Journal of Ecology

Forest response to permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland

Journal:	*Journal of Ecology*
Manuscript ID	Draft
Manuscript Type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Dearborn, Katherine; Wilfrid Laurier University, Biology Wallace, Cory; Wilfrid Laurier University, Geography and Environmental Studies Patankar, Rajit; Wilfrid Laurier University, Biology; National Ecological Observatory Network Baltzer, Jennifer; Wilfrid Laurier University, Biology
Key-words:	Plant population and community dynamics, active layer, boreal forest, eastern larch, black spruce, ForestGEO, organic layer thickness, peatland, permafrost

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1   **Title:** Forest response to permafrost thaw is strongly mediated by organic layer thickness

2   in a boreal peatland

3

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14

15   **Abstract**

16

17   1. Boreal peatlands are frequently underlain by sporadic or discontinuous permafrost,

18   which is thawing rapidly. A common ecological response to thaw is the conversion of

19   raised forested plateaus to treeless wetlands, but unexplained spatial variation in

20   responses, combined with a lack of stand-level data make it difficult to predict future

21   trajectories of boreal forest composition and structure.

22   2. We sought to characterize patterns and identify drivers of forest structure, composition,

23   mortality, and recruitment in a boreal peatland experiencing permafrost thaw. To do this,

24   we established a large (10 ha) permanent forest plot (completed in 2014), which includes

25   40,584 mapped and measured trees. In 2018, we conducted a comprehensive mortality

26   and recruitment recensus. We also measured frost table depth, soil moisture, soil

27   humification, and organic layer thickness within the plot between 2012 and 2018, and

28   used habitat association tests to link these variables to forest characteristics and

29   dynamics.

30   3. Forest composition and structure varied markedly throughout the plot and were

31   strongly governed by patterns in permafrost presence and organic layer thickness.

32   Overall, there was a net loss of trees from the plot at a rate of 0.7% yr^{-1}. Mortality of

33   black spruce, the dominant tree species, was more than double that of recruitment and

34   was strongly associated with rapid permafrost thaw and thick organic soils. In contrast,

35   recruitment of larch was over four times greater than mortality, and occurred primarily in

36   low-lying, permafrost-free wetlands with surficial mineral soil.

37   4. Synthesis: The trends in tree demography and underlying drivers suggest that spruce-

38   dominated permafrost plateaus will be converted into larch-dominated wetlands as

39   permafrost thaw progresses in boreal peatlands, particularly in areas with surficial

40   mineral soil. In the longer term, thaw could increase the hydrologic connectivity of the

41   landscape, resulting in widespread drainage and re-vegetation by spruce, but we did not

42   find evidence that this is occurring yet. Given the increasing rates of permafrost thaw,

43   and positive feedbacks between thaw and forest change, we predict that larch abundance

44   will continue to increase in boreal peatlands over the coming decades, leading to shifts in

45   ecosystem function, wildlife habitat, albedo, and potentially snow dynamics.

46

47   **Keywords**

48

49   Active layer, boreal forest, eastern larch, black spruce, ForestGEO, organic layer

50   thickness, peatland, permafrost

51

52   **Introduction**

53

54   Boreal peatlands store vast amounts of carbon (Kurz et al., 2013; Tarnocai et al.,

55   2009) and provide critical habitat for wildlife (Bradshaw, Hebert, Rippin, & Boutin,

56   1995). They are also spatially extensive. The boreal forest is the second largest forested

57   biome in the world, and approximately 25-30% of it is composed of peatlands (Gorham,

58   1991). Boreal peatlands are characterized by poor drainage, sparse forest canopies, thick

59   organic soils (>40 cm), and the frequent presence of sporadic (10-50% coverage) or

60   discontinuous (50-90% coverage) permafrost (Helbig, Pappas, & Sonnentag, 2016;

61   National Wetlands Working Group, 1997). This permafrost plays a critical role in

62   governing hydrological and ecological processes (Baltzer, Veness, Chasmer, Sniderhan,

63   & Quinton, 2014; Connon, Quinton, Craig, & Hayashi, 2014). Near its southern limits, it

64   is relatively warm (near 0°C), making it vulnerable to rapid thaw with even minor

65   amounts of climate warming (Tarnocai, 2006). As a result, boreal peatlands are poised to

66   undergo rapid landcover change in the near future, and there is evidence that this change

67   is already underway (Helbig et al., 2016). Given these changes and the importance of

68   boreal peatlands as carbon stores, wildlife habitat, and to the livelihoods and cultures of

69   local inhabitants, understanding potential post-thaw forest trajectories is critical.

70

71   A frequent outcome of permafrost thaw in boreal peatlands is the conversion of

72 raised forested plateaus to treeless wetlands (Baltzer et al., 2014; Carpino, Berg, Quinton,

73 & Adams, 2018; Osterkamp et al., 2000; Vitt, Halsey, & Zoltai, 2000). Permafrost often

74 elevates the ground surface above the surrounding wetlands in these systems due to the

75 volumetric expansion of water as it freezes. These raised permafrost "plateaus" are well

76 drained and densely treed compared to the surrounding wetlands. As thaw progresses,

77 plateaus subside, resulting in local flooding and forest loss (Baltzer et al., 2014; Quinton,

78 Hayashi, & Chasmer, 2011). This process has accelerated in recent decades, reaching

79 rates as rapid as half a percent per year (Baltzer et al., 2014). However, trajectories of

80 forest response to thaw are not always consistent, and in some cases different tree species

81 have shown contrasting responses, leading to an increase in the dominance of one species

82 over another (Lara et al., 2016).

83

84   There are several abiotic and biotic factors that could be mediating forest response

85 to thaw, including organic layer thickness. Tree recruitment in boreal peatlands tends to

86 be higher when nutrient-rich mineral soils are near the surface (i.e. when organic layers

87 are thin) (Préfontaine & Jutras, 2017), suggesting that the benefits of higher nutrient

88 availability could counteract some of the mortality resulting from plateau subsidence and

89 flooding. It is also possible that plateaus underlain by mineral soil will experience less

90 subsidence and therefore undergo lower rates of forest loss, since they generally contain

91 less pore space (and therefore less frozen water) than permafrost composed of organic

92　　material, although the presence of ice lenses would result in rapid subsidence if/when the

93　　thaw front reaches these lenses.

94

95　　　　Species-specific nutrient and moisture requirements are also likely to affect

96　　trajectories of forest change. North American boreal peatlands typically consist of a

97　　combination of *Picea mariana* (black spruce), *Larix laricina* (eastern larch), and *Betula*

98　　*spp.* (birch) (Islam, Macdonald, & Zwiazek, 2003; Lara et al., 2016). Eastern larch is

99　　more flood-tolerant than black spruce (Islam & Macdonald, 2004; Montague & Givnish,

100　　1996), suggesting it may begin to replace black spruce as permafrost thaw proceeds.

101　　However, it is also more nutrient demanding (Islam & Macdonald, 2005), which could

102　　limit this process to nutrient-rich sites. Birch can be highly vulnerable to the effects of

103　　ground subsidence because it tends to be most abundant along plateau-wetland edges

104　　(Lara et al., 2016; Osterkamp et al., 2000). However, its rapid growth rate and propensity

105　　to reproduce vegetatively (Bret-Harte, Shaver, & Chapin, 2002) could give it a

106　　competitive edge over conifers when gaps form in the canopy.

107

108　　　　Due in part to the remote nature of boreal peatlands, forest response to permafrost

109　　thaw has primarily been quantified using remotely sensed imagery (Baltzer et al., 2014;

110　　Chasmer & Hopkinson, 2017; Helbig et al., 2016; Jorgenson et al., 2010). These methods

111　　can quantify land cover change across broad spatial extents, but cannot elucidate dynamic

112　　processes or differential responses of tree species (Baltzer et al., 2014; Helbig et al.,

113　　2016; Lara et al., 2016). A few studies have used dendrochronology to quantify growth

114　　responses to changing permafrost conditions (Sniderhan & Baltzer, 2016; Zhang, Bai,

115   Hou, Chen, & Manzanedo, 2019), but these methods cannot capture fine-scale

116   demographic dynamics. There is also a network of permanent forest plots in the

117   Northwest Territories (Gillis, Omule, & Brierley, 2005), but they exclude trees less than

118   5 cm in diameter (which are very common in peatlands), contain no spatial information,

119   and are small (400 m^2). Large forest dynamics plots provide an opportunity to examine

120   fine-scale spatial patterns in mortality and recruitment of individual species across local

121   gradients in edaphic conditions, thereby enhancing our understanding of warming-

122   induced landcover change (Anderson-Teixeira et al., 2015).

123

124   Pronounced variation in rates and trajectories of change, combined with a lack of

125   species-specific recruitment and mortality data at high latitudes make it difficult to

126   anticipate forest response to permafrost thaw in boreal peatlands. To address this

127   uncertainty, we used forest structure and dynamics data coupled with measurements of

128   key abiotic variables to characterize recent forest change in a unique 10-ha mapped forest

129   plot. The plot (established between 2012 and 2014) encompasses a mosaic of rapidly

130   thawing permafrost plateaus and permafrost-free wetlands, and traverses a strong

131   gradient in organic layer thickness. We asked: (1) How do forest structure, mortality, and

132   recruitment vary spatially and among species within this boreal peatland? (2) What are

133   the abiotic controls on forest composition, structure, mortality, and recruitment? (3) To

134   what extent has recent permafrost thaw driven mortality and recruitment of the dominant

135   species? Our results establish direct links between abiotic variables and fine-scale forest

136   dynamics, information that is necessary to improve predictions of future forest

137   composition and structure in permafrost peatlands.

138

139   **Materials and Methods**

140

141   *Study site*

142

143   The study site is located at Scotty Creek (61˚18'38" N, 121˚17'36" W), a 152 km^2

144   basin located approximately 50 km south of Fort Simpson, Northwest Territories. The

145   area is undisturbed boreal forest. Mean annual air temperature in Fort Simpson is -2.8˚C

146   and the total annual precipitation is 388 mm, approximately 60% of which falls as rain

147   (1981-2010 climate normals; Environment and Climate Change Canada). Permafrost in

148   the area is sporadic or discontinuous, which results in a mosaic of raised forested

149   permafrost plateaus, permafrost-free wetlands (ranging from nutrient-rich fens to

150   ombrotrophic bogs), and lakes (Quinton et al., 2011).

151

152   *Plot initiation and recensus*

153

154   An 800 m (east-west) by 120 m (north-south) forest plot was established between

155   2012 and 2014 as part of the Smithsonian Forest Global Earth Observatory (ForestGEO),

156   a global network of 61 methodologically identical permanent plots (Anderson-Teixeira et

157   al., 2015). These plots support spatially explicit investigations of forest dynamics across

158   local environmental gradients (Furniss, Larson, & Lutz, 2017; Harms, Condit, Hubbell, &

159   Foster, 2001) and comparative studies at the global scale (Allen et al., 2010; Chisholm et

160   al., 2014; Chu et al., 2018; Lutz et al., 2018). The Scotty Creek plot is the only boreal

161   forest plot in the network. It is the most northerly, experiences the most extreme (cold

162   and dry) climate and climate change, and has the second lowest woody biomass of all

163   plots (Anderson-Teixeira et al., 2015; Lutz et al., 2018). Elevation varies by less than two

164   meters within the plot, and relates strongly to permafrost conditions.

165

166   In 2012, 287 aluminum posts were installed at 20 m intervals throughout the

167   Scotty Creek ForestGEO plot using a GNSS receiver (Leica Viva GS10, Leica

168   Geosystems AG, Heerbrugg, CH) with differential correction via an on-site base station

169   (horizontal accuracy of 8 to 15 mm), dividing the plot into 240 20 m × 20 m grid cells.

170   Between 2012 and 2014, every live stem with a diameter at breast height (DBH; 1.3 m

171   height) ≥ 1 cm was tagged, measured, and mapped following standard ForestGEO

172   protocols (Condit, 1998). Stems were identified to species except in the case of shrub

173   species that exhibited high rates of introgressive hybridization (*Salix* and *Betula* spp.) and

174   were considered species complexes (Porsild & Cody, 1990). For *Salix* and *Betula* spp.,

175   identification was to genus except in the case of the tree form of *Betula neoalaskana*

176   Sarg., for which unhybridized trees were clearly identifiable. Multi-stemmed individuals

177   were common due to the high rates of clonal reproduction in shrub taxa. These

178   individuals were identified using a single numeric tag corresponding to the entire genet

179   and individual stems were uniquely identified within that genet using lettered tags.

180

181   In summer 2018, we conducted a complete mortality and recruitment recensus.

182   For each tree, we recorded its status (alive or dead). We recorded probable cause of

183   mortality for all dead stems; this included waterlogging (dead stem was either standing or

184   had fallen over in, or immediately adjacent to, fully saturated soil), falling over (stem fell

185   over from below breast height, likely due to blow-down, but was not located in or

186   immediately adjacent to standing water), physical damage (main stem snapped off above

187   breast height), browsing (evidence of heavy browsing), or biological/unknown (dead

188   stem was standing and cause of death was unknown, but likely attributable to fungal

189   decay, insect damage, or senescence). Finally, we tagged, measured, mapped, and

190   identified all new stems with DBH ≥ 1 cm as described for the original census, hereafter

191   referred to as "recruits".

192

193   *Abiotic variables*

194

195   We measured key abiotic variables at 20 m intervals throughout the plot (i.e.

196   adjacent to each of the 287 aluminum posts) between 2012 and 2018. We obtained

197   volumetric soil water content measurements from the top 5 cm of soil using TDR (time

198   domain reflectometry) probes (ThetaProbe, Delta-T Devices, Cambridge, UK, and

199   Stevens Hydra Probe, Stevens Water Monitoring Systems Inc., Oregon, US) on July 19,

200   2012. We subsequently adjusted these measurements using site-specific calibrations

201   (Warren, 2015). We also obtained soil moisture measurements from subsections of the

202   plot on two additional days in 2012, four days in 2013, and one day (at multiple depths)

203   in 2017. These repeated measurements correlated strongly with the July 19, 2012

204   measurements (Appendix 1). We therefore considered the July 19, 2012 measurements to

205   be representative of spatial patterns in soil moisture, and used them in all subsequent

206   analyses. We measured snow depth between March 21 and 26, 2013 using a GPS

207   automatic snow depth probe with ±5 cm accuracy (Snow-Hydro LLC, Fairbanks, US).

208   Finally, we measured organic layer thickness (using a 1.5 m auger), fibric layer thickness,

209   and peat humification at a depth of 5 cm (using the qualitative von Post scale; von Post,

210   1922) between August 5 and 8, 2018.

211

212   We measured frost table depth as depth to refusal using a 2 m steel rod on July 19,

213   2012 and August 5, 2018, and on multiple dates (May 27, May 31, and August 27) across

214   the westernmost 500 m of the plot in 2013. To quantify changes in frost table depth

215   between 2012 and 2018, we first adjusted the values to make them comparable, since

216   active layers were not measured at their seasonal maximums in either year due to logical

217   constraints of the remote field site. Full details of this adjustment are provided in

218   Appendix 2 but briefly, we used repeated thaw measurements from 2013 to determine a

219   seasonal rate of active layer development (in cm per thawing degree day). We used this

220   rate to extend the frost table measurements made in 2012 and 2018 to an equivalent

221   number of thawing degree days to make depths comparable (1855; the thawing degree

222   day accumulation on August 27, 2013).

223

224   Next we subtracted adjusted 2012 values from adjusted 2018 values at each

225   location and assigned a score to each point based on the amount of thaw that occurred

226   between years (0 = permafrost-free in both 2012 and 2018, 1 = 0-30 cm of thaw, 2 = >30

227   cm of thaw, and 3 = permafrost present in 2012, but not in 2018). A categorical variable

228   was necessary to differentiate between sites that had permafrost and had undergone no

229   change in thaw depth versus those that had no permafrost in 2012 or 2018 and similarly

230   had undergone no change. Next, we summed scores at the four corners of each grid cell

231   to generate an aggregate thaw severity score that ranged from 0 (no change; all four

232   corners were permafrost-free in 2012 and 2018) to a maximum of 12 (major change; all

233   four corners had permafrost in 2012, but not in 2018).

234

235   *Data analysis*

236

237   *Characterizing patterns in forest composition, structure, mortality and recruitment*

238

239   To quantify forest compositional and structural attributes of the plot, we

240   calculated stem density, basal area, and species richness in each 20 m x 20 m grid cell.

241   Hybridizing genera (*Betula* spp. and *Salix* spp.) were treated as single species, meaning

242   species richness is somewhat underestimated. We also tallied the number of mortality and

243   recruitment events for each species in each grid cell, and calculated overall rates of

244   mortality and recruitment (as percentages of initial stem counts) across all grid cells. We

245   included multiple stems produced by the same individual as separate stems in these

246   calculations because each stem is functionally distinct. However, we also performed

247   analyses at the genet level to ensure that our findings did not depend on treatment of

248   multi-stemmed individuals (see Appendix 3). All data manipulation and analyses were

249   performed in the R statistical platform (v. 3.2.1).

250

251   *Characterizing patterns in abiotic variables*

252

253   Since the six measured abiotic variables (soil moisture, active layer depth, organic

254   layer thickness, fibric layer depth, soil humification, and snow depth) covaried strongly,

255   we sought to summarize major gradients using principal components analysis (PCA). As

256   three of these variables were categorical (see Appendix 4) we used mixed PCA (package

257   PCAmixdata) (Chavant, Kuentz-Simonet, Labenne, & Saracco, 2017), which performs a

258   standard PCA on numeric variables, a multiple correspondence analysis (MCA) on

259   categorical variables, and then combines the two into a single ordination. Explained

260   variance dropped notably between the second and third PC, and the difference in

261   explained variance between each of the subsequent PCs did not exceed 2%, so we

262   extracted values of the first two principal components for each 20 m post for use in

263   further analysis. We then averaged the values from the four corner posts of each grid cell

264   to generate a mean value of each principal component for each grid cell.

265

266   *Testing for associations between abiotic variables and forest attributes/dynamics*

267

268   To test whether initial stems, deaths, and recruits of each of the dominant taxa

269   (*Picea mariana* (Mill.) Britton, Stems & Poggenburg, *Larix laricina* (Du Roi) K. Koch,

270   and *Betula* spp.) were significantly associated with the first or second principal

271   components, we used an adjusted habitat association test developed for use with

272   continuous environmental variables (Itoh, Ohkubo, Nanami, Tan, & Yamakura, 2010).

273   Specifically, we used a kernel density function to estimate the probability of initial stem,

274   death, and recruit occurrences of each of the dominant taxa across the full range of PC1

275   and PC2 values. Next, we used the same function to estimate the probability of

276   occurrence of PC1 and PC2 values. We then divided the former by the latter to generate

277   "adjusted" probabilities of initial stem, death, and recruit occurrence that took into

278   account the frequency of PC1 and PC2 values.

279

280   We extracted the mean PC1 and PC2 values from these adjusted distributions for

281   use as test statistics. Other studies have used the standard deviation or the value at

282   maximum probability as test statistics (Itoh et al., 2010), but we felt the mean would best

283   capture the affinity of initial stems/deaths/recruits for particular values of PC1 or PC2.

284   We then used torus translation to generate null distributions of PC1 and PC2 means. To

285   do this, we held the positions of initial stems/deaths/recruits constant and shifted the 20

286   m-resolution maps of PC1 and PC2 values in every combination of x and y directions

287   (preserving all spatial autocorrelation in the values), then flipped the original maps

288   vertically as well as horizontally and repeated each shift for a total of 960 shifts per PC

289   (calculating the mean PC value each time). Finally, we extracted the 2.5 and 97.5

290   percentiles of the resulting distributions of means and compared observed means to these

291   bounds.

292

293   *Testing for associations between permafrost thaw and forest dynamics*

294

295   Because of the importance of permafrost thaw in peatland landcover changes

296   (Baltzer et al., 2014), we sought to determine the extent to which thaw was driving forest

297   dynamics. We evaluated associations between mortality and recruitment of the dominant

298   taxa and thaw severity (represented by three categories of thaw severity scores: 0, 1-5,

299 and >5) using a categorical torus translation test (Harms et al., 2001). We also evaluated

300 associations between causes of *P. mariana* deaths (biological/unknown, falling/physical

301 damage, and waterlogging) and thaw severity using the same test. We restricted this last

302 analysis to *P. mariana*, since we did not find obvious evidence of waterlogging-induced

303 mortality in other taxa.

304

305 **Results**

306

307 *Spatial patterns in species composition, forest structure, and edaphic conditions*

308

309 The Scotty Creek ForestGEO plot is dominated in both stem density and basal

310 area by three common boreal species. In the initial census, *P. mariana* comprised 80.1%

311 of stems and was distributed throughout the plot, *L. laricina* made up 11.2% and occurred

312 mainly in the eastern half of the plot, and *Betula* spp. comprised 7.3% with high density

313 patches in the eastern and western ends of the plot. The remaining 1.4% of stems was

314 composed of *Salix* spp., *Alnus alnobetula* (Ehrh. K.Koch, *Picea glauca* (Moench) Voss,

315 and *Pinus banksiana* Lamb., all of which generally occurred in the eastern half of the plot

316 (Figs 1 & 2). Botanical nomenclature follows (Porsild & Cody, 1990)

317

318 *Salix* spp. (likely composed of *Salix glauca* L., *Salix planifolia* Pursh, *Salix*

319 *bebbiana* Sarg., *Salix pyrifolia* Andersson, *Salix serissima* (L.H. Bailey) Fernald, and

320 their hybrids) and *A. alnobetula* are shrub species, while *P. mariana*, *L. laricina*, *P.*

321 *glauca*, and *P. banksiana* are trees with very few records of multi-stemmed individuals.

322   *Betula* spp. were predominantly shrub species (likely composed of *Betula occidentalis*

323   Hook., *Betula glandulosa* Michx., *Betula pubescens* Ehrh., *Betula pumila* L., and their

324   hybrids). The exception was *B. neoalaskana*, which is characterized by tree form, but

325   hybridizes with *Betula* spp. shrubs as well. Tree and shrub stems were very small, with

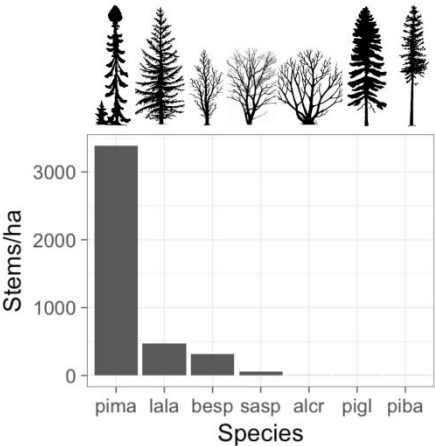326   73% of tree stems less than 5 cm DBH, and 89% of shrub stems less than 2 cm DBH

327   (Appendix 5).

328

329

330   Figure 1: Number of stems per hectare of each species present in the Scotty Creek ForestGEO

331   plot as of the original census completed in 2014 (pima = *Picea mariana*, lala = *Larix laricina*,

332   besp = *Betula* spp., sasp = *Salix* spp., alcr = *Alnus alnobetula*, pigl = *Picea glauca*, piba = *Pinus*

333   *banksiana*). See Appendix 6 for counts of stems versus individuals for each species. Tree

334   silhouettes taken from Natural Resources Canada website (https://tidcf.nrcan.gc.ca/en/trees/).

335

336
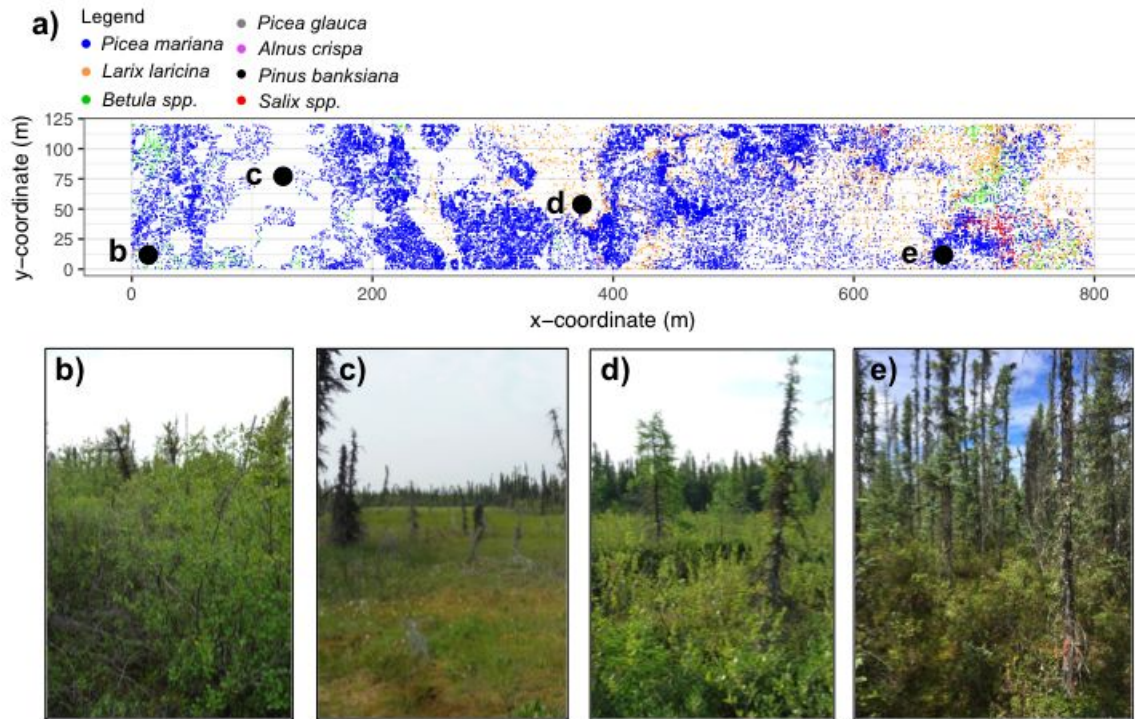
Figure 2: a) Map of all stems in the Scotty Creek ForestGEO plot as of the initial census

completed in 2014 (see Appendix 6 for separate maps of each species), with photos showing b) a

dense thicket of *Betula* spp. shrubs underlain by permafrost, c) a permafrost-free bog with a few

scattered *P. mariana*, d) a permafrost-free fen with a sparse canopy of *L. laricina*, and e) a dense

forest dominated by *P. mariana* and underlain by permafrost. Approximate locations of these

pictures are denoted by the corresponding letters on the map.

343

The first two axes in the mixed principal components analysis captured 34.7% of

variance in the six abiotic variables (subsequent axes explained an additional 10% or

less) (Appendix 7). The first axis (PC1) explained 21.4% of variance and reflected a

gradient in permafrost presence and soil moisture. High values represented dry soils atop

permafrost plateaus, while low values represented permafrost-free wetlands. The second

axis (PC2) explained an additional 13.3% of the variance and reflected a gradient in

350   organic layer thickness, peat decomposition, and maximum snow depth. Areas with high

351   values had more surficial mineral soils (within 1.5 m of the surface), more highly

352   decomposed peat, and a deeper snowpack, whereas areas with low values had thick

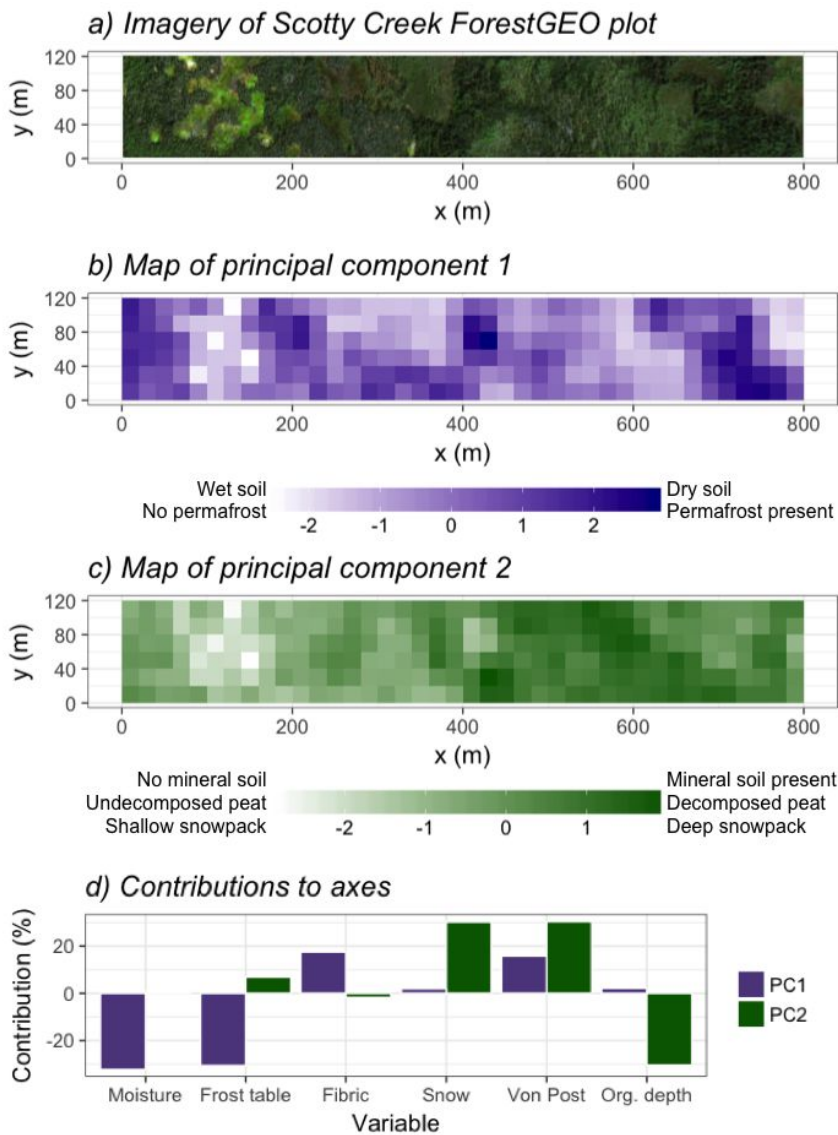353   organic layers (>1.5 m), undecomposed peat, and shallow snowpacks (Fig 3).

354

355

356   Figure 3: Mixed principal components analysis of abiotic variables measured at 20 m intervals

357   throughout the Scotty Creek ForestGEO plot between 2012 and 2018. Panel a) shows satellite

358   imagery of the plot (Esri World Imagery; Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA,

359   USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community).

360   Panels b) and c) depict maps of averaged values of the first and second principal components,

361   respectively, for each of the 240 grid cells in the plot (i.e. each value is an average of the values at

362   the four corners of a grid cell), and the scale bars are labeled with variables that had contributions

363   of greater than 20% to each axis. Panel d) depicts the contributions of all six variables to axes 1

364   and 2 (expressed as percentages of total contributions and oriented in accordance with the

365   direction they load onto each axis).

366

367   Patterns in species richness and basal area corresponded with gradients in both

368   principal components, while patterns in stem density were more erratic. Mean stem

369   density at the grid cell scale was 4227 ± 3125 stems/ha and tended to be low in areas with

370   low PC1 values (i.e. permafrost-free wetlands), but did not clearly correspond with

371   patterns in PC2 (Fig 4a). Species richness of trees and tall shrubs was generally low

372   (mean of 2.6 ± 1.2 species per grid cell), but increased with increasing values of PC1 and

373   PC2, meaning it was highest in well-drained areas underlain by permafrost and mineral

374   soil (Fig 4b). Mean basal area at the grid cell scale was 6.7 ± 5.1 m^2 ha^{-1} and, like species

375   richness, increased with increasing values of PC1 and PC2 to a maximum of 25.2 m^2 ha^{-1}
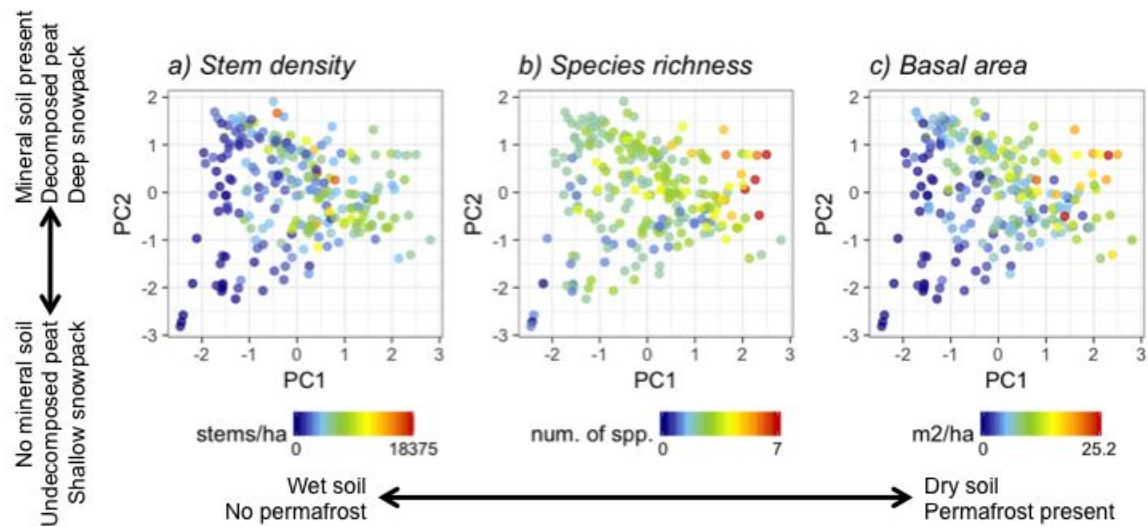
376   (Fig 4c).

377

Figure 4: Ordination plots showing each of the 240 20 m × 20 m grid cells in two-dimensional space defined by the first and second principal components depicted in Figure 3. Grid cells are colour-coded according to their a) stem density, b) species richness, and c) basal area.

Spatial patterns of forest dynamics

Overall, the plot experienced a net loss of stems at a rate of 0.7% yr⁻¹ between censuses (2013 to 2018), but mortality and recruitment varied spatially and among species. Mortality of *P. mariana* was more than double that of recruitment (2586 deaths vs. 992 recruits), but because initial stem density was so high, they only experienced a 1.0% yr⁻¹ net loss of stems. In contrast, recruitment of *L. laricina* was more than four times that of mortality (128 deaths vs. 566 recruits), resulting in a 1.9% yr⁻¹ net gain in stems. Mortality of *Betula spp.* was only marginally greater than recruitment, but because rates were high, *Betula* spp. still experienced a 0.7% yr⁻¹ net loss of stems (Fig 5) (see Appendix 9 for rates of *Betula* spp. genets). The remaining species (*Salix spp.*, *A. crispa*,

394 *P. glauca*, and *P. banksiana*) experienced net losses as well, though their initial densities

395 were so low that these losses did not notably influence forest composition or structure.

396 The net change in basal area was predominantly negative for all species due to the small

397 diameters of new recruits, although *L. laricina* showed net gains in basal area of between

398 1% and 77% in approximately half (51%) of the grid cells it occupied (Appendix 8).

399

400 The diameters of stems that died between 2013 and 2018 were very similar in

401 distribution to the diameters of surviving stems, meaning mortality occurred more or less

402 equally across size classes. A Kolmogorov-Smirnov test revealed that the diameter

403 distributions of deaths and survivors were significantly different ($p < 0.05$ for all species),

404 but this is likely an artifact of large sample size and unlikely to be ecologically significant

405 (see Appendix 5). In general, mortality and recruitment rates of shrub species were higher

406 than those of tree species, mainly because clonal stems had high turnover rates (see
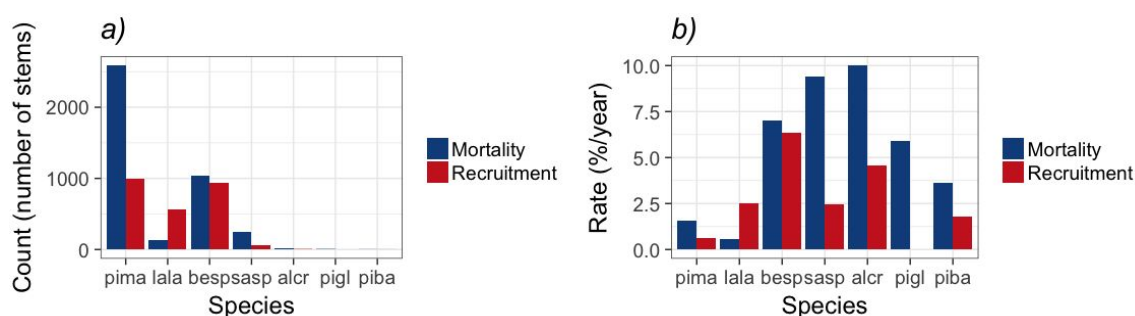
407 Appendix 9).

408

409

410 Figure 5: The a) numbers of stem deaths and recruits, and b) rates of stem mortality and

411 recruitment of each species in the Scotty Creek ForestGEO plot between the initial census

412 completed in 2014 and the recensus in 2018 (see Fig 1 for species abbreviations and Appendix 8

413 for basal area losses and gains).

414

415   Mortality and recruitment patterns varied spatially across the plot (Fig 6).

416   Specifically, eastern grid cells experienced net gains in stems and western grid cells

417   experienced net losses (Fig 6a). Net losses in the western half were attributable to a

418   decline in *P. mariana* abundance (Fig 6b), whereas net gains on the eastern side were

419   driven by an increase in *L. laricina* abundance (Fig 6c). *Betula* spp. dynamics were

420   variable between adjacent grid cells, but there was no overall pattern in net gains or

421   losses across the plot (Fig 6d; see Appendix 9 for a map of net change in *Betula* spp.
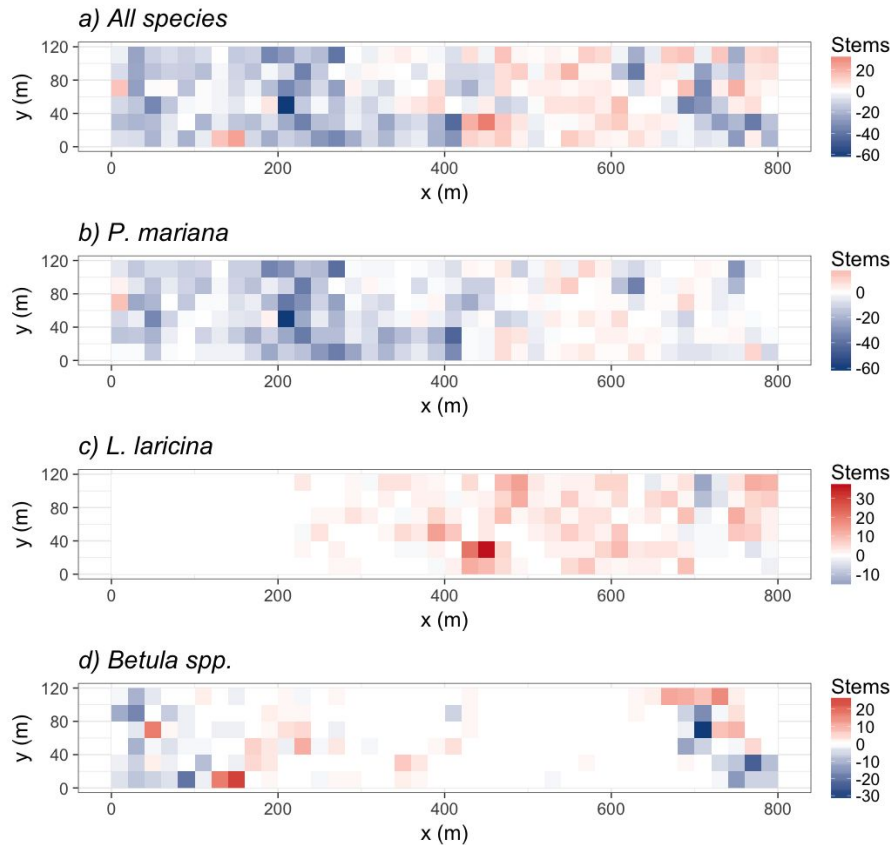
422   individuals).

423

a) All species

b) P. mariana

c) L. laricina

d) Betula spp.

424

425   Figure 6: Maps of net change in the number of stems of a) all species combined, b) *Picea*

426   *mariana,* c) *Larix laricina*, and d) *Betula* spp. in each of the 240 20 m × 20 m grid cells in the

427   Scotty Creek ForestGEO plot between censuses. Darker blue colours indicate high net losses of

428   stems (i.e. more deaths than recruits), while darker red colours indicate high net gains. Note the

429   difference in scales between maps. See Appendix 8 for maps of net change in basal area of each

430   species.

431   *Abiotic drivers of forest dynamics*

432

433   The abiotic variables governing the initial distributions of *P. mariana* and *Betula*

434   spp. were different from those governing the distribution of *L. laricina*. The abundance of

435   both *P. mariana* and *Betula* spp. stems was positively associated with the presence of

436   permafrost and correspondingly well-drained soils (high PC1) according to habitat

437   association tests. However, neither species was sensitive to gradients in organic layer

438   thickness (PC2). In contrast, *L. laricina* abundance was not significantly associated with

439   gradients in permafrost presence or soil moisture (PC1), but was positively associated

440   with thin organic layers (high PC2) (Fig 7, Tables 1 and 2).

441

442   Abiotic drivers of mortality often differed from those of recruitment, leading to

443   spatial shifts in the distributions of stems, and the magnitude and direction of these shifts

444   varied among species. *P. mariana* deaths and recruits were both associated with dry soils

445   underlain by permafrost (high PC1), like their initial stem densities. However, *P. mariana*

446   recruits were also associated with thin organic soils (high PC2), even though deaths and

447   initial stems were not. Net losses of *P. mariana* were therefore greatest in areas with

448   thick organic soils (Fig 7, Tables 1 and 2). *L. laricina* deaths occurred randomly in

449   relation to environmental conditions (PC1 or PC2). In contrast, recruits were significantly

450   associated with wet, permafrost-free soils (low PC1) and thin organic layers (high PC2).

451   As a result, net gains of *L. laricina* stems were highest in wet, permafrost-free areas with

452   surficial mineral soil (Fig 7, Tables 1 and 2). Both deaths and recruits of *Betula* spp. were

453   associated with dry soils underlain by permafrost (high PC1), but were not sensitive to

454   organic layer thickness (PC2), similar to their initial stem densities. As a result, there

455   was no spatial shift in the abundance of *Betula* spp. stems within the plot. This was

456   consistent when analysis was done at the genet level as well.

457

458   *Permafrost thaw and forest dynamics*

459

460   The extent to which permafrost thaw drove mortality and recruitment varied

461 notably among the three dominant species. *L. laricina* and *Betula* spp. deaths were not

462 significantly associated with areas that experienced minor or major thaw (i.e. deaths were

463 distributed randomly in relation to permafrost dynamics), but *P. mariana* deaths were

464 positively associated with areas that experienced minor as well as major thaw (Appendix

465 10). Interestingly, *P. mariana* and *L. laricina* recruitment showed very different trends

466 with respect to permafrost dynamics. *P. mariana* recruitment was negatively associated

467 with permafrost-free areas and positively associated with areas that experienced major

468 thaw, whereas *L. laricina* recruitment was positively associated with permafrost-free

469 areas (though not significantly) and negatively associated with major thaw. *Betula* spp.

470 recruits followed a similar pattern to that of *P. mariana* recruits.
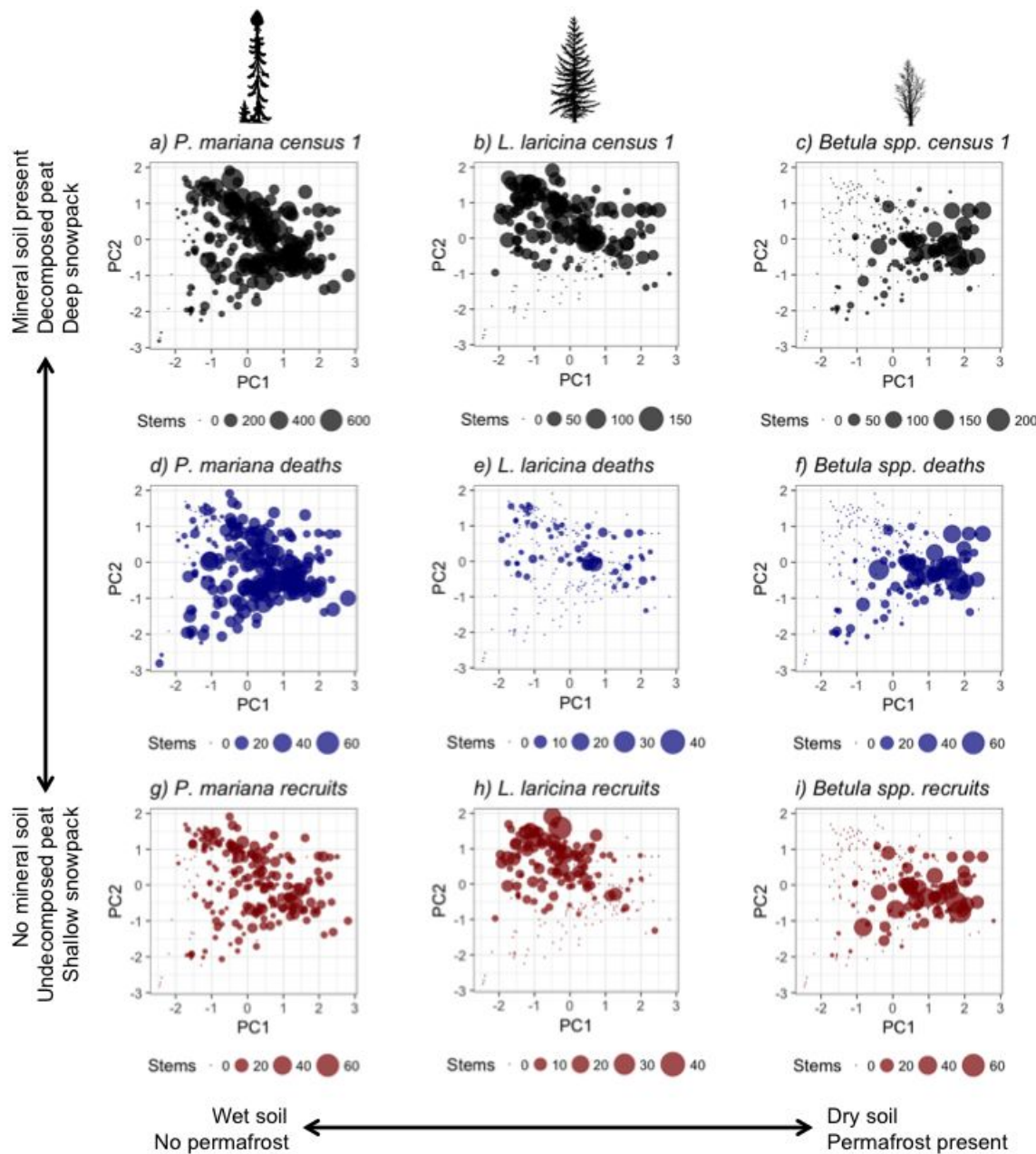
471

Figure 7: Ordination plots showing each of the 240 20 m × 20 m grid cells in two-dimensional

space defined by the first and second principal components depicted in Fig 3. Grid cells are sized

according to the number of stems of each of the three most dominant species in the initial census

(black, letters a-c), the number of deaths (blue, letters d-f), and the number of recruits that

occurred between censuses (red, letters g-i). Note that scales differ between species, as well as

478   between initial census values and deaths/recruits, and that circles are semi-transparent to show

479   overlap.

480

481   Table 1: Observed mean values of PC1 for each species (adjusted according to the probability of

482   that species occurring at a given value of PC1, given the distribution of PC1 values) compared to

483   95% confidence intervals derived from 960 torus translations of the grid cells. Note that high

484   values of PC1 correspond with low soil moisture content and shallow active layers (Fig 3), and

485   that asterisks indicate the observed mean is below (-) or above (+) the 2.5% or 97.5% bound,

486   respectively, of the distribution of torus translated values.

	Species	Torus mean lower bound	Torus mean upper bound	Observed mean (adj.)
Census 1	*P. mariana*	-0.18	0.51	**0.71*(+)**
	L. laricina	-0.27	0.69	0.18
	Betula spp.	-0.63	1.11	**1.64*(+)**
Deaths	*P. mariana*	-0.18	0.51	**0.76*(+)**
	L. laricina	-0.79	1.30	0.56
	Betula spp.	-0.58	1.03	**1.48*(+)**
Recruits	*P. mariana*	-0.15	0.48	**0.83*(+)**
	L. laricina	-0.36	0.81	**-0.56*(-)**
	Betula spp.	-0.54	0.93	**1.37*(+)**

487

488   Table 2: Observed mean values of PC2 for each species (adjusted according to the probability of

489   that species occurring at a given value of PC2, given the distribution of PC2 values) compared to

490   95% confidence intervals derived from 960 torus translations of the grid cells. Note that high

491   values of PC2 correspond with thin organic layers, decomposed peat, and deep snowpacks

492   (Figure 3), and that asterisks indicate the observed mean is below (-) or above (+) the 2.5% or

493   97.5% bound, respectively, of the distribution of torus translated values.

	Species	Torus mean lower bound	Torus mean upper bound	Observed mean (adj.)
Census 1	*P. mariana*	-0.97	0.12	0.02
	L. laricina	-1.23	0.61	**0.75*(+)**
	Betula spp.	-1.67	0.94	-0.29
Deaths	*P. mariana*	-1.17	0.27	-0.55
	L. laricina	-1.73	0.79	0.35
	Betula spp.	-1.67	0.94	-0.46
Recruits	*P. mariana*	-0.82	-0.09	**-0.02*(+)**
	L. laricina	-1.31	0.71	**0.99*(+)**
	Betula spp.	-1.54	0.84	-0.39

494

495   *Permafrost thaw and causes of mortality*

496

497   Causes of mortality varied among species, though biological/unknown causes

498   were the most common. Biological/unknown causes accounted for 84% and 77% of *L.*

499   *laricina* and *Betula* spp. deaths, respectively, with the remainder due to stems falling over

500   or physical damage. Most *P. mariana* mortality was also due to biological/unknown

501   causes (59%), but the remainder was due to a combination of waterlogging (23%) and

502   falling over or physical damage (18%) (Fig 8a). Waterlogged *P. mariana* stems were

503   positively associated with minor amounts of vertical thaw (thaw severity scores of 1 to

504   5), while other causes (biological/unknown, falling over, or physical damage) were

505   positively associated with major thaw (scores of 6-12) (Appendix 10). Most

506   waterlogging occurred in the western half of the plot (i.e. areas with no underlying

507   mineral soil) (Fig 8b,c), but there was no discernable east-west gradient in the magnitude

508   of thaw (Fig 8d).

509

a) Causes of P. mariana deaths

b) Photo of waterlogged P. mariana

c) Map of P. mariana deaths

d) Severity of permafrost thaw between 2012 and 2018

510
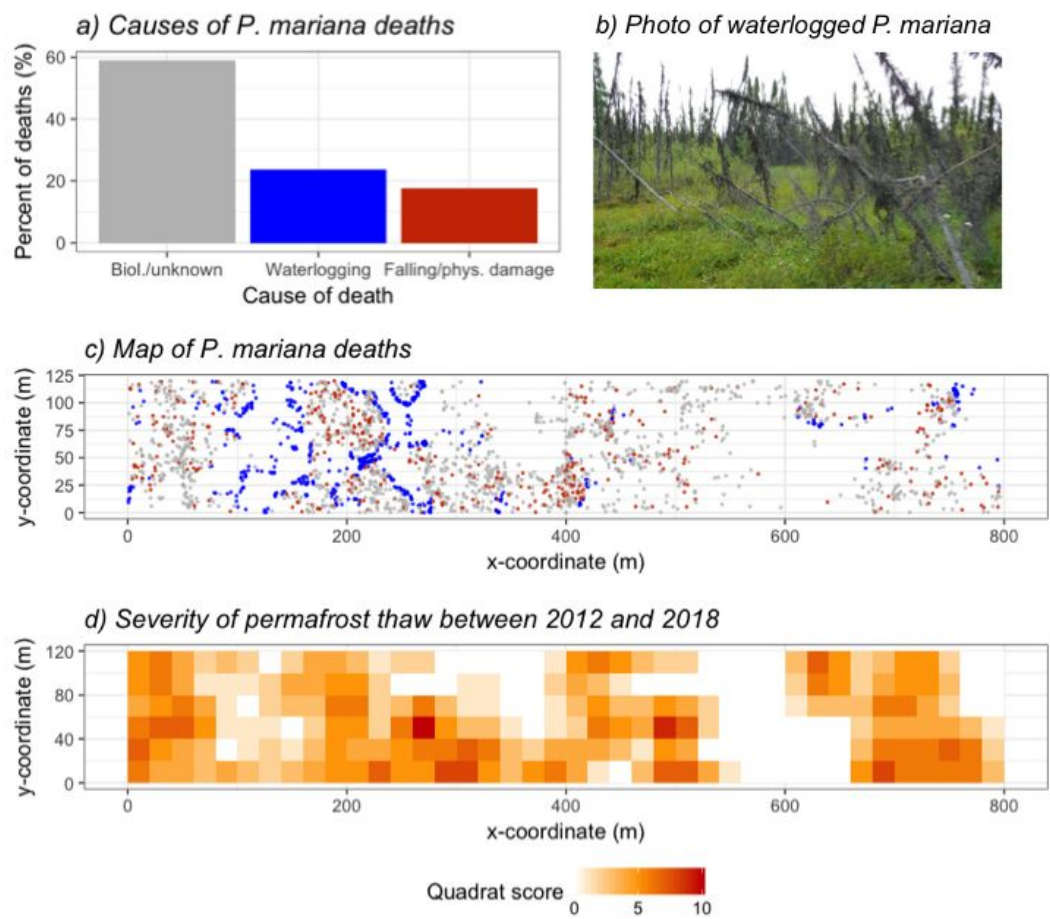
Figure 8: a) The proportion of *P. mariana* deaths that occurred as a result of biological/unknown

causes, waterlogging, and falling over/physical damage; b) a photo of *P. mariana* deaths that

occurred as a result of waterlogging along the margins of a subsiding permafrost plateau in the

western half of the plot; c) a map of *P. mariana* deaths throughout the plot, colour-coded by

cause (see panel a) for colour meanings); d) a map of change in frost table depth between 2012

and 2018 for each grid cell (white values had no permafrost and higher values indicate greater

thaw - see methods for explanation of score).

518

Discussion

520

521   We found that spatial patterns of forest composition, structure, mortality, and

522   recruitment in the Scotty Creek ForestGEO plot were driven in part by gradients in soil

523   moisture associated with permafrost conditions, but that they were also driven to a large

524   extent by soil organic layer thickness. Species richness, basal area, and stem density were

525   all higher atop well-drained plateaus than in surrounding permafrost-free wetlands, but

526   basal area and species richness were also positively associated with thin organic layers

527   (i.e. access to mineral soil), which varied substantially across the 800 m gradient captured

528   by the plot. The plot experienced a net loss of stems at a rate of 0.7% yr^{-1} between 2013

529   and 2018, which was partially driven by waterlogging of *P. mariana* associated with

530   lateral permafrost thaw along permafrost plateau margins, and partially by indirect effects

531   of vertical permafrost thaw within plateau interiors. Mortality occurred throughout the

532   diameter range, meaning permafrost thaw was an agent of mortality for both smaller and

533   larger trees. However, high recruitment of *L. laricina* and to a lesser extent *P. mariana* in

534   areas with thin organic soils resulted in localized net gains of stems. Collectively, these

535   results suggest that permafrost thaw is driving forest loss in the Scotty Creek basin, but

536   that access to mineral soil and species-specific responses to thaw strongly mediate these

537   dynamics.

538

539   Permafrost thaw is an ongoing and accelerating process in our study area and

540   throughout the circumpolar north (Jorgenson et al., 2010; Quinton et al., 2011). Mean

541   annual temperature in our study area has increased substantially over the past century

542   from -4.1°C (between 1896 and 1970) to -2.8°C in recent decades (1981-2010) (Quinton,

543   Hayashi, & Chasmer, 2009). Given that permafrost in this region is already near 0°C and

544   is often maintained by canopy shading, forest fragmentation associated with thawing

545   permafrost plateaus has greatly increased the rate of thaw since the 1970s (Baltzer et al.,

546   2014). Temperatures are projected to continue increasing at northern latitudes over the

547   coming decades (Hartmann, Klein Tank, & Rusticucci, 2013) and, as a result, the rate of

548   thaw will likely continue to accelerate. Therefore, thaw-driven shifts in forest

549   composition or structure are unlikely to be ephemeral.

550

551   The overall mortality rate in the Scotty Creek ForestGEO plot was 2.0% yr^{-1}

552   across all species and diameter classes. In the Canadian boreal forest, permanent forest

553   plots are primarily located in permafrost-free regions of the southern boreal forest, and

554   exclude stems that are less than 5 cm DBH (Gillis et al., 2005), making direct

555   comparisons with our results difficult. Mortality rates in these southern plots began to

556   exceed 2.0% yr^{-1} in western Canada after the early 2000s due in part to climate-induced

557   drought stress (Birch et al., 2019; Peng et al., 2011). When we removed stems smaller

558   than 5 cm DBH from our data, we found a mortality rate of 1.9% yr^{-1} at Scotty Creek,

559   suggesting that the direct and indirect effects of vertical and lateral permafrost thaw in

560   northern portions of the boreal forest are resulting in comparable mortality rates to

561   climate-induced drought stress in the southern portions.

562

563   Given the high latitude and extreme climate of the Scotty Creek plot, we expected

564   stem mortality and recruitment rates to be lower than those in other ForestGEO plots

565   (Stephenson & van Mantgem, 2005). However, the mortality rate we observed is

566   comparable to those in other forest types, which tend to range between 1% and 5% yr^{-1}

567   for most species and diameter classes (Condit, Hubbell, & Foster, 1995; Furniss et al.,

568   2017; Gonzalez-Akre et al., 2016; Itoh et al., 2012). Furthermore, the large discrepancies

569   between mortality and recruitment rates of the two dominant species in the Scotty Creek

570   plot (net loss of *P. mariana* and net gain of *L. laricina*) are fairly unique amongst large

571   forest plots. Other plots have observed discrepancies, but they tend to correspond with

572   species-specific diseases, are found in less dominant species, or are related to known

573   successional trends (Furniss et al., 2017; Gonzalez-Akre et al., 2016; Lutz et al., 2014).

574   Given that the forest at Scotty Creek is not currently undergoing succession (i.e. *L.*

575   *laricina* is not a late-successional species), permafrost thaw is almost certainly

576   responsible for the discrepancies we observed, and may be initiating unprecedented shifts

577   in boreal forest composition.

578

579   We found that organic layer thickness strongly mediated forest response to

580   permafrost thaw. Despite the occurrence of thaw and associated flooding throughout the

581   plot, net gains of stems frequently occurred in areas with thin organic layers. This was

582   particularly true for *L. laricina*, which can produce aerenchymatous tissue in the stem

583   that facilitates root aeration, thereby maintaining higher root mass and root hydraulic

584   conductivity than *P. mariana* in saturated soils (Islam et al., 2003). Partially because of

585   the need to produce new foliage every spring, *L. laricina* is also notably more nutrient

586   demanding than *P. mariana* (Islam & Macdonald, 2005), which explains why recruitment

587   was so strongly associated with the presence of surficial mineral soil.

588

589   Though we expected the flood-tolerant *L. laricina* to fare better than *P. mariana*

590   as soils became increasingly waterlogged, the fact that *L. laricina* recruitment was more

591   than four times greater than mortality was surprising. It is likely that the loss of *P.*

592   *mariana* from recently flooded sections of the plot provided new openings in the canopy

593   for *L. laricina* to colonize. This is supported by the fact that *L. laricina* recruitment was

594   strongly associated with high soil moisture even though initial stem distributions were

595   not. Larch growth has responded positively to permafrost thaw in other regions, perhaps

596   because it is capable of rapidly taking advantage of nutrients released at the thaw front

597   (Islam & Macdonald, 2005; Keuper et al., 2012; Prokushkin et al., 2018; Zhang et al.,

598   2019). *L. laricina* has also advanced northward in North America in response to climate

599   warming over the past few decades (Mamet, Brown, Trant, & Laroque, 2019). The

600   increase in *L. laricina* dominance at Scotty Creek has so far been restricted to areas with

601   surficial mineral soil, but it is possible that coalescing taliks (pockets of ground beneath

602   the active layer that remain unfrozen throughout the winter) and degrading permafrost

603   "dams" will facilitate the movement of nutrient-rich groundwater to formerly isolated

604   bogs as thaw progresses (Connon, Devoie, Hayashi, Veness, & Quinton, 2018; Connon et

605   al., 2014). This could enable *L. laricina* to overtake *P. mariana* in other areas as well.

606

607   Despite our expectation that *P. mariana* mortality would be driven primarily by

608   waterlogging associated with permafrost thaw, we found that most deaths were due to

609   biological or unknown causes, and that deaths due to stems falling over or incurring

610   physical damage were almost as common as deaths due to waterlogging. Some deaths

611   were likely the delayed result of damage incurred during a wet snowfall event in late

612   spring 2012 (J. Baltzer, personal observation). This is supported by damage assessments

613   done on large stems (those >10 cm DBH) in 2012. Notably, 36% of live stems with

614   snapped crowns in 2012 had died by 2018. This is a considerably higher mortality rate

615   than we found amongst stems with other types of damage (26% or less) or no damage

616   (only 8%) (Appendix 11). As climate warms, spring snowfall and frost events could

617   become increasingly common sources of damage or mortality for boreal trees (Man,

618   Kayahara, Foley, & Wiseman, 2013). These events will likely affect *P. mariana* more

619   severely than *L. laricina*, since the top-heavy crown architecture of the former makes it

620   particularly susceptible to damage via snow loading, and because deciduous species are

621   generally less susceptible to overwinter damage than evergreens due to reduced canopy

622   snow capture (Man et al., 2013; Nykänen, Peltola, Quine, Kellomäki, & Broadgate,

623   1997). Lastly, windthrow could become increasingly common in peatlands as stems are

624   lost to waterlogging and damage, since trees at forest edges or in thinned stands are more

625   susceptible to windthrow than those in dense stand interiors (Peltola, Kellomäki,

626   Väisänen, & Ikonen, 1999).

627

628   Causes of *P. mariana* deaths other than waterlogging (i.e. biological/unknown,

629   falling over, or physical damage) were positively and significantly associated with high

630   rates of vertical permafrost thaw, supporting the mounting evidence that trees growing

631   atop plateaus may be suffering from thaw-induced drought stress. The water table is

632   perched atop the frost table at this site such that any deepening of the latter makes it

633   difficult for shallow-rooted *P. mariana* to access adequate moisture (Sniderhan &

634   Baltzer, 2016). Drought stress can cause reductions in physiological function and growth

635   (Patankar, Quinton, Hayashi, & Baltzer, 2015; Sniderhan & Baltzer, 2016) or outright

636   mortality (Peng et al., 2011). It may also leave trees more vulnerable to insects or

637   pathogens, thereby indirectly increasing mortality rates (Desprez-Loustau, Marçais,

638   Nageleisen, Piou, & Vannini, 2006). Furthermore, the thinning of forest stands within

639   plateau interiors feeds back positively on the rate of vertical thaw, since it increases the

640   amount of incident radiation reaching the ground surface (Baltzer et al., 2014; Lara et al.,

641   2016). As such, the rate of *P. mariana* loss we observed in the Scotty Creek plot is likely

642   to accelerate in the future.

643

644   In contrast to our expectations, *P. mariana* deaths due to waterlogging were

645   associated with minor rates of permafrost thaw. This may be partially attributable to the

646   fact that surface subsidence can occur without any change in active layer thickness (i.e.

647   the depth from the surface to permafrost can remain constant as the surface sinks).

648   Additionally, waterlogging is a response to lateral thaw (i.e. disappearance of permafrost)

649   along abrupt plateau margins, which our active layer measurements often failed to

650   capture. Measurements tended to fall within permafrost-free wetlands or plateau interiors,

651   where vertical thaw was occurring, but permafrost persisted between years. Locations

652   where we did capture lateral thaw were immediately adjacent to permafrost-free

653   wetlands, which experienced no change in active layer depth between 2012 and 2018,

654   and were thus assigned a zero in our thaw severity rating. These zeros lowered the

655   aggregate thaw severity scores of grid cells in which lateral thaw was observed at one or

656   two grid cell corners. In short, the coarseness of our thaw depth measurements masked

657   dynamic processes at plateau margins but effectively, the minor thaw category often

658   corresponded with degrading plateau margins.

659

660   We found that *Betula* spp. experienced a very high turnover of stems, but spatial

661   patterns in abundance were stable between censuses. Areas dominated by *Betula* spp. also

662   tended to have highly decomposed peat (high von Post scores) and showed evidence of

663   fire (surficial charcoal; K. Dearborn, personal observation). It is possible that *Betula* spp.

664   rapidly colonized these areas following small burns, and subsequently prevented conifers

665   from colonizing. *Betula* spp. are competitive, fast-growing, and produce high quality

666   litter compared to evergreen species (Aerts, Verhoeven, & Whigham, 1999; Bret-Harte et

667   al., 2002). These characteristics could maintain patches of high *Betula* spp. abundance for

668   extended time periods following small burns, similar to the long-term replacement of

669   conifer forests by shrub fields following severe burns in the Cascade Mountains

670   (Lauvaux, Skinner, & Taylor, 2016). Their ability for clonal reproduction also means that

671   once they become dominant, they likely remain that way with limited opportunity for

672   succession toward a forested state, since rates of individual or genet mortality are low

673   (Appendix 9).

674

675   **Conclusions**

676

677   Our results, combined with the ongoing and projected increases in annual and

678   summer boreal temperatures, suggest that permafrost thaw will continue to elevate black

679   spruce mortality in boreal peatlands. A corresponding increase in larch abundance might

680   maintain sparse forest cover, but is also likely to alter a range of key ecosystem functions.

681   For instance, an increase in soil nutrient content and corresponding shift towards more

682   minerotrophic plant communities could occur, since larch needles fall every year and are

683   higher quality and more readily decomposable than spruce needles (Aerts et al., 1999;

684   Carlyle & Malcolm, 1986). The thinning of forest stands and increasing dominance of

685   deciduous species could also increase surface albedo in the winter, with potential

686   consequences for snow cover duration (Lundquist, Dickerson-Lange, Lutz, & Cristea,

687   2013). Finally, a loss of raised plateau habitat will likely be detrimental to caribou

688   whether a sparse canopy is maintained or not, since the lichens growing atop plateaus

689   form an important component of their diet (Joly, Chapin, & Klein, 2010). In any case, the

690   high disparities between mortality and recruitment among the dominant tree species

691   suggest high rates of community change for the boreal region, even higher than those

692   reported for more southerly boreal forests (Birch et al., 2019).

693

694   In the longer term, it is possible that extensive permafrost thaw and increasing

695   hydrological connectivity within the watershed will result in sufficient landscape

696   drainage to cause widespread drying of the landscape (Connon et al., 2014; Haynes,

697   Connon, & Quinton, 2018). If this occurs, successional processes will likely initiate an

698   increase in black spruce cover over time (Préfontaine & Jutras, 2017; Zoltai, 1993).

699   However, we did not find any indication that this is occurring yet. Instead, the evidence

700   we found of positive feedbacks between spruce loss and vertical thaw atop plateaus,

701   combined with previously uncovered evidence of positive feedbacks between plateau

702   subsidence and lateral thaw (Baltzer et al., 2014) suggest that the conversion of plateau-

703   wetland mosaics into more homogeneous, larch-dominated wetlands is likely to

704   accelerate in the coming decades.

705

706   **Acknowledgements**

707

725

726   **Authors' Contributions**

727

728   JB conceived ideas, obtained funding, and contributed substantially to data

729   analysis and writing, KD led the plot recensus in 2018, conducted data analysis, designed

730   figures, and wrote the manuscript, RP and CW led plot establishment, collected abiotic

731   data, and provided feedback on methodology, data analysis, and writing. All authors gave

732   final approval for publication.

733

734   **Data Availability**

735

736   Forest census data will be archived in the ForestGEO online data portal

737   (http://ctfs.si.edu/datarequest/).

738

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740

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Supporting information to the paper:
Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland. *Journal of Ecology*.

Appendix 1: Soil volumetric water content correlation matrix

Table 1: Pearson correlations among volumetric water content measurements taken on various dates, at various depths, and in various subsets of the Scotty Creek ForestGEO plot (Warren 2015). Measurements were taken immediately adjacent to posts as described in the methods section of the manuscript, and the depth at which measurements were taken is noted in brackets after each date. Note that the July 19, 2012 measurements are the only set of measurements completed across the entire plot, and thus are the measurements used in our analysis. The remaining measurements from 2012, and all measurements from 2013 were taken across the westernmost 500 m of the plot (meters 0 to 500), while the measurements from 2017 were taken between meters 180 and 480. All correlations were positive and significant at the 0.05 level.

	Jul 19, 2012 (<5 cm)	Jul 31, 2012 (<5 cm)	Aug 2, 2012 (<5 cm)	May 27, 2013 (<5 cm)	May 31, 2013 (<5 cm)	Aug 27, 2013 (<5 cm)	Aug 28, 2013 (<5 cm)	Sep 4, 2017 (6 cm)	Sep 4, 2017 (12 cm)	Sep 4, 2017 (20 cm)
Jul 19, 2012 (<5 cm)	1									
Jul 31, 2012 (<5 cm)	0.94	1								
Aug 2, 2012 (<5 cm)	0.96	0.99	1							
May 27, 2013 (<5 cm)	0.94	0.93	0.93	1						
May 31, 2013 (<5 cm)	0.94	0.95	0.97	0.94	1					
Aug 27, 2013 (<5 cm)	0.93	0.94	0.96	0.90	0.94	1				
Aug 28, 2013 (<5 cm)	0.93	0.93	0.94	0.92	0.93	0.94	1			
Sep 4, 2017 (6 cm)	0.27	0.35	0.32	0.30	0.28	0.29	0.31	1		

Sep 4, 2017 (12 cm)	0.48	0.57	0.54	0.53	0.51	0.50	0.52	0.76	1	
Sep 4, 2017 (20 cm)	0.47	0.55	0.52	0.48	0.49	0.48	0.47	0.65	0.88	1

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Supporting information to the paper:
Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland. *Journal of Ecology.*

Appendix 2: Adjustments to 2012 and 2018 frost table depth measurements

      To ensure that frost table depths were comparable between 2012 and 2018, we used known intraseasonal rates of thaw derived from repeat measurements taken across the westernmost 500 m of the plot in 2013 (i.e. at 182 of the 287 posts). Specifically, we used the difference in frost table depth between May 31 and August 27, 2013 (in cm), and the difference in thawing degree days (TDD, derived from Fort Simpson station data) between the same two dates to calculate rates of thaw (in cm/TDD) at each post within this subset of the plot. We then used multiple linear regression to model the relationship between rate of thaw and a selection of abiotic variables that had the strongest correlations with rates of thaw (soil moisture, organic layer thickness, and tree density within a 5 m radius of the post). We used this model ($R^2 = 0.31$, $p = 0.07$) to estimate rates of thaw (in cm/TDD) at the 105 posts in the easternmost portion of the plot for which we did not have known rates. Next, we calculated the difference in TDD between August 27, 2013 and July 19, 2012, as well as between August 27, 2013 and August 5, 2018. We then multiplied known and estimated rates of thaw at each post by differences in TDD between dates to make the 2012 and 2018 frost table depths comparable (in terms of TDD) to August 27, 2013 depths. Finally, we subtracted adjusted 2012 values from adjusted 2018 values to estimate the amount of thaw (in cm) that occurred between 2012 and 2018.

Supporting information to the paper:
Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to
permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland.
Journal of Ecology.

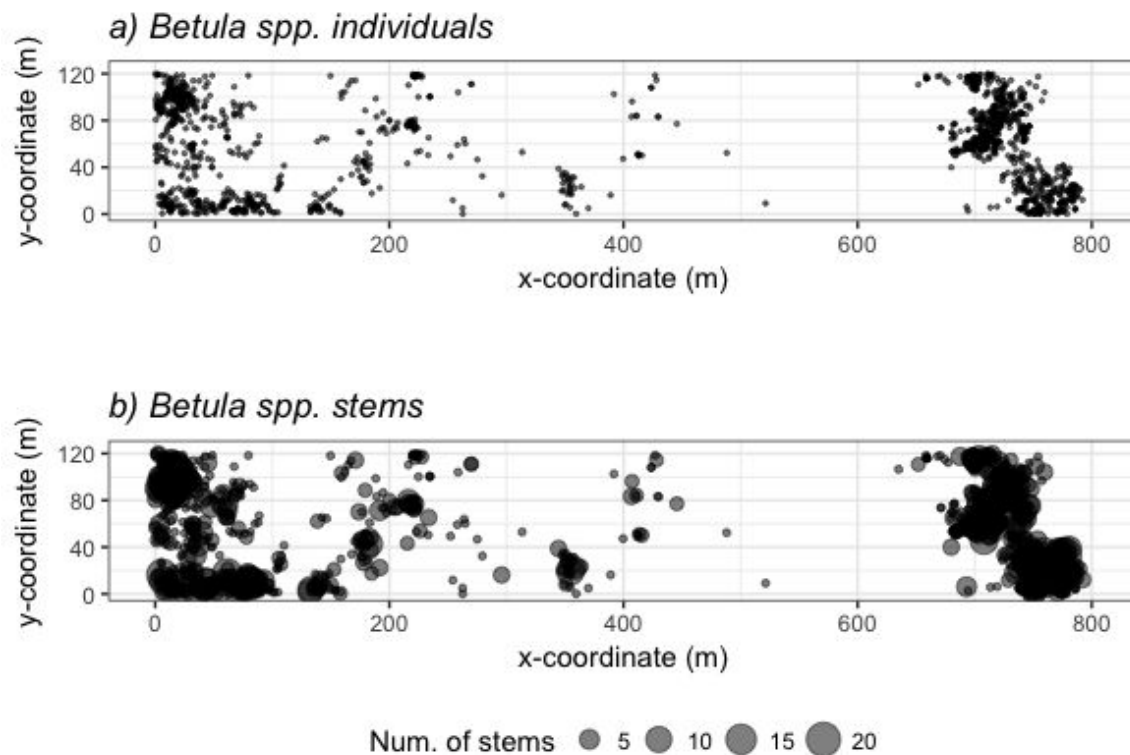Appendix 3: Maps of *Betula* spp. individuals (genets) and *Betula* spp. stems (ramets)

Figure 1: Map showing the a) locations of *Betula* spp. individuals (1349 total genets comprising
2973 ramets) in the Scotty Creek ForestGEO plot and b) locations of *Betula* spp. individuals
resized according to the number of multiple stems (ramets) making up each individual.

Supporting information to the paper:
Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland. *Journal of Ecology.*

Appendix 4: Categorization of abiotic variables

Several of the abiotic variables we included in our principal components analysis were categorical. The von Post score is inherently categorical, and we converted organic layer thickness and 2012 frost table measurements into categorical variables as well, since over 50% of the values of these two variables were censored beyond the limits of our equipment (i.e. beyond the length of the auger or frost probe). We explored several methods of including censored quantitative data in regression-based analyses, but all of them required that less than half of the values be censored (Tobin 1958; Buettner et al. 2014; Fisher et al. 2016). We therefore categorized 2012 frost table depth measurements into one of three categories (less than 50 cm, between 50 cm and 200 cm, and greater than 200 cm), and the organic layer thickness measurements into one of three categories (less than 60 cm, between 60 cm and 150 cm, and greater than 150 cm) prior to performing our principal component analysis. We performed a sensitivity analysis using higher numbers of categories for each variable, but the results of the principal components analysis were not notably affected.

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Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland. *Journal of Ecology.*

Appendix 5: Frequency histograms of surviving stem diameters and diameters of stems that died for each of the three dominant species in the plot
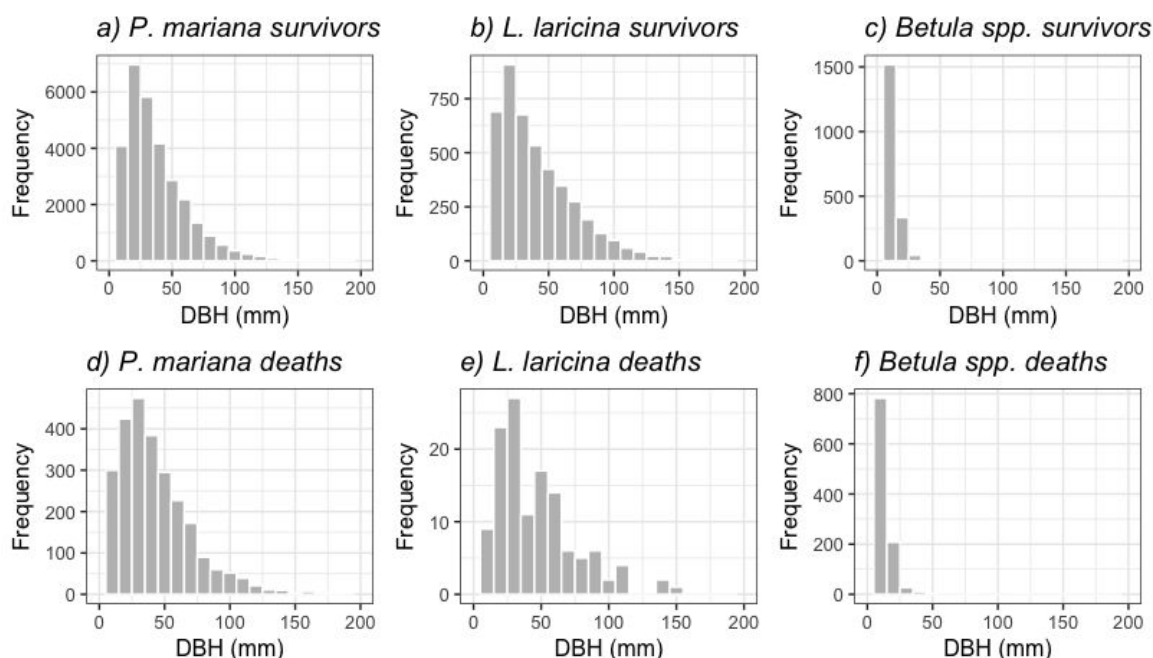
Figure 1: The distribution of surviving stem diameters of *Picea mariana*, *Larix laricina*, and *Betula spp.* (a-c), as well as distributions of diameters of *P. mariana*, *L. laricina*, and *Betula spp.* stems that died between the initial census (completed in 2014) and recensus in 2018 (d-f).

Supporting information to the paper:
Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland. *Journal of Ecology.*

Appendix 6: Stem counts for each species

Table 1: The number of ramets and genets of each species in the Scotty Creek ForestGEO plot as of the initial census completed in 2014.

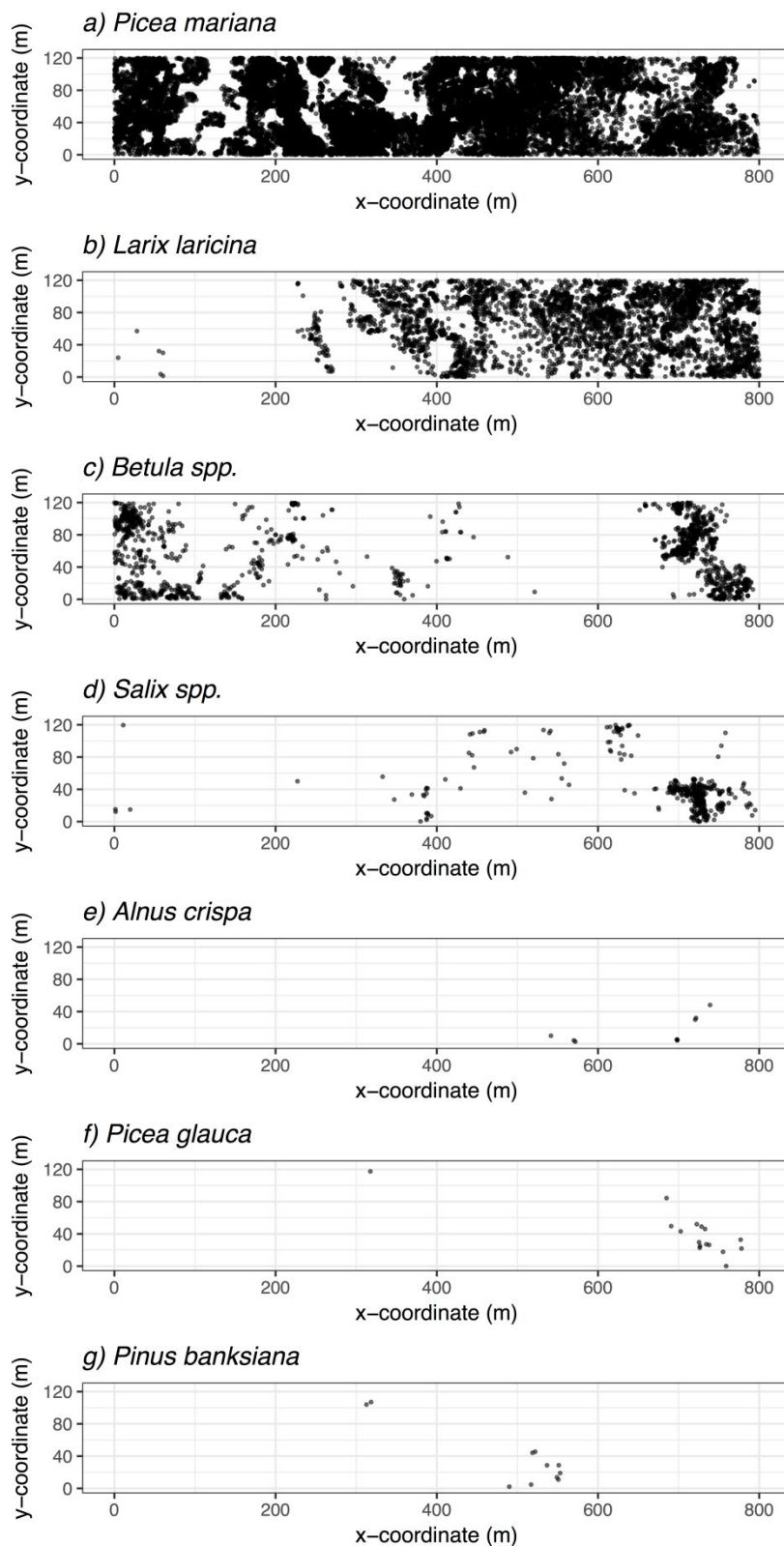| Species	Number of ramets	Number of genets
Picea mariana	32490	32034
Larix laricina	4550	4394
Betula spp.	2973	1349
Salix spp.	520	386
Alnus crispa	22	10
Picea glauca	17	16
Pinus banksiana	11	11
All species	40583	38200

Figure 1: Maps of the distributions of each genet (individual) of the species present in the Scotty Creek ForestGEO plot.

Supporting information to the paper:
Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland. *Journal of Ecology.*

Appendix 7: Results of principal components analysis on abiotic variables.

Table 1: Eigenvalues and variance explained for each axis in the mixed principal components analysis.

Axis	Eigenvalue	Proportion variance explained	Cumulative variance explained
PC1	2.57	21.38	21.38
PC2	1.60	13.34	34.72
PC3	1.27	10.55	45.28
PC4	1.10	9.19	54.47
PC5	1.05	8.72	63.18
PC6	0.98	8.13	71.31
PC7	0.86	7.17	78.48
PC8	0.80	6.63	85.10
PC9	0.67	5.58	90.68
PC10	0.57	4.76	95.44
PC11	0.40	3.32	98.76
PC12	0.15	1.24	100.00

Supporting information to the paper:
Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland. *Journal of Ecology.*

Appendix 8: Change in basal area (in m^2) between the initial census completed in 2014 and the recensus in 2018.
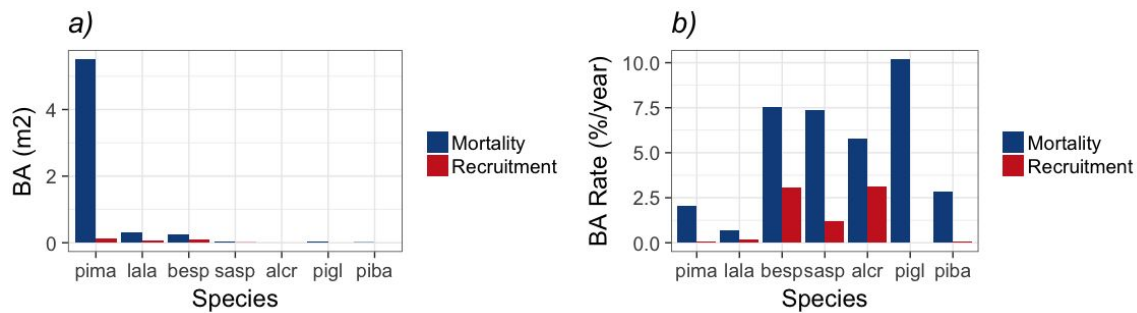

Figure 1: The a) amount of basal area lost and gained, and b) rates of basal area loss and gain for each species in the Scotty Creek ForestGEO plot between the initial census completed in 2014 and the recensus in 2018.
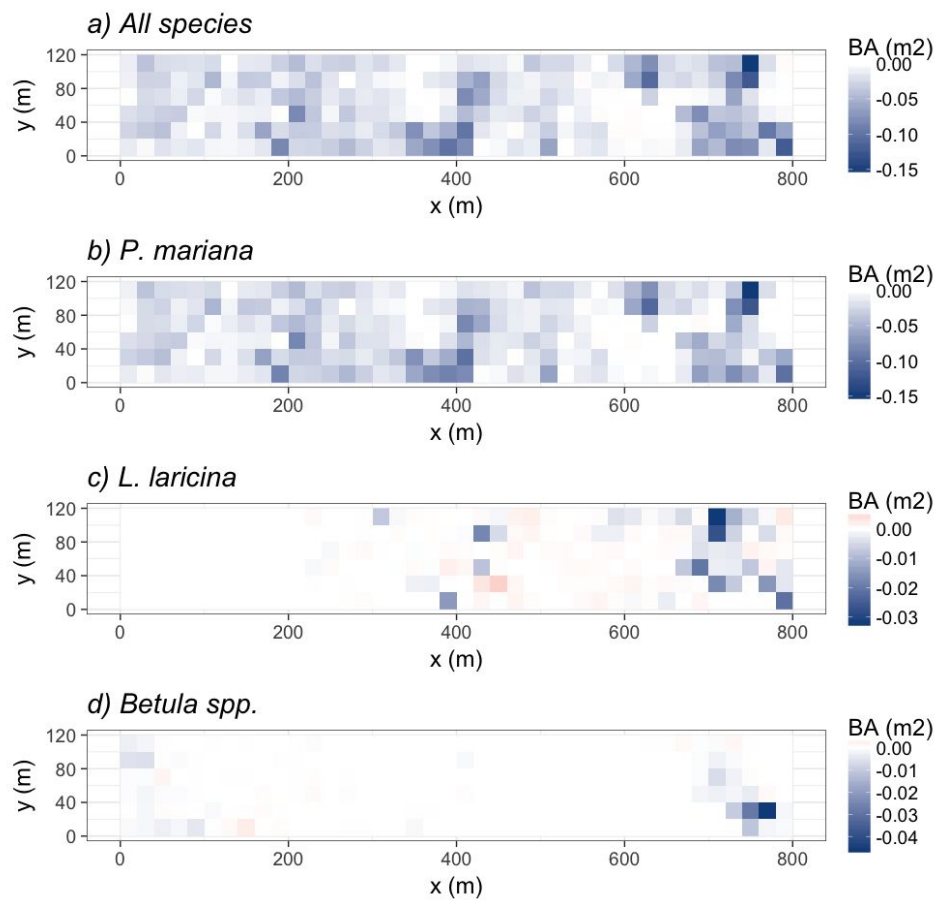
Figure 2: Maps of net change in the basal area of a) all species combined, b) *Picea mariana*, c) *Larix laricina*, d) *Betula spp.* in each of the 240 20 m × 20 m grid cells in the Scotty Creek ForestGEO plot between the initial census completed in 2014 and the recensus completed in 2018. Darker blue colours represent higher net losses of basal area. Note the difference in scales between maps.

Supporting information to the paper:
Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to
permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland.
Journal of Ecology.

Appendix 9: Comparison of *Betula spp.* dynamics when each multi-stemmed individual
is treated as a separate data point (genets) versus when stems originating from the same
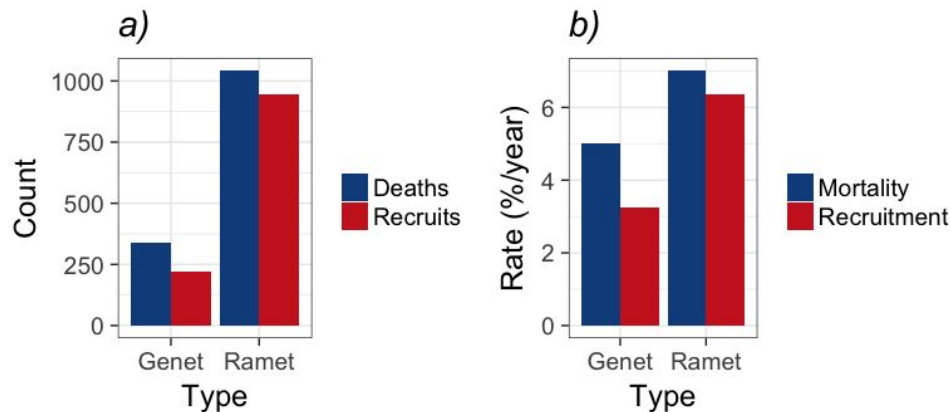individual (ramets) are combined into a single data point.

Figure 1: The a) numbers of deaths and recruits, and b) rates of stem mortality and recruitment of
Betula spp. when each multi-stemmed plant is treated as a separate data point (ramets) compared
to numbers and rates when stems originating from the same *Betula spp.* individual were
combined into a single data point (genets). Values refer to mortality and recruitment that occurred
between the initial census completed in 2014 and the recensus in 2018.
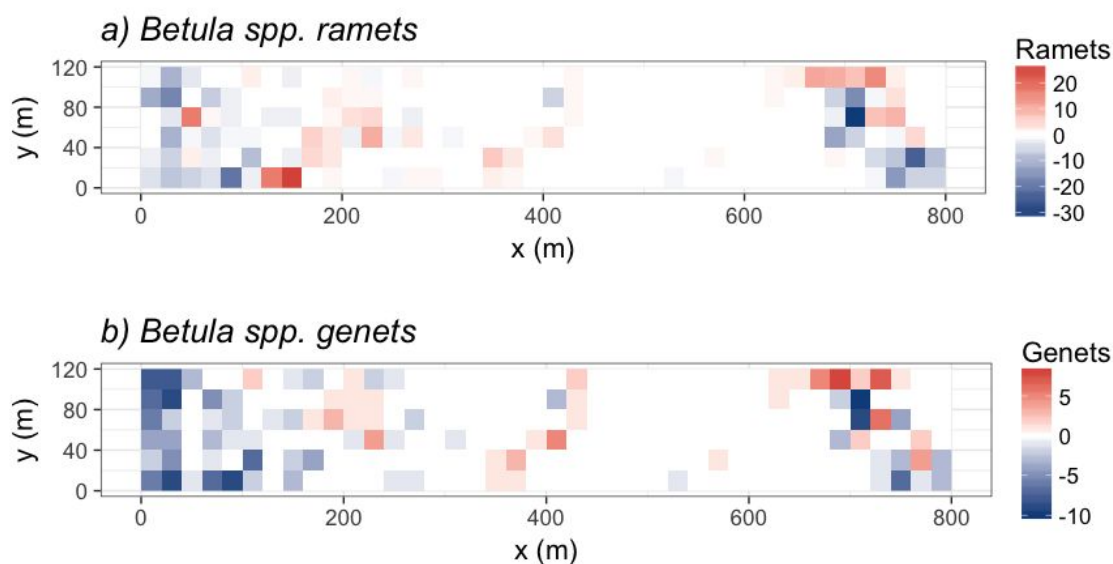

Figure 2: Maps of net change in the number of *Betula spp.* when a) stems in multi-stemmed
individuals (ramets) were treated as separate data points, and b) when stems originating from the
same individual (genets) were combined into a single data point. Darker blue colours indicate

high net losses of stems between 2013/2014 and 2018 in a given 20m x 20m grid cell (i.e. more deaths than recruits), while darker red colours indicate high net gains of stems. Note the difference in scales between maps.

Supporting information to the paper:
Dearborn, K.D., Wallace, C.A., Patankar, R., and Baltzer, J.L. Forest response to permafrost thaw is strongly mediated by organic layer thickness in a boreal peatland. *Journal of Ecology.*

Appendix 10: Results of categorical habitat association tests between the degree of vertical permafrost thaw and the deaths and recruits of each of the three dominant species (*Picea mariana*, *Larix laricina*, and *Betula spp.*), as well as the three causes of *P. mariana* mortality.

Table 1: Results of categorical torus translation test of association between three categories of vertical permafrost thaw (no permafrost, minor thaw and major thaw – see methods for explanation of categories) and deaths of the three dominant species (*Picea mariana*, *Larix laricina*, and *Betula spp.*) in the Scotty Creek Forest Dynamics Plot. Values indicate the number of torus-translated maps in which the true relative density of deaths in a given habitat is greater than, less than, or equal to translated maps. Using a two-tailed test and alpha=0.05, a relative density greater or less than 97.5% of the torus-translated maps (234 out of 240) indicates a positive or negative association, respectively.

	No permafrost			Minor vertical thaw			Major vertical thaw		
	Greater	Less	Equal	Greater	Less	Equal	Greater	Less	Equal
P. mariana	0	**239***	1	**239***	0	1	**237***	2	1
L. laricina	97	131	12	187	44	9	73	160	7
Betula spp.	0	**239***	1	163	76	1	232	7	1
All spp.	0	**239***	1	**235***	4	1	**239***	0	1

Table 2: Results of categorical torus translation test of association between three categories of vertical permafrost thaw (no permafrost, minor thaw and major thaw – see methods for explanation of categories) and recruits of the three dominant species (*Picea mariana*, *Larix laricina*, and *Betula spp.*) in the Scotty Creek Forest Dynamics Plot. Values indicate the number of torus-translated maps in which the true relative density of recruits in a given habitat is greater than, less than, or equal to translated maps. Using a two-tailed test and alpha=0.05, a relative density greater or less than 97.5% of the torus-translated maps (234 out of 240) indicates a positive or negative association, respectively.

	No permafrost			Minor vertical thaw			Major vertical thaw		
	Greater	Less	Equal	Greater	Less	Equal	Greater	Less	Equal
P. mariana	1	**238***	1	161	73	6	**237***	2	1
L. laricina	224	14	2	91	147	2	2	**237***	1
Betula spp.	0	**239***	1	222	16	2	208	31	1
All spp.	4	**235***	1	208	31	1	215	23	2

Table 3: Results of categorical torus translation test of association between three categories of vertical permafrost thaw (no permafrost, minor thaw and major thaw – see methods for explanation of categories) and the three causes of *Picea mariana* mortality. Values indicate the number of torus-translated maps in which the true relative density of a given cause of death in a given habitat is greater than, less than, or equal to translated maps. Using a two-tailed test and alpha=0.05, a relative density greater or less than 97.5% of the torus-translated maps (234 out of 240) indicates a positive or negative association, respectively.

	No permafrost			Minor vertical thaw			Major vertical thaw		
	Greater	Less	Equal	Greater	Less	Equal	Greater	Less	Equal
Biol./unknown	0	**239***	1	215	23	2	**239***	0	1
Waterlogging	0	**238***	2	**239***	0	1	2	**237***	1
Falling/damage	0	**239***	1	219	20	1	**239***	0	1

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Appendix 11: The percentage of large (>10 cm DBH) damaged stems that died between 2012 when damage assessments were completed and 2018 when the plot was recensused.
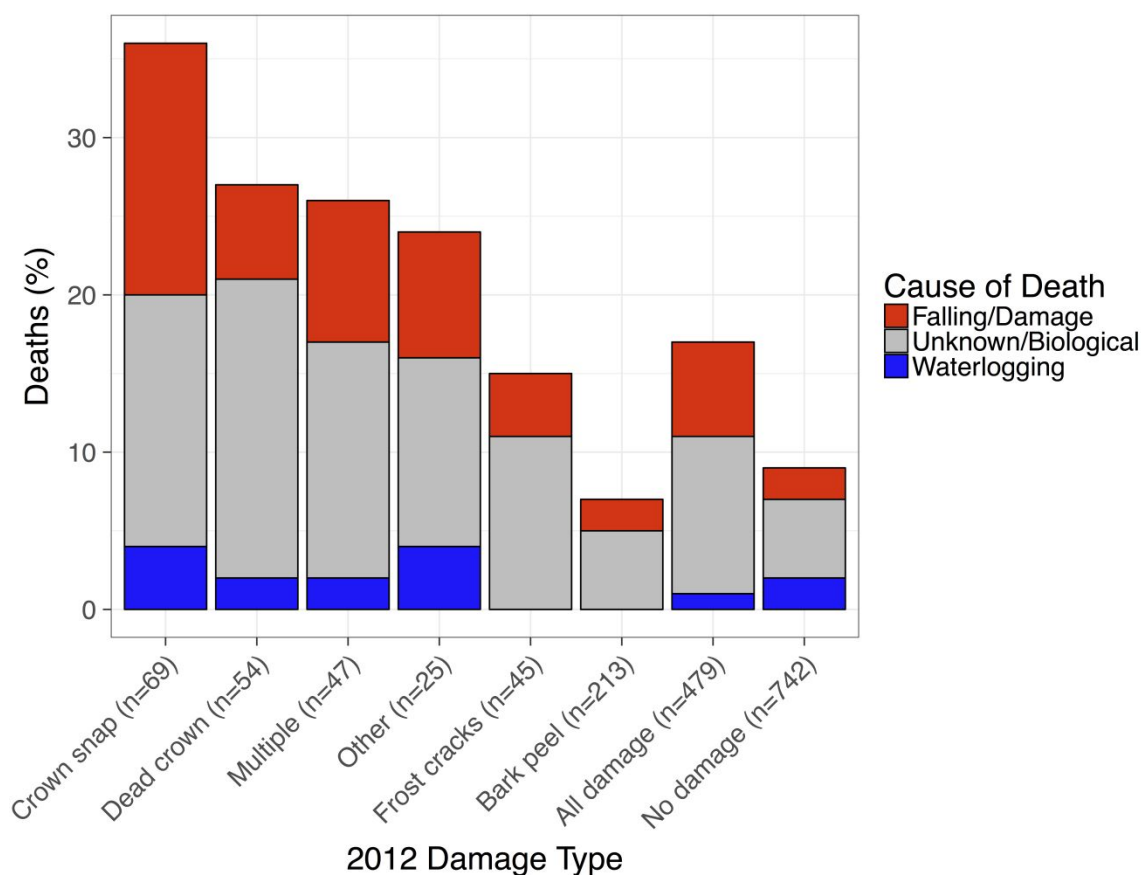

Figure 1: Percentage of damaged stems that died between 2012 when damage assessments were completed and 2018 when stems were recensused. Bars are colour coded by cause of death (see methods), and the number of trees in each damage category is noted in brackets after the name of the damage type. Note that damage assessments were only done on large stems (>10cm DBH), and that damage types that occurred on fewer than 10 trees are not shown (though they are included in the "All damage" category).