Northernmost North American *Pinus contorta* var. *latifolia* (lodgepole pine) sociations and vegetation diversity relative to its central range east of the Rocky Mountains

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Lodgepole pine (*Pinus contorta* var. *latifolia*) stands were sampled in central Yukon, Canada (61.5–64°N latitude), which represented the northernmost 9% of the tree's North American range. Within this area, lodgepole pine occupied only ~2% of the landscape. This study determined: 1) what forest sociations occurred (i.e. structural dominance-types); 2) how plant growth form composition and richness differed from the central portion of the species' geographical range; and 3) if stands were biased towards occurring on more thermally favorable south-facing slopes. Five lodgepole pine sociations were recognized among 100 relevés: *Rhododendron groenlandicum* (Labrador tea); *Cladonia arbuscula* (green reindeer lichen); *Calamagrostis purpurascens* (purple reedgrass); *Hylocomium splendens* (stairstep moss) and *Alnus viridis* (green alder, n = 4 relevés). *Rhododendron* stands were proportionally more common on low gradient sites and had more total plant cover than the other sociations. *Cladonia* and *Calamagrostis* stands were typically associated with dry coarse-textured soils and warm dry sites, respectively; whereas the composition of the *Hylocomium* sociation reflected the detrimental influences of atypically dense forest canopies on understory vascular plants. Only the *Calamagrostis* sociation was unique to the study region. Species richness among common northern lodgepole pine sociations averaged 16–19 taxa per relevé (p > 0.05). Northern compared to central range (n = 1394) relevés were compositionally different based on little overlap of their datasets in the ordination space. Northern vegetation had less (p < 0.001) total plant (129% vs 184%), deciduous shrub (9% vs 26%), broad-leaved herb (5% vs 25%), and bryophyte (27% vs 54%) cover; had greater macro-lichen cover (13% vs 5%) and lower floristic richness (11 vs 24 taxa) and was less than half as phytosociological diverse. Lodgepole pine stands in the northernmost portion of their range were not biased towards occurring on south-facing slopes, which suggested an ecological potential for range expansion.

The presence of a plant at or near the limits of its geographical range is dependent upon the occurrence of acceptable climate and site conditions, excluding consideration of factors such as dispersal, interspecific competition, and history. If a regional climate is unfavorable, the plant is typically limited to localities and microsites where constraints are sufficiently mitigated (Daubenmire 1952). In the case of trees, they have broad ecological amplitudes and adapt to a multitude of environmental circumstances. Their understory plants, in contrast, are often sensitive to differences in moisture balance, soil nutrient status, tree canopy density and its influence on the amount of photosynthetically active radiation that reaches the forest floor, and the effects of tree succession (Hart and Chen 2006, De Grandpre et al. 2011, Strong 2011), possibly more so in marginal habitats. This sensitivity is represented by cover variation and differential dominancy among individual species and growth forms. Such differences are more apparent in mature seral than climax boreal forest stands due to compositional convergence during ecological succession.

In mountainous terrain, the location of a tree and understory combination varies with elevation, slope orientation or aspect, and slope gradient (Bonan and Shugart 1989), which are proxies for heat and moisture availability. Such synecological responses have been long known. More than 60 years ago, Daubenmire (1952) reported shifts in aspect occurrence among northern Idaho *Pseudotsuga/Physocarpa* (Douglas-fir/ninebark) and *Abies/Paxistima* (fir/mountain lover) stands with elevation. Similar changes also occur in response to latitude. *Populus tremuloides* (trembling aspen) stands shift from north facing slopes at low elevations in the southern portions of its range in Nevada and Utah (Mueggler 1988, p. 3) to steep south-facing slopes in central Alaska (Youngblood 1995) near the species' northernmost occurrence.

Pinus contorta var. *latifolia* (lodgepole pine) is a common tree species in the mountains and foothills of western North America from 36°N latitude in Colorado (USA) to ~61°N in southern Yukon (Canada) (Lotan and Critchfield 1990). The associated understory vegetation varies with local

ecological circumstances, but regional trends occur. In the southernmost portion of the *P. contorta* range, for example, *Juniperus communis* (ground juniper) typifies understory vegetation at low elevations, whereas *Vaccinium scoparium* (grouseberry) occurs at high elevations in upper subalpine areas (Alexander et al. 1986, Hess and Alexander 1986). From southern Wyoming (USA) to the extreme southwest corner of Alberta (Canada), mid-elevation *P. contorta* understory vegetation includes species such as *Calamagrostis rubescens* (pine grass), *Rubus parviflorus* (thimbleberry), *Paxistima myrsinites* (mountain lover) or *Xerophyllum tenax* (common bear grass) (Arno et al. 1985, Cooper et al. 1987). North of ~50°N and east of the Rocky Mountain continental drainage divide, *Menziesia glabella* (false azalea, La Roi and Hnatiuk 1980, Beckingham et al. 1996), *Rhododendron groenlandicum* (Labrador tea, Strong 2002a), and *Viburnum edule* (low-bush cranberry, Beckingham et al. 1996) are characteristic and often prominent understory species on subalpine, and in middle and low elevation forest sites, respectively. The two latter species occur in the east–west transition zone between eastern boreal and western cordilleran biomes. Between 58–60°N in northern British Columbia (Fig. 1), Annas (1977) reported *P. contorta* understory vegetation dominated by either *R. groenlandicum* and bryophytes, or mixtures of low-growing ericaceous and evergreen plants with either bryophytes or lichens as co-dominants. Similar forest understory types have also been described immediately to the north in Yukon (Lipovsky and McKenna 2005) and in southwest Northwest Territories (Jeffrey 1964). Less extensive and discontinuously-distributed stands of *P. contorta* do extend as far north as ~64°N in the territory of Yukon (Fig. 1), but little is known of their botanical composition or site relationships, or how similar their composition is to other portions of the species' range.

The objectives of this research were to: 1) classify and summarize the botanical composition of *P. contorta* var. *latifolia* communities (referred to as sociations) that occur in the northernmost portion of the species' geographical range; 2) summarize the site conditions associated with each sociation; 3) test the hypothesis that *P. contorta* stands are biased toward occurring on more thermally-favorable south-facing slopes; and 4) compare the botanical composition of northern and central range *P. contorta* relevés using ordination; and 5) determine how *P. contorta* vegetation in these two areas differed with respect to growth form composition. The two latter objectives address an aspect of ecological diversity research thought 'under investigated' by Hart and Chen (2006, p. 393), particularly for northern boreal forests.

Material and methods

Study area

Pinus contorta stands have a scattered distribution north of 61°N latitude and comprise only 2% of the land cover in the northernmost 9% of the species' North American range (Fig. 1). Between 60° and 61°N in Yukon, *P. contorta* occupies ~16% of the land in the boreal forest portion of its range (Strong 2013). Its northernmost present-day occurrence is at ~64°N in the Dawson City area (Fig. 1). Mountains and foothills are common throughout the southern half of Yukon. Less steeply sloping terrain occurs in valley bottoms and at higher elevation as remnants of an ancient plateau. *Picea albertiana* ssp. *albertiana* (western white spruce, Strong and Hills 2006) and *Picea mariana* (black spruce) stands dominate upland forests, with *P. tremuloides* on well to moderately-well drained sites in lower valley locations (Strong 2009) and with graminoid-dominated vegetation on steep south–southwest facing slopes. *Populus tremuloides* and *Pinus contorta* stands seldom exceed 15 m in height, but *Picea albertiana* trees reach 25 m (Strong 2009). The studied area occurs within the Northern Cordilleran High Boreal (NCh) and Boreal (NCb) ecoclimatic regions (Strong 2013) between 61.5° and 64°N latitude in the central portion of the territory (Fig. 1, hereafter referred to as northern range). The latter ecoclimatic region occurs at lower elevations. Median summer temperatures are 10° and 11°C, whereas winter temperatures are −17° and −16°C by region, respectively. The NCh typically receives 324 mm of precipitation per year, with most falling in summer (208 mm). The NCb is drier (median annual 279 mm) than the NCh (Strong 2013, also Jätzold 2000).

Northern range stand selection and field sampling

Vegetation sampling included only *P. contorta*-dominated stands. Potential locations for sampling (n = 187) were identified using unpublished 1:50 000-scale Yukon Energy, Mines and Resources forest cover mapping. Candidate areas for sampling were limited to forest cover map polygons with
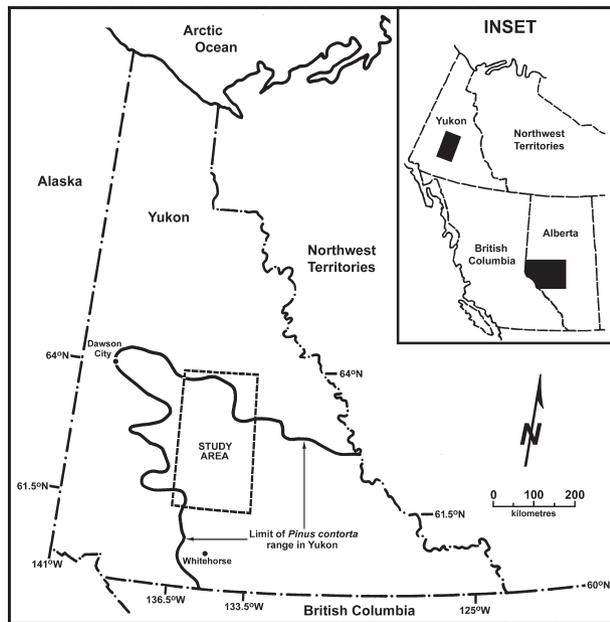

Figure 1. Location of the study area relative to the northernmost distribution limits of *Pinus contorta* var. *latifolia* (lodgepole pine) in Yukon, Canada. Inset shows the source area of the central range relevé data relative to Yukon. Limits of the *Pinus contorta* range in Yukon were compiled from Yukon Energy, Mines and Resources forest cover mapping.

a >50% *P. contorta* content that occurred within a 45 min hike from an accessible road. Locations beyond this distance were considered, if they occurred within a 15–20 min hike. More than one stand was sometimes sampled within a forest cover map polygon, if the stands differed 1) in compass bearings by ≥45°, or 2) by >5% slope gradient; or were separated, 3) by a distance of least 500 m, 4) by non-*Pinus* vegetation, or 5) had a different type of understory vegetation. Samples were obtained from as broad an area as possible given the constraint of access. These criteria separated nearby stands due to real and potential ecological differences in site conditions, which avoided pseudo-replication concerns. Recent burns (≤15 years old) were excluded from sampling. At the end of the field season, all candidate areas had been either sampled or eliminated from consideration for various reasons (e.g. misclassification of the forest cover map polygons and anthropogenic disturbance).

Stand-level species composition and abundance sampling was based on 20×30 m plots, with a centrally located 30-m transect. Along the transect, five 2.5×2.5 m quadrats each with a nested 1×1 m quadrat were used to visually estimate the canopy cover of vascular plants 1.0–2.5 m (tall shrub stratum) and <1 m tall (low shrub and herb stratum), respectively. Terrestrial bryophyte and macro-lichen cover estimates were made in the smaller quadrats. The lower left corner of each quadrat was placed at 5-m intervals along each transect beginning at the 5-m mark. The 20×30 m plot was used to assess the canopy cover of trees and shrubs >2.5 m tall. Vascular plant and bryophyte, and lichen nomenclature were based on the 'Integrated Taxonomic Information System' (<www.itis.gov.index.html>) and a North American checklist (<www.ndsu.edu/pubweb/~esslinge/chcklst/chcklst7.htm>), respectively, except where noted.

Point-centered quarter sampling was used to estimate the density of trees >2.5 m tall and to sample stem basal diameters, with sampling points located at the 0-, 10-, 20- and 30-m marks along each vegetation sampling transect. Heights and ages were determined for the two tallest *P. contorta* within each plot. Trees that existed prior to the last stand-replacing wildfire were excluded from consideration. Tree heights were determined using a measuring tape and clinometer. Stand ageing was based on annual growthring counts for the two tallest trees in each plot. Increment cores were extracted just above the root collar. Growthrings were counted using a dissecting scope, due to their narrow spacing, after trimming the surface of each core to clearly expose the rings. The oldest cored tree was considered the stand's age. Soil moisture and nutrient regimes, and drainage (Luttmerding et al. 1990, p. 35, 38 and 43, respectively); soil subgroup (Soil Classification Working Group 1998); and soil humus form (Green et al. 1993) were classified based on a pit dug near the start of each sampling transect.

Canadian National Topographic Series maps (1:50 000-scale, 1963–1990) were used to determine if *P. contorta* stand occurrences were biased with respect to slope orientation. To create an extrinsic hypothesis for the comparison (Sokal and Rohlf 1981), slope gradient (≤5% or >5%) and aspect (181–90°N or 91–180°S when >5%) frequencies were tabulated based on four points at a 250 m spacing that radiated outward in the four cardinal directions from each vegetation plot center. Points that occurred in terrain without definable characteristics (n = 10) or in waterbodies (n = 26) were deleted from consideration (net sample = 1564 points).

Central range relevé data

To compare the compositional similarity of northern *P. contorta* relevés to their more southern counterparts (Fig. 1, inset), plant percent cover data were compiled from 24 Alberta studies and a relevé database. The included data were limited to relevés located between 52.5° and 55.5°N in west–central Alberta. This area was chosen for comparison because 1) it approximated the central portion of the species' north–south geographical range, 2) included the southern portion of the boreal–cordilleran transition zone (i.e. ecologically similar to northern range), and 3) included the most extensive area of east–west *P. contorta* development along the eastern slopes of the Rocky Mountains (Strong 1992), and 4) a large number of relevés were available for comparison, unlike adjoining areas. About 70% of relevés (969 of 1394) were from the Alberta Ecological Site Information System (data available from srd.data@gov.ab.ca), which included stand composition data from numerous internal government studies, permanent forest plot sites, and the Banff/Jasper National Park biophysical analysis. See Supplementary material Appendix 1 for additional relevé sources. The sampling designs used in these studies were varied, but three-fourths were based on 400–600-m² plots. If subsampling occurred within a plot, it was typically limited to one tall shrub, and one low shrub and herb quadrat. Within the central range, 176 stands were sampled using the same or a very similar design as applied in the northern range (Supplementary material Appendix 1).

Only relevés dominated by *P. contorta*, with a ≥20% canopy cover were included in the central range dataset, which was the typical minimum among most northern relevés. Taxon cover values were combined when in more than one stratum. Due to different methods of data collection and summarization among studies, taxon cover values in each relevé were converted to integers, with original values <0.56 deleted. The same protocol was applied to northern relevés, when compared with the central range. Taxa were excluded if present in less than 1% of all relevés, except if an unusually large cover value occurred.

Data analysis

Cluster analysis based on Euclidean distance as the (dis)similarity measure and Ward's method of group linkage (Statsoft 1995) was used to initially group northern range relevés based on taxa percent cover. These algorithms produced the most distinctive groupings among several tested possibilities. Scrutiny, however, identified inconsistencies among the resulting six groups that formed at a low level of amalgamation (~18% error). These inconsistencies included relevés that either lacked an overtly dominant understory taxon or had an abundant taxon that was more characteristic of another group. Also, not all groups had substantial and

significantly different (p < 0.05, Kruskal–Wallis testing) taxon cover values, except for the degree of *Hylocomium splendens* (stairstep moss) development. As a result, each inconsistent relevé (n = 16) was reassigned to an appropriate group and two compositionally similar cluster groups were amalgamated. These reassignments did not change the fundamental composition of the initial groups, but did increase their compositional contrast. The final groupings are referred to as sociations based on their classification and naming according to dominant taxa by strata (Mueller-Dombois and Ellenberg 1974). A slash (/) in a sociation name indicates a change in stratum and a dash (–) identifies co-occurring taxa.

Detrended correspondence analysis (McCune and Mefford 1999) was used to illustrate the compositional distinctiveness of the recognized sociations, with the proportion of explained variance determined using relative Euclidean distance. The same procedures were used for simultaneous ordination of the compositionally-truncated northern and central range relevé datasets.

Comparisons of plant abundance and stand characteristics to determine if differences occurred between and among groupings were based on Mann–Whitney U-tests and Kruskal–Wallis tests, respectively, due to the lack of sample normality according to Kolmogorov–Smirnov one-sample tests. Within significant Kruskal–Wallis tests, non-parametric Scheffé rank tests (Miller 1966, formula 110) at the ∝ 0.05 level were used to identify which sociations differed with regards to the abundance of an individual taxon. G-test for goodness of fit (Sokal and Rohlf 1981, pp. 694–698) was used to compare observed slope and aspect frequencies, with expected landscape proportions. STATISTICA software (Statsoft 1996) was used for statistical testing, whereas G-test and Scheffé rank procedures were manually performed. Richness, or number of taxa, and dominance concentration (Strong 2002b) were determined for each relevé. For the latter, a value of zero and one represent no and maximum abundance concentration, respectively. Constancy was defined as the percent occurrence of a taxon among relevés.

Results

Northern range sociations

A total of 100 relevés were compiled between 61.592–63.574°N latitude and 133.524–136.633°W longitude at elevations ranging from 517–919 m. Sampling was conducted between 17 Jun and 21 Jul 2012. On average, plots occurred 695 m (maximum 3450 m) from a road. Total tree canopy cover ranged from 22–80% (average 49%). *Pinus contorta* had an average cover of 34%. *Picea albertiana* and *P. mariana* were of secondary abundance and occurred in all vegetation strata (Table 1). *Pinus contorta* trees reached 21 m in height. Maximum basal diameter was 30 cm, but typically ranged from 15–21 cm based on first and third quartile values. Stands ranged from 19 to 196 years old. Floristic richness among relevés totalled 95 taxa.

Five *P. contorta* sociations were recognized among northern stands. Each differed (p < 0.05) from the others based on one or more understory taxa (Table 1). The *P. contorta//Rhododendron groenlandicum–Vaccinium vitis-idaea–Hylocomium splendens* sociation was distinguished by the large proportion of cover and high constancy of *R. groenlandicum* and *V. vitis-idaea* (bog cranberry) in the low shrub and herb stratum. The abundance of *H. splendens* also differentiated it from all except the *P. contorta–Picea* spp.//*H. splendens–Peltigera aphthosa* sociation (Table 1). The distinctive composition of the *P. contorta//R. groenlandicum–V. vitis-idaea–H. splendens* sociation was reflected in the segregation of its relevés from other sociations in ordination space (Fig. 2). In addition, the sociation had the greatest percentage of total plant and total understory vascular plant cover, and possibly the lowest degree of dominance concentration among taxa. It, however, had the same floristic richness (range 16–19 per relevé) as the three other commonly occurring sociations (Table 1).

The *Pinus contorta–Alnus viridis* sociation was distinguished by its large proportion of *A. viridis* ssp. *crispa* (green alder) with a height of 2.5–5.0 m, and a poorly developed low shrub and herb stratum (average 11% cover). This unique composition isolated *P. contorta–Alnus viridis* relevés from others in Fig. 2. Floristic richness appeared to be relatively low compared to the other sociations, whereas dominance concentration was likely greater (Table 1). Tree densities averaged 2241 stems ha^{-1}. This density was similar to the *P. contorta–Picea* spp.//*V. vitis-idaea–Cladonia arbuscula* sociation, which had the lowest densities among the four Kruskal–Wallis compared types. However, *P. contorta* tree canopy cover was similar to most of the other sociations (Table 1). The *P. contorta–A. viridis* sociation was relatively uncommon in the study area based on the few stands that were found for sampling (n = 4).

The *Pinus contorta–Picea* spp.//*Vaccinium vitis-idaea–Cladonia arbuscula* sociation had a more open tree canopy and a greater abundance of terrestrial macro-lichens than the other sociations (Table 1). Lichens had an average cover of ~45%, with *Cladonia arbuscula* ssp. *mitis* (green reindeer lichen) composing the largest portion (Table 1). *Calamagrostis purpurascens* (purple reedgrass) was the only high constancy vascular species in the low shrub and herb stratum, but had little canopy cover (average 3%). Tree densities were among the lowest and *P. contorta* trees were on average > 47 years older than the other sociation (Table 1). Most of the older trees had a large fire scar on their lower trunk.

Pinus contorta//Calamagrostis purpurascens understory vegetation was dominated by a modest cover of *C. purpurascens*. Other herbs and low-growing shrubs also occurred, but all had moderate to low constancy. *Peltigera* spp. (dog tongue lichens) and *H. splendens* were the most consistently occurring taxa. Among sociations, the *P. contorta//C. purpurascens* type had the least amount of total plant and nonvascular plant cover (Table 1). *Pinus contorta//C. purpurascens* relevés were separated in ordination space from the *R. groenlandicum-* and *C. arbuscula-* dominated understory types (Fig. 2).

Hylocomium splendens in conjunction with *Peltigera aphthosa* (studded dog tongue lichen) were the most

Table 1. Plant composition by stratum, stand characteristics and site conditions of *Pinus contorta* var. *latifolia* (lodgepole pine) sociations at their northernmost ecological extreme in North America. See acronyms in variable list for the taxa that form each sociation name.

Variable[a]	Sociation[b]					p-value
	PICO// RHGR– VAVI– HYSP	PICO– ALVI	PICO– PIC// VAVI– CLAR	PICO// CAPU	PICO– PIC// HYSP– PEAP	
Number of relevés	15	4	11	21	49	
Tree stratum (>2.5 m tall)	Average percent cover [standard deviation] constancy[c], Scheffé rank test result					
Pinus contorta var. *latifolia* [PICO][b]	36[8]10b[d]	37[6]10	24[9]10a	38[5]10b	34[7]10b	<0.001
Alnus viridis ssp. *crispa* [ALVI]	8[16]4a	60[18]10	+[+]1a[e]	+[+]+a	2[5]2a	0.027
Picea albertiana [PIC]	3[3]7a	5[7]7	8[7]9a	3[4]8a	9[10]4a	0.009
Picea mariana [PIC]	6[8]7ab	1[2]5	6[7]7ab	2[3]4a	11[14]8b	0.015
Salix bebbiana	1[1]1	9[14]7	+[+]2	1[2]5	1[2]4	0.192
Tall shrub stratum (1.0–2.5 m tall)						
Alnus viridis ssp. *crispa*	+[1]1	3[4]5	0	0	+[+]+	0.1
Picea albertiana	1[1]3	+[1]2	2[2]5	1[1]4	1[1]4	0.527
Picea mariana	2[6]3ab	0	1[2]4b	+[+]1ab	3[5]6a	<0.001
Low shrub and herb stratum (<1 m tall)						
Alnus viridis ssp. *crispa*	0	2[3]7	0	0	+[+]+	0.585
Calamagrostis purpurascens [CAPU]	1[2]5a	+[+]2	3[3]9a	16[9]9b	2[5]5a	<0.001
Geocaulon lividum	3[4]a	0	4[5]5a	1[2]1a	2[5]4a	0.027
Linnaea borealis	1[1]6	+[+]5	1[2]4	4[5]7	2[3]8	0.053
Picea albertiana	+[+]3ab	2[3]7	2[2]7b	1[2]4ab	+[+]2a	0.002
Picea mariana	4[9]5a	3[2]7	+[1]3a	+[+]+a	2[4]5a	0.004
Rhododendron groenlandicum [RHGR]	26[14]10b	1[1]5	1[3]3a	+[+]1a	1[2]2a	<0.001
Rosa acicularis	+[+]3	2[4]5	+[1]4	2[2]6	1[2]3	0.091
Vaccinium vitis-idaea [VAVI]	27[12]10b	+[+]10	9[11]7a	4[7]5a	8[12]7a	<0.001
Cetraria ericetorum	0a	0	+[+]5a	+[+]4a	+[+]2a	0.004
Cladonia arbuscula ssp. *mitis* [CLAR]	3[3]9a	+[+]2	27[15]10b	+[1]5a	2[5]8a	<0.001
Cladonia amaurocraea	+[+]1a	0	1[3]8b	+[+]1a	+[+]2a	<0.001
Cladonia cornuta	+[+]1a	0	+[+]4a	+[+]3a	+[1]5a	0.038
Cladonia gracilis ssp. *turbinata*	+[+]3a	+[+]5	0a	+[+]7a	+[1]6a	0.037
Cladonia phyllophora	0a	+[+]5	+[1]2a	+[+]+a	+[+]4a	0.014
Cladonia spp.	+[+]2a	+[+]7	3[5]8b	+[+]7ab	+[+]5ab	<0.001
Flavocetraria cucullata	+[+]3a	+[+]2	3[5]8b	+[+]4a	+[+]5a	<0.001
Dicranum acutifolium	+[+]1	+[1]5	+[+]4	0	+[+]	0.073
Hylocomium splendens [HYSP]	43[21]10b	8[7]10	3[6]7a	2[3]7a	33[27]10b	<0.001
Peltigera aphthosa [PEAP]	6[6]9ab	+[+]5	3[4]7ab	2[3]7a	6[7]10b	0.005
Peltigera malacea	+[1]3a	+[+]2	4[6]6a	2[2]6a	1[2]4a	0.012
Pleurozium schreberi	12[14]7b	0	2[5]4a	+[+]1a	1[1]4a	<0.001
Stand characteristics	Average [standard deviation] Scheffé rank test results					
Total plant cover (%)	190[32]c	139[13]	113[31]ab	89[14]a	133[35]b	<0.001
Total tree (>2.5%) canopy cover (%)	45[8]ab	46[4]	38[13]a	44[4]a	56[12]b	<0.001
Total vascular plant cover (%)	124[24]b	130[7]	63[27]a	79[14]a	86[18]a	<0.001
Total nonvascular plant cover (%)	66[26]b	9[6]	49[18]b	10[8]a	47[28]b	<0.001
Total understory vascular plant cover<1 m tall (%)	67[22]b	11[5]	22[19]a	33[14]a	23[19]a	<0.001
Average number of taxa per relevé	16[4]	14[2]	19[2]	18[3]	18[4]	0.097
Number of vascular taxa per relevé	10[3]	9[1]	8[3]	10[2]	9[2]	0.147
Dominance concentration (*Dw*)	0.53[0.08]a	0.66[0.09]	0.58[0.08]a	0.60[0.06]a	0.60[0.06]a	0.013
Stand age (years)	76[29]bc	63[12]	123[41]c	53[15]a	73[25]b	<0.001
Tree dense (stems ha^{-1}×100)	31.6[17.5]ab	22.4[7.6]	23.7[15.7]a	38.5[27.6]ab	51.0[34.5]b	0.005
Tree height (m)	15.0[2.4]	16.5[0.5]	14.9[2.7]	13.7[3.4]	15.2[2.4]	0.271
Tree basal diameter (cm)	13[3]	16[1]	13[3]	11[4]	11[4]	0.108
Typical site conditions						
Compass bearing when >5% slope gradient (degrees)	variable	variable	150–222[f]	150–270[f]	variable	–
Slope gradient range when >5% (%)	10–30	10–20	8–20	10–45	8–50	–
Percent of relevés with ≤5% slope gradient	67	50	36	52	45	–
Soil drainage class	well–moderate	well– moderate	well	well	well	–
Moisture regime class	submesic– mesic	submesic– mesic	subxeric– submesic	submesic – subxeric	submesic	–
Nutrient regime class	poor	moderate	poor	poor	poor	–

Notes: comparisons based on Kruskal–Wallis tests. *Pinus contorta–Alnus viridis* sociation excluded from analysis due to small samples size.
[a]includes only plant taxa with >45% constancy in at least one sociation.
[b]see acronyms in list of variables for the scientific name of taxa. Taxa acronyms are in brackets, e.g. [PICO].
[c]constancy classes (%): +[≤5]; 1[6–15]; 2[16–25]; 3[26–35]; 4[36–45]; 5[46–55]; 6[56–65]; 7[66–75]; 8[76–85]; 9[86–95]; and 10[96–100].
[d]sociations followed by the same letter do not differ at the ∝0.05 level based on Scheffé rank tests.
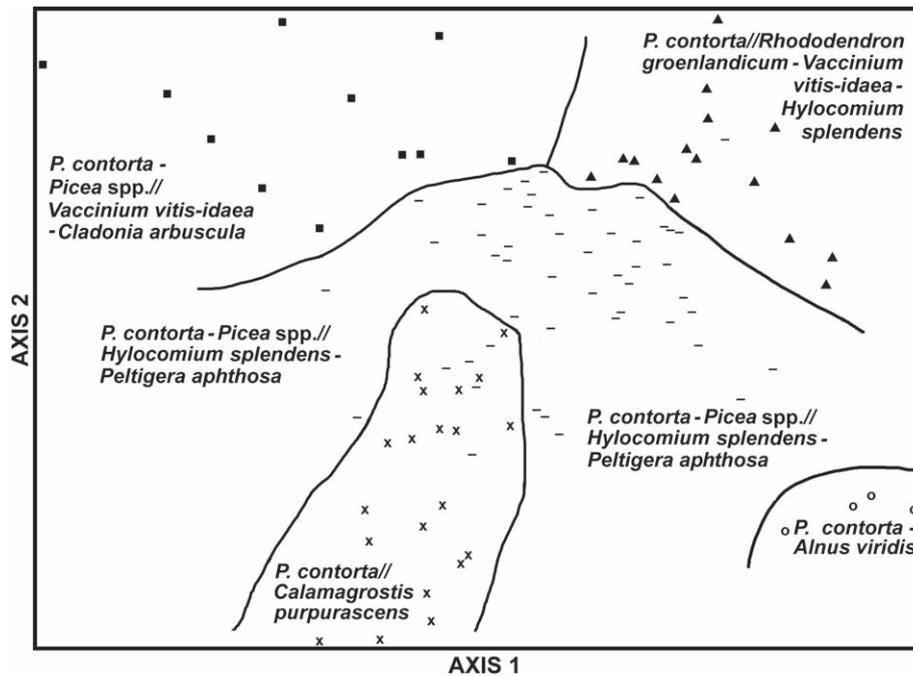[e]'+' represents a value ≤0.55.
[f]values presented in clockwise order.

Figure 2. An ordination of northern *Pinus contorta* var. *latifolia* relevés (lodgepole pine, n = 100) based on detrended correspondence analysis. Lines delineate spaces where occurrences of sociation relevés were most concentrated. Taxa composition explained 48% of the variance in relevé locations on axis 1 and axis 2, with a third axis explained an addition 11%.

consistently occurring understory taxa in the *Pinus contorta–Picea* spp.//*Hylocomium splendens–Peltigera aphthosa* sociation. Their combined cover averaged 39%. Understory vascular plant cover totalled 23%, with *V. vitis-idaea* and *Linnaea borealis* (twinflower) the most constant species, but they had low cover (Table 1). Tree stems were 24% to 56% denser and stands contained more *P. mariana* cover than the other sociations. *Pinus contorta–Picea* spp.//*H. splendens–P. aphthosa* relevés occurred between the other sociations in ordination space, with some intermingling along margins (Fig. 2). The degree of overlap with the *P. contorta*//*C. purpurascens* sociation was less than suggested in Fig. 2, when viewed in three-dimensional ordination space. *Pinus contorta–Picea* spp.//*H. splendens–P. aphthosa* vegetation was the most sampled sociation within the northern dataset.

Northern sociation site conditions

The number of sampled *P. contorta* stands on south (n = 35), north (n = 15), and ≤ 5% gradient (n = 50) sites differed from the expected proportions (G-test = 6.77, p = 0.034), with ≤ 5% gradient slopes deviating most from an expected value of 37.3. *Pinus contorta* occurrences on both north and south slopes were either equal to or less than expected. The *P. contorta*//*R. groenlandicum–V. vitis-idaea–H. splendens* sociation was proportionally most common on low gradient sites, but the *P. contorta–Picea* spp.//*H. splendens–P. aphthosa* sociation occurred most frequently (Table 1). The *P. contorta–Picea* spp.//*V. vitis-idaea–C. arbuscula* and *P. contorta*//*C. purpurascens* sociations were associated with south aspects (91–270°) when slopes exceeded a 5% gradient (n = 7 of 7 and 9 of 10 stands, respectively). The

other sociations had similar proportions of north and south slopes.

Site conditions did not substantially differ among sociations (Table 1). About three-fourths of sites had Eluviated Eutric Brunisolic soils, although confirmation of a continuous ≥ 2 cm thick Ae horizon was sometimes complicated by the presence of several centimeters of ash-colored White River tephra at the top of the solum. The remaining stands were classified as Orthic Eutric Brunisols (i.e. < 2 cm Ae horizon). The proportion of Orthics was similar among sociations. Most sites had well drained soils, with a submesic moisture regime, although the *P. contorta*//*R. groenlandicum–V. vitis-idaea–H. splendens* and *P. contorta–A. viridis* sociations sometimes occurred on sites trending toward a mesic moisture regime. Members of the *P. contorta*//*V. vitis-idaea–C. arbuscula* sociation had subxeric moisture regimes due to their occurrence on deep sand deposits compared to less coarse-textured substrates (e.g. loams and finer sands) than were found with the other sociations. Except for members of the *P. contorta–A. viridis* sociation, all sites were considered to have poor nutrient regimes. Hemimors or humus forms with little or no integration of organic matter into the upper mineral soil horizon were characteristic of the five sociations. Seventy-four percent of all sampled sites occurred in the NCb ecoclimatic region, with 18–28% of each sociation from the NCh region.

Northern versus central range

Central range relevés occurred in the Upper Boreal–Cordilleran (37%), Subalpine (33%), Lower Boreal–Cordilleran (24%), and Montane (6%) ecoclimatic regions

(Strong 1992). When simultaneously ordinated, northern relevés were positioned to one-side of those from central range in the three-dimensional ordination space. This displacement was best illustrated along axis 2 and axis 3 of the ordination (Fig. 3). Four of the 100 northern relevés occurred in the fringe of the central range relevé loci swarm (n = 1394). These overlapping relevés were members of the *P. contorta–Picea* spp.//*H. splendens–P. aphthosa* (n = 2) and *P. contorta*//*R. groenlandicum–V. vitis-idaea–H. splendens* (n = 2) sociations. Taxa (n = 246) composition and abundance explained 36% of the variation in loci location among ordinated relevés. All taxa with ≥1% cover in northern relevés (n = 56) occurred among central range relevés.

Pleurozium schreberi (Schreber's moss), *Linnaea borealis*, and *Cornus canadensis* (bunchberry) had the highest constancy (>80%) among central range taxa, whereas *P. schreberi* (average 27% cover), *H. splendens* (12% cover), and *Ptilium crista-castrensis* (knight's plume, 11% cover) were the most abundant species. In comparison, *H. splendens* (83% constancy), *P. schreberi* (76% constancy) and *V. vitis-idaea* (60% constancy) were the most consistently occurring species among northern *P. contorta* relevés, with *H. splendens* (24% cover) and *V. vitis-idaea* (11% cover) the most abundant. Cover and constancy values for less abundant taxa are not presented.

Total plant cover averaged 184% among central range relevés, but only 129% in those from the northern portion of the range. Relative to the central range, northern *P. contorta* stands contained on average less deciduous shrub, broad-leaved herb (forbs and ferns), and bryophyte
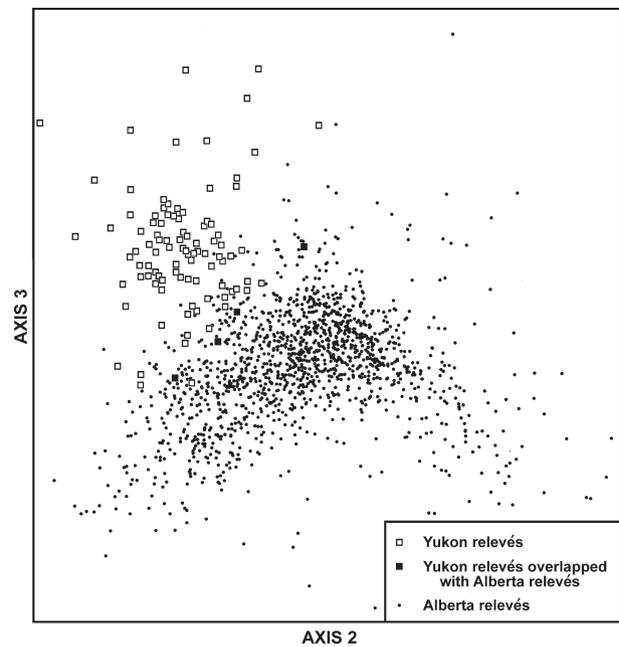

Figure 3. An ordination of 100 northern and 1394 central range *Pinus contorta* var. *latifolia* (lodgepole pine) relevés using detrended correspondence analysis. Axis 2 and axis 3 best illustrated the compositionally-based separation of the two datasets.

cover (Table 2, column A vs B), but greater fruticose and foliose lichen cover (i.e. 12.9% vs 5.2%). Total tree species cover was greater, evergreen shrub cover was less, and

Table 2. Percent canopy cover and taxa richness by growth form in the northern and central portions of the *Pinus contorta* var. *latifolia* (lodgepole pine) range east of the Rocky Mountains in western North America.

Variable	Northern range (61.5–64.0°N)	Central range (52.5–55.5°N)		p-value	
Number of relevés	100	1394	176		
	Average percent cover [standard deviation]				
All plants	(A)	(B)	(C)[a]	A vs B	A vs C
Trees	128.6 [43.1]	184.1 [61.3]	168.3 [40.6]	<0.001	<0.001
Deciduous shrubs	54.5 [16.8]	49.6 [17.2]	41.3 [9.6]	<0.001	<0.001
Evergreen shrubs	9.3 [17.2]	26.0 [23.4]	28.5 [21.7]	<0.001	<0.001
Graminoids	15.0 [20.9]	18.4 [21.2]	14.5 [15.1]	<0.001	0.036
Broad-leaved herbs	5.3 [8.0]	5.8 [9.6]	8.8 [11.3]	0.084	0.002
Bryophytes	4.8 [5.4]	25.0 [22.3]	27.1 [23.3]	<0.001	<0.001
Macro-lichens	26.8 [28.4]	54.0 [33.8]	44.9 [33.2]	<0.001	<0.001
Dominance concentration (*Dw*)	12.9 [14.6]	5.2 [9.0]	3.1 [6.7]	<0.001	<0.001
	0.47 [0.07]	0.52 [0.09]	0.48 [0.09]	<0.001	0.960
	Average number of taxa per relevé [standard deviation]				
All taxa	11.2 [2.7]	24.2 [10.4]	16.9 [5.1]	<0.001	<0.001
Trees	3.0 [0.7]	2.5 [1.0]	1.9 [0.8]	<0.001	<0.001
Deciduous shrubs	1.2 [1.0]	3.9 [2.2]	2.9 [1.3]	<0.001	<0.001
Evergreen shrubs	1.1 [0.9]	2.5 [1.4]	1.9 [1.1]	<0.001	<0.001
Graminoids	0.6 [0.6]	1.0 [0.8]	0.9 [0.7]	<0.001	<0.001
Broad-leaved herbs	1.1 [0.9]	7.2 [4.9]	5.3 [3.6]	<0.001	<0.001
Bryophytes	1.4 [0.9]	4.3 [2.7]	2.9 [1.3]	<0.001	<0.001
Macro-lichens	2.6 [2.0]	2.8 [3.4]	0.9 [1.0]	0.012	<0.001

Notes: data include only taxa with 1% or more canopy cover within individual relevés. Probability value (p) from pair-wise comparisons by Mann–Whitney U-tests.
[a]a subset of column B relevés with the same or very similar plot sampling design as used for column A (i.e. standardized design). Column B relevés sampled using various designs (i.e. mixed design).

graminoid cover was the same in northern and central range relevés (Table 2). Although northern and central range relevés had a similar intermediate level of dominance concentration, those in the central range had a slightly greater degree of concentration (Table 2). No significant difference in dominance concentration occurred between datasets that employed the standardized sampling design (Table 2, A vs C). An average of 11 and 24 taxa occurred in northern and central range relevés, respectively. Individual plant growth forms in northern relevés were less floristically rich than those in central range, except for trees taxa (Table 2). The greatest differential in growth form richness between the northern and central datasets was with broad-leaved herbs.

Where large differentials in growth form cover occurred between the northern and central range datasets that involved mixed sampling designs (Table 2, A vs B), a similar difference also occurred between relevés sampled using the standardized plot design (Table 2, A vs C). Differentials were typically greater for the mixed than the standardized sampling design. One notable exception was lesser macro-lichen richness in the standardized central range dataset (Table 2, cf. B and C).

Discussion

Data constraints

There were plot design differences and related issues that could have biased the comparison of northern and central range relevés. These included different plot and quadrat sizes, and configurations; different intensities of understory subsampling (Kenkel and Podani 1991, Jalonen et al. 1998, Keeley and Fotheringham 2005); overlooked taxa and inconsistencies in canopy cover estimations (Helm and Mead 2004, Milberg et al. 2008); and different levels of sampling effort among individual field observers. Where major deviations in growth form abundance occurred (Table 2), however, the direction and the magnitude of the differential were similar whether based on mixed sampling designs that involved > 30 botanists, or based on a sampling design comparable to that used in the northern range (i.e. standardized) with cover assessments essentially by one botanist. Therefore, divergences in growth form abundances between two portions of the range were more likely a function of ecology rather than sampling design or degree of sampling effort.

Cover differences between the mixed and standardized central range sampling designs were likely related to broad botanical differences among included macro-ecosystems in each dataset. Standardized central range relevés were sampled in the Upper Boreal–Cordilleran and Subalpine ecoclimatic regions, whereas the mixed designs also included relevés from the Lower Boreal–Cordilleran and Montane ecoclimatic regions (Strong 1992). The two latter regions occurred at lower elevations and had warmer climates than the two former. Therefore, the lower areas had a greater potential for more robust and floristically-diverse forest understory vegetation, chiefly more deciduous shrubs and broad-leaved herbs. The inclusion of only taxa with ≥ 1% cover in individual relevés (cf. Vittoz and Guisan 2007) and analyses by rank-order (i.e. Mann–Whitney U-tests) rather than by cover values (e.g. by t-tests) likely reduced the importance of plot sampling intensity and inconsistencies in cover estimation among observers. Therefore, most differences in growth form abundances between the northern and central ranges were too great (i.e. 0.4–5.2 ×) to just represent sampling error. Differences in plot sizes among northern and central range relevés (Fig. 3) were not expected to have a substantial influence on ordination results, because 75% of plots were of a similar size (500 ± 100 m^2) and they exceeded a 300 m^2 affect-threshold (Otýpková and Chytrý 2006).

The previously identified plot design and sampling issues have greater implications for assessing taxa richness than cover abundance differences, because richness is known to vary with the amount of surveyed area and the intensity of sampling. Inclusion of only taxa with ≥ 1% cover would reduce the importance of plot size and sampling intensity; however, the small but statistically significant differences in taxa richness between the northern and central portions of the range should be viewed with caution.

Northern sociations

Although ordination (Fig. 3) showed that northern *P. contorta* relevés were compositional different from those in the central range, northern sociations were similar to community types reported in other localities. The composition and structure of the *P. contorta*//*R. groenlandicum*–*V. vitis-idaea*–*H. splendens* sociation approximated the *P. contorta*/*Ledum groenlandicum* [= *R. groenlandicum*]/*V. vitis-idaea*/*P. schreberi* type described by Strong (2002a, pp. 156–158), although with reduced *P. schreberi* and *P. crista-castrensis* cover. It also most closely approximated climatic reference vegetation for the Northern Cordilleran Boreal (NCb) ecoclimatic region (Strong 2013), based on its presence on low gradient submesic–mesic sites that more strongly reflected the influences of regional climate than local site conditions (Ecoregions Working Group 1989, p. 1). However, this sociation was probably associated with slightly cooler sites than the *P. tremuloides*–*P. albertiana*/*Shepherdia canadensis* climatic reference type for the NCb region (Strong 2013), based on the former's occurrence at higher elevations on low gradient sites (median 646 m, n = 50 versus 598 m, n = 100, Strong 2009), Mann–Whitney U-test, p = 0.002).

Why *Pinus contorta*–*A. viridis* communities formed was unclear, in part, because of too few samples. The presence of a tall shrub stratum suggested warmer and somewhat moister site conditions than associated with the other sociations. Oswald and Brown (1986, p. 52) recognized a similar plant community on comparable site conditions, but provided no obvious clues to its particular synecology.

The *P. contorta*–*Picea* spp.//*V. vitis-idaea*–*C. arbuscula* and *P. contorta*//*C. purpurascens* sociations represented edaphic vegetation associated with coarse-textured dry soils and warm dry sites, respectively. Plant communities with understory vegetation similar to the *P. contorta*–*Picea* spp.//*V. vitis-idaea*–*C. arbuscula* sociation were reported in

southern Yukon (Lipovsky and McKenna 2005, G3B-P type), northern (Annas 1977) and central British Columbia (Coxson and Marsh 2001). At ecological climax, the *Cladonia*-dominated understory vegetation would likely persist in conjunction with open-growing *P. albertiana* (Kojima 1996), unlike the other sociations with a ground cover of feathermosses such as *H. splendens* or *P. schreberi*. No reports of the *P. contorta*//*C. purpurascens* sociation were found outside Yukon.

Stands of the *P. contorta*//*H. splendens–P. aphthosa* sociation were interpreted as having understory vegetation that developed in response to an atypically dense overstory. A dense tree canopy reduces the quantity of photosynthetically active radiation that reaches the forest floor, thereby eliminating shade-intolerant and minimizing semi-shade tolerant vascular plants, which favors bryophyte development. Based on a review of individual *P. contorta*//*H. splendens–P. aphthosa* relevés, it appears that some members of this sociation would have been part of the *P. contorta*//*C. purpurascen*s or the *P. contorta*//*R. groenlandicum–V. vitis-idaea–H. splendens* sociations, if not for the overly dense overstory. The *P. contorta*/feather moss type (UFe.5 ecosite) recognized by Beckingham et al. (1996) was similarity to the *P. contorta*//*H. splendens–P. aphthosa* sociation.

Biodiversity

Pinus contorta-dominated stands at their northernmost geographical limit had lower total plant cover and taxa richness, differed in their overall taxa composition, and differed substantially in understory vegetation growth forms relative to the central portion of the range. These botanical differences were probably part of an ecological continuum rather than an abrupt change in plant community composition. This gradient was likely a response to the cooling and shortening of the growing season with increasing latitude. The most distinctive differences in botanical composition included a reduction in the amount of deciduous shrub, broad-leaved herb, and bryophyte cover in northern stands. *Pinus contorta* understory vegetation in the central range included species such as *Viburnum edule*, *Rosa acicularis* (wild rose), *Shepherdia canadensis*, *Chamerion angustifolium* (fireweed), *Mertensia paniculata* (bluebell), and *Cornus canadensis* (Beckingham et al. 1996). These species also occurred in northern *P. contorta* relevés, but were typically minor components. The reduced abundance of deciduous shrubs and broad-leaved herbs might be attributable to their sensitivity to a colder and more arid northern climate, and possibly greater light attenuation than more southern stands (Lappi and Stenberg 1998, Strong 2011). However, the reduced abundance of bryophytes among northern stands was more difficult to explain, but may also be related to reduced moisture availability (e.g. median 539–464 mm [central range, Strong 1992] versus 324–279 mm [northern range, Strong 2013] of annual precipitation).

Northern *P. contorta* vegetation appeared less phytosociologically diverse than its central range. As examples, La Roi and Hnatiuk (1980) reported five sociations along 180 km of road based traverse in Jasper National Park, which was less than one-third the distance used in the northern range (~ 612 km). As well, a total of 22 *P. contorta* sociations were recognized among five studies (Supplementary material Appendix 1 – Strong 1996, 1999a, 1999b, 2001, 2005) located immediately east of Jasper National Park in the Subalpine and Upper Boreal–Cordilleran ecoclimatic regions of the central range. These studies had a combined area of 220 km². If northern range plots occurred on average within 0.7 km of an accessible road, the studied area represented 857 km², but with only five recognized sociations. Similarly poor phytosociological diversity was also evident in a plant community classification developed by Oswald and Brown (1986) in south–central Yukon. In their study, 16 sociation-equivalent *P. contorta* types were recognized within 34 180 km² (note: at least one-third of the landscape in their study area consisted of alpine and subalpine ecosystems that lacked forest vegetation). Although the comparison of plant community diversity among studies was complicated by the difficulty of determining the amount of studied area, the diversity of sociations near the northernmost distributional limit of *P. contorta* appeared much less than half that of its central range.

Potential northern range expansion

The common occurrence of *P. contorta* on sites with ≤ 5% gradients (i.e. reflective of the regional climate) and north exposures (i.e. cold sites compared to south slopes) implied that the local climatic conditions was not sufficiently rigorous to restrict stand occurrences mostly to warmer south-facing slopes in the northern range (i.e. proposed hypothesis rejected, see introduction). The general occurrence of stands on low gradient sites also supported the interpretation by Johnstone and Chapin (2003) that ecological potential exists for range expansion under the current climatic regime. However, the extensive occurrence of shade-tolerant and self-perpetuating *Picea albertiana* forests on most upland sites at the margins of the range will likely inhibit actual outward migration of shade-intolerant and fire-dependent *P. contorta* at present. No studies have been conducted in the northern range to estimate the current fire-return interval. Drury and Grissom (2008), however, determined a ~ 90 ± 32 year fire-return interval in the Yukon Flats National Wildlife Refuge of eastern–central Alaska, which is located northwest of the study area. Both areas have boreal forest vegetation and a substantial early summer climatic moisture deficit (Jätzold 2000), therefore, possibly similar fire-return intervals at least in lower elevation terrain. In comparison, fire-return intervals ranged from 113–226 (average 172) years in the boreal forest portions of Kluane National Park (Yukon), southwest of the study area, when all fire sources were considered (Hawkes 1983, p. 45). Both the Yukon Flats and Kluane area had longer return-intervals than the boreal–cordilleran portion of the central *P. contorta* range (median ≤ 67 years, Amoroso et al. 2011). Among different future climate warming scenarios, McCoy and Burns (2005) determined that central Yukon fire frequencies and the average annual amount of burned area would likely double relative to current levels by 2069. Although doubling the amount of

annual burning would encompass only ~0.6% of the landscape, these fires might be disproportionately concentrated in warmer and drier areas at low elevations (cf. Jätzold 2000), where *P. contorta* primarily occur. Under such circumstances, *P. contorta* might be able to increase its within range density. If outward migration occurs, northward migration would likely be blocked by the cold higher elevation climates of the Mackenzie Mountains (cf. Strong 2013), with some expansion to the northeast into east-central Yukon. More rapid and extensive expansion would more likely occur northwest of the study area at lower elevations into east–central Alaska (Fig. 1).

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