# ASSOCIATIONS OF SECONDARY BARK BEETLES WITH DYING AND LIVE LODGEPOLE PINE IN THE POST-OUTBREAK PHASE OF MOUNTAIN PINE BEETLE, DENDROCTONUS PONDEROSAE (HOPKINS), IN THE CENTRAL INTERIOR OF BRITISH COLUMBIA, CANADA

by

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#### Abstract

Dendroctonus ponderosae (Hopkins) or mountain pine beetle is a native bark beetle (Coleoptera: Curculionidae: Scolytinae) that feeds on more than 20 species of pine in western North America. In British Columbia, its principal host is lodgepole pine (Pinus contorta var. latifolia Engelmann). As a "primary" bark beetle, D. ponderosae kills its host at epidemic stages, exerting profound landscape-level mortality. As of 2012, D. ponderosae has caused the loss of 726 million cubic meters of timber, covering an area of 17.5 million hectares of mature pine forest in British Columbia and Alberta. Small diameter hosts are not suitable for *D. ponderosae*, however, creating a niche for the "secondary" bark beetles, including Ips pini (Say), Pseudips mexicanus (Hopkins), and Orthotomicus latidens (LeConte). At the post-epidemic stage of *D. ponderosae*, we found the rate of new mortality was approximately 4%, which 1% of the mortality was associated with a complex of secondary bark beetles, and not D. ponderosae, as the principal mortality agent in those stands. This finding suggests that at high population densities, secondary bark beetles are potential mortality agents of residual pines, sustaining the apparent outbreak of D. ponderosae by killing smaller diameter trees, with the highest rate of mortality among younger stands.

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	Number	Characteristics (SPATIAL partition)										
Bark beetles	of host species	Predominant regions on tree (Location)	Gallery shape, and length <b>(Appendices F</b> and <b>G)</b>	Beetle morphological features	Unique characteristics for identification							
Dendroctonus ponderosae (Hopkins)	>30 hosts of pines, 8 non-pine hosts, 11 exotics	Main bole, below 5 m on healthy trees (at outbreaks)	Hook-(J)shaped, gallery 30 cm long, monogamous, female-initiated	Dark brown to black, 3.7–7.5 mm	No spines, broader than <i>Hylurgops</i>							
lps pini (Say)	>10 hosts of pines, 7 non-pine hosts, all pine hosts overlapped with <i>D. ponderosae</i>	Top larger branches, and spreading downward or main bole in absence of competitors	Star-(X,Y)shaped, each arm 13–25 cm long polygamous (up to 8 females), male-initiated	Dark reddish brown to nearly black, 3.5–4.2 mm	4 declivity spines, with third spine elongated (male) Antenna club is sub- capitated, bi-sinuate							
<i>Hylurgops</i> spp. (LeConte), sour sap bark beetles	Most conifers: pines, spruces, firs, Douglas fir, western hemlock	Large roots, and root collar regions	Aggregated feeding by larvae without a pattern, black stain on gallery to separate from <i>D. murrayanae</i>	Reddish brown to black, 3.1–5.7mm (depending on species	Hylurgops porosus: known vector of Leptographium wageneri (W.B. Kendr.) M.J.Wingf. that stain the gallery black							
<i>Orthotomicus latidens</i> (LeConte)	>10 hosts of pines, 6 non-pine hosts, most pine hosts overlapped with <i>D. ponderosae</i>	Thinner bark of smaller trees, upper canopy of larger trees	Horizontal-(L,Y)shaped, each arm 3–5 cm long, monogamous, male-initiated	Dark reddish brown, 2.3–3.6 mm	3 declivity spines Antenna club is broadly sinuate to nearly straight							
Pseudips mexicanus (Hopkins)	>15 hosts of pines, which 8 is exotics, 10 overlapped pine hosts with <i>D. ponderosae</i>	Root collar regions, below 1 m	Curved-(C,S)shaped, each arm 5–6 cm long, polygamous (up to 3 females), male- initiated	Dark reddish brown, 3. <del>6–</del> 5.0 mm	3 declivity spines Antenna club is strongly arcuate							

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	Number	Characteristics (SPATIAL partition)										
Bark beetles	of host species	Predominant regions on tree (Location)	Gallery shape, and length <b>(Appendices F</b> and <b>G)</b>	Beetle morphological features	Unique characteristics for identification							
Dendroctonus murrayanae (Hopkins)	5 hosts of pines: lodgepole, jack, red, whitebark, and eastern white 3 spruces	Large roots, and root collar regions, below 0.6 m	Aggregated feeding chambers by larvae , 13–23 cm long, monogamous, female-initiated	Dark brown to black body with reddish brown elytra, 5.0–7.3mm	Aggregated feeding chamber with red frass (if fresh), median longitunidal subcarinate line above the epistomal process							
<i>Pityogenes</i> spp. (Bedel), i.e. primarily <i>P. knechteli</i> (Swaine) found in lodgepole pine	Most pines, and some spruce (species dependent)	Mostly on smaller trees, or on the smaller branches, larger twigs, thinner barks of larger trees	Star-(*)shaped, polygamous (up to 10 females), male-initiated	Dark reddish brown to nearly black, 1.8–3.7 mm (depending on species)	<ul> <li>2,3 large teeth spines on male declivity, deeply excavated frons on female, among the smallest of beetle.</li> <li>Antenna club is compressed with two sutures</li> </ul>							
Pityophthorus spp. (Eichhoff), >10 species of this genus attacks lodgepole pine	Most conifers, and some deciduous, (species dependent)	Mostly on smaller trees, or on the smaller branches, twigs, thinner barks of larger tree	Star-(*)shaped, mainly polygamous (up to 5 or more females, initiated by male), but some monogamous	Yellowish brown to almost black, 0.8–3.2mm (depending on species)	Chitinized septa on antennal clubs (refer Bright, 1981), among the smallest of beetle based on size							
Ambrosia beetles, i.e. primarily <i>Trypodendron lineatum,</i> and <i>Gnathotrichus</i> spp.	Most conifers, and some deciduous (species dependent)	Primarily in sapwood, between the outermost phloem and hardwood in the center	Pinsized-hole of tunnels (into the wood), 3-dimensional galleries within sapwood	Dark reddish brown to black, 2.0–3.7 mm (depending on species)	<ul> <li>'Hole' tunnels, with black stain fungus surrounding the 'hole'</li> <li><i>T. lineatum</i>: unmarked suture in antenna club, pronotum is flattened and subquadrate (if male) or subcircular (if female)</li> </ul>							

Table 2.Temporal niche partitioning in lodgepole pine by various bark beetles: Dendroctonus ponderosae, Ips pini, Hylurgops spp.,<br/>Orthotomicus latidens, Pseudips mexicanus, Dendroctonus murrayanae, Pityogenes spp., Pityophthorus spp., and ambrosia beetles,<br/>in lodgepole pine in British Columbia

		Characteristics (TEMPORAL partition)	<u>, , , , , , , , , , , , , , , , , , , </u>
Bark beetles	Peak flight period(s)	Mean generation time	Number of generation(s) per year
Dendroctonus ponderosae (Hopkins)	End-July to mid-August	Lodgepole pine: more than 28 days at constant 24°C	Univoltine, up to 2 broods per year
Ips pini (Say)	Mid-May (last season adults), end-July (re-emergent or brood 1), end-Aug to early-Sept (re-emergents)	Lodgepole pine: about 34 days at 25–35°C, or about 60 days (in field, Alberta)	Bivoltine, up to 3 broods per year (in BC)
<i>Hylurgops</i> spp. (LeConte) sour sap bark beetles	All summer throughout the growing period	Unknown, possibly more than one year per generation, common to other root-feeders	Semivoltine, one generation every 1.5–2.5 years
<i>Orthotomicus latidens</i> (LeConte)	End-May to early-June, end-July (re-emergent or brood 1)	Lodgepole pine: 64–124 (mean: 77) days at 25–35°C	Univoltine, up to 2 broods per year
<i>Pseudips mexicanus</i> (Hopkins)	End-May to early-June, early to mid-Aug (re-emergent or brood 1)	Lodgepole pine: 49 days at constant 26.5°C	Univoltine, up to 2 broods per year

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÷	C	haracteristics (TEMPORAL partition)	
Bark beetles	Peak flight period(s)	Mean generation time	Number of generation(s)per year
Dendroctonus murrayanae (Hopkins)	Mid-June to mid-July	Lodgepole pine: >26 days (in the field)	Univoltine
<i>Pityogenes</i> spp. (Bedel), i.e. primarily <i>P. knechteli</i> (Swaine) found in lodgepole pine	P. knechteli: end-May, early-July to early-August (re-emergent or brood 1)	P. knechteli in lodgepole pine: about 6–8 weeks in field, Alberta (estimate from Reid 1955)	<i>P. knechteli</i> : Univoltine, up to 2 broods per year
Pityophthorus spp. (Eichhoff), >10 species of this genus attacks lodgepole pine	Unknown, possibly highly variable, depending on species	Unknown, possibly highly dependent on the latitude, elevation and host	Univoltine (in general), but can vary by latitude and elevation (Bright 1981)
Ambrosia beetles, i.e. primarily <i>Trypodendron lineatum,</i> and <i>Gnathotrichus</i> spp.	T. lineatum: end-April to May, & mid-summer Gnathotrichus spp.: May-June, & throughout summer	Ambrosia beetles (in general): 6–10 weeks in the field <i>T. lineatum:</i> 9–10 weeks	Univoltine, up to 2 broods per year

								Deciduous										
Site	Plot	Total	trees	Lodge pin (Pl	pole ie i)	Inter spru (Sx	rior Ice ()	Bla spr (S	ack uce b)	Subalı fir (Bl	Subalpine fir (Bl)		las )	Trembling aspen (At)		Pa bii (Ej	Paper birch (Ep)	
		n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	
Mac1	A	76	9	52	68	0	0	0	0	0	0	0	0	24	32	0	0	
Mac1	В	150	18	126	84	4	3	0	0	0	0	0	0	17	11	3	2	
Mac2	Α	21	3	12	57	6	29	0	0	0	0	0	0	3	14	0	0	
Mac2	В	72	9	71	99	1	1	0	0	0	0	0	0	0	0	0	0	
Mac3	Α	11	1	11	100	0	0	0	0	0	0	0	0	0	0	0	0	
Mac3	В	77	9	61	79	14	18	0	0	0	0	2	3	0	0	0	0	
Mac3	С	67	8	67	100	0	0	0	0	0	0	0	0	0	0	0	0	
Mac4	Α	55	7	37	67	16	29	0	0	1	2	0	0	0	0	1	2	
Mac4	В	82	10	63	77	15	18	0	0	4	5	0	0	0	0	0	0	
Mac5	Α	33	4	30	91	1	3	0	0	0	0	2	6	0	0	0	0	
Mac5	В	57	7	20	35	25	44	8	14	0	0	4	7	0	0	0	0	
CCk	Α	51	6	35	69	3	6	0	0	13	25	0	0	0	0	0	0	
CCk	В	28	3	17	61	1	4	0	0	10	36	0	0	0	0	0	0	
CLk	Α	24	3	14	58	7	29	3	13	0	0	0	0	0	0	0	0	
CLk	В	23	3	8	35	3	13	11	48	0	0	0	0	1	4	0	0	
Total		827	100	624	75	96	12	22	3	28	3	8	1	45	5	4	1	

Table 3.Summary of coniferous and deciduous tree species surveyed in 10 x 10 m plots across seven sites in the central interior of British<br/>Columbia, Canada, 2009–2010

			S	tand	density	of lodger	pole p	ine				Stand matu	urity of lo	dgepole p	oine	
Site	Plot			2009			2010		Class <sup>†</sup>	D	iameter (	cm)		Class <sup>‡</sup>		
			Alive	Dead	Ratio	Alive	Dead	Ratio		Min	Max	Mean	Min	Max	Mean	
Mac1	Α	52	37	15	0.4	37	15	0.4	м	0.7	14.5	5.1	1.5	10.6	5.3	Y
Mac1	В	126	58	68	1.2	54	72	1.3	н	0.9	17.0	5.8	2.0	14.0	7.8	Y
Mac2	Α	12	8	4	0.5	6	6	1.0	L	1.1	18.4	7.6	1.7	9.3	5.6	Y
Mac2	В	71	34	37	1.1	24	47	2.0	н	0.4	15.5	6.5	1.5	14.7	8.2	Y
Mac3	Α	11	7	4	0.6	6	5	0.8	L	3.5	21.2	10.3	3.2	16.0	9.8	YO
Mac3	В	61	23	38	1.7	20	41	2.1	н	1.6	14.2	6.9	2.4	13.4	9.0	Y
Mac3	С	67	0	0	-	40	27	0.7	Н	2.1	13.6	7.3	3.9	16.5	9.6	Y
Mac4	Α	37	6	31	5.2	4	33	8.3	м	3.8	23. <del>9</del>	12.0	4.0	24.8	15.0	0
Mac4	В	63	21	42	2.0	21	42	2.0	Н	3.1	20.7	9.9	2.0	21.2	13.4	0
Mac5	Α	30	10	20	2.0	9	21	2.3	М	1.5	19.9	10.9	2.4	16.8	12.4	YO
Mac5	В	20	10	10	1.0	8	12	1.5	L	1.7	20.2	10.6	2.1	15.8	10.7	YO
CCk	Α	35	10	25	2.5	10	25	2.5	М	1.8	22.2	11.8	2.2	20.3	12.6	0
CCk	В	17	8	9	1.1	8	9	1.1	L	8.5	26. <del>9</del>	17.3	10.6	22.0	17.5	0
CLk	Α	14	2	12	6.0	2	12	6.0	L	5.9	26.5	16.6	10.1	25.6	18.8	0
CLk	В	8	2	6	3.0	2	6	3.0	L	3.6	20.4	13.8	5.4	20.4	15.2	0
Total		624	236	321	1.4	251	373	1.5	М	0.4	26.9	8.4	1.5	25.6	10.1	YO

Table 4.Stand density and maturity categorizations based on lodgepole pine surveyed for this study in seven plots, comprising 15 plots in<br/>the central interior of British Columbia, Canada, 2009–2010. Each plot was unique, with a variety of alive and dead lodgepole<br/>pine, mean diameters, and mean heights. Refer to text (M1.3) for further details in the methods of categorization

<sup>†</sup> L (low density, 0-25 pine/plot), M (medium density, 26-59 pine/plot), H (high density, ≥60 pine/plot)

<sup>\*</sup> O (old or 'mature', average diameter ≥ 10cm, max. diam. ≥ 20cm, average height ≥ 10m, max. height ≥ 20m), YO (young-old, meet more than 2 but less than 4 of the old (O) requirements, 2 ≤ YO < 4), Y (young, average diameter < 10cm, max. diam. < 20cm, average height < 10m, max. height < 20m)</p>

Table 5.Differences in diameter-at-breast-height (dbh) and height as a function of current lodgepole pine condition in 2010<br/>(category: dead or alive) in the post-outbreak stage of a *Dendroctonus ponderosae* outbreak in British Columbia, Canada.<br/>The results with a significance difference are **in bold** 

	Sample	size	Me	ean diameter-a	at-breast-	height		Mean height								
Site	Lodgepole pine	Plots	Alive(cm) (± SE)	Dead(cm) (± SE)	t	df	p-value	Alive(m) (± SE)	Dead(m) (± SE)	t	df	p-value				
Mac1	178/177*	2	6.4(±1.0)	4.4(±1.1)	3.86	175	<0.001	7.9(±1.8)	4.7(±1.9)	6.94	174	<0.001				
Mac2	83	2	4.9(±1.4)	8.1(±1.6)	4.16	80	<0.001	6.0(±1.7)	7.9(±1.9)	2.12	80	<0.05				
Mac3	72	2	8.1(±2.2)	8.7(±2.4)	0.68	69	0.50	9.4(±1.3)	9.0(±1.5)	0.46	69	0.64				
Mac4	100	2	9.0(±1.7)	11.4(±2.0)	2.27	97	<0.05	14.0(±1.9)	14.1(±2.2)	0.08	97	0.93				
Mac5	50	2	9.4(±2.5)	11.4(±3.0)	1.19	47	0.24	12.3(±2.2)	11.3(±2.6)	0.71	47	0.48				
CCk	52	2	15.9(±3.5)	13.5(±3.9)	1.42	49	0.16	17.9(±2.9)	13.3(±3.3)	3.13	49	<0.01				
CLk	22	2	15.8(±4.7)	15.6(±5.8)	0.06	19	0.95	18.8(±4.3)	16.8(±5.2)	0.66	19	0.52				
Total	624	15	9.9(±1.4)	10.4(±1.5)	1.40 608		0.16	12.1(±1.6)	11.2(±1.6)	2.54	607	<0.05				

\*The difference in sample size between the diameter and height was due to one lodgepole pine height determined to be non-measurable (on ground, with missing top)

Table 6.Summary of diameter-at-breast-heights (in cm) measured on live lodgepole pine surveyed in the central interior<br/>regions of British Columbia, Canada, 2009 and 2010. The table shows the total number of residual live lodgepole<br/>pine within the site, the measurements (in cm) of the smallest, largest and mean diameter size of the residuals, the<br/>changes in the number of dead trees within year 2009 and 2010, and as a result, the changes in mean diameter-at-<br/>breast-height of the residuals within each site

Site	Plot		200	9			20:	LO		New mortality	Changes in mean diameter
		Alive (n)	Min	Max	Mean	Alive (n)	Min	Max	Mean	(2009 to 2010)	(cm)
Mac1	Α	37	1.4	12.5	5.6	37	1.4	12.5	5.6	0	=
Mac1	В	58	1.6	11.3	7.0	54	1.6	11.3	7.1	+ 4	<b>个 0.1</b>
Mac2	Α	8	1.1	11.6	5.0	6	1.1	5.0	3.0	+ 2	↓ 2.0
Mac2	В	34	1.1	9.6	5.4	24	1.1	9.6	5.0	+ 10	↓ 0.4
Mac3	Α	7	3.5	14.6	9.4	6	3.5	14.6	9.4	+ 1	=
Mac3	В	23	2.6	10.7	6.8	20	2.6	10.7	6.6	+ 3	↓ 0.2
Mac3	С		-		-	40	2.1	10.3	6.1	N.A.	N.A.
Mac4	Α	6	6.3	13.2	9.2	4	6.3	11.3	8.9	+ 2	↓ 0.3
Mac4	В	21	5.0	12.5	8.6	21	5.0	12.5	8.6	0	=
Mac5	Α	10	2.5	12.9	8.9	9	2.5	12.9	9.1	+ 1	↑ 0.1
Mac5	В	10	2.9	14.4	9.9	8	2.9	14.4	9.9	+ 2	=
CCk	Α	10	10.6	22.2	14.6	10	10.6	22.2	14.6	0	=
CCk	В	8	12.0	22.0	17.0	8	12.0	22.0	17.0	0	=
CLk	Α	2	14.9	15.2	15.1	2	14.9	15.2	15.1	0	=
CLk	В	2	16.1	16.8	16.5	2	16.1	16.8	16.5	0	Ξ
Total		236	1.1	22.2	7.7	251	1.1	22.2	7.5	+ 25	↓ 0.2

Table 7.Summary of tree height measurements (in m) of the live lodgepole pines surveyed in the central interior regions of<br/>British Columbia, Canada, 2009 and 2010. The table shows the total number of residual live lodgepole pine within the<br/>site, the measurements (in m) of the smallest, largest and mean height of the residuals, the changes in the number of<br/>dead trees within year 2009 and 2010, and, as a result, the changes in mean height of the residuals within each site

Site	Plot		200	9			201	10		New mortality	Changes in mean height
		Alive (n)	Min	Max	Mean	Alive (n)	Min	Max	Mean	(2009 to 2010)	(m)
Mac1	Α	37	2.0	10.6	6.0	37	2.0	10.6	6.0	0	=
Mac1	В	58	3.0	13.5	9.6	54	54 3.0 13.5 9.7		+ 4	↑ 0.1	
Mac2	Α	8	1.7	8.6	4.5	6	1.7	4.9	3.3	+ 2	↓ 1.2
Mac2	В	34	2.4	13.8	7.6	24	2.4	13.1	7.3	+ 10	↓ 0.3
Mac3	Α	7	3.2	12.3	8.9	6	3.2	12.3	8.4	+ 1	↓ 0.5
Mac3	В	23	5.0	13.3	9.9	20	5.0	13.3	9.6	+ 3	↓ 0.3
Mac3	С	-	-	-		40	4.0	14.2	8.4	N.A.	N.A.
Mac4	Α	6	11.8	17.4	14.7	4	13.2	16.2	14.7	+ 2	=
Mac4	В	21	3.1	19.0	13.5	21	3.1	19.0	13.5	0	-
Mac5	Α	10	5.0	15.7	12.4	9	5.0	15.7	12.7	+ 1	个 0.3
Mac5	В	10	6.3	14.2	11.8	8	6.3	14.2	11.9	+ 2	<b>个 0.1</b>
CCk	Α	10	14.0	19.7	17.0	10	14.0	19.7	17.0	0	<u>-</u>
CCk	В	8	14.1	21.6	18.5	8	14.1	21.6	18.5	0	=
CLk	Α	2	14.0	19.7	17.0	2	14.0	19.7	17.0	0	=
CLk	В	2	14.1	21.6	18.5	2	14.1	21.6	18.5	0	=
Total		236	1.7	21.6	10.0	251	1.7	21.6	9.8	+ 25	↓ 0.2

 Table 8A.
 Summary of the presence of various bark beetles associated with lodgepole pine mortality in 2010 in the seven plots surveyed in the central interior region of British Columbia.

	Stand	Lodge	Lodgepole pine			Bark beetles associated with dead lodgepole pine in 2010																
Site	density and	Dead	<b>B</b> . 1	Гор	M	в	2°E	3B	2°BE	I (D)	I	P	H-L	PB	c	)L	P	M	P	T	AA	ИВ
	maturity	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Mac1	H-Y	85	10	11	21	25	20	23	4	5	12	14	16	18	3	3	4	5	5	6	2	2
Mac2	M-Y	53	3	6	29	55	34	64	4	8	14	26	29	55	9	17	8	15	9	17	8	15
Mac3	M-Y	46	6	13	29	63	24	52	4	9	11	24	22	48	7	15	2	4	6	13	9	20
Mac4	M-0	75	6	8	36	48	42	56	1	1	7	9	40	53	7	9	6	8	0	0	21	28
Mac5	L-YO	33	2	66	25	76	23	70	1	3	5	15	22	67	3	9	0	0	1	3	18	55
CCk	M-0	34	3	9	22	65	19	56	0	0	1	3	16	47	10	29	3	9	0	0	14	41
CLk	L-0	18	3	17	10	56	14	78	0	0	1	6	5	28	7	39	1	6	0	0	5	28
Total	M-YO	373	41	11	195	52	200	54	23	6	70	19	171	46	48	13	27	7	25	7	77	21

The frequency (n) represents the total number of lodgepole pine and the percentage composition (%) of the explanatory variables over the dead lodgepole pine surveyed within each plot

Abbreviations: B.Top=Broken top trees, MPB=mountain pine beetle or *Dendroctonus ponderosae*, 2°BB=secondary bark beetles, 2°BB (D)=Trees killed by the presence of predominantly secondary bark beetles (some trees had other agents of mortality weakening the trees, but is of minor significance), IP=Ips pini, OL=Orthotomicus latidens, PM=Pseudips mexicanus, H-LPB=Hylurgops spp. and/or *Dendroctonus murrayanae* (lodgepole pine beetle),

PT=Ps pint, OL=Orthotomicus intraens, PM=Pseudips mexicanus, H-LPB=nylargops spp. and/or Denaroctonus marrayande (lodgepole pine bee PT=Pityogenes spp. and/or Pityophthorus spp., AMB=ambrosia beetles

<sup>+</sup> Density (L=low, 0-25 pine/plot; M=medium, 26-59 pine/plot; H=high, ≥60 pine/plot) and maturity (Y=young, YO=young-old, O=old) (refer Table 2 for more details of classifications)

		Stand	Lodge	pole p	oine					Ba	ark bee	tles as	sociat	ted with o	lead l	odgepol	e pin	e in 2010	)				
Site	Plot	and	Dead	<b>B</b> . 1	бр	M	×8	2°E	38	2°B	B (D)		Ρ	H-L	PB	C	)L	P	M	P	τ	AN	ИВ
		maturity <sup>†</sup>	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Mac1	A	M-Y	15	5	33	5	67	4	27	0	0	2	13	2	13	0	0	2	13	4	27	0	0
Mac1	в	H-Y	72	5	7	16	22	16	22	4	6	10	14	14	19	3	4	2	3	1	1	2	3
Mac2	Α	L-Y	6	0	0	4	67	5	83	0	0	2	33	2	33	2	33	2	33	1	17	0	0
Mac2	в	H-Y	47	3	6	25	53	29	62	4	9	12	26	26	55	7	15	6	13	8	17	8	17
Mac3	Α	L-YO	5	3	60	2	40	1	20	0	0	1	20	1	20	0	0	0	0	1	20	0	0
Mac3	в	H-Y	41	3	7	27	66	23	56	4	10	10	24	21	51	7	17	2	5	5	12	9	22
Mac3	с	H-Y	27	8	30	23	85	24	89	9	33	19	70	21	78	2	7	3	11	4	15	0	0
Mac4	Α	M-O	33	4	12	16	48	22	67	1	3	1	3	22	67	2	6	1	3	0	0	9	27
Mac4	в	H-O	42	2	5	20	48	20	48	0	0	6	14	18	43	5	12	5	12	0	0	12	29
Mac5	Α	M-YO	21	1	5	16	76	16	76	1	5	3	14	16	76	3	14	0	0	1	5	13	62
Mac5	В	L-YO	12	1	8	9	75	7	58	0	0	2	17	6	50	0	0	0	0	0	0	5	42
CCk	Α	M-0	25	0	0	14	56	11	44	0	0	0	0	9	36	5	20	1	4	0	0	8	32
CCk	в	L-0	9	3	33	8	11	8	89	0	0	1	11	7	78	5	56	2	22	0	0	6	67
CLk	Α	L-0	12	1	8	7	58	11	92	0	0	1	8	4	33	4	33	1	8	0	0	4	33
CLk	В	L-0	6	2	33	3	50	3	50	0	0	0	0	1	17	3	50	0	0	0	0	1	17
Total		M-YO	373	41	11	195	52	200	54	23	6	70	19	171	46	48	13	27	7	25	7	77	21

Table 8B.A more detailed view of Table 8A with each site broken into their respective plots of various bark beetles associated with the<br/>total lodgepole pine mortality in 2010. The frequency (n) represents the total number of lodgepole pine and the percentage<br/>composition (%) of the explanatory variables over all the lodgepole pine surveyed within each plot

Abbreviations: B.Top=Broken top trees, MPB=mountain pine beetle or *Dendroctonus ponderosae*, 2°BB=secondary bark beetles, 2°BB (D)=Trees killed by the presence of predominantly secondary bark beetles (some trees had other agents of mortality weakening the trees, but is of minor significance),

IP=/ps pini, OL=Orthotomicus latidens, PM=Pseudips mexicanus, H-LPB=Hylurgops spp. and/or Dendroctonus murrayanae (lodgepole pine beetle), PT=Pityogenes spp. and/or Pityophthorus spp., AMB=ambrosia beetles

<sup>†</sup> Density (L=low, 0-25 pine/plot; M=medium, 26-59 pine/plot; H=high, ≥60 pine/plot) and maturity (Y=young, YO=young-old, O=old) (refer Table 2 for more details of classifications)

 Table 9A.
 Summary of the live and dead lodgepole pines, the presence of *Dendroctonus ponderosae* in 2009 and 2010, and other weakening agents affecting the tree mortality (i.e. root collar damage by insects (RC), wood borers (WB), and western gall rusts (WGR) in 2010) in the seven plots surveyed in the central interior region of British Columbia.

The frequency (n) represents the total number of live and dead lodgepole pine or the variable of interest with the percentage composition (%) of the explanatory variables over all the lodgepole pines surveyed within each site

	Stand	Total			200	)9						20	10		-			Others	(2010	)	
Site	density and	lodgepole	AI	ive	De	ad	м	PB		Ali	ve	De	ead	М	PB	R	с	w	8	w	<u>G</u> R
	maturity <sup>†</sup>	pine	n	%	n	%	n	%		n	%	ń	%	n	%	n	%	n	%	<u>n</u>	%
Mac1	M-Y	178	95	53	83	47	20	11	1	91	51	87	49	21	13	61	34	8	4	117	66
Mac2	H-Y	83	42	51	41	49	28	34		30	36	53	64	29	35	30	36	23	28	30	36
Mac3	L-Y	72	30	42	42	58	28	39		26	36	46	64	29	40	30	42	22	31	47	65
Mac4	H-Y	100	27	27	73	73	36	36	:	25	25	75	75	36	36	32	32	23	23	3	3
Mac5	L-YO	50	20	40	30	60	24	48		17	34	33	66	25	50	33	66	12	24	22	44
CCk	H-Y	52	18	35	34	65	22	42		18	35	34	65	22	42	17	33	12	23	1	2
CLk	H-Y	22	4	18	18	82	10	45		4	18	18	82	10	45	13	59	13	59	1	5
Total	M-YO	624	-	-	*	-	168	27	2	51	40	373	60	195	31	238	38	113	18	221	35

Abbreviations: MPB=mountain pine beetle or Dendroctonus ponderosae, RC=root collar damage by insects, WB=wood borers, WGR=western gall rusts

<sup>†</sup> Density (L=low, 0-25 pine/plot; M=medium, 26-59 pine/plot; H=high, ≥60 pine/plot) and maturity (Y=young, YO=young-old, O=old) (refer **Table 2** for more details of classifications)

		Stand	Total			20	09					201	10					Others (	2010)		
Site	Plot	density and	lodgepole	A	ive	De	ad	М	<b>2</b> 8	Ai	ive	De	ad	М	РВ	R	с	w	В	W	GR
		maturity	pine	n	%	n	%	<u>n</u>	%	n	%	n	%	n	%	n	%	n	%	n	%
Mac1	A	M-Y	52	37	71	15	29	5	10	37	71	15	29	5	10	7	13	2	4	36	69
Mac1	в	H-Y	126	58	46	68	54	15	12	54	43	72	57	16	13	54	43	6	5	81	64
Mac2	Α	L-Y	12	8	67	4	33	3	25	6	50	6	50	4	33	4	33	4	33	11	92
Mac2	в	H-Y	71	34	48	37	52	25	35	24	34	47	66	25	35	26	37	19	27	19	27
Mac3	Α	L-YO	11	7	64	4	36	2	18	6	55	5	45	2	18	2	18	2	18	3	27
Mac3	в	H-Y	61	23	38	38	62	26	43	20	33	41	67	27	44	28	46	14	23	12	20
Mac3	с	H-Y	67	-	•	-	-	-	•	40	60	27	40	23	34	22	33	6	9	32	48
Mac4	Α	M-0	37	6	16	31	84	16	43	4	11	33	89	16	43	15	41	8	22	2	5
Mac4	в	H-O	63	21	33	42	67	20	32	21	33	42	67	20	32	17	27	15	24	1	2
Mac5	Α	M-YO	30	10	33	20	67	16	53	9	30	21	70	16	53	19	63	10	33	13	53
Mac5	В	L-YO	20	10	50	10	50	8	40	8	40	12	60	9	45	14	70	2	10	9	45
CCk	Α	M-0	35	10	29	25	71	14	40	10	29	25	71	14	40	6	17	6	17	1	3
CCk	в	L-0	17	8	47	9	53	8	47	8	47	9	53	8	47	11	65	6	35	0	0
CLk	Α	L-O	14	2	14	12	86	7	50	2	14	12	86	7	50	11	79	10	71	0	0
CLk	B	L-0	8	2	25	6	75	3	38	2	25	6	75	3	38	2	25	3	38	1	13
Total		M-YO	624	-	-		-	168	27	251	40	373	60	195	31	238	38	113	18	221	35

 Table 9B.
 A more detailed view of Table 9A with each site broken into its respective plots of live and dead lodgepole pine in 2009 and 2010, indicating the presence of *Dendroctonus ponderosae* and other potentially weakening agents of lodgepole pine

Abbreviations: MPB=mountain pine beetle or Dendroctonus ponderosae, RC=root collar damage by insects, WB=wood borers, WGR=western gall rusts

<sup>†</sup> Density (L=low, 0-25 pine/plot; M=medium, 26-59 pine/plot; H=high, ≥60 pine/plot) and maturity (Y=young, YO=young-old, O=old) (refer Table 2 for more details of classifications)

**Table 10A.** Likelihood of tree mortality as a function of presence/absence of signs of various insects and root collar damage by insects in<br/>624 lodgepole pine across 15 plots in British Columbia, Canada in 2010, with the best models ranked by decreasing AIC value.<br/>p(tree death) =  $exp^{B_0+B_1x_1+...+B_kx_k}$ , where  $x_k$  are covariates listed below and coefficients are estimates (± SE)<br/> $1 + exp^{B_0+B_1x_1+...+B_kx_k}$ 

Model	Intercent		Explanato	ry variables of a	gent of mortal	ity of lodgepo	le pine <sup>†</sup>			
rank	mercept	DBH	мрв	RC	2BB	IP	OL	РМ	a.ı.	AIC
	0.963***	-0.221***			6.111***					F 74
Ŧ	(±0.205)	(±0.032)			(±0.624)				021	5/1
	-0.102 <sup>NS</sup>			-1.219***	4.787***				601	607
2	(±0.109)			(±0.279)	(±0.511)				021	607
2	-0.234*		-1.368 *		5.105***				621	<b>610</b>
3	(±0.102)	-	(±0.456)		(±0.618)				021	010
٨	-0.324**				3.987***				677	620
4	(±0.098)				(±0.464)				022	020
5	0.357**	-0.087***	1.957***			2.269***	2.636***		610	776
	(±0.174)	(±0.025)	(±0.323)			(±0.615)	(±0.759)		019	720
6	-0.142 <sup>NS</sup>		1.203***			2.247***	2.289**		620	727
	(±0.099)		(±0.225)			(±0.610)	(±0.743)		020	/3/
7	-0.289 <sup>NS</sup>	-0.064**	1.896***			2.294***			620	746
/	(±0.171)	(±0.024)	(±0.311)			(±0.610)			020	740
Q	0.424*	-0.087**	2.179***				2.650***		620	747
0	(±0.173)	(±0.025)	(±0.308)				(±0.751)		020	/4/
٥	-0.092 <sup>NS</sup>		1.330***			2.314***			601	753
	(±0.098)		(±0.221)			(±0.607)			021	/52
10	-0.085 <sup>NS</sup>		1.463***				2.373**		621	750
10	(±0.098)		(±0.218)				(±0.737)		021	/58

<sup>\*</sup> Abbreviations: DBH=diameter at breast height in centimeters, MPB=mountain pine beetle or *Dendroctonus ponderosae*, RC=root collar damage by insects, 2BB=Secondary bark beetles, IP=*Ips pini* (Say), OL=*Orthotomicus latidens* (LeConte), PM=*Pseudips mexicanus* (Hopkins)

Significance: \* (p<0.05), \*\* (p<0.01), \*\*\* (p<0.001), N.S. (not significant, p>0.05)

- continued next page -

– continuation –

Model	1		Explanator	ry variables of a	gent of morta	ality of lodgepo	le pine <sup>†</sup>			ALC
rank	Intercept	DBH	МРВ	RC	288	IP	OL	PM	<b>a</b> .r.	AIC
11	0.381* (±0.171)	-0.072** (±0.024)	2.096*** (±0.300)			anna an Teal (1999) ann an t- Le Ur Sterreger Chron		2.298* (±1.046)	620	762
12	0.115 <sup>NS</sup> (±0.088)					2.742*** (±0.600)	2.629*** (±0.734)		621	766
13	0.380* (±0.170)	-0.069** (±0.024)	2.182*** (±0.295)						621	769
14	-0.048 <sup>NS</sup> (±0.097)		1.508*** (±0.217)					2.193* (±1.037)	621	770
15	-0.033 <sup>NS</sup> (±0.097)		1.624*** (±0.214)						622	776
16	0.210* (±0.085)					2.896*** (±0.596)			622	791
17	0.273** (±0.084)						2.863*** (±0.727)		622	809
18	0.328*** (±0.083)							2.930** (±1.022)	622	824
19	0.166 <sup>NS</sup> (±0.102)			0.630*** (±0.173)					622	832
20	-0.072 <sup>NS</sup> (±0.157)	0.057** (±0.017)							622	833

<sup>†</sup>Abbreviations: DBH = diameter at breast height in centimeters, MPB=mountain pine beetle or *Dendroctonus ponderosae*, RC=root collar damage by insects, 2BB = Secondary bark beetles, IP=*Ips pini* (Say), OL=*Orthotomicus latidens* (LeConte), PM=*Pseudips mexicanus* (Hopkins)

Significance: \* (p<0.05), \*\* (p<0.01), \*\*\* (p<0.001), N.S. (not significant, p>0.05)

**Table 10B.** Likelihood of tree mortality as a function of lodgepole pine mortality across pine diameter sizes (in cm), the presence/absence of<br/>various bark beetles, and root collar damage by insects in each individual sites in British Columbia, Canada in 2010, with the best<br/>models ranked by decreasing AIC value. p(tree death) =  $exp^{B_0 + B_1x_1 + ... + B_kx_k}$ , where  $x_k$  are covariates listed below and<br/>coefficients are estimates (± SE) $1 + exp^{B_0 + B_1x_1 + ... + B_kx_k}$ 

Model	Cite	Intercept	Ex	planatory variab	oles of agent o	f mortality of k	odgepole pine <sup>†</sup>		d.f.	AIC
rank	Site	(± SE)	DBH	МРВ	RC	2BB	IP	OL		
4		2.747***	-0.712***	3.025*		6.816***				1.00
T	Mac1	(±0.486)	(±0.116)	(±1.361)		(±1.587)			1/4	160
2	Maal	2.508***	-0.640***			8.911***			175	161
	IVIACI	(±0.454)	(±0.105)			(±1.593)			1/5	101
2	Maci	2.181***	-0.546***	4.465***			3.570**		174	190
	IVIACT	(±0.417)	(±0.092)	(±0.957)			(±1.194)		1/4	103
٩	Mac1	-0.788**	-0.151**						176	220
	INIGCT	(±0.295)	(±0.046)						170	233
10	Mac1	-0.169 <sup>NS</sup>					2.567*		176	240
	IVIACT	(±0.156)					(±1.056)			240
11	Mac1	-0.166 <sup>NS</sup>		1.082*					176	246
**	IVIACI	(±0.160)		(±0.509)					1/0	240
4		-0.372 <sup>NS</sup>				3.868***			01	70
1	Macz	(±0.291)				(±1.056)			81	79
	Mag2	-0.148 <sup>NS</sup>		3.481***					01	07
Z	IVIAC2	(±0.273)		(±1.054)					81	8/
2	Maca	-1.208*	0.295***						01	07
	IVIdLZ	(±0.530)	(±0.085)						01	97
٨	Maca	0.113 <sup>NS</sup>			1.496**				01	104
<b>4</b>	IVIdCZ	(±0.275)			(±0.562)				01	104
5	Mac2	0.322 <sup>NS</sup>					2.243*		Q1	105
J	IVIGLE	(±0.244)					(±1.066)		01	COT

<sup>†</sup>Abbreviations: DBH = diameter at breast height in centimeters, MPB=mountain pine beetle or *Dendroctonus ponderosae*, RC=root collar damage by insects, 2BB = Secondary bark beetles, IP=*Ips pini* (Say), OL=*Orthotomicus latidens* (LeConte)

Significance: \* (p<0.05), \*\* (p<0.01), \*\*\* (p<0.001), N.S. (not significant, p>0.05)

Sites (n): Mac1 = Mackenzie 1 (n=178, 2 plots), Mac2 = Mackenzie 2 (n=83, 2 plots)

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Model	Cit-	Intercept	E:	xplanatory varia	bles of agent c	of mortality of	lodgepole pine <sup>†</sup>		46	AIC
rank	Site	(± SE)	DBH	МРВ	RC	2BB	IP	OL	u.r.	AIC
1	Mac3	-0.916*** (±0.232)				4.766*** (±1.037)			137	123
2	Mac3	0.704** (±0.236)		1.128** (±0.438)			3.329** (±1.049)		136	155
3	Mac3	-0.390* (±0.195)					3.758*** (±1.036)		137	160
4	Mac3	-0.493* (±0.221)		1.696*** (±0.396)					137	176
5	Mac3	-0.301 <sup>№</sup> (±0.217)			1.112** (±0.371)				137	187
6	Mac3	-0.911* (±0.433)	0.139* (±0.055)						137	189
1	Mac3-C	-2.277*** (±0.525)				5.413*** (±1.148)			65	39
2	Mac3-C	-1.466*** (±0.370)					4.357*** (±1.092)		65	58
3	Mac3-C	-3.984*** (±1.025)	0.476*** (±0.128)						65	75
4	Mac3-C	-1.224*** (±0.360)		2.265*** (±0.596)					65	78
5	Mac3-C	-0.901** (±0.329)			1.460** (±0.552)				65	87

\* Abbreviations: DBH = diameter at breast height in centimeters, MPB=mountain pine beetle or *Dendroctonus ponderosae*, RC=root collar damage by insects, 2BB = Secondary bark beetles, IP=*Ips pini* (Say), OL=*Orthotomicus latidens* (LeConte)

Significance: \* (p<0.05), \*\* (p<0.01), \*\*\* (p<0.001), N.S. (not significant, p>0.05)

Sites (n) : Mac3 = Mackenzie 3 (n=139, 3 plots), Mac3-C = Mackenzie 3-Plot C (n=67)

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#### – continuation –

Model	Site	Intercept	E	kplanatory varia	bles of agent o	of mortality of	lodgepole pi	ne <sup>†</sup>	-1 E	AIC
rank	Site	(± SE)	DBH	МРВ	RC	2BB	IP	OL	a.r.	AIC
1	Mac4	-0.578* (±0.261)		2.255** (±0.773)					98	103
2	Mac4	-0.296 <sup>NS</sup> (±0.588)	0.141* (±0.058)						98	110
1	Mac5	0.514 <sup>NS</sup> (±0.516)		4.041*** (±1.222)	-2.605* (±1.176)				47	52
2	Mac5	-0.241 <sup>NS</sup> (±0.403)		2.234** (±0.736)					48	57
1	CCk <sup>‡</sup>	2.267* (±0.888)	-0.176** (±0.067)		1.726* (±0.879)			2.350 <sup>0.0503</sup> (±1.201)	48	62
2	CCk <sup>‡</sup>	2.920** (±1.009)	-0.255** (±0.089)	1.885* (±0.943)	1.691* (±0.853)				48	63
3	CCk <sup>‡</sup>	1.941* (±0.828)	-0.116* (±0.055)					2.242* (±1.136)	49	64
4	CCk	2.185* (±0.865)	-0.145* (±0.061)		1.622* (±0.802)				49	65
5	CCk	2.567** (±0.925)	-0.192* (±0.076)	1.807* (±0.889)					49	65

\* Abbreviations: DBH = diameter at breast height in centimeters, MPB=mountain pine beetle or *Dendroctonus ponderosae*, RC=root collar damage by insects, 2BB = Secondary bark beetles, IP=*lps pini* (Say), OL=*Orthotomicus latidens* (LeConte)

<sup>+</sup>AIC values were significant (or close to it) when tested using generalized linear model, and close to significant (p<0.063) when tested using generalized linear mixed effect models, compared to the other models that remained significant when scrutinized from either tests

Significance: \* (p<0.05), \*\* (p<0.01), \*\*\* (p<0.001), N.S. (not significant, p>0.05)

Sites (n) : Mac4 = Mackenzie 4 (n=100, 2 plots), Mac5 = Mackenzie 5 (n=50, 2 plots), CCk = Crassier Creek (n=52, 2 plots)

		DBH	Hgt	Dead	/Alive	М	РВ	Sec	condar	y bark bee	etles (2	BB) (fin	al in 20	)10)		Others			
Site	Plot	(cm)	_(m)	2009	2010	2009	2010	2BB	IP	H-LPB	OL	PM	PT	AMB	RC	WGR	WB	Kill	BT
M1	В	9.2	9.7	Α	Α		<u> </u>	✓	✓							1		?	
M1	В	8.7	10.2	Α	D			✓	✓						✓	✓		✓	
M2	В	9.5	13.8	Α	D	✓	✓	✓	1	✓	✓	1			1		✓	✓	
M2	В	5.7	9.5	Α	D			$\checkmark$	✓		✓		✓		✓	✓	✓	✓	
M2	В	9.0	13.1	Α	Α	✓	✓	✓	✓			✓			✓			?	
M2	В	7.3	8.4	Α	D	✓	✓	✓	✓		✓				✓			✓	
M2	В	8.2	13.2	D	D	✓	✓	✓	✓	✓	✓	✓	✓		$\checkmark$			✓	
M2	В	6.5	7.2	Α	D			✓	✓	$\checkmark$			✓			✓	$\checkmark$		✓
M2	В	10.2	12.9	D	D	✓	✓	✓		✓					✓	✓			
M2	В	8.1	11.1	Α	D			✓	✓	✓		✓	✓	✓	✓				✓
M3	Α	9.0	11.6	Α	D			✓	✓	✓			✓						✓
М3	В	10.9	13.1	D	D	✓	✓	✓	✓	✓					✓			✓	
M3	В	7.4	11.0	Α	D	✓	✓	✓	✓	✓	✓	✓	✓			✓		$\checkmark$	
M3	В	7.3	10.5	Α	D	✓	✓	✓	✓		✓	✓	✓		✓			✓	
М3	В	8.1	9.4	Α	Α		✓								✓				
M3	С	10.7	13.5		D		✓	✓	✓	✓		✓	✓				✓	✓	
M3	С	5.7	9.0	-	D			✓	✓	✓									✓
M3	С	8.2	8.5		Α			✓	✓						✓	✓		?	
M3	С	8.4	11.3	-	D			1	✓	✓						✓		✓	
M5	В	13.6	12.9	Α	D		✓	1	1						✓				✓
CCk	Α	14.6	17.1	Α	Α	1	✓	✓			✓							?	

 Table 11.
 A detailed summary of 21 lodgepole pines with frass and their interactions with various insects, broken tops, or the other agents of tree mortality recorded in 2010 at the post-outbreak stage of *Dendroctonus ponderosae* in central British Columbia, Canada

 Abbreviations:
 DBH=diameter at breast height (in cm), Hgt=height (in m), MPB=mountain pine beetle or Dendroctonus ponderosae,

 2BB=Secondary bark beetles, IP=Ips pini (Say), H-LPB=Hylurgops spp. and/or Dendroctonus murrayanae (Hopkins),

 OL=Orthotomicus latidens (LeConte), PM=Pseudips mexicanus (Hopkins), PT=Pityogenes spp. and/or Pityophthorus spp.,

 AMB=ambrosia beetles, RC=root collar damage by insects, WGR=western gall rust, WB=wood borers, BT=Broken top trees

			DBH	Hgt	M	PB	Se	condar	y bark bee	etles (2)	BB) (fina	al in 20	10)		Others			
Tree	Site	Plot	(cm)	(m)	2009	2010	2BB	IP	H-LPB	OL	PM	PT	AMB	RC	WGR	WB	Frass	BT
1	M1	В	3.0	5.9											1			
2	M1	В	3.5	8.0											$\checkmark$			✓
3	<b>M</b> 1	В	8.7	10.2			✓	✓						✓	✓		✓	
4	M1	В	5.6	8.6											✓			✓
5	M2	Α	11.6	8.6		✓								✓	✓			
6	M2	Α	10.0	7.2			✓			✓	✓			✓	✓			
7	M2	В	9.5	13.8	✓	✓	✓	✓	✓	✓	✓			✓		✓	✓	
8	M2	В	5.7	9.5			✓	✓		$\checkmark$		✓		✓	$\checkmark$	✓	✓	
9	M2	В	7.3	8.4	$\checkmark$	✓	✓	✓		✓				✓			✓	
10	M2	В	3.7	5.5										✓				
11	M2	В	8.3	11.7														
12	M2	В	6.5	7.2			✓	✓	✓			✓			✓		✓	✓
13	M2	В	5.6	7.6			✓		✓	✓		✓						
14	M2	В	4.0	3.4											✓			✓
15	M2	В	8.1	11.1			✓	✓	✓		✓	✓	✓	✓			✓	$\checkmark$
16	M2	В	5.1	4.1														
17	M3	Α	9.0	11.6			✓	✓	✓			✓					✓	$\checkmark$
18	M3	B	10.5	12.7	✓	✓	✓			✓				✓				
19	M3	В	7.4	11.0	✓	✓	✓	✓	✓	✓	✓	✓			✓		✓	
20	M3	В	7.3	10.5	✓	✓	✓	✓		✓	✓	✓		✓			✓	
21	M4	Α	13.2	17.4	✓	✓	✓	✓	✓					✓	✓	✓		
22	M4	Α	6.6	11.8			✓	<u>√</u>	✓	✓							· · · · · · · · · · · · · · · · · · ·	
23	M5	Α	7.0	9.7			✓		✓						$\checkmark$			
24	M5	В	6.7	9.8										✓	✓			
25	M5	В	13.6	12.9		✓	✓	✓						✓			✓	✓

 Table 12.
 A detailed summary of 25 lodgepole pines with new mortality recorded in the five sites near Mackenzie in 2010 at the post-outbreak stage of *Dendroctonus ponderosae*, exhibiting the multiple interactions of bark beetles in the trees in the stands

Abbreviations: DBH=diameter at breast height (in cm), Hgt=height (in m), MPB=mountain pine beetle or Dendroctonus ponderosae, 2BB=Secondary bark beetles, IP=Ips pini (Say), H-LPB=Hylurgops spp. and/or Dendroctonus murrayanae (Hopkins), OL=Orthotomicus latidens (LeConte), PM=Pseudips mexicanus (Hopkins), PT=Pityogenes spp. and/or Pityophthorus spp., AMB=ambrosia beetles, RC=root collar damage by insects, WGR=western gall rust, WB=wood borers, BT=Broken top trees

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Figure 1. The epidemiology of *Dendroctonus ponderosae* (black line/shade), and their four phases of population cycles (endemic, incipient, epidemic, and post-epidemic), in relation to secondary bark beetle populations (red line/shade), and the potential extension of the outbreak by bark beetles associated with additional tree mortality, in the post-outbreak stage of *Dendroctonus ponderosae*. This new mortality may arise from the secondary species that are consuming smaller-diameter residual pines



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Figure 2.Tree abundance in seven study sites in the central interior of British Columbia,<br/>Canada, 2009–2010





Α.

Total lodgepole pine surveyed by sites (n=624)





Figure 3.Status of lodgepole pine (alive/dead) in seven study sites in the centralinterior of British Columbia, Canada, 2009–2010



\* Total excludes a 15<sup>th</sup> plot (Mac3-C) established in 2010 (27 dead trees of 67 trees total) because no baseline measurement was taken in 2009 to permit reference of time of death

Figure 4A.Vigour of lodgepole pine surveyed in each of 14 plots in the central interior of<br/>British Columbia, Canada, 2009–2010



alive/dead lodgepole pine surveyed by site-plot

Total: 557

Figure 4B. Percentages of lodgepole pine of different vigours surveyed in each of



14 plots in the central interior of British Columbia, Canada, 2009–2010

Total: 557

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20 Mac1 15 n=87 10+ 5 0+ 20 · Mac2 15 n=53 10 5. ٥. 20 Mac3 15 n=46(+27) 10 5. 0 20 Mac4 15 n=75 10 5 0 20 Mac5 15 n=33 10 5 O 20. **Crassier Creek** 15 40 Mackenzie 1 n=34 10. Mackenzie 2 5 35-Mackenzie 3 0{ 20 Mackenzie 4 **Chief Lake** 15 Mackenzie 5 n=18 10 **Crassier Creek** 5. Chief Lake 0-All 7 sites 20 **Overall 7 sites** 15 n=346(+27) 10 5. 0 ò 5 10 15 20 25 30 5 0 10 15 20 25 ò 5 30 Diameter (cm) of lodgepole pine  $\rightarrow$ 

**Figure 5B.** Density distribution of dead lodgepole pines by site in seven sites in the central interior of British Columbia, Canada, 2010
Figure 6. Distribution of dbh of live residuals (Figure 6A) and dead lodgepole pines (Figure 6B) in the central interior of British Columbia, Canada, 2009 and 2010





**Figure 7.** Relationship between mean tree diameter and mean stand density per site among the seven sites of the central interior of British Columbia, Canada

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# Figure 8. Spatial niche partitioning in same lodgepole pine host by bark beetles in central British Columbia, Canada



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# Figure 9. Temporal niche partitioning of flight dispersal periods by bark beetles in central British Columbia, Canada



Figure 10. Semiochemical attraction and repellence by bark beetles in central British Columbia, Canada



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### Introduction

British Columbia has a richer diversity of ecosystems than any other Canadian province. The province possesses 16 biogeoclimatic zones; a complex of geological terrains and varying climatic regions, ranging from continental to alpine tundra to maritime. This westernmost province of Canada supports a wide variety of biota from the depths of the Pacific Ocean to the peaks of the Rocky Mountains, with its multitude of ecosystems of kelp beds, estuaries, wetlands, mountain slopes, alpine meadows and desert-like steppes. The province is larger than any European country, except Russia, with a total land area of 95 million hectares.

Almost 60% of the land is forested: approximately 55 million hectares or roughly 11 billion cubic meters of timber (BCMOE 2007, BCMoFML 2010). Coniferous forests make up 83% of the forested land, with lodgepole pine constituting more than two billion cubic meters of growing stock. Mature lodgepole pine, as the leading tree species, comprises almost a third of the annual provincial timber harvest: approximately 1.35 billion cubic meters of timber or 14 million hectares of mature pine (BCMoFR 2007, 2008, BCMoFML 2010). This natural resource, a natural treasure of the province, generates substantial revenues to support the local economy in the form of a wide variety of forest products and sustains innumerable ecological functions, such as supporting plants and wildlife biodiversity and other provisions of invaluable non-timber forest products and services (Hamre 1975, Fahey and Knight 1986, Campbell et al. 2009). In terms of human economics, the accrued benefits of ecosystem services worldwide have an average value of 33 trillion U.S. dollars.

Proportionally for the size of British Columbia, the estimated value of ecosystem services is valued at more than 200 billion U.S. dollars (Costanza et al. 1997).

Pinus contorta var. latifolia Engelmann, the dominant inland form of lodgepole pine among the four major geographical varieties (Lotan and Perry 1983), exhibits one of the most widespread geographical ranges among the pines in North America, ranging from central Yukon to the Rocky Mountains in British Columbia, and from Colorado to the Black Hills in South Dakota in the United States (Lowery 1984). Lodgepole pine is a ubiquitous species that has a wide range of environmental tolerance, occurring at elevations from 500 to 3600 meters, with a preference for cool and dry habitats over warm and moist sites, but persisting even on poor soils in British Columbia and Alberta (Smithers 1961). Lodgepole pine is a serotinous subclimax species. As a fire-maintained species, it is highly adapted to regenerate quickly to overcome competition from other species, as the seedlings are intolerant to shade and are poor competitors (Fowells 1965). This species has multiple uses, aesthetic and recreational functions, and ecological roles, acting as a carbon sink, foraging material, and/or wildlife habitat. Given its timber and non-timber yields, lodgepole pine is important to the province of British Columbia (McDougal 1973, Pfister and Daubenmire 1975, Lotan and Perry 1983, Lotan and Critchfield 1990).

Lodgepole pine is associated with a variety of insect groups such as terminal, shoot and twig insects, sap-sucking insects, folivores, seed and cone feeders, lower stem and root insects, bark beetles, ambrosia beetles, and wood borers (Keen 1952, Smithers 1961, Coulson and Witter 1984). Among these groups of insects, which are classified according to the type and part of tree on which they feed and reproduce, bark beetles cause more

mortality to lodgepole pine than any other abiotic factor, forest fires or annual harvests of anthropogenic origin, and any biotic disturbance agents, combined (Amman 1975, BCMoFML 2010). The name bark beetle is derived from the beetle's habit of breeding under the bark, or in the subcortical tissue region of trees, primarily conifers (Wood 1982b). There are more than 50 species of scolytid bark beetles associated with lodgepole pine in Canada (Bright 1976).

The colonization behaviour of bark beetles can vary from "primary" to "secondary" users of lodgepole pine as host. "Primary" refers to the more aggressive beetles that can attack and kill healthy trees (Rudinsky 1962). In contrast, "secondary" bark beetles reproduce in unthrifty trees, such as those stricken by diseases or drought, and in recently-killed trees, such as in windfalls, freshly cut logs, and logging slash (Swaine 1918, Wood 1982b, Safranyik et al. 1999b, 2000, 2004). If a live tree is colonized, the secondary species are often found at a distance away from the main bole, in the lower bole or upper limbs of decadent trees. Under normal circumstances, secondary bark beetles might further weaken the tree, or only on occasion cause mortality. Secondary bark beetles are not usually a significant source of tree mortality, however (Keen 1952, Furniss and Carolin 1977).

The majority of bark beetles are secondary, and only a few species are primary (Rudinsky 1962). Bark beetles play an important role in promoting a heterogenous forest community, supporting a multitude of wildlife, biodiversity, and ecological functions (Chan-McLeod 2006, Burton 2008). Bark beetles may promote higher growth and vigor by removing stagnated and weakened trees, accelerating the deterioration of dead or dying trees, and by recycling nutrients (Wood 1982b, Romme et al. 1986, Brown et al. 2010).

# The outbreak of Dendroctonus ponderosae in British Columbia and subsequent lodgepole pine mortality

In the following section, the biology and ecology of *Dendroctonus ponderosae* and each of the secondary bark beetles in the north-central region of British Columbia are briefly described. All of these insects may colonize lodgepole pine, but reduce competition by partitioning the resource spatially and temporally, often via complex chemical cues. A description of the spatial and temporal partitioning can be found in **Tables 1** and **2**, respectively, while the known chemical ecology of these species is provided in **Appendix A**.

# The bark beetles of lodgepole pine in British Columbia "Primary" bark beetle Dendroctonus ponderosae (Hopkins), mountain pine beetle

*Dendroctonus ponderosae* (Hopkins) is a primary phloeophagous generalist on more than 30 species of pines (Furniss and Schenk 1969, Smith et al. 1981). In British Columbia, its primary host is lodgepole pine. Among all the mortality agents of pines, *D. ponderosae* inflicts the highest rate of tree mortality in the western hemisphere of North America, ranging from the provinces of British Columbia and Alberta in Canada to the 12 western states of United States (Furniss and Carolin 1977, Wood 1982b, Amman and Cole 1983). The insect prefers the largest-diameter mature pines during outbreaks (Amman 1975, Raffa 1988, Boone et al. 2011).

*Dendroctonus ponderosae* is the principal mortality agent in this study, infesting the main bole, below 5 m, of apparently healthy lodgepole pine of at least 10 cm in diameter at epidemic phases (Hopkins 1909, Unger 1993, Safranyik and Carroll 2006, Gibson et al. 2009) (**Table 1**). It is considered a primary bark beetle. *Dendroctonus ponderosae* has four larval instars. Each instar takes, on average, 28–30 days to develop at constant 24°C (in phloem of

high quality, as in epidemic conditions). Maturation feeding ranges from days to months as the adults emerged synchronously (Safranyik and Whitney 1985, Bentz et al. 1991). *Dendroctonus ponderosae* has one generation per year in British Columbia, with peak emergence usually occurring at the end of July to mid-August, and lasting between 7–10 days. Occassionally, parent adults may re-emerge to establish a second brood (Reid 1962a, Safranyik and Carroll 2006).

# "Secondary" bark beetles Ips pini (Say), pine engraver

*Ips pini* is the most common sympatric with *D. ponderosae*, and is one of the most aggressive species of secondary bark beetles, with the capacity to cause mortality of sapling or pole-sized lodgepole pine with a diameter of 5 cm and greater (Roe and Amman 1970, Furniss and Carolin 1977). *Ips pini* may also kill larger trees with weakened defenses, such as trees with concurrent attacks from other species of bark beetles (Weaver 1934, Rudinsky 1962, Ayres et al. 2001), or any other disturbance agents in the forest (Kennedy 1969, Klepzig et al. 1991, Santoro et al. 2001, Lombardero et al. 2006, Fettig et al. 2010). *Ips pini* has a transcontinental distribution in most pine species, and is most commonly found in downed materials such as windfalls, freshly cut logs, and thin-barked portions of slash. Suitable breeding material includes the tops and branches of trees recently killed or weakened by *D. ponderosae* (Reid 1957a, Bright 1976, Kegley et al. 1997), as in this study **(Table 1)**.

*Ips pini* has three larval instars, with a life cycle of between 34–60 days in lodgepole pine (Reid 1955, Miller and Borden 1985), between 31–48 days in white pine (Prebble 1933), between 40–55 days in ponderosa pine (Kegley et al. 1997), approximately 15 days at constant 25°C to 65 days under normal seasonal temperatures in red pine (Ayres et al. 2001) or 33–35 days in jack pine, in addition to 6–11 days for maturation feeding under the bark (Thomas 1961, Schenk and Benjamin 1969). *Ips pini* overwinter near their brood trees in the duff as adults, which provides close proximity to available host materials upon emerging from hibernation early the next spring (Schmitz 1980, Safranyik et al. 1999a). Normally a bivoltine species in Ontario, Canada, *I. pini* can have up to three broods, with peak flights starting in mid-May, the second in end of July, and, in warmer summers, a smaller peak of reemerging parents or brood adults flying in late August to early September (Thomas 1961, Bright 1976, Safranyik et al. 1996, 2000, Ayres et al. 2001) **(Table 2)**.

#### Hylurgops spp. (LeConte), sour sap bark beetles

*Hylurgops* spp. commonly infest the phloem at the lower bole of recently cut lodgepole pine stumps, or at the root collar region of the larger main roots of dead or severely weakened conifers (Keen 1952, Wood 1982b, Safranyik et al. 1999a, 2000, 2004) **(Table 1)**. Similar to other root inhabiting insects, this genus exhibits a semivoltine life cycle. For example, *Hylurgops rugipennis* (Mann.) has approximately one generation every 1.5–2.5 years due to the varying rate of development from temperature differences within the subcortical tissues of the roots (Reid 1957a, 1957b). The most abundant *Hylurgops* spp. is *Hylurgops porosus* (LeConte) (Safranyik et al. 2000, 2004, Schweigkofler et al. 2005). This species is likely responsible for dark staining in the phloem where it occurs. *Hylurgops porosus* and *Hylurgops rugipennis* have a flight period throughout the growing season, based on the extended period of emergence from the stumps. These insects breed in the base of trees killed by *D. ponderosae* without competing directly with the more aggressive species in the upper bole (Safranyik et al. 1999a, 2000, 2004) **(Table 2)**.

#### Orthotomicus latidens (LeConte), smaller western pine engraver

*Orthotomicus latidens* is a ubiquitous species, breeding in ephemeral, patchy habitats, such as in wind-downed or diseased trees, and in tops and branches of trees recently killed by *D. ponderosae* (Keen 1952, Bright 1976, Miller and Borden 1985, Miller et al. 1986, Reid 1999) **(Table 1)**. *Orthotomicus latidens* has three larval instars, with an estimated mean generation time of 64–124 days in lodgepole pine. Maturation feeding can last from weeks to months to synchronize adult emergence, as most *O. latidens* overwinter under the bark (Miller and Borden 1985). *Orthotomicus latidens* is univoltine in south-central British Columbia, and can produce up to two broods per year. The main flight period occurs in spring, around late May to early June, with a second flight peak in late July from re-emerging adults (Miller and Borden 1985) **(Table 2)**.

## Pseudips mexicanus (Hopkins), Monterey pine engraver

*Pseudips mexicanus* often occur together with endemic *D. ponderosae* (Smith et al. 2011), preferring the lower boles of suppressed trees below a height of 1.0 m (Smith et al. 2009) **(Table 1)**. *Pseudips mexicanus* has four larval instars, and can complete its life cycle in approximately 50 days at 26.5°C. The insect may emerge in less than four days of maturation feeding (Smith et al. 2009). *Pseudips mexicanus* primarily overwinter as larvae and adults (Struble 1970), based on the finding of amorphous galleries in lodgepole pine (Smith et al. 2009). *Pseudips mexicanus* is univoltine in lodgepole pine in British Columbia and California, with the ability to produce up to two broods per year, with two peak flights. The first flight peaks around late May to early June. A subsequent flight from re-emerging adults peaks in early to mid-August (Bright and Stark 1973, Smith et al. 2009).

In California, *P. mexicanus* may have up to three generations per year in Monterey pine (Struble 1970) **(Table 2)**.

#### Dendroctonus murrayanae (Hopkins), lodgepole pine beetle

*Dendroctonus murrayanae* is most commonly associated with lodgepole pine, but is also found in four other species of pines and three species of spruce. Lodgepole pine beetle prefers the lower boles near the roots on overmature or weakened standing pines or the stump areas of windfallen trees. This insect is seldom found more than 60 cm above ground level (Keen 1952, Bright 1976, Wood 1982b) **(Table 1)**. *Dendroctonus murrayanae* has four larval instars, with larval offspring aggregating and feeding gregariously side-by-side in communal chambers, and taking more than 26 days to mature into adults from second-instar larvae (Furniss and Kegley 2008). *Dendroctonus murrayanae* is univoltine, overwintering as larvae . Flight to attack new hosts occurs in mid-June to mid-July, with eggs hatching into larvae in August before winter (Safranyik et al. 2004, Furniss and Kegley 2008) **(Table 2)**.

#### Pityogenes spp. (Bedel), twig beetles

*Pityogenes* spp. are predominantly found among the smaller-diameter slash and stems in most species of pines and in several species of spruces, with each species having their preferred host (Bright and Stark 1973) **(Table 1)**. The most common and important species of *Pityogenes* associated with lodgepole pine in the western hemisphere of North America is *Pityogenes knechteli* (Swaine) (Reid 1955, Bright 1976, Safranyik et al. 2004), which can increase to outbreak levels and kill up to 16% of live trees after a *D. ponderosae* epidemic (Evenden and Gibson 1940). *Pityogenes* spp. have four or five larval instars, with varying rates of development, depending on tree species. *Pityogenes knechteli* has a mean generation time of about 6–8 weeks to complete its life cycle from egg to adults (Reid 1955), and is univoltine, with the capacity to have up to two broods per year. The main dispersal period peaks at the end of May. Re-emergent adults establishing a second brood may produce a second lower peak from early June to August (Reid 1955, Safranyik et al. 2004) (Table 2).

#### *Pityophthorus* spp. (Eichhoff), twig beetles

Multiple species of *Pityophthorus* may occur in almost all of the commercially important conifers and on some deciduous trees. There are more than ten species of *Pityophthorus* that regularly occur in lodgepole pine, but the species within this genus are difficult to distinguish (Bright 1976) **(Table 1)**. *Pityophthorus* spp. are more common on smaller trees, and only found in twigs or the thinner-barked sections of larger trees. *Pityophthorus* spp. have two or three larval instars, and are presumably univoltine in general, depending on latitude and elevation (Bright 1981) **(Table 2)**. This genus might be widespread, but its impact on tree mortality is likely minimal, including on lodgepole pine. Thus, research on their biology and population dynamics is limited. Literature on life tables, population structure, host selection behaviour or dispersal patterns for this genus is almost nonexistent.

## Ambrosia beetles (Trypodendron lineatum [Oliver] , Gnathotrichus [LeConte])

The three native species of ambrosia beetles most commonly found in the western hemisphere of North America are the striped ambrosia beetle, *Trypodendron lineatum* (Oliver), *Gnathotrichus sulcatus* (LeConte) and *Gnathotrichus retusus* (LeConte) (Daterman and Overhulser 2002). Ambrosia beetles are found in a broad range of coniferous and broadleaved trees of at least 10 cm in diameter (Wood 1957) **(Table 1)**. Lodgepole pine is not always their

most preferred host, in comparison to most of the other species or genera of bark beetles above. Ambrosia beetles are often univoltine, laying up to two broods per year, with an estimated mean generation time of 6–10 weeks from egg to emergence (Daterman and Overhulser 2002). *Trypodendron lineatum* begins its flight as early as March, peaking in late April to May. The main flight of *Gnathotrichus* species is around May to June with flight throughout summer, depending on the warmth of days (Daterman et al. 1965, Daterman and Overhulser 2002) **(Table 2)**. *Trypodendron lineatum* begins flight earlier in the spring than *Gnathotrichus* spp. because *T. lineatum* prefer aged timber of at least 3–5 months old, or trees that have died the previous autumn or winter (Borden 1988). Ambrosia beetles are appropriately grouped together because all species of this tribe bore into the inner sapwood to feed on their cultivated 'garden' of mycelial growth of ambrosial fungi that they vector, instead of consuming the phloem or woody tissue of the trees.

## **Epidemiology of bark beetle populations**

There are four phases in the population dynamics of *Dendroctonus ponderosae*: endemic, incipient-epidemic, epidemic or outbreak, and post-epidemic (Safranyik and Carroll 2006).

At endemic phases, *D. ponderosae* exhibits similar colonization behavior to that of a "secondary" bark beetle, reproducing in weakened, dying or dead trees. There are insufficient numbers of beetles to overcome even a single large-diameter live tree within the stand; thus, the insects are restricted to subsistence on low-quality hosts (Evenden et al. 1943). The population reaches incipient-epidemic levels under favorable conditions, such as declining tree resistance from a series of stress events like fire or drought. This allows the population to reach an epidemic threshold to successfully attack and overcome

the tree defenses and begin to kill live large-diameter trees within the stand (Berryman 1982a, Raffa and Berryman 1983). This critical turning point reflects a threshold upon which a population may decline to endemic stages or to continue to build up to a full-scale outbreak if ideal conditions for beetle survival, development and establishment persist. Such conditions may include, but are not limited to, stressed trees, forest disturbance events, and the insects' interactions or associations with other secondary bark beetles that facilitate an epidemicity (Weaver 1934, Roe and Amman 1970, Carroll et al. 2006a, Safranyik and Carroll 2006, Fettig et al. 2010, Koopmans 2011, Smith et al. 2011).

Once populations enter epidemic stages, *D. ponderosae* acts as a "primary" bark beetle to exert stand-replacing mortality at a landscape-level. This stage of the population is highly resilient to large losses. The outbreak is sustained as long as an abundance of preferable hosts is available, such as mature pines. The insects also require favourable weather conditions, such as mild winters or warm summers or prolonged stress events like droughts and diseases. When there are insufficient supply of large-diameter host trees to sustain the outbreak or when the population suffers huge losses from lethal low temperatures, the population enters the post-epidemice phase (Safranyik and Carroll 2006).

Secondary bark beetles may exhibit similar population phases, but with less steep population growth and peaks at lower population sizes. Secondary bark beetles may be facultative mortality agents of lodgepole pine for two to three years following an outbreak of *D. ponderosae*. High numbers may build due to increased host abundance from the weakened, dying, or dead host pines from a *D. ponderosae* outbreak or simply under favourable climatic conditions, owing to an extended period of growth and development

while minimizing mortality rates (Keen 1952, Unger 1993, Kegley et al. 1997). The secondary bark beetles potentially causing new lodgepole pine mortality among live residuals in British Columbia following an outbreak of *Dendroctonus ponderosae* include sympatric species such as *Ips pini* (Say), *Hylurgops* spp., *Orthotomicus latidens* (LeConte), *Pseudips mexicanus* (Hopkins), *Dendroctonus murrayanae* (Hopkins), *Pityogenes* spp. (Bedel), *Pityophthorus* spp. (Eichoff), as well as ambrosia beetles.

## Importance of the outbreak of *Dendroctonus ponderosae* and its effect on the economy and environment

The present outbreak of *D. ponderosae* in western Canada is the most destructive outbreak by a forest insect in recorded history (Kurz et al. 2008). The latest reports, as of 2012, indicate that D. ponderosae had caused a mortality of mature lodgepole pine over an estimated cumulative area of 17.5 million hectares in British Columbia and Alberta, or a total of 726 million cubic meters of timber, since the outbreak began around 1997 (Walton 2010, BCMoFLNRO 2011). The mortality to date is larger than the combined total of all other bark beetles' mortality in the western coniferous forests of the United States recorded since 1997 to the present day (16.8 million hectares; USDAFS 2011), and the scale of mortality is at least six times larger than the combined total of all recorded outbreaks in the province from 1910 to 1995 (Unger and Fiddick 1979, Wood and Unger 1996). At present, more than 250 thousand trees, or a total of more than 3.6 million cubic meters of pine forests (jack pine, Pinus banksiana Lamb. and the lodgepole-jack pine hybrid) at risk in Alberta have been removed, as preventive measures (ABSRD 2010, 2011) to reduce the beetles' spread eastwards into the boreal forests of North America (Safranyik et al. 2010, Cullingham et al. 2011, Giroday et al. 2011). Currently, the insect has spread as far east as the Alberta-

Saskatchewan border (Brian H. Aukema 2012, personal communication).

Currently, the *D. ponderosae* population in British Columbia is experiencing a decline as its preferred host, larger diameter, mature lodgepole pine, has been killed since the outbreak peaked in 2005-2007 (Westfall and Ebata 2010, Sambaraju et al. 2012). The scale of this outbreak is so extensive and unprecedented that beetle populations with exhausted host supplies have begun to attack small tree in dense stands or mixed-species stands around the peripheries of the outbreak. For instance, pine stands as young as 18 years of age or as small as 8 cm in average diameter around the Prince George Forest District (Westfall 2004) have been attacked, and non-pine trees (such as interior hybrid spruce, *Picea engelmanni* Parry x *Picea glauca* (Moench) Voss) have signs of colonization by the beetles, though these events are rare occurrences (Evenden et al. 1943, Furniss and Schenk 1969, Huber et al. 2009, Safranyik et al. 2010).

Concomitant with the decline of numbers of *D. ponderosae* in the central interior of British Columbia, there has been an increase in secondary bark beetle populations breeding in an abundance of unoccupied phloem, such as the limbs, branches and twigs of the crowns, and root collar regions of pines whose stems have been colonized by *D. ponderosae* (Evenden and Gibson 1940, Rudinsky 1962, Furniss and Carolin 1977, Safranyik et al. 1996, 1999a, 2000). Those areas may be considered poor quality substrate for *D. ponderosae*, or outright unsuitable, but may be excellent host material for secondary bark beetles (Reid and Robb 1999, Safranyik et al. 1999a, 1999b, 1999c, 2000, 2004). At the same time as *D. ponderosae* may deplete hosts, so too secondary bark beetles may reproduce by attacking almost any surrounding trees as resources become scarcer. The trees at risk are primarily residuals,

comprising the smaller diameter classes or next generations of trees as the future mid-term timber supply for the province (Roe and Amman 1970). The outcome may be extension of the bark beetle outbreak from the additional mortality of the pole-sized trees, for up to three years, depending on the abundance and years of accumulation from the populations built up, after the collapse of populations of *D. ponderosae* (Evenden and Gibson 1940, Kennedy 1969, Roe and Amman 1970, Kegley et al. 1997, Safranyik and Carroll 2006, Westfall 2006).

Westfall (2006) noted that *I. pini* accounted for 20% of young lodgepole pine mortality in plantations. In recent years, annual surveys of the forest health conditions in British Columbia by Westfall (2005) and Westfall and Ebata (2007, 2008, 2009, 2010) have reported that young pine mortality has been on the rise, totaling almost 800 thousand hectares out of the approximately two million hectares of available young, lodgepole pine leading stands between the ages of 20–55 years in the province. Such losses are depicted schematically in **Figure 1**.

These estimates represent increasing mortality within the mid-term supply in the province, or an additional 5% mortality following the current outbreak (0.8 million hectares/17.5 million hectares). While the causative agents of mortality are unknown, outbreaks of secondary bark beetles should not be treated as an event of limited or non-significance. These estimates came from calculations from aerial surveys for *D. ponderosae* at the landscape level. At present, no detailed assessments of stand characteristics have been analysed on an annual basis that would allow (I) estimates of the rate of residual mortality in the post-outbreak stands and (II) identification of bark beetles (primary and secondary) that may be associated with such mortality.

## Objectives

There were two main objectives in this study: (I) to assess a variety of stands in the declining phase of an outbreak of *Dendroctonus ponderosae* over a two-year period to determine the extent and rate of lodgepole pine mortality, and (II) to examine the relationship between the rate of mortality and associations with *Dendroctonus ponderosae*, secondary bark beetles, and root collar damage by insects or other agents of mortality.

## Authorship

While the work in this thesis is my own, I use the first person plural pronoun throughout. This work is being prepared for submission to a peer-reviewed journal with co-authors Allan Carroll and Brian Aukema. As such, I retain 'we' and 'our' throughout the thesis to signify joint authorship.

### **Materials and Methods**

# Section 1: What do stands look like in the post-outbreak phase of an epidemic of Dendroctonus ponderosae?

Forest profiles may be altered as *D. ponderosae* activity shifts the balance of dead and live lodgepole pine composition in stands throughout the course of an outbreak. Thus, the first goal was to survey the patterns of mortality over two years in several stands along a gradient of activity of *D. ponderosae* in central British Columbia, focusing primarily on stands where populations of *D. ponderosae* were declining, or in a

"post-outbreak" mode (Safranyik and Carroll 2006).

## Part I. Stand selection

Stands were selected where lodgepole pine was the dominant species and there was evidence of recent tree-killing activity by *D. ponderosae*. The latter criterion was judged by an abundance of trees in the "green, red, and grey-attack" categories (referencing the colour of the crown in years prior to, during, and following tree death (Safranyik et al. 1974, Aukema et al. 2006). "Green-attack" represents live trees, subsequently examined in following years for new tree mortality associated with *D. ponderosae* and/or secondary bark beetles. "Red-attack" denotes recent colonization by *D. ponderosae* and tree death within the past year or two, as foliage fades to a chlorotic yellow, then red, within one year. "Grey-attack" represents lodgepole pine killed by *D. ponderosae* in previous years (i.e. often more than two years old). A photographic reference guide of the crown conditions are provided in **Appendix B**. The presence or absence of *D. ponderosae* and/or secondary bark beetles was evaluated based on visual observation of pitch tubes, boring dust at the base of the tree, and galleries under the bark. In total, seven study sites were selected as representative samples of lodgepole pine distributions in the central interior region of British Columbia were selected: five near Mackenzie (Mackenzie Forest District at 55° 29' N, 123° 26' W, elevation: ~800m), one near Crassier Creek (Peace River Forest District at 55° 39' N, 122° 17' W, elevation: ~1050m), and one near Chief Lake (Prince George Forest District at 54° 13' N, 123° 04' W, elevation: ~750m). The Mackenzie Forest District is located between the Peace River Forest District and the Prince George Forest District, in the center of British Columbia. All seven sites were located at least one kilometer apart from each other. A map of the study sites, their locations relative to tree-killing activity by *D. ponderosae* recorded by aerial surveys and photographs of the study sites are provided in **Appendix C** and **Appendix D**.

#### Part II. Stand establishment

In each of the seven sites, two plots measuring 10 x 10 meter (0.01 hectares) were placed at random in the spring of 2009. At one site in Mackenzie, a third plot of similar size was also established in the second year of the study. Within each plot, a census of each tree was recorded over two years: species of tree, diameter at breast height (DBH, 1.3m), height, and condition (alive or dead) (Avery and Burkhart 2002). The diameter of trees were measured using a DBH tape, or a caliper for smaller trees, and the tree height was recorded using a Haglöf vertex IV hypsometer, or a tape measurer for smaller trees. The first survey to establish the stand profiles was conducted in mid-summer 2009, the second survey in early summer of 2010, before the primary flight of *D. ponderosae*, and the third survey late-summer of 2010 to detect any trees that had died in 2010.

## Part III. Stand classifications (density and maturity)

Forest stands can be measured both qualitatively and quantitatively. Forest productivity can be evaluated using qualitative measures such as climate, soil and vegetation characteristics, or quantitatively using an economical value in wood productivity (Ford-Robertson and Winters 1983). Quantitative methods are often favored because measurements of stand density can be made if the topographic or climatic conditions permit classification of certain qualitative biogeoclimatic zones. These measurements facilitate comparison among sites' potential productivity relative to one another, which is a useful tool for forest managers. Stand density is important because density is directly proportionate to growth rate and the stand's consequential future merchantable yield. For example, in an ideal pure lodgepole pine stand, the optimum density of 1,980 trees/hectare might yield 280  $m^3$ /hectare of merchantable timber, compared to 4,450 trees/hectare yielding only 21 m<sup>3</sup>/hectare (Lotan and Critchfield 1990). The four most common measurements of stand density use diameter, height, form, and number of trees per unit area (Bickford 1957). This study used two quantitative measures of stand density as direct and indirect measures of the current and potential productivity of the forest.

The first method of stand density estimation used the number of lodgepole pine stems per hectare. The stand density per hectare for each site was estimated by multiplying the quantity of trees within the 10 x 10 meter plots by 100, since all plots were standardized to a fixed area of 0.01 hectare (1 hectare = 100 plots of 0.01 hectare / 10 x 10 meter). Based on the survey data, the sites and plots were grouped into three categories:

(I) low density at 0–25 lodgepole pine per 10 x 10 meter plot (0–2500 stems/hectare),

(II) medium density at 26–60 pines per plot (2600–6000 stems/hectare), and
(III) high density with more than 60 pines per plot (>6000 stems/hectare).

The second method of stand density estimation evaluated the height and diameter of the trees (Briegleb 1952). Stands were classified as 'old' if the trees exhibited an average diameter of at least 10 cm, including more than one large diameter pine of at least 20 cm in circumference, and mean height of at least 10 m, with more than one pine at least 20 m tall. In contrast, a stand was classified as 'young' if the mean diameter of lodgepole pine was less than 10 cm and the average height was less than 10 m, with no lodgepole pine larger than 20 cm DBH or taller than 20 m. If all of the criteria for an 'old' stand were not met, the plot or site was considered a 'young' stand with high annual growth potential. If the surveyed pines met at least two, but less than four, of the criteria, the site or plot was considered a 'young-old stand'; a stand with a moderate rate of growth that will gradually diminish as the stand matures.

The effect of diameter and height of lodgepole pine on pine condition (dead or alive) was examined using a logistic regression in a mixed effect model. Fixed effects included diameter at breast height and tree height, fitted as continuous variables. Sites and plots were modeled as random effects.

# Section 2: Which insects and/or pathogens are most closely associated with new tree mortality?

For reference, a flow chart of the methodology is provided in **Appendix E**. An initial survey for all plots, except for the fifteenth plot in Mackenzie, was performed at the beginning of the summer in June or July of 2009. The survey involved visual examination of all trees for any signs of bark beetle infestation. If a lodgepole pine was dead or showing signs of dying,

such as yellowing or reddish foliage or drying phloem, the putative source of tree mortality was sought by peeling back a small section of the bark, approximately 30 cm x 30 cm, to look for any signs of *D. ponderosae* and/or any secondary bark beetles. The presence or absence of bark beetles or their galleries was noted and photographed. This inspection was performed at the roots, at breast height (1.3 m), and at approximately three meters high. In each plot, the lodgepole pines were also checked for the presence or absence of root collar damage by insects at the bases of the trunks by scraping away leaf litter and the tree bark, digging down up to 50 cm below root collar of the main trunk. Western gall rusts (*Endocronartium harknessii*) were noted as well, when found on the upper branches of the lodgepole pines, or the main bole of smaller trees. A photographic reference for each gallery type by species of the insect, and the descriptions of the insects themselves, occasionally encountered, are included in **Appendix F**.

The plots were established and surveyed once in 2009. In 2010, a mortality survey was performed twice in all 15 plots, once before August 15, and another after August 15 (i.e. before and after the peak flight period of *D. ponderosae* and secondary species, determined from unpublished data of pheromone traps in the locality). In the second and third surveys, the live lodgepole pine in the 10 x 10 m plots were re-examined for any new mortality. Trees that were dying or dead were checked for corresponding bark beetle activity. If the survey before August 2010 detected the presence of *D. ponderosae*, the beetles were concluded to have arrived in the 2009 flight season. If a tree remained alive and vigorous, the conclusion was that there was no beetle colonization (or an unsuccessful one). For data quality purposes, all dead trees were revisited and measured a second time

(third survey) in 2010, using similar methods of examination as in 2009 (**Appendix E**); i.e. diagnosis of the galleries by removing sections of the bark, with the inference that detection of *D. ponderosae* at this stage reflected a recent arrival within the 2010 flight period.

Though all seven sites were surveyed in 2009, three of the Mackenzie sites were surveyed before the peak flight period of *D. ponderosae* in 2009 (before 13 August, determined from unpublished data of pheromone traps in the locality), which meant that the records of 2009 from those three sites might not reflect the arrivals of all the *D. ponderosae* of the same year; the remaining sites were surveyed after *D. ponderosae* flight, accounting for their arrival by 2009. Overall, the survey of 2010 that was performed twice (second and third surveys) served the dual purpose of monitoring for bark beetle activity before and after their main flight seasons in 2010, and this standardized those three sites with the rest, while ensuring consistency in the records from the 2009 survey.

An additional plot in one of the high-insect activity sites near Mackenzie, site 3-plot C (Mac3-C) was surveyed in 2010 and added into the overall survey of tree mortality associated with various insects and pathogens. Mac3-C was randomly selected and surveyed for meeting the profile criteria as a high risk stand for mortality of secondary bark beetles. Since this plot was not surveyed in 2009, analysis of the rates of mortality was excluded, but studies of the associations of various insects, including bark beetles, with the overall tree mortality was included in the analysis. This stand, on its own, is treated in depth in **Appendix I**.

The effects of tree diameter, *D. ponderosae*, root collar damage by insects (such as Warren root collar weevil, *Hylobius warreni* Wood), and the presence/absence of secondary bark beetles or individual secondary bark beetles such as *I. pini* (Say), *O. latidens* (LeConte), and *P. mexicanus* (Hopkins), on associated pine mortality (i.e. live/dead) were examined using generalized linear mixed effect models for binary response data. Fixed effects included diameter at breast height and tree height, fitted as continuous variables, and the presence or absence of *D. ponderosae*, root collar damage by insects, and the presence of any secondary bark beetles or individual species of secondary bark beetles, fitted as categorical variables. Terms for the stand variations within the seven sites, or the 15 plots within the sites, were modeled as random effects. The most parsimonious models were selected based on Akaike Information Criteria (AIC), a measure of relative goodness of fit (Akaike 1974), with the lowest AIC score for a given response variable representing the best fit. All data analysis was conducted using R (Dalgaard 2008, R Development Core Team 2010).

#### Results

# Section 1: What do stands look like in the post-outbreak phase of an epidemic of Dendroctonus ponderosae?

Within the 15 plots, 827 trees were surveyed, consisting of 624 lodgepole pines, 96 interior hybrid spruces [*Picea engelmanni* Parry x *Picea glauca* (Moench) Voss], 45 trembling aspens [*Populus tremuloides* Michx.], 22 black spruces [*Picea mariana* (Mill) BSP], 28 subalpine firs [*Abies lasiocarpa* (Hook) Nutt], eight Douglas-firs [*Pseudotsuga menziesii* (Mirb.) Franco], and four paper birches [*Betula papyrifera* Marsh.] (Figure 2, Table 3). Eighty eight percent (550/624) of the lodgepole pines were located in the sites near Mackenzie. All plots located near Mackenzie had 50% – 100% lodgepole pine composition, except for one, which had only 35% lodgepole pine (Table 3). The remaining 12% (74/624) of the lodgepole pines occurred in plots near Chief Lake and Crassier Creek (Figure 4). In these latter plots, lodgepole pines were more mature and found in mixed-species compositions, characteristic of lodgepole pine as a subclimax species. Even so, the lowest composition of lodgepole pine was 35% in the CLk site, plot B (Table 3).

The density of lodgepole pine varied among sites, from eight to 126 stems per 10 x 10 m plot (or 800–12,600 stems per hectare) **(Table 4)**. Based on the stand 'maturity' criterion, six of the 15 plots were young, six could be considered old, and the remaining three plots were transitioning young-old plots. These categorizations were derived from the diameter and height of the trees in the plots (BCMoFLNRO 2011; Briegleb 1952) **(Table 4)**.

Of the 557 lodgepole pines surveyed in 2009, 42% (236/557) were alive and 58% (321/557) were dead. If lodgepole pine in Mac3-C was included, the final tallied results were 40% live (251/624) and 60% dead (373/624) lodgepole pine. Only 557 lodgepole pines

from the 14 plots were used in the determination of the annual rate of tree mortality, since the remaining 67 (Mac3-C) of total 624 lodgepole pines were only surveyed in 2010, precluding calculations of the changes in mortality from 2009.

Surveys in 2010 revealed that an additional 25 lodgepole pines had died, decreasing the percentage of live lodgepole pines to 38% (211/557), and increasing the percentage of dead pines to 62% (346/557) (Figure 3). The 25 dead trees in 2010 yielded, then, an annual rate of pine mortality of approximately 4% (25/557 trees). The rate of mortality was highly variable between sites, ranging between zero and 15% depending on the lodgepole pine density and its maturity class. Among the sites near Mackenzie, site two (Mac2) exhibited the highest rate of mortality at 14% (12/83) in 2010, supplying almost half of the new mortality (12/25) (Figure 4). This was a relatively young stand (Table 4); plot A within that site (Mac2-A) exhibited a low stocking density, and displayed a mortality rate of 17% (2/12), while plot B within that site (Mac2-B), exhibited a high density of trees and a mortality rate of 14% (10/71). The plot with the highest cumulative lodgepole pine mortality, 89% (33/37 trees), occurred within the fourth site of Mackenzie (Mac4-A; a medium density 'old' stand). Comparisons between diameters and heights of live vs. dead lodgepole pine

On average, the 624 lodgepole pines had mean measurements of 8.4 cm in diameter and 10.1 m in height. Overall, the dead lodgepole pines exhibited slightly larger diameters than the live residuals (9.9  $\pm$  1.4cm vs. 10.4  $\pm$  1.5cm), although this difference was not statistically significant (t<sub>608</sub> = 1.40, p = 0.16) **(Table 5)**. In contrast, live trees were taller than dead trees (12.1  $\pm$  1.6m vs. 11.2  $\pm$  1.6 m) (t<sub>617</sub> = 2.54, p<0.05) **(Table 5)**. There was, however, considerable plot to plot variation and year-to-year differences could alter a stand's profile with only minor mortality. For example, plots Mac2-A and Mac4-A sustained the deaths of only two trees within each plot from 2009 to 2010. Although Mac2-A was a 'young' stand with a low density (n=12, live=8 in 2009), the death of two of its largest live lodgepole pines (tree #1: 11.6 cm and 8.6 m, tree #2: 10.0 cm and 7.2 m) decreased the plot's average diameter from 5.0 cm to 3.0 cm and average height from 4.5 m to 3.3 m. In the moderately dense stand of Mac4-A, the death of the largest tree (13.2 cm and 17.4 m) was sufficient to shrink the stand's mean diameter range from 6.3–13.2 cm to 6.3–11.3 cm, and the height range from 11.8–17.4m to 13.2–16.2m. These results are illustrated graphically in **Figures 5** and **6**, with numerical summaries presented in **Tables 6** and **7**.

# Section 2: Which insects and/or pathogens are most closely associated with new tree mortality?

Overall, 60% of the lodgepole pines surveyed (373/624) within the 15 plots in 2010 were dead. The 373 dead lodgepole pines comprised a combination of 321 dead pines from the 14 plots surveyed in 2009, 25 new dead trees near Mackenzie in 2010, and 27 dead trees from the new plot of Mac3-C in 2010 (Figure 3).

Among the 373 dead trees, 191 had signs of *D. ponderosae* in 2009. Surveys detected an additional four pines with *D. ponderosae* in 2010 (**Table 8A**). By the end of summer in 2010, two out of those four attacked trees had died. More than 80% (163/193) of the trees with galleries of *D. ponderosae* were associated with plots near Mackenzie. This figure was consistent with the majority of the lodgepole pines being found near Mackenzie (550/624 lodgepole pines surveyed, or 88%) (**Figure 2**). Among the seven sites in Mackenzie Forest District in 2010, *D. ponderosae* were most frequent in a low density

'young-old' stand (Mac5) at 76% (25/33) and least frequent in a high density 'young' stand (Mac1) at 23% (21/87) **(Table 9)**.

Secondary bark beetles were found in 54% of the dead trees (200/373) (Table 8). Among the 200 trees with secondary bark beetles, the frequency of each species detected in the survey were 35% I. pini (70/200), 86% Hylurgops spp. and/or D. murrayanae (171/200), 24% O. latidens (48/200), 14% P. mexicanus (27/200), 13% Pityogenes spp. and/or Pityophthorus spp. (25/200), and 39% ambrosia beetles (77/200). Most of the time, when galleries of Hylurgops spp. and/or D. murrayanae overlapped, Hylurgops spp. appeared to be the more likely agent associated with the dead trees rather than *D. murrayanae*, based on the type and location of the galleries (extending below the root collar) and/or on the presence of the black stain fungus (Appendix F and photos in Appendix G). The presence of O. latidens with P. mexicanus were associated with the larger trees (n: 13/27, d: 13.3 cm, h: 14.9 m) in comparison to the presence of *P. mexicanus* in the absence of *O. latidens* (n: 14/27, d: 11.8 cm, h: 13.6 m). The presence of ambrosia beetles was highly variable. These insects appeared to prefer older, more mature stands. The highest occurrence of trees with these xylophagous insects was in Mac5, 55% of the time (18/33), followed by Crassier Creek, 41% of the time (14/34) (Table 8). The survey found 30% or more (113/373) of the dead trees to contain wood borers, evidenced by the wood shavings of the larval galleries by the wood borers that often intermingled with those of the secondary bark beetles (Table 8).

The presence of feeding damage around the root collar by insects from plot to plot was also highly variable, from a low 13% of the time (7/52) in Mac1-A to a high 79% of the time (11/14) in CLk-A. Most of the more mature sites had higher occurrences of root collar damage compared to the younger sites. On average, the presence of root collar damage on most plots (11/15) encompassed about one third or more of the plots' area, where four of those plots had root collar damage presences of more than 50% of the plot area **(Table 8)**.

Western gall rust occurred on approximately one third of all lodgepole pines surveyed (221/624) and occurred on 30% (113/373) of the dead trees **(Table 8)**. One site was responsible for more than half of these occurrences, Mac1 at 66% (117/178). Western gall rust was most frequently noted on the smaller trees.

In general, galleries of *D. ponderosae* and secondary bark beetles were found in almost equal abundance in trees of similar diameter and height. For example, galleries of *D. ponderosae* were found in trees with mean diameter of 13.6 cm (6.0–26.9 cm) and mean height of 14.8 m (5.9–25.6 m), and galleries of secondary bark beetles were found in trees with mean diameter of 13.0 cm (4.5–26.9 cm) and mean height of 14.2 m (4.0–25.6 m). Trees with secondary bark beetles, but without indication of *D. ponderosae*, were much smaller (đ: 6.6–10.8 cm, ħ: 7.8–11.9 m). These relationships of the tree size measurements with individual bark beetles and/or their interactions are further explored in **Appendix H**.

When all 624 trees were examined, the best model explaining the likelihood of lodgepole pine mortality indicated that the probability of tree death was associated with the presence of any of the assemblage of secondary bark beetles, and decreased with increasing diameter of the lodgepole pines (AIC: 571) (Table 10A). No term for the presence of

*D. ponderosae* occurred in that model. The best model that demonstrated tree death increased with presence of *D. ponderosae* in the post-outbreak stands showed that the probability of tree death increased simultaneously with the presence of *I. pini* and/or *O. latidens* in the same trees, and was only the 5<sup>th</sup> best model overall (AIC: 726, **Table 10A**). Examining the effect of *D. ponderosae* in the tree on its own was only the 15<sup>th</sup> best model in predicting tree death (AIC: 775). Other secondary insects or damage on their own were similarly unsuitable: *I. pini* reflected the 16<sup>th</sup> best model (AIC: 791); *O. latidens* reflected the 17<sup>th</sup> best model (AIC: 809); *P. mexicanus* the 18<sup>th</sup> best model (AIC: 824); root collar damage by insects the 19<sup>th</sup> best model (AIC: 832). Physical attributes such as diameter produced only the 20<sup>th</sup> best model(AIC: 833). In contrast, a model containing the complex of secondary bark beetles was the 4<sup>th</sup> best model overall (AIC: 628) (**Table 10A**).

These results were highly variable across sites. The top models for each of the sites are shown in **Table 10B**. Among the seven sites, almost half had secondary bark beetles associated as the primary indicator of tree death (3/7), two had *D. ponderosae* as the most significantly associated mortality agent (2/7), and the remaining sites showed no relationships with bark beetles as agents of mortality (2/7). A detailed study of one of those stands, Mac3-C, is provided in **Appendix I**.

Secondary bark beetles may be attacking or colonizing many more trees than just those killed. In 2010, 21 of the lodgepole pine contained frass from new activity by bark beetles in 2010 (mean diameter, đ: 8.9 cm, mean height, ħ: 11.3m; **Appendix J**). All of these trees originated from the plots near Mackenzie (20/21) and Crassier Creek (1/21). Among the 21 lodgepole pines, 57% had *D. ponderosae* (12/21), 95% had an assemblage of secondary bark beetles (20/21), 86% had *I. pini* (18/21), 52% had *Hylurgops* spp. and *D. murrayanae* (11/21), 33% had *O. latidens* (7/21), 33% had *P. mexicanus* (7/21), 38% had *Pityogenes* spp. and/or *Pityophthorus* spp. (8/21), 5% had ambrosia beetles (1/21), 62% had root collar damage by insects (13/21), 14% had wood borers (3/21), and 38% had western gall rust (8/21) (Table 11). A full accounting of tree sizes and interactions among the insects in trees with frass, and the respective sizes of those trees is provided in **Appendix K**.

Among the 21 trees with frass, half had died (10/21) by 2010. Some trees had been dead since the first survey in 2009 (3/21). Others looked alive, having predominantly green needles (4/21). The last four trees (three dead, one alive) occurred in Mac3-C and were surveyed in 2010 **(Table 11)**. Among the 10 trees that died in 2010 with frass, some of the trees displayed a high likelihood that the mortality was the work of bark beetles (6/10), without evidence of other critical mortality agents. The other four trees with frass had some form of mechanical injury, such as broken tops (4/10). All 10 trees harboring bark beetles had at least part of the complex of secondary bark beetles (đ: 8.3 cm, ħ: 10.6 m). *Ips pini* was the most commonly associated individual secondary species found 90% of the time (9/10) (d: 8.4 cm, ħ: 10.6 m) **(Table 11)**.

Although these models indicate that secondary bark beetles may be as, or more, associated with dead trees than *D. ponderosae* in the post-outbreak period, correlation is not causation. The trees could have been heavily infested with secondary bark beetles well in advance of (or after) colonization by *D. ponderosae*. Hence, the associations of bark beetles with trees that died in 2010 was also studied. The rate of new mortality in the stands was approximately 4% (25/624) in 2010. These trees are displayed in **Table 12**. Eight of these trees had *D. ponderosae*; six trees in 2009, and two new dying trees in 2010 (total of 8/25). Six of the 25 trees appeared to have no colonization by *D. ponderosae* or any structural defects, displaying only colonization by secondary bark beetles **(Table 12)**. Thus, annual new mortality for 2010 associated with activity by secondary bark beetles appeared to be only 1% overall (6/624). Of the eight trees that had evidence of attack by *D. ponderosae*, only one did not have heavy amounts of colonization by secondary bark beetles such as *I. pini* or structural defects such as a broken top **(Table 12)**.

In total, sixteen of the 25 trees had an assemblage of secondary bark beetles, and ten of them contained frass (10/25), an indicator of fresh attack by secondary bark beetles. Among the 16 trees with secondary bark beetles, the individual species included *I. pini* (11/16), *Hylurgops* spp. and/or *D. murrayanae* (9/16), *O. latidens* (9/16), *P. mexicanus* (5/16), and *Pityogenes* spp. and/or *Pityophthorus* spp. (7/16) and one tree with ambrosia beetles (1/16) **(Table 12)**. Just over half of these trees, 52%, had root collar damage by insects (13/25) as well. Among the 25 trees, 28% (7/25) had broken tops. Four of the seven trees with broken tops had been attacked by various species of bark beetles other than *D. ponderosae*.
## Discussion

The findings are consistent with evidence that species of secondary bark beetles can kill trees in the post-outbreak phase of a landscape-level eruption of a primary bark beetle. To date, much information on colonization activity by secondary bark beetles such as pine engravers has focused on their reproduction in habitats disturbed by fires or storms (Kennedy 1969, Miller et al. 1986, Amman and Ryan 1991, Rasmussem et al. 1996, McCullough et al. 1998, Reid and Robb 1999, Lombardero et al. 2006, Ryall et al. 2006, Gandhi et al. 2007, Aukema et al. 2010, Fettig et al. 2010). Studies on tree-killing activity by these insects have been restricted primarily to instances where trees have been heavily stressed by drought (Raffa et al. 2008) or competition, where pine engravers have been known to kill small groups of trees of 5–8 inches DBH (Kegley et al. 1997). Studies of activity by secondary bark beetles in concert with other biotic disturbance agents such as rootboring insects (Aukema et al. 2010) or *D. ponderosae* (Safranyik et al. 1999a, 1999b, 2004) have been less abundant. To our knowledge, this is the first study to quantify the frequency of association of the members of the bole-infesting assemblage of bark beetles colonizing lodgepole pine during the post-outbreak phase of *D. ponderosae* epidemic over a large spatial area.

Results from this study indicated that that year-over-year mortality was associated with pines of decreasing diameter, or likely those stressed by interspecific competition prior to *D. ponderosae* removing the largest and most dominant pines in the stands. Females of *D. ponderosae*, attacking vigorous trees, produce vertical J-shaped galleries that overcome host defenses by increasing the rate of depletion and cumulative resins produced

by blocking water conduction in the xylem. In contrast, females of many species of secondary bark beetles simply lay eggs in north-south or randomly-oriented galleries as larval galleries radiate laterally across the grain of the wood. In this study, although galleries of secondary bark beetles may have been highly abundant, without exhaustive sampling of a whole tree, it is impossible to prove that trees putatively killed by secondary bark beetles did not have D. ponderosae. For example, even a failed attack by a few D. ponderosae, undetected in our sampling scheme, may have introducted pathogenic blue stain fungi that contributed to the demise of a tree (Kim et al. 2005, Six and Wingfield 2011). Likewise, other potential mortality factors in the stands cannot be excluded (Smithers 1961, Amman 1975, Unger and Fiddick 1979, Westfall and Ebata 2010), including pathogens like western gall rust (Peterson 1960), Comandra blister rust (Johnson 1986), Atropellis canker (Lightle and Thompson 1973), Armillaria root disease (Baranyay and Stevenson 1964, Tkacz and Schmitz 1986, Williams et al. 1986), Dothistroma needle blight (Peterson 1982, Bradshaw 2004, Welsh et al. 2009), or parasitic plants like lodgepole pine dwarf mistletoe (Hawksworth and Dooling 1984).

The amount and surface area covered by galleries of secondary bark beetles (results not shown) provide reasonable evidence that secondary bark beetles were associated with up to 25% of the direct mortality seen in the post-outbreak phase of this *D. ponderosae* epidemic. Secondary bark beetles are excellent competitors with *D. ponderosae* in outbreak or post-outbreak phases. For example, the more aggressive species of secondary bark beetles, such as *I. pini* or *Pityogenes knechteli*, have been recorded to have higher attack densities than *D. ponderosae* (optimal attack density *I. pini* is potentially higher than

100 attacks/m<sup>2</sup> vs. *D. ponderosae* around 60–70 attacks/m<sup>2</sup>, and higher still for *P. knechteli*) (Raffa and Berryman 1983, Berryman et al. 1985, Rankin and Borden 1991, Borden et al. 1992, Poland and Borden 1994b, Raffa 2001). The fungal associate of *I. pini* is highly adapted to colonize and develop in highly stressed and dying trees compared to *D. ponderosae* fungi that grow best in healthy vigorous phloem (Six and Paine 1998, Solheim and Krokene 1998, Kopper et al. 2004, Kim et al. 2005). Many species of secondary bark beetles are usually bivoltine, with parents often emerging to establish second, or sometimes third, broods in a longer than usual growing season (Safranyik et al. 1996, 2000).

To reduce competition, the insects partition hosts in space and time, often through sophisticated communication signals that may repel competing species (Figure 8, Table 1). For example, many scolytids exhibit spatial partitioning within a tree (Reid 1955, Safranyik et al. 2000, Ayres et al. 2001, Aukema et al. 2004, 2010, Wermelinger et al. 2007). In this system, the more aggressive bark beetles such as *D. ponderosae* often occupy the main bole of the tree, between the root collar and regions up to 5 m high. Smaller secondary bark beetles, such as *I. pini* and *O. latidens*, occupy the upper bole and larger branches, and *Pityogenes* spp. and/or *Pityophthorus* spp. occupy the thinner and higher phloem sections of the smaller branches and twigs (Poland and Borden 1994a, 1994b, Safranyik et al. 2000). Below the lower bole, the larger secondary bark beetles, such as *P. mexicanus*, *Hylurgops* spp. and/or *D. murrayanae* are primarily found in the root collar regions and on the larger roots (Furniss and Carolin 1977, Wood 1982b, Safranyik et al. 2000). The niche partitioning strategy exhibited was consistent with the location of attacks by the bark beetles sampled in this study (Figure 8, Table 1).

Differences in peak flight time between species also minimize competition with sympatrics. For example, Safranyik et al. (2000) captured the earliest flights of *Hylurgops porosus* and *Trypodendron lineatum* before flights of *I. pini, P. knechteli*, and *D. ponderosae* in British Columbia. Temporal partitioning may also avoid predation, synchronize growth capacity with symbiotes, and promote colonization during a period when the hosts are most stressed or most abundant (Reid 1955, 1962a, Amman and Cole 1983, Safranyik et al. 1999b, 2000, 2004, Safranyik and Carroll 2006). Benefits of earlier or later flights are often balanced against the risk of mortality, such as arriving too late at a host, with competitors depleting most of the available common resources (Hardin 1960, Stephens and Krebs 1986, Bell 1990). A summary of the temporal partitioning between the bark beetles in this system is depicted in **Figure 9**, with more descriptions provided in **Table 2**.

Bark beetles procure and partition hosts by responding to a host of chemical signals, including host monoterpenes and pheromones synthesized by their symbiote microbes, produced *de novo* from the insects' hindguts, and/or oxidized products from the metabolized precursors ingested in the host phloem (Byers 1987, 1989, 1995, Seybold et al. 2000, Raffa 2001). The combination of pheromones/allomones and host monoterpenes benefit the bark beetles by inducing a suite of behavioral responses in conspecifics or sympatrics from an aggregation or a deterence response. These results to maintain an optimal colonization density, which influenced the insects' behaviour to locate, accept, or feed upon the host trees. Such signals can also adversely affect the population by serving as kairomones to predators, parasites and competitors of bark beetles (Borden 1982, Wood 1982a). Discussion of the pheromone systems of the bark beetles infesting lodgepole pine in this study can be found in **Figure 10** and **Appendix A**.

Our findings extend the current understanding of the bole-infesting assemblage of bark beetles in lodgepole pine in central British Columbia, Canada. In its endemic phase, *D. ponderosae* acts almost as a secondary bark beetle, persisting in unthrifty trees with secondary bark beetles such as *P. mexicanus* and *I. pini* (Smith 2008, Smith et al. 2009). When conditions permit an increase in numbers, *D. ponderosae* may recruit enough conspecifics to be able to strip-attack a lodgepole pine (Carroll et al. 2006a, Safranyik and Carroll 2006, Koopmans 2011). Secondary bark beetles may aid in this transition by increasing the nutritional quality of the host or promoting more favourable growth conditions for the beetles, perhaps by prior fungal inoculations (Reid 1963, 1969, Ayres et al. 2000, Bleiker and Six 2007), diluting the rate of predation (Aukema et al. 2004, Aukema and Raffa 2004, Boone et al. 2008), and reducing or exhausting their common host defenses (Christiansen et al. 1987, Boone et al. 2011).

As *D. ponderosae* gains the ability to kill trees, secondary bark beetle populations build in the spatially-partitioned resource, relegated to unused phloem in tree tops or branch tips. As *D. ponderosae* exhausts its host supply over a period of approximately a decade (Evenden and Gibson 1940, Kennedy 1969, Roe and Amman 1970, Alfaro et al. 2004, Taylor and Carroll 2004), a delayed-density dependent response in the populations of secondary bark beetles gradually introduces a negative feedback in the declining populations of the *D. ponderosae* e entering the post-outbreak stage, by accelerating the collapse of *D. ponderosae* populations due to strong interspecific competition and increasing host exhaustion (Safranyik and Carroll 2006). Secondary bark beetles, however, may continue to infest and kill smaller diameter pines for one to three years after the collapse of an outbreak, especially if stand vigour is reduced (Kennedy 1969, Kegley et al. 1997). In our study, year-to-year mortality was as high as 15% of the trees surveyed, depending on the locale.

# Conclusion: Synthesis and implications for control and management

The potential mortality from secondary bark beetles after an epidemic of *D. ponderosae* can vary spatially and temporally. Since D. ponderosae in the central interior region of British Columbia is at the northern edge of its distribution, the associated composition and sympatric species of D. ponderosae should not be generalized to be the same in all regions of the beetle's range. The breadth of complexity in the host, insect, predators and environmental interactions are highly variable. Dendroctonus ponderosae may exhibit developmental differences in the northern boreal compared to its southern regions, for example. These differences can affect the distribution and possibly the rate of mortality at the northern edges of the outbreak. Our numbers were possibly more conservative in estimating the rate of mortality, in comparison to the growth seasons in the southern regions, which are potentially warmer and longer, with more interactions between the secondary bark beetles within the bole-infesting assemblage. This section focuses on the potential applications of the information collected in this study and/or previous studies to provide practical suggestions for forest managers to mitigate lodgepole pine mortality from bark beetles, with special reference to the incipient and post-epidemic stages, in an ongoing effort to monitor, control, manage, minimize and prevent outbreak occurrences by bark beetles in the future.

#### Mechanical intervention: Stand hygiene and healthy sanitation practices

There are several direct control tactics that can be implemented to minimize the risk of mortality from epidemic bark beetles. Since *D. ponderosae* and secondary bark beetles are sympatrics using the same hosts, and their population dynamics are intricately connected to one another (Carroll et al. 2006a, Koopmans 2011, Smith et al. 2011), the interventions with the highest impacts will be implemented during non-epidemic periods.

#### Part I. Prevention: Cultural controls

Cultural practices are excellent preventive tools to manage bark beetles or other agents of mortality of lodgepole pine because such practices may increase the defensive threshold of the trees (Shore et al. 2006, Whitehead et al. 2006). A primary consideration is to have a well-thought plan to maintain stand hygiene, by carefully selecting sites suitable for lodgepole pines and/or harvesting species preferred by bark beetles before they become susceptible (McGregor and Cole 1985). Techniques may include silvicultural tactics such as monitoring the stocking density or spacing treatments, applying regular thinnings to dense stands and/or pruning of individual trees (Mitchell et al. 1983), fertilizing and irrigating during dry summer months (Brockley 2001, Brockley and Sanborn 2009), and reducing the competition for space, light, moisture and nutrients.

Stands may also be mixed with other softwood or hardwood species (site permitting), which may decrease mortality originating from one dominant agent of mortality, providing refuges and resources for wildlife and decreased susceptibility to disturbances (McGregor and Cole 1985, Burton 2008). However, potential benefits in planting mixed stands need to be balanced against the trade-off between competition and facilitation in the growth of lodgepole pine in mixed plantations, since different species can offset any potential benefits by retarding the growth of the principal harvest, for example.

### Part II. Treatment: Direct controls

When infestations by bark beetles are detected, prompt removal may be recommended using proper salvaging methods. Some direct control methods may include treating the slash immediately, using methods such as 'lop and scatter', 'pile and burn', chipping, and debarking (Klein 1978, Six et al. 2002). Any harvesting practices, including salvage logging, are only as effective as their proper execution, especially critical during the beetles' flight season. Among the precautions to take during harvesting is prevention of injury to trees, or to roots from soil compaction, which can stress trees, making the remaining trees more susceptible to attack by bark beetles.

Solar radiation can be applied on smaller piles of wood, or by homeowners planning to use recently cut firewood that may or may not contain bark beetles, by wrapping and sealing the wood in thick, clear plastic sheets placed in a sunny location to increase the heat treatment, rendering them unsuitable for bark beetles and killing the beetles within by increasing the desiccation rate of the logs. Such methods can be labor-intensive, and their effectiveness is unpredictable as this process is dependent on solar gain. Therefore, the practice is probably more suitable in southern or warmer regions (Graham 1924, Patterson 1930, Buffam and Lucht 1968, Mitchell and Schmid 1973, Sanborn 1996, Negrón et al. 2001). Alternatively, the logs can be misted if an abundant water is nearby, making them unsuitable for bark beetle development and emergence (McMullen and Betts 1982, Safranyik and Linton 1982). This idea is likely impractical in areas where lodgepole pine normally grows in inland areas, however.

Prescribed burning is another viable option in more rural areas, where an area is less accessible or sanitation logging is not practical (Munger and Westveld 1931, Klein 1978, Swain and Remion 1981, McMullen et al. 1986). The fire must be of sufficient intensity to cause significant mortality (Stock and Gorley 1989, Safranyik et al. 2001), and needs to be balanced against the difficulty and dangers of controlling such treatments (Hirsch et al. 1998). Moreover, ecological tradeoffs of scarring the soil, causing infections and/or scorching the trees may occur, making the trees more attractive to attacks by bark beetles instead. At epidemic levels, the best direct mechanical control may be to quickly remove, burn, or chip the trees on site to prevent beetles from emerging to kill other susceptible hosts nearby, which may slow the spread but may not stop expansion (Hopping and Mathers 1945, Klein 1978).

## **Biological manipulation: Semiochemicals**

Tremendous progress has been made over the years to elucidate the attraction and repellence by semiochemicals produced by the beetles and/or hosts, with hopes to exploit and manipulate the responses by insects **(Appendix A)**. The semiochemicals can be used in a variety of ways, as a direct method to monitor and control the species of interest or, indirectly, by employing the assistance of sympatrics to increase the level of competition, or to attract the common enemies of bark beetles utilizing those semiochemicals as kairomones (Birch 1978, Borden 1982, Wood 1982a, Byers 1989, 1995, Raffa 2001, Boone et al. 2008).

## Part I. Monitoring the populations of bark beetles

A survey of bark beetle populations is recommended as one of the first tools for forest managers to monitor and track population densities over time, as population dynamics of the bark beetles are reciprocally dependent and linked to one another (Berryman 1982b). There are several ways to detect and estimate the populations: by the physical appearance of symptoms and signs of bark beetle activity on the host trees, such as the number of resinous pitch tubes or streaming pitch and frass presence, by 'chopping and checking' for eggs, larvae, pupae and adults under the bark, and from the number of trees with fading foliage, woodpecker activity (or their ratios of infestation to host or area for relative comparison), all of which can be both labor- and budget-intensive for management purposes. Another, more convenient, way is to utilize semiochemicals to estimate the population in the vicinity. Monitoring using bark beetle pheromones is highly espoused because it discloses the population density of bark beetles over time. Continuous screening on an annual basis can allow intervention actions to be taken to prevent or minimize potential future mortality by detecting increases in local populations, before they exceed epidemic thresholds. Care need to be taken in evaluation of trap catch data, however, as numbers of insects in pheromone traps may not correlate well with actual numbers emerging from host trees (Bentz 2006).

### Part II. Aggregation and anti-aggregation mechanisms

The goal of a 'push-and-pull' strategy is essentially to push bark beetles away from susceptible resources using a repellent mechanism (i.e. anti-aggregant), and pull populations towards an alluring stimulus (i.e. baited lures or trapped logs) (Lindgren and Borden 1993, Miller et al. 1995, 2005, Miller and Borden 2000, Cook et al. 2007, Gillette and Munson 2009). Although the use of bark beetle pheromones or host volatiles are advocated, forest managers are recommended to consult specially-trained professionals in bark beetle management or rely heavily upon data from prior monitoring. Some pheromones may have multifunctional responses, individually or when mixed in different blends, and may unintentionally attract more bark beetles to surrounding live trees from migration events. This may potentially initiate incipient to epidemic conditions for bark beetles from events of 'spill-over', sudden stressful disturbances or untimely treatments due to human errors or budget restrictions.

# Part III. Induced competition and predatory response

In addition to interrupting the regular communication signals of bark beetles with their conspecifics, the properties of the pheromones that attract bark beetles can be similarly manipulated to induce a kairomonal attraction by predators, parasitoids, and/or competitors. Amplified levels of interspecific and intraspecific competition between the sympatrics of secondary bark beetles with each other and/or *D. ponderosae* may result in drastic reduction of brood fecundity, brood production and per capita survival for both species (Rankin and Borden 1991, Poland and Borden 1994a, 1994b, Devlin and Borden 1994, Safranyik et al. 1996, 1998, 1999c). Multiple studies have demonstrated attraction of invertebrate

predators such as the clerid beetles or other generalist predators and parasitoids to pheromones of secondary bark beetles, sometimes synergistically with host volatiles (Reid 1957b, Miller et al. 1987, 1991, Raffa 1991, 2001, Erbilgin and Raffa 2001, Aukema and Raffa 2002, Miller and Borden 2003, Erbilgin et al. 2003, Aukema et al. 2004, Boone et al. 2008). Though this study did not examine the interactions between bark beetles and their natural enemies, this aspect of controlling bark beetles by semiochemical manipulation may have great potential, especially in a holistic IPM (integrated pest management) approach in conjunction with the other control methods. Furthermore, if semiochemicals can induce higher competition and predatory responses, another option that holds potential to cause significant mortality of bark beetle populations at epidemic stages is application of epizootic fungal pathogens (Klepzig and Six 2004, Six and Klepzig 2004, Aanen et al. 2009, Six and Wingfield 2011); there is much to learn about these mutualistic or antagonistic interactions.

# **Chemical control**

Broadcast insecticides are often ineffective and impractical in the control of bark beetles, which are naturally protected under the bark. Although there exist several topical insecticides such as lindane or monosodium methanearsonate, some which have only recently been banned in Canada and the United States, some registered ones, such as chlorpyrifos (more effective for defoliators) are expensive treatments that need to be applied regularly, sometimes twice in a season, to maintain effectiveness for the short-term (Berisford et al. 1980, Brady et al. 1980, Maclauchlan et al. 1988). Broadcast insecticides pose dangers of dermal and oral toxicity to the applicators, increased risk of groundwater

runoff and soil sediment contamination, and potential non-target effects to beneficial insects (Buckner 1974, CPPA 1985, Morrissey et al. 2007, Morrissey and Elliott 2011). The use of pesticides can be termed a 'wicked problem' (Rittel and Webber 1973), where pesticides are a superficial treatment on the surface of a larger and more insidious issue of poor forest management (Burton 2006, Wallenius et al. 2011).

### Best control methods of bark beetles at different population densities

Under non-epidemic conditions, recent mortality from disturbance events or stressed trees (fire-injured, girdled, drought, etc.) may be attractive to D. ponderosae and/or secondary bark beetles (Waring and Pitman 1983, Geiszler et al. 1984, Miller et al. 1986, Amman and Ryan 1991, Rasmussem et al. 1996, Santoro et al. 2001, Gandhi et al. 2007, Fettig et al. 2010). Such susceptible trees should be removed, if infested, before beetles emerge. Sanitation may be augmented by the use of trap trees and/or baited semiochemical traps to increase the effectiveness of such operations. For example in western Canada, several tried-and-true logging sanitation practices use "post-logging mopup" (Borden et al. 1983a) or trapping strategies using "containment and concentration" (Borden et al. 1983b) and can effectively reduce the residual populations over several years and slow the spread of the infestations of bark beetles, compared to a do-nothing strategy (Cole and Amman 1980, Borden and Lacey 1985). However, if populations manage to attain epidemic stages, treatment is rarely successful, as a suppression rate of 90% in the treated trees is required to compensate for the rate of increase at outbreak levels (Carroll et al. 2006b).

In post-epidemic phases, depending on the extensiveness of the outbreak and feasibility, future mortality could be minimized by using the strategies of "containment and concentration" with trap logs. The tactic of using logs as trapping materials for the insects referred to reduce the population levels of secondary bark beetles, and has limited feasibility in effectiveness for 'primary' bark beetles, such as *D. ponderosae* that primary attack live trees. Such logs would need to be promptly salvaged before the beetles emerge, hastening the collapse of the population to endemic levels. Follow-up treatments may be repeated every season until local populations return to endemic levels.

Early detection of outbreak status may be achieved by aerial surveys and digital remote sensing techniques from aircraft- or satellite-borne sensors (Wulder et al. 2006). Aerial survey techniques can provide the valuable information on forest health conditions, locate the focal point(s) of potential infestations, and delineate the scale and direction of advance of outbreaks. Subsequent follow-up by systematic ground surveys is required to confirm the agent(s) of mortality to be bark beetles and, if so, to further ascertain and identify the extent of the epidemic and/or other potential weakening agents, and the associated risk to the surrounding live residuals susceptible to those populations (Carroll 2007).

Early detection and continuous monitoring are important to maximize and buy time for forest managers to act promptly for the following reasons: (I) to forecast the potential outbreak and determine the magnitude of the problem, (II) to gather and assemble previous spatial and temporal information about past, or similar, successful management treatments on stands, and (III) to formulate integrated management strategies to contain the expanding populations, with an action plan that prioritizes and balances the ecological and economical

benefits in the application of containment treatments as well as the response (Vite 1976, McGregor and Cole 1985, Hall 2004). Prevention is the only long-term solution that provides more benefits than the active direct control methods of the short term (Shore et al. 2006, Whitehead et al. 2006). Management budgets are normally a limiting factor in effectively implementing preventative tactics. These factors are balanced against the fact, however, that bark beetles are normal, native, agents of disturbance and, as such, will always have some activity in a thriving forest.

#### Public participation, education, awareness and regulation

In all of the preceding management options, it is important to communicate with stakeholders and/or those individuals who are affected as a consequence of the management actions. This may involve providing public access to information, or providing more education on forest management in resource-based communities. This may take forms such as curricula for high school students, introducing forestry-related topics in the syllabus of science classes, including forest health with special reference to the population dynamics of insects, or bark beetles, since they are the most important mortality agent in the forests. In the age of information technology, having a dedicated website and/or online discussion forums by the province and/or federal forest service may serve as an outlet to inform the general public of action plans by the government, providing a participation forum for concerned individuals, and provide a forum of discussions engaging the parties responsible for timber supply management within respective communities. Consultative processes can increase the levels of satisfaction and provide a platform of communication for all the parties, to articulate their concerns, exchange ideas, and update each other with pertinent information for a diplomatic compromise between all parties where conflicting management objectives may exist.

# Importance and consequences of bark beetle outbreaks

Although the previous sections focus on outbreak management, this is not to suggest that all outbreaks of bark beetles are bad. Indeed, *D. ponderosae* is a natural disturbance agent, performing the same ecological function as an abiotic disturbance agent, such as a stand-replacing fire (Lotan et al. 1985, Taylor et al. 2006, Alfaro et al. 2008).

The role and importance of bark beetles needs to be recognized as part of a valuable forest community: economic progress must be balanced with ecological function and the social and aesthetic values for individuals and communities alike. Bark beetles can encourage a higher level of productivity with higher growth yields by increasing resource availability, such as space and growth for plant succession or enhancing the service of nutrients recycling (Rudinsky 1962, Wood 1982b, Romme et al. 1986, Brown et al. 2010). Bark beetles may provide undervalued, inestimable services to wildlife as habitat enhancers, bettering soil and water quality, and last but not least, improve recreational outlets or visual aspects of the landscape by encouraging habitat heterogeneity (McGregor and Cole 1985).

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### Appendices

Appendix A. Niche partitioning by chemical profiles by various bark beetles:
 Dendroctonus ponderosae, Ips pini, Hylurgops spp., Orthotomicus latidens,
 Pseudips mexicanus, Dendroctonus murrayanae, Pityogenes spp.,
 Pityophthorus spp., and ambrosia beetles, in lodgepole pine in British Columbia

- **Appendix B.** Photographic guide to green-, red-, and grey-attack stages of lodgepole pine in sites in the central interior of British Columbia
- Appendix C. Map of the seven study site locations (Appendix C1), in relation to the three forest district regions in British Columbia (five in Mackenzie Forest District, one in Peace River Forest District, one in Prince George Forest District), and relative to the distribution of lodgepole pine (green) and *Dendroctonus ponderosae* outbreak (red) from 1999 to 2009 in the provinces of British Columbia and part of Alberta, with snapshot of the outbreak in the year 1999, 2004, and 2008 (Appendix C2)

Appendix D. Photographs of each of the seven sites in this study of the central interior of British Columbia were exemplified for each site,
[Appendix D1] Mackenzie Site # 1 (Mac1)
[Appendix D2] Mackenzie Site # 2 (Mac2)
[Appendix D3] Mackenzie Site # 3 (Mac3)
[Appendix D4] Mackenzie Site # 4 (Mac4)
[Appendix D5] Mackenzie Site # 5 (Mac5)
[Appendix D6] Crassier Creek (CCk)
[Appendix D7] Chief Lake (CLk)

- **Appendix E.** Survey methodology to examine and monitor the mortality of lodgepole pine, with the figures illustrating:
  - [Appendix E1] A flow chart detailing site establishment, and tree examination for presence of bark beetles or their galleries in the first year of survey in 2009 and for new mortality in 2010
  - [Appendix E2] Signs of bark beetles activity included the presence of pitch tubes and frass

Appendix F. Photographic guide and descriptions of the various insects (i.e. adult bark beetles and their galleries) and other agents of lodgepole pine mortality in sites in central interior of British Columbia

> [Appendix F1] Dendroctonus ponderosae (Hopkins), mountain pine beetle, with examples of their prevalence and desperation, including on the surrounding residuals, which were non-suitable host (smaller diameter lodgepole pines of 8 cm or less), resulting in the bark cracking (Appendix F1.2)

[Appendix F2] Ips pini (Say), pine engraver

[Appendix F3] Hylurgops spp. (LeConte), sour sap bark beetles

[Appendix F4] Orthotomicus latidens (LeConte), smaller western pine engraver

[Appendix F5] Pseudips mexicanus (Hopkins), Monterey pine engraver

[Appendix F6] Dendroctonus murrayanae (Hopkins), lodgepole pine beetle

[Appendix F7] Pityogenes spp. and/or Pityophthorus spp.

[Appendix F8] Ambrosia beetles (with 'pin-holes')

[Appendix F9] Overlapping galleries of Hylurgops spp. – D. murrayanae

[Appendix F10] Root collar damage by insects

[Appendix F11] Wood borers

[Appendix F12] Western gall rust

[Appendix F13] Interactions of Dendroctonus ponderosae – Ips pini

[Appendix F14] Interactions of Dendroctonus ponderosae – O. latidens

[Appendix F15] Interactions of Dendroctonus ponderosae – Ips pini – O. latidens [Appendix F16] Interactions of Ips pini – Hylurgops spp. and/or D. murrayanae – Orthotomicus latidens – Pseudips mexicanus

[Appendix F17] Interactions of *Pseudips mexicanus – Orthotomicus latidens* [Appendix F18] Interactions of *Ips pini – Hylurgops* spp. and/or *D. murrayanae* and/or *Hylastes* spp. – ambrosia 'pin-holes'

[Appendix F19] Miscellaneous observation: some of the difficulties in diagnosing the 'true' mortality source, due to other (old) damages, such as rotting heartwood, decaying fungus, woods hollowed out by carpenter ants or termites, and wood-peckering damage holes

- [Appendix F20] Miscellaneous observation of Orthotomicus latidens tunneling randomly and intermixing with/into Dendroctonus ponderosae gallery in the older stands (perhaps due to their overwintering behaviors or maturation feeding of tenerals/adults from the previous season, since no egg galleries were present?)
- Appendix G. Detailed descriptions of each agent of lodgepole pine mortality (supplements to the photographic guide of Appendix F) of the adult bark beetles associated under the bark (Appendix G1) and their characteristic galleries (Appendix G2) in sites in central interior of British Columbia
- **Appendix H.** The relationships between the physical attributes of tree sizes with various signs of bark beetle activity, other biotic disturbances, and their interactions in sites in central interior of British Columbia
- Appendix I. 'The perfect mortality-storm' of lodgepole pine, a combined effect of stand density and stand maturity interacting with high secondary bark beetles activity in the case study of Mackenzie site 3, plot C (Mac3-C)

- Appendix J. Twenty one lodgepole pine with frass were found near Mackenzie and Crassier Creek at the post-outbreak stage of *Dendroctonus ponderosae*. The frasses were indicators of newly attacked trees in 2010, while, exhibiting the multiple interactions of the trees in the stands with the bark beetles, broken tops, and the other agents of tree mortality.
  - [Appendix J1] Summary of the cross-interactions between the bark beetles, as potential mortality agents, and the differences in the distribution of diameter-at-breast-height (in cm) in trees with their presence versus their absence
  - [Appendix J2] Summary of the cross-interactions between the bark beetles, as potential mortality agents, and the differences in the distribution of height (in m) in trees with their presence versus their absence
  - [Appendix J3] Summary of the cross-interactions between bark beetles with non-bark beetles elements, and their abundance among the dead or alive trees in the stand, and the differences in the distribution of diameter-at-breast-height (in cm) in trees with their presence versus their absence
  - [Appendix J4] Summary of the cross-interactions between bark beetles with non-bark beetles elements, and their abundance among the dead or alive trees in the stand, and the differences in the distribution of height (in m) in trees with their presence versus their absence
- Appendix K. The relationships between the physical attributes of tree sizes with various new signs of bark beetle activity in trees (frass trees of 2010) in sites in central interior of British Columbia
- **Appendix L.** Justification for grouping *Hylurgops* spp. and *Dendroctonus murrayanae* in the same category

#### Appendix A. Niche partitioning by chemical profiles by various bark beetles

*Dendroctonus ponderosae* is attracted to trans-verbenol and cis-verbenol by females, (+)-exo-brevicomin produced by males and the host monoterpenes of myrcene as a synergist attractant, and to alpha-pinene and beta-phellandrene emitted as tree volatiles indicating susceptibility or as potential hosts (Vite and Pitman 1968, Pitman and Vite 1969, Renwick and Vite 1970, Hughes 1973a, 1973b, 1974, Billings et al. 1976, Borden et al. 1983c, Lindgren and Borden 1989, Miller and Lafontaine 1991, Miller and Borden 2003).

In British Columbia, *I. pini* is attracted to the racemic blend of (±)-ipsdienol, produced by males and had a higher response by females, and to lanierone as a synergistic compound. *Ips pini* is also attracted to the host monoterpene of beta-phellandrene, but their pheromone ipsdienol is repellent to *D. ponderosae*, *O. latidens*, and *P. mexicanus* (Angst and Lanier 1979, Lanier et al. 1980, Miller et al. 1989, 1996, 1997, 2005, Miller and Borden 1990a, Safranyik et al. 1996, Savoie et al. 1998) **(Figure 10)**.

The opposite is true for *O. latidens* attraction to the pheromone ipsenol or *D. ponderosae* pheromones of trans-verbenol and exo-brevicomin, which are attractive to the producing species, but repellent to *I. pini* (Angst and Lanier 1979, Hunt and Borden 1988, Miller and Borden 1990b, 2000, Miller et al. 1991, Borden et al. 1992, Miller 2000, Pureswaran et al. 2000) **(Figure 10)**. Verbenone is an anti-aggregation pheromone by *D. ponderosae* that is repellent to its own kind, *I. pini* and *O. latidens* demonstrated the effectiveness of these pheromones to minimize competition by indicating the full occupancy within that individual-host (Renwick and Vite 1970, Ryker and Yandell 1983, Lindgren and

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Borden 1989, Amman et al. 1991, Shore et al. 1992, Miller et al. 1995, Lindgren and Miller 2002).

Cross-attractions within the secondary bark beetle circles are common, for example, Pityogenes knechteli, a sympatric of *I. pini*, uses similar pheromones of ipsdienol as attractants, but the differences are most likely in the enantiomeric ratios of ipsdienol or the presence of some synergist from host volatiles or either species, and both were equally repelled by the pheromone ipsenol (Miller and Borden 1992, 2003, Devlin and Borden 1994, Savoie et al. 1998); similarly, P. mexicanus is attracted to the synonomes pheromone of O. latidens, attracted by ipsenol and repelled by ipsdienol (Savoie et al. 1998). Thus, the biosynthesis of the oxidized monoterpenes of ipsdienol, ipsenol, and verbenone can act as an effective synomones for those five species, including D. ponderosae, to coexist within the vicinity of each other to maximize the use of the same host-individual trees, by avoiding the competition within and among species from the potential overlapping niches otherwise without using chemical signals (Miller and Borden 1992, Poland and Borden 1994a, 1994b, Devlin and Borden 1994, Savoie et al. 1998, Miller 2000, Safranyik et al. 2000) (Figure 10); these beetles have been observed to occur together, including in this study, normally in several assortments of two or three species predominating, but it is less common for all of them to coexist together because when they do, the high levels of competitions (exploitation, exclusion, interference) severely restricts any potential growth for all species involved.

Limited is known about the semiochemical attractions and anti-aggregations mechanisms of *Hylurgops* spp. and/or *D. murrayanae*, but other studies had shown

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association of these beetles at endemic levels with *D. ponderosae* and other secondary bark beetles, following tree mortality events by an outbreaking population or stand thinning; showing some cross attractions between these species with the other secondary bark beetles pheromones, in addition to the potential synergistic effects from host volatiles (Reid 1955, Safranyik et al. 1999a, 1999b, 2000, 2004, Furniss and Kegley 2008); consistent with the studies by Miller et al. (1991) and Miller and Borden (2003) that found ipsenol and ipsdienol to be attractive to *Hylurgops porosus*.

Beta-phellandrene in lodgepole pine is most attractive to *D. ponderosae* and some of the secondary bark beetles because it is the most abundant monoterpene in the pine (Shrimpton 1972, Miller and Borden 1990a, 1990b, 2003), therefore, potentially used for host species recognition to locate suitable host. In addition, Wallin and Raffa (2000) found that *I. pini* exhibited differences in post-landing behavioral responses – in host-entry, orientation within host and gallery construction – to the different concentrations of host monoterpenes, perhaps using absolute concentrations of various monoterpenes as predictors of host defensive capacity than solely on one particular monoterpene or its concentration in their decision to either colonize the host found, or perhaps, to locate another more suitable ones.

Ethanol, probably released by microorganisms in decaying woody tissue (Moeck 1970, Montgomery and Wargo 1983) and other stress-chemicals produced by stressed plants (Kimmerer and Kozlowski 1982), is also a known attractant to a wide variety of species of secondary bark beetles (Visser 1986, Byers 1995, Hobson 1995). A summary of the various other host monoterpenes or pheromones that are attractive and repellant to the bark beetles or towards their enemies, using those compounds as kairomones (Borden 1982,

Wood 1982a, Byers 1995) are provided in the following table (below).

	Characteristics (CHEMICAL profile partition)			
Bark beetles	Aggregation, or attractant (by host volatile/as kairomone)	Anti-aggregation, or repellent (by another species)	Other mechanisms of communications	
Dendroctonus ponderosae (Hopkins)	trans-verbenol (female) +exo-brevicomin (male) myrcene (host volatile) alpha-pinene (host volatile) beta-phellandrene (host volatile)	verbenone (D. ponderosae) ipsdienol (Ips pini)		
Ips pini (Say)	racemic <i>ipsdienol</i> (male) in BC, but enantiomer ratios vary by region to 'escape' predation lanierone (male) as synergist beta-phellandrene (host volatile) 3-carene (host volatile)( some response)	trans-verbenol ( <i>D. ponderosae</i> ) (±)-exo-brevicomin ( <i>D. pond.</i> ) verbenone ( <i>D. ponderosae</i> ) ipsenol ( <i>O. latidens</i> ) myrcene (host volatile) conopthorin (green leaf volatile)	beta-pinene (host volatile): elicit host entry, but inhibit gallery construction alpha-pinene (host volatile): elicit within-host orientation, gallery construction, but inhibit host entry	
<i>Hylurgops</i> spp. (LeConte) i.e. primarily <i>H. porosus</i>	ipsdienol (kairomone) 3-carene (host volatile)(some response) beta-phellandrene (host volatile)(some response) terpinolene (host volatile)(some response)	unknown, probably conopthorin (green leaf volatile)		
Orthotomicus latidens (LeConte)	ipsenol (male) beta-phellandrene (host volatile)	ipsdienol ( <i>Ips pini</i> ) verbenone ( <i>D. ponderosae</i> )		
<i>Pseudips mexicanus</i> (Hopkins)	ipsenol (male), most likely with differences in enantiomeric ratios than <i>O. latidens</i> 3-carene (host volatile)(some response) beta-phellandrene (host volatile)(some response)	ipsdienol ( <i>Ips pini</i> )		

Appendix A. Niche partitioning by chemical profiles in lodgepole pine by various bark beetles: Dendroctonus ponderosae, Ips pini, Hylurgops spp., Orthotomicus latidens, Pseudips mexicanus, Dendroctonus murrayanae, Pityogenes spp., Pityophthorus spp., and ambrosia beetles

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## – continuation –

	Characteristics (CHEMICAL profile partition)			
Bark beetles	Aggregation, or attractant (by host volatile/as kairomone)	Anti-aggregation, or repellent (by another species)	Other mechanisms of communications	
<i>Pityogenes</i> spp. (Bedel), i.e. primarily <i>P. knechteli</i> (Swaine) found in lodgepole pine	ipsdienol (male), most likely with differences in enantiomeric ratios than <i>I. pini</i> hexanol (male)(at low concentration) beta-pinene (host volatile)(some response)	3-carene (inhibit attractant) alpha-pinene (inhibit attractant) hexanol (male) (at high concentration)		
Ambrosia beetles, i.e. primarily Trypodendron lineatum, and Gnathotrichus sulcatus Gnathotrichus retusus	4,6,6-lineatin (female) sulcatol (male) sulcatol (male)	unknown, probably conopthorin (green leaf volatile)		
Non-bark beetles I. Wood borers, <i>Monochamus</i> spp. (Coleoptera: Cerambycidae) (kairomonal responder)	Ethanol and/or host volatiles and/or turpentines (in general, but response to individual monoterpene is dependent on species, i.e. beta-phellandrene/alpha-pinene/ beta-pinene/3-carene) Bark beetle pheromones (primarily from <i>lps</i> DeGeer spp., i.e. ipsdienol/ipsenol) Synergism between bark beetle pheromones and monoterpenes had mixed results than the individual attractant (higher synergistic response in eastern Ontario, but not synergistic in west coast British Columbia, requiring further study) Smoke volatiles (post-fire, as indicator of damage or weaken host)	conopthorin (green leaf volatile)	similar to the wood borers responses, bark beetle pheromones or/with host volatiles increases the attractions of predators (e.g. clerid beetles) woodpeckers and parasitoids use acoustic vibration to detect the beetle, versus chemical cues, while, mites and nematodes, or epizootics microorganisms and fungi require the beetles for phoretic transport and/or as host, non- to less-dependent on manipulation using the chemical signals	

Appendix B. Photographic guide to green-, red-, and grey-attack stages of lodgepole pine in sites in the central interior of British Columbia. Stands were selected based on colour of crown as a proxy for time since attack by *Dendroctonus ponderosae*. New mortality of trees originated from outbreaks of bark beetles, either from an ongoing epidemic of *Dendroctonus ponderosae* or additional activity by secondary bark beetles, or their interactions thereof, potentially with other disturbance agents



Gradient of lodgepole pine attack in stand in Mackenzie



<== "green-attack" to "chlorotic-yellow" to "bright-red" to "maroon-red" to "gray-attack" ==>



## Appendix C2.

Map of the seven study site locations, relative to the distribution of lodgepole pine (green) and *Dendroctonus ponderosae* outbreak (red) from 1999 to 2009 in the provinces of British Columbia and part of Alberta, with snapshot of the outbreak in the year 1999, 2004, and 2008







Appendix D1. Photographs of Mackenzie site 1 (Mac1) in Mackenzie Forest District



Appendix D2. Photographs of Mackenzie site 2 (Mac2) in Mackenzie Forest District



# Appendix D3. Photographs of Mackenzie site 3 (Mac3) in Mackenzie Forest District



Appendix D4. Photographs of Mackenzie site 4 (Mac4) in Mackenzie Forest District



Appendix D5. Photographs of Mackenzie site 5 (Mac5) in Mackenzie Forest District



Appendix D6. Photographs of Crassier Creek (CCk) in Peace River Forest District



Appendix D7. Photographs of Chief Lake (CLk) in Prince George Forest District

Appendix E1. Flow chart of survey methodology to diagnose and monitor of insects associations with old and new lodgepole pine mortality



- frass pitch tube tree with frass and attack-holes tree with pitch tube 🕊 2.3
- Appendix E2. Pictures of frass and pitch tubes (refer to Appendixes E and F for more detailed examination of insects by species and/or by their distinctive galleries)

Appendix F1.1. Photographs of galleries of *Dendroctonus ponderosae* (Hopkins) (refer to Appendix G2 for further details of gallery)



**Appendix F1.2.** Miscellaneous observations of *Dendroctonus ponderosae* galleries in non-suitable hosts (≤ 8 cm lodgpole pines)



Appendix F2.Photographs of galleries of *Ips pini* (Say)<br/>(refer to Appendix G2 for further details of gallery)

## **Appendix F3.** Photographs of galleries of *Hylurgops* spp. (LeConte) (refer to **Appendix G2** for further details of gallery)



Appendix F4.Photographs of galleries of Orthotomicus latidens (LeConte)<br/>(refer to Appendix G2 for further details of gallery)





Appendix F5.Photographs of galleries of *Pseudips mexicanus* (Hopkins)<br/>(refer to Appendix G2 for further details of gallery)

Appendix F6.Photographs of galleries of Dendroctonus murrayanae (Hopkins)<br/>(refer to Appendix G2 for further details of gallery)



Appendix F7. Photographs of galleries of *Pityogenes* spp. and/or *Pityophthorus* spp.




## Appendix F8. Photographs of galleries of ambrosia beetles (refer to Appendix G2 for further details of gallery)

Appendix F9.Photographs of galleries of Hylurgops spp. and/or Dendroctonus<br/>murrayanae (refer to Appendix G2 for further details of gallery)





Appendix F10. Photographs of root collar damage by insects (refer to Appendix G2 for further details and descriptions)



Appendix F11. Photographs of wood borers (refer to Appendix G2 for further details and descriptions)



\*

emergent adults 'under the bark'



Appendix F12.Photographs of western gall rust<br/>(refer to Appendix G2 for further details and descriptions)

Appendix F13. Photographs of interactions between the galleries of *Dendroctonus ponderosae* and *Ips pini* 





Appendix F14.Photographs of interactions between the galleries of<br/>Dendroctonus ponderosae and Orthotomicus latidens



Appendix F15.Photographs of interactions between the galleries of<br/>Dendroctonus ponderosae, Ips pini and Orthotomicus latidens

Appendix F16.Photographs of interactions between the galleries of secondary<br/>bark beetles: Ips pini, Hylurgops spp. and/or Dendroctonus<br/>murrayanae, Orthotomicus latidens, and Pseudips mexicanus



**Appendix F17.** Photographs of interactions between the galleries of *Orthotomicus latidens* and *Pseudips mexicanus* 

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Appendix F18. Photographs of interactions between the galleries of secondary bark beetles: *Ips pini, Hylurgops* spp. and/or *Dendroctonus murrayanae* and/or *Hylastes* spp., and ambrosia beetles ('pin-holes' characteristics)



**Appendix F19.** Miscellaneous observations in the diagnosis, and/or the difficulties to ascertain the 'true' agent of tree mortality



rot and decay fungus



Woodpeckering holes



carpenter ants



rot and decay fungus

Appendix F20. Miscellaneous observations of the interactions between the galleries of *Dendroctonus ponderosae* and *Orthotomicus latidens* that tunneled randomly, intermixing with/into *Dendroctonus ponderosae* gallery (potentially due to their overwintering behavior or maturation feedings of the teneral/adults from the previous summer?)





#### Appendix G. References of the agent of lodgepole pine mortality

#### Appendix G1: identification of adult bark beetles associated under the bark

The bark beetles associated with the trees were identified either from visual inspection of the adult(s), if present, or from their associated reproductive galleries. This appendix details the characteristics of the adult insects. Adults of *Dendroctonus ponderosae* are dark brown to black and range from 3.7–7.5 mm long, with females normally larger than males (Unger 1993). Adults of *lps pini* range from dark reddish brown to nearly black, with sizes from 3.5–4.2 mm long (Hopping 1964). Adults of *Hylurgops* spp. are reddish brown to black in color, depending on species, and ranges between 3.1–5.7 mm, with a more slender appearance than *D. ponderosae* (Furniss and Carolin 1977, Wood 1982b). Adults of *Orthotomicus latidens* are dark reddish brown and ranges from 2.3–3.6 mm long (Wood 1982b), distinguishable from *I. pini* and *P. mexicanus* due to its smaller size. Adults of *Pseudips mexicanus* are dark reddish brown and approximately 3.6–5.0 mm long (Struble 1970, Wood 1982b).

Adults of *Dendroctonus murrayanae* have dark brown to black body with reddish brown elytra, and ranging from 5.0 to 7.3 mm in size (Keen 1952, Wood 1982b). Adults of *Pityogenes* spp. are dark reddish brown to nearly black, and range from 1.8–3.7 mm long, while adults of *Pityophthorus* spp. are yellowish brown to almost black, ranging from 0.8–3.2 mm in size (Reid 1955, Bright and Stark 1973, Bright 1976, 1981). Ambrosia beetles are dark reddish brown to black and depending on the species, ranges from 2.0–3.7 mm in measurement (Borden 1988, Daterman and Overhulser 2002). Among the two most common ambrosia beetles, *Trypodendron lineatum* is 2.7–3.5 mm long, with the adults ranging from brown to black, distinguished by their bicolored elytra, usually with five dark stripes alternating with four lighter stripes (Wood 1957, 1982b). In contrast, *Gnathotrichus* spp. are dark reddish brown to almost black in color, and on average about 3.7 mm in length (Daterman and Overhulser 2002), with a longer, slender appearance, compared to the stouter *Trypodenderon lineatum*.

Most pine engravers can be identified to species and sex based on their antennal club or secondary sexual characters and by the number and shape of their declivital spines at the end of the beetles' elytra (Hopping 1963a, Lanier and Cameron 1969). *Ips pini* has four spines, while O. latidens and P. mexicanus with only three spines. All three species can be distinguished via the antenna club, mean size, and differences in their declivital characteristics (I. pini: Fig. 7,8,26,27 in Hopping 1963a, O. latidens: Fig. 3,4,20 in Hopping 1963c, P. mexicanus: Fig. 1,2,21 in Hopping 1963a, Lanier and Cameron 1969). The distinguishing characteristics for *I. pini* entail the four spines, with the third spine in males being the largest, elongated or sub-capitated, whereas females possess a short, conical third spine, identical to the second spine (Fig. 7,8,9 in Hopping 1964, Fig. 45 in Bright 1976). In *I. pini*, the sutures of the antennal club are bi-sinuate (Fig. 92 in Bright 1976, Fig.2 in Angst and Lanier 1979). For O. latidens, the males' third declivital spines are larger and longer, shaped like a 'long cylinder', compared to females with a smaller third declivital spine, which is shaped more like a 'tapered triangle' (Fig. 42 in Bright 1976, Miller and Borden 1985), and the suture of antenna club is broadly sinuate to nearly straight (Fig. 89 in Bright 1976). In *P. mexicanus*, the sutures of the antenna club are strongly arcuate. On the frons, males have a prominent median tubercle on the epistomal margin, whereas the females exhibit a bare spot in that area with a small carina or a shallow fovea. Most males have a longer third

spine, which extend in parallel, than the females, with the spine turning obliquely inwards (Fig. 7,8 in Lanier and Cameron 1969, Hopping 1963b).

*Hylurgops* spp. have an anteriorly constricted pronotum, or more slender appearance than the *Dendroctonus* genus, and is more likely found at the base or the roots of the tree(Bright 1976, Wood 1982b). *Dendroctonus murrayanae* can be distinguished from *Hylurgops* spp. or *D. ponderosae* from the stout appearance characteristic of the genus *Dendroctonus* or based on the presence of a median longitunidal, subcarinate line located above the epistomal process (Fig. 2 in Furniss and Kegley 2008).

Synonymous with the common name of twig beetles, *Pityogenes* spp. and *Pityophthorus* spp. are among the smallest of bark beetles. Males of *Pityogenes* spp. have two or three large teeth-like spines on their elytral declivity, and females have a deeply excavated frons. *Pityophthorus* spp. are so numerous that to identify them can be challenging. One difference between *Pityogenes* spp. and *Pityophthorus* spp. are their antennal clubs, compressed with two sutures in *Pityogenes* spp., but chitinized septa in *Pityophthorus* spp. (Bright and Stark 1973, Bright 1976, 1981).

#### Appendix G2. identification of bark beetle galleries under the bark

The common method of identifying the beetles associated with trees is based on the characteristics of beetle galleries, after most of the parent bark beetles or their broods have re-emerged and dispersed to seek, feed, and reproduce in other hosts. The common gallery features, including the length and shape of the gallery of *D. ponderosae* and the secondary bark beetles are included as a reference guide to identify the beetles associated with the mortality of the tree surveyed (BCMoF 1994) **(Appendix F)**.

*Dendroctonus ponderosae* is a monogamous species, and females normally initiate the construction of a long, nearly straight, vertical egg gallery in the soft inner cambium beneath the bark. The gallery has a characteristic hook, or J-shaped, where the beetle entered, with the gallery initially heading downward, then ascending diagonally for about 3–5 cm, before turning upward, slightly grooving, following the grain of the wood (Wood 1982b, Gibson et al. 2009) **(Appendix F1)**. Galleries are approximately 30 cm long under optimal conditions, however, length may approach 1.5 m (Reid 1962b, Safranyik and Carroll 2006).

*Ips pini* is a polygamous species, with one male creating a nuptial chamber to mate with up to seven females, which individually create galleries of 13–25 cm long (Furniss and Carolin 1977) **(Appendix F2)**. *Orthotomicus latidens* is monogamous, with the female constructing up to four egg gallery arms of 2–3 cm long for each of the arm, which extends from the male-initiated nuptial chamber (Reid 1999) **(Appendix F4)**. *Pseudips mexicanus* is polygamous, with the males mating up to three females. Females construct galleries of approximately 5 cm long on each of the arms (Smith et al. 2009) **(Appendix F5)**. The harem size for each can be inferred from the number of egg galleries by the females, which radiates from the nuptial chamber initiated by males, except for *O. latidens* since this species is always monogamous. *Ips pini* and *O. latidens* galleries radiate from the nuptial chamber to produce an X or Y or star shaped galleries (Fig. 5,6 in Kegley et al. 1997 vs. Fig. 23 in Bright and Stark 1973), while *P. mexicanus* create an almost circular curving of a C or S shaped galleries radiating away from the nuptial chambers (Fig. 5 in Hopping 1963b, Fig. 1 in Smith et al. 2009). The galleries of *I. pini* and *O. latidens* can be differentiated based on their sizes,

spacing of the egg niches, and lengths of the galleries (Appendix F2 vs. Appendix F4). Females of *O. latidens* lay their eggs singly on both sides of tunnel of the egg gallery at an average rate of 0.95 egg niches/mm, almost double the rate of *I. pini* at 0.54 egg niches/mm (Miller and Borden 1985). In term of size, the adults of *O. latidens* are smaller (2.3–3.6 mm) than *I. pini* (3.5–4.2 mm), and produce shorter galleries (each arm approximately 3 cm long, vs. each arm approximately 13–25 cm in length). These differences of size, higher density of egg niches, and gallery characteristics help distinguish each species based on their ovipositional behaviour and their gallery systems.

The sour sap bark beetles of the genera *Hylurgops* and *Hylastes* are known to vector the ophiostomatoid fungus, *Leptographium wageneri* (W.B.Kendr.) M.J. Wingf., which causes the black-stain root disease, exhibiting symptoms of a dark stain on the tracheids of the phloem (Schweigkofler et al. 2005). This black stain signature is used to distinguish the *Hylurgops* spp. from *D. murrayanae* since larvae of both species often overlap when they occur together in the root crowns region of the tree (Bright 1976, Wood 1982b)

(Appendix F3, Appendix F6, Appendix F9). Though *Hylastes macer* (LeConte) is more commonly associated with the *Leptographium* fungus, with 63–75% association vs. *Hylurgops porosus* (LeConte) at only 30% (Schweigkofler et al. 2005), *Hylurgops porosus* is probably the more important vector (Safranyik et al. 1999a, 2000, 2004). Thus, galleries with dark stains were assumed to predominantly have originated from *Hylurgops* spp.

### (Appendix F3).

Dendroctonus murrayanae, monogamous like other Dendroctonus spp., attack individual trees at low densities, not in groups, constructing galleries of 13–23 cm in length. Dendroctonus murrayanae laid their eggs in a strung-out mass on the more downward or inward-curved side of the gallery in a shallow excavation. The larvae exhibit aggregated feeding while leaving trails of red frass (BCMoF 1994, Furniss and Kegley 2008)

### (Appendix F6).

*Pityogenes* spp. and/or *Pityophthorus* spp. frequently occur on smaller trees, or smaller branches/larger twigs/thinner barks of larger trees. They produce star-shaped galleries, with multiple branches of tunnelling from five to ten females from the nuptial chamber, similar but considerably smaller tunnels than those of *I. pini* or *O. latidens* (Bright and Stark 1973, Bright 1976, 1981) **(Appendix F7)**.

Ambrosia beetles are sapwood borers. Their galleries are easily distinguishable from the other bark beetles galleries, based on their characteristic 'pin-hole' tunnels with black stain fungi discolouring the entrance of their tunnel on the phloem (Daterman and Overhulser 2002) (Appendix F8). Ambrosia beetles produce an extensive network of three-dimensional galleries, extending primarily into the woody tissue. The chambers or cradles for larvae development branch several times, above and below the main tunnel. Ambrosia beetles often occur on the larger trees of at least 10 cm in diameter (Wood 1957, 1982b).

Although wood borers are not bark beetles, they are found quite extensively in dead trees, together with other phloeophagous insects (Wilson 1975). Wood borers also tunnel into the hardwood, but can be distinguished from ambrosia beetles by their larger larval sizes, the wider galleries going in random directions leaving a trail of roughen wooden shavings, or D-shaped or larger O-shaped tunnels, boring into the sapwood (Appendix F11). Aside from damage by insects, including in the roots (Appendix F10), the presences of other deformities and/or pathogens on lodgepole pine were also examined. The most abundant of them all, in the younger stands, was the fungi *Peridermium harknessii* Moore, which causes western gall rust on the pines (Peterson 1960). Western gall rusts exhibit symptoms such as trunk cankers and branch galls on lodgepole pine (Appendix F11). The formations of those woody galls were the product of fungal infection, resulting in the cambial cells to divide rapidly. This pathogen is an obligate parasite that requires live host to successfully propagate, which is a potential mortality agent of lodgepole pine by itself if the trees were heavily infested, or increases the susceptibility of mortality by subsequent colonizations from bark beetles.

#### Appendix H: Size relationships of trees with various signs of bark beetle activity

The dominant density distribution of *Dendroctonus ponderosae* can be split based on the stand's maturity levels; beetles in the 'young' stands were predominantly in trees of at least 10 cm versus the older stands in trees of at least 15 cm. When the trees were associated with the complex of secondary bark beetles or D. ponderosae and with other bark beetles, the hosts were more likely to be larger and taller, in comparison to the trees with individual secondaries only, in the absence of *D. ponderosae*. For example, 81% (161/200) of the secondary bark beetles associated with *D. ponderosae* presence were in the larger trees (đ: 14.0 cm , h: 15.1 m), compared to the remainder 19% of the trees with secondaries, but without D. ponderosae (39/200) (d: 9.1 cm, h: 10.4 m). When the density distribution of secondary bark beetles were examined in comparison to those of D. ponderosae, those bark beetles were closely associated to one other, with their highest distribution to resemble those at the mean diameters of *D. ponderosae*. These could vary depending on the stand dynamics. In 'young' stands, the density distribution of secondaries associated with D. ponderosae were generally lower to indicate that not all the D. ponderosae mortalities were occupied by secondary bark beetles. In the 'old' stands, the density distributions of the secondary bark beetles were close to or lower than those of *D. ponderosae*, since not many young susceptible trees were left in the more mature stands, with the majority of those larger diameter trees normally had been colonized by D. ponderosae.

#### Individual secondary bark beetles

Although individual species of secondary bark beetles were associated with the dead trees at a lower rate (around 25% or less), *I. pini* were found almost exclusively in the intermediate diameter tree class of younger stands around 10 cm (distribution: 5.7–17.1 cm) and very low in the 'old' stands. When the density distribution of *I. pini* was plotted, the beetles were found in smaller diameter trees than those of *D. ponderosae* and/or most secondary bark beetles; *I. pini* had a density distribution that closely resembles those of the complex of secondary bark beetles.

*Hylurgops* spp. and/or *D. murrayanae* were the most abundant secondary bark beetles associated with the dead trees (171/373), with a mean of 13.3 cm. These insects were found in trees around 10 cm in the 'young' stands or 15 cm or more in the 'old' stands, similar to *D. ponderosae*.

Galleries of *O. latidens* were found in dead trees with a mean of 12.6 cm. Such trees occurred slightly more in Mackenzie (29/48) than the 'older' stands of Crassier Creek and Chief Lake combined (17/48), but had the highest presence of individual secondary bark beetles presence in the 'old' stands than most of the other bark beetles or when compared to the individual younger stands **(Table 8)**. Their distribution were more spread out from the mean, towards the relatively smaller diameter trees when associated with *D. ponderosae* or *I. pini* in the 'old' and 'young' stands respectively. When *O. latidens*\_was found with *I. pini*, *O. latidens* were found in smaller trees than the majority of *I. pini*.

Trees with *P. mexicanus* was among the lowest frequency of secondary bark beetles in the stands associated with the dead trees (27/373). These trees had a mean diameter of 12.5 cm. When evidence of *P. mexicanus* was present, the insects were most commonly associated with *D. ponderosae* (presence: absence ratio of 5.8), and occasionally with *O. latidens* (ratio of 0.4). Since there are very few observations of *P. mexicanus*, the graphs of their density distribution is often not evenly distributed (non-bell shaped curve) when plotted in each individual site.

*Pityogenes* spp. and/or *Pityophthorus* spp., or the twig beetles were the least frequently recorded (25/373). They occurred in the smaller diameters and twigs (mean: 8.6 cm), mostly beyond the main bole area surveyed. While the lower diameter distribution of associated trees overlapped with *D. ponderosae*, the diameter distribution most closely matched the distribution of *I. pini* as they would peak in the smaller diameter than *I. pini*.

Ambrosia beetles were distributed in the largest diameter trees on average (đ: 15.0 cm, ħ: 16.0 m), compared to any other bark beetles including *D. ponderosae*.

## Other biotic disturbances: root collar damage by insects, wood borers and western gall rust

The four most abundant disturbance agents associated with the dead trees (n: 373), except for root collar damage and western gall rusts that included live trees (n: 251) as well, are *Hylurgops* spp. and/or *D. murrayanae* at 46% (171/373), root collar damage at 38% (238/624), and western gall rust at 35% (221/624), and the wood borers at 30% (113/373).

Root collar damage occurrences and their density distributions were similar to those of secondary bark beetles. Both groups followed closely the density distribution of trees with signs of *D. ponderosae*, having the focal peak point at the mean diameters of *D. ponderosae*. The difference between root collar damage and *D. ponderosae* was the former occurred at lower density than the distribution means of the latter, but extended their distribution towards the smaller diameter classes, and only occasionally in the larger trees of the older stands.

The signs of trees colonized by wood borers closely resembled those of the secondary bark beetles, with lower density and more spread out distributions over the smaller diameters of tree colonized by *D. ponderosae*.

The fungal parasite infections of western gall rust (*Endocronartium harknessii*) did not show any correlation with the other disturbance agents, and were found in stands with trees of mean diameter 6.5 cm and 7.9 m. The density distribution that showed the highest peaks around lodgepole pine are 9 cm or less in all types of stands, with almost all the infections were recorded solely in the Mackenzie Forest District.

#### Interactions among the bark beetles and with other biotic disturbances

The interactions between two individual species of bark beetles were cross-compared in two ways, by including or excluding the presence of the other bark beetles, or by excluding the presence of the secondary species examined.

The individual species of the secondary bark beetles were associated most often with *D. ponderosae* (all had ratios of presence to absence of 2.7 or higher). *Dendroctonus ponderosae* was found with *I. pini* 79% of the time (55/70), with *Hylurgops* spp. and/or *D. murrayanae* 88% of the time (151/171), with *O. latidens* 73% of the time (35/48), with *P. mexicanus* 85% of the time (23/27). *Dendroctonus ponderosae* was rarely found in the same tree with *Pityogenes* spp. and/or *Pityophthorus* spp., 56% of the time (14/25), but was found most frequently with ambrosia beetles, 91% association (70/77) **(Table 8)**.

Among the individual secondary bark beetles, *Hylurgops* spp. and/or *D. murrayanae* had the highest interactions, in relative numbers and percentages, with the other species of secondaries, comparable to those with *D. ponderosae*. These insects were found in the same tree as *I. pini* at 86% of the time (60/70), *O. latidens* at 69% of the time (33/48), *P. mexicanus* at 85% of the time (23/27), *Pityogenes* spp. and/or *Pityophthorus* spp. at 72% of the time (18/25), and ambrosia beetles at 94% of the time (72/77).

*Pityogenes* spp. and/or *Pityophthorus* spp. were among the smallest bark beetles in this study, which was found among the smallest of the dead trees (đ: 8.6 cm, ħ: 10.3 m). When *Pityogenes* spp. and *Pityophthorus* spp. occurred individually on their own, the trees were smaller and shorter (đ: 5.0 cm, ħ: 5.5 m). While, ambrosia beetles were almost always

associated with the largest and tallest dead trees (đ: 15.0 cm, h: 16.0 m). Their highest association was with *D. ponderosae* at 94% of the time (72/77) (đ: 15.3 cm, h: 16.2 m).

In the realm of exclusive interactions between two species of bark beetles only, D. ponderosae exhibited the highest exclusive interaction with Hylurgops spp. and/or D. murrayanae at 23% (39/171) of the total occurrences. Ips pini never occured in the same trees with O. latidens only or P. mexicanus only. Pseudips mexicanus was not associated exclusively with any bark beetles, except with O. latidens on some occasions. Similarly, no associations were detected between Pityogenes spp. and/or Pityophthorus spp. with any other species of bark beetles, except with I. pini only.

Insects that feed around the root collar were also frequently associated with *D. ponderosae*, in 64% of the occurrences (152/238). Root collar damage was associated with the assemblage of secondary bark beetles 63% of the time (150/238), and *Hylurgops* spp. and/or *D. murrayanae* 55% of the time (131/238). Those three groups of interactions were found in larger trees (d: 13.8–14.1 cm, h: 14.8–15.2 m) in comparison to those without root collar damage by insects (d: 8.5–10.7 cm, h: 10.7–12.7 m). Analogously, wood borers had a high correlation with all the four groups, including root collar damage by insects, at a rate of around 80% or higher. Trees with wood borer activity had signs of secondary bark beetle activity 96% of the time (109/113), *D. ponderosae* 85% of the time (96/113), *Hylurgops* spp. and/or *D. murrayanae* 84% of the time (95/113), and root collar damage by insects 79% of the time (89/113).

The fungus disease, western gall rust, had no correlation with the bark beetles or the non-bark beetle groups. In general, the disease were found on the larger trees (d: 7.9-11.7 cm, h: 9.3-13.1 m).

# Appendix I: Case study of Mac3-C: The perfect mortality-storm from a combined effect of stand density and maturity from secondaries

The goal of setting up Mac3-C in 2010 was to demonstrate the role of bark beetle outbreaks as an important agent of lodgepole pine mortality and their continuous significance in the stands, especially the secondary bark beetles at the post-outbreak stage after the main wave of mortality at the outbreak stage by *D. ponderosae*. Sometimes, such cases of high mortality by secondaries were considered an outlier, when the samples were irregularly detected, or the rate of mortality was higher or lower than the conventional mean, but such issues were also caused by a limited sample size or limited monitoring periods or less common events requiring certain predisposition factors or due to preconceived bias and a narrow scope of predetermined conclusion in hindsight, before collecting, examining, or interpreting the field data. The evaluation of a worst case scenario of tree mortality by outbreaks of secondary bark beetles can provide additional insights on the bark beetles populations at the post-outbreak stage, in their associations among the dead and their interactions with the live residuals lodgepole pines. For that reason, an additional plot (Mac3-C) was 'randomly' selected and surveyed for meeting the profile criteria as a high risk stand for mortality by secondary bark beetles.

Mac3-C is a young, high density, pure lodgepole pine plot with 40 live and 27 dead pines (đ: 7.3 cm, ħ: 9.6 m) **(Table 4)**, and it is a good example of a stand with a more severe situation of a secondary bark beetle outbreak, *I. pini* in particular. In general, 54% of the dead trees contained an assemblage of secondary bark beetles (200/373), and in Mac3-C, the secondaries were associated in the stand at the rate of 35% (24/67), or with the dead trees at 89% (24/27), which was much higher than the 54% average. Normally, the role of an individual species of secondary bark beetles as an agent of tree mortality was insignificant; however, this was not the case for *l. pini* in Mac3-C. *Ips pini* was associated with the dead trees at an average rate of 19% (70/373) in the 15 plots, but more than a quarter of *l. pini* were detected in the single plot of Mac3-C (19/67), or a 70% association with the dead trees of Mac3-C (19/27), which was at least three times higher than the 19% average. Among the 27 dead pines, the following bark beetles were associated at a higher rate even, where *D. ponderosae* was found in 85% of the trees (23/27), and *Hylurgops* spp. and/or *D. murrayanae* 78% of the time (21/27). The presence of *P. mexicanus* 11% of the time (3/27), and *O. latidens* 7% of the time (2/27), were almost negligible in comparison. Root collar damage by insects were examined on all 67 live and dead lodgepole pines in the stand, where the rate of infestation was one out of every three pines (22/67) (**Tables 8** and **9**).

The classic paradigm was the younger the stands, the smaller the mean diameter and the shorter the mean height of the lodgepole pines. This proved agreeable with the field observations and/or in the comparisons made between the stands. For example, the high density 'young' plot of Mac3-C (đ: 7.3 cm, ħ: 9.6 m) was contrasted against the polar opposite of the low density 'old' plot of CLk-A (đ: 16.6 cm, ħ: 18.8 m). In general, the difference in diameter sizes between the presence and absence of bark beetles was approximately double, and the magnitude of the height differences was between a half-fold to a one-fold increase. For example, the presence of *D. ponderosae* in the 15 overall plots (đ: 13.6 cm, ħ: 14.8 m), versus their absence (đ: 6.0 cm, ħ: 8.0 m) was approximately double in measurements; in Mac3-C, the presence (đ: 10.3 cm, ħ: 12.9 m) to absence (đ: 5.8 cm, ħ: 7.9 m) was slightly less than double; and in the lower density 'older' site (CLk-A), the presence (đ: 20.9 cm, ħ: 22.0 m) to absence (đ: 12.4 cm, ħ: 15.5 m) remained high, though the least different between the three comparisons. The presence of bark beetles was mostly found in the larger and taller lodgepole pines, in comparison to the absence of bark beetles in the trees, where the healthy and dead trees without bark beetles were smaller and shorter. This was generally true for all species of bark beetles in all type of plots, except for the very low numbers or almost non-occurrences of *I. pini* and *Pityogenes* spp. and/or *Pityophthorus* spp. in the 'older' plots.

If the stands were grouped according to the maturity level ('young' or 'old'), the trees with *D. ponderosae* were smaller and shorter (d: 9.8-12.2 cm, h: 11.7-12.9 m) in the younger stands in Mackenzie (Mac3-C, Mac3-B, Mac2-B, Mac1-B), than those of the older stands ( $d \ge 15 \text{ cm}$ ,  $h \ge 15 \text{ m}$ ) in Mackenzie (Mac4-B), Crassier Creek (CCk-A) or Chief Lake (CLk-A). The complex of secondary bark beetles mimicked closely the distribution of *D. ponderosae*. The only minor difference is trees with secondaries were slightly smaller and shorter. For example, the measurements of the dead trees associated with the secondary bark beetles in Mac3-C (d: 9.6 cm, h: 12.0 m) and CLk-A (d: 17.7 cm, h: 19.0 m), were relatively similar to the measurements of *D. ponderosae* in Mac3-C (d: 10.3 cm, h: 12.9 m) and CLk-A (d: 20.9 cm, h: 22.0 m).

The reverse of the classic paradigm, as above, occurred only in the low density 'old' stand (CLk-A), where the presence of certain secondaries such as *I. pini*, *O. latidens*, *P. mexicanus* and ambrosia beetles were associated with the smaller and shorter lodgepole pines, in comparison to their absence. Some possible explanations for the phenomena in CLk-A were the low presence of the secondary bark beetles, thus, skewing and lowering the mean diameters, mean heights and their ranges, or the lower availability of suitable hosts and higher presence of live 'residuals' that are more resistant to bark beetles, or possibly, the more mature stand conditions were not the best for the populations of secondaries to increase to outbreak levels to cause 'residual' mortality.

Lodgepole pine mortality associated with bark beetles can be highly variable from stand to stand, depending on the interactions of bark beetles with the pine densities and/or with the plot maturity. Two comparisons of tree mortality by bark beetles were made between Mac3-C with the other plots; the first being the similarity of some of the plots to Mac3-C, and the second, the differences in the plots in stand density and stand maturity to Mac3-C. The measurements of Mac3-C and the 15 overall plots were standardized as the baseline for all the comparisons.

#### Ratios among stands, as comparable indicators of mortality associated-agents

The most noticeable difference between Mac3-C with the other plots was the ratio of dead to live lodgepole pines. Ratio was used as a relative measure of the interactions, in the relative comparisons between the plots. The higher the ratio number, the higher the proportion of dead to live trees within the plot. The advantage of using ratio to compare the presence to absence was the adjustment was made automatically on the appropriate scale, relative to the plot density, since the ratio of other than 1.0 represents the severity of the mortality agent, values above 1.0 meant higher presence than absence, and anything below 1.0 signified more absent than present. For example, if the ratio is 2.0, the occurrences of

present to absent of that mortality agent is twice as high, and a ratio of 0.5 meant the numbers present to absent is half of that.

The first three comparisons (Mac3-B, Mac2-B, Mac4-B) were highly similar in density and maturity to Mac3-C, though there were some minor differences. The commonality among these plots was their high density of lodgepole pines ( $\geq$ 60 stems/plot) and as 'young' stands, except for Mac4-B that was an older mature stand **(Table 4)**.

Mac3-C had a ratio of 0.7, compared to the other 3 plots with similar density, where their ratio were 2.0 or higher, while the overall ratio of all the 15 plots was around 1.5. This implies that the lower value of Mac3-C had more live trees than dead trees, within the stand. In term of meeting the goals of this study, the lower the ratio, the higher the potential availability of hosts for the secondary bark beetles, as long as the residuals were within the suitable range as viable hosts, which was the case for Mac3-C (ratio: 0.7, đ: 7.3 cm, ħ: 9.6 m) **(Table 4)**.

In the second part of the comparison, the goal was to vary the stand density and stand maturity, but still be as inclusive as possible in examining the interactions between the guilds of bark beetles with their lodgepole pine hosts. Several inherent variability in density and maturity within the plots were contrasted against Mac3-C (high density 'young' plot): the four variable plots had the characteristics of a very high density 'young' plot (Mac1-B), a medium density 'young-old' plot (Mac5-A), a medium density 'old' plot (CCk-A), and a low 'old' density plot (CLk-A) **(Table 4)**. Among these plots, the ratio of dead to alive trees for the very high density plot was 1.3, for the 'young-old' and 'old' stands of medium density

were slightly above 2.0, and for the low density old' stand was 6.0. All the values were well above Mac3-C ratio of 0.7, or all plots had lower abundance of live residuals than Mac3-C.

The ratio of presence to absence of *D. ponderosae* was fairly high and consistent in all the plots, at a ratio of 0.5 or higher, except for the very high density plot of Mac1-B at 0.1. One probable explanation for the Mac1 plots was Mac1-A and Mac1-B were 'younger' stands, where the trees were smaller in diameters (đ: 5.6 cm), shorter in heights (ħ: 7.0), and of limited suitability as hosts for *D. ponderosae*. The assemblage of secondary bark beetles had similar ratios of presence to absence of 0.5 or higher within all plots, except for Mac1-B. Most of those ratios followed closely the trends of *D. ponderosae*, except for some minor differences. Those differences were due to plot to plot variations, including the availability of larger trees or more mature plots, which effectively limits the numbers of mortality to some extent, or potentially the number of suitable hosts for *D. ponderosae* and the subsequent increase in the populations of secondary bark beetle, as the case for Mac1.

The more distinct the deviation in stand density or maturity from Mac3-C or the 15 overall plots, the higher the variability between the ratios of dead to live trees; the average ratio of presence to absence in *D. ponderosae* and secondary bark beetles (d: 13.0–13.6 cm, h: 14.2–14.8 m) for the 15 overall plots were both 0.5; in Mac3-C, the ratios were 0.5 and 0.6 respectively (d: 9.6–10.3 cm, h: 12.0–12.9 m); in a high density 'young' stand (Mac3-B), or in a plot similar to Mac3-C, the presence of *D. ponderosae* and secondary bark beetles were more similar, at 0.8 and 0.6 (d: 9.8–9.9 cm, h: 11.5–11.7 m) than in the polar opposite stand of Mac3-C or a low density 'older' stand (CLk-A), where the two ratios were proportionally higher at 1.0 and 3.7 (d: 17.7–20.9 cm, h: 19.0–22.0 m).

The differences in ratio demonstrates the complexity of the maturity of the stand, as a direct measure of the numbers of dead to live trees, or as an indirect measure of more suitable hosts for the bark beetles from the larger and taller trees.

Mac3-C had the highest ratio of *l. pini* at 0.4, which was minorly significant in comparison to the overall and the other plots (ratios of 0–0.2). The ratios of presence to absence of *Hylurgops* spp. and/or *D. murrayanae*, *O. latidens*, *P. mexicanus* in Mac3-C (0.5, ~0, ~0) were not significantly different from the overall measurements (0.4, 0.1, ~0). However, in certain plots, some species of secondary bark beetles were found more concentrated in the 'young-old' or 'old' plots. *Hylurgops* spp. and/or *D. murrayanae* and ambrosia beetles had the highest ratio of presence to absence at 1.1 and 0.8 in medium dense 'young-old' plot (Mac5-A), well above the average ratio of 0.4 and 0.1 in the 15 overall plots. *Orthotomicus latidens* had the highest ratio of presence to absence in low density 'old' plot (CLk-A) at 0.6, compared to the average ratio of 0.1 from the 15 overall plots. *Pseudips mexicanus* had one of the lowest ratios of presence to absence among the associations of bark beetles in the stands (0.1 or less), regardless of plot density or maturity level.

Similarly, the presence to absence ratio of the non-bark beetle elements (root collar damage by insects and wood borers) in Mac3-C and Mac3-C type of plots were more similar to the 15 overall plot, than the non-Mac3-C type of plots, which had greater variation: the 15 overall plots had ratios of 0.6 for root collar damage and 0.2 for wood borers, Mac3-C type of plots had ratios of 0.4–0.8 for root collar damage by insects and 0.1–0.4 for wood borers, the non-Mac3-C type of plots, in this case CLk-A, had the highest ratios of 3.7 for root collar

damage and 2.5 for wood borers. These last 2 ratios were 5 times or higher, in some stands, than the average ratios observed in the overall plots.

For the fungus disease of western gall rust, the ratio for Mac3-C type of plots can vary from 0.2 to 0.9 compared to the 15 overall plots (0.5), but the highest ratio was found in the very high density 'young' stand (Mac1-B) at 1.8, at least twice or more, higher than the average ratios. Among all, western gall rust was the only mortality agent associated with the smaller and shorter lodgepole pines (d: 5.5–7.9 cm, h: 8.1–10.6 m) in all plots, except in Mac1-B, relative to those trees that did not had any western gall rusts (d: 6.6–13.3 cm, h: 6.9–14.5 m).

In summary, these ratios indirectly supports the warrant for a more detailed inspection of Mac3-C, with its low stand ratio of 0.7 (high amount of 'residuals') and qualifying as a high 'risk' stand for potential tree mortality from outbreaks of secondaries, in particular *I. pini* that was recorded at a ratio of 0.4 (above the average values from any of the other stands surveyed).

#### Exception than the rule: Higher associations of secondary bark beetles in Mac3-C

The highlight of Mac3-C was the percentage of *I. pini* found associated most abundantly with the lodgepole pines. Mac3-C was not an unusual plot, as the presence to absence ratio of *D. ponderosae* and the complex of secondary bark beetle in Mac3-C and the 15 overall plots were similar at around 0.5.

One of the reason for the more pronounced increase in *I. pini* was because of the higher abundance of live residuals (ratio: 0.7), and the trees in Mac3-C were highly suitable potential hosts for *I. pini*, as the plot was a monoculture plantation of intermediate, pole-sized diameter of lodgepole pines (đ: 5.7–17.1 cm, ħ: 5.8–20.0 m). The pine engravers were seldom found on the larger trees in the older plots, possibly due to the beetles occurring at the higher canopy levels or above the sampled area, since unlike smaller trees, the larger ones were more fully utilized by *D. ponderosae*, limiting the 'free' resources available for subsequent use by the secondaries to cause potential outbreaks.

Since *I. pini* is a moderately aggressive bark beetle that occasionally outbreak given the proper circumstances, in this case, the initial host abundance from the dead trees of *D. ponderosae* outbreak, new mortality of nearby live residuals was predicted when the increase in population of *I. pini* was sufficient to overcome the defenses of the pole-sized trees, which disregard whether the trees were healthy or had been weaken by *D. ponderosae* or compromised by any secondary bark beetles or the other mortality agents.

*Hylurgops* spp. and/or *D. murrayanae* was found in the largest of trees, with the differences between their presence and absence from the trees was approximately the
doubling of the diameters size or heights of the trees, displaying differences ranging from 4.1 to 9.1 cm and 3.8 to 8.3 m. For *O. latiden*, their presence was most noticeable in the older plots, and for *P. mexicanus*, no correlation of plot density or stand maturity affected the distribution of this species.

Each stand had its own characteristic interactions between stand density and maturity, or indirectly, the signature of interactions between the insects and hosts. In this manner, the presence of Pityogenes spp. and/or Pityophthorus spp. was associated with the smallest of trees among all the recorded bark beetles in most sites, and were not present in the older sites, possibly due to the unsampled regions at higher canopy level, where there is a higher availability of exclusive phloem material for them and less suitable for D. ponderosae. However, the beetles were associated with the larger trees (d: 7.3–14.6 cm, h: 9.6–14.6 m) when present in the stand, than their absence in the smaller trees (đ: 5.8–10.8 cm, h: 7.7–12.3 m). In contrast, ambrosia beetles was found among the largest of trees in all the compared sites, except for Mac3-C and CLk-A. The differences between their presence (d: 10.2–18.4 cm, h: 11.7–18.2 m) and absence (d: 5.7–9.8 cm,  $\hbar$ : 7.7–12.3 m) from the trees was approximately the doubling of the diameters size, but less so in height. Mac3-C had a similar trend of the general interactions of the 15 overall plots for Pityogenes spp. and/or Pityophthorus spp., where they were found among the smallest of trees, but no ambrosia was found in this plot.

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# Summary of case study of Mac3-C, in comparison to similar type of stands

The average value of the 15 plots, or within a plot, is subject to random fluctuations, since the resulting mean is only an arbitrary series of measurements of the most frequent values recorded, not an absolute dictum; in this case, the majority of the data was collected from the 'young' residual stands in Mackenzie, and the mean value of this case study primarily reflect the pole-sized diameter lodgepole pines of Mackenzie, which Mac3-C did not deviate from the overall measurements. The purpose of these comparisons of the interactions, means and ratios were to differentiate the plots, since any deviations from the mean, signify that some characteristics of the bark beetles or the non-bark beetle elements were correlated as major agents of tree mortality under different circumstances, or by varying the density or maturity levels.

In the younger stands of Mackenzie (Mac3-C, Mac3-B, Mac2-B, Mac1-B), the bark beetles and root collar damage by insects were associated with lodgepole pine of diameters around 8–10 cm, versus the older stands of Mackenzie (Mac4-B), Crassier Creek (CCk-A) or Chief Lake (CLk-A), which was around 13 cm or more: *D. ponderosae* ( $d_{young}$ : 9.8–10.3 cm vs.  $d_{old}$ : 15.4–20.9 cm), *I. pini* ( $d_{vg}$ : 8.7–10.2 cm vs.  $d_{old}$ : 13.6–14.7 cm), *Hylurgops* spp. and/or *D. murrayanae* ( $d_{vg}$ : 9.9–10.1 cm vs.  $d_{old}$ : 15.7–22.5 cm), *O. latidens* ( $d_{vg}$ : 7.8–9.0 cm vs.  $d_{old}$ : 12.8–16.5 cm), *P. mexicanus* ( $d_{vg}$ : 7.4–11.8 cm vs.  $d_{old}$ : 14.1–19.8 cm), and root collar damage by insects ( $d_{vg}$ : 9.1–9.6 cm vs.  $d_{old}$ : 14.5–18.6 cm).

In term of heights, the bark beetles in the younger stands were found in the shorter lodgepole pines, around 10 to 13 m, versus the older stands, which was around 14 m or more: *D. ponderosae* ( $\hbar_{young}$ : 11.7–12.9 m vs.  $\hbar_{old}$ : 17.2–22.0 m), *I. pini* ( $\hbar_{yg}$ : 11.5–12.0 m vs.

h<sub>old</sub>: 11.4–18.3 m), *Hylurgops* spp. and/or *D. murrayanae* (h<sub>yg</sub>: 11.5–12.7 m vs.

h<sub>old</sub>: 17.4–24.7 m), *O. latidens* (ħ<sub>yg</sub>: 10.0–11.2 m vs. ħ<sub>old</sub>: 16.7–17.9 m), *P. mexicanus* (ħ<sub>yg</sub>: 10.8–14.3 m vs. ħ<sub>old</sub>: 16.7–19.5 m), and root collar damage by insects (ħ<sub>yg</sub>: 11.4–12.1 m, ħ<sub>old</sub>: 14.3–20.1 m).

The reverse was true with western gall rust, found associated with the smaller trees (đ: 5.5–7.9 cm, ħ: 8.1–10.6 m), relative to their absence (đ: 6.6–13.3 cm, ħ: 6.9–14.5 m).

If the stands were grouped according to their maturity, the individual secondary bark beetles in the younger stands of Mackenzie, were mostly associated to the larger trees ( $\hat{d}$ : 7.4–15.6 cm,  $\hat{h}$ : 10.3–13.2 m) versus the average-sized tree in the plots ( $\hat{d}$ : 5.8–7.3 cm,  $\hat{h}$ : 7.8–9.6 m). However, those trees with secondaries in the younger stands were smaller and shorter than those from the older stands ( $\hat{d}$ : 12.8–22.5 cm,  $\hat{h}$ : 16.7–24.7 m).

The assemblage of secondary bark beetles was the main mortality agent associated with the dead trees in Mac3-C. Among the individual or groups of secondaries, the most significant secondary bark beetles in Mac3-C was *I. pini*, found most abundantly (ratio 0.4) in this stand than any other stands, and was associated with the dead trees as the second best model (AIC: 58) after secondary bark beetles (AIC: 39) **(Table 10B)**.

The presence to absence ratio is a gauge of the stand density and maturity, but is also an indirect measure of the stand as a suitability index for secondary bark beetles. The highest ratio of 0.4 in *I. pini* in Mac3-C is an example exhibiting the species preference for a high density 'young' stand. In general, *Hylurgops* spp. and/or *D. murrayanae* was found most abundantly among the individual species of secondary bark beetles, in all the different stages of the stands, but 'young-old' stand (Mac5-A) works best for them, since the ratio of 1.1 indicates an increase of at least two-fold or more than the other sites. *Orthotomicus latidens* was predominantly associated with the dead trees in the 'older' stands (CLk-A or CCk-A) at ratios of 0.4 and 0.2.

In summary, Mac3-C is a high-risk plot of pure lodgepole pine, perfect to examine the rate of mortality from secondary bark beetles. Host abundance, or the availability of residual pines in the plot highly influence the population dynamics of bark beetles in Mac3-C, with the rise of one population into the outbreak phase, corresponding to a drop for another species, which in turn cause an extended period of mortality among the 'ripe residuals' on overtime.

<u> </u>	Lodgepole pines with frass	Dendroctonus ponderosae	Any secondary bark beetles	ips pini	Hylurgops spp. and/or Dendroctonus	Orthotomicus latidens	Pseudips mexicanus	Pityogenes spp. and/or Pityophthorus spp.	Ambrosia beetles
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presence <sup>†</sup> (+)	8.9	9.7	8.9	8.5	8.6	8.6	8.6	7.9	8.1
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absence <sup>*</sup> (-)	-	7.7	8.1	11.0	9.2	9.0	9.0	9.5	8.9
		(5.7 – 9.2)		(8.1 - 14.6)	(5.7 – 14.6)	(5.7 – 13.6)	(5.7 – 14.6)	(5.7 – 14.6)	(5.7 – 14.6)
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presence <sup>†</sup> (+)	8.5	9.3		_	8.4	7.6	8.6	7.9	8.1
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absence <sup>‡</sup> ()	11.0	11.0	-	-	10.2	14.6	0	0	0
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Appendix J1. Distribution of diameter-at-breast height (in cm) of lodgepole pine with frass, and their association with *Dendroctonus* ponderosae and secondary bark beetles

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•	Lodgepole pines with frass	Dendroctonus ponderosae	Any secondary bark beetles	lps pini	Hylurgops spp. and/or Dendroctonus murrayapae	Orthotomicus latidens	Pseudips mexicanus	Pityogenes spp. and/or Pityophthorus spp.	Ambrosia beetles
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Orthotomicus latidens			• • • • • • • • • • • • • • • • • • • •						
presence <sup>†</sup> (+)	<b>8.6</b> (5.7 - 14.6)	9.1 (7.3 - 14.6)	-	7.6 (5.7 – 9.5)	8.4 (7.4 - 9.5)	_	8.1 (7.3 – 9.5)	7.2 (5.7 – 8.2)	0
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absence <sup>*</sup> (-)	9.0 (5.7 – 13.6)	10.4 (8.1 – 13.6)	-	9.0 (5.7 – 13.6)	8.7 (5.7 – 10.9)	-	9.3 (8.1 – 10.7)	8.6 (6.5 – 10.7)	8.1
Pseudips mexicanus								an a	
	and the states		M. Standard	Sector Prints	denie Basie i	tion of some	Same a	a harver from the se	in <b>state and s</b> ame
presence <sup>+</sup> (+)	8.6 (7.3 - 10.7)	8.7 (7.3 – 10.7)	-	8.6 (7.3 – 10.7)	8.8 (7.4 – 10.7)	8.1 (7.3 – 9.5)	-	8.3 (7.3 – 10.7)	8.1
					Z BE CONTROL		HEST OF ME	ALL DE LE MALL	tute of the
absence <sup>‡</sup> (–)	9.0 (5.7 – 14.6)	10.8 (7.3 – 14.6)	-	8.5 (5.7 – 13.6)	8.5 (5.7 – 10.9)	9.2 (5.7 – 14.6)	-	7.1 (5.7 – 9.0)	0
Pityogenes spp. and/or Pityo	ohthorus spp.								NA LALA
presence <sup>+</sup> (+)	7.9 (5.7 – 10.7)	8.4 (7.3 – 10.7)	-	7.9 (5.7 – 10.7)	8.3 (6.5 – 10.7)	7.2 (5.7 – 8.2)	8.3 (7.3 – 10.7)	-	8.1
		DATER 1				Deces 2 -Leave	in the Tables		
absence <sup>*</sup> (-)	9.5 (5.7 – 14.6)	10.4 (7.3 – 14.6)	-	9.1 (5.7 – 13.6)	8.9 (5.7 – 10.9)	10.5 (7.3 – 14.6)	9.3 (9.0 – 9.5)		0
Ambrosia beetles				A. 44		and the second		Same Second - Same	
presence <sup>+</sup> (+)	8.1	0	+	8.1	8.1	0	8.1	8.1	
	in the second	An de Carte	······································	Sec. 20	distant 10 total	in sector and		And the second the second second	
absence <sup>*</sup> (-)	8.9 (5.7 – 14.6)	9.7 (7.3 – 14.6)	-	8.6 (5.7 – 13.6)	8.7 (5.7 – 10.9)	8.6 (5.7 – 14.6)	8.7 (7.3 – 10.7)	7.8 (5.7 – 10.7)	-

<sup>†</sup> The interactions of the two terms may include the presence of (1) *Dendroctonus ponderosae*, or (2) any secondary bark beetles, or (3) others/non-bark beetles (root collar damage by insects, wood borers, or western gall rust)

\* In contrast, the second relationship showed the absence of the 'horizontal' term (opposite of cross-interactions) with the hosts, with the only residuals are the non-bark beetles (others: root collar damage by insects, wood borers, or western gall rust)

Appendix J2.	Distribution of height (in m) of lodgepole pine with frass, and their association with Dendroctonus ponderosae and secondary
	bark beetles

	Lodgepole pines with frass	Dendroctonus ponderosae	Any secondary bark beetles	lps pini	Hylurgops spp. and/or Dendroctonus	Orthotomicus latidens	Pseudips mexicanus	Pityogenes spp. and/or Pityophthorus spp.	Ambrosia beetles
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Lodgepole pines with frass				. is bould		. Z (totali 🕬			
presence <sup>+</sup> (+)	11.3 (7.2 - 17.1)	12.4 (8.4 - 17.1)	11.4 (7.2 – 17.1)	11.0 (7.2 – 13.8)	11.6 (7.2 13.8)	12.0 (8.4 - 17.1)	12.3 (10.5 – 13.8)	11.0 (7.2 – 13.5)	11.1
	A CONTRACTOR OF A CONTRACT OF		a state of the state	and the second	1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1	and the state of the second			312.J <b>26</b>
absence <sup>*</sup> (–)	—	9.8 (7.2 – 11.6)	9.4	13.1 (9.4 – 17.1)	10.9 (8.4 – 17.1)	11.0 (7.2 – 13.5)	10.8 (7.2 – 17.1)	11.5 (8.4 – 17.1)	11.3 (7.2 – 17.1)
Dendroctonus ponderosae									
presence <sup>†</sup> (+)	12.4 (8.4 - 17.1)	_	12.7 (8.4 – 17.1)	12.2 (8.4 – 13.8)	12.9 (11.0 – 13.8)	12.3 (8.4 - 17.1)	12.5 (10.5 – 13.8)	12.1 (10.5 – 13.5)	0
				********	Contribution of the last	Sector Andrea			1
absence <sup>*</sup> (–)	7.7 (5.7 – 9.2)	-	7.7 (5.7 – 9.2)	7.7 (5.7 – 9.2)	7.5 (5.7 – 9.0)	5.7	8.1	7.3 (5.7 – 9.0)	8.1
Any secondary bark beetles		and so that a straight of the		Constant Said on Said					
presence <sup>†</sup> (+)	11.4 (7.2 - 17.1)	12.7 (8.4 – 17.1)	_	_	-		-		
	Contraction in the second			94 × 2 + 2 + 1	A. S. A. Martin	utic Section R			
absence <sup>*</sup> ()	9.4	9.8 (7.2 11.6)	_	-		_	-	—	-
lps pini				100 A 2 2 2			in Canada		
presence <sup>+</sup> (+)	11.0 (7.2 – 13.8)	12.2 (8.4 – 13.8)		-	11.5 (7.2 – 13.8)	11.1 (8.4 – 13.8)	12.3 (10.5 13.8)	11.0 (7.2 – 13.5)	11.1
			S. OKADAR	An Sector		ALC: ALC: NO	Active applies		CALL OF LAND
absence <sup>*</sup> (-)	13.1 (9.4 – 17.1)	13.1 (9.4 – 17.1)	_		10.5	17.1	0	0	0
Hylurgops spp. and/or Dendro	octonus murrayano		an madalan di Sangan di Sangan di Kanan dalam da kana d	in me rotal (. 1411) in the second		ALL RATES - LONG THE REPORT OF A	and a state of the	and a second	and the second of the second
presence <sup>*</sup> (+)	11.6	12.9	-	11.5 (7.2 - 12.9)	-	12.7	12.5	11.3	11.1
	( <i>1.2 - 13.8)</i>	(11.0 - 13.8)	art and a star from	(7.2 - 13.8)		(5.CI = U.I.)	(8.51 ~ U.II)	(7.2 = 13.3)	
absence <sup>‡</sup> ()	10.9	11.9 (8.4 17.1)		10.4	—	11.4	11.8	10.0	0
	(0.4 - 1/.1)	(0.4 - 17.1)		(0.4 - 13.1)		(0.4 - 17.1)	(10.5 - 13.1)	(3.3 - 10.3)	

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### – continuation –

	Lodgepole pines with frass	Dendroctonus ponderosae	Any secondary bark beetles	lps pini	Hylurgops spp. and/or Dendroctonus	Orthotomicus latidens	Pseudips mexicanus	Pityogenes spp. and/or Pityophthorus spp.	Ambrosia beetles
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Orthotomicus latidens									
	No. of Concession, Name		1	1		A State State	ALC: MARC	CONCEPT OF ANY	
presence <sup>†</sup> (+)	12.0	12.3 (8.4 - 17.1)	-	11.1 (8.4 - 13.8)	12.7 (11.0 - 13.8)	-	12.1 (10.5 – 13.8)	11.1 (9.5 – 13.2)	0
				L			Sec. Con Berthins	Same + Marina	
absence <sup>‡</sup> (–)	11.0 (7.2 – 13.5)	12.5 (9.4 – 13.5)		10.9 (7.2 – 13.5)	11.2 (7.2 – 13.5)	-	12.6 (11.1 – 13.5)	10.9 (7.2 – 13.5)	11.1
Pseudips mexicanus			ann an 1700 Tha Guide ann an Star an Star Star Star		er is the second states of the constitution of second	and the second	er - mangel - 122 Victor (* 112. 1000 m. 114	n 18 in an an an ann an an an an an an an an a	
	C. Then	<b>43.4 4</b> 1.5 5	a watata	a the second		and the Real Barrier of		A CONTRACTOR OF THE OWNER OF THE	the state of the second
presence <sup>*</sup> (+)	12.3	12.5	-	12.3	12.5 (11.0 - 12.8)	12.1 (10 5 - 13 8)	-	11.9 (10.5 - 13.5)	11.1
	(10.5 - 13.8)	(10.5 = 15.8)	ALC: Same Same	(10.5 = 15.8)	(11.0 – 15.5)	(10.5 15.0)	a de reise velte ve		The States
absence <sup>‡</sup> (–)	10.8 (7.2 - 17.1)	12.3 (8.4 – 17.1)		10.1 (7.2 – 13.1)	10.9 (7.2 – 13.1)	11.7 (8.4 – 17.1)	-	9.4 (7.2 – 11.6)	0
Pityogenes spp. and/or Pityo	ohthorus spp.								Sec. Prairie
presence <sup>†</sup> (+)	11.0	12.1	-	11.0	11.3	11.1	11.9	-	0
and the first of the second	(7.2 – 13.5)	(10.5 – 13.5)	and the second states of the	(7.2 – 13.5)	(7.2 – 13.5)	(9.5 – 13.2)	(10.5 – 13.5)	ere en server al a server a server	an a
	11.6	12.6	_	11.0	12.0	13 1	135		11.1
absence" (–)	(8.4 - 17.1)	(8.4 - 17.1)	-	(8.4 - 13.8)	(9.0 - 13.8)	(8.4 - 17.1)	(13.1 - 13.8)		
Ambrosia beetles									
presence <sup>+</sup> (+)	11.1	0		11.1	11.1	0	11.1	11.1	_
	a to be to be start			akasi (Peret	240 P. 10 10 10				<u> Mélés medit ér</u>
absence <sup>‡</sup> (–)	11.3	12.4	-	11.0	11.7	11.9	12.5	10.9	-
	(7.2 - 17.1)	(8.4 - 17.1)		(7.2 - 13.8)	(7.2 <b>– 13</b> .8)	(8.4 - 17.1)	(10.5 - 13.8)	(7.2 – 13.5)	

<sup>†</sup> The interactions of the two terms may include the presence of (1) *Dendroctonus ponderosae*, or (2) any secondary bark beetles, or (3) others/non-bark beetles (root collar damage by insects, wood borers, or western gall rust)

<sup>\*</sup> In contrast, the second relationship showed the absence of the 'horizontal' term (opposite of cross-interactions) with the hosts, with the only residuals are the non-bark beetles (others: root collar damage by insects, wood borers, or western gall rust)

	Lodgepole pines	Dead	New mortality (live to dead)	Residuals (live)	Mac3-C* (dead) (2010)	Mac3-C* (live) (2010)	Root collar damage by	Others: Wood borers	Others: Western gall
	(+)	(2009 and 2010) (+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Lodgepole pines with frass									
presence <sup>†</sup> (+)	8.9 (5.7 – 14.6)	9.8 (8.2 – 10.9)	8.3 (5.7 – 13.6)	10.2 (8.1 – 14.6)	8.3 (5.7 – 10.7)	8.2	8.8 (5.7 – 13.6)	8.6 (5.7 – 10.7)	8.0 (5.7 – 10.2)
Dendroctonus ponderosae			in a bit is	AND A REAL	<u>/1511568</u>	i da da		Same 2. Se	
presence <sup>+</sup> (+)	9.7 (7.3 – 14.6)	9.8 (8.2 – 10.9)	9.0 (7.3 – 13.6)	10.6 (8.1 - 14.6)	10.7	0	9.3 (7.3 – 13.6)	10.1 (9.5 – 10.7)	8.8 (7.4 – 10.2)
absence <sup>‡</sup> (–)	7.7 (5.7 – 9.2)	0	7.6 (5.7 – 9.0)	9.2	7.1 (5.7 – 8.4)	8.2	7.7 (5.7 – 8.7)	5.7	7.8 (5.7 – 9.2)
Any secondary bark beetles									
presence <sup>+</sup> (+)	8.9 (5.7 – 14.6)	9.8 (8.2 – 10.9)	8.3 (5.7 – 13.6)	10.9 (9.0 – 14.6)	8.3 (5.7 – 10.7)	8.2	8.9 (5.7 – 13.6)	8.6 (5.7 – 10.7)	8.0 (5.7 – 10.2)
		Sander C		A State Shot	1 0 J		ale i zloviti	San Litte Street	
absence <sup>‡</sup> (–)	8.1	0	0	8.1	0	0	8.1	0	0
lps pini						den antica			and the second
presence <sup>†</sup> (+)	8.5 (5.7 – 13.1)	9.6 (8.2 – 10.9)	8.3 (5.7 – 13.6)	9.1 (9.0 – 9.2)	8.3 (5.7 – 10.7)	8.2	8.8 (5.7 - 13.6)	8.6 (5.7 – 10.7)	7.7 (5.7 – 13.6)
absence <sup>‡</sup> (–)	11.0 (8.1 – 14.6)	10.2	0	11.4 (8.1 – 14.6)	0	<b>0</b> 0	9.2 (8.1 – 10.2)	0 0	10.2
Hylurgops spp. and/or Dendro	ctonus murrayan	ne A A A A A A A A A A A A A A A A A A A							and the second second
presence <sup>†</sup> (+)	<b>8.6</b> (5.7 - 10.9)	9.8 (8.2 – 10.9)	8.1 (6.5 – 9.5)	C	8.3 (5.7 – 10.7)	0	9.4 (8.1 – 10.9)	10.1 (9.5 – 10.7)	8.1 (6.5 – 10.2)
						tin in Local			ent all des all all all all all all all all all al
absence <sup>‡</sup> (–)	9.2 (5.7 – 14.6)	0	8.5 (5.7 – 13.6)	10.2 (8.1 - 14.6)	0	8.2	8.5 (5.7 – 13.6)	5.7	8.0 (5.7 – 9.2)

Appendix J3. Distribution of diameter-at-breast height (in cm) of lodgepole pine with frass, and their association with bark beetles, root collar damage by insects or other interactions

- continue next page -

#### continuation

	Real Sector States Sector	a anna an tao an	ANY AVERAGE			the states the states		in the second	1750 <b>(</b> 1772)
absence <sup>‡</sup> ()	9.0 (5.7 – 13.6)	10.6 (10.2 – 10.9)	9.2 (6.5 - 13.6)	8.8 (8.1 - 9.2)	8.3 (5.7 – 10.7)	8.2	9.6 (8.1 – 13.6)	10.7	8.5 (6.5 – 10.2)
Pseudips mexicanus	and the state of the			ana ana biran ti inana ana ar					
		COLOR MANAGEMENT		and the second second second	and the second	A SHE MARK S			State of Street
presence' (+)	8.6 (7.3 – 10.7)	8.2	8.1 (7.3 – 9.5)	9.0	10.7	U	8.4 (7.3 – 9.5)	(9.5 – 10.7)	7.4
State of the second		287284282 R. 43	Service Adda	CALL AVELOW	17 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	HIGH PLOSE		A DE LA DE L	<b>NAME</b>
absence <sup>‡</sup> (–)	9.0 (5.7 14.6)	10.6 (10.2 – 10.9)	8.5 (5.7 – 13.6)	10.6 (8.1 – 14.6)	7.1 (5.7 – 8.4)	8.2	9.1 (5.7 – 13.6)	5.7	8.1 (5.7 – 10.2)
Pityogenes spp. and/or Pityop	hthorus spp.	alan - A da an an ann an Alba - a suid dan alb - Alba Alba an a	nan ar 1877 lag bar kini ta da shekara <b>ranara</b>	and with the state of the state	and a second state of the second	anary and a statement of the second and the second	na se anna an a	the case and a set of the set of the set of the	
		Contrain Provinsion	Tall See Charles	MILLION SACE	A Distant	A CALLER OF			
presence <sup>†</sup> (+)	7.9 (5.7 – 10.7)	8.2	7.3 (5.7 – 9.0)	0	10.7	0	7.3 (5.7 – 8.2)	8.2 (5.7 – 10.7)	6.5 (5.7 – 7.4)
	Parts on Design	120576724672	Sector Park	Section of the				Mart also	14 15 CM
absence <sup>*</sup> (–)	9.5 (5.7 – 14.6)	10.6 (10.2 – 10.9)	9.8 (7.3 13.6)	10.2 (8.1 – 14.6)	7.1 (5.7 - 8.4)	8.2	9.5 (7.3 – 13.6)	9.5	8.9 (8.2 – 10.2)
Ambrosia beetles									
	and the second second	the second	and the second second						A Carlos Parasan
presence <sup>†</sup> (+)	8.1	0	8.1	0	0	0	8.1	0	0
						with the set of the set	A		
absence <sup>‡</sup> (–)	8.9	9.8	8.3	10.2	8.3	8.2	8.9	8.6	8.0
	(5.7 – 14.6)	(8.2 - 10.9)	(5.7 – 13.6)	(8.1 - 14.6)	(5.7 - 10.7)		(5.7 – 13.6)	(5.7 - 10.7)	(5.7 - 10.2)
	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
		(2009 and 2010)	(2009 to 2010)	(2009 to 2010)	(2010)	(2010)			
	Lodgepole pines						Root collar	Others:	Others:
	with frass	Dead	New mortality (live to dead)	Residuals (live)	Mac3-C* (dead)	Mac3-C* (live)	damage by insects	Wood borers	Western gall rust

<sup>†</sup> The interactions of the two terms may include the presence of (1) *Dendroctonus ponderosae* or (2) secondary bark beetles with the hosts, with some of them interacting with non-bark beetles/others (root collar damage by insects, wood borers, or western gall rust)

<sup>\*</sup> In contrast, the second relationship showed the absence of the 'horizontal' term (opposite of cross-interactions) with the hosts, with the

only residuals are the non-bark beetles (others: root collar damage by insects, wood borers, or western gall rust)

\* Mac3-C was surveyed on 2010 only, without any prior information of the stand for mortality monitoring (2009)

	Lodgepole pines	Dead	New mortality (live to dead)	Residuals (live)	Mac3-C* (dead)	Mac3-C* (live)	Root collar damage by	Others: Wood borers	Others: Western gall
	with frass (+)	(2009 and 2010) (+)	(2009 to 2010) (+)	(2009 to 2010) (+)	(2010) (+)	(2010) (+)	insects (+)	(+)	rust (+)
Lodgepole pines with frass									
	County (manufactor)	A Street State		Adada Se	and finishes	se tinteks.		A Antal	Alment
presence <sup>†</sup> (+)	11.3	13.1	10.6	12.3	11.3	8.5	11.3	12.3	10.0
	(7.2 – 17.1)	(12.9 – 13.2)	(7.2 - 13.8)	(9.4 - 17.1)	(9.0 – 13.5)		(8.4 – 13.8)	(9.5 - 13.8)	(7.2 - 12.9)
Dendroctonus ponderosae	State Annual State	an 20 de la com					an a' m Ar ann a' a	aran Irina	San Lainis
presence <sup>†</sup> (+)	12.4	13.1	11.3	13.2	13.5	0	11.9	13.7	12.0
	(8.4 - 17.1)	(12.9 – 13.2)	(8.4 – 13.8)	(9.4 – 17.1)	Line of the second is the second	na marka Peseta P. Malaria P. Ma	(8.4 – 13.8)	(13.5 – 13.8)	(11.0 – 12.9)
					<b>. 2</b> 6. a.				
absence <sup>*</sup> (–)	9.8	0	9.9	9.7	10.2	8.5	9.8	9.5	9.4
	(7.2 – 11.6)		(7.2 - 11.6)		(9.0 - 11.3)		(8.5 - 11.1)		(7.2 - 11.3)
Any secondary bark beetles	and the second state of th	nan antar in standard in suite a suite and suite and the states	A TRANSMENT OF A PARTY AND A PARTY	Second の構成していたけたいないの違い。	A Marine Marine Street and a street and the South	and a statistic statistic statis	an anti-anti-anti-anti-anti-	an a she was a subscription of	and a state of the
					and the second second	Service Marine		12.2	
presence <sup>*</sup> (+)	11.4	13.1	10.6	13.3	11.3	8.5	11.4	12.3	10.0
	{/.2 - 1/.1)	(12.9 – 13.2)	(7.2 - 13.8)	(9.7 – 17.1)	(9.0 - 13.5)		(8.4 - 15.8)	(9.5 – 13.6)	(7.2 - 12.9)
	0.4	0	0	9.4	0	0	A P	∩ ∩	0
absence' (-)	5.4	U	0	5.4	Ū	Ū	5.4	Ū	0
lps pini								and a thick	ALL NO ALL
	11.0	13.2	10.6	11.4	11.3	8.5	11.3	12.3	9.6
presence (+)	(7.2 - 13.8)	(13.1 - 13.2)	(7.2 - 13.8)	(9.7 - 13.1)	(9.0 - 13.5)		(8.4 - 13.8)	(9.5 - 13.8)	(7.2 - 11.3)
			States and the second		1. 16 M. 1. 16	A. A. A. A.	S. W. C. Walter	Contraction of the second	A. 1. 1. 1.
absence <sup>‡</sup> ()	13.1	12.9	0	13.3	0	0	11.2	0	12.9
	(9.4 - 17.1)			(9.4 – 17.1)			(9.4 – 12.9)		
Hylurgops spp. and/or Dendroo	tonus murrayand	1e							
	the state of the second second		11. S. 1. 1. 1.	Contract Of Contract	Colline College	Car Lin Councilo			and the second
presence <sup>+</sup> (+)	11.6	13.1	10.9	0	11.3	0	12.8	13.7	10.6
anna a sheker ta se di ke darta ta a na na da bahar ana sheker a sa s	(7.2 – 13.8)	(12.9 – 13.2)	(7.2 – 13.8)	an an an Saint Andre an Andre an Andre	(9.0 – 13.5)	. Internet wetter in the second second	(11.1 – 13.8)	(13.5 – 13.8)	(7.2 – 12.9)
	A STATE OF A STATE					in the second second		NAME OF A PARTY	and the second
absence <sup>‡</sup> (–)	109	0	10.3	12.3	0	8.5	10.3	9.5	9.5
	(8.4 - 17.1)		(8.4 – 12.9)	(9.4 - 17.1)			(8.4 - 13.1)		(8.5 – 10.2)

Appendix J4.	Distribution of height (in m) of lodgepole pine with frass, and their association with bark beetles, root collar damage by
	insects or other interactions

– continue next page –

#### continuation

	Lodgepole pines with frass (+)	Dead (2009 and 2010) (+)	New mortality (live to dead) (2009 to 2010) (+)	Residuals (live) (2009 to 2010) (+)	Mac3-C* (dead) (2010) (+)	Mac3-C* (live) (2010) (+)	Root collar damage by insects (+)	Others: Wood borers (+)	Others: Western gall rust (+)
Orthotomicus latidens							<u>``</u>		
		en and the						Marine 2 Jake	Ling Traile
presence <sup>†</sup> (+)	12.0	13.2	10.6	17.1	0	0	11.1	11.7	10.3
presence (+)	(8.4 - 17.1)		(8.4 – 13.8)				(8.4 – 13.8)	(9.5 – 13.8)	(9.5 – 11.0)
a second s	and a state of the		5. THE APRIL		in a start and a start and		Carle Bar	designed to the	
absence <sup>‡</sup> ()	11.0	13.0	10.6	10.7	11.3	8.5	11.4	13.5	10.0
	(7.2 – 13.5)	(12.9 – 13.1)	(7.2 – 12.9)	(9.4 – 13.1)	(9.0 – 13.5)		(9.4 – 13.1)		(7.2 – 12.9)
Pseudips mexicanus		new constants and the second		and a second	and the second of the second attempts of the second	The second starts of the SP is the second start second starts	u na mata i una destructura de la contra da seculada	Barthathan a' share ne - shareesti kalim	a contract of the construction of the
Sector Sector Sector	and the state of the second second			E. Just And St.		Linds Dates			A . at the rise of
presence <sup>*</sup> (+)	12.3	13.2	11.6	13.1	13.5	0	12.3	13.7	11.0
	(10.5 - 13.8)	ar an	(10.5 – 13.8)			teres and the standard second to	(10.5 – 13.8)	(13.5 – 13.8)	
		the subscript in the							
absence <sup>‡</sup> ()	10.8	13.0	10.0	12.1	10.2	8.5	10.6	9.5	9.9
	(7.2 - 17.1)	(12.9 – 13.1)	(7.2 – 12.9)	(9.4 - 17.1)	(9.0 – 11.3)		(9.4 - 13.1)		(7.2 - 12.9)
Pityogenes spp. and/or Pi	tyophthorus spp.	and an tail the second second second	and the second second second second	ant share to accord the same	and an and a state of the second second		n a statue a second a second a		
					12.5	0	11.1	11 E	0.2
presence <sup>*</sup> (+)	11.0	13.2	10.2	U	13.5	U	11.1	11.5	9.2
	(7.2 - 13.5)		(7.2 – 11.0)				(9.5 - 13.2)	(9.5 – 15.5)	(7.2 - 11.0)
	11 5	12.0	11.2	17 2	10.2	<b>8</b> 5	11 /	13.8	10.5
absence" ()	11.5	(12.0	(9.4 - 13.9)	12.5 (9 A - 17 1)	(9.0 - 11.3)	0.5	(84-138)	13.0	(85-129)
Ambrosia bootlos	(0.4 - 17.1)	(12.3 - 13.1)	(0.4 - 10.0)	(3.4 17.1)	(5.0 11.5)		(0.4 15.0)		(0.0 22.0)
Ambrosid beeties	A CALL AND A CALL					Sec.	Contraction of the second	- AN	· · · · · · · · · · · · · · · · · · ·
1		0	11 1	<u>.</u>	0	0	11.1	0	0
presence (+)	****	v	****	v	·	•		-	-
	0	an an an ann an thair	and the second states	C. C. A. C. M.	and the first	ar is the second	6	CARGE CONTRACTOR	
absence <sup>‡</sup> ()	11.3	13.1	10.6	12.3	11.3	8.5	11.3	12.3	10.0
ausence (~)	(7.2 - 17.1)	(12.9 - 13.2)	(7.2 - 13.8)	(9.4 - 17.1)	(9.0 - 13.5)		(8.4 - 13.8)	(9.5 - 13.8)	(7.2 - 12.9)

<sup>†</sup> The interactions of the two terms may include the presence of (1) *Dendroctonus ponderosae* or (2) secondary bark beetles with the hosts, with some of them interacting with non-bark beetles/others (root collar damage by insects, wood borers, or western gall rust)

\* In contrast, the second relationship showed the absence of the 'horizontal' term (opposite of cross-interactions) with the hosts, with the only residuals are the non-bark beetles (others: root collar damage by insects, wood borers, or western gall rust)

\* Mac3-C was surveyed on 2010 only, without any prior information of the stand for mortality monitoring (2009)

#### Appendix K: Size relationships of trees with frass with bark beetle activity

If lodgepole pines were associated to *D. ponderosae*, the trees were larger and taller (12/21) (d: 9.7 cm, h: 12.4 m) than trees without *D. ponderosae* (9/21) (d: 7.7 cm, h: 9.8 m) (Table 11, Appendix I). Any trees associated to *D. ponderosae*, with any interactions between *D. ponderosae* and secondaries or non-bark beetles, were larger (d: 8.4–10.1 cm, h: 11.9–13.7 m), than the trees in the absence of *D. ponderosae* (d: 5.3–8.1 cm,

ħ: 9.4–11.1 m) **(Table 11)**.

Within the secondary bark beetle castes, *I. pini* was associated the highest with all the other bark beetles. For example, among the 11 *Hylurgops* spp. and/or *D. murrayanae* found, they were associated from highest to lowest in the following order: *I. pini* (10/11), followed by *D. ponderosae* (6/11) and *Pityogenes* spp. and/or *Pityophthorus* spp. (6/11); for *O. latidens*, this species was associated the highest with *I. pini* (6/7) and *D. ponderosae* (6/7); for *P. mexicanus*, the highest interaction was with *I. pini* (7/7) and *D. ponderosae* (6/7)

# (Table 11, Appendix I).

One common features among the secondary bark beetles interactions were the more uniform distribution of measurements of the tree diameter (d: 8.5-8.6 cm), less so in tree height (h: 11.0-12.3 m). In their absence, the trees were slightly larger in diameter (d: 9.0-11.0 cm), but comparable in tree height measurement (h: 10.8-13.1 m). The overall relative similarity of measurements was possibly due to the limited sample size. The only obvious observation of host selection was the presence of *I. pini* in smaller lodgepole pines (18/21) (d: 8.5 cm, h: 11.0 m), in comparison to their absence (3/21) (d: 11.0 cm, h: 13.1 m) (Appendix I). From the four surviving green residuals, all trees had some secondary bark beetles (4/4), *I. pini* in half of them (2/4), failed or ongoing colonization of *D. ponderosae* in half of them (2/4), and *O. latidens* and *P. mexicanus* in one of the tree for each species (Appendix I). The one tree with *P. mexicanus*, was found also associated with *D. ponderosae* and *I. pini*. This sort of multiple layers of interactions between the secondary bark beetles demonstrate the lethal potential of secondaries as a possible mortality agent of weaken trees. In this case, as an opportunist, in others, as the aggressor species that attacked live residuals, for example, several of the live trees were exclusively infested with an individual secondary species such as *I. pini* (1/2) or *O. latidens* (1/1) (Table 11).

The twig bark beetles, *Pityogenes* spp. and/or *Pityophthorus* spp. was associated with the smaller diameter trees (d: 7.9 cm, h: 11.0 m) versus their absence from the trees (d: 9.5 cm, h: 11.5 m). This generalization of smaller trees associated with twig beetles was true for all the twig beetle interactions with the other groups, but the difference in magnitude was most noticeable in their interaction with *O. latidens* (d: 7.2 cm, h: 11.1 m), versus the absence of the twig beetles, in the presence of *O. latidens* only (d: 10.5 cm, h: 13.1 m) (Appendix I). In contrast, ambrosia beetles were found the least among the frass trees (1/21). For that reason, no comparisons were made, since the sample size was limited, and insufficient to exhibit even the weakest of any interactions.

Root collar damage by insects were found in 62% (13/21) (đ: 8.8 cm, ħ: 11.3 m) of the trees with frass. Root collar damage by insects were most commonly associated with the complex of secondary bark beetles (12/13), followed by *I. pini* (11/13) *D. ponderosae* 

(9/13), Hylurgops spp. and/or D. murrayanae (5/13), O. latidens (5/13), P. mexicanus (5/13), and with Pityogenes spp. and/or Pityophthorus spp. (4/13) (Table 11, Appendix I).

Wood borers were found in 14% of the trees with frass (3/21). All were associated with the complex of secondary bark beetles (3/3) and *I. pini* (3/3), and two out of the three trees were associated with the other mortality agents, except for their absence in ambrosia beetles (Appendix I). One possibility for the highest association of *I. pini* with the wood borers was the attractions to the host volatiles of weaken trees, or the presence of new mortality, which signal the presence of a suitable host, in addition to the emitted pheromones by the secondaries.

38% (8/21) of the trees with frass had western gall rusts, which had the highest association with the complex of secondary bark beetles (8/8), followed by *I. pini* (7/8) (Table 11). The recorded observation that only two trees were associated with *D. ponderosae*, versus the presence of secondaries in all the interactions with western gall rusts exhibited the differences in behaviors and colonization preferences between *D. ponderosae* and *I. pini*; *Dendroctonus ponderosae* is more likely to attack healthy, vigorous tree of larger diameter because the phloem nutrition of those trees are highest when they had not been compromised; in contrast to secondary bark beetles, particularly *I. pini* that are moderately aggressive, will attack almost any weakened hosts, including ones with western gall rust.

In summary, 21 trees with frass were associated with bark beetles. The highest among them were *I. pini* (18/21), followed by *D. ponderosae* (13/21), *Hylurgops* spp. and/or *D. murrayanae* (11/21), *Pityogenes* spp. and/or *Pityophthorus* spp. (8/21), *O. latidens* (7/21),

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and *P. mexicanus* (7/21) **(Table 11)**. The presence of *D. ponderosae* in the lodgepole pine was associated with the larger and taller trees (đ: 9.7 cm, ħ: 12.4 m), versus their absence (đ: 7.7 cm, ħ: 9.8 m). In contrast, the presence of *I. pini* and *Pityogenes* spp. and/or *Pityophthorus* spp. were associated with the smaller trees (đ: 7.9–8.5 cm, ħ: 11.0 m), in comparison to their absence (đ: 9.5–11.0 cm, ħ: 11.5–13.1 m). Most secondary barkbeetles, excluding *I. pini* were associated with trees of slightly smaller, if not comparable, in diameter size and heights in their presence (đ: 8.6 cm, ħ: 11.6–12.3 m), versus their absence (đ: 9.0– 9.2 cm, ħ: 10.8–11.0 m) **(Appendix I)**.

# Appendix L: Justification for grouping Hylurgops spp. and Dendroctonus murrayanae in the same category

The two most common bark beetles at the root collar regions, *Hylurgops* spp. and/or *D. murrayanae*, were found very similarly within their habitat environments, including their numbers, occurrences and interactions with each other or with other bark beetles. In total, the grouped measurements of bark beetles of the roots, *Hylurgops* spp. (d: 13.3 cm, h: 14.7 m) and *D. murrayanae* (d: 13.5 cm, h: 14.8 m), had comparable diameter and height (d: 13.3 cm, h: 14.6 m), similar to the average combined measurements of their individual occurrences. This comparison of the two showed some overlapping, and was combined into one category because both had some similarities in the measurements, so as not to underevaluate the presence of one or the other.