

1 **Tree ring-based reconstruction of the long-term**  
2 **influence of wildfires on permafrost active layer dynamics**  
3 **in Central Siberia**

4  
5 **Running title: Fire effects on permafrost active layer dynamics**

6  
7 Anastasia A. Knorre<sup>a,b</sup>, Alexander V. Kirilyanov<sup>c,d,a\*</sup>, Anatoly S. Prokushkin<sup>d,a</sup>,  
8 Paul J. Krusic<sup>c</sup>, Ulf Büntgen<sup>c,e,f,g</sup>

9  
10 <sup>a</sup>*Institute of Ecology and Geography, Siberian Federal University, Krasnoyarsk,*  
11 *660041, Russia*

12 <sup>b</sup>*State Natural Reserve 'Stolby', Kar'ernaya 26A, Krasnoyarsk, 660006, Russia*

13 <sup>c</sup>*Department of Geography, University of Cambridge, CB2 3EN, UK*

14 <sup>d</sup>*Sukachev Institute of Forest SB RAS, Akademgorodok, Krasnoyarsk, 660036, Russia*

15 <sup>e</sup>*Global Change Research Institute CAS, 603 00 Brno, Czech Republic*

16 <sup>f</sup>*Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland*

17 <sup>g</sup>*Department of Geography, Masaryk University, Kotlářská 2, 61137, Czech Republic*

18  
19  
20  
21  
22 *\* Corresponding author: kirilyanov@ksc.krasn.ru (Alexander V. Kirilyanov)*

24 **Abstract**

25 Although it has been recognized that rising temperatures and shifts in the hydrological cycle  
26 affect the depth of the seasonally thawing upper permafrost stratum, it remains unclear to what  
27 extent the frequency and intensity of wildfires, and subsequent changes in vegetation cover,  
28 influence the soil active layer on different spatiotemporal scales. Here, we use ring width  
29 measurements of the subterranean stem part of 15 larch trees from a *Sphagnum* bog site in  
30 Central Siberia to reconstruct long-term changes in the thickness of the active layer since the  
31 last wildfire occurred in 1899. Our approach reveals a three-step feedback loop between above-  
32 and belowground ecosystem components. After all vegetation is burned, direct atmospheric  
33 heat penetration over the first ~20 years caused thawing of the upper permafrost stratum. The  
34 slow recovery of the insulating ground vegetation reverses the process and initiates a gradual  
35 decrease of the active layer depth. Due to the continuous spreading and thickening of the peat  
36 layer during the last decades, the upper permafrost horizon has increased by 0.52 cm/year. This  
37 study demonstrates the strength of annually resolved and absolutely dated tree-ring series to  
38 reconstruct the effects of historical wildfires on the functioning and productivity of boreal forest  
39 ecosystems at multi-decadal to centennial time-scale. In so doing, we show how complex  
40 interactions of above- and belowground components translate into successive changes in the  
41 active permafrost stratum. Our results are particularly relevant for improving long-term  
42 estimates of the global carbon cycle that strongly depends on the source and sink behavior of  
43 the boreal forest zone.

44

45

46

47 *Keywords:* Boreal forest, Ecological interaction, Ecosystem response, Seasonally thawing soil  
48 layer, *Sphagnum*, *Larix gmelinii*

## 49 **1. Introduction**

50 Comprising up to 24% of the Northern Hemisphere landmass (Zhang et al., 1999; 2000), the  
51 permafrost zone is a particularly important component of the circumpolar boreal forest. Both,  
52 soil-forming activities (Ershov 1994, 1995; Gubin and Lupachev, 2008), as well as water and  
53 nutrient supply for plants (Sugimoto et al., 2002; Saurer et al., 2016; Prokushkin et al., 2018),  
54 predominantly depend on the freeze-thaw processes of the upper permafrost stratum, the so-  
55 called active layer (Permafrost Subcommittee, 1988). Operating at large spatial and temporal  
56 scales, a multitude of effects, related to the current global climate change, have been reported  
57 as responsible for changes in the behavior of different components of the permafrost-sphere  
58 (Grosse et al., 2016); and these influences are expected to increase under predicted future  
59 warming (IPCC, 2013). In this regard, far reaching ecological consequences are expected well-  
60 beyond the widespread permafrost body itself (Chadburn et al., 2017; Gasser et al., 2018;  
61 Lawrence and Slater, 2005; Nelson et al., 2001; Schuur et al., 2015; Tei et al., 2017). A key  
62 example of indirect effects of warmer temperatures on permafrost thawing is a change in the  
63 hydrological and biogeochemical fluxes that are characteristic of high northern latitudes  
64 (McGuire et al., 2002; Pokrovsky et al., 2005).

65         Trees of genus *Larix* dominate over 20% of boreal forests and are the most wide-spread  
66 in the permafrost zone of Eurasia (Abaimov et al., 1997). Being well adapted to harsh  
67 environments, larch trees are resistant to extremely low winter temperatures and the effects of  
68 late spring and early autumn frosts. One of the genus' main protective adaptations to low soil  
69 temperatures, and a particularly shallow active layer, is production of adventitious roots  
70 (Cooper, 1911; Sukachev, 1912). Adventitious rooting is also observed in other species in the  
71 boreal forests, e.g. black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* (L.)  
72 Mill.), Scots pine (*Pinus sylvestris* L.), Siberian fir (*Abies sibirica* Ledeb) and Siberian pine  
73 (*Pinus sibirica* Du Tour). Tree-rings studies of roots help in understanding the adaptive strategy

74 of trees on permafrost. Studies on the timing of root initiation of conifers in Canada  
75 (Fayle,1968; Krause and Morin, 2005) and Siberia (Kajimoto, 2010) suggest a process of  
76 renewal of the adventitious roots due to reductions of deeper soil temperature and decrease of  
77 active layer thickness with stand maturation. However, despite the importance of roots for tree  
78 stabilization, as well as absorption and transport of water and minerals, investigations of tree  
79 roots in boreal and especially permafrost zones are relatively rare and mainly focused on root  
80 biomass estimations and above- to belowground carbon partitioning (Baret et al., 2015; Kurz et  
81 al., 1996; Mokany et al., 2006 and references therein). Most tree-ring studies of roots are  
82 devoted to specific questions, like understory competition (Zaitsev et al., 2018), effect of  
83 thinning (Krause et al., 2014; Lemay et al., 2017; Vincent et al., 2009; Ruel et al., 2003), species  
84 adaptation to local soil conditions (Kajimoto et al., 2003; Krause and Morin, 2005).

85         Wildfires are the major driver of forest structure and species composition in the boreal  
86 zone and their impact should be considered when assessing spatiotemporal changes in the  
87 energy exchange, biogeochemistry, hydrology and carbon storage of the boreal forest (Certini,  
88 2005; Conard and Ivanova, 1997; Köster et al., 2017). Various ecosystem components  
89 including stand composition, ground vegetation, organic layer and soils, soil microbial  
90 community and zoobiota are heavily affected by wildfires (Bezkorovainaya et al., 2016; Gibson  
91 et al., 2018; Masyagina et al., 2016; Moore, 1996; Sorokin et al., 2000; Tiedemann et al., 1979;  
92 Viereck and Schandelmeier, 1980; Waldrop and Harden, 2008 and reference therein). The mean  
93 return interval of extensive fires in the larch dominated areas of the middle taiga, in the south  
94 of permafrost zone in Central Siberia, is  $77\pm 20$  years. The frequency of wildfires decreases with  
95 latitude to  $82\pm 7$  years in the northern taiga zone at  $\sim 64^\circ\text{N}$ , and up to  $320\pm 50$  years at the treeline  
96 ecotone  $\sim 71^\circ\text{N}$  (Kharuk et al., 2011; Panyushkina and Arbatskaya, 1999; Vaganov and  
97 Arbatskaya, 1996). Although it has been argued that the frequency and intensity of wildfires  
98 will increase under warmer temperatures (Kharuk et al., 2013), little is known how fires will,

99 directly and/or indirectly, contribute to changes in the seasonally thawing active layer.  
100 Considering most of northern Eurasia's permafrost area is covered by larch forests (Abaimov  
101 et al., 1997), and the importance of wildfires in boreal zone, it is worthwhile to assess possible  
102 fire effects on permafrost active layer dynamics in larch dominated ecosystems. The impact of  
103 wildfire on forest ecosystems in the permafrost zone has been intensively studied in Siberia  
104 (Sofronov and Volokitina, 2010 and references therein). However, our knowledge of the long-  
105 term effect of fire on active soil layer is still limited. Though it is well-known that seasonal  
106 thaw depth increases after wildfire (e.g. Mackay, 1970; Pozdnyakov, 1986; Yoshikawa et al.,  
107 2002), and decreases with subsequent re-vegetation (e.g. Fisher et al., 2016; Loranty et al.,  
108 2018; Mackay, 1995; Shiklomanov et al., 2010), the rates of these processes are unknown for  
109 Siberia. This pending task appears particularly relevant to current debates on the amount of  
110 carbon and methane that might be released from melting permafrost in a warmer future  
111 (Anisimov, 2007; Koven et al., 2011; Schaefer et al., 2011; Schuur et al., 2015).

112 Here, we present the first tree ring-based reconstruction of long-term changes in the  
113 depth of the seasonally thawing upper permafrost stratum that occurred after a massive wildfire  
114 burned most of a forest ecosystem in 1899. Conducted in an undisturbed, natural forest in  
115 Central Siberia, our study aims to test the hypothesis that fire-induced modifications of the  
116 active layer depth are directly related to the rate of change in the insulating vegetation cover,  
117 and thus may range from decades to centuries.

118

## 119 **2. Material and Methods**

120 This study was conducted in an undisturbed Gmelin larch (*Larix gmelinii* (Rupr.) Rupr.)  
121 dominated *Sphagnum* bog, in the Kochechum River valley, in Central Siberia (64°19'30''N,  
122 100°14'53'E and 147 m a.s.l.) (Fig. 1a). Details on stand and soil characteristics are given in a  
123 recent study by Prokushkin et al. (2018). Located within the continuous permafrost zone, the

124 region is characterized by a severe continental climate. Based on meteorological measurements  
125 from the nearby instrumental station in Tura, the mean annual temperature since 1929 is  $-8.9^{\circ}$   
126 C. The warmest ( $+16.6^{\circ}$  C) and coldest ( $-35.9^{\circ}$  C) monthly means are most often recorded in  
127 July and January, respectively. The average amount of annual precipitation is 357 mm, and the  
128 growing season is generally restricted to  $\sim 70$ – $90$  days between the end of May and the  
129 beginning of September (Bryukhanova et al., 2013; Shishov et al., 2016).

130 In this study we follow the approach proposed by Borggreve (1889), who suggested that  
131 tree seeds, which germinate on the surface of a *Sphagnum* bog, allow moss expansion to be  
132 estimated. This is based on the fact that *Sphagnum* grows vertically during succession, but a  
133 tree's root collar (hypocotil) remains at the same position at which its seed germinated. The  
134 upright developing *Sphagnum* mat thus buries the lower part of a tree stem which can, in the  
135 case of larch, produce adventitious roots (Cooper, 1911; Kajimoto et al., 2003; Sukachev,  
136 1912). Assuming that seed germination occurred on the *Sphagnum* surface, tree age at the collar  
137 provides precise information of the annual rates of vertical moss growth (Borggreve, 1889;  
138 Dubakh, 1927; Schulze et al., 2002; Knorre et al., 2003; Prokushkin et al., 2006).

139 For larch growing on *Sphagnum*-dominated permafrost sites, it was found that tree-ring  
140 formation ceases at different positions along those portions of roots and stem that are buried in  
141 moss in different years (Fig. 2). Consequently, we use data on cambium cessation at different  
142 locations along the larch tap-roots and stems, below the current moss surface, to reconstruct  
143 changes in the active soil layer thickness.

144 Ten and five larch trees between 0.6–3.0 m high were sampled in late July 2002 and  
145 2005, respectively. From each tree, a total of 3–11 discs were cut along the buried stem section  
146 from the current surface of the moss layer down to the level of the root collar (Fig. 1b). For  
147 each disc sample, ring widths were measured along the two longest, undisturbed and continuous  
148 radii using a LINTAB measuring system (RINNTECH e.K., Heidelberg, Germany). The disc-

149 specific ring width series were visually cross-dated and then averaged with the TSAP-win  
150 software (Rinn, 2003). The resulting within-disc chronologies were further cross-dated between  
151 discs from different positions of the same tree. The cross-dated ring width chronologies were  
152 then used to define the calendar year of the first, oldest (innermost) and last, youngest  
153 (outermost) tree ring at each sample depth of the belowground stem section. The calendar year  
154 of the innermost ring at the root collar was considered the year of tree establishment, whereas  
155 the year of the outermost ring referred to the last year of cambium activity at this particular  
156 stem position. Due to heavily suppressed wood formation, the outermost rings in 3 out of 75  
157 discs could not be accurately cross-dated and were therefore excluded from further analysis.

158         To test the hypothesis of a thermally-induced cessation of cambial activity within the  
159 belowground part of a tree, a set of waterproof sensors (S-TMB-M002; Onset Computer  
160 Corporation, Bourne, MA, USA) were installed to measure soil temperatures at 5, 10, 20 and  
161 40 cm stem depth below the *Sphagnum* surface. All sensors were connected to a HOBO Micro  
162 Station Data Logger (H21-002; Onset Computer Corporation, Bourne, MA, USA), which  
163 recorded mean temperatures each hour at each depth from the end of the 2007 growing season  
164 until the end of the 2008 growing season. The hourly data were then averaged to produce a time  
165 series of daily temperature means at different soil/stem depths.

166         To date the wildfire at our site, fire-scars on two trees that survived the last fire, growing  
167 at the edge of the *Sphagnum* bog, were dendrochronologically analyzed. To estimate the spatial  
168 extent of this wildfire fire scars on trees at 8 sites, located up to 22 km away, were also dated.  
169 To reconstruct the active soil layer thickness during the first decades after fire, we complement  
170 our data with measurements of seasonal permafrost active layer depth at four sites affected by  
171 different wildfires in 2005, 1994, 1990 and 1981. These additional measurements were obtained  
172 between mid-July and mid-August 2005.

173

174 **3. Results and Discussion**

175 The tree-ring analysis of fire scars from trees in the region indicate that the last major wildfire  
176 at the study site occurred in 1899 AD and affected an area of at least 250 km<sup>2</sup>. The vast spatial  
177 extent of the fire and low number of survived trees at the edge of the studied ecosystem suppose  
178 high severity of the wildfire at the site. This suggests the fire completely devastated the site,  
179 burning nearly all trees, as well as the understory vegetation, including the extensive moss layer  
180 and large parts of the organic upper soil horizon.

181 Tree-ring dating of wood samples from the root collar indicates that the regeneration  
182 rate of new larch trees was particularly high during the first decades after the wildfire (Fig. S1),  
183 which is due to favorable soil temperature regime and, most probably, a lack of competition for  
184 new seedlings since the ground vegetation had been completely removed by wildfire (Sofronov  
185 and Volokitina, 2010). About 50% of all of the trees germinated within the first 10 years after  
186 the fire, and all of the larch seedlings established between 1900 and 1932 AD. Therefore, the  
187 age of the individual larches that were sampled varies from 71–103 years, with a mean of 91  
188 years ( $\pm 9.4$  standard deviation; STDEV). As a direct consequence of the post-fire reforestation  
189 that coincided with the spatial expansion and vertical rise of the *Sphagnum* mat, the root collars  
190 of the sampled trees are now buried under a 20–45 cm thick moss layer. The mean root collar  
191 depth is 32.5 cm ( $\pm 6.5$  STDEV).

192 Recovery of ground vegetation reduced the depth of the permafrost active layer. Sealing  
193 the roots and stems in permafrost leads to cessation of cambial activity. Since the outermost  
194 tree ring of each disc refers to the year in which cambial activity stopped, we found a positive  
195 relationship between cessation and moss-peat layer thickness, with the upper levels of the  
196 buried stem dying later (Fig. 2, S1). The average difference, in calendar years, of the formation  
197 of the last (outermost) tree-rings in the uppermost discs collected at the current moss-layer  
198 surface, and the lowermost root collar disks was 35.6 years ( $\pm 13.1$  STDEV), and ranged from



199 6–58 years for trees established in between 1900 and 1932. In general, belowground stem parts  
200 at positions closest to the current moss surface, on average, live longer than deeper stem layers  
201 (Fig. 2, S1). The duration of cambial activity for buried stems, at around 30–45 cm depth,  
202 ranged between 24 and 69 years, compared to 61–97 years of cambial activity at the moss  
203 surface. At our study site, the cessation of cambial activity in larch stems started in 1946 (Fig.  
204 3). Using the information of cessation dates and *Sphagnum* layer thickness for all the trees at  
205 our site (as an example shown to Fig. 2 for tree N5), we find a significant linear relationship  
206 ( $R=0.81$ ,  $p<0.001$ ) between these two variables (Fig. 3). Consequently, the most recent cases  
207 of cambial termination are observed at a depth of 10–15 cm below the moss surface.

208         Seasonal measurements of temperature at different moss depths confirm the importance  
209 of low temperatures on belowground stem growth at depths of 10–40 cm (Fig. 4). At a depth of  
210 10 cm, the 5°C level, that is widely accepted as the lower temperature limit for xylogenesis  
211 (Rossi et al., 2007, 2008; Körner 2012), is reached by the middle of June, and never reached at  
212 a depth of 20 cm. Though the temperatures at a depth of 15 cm were not measured, we theorize  
213 that a suitable period for tree-ring formation below 15 cm is too short and arrives, if ever, late  
214 in the season (Bryukhanova et al., 2013).

215         The combination of tree-rings in buried stems, active layer thickness at sites affected by  
216 wildfire in different years, as well as features of *Sphagnum* growth (Prokushkin et al., 2006),  
217 permit the reconstruction of changes in the seasonal thaw depth of the upper permafrost layer  
218 over the last century (Fig. 5). The forest fire that occurred in 1899 and killed most of the larch  
219 trees also burned the insulating layer of ground vegetation. As a consequence of this removal,  
220 seasonal thawing of permafrost started earlier in spring. In 1-2 years after the fire the active  
221 layer is up to 1.5 m thick. Rain water, which is not intercepted by the ground vegetation,  
222 supplies additional heat from the atmosphere to the soil. These favorable conditions stimulate  
223 successful regeneration of larch (current density at the site is 5700 trees/ha) and formation of

224 deep rooting systems. During the first years after wildfire seasonal tree growth extends from  
225 late May till early September. During this period the ground vegetation, is largely represented  
226 by patches of *Sphagnum* and other vegetation that extend mostly horizontally, and gradually  
227 occupy the area with time. Vertical growth of *Sphagnum* occurs primarily in slight depressions.  
228 According to our estimates (Prokushkin et al., 2006) the duration of this recovery period is  
229 approximately 20 years (Fig. 3). The decomposition rate of litter during this period is high due  
230 to optimal hydro-thermal conditions, and vertical growth rates of mosses are low.

231         Formation of a continuous ground vegetation layer insulates the soil. Vertical growth of  
232 *Sphagnum* leads to a delay in seasonal permafrost thawing in summer and a gradual decrease  
233 of active soil layer thickness from year to year. Our data suggest that the rising permafrost table  
234 leads to the progressive cessation of growth of the buried stem, as well as adventitious roots  
235 beneath the moss layer. Cambium cessation of buried stems started in the 1940s at the current  
236 depth of ~40 cm. If 20 years are necessary for *Sphagnum* to cover the surface (Prokushkin et  
237 al., 2006) (Fig. 5, stage i), then it would take 25-30 years for the moss to develop a 15 cm thick  
238 layer, assuming an annual rate of 0.5-0.6 cm/year (Prokushkin et al., 2006; Knorre et al., 2006),  
239 which is large enough to insulate the ground sufficiently for the permafrost to rise (Fig. 5, stage  
240 ii). As the peat layer continues to grow, the permafrost rises, and cessation of cambial activity  
241 occurs at higher and higher levels along the buried stems (Fig. 5 stage iii).

242         The data presented in Fig. 3 are used to estimate the rate of post-fire permafrost “rise”,  
243 i.e. reduction of the active layer post 1940s. The slope of the regression (0.52 cm/year) indicates  
244 the rate at which the height of cambial activity cessation, along the buried stem, rises following  
245 the active layer thinning. Our estimate for the rate of permafrost recovery (0.52 cm/year) is in  
246 line with the rate of vertical moss growth in the region (Prokushkin et al., 2006, Knorre et al.,  
247 2006). Some difference in the rate of permafrost rise between the trees (Fig. 3) could be related

248 to the difference in thermo-hydrological conditions and various elements of micro-topography  
249 (mounds and troughs), and variations in density of the insulating moss cover.

250 In the forest ecology community, the general understanding of post-fire dynamics of  
251 vegetation and consequent changes in active soil layer thickness in the permafrost zone is that  
252 the seasonally thawing soil layer usually deepens quickly over the first post-fire years, and  
253 slowly recovers following re-vegetation (e.g. Brown et al., 2015; Pozdnyakov, 1986). These  
254 conclusions are supported by a number of multi-decadal observations of soil layer thickness in  
255 Canada and Alaska (Brown et al., 2000; Mackay, 1995; Viereck et al., 2008). Though these  
256 data provide unique information, their obtainment requires repeated measurements over several  
257 decades and are mostly devoted to particular habitats (Burn, 1998; Minsley et al., 2016). Our  
258 study case is also site-specific. The proposed technique was tested at only site which is  
259 characterized by high accumulation rates of insulating soil organic matter. To understand the  
260 spatial applicability of this methods, it needs to be verified at a variety of permafrost sites  
261 dominated by moss across the boreal forest, which occupy up to 55% of the studied region  
262 (Korets et al., 2016). Moreover, this new tree-ring based approach can provide annually  
263 resolved data from many sites within one field season, which is not possible with the direct  
264 observation methods.

265

#### 266 **4. Conclusions**

267 Here we demonstrate a new technique for reconstructing the post-wildfire recovery of  
268 permafrost in Central Siberia based on dendrochronological dating of stems buried in the moss  
269 layer. Our case study is supported with direct measurements of active layer thickness at the  
270 chronosequence of forest ecosystems affected by fires over the past decades. The data indicate  
271 the proposed technique is successful in reconstructing the dynamics of ground cover recovery  
272 and soil active layer thickness changes with annual resolution, and shows that the effect of

273 wildfire on active soil thickness persists for several decades. This implies long-term  
274 consequences for carbon, nutrient and water balance of the ecosystem, resulting in increased  
275 microbial and zoobiota activity in a deeper and warmer active soil layer (Fig. 5). Further  
276 investigations on root tree-rings in the permafrost zone are needed at more sites to quantify the  
277 effect of the current climate changes on the active soil layer thickness.

278

## 279 **Acknowledgments**

280 We are grateful to Dr. Andrea H. Lloyd for her critical comments on early version of the  
281 manuscript. Additional sample analysis and paper writing was supported by the Russian  
282 Science Foundation (project RSF 18-14-00072). Ministry of Education and Science of the  
283 Russian Federation (project # 5.3508.2017/4.6) partly supported the work of AAK at the final  
284 stage of paper writing. ASP thanks to the Russian Foundation for Basic Research (project RFBR  
285 18-05-60203). Two anonymous referees kindly provided useful comments and suggestions.

286

## 287 **Author contributions**

288 AVK initiated the study. AAK, ASP and AVK collected the material, AAK measured the  
289 material and prepared the first draft of the manuscript. UB and PJK worked on the final version  
290 of the paper with comments from AVK and ASP. All authors provided critical discussion.

291

## 292 **References**

- 293 Abaimov, A.P., Bondarev, A.I., Zyryanova, O.A., Shitova, S.A., 1997. Polar forests of  
294 Krasnoyarsk region. Novosibirsk, Nauka, 208 pp. (in Russian).
- 295 Anisimov, O.A., 2007. Potential feedback of thawing permafrost to the global climate system  
296 through methane emission. *Environ. Res. Lett.* 2, 045016.
- 297 Baret, M., Pepin, S., Ward C., Pothier, D., 2015. Long-term changes in belowground and  
298 aboveground resource allocation of boreal forest stands. *For. Ecol. Manag.* 350, 62-69.

299 Bezkorovainaya, I.N., Evgrafova, S.Y., Klimchenko, A.V., Zakharchenko, L.P., 2016.  
300 Biomass and potential activity of soil biota in cryogenic forest ecosystems of Central  
301 Siberia. Russian J. For. Res. 2, 127-134 (in Russian).

302 Borggreve, B. 1889. Über die Messung des Wachstums von Hochmooren. Mitteilungen des  
303 Vereins zur Förderung der Moorkultur im Deutschen Reich 7, 20–23.

304 Brown, J., Hinkel, K.M. & Nelson, F.E. 2000. The Circumpolar Active Layer Monitoring  
305 (CALM) Program: Research designs and initial results. Polar Geography 24(3): 166-254.

306 Brown, D. R. N., Jorgenson, M. T., Douglas, T. A., Romanovsky, V. E., Kielland, K.,  
307 Hiemstra, C., Euskirchen, E. S., Ruess, R. W., 2015. Interactive effects of wildfire and  
308 climate on permafrost degradation in Alaskan lowland forests, J. Geophys. Res. Biogeosci.  
309 120, 1619–1637.

310 Bryukhanova, M. V., Kirilyanov, A. V., Prokushkin, A. S., Silkin, P. P., 2013. Specific  
311 features of xylogenesis in Dahurian larch, *Larix gmelinii* (Rupr.) Rupr., growing on  
312 permafrost soils in Middle Siberia. Russian J. Ecol. 44 (5), 361-366.

313 Burn, C. R., 1998. The response (1958-1997) of permafrost and near-surface ground  
314 temperatures to forest fire, Takhini River valley, southern Yukon Territory. Can. J. Earth  
315 Sci. 35, 184-199.

316 Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143 (1), 1-  
317 10.

318 Chadburn, S.E., Burke, E.J., Cox, P.M., Friedlingstein, P., Hugelius G., Westermann, S.,  
319 2017. An observation-based constraint on permafrost loss as a function of global warming.  
320 Nature Climate Change 7, 340-345.

321 Conard, S.G., Ivanova, G.A., 1997. Wildfire in Russian Boreal Forests—Potential Impacts of  
322 Fire Regime Characteristics on Emissions and Global Carbon Balance Estimates.  
323 Environmental Pollution 98 (3), 305-313.

324 Cooper, W.S., 1911. Reproduction by layering among conifers. Bot. Gaz. 52, 369–379.

325 Dubakh, A.D., 1927. Moss Growth and Peat Accumulation in Byelorussian Bogs, Izv.  
326 Leningrad. Les. Inst. 35, 190–199 (in Russian).

327 Ershov, Yu.I., 1994. Mesomorphic soil formation in cryogenic-taiga semihumid region of  
328 Central Siberia. Pochvovedenie (Eurasian Soil Sci.) 10, 10–18 (in Russian).

329 Ershov, Yu.I., 1995. Features of forest soil formation in the north of Central Siberia.  
330 Pochvovedenie (Eurasian Soil Sci.) 7, 805–810 (in Russian).

331 Fayle, D.C.F., 1968. Radial growth in tree roots. Tech. Rep. Fac. For. Univ. Toronto, 9, 183  
332 pp.

333 Fisher, J.P., Estop-Aragónés, C., Thierry, A., Charman, D.J., Wolfe, S.A., Hartley, I.P.,  
334 Murton, J.B., Williams, M., Phoenix, G.K., 2016. The influence of vegetation and soil  
335 characteristics on active-layer thickness of permafrost soils in boreal forest. *Glob. Chang.*  
336 *Biol.* 22(9), 3127-3140.

337 Gasser, T., Kechiar, M., Ciais, P., Burke, E.J., Kleinen, T., Zhu, D., Huang, Y., Ekici, A.,  
338 Obersteiner, M., 2018. Path-dependent reductions in CO<sub>2</sub> emission budgets caused by  
339 permafrost carbon release. *Nature Geoscience*. In Press. DOI 10.1038/s41561-018-0227-0.

340 Gibson, C.M., Chasmer, L.E., Thompson, D.K., Quinton, W.L., Flannigan, M.D., Olefeldt D.,  
341 2018. Wildfire as a major driver of recent permafrost thaw in boreal peatlands. *Nature*  
342 *Communications* 9, 3041.

343 Grosse, G., Goetz, S., McGuire, A.D., Romanovsky, V.E., Schuur, E.A.G., 2016. Changing  
344 permafrost in a warming world and feedbacks to the Earth system. *Environ. Res. Lett.* 11,  
345 040201.

346 Gubin, S.V., Lupachev, A.V., 2008. Soil formation and the underlying permafrost. *Eurasian*  
347 *Soil Science* 41 (6), 574–585.

348 IPCC, 2013. Climate change 2013: The Physical Science Basis. Contribution of Working  
349 Group I to the Fifth Assessment Report of Intergovernment Panel on Climate Change  
350 [Stoker, T.F., D. Qin, G.-K.Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y.  
351 Xia, V. Bex and P.M. Middley (eds.)]. Cambridge University Press, Cambridge, United  
352 Kingdom and New York, NY, USA, 1535 pp.

353 Kajimoto, T., Matsuura, Y., Osawa, A., Prokushkin, A.S., Sofronov, M.A., Abaimov, A.P.,  
354 2003. Root system development of *Larix gmelinii* trees affected by micro-scale conditions  
355 of permafrost soils in central Siberia. *Plant Soil* 255, 281–292.

356 Kajimoto, T., 2010. Root system development of larch trees growing on permafrost. In:  
357 Osawa, A., Zyryanova, O.A., Matsuura, Y., Kajimoto, T. & Wein R.W. (Eds.), *Permafrost*  
358 *Ecosystems: Siberian Larch Forests*, Ecological studies, 209, 303-330.

359 Kharuk, V.I., Dvinskaya, M.L., Ranson, K.J., 2013. Fire return intervals within the northern  
360 boundary of the larch forest in Central Siberia. *Int. J. Wildland Fire* 22(2): 207-211.

361 Kharuk, V.I., Ranson, K.J. Dvinskaya, M.L., Im, S.T., 2011. Wildfires in northern Siberian  
362 larch dominated communities. *Environ. Res. Lett.* 6, 045208

363 Knorre, A.A., Vaganov, E.A., Shashkin, A.V., Schulze, E-D., 2003. A method of theoretical  
364 and experimental evaluation of carbon accumulation in bog ecosystems. *Doklady Biol. Sci.*  
365 388, 49-51.

366 Knorre, A.A., Kirdyanov, A.V., Vaganov, E.A., 2006. Climatically-induced interannual  
367 variation in aboveground biomass productivity in the forest-tundra and northern taiga of  
368 central Siberia. *Oecologia* 147, 86-95.

369 Korets, M. A., Ryzhkova, V. A., Danilova, I. V., Prokushkin A. S., 2016. Vegetation cover  
370 mapping based on remote sensing and digital elevation model data. *Materials of the XXIII*  
371 *ISPRS Congress “The International Archives of the Photogrammetry, Remote Sensing and*  
372 *Spatial Information Sciences”*, vol. XLI-B8, 699-704.

373 Koven, C.D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D.,  
374 Krinner, G., Tarnocai, C., 2011. Permafrost carbon-climate feedbacks accelerate global  
375 warming. *PNAS* 108 (36), 14769-14774.

376 Körner, C., 2012. *Alpine treelines: functional ecology of the global high elevation tree limits.*  
377 Springer, Berlin.

378 Köster, E., Köster, K., Berninger, F., Aaltonen, H., Zhou, X., Pumpanen, J., 2017. Carbon  
379 dioxide, methane and nitrous oxide fluxes from a fire chronosequence in subarctic boreal  
380 forests of Canada. *Sci. Total Environ.* 601–602, 895-905.

381 Krause. C., Lemay, A., Tremblay, S., Ruel, J.-C., Plourde, P.-Y., 2014. How does the root  
382 system inhibit windthrow in thinned black spruce sites in the boreal forest? *Trees* 28,  
383 1723–1735.

384 Krause, C., Morin, H., 2005. Adventive-root development in mature black spruce and balsam  
385 fir in the boreal forests of Quebec, Canada. *Can. J. For. Res.* 35, 2642–2654.

386 Kurz, W.A., Beukema, S.J., Apps, M.J., 1996. Estimation of root biomass and dynamics for  
387 the carbon budget model of the Canadian forest sector. *Can. J. For. Res.* 26(11), 1973-  
388 1979. Lawrence, D.M., Slater, A.G., 2005. A projection of severe near-surface permafrost  
389 degradation during the 21<sup>st</sup> century. *Geophys. Res. Lett.* 32, L24401.

390 Lemay, A., Krause, C., Rossi, S., Achim, A., 2017. Xylogenesis in stems and roots after  
391 thinning in the boreal forest of Quebec, Canada. *Tree Physiol.* 37, 1554–1563.

392 Loranty, M. M., Berner, L. T., Taber, E, D. Kropp, H., Natali, S. M., Alexander, H. D.,  
393 Davydov, S. P., Zimov, N. S. 2018. Understory vegetation mediates permafrost active  
394 layer dynamics and carbon dioxide fluxes in open-canopy larch forests of northeastern  
395 Siberia. *PLoS ONE* 13(3), e0194014.

396 Mackay, J. R. 1970. Disturbances to the tundra and forest tundra environment of the western  
397 Arctic. *Can. Geotech. J.* 7, 420-432.

398 Mackay, J.R., 1995. Active layer changes (1968 to 1993) following the forest-tundra fire near  
399 Inuvik, N.W.T., Canada. *Arctic and Alpine Research* 27(4), 323-336.

400 Masyagina, O.V., Tokareva, I.V., Prokushkin A.S., 2016. Post fire organic matter  
401 biodegradation in permafrost soils: Case study after experimental heating of mineral  
402 horizons. *Sci. Total Environ.* 573, 1255–1264.

403 McGuire, A.D. Wirth, C., Apps, M., Beringer, J., Clein, J., Epstein, H., Kicklighter, D.W.,  
404 Bhatti, J., Chapin III, F.S., de Groot, B., Efremov, D., Eugster, W., Fukuda M., Gower T.,  
405 Hinzman, L., Huntley B., Jia, G.J., Kasischke E., Melillo, J., Romanovsky, V., Shvidenko  
406 A., Vaganov, E., Walker, D., 2002. Environmental variations, vegetation distribution,  
407 carbon dynamics and water/energy exchange at high latitudes. *J. Veg. Sci.* 13, 301-14.

408 Minsley, B.J., Pastick, N.J., Wylie, B.K., Brown, D.R.N., Kass, M.A., 2016. Evidence for  
409 nonuniform permafrost degradation after fire in boreal landscapes. *J. Geophys. Res. Earth*  
410 *Surf.* 121, 320–335.

411 Mokany, K., Raison, R.J., Prokushkin A.S., 2006. Critical analysis of root : shoot ratios in  
412 terrestrial biomes. *Glob. Chang. Biol.* 12(1), 84-96.

413 Moore, P.D., 1996. Fire damage soils our forests. *Nature* 384, 312–313.

414 Nelson, F.E., Anisimov, O.A., Shiklomanov N.I., 2001. Subsidence risk from thawing  
415 permafrost. *Nature* 410, 889–890.

416 Panyushkina, I.P., Arbatskaya, M.K., 1999. Dendrochronological approach to study  
417 flammability of forests in Evenkia (Siberia). *Siberian Journal of Ecology* 2, 167-173 (In  
418 Russian).

419 Permafrost Subcommittee: 1988, Glossary of permafrost and related ground-ice terms,  
420 Associate Committee on Geotechnical Research, National Research Council of Canada,  
421 Ottawa, Technical Memorandum No. 142, 156 pp.

422 Pokrovsky, O.S., Schott, J., Kudryavtzev, D.I., Dupré, B., 2005. Basalt weathering in Central  
423 Siberia under permafrost conditions. *Geochimica et Cosmochimica Acta* 69 (24), 5659–  
424 5680.

425 Pozdniakov, L.K., 1986. Permafrost forestry. Nauka, Novosibirsk, 192 pp. (in Russian).

426 Prokushkin, A.S., Knorre, A.A., Kirdeyanov, A.V., Schulze, E.-D., 2006. Productivity of  
427 mosses and organic matter accumulation in the litter of *Sphagnum* larch forest in the  
428 permafrost zone. *Russian J. Ecol.* 37 (4), 225-232.



429 Prokushkin, A.S., Hagedorn, F., Pokrovsky, O.S., Viers, J., Kirilyanov, A.V., Masyagina  
430 O.V., Prokushkina M.P., McDowell W.H., 2018. Permafrost regime affects the nutritional  
431 status and productivity of larches in Central Siberia. *Forests* 9, Article 314.

432 Rinn F., 2003, TSAP-Win – Time series analysis and presentation dendrochronology and  
433 related applications. Frank Rinn, Heidelberg.

434 Rossi, S., Deslauriers, A., Anfodillo, T., Carraro, V., 2007. Evidence of threshold  
435 temperatures for xylogenesis in conifers at high altitudes. *Oecologia* 152: 1–12.

436 Rossi, S., Deslauriers, A., Gricar, J., Seo J.-W., Rathgeber, C.B.K., Anfodillo, T., Morin, H.,  
437 Levanic, T., Oven, P., Jalkanen, R., 2008. Critical temperatures for xylogenesis in conifers  
438 of cold climates. *Glob. Ecol. Biogeogr.* 17: 696–707.

439 Ruel, J.-C., Larouche, C., Achim, A., 2003. Changes in root morphology after precommercial  
440 thinning in balsam fir stands. *Can. J. For. Res.* 33, 2452–2459.

441 Saurer, M., Kirilyanov, A.V., Prokushkin, A.S., Rinne, K.T., Siegwolf, R.T.W., 2016. The  
442 impact of an inverse climate-isotope relationship in soil water on the oxygen-isotope  
443 composition of *Larix gmelinii* in Siberia. *New Phytologist*, 209, 955–964.

444 Schaefer, K., Zhang, T., Bruhwiler, L., Barrett, A.P., 2011. Amount and timing of permafrost  
445 carbon release in response to climate warming. *Tellus B* 6, 165–180.

446 Schulze, E.-D., Prokushkin, A.S., Arneth, A., et al., 2002. Net ecosystem productivity and  
447 peat accumulation in a Siberian aapa mire, *Tellus B* 54(3), 531–536.

448 Schuur, E.A.G., McGuire, A.D., Schädel, C., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius,  
449 G., Koven, C.D., Kuhry, P., Lawrence, D.M., Natali, S.M., Olefeldt, D., Romanovsky,  
450 V.E., Schaefer, K., Turetsky, M.R., Treat, C.C., Vonk, J. E., 2015. Climate change and the  
451 permafrost carbon feedback. *Nature* 520, 171-179.

452 Shiklomanov, N.I., Streletskiy, D.A., Nelson, F.E., Hollister R. D., Romanovsky V. E.,  
453 Tweedie, C. E., Bockheim, J. G., Brown, J., 2010. Decadal variations of active layer  
454 thickness in moisture-controlled landscapes, Barrow, Alaska. *J. Geophys. Res.* 115,  
455 G00I04.

456 Shishov, V.V., Tychkov, I.I., Popkova, M.I., Ilyin, V.A., Bryukhanova, M.V., Kirilyanov,  
457 A.V., 2016. VS-oscilloscope: a new tool to parameterize tree radial growth based on  
458 climate conditions. *Dendrochronologia* 39. 42-50.

459 Sofronov, M.A., Volokitina, A.V., 2010. Wildfire Ecology in Continuous Permafrost Zone.  
460 In: Osawa, A., O.A. Zyryanova, Y. Matsuura, T. Kajimoto and R.W. Wein (Eds.):  
461 Permafrost Ecosystems: Siberian Larch Forests, *Ecological studies* 209, 59-82.

462 Sorokin, N.D., Evgrafova, S.Y., Grodnitskaya, I.D., 2000. Effects of ground fires on the  
463 biological activity of cryogenic soils in northern Siberia. *Eurasian Soil Sci.* 3, 274-277.

464 Sugimoto, A., Yanagisawa, N., Naito, D., Fujita, N., Maximov, T.C., 2002. Importance of  
465 permafrost as a source of water for plants in east Siberian taiga. *Ecological Research* 17,  
466 493–503.

467 Sukachev, V.N., 1912. Vegetation of the upper basin of Tungir river (Oljekma okrug of  
468 Yakutsk district). *Transactions of Amur Expeditions* 1, 1-286 p. (in Russian).

469 Tei, S., Sugimoto, A., Yonenobu, H., Matsuura, Y., Osawa, A., Sato, H., Fujinuma, J.,  
470 Maximov, T., 2017. Tree-ring analysis and modeling approaches yield contrary response  
471 of circumboreal forest productivity to climate change. *Glob. Chang. Biol.* 23(12), 5179-  
472 5188.

473 Tiedemann, A.R., Conrad, C.E., Dieterich, J.H., Hornbeck, J.W., Megahan, W.F., Viereck,  
474 L.A., Wade, D.D., 1979. Effects of fire on water – a state-of-knowledge review USDA  
475 Forest Service General Technical Report WO-10.

476 Vaganov, E.A., Arbatskaya, M.K., 1996. Climate history and wildfire frequency in the central  
477 part of Krasnoyarsky krai. I. Climatic conditions in growing season and seasonal wildfires  
478 distribution. *Siberian J. Ecol.* 3, 9–18.

479 Viereck, L.A., Schandelmeier, L.A., 1980. Effects of Fire in Alaska and Adjacent Canada: A  
480 Literature Review. BLM-Alaska Technical Report 6. U. S. Department of the Interior,  
481 Bureau of Land Management. 124 pp.

482 Viereck, L.A., Werdin-Pfisterer, N.R., Adams, P.C., Yoshikawa, K., 2008. Effect of Wildfire  
483 and Fireline Construction on the Annual Depth of Thaw in a Black Spruce Permafrost  
484 Forest in Interior Alaska: A 36-Year Record of Recovery. *Proceedings of the Ninth*  
485 *International Conference on Permafrost, 1845-1850.*

486 Vincent, M., Krause, C., Zhang, S.Y., 2009. Radial growth response of black spruce roots and  
487 stems to commercial thinning in the boreal forest. *Forestry* 82, 557–571.

488 Waldrop, M.P, Harden, J.W. 2008. Interactive effects of wildfire and permafrost on microbial  
489 communities and soil processes in an Alaskan black spruce forest. *Glob. Chang. Biol.* 14,  
490 2591–2602.

491 Yoshikawa, K., Bolton, W. R., Romanovsky, V. E., Fukuda, M., Hinzman, L. D., 2002.  
492 Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska, *J. Geophys.*  
493 *Res.*, 107, 8148,

494 Zaitsev, G.A., Kulagin, A.Yu., Davydychev A.N., 2018. The particularities of the growth of  
495 Siberian fir (*Abies sibirica* Ledeb.) in the first stages of ontogeny in conifer forests (Ufa  
496 plateau, Pre-Ural). *Trees* 32: 511–518.

497 Zhang, T., Barry, R. G., Knowles, K., Heginbottom, J. A., Brown, J., 1999. Statistics and  
498 characteristics of permafrost and ground-ice distribution in the Northern Hemisphere. *Polar*  
499 *Geography*, 23(2). 132–154.

500 Zhang, T., Heginbottom, J.A., Barry, R.G., Brown, J., 2000. Further statistics on the  
501 distribution of permafrost and ground ice in the Northern Hemisphere. *Polar Geography*,  
502 24(2), 126-131.

503  
504  
505  
506  
507  
508  
509  
510  
511  
512  
513  
514  
515  
516  
517  
518  
519  
520  
521  
522  
523  
524  
525  
526

527 **Figure Captions**

528 **Figure 1.** (a) Study site, (b) excavated larches with adventitious roots (cut), and (c) location of  
529 the sampling area within Central Siberia (red circle).

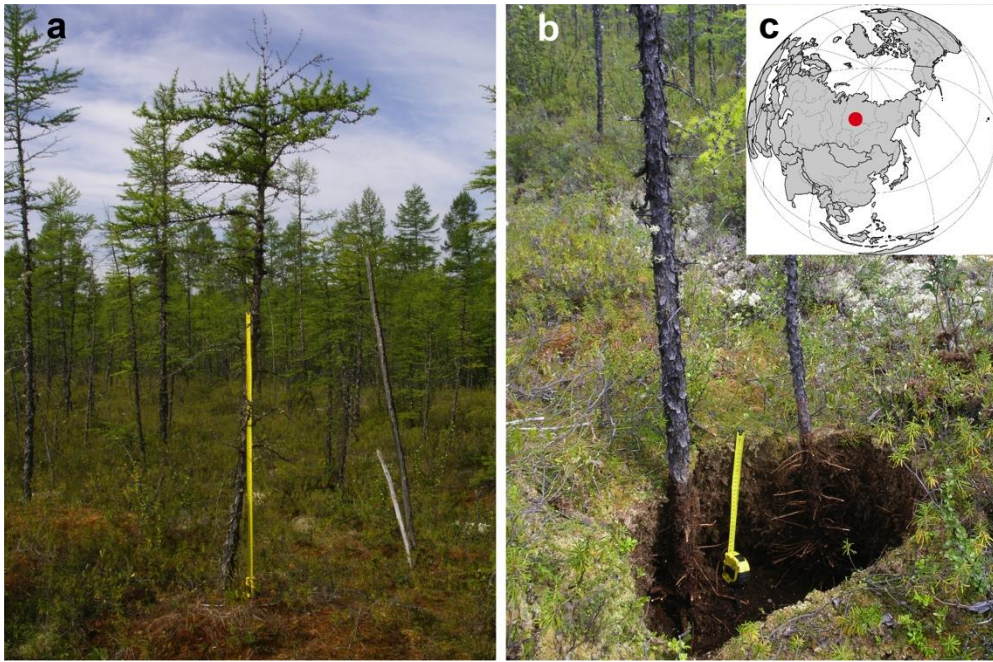
530 **Figure 2.** Averaged tree-ring width measurement series that represent different below-surface  
531 stem heights of tree N5.

532 **Figure 3.** Precise calendar dates of the outermost, last tree rings, formed at different stem  
533 depths below the upper *Sphagnum* surface before death (ranging from ~ 10 to ~ 50 cm). The  
534 linear function is a least square approximation of the permafrost rise rate, and the three-step  
535 feedback loop of: i) thawing of the upper permafrost stratum, ii) decreasing active layer depth,  
536 and iii) increasing of the upper permafrost horizon by 0.52 cm/year is shown at the bottom of  
537 the figure.

538 **Figure 4.** Temperature dynamics at four depths (5, 10, 20 and 40 cm) of a moss-peat layer at  
539 the studied site. The temperature sensors were installed in late summer 2007. The dashed  
540 horizontal line indicates the physiological minimum threshold for root growth of frost-tolerant  
541 species 2.3°C (Schenker et al., 2014), and the solid line corresponds to 5°C, a widely accepted  
542 low temperature limit for xylogenesis (Rossi et al., 2007, 2008; Körner 2012).

543 **Figure 5.** Schematic representation of the post-wildfire development of a forested *Sphagnum*  
544 bog ecosystem in the continuous permafrost zone in Central Siberia together with the main  
545 features of our sampling design and data recording.

546



547

548 **Figure 1.** (a) Study site, (b) excavated larches with adventitious roots (cut), and (c) location of  
549 the sampling area within Central Siberia (red circle).

550

551

552

553

554

555

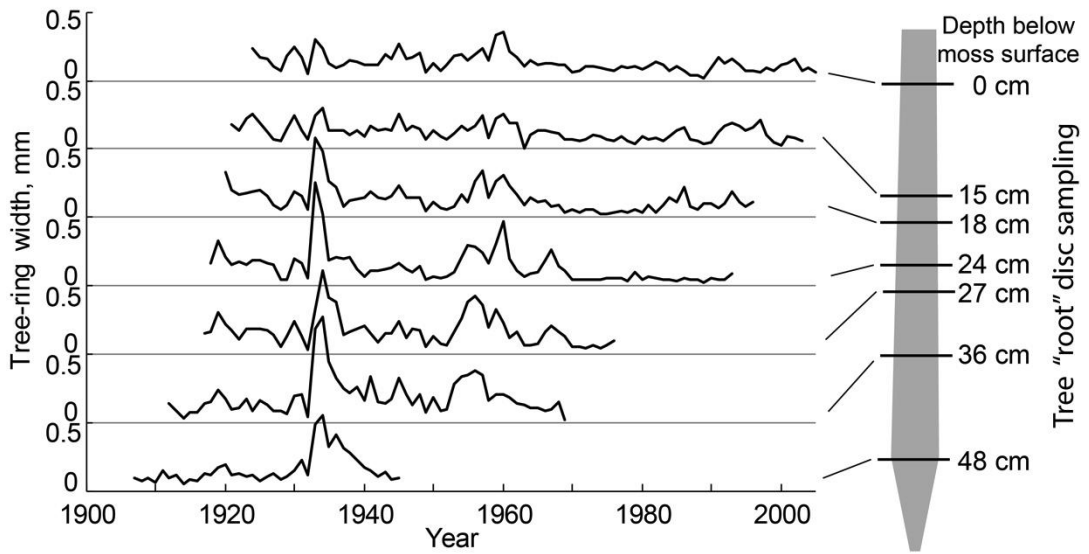
556

557

558

559

560



561

562 **Figure 2.** Averaged tree-ring width measurement series that represent different below-surface

563 stem heights of tree N5.

564

565

566

567

568

569

570

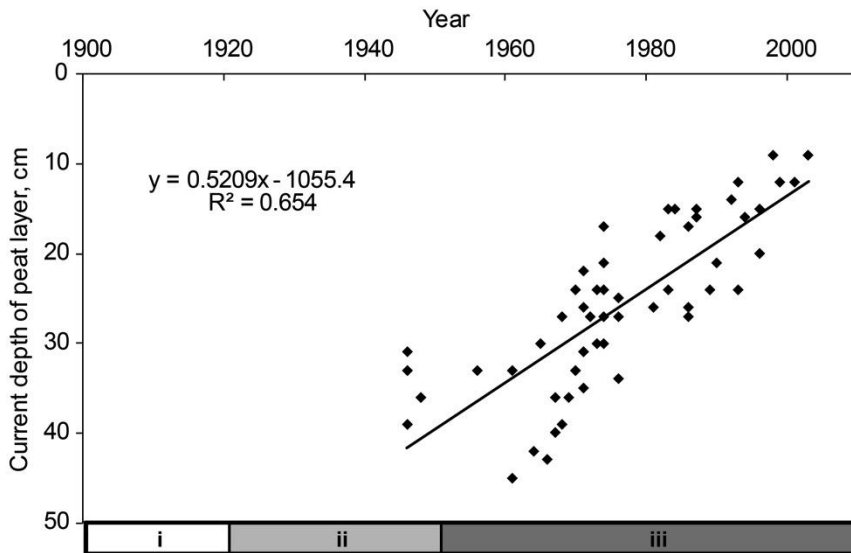
571

572

573

574

575



576

577 **Figure 3.** Precise calendar dates of the outermost, last tree rings, formed at different stem  
 578 depths below the upper *Sphagnum* surface before death (ranging from ~ 10 to ~ 50 cm). The  
 579 linear function is a least square approximation of the permafrost rise rate, and the three-step  
 580 feedback loop of: i) thawing of the upper permafrost stratum, ii) decreasing active layer depth,  
 581 and iii) increasing of the upper permafrost horizon by 0.52 cm/year is shown at the bottom of  
 582 the figure.

583

584

585

586

587

588

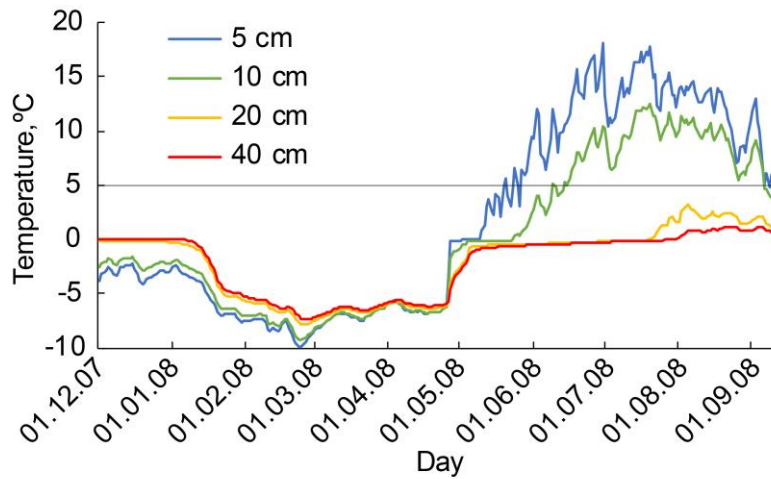
589

590

591

592

593



594

595 **Figure 4.** Temperature dynamics at four depths (5, 10, 20 and 40 cm) of a moss-peat layer at  
 596 the studied site. The temperature sensors were installed in late summer 2007. The dashed  
 597 horizontal line indicates the physiological minimum threshold for root growth of frost-tolerant  
 598 species 2.3°C (Schenker et al., 2014), and the solid line corresponds to 5°C, a widely accepted  
 599 low temperature limit for xylogenesis (Rossi et al., 2007, 2008; Körner 2012).

600

601

602

603

604

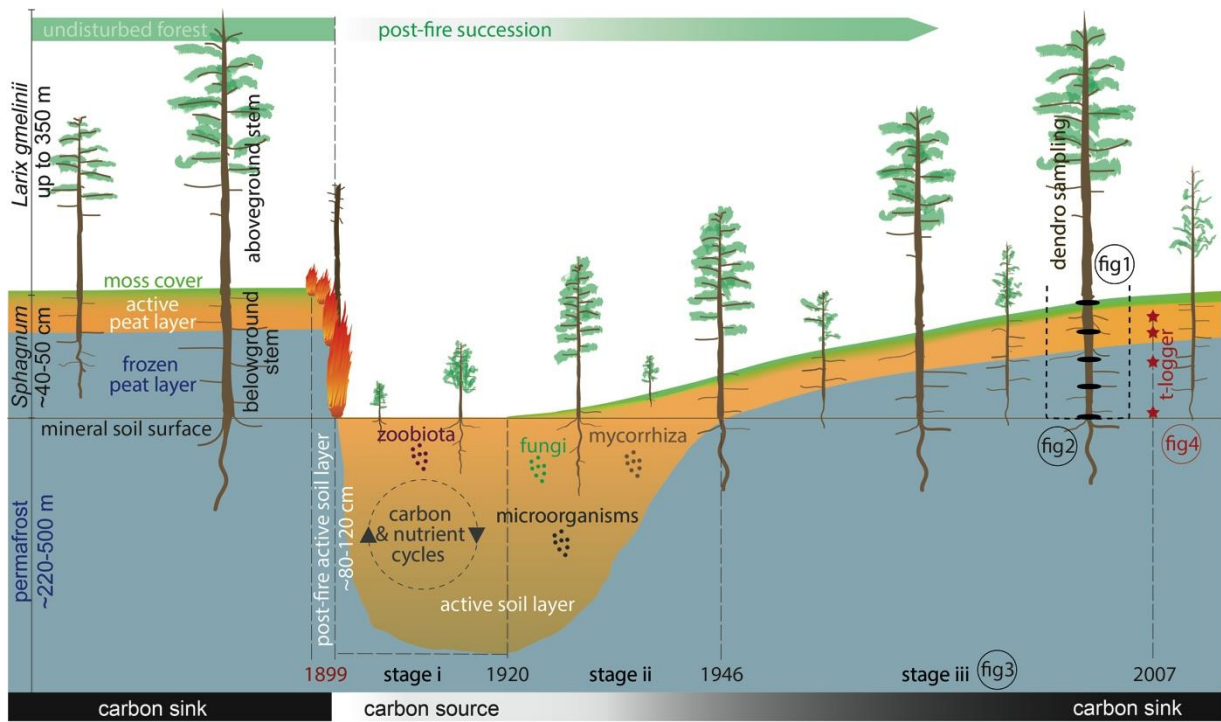
605

606

607

608





609

610 **Figure 5.** Schematic representation of the post-wildfire development of a forested *Sphagnum*  
 611 bog ecosystem in the continuous permafrost zone in Central Siberia together with the main  
 612 features of our sampling design and data recording.