

Range of Natural Variation in Structural Attributes of Young Stands: Refining Current Indicators

FIA-FSP Project no. Y071269

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Abstract

Most natural disturbances leave structural legacies that are used by a variety of organisms as forest regrows. Forest management prescribes retention of “wildlife tree patches” in harvested stands. Ecosystem-based management assumes that, as levels of retention move beyond natural levels, risk to biodiversity increases. This study estimates RONV for structural attributes remaining after fire, insects and wind disturbances within a variety of ecosystems of the SBS and ESSF biogeoclimatic subzones of interior BC, to allow risk assessment following a variety of management options.

We measured structural legacies (live and dead standing stems and downed wood) in 140 plots in 27 sites that had been disturbed by fire, wind and insects over the past 50 years. In the study area, fire caused the most extensive catastrophic disturbances; beetles were extensive, but often not catastrophic; wind disturbance was least common. We encountered considerable difficulty in locating unsalvaged disturbances and identified only four of wind or insect origin that were more than 10 years old.

Immediately following disturbance, fire left the most snags, and wind created the most downed wood. Even the most severe beetle disturbances left live trees. Wind and beetles left more large than small snags and downed wood. Size-class distribution of snags following fire initially was negatively exponential, but became unimodal over time as the smallest snags fell.

A multivariate classification model was able to distinguish between the three types of disturbance. Overall, the range of natural variability was large, and covered all possible values of retention. However, the mean and standard deviation of numbers of snags and volume of downed wood left after disturbance can guide risk analyses.

April 30, 2007

Keywords: snags, coarse woody debris, large live trees, stand structure, natural disturbance, young seral, wildlife tree patch

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Introduction

Structural attributes of old forests, including downed wood, large live trees, dead and decaying trees, and patches of shrubby vegetation, provide critical habitats for a variety of mammals, birds, invertebrates, plants and lichens (Bunnell et al. 2003, Price and Hochachka 2001, Schoonmaker and McKee 1988). Most natural disturbances leave some structural attributes in the newly-regenerating stand (Hansen et al. 1991, Franklin et al. 2000). Legislation (e.g., Forest and Range Practices Act) and land-use plans (e.g., Sustainable Resource Management Plans, Landscape Unit Plans, Forest Stewardship Plans) prescribe retention of wildlife tree patches — with a variety of structural features — in young managed stands. However, high uncertainty about the threshold amount of structure needed to maintain biodiversity currently limits the usefulness of wildlife tree patches as an indicator of sustainability. A risk assessment undertaken by the Babine Watershed Monitoring Trust (www.babinetrust.ca) highlighted resolution of this uncertainty as a top priority within the Central Interior of BC.

Currently, many managers are setting targets for stand-level retention with little or no science to support those targets. For example, in areas with high mountain pine beetle infestation, the target for stand structure retention has been doubled from the provisions in provincial policy to reflect the widely held belief that disturbance by mountain pine beetles would leave high levels of structure (MSRM 2003). The question remains, however: What portion of harvested stands should be included within wildlife tree patches to minimise the impacts of forestry on biodiversity?

Two complementary lines of research address this question: first, studies can examine the response of selected species to different amounts of structure, providing good answers for some species but in a “piece-meal” approach; second, research determining the range of natural variability (RONV) of structural attributes for particular ecosystems provides a more holistic, coarse-filter, approach. The latter approach assumes that organisms have adapted to RONV, and likely provides a less accurate answer for a given species. It can, however, provide broadly applicable answers that can be implemented relatively quickly. Analogous to efforts to maintain biodiversity over the landscape, an efficient approach defines coarse-filter thresholds based on RONV, and modifies thresholds for species of particular interest based on fine-filter research.

Much work has been undertaken to define the RONV for the frequency and size of disturbance (Bergeron et al. 2002, DeLong 2002), but little has described the RONV for stand-level attributes remaining after disturbance (Bergeron et al. 1999, Franklin et al. 2000; but see related work in Prince George area by DeLong and Kessler 2000). Estimates of RONV in post-disturbance structural attributes must consider six factors. First, different types and intensities of disturbance leave different structural legacies (Franklin et al. 2000). In the area of interest, fire and insects are the primary stand-replacing disturbance agents, with windthrow secondarily important, particularly as it interacts with other agents (Burton et al., 2005). Second, ecosystems (represented by biogeoclimatic subzones and site series groups) vary in their susceptibility to disturbance agents because of differences in climate, age structure and species composition (Stocks et al. 2002, Burton et al., 2005). Third, ecosystem productivity (site series groups) influences structural attributes. Fourth, stand type and age prior to disturbance also limits the structure that can remain. Fifth, structural legacies change over time as trees grow and die, snags

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fall and downed wood decays (Hansen et al. 1991, Franklin et al. 2000, Lofroth 1998, DeLong et al. 2005). Sixth, remnant patterns can vary with disturbance size (Eberhardt and Woodard 1987, Anderson 2004).

This study estimates RONV for structural attributes remaining after fire, insects and wind disturbances within a variety of ecosystems of the SBS and ESSF biogeoclimatic subzones of interior BC. It looks at changes in structural legacies over time by examining a chronosequence of stands disturbed over the past 50 years. The data are also used to test a disturbance classification system that considers the amount and dispersion of overstory removal, understory removal and forest floor disturbance (Roberts 2004). This system aims to provide a more complete characterisation of disturbance, to help in the design of management techniques that better mimic natural processes, and to aid our understanding of the impact and implications of existing management practices.

Methods

Study Area

The study area includes the SBSmc2 and ESSFmc subzones of the Northern Interior Forest Region, with field work completed in and around the Babine River Watershed of the Skeena-Stikine Forest District (centred on 1:250,000 NTS sheet 93M, but expanded to include sheet 93L and parts of 93E to increase sample size). The Babine Watershed is the focus of a series of special management requirements, in which forestry activities are expected to protect high-value salmon, grizzly bear, biodiversity and wilderness resources (see www.babinetrust.ca).

Study Design

We characterised RONV in the density and size-class distribution of large live trees, snags and downed wood in young (< 50 years), naturally-disturbed stands of different disturbance origin (fire, bark beetle, windthrow) in two biogeoclimatic subzones (SBSmc2 and the ESSFmc). Within subzones and disturbance types, we sampled in different site series groups (mesic, mesic-rich and mesic-poor), as available, to control for productivity. We used the age of standing trees to attempt to eliminate immature prior stands. Rather than stratifying by disturbance size and time since disturbance, we included a range of disturbance sizes and stand ages in our sample.

We examined disturbances at three scales, landscape, disturbance and within-disturbance, using existing databases, air photo interpretation and field sampling respectively.

Landscape Scale: Existing Databases

At the broadest, landscape scale, we searched for fire and beetle disturbances using the BC Natural Disturbance database for beetles and fire and current Forest Cover mapping for fire. We filtered beetle disturbance data in the Natural Disturbance database for severity, keeping disturbances described as over 30% disturbed (the most severe category listed) with a stand composition of over 50% of the target species. This filtering eliminated the least severe attacks but still necessitated reconnaissance surveys prior to detailed ground surveys. Existing databases

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did not list wind disturbances. We augmented our list of disturbances through discussion with local ecologists and foresters, and through an aerial reconnaissance flight.

We assessed prevalence of different disturbances qualitatively.

We then selected disturbances to study more closely that matched with our sampling design, that had not been salvage-logged (or at least, had unsalvaged portions), and that were recorded on air photos.

Disturbance Scale: Air Photo Interpretation

At the disturbance scale, we used existing Forest Cover mapping to ascertain the size and extent of disturbances originating from fire, and used a combination of aerial photographs and maps derived from the Natural Disturbance Database to estimate the size and extent of disturbances originating from bark beetle attack or wind. Measures of bark beetle and wind disturbances were necessarily approximate, as the boundaries were not well defined and, in the case of recent beetle attacks, are still fluid. Within disturbances, we examined and interpreted historical and recent photos as available. We estimated the area of undisturbed remnant patches and estimated the proportion of the total area with varying densities of standing live trees within using standard stereogrammetry and parallax techniques. For very large disturbances, we limited air photo interpretation to a subsample of the disturbed area, the selection of which was generally determined by air photo availability. Snags were not possible to assess remotely, especially when mixed with live trees.

Air photo interpretation was not possible for recent or current disturbances, because they are not identifiable on existing (2003 or earlier) air photographs. For older disturbances, we typed disturbance severity and estimated canopy closure using a fairly conservative assessment of the disturbance boundary, to avoid including large areas of edge where disturbance severity was minimal.

Within-disturbance Scale: Field Sampling

At the finest scale, we used field sampling to examine structure within disturbed areas. We sampled all accessible, unsalvaged disturbed stands up to a maximum of 6 sites per disturbance type/subzone combination. At most sites, we used 3 to 9 plots to capture variation in disturbance intensity and/or site differences within a disturbance, increasing sampling effort with increasing patch size and heterogeneity (Table 1). We used two plots in each of three small sites resulting from the same wind storm, and a single site in a small, partially-salvaged mountain pine beetle disturbance.

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Table 1. Characteristics of disturbances used to estimate the range of natural variability in structural legacies.

Site	Disturbance Type ¹	Age ²	Number of plots						
			ESSFmc			SBSmc2			Total
			M ³	MP	MR	M	MP	MR	
Upper Fulton East	SB and MPB	2				3		3	6
Blunt 226 Rd	BBB	1	3		3				6
Blunt FSR 20-23km	BBB	1	4		3				7
Goat Mtn	BBB	1	1		3				4
Howson Cr BBB	BBB	1			2			4	6
Nichyeskwa 455 Rd	BBB	2						3	3
Babine River MPB	MPB	1				4			4
Howson Cr MPB	MPB	1					1		1
Bulbous Toe	MPB	2				2	4	1	7
Klo Fire	Fire	1	4		4				8
Smithers Landing Fire	Fire	1				3			3
Babine River	Fire	2				4		4	8
Boucher Cr/Lake/465 Rd	Fire	2				5		2	7
McKendrick Pass	Fire	2	1		2				3
Swiss Fire	Fire	2	4	1	3				8
Torkelson	Fire	2				3			3
Upper Fulton B	Fire	2				3	1	3	7
Onion Fire	Fire	3	3	2		4			9
Otto Fire	Fire	3	3		3				6
Upper Van Fire North	Fire	3	4		4				8
Upper Van Fire South	Fire	3				3			3
Van Fire	Fire	3				1		6	7
Francois Lake Woodlot	Wind and MPB	1				3		3	6
Gates Rd A	Wind and MPB	1						2	2
Gates Rd B	Wind and MPB	1				1		1	2
Gates Rd C	Wind and MPB	1				2			2
Chisholm Lake	Wind	2				4			4
Total			27	3	27	45	6	32	140

¹ BBB = balsam bark beetle; SB = spruce beetle; MPB = mountain pine beetle

² 1 = disturbed 1998 – 2007; 2 = disturbed 1978 – 1998; 3 = disturbed 1958 – 1978

³ M = mesic; MP = mesic-poor; MR = mesic-rich site series

Disturbance types were not distributed equally or independently. Almost all balsam bark beetle disturbances were within the ESSFmc subzone, while all mountain pine beetle disturbances, as well as wind disturbances, were within the SBSmc2 subzone. The Upper Fulton East site was the result of at least two different disturbance agents (mountain pine beetle and spruce beetle), and may have been impacted by wind as well. The recent windthrow sites included trees killed by mountain pine beetles. Other sites seemed to have resulted from a single disturbance agent. We

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have a complete range of ages (i.e. time since disturbance chronosequence) for fire-initiated stands but not for bark beetle attack or windthrow.

At each plot, we assessed site series (Banner et al. 1993) to indicate productivity, and noted elevation and aspect. We measured and classified downed wood along a triangular, 90-m transect, recording standard information including diameter, decay and length class (BC MELP and BC MOF 1998). We measured all pieces > 7.5 cm diameter for the first 15m of each transect leg, and pieces > 20 cm diameter for the remaining 15 m to provide a better representation of large pieces (Lloyd, 2005). Within three 5.64-m sub-plots (100m² area), one at each apex of the triangle, we measured and classified standing residual trees (live and dead) over 7.5 cm dbh that were considered to have been present prior to the disturbance. We also recorded crown closure at four points within each sub-plot and noted the % of disturbed soil and residual shrubs.

Data Analysis

We analysed the data using descriptive statistics, aiming to define patterns as hypotheses for future testing. We calculated the number of standing live and dead stems per hectare, and volume of downed wood per hectare. Because we consider each site as an independent sample, we then averaged the values across plots to give a single estimate per site. We explored patterns in structural attributes as a function of disturbance type, time since disturbance, subzone and productivity using univariate and multivariate models, removing non-significant interaction terms, and transforming data to improve normality as appropriate. We examined data from plots within sites to look at heterogeneity within sites (based on coefficient of variation in stem number among plots). We also examined patterns related to productivity within stands to control for high variation among stands. We combined classes when we were unable to detect differences among them. We stratified analyses as necessary to look at structure within and outside remnant patches.

We used principal components analysis (PCA) to summarise 51 structural attributes (including the abundance and composition – coniferous or deciduous – of different size classes of live trees, dead trees, and downed wood) in terms of two or three dominant eigenvectors. We plotted eigenvalues in multivariate space and used analysis of variance to discern if disturbance type, time since disturbance, subzone and productivity generated significant differences in these multivariate stand attributes. The SAS procedures GLM, CORR and REG (SAS Institute 1992) were used for analysis of variance and analysis of covariance in exploring differences and trends in factors potentially affecting stratum-based disturbance differences and PCA scores. We further looked for natural disturbance clusters to help us evaluate the Roberts (2004) system of disturbance classification, the degree to which it can be applied to fire, insect, and windthrow disturbances, and whether the three Roberts' three dominant axes (overstory, understory, and forest floor disruption) were well correlated with the trends in residual structure recognized by the PCA analysis.

Results

Landscape Scale: Existing Databases

Within 1:250,000 NTS sheet 93M (including most of the Babine Watershed), the BC Natural Disturbance Database records many stands disturbed by bark beetles, and a few by fire over the past decade (Table 2). The database does not record wind disturbances.

Table 2. Number of polygons and area affected by fire and bark beetles in common biogeoclimatic subzones in and around the Babine Watershed within the last decade (Taylor 2005, <http://www.pfc.forestry.ca/fires/disturbance/>)

BEC subzone	Fire		Mountain Pine Beetle		Spruce Beetle		Balsam Bark Beetle	
	#	Ha	#	Ha	#	Ha	#	Ha
SBSmc2	3	2,900	315	2,500	13	600	130	54,000
ESSFmc	3	235	24	100	5	900	138	87,000

These data, however, are somewhat misleading. While there have been comparatively few fires within the last decade, there have been several large fires and numerous small ones within the last 50 years. Not all of these were recorded in the Natural Disturbance Database. Balsam bark beetles have disturbed large areas, but rarely at a severity sufficient to replace stands. In general, bark beetle disturbances are less well-defined than fires, spreading over a much longer time frame. Mountain pine beetle disturbances have generally been smaller and less extensive in the study area until the recent wave. Of those listed, more than 90% were less than 1ha in area, and we only found one unsalvaged disturbance more than a decade old. Spruce beetles have also been a less extensive disturbance agent in the study area, and stands have generally been salvaged soon afterwards. We found a single disturbance with evidence of unsalvaged spruce beetle attack.

Wind is rare within the study area. Although blowdown is common along some block edges (Burton, 2001), finding wind-disturbed stands was challenging. We expanded the geographic scope of our study slightly to include stands disturbed by 1994 and 2004 windstorms to the south and east within the Morice TSA.

From closer examination of the disturbance database as well as the forest cover database and discussions with local ecologists and foresters, filtering out those (particularly bark beetle) disturbances affecting only small portions of a stand, we conclude that fire has been the dominant stand-replacing disturbance over the past 50 years in the SBSmc2 portion of the study area (Table 3). Balsam bark beetles are the most prevalent disturbance agent within the ESSFmc, although not all of the area listed is severely disturbed.

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Table 3. Number of polygons and area affected by fire and moderate-severe bark beetle attack in common biogeoclimatic subzones in and around the Babine Watershed (93M mapsheet; fires since 1956, beetle attack since 1975)

BEC subzone	Fire		Mountain Pine Beetle		Spruce Beetle		Balsam Bark Beetle	
	#	Ha	#	Ha	#	Ha	#	Ha
SBSmc2	16	14,843	1830	1,065	139	4,593	15	3,047
ESSFmc	6	4,506	20	3	12	268	20	9,320

Levels of salvage logging were considerably higher than we had anticipated. Many natural disturbances were completely modified, and hence unavailable for study. For example, a 1986 mountain pine beetle attack in the Morrison, and a mountain pine/spruce beetle disturbance along Chapman Lake in the late 1980's have been salvaged completely. These disturbances are not included in the BC Natural Disturbance database. Salvage was biased to more productive stands on flat ground; hence our sample was biased to less productive stands on steep ground.

Disturbance Scale: Air Photo Interpretation

Within the northern part of the Bulkley TSA, which includes the middle and upper part of the Babine watershed, we located 18 forest fires dating from since 1958, in which unsalvaged portions likely remained. Other fires have likely occurred during this time, but are no longer easily detectable on the landscape. The detected fires ranged in size from 5 ha to about 9,000 ha, with most (13 out of 18) being less than 100 ha (Table 4).

Table 4 Size distribution of fires with unsalvaged areas in the northern part of the Bulkley TSA

Fire area (ha)	no. of incidences
<10	2
10-100	11
100-1000	3
>1000	2

Of the 18 fires, only the largest four had identifiably undisturbed polygons within them (Table 5). Smaller fires included areas of residual trees and shrubs, but these were either too small to delineate at the scale of the photograph, or were complexed with areas that had been burned. Most of the disturbance area (from two-thirds to all of the disturbance) had less than 5% canopy cover remaining.

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Table 5 Area and disturbance severity in nine study fires in the northern part of the Bulkley TSA

Site	total area (ha)	undisturbed area (ha)	canopy cover estimate (% of disturbed area)			
			<5	5-15	15-25	25-35
Babine River	18	0	85	15	0	0
Boucher Cr	32	0	81	9	10	0
McKendrick Pass	42	0	93	0	7	0
Torkelson	7	0	100	0	0	0
Upper Fulton B	97	0	76	12	12	0
Onion Fire	421	40	81	17	2	0
Otto Fire	1423	129	64	25	11	0
Upper Van Fire	838	3	94	3	3	0
Van Fire	9007	254	76	23	1	0

Defining the limits of bark beetle effects proved more challenging, because the intensity of attack was highly variable, and the results depended on the tree species composition of the affected stand. The filtered disturbances (severity > 30%; > 50% target species) generally followed a Poisson distribution with disturbance size (Table 6). The pattern of mountain pine beetle disturbances will likely change as the outbreak develops within the study area.

Table 6 Area and number of polygons affected by moderate-severe beetle outbreak (93M mapsheet)

BEC subzone	disturbance area (ha)	disturbance agent		
		mountain pine beetle (no. polygons)	spruce beetle (no. polygons)	balsam bark beetle (no. polygons)
SBSmc2	<5	1803	62	9
	5-10	10	24	0
	10-100	16	46	2
	100-1000	1	6	3
	1000+	0	1	1
ESSFmc	<5	20	6	12
	5-10	0	3	0
	10-100	0	2	2
	100-1000	0	1	3
	1000+	0	0	3

Unfortunately, aerial reconnaissance during August 2006 showed that almost all of the areas identified had either been salvaged or were of limited severity. We located one unsalvaged mountain pine beetle area of recent origin in the northern part of the Bulkley TSA, one in the

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southern part, and one of 1980s origin in the southern part. We were unable to locate any unsalvaged spruce beetle areas, although one area was thought to be of mixed mountain pine beetle and spruce beetle origin, from the 1980s. Aerial reconnaissance confirmed the presence of two or three very large BBB disturbances of current origin in the northern part of the Bulkley TSA, and another in the south part. These disturbances were patchy, but in some areas exceeded 50% of the stand. Only one unsalvaged balsam bark beetle disturbance of older (1980s) origin was locate, less than 5 ha in extent.

In contrast with fire disturbance, canopy cover remaining after both wind and beetle disturbance was generally higher than 5%. Balsam bark beetles, in particular, left high canopy cover across the entire disturbed stand (Table 7).

Table 7 Area and disturbance severity in four beetle and wind disturbances in the northern part of the Bulkley TSA

Site	Disturbance agent	total area (ha)	canopy cover estimate (% of disturbed area)				
			<5	5-15	15-25	25-35	35-45
Bulbous Toe	MPB ¹	100	0	43	32	7	18
Upper Fulton E	MPB + SB	33	0	27	21	51	0
Nichyeskwa	BBB	35	0	0	31	69	0
Chisholm Lake	Wind	25	0	0	61	24	14

¹ BBB = balsam bark beetle; SB = spruce beetle; MPB = mountain pine beetle

Within-disturbance Scale: Field Sampling

Effects of Disturbance Type

Measured in the first decade after disturbance, fire left few live trees and created three times more snags than either wind or beetles (Figure 1a). Snags in windthrown stands mostly resulted from tree death prior to the wind disturbance (primarily due to mountain pine beetles). Wind created three times more downed wood than fire or beetles (Figure 1b). Downed wood in recent fire- or beetle-initiated disturbance probably originated mainly from tree and snag fall prior to the disturbance, rather than from the disturbance itself.

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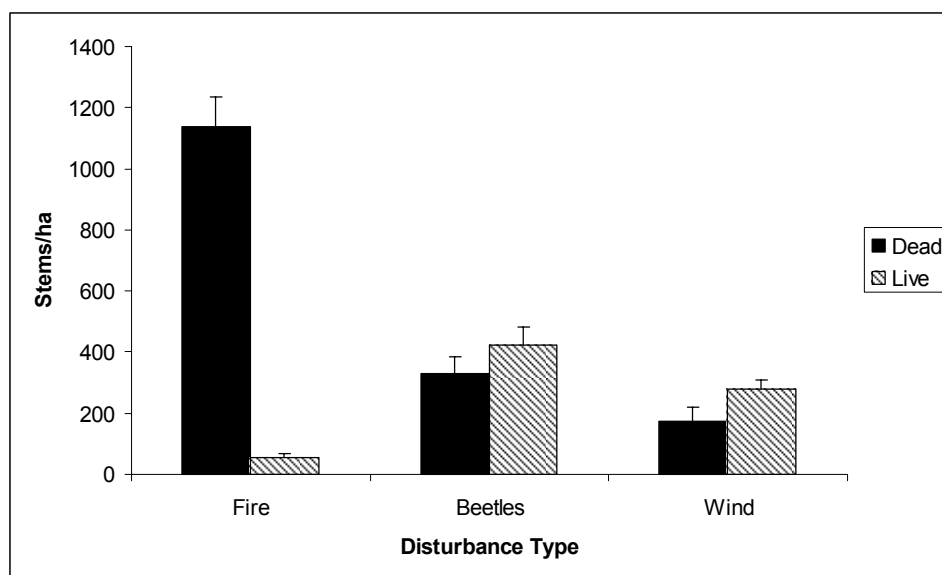


Figure 1a. Number of standing dead and live trees remaining within the first decade after disturbance by beetles, fire and wind (bars are standard error; fire $n = 2$; beetles $n = 6$; wind $n = 4$; live trees: $F_{2,9} = 8.8$, $p = 0.008$; dead standing: $F_{2,9} = 40$; $p < 0.001$).

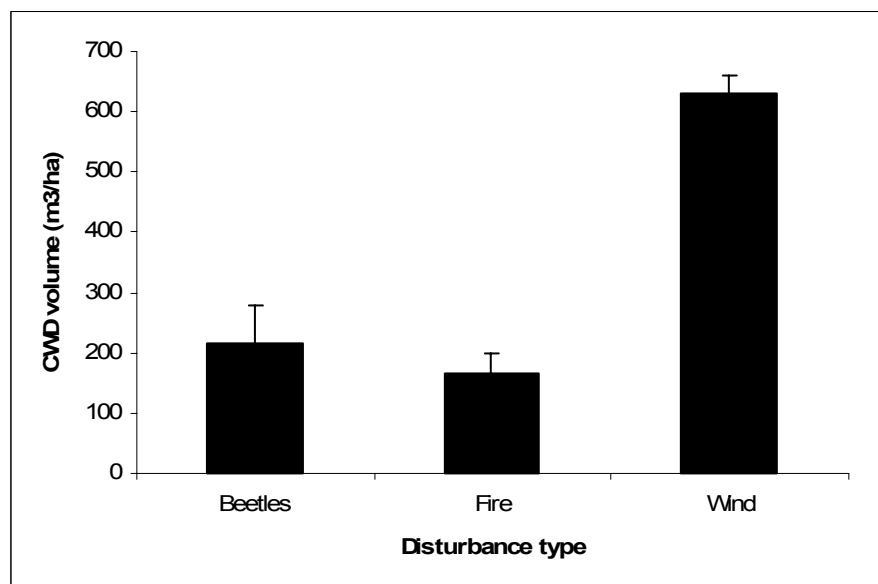


Figure 1b. Volume of downed wood present within the first decade after disturbance by beetles, fire and wind (bars are standard error; downed wood: $F_{2,9} = 17.6$, $p = 0.001$).

Remnant live trees within fires were distributed more patchily than were remnants within wind and beetle-disturbed stands (Figure 2; $F_{2,23} = 10.8$; $p < 0.001$). Snags were distributed more patchily in windthrown stands ($F_{2,19} = 36.5$; $p < 0.001$). This latter result is likely due to patchy death due to mountain pine beetles rather than a feature of wind disturbances (all recent wind disturbances included patches of mountain pine beetle mortality).

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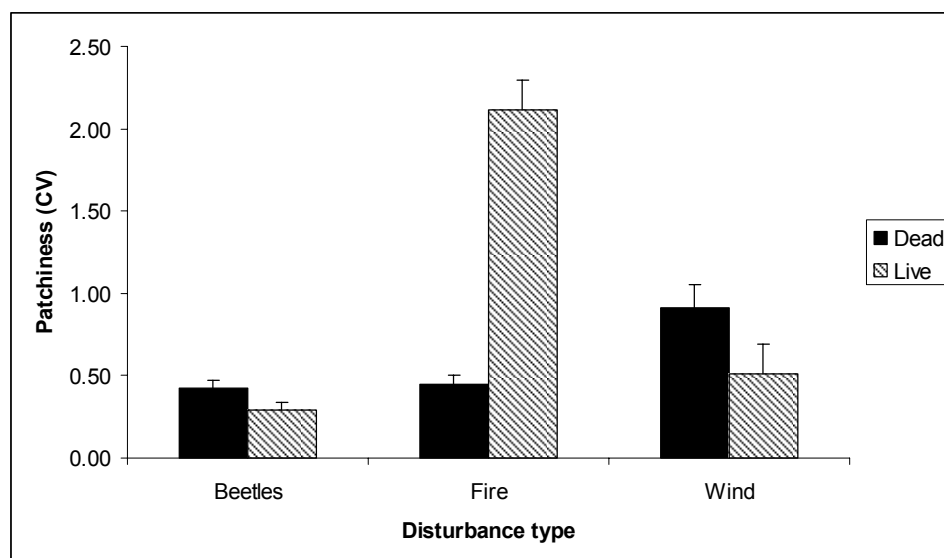


Figure 2. Patchiness (coefficient of variation of number of stems among plots within sites, averaged across sites; bars are standard errors; disturbed over past 50 years) in dead and live standing structure after disturbance by beetles, fire and wind.

Because of the patchiness in remnant structure within fire disturbances, we stratified plots by severity (two classes: partial and total disturbance) to calculate mean number of stems remaining (Table 8). While snags were uniformly distributed in partial and total disturbance plots, live trees were not, although sample size of recent disturbances was too small ($n = 2$) to analyse.

Table 8. Estimates of standing dead and live trees following fire by disturbance severity ($n = 2$ fires in past decade).

Status	Partial disturbance	Total disturbance
Dead standing	1139 \pm 83	1108 \pm 151
Live	330 \pm 198	0 \pm 0

The diameter-class distribution of snags varied by disturbance type. Following fires, remnant snags followed the reverse-J distribution typical of an undisturbed old forest (Figure 3). Live trees left after beetles and wind also followed the reverse-J distribution, but dead trees did not. Beetles preferentially killed larger trees: in diameter classes above 27.5 cm, there were more dead than live trees; in small classes, there were more live trees (Figure 3). Snags in windthrown stands were dominated by larger trees. Although smaller trees in the sub-canopy would be more protected from wind, we suspect that this result is due to selection by mountain pine beetles rather than selection by wind. Fires left very few live trees; these were located in skipped patches defined as “partial” disturbances above.

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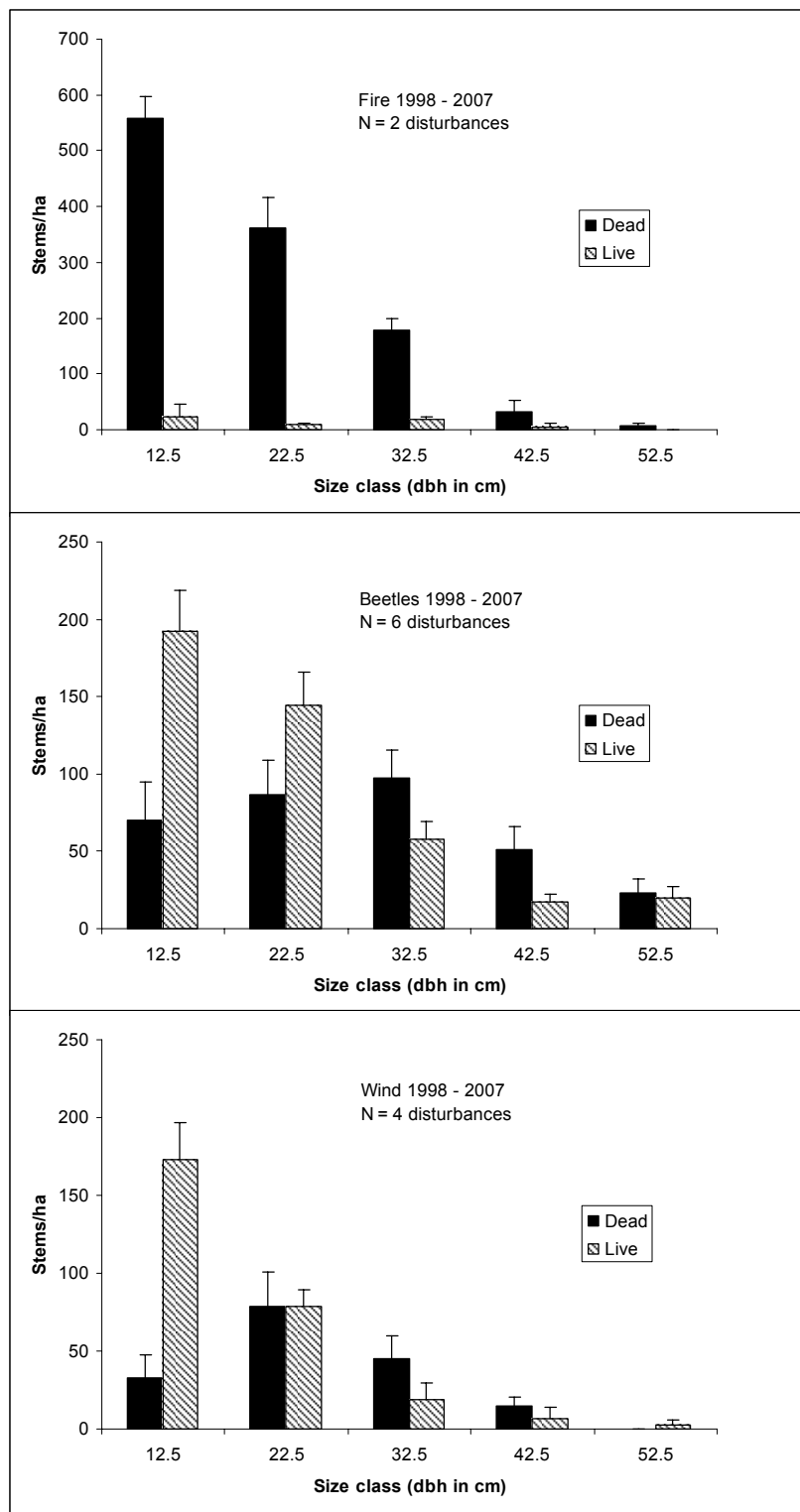


Figure 3. Diameter-class distribution of standing live and dead trees in the first decade after stand-replacing disturbance caused by beetles, fire or wind (Y-axis for fire is a different scale; bars are standard errors).

Differences Among Ecosystems

Within disturbances, subzone and productivity (based on groups of site series) had little influence on the standing live and dead structure except in stands disturbed by balsam bark beetles. In mesic stands within the ESSFmc, 75% (6/8) plots had more dead than live subalpine fir; in mesic-rich stands within the ESSFmc, 45% (5/11) plots had more dead than live fir; and in mesic-rich stands within the SBSmc2, 0% (0/5) plots had more dead than live fir. This pattern likely reflects a change in the proportion of subalpine fir in the stand, with beetles killing a smaller proportion of fir in mixed stands (Figure 4).

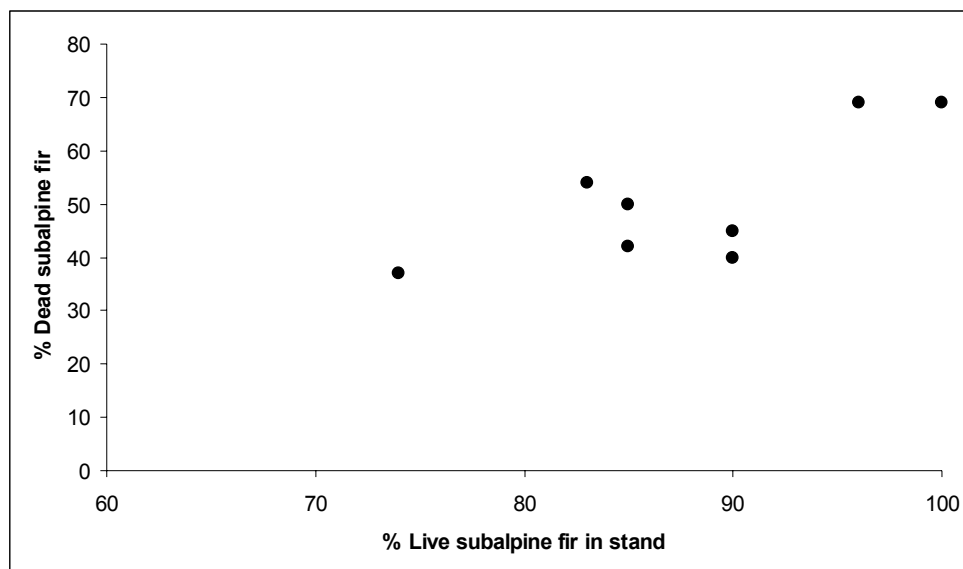


Figure 4. Percent of dead subalpine fir within a stand as a function of the amount of fir in the stand ($F_{1,6} = 10.8$; $p = 0.02$ based on transformed data).

Similarly, subzone and productivity had relatively little influence on downed wood volumes compared to disturbance type. Within disturbance types, mesic-rich sites had a higher proportion of large-diameter downed wood (chi-squared test, $P < 0.01$); no other patterns were apparent.

Change in Remnant Structure over Time

Our data provide reasonable estimates of changes over time for fire disturbance, but not for beetles or wind. We found a single wind disturbance over 10 years old; and hence cannot generalise beyond this case. Neither can we generalise about beetles: the single balsam bark beetle disturbance and single mountain pine beetle disturbance older than 10 years show different patterns.

Over time after a disturbance, the number of snags decreases, while the number of live trees does not change (Figure 5a; Dead standing: $F_{1,11} = 12.5$; $p = 0.005$; Live: $F_{1,11} = 1.1$; $p = 0.3$). Downed wood volumes increase as snags fall (Figure 5b; $F_{1,11} = 6.6$; $p = 0.03$).

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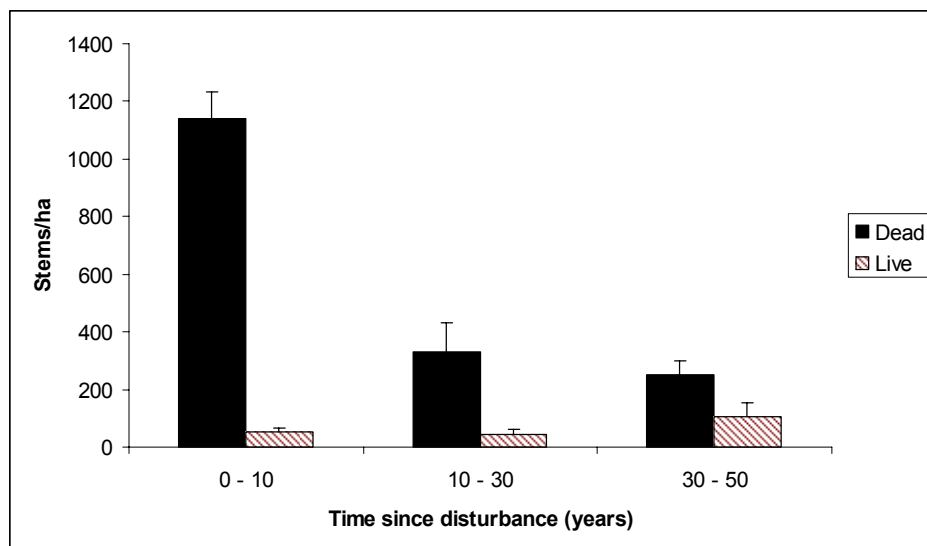


Figure 5a. Number of standing dead and live trees remaining after disturbance by fire (bars are standard error)

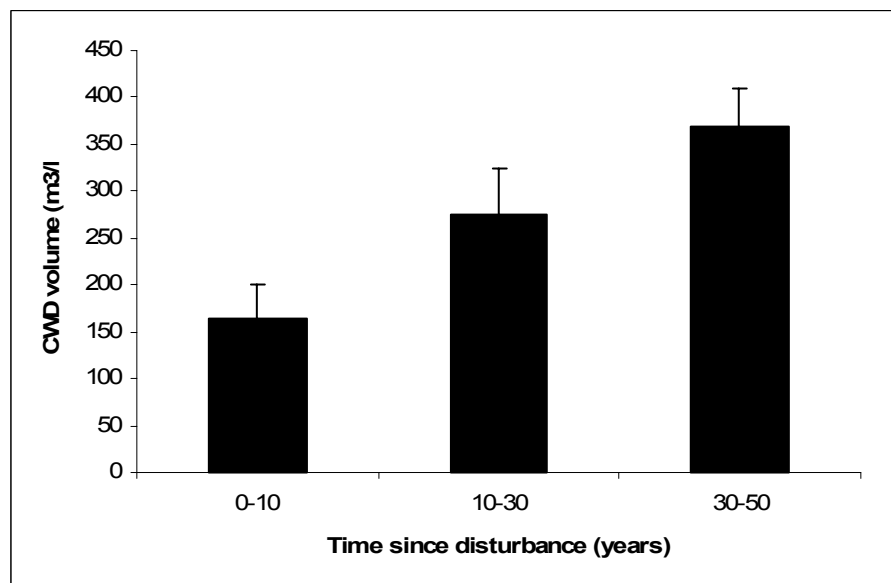


Figure 5b Change in mean volume of downed wood over time since disturbance by fire (bars are standard error)

Over time, the reverse-J distribution in diameter class distribution of standing dead trees left by fire changes (Figure 6a-b). The smallest snags no longer represent the biggest group, likely because they have fallen and recruited into downed wood. The total number of standing dead trees also decreases. The number of live trees in the smaller diameter classes is higher in the older fires (Figure 6a-b). These trees may be post-disturbance colonisers, or may have been released following the disturbance. The latter is more likely because these small trees are usually

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subalpine fir and spruce rather than pine. Conversely, the higher number of live trees in the older fires may be an artefact of disturbance size: the older disturbances are larger, with a higher proportion of skipped areas (see Table 5).

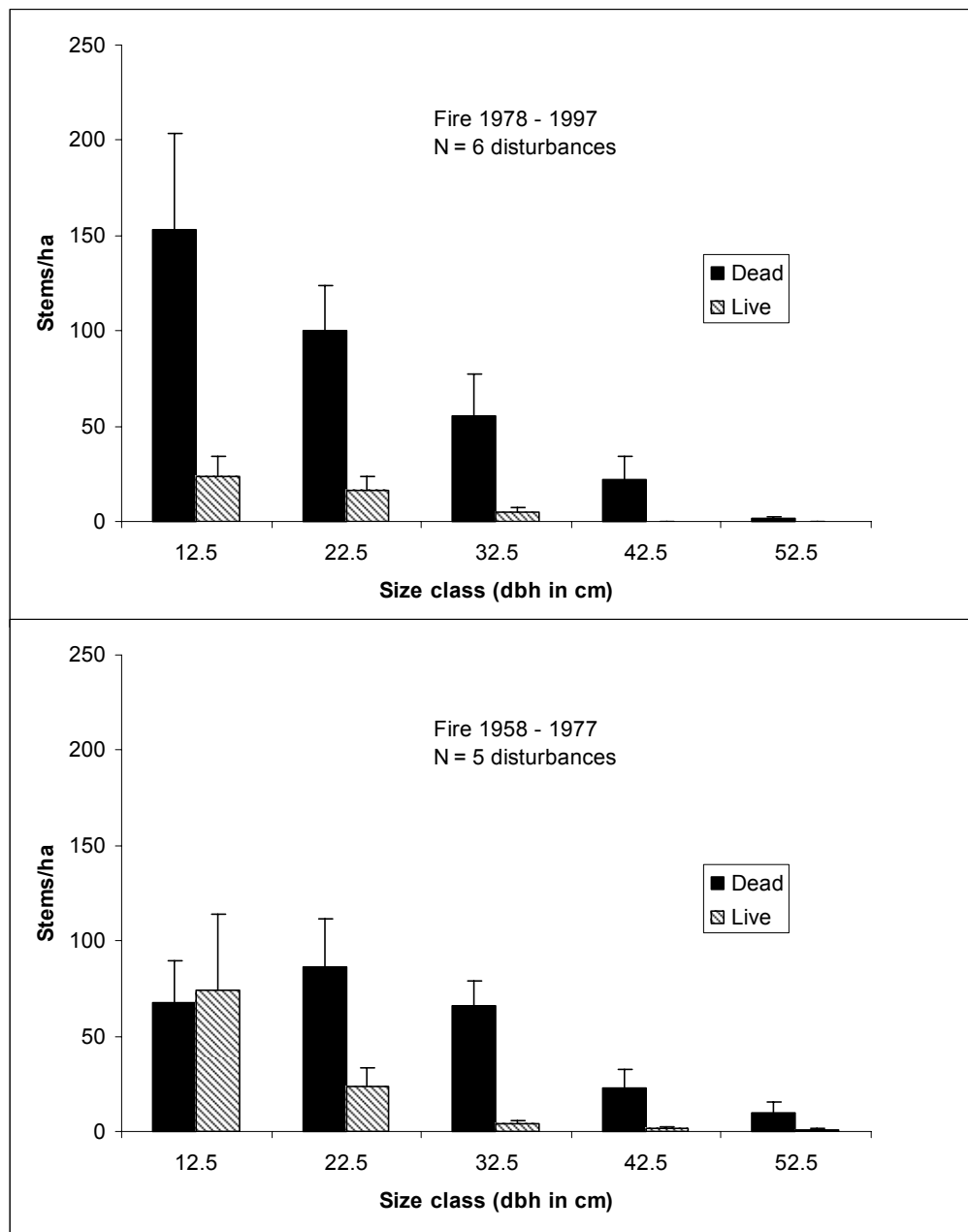


Figure 6. Change in diameter-class distribution of live and dead standing trees over time since disturbance by fire (compare with Figure 1a for first decade after disturbance; bars are standard errors).

The legacy of patchiness (see Table 8) in live trees after fire continued over time (effect of time since disturbance: $F_{1,19} = 1.6$; $p = 0.2$; effect of severity: $F_{1,19} = 52$; $p < 0.001$), while dead stems

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continued to be uniformly distributed within disturbances (effect of time since disturbance: $F_{1,18} = 17.9$; $p < 0.001$; effect of severity: $F_{1,18} = 0$; $p = 1$).

For downed wood, volume and diameter class distribution in the first decade reflected downed wood present prior to disturbance (Figure 7). In subsequent decades, the volume and proportion of large-diameter logs was higher, perhaps as fire-killed snags fell and were recruited into the downed wood. The older sites had more downed wood in all size classes, but a higher proportion in the larger classes.

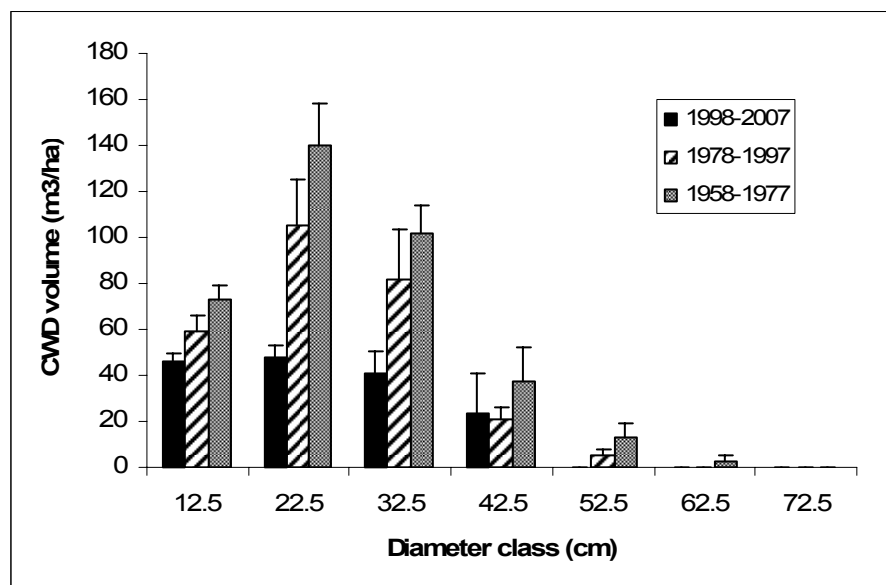


Figure 7 Change in diameter-class distribution of downed wood over time since disturbance by fire (bars are standard error).

Analyses of decay class corroborates this pattern. In recently-disturbed sites, the downed wood present after a fire represented a range of decay classes from sound and recently fallen (decay class 1) to soft and powdery (decay class 5). This suggests that much of the volume present at this stage originated prior to the disturbance (Figure 8). In older sites (10-50 years after disturbance), there was a large volume of moderately sound to somewhat decayed wood (decay classes 2-3), likely a result of snag fall since the disturbance. 10 – 30-year-old disturbances had the highest volume of decay in classes 2 and 3; 30 – 50-year-old disturbances had the highest volume in classes 3 and 4 (Figure 7). This shift likely represents a pulse of recruitment from snag fall.

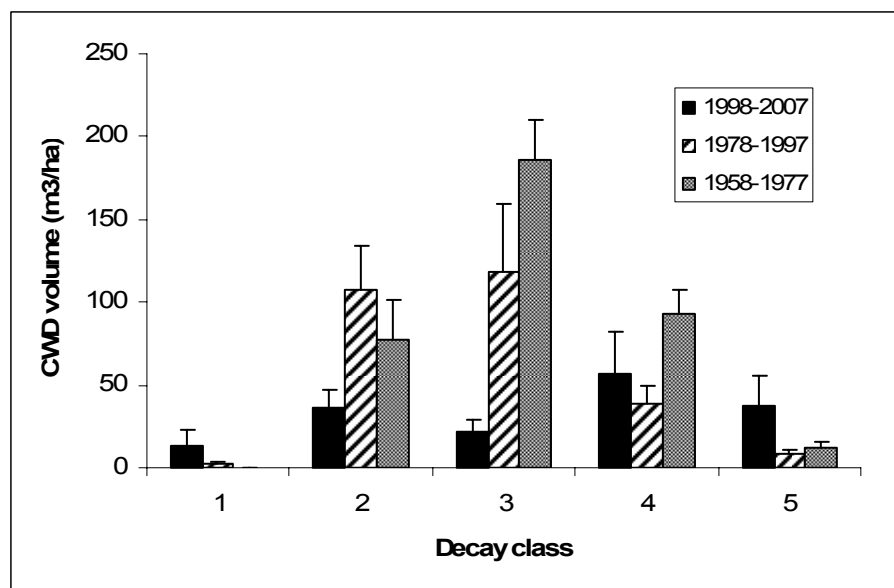


Figure 8 Change in decay class distribution of downed wood over time since disturbance by fire (bars are standard error).

Most fire-disturbed sites had little or no volume in decay class 1 (sound logs with bark and branches still attached), even when snags were present and snag fall was therefore likely. Older fire sites lacked decay class 1 downed wood altogether, and it is likely that newly-recruited downed wood would be assigned to a more advanced decay class regardless of time since fall. Decay class 1 logs were more consistently present in beetle-disturbed sites (7 out of 9 sites, including 3 out of 3 sites 10-30 years old), although mean volumes were low (<25 m³/ha). Decay class 1 logs accounted for nearly half the volume present in young wind-disturbed sites but were not present in the single site that was 10-30 years old (Figure 9). Decay class 1 logs are more likely to originate from fallen green trees, whereas snags of fire origin may have lost the attributes of decay class 1 logs at the time of disturbance.

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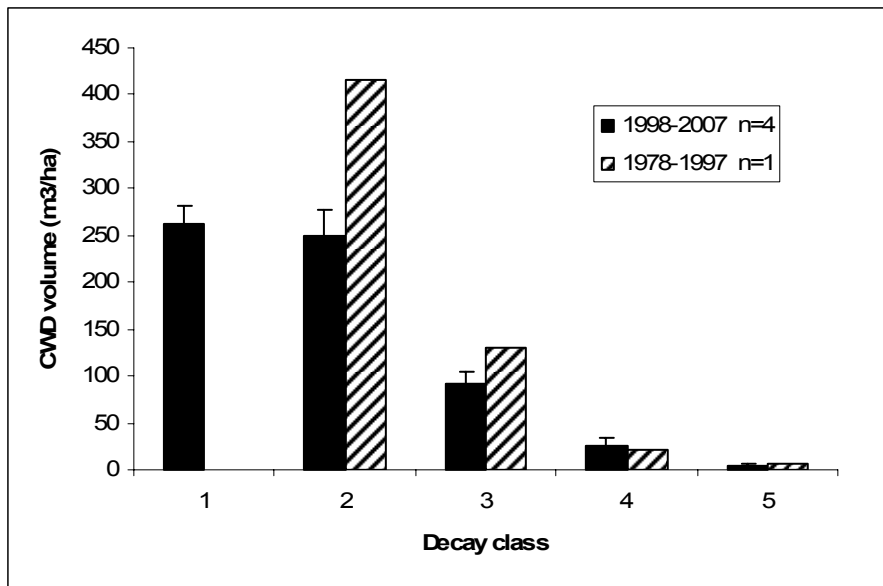


Figure 9 Changes in decay class distribution of downed wood over time since disturbance by wind (bars are standard error)

Disturbance Classification

We ran principal components analyses on a set of 51 variables, including standing live and dead trees and downed wood as analysed singly above, as well as disturbance to understory, shrub and overstory layers and a variety of other variables. We used PCA to reduce collinearity and to portray the clustering. The analysis shows a fairly continuous gradation in attributes within and among disturbance types, though some clustering emerges as well (Figure 10).

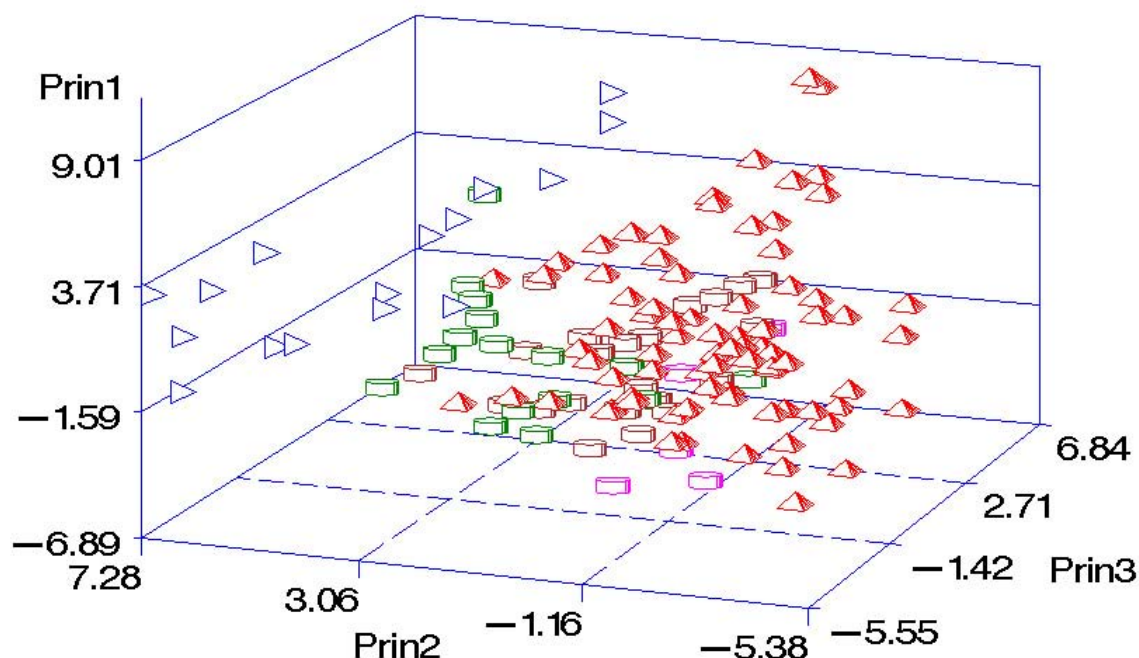


Figure 10. Clustering of plot locations in three-dimensional space defined by the first three principal components scores derived from 51 structural variables. Pyramid = fire; flag = wind; cylinder = insect outbreak, with green = spruce beetle, and brown = balsam bark beetle, and magenta = mountain pine beetle.

There are no strong underlying gradients in the clouds of structural diversity portrayed in Figure 10. The first principal component (Prin1) explains 20.6% of the variation in the 51 structural variables, and is most strongly correlated ($r=0.26$) with the total density of downed wood pieces per ha. The second principal component (Prin2) explains 15.6% of the variation, and is most strongly correlated ($r=-0.26$) with visual estimates of percent soil disturbance. The third principal component (Prin3) explains a further 12.5% of the variation, and is most strongly correlated ($r=0.28$) with the density per hectare of large downed wood pieces having diameters of 60 to 80 cm. Collectively, these three axes explain 48.7% of the variation in the data collected, recognising that the structural data are highly weighted to attributes describing downed wood.

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Can this natural variability in residual stand structure, or disturbance legacies, be captured by the Roberts (2004) model of disturbance classification? That is, does the Roberts model portray similar or different aspects of these stands, in comparison to the multivariate principal components analysis? Figure 11 shows the distinct (non-overlapping) clusters associated with fire, wind and insect disturbances when plotted according the relative extent of overstory (canopy), understory (shrub and regeneration), and forest floor (or soil) disturbance. Despite the variability in many structural attributes portrayed in Figure 10 it is immediately obvious that all insect disturbances have caused a wide range of tree mortality but have left understory vegetation and the forest floor relatively undisturbed. In contrast, wind disturbances generally resulted in moderately high canopy death and low (but non-zero) levels of disruption to the forest floor and soil. Many of the fire plots shown in Figure 11 are masked, because so many experience 100% disturbance of all three layers, and the ability to so completely impact all three layers is unique among the disturbance types sampled. Although partly related to our sampling design (i.e., avoiding edges and edge effects when locating plots), relatively few fire plots had intermediate or low impact on trees, vegetation and soil.

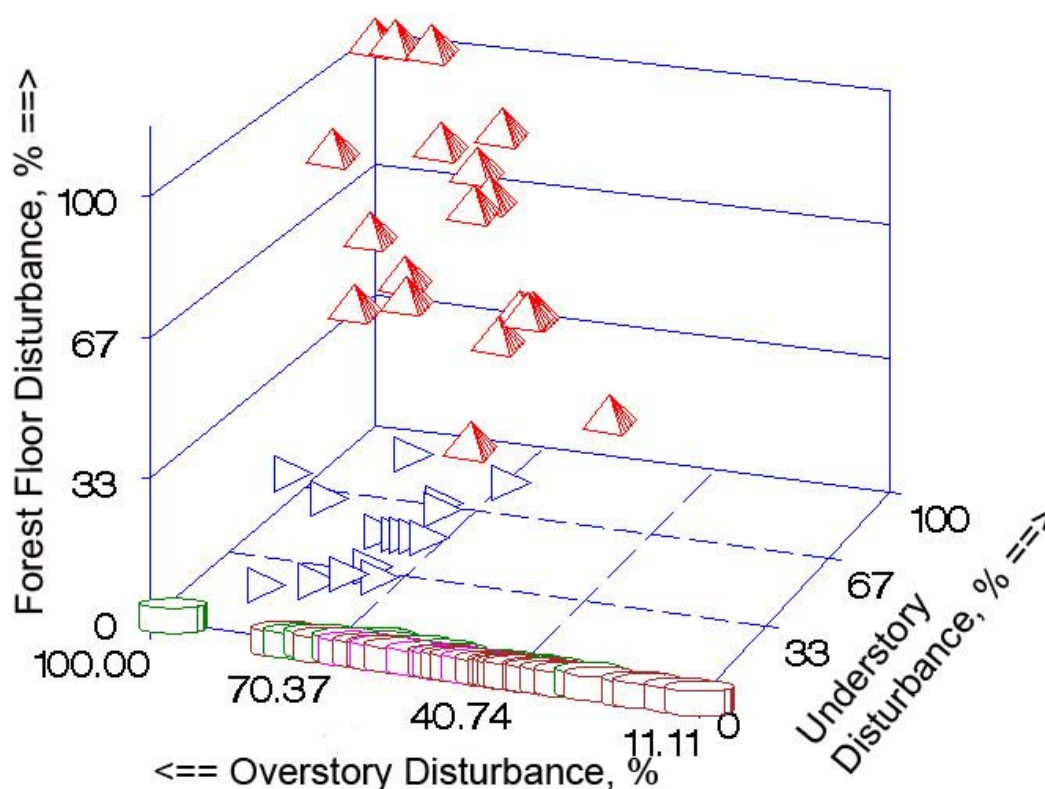


Figure 11. Position of sample plots in the three-dimensional space defined by the three-axis model of Roberts (2004). Pyramid = fire; flag = wind; cylinder = insect outbreak, with green = spruce beetle, and brown = balsam bark beetle, and magenta = mountain pine beetle.

The interrelationship of disturbance levels by stratum and the structure-based PCA scores is weak as a whole, but warrants further inspection. As evident in Figure 12, a large proportion of the overstory disturbance scores, especially those resulting from forest fires, indicate 100% tree mortality. Understory disturbance likewise exhibits a large number of 100% mortality values, but also have many 0% disturbance, typically associated with most insect outbreaks (Figure 13). Similar patterns of a negative slope and clusters of 0% and 100% disturbance are also found for forest floor or soil disturbance. The predominance of these 100% and 0% mortality levels suggests that relationships with principal components scores might be stronger if these ceiling and floor values were excluded. This proved true for the relationship between overstory disturbance and PCA-1 (Figure 12), but not understory disturbance and any principal component (see Figure 13 for the best correlate), nor for forest floor disturbance and any principal component.

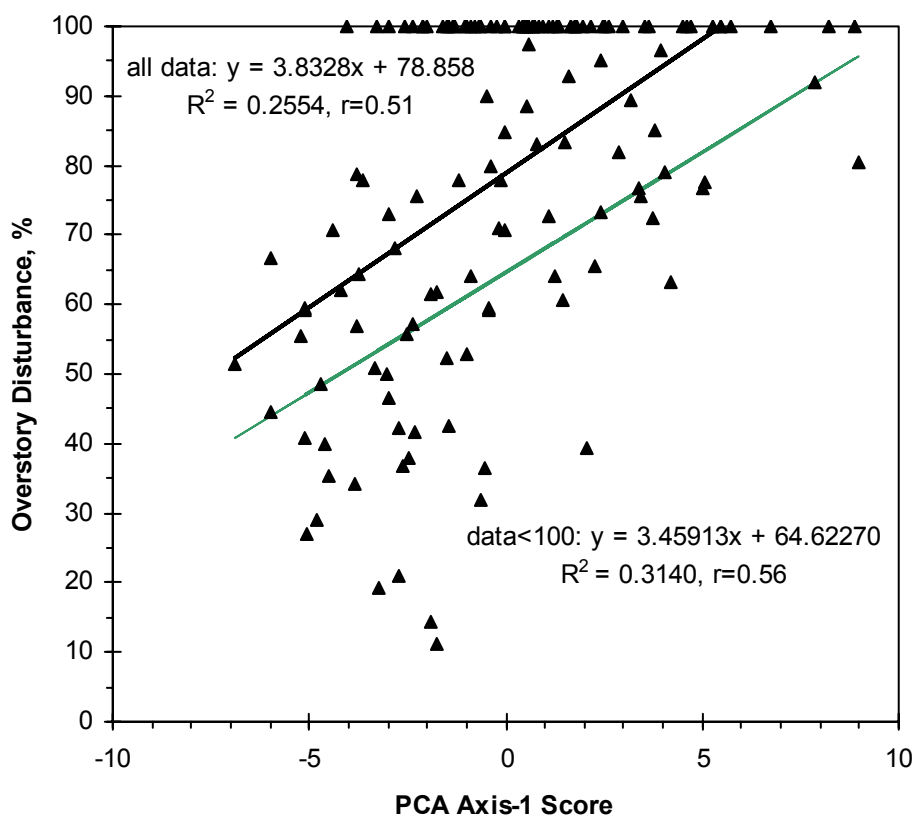


Figure 12. Overstory disturbance scores plotted against PCA scores on the first principal component axis. The large number (63 of 140) plots with 100% overstory mortality were mostly fire-origin plots; the correlation of overstory disturbance to PCA-1 is slightly greater if those 100% scores are excluded.

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These relationships and associated cluster patterns of individual disturbance patterns suggest some real functional differences among some disturbances. Those disturbance polygons that are dominated by either 0% or 100% mortality in any layer are qualitatively different from those plots and stands which maintain intermediate levels of disturbance legacies.

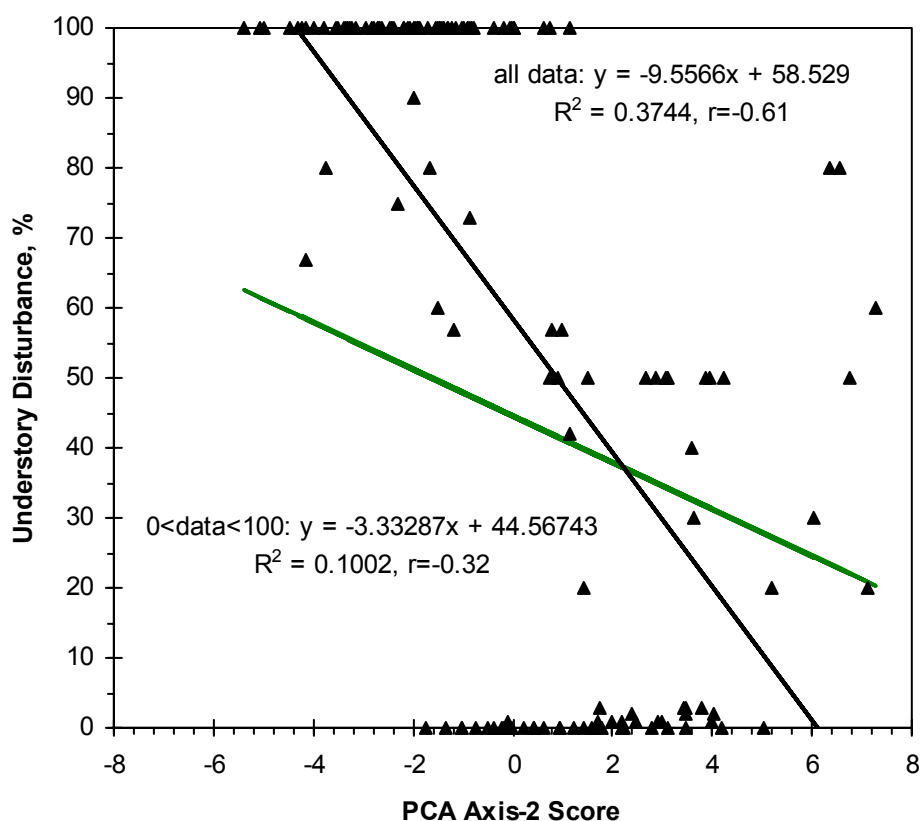


Figure 13. Understory disturbance scores plotted against PCA scores on the second principal component axis. Relatively few (46 of 140) plots have neither 0% nor 100% understory mortality; the correlation of overstory disturbance to PCA-2 is not improved if those 0% and 100% scores are excluded.

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These potential indicators of residual structure after disturbance also exhibit some significant differences with the environmental attributes explored in this sample survey.

Although overstory disturbance levels did not differ significantly between BEC zones, understory and forest floor disturbance percentages were significantly greater in the ESSFmc than in the SBSmc2 (Table 9). Plot scores on the second principal component axis were also significantly higher in the SBSmc2 than in the ESSFmc (Table 9).

Table 9. Mean (+/- standard error) levels of disturbance and PCA indicators in different biogeoclimatic zones, and significant differences between them.

Attribute	SBSmc2		ESSFmc		ANOVA* Results	
	mean	S.E.	mean	S.E.	F	prob>F**
number of plots	83		57			
overstory disturbance, %	78.0	2.5	80.1	3.6	2.26	0.14
understory disturbance, %	54.5	4.6	64.4	6.2	4.56	0.03
forest floor disturbance, %	45.5	5.1	64.4	6.2	6.51	0.01
PCA-1	0.450	0.364	-0.655	0.403	0.01	0.9
PCA-2	0.971	0.315	-1.414	0.276	18.18	<0.0001
PCA-3	-0.326	0.276	0.475	0.328	0.04	0.9

* Type III sums of squares results from a single four-way main effects analysis of variance model.

** differences between zones are significant if prob>F is 0.05 or less.

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Levels of overstory disturbance appear to have been significantly greater on medium-productivity sites than on medium rich sites, with medium-poor sites (though low in number) being intermediate (Table 10). The third principal component, PCA-3, is particularly sensitive to picking up the variation in site type, with poorer sites typically scoring <-0.77 , and richer sites scoring $>+0.20$ (Table 10).

Table 10. Mean (+/- standard error) levels of disturbance and PCA indicators in different site types, and significant differences among them.

Attribute	Medium-Poor		Medium		Medium-Rich		ANOVA* Results	
	mean	S.E.	mean	S.E.	mean	S.E.	F	prob>F**
number of plots	9		72		59			
overstory disturbance, %	76.1 ab	6.1	85.5 a	2.3	71.2 b	3.7	7.54	0.0008
understory disturbance, %	2.0	16.6	66.2	4.9	57.0	5.8	1.45	0.2393
forest floor disturbance, %	0.0	17.2	59.2	5.6	56.7	6.0	1.11	0.3339
PCA-1	-2.287	0.934	0.593	0.397	-0.542	0.394	1.46	0.2354
PCA-2	-0.166	0.734	-0.297	0.340	-0.029	0.369	2.8	0.0645
PCA-3	-1.173 b	0.582	-0.360 ab	0.291	0.778 a	0.335	4.2	0.0170

* Type III sums of squares results from a single four-way main effects analysis of variance model.

** differences between zones are significant if prob>F is 0.05 or less.

a,b,c results of Tukey multiple comparison test on factors found significant by anova; means sharing the same letter are not significantly different from each other at the 95% confidence level.

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All factors tested varied significantly with the agent of disturbance (Table 11).

As noted above, fires resulted in the greatest level of disturbance at all layers of the forest ecosystem, with windthrow having a significantly higher effect on understory disturbance than insects, though no greater effect on the forest floor (Table 11). Principal components analysis is adept at pulling apart the distinctive features of these different disturbance types, with fire scoring significantly more negative values on the PCA-2 axis, insects scoring the most negatively on the PCA-1 axis, and windthrow getting the negative scores on the PCA-3 axis (Table 11).

Table 11. Mean (+/- standard error) levels of disturbance and PCA indicators after different types of disturbance, and significant differences among them.

Attribute	fire		insects		wind		ANOVA* Results	
	mean	S.E.	mean	S.E.	mean	S.E.	F	prob>F**
number of plots	80		44		16			
overstory disturbance, %	94.2 a	1.5	50.0 c	2.7	81.4 b	1.8	95.41	<0.0001
understory disturbance, %	93.0 a	1.8	0.6 c	0.1	45.6 b	4.7	429.36	<0.0001
forest floor disturbance, %	92.5 a	1.8	0.0 b	0.0	3.0 b	1.1	518.68	<0.0001
PCA-1	0.898 b	0.298	-2.818 c	0.332	3.260 a	0.666	36.07	<0.0001
PCA-2	-1.760 c	0.194	1.536 b	0.259	4.577 a	0.483	106.1	<0.0001
PCA-3	-0.596 b	0.246	1.791 a	0.291	-1.946 c	0.679	27.21	<0.0001

* Type III sums of squares results from a single four-way main effects analysis of variance model.

** differences between zones are significant if prob>F is 0.05 or less.

a,b,c results of Tukey multiple comparison test on factors found significant by anova; means sharing the same letter are not significantly different from each other at the 95% confidence level.

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There is little evidence of the effect of time since disturbance in our descriptions of disturbance levels by stratum (Table 12). This is as it should be, because we were trying to describe direct disturbance effects in estimating those values. Older disturbances scored highest on the PCA-1 axis, while the most recent disturbances scored significantly higher on the PCA-2 and (to a lesser extent) on the PCA-3 axis (Table 12).

Table 12. Mean (+/- standard error) levels of disturbance and PCA indicators in natural disturbances of different ages, and significant differences among them.

Attribute	1 decade		2-3 decades		4-5 decades		ANOVA* Results	
	mean	S.E.	mean	S.E.	mean	S.E.	F	prob>F**
number of plots	51		56		33			
overstory disturbance, %	65.2	3.7	83.0	2.8	93.1	2.8	1.65	0.1963
understory disturbance, %	31.1	5.6	63.9	5.8	91.8	3.2	0.84	0.4321
forest floor disturbance, %	20.8	5.5	59.7	6.2	92.1	3.1	0.47	0.6236
PCA-1	-1.579 c	0.447	0.352 b	0.408	1.844 a	0.427	12.29	<.0001
PCA-2	0.844 a	0.488	-0.102 b	0.336	-1.131 c	0.266	106.1	<.0001
PCA-3	0.622 a	0.402	-0.690 b	0.285	0.209 ab	0.406	4.62	0.0115

* Type III sums of squares results from a single four-way main effects analysis of variance model.

** differences between zones are significant if prob>F is 0.05 or less.

a,b,c results of Tukey multiple comparison test on factors found significant by anova; means sharing the same letter are not significantly different from each other at the 95% confidence level.

Discussion

Our study was able to estimate the structural legacies following fire, beetle and wind disturbances in two subzones of interior BC. Figures 1 and 3, in particular, provide our estimates of the natural range of variability for these disturbances. Fire was the most prevalent, and catastrophic, disturbance agent in the SBSmc2. It created the most snags, leaving few, patchily distributed living trees (less than 5% canopy cover), and a low volume of downed wood (at least initially). Large fires (> 1,000 ha) all included undisturbed areas; smaller fires included areas of partial retention, but not undisturbed patches. Many of the small fires were the result of post-harvest prescribed fire escapes up steep hills.

Balsam bark beetles were the predominant disturbance agent within the ESSFmc. Severity was mild to moderate, leaving fairly uniform stands of mixed live and dead stems (canopy cover 25 – 35% or more) and a low volume of downed wood. Mountain pine beetle disturbances in the study area to date are small and follow a similar pattern to other beetles. As the current outbreak continues, disturbance may match the severity of fire as in forests to the east of the study area. Wind, which is rare in the study area, provides the most downed wood immediately following disturbance.

Immediately following beetle and wind disturbance, the size-class distribution of dead trees follows a unimodal pattern, with most snags in the 27.5 – 37.5 cm class (beetles) or 17.5 – 27.5 cm class (wind). Fire-produced snags initially follow the negative exponential size-class distribution typical of live trees in oldgrowth stands, but change over time to match the pattern in wind and beetle-disturbed stands. Downed wood also follows a unimodal pattern in size-class distribution, particularly as time since disturbance increases. Most of the downed wood volume present 10-30 and 30-50 years after disturbance is in larger-diameter pieces, indicating that these are present after disturbance, and persist for at least 50 years afterwards.

Our study likely underestimates the structural legacies of natural disturbances because the most productive stands had been salvaged. While the data provide a good estimate for retention on steep, less-productive sites, they should be applied with caution elsewhere. Additional caution is necessary because our study was retrospective in nature. We did not compare post-disturbance structure to the number of live and dead stems and volume of downed wood present in the stand before disturbance. In addition, the unbalanced design, while reflecting natural disturbance patterns, increases the difficulty in defining clear patterns.

Examination of information at different scales is critical. For example, interpretation of air photos at 1:10,000 was unable to distinguish between burned and unburned areas in fires, classing such areas as partially disturbed, whereas field sampling detected distinct patchiness.

We found that local knowledge provided more reliable information on disturbances than existing databases. The Forest Cover database was more accurate in terms of disturbance size and extent than the BC Natural Disturbance database; Forest Cover also identified sites that the Natural Disturbance database missed, but included some others where the disturbance agent was not accurately identified.

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Information on beetle disturbances was limited to the BC Natural Disturbance database. Unfortunately, disturbance severity is not well captured in this database: severity of mapped disturbance was often minor, resulting in apparently extensive disturbances that were barely (or not at all) detectable in the field. Even after filtering the database for the most severe disturbances and for target species, field reconnaissance proved stands to have minor disturbance. We found that spruce beetle and mountain pine beetle attacks identified in the database often could not be located in the field; it was not always clear whether the disturbance was incorrectly mapped, or whether it had been salvaged. Lack of information on salvage severely hampered our efforts to locate sites.

Wind disturbances were not present in either disturbance database. The limited number of sites located indicates that wind is a relatively uncommon disturbance agent.

Disturbance classification.

We identified natural disturbance clusters to help us evaluate the Roberts (2004) system of disturbance classification, and the degree to which it can be applied to fire, insect, and windthrow disturbances and by extension (through use of existing data from databases such as those maintained by the Northern Interior Vegetation Management Association, NIVMA, www.nivma.bc.ca) those due to forest harvesting activities. This evaluation explored the degree to which a unified disturbance classification system can identify common attributes of different disturbance events (and management options) independent of the agent of disturbance.

Structural analysis using PCA and the three-axis model of Roberts (2004) reveals both clustering and continua of structural legacies after these natural disturbances. In many ways, forest fires are the most analogous to industrial clear-cut harvesting in that disturbance levels are very high (if not 100%) in all layers of the forest. These high levels are biased by the fact that sample plots were located in the centre of old burns, largely free of edge effects. As illustrated in Figures 10 and 11, however, there are natural precedents for intermediate levels of overstory, understory, and forest floor disturbance even in fires, consistent with “mixed crown” fire behaviour. Those intermediate levels of disturbance are much more prevalent in disturbances generated by insects or wind, where all canopy trees are rarely killed, and where the understory (vegetation, tree seedlings and samplings) are left relatively unscathed. This makes windthrow and insect outbreaks (even at their most severe as documented in this study) qualitatively different from forest fires, in that they can function as “releasing disturbances” that accelerate succession to understory species (often more shade-tolerant species such as spruce and fir), rather than “resetting” stand development to shade-intolerant species such as pine.

Guidance to Management

Current efforts to implement ecosystem-based management use natural variability to guide management. As management moves away from the structure and function of unmanaged stands, the uncertainty that biodiversity will be maintained increases. At greater deviations from natural, risk to biodiversity increases. Managing within the range of natural variability provides the best chance that biodiversity will not be compromised.

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Risk assessment suggests that risk to biodiversity related to stand structure increases sigmoidally as the percentage of retained patches or structural attributes moves away from the amount of remnants left following natural disturbance (Figure 14; BWMT 2005).

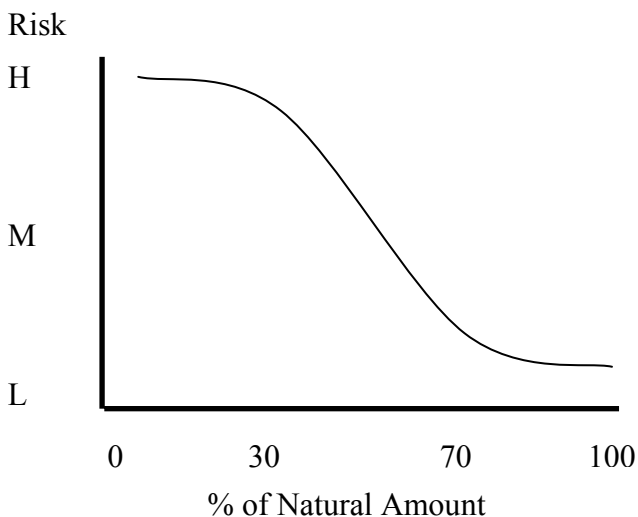


Figure 14. Percent structural retention as a proportion of natural remnants.

The area in wildlife-tree patches and their distance apart provide the simplest estimate of structural retention. Adding explicit information on volume of downed wood, and numbers of snags and live trees reduces uncertainty about levels of risk. If only wildlife-tree patch indicators are used (i.e., omitting downed wood, snags and live trees), moderate uncertainty arises because wildlife-tree patches vary considerably in content. Uncertainty also exists because some reserves are temporary.

The recovery period for stand structure is long. Stand heterogeneity and large structures take more than a century to develop. Some mitigation is possible (e.g., creating snags), but potential is limited (e.g., tree size limits snag size) and activities are unlikely to be cost effective.

Harvesting can never leave as much structure as natural disturbances because biomass is removed from the site. Beetle and wind disturbances leave all biomass on site; fire removes some biomass. Current stand-level retention targets in the study area range from 1% to 11% of the area of a harvested stand (Province of BC, 2006). In beetle-disturbed stands, the Chief Forester provided guidance to leave from 10% to 25% of the cutblock in wildlife tree patches (highest retention in cutblocks > 1,000ha; Snetsinger, 2005). The current regulations do not stipulate what types of structure should remain within patches, and although guidebooks suggest structure should be representative, evidence suggests that trees within patches are smaller than those outside and that wildlife tree patches contain very few “functional” (i.e. >20cm dbh) snags (B.C. MoF, 2005).

Hence, current harvesting practices result in retention of standing live and dead stems that is considerably lower than the range following natural disturbance as described in our study

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(particularly following beetle or wind disturbance). Current practices may pose high risk, if landscape-level retention is insufficient.

In addition, current retention levels will result in mid-seral (30-50 years and later) downed wood volumes that are not only lower than the RONV but will include only soft, decayed pieces instead of a mix of sound and decayed wood. Structurally intact downed wood provides habitat attributes such as large concealed spaces (Keisker 2000) that are not common on the landscape.

In a study of stand structure remaining after harvest in the neighbouring Morice TSA, post-harvest downed wood volumes varied between 25 and 250 m³/ha in the SBSmc2 and between 25 and 350 m³/ha in the ESSFmc (Lloyd 2003). 85% of this area was outside Wildlife Tree Patches and other reserves and contained no snags and almost no standing trees (Lloyd, unpubl. data). This has long-term implications for the long-term volume and state of decay of the downed wood in the 85% of the area not occupied by WTPs and other reserves. This study shows that standing dead trees continue to fall and be recruited into the downed wood pool for at least 50 years after natural disturbance resulting in a range of decay classes across the disturbed area that includes fairly sound wood and that persists well into the mid seral stages of stand development. As harvested stands include few or no standing stems, live or dead, this continuous recruitment will not occur except in Wildlife Tree Patches, and stands in middle or later seral stages will contain only well-decayed wood resulting from the initial harvest over most of their area.

In practice, volumes of downed wood usually remaining after harvest in the study area are about three orders of magnitude higher than the minimum 4 logs/ha mandated under the Forest and Range Practices Act (Lloyd 2003). While commercial timber extraction precludes levels of retention that are consistent with natural levels, this study highlights the discrepancies that exist between downed wood volumes and (especially) number of live and dead standing stems following natural and managed disturbances.

Assuming no decline in post-harvest downed wood volumes since the 2003 study, it appears that the primary focus of management effort should be on increasing the number of standing stems remaining after harvest. This will not only bring the number of standing stems more into line with the RONV but, when they fall, will produce the relatively sound downed wood in mid and later seral stages that will be missing in stands harvested by current standards. Retention of standing dead stems is complicated by Workers Compensation Board regulations, such that extensive snag retention is impractical outside reserve areas or other no-work zones. Current downed wood guidelines drawn up by the provincial Wildlife Tree Committee emphasise the need to maintain a range of size and decay classes following harvest. We believe that emphasis should be placed rather on maintaining large logs, as a higher proportion of these are recruited some time after the natural disturbance. Emphasis on maintaining the range of decay classes is broadly justified, however the prevalence of decay class 2 and 3 after natural disturbance should be noted (decayed wood makes up a small proportion of total volume) as this persists into the mid seral stages and beyond.

This brief survey has demonstrated that there are natural templates and precedents for all combinations of tree mortality and disruption to the forest understory and forest floor. Many different combinations of residual structure and composition are found in the form of live and dead trees in the overstory, and in the volume and density of logs found on the ground. In

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providing guidance for sustainable forest management by building on a foundation of emulating natural disturbances, the challenge will be in maintaining and replicating, in the managed forest, the range of natural variability found in natural forests. Even if some sufficient level of residual tree patches and residual downed wood is identified within clearcut openings to emulate fire disturbance, there will still be considerable forest variability missing at the landscape level. Forest harvesting will have to adopt a wide range of techniques in order to undertake partial cutting, variable retention, and the protection of advance regeneration if and where management is truly designed to emulate natural disturbances.

The current mountain pine beetle disturbance is evidence that BC's interior has already moved beyond the natural range of variability due to anthropogenic influences. The current low levels of within-stand retention can only exacerbate this change.

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