Retention level affects dynamics of understory plant community recovery in northern temperate hemlock-cedar forests

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ABSTRACT
Retention forestry is replacing clear-cutting as the dominant silvicultural practice in many parts of the world. Higher retention levels are thought to promote faster, more complete ecological recovery after logging, but this hypothesis is insufficiently tested. We compared plant community dynamics in 0%, 40% and 70% retention stands to unharvested stands for 24 years after logging at the Date Creek Research Forest near Kispiox, BC, Canada. The study has a before-after control-impact experimental design with four replicates of each treatment. For terricolous understory plants, we used the similarity of cover, species richness and composition to pre-harvest and unharvested conditions as indicators of ecological integrity. Changes in cover, richness and composition were greatest at 0% retention. For nonvascular plants, changes were generally intermediate at 40% retention and smallest at 70% retention, and recovery increased with retention. The dominant moss Hylocomium splendens responded negatively to harvest in proportion to retention level, while most other species responded positively, shifting community composition. Most vascular plants responded positively to harvest, especially at 0% retention, with the exception of two late seral species, Platanthera orbiculata and Oplopanax horridus. Generally, understory communities in these largely unfragmented northern cedar-hemlock forests displayed less sensitivity to low retention levels than studies conducted elsewhere. For some vascular plant indicators, changes at 70% retention were equal to or greater than those at 40%. Thus, most-but not all-vegetation responses supported the hypothesis that higher retention enhances ecological recovery after logging. The non-linear results were apparently driven by suppression of understory conifer growth in small gaps at 70% retention and illustrate that evaluating ecological integrity strictly in terms of departure from an un-impacted benchmark system risks oversimplifying complex forest dynamics.

1. Introduction
New conceptual and multidisciplinary approaches are proposed to manage the structure and dynamics of forest ecosystems to promote their long-term productivity, biodiversity and adaptability (Puetzmann et al., 2009; Messier et al., 2013). Retention forestry is an approach that focuses on the type and quantity of forest structures left behind during logging operations to maintain identified ecological, social and economic values (Gustafsson et al., 2012; Lindenmayer et al., 2012; Fedrowitz et al., 2014). How forest ecosystem attributes and functions change and recover after different frequencies and intensities of canopy removal is still under investigation. Hypothesized benefits of retaining some canopy trees during logging are reduced negative effects of harvest on forest specialist species and faster ecological recovery after harvest compared to clear-cutting (Gustafsson et al., 2012; Fedrowitz et al., 2014), but few well-designed studies have existed for long enough to determine rates of recovery. In a recent meta-analysis of 78 studies, more than 70% were five years or less in duration (Fedrowitz et al., 2014).

The Date Creek Experimental Forest in northwestern British Columbia (BC), Canada (Coates and Burton, 1997) offers an excellent opportunity to test whether retention forestry lessens effects of harvest and hastens ecological recovery. Four replicates of three retention levels and an unharvested control (0%, 40%, 70% and 100% retention) were applied to ~20 ha treatment units in 1992. Potentially confounding environmental effects (Lindenmayer and Laurance, 2012) were minimized using a randomized complete block design. The understory plant community was measured pre-harvest and regularly for
24 years post-harvest, creating a strong before-after control-impact (BACI) experimental design with one of the longest datasets in North America, including measurements of light availability over time. Here, we use the long-term response of the understory plant community as an indicator of ecological integrity, defined as departure from the condition of an un-impacted benchmark system (Haessler and Kneeshaw, 2003). We compare the dynamics of understory tree, vascular and nonvascular plant functional groups and species at three retention levels and evaluate whether the vegetation remains closer to, and recovers more quickly to pre-harvest and unharvested conditions at higher levels of canopy retention.

Although few large scale forestry experiments have tracked the recovery of plant communities for as long as Date Creek, much knowledge about understory responses to logging has been acquired over shorter time frames or by using the chronosequence approach. Logging creates a stressful microclimate for understory plants acclimated to mature closed forest canopies, including higher understory light levels, greater air and soil temperature and moisture fluctuations (Heithecker and Halpern, 2006) and abrupt changes in soil nutrients and microbiota (Brundrett, 1991; Prescott, 2002). Higher levels of retention ameliorate these stresses (Heithecker and Halpern, 2006; Caners et al., 2013b), reducing the magnitude of understory change (Craig and Macdonald, 2009). As tree seedlings and saplings replace harvested trees, the micromlate approaches mature forest conditions and understory vascular plants recover to near undisturbed levels in some forests (Halpern and Spies, 1995). Although logging impacts are short-lived for many temperate forest plants and species richness is often higher in managed forests (Boch et al., 2013), species composition can be substantially or permanently altered by traditional clear-cut logging (Haessler et al., 2002).

Life history or functional traits of plant species can help to predict their differing responses to harvest and recovery over time (Lavelle and Garnier, 2002). We expect early seral species with little or no presence in undisturbed forest to quickly increase after disturbance (Halpern, 1989), then to decline as light and nutrient availability decline. Most forest generalist species can survive disturbances ranging from 40% retention (Zenner et al., 2012) to full clear-cut logging and burning (Halpern 1989) and respond positively to the new environment (Bond and Midgley, 2001). We expect forest generalists to increase after harvest but to lag behind early seral species in recovery due to greater tolerance of diminishing resource availability. Sensitive late seral species are reduced in cover or extirpated in the forest generalist community (Halpern et al., 2005), and we expect negligible to slow recovery times (Craig and Macdonald, 2009) and not return to unharvested forest conditions.

Shrubs in composition can also occur between life forms that differ in response to disturbance. In the understory of northern temperate forests a carpet of feather moss impedes establishment of tree seedlings. Partial logging can reduce feather moss cover and allow tree seedling germination (LePage et al., 2000) because most bryophytes are more sensitive to overstory removal than most vascular plants (Frego, 2007). Within bryophytes, mosses are less sensitive than liverworts (Bartels et al., 2017), but both groups contain sensitive species that persist only in intact forests, as well as species that thrive after disturbance (Caners et al., 2013b). Based on the hypothesis that retention increases ecological integrity, we expect retention to have a stronger stabilizing effect on nonvascular plants than on vascular plants, and to have the strongest stabilizing effect on liverworts.

We used a conceptual model to simplify interpretations of plant community dynamics, identifying four alternative responses to harvest that support the hypothesis that retention maintains ecological integrity via a stabilizing effect (the retention-stability hypothesis; Fig. 1). A positive response to harvest with recovery occurs when an indicator increases as retention decreases, then returns to pre-harvest (or unharvested) levels over time (Fig. 1a). Retention has a stabilizing effect if the peak of change (largest departure from pre-harvest levels) or recovery time (length of time the indicator remains different from pre-harvest levels) are reduced at higher retention levels. A positive response to harvest without recovery occurs when an indicator increases with decreasing retention but remains at an elevated level (Fig. 1b). A negative response with recovery (Fig. 1c) and a negative response without recovery (Fig. 1d) occur when an indicator decreases with decreasing retention, but otherwise correspond to the respective positive responses. “Without recovery” scenarios (1b and 1d) could represent indicators that require more time to recover, or are irrevocably shifted because a threshold has been passed.

2. Methods

2.1. Study area

This study of understory plant community responses was a component of the larger 4000 ha Date Creek Silvicultural Systems Experiment (55° 22’ N, 127° 50’ W) located 21 km north of Hazelton in northwestern BC (Coates et al., 1997). It was established in 1992 to meet timber production goals while also retaining live trees, snags or logs that serve important ecological functions in post-harvest stands. The study area was located within the moist cold subzone of the Interior Cedar-Hemlock biogeoclimatic zone, a transitional zone between interior and coastal forest ecosystems lying at the northern temperate forest limit (Banner et al., 1993). Between 370 and 665 m in elevation, the area averages 535 mm annual precipitation (238 mm during the growing season) and has a mean annual temperature of 4.4 °C. Morainal parent materials with loamy sand to clay loam textures are dominant. Soils are Eluviated Dystric Brunisols, Orthic Brunisols and Orthic Humo-Ferric Podzols (Soil Classification Working Group, 1998) with 4–14 cm thick forest floors layers.

Treatment units were located in mature stands dating from an 1885 fire and in old-growth stands aged ≥ 350 years. The ~140 year old mature stands were dominated by western hemlock (Tsuga heterophylla, 65% of stand basal area), western red-cedar (Thuja plicata, 18% basal area) and hybrid spruce (a complex of Picea glauca, Picea stichensis and Picea engelmannii, 8% basal area) with six minor tree species: subalpine fir (Abies lasiocarpa), amabilis fir (Abies amabilis), lodgepole pine (Pinus contorta var. latifolia), paper birch (Betula papyrifera), trembling aspen (Populus tremuloides) and black cottonwood (Populus balsamifera ssp. trichocarpa) (plant nomenclature follows MacKenzie et al. 2016; authorities are in Appendix A). Old growth stands lacked pine, birch, aspen and cottonwood, and were dominated by western hemlock (81% basal area), with minor western red-cedar, amabilis fir, subalpine fir and hybrid spruce. Understories had a thick growth of feather mosses (80% cover), Pleurozium schreberi, Hlycochonium splendens, Ptitum cris- castrensis and Rhytidiadelphus spp. The sparse shrub and herb layers (4–8% cover) had scattered oval-leaved blueberry (Vaccinium ovalifo- lium), Alaskan blueberry (V. alaskaena), black huckleberry (V. membranaceum), bunchberry (Cornus canadensis), five-leaved bramble (Rubus pedatus), one-sided wintergreen (Orthilia secunda) and prince’s pine (Chimaphila umbellata). Wetter sites had devil’s club (Oplopanax horridus), black gooseberry (Ribes lacustre), highbush-cranberry (Viburnum edule), oak fern (Gymnocarpium dryopteris), lady fern (Athyrium filix-femina) and leafy mosses (Mniaceae spp.).

2.2. Experimental design and treatments

Three logging treatments were applied at Date Creek and compared to unharvested forest: 0% (clear-cut) retention, 40% retention and 70% retention (Table 1). All conifer trees were removed in the 0% retention treatment. A few scattered aspen and birch were retained, and very few