temperature, (c) soil temperature, and (d) soil moisture across a gradient of overstory retention. 0% retention represents the clearcut areas of the 15% aggregated-retention treatment (see Fig. 1). Values for 15 and 40% retention are from dispersed treatments only. *P*-values are from one-way randomized block ANOVAs. Retention levels with different letters differ significantly based on a Tukey HSD test. Modified from Heithecker and Halpern (2006).

Fig. 3. Treatment-level responses (mean +1 S.E.) of bryophytes. (a) Absolute change in percent cover, (b) proportion of species showing declines in frequency, and (c) change in species richness (number of taxa per quadrat array consisting of 24, 0.1 m^2 quadrats). Means for aggregated treatments are calculated as weighted averages of plots from harvested areas and aggregates. *P* values represent the significance of a main effect of treatment in a single-factor randomized block ANOVA. Treatments with different letters differ significantly based on a Tukey HSD test. Modified from Dovčiak et al. (2006).

Fig. 4. Local extinctions of late-seral herbs from all plots within experimental treatments (control or dispersed retention) or environments within treatments (harvest areas or forest aggregates in aggregated retention). Values are means (+1 S.E.; *n* = 6) per experimental treatment or environment within treatment. Numbers of plots vary: 100%, 40%D, and 15%D, *n*

= 32; 40%A aggregates, *n* = 25 (24); 15%A aggregates, *n* = 10; 40%A harvest areas, *n* = 12; 15%A harvest areas, *n* = 22). Modified from Halpern et al. (2005).

Fig. 5. Capture rates for the western red-backed vole before and after harvest treatments. Significance levels are from a randomized-block ANCOVA examining the effect of basal area retention (%BA) on post-treatment captures. The %BA x time interaction tested if the effect was similar in both post-treatment years. Modified from Gitzen et al. (2007).

Fig. 6. Public perceptions of scenic beauty (higher scores correspond to "greater perceived beauty") as a function of level and pattern of retention. Dashed lines represent estimates of the limits of scenic beauty obtained from a larger sample of scenes. Modified from Ribe (2005).

Fig. 7. Examples of microclimatic gradients with distance from the aggregate edge at the Butte experimental block in southern Washington. (a) Transmitted light (PPFD), (b) mean air temperature (1 m above the ground surface), (c) maximum air temperature, and (d) mean soil temperature (15 cm depth). Values are means ($\pm$1 S.E.) at each distance along two transects facing south or west (S/W) and north or east (N/E). Solid horizontal lines are 95% confidence intervals of the mean (*n* = 20) for reference stations in nearby undisturbed forest (100% retention). Modified from Heithecker and Halpern (2007).

Fig. 8. Gradients in abundance (mean +1 S.E.; *n* = 4) of selected groups of spiders and carabid beetles across forest aggregates. (a) Linyphiidae (spiders of interior forest), (b) Carabidae (beetles), (c) Gnaphosidae and (d) Lycosidae (the latter two, spiders of open, xeric conditions). Positions with different letters differ statistically ($p \leq 0.05$) based on a priori contrasts with a Dunn-Sidak multiple-comparison adjustment. Positions codes: Center, aggregate center (56 m from edge), Intmd, intermediate (~15 m from edge), Edge, edge; and Harvest, clearcut area. Modified from Halaj et al. (2008).

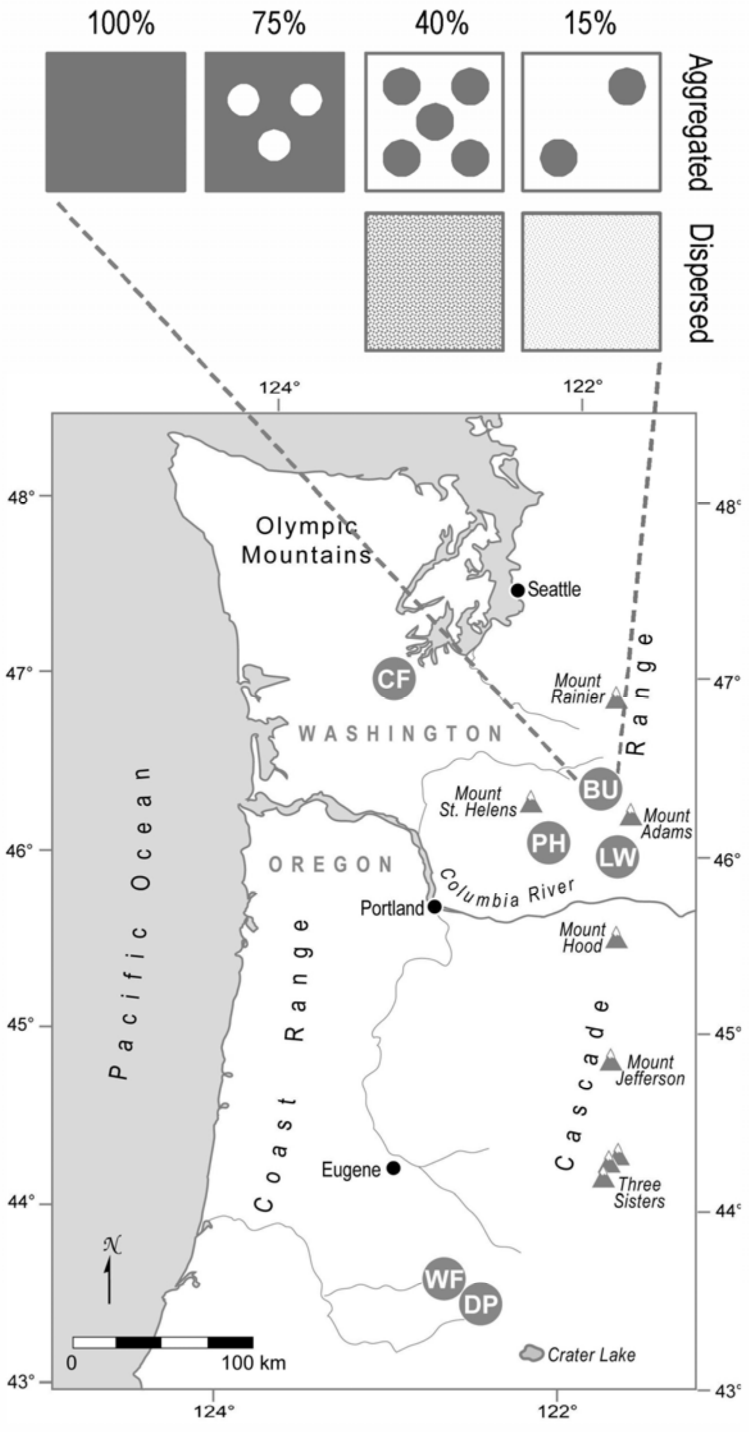

100%
75%
40%
15%
Aggregated
Dispersed
124°
122°
48°
47°
46°
45°
44°
43°
Olympic Mountains
Seattle
CF
Mount Rainier
WASHINGTON
Cascade Range
BU
Mount St. Helens
Mount Adams
PH
LW
OREGON
Columbia River
Portland
Mount Hood
Pacific Ocean
Coast Range
Mount Jefferson
Eugene
Three Sisters
N
WF
DP
Crater Lake
0
100 km

Figure 1.

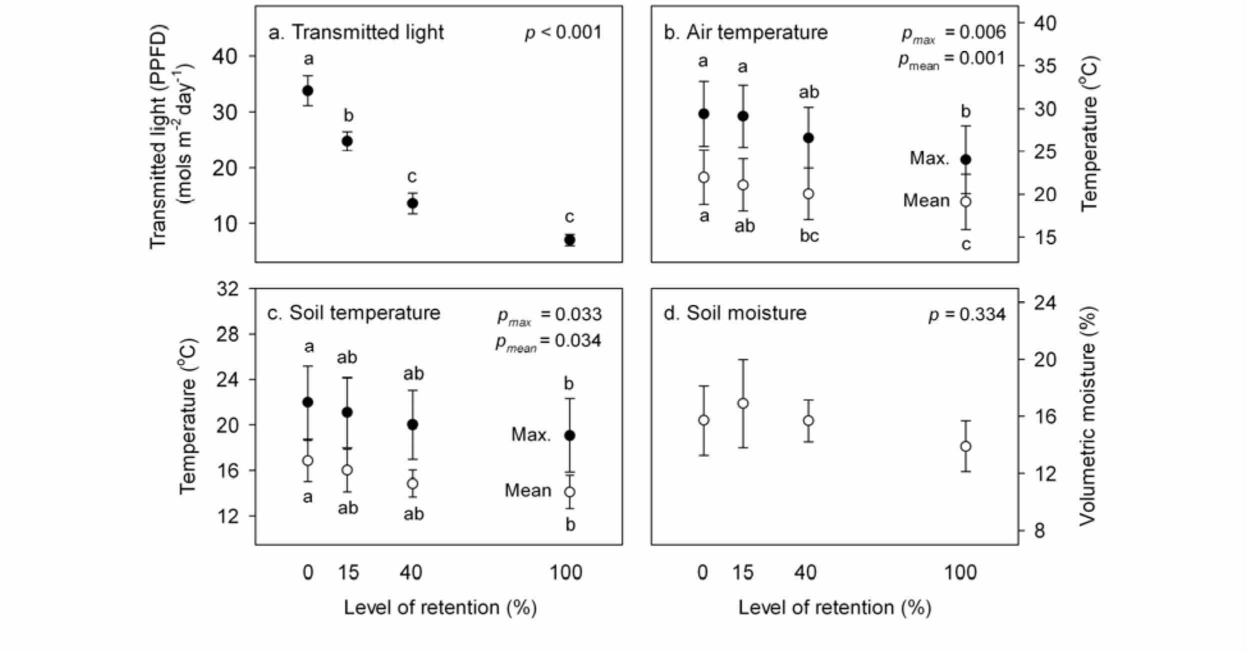

a. Transmitted light
$p < 0.001$
Transmitted light (PPFD)
(mols m^{-2} day^{-1})
40
30
20
10
a
b
c
c
b. Air temperature
p_{max} = 0.006
p_{mean} = 0.001
a
a
ab
b
Max.
Mean
a
ab
bc
c
40
35
30
25
20
15
Temperature (°C)
c. Soil temperature
p_{max} = 0.033
p_{mean} = 0.034
Temperature (°C)
32
28
24
20
16
12
a
ab
ab
b
Max.
Mean
a
ab
ab
b
d. Soil moisture
$p = 0.334$
24
20
16
12
8
Volumetric moisture (%)
0
15
40
100
Level of retention (%)
0
15
40
100
Level of retention (%)

Figure 2.

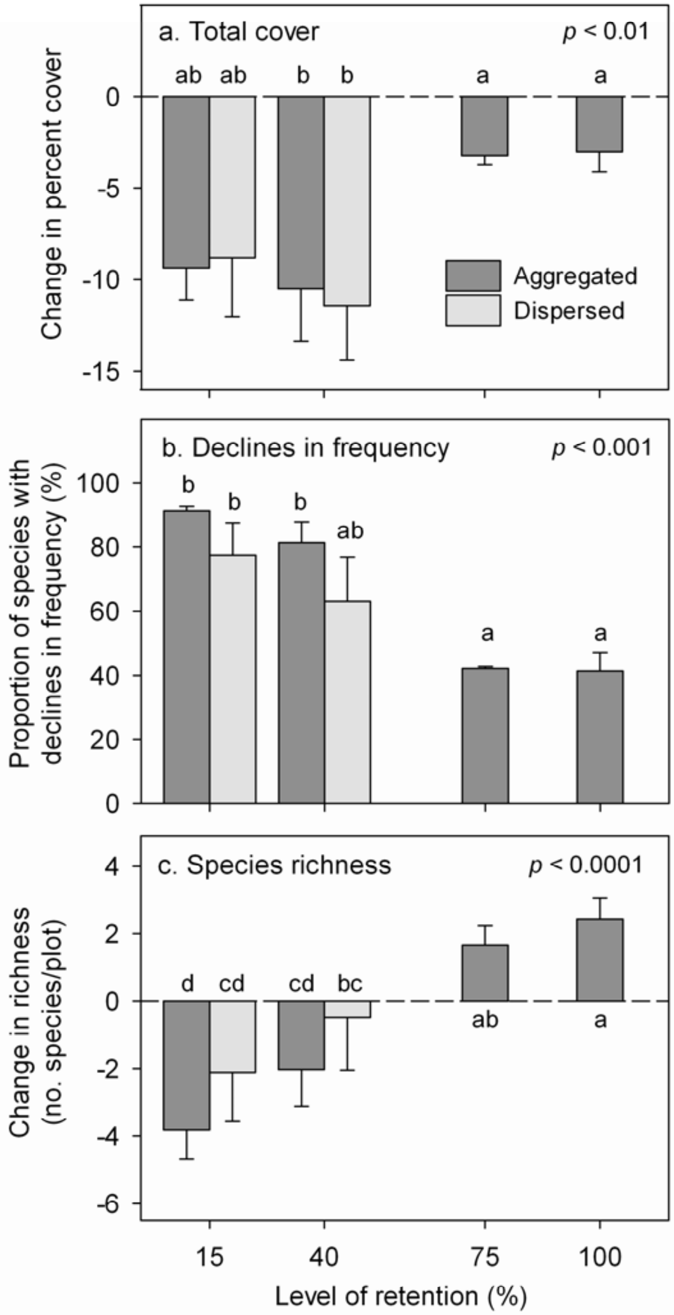

a. Total cover
p < 0.01
Change in percent cover
0
-5
-10
-15
ab
ab
b
b
a
a
Aggregated
Dispersed
b. Declines in frequency
p < 0.001
Proportion of species with declines in frequency (%)
100
80
60
40
20
0
b
b
b
ab
a
a
c. Species richness
p < 0.0001
Change in richness (no. species/plot)
4
2
0
-2
-4
-6
d
cd
cd
bc
ab
a
15
40
75
100
Level of retention (%)

Figure 3.

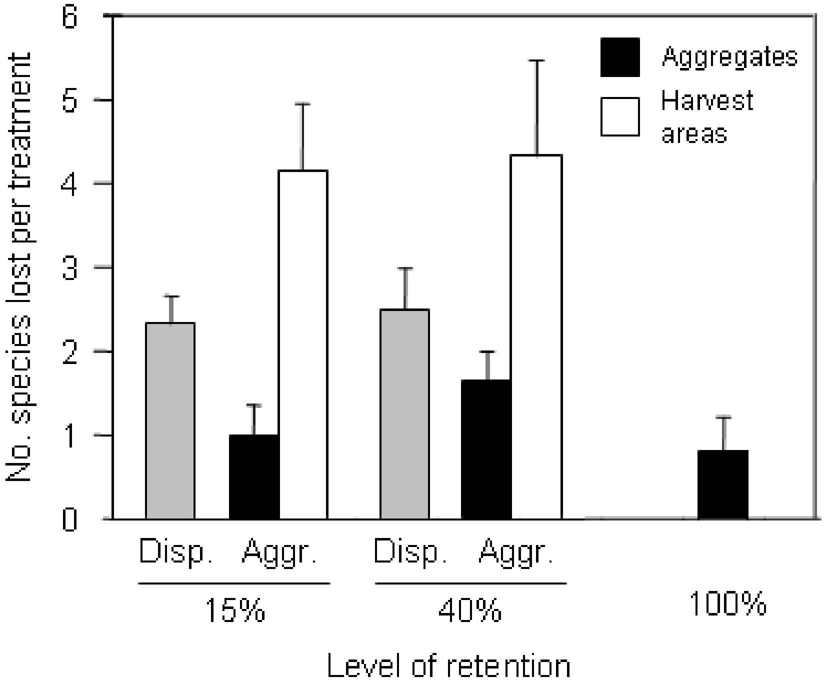

No. species lost per treatment
0
1
2
3
4
5
6
Aggregates
Harvest areas
Disp.
Aggr.
Disp.
Aggr.
15%
40%
100%
Level of retention

Figure 4.

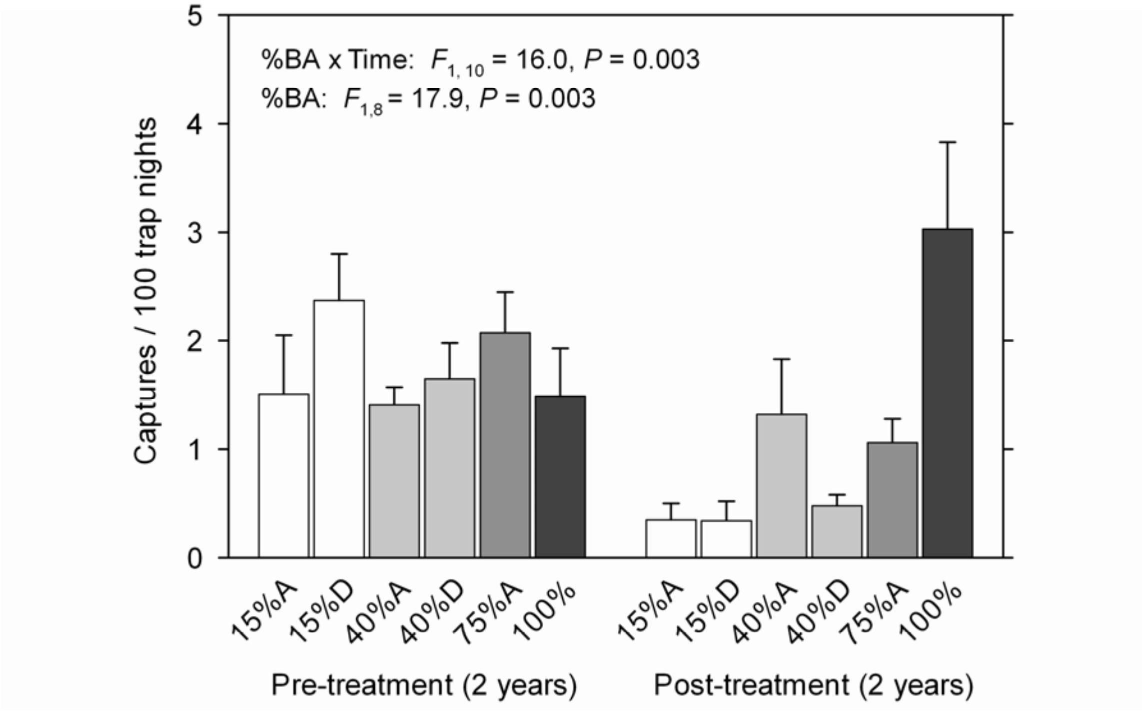
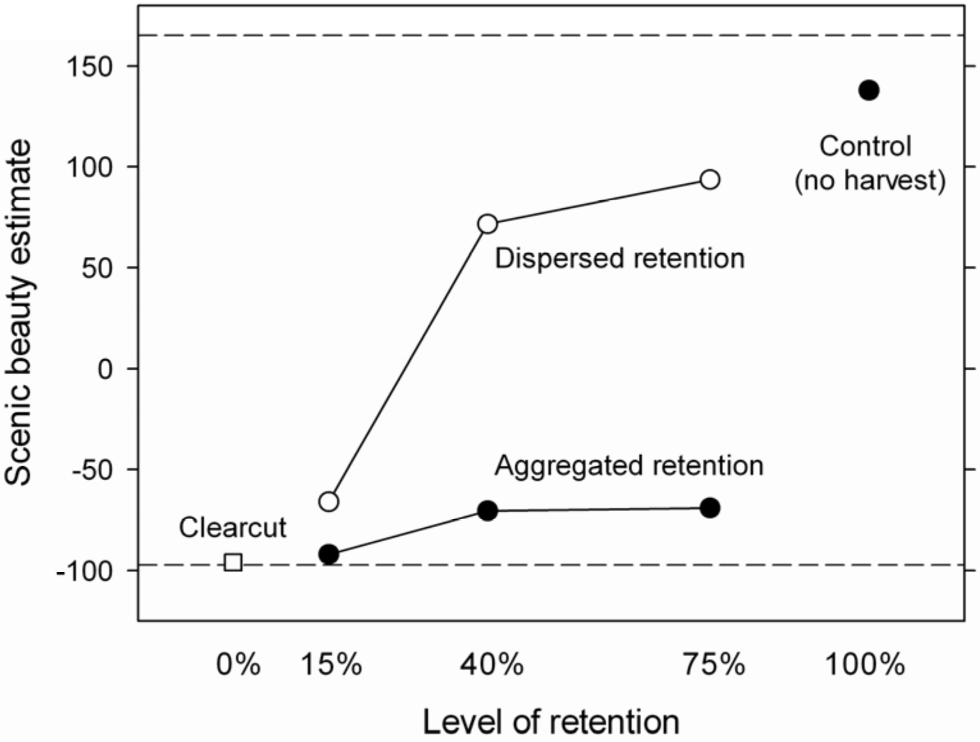

%BA x Time: $F_{1,10}$ = 16.0, P = 0.003
%BA: $F_{1,8}$ = 17.9, P = 0.003
Captures / 100 trap nights
0
1
2
3
4
5
15%A
15%D
40%A
40%D
75%A
100%
15%A
15%D
40%A
40%D
75%A
100%
Pre-treatment (2 years)
Post-treatment (2 years)

Figure 5.



150
100
50
0
-50
-100
Scenic beauty estimate
Control
(no harvest)
Dispersed retention
Aggregated retention
Clearcut
0%
15%
40%
75%
100%
Level of retention

Figure 6.

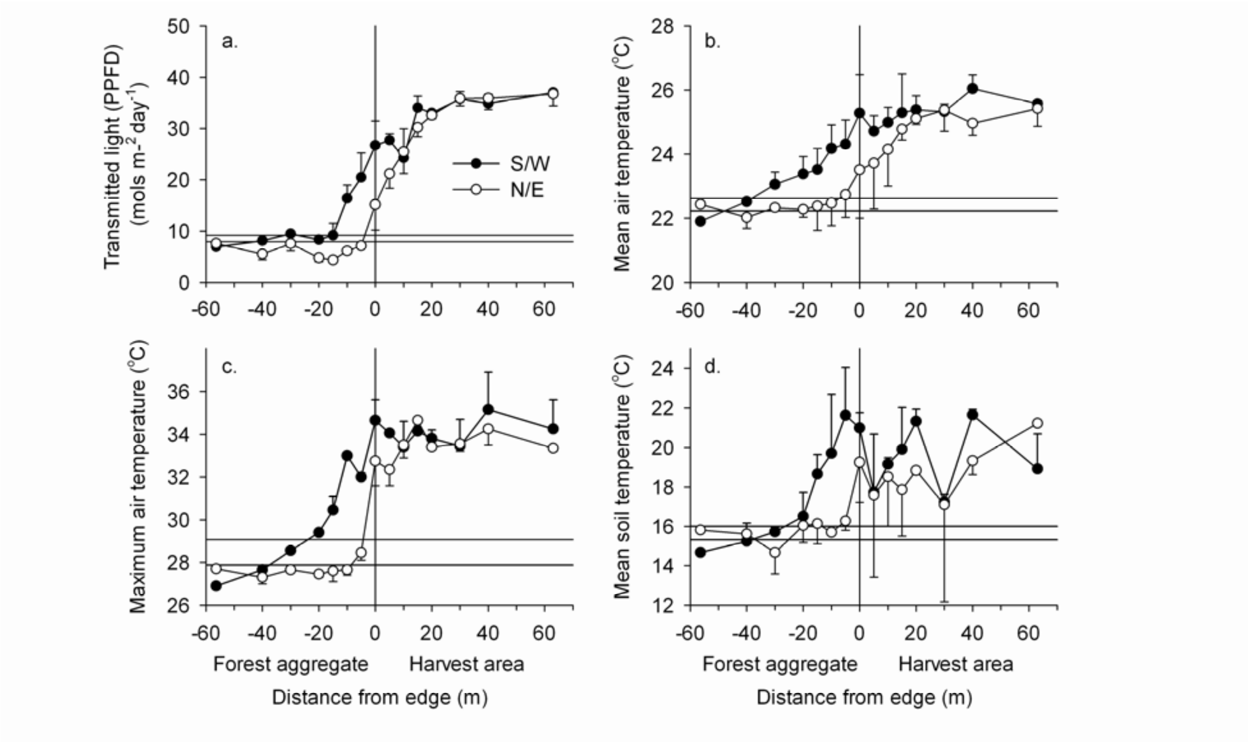

a.
Transmitted light (PPFD) (mols m-2 day-1)
0
10
20
30
40
50
S/W
N/E
b.
Mean air temperature (°C)
20
22
24
26
28
c.
Maximum air temperature (°C)
26
28
30
32
34
36
d.
Mean soil temperature (°C)
12
14
16
18
20
22
24
-60
-40
-20
0
20
40
60
Forest aggregate
Harvest area
Distance from edge (m)

Figure 7.

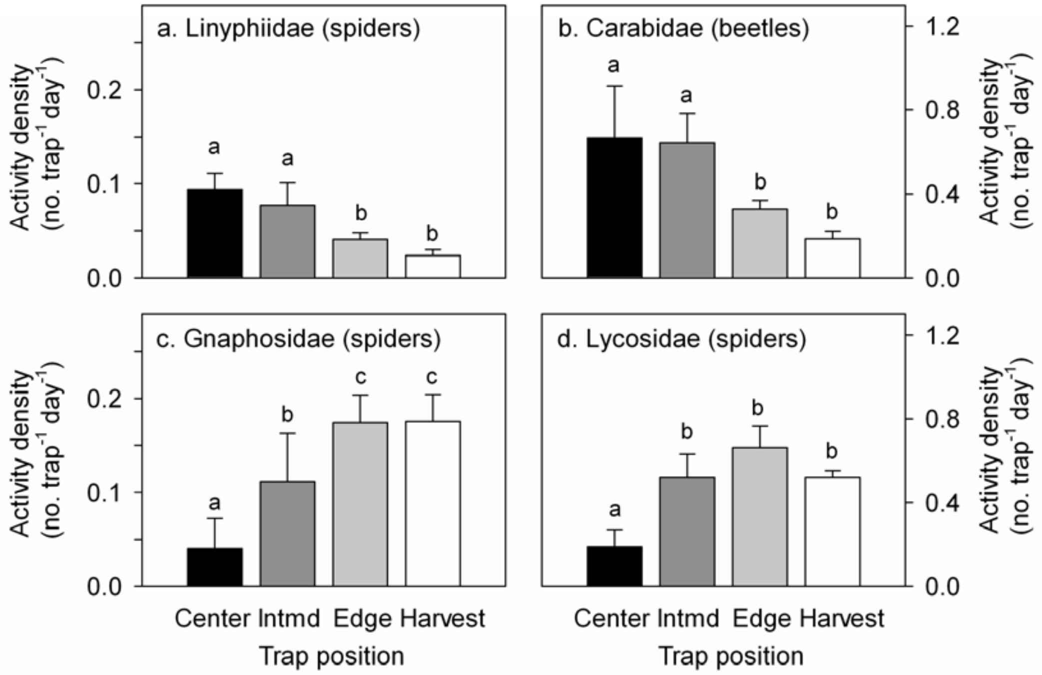

a. Linyphiidae (spiders)
b. Carabidae (beetles)
c. Gnaphosidae (spiders)
d. Lycosidae (spiders)
Activity density (no. trap-1 day-1)
0.0
0.1
0.2
0.4
0.8
1.2
a
b
c
Center
Intmd
Edge
Harvest
Trap position

Figure 8.

Table 1

Summary of responses to level and pattern of retention and the ecological integrity of forest aggregates (role as refugia and susceptibility to edge effects) from component studies of the DEMO experiment.

	Retention[a]		Integrity of aggregates[b]		
Component studies	Level	Pattern	Refugia	Edge effects	Source
Physical environment					
Soil disturbance	N	N	—	Y	Halpern and McKenzie, 2001; Nelson and Halpern, 2005a
Slash accumulation	Y	Y	—	Y	Halpern and McKenzie, 2001; Nelson and Halpern, 2005a
Microclimate	Y	—	—	Y	Heithecker and Halpern, 2006; Heithecker and Halpern, 2007
Biological responses					
Overstory: bole damage	N	Y	—	—	Moore et al., 2002
Overstory: mortality	Y	Y	—	—	Maguire et al., 2006
Overstory: growth	N	Y	—	—	Maguire et al., 2006
Regeneration: mortality[c]	Y	Y	—	—	Maguire et al., 2006
Forest-floor bryophytes	Y	N	Y	Y	Nelson and Halpern, 2005b; Dovčiak et al., 2006
Vascular plants	Y	N	Y	Y	Halpern et al., 2005; Nelson and Halpern, 2005a

Table 1 (Cont.)

	Retention[a]		Integrity of aggregates[b]		
Component studies	Level	Pattern	Refugia	Edge effects	Source
Mycorrhizal fungi	Y	N	—	—	Luoma et al., 2004
Canopy arthropods	N	N	Y	N	Schowalter et al., 2005
Litter-dwelling arthropods	Y	N	Y	Y	Halaj et al., 2008
Amphibians	N	N	—	—	Maguire et al., 2005
Forest-floor small mammals	Y	N	—	—	Gitzen et al., 2007
Public perceptions					
Scenic beauty	Y	Y	—	—	Ribe, 2005
Overall acceptability	Y	N	—	—	Ribe, 2006

[a] ‘Y’ (Yes) indicates that many of the variables tested showed significant responses to level or pattern of retention; ‘N’ (No) indicates that significant responses to level or pattern of retention were rare or absent; ‘—’ indicates not tested.

[b] ‘Y’ (Yes) indicates that aggregates served as refugia for forest-associated species or that edge effects were detected; ‘N’ (No) indicates that aggregates did not serve as refugia for forest-associated species, or that no edge effects were detected; ‘—’ indicates not applicable or not tested.

[c] Planted conifers (harvested areas only).