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Site Preparation Severity influences Lodgepole Pine Plant Community Composition, Diversity and Succession over 25 years

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Abstract

Lodgepole pine ecosystems of central British Columbia face cumulative stresses and management practices are increasingly scrutinized. We addressed tradeoffs between “light-on-the-land” versus more aggressive silvicultural approaches by examining plant communities and indicator species (non-natives, berry-producers, epiphytes, mycotrophs, pine rust alternate hosts) across a gradient of 5-6 site preparation treatments at the Bednesti trial (established 1987). We tested whether more severe site preparation (1) caused plant community composition to diverge from a 35-46-yr-old reference forest; (2) accelerated succession by hastening crown closure; or (3) delayed succession by promoting seral species. Non-metric multi-dimensional scaling (NMDS) ordination showed all treatments converging toward the reference forest composition. At 10 yr, succession was incrementally delayed by more severe treatments; at 25 yr, only burned windrows were still delayed. Mixed effects models based on site preparation severity were better than crown closure models for 11 of 13 variables tested, suggesting belowground processes mostly drive succession in these infertile ecosystems. Invasive hawkweeds persisted on all treatments at 25 yr. Limited, contradictory data did not support using mechanical or fire treatments to reduce alternate hosts of pine stem rusts. Long-term trials like Bednesti highlight the need for ecosystem-specific strategies and diverse approaches to accommodate conflicting benefits and risks of disturbance in forests.

Key words: silviculture, biodiversity, ecological disturbance, invasive species, *Pinus contorta*

Introduction

Lodgepole pine (*Pinus contorta* var. *latifolia*) forests dominate the plateau landscape of the central interior of British Columbia (BC), Canada. Over the past 50 yr this landscape has come to represent the heartland of BC's forest industry as lodgepole pine supplanted Douglas-fir (*Pseudotsuga menziesii*) and interior spruce (*Picea glauca* x *engelmannii*) as the dominant tree harvested and replanted¹. Formerly, silviculturists viewed lodgepole pine ecosystems as resilient and relatively problem-free. This perception has changed in the 21st Century as BC's great mountain pine beetle (*Dendroctonus ponderosae*) outbreak (Shore et al. 2004) coincided with other stresses on lodgepole pine forests, including a growing incidence of stem and foliar diseases (Woods et al. 2017), large wildfires (Ghoussoub 2017) and timber supply shortages (Burton 2010), as well as regional declines in woodland caribou (*Rangifer tarandus caribou*) populations (Cichowski and Williston 2005). One outcome of the confluence of forest management challenges is that silvicultural practices in lodgepole pine forests are now subject to increased professional and public scrutiny.

We revisited the Bednesti experiment, a 25-yr old well-replicated, randomized silvicultural site preparation trial established in 1987 on an infertile upland site typical of central BC (Bedford and Sutton 2000). Its objective was to improve understanding of biological and management factors affecting lodgepole pine establishment and growth, and to devise management strategies to improve productivity, principally through use of mechanical site preparation equipment. Our current study examines the composition, diversity and dynamics of plant communities (vascular plants, bryophytes, macrolichens) in the experiment and an adjacent unmanaged reference forest with the aim of addressing tradeoffs in managing timber and non-timber resources in these increasingly stressed forest ecosystems.

The replicated, randomized design and range of alternative forest disturbances included at Bednesti and a partner study site in northeast BC have provided outstanding opportunities to explore questions related to resilience and restoration success in northern forests (Haeussler et al. 1999, 2002, 2004). Here, we explore

¹Province of BC RESULTS database (unpubl. data 1953-2014) indicates that lodgepole pine reforestation exceeded Douglas-fir in 1980 and interior spruce in 1995, currently accounting for 30% of total provincial planting.

how initial disturbance severity interacts with subsequent tree growth and crown closure to influence community composition and diversity, as well as the abundance of culturally and ecologically significant plants (edible berries, epiphytes, late seral herbs) or plants that pose risks to biodiversity and forest health. The latter include invasive non-native plants –notably hawkweeds of the *Pilosella* subgenus (Wilson 2006), and alternate (telial) hosts of two rusts that kill and damage lodgepole pine, comandra blister rust (*Cronartium comandrae*) and stalactiform blister rust (*Cronartium coleosporioides*) whose respective alternate hosts in central BC are false toadflax (*Geocaulon lividum*) and herbs of the broomrape family (Orobanchaceae).

We proposed three alternative hypotheses regarding successional trajectories:

H1: Silvicultural site preparation alters lodgepole pine plant community successional trajectories, causing higher severity treatments to diverge in composition from lower severity treatments and older reference forests between 10 and 25 years, indicating lack of ecological resilience (Holling 1973).

H2: Silvicultural site preparation does not cause successional trajectories to diverge, rather it accelerates the rate of convergence toward reference forest composition on high severity treatments compared to low severity treatments by increasing tree size and crown closure, thereby speeding replacement of early seral by late seral species.

H3: Silvicultural site preparation does not cause successional trajectories to diverge, rather it delays succession toward reference forest composition on higher severity treatments by creating favourable conditions for establishment and persistence of early seral species, delaying their replacement by late seral species.

For indicator plants, we anticipated that the range of treatment severities in the study would create both benefits and risks for forest managers (i.e., tradeoffs) that are better evaluated over a successional trajectory than at a single point in time.

Methods

Bednesti study area: Bednesti (53°52'N, 123°29'W, 825 m elev.) is located in central BC, 50 km west of

Prince George, in the dry, warm subzone of the Sub-Boreal Spruce biogeoclimatic zone and is intermediate between the Lodgepole Pine-Black Spruce-Feathermoss (SBSdw3/05) and Interior Spruce-Pink Spirea-Prickly Rose (SBSdw3/01) site series (DeLong et al. 1993). Estimated mean annual temperature is 3.4°C with 595 mm precipitation and 231 mm snow (Wang et al. 2012). The gently undulating terrain (<10% slope) is a compact basal till with scattered pockets of sand and gravel. Soils are Podzolic to Brunisolic Gray Luvisols with 3-6 cm thick organic horizons (LFH) (Soil Classification Working Group 1998), sandy loam to silt loam surface texture and 10-65% coarse fragments. A compact horizon at 10-50 cm depth restricts tree rooting, causing soils to be excessively wet in spring and drought prone in late summer

The sub-boreal plateau of central BC has a history of stand-replacing wildfires with 80-125 yr return intervals (DeLong and Tanner 1996) and recurrent outbreaks of mountain pine beetle. Cattle graze widely, but the study site was not regularly or recently grazed due to sparse forage. The primary human use was most likely blueberry-picking. In 1960, Bednesti supported mature wildfire-origin lodgepole pine with a subcanopy of black spruce (*Picea mariana*) and interior spruce. The understory was dominated by velvet-leaved blueberry (*Vaccinium myrtilloides*), bunchberry (*Cornus canadensis*) and red-stemmed feathermoss (*Pleurozium schreberi*). It was strip logged in 1963-64. Leave strips were removed in 1971. A 1986 survey found insufficient conifer stocking.

Experimental design and treatments: Vegetation was sheared and piled in long windrows with a brush blade mounted on a D8 crawler tractor in winter 1986-87. Snowpacks and frozen ground minimized soil disturbance. Treatment plots measuring ~30 m x 25 m were laid out between windrows, avoiding wet and excessively disturbed areas. Neighbouring plots were grouped into five blocks. Five (1997, 10 yr) or six (2012, 25 yr) of 10 site preparation treatments tested at Bednesti were selected for vegetation sampling to encompass a gradient from low to high disturbance severity:

SH: Sheared (U or UC in earlier publications). Vegetation was sheared at ~10 cm height with a brush blade on snow, creating little soil exposure and leaving LFH layers, budbanks and seedbanks mostly undisturbed. Severity ranking: low.

DT: Disk Trenching. After shearing (see SH), a TTS Delta powered disk trencher mounted on a rubber-tired skidder created continuous shallow, linear furrows spaced 3 m apart. Mineral soil was 48% exposed with LFH, budbanks and seedbanks buried or coarsely mixed. Severity ranking: moderately low.

CM: Coarse Mixing. After shearing, an Eden relief bedding plow with 6 hydraulic disks mounted on a crawler tractor created 1.6 m planting beds flanked by 50 cm trenches of exposed subsurface soil. In raised beds, intact LFH was buried beneath loose chunks of soil and organic matter. Mineral soil exposure was ~100% with budbanks and seedbanks buried, uprooted and coarsely mixed. Severity ranking: medium.

PI: Plowed and Inverted (sampled at 25 yr only). After shearing, a three-bottom agricultural breaking plow mounted on a crawler tractor created side-by-side inverted furrow slices. Mineral soil exposure was ~100% with LFH, budbanks and seedbanks inverted and buried under 10-15 cm of soil. Severity ranking: medium.

FM: Fine Mixing. A high-speed rotating drum (Madge Rotoclear) pulled behind a crawler tractor created 15 cm of finely chopped organic matter intimately mixed with soil. Mineral soil exposure was 100% with most roots and rhizomes finely comminuted. Severity ranking: high. For logistical reasons, these plots were grouped at the south end of the site.

BW: Burned Windrow. After shearing, slash was piled in long rows and burned. LFH, fine and medium slash were completely consumed forming a thick ash layer. Mineral soil exposure was minimal, but budbanks and seedbanks to 10-15 cm depth were consumed by intense heat. Plots were laid out in well-burned 10 m x 50m strips adjacent to each block. Severity ranking: high.

RF: Reference Forest. In 2012, we located 5 unmanaged naturally-regenerated forest plots immediately north of the Bednesti experiment. RF plots were assigned to the block situated directly south on ecologically similar soils. We cored several dominant trees in each plot and found that two were ~35 yr old and three were ~46 yr old, corresponding to natural regeneration after the 1963-4 and 1971 two-pass strip logging operation. We were unable to use a mature, wildfire origin stand as a reference area, because all mature pine on comparable soils near Bednesti were killed by mountain pine beetles and subsequent salvage logging. RF plots had rare beetle mortality and represented the oldest live lodgepole pine stand in the local area.

Site preparation was carried out late in 1987. In spring 1988, 80 one-yr-old Styroblock™ PSB 211 lodgepole pine seedlings were planted in each treatment unit at a target density of 1200 stems ha⁻¹ with 48 inner seedlings serving as measurement trees surrounded by an outer ring of 32 unmeasured buffer trees. Tree spacing averaged 2.9 m x 2.9 m, but exact spacing varied with the configuration of planting spots in each

treatment.

SH, DT, CM and PI treatments were randomly assigned to plots within blocks. BW, FM and RF plots were assigned to the closest block of other treatments. The experimental area was topographically uniform with no systematic soil or vegetation gradient. Haeussler et al. (1999) found no evidence of a block effect, and concluded the largest source of pre-treatment variation in plant community composition was the distribution of small patches of trembling aspen (*Populus tremuloides*) or green alder (*Alnus viridis*) scattered independently of blocks across the site.

Vegetation sampling: 10-yr vegetation sampling took place August 16-27, 1997; 25+-yr sampling from August 14-25, 2012. Except as noted, identical methods were used on both dates. All plant identification and ocular estimates were made by the senior author. In 25 plots at 10 yr (SH, DT, CM, FM, BW) and 35 plots at 25+ yr (SH, DT, CM, PI, FM, BW and RF), we randomly located 3 vegetation subplots. Subplots were positioned centrally within the narrow burned windrows (BW) to minimize edge effects. Ten-yr subplots were unmarked and a new randomization was done at 25 yr. Each subplot was a nested set of rectangular quadrats to sample four vegetation layers: (i.) tall shrubs and trees > 2 m height (5 m x 5 m); (ii.) low shrubs and trees < 2 m height (3 m x 3 m); (iii.) herbs and dwarf shrubs (1 m x 3 m); (iv.) forest floor mosses, liverworts and macrolichens (1 m x 1 m in 1997; 0.33 m x 3 m in 2012). An ocular estimate of percent cover was recorded for each species (or taxon, Appendix I). At 10 yr, to aid in quantifying treatment severity, we recorded the surface area % of mineral soil, rocks and stones, organic matter and woody debris on each 3 m x 3 m quadrat and % disturbed vs. undisturbed ground area.

At 25+ yr, we spent 20-30 minutes recording occurrence of mycoheterotrophic and mixotrophic species (hereafter, mycotrophs) within the "measurement area" (defined below) of each plot. Mycotrophs are vascular plants in the Orchidaceae, Pyrolaceae, Monotropaceae, Lycopodiaceae and Botrychiaceae that obtain all or some of their nutrition from mycorrhizal connections to conifers and other forest plants (Massicotte et al. 2012). Among vascular plants of northern forests, this functional group is the most sensitive to tree cutting and forest

160 floor disturbance (Haeussler et al. 2007). We also sampled epiphytic macrolichens, liverworts and mosses on 5
161 randomly selected pines per plot. All epiphytes located on the trunk below breast height and on three 10-cm
162 sections (proximal, distal and mid portion) taken from three random branches radially distributed around the
163 trunk below breast height were collected and identified to species or sub-genus in the laboratory.

164 Total height and diameter at breast height were recorded for each lodgepole pine sample tree from 11 to 25
165 yr after planting (at 10 yr, basal diameter was measured). The “measurement area” of each plot was
166 determined by stem-mapping the perimeter defined by points of origin of the outer ring of measurement trees,
167 then extending the boundary 1.5 m outward to encompass tree crowns. These data were used to calculate
168 mean height, mean diameter and basal area per hectare for each experimental plot at 10 and 25 yr. We
169 extrapolated backward one yr from the 11- to 25-yr curves to obtain 10 yr diameters. For RF plots we used the
170 mean diameter and height of the 5 epiphyte sample trees and a prism sweep to determine basal area. We
171 estimated stem volume per hectare as (basal area x height)/3 and the crown volume index as (mean percent
172 cover of pine)x(mean height). Pine health was surveyed 12 times between 7 yr and 25 yr on four treatments
173 only (SH, DT, CM, BW). The cumulative number of trees that died from rust infection or had detectable rust
174 cankers on or within 10 cm of the main stem by 25 yr was tallied by plot separately for comandra blister rust (*C-*
175 *RUST*) and stalactiform blister rust (*S-RUST*).

176 **Data analysis:** We used multivariate analysis of plant community composition and mixed effects modeling of
177 individual response variables to test the hypotheses over gradients of site preparation severity, tree size and
178 crown closure. To evaluate H1 vs.H2-3, we examined multivariate and univariate indicators of plant composition
179 for evidence of diverging vs. converging successional trajectories. Divergence was defined throughout as an
180 increase in the Bray-Curtis Distance (BCD) between two plant communities with time; convergence as a
181 decrease in BCD. To test H2 vs. H3, we first determined if tree size and crown closure increased with site
182 preparation severity, then evaluated if composition converged more rapidly at high (H2) or low (H3) severity.
183 Next we determined whether tree size or crown closure (H2) provided better model fits than severity (H3) for

univariate indicators. We also examined if higher severity increased richness and abundance of late (H2) vs. early seral (H3) plant indicators.

explanatory variables (Table 1a): We scored the 7 treatments on an index of relative severity (after Roberts 2007):

$$S = [V/V_{max} + FF/FF_{max}]/2 \tag{1}$$

$$V = AG + BB + SB, \text{ where } AG = \% \text{ removal of above-ground vegetation; } BB = \% \text{ destruction of soil budbank; } SB = \% \text{ destruction of soil seedbank.} \tag{2}$$

$$V_{max} = \text{maximum score.} \\ FF = CWD + LFH + MS, \text{ where } CWD = 100 - \% \text{ cover of woody debris relative to max; } LFH = \% \text{ removal of LFH layer; } MS = \text{alteration of top 10 cm of mineral soil relative to max.} \tag{3}$$

$$FF_{max} = \text{maximum score.}$$

Scores for vegetation (*V*) and forest floor (*FF*) components were estimated from written records, 1987-88 photos and 10-yr ground cover data. We also considered two binary alternatives to *S*: a high severity threshold (0 = all unburned treatments; 1 = BW) and a low severity threshold (0 = all site preparation treatments; 1 = RF).

The first axis of a principal components analysis (PCA) of lodgepole pine height, diameter, basal area ha⁻¹, stem volume ha⁻¹, % cover and crown volume index (representing 81% of total variation) served as an integrated index of pine size (*PSIZE*). Crown closure (*CC*) was estimated by summing % cover estimates of lodgepole pine plus all other tree species of equal or greater height. Although few non-pine species occurred in the tree canopy, *PSIZE* and *CC* were only moderately correlated (*r* = 0.54) because *PSIZE* encompassed the entire plot (48 measurement trees) whereas *CC* was estimated on 3 randomly selected 5 m x 5 m quadrats per plot. Other explanatory variables included plot geographic coordinates to test for spatial pattern, and % cover of blister rust alternate hosts.

multivariate analysis: Non-metric multi-dimensional scaling (NMDS) with the vegan package in R (Oksanen et al. 2017) was used for unconstrained ordination of plant community composition (% cover of vascular plants, bryophytes and macrolichens with subplots pooled at the plot scale, 60 plots x 134 taxa).

Cover was subjected to a Wisconsin double standardization and square root transformation. BCD was selected as the distance metric. We ran the ordination with $k = 1$ to 7 dimensions with maximum of 1000 random starts to find a convergent solution. Stress levels and Shepard plots of the ordination distances against original dissimilarities at $k = 1$ to 7 were used to choose the number of dimensions. We reran the NMDS several times at the best k , beginning with the best previous solution, to find a stable configuration. The strength of fit (r^2) and significance level of explanatory variables (Table 1a) were determined by 999 Monte Carlo permutations. For variables with $P < 0.05$, correlation coefficients (r) with individual NMDS axes were examined, and these variables were overlain on the ordination.

univariate analysis: We fit linear mixed effects models with the nlme package in R (Pinheiro et al. 2015) for each response variable (Table 1b). Subplot data were pooled at the plot scale and response variables were normalized with a power transformation, as needed. Random effects were plot nested within block for models encompassing 2 dates ($n = 50$ or 60); block only for one-yr models ($n = 25$ or 35). These models are equivalent to a Randomized Complete Block Design with a split plot for repeated measures in classical ANOVA. After examining scatterplots, we worked our way through an appropriate set of full to reduced fixed effects models. Severity was modeled as linear (S), quadratic ($S + S^2$) or cubic ($S + S^2 + S^3$) functions, with and without a YR intercept and $S \times YR$ interaction terms, and with BW or RF substituting for S (linear only). The best severity model based on satisfactory distribution of residuals and lowest Akaike information criterion (AIC) was compared to the best tree size/crown closure model with $PSIZE$ or CC as linear, quadratic or cubic variables. CC full models were identical to S full models, but $PSIZE$ models did not require YR intercepts or interaction terms. For infrequent taxa (non-hawkweed invasives, $TOAD$), we substituted Kruskal-Wallis non-parametric ANOVA (K-W; stats package, R Core Team 2017) to contrast appropriate combinations of treatments or years. For count variables with many zeroes ($C-RUST$, $S-RUST$), we fit a poisson mixed effects model (lme4 package in R Version 1.1-12; Bates et al. 2015) without the low severity threshold (RF wasn't sampled for rusts) and added % cover of alternate hosts (Table 1a) as candidate fixed effects.

To evaluate ecological impacts of hawkweed invasion we examined correlations between hawkweed cover and the diversity (richness, evenness, Shannon's index) and cover of native herb species on 1 m x 3 m quadrats at 10 yr ($n = 75$) and 25 yr ($n = 105$).

Results

Tree size and crown closure: *PSIZE* and *CC* increased non-linearly with site preparation severity (Table 2i, Fig. 1). There was a moderate increase from low to medium severity but little additional increase to high severity (cf. Bedford and Sutton 2000, Boateng et al. 2012). Site preparation followed by planting clearly accelerated stand development because *PSIZE* in high severity treatments at 25 yr was similar to reference forests at 35-46 yr, while *CC* in low severity treatments at 25 yr and medium-high severity treatments at 10 yr equaled that of reference forests.

Plant community composition: An NMDS with $k = 3$ dimensions, stress = 0.137 and Shepard plot $R^2 = 0.981$ (Table 3a) was selected. Neither blocks (goodness of fit $r^2 = 0.057$; $P = 0.60$), nor geographic coordinates (Table 3b) were significantly correlated with the ordination, confirming our view that spatial gradients in terrain and pre-1960s vegetation were weak, and that treatments not randomly assigned to plots within blocks could reasonably be incorporated into the experimental design.

Differences in community composition related to stand age (or sampling date) greatly outweighed differences due to site preparation. NMDS Axis1 was strongly correlated with stand age and pine size ($r > 0.9$, Table 3b) and cleanly separated 10-, 25-, 36-, and 46yr-old plant communities (vertical lines in Fig. 2a). NMDS Axis2 was highly correlated with severity and crown closure ($r < -0.89$, Table 3b). Low severity treatments (RF, SH, DT) were located high on Axis2, medium-high severity treatments (CM, PI, FM) near centre, and burned windrows (BW) at the bottom in both yr (Fig. 2a). At 10 yr, BW was separate from all other treatments, but at 25 yr BW overlapped slightly with FM, and FM, PI, and CM were no longer distinct from SH and DT, indicating convergence. No significant explanatory variables were strongly correlated with Axis3 (Table 3b, not graphed). Successional trajectories proceeded laterally to the right in low severity and diagonally up and right in medium

and high severity plant communities.

Ten yr plant communities (Fig. 2b, left) were characterized by pioneering native and non-native forbs (*Epilobium ciliatum* [Ec], *Trifolium* spp. [Tr], *Hieracium* spp. [Ha, Hp], *Taraxacum officinale* [To]), graminoids (Poaceae [Po, Fo], *Carex* spp. [Cx], *Juncus* spp. [Ja, Je]) and pioneering bryophytes (*Ceratodon purpureus* [Cp], *Polytrichum juniperinum* [Pj]). Shade tolerant and mycotrophic forbs (*Chimaphila menziesii* [Cm], *Orthilia secunda* [Os], *Goodyera repens* [Gr], *Linnaea borealis* [Lb], *Lycopodium* spp. [Ld, La]), late seral feathermosses (*Hylcomium splendens* [Hs], *Pleurozium schreberi* [Pl]), liverworts (*Barbilophozia* [Bh, Bl], *Lophozia* spp. [Lo]), and many epiphytic and *Peltigera* lichens [Lp, Pe] were associated with 25+ yr plant communities (Axis1, right). Species associated with higher site preparation severity, irrespective of stand age, included green alder [Av], trembling aspen [Pt], yarrow (*Achillea millefolium* [Ac]), white meadow-sweet (*Spiraea betulifolia* [Sb]) and fireweed (*Epilobium angustifolium* [Ea]) (lower Axis2). Spruces (Pc), subalpine fir (*Abies lasiocarpa*, Al), black gooseberry (*Ribes lacustre* [Rl]) and several mosses [Ep, Ap] were negatively associated with severity (upper Axis2). Willows [Sa], velvet-leaved blueberry [Vm], *Rosa acicularis* [Ra], *Lonicera involucrata* [Li] and *Rubus pubescens* [Rp] were relatively insensitive to forest age and severity (centre Axis2) (more in Table A-1).

Mixed effects models for plant community composition (Table 2ii, Fig. 3) and plot pair comparisons (Fig. 4) reinforced the NMDS results. A severity model with separate YR intercepts and parallel curves predicted that treated plant communities were 15% more similar to reference forests at 25 yr than at 10 yr at all levels of S. There was a gentle decline in *RFSIM* from low to medium severity, but a rapid decline at $S > 0.8$ in both yr. Reference forests were 65% similar to one another, thus $RFSIM > 60\%$ on low severity treatments at 25 yr, represents nearly full convergence when allowing for experimental error. Community composition converged over the full range of treatments. Crown closure better predicted *CONVG* than severity (Fig. 3b, Table 2ii), but contrary to H2, the rate of convergence declined linearly as CC increased. Of 299 plot-pairs sampled in both yr, 74% were compositionally more similar at 25 yr than at 10 yr, while 26% diverged (Fig. 4). Among diverging plot pairs, 80% were $>65\%$ similar at 10 yr, suggesting divergence was mostly due to experimental error (i.e.,

randomly relocating subplots). All 4 diverging plot pairs that were <55% similar at 10 yr included an anomalous DT plot situated in an aspen clone.

Species diversity: 167 taxa (98 native trees, shrubs and herbs, 8 non-native herbs, 61 bryophytes and macrolichens) were recorded in sample quadrats, including 154 in experimental plots, and an additional 12 (1 tree, 5 forbs, 3 bryophytes, 3 liverworts) found only in RF. We recorded 98 taxa in plots sampled at 10 yr, and 118 taxa in those same plots at 25 yr. Of 30 taxa recorded only at 10 yr, 73% were early seral forbs, grasses, and mosses; of 51 taxa recorded only at 25 yr, there were 7 shade-loving forbs, 4 bryophytes, and 22 lichens.

Plot scale richness increased across the board from 10 to 25 yr. Richness declined linearly with severity at 10 yr, but at 25+ yr, the relationship was cubic, with the most taxa at low and high S and fewest at $0.6 < S < 0.7$ (RICH, Table 2iii, Fig. 5a). The crown closure model, predicting negative linear relationships with CC in both years, fit almost as well (AIC = 386 vs. 385). Species evenness, also decreased linearly with CC, but, unlike richness, it declined with stand age, and the crown closure model fit considerably better than the severity model (EVEN; Fig. 5b, Table 2iii). Richness of epiphytes (EPIRICH) and mycotrophs (MYCRICH) were insensitive to site preparation severity but were higher in reference forests than in 25 yr-old experimental stands (Fig. 5c, d; Table 2iii). Also, there were more epiphytic taxa on open-canopied pines than beneath denser canopies.

Invasive non-native plants: Eurasian hawkweeds of the subgenus *Pilosella* (*Hieracium caespitosum*, *H. piloselloides*, *H. aurantiacum*) were pervasive in both yr. Clovers (*Trifolium hybridum*, *T. pratense*) were common on burned windrows at 10 yr but not at 25 yr. Dandelion (*Taraxacum officinale*), birds-foot trefoil (*Lotus corniculatus*), Kentucky bluegrass (*Poa pratensis*) and Canada thistle (*Cirsium arvense*) were rare. In reference forests we found one patch of hawkweed ($0.1 \pm 0.1\%$ cover) and no other non-natives. In the experimental area, hawkweed cover was 10% at 10 yr and 2% at 25 yr. Total non-native cover was barely higher. The best models (HAWK, NNAT; Table 2iv, Fig. 6a-b) predicted a monotonic increase with severity at 10 yr, but a more complex cubic relationship at 25 yr with highest invasive cover at $S = 0.3$ and lowest at $0.7 < S < 0.9$. Although declining non-native cover suggested shading was important, the best tree size/crown closure models (cubic

PSIZE functions) fit less well than severity models.

There was no evidence of negative correlations between hawkweed abundance and native herb diversity or cover. Correlations were mostly non-significantly positive, but at least one major understory plant (bunchberry, $r = -0.31$; $P = 0.006$) was significantly negatively associated with hawkweeds. Non-natives other than hawkweeds were 25 times more abundant on burned than unburned plots at 10 yr (5% vs. 0.2% cover; K-W: $X^2_1 = 3.9$, $P = 0.049$) and >50 times more abundant at 25+ yr (0.08% vs. 0.0015%, K-W: $X^2_1 = 8.3$, $P = 0.004$). Overall, these invasives were 128 times more abundant at 10 yr than at 25+ yr (K-W: $X^2_1 = 4.9$, $P = 0.03$).

Berry-producers: Velvet-leaved blueberry was the dominant berry-producer at Bednesti except on burned windrows where the dominant berry producers were wild strawberry (*Fragaria virginiana*) and prickly rose (*Rosa acicularis*). Best-fit models were complex functions showing that berry producers declined with stand age and treatment severity, peaking at $0.2 < S < 0.5$ at 25 yr (*BLUEB*, *BERRY*; Fig. 6c-d, Table 2iv). Tree size and crown closure were poorer predictors than severity.

Lodgepole pine blister rusts and their alternate hosts: Comandra blister rust infection of pine was observed in every surveyed plot (SH, DH, PI, BW) with cumulative infection ranging from 1 to 8 trees per plot at 25 yr. False toadflax was recorded on just one 25-yr old SH and three RF subplots. Consequently, we couldn't detect a relationship between false toadflax abundance and rust infection ($P > 0.90$), nor differences in false toadflax abundance between 10 and 25+ yr (K-W $X^2_1 = 2.2$, $P = 0.14$). At 25+ yr, false toadflax was significantly more abundant at low (RF, SH, DT) than medium or high severity (CM, PI, FM, BW; K-W: $X^2_1 = 4.2$, $P = 0.04$). Perversely, the probability of comandra rust infection increased with severity (*C-RUST*; Table 2iv, Fig. 7): a poisson model with S had significantly better fit than the null model (AIC 91 vs.96, $P = 0.009$), and slightly better fit than a *PSIZE* model (AIC = 94).

We were unable to fit a model for stalactiform rust because infection ranged from 0 to 2 trees per plot with 13 of 20 plots having no stalactiform rust. But Orobanchaceae hosts were ubiquitous, averaging 0.7% cover.

330 Cow-wheat (*Melampyrum lineare*) was common in both yr; scarlet paintbrush (*Castilleja miniata*) was mostly on
331 burned windrows at 25 yr ($K-W \chi^2_1 = 13.7$, $P = 0.0002$); yellow rattle (*Rhinanthus minor*) was seen on trails but
332 not recorded in quadrats. The best fits for cow-wheat and total Orobanchaceae cover were high severity
333 threshold models with a significant $YR \times BW$ interaction (*COWWH*, *OROB*; Table 2iv, Fig. 6e-f). On unburned
334 treatments, *OROB* dropped from >2% at 10 yr to 0.4% at 25+ yr. Burned windrows had significantly less
335 *COWWH* and *OROB* than unburned plots at 10 yr, but more *OROB* at 25 yr due to an increase in scarlet
336 paintbrush. *PSIZE* and *CC* models had a much poorer fit (Table 2iv).

337 **Hypotheses:** In summary, there was no evidence that plant community composition on treatments of lower vs.
338 higher severity diverged over time, refuting H1 (Figs. 2-4). Tree size and crown closure increased with site
339 preparation severity (Fig 1), but the rate of convergence decreased rather than increased at higher crown
340 closure and severity (Fig 3b), refuting H2 and lending support to H3. Eleven of 13 variables had a better fit with
341 a crown closure model than a severity model, further refuting H2. Closer examination of community composition
342 suggests that H3 was fully supported at yr 10, but changes after yr 10 supported H3 on burned windrows only.
343 Specifically, on burned windrows 7 of 15 indicators suggested delayed succession between 10 and 25 yr,
344 whereas 2 suggested accelerated succession; on intermediate treatments (CM, PI, FM), 2-3 indicators each
345 suggested delayed succession, whereas 3-4 indicators suggested accelerated succession.

346 Discussion

347 In the 1980s, management of public forest lands in central BC followed trends in Fennoscandia and the
348 southeastern US by shifting from reliance on natural pine regeneration to intensive site preparation, artificial
349 regeneration and control of competing vegetation to enhance wood yields. The pendulum swung back in
350 following decades to less intensive practices intended to achieve satisfactory reforestation at minimal cost
351 (Hawkins et al. 2006). In the 2010s, most newly logged pine sites are planted with good quality seedlings onto
352 unprepared sites with minimal soil disturbance. Twenty-fifth yr monitoring of successional trajectories and plant
353 indicators at Bednesti can help to evaluate some of the resource management tradeoffs associated with these

shifts in practices and priorities.

Successional trajectories: We proposed three hypotheses regarding patterns of forest succession following site preparation treatments that ranged from winter shearing of above-ground vegetation through several intensities of soil mixing to a very severe burn. Hypothesis H1 posited that this range of disturbances could launch the plant communities onto divergent successional trajectories whereby plant community composition across treatments became less similar over time. The evidence from plant community ordination and convergence analyses refutes H1. Overwhelmingly, the Bednesti experimental plant communities became more similar to each other and to the composition of nearby reference forests. At 25-yr, their similarity to reference forest composition (50-60%) was not much less than the 65% observed among the 5 reference forest plots themselves. Those pine stands were logged at the same time as the experimental area, but restocked naturally, and are excellent controls for what the experimental plant communities would have become with sufficient natural pine regeneration. Following Holling's (1973) definition of ecological resilience, we conclude that the Bednesti plant communities absorbed the full range of experimental disturbances without shifting to an alternative domain of successional attraction, such as an aspen forest. In that sense, the rehabilitation has successfully restored these sub-boreal plant communities. Avoiding soil compaction and stripping of organic layers (Mackenzie et al. 2005) and planting lodgepole pine were two important site-level management practices that helped maintain or restore resilience. A surrounding landscape that had abundant mature lodgepole pine forests prior to the early 2000s was likely also important in allowing dozens of late seral bryophytes, lichens and mycotrophs to colonize the experiment after ten years.

Our second hypotheses, H2, posited that more severe site preparation would accelerate plant community succession relative to less severe treatments by increasing tree growth rates, speeding crown closure and increasing competition for light and other resources, thereby favouring shade- and stress-tolerant late seral plants (Grime 1979) over intolerant, resource-demanding early seral species (cf. Thompson et al. 2013). Conversely, H3 postulated that more severe site preparation would delay successional replacement of early

seral by late seral plants. Haeussler et al. (1999, 2002) showed that low severity site preparation retains a high proportion of residual and budbanking forest plants whereas higher severity site preparation promotes establishment from seeds and spores. H3 postulated that more severe treatments create a pulse of resource availability that, while not sufficient to derail successional trajectories (as in H1), do allow pioneer species to thrive longer than on lower severity treatments. These alternative scenarios are relevant to managers seeking to balance species and habitat diversity with timber production while discouraging pests and invasive species.

The evidence regarding H2 and H3 was mixed. Our data clearly show that succession was slower on higher severity treatments (H3) at 10 yr. But between 10 and 25 yr, there appears to have been a shift toward scenario H2. The balance of evidence suggests that during this period, successional replacement of early seral species on higher severity plowing and mixing treatments began to equal or surpass that on low severity treatments. At 25 yr, only burned windrows still satisfied H3. Despite having larger trees with denser canopies than the less severe treatments, burned windrows retained significant cover of seral species like fire-moss, yarrow, fireweed, strawberry and paintbrush. Neither soil disturbance nor more rapid growth of overstory trees influenced establishment of late seral mycotrophs and epiphytes.

The wide spacing and generally airy open crowns of planted pines at Bednesti evidently did not provide the strong gradient of light competition that rapidly eliminates early seral vegetation during the stem exclusion stage of forest development on more fertile soils (Coomes and Grubb 2000) or at higher planting densities. It is possible that, despite higher crown closure and having subplots centrally located to minimize edge effects, burned windrow plots (10 m x 50 m) were successional delayed because more side light reached their understories than those of other treatment plots (25 m x 30 m). We think such treatment artefacts were relatively minor and that belowground factors, including differential budbank and seedbank survival and mineral soil exposure for seedling establishment (earlier described by Haeussler et al. 1999, 2002), soil chemical properties (Mackenzie et al. 2005; Boateng et al. 2010) and soil biology (not studied at Bednesti) were more important than aboveground light competition in explaining differences in successional rates..

At the nutritionally poor Bednesti site, below-ground interactions are likely to be more important as successional drivers (Aerts 1999) than on a mesotrophic ecosystem such as Bednesti's partner site (Inga Lake) where the same silvicultural treatments had substantially different outcomes (Haeussler et al. 2004). Bardgett et al.'s (2005) synthesis of the role of plant-soil feedbacks in succession, complemented by data from central BC (Kranabetter et al 2009; Kranabetter and Mackenzie 2010), provides a possible process-based explanation for the observed plant community dynamics, particularly delayed succession on burned windrows. Typically, forest soil biological communities switch from bacterially-dominated to fungally-dominated during early primary succession. In tandem, the succession of vascular plants involves a progression from short-lived non-mycorrhizal and nitrogen-fixing species that utilize inorganic forms of nitrogen and other nutrients (e.g., clover, sedges), to longer-lived arbuscular-mycorrhizal species that also derive much of their nutrition from inorganic sources (e.g., fireweed). Dominance then shifts to woody ectomycorrhizal (e.g., conifers) and ericoid-mycorrhizal (e.g., blueberries) species that acquire nutrients from organic sources, shade-dependent mycotrophic species that derive C and N directly from trees or other established plants (Read et al. 2004), and feathermosses that host nitrogen-fixing cyanobacteria (DeLuca et al. 2002).

Kranabetter and Mackenzie (2010) showed that on infertile sites, ectomycorrhizal and ericoid-mycorrhizal plants dominate early stages of secondary succession, whereas on richer sites, non-mycorrhizal and arbuscular-mycorrhizal plants persist longer due to sustained availability of inorganic nutrients. We believe that treatment severity at Bednesti altered the proportions and relative competitiveness of these four plant mycorrhizal functional types. Our results suggest that fire may be inherently different from mechanical treatments in ways that influence nutrient acquisition by plants, but our study lacked low and medium severity burns and also lacked an extreme mechanical treatment with comparable bud- and seedbank damage to burned windrows. Boateng et al. (2010) found higher soil pH, CEC and exchangeable Ca and K on burned windrows over 20 yr, but no long term changes in soil nitrogen or pine foliar nutrients other than boron. No soil biology data are available to explicitly link soil properties to the plant successional trajectories documented

here. Such process-based work could be a fruitful topic for further research.

Management indicator species: The shift to less intensive management in central BC in the 2000s, though driven mainly by economics, was also motivated by a desire to protect soils and other forest values such as biodiversity through prescriptions that are “lighter on the land” (Boateng et al. 2012). Our results for indicator plant species can help assess the merits of this approach.

The distribution of invasive non-native herbs at Bednesti provides no easy answers for silviculturists seeking to protect biodiversity. There is abundant scientific evidence that severe soil and vegetation disturbance, whether by mechanical means or fire, increases risks of non-native plant invasion (Langor et al. 2014). At Bednesti, non-hawkweed invasives were most frequent on burned windrows, but these species were minor and short-lived –as expected of agronomic plants and weeds on nutrient-deficient sites. Hawkweeds, on the other hand, persisted to 25 yr at low to high disturbance. *Pilosella* hawkweeds are unusually aggressive invaders in poor soils, forming dense mats that competitively exclude other plants (Kloppel et al. 2003). It is believed they can sequester nitrogen in poor soils (Giroday and Baker 2006), possibly through a positive feedback mechanism with soil microbiota. Although we detected no clear negative impact on native herbs, we believe these hawkweeds pose the first persistent threat to the integrity of central BC lodgepole pine forests from non-native plants. More research is needed to clarify how they maintain themselves in infertile forest understories, their effects on plant competitive relationships and soil biogeochemical processes, and whether they will disappear as the feathermoss carpet thickens at 30-40 yr. Planting pine at higher densities and in mixtures with conifers that cast deeper shade may be one strategy to reduce hawkweeds. But this strategy will also reduce abundance and persistence of valued native plants, including berry producers.

For berry-producers, results were straightforward: medium to high severity treatments reduced abundance, particularly of velvet-leaved blueberry. We anticipated that losses of ericoid-mycorrhizal blueberries would be offset by increases in raspberry, wild strawberry and prickly rose, but on this infertile ecosystem, increases in early seral berry-producers, mostly on burned windrows, did not offset losses. Low intensity fire is one of the

best ways to stimulate velvet-leaved blueberry resprouting and berry production (Duchesne and Wetzel 2004). Due to piling of fuels, fire severity at Bednesti greatly exceeded the optimal 0.3 cm depth-of-burn reported by these authors. For berry producers, notably *Vaccinium*, broadcast burning appears to better distribute burn impacts and exchangeable cations than the current central BC approach of piling and burning logging slash at roadside.

One clear tradeoff of a light-on-the-land strategy is that forest soils, soil biota, seedbanks and budbanks are not periodically rejuvenated as under a wildfire regime (Zackrisson et al. 1996). Foresters have wondered whether prevalence of pine stem rusts could likewise be a result of fire suppression and whether greater use of prescribed fire or mechanical site preparation could reduce rust damage in plantations. At one central BC site, comandra rust incidence was >85% when false toadflax was present within 1 m of the tree and decreased to 45% when >15 m away (Reich 2011). At Bednesti, false toadflax was found only in older, less-disturbed pine stands, providing tentative support for the view that soil disturbance could reduce this host in the early years when pines are most liable to infection. Contrary to these findings and an earlier analysis by Reich et al. (2015), our *C-RUST* model predicted increased infection on more severe treatments.

We also found no clear relationship between Orobanchaceae abundance and stalactiform rust infection. While Orobanchaceae hosts were present in every Bednesti plot at 10 and 25 yr, stalactiform rust was rarely present. Given co-occurrence of the two stem rusts, the diverse niches of their various hosts, and lack of clarity on how the susceptibility of pine varies with environmental factors that influence abundance of the alternate host, it isn't possible to conclude whether more or less site preparation would reduce rust damage. Much larger treatment units and detailed pre- and post-treatment monitoring are needed to disentangle the complex relationships among the physical and biotic factors that influence infection rates.

Conclusions

Management of lodgepole pine ecosystems for resilient forests that provide a long term supply of timber while sustaining biodiversity, wildlife habitat and other non-timber values involves tradeoffs between creating

and prolonging open early seral habitats with a rich variety of plants and speeding up the development of closed forest habitats to support species at risk from the loss of mature and old growth forests. For BC lodgepole pine ecosystems, such tradeoffs have been accentuated by the 2000s mountain pine beetle epidemic because 20-40-yr-old plantations are now the dominant category of closed pine forest. Aside from unexpectedly strong persistence of non-native hawkweeds, our study found the plant communities of nutrient-limited lodgepole pine ecosystems to be resilient to a broad spectrum of silvicultural site preparation. The appearance of 51 new species, mainly bryophytes and lichens, 10-25 yr after disturbance suggests, however, that nearby mature pine forests played a role in this resilience that cannot be taken for granted in the aftermath of the beetle.

Severe treatments enhanced growth of lodgepole pine, but there was minimal evidence that they accelerated the development of plant communities. Succession was actually delayed on higher severity treatments over the first decade, but by 25 yr only the most extreme treatment (windrowed and burned slash) was still delayed. Less severe broadcast burning will likely provide many benefits of fire while avoiding extreme impacts such as the loss of blueberries. We now disagree with our 10-yr recommendation (Haeussler et al. 2002) that medium severity treatments are a good way to balance benefits and risks of site preparation. Instead, 25-yr results suggest managers should address tradeoffs by adopting a diversity of low, medium and high severity practices within stands and across landscapes. Since 1988, the Bednesti study has provided insights into the complexity of practicing ecosystem-specific silviculture that balances benefits and risks for plants and other forest values. Long term maintenance and monitoring of experiments like Bednesti are needed to allow forest management to adapt to ever-changing conditions and concerns.

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Tables

Table 1. Description of explanatory and response variables.

(a) Explanatory variables			
Abbreviation	Description	Units	Range of Values
<i>S</i>	Site preparation severity. Equation (1) in text	none	0 to 1
<i>BW</i>	Dummy variable for burned windrow	none	0 = unburned; 1 = burned
<i>RF</i>	Dummy variable for reference forest	none	0 = experimental plot; 1 = reference forest
<i>YR</i>	Year of sampling	years	1997 = 0; 2012 = 15
<i>AGE</i>	Age of lodgepole pine stand	years	10 – 46
<i>PSIZE</i>	Size of lodgepole pine from Axis1 of PCA of height, diameter, basal area, stem volume and crown volume index.	none	0 – 1.6
<i>CC</i>	Tree crown closure = ocular estimate of cover of lodgepole pine and other canopy trees of equal or greater height	%	16 – 80
<i>NORTH</i>	North:South geographic coordinate of plot	none	0 – 8
<i>EAST</i>	East:West geographic coordinate of plot	none	0 – 8
<i>TOAD</i>	Mean cover of <i>Geocaulon lividum</i> in plot (<i>C-RUST</i> only)	%	0 – 0.03
<i>COWWH</i>	Mean cover of <i>Melampyrum lineare</i> in plot (<i>S-RUST</i> only)	%	0 – 5.8
<i>OROB</i>	Mean cover of Orobanchaceae (<i>Melampyrum</i> + <i>Castilleja</i>) in plot (<i>S-RUST</i> only)	%	0 – 5.8
(b) Response variables			
Abbreviation	Description	n	Treatments and Years
i. Tree Size and Crown Closure			
<i>PSIZE</i>	Size of lodgepole pine (see above).	60	all
<i>CC</i>	Tree crown closure (see above)	60	all

ii. Plant Community Composition			
<i>RFSIM</i>	Mean similarity (1 – BCD)* of each plot at 10 yr and 25 to the 5 (or 4 other) RF plots	60	SH, DT, CM, FM, BW at 10 and 25 yr; PI and RF at 25 yr only
<i>CONVG</i>	Mean change in similarity $[(1-BCD)_{25} - (1-BCD)_{10}]$ for each plot relative to all other plots (positive = converging; negative = diverging)	25	SH, DT, CM, FM, BW
iii. Species Diversity			
<i>RICH</i>	Species richness, subplot data pooled at plot scale	60	All
<i>EVEN</i>	Pielou's species evenness index, plot scale data	60	All
<i>EPIRICH</i>	Richness of epiphytes on lodgepole pine, 5 trees per plot	35	7 treatments at 25+ yr
<i>MYCRICH</i>	Richness of mycoheterotrophs and mixotrophs, plot scale data	35	7 treatments at 25+ yr
iv. Abundance of Management Indicator Species			
<i>HAWK</i>	Mean cover of <i>Pilosella</i> hawkweeds in plot	60	All
<i>NNAT</i>	Mean cover of all non-native plants in plot	60	All
<i>BLUEB</i>	Mean cover of <i>Vaccinium myrtilloides</i> in plot	60	All
<i>BERRY</i>	Mean cover of all berry-producing plants in plot	60	All
<i>TOAD</i>	Mean cover of <i>Geocaulon lividum</i> in plot	60	All
<i>COWWH</i>	Mean cover of <i>Melampyrum lineare</i> in plot	60	All
<i>OROB</i>	Mean cover of <i>Melampyrum</i> + <i>Castilleja</i> in plot	60	All
<i>C-RUST</i>	Cumulative number of trees infected with comandra blister rust in plot from 1994 to 2012	20	SH, DT, CM, BW
<i>S-RUST</i>	Cumulative number of trees infected with stalactiform blister rust in plot from 1994 to 2012	20	SH, DT, CM, BW

*BCD is the Bray-Curtis distance metric

Table 2. Comparison of best-fitting disturbance severity and tree size/crown closure models for each response variable, with best overall model indicated by bold Akaike information criterion (AIC).

Response Variable*	Power†	Severity Model		Tree Size/Crown Closure Model	
		Equation	AIC	Equation	AIC
i. Tree Size and Crown Closure					
PSIZE	1	$Y = (-0.67 + 0.1 \times AGE - 0.0012 \times AGE^2) - (1.34 + 0.0045 \times YR) \times S + (3.44 + 0.0099 \times YR) \times S^2 - (2.09 - 0.01 \times YR) \times S^3$	-80	n/a	
CC	1	$Y = (26.4 + 20.8 \times RF) - (94.8 - 15 \times YR) \times S + (371 - 36.8 \times YR) \times S^2 - (249 - 23 \times YR) \times S^3$	439	n/a	
ii. Plant Community Composition					
RFSIM	1	$Y = (0.51 + 0.0096 \times YR) - 0.38 \times S + 0.80 \times S^2 - 0.38 \times S^3$	-200	$Y = (0.48 + 0.021) \times YR - (0.001 - 0.0002 \times YR) \times CC$	-190
CONVG	1	$Y = 0.067 - 0.056 \times S$	-116	$Y = 0.08 - 0.001 \times CC_{10}$	-120
iii. Species Diversity:					
RICH	1	$Y = (39.7 + 0.43 \times YR) - (11.9 + 1.01 \times YR) \times S - (4.46 \times YR) \times S^2 + (4.18 \times YR) \times S^3$	385	$Y = (41.9 + 0.82 \times YR) - 0.22 \times CC$	386
EVEN	1	$Y = (0.75 - 0.0086 \times YR) + 0.28 \times S - 1.13 \times S^2 + 0.74 \times S^3$	-147	$Y = 0.82 - (0.0035 + 0.000086 \times YR) \times CC$	-159
EPIRICH	1	$Y = 12.7 + 7.1 \times RF$	149	$Y = 21.5 - 0.13 \times CC$	177
MYCRICH	1	$Y = 3.5 + 2.5 \times RF$	133	$Y = 0.26 + 2.96 \times PSIZE$	139
iv. Abundance of Management Indicator Species					
HAWK	1/3	$Y = (2.27 - 0.14 \times YR) + (0.67 + 0.56 \times YR) \times S - (1.23 \times YR) \times S^2 + (0.69 \times YR) \times S^3$	92	$Y = 2.41 - 2.41 \times PSIZE - 4.97 \times PSIZE^2 + 1.70 \times PSIZE^3$	99
NNAT	1/3	$Y = (2.22 - 0.13 \times YR) + (0.81 + 0.55 \times YR) \times S - (1.23 \times YR) \times S^2 + (0.69 \times YR) \times S^3$	92	$Y = Y = 244 - 2.49 \times PSIZE - 5.17 \times PSIZE^2 + 1.78 \times PSIZE^3$	98
BLUEB	0.5	$Y = (12.7 - 0.71 \times YR) - (49.8 - 3.87 \times YR) \times S + (86.2 - 6.63 \times YR) \times S^2 - (47.8 - 3.43 \times YR) \times S^3$	165	$Y = 5.24 - 0.048 \times CC$	187

BERRY	0.5	$Y = (6.54 - 0.21 \times YR) + (2.69 - 0.83 \times YR) \times S - (1.4 \times YR) \times S^2 + (0.78 \times YR) \times S^3$	177	$Y = 5.1 - 0.99 \times PSIZE$	183
COWWH	0.25	$Y = (1.1 - 0.032 \times YR) - (0.59 - 0.036 \times YR) \times BW$	23	$Y = (1.17 - 0.021 \times YR) - 0.0039 \times CC$	37
OROB	0.3	$Y = 1.18 - 0.04 \times YR - (0.69 \times BW - 0.07 \times YR) \times BW$	45	$Y = 1.22 - 1.08 \times PSIZE + 0.50 \times PSIZE^2$	66
C-RUST	1	$Y = 2.29e^{0.99S}$	91	$Y = 1.18e^{1.13 \times PSIZE}$	94
S-RUST	no satisfactory model due to low rates of stalactiform blister rust infection on lodgepole pine				

*defined in Table 1b.

†Value of the exponent in a normalizing power transformation of the dependent variable (1 = untransformed). Parameter estimates are for the transformed variable (also see Y axes in Figs. 3, 5-6).

Table 3. Results of a non-metric multi-dimensional scaling (NMDS) ordination of vegetation cover by species at Bednesti at 10 yr (5 treatments, 25 plots) and 25+ yr (7 treatments, 35 plots) with explanatory variables (defined in Table 1a) ranked by the strength of their fit (r^2) with the overall NMDS solution.

(a) NMDS Ordination Properties					
Input	Number	Output		Value	
Plots	60	Dimensions		3	
Species	134	Stress		0.1367623	
		Shepard plot non-metric fit:		R ² = 0.981	
(b) Correlations of Explanatory Variables with the NMDS Ordination					
Variable	r ²	Monte Carlo	Correlation Coefficients (r) with NMDS Axes*		
		P-value	Axis1	Axis2	Axis3
PSIZE	0.927	0.001	0.906	-0.411	0.100
AGE	0.886	0.001	0.997	-0.018	0.080
YR	0.880	0.001	0.942	-0.239	0.236
S	0.659	0.001	-0.326	-0.924	0.201
CC	0.541	0.001	-0.320	-0.944	0.085
NORTH	0.122	0.07	--	--	--
EAST	0.043	0.46	--	--	--

*For variables with $P < 0.05$, r-values are shown for each axis (strongest correlations highlighted).

Appendix Table A-I. Plant species codes from Figure 1b with scientific and common names and seral stage classification.

Codes	Scientific Name	Common Name	Seral stage [†]
Trees and Shrubs			
Al	<i>Abies lasiocarpa</i>	subalpine fir	late
Pc	<i>Picea</i> spp.	interior spruce and black spruce	generalist
Pn	<i>Pinus contorta</i> var. <i>contorta</i>	lodgepole pine	generalist (e)
Pt	<i>Populus tremuloides</i>	trembling aspen	generalist (e)
Av	<i>Alnus viridis</i> ssp. <i>crispa</i>	green alder	generalist
Li	<i>Lonicera involucrata</i>	black twinberry	generalist
Rl	<i>Ribes lacustre</i>	black gooseberry	generalist (l)
Ra	<i>Rosa acicularis</i>	prickly rose	generalist
Ri	<i>Rubus idaeus</i>	red raspberry	early
Sa	<i>Salix</i> spp.	willows	generalist (e)
Sb	<i>Spiraea betulifolia</i>	white meadow-sweet	generalist
Vm	<i>Vaccinium myrtilloides</i>	velvet-leaved blueberry	generalist
Native forbs and dwarf shrubs			
Ac	<i>Achillea millefolium</i>	yarrow	early
An	<i>Anaphalis margaritacea</i>	pearly everlasting	early
Cm	<i>Chimaphila menziesii</i>	Menzies' pipsissewa	late
Co	<i>Cornus canadensis</i>	bunchberry	generalist
Ea	<i>Epilobium angustifolium</i>	fireweed	generalist (e)
Ec	<i>Epilobium ciliatum</i>	purple-leaved willowherb	early
Fv	<i>Fragaria virginiana</i>	wild strawberry	early (g)
Ga	<i>Gentianella amarella</i>	northern gentian	early
Gr	<i>Goodyera repens</i>	dwarf rattlesnake orchid	late
Ha	<i>Hieracium albiflorum</i>	white hawkweed	early
Lb	<i>Linnaea borealis</i>	twinline	generalist
La	<i>Lycopodium annotinum</i>	stiff club-moss	late
Ld	<i>Lycopodium dendroidium</i>	ground-pine	late
Ml	<i>Melampyrum lineare</i>	cow-wheat	generalist
Os	<i>Orthilia secunda</i>	one-sided wintergreen	late
Vc	<i>Vaccinium caespitosum</i>	dwarf blueberry	generalist

Vi	<i>Viola</i> spp.	violets	generalists
Native graminoids			
As	<i>Agrostis scabra</i>	hair bentgrass	early
Cc	<i>Calamagrostis canadensis</i>	bluejoint reedgrass	generalist
Cr	<i>Calamagrostis rubescens</i>	pinegrass	generalist
Cx	<i>Carex</i> spp.	sedges	early
Fo	<i>Festuca occidentalis</i>	western fescue	generalist
Ja	<i>Juncus arcticus</i>	arctic rush	early
Je	<i>Juncus ensifolius</i>	dagger-leaf rush	early
Po	Poaceae	miscellaneous native grasses	generalists (e)
Non-native herbs			
Cs	<i>Cirsium arvense</i>	Canada thistle	early
Lc	<i>Lotus corniculatus</i>	birdsfoot trefoil	early
Hp	<i>Hieracium</i> spp. (<i>Pilosella</i> subgenus)	Pilosella hawkweeds	early
To	<i>Taraxacum officinale</i>	dandelion	early
Tr	<i>Trifolium</i> spp.	clovers	early
Bryophytes			
Ap	<i>Aulacomium palustre</i>	glow moss	generalist
Bh	<i>Barbilophozia hatcheri</i>	Hatcher's leafy liverwort	late
Bl	<i>Barbilophozia lycopodioides</i>	common leafy liverwort	late
By	<i>Bryum</i> spp.	thread-mosses	early
Br	<i>Brachythecium</i> spp.	ragged mosses	generalists (e)
Cp	<i>Ceratodon purpureus</i>	fire-moss	early
Di	<i>Dicranum</i> spp. (other than <i>D. polysetum</i>)	heron's-bill moss	late
Dp	<i>Dicranum polysetum</i>	wavy-leaved moss	generalist
Ep	<i>Eurhynchium pulchellum</i>	elegant beaked-moss	generalist (l)
Hs	<i>Hylocomium splendens</i>	step moss	late
Lo	<i>Lophozia</i> spp.	leafy liverworts	late
Pl	<i>Pleurozium schreberi</i>	red-stemmed feathermoss	generalist
Ph	<i>Pohlia</i> spp.	pohlia mosses	early (g)

Pj	<i>Polytrichum juniperinum</i>	juniper haircap moss	early
Pt	<i>Ptilium crista-castrensis</i>	knight's plume feather moss	late (g)
Pp	<i>Ptilidium pulcherrimum</i>	western naugahyde liverwort	generalist
Lichens			
Ce	<i>Cetraria islandica</i>	Icelandmoss	generalist
Hy	<i>Hypogymnia</i> spp.	bone lichens	epiphyte
Lp	<i>Pezizomycotina</i> lichens	miscellaneous lichens	epiphytes
Py	<i>Parmeliopsis hyperopta</i>	grey starburst	epiphyte
Ps	<i>Parmelia sulcata</i>	hammered crottle lichen	epiphyte
Pe	<i>Peltigera aphthosa</i>	silver-edge pelt lichen	generalist
Pg	<i>Platismatia glauca</i>	ragbag lichen	epiphyte
Rm	<i>Ramalina</i> spp.	ribbon lichens	epiphyte

t(e),(g) or (l) indicates that listed seral stage is transitional to early, generalist or late, respectively. Epiphytes may be generalists or late seral but require tree substrate and generally increase with age.

Note: Nomenclature throughout manuscript follows Klinkenberg (2017). 167 taxa were recorded (to the species or subgenus level). The NMDS included 134 taxa because epiphytes recorded only on sample pines at 25+ yr were excluded (no matching 10 yr data) and some infrequent or difficult taxa were lumped by genus or family. For display purposes, Fig. 1b and Table 1-A show 66 common or influential taxa and some related species with similar NMDS coordinates were lumped (e.g., Lp).

Reference

Klinkenberg, B. (Editor) 2017. E-Flora BC: Electronic Atlas of the Flora of British Columbia [online]. Univ. Brit. Col., Vancouver, BC. Available from: <http://www.eflora.bc.ca> [accessed 12 June 2017].

Figure 1

Best-fitting models for the relationship between site preparation severity (S) and (a) pine size ($PSIZE$) and (b) percent crown closure of all tree species (CC) (details in Tables 1, 2i). Unfilled circles, black circles and black squares represent 10-, 25- and 35-46-yr-old plots, respectively.

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First two axes of a non-metric multi-dimensional scaling (NMDS) ordination of plant community composition of (a) Bednesti treatment plots with overlain explanatory variables (Table 1a). Vertical lines indicate mid-points for samples of a given stand age. (b) Ordination of plant taxa that are common or strongly associated with the NMDS axes (label colour indicates seral stage: red = early, black = generalist, blue = late, green = epiphytic lichen; names in Table A-1). Ellipses outline location of 10-, 25-, and 35-46-yr old plots with symbols from (a) indicating centroids for each treatment.

190x254mm (300 x 300 DPI)

Figure 3

Best-fitting models for plant community composition response variables (a) *RFSIM* and (b) *CONVG* (described in Tables 1b, 2ii). In (a), unfilled circles and the dashed line depict 10-yr response; black symbols and the solid line depict 25+-yr response (square symbols compare each reference forest plot to 4 other reference forest plots). In (b), unfilled symbols and the solid line depict the mean change in community similarity between 1997 and 2012 with plots above the dotted line converging in composition, those below diverging, relative to all other plots.

254x190mm (300 x 300 DPI)

Figure 4

Similarity in plant species composition at 25 yr plotted against similarity at 10 yr for all pairs of plots sampled in both years (SH, DT, CM, FM, BW treatments). The diagonal line separates plot pairs that are converging between the two dates from plot pairs that are diverging. Symbols identify treatments for each plot pair.

254x190mm (300 x 300 DPI)

Figure 5

Best fitting models for species diversity response variables (a) species richness; (b) species evenness; (c) epiphyte species richness; (d) mycotroph species richness (details in Tables 1b, 2iii). Unfilled circles, black circles and black squares represent 10-, 25- and 35-46-yr-old plots, respectively. Dashed lines predict 10-yr response; solid lines predict 25- to 46-yr response; dotted vertical lines in (c) and (d) indicate low severity thresholds.

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Best fitting models predicting abundance of (a) *Pilosella* hawkweeds; (b) all non-native plants; (c) velvet-leaved blueberry; (d) all berry-producers; (e) cow-wheat; (f) all Orobanchaceae (details in Tables 1b, 2iv). Unfilled circles, black circles and black squares represent 10-, 25- and 35-46-yr-old plots, respectively. Dashed lines predict 10-yr response; solid lines predict 25- to 46-yr response; dotted vertical lines in (e) and (f) indicate high severity thresholds.

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Figure 7

Best-fitting poisson model predicting the cumulative number of pine trees infected by Comandra blister rust per plot between 1994 and 2012 (details in Tables 1b, 2iv).

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