

# A Comparison of Forest Edges and Interiors on the Infestation Dynamics of *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae: Scolytinae)

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## Abstract

The western balsam bark beetle, *Dryocoetes confusus* Swaine, is ubiquitous throughout mature subalpine fir ecosystems in British Columbia and is considered the most serious mortality-causing disturbance. Harvesting subalpine fir has increased recently; however, little is known about how this anthropogenic disturbance affects the population dynamics of *D. confusus*. Using high resolution photography and ground surveys, this study compared stand composition and *D. confusus* attack levels along natural forest edges and edges created by harvest <10 years or >15 years ago, to forest interiors, where no anthropogenic disturbance had occurred. Subalpine fir density and *D. confusus* attack were lower in natural forest edges than in harvested edges. There were differences in attack levels between harvest treatments, but the overall impact by *D. confusus* was similar to *D. confusus*-caused mortality seen in forest interiors. More recent attack differed among edge treatments, with the highest levels in the <10 years since harvest treatment and the lowest levels in natural edges. This short period of increased activity by *D. confusus* post-harvest has minimal impact beyond what is considered the natural range of mortality in unmanaged stands.

**Keywords:** western balsam bark beetle, subalpine fir, effect of harvest edges on insect dynamics

## Introduction

The western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae: Scolytinae), plays a major role in the natural succession processes of subalpine fir ecosystems, which are dominated by Engelmann spruce (Sx), *Picea engelmannii* Parry ex Engelm. (Pinales: Pinaceae) and subalpine fir, *Abies lasiocarpa* (Hook.) Nutt (Pinales: Pinaceae) (Lloyd et al. 1990; Maclauchlan & Brooks 2021, 2023; Maclauchlan et al. 2023). In association with a blue stain fungus, *Grosmannia dryocoetidis* (Ophiostomatales: Ophiostomataceae) (Molnar 1965), *D. confusus* is considered the most serious mortality-causing disturbance of mature subalpine fir in British Columbia (B.C.) and has been re-

1

sponsible for the loss of millions of cubic metres of timber through unsalvaged losses (BCFLNRO 2015; Maclauchlan 2016; Maclauchlan et al. 2023).

Subalpine fir grows at moderate to high elevations throughout the B.C. interior, predominately in the Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone and to a lesser degree in the Sub-Boreal Spruce biogeoclimatic zone and other ecosystems (Lloyd et al. 1990; Coupé et al. 1991; Meidinger & Pojar 1991). It prefers wetter sites to dry ones, and summer rainfall is a limiting factor for growth (Peterson et al. 2002). Winters are cold with significant snowpack and summers are cool (Parish & Thomson 1994), depending on elevation. Temperatures can range from below  $-45^{\circ}\text{C}$  in the winter to above  $32^{\circ}\text{C}$  in the summer (Alexander et al. 2004).

*Dryocoetes confusus* is ubiquitous throughout mature subalpine fir stands, with tree size, health, and density being the most important factors in the beetles' host selection process (Stock 1991; McMillin et al. 2003; Maclauchlan et al. 2023). Beetles select slow-growing, stressed trees over faster growing, more healthy trees (Bleiker et al. 2003; Lalande et al. 2020) and can kill 0.5–3.5% of stems in a stand each year; sometimes causing over 50% mortality in a stand (Maclauchlan 2016; Maclauchlan et al. 2023). Coupled with other mortality factors over the life of a stand, total mortality can reach up to 80% after several years of attack (Maclauchlan et al. 2023). Bark beetles and other disturbances change stand structure, species composition, and even the function of these forests (Flower et al. 2015; Seidl et al. 2016; Rodman et al. 2022). *Dryocoetes confusus* is altering subalpine fir landscapes in concert with anthropogenic and climate disturbance. Tree mortality and windthrow create canopy gaps or forest fragmentation, which, in turn, may contribute to conditions that are suitable for regeneration. This creates a very slow canopy turnover, but one that is continuous over a long time. However, with increasing erratic climate events and harvesting in these fragile ecosystems, this natural slow, small, gap-dynamic pattern may be disrupted causing more spatial fragmentation. Forest fragmentation is a documented conservation (D'eon & Glenn 2005) and habitat concern, although there are wide ranging views on the effects of harvesting and subsequent fragmentation on forest values. *Dryocoetes confusus* may be attracted to trees damaged by disturbance events, such as wind, snow breakage, or harvesting, and may infest fresh, live windthrow and broken stems (Stock 1991). Harvesting creates forest edges that may be more vulnerable to wind disturbance (Harper et al. 2005). The role of storm-damaged trees in *D. confusus* population dynamics is not as well understood (McMillin et al. 2003; Maclauchlan & Brooks 2021) as with some *Dendroctonus* beetles, such as spruce beetle (*D. rufipennis*), and Douglas-fir beetle (*D. pseudotsugae*) (Furniss 1962; Schmid & Frye 1977) that are also attracted to fresh windthrow. As a result, we do not fully understand how harvesting and the creation of unnatural forest edges may affect *D. confusus* activity, tree health and mortality, and subsequent forest structure.

As the salvage harvesting of mountain pine beetle-killed (*Dendroctonus ponderosae* Hopkins [Coleoptera: Curculionidae: Scolytinae]) lodgepole pine (PL) *Pinus contorta* var. *latifolia* in B.C. concludes, due both to its reduction in merchantability (Chen & Walton 2015) and accessibility, more non-pine forests, often these higher elevation forests, are targeted for harvest. Consequently, there has been increasing interest in the health and sustainability of subalpine fir dominated forests. For example, the volume of harvested subalpine fir in northern B.C. has increased from 12% to 24% of the total harvest since 2016 (R. Midgley, pers. comm.). The objective of this study was to better understand and describe the response of *D. confusus* to the creation of harvested stand edges. Harvesting may cause stress on trees at the edge of harvest blocks, which may in turn attract *D. con-*

*confusus*, thus elevating attack levels along these edges. The authors approached this objective by comparing levels of *D. confusus* attack along stand edges created by harvest less than 10 years ago and more than 15 years ago, to natural forest edges and interior forests where no anthropogenic disturbance had occurred.

## Methods

The importance of stand edges (natural or harvested) on *D. confusus* attack levels versus those in the interior of unharvested stands in subalpine fir forests was compared using large-scale aerial photography and detailed ground surveys. Areas in southern B.C. within the Thompson Okanagan Region, having trace to moderate levels of *D. confusus* activity, were selected to compare attack levels along harvested and natural stand edges (Table 1). The study area was chosen based on recorded *D. confusus* activity information gathered during the annual B.C. Aerial Overview Survey (AOS) (<https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/aerial-overview-surveys/data-files>). The 70 mm photography and ground surveys were conducted over an area of 100 ha in high elevation terrain east of Vernon, B.C., near Cherry Ridge (50° 18' 33.51" N; 118° 29' 8.74" W), Home Lake (50° 5' 57.15" N; 118° 46' 52.55" W), and Buck Mountain (50° 5' 21.63" N; 118° 52' 55.69" W).

### Large-scale aerial photography protocol

Once potential areas of interest were identified from the AOS data, detailed helicopter reconnaissance flights were undertaken to locate individual stands suitable for the study. Stands were selected based on time of harvest (<10 years since harvest or >15 years since harvest). At the same time, natural, unharvested stands (interior forests and natural forest edges) in proximity to the recent (<10 years) or old harvested edges (>15 years) with similar *D. confusus* pressure were also identified. Interior forest locations were at least 600 m from selected harvest blocks or natural stand edges. Harvested and natural stands were categorized as “edge” and “interior”: edge being that part of the stand adjacent to a harvest block or natural opening, and interior being that part of the stand not directly adjacent to an artificial (harvest) or natural edge (Table 1). Attack levels of *D. confusus* were analysed using large-scale aerial 70 mm photography and detailed ground surveys in the four treatment categories: <10 years since harvest, >15 years since harvest, natural edge, and interior (no harvest). There were fewer stands that met the criteria in the <10 years since harvest category and in the natural edge stands, which in turn influenced the number of possible ground surveys in these two categories. Road access was also a limiting factor in conducting the ground surveys.

The high ground resolution provided by 70 mm photography (Pitt et al. 1997) allowed detailed analyses of vegetation and site conditions. To maximize productivity, flight lines for the 70 mm photography were pre-determined on maps and distributed evenly among treatments in natural and harvested areas. Interior plots ran parallel to the direction of helicopter travel, avoiding other plot edges. Edge plots ran in a straight line along the original harvested edge or forested edge of natural openings.

**Table 1. 70 mm photo plot location within the stand and number of photo plots per treatment**

Treatment	Photo plots	
	Edge	Interior
Natural edge	39	
Interior (no harvest)		248
<10 years since harvest	55	34
>15 years since harvest	96	24
<b>Total</b>	<b>190</b>	<b>306</b>



A camera boom system mounted longitudinally under the helicopter was used to acquire the stereo photo pairs, which were taken at intervals along flight lines (Hall & Aldred 1992). The boom system was developed and produced by the B.C. Ministry of Forests Inventory Branch (Grace 1981). Two customized Hasselblad MK-70 photogrammetric cameras fitted with Carl Zeiss 100 mm planar lenses were mounted at each end of the boom and wired to a control board in the passenger compartment, allowing for remote firing of the cameras at the desired locations. Both cameras were triggered simultaneously, at predetermined intervals, to obtain overlapping images of the ground. The photo scale of each image was dependent on the flying height of the helicopter at the time of image exposure and the focal length of the camera lenses. Simultaneously exposed frames made up each photo pair. AGFA AviPhot Chrome 200 PE1 200 ASA 70 mm X 30.5 m colour reversal film was used, exposed at f5.6 for 1/500 second. No lens filters were used. Flying height averaged 100 m above ground level and ranged from 80 m to 137 m. Helicopter air speed averaged 20–30 knots while the photos were being taken. Helicopter speed was kept slow to avoid blur. The 70 mm photos were taken in early autumn under clear, calm flying conditions, when foliar colour fade of *D. confusus* attack was most visible from the air.

All photo plot assessments were performed using a four-power stereoscope and parallax bar on a tabletop light table. An AP190 Stereocord system was used to establish the linear plots. Plots were rectangular with a fixed ground width of 5.0 m and a varying

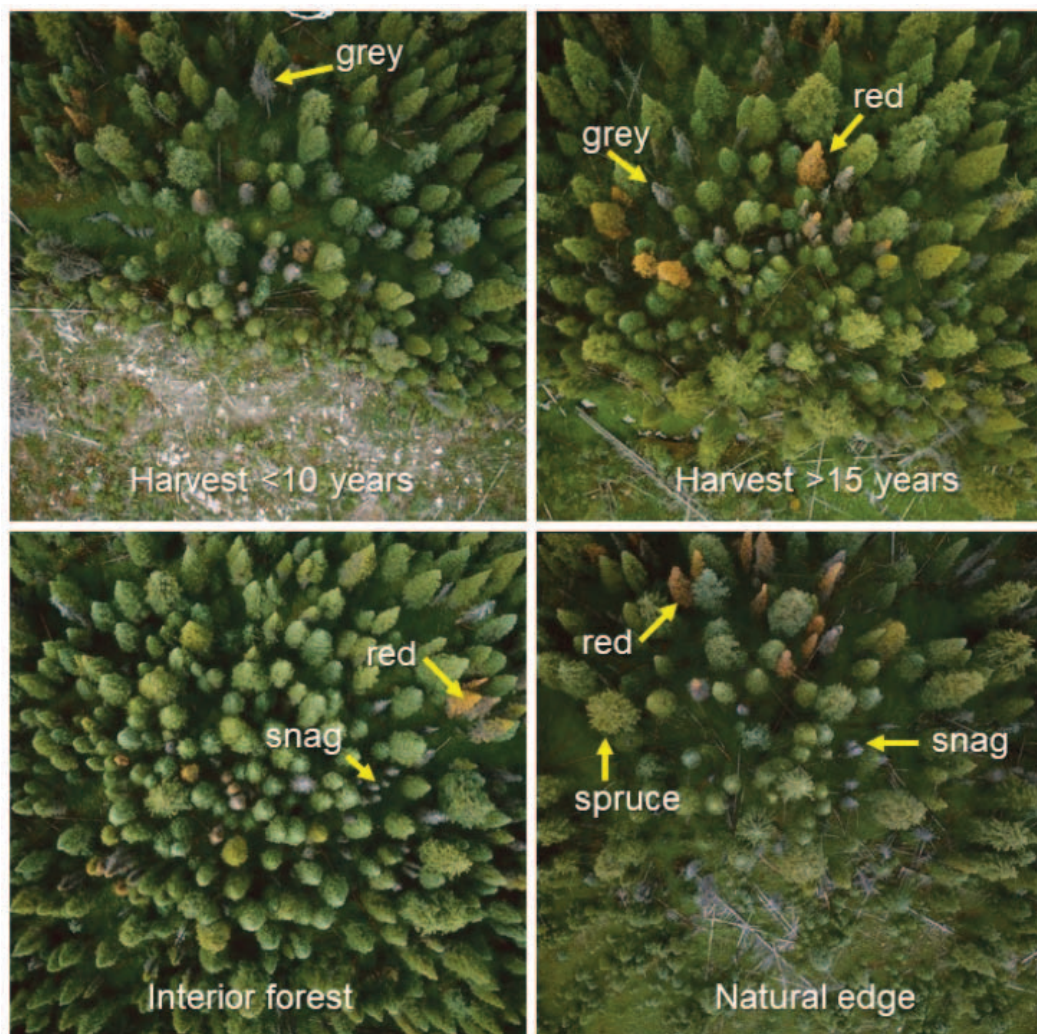


Figure 1. Four 70 mm photographs showing examples of <10 years since harvest, >15 years since harvest, natural edge, and forest interior. The arrows indicate *D. confusus* attack classification: red, grey, and snag.

length of 23.6 to 40.1 m. A 5 m plot width was selected because it yielded a median of five live subalpine fir per plot, which was considered to be a sufficient number of trees for assessment purposes. Edge effects photo plots had a fixed length of 30 mm and a width of 3.6 to 6.4 mm, accurate to within 0.1 mm, to reduce the number of overlays required. These were printed onto clear Mylar® overlays. Thirty mm produced a plot of maximum length, while still ensuring that all trees were in stereo. Standard stereo photo measurement techniques were used to measure the exact flying height and photo scale (Warner et al. 1996). During photo plot assessment, the plot line was treated as if it was located at ground rather than at canopy level. If the germination point of a given tree was within the plot line, it was considered as being “in,” regardless of whether or not its crown was inside the plot line. Both dominant and co-dominant trees were included. Co-dominant trees were defined as those trees with an average of two thirds or more of the height of dominant trees in the photo, easily identifiable through photo interpretation and based on crown width. The height of one tree per 70 mm photo plot was measured. The total ground-equivalent area analysed was 7.61 ha.

Trees within photo plots were assessed for species and status (live/dead). Additionally, *D. confusus* attack status was assigned for all dead (faded) subalpine fir in each plot. Subalpine fir presumably killed by *D. confusus* were classified into three attack categories, which corresponded to time since attack: red, grey, and snag (Figure 1). Other species were noted and recorded. *Dryocoetes confusus* attack classification is described below:

- Red — subalpine fir with foliage that was noticeably fading in colour or was bright red.
- Grey — subalpine fir with significant foliage loss and remaining foliage was dull red.
- Snag — subalpine fir that had lost most or all foliage, fine branches, and often larger branches and tops.

The causal agent of mortality cannot be absolutely determined from the photo plots but most mortality in subalpine fir is due to *D. confusus* attack (Lalande et al. 2020; Maclauchlan et al. 2023) and ground surveys provided a comparison and verification of the mortality agent. In ground surveys, we can ascertain whether a tree with green foliage is attacked, whereas in aerial photographs, we cannot. Other foliage attributes and attack status descriptors are identical to the aerial photo plot analysis.

### Ground surveys

Ground surveys (BCMOF 1995, 2001) were conducted at the 70 mm study sites to augment the information collected through the large-scale aerial photographic analysis. During the ground surveys, both standing and downed subalpine fir were assessed for the presence of *D. confusus* attack. One hundred and seven ground surveys were conducted in the summer (July–October) when access and ground conditions were optimal (Table 2). Ground surveys were conducted along the edges of the two harvest treatments (<10 years since harvest and >15 years since harvest), along the edge of natural openings, and within

**Table 2. Location in the stand and number of ground surveys conducted by treatment**

Treatment	Location	Ground surveys (N)
Interior (no harvest)	interior	43
Natural edge	edge	23
<10 years since harvest	edge	7
>15 years since harvest	edge	34
	<b>Total</b>	<b>107</b>

stand interiors (Table 2). In total, 10.7 ha were assessed. Surveys conducted in forest interiors were used for comparison with all other treatments.

Each ground survey measured 100 m x 10 m. All standing subalpine fir and other species (live or dead) over 15 cm diameter at breast height (DBH) were tallied and assessed for forest health factors. Trees with broken tops that were >3.0 m in height and treetops that met the size criteria were also tallied and assessed. The DBH of all *D. confusus*-attacked subalpine fir were measured and recorded. Additional attributes, including foliage colour, estimated time on the ground, and attack status were recorded for each down subalpine fir tree using the following:

#### Foliage colour and estimated time on the ground

- Green foliage; fallen within past year
- Red or fading foliage; on ground about two years
- Older snag, often decayed; many years on ground

#### *Dryocoetes confusus* attack status

- Current attack on tree with green foliage
- Brood or emergence (exit holes) visible on tree with red or grey foliage
- Old galleries, exit holes; no insects remaining in tree (snag)
- No *D. confusus* attack present

Downed trees that were very decayed (soft) were not assessed. As we encountered downed trees, we examined the stumps to determine whether they had been cut or had fallen naturally.

ANOVA, Tukey's multiple comparison test, and *t*-tests ( $p < 0.05$ ) were performed using the statistical computing package SYSTAT 10.2 for Windows (SPSS Inc., Chicago, IL).

## RESULTS

### Photo plots: Harvest history and edge effects on *D. confusus* attack

In total, 496 photo plots (190 edge and 306 interior plots) were established (equivalent of 7.61 ha assessed). Interior photo plots had significantly more live subalpine fir and more total trees than any of the natural or harvested edge photo plots (*t*-test;  $p < 0.05$ ) (Table 3).

The height of one tree per 70 mm photo plot was measured, for a total of 496 trees. Trees in the natural edge treatment were significantly shorter (average 20.3 m) ( $p < 0.01$ ) than those in the <10 years (average 23.3 m) and >15 years harvested edge treatments (average 23.5 m). No significant differences in tree height existed between the randomly placed natural interior treatment (average 23.9 m) and the interior plots paired with the two harvested treatments (<10 years average 23.2 m; >15 years average 22.9 m).

**Table 3. Average stems per hectare (SPH) for all edge and interior photo plots**

Plot location	N	Average SPH	
		Live subalpine fir	Total trees
Edge	190	304 ± 21.0 <sup>a</sup>	634 ± 24.1 <sup>a</sup>
Interior	306	406 ± 17.1 <sup>b</sup>	831 ± 15.8 <sup>b</sup>

Notes: Means followed by the same letter are not significantly different (*t*-test;  $p > 0.05$ ).

The authors compared the average stem density of unattacked, red, grey and snag subalpine fir, and that of other species by treatment (Table 4). Spruce comprised a significantly greater proportion of the assessed trees in natural edge plots than in harvested edge plots. The average stem density of green, unattacked subalpine fir in the edge plots of harvested stands (<10 years, >15 years) was virtually identical, as was total live tree



stem density. The stem density of spruce and other species was similar in the two harvested treatments (Table 4). All interior stands, regardless of treatment or density, averaged about 5% red attack. Comparatively, in edge plots, the two harvest treatments had significantly higher subalpine fir density than natural edge plots and averaged about 3% red attack, whereas the natural edge plots had just under 1% red attack. Grey attack predominated in both edge and interior plots of the <10 years since treatment, whereas snags was the most common dead tree category in the >15 years since harvest treatment (Table 4).

**Table 4. Average stems per hectare (SPH) of live subalpine fir (BI), *D. confusus*-attacked subalpine fir, and other live species, by treatment and photo plot (PP) location**

Treatment	Location	N PP	Average SPH						
			Live	Red	Grey	Snag	Total BI	Other species live	Total live
<10 years since harvest	edge	55	309	17	90	70	486	102	411
>15 years since harvest	edge	96	308	15	62	77	462	120	428
Natural	edge	39	193	2	29	34	258	526	719
<10 years since harvest	interior	34	344	31	120	104	599	106	450
>15 years since harvest	interior	24	412	28	42	65	548	106	518
Natural	interior	248	414	34	114	94	656	210	624

Red and grey attack can be combined (Table 5), since from a biological perspective this better reflects the amount of attack occurring since harvest. The difference in attack among treatments for edge and interior photo plots were compared. The percentage of combined red and grey attack in edge plots was significantly different among all three treatments, with the highest level of red and grey attack in the <10 years since harvest treatment and the lowest in the natural stand edge, at  $22.7 \pm 3.36$  and  $8.4 \pm 2.75$ , respectively (Table 5). Snags were significantly more abundant in both the <10 years and >15 years since harvest edge plots than in the natural stand edge plots. There was no signifi-

**Table 5. Comparison of average percentage unattacked and *D. confusus*-attacked subalpine fir in interior and edge plots by treatment. Photo plots, which did not contain subalpine fir, were excluded from this analysis (-12 photo plots)**

Tree status	Treatment (N)		
	Edge plots (Average % subalpine fir $\pm$ SE)		
	<10 years since harvest (55)	>15 years since harvest (95)	Natural (28)
No attack	$58.7 \pm 3.85a$	$68.7 \pm 3.09b$	$84.6 \pm 3.72c$
Red & grey	$22.7 \pm 3.36a$	$15.4 \pm 2.28b$	$8.4 \pm 2.75c$
Snag	$18.5 \pm 3.46a$	$15.8 \pm 2.08a$	$6.5 \pm 2.44b$
	Interior plots (Average % subalpine fir $\pm$ SE)		
	<10 years since harvest (34)	>15 years since harvest (24)	Natural (248)
No attack	$58.9 \pm 3.49a$	$73.9 \pm 4.15b$	$63.7 \pm 1.60a$
Red & grey	$23.8 \pm 3.41a$	$16.1 \pm 4.77a$	$22.1 \pm 1.37a$
Snag	$17.3 \pm 2.85a$	$10.0 \pm 2.19b$	$14.2 \pm 0.95a$

Notes: Means within plot location followed by the same letter are not significantly different (ANOVA, Tukey's multiple range test  $P > 0.05$ ).

cant difference in the percentage of red and grey attack (combined) in interior plots among treatments (Table 5), which ranged from  $16.1 \pm 4.77$  in the >15 years since harvest to  $23.8 \pm 3.41$  in the <10 years since harvest. Snag levels were significantly lower in the interior plots of the >15 years since harvest treatment compared with both the natural or <10 years since harvest treatments (Table 5). There were fewer snags along natural edges than in the interior of natural stands.

There was no significant difference in stem density between stands harvested less than 10 years ago and those harvested more than 15 years ago (Figure 2). In all treatments except for the natural edge treatment, subalpine fir density was significantly greater than any other species occurring in the stands.

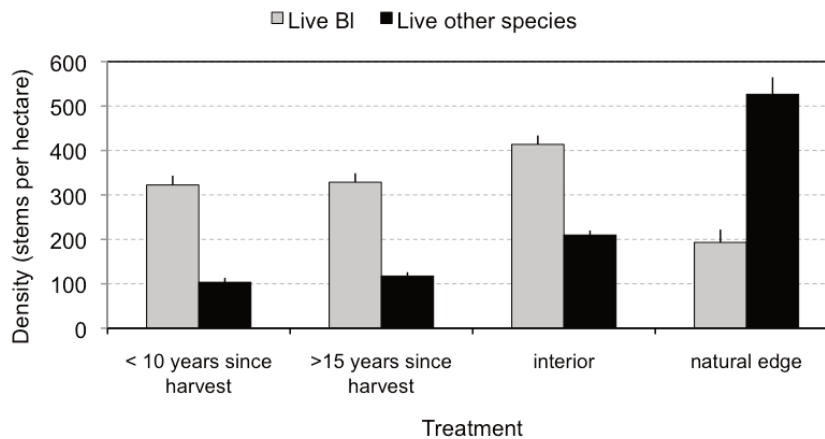


Figure 2. Comparison of average density (stems per hectare) ( $\pm$  S.E.) of live subalpine fir and other species by treatment.

When plots were combined (edge and interior) within a treatment, and time of harvest was compared, the ratio of dead subalpine fir to total subalpine fir was significantly less in the oldest harvest regime. The natural edge plots had the overall lowest ratio of dead subalpine fir, in part because there was more interior spruce, which would therefore not be affected by *D. confusus*.

The authors compared differences in percent attack of red, grey, and snags by treatment regime (Figure 3), regardless of photo plot location. Attack levels were lowest in the natural edge category, while both the natural interior and harvested treatments had high levels of red and grey trees, and snags.

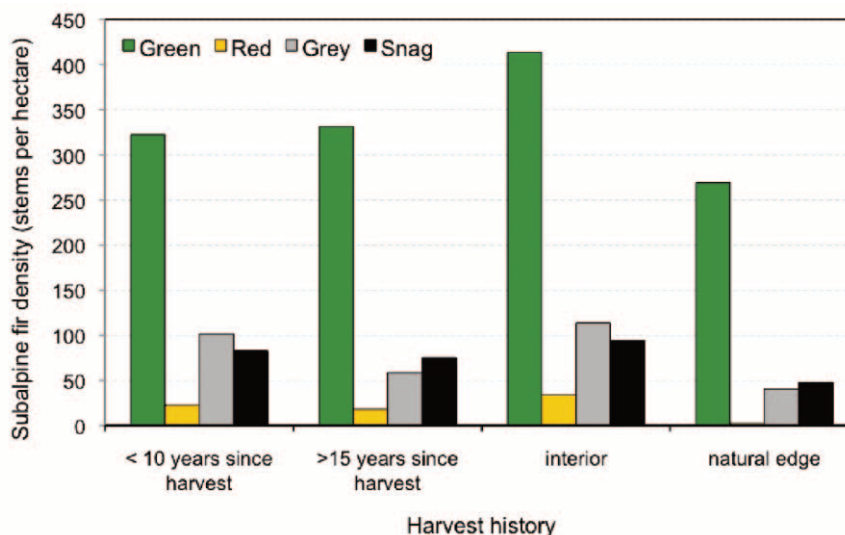


Figure 3. Average density (stems per hectare; SPH) of live and *D. confusus*-killed subalpine fir, by treatment, as determined from 70 mm photo plots.



## Ground surveys for standing and down trees

In all four treatments, *D. confusus*-attacked subalpine fir had a significantly larger diameter than either the unattacked subalpine fir or those, which died from other causes (Table 6). Due to the nature of this trial, only a small number of other species were measured during the surveys. Sixteen live lodgepole pine and 26 interior spruce had an average DBH of 27.7 cm and 39.0 cm, respectively. There was no significant difference in the average percent subalpine fir mortality between treatments (Table 6). Other species mortality was low in all treatments, ranging from 1.1% to 5.4%. The highest level of other species mortality was in the natural edges treatment, which had a much higher proportion of interior spruce (Figure 4).

**Table 6. Average DBH (cm) ± SE of standing live, unattacked subalpine fir (BI), *D. confusus*-attacked, and dead due to other causes subalpine fir, by treatment. The average percent of *D. confusus*-attacked subalpine fir is shown in parentheses**

Treatment (N)	Live BI (N)		<i>D. confusus</i> -attacked BI (N), (Avg. % attack)		Dead BI (N) (other mortality cause)	
	N	Avg. DBH ± SE	N	Avg. DBH ± SE	N	Avg. DBH ± SE
<10 years since harvest (7)	69	22.3 ± 0.72a	131 (39.5)	23.3 ± 0.50b	65	21.5 ± 0.74a
>15 years since harvest (34)	368	25.8 ± 0.42a	370 (35.0)	28.5 ± 0.43b	292	25.1 ± 0.50a
Interior (43)	461	25.7 ± 0.38a	471 (38.5)	28.6 ± 0.39b	321	25.6 ± 0.47a
Natural edge (23)	199	22.7 ± 0.48a	136 (31.8)	27.2 ± 0.64b	175	24.4 ± 0.57c
<b>Total trees measured</b>	<b>1,097</b>		<b>1,108</b>		<b>853</b>	

Notes: Means followed by the same letter are not significantly different (ANOVA, Tukey's multiple range test  $P > 0.05$ ).

The distribution of tree species within the surveyed stands and average stand density by treatment was compared (Figure 4). Surveys done in areas that had been harvested (<10 years and >15 years) had a very similar live tree composition and density, while those surveys done at natural edges had a much higher percentage of interior spruce and

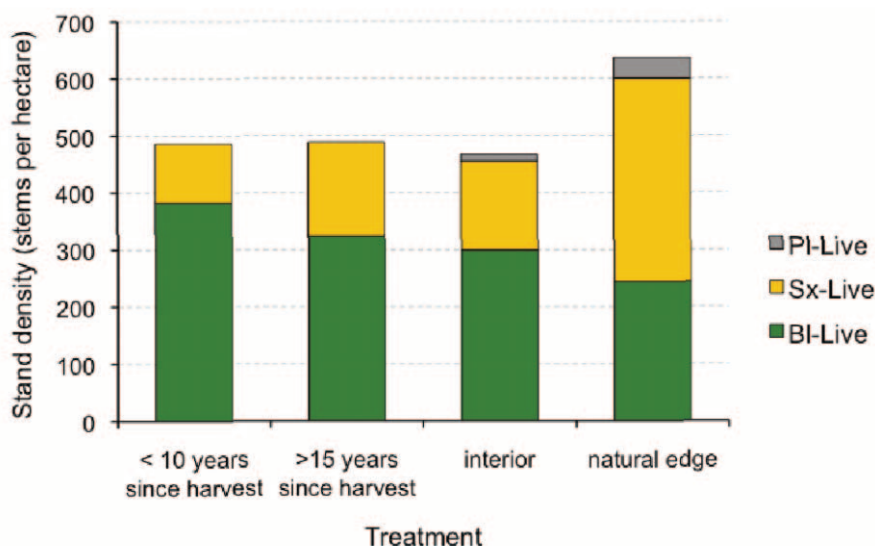


Figure 4. Average stand density and species distribution by treatment based on 107 ground surveys and more than 5,700 trees assessed.

generally higher densities. The distribution of tree species within the interior of natural stands was very similar to that of harvested areas (Figure 4).

Various forest health factors, in addition to *D. confusus*, were recorded during the ground surveys. In general, abiotic factors such as dead and broken tops (likely due to windfall), forks, and scarring (again, likely due to other trees falling and scraping standing trees) were most prevalent. *Echinodontium tinctorium*, or toothed conk (Russulales: Echinodontiaceae) was present at low levels on suppressed trees or on trees with prior wounding. None of these factors was as dominant as *D. confusus*.

Over 95% of stems on the ground were natural blowdown, either from wind or snow, and some had top breakage. The majority of fallen trees had been on the ground for over two years, and thus were categorised as snags. Most down subalpine fir had evidence of past *D. confusus* attack.

## Discussion

Density, climate, and individual growth parameters of subalpine fir play a pivotal role in the population fluctuations of *D. confusus* (Bleiker et al. 2003; McMillin et al. 2003; Lalande et al. 2020; Howe et al. 2022; Maclauchlan et al. 2023). The 70 mm photographic plots showed *D. confusus* attack was higher along harvested forest edges compared to natural forest edges, with the highest levels of attack observed in the more recently created harvested edges (<10 years since harvest). The lowest level of attack occurred in the natural forest edges. There was little difference in levels of attack in stand interiors, whether situated near harvested or natural edges.

The density of subalpine fir, live or dead, was lowest in natural forest edges compared to all other treatments, even though total stand density was higher, mainly due to the spruce component. Natural forest edges in the ESSF biogeoclimatic zone are frequently wet, and potentially comprise a preferred growing habitat for interior spruce. This would explain in part both the differences in species composition and attack levels in harvested and natural edges. Trees growing at the edge of natural openings may be more windfirm as they have acclimated to this exposed growing condition. Trees have more growing space, with the potential for augmented, faster annual growth (Parish et al. 1999; Bleiker et al. 2003; Harper et al. 2005; Vitali et al. 2016). The abiotic stressors placed on new, man-made edges, such as increased wind damage and greater temperature fluctuations, temporarily augmented subalpine fir susceptibility to *D. confusus*. However, over time, the density of live subalpine fir in mature stands will decline (Maclauchlan et al. 2023), allowing tree growth to accelerate due to more light and less competition (Parish et al. 1999; Vitali et al. 2016). Subsequently, *D. confusus* attack may decline or equilibrate until sub-dominant trees fill these gaps created by dead trees, providing new host resources for *D. confusus*.

Ground surveys showed little difference in *D. confusus* attack among harvest treatments and the natural forest interior, likely reflecting the innate population pulses exhibited by *D. confusus* (Lalande et al. 2020; Howe et al. 2022; Maclauchlan et al. 2023). There was lower, but not significantly so, attack along the natural forest edge, similar to our observations in the photo plots. Older snags were the most encountered category of downed subalpine fir. Although there was slight variation among treatments of *D. confusus* attack on downed trees, the most interesting observation was the amount of windthrow with no evidence of attack (McMillin et al. 2003; Maclauchlan & Brooks 2021; Maclauchlan et al. 2023). Unattacked, windthrown subalpine fir ranged from approximately 30% to 40%, with the highest proportion of unattacked windthrow occurring in

the natural edge category, mirroring attack trends recorded in standing trees from ground surveys and photo plots.

Snags and downed woody debris play a fundamental role in maintaining the long-term ecological functioning of subalpine fir ecosystems (Hansen et al. 1991). Coarse woody debris is an important habitat component for some plant and animal species (Feller 2003) and recent studies have shown that it plays a crucial role in conserving biodiversity, forest regeneration, global carbon sinks, and soil development (Russell et al. 2015; Prescott et al. 2017). Wang et al. (2021) claimed that carbon stored in coarse woody debris in later successional subalpine fir forests was four times higher than in earlier successional forests. Maclauchlan et al. (2023) found that most of the windthrown subalpine fir was first killed by *D. confusus*, thereby adding to forest floor woody debris. However, fresh windthrow was not particularly attractive as host material for *D. confusus*.

The role of natural and anthropogenic disturbance in shaping forest structure, composition, and processes has received increased attention over the past few decades (Dang et al. 2014; Flower & Gonzalez-Meler 2015). Disturbance events such as snow accumulation, windstorms, forest fires, and insect outbreaks all play essential roles in both small- and large-scale processes of all forest ecosystems. Harvesting creates new edges, thus exposing trees to increased abiotic extremes of wind (Burton 2001; Harper et al. 2005), sunlight, and precipitation, typically in the form of snow. This rapid edge creation through harvesting may stress edge trees, potentially causing growth reduction in some trees, or a release in growth in others due to increased light and growing space. Edge creation may also result in increased levels of windthrow well above background levels typically experienced in forest interiors (Esseen & Renhorn 1998; Burton 2001). With time, harvested edges may approach a similar ecological functioning as natural stand edges, with lower stem density, more moisture availability and growing space, and thus a diversity of fast- and slow-growing trees, which would provide *D. confusus* with a selection of host availability similar to that encountered in forest interiors.

In conclusion, the most noticeable finding was the lower subalpine fir density and lower level of *D. confusus* attack in the natural forest edges compared with subalpine fir forests near anthropogenically altered settings. Until forest edges become windfirm, elevated incidence of windthrow may create additional, although not always preferred, habitat for *D. confusus*. Over time, the amount of windthrow will begin to mirror that found in natural edges. Also, this rapid exposure of subalpine fir to increased sunlight, growing space and other abiotic factors can both increase and decrease a tree's susceptibility to attack by *D. confusus*. This insect briefly takes advantage of stressed edge trees and fresh windthrow, but within a few generations, the natural population pulses indicative of this insect's host selection and population dynamics resume. The results of this study highlight that harvest and other disturbances in high elevation subalpine fir forests only minimally and for short durations, disrupt the natural, low level and spatially discrete population surges of *D. confusus*. Therefore, although there is a short period of increased mortality caused by *D. confusus* post-harvest, the impact is relatively small and not outside the range of mortality seen in natural, unmanaged stands.

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