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

Running title: Fire effects on permafrost active layer dynamics

Anastasia A. Knorre[a,b], Alexander V. Kirdyanov[b,c,d*], Anatoly S. Prokushkin[b], Ulf Büntgen[c,e,f,g,]

[a]*State Natural Reserve 'Stolby', Kar'ernaya 26A, Krasnoyarsk, 660006, Russia*

[b]*Sukachev Institute of Forest SB RAS, Akademgorodok, Krasnoyarsk, 660036, Russia*

[c]*Department of Geography, University of Cambridge, CB2 3EN, UK*

[d]*Institute of Ecology and Geography, Siberian Federal University, Krasnoyarsk, 660041, Russia*

[e]*Global Change Research Institute CAS, 603 00 Brno, Czech Republic*

[f]*Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland*

[g]*Department of Geography, Masaryk University, Kotlářská 2, 61137, Czech Republic*

* *Corresponding author: kirdyanov@ksc.krasn.ru (Alexander V. Kirdyanov)*

Submitted as an original research article to ***STOTEN***, 7th July 2018

Highlights

A novel technique based on dating of cambial activity cessation in tree stems buried under moss layer demonstrate a good efficiency for estimating the post-fire permafrost rise as well as reconstruction of a dynamics of ground cover recovery and soil active layer thickness changes.

A thickness of 10-15 cm of the Sphagnum layer was shown to be crucial for interrupting tree-ring production in larch roots and buried stem layers.

Wildfires exert a long-term effect on active soil layer thickness and forest ecosystems in continuous permafrost zone in northern Eurasia.

Abstract

Although it has been recognized that rising temperatures and shifts in the hydrological cycle affect the depth of the seasonally thawing upper permafrost stratum, it remains unclear if and how the frequency and intensity of wildfires and subsequent changes in vegetation cover influence this soil active layer at different spatiotemporal scales. Here, we use ring width measurements of the below-surface stem part of 15 larch trees from a *Sphagnum* bog site in Central Siberia to reconstruct long-term changes in the thickness of the active layer since the last wildfire occurred in 1899. Our novel dendroecological approach reveals a three-step feedback loop between above- and belowground ecosystem components: The thawing upper permafrost stratum increased over the first ~20 years after the fire killed almost all vegetation and thus enhanced the direct atmospheric heat penetration into the upper soil horizon. The slow recovery of the insulating ground vegetation then reversed the process and initiated a gradual decrease of the active layer depth. Due a continuous spatial and vertical thickening of the moss cover during the last decades, the upper permafrost horizon increased by 0.52 cm/year. This study, for the first time, demonstrates the strength of annually resolved and absolutely dated tree-ring chronologies to assess the effects of historical wildfires on the functioning and productivity of boreal forest ecosystems at centennial time-scale, and how the complex interaction of above- and belowground components translate into changes in the active permafrost stratum. Our results are also relevant for improving estimates of long-term changes in the terrestrial carbon pool that strongly depend on the ecosystem productivity of the boreal forest.

Keywords: boreal forest, bog, carbon cycle dynamics, ecological interaction, ecosystem response, forest ecology, permafrost, Siberia, seasonally thawing soil layer, tree rings, wildfires, *Larix gmelinii*

1. Introduction

Underling up to 24% of the Northern Hemisphere landmass (Zhang et al., 1999; 2000), permafrost is an important component of the widespread, circumpolar, boreal forest biome. Both, soil-forming activities (Ershov 1994, 1995; Gubin and Lupachev, 2008), as well as water and nutrient supply for plants (Sugimoto et al., 2002; Saurer et al., 2016; Prokushkin et al., 2018), predominantly depend on thaw-freeze processes of the upper permafrost layer. Generally operating at large spatial and temporal scales, a multitude of effects of ongoing global climate change have been reported for the behavior of different components of the permafrost-sphere (Groose et al., 2016), with their influences likely to increase under predicted warming (IPCC, 2013). In this regard, far reaching ecological consequences are expected well-beyond the permafrost body itself (Chadburn et al., 2017; Lawrence and Slater, 2005; Nelson et al., 2001; Schuur et al., 2015), such as changes in the intertwined hydrological and biogeochemical fluxes that are characteristic for the high northern latitudes (McGuire et al., 2002; Pokrovsky et al., 2005).

Moreover, wildfires are major drivers of forest structure and species composition, thus influencing the energy exchange, biogeochemistry, hydrology and carbon storage of the boreal forest (Certini, 2005; Conard and Ivanova, 1997). Although it has been argued that the frequency and intensity of wildfires will increase under rising temperatures (Kharuk et al., 2013), it is unclear how fires will, directly or indirectly, contribute to changes in the seasonally thawing upper permafrost stratum, the so-called active layer (Permafrost Subcommittee, 1988). Since most of northern Eurasia's permafrost area is covered by undisturbed larch (*Larix* spp) forests (Abaimov et al., 1997), and wildfires are a natural component of this boreal ecosystem, it is worthwhile to assess possible fire effects on permafrost active layer dynamics. This pending task appears particularly relevant to current debates on the amount of carbon and methane that might be released from melting permafrost in a warmer future (Anisimov, 2007; Koven et al., 2011; Schaefer et al., 2011; Schuur et al., 2015). Thus, greenhouse gas fluxes from the cryosphere into the atmosphere may be sufficiently affected by alterations in the return frequency, severity and spatial extent of wildfires and their impact on permafrost active layer dynamics.

Here, we present the first tree ring-based reconstruction of long-term changes in the depth of the seasonally thawing upper permafrost stratum that occurred after a massive wildfire in 1899 killed most of a *Sphagnum* forest-bog ecosystem. Conducted in an undisturbed, natural forest in Central Siberia, our study aims to test the hypothesis that fireinduced modifications of the depth of the permafrost active layer are directly related to the rate of change in the insulating vegetation cover, and thus may range from multi-decadal to centennial time-scales.

2. Material and Methods

The genus *Larix* is well adapted to the harsh environmental conditions of the widespread boreal permafrost zone in northern Eurasia. Larch trees are resistant to extremely low and extended winter temperatures, as well as to late spring and early autumn frosts. Due to the possibility of producing adventitious roots (Cooper, 2011; Sukachev, 1912), larch trees are also tolerant to very low soil temperatures and a particularly shallow active permafrost layer (Abaimov, 2010). This phenomenon is especially well pronounced in *Sphagnum* ecosystems, in which an extensive moss and peat layer translates into exceptionally high insulation rates of direct solar radiation, and subsequently cold soil conditions.

This study was conducted in an undisturbed (Fig. 1a), Gmelin larch (*Larix gmelinii* (Rupr.) Rupr.) dominated *Sphagnum* bog in the Kochechum River valley in Central Siberia (64°19’30’’N, 100°14’53’E, and 147 m asl). Located within the continuous permafrost zone, the region is characterized by a severe continental climate. Based on meteorological measurements from the nearby instrumental station in Tura that operates since 1929, mean annual temperature is -8.9° C, with the warmest (+16.6° C) and coldest (-35.9° C) monthly means mainly occurring in July and January, respectively. The average amount of annual precipitation is 357 mm, and the growing season is generally restricted to ~70-90 days between the end of May and the beginning of September (Bryukhanova et al., 2013; Shishov et al., 2016).

Dendroecological standard techniques were used to reconstruct the fire history in this region (Panyushkina and Arbatskaya, 1999; Kharuk et al., 2005, 2008). Moreover, we follow Borggreve (1889), who suggested that tree seeds which germinate on the surface of a *Sphagnum* bog may allow moss growth rates to be estimated. This approach is based on the fact that *Sphagnum* grows vertically during succession, but a tree’s root collar (hypocotil) remains at the same position at which its seed germinated. The vertically growing *Sphagnum* thus buries the lower part of a tree stem, which can, in the case of larch, produce adventitious roots (Cooper, 2011; Kajimoto, 2010; Kajimoto et al., 2003; Sukachev, 1912). Assuming that seed germination occurred on the surface of a *Sphagnum* mat, tree age at the collar provides precise, annually resolved information of the rate of vertical moss growth (Borggreve, 1889; Dubakh, 1927; Schulze at al., 2002; Knorre et al., 2003; Prokushkin et al., 2006).

For larch growing on permafrost at *Sphagnum*-dominated sites, it was found that tree-ring formation ceases at different positions along the root and buried in moss stem in different years (Fig. 2). Here we use data on cambium activity cessation at different locations along the larch tap roots and stems below the current moss surface to reconstruct the dynamics of active soil layer thickness.

Ten and five larch trees between 0.6-3.0 m high were sampled in 2002 and 2005, respectively. The moss-buried, belowground stem parts were entirely excavated (Fig. 1b), before being transported to the laboratory at the Sukachev Institute of Forest SB RAS in Krasnoyarsk. For each tree, a total of 4-11 discs were cut along the buried stem section from the current surface of the moss layer (i.e. 0 cm for each individual) down to the level of the root collar (e.g. between 27 and 45 cm depending on individual trees). For each disc sample, ring widths were measured along the two longest, undisturbed and continuous radii using a LINTAB measuring system (RINNTECH e.K., Heidelberg, Germany). The disc-specific ring width series were visually cross-dated and then averaged in TSAP-win (Rinn, 2003). The resulting disc chronologies were further cross-dated between discs from different positions of the same tree. The cross-dated ring width chronologies were then used to define the calendar year of the first, oldest (innermost) and last, youngest (outermost) tree ring at each sample depth of the belowground “stem section. The calendar year of the innermost ring at the root collar was considered the year of tree establishment, whereas the year of the outermost ring referred to the year when cambium activity ceased at this particular stem position. Due to heavily suppressed wood, the outermost rings of three out of 77 discs could not be accurately cross-dated and were therefore excluded from any further analysis.

To test the hypothesis of a thermal-induced cessation of cambial activity within the belowground part of a tree, a set of waterproof sensors S-TMB-M002 (Onset Computer Corporation, Bourne, MA, USA) were installed to measure temperatures at 5, 10, 20 and 40 cm soil/stem depth below the *Sphagnum* upper surface. All sensors were connected to a HOBO Micro Station Data Logger H21-002 (Onset Computer Corporation, Bourne, MA, USA) that recorded mean hourly temperature at each depth from the end of the 2007 growing season until the end of the 2008 growing season. Data were then averaged to represent daily temperature means at each of the depths.

To reconstruct the post-fire dynamics of active soil layer thickness, we complement our data with the measurements of seasonal upper permafrost layer thaw depth for a sequence of sites affected by wildfires in 2005, 1990, 1994, 1981 and 1947, as well as several control sites nearby that were not affected by fire for at least 150 years. These additional measurements were conducted between mid-July and mid-August 2005, i.e. still before the maximum upper permafrost thaw that usually occurs in September.

3. Results and Discussion

Killing almost all trees, as well as the entire understory vegetation, including the extensive moss layer and large parts of the organic upper soil horizon, the last major wildfire devastated the study site in 1899 AD.

The regeneration rate of larch trees was particularly high during the first decades after wildfire, because of a favorable soil temperature regime and, most probably, a lack of competition for the new seedlings since ground vegetation had been completely removed by wildfire. The vast majority of trees germinated within the first 10 years after the fire (50%) and all of the larch seedlings established within the first 34 years between 1900 and 1932 AD. The age of the individual larches that were sampled thus varies from 71-103 years, with a mean of 91 years (±9.4 years standard deviation). As a direct consequence of the post-fire reforestation that coincided with the expansion and vertical growth of *Sphagnum*, the root collars of the sampled trees are now buried under a 20-45 cm thick moss layer. The mean root collar depth is 32.5 cm (±6.5 cm).

Recovery of ground vegetation reduced the depth of the permafrost active layer and sealing the roots and stems in permafrost leads to cessation of cambial withering away. Since the outermost tree ring of each tree disc refers to the year in which cambial activity stopped, we found a positive linear relationship between cessation and moss-peat layer thickness with the upper levels of the buried stem dying later (Fig. 2). The average difference in calendar years of formation of the last (outermost) tree-rings at the uppermost disk (collected from the current surface of moss layer) and the root collar was 35.6 (± 13.1) years and ranged from 6 (for a tree established in 1932) to 58 years (for a tree established in 1900). In general, belowground stem parts at positions closer to the current moss surface on average live longer than at deeper stem layers (Fig. 2). The duration of cambial activity for stems buried 30-45 cm deep was 24-69 years, compared to 61-97 years of cambial activity at the moss surface (0 cm).

The most recent cases of cambial activity cessation are observed in the larch stem levels currently buried at the depth of 10-15 cm (Fig. 3). Seasonal dynamics of temperature at different depth of a moss layer (Fig. 4) confirm the predominant role of low temperature as a triggering factor for this activity cessation. In summer 2008, temperature at the depth of 20 cm reached 2.3°C, the physiological minimum threshold for root growth of frost-tolerant species (Schenker et al., 2014), just for a few days at the first half of July and never reaches even 3.0°C. At the depth of 10 cm, temperature becomes >2.3°C on 31 May. However, the level of 5°C, which is a widely accepted as a low temperature limit for xylogenesis (Rossi et al., 2007, 2008; Körner 2012) and a threshold for root and shoot growth of *Larix decidua* Mill. (Häsler et al., 1999), is reached only in the middle of June (14 June 2007). Seasonal growth analysis data from the region testify that by this date, up to 25% of the final tree-ring width is already completed and lignification of early wood started (Bryukhanova et al., 2013). Results of dendroclimatic analysis also confirm that climatic conditions at the very beginning of growing season are the most important for larch stem growth (Benkova et al., 2015; Kirdyanov et al., 2013; 2016). Though temperature data for the depth of 15 cm were not measured, we may conclude that the period when temperature is suitable for tree growth at this depth is too short and appears late in the season.

Our data on tree-rings in buried stems, active layer thickness for a sequence of sites affected by wildfire in different years and features of *Sphagnum* growth (Prokushkin et al., 2006) allow reconstruction of changes in seasonally thawing depth of the upper layer of permafrost and the dynamics of this particular forest-bog ecosystem over the last century (Fig. 5). A forest fire occurred in 1899 and killed most of the larch trees as well as burned the insulating layer of ground vegetation. As a consequence of removal of the ground vegetation and the forest canopy, seasonal thawing of permafrost starts earlier in spring and in 1-2 years after fire the active layer can be up to 1.5-2 m thick in late summer (Abaimov et al., 1997; our own observations in the region of sites fired in 1980-2005). Rain water, which is not intercepted by the ground vegetation, supplies additional heat flow from the atmosphere into the soil. These favorable conditions stimulate successful regeneration of larch (current density of the tree stand is 5700 trees/ha) and formation of deep rooting systems. Seasonal tree growth can last from late May till the end of vegetation period (early September) during the first years after fire. Ground vegetation during this period is mostly presented by separate patches of *Sphagnum* and other vegetation which extend mostly horizontally and gradually occupy the area with time. Vertical growth of *Sphagnum* occurs primarily in slight depressions. According to our estimates (Prokushkin et al., 2006) duration of this period is approximately 20 years (indicated as stage I on Fig. 3). Decomposition of litter is of high rate during this period due to optimal hydro-thermal conditions and vertical growth rates of mosses are low.

Formation of a continuous ground vegetation layer insulates the soil. Vertical growth of *Sphagnum* leads to a delay in seasonal permafrost thawing in summer and a gradual decrease of active soil layer thickness from year to year. Our data suggest that the rising permafrost table leads to the progressive death of the buried stem as well as adventitious roots beneath the moss layer. Cambium cessation of buried stems started in the 1950s at a current depth of ~40 cm. If 20 years are necessary for *Sphagnum* to cover the surface (Prokushkin et al., 2006), the following 25-30 years for the moss to grow up with the annual rate of 0.5-0.6 cm/year (Prokushkin et al., 2006; Knorre et al., 2006), to form a layer of approx. 15 cm thick which is enough to start cambium cessation of larch stems at lower levels of peat (period II on Fig. 3). As peat layer continues to grow up, permafrost is rising and cessation of cambial activity occurs at higher and higher levels along the buried stems (period III on Fig. 3).

Data on Fig. 3 provide the estimation of the rate of post-fire permafrost "rise", i.e. decrease of the seasonal soil thaw depth after 1950s. The mean slope of the regression line (0.52 cm/year) indicate the rate of progressive rise of the buried stem sections with cambial activity ceased due to permafrost rise (decrease of active soil layer). Our estimate for the rate of permafrost (0.52 cm/year) is quite in line with the rate of vertical moss growth in the region (Prokushkin et al., 2006, Knorre et al., 2006). Some difference in the rate of permafrost rise between the trees (Fig. 3) could be related by the difference in thermo-hydrological conditions at various elements of micro-topography (mounds and troughs) and variations in density of the insulating moss cover.

Conclusion

In this study, we used tree-rings of tap roots and buried in moss lower part of a Gmelin larch stems to reconstruct the post-fire ecosystem dynamics based on cambial activity cessation dates in a forested *Sphagnum* bog ecosystem in northern Central Siberia. A thickness of 10-15 cm of the *Sphagnum* layer was found to be crucial for interrupting tree-ring production in larch roots and buried stem layers. In general, our case study indicates a good efficiency of a proposed technique for estimating the post-fire permafrost rise as well as reconstruction of a dynamics of ground cover recovery and soil active layer thickness changes. The reconstructed dynamics of ground cover recovery and soil active layer thickness changes on The effect of fire on active soil thickness evident for at least six decades that implies a long Further investigations on root tree-rings in the permafrost zone are needed on a broader scale to get data on the effect of the current climate changes on the active soil layer thickness coupled with ecosystem productivity and tree growth in the largest monodominant vegetation belt on the globe.

Acknowledgments

We are grateful to Andrea H. Lloyd for her critical comments. Additional sample analysis and paper writing was supported by the Russian Science Foundation (project RSF 18-14-00072). Ministry of Education and Science of the Russian Federation (project # 5.3508.2017/4.6) partly supported the work at the final stage of paper writing. ASP thanks to the Russian Foundation for Basic Research (project RFBR 18-05-60203)

Author contributions

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

References

Abaimov, A.P., Bondarev, A.I., Zyryanova, O.A., Shitova, S.A., 1997. Polar forests of Krasnoyarsk region. Novosibirsk, Nauka, 208 pp. (in Russian).

Abaimov, A.P., 2010. Geographical distribution and genetics of Siberian larch species. In: Osawa, A., O.A. Zyryanova, Y. Matsuura, T. Kajimoto and R.W. Wein (Eds.): Permafrost Ecosystems: Siberian Larch Forests, Ecological studies 209, 41-58.

Anisimov O.A., 2007. Potential feedback of thawing permafrost to the global climate system through methane emission. Environ. Res. Lett. 2, 045016

Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, T L.G., Vinson, S., 1993. Boreal forests and tundra. Water, Air, and Soil Pollution 70 (1-4), 39-53.

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

Bryukhanova, M. V., Kirdyanov, A. V., Prokushkin, A. S., Silkin, P. P., 2013. Specific features of xylogenesis in Dahurian larch, Larix gmelinii (Rupr.) Rupr., growing on permafrost soils in Middle Siberia. Russian Journal of Ecology 44 (5), 361-366.

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

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

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

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

Demchenko, P.F., Eliseev, A.V., Arzhanov M.M., Mokhov, I.I., 2006. Impact of global warming rate on permafrost degradation. Izvestia Atmospheric and Oceanic Physics 42, 32-39.

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

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

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

Genet, H., McGuire, A.D., Barrett, K., Breen, A., Euskirchen, E.S., Johnstone, J.F., Kasischke, E.S., Melvin, A.M., Bennett, A., Mack, M.C., Rupp, T.S., Schuur, A.E.G., Turetsky, M.R., Yuan, F., 2013. Modeling the effects of fire severity and climate warming on active layer thickness and soil carbon storage of black spruce forests across the landscape in interior Alaska Environ. Res. Lett. 8, 045016.

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

Gubin, S.V., Lupachev, A.V., 2008. Soil Formation and the Underlying Permafrost. Eurasian Soil Science 41 (6), 574–585.

Häsler, R., Streule, A., Turner, H., 1999. Shoot and root growth of young *Larix decidua* in contrasting microenvironments near the alpine timberline. Phyton 39,.47-52.

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

Ivanova, G.A., 1996. Extremely fire risk seasons in forest of Evenkia. Siberian Journal of Ecology 1, 29-34 (in Russian).

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

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

Kirdyanov, A.V., Bryukhanova, M.V., Knorre, A.A., Tabakova, M.A., Prokushkin, A.S., 2016. Dendrochronological research of trees growing on permafrost in Siberia, Russia. In: Conference Proceedings of the 16th International Multidisciplinary Scientific GeoConference SGEM2016 (June 30- July 7, Albena, Bulgaria), STEF92 Technology Ltd., Book 3 Vol. II, 517-524 pp.

Kirdyanov, A.V., Prokushkin, A.S., Tabakova, M.A., 2013. Tree-ring growth of Gmelin larch under contrasting local conditions in the north of Central Siberia. Dendrochronologia 31(2): 114-119.

Kharuk, V.I., Dvinskaya, M.L., Ranson, K.J., 2005. The spatiotemporal pattern of fires in northern taiga larch forests of Central Siberia. Russ. J. Ecol. 36 (5), 302 – 311.

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

Kharuk, V.I., Ranson, K.J., Dvinskaya., M.L., 2008, Wildfires dynamic in the larch dominance zone. Geophysical Research Letters 35, L01402.

Knorre, A.A., Vaganov, E.A., Shashkin, A.V., Schulze, E-D., 2003. A method of theoretical and experimental evaluation of carbon accumulation in bog ecosystems. Doklady Biological Sciences 388, 49-51.

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

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

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

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

Lawrence, D.M., Slater, A.G., 2005. A projection of severe near-surface permafrost degradation during the 21st century. Geoph. Res. Lett. 32, L24401, DOI:10.1029/2005GL025080.

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

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

Osawa, A., Kajimoto, T., 2010. Development of Stand Structure in Larch Forests. . In: Osawa, A., Zyryanova, O.A., Matsuura, Y., Kajimoto, T. & Wein R.W. (Eds.), , Permafrost Ecosystems: Siberian Larch Forests, Ecological studies, 209. 502 pp.

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

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

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

Prokushkin, A.S., Knorre, A.A., Kirdyanov, A.V., Schulze, E.-D., 2006. Productivity of mosses and organic matter accumulation in the litter of sphagnum larch forest in the permafrost zone. Russian Journal of Ecology 37 (4), 225-232. Prokushkin, A.S., Hagedorn, F., Pokrovsky, O.S., Viers, J., Kirdyanov, A.V., Masyagina O.V., Prokushkina M.P., McDowell W.H., 2018. Permafrost Regime Affects the Nutritional Status and Productivity of Larches in Central Siberia. Forests 9, 314.

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

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

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

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

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

Schulze, E.-D., Prokushkin, A.S., Arneth, A., et al., 2002. Net Ecosystem Productivity and Peat Accumulation in a Siberian Aapa Mire, Tellus B. 54(3), 531–536.

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

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

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

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

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

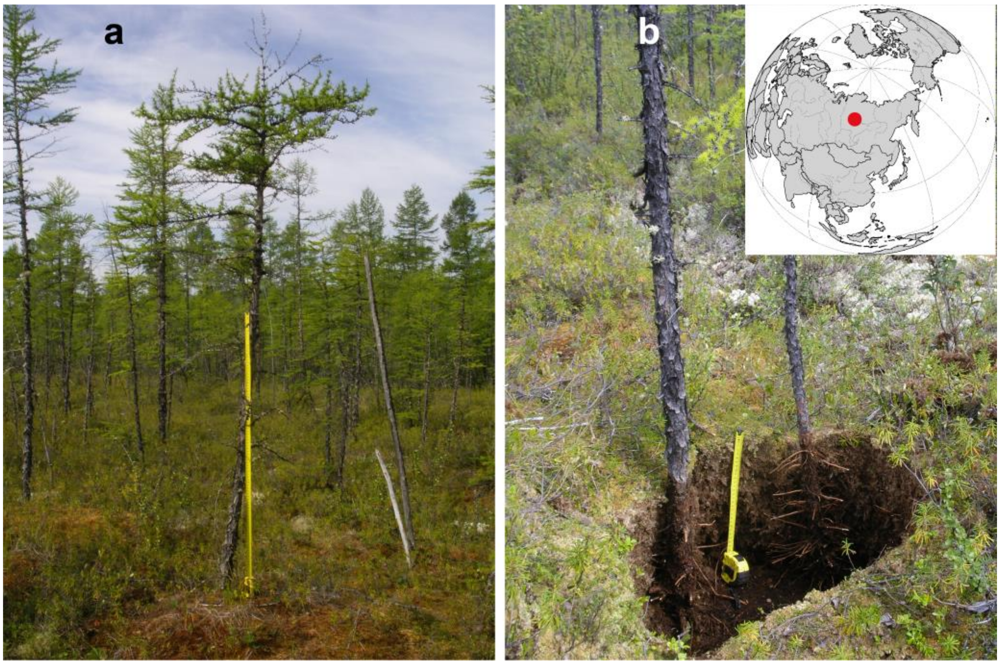

Figure 1. (a) Studied larch stand established on a *Sphagnum* bog, (b) sampled trees with adventitious roots of larch (cut) and frozen peat layer at the bottom of a ground vegetation layer. Insert shows the study site location (red circle).

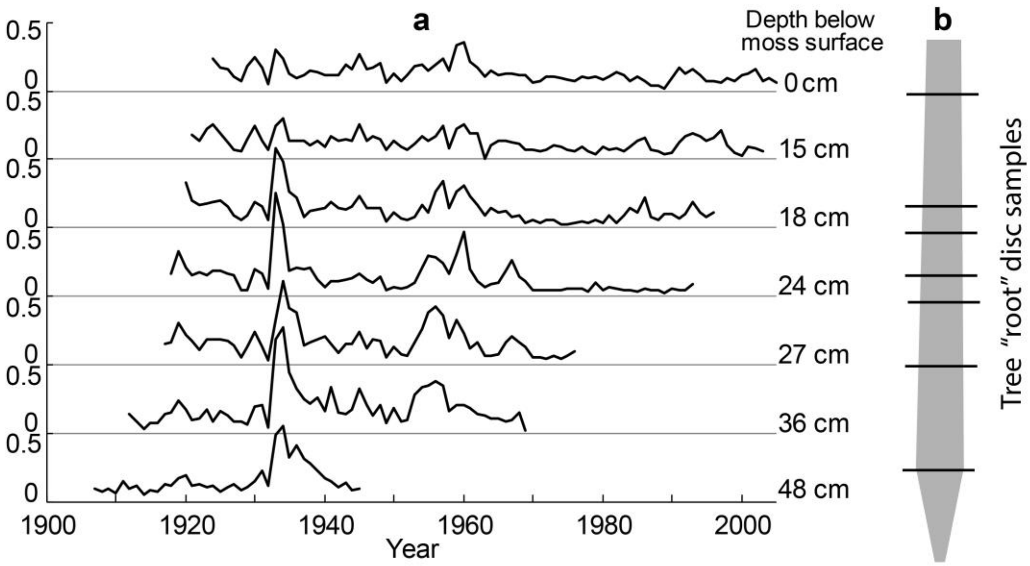

Figure 2. (**a**) Tree-ring width chronologies obtained for tree discs of tree N5 from different depths of a moss layer. (**b**) The serial section technique with the tree disc samples along the "root" shown on the panel (**a**) for the tree N5

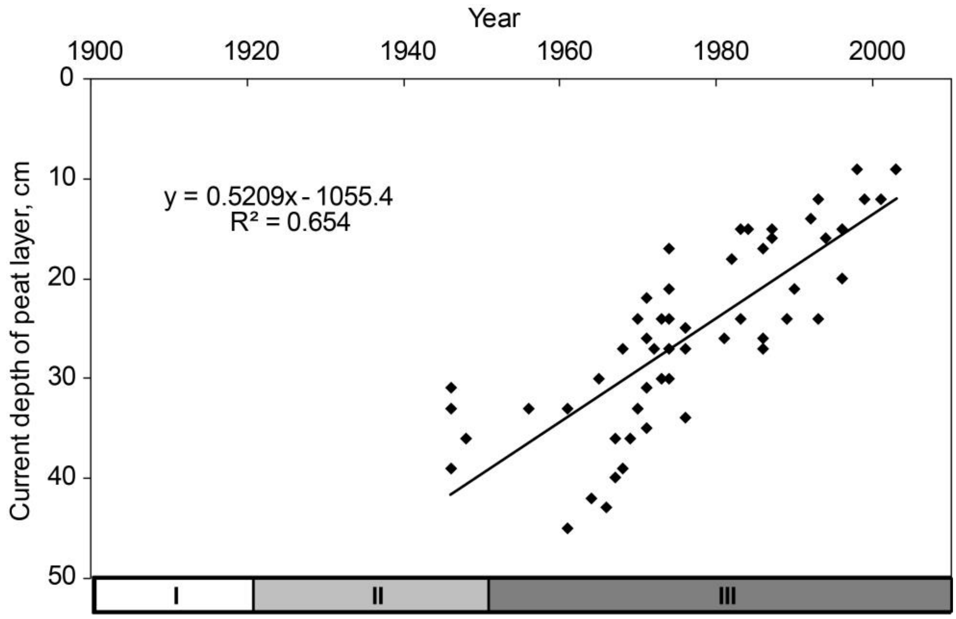

Figure 3. The cessation dates of "root" cambium activity of buried in a moss and peat layer at different depths. Line presents least square approximation of the permafrost rise rate. I – period of increased active layer thickness and "horizontal" distribution of *Sphagnum* when insulating moss layer gradually occupies the area, II – period of vertical growth of mosses till the height of approx. 15 cm which is crucial to suppress cambial activity of larch below, III – period of rising permafrost which follows the moss layer growth. ºC

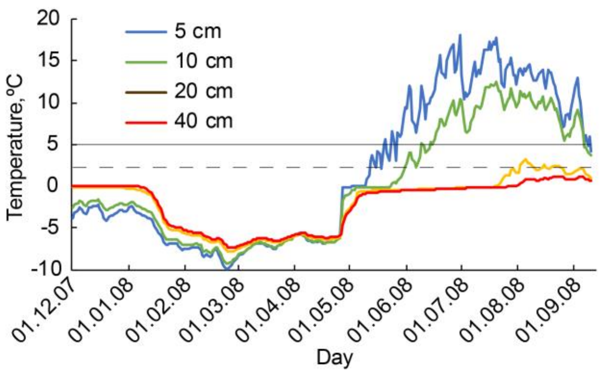

Figure 4. Temperature dynamics at four depths (5, 10, 20 and 40 cm) of a moss-peat layer at the studied site. The temperature sensors were installed in late summer 2007. The dashed horizontal line indicates the physiological minimum threshold for root growth of frost-tolerant species 2.3°C (Schenker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

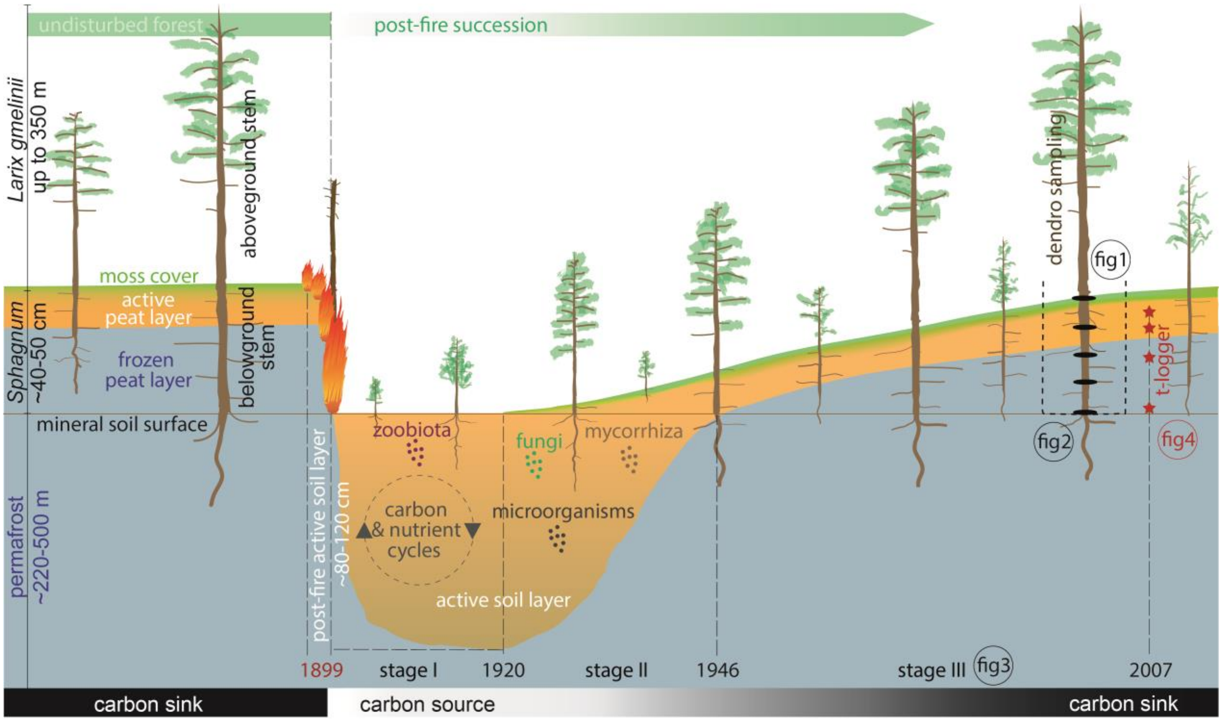

Figure 5. Schematic representation of post-wildfire evolution of a forested bog ecosystem in the continuous permafrost zone in Siberia. The diagram shows the main features of the studied ecosystem development after fire event in 1899 and some facts about permafrost area in the region. It also refers to the sampling design and source of data presented in figures of the paper (fig 1-4 in circles).