

Permafrost landslides promote soil CO₂ emission and hinder C accumulation

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ABSTRACT

In boreal forests developed on permafrost, landslide processes are widespread. They occur primarily in years of above average summer-autumn precipitation and can cover up to 20% of total area of slopes adjacent to rivers. Permafrost landslides will escalate with climate change. These processes are the most destructive natural disturbance events and result in complete disappearance of initial ecosystems (vegetation cover and soil). We have studied sites of landslides of different ages along the Nizhnyaya Tunguska River and the Kochechum River (key site Tura) to analyze postsliding ecosystem succession. Just after the event (as at the 1-year-old site), as compared to the non-affected control site we registered a drop in soil respiration, a 3 times lower microbial respiration rate, and a 4 times smaller mineral soil C and N content at G-plots - bare soil (melkozem) at middle location of a site. Results show that regeneration of soil respiration and eco-physiological status of microbial communities in soil during post disturbance succession starts with re-establishment of the vegetation and the following accumulation of the organic soil layer. During the 35-years succession under observation the, at the oldest site the accumulated litter contained similar C and N stocks as the control sites. However, the mineral soil C and N stocks and the microbial biomass even of the oldest landslide area did not reach the value of these parameters in control plots. We conclude that forested ecosystems in permafrost area disturbed after landsliding require decades for final successful restoration. In addition, the degradation of permafrost due to landslides clearly hinders the accumulation of soil organic matter in the mineral soil.

Keywords: landslides; soil microorganisms; permafrost; soil organic carbon; soil temperature; soil water content; environmental impact; natural disturbance; soil respiration; CO₂; soil C and N content; reforestation; *Larix*; soil microbiota; Siberia; boreal ecosystems.

1. Introduction

Last decades many questions arose concerning permafrost degradation threat under changes in northern latitudes. Most researches pointed out to the direct connection between current global climate changes and substantial permafrost degradation (IPCC 2013, Jorgenson and Grosse, 2016), Romanovsky et al. (2010) reported about increasing of permafrost temperature by up to 2°C in Siberian regions during last 40 years, seasonally affected 1-3°C increase of air temperature in central Siberia has registered during 1960-2010 (Tchebakova et al. 2011). According to Shan et al. (2015), the average annual temperature in permafrost area of China has increased by 3.2°C over 60 years. A warming trend in atmospheric temperature in Iceland has been observed over the last two centuries - an increase of about 0.7 °C per century (Nawri and Björnsson, 2010). An important negative consequences of permafrost degradation for environment are likely intensive emissions of greenhouse gases (GHG) stored in permafrost soil organic matter of high-latitude regions in Siberia (Russian Federation) (Gentsch et al., 2015) and dissolved organic carbon laterally transferred to aquatic ecosystems (Liu et al. 2018). Released GHG from thawing permafrost as a largest terrestrial feedback amplify in turn atmosphere warming and farther permafrost degradation (Abbott and Jones 2015). For sake of justice, we have to admit that some recent studies were made on dark soil CO₂ fixation that can be accounted as a re-use of 0.1-5% of net soil respiration value in permafrost soils (Šantrůčková et al. 2018). However, that can unlikely compensate GHG emissions in high latitudes due to climate change.

In boreal ecosystems, there were repeatedly stated that the most influence on the permafrost degradation was put by wildfires (Flannigan et al. 1998, Wondzell and King 2003, Kharuk et al. 2011), pathogen and insect outbreaks (Eng et al. 2004) and logged areas (Smith et al. 1986). In permafrost region of Siberia, ground forest fires are typically occurred; this type of wildfires causes vegetation cover and litter damage whereas tree layer can survive and mineral soil stay undisturbed (Masyagina et al. 2015). In the beginning of XXI century, one another driver become essential to provoke permafrost degradation. These are landslide processes (e.g., solifluctions) which are increased its occurrence in permafrost zone of central Siberia (Abaimov et al., 2002, Geertsema and Schwab 2004, Kharuk et al. 2016), and mostly attributed to south-exposed river slopes (Prokushkin et al. 2010). Landslide are more disturbing factor for forest ecosystem and permafrost

than wildfires or clear-cuttings since solifluction eliminates entire ecosystem including vegetation and productive soil (Shishov et al. 1999; Prokushkin et al. 2010) and radically alter wildlife habitat. Soil landslides usually occur on the thickest soil active layer (e.g., south and west slopes), and can be provoked by biotic (pathogen and insects outbreaks) and abiotic disturbance (wildfires, logging) agents or local climate anomalies such as overwetting of seasonally thawed layer due to climate change (as a result of combination of high air and soil temperatures and excessive precipitation in summer, or intensive nival thawing) (Kharuk et al. 2016). Thus, new ecosystem succession starts on parent material. In the first years after the landslide, local temporal streams form due to melting of outcropping permafrost layer. At the same time, erosion starts after landslides, and large amount of soil and organic material enters streams as sediment, which results in deterioration of the water quality (Geertsema et al. 2009); washout of humus and nutrients from soil accumulative horizons changes soil fertility properties (Sorokin 2005, Prokushkin et al. 2010). New ecological conditions appeared at areas disturbed by landslides lead to changes in environment, species composition, soil carbon and nitrogen content as well as to soil respiration fluctuations, soil microbial community variation and GHG emissions (Bugaenko et al. 2005; Masyagina et al. 2013). All these factors initialize, in turn, the first phase of recovering succession for newly forming ecosystem. Landsliding is an important landscape-forming factor that is increasing site and habitat diversity (Pozdnyakov 1986, Abaimov 2002, Geertsema and Pojar 2007). Various heterogeneous conditions (microclimatic and edaphic) are developing at a place of a landslide, especially on permafrost soils. Therefore, landslide areas of various age and types represents a mosaic of successional stages across landscapes. Landslides impact soil chemistry: the contents of C, N, and P along with the base cations (Ca, Mg, K) and pH values are different in soils subjected to landslides than in intact soil, and the C/N ratio is affected by landslides (Pozdnyakov 1986, Huggett 1998). Therefore, soil C and N content, soil microbial activity, vegetation regeneration and soil respiration are highly variable at different microsites (e.g., depending on microtopography). However, the positive side is that landslide (as a thermokarst disturbance type) delivers organic matter (OM) to downslope or downstream ecosystems where it may or may not be released to the atmosphere (Abbott and Jones, 2015); while wildfires causes direct mineralization of OM to the atmosphere. So, during the landslide event, an active layer of soil (together with vegetation) slides down on a rupture surface of permafrost and can be accumulated at river terraces (coastal sediments), and in that way soil carbon can be preserved or stabilized over long time period. Last decades, the formation and consequences of landslides, as well as soil-vegetation regeneration patterns in high latitudes are attracting little attention, though an increasing regularity of landslides in permafrost areas is one of the challenging concerns of global change (Bugaenko et al. 2005; Prokushkin et al. 2010; Kharuk et al. 2016). For example in 2001, within 100 kilometers along the middle stream of

Nizhnyaya Tunguska River (Siberia) 72 solifluction areas were observed (Abaimov et al., 2002). For the period of 2000-2012, Kharuk et al. (2016) found 145 landslides at the territory of 62000 km² located just on the north of Tura with using analysis of satellite imagery. In British Columbia a half of all watersheds located at NE part is covered by landslides (Swanson et al. 1992).

In this study, we address to the changes in physical, chemical and biological parameters along landslides chronology. The main hypothesis is that permafrost landslides (by the example of larch ecosystems in permafrost region of Siberia) promoting soil CO₂ emission, because of acceleration of soil microbial processes in more favorable microenvironments (increased soil temperature and water content) and abundant substrate emerged after landslide disturbance. Another point we want to check is whether landslides provoke transformation in soil microbial community and biotope structure, abundance and biological species diversity.

2. Study area and site characteristics

The study area is located within the northern part of central Siberia (Krasnoyarsk region, Russian Federation), in the area underlying by continuous permafrost, and was indicated as Tura site. This region has cold continental climate. Mean annual temperature is -9.5°C with mean monthly temperature ranging from -36°C in January to 16°C in July. Average annual precipitation for the region is 300-350 mm. About 30-40% of annual precipitation falls as snow, with the snow depth being 40-50 cm. The growing season is about 115 days, with a frostless period of 55-56 days (Butorina, 1979).

To study specificity of different solifluction stages of forest successions depending on age class and degradation degree, we have selected three sites disturbed by landslides of different age classes on south-east- and south-west-facing slopes in a valley of Nizhnyaya Tunguska River and Kochechum River (64°N 100°E, Fig. 1-2, Table 1-2). Along with landslide sites, adjacent control (intact, not disturbed by landslide) plots were chosen to estimate the effect of soil sliding on ecosystem processes. The control sites are described as larch stands (*Larix gmelinii* (Rupr.) Rupr.). The total area being affected by landslides (zone of depletion and accumulation) was about 1165 m² for L2009, 11200 m² for L2001 and 5700 m² for L1972 (Table 1). Prokushkin et al. (2010) assessed the loss of C occurred due to soil (18000-88000 kg C ha⁻¹), live wood (13000-24000 kg C ha⁻¹) and O-horizon (8000-12000 kg ha⁻¹) disturbance by landslide events at the same locations as our ones (L2001 and L1972). Carbon loss with mineral soil due to landslides in Tura is comparable or bigger by the value due to landslide in arctic tundra affected by thermokarst (12 kg C m⁻², Abbot and Jones, 2015). The chosen areas are characterized by different forest types,

amounts of mineral and organic matter, and ecological conditions. Successful regeneration of Gmelin larch (*Larix gmelinii* (Rupr.) Rupr.) has been noticed at all solifluction sites (Prokushkin et al. 2010).

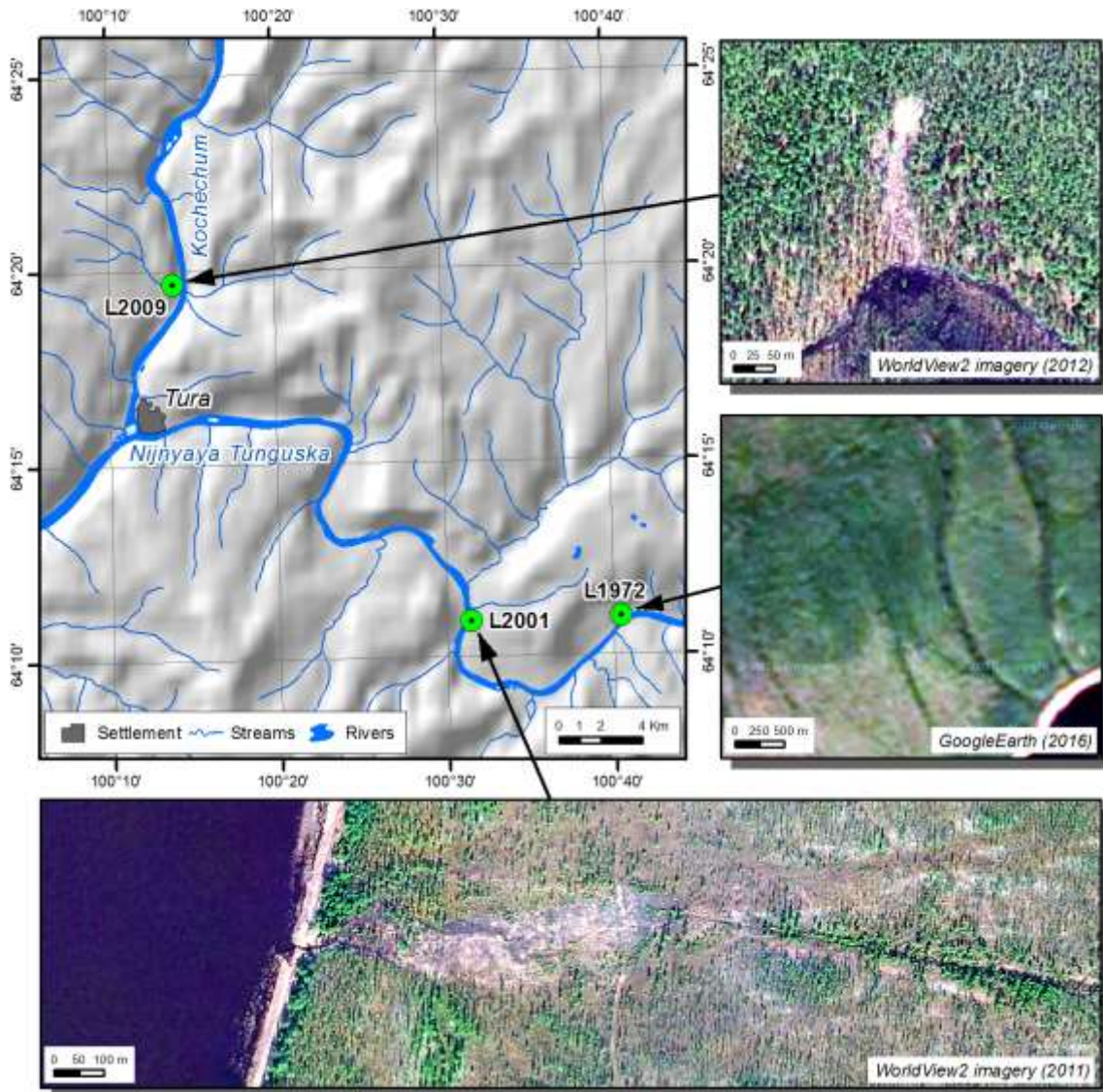


Fig. 1. Study sites location and satellite views of studied landslides (L2009 – 3-years old as for 2012, L2001 – 10-years old as for 2011, L1972 – 44-years old as for 2016)

Our surveys have been conducted in the middle slope position on the landslide sites in August of 2004-2013 (Table 1-2, Fig. 1-2). At every landslide site as well as in control adjacent stand at the middle part of the slope we settled 20-m transects where small plots (3x3 m) in three repetitions have been organized. These small plots were used for soil sampling, field measurements of soil respiration and temperature, and plant species composition description. In

order to study variability of environmental conditions and microtopography caused by landslide disturbance we established two types of small plots (3x3 m) at landslide sites – Edge microsite (E-plots) and Ground microsite (G-plots). The E-sites represent boundary layer between intact stand and one destroyed by solifluction. It looks like mixture of soil and dead trunks of trees where can still survive some species. Between edges, there are G-plots established which represents a fine-grained layer (bare ground, melkozem) with no plants or trees just after landslide event. Totally, we settled 27 small plots (3x3 m) at disturbed by landslide and control plots. Under landslide impact, edges and central zones (bare ground) have been drastically changed with respect to nutrient contents and ecological conditions (Prokushkin et al. 2010).



Fig. 2. Studied landslides after one year (L2009 as for 2010) (A), six years (L2001 as for 2007) (B) and 35 years (L1972 as for 2007) (C) of succession. Red line points to the middle part of landslide area (photo by Masyagina O.V.)

Table 1 Landslide sites characteristic

Parameter	L2009	L2001	L1972
Year of landslide event	2009	2001	1972
River valley	Kochechum	Nizhnyaya Tunguska	Nizhnyaya Tunguska
Direction	South-west	South-east	South-west

Location	64.328N 100.231E	64.182N 100.525E	64.183N 100.675E
Time passed since disturbance, (years)	1 (as for 2010)	6 (as for 2007)	35 (as for 2007)
Slope inclination, dip (steepness), (°)	5-7	19-27	11-20
Slope length, (m)	95	390	290
Maximum width of a site, (m)	15	33	37
Minimum width of a site, (m)	14	12	7
Site area, (m ²)	1165	11200	5700
The volume of washout of soil, (m ³)	252	5365	3725
Loss of wood, m ³	ND	72.8	91.2
Height of vegetation cover and litter (L2001 and L1972 as of 2007, L2009 as for 2013),	0.1	1.1±0.6	5.7±0.9

ND – no data

Table 2 Control sites characteristics

	C2009	C2001	C1972
Stand type adjacent to the middle part of landslide	<i>Vaccinium</i> dry moss larch stand (dominated by <i>Rhytidium rugosum</i> (Hedw.) Kindb.)	<i>Ledum-Vaccinium</i> green moss larch stand (dominated by <i>Pleurozium schreberi</i> (Brid.) Mitt.)	<i>Ledum-Vaccinium</i> green moss larch stand (dominated by <i>Pleurozium schreberi</i> (Brid.) Mitt.)
Soil type*	Typic Aquorthels?	Typic Aquorthels	Typic Aquorthels
Tree species composition	7L3P	10L	10L
Age, years	100-200	150	90-150
Mean H, m	12	13	9
Mean D, cm	20	14	10
Crown closure	0.6	0.4	0.7
Forest yield, m ³ ha ⁻¹	110	50	90

*Keys to Soil Taxonomy (1998). Note: L – Larix, P – Picea.

3. Methods

3.1. Field measurements

The quantity of vascular plants, moss, lichen species (pcs) and *Larix* seedlings (pcs ha⁻¹) were accounted within small plots (3x3 m) located at the middle part of the slope along with the red line showed at Fig. 1 before soil respiration and temperature measurements and sampling procedure. Descriptions of plant species composition of control (intact) and landslide communities were made according to standard geobotanical methods (Sukachev and Zonn, 1961; Ponyatovskaya, 1964; Westhoff & van der Maarel, 1973; Andreeva et al. 2002) in 2004 (for L2001, L1972 and adjacent control sites) and in 2013 (for L2009 and its control site). The names of vascular species were determined according to Cherepanov (1995), the names of lichens and bryophytes were done according to Konstantinov et al. (1992), Andreev et al. (1996), Ignatov et al. (2006) and “A checklist of the lichen flora of Russia” (2006).

Soil respiration rates (SR, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$) were measured at small plots (3x3 m) on the base of 3-5 soil PVC collars (D=10 cm) with Li-Cor 6200 (LI-COR, USA) at landslide and control sites in July 2007, 2009.

Soil temperature (ST, °C) was measured at 5 cm depth with electronic thermometer Checktemp 1 (USA) at the same time of measuring soil respiration. Soil temperature at 5 cm depth was chosen because is important depth for root systems of juvenile plants. Furthermore, we decided to use this depth for ST measuring instead of litter layer, which characterizes by high microbial activity and large root's contribution, because at landslide plots litter layer is usually eliminated by the solifluction disturbance.

3.2. Field sampling

To assess how soil sliding affects ecosystem re-establishment, mineral soil samples for C, N and MSWC analyses and also for conducting of incubation experiments on measuring soil heterotrophic respiration (MR) and soil microbial biomass (MB), were collected on each site in August 2007 (for L2001 and L1972) and in August 2009 (for L2009). Soil samples for soil microbial community structure and PCR analyses were obtained at control, E-plots and G-plots at L2001 and L1972 in August 2010. Mineral soil samples were excavated down to the top 5 cm soil of active layer with 3-4 repetitions, and then they were put to the refrigerator and kept at 4°C until aircraft transportation. After the flight, samples were transported to the laboratory and processed according to appropriate methods.

3.3. Laboratory analyses and incubation

Gravimetric mineral soil water content (MSWC, %) was determined in soil samples collected at depth 0-5 cm at the same time as soil respiration measuring.

Mineral soil C, N contents and C/N ratio were sieved to obtain <2-mm fraction, then the contents were determined on Vario Isotope Cube analyzer coupled with IRMS (Elementar, UK/Germany) after soil samples were dried at 60°C for 48 h.

Soil heterotrophic microbial biomass (MB, mg C g⁻¹ of dry soil) was assessed by the substrate-induced respiration (SIR, mg C g⁻¹ of dry soil hour⁻¹) determination with subsequent recalculation on microbial biomass carbon (C-CO₂) according to Eq. (1) (Sparling 1995). To assess SIR values, fresh mineral soil (2 g) of soil water capacity equal to 60% was placed to 15 ml glass flasks, then there was added a 0.1 ml of glucose-mineral solution to achieve glucose concentration in soil equal to 10 mg g⁻¹ of soil. After that, flasks were closed with resin stoppers hermetically and incubated at 22°C. Soil gases from flasks were taken twice. First, just after glucose-mineral mixture was added and last - in few hours. CO₂ concentration was analyzed with gas

chromatographer Agilent 6890N at a Collective Using Center of Sukachev Institute of Forest SB RAS (Krasnoyarsk, Russia) (Masyagina et al. 2015).

$$MB = 50.4 \times SIR \quad (1)$$

Microbial respiration (MR, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$) of soil microbiota as a CO_2 emission rate during 24 h of soil incubation at 22°C and 60% of soil water capacity has been obtained (Masyagina et al. 2015).

Coefficient of microbial activity $q\text{CO}_2$ (Sparling 1995, Ananieva 2003) was calculated with Eq. (2).

$$q\text{CO}_2 = MR / MB \quad (2)$$

DNA amount methods will be placed here

To assess soil microbial community structure we used method of surface plating at Petri dishes contained dense nutrient medium and colonies calculating (Methods of soil microbiology and biochemistry 1991). The amount of 20-30 ml of medium contained agar-agar was put in Petri dishes, and after hardening at room temperature all Petri dishes were turned over to condensated water to go up. After preliminary soil dispersion, 1:1000 dilution of soil suspension solution has been made. This diluted solution was plated at Petri dishes in 3 repetitions. Plated dishes were turned over and placed into thermostat device at 28°C . Bacteria colonies were calculated after 3 days, actinomycetes colonies – 7-20 days, fungi and yeast colonies – 5-7 days. After colonies at Petri dishes been calculated, we determined mean number of colonies per 1 g of dry soil according to the Eq. 3 (Methods of soil microbiology and biochemistry 1991):

$$a = b * c * d / e, \quad (3)$$

where a – cells number in 1 g of dry soil; b – mean number of colonies at Petri dishes; c – dilution of the soil suspension solution; d – drops number in 1 ml suspension; e – weight of dry soil taken for analysis.

For quality and quantity characteristic of soil microflora we used following mediums:

Starch-and-ammonia medium was used for actinomycetes and bacteria determination (g per liter of tap water). It consists of $(\text{NH}_4)_2\text{SO}_4$ (2 g), K_2HPO_4 (1 g), MgSO_4 (1 g), NaCl (1 g), CaCO_3 (3 g), soluble starch (10 g), agar-agar (20 g). Starch was first mixed with small amount of water and then added to medium.

Meat infusion agar medium for bacteria accounts consists of meat broth, peptone (10 g l^{-1}), NaCl (5 g l^{-1}), agar-agar (20 g l^{-1}), and solution was bring up to pH 7.

Lockheed's soil agar medium consists of K_2HPO_4 (0.2 g), agar-agar (20 g), soil extract (1 l). Soil extract was prepared from strongly ameliorated fertilized soil. Sifted soil (3 mm mesh) was mixed with the equal amount (by weight) of tap water. The mixture was autoclaved 1 hour at 120°C, and then hot suspension was filtered through paper filter by pumping.

Wort agar medium was prepared from diluted wort solution with sugar content about 4-5°B. Agar-agar (20 g l⁻¹) was added to mixture, and then solution was bring up to pH 7. Before plating there was streptomycin added to the suspension to prevent bacteria growth.

Total value of microorganisms was calculated as a sum of all colonies observed at all applied mediums (starch-and-ammonia medium, meat infusion agar medium, Lockheed's soil agar medium and wort agar medium). Hydrolytic microflora was accounted at meat infusion agar medium, copiotrophs – at starch-and-ammonia medium, oligotrophs – at Lockheed's soil agar medium and microscopic fungi – at wort agar medium (Dobrovol'skaya et al. 1990).

3.4. Data analyses

Studied parameters (ST, MSWC, C and N availability, C/N, SR, MR, MB, qCO₂, DNA amount, number of soil microbiota groups and plant species) were tested for normality prior to analysis to stabilize variance. The non-normally distributed variables were logarithmically transformed prior to analysis to stabilize variance. Two-way factorial analysis of variances (ANOVAs) were used to test the main effects of age class of landslide and microsite types (E- and G-plots) on variables: ST, MSWC, C and N availability, C/N, SR, MR, MB, qCO₂, PCR, number of soil microbiota groups and plant species (Table 3). Tukey HSD (p adjusted) was used for Tukey multiple comparisons of means. The analyses of the obtained data were performed using RStudio version 1.1.423 – © 2009-2018 RStudio, Inc.

4. Results and discussion

The landslide is an important factor of mesorelief and microrelief formation along northern rivers (Pozdnyakov, 1986). Periodic landslides at south-east- and south-west-facing slopes caused specific ridge-trench look alike relief form and influence plant communities on slopes. It is expecting that under climate change the impact of landslide will progress in high latitude ecosystems. Here we study long-term and short-term changes of the important parameters of ecosystem after landslide in high latitude forest communities, and how forest restoration process develops.

4.1. Landslide disturbance influence on microenvironment

Hydrothermal conditions play essential role especially at primary stage of landslide ecosystem succession (Masyagina et al. 2013). In our survey, both soil temperature at 5 cm depth and mineral soil water content at 0-5 cm soil horizon are important factors at landslide plots (Table 3). Temperature regime (at 5 cm depth) measurements revealed increased mineral soil temperature values at landslide sites compare to control sites. Soon after landslide disturbance (1-7 years) occurred, we observe a big difference in ST values between landslide plots and intact communities (Fig. 3). In particular, at L2009, site of initial successional stage, in a year after landslide event ST was 10°C higher at E-plot and 17.6°C higher at G-plot compare to adjacent intact stand. At L2001 site, 4-7 years after disturbance ST values were 12°C higher at E-plot and 15°C higher at G-plot compare to adjacent control stand. Observed significant differences are obviously caused by the lack of tree cover (Prokushkin et al. 2010) especially at central part with bare soil (G-plots). Abbott and Jones (2015) also assessed soil temperature as main environmental factor in arctic thermokarst, and important predictor of ecosystem respiration. Even after 33-35 years (L1972) where was statistical evidence of 2°C-difference in ST between control plots and G-plots, which points possibly to the final successional stage achievement. Therefore, restoration of soil temperature to the intact community's level were provided by the reestablishment of ground moss-lichen cover and its thermal insulating properties.

Soil water content is another important ecological factor relating to the recovery process of disturbed ecosystem. Mineral soil water content at 0-5 cm horizon did not vary greatly among intact larch stands, and was in range 14-46%. In one year after landslide (L2009), there were statistically lower values of MSWC at G-plots compare to intact stand. At L2001, 5-6 years after disturbance, the same difference between median values of MSWC between G-plots and control plots was observed, however, it was not statistically significant (Fig. 3). At 35 years after landslide disturbance (L1972), the difference between MSWC values was minimal at damaged and control sites.

Table 3. Statistical results (F-values) of two-way ANOVAs for some physical, chemical and biological parameters at landslides in permafrost zone

Source of variation	Landslide	Microsite	Landslide : Microsite
Soil temperature at 5 cm depth, °C	124.1**	582.8**	178.2**
Mineral soil water content at 0-5 cm horizon, %	20.51**	5.57**	1.04
Total soil C at 0-5 cm horizon, %	55.35**	236.90**	63.51**
Soil organic C at 0-5 cm horizon, %	0.56	10.79**	1.44
Total soil N at 0-5 cm horizon, %	66.37**	161.36**	44.56**
C/N at 0-5 cm soil horizon	27.46**	26.22**	6.39**
Soil respiration, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	47.05**	4.77**	0.83

Microbial respiration at 0-5 cm mineral soil horizon, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	15.56**	11.81**	6.12**
Microbial biomass at 0-5 cm mineral soil horizon, mg C g^{-1} dry soil	3.11*	8.81**	1.97
qCO ₂	38.36**	9.55**	2.90**
Basal respiration, $\mu\text{g C g}^{-1}$ dry soil day ⁻¹	49.44**	11.55**	6.36**
DNA amount, mln. fragment DNA copies g ⁻¹ soil	8.75**	7.97**	0.74
Number of hydrolytic microflora colonies, thous. KOE g ⁻¹ dry soil	4.95**	13.27**	8.20**
Number of microscopic fungi colonies, thous. KOE g ⁻¹ dry soil	2.96	1.09	1.49
Number of copiotrophs colonies, thous. KOE g ⁻¹ dry soil	21.64**	7.63**	10.34**
Number of oligotrophs colonies, thous. KOE g ⁻¹ dry soil	21.98**	14.64**	24.56**
Number of actinomycetes colonies, thous. KOE g ⁻¹ dry soil	0.20	3.60**	15.79**
Number of vascular plant species, pcs.	3.55*	10.64**	2.84*
Number moss species, pcs.	8.30**	9.57**	2.28
Number of lichen species, pcs.	13.94**	17.43**	3.10*
Total species number, pcs.	0.76	1.68	1.10
Larix seedlings, thous. pcs. ha ⁻¹	511.8**	1111.1**	215.8**

* P<0.05, ** P<0.01

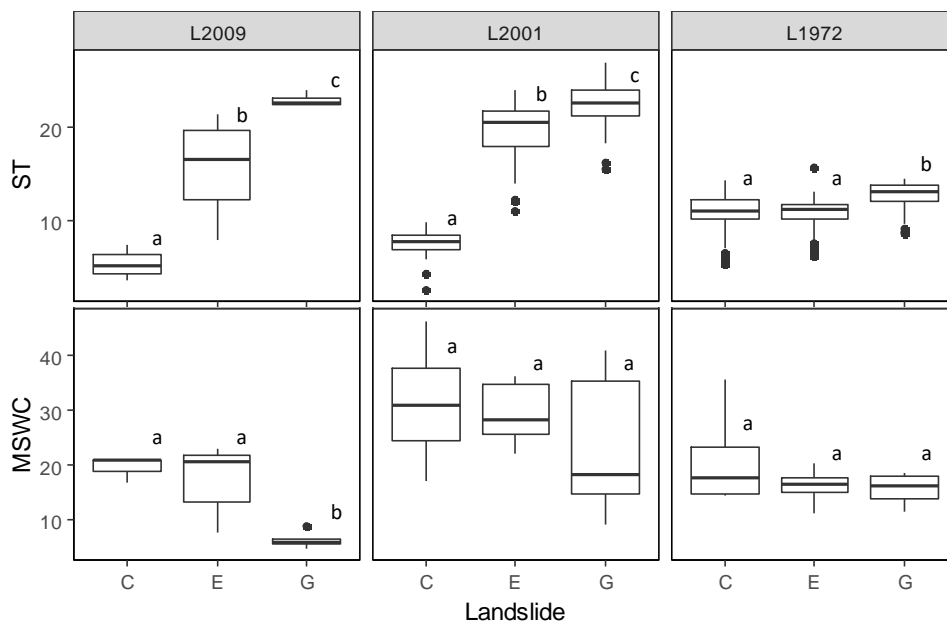


Fig. 3. The effect of landslide and its microsite type (E – right or left edge of landslide, G – ground) on soil temperature at 5 cm depth (ST, °C) and mineral soil water content (MSWC, %) at 0-5 cm mineral soil horizon at landslides of different ages (L2009, L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates median, box boundaries indicate 25th and 75th percentiles, and whiskers indicate highest and lowest values, dots above or below whiskers indicate outliers. Medians followed by different letters in the same curve are significantly different at P<0.05 according to Tukey multiple comparisons of means analysis.

Separately, we have to emphasize specific role of microtopography conditions at permafrost area. Consequences of landslides as well as wildfires and clear-cuttings are very

complicated at cryogenic soils. For example, range and degree of environment transformation of ecosystems disturbed by landslides is very wide, and that can give a start to variety of different communities. Thus, highly varied microenvironment developed due to landslide disturbance is supposed to be favorable (high ST and sufficient MSWC) for successful seed germination and further prevalence of vascular species. Increased insolation due to the absence of shading from trees and shrub's layer contributes to this too. Due to high variability of hydrothermal conditions, time of succession and environment transformation will be non-homogenous as well. Finally, development of ground cover plants and tree seedlings lead to stabilization of soil temperature, restoration of thermal insulating effect of green moss and lichen cover, and raising of the level of permafrost.

4.2. Landslide disturbance influence on C and N availability

Carbon and nitrogen contents in mineral soil of all landslide sites were significantly smaller (2-6 times) than that of control sites (Fig. 4). This was supported by the studies of Prokushkin et al. (2010) at the same sites (L2001 and L1972); additionally, the authors observed the decreasing of pH and biogenic elements (C, N, P, Potassium, Ca) particularly at G-plots. According to Leibman (2009), these changes can be attributed to geochemical processes on slopes exposed by landsliding, which can cause a redistribution of elements within the active layer and upper permafrost. Moreover, in the middle part of landslide, the topsoil part, being enriched in organic matter, was lost by the landslide disturbance (bare ground). C/N values in mineral soil (0-5 cm) at landslide sites varies wider (from 17 to 24) than that of control sites (from 20 to 24). All these factors can influence soil microbial, biotope communities' structure, and consequently successional processes.

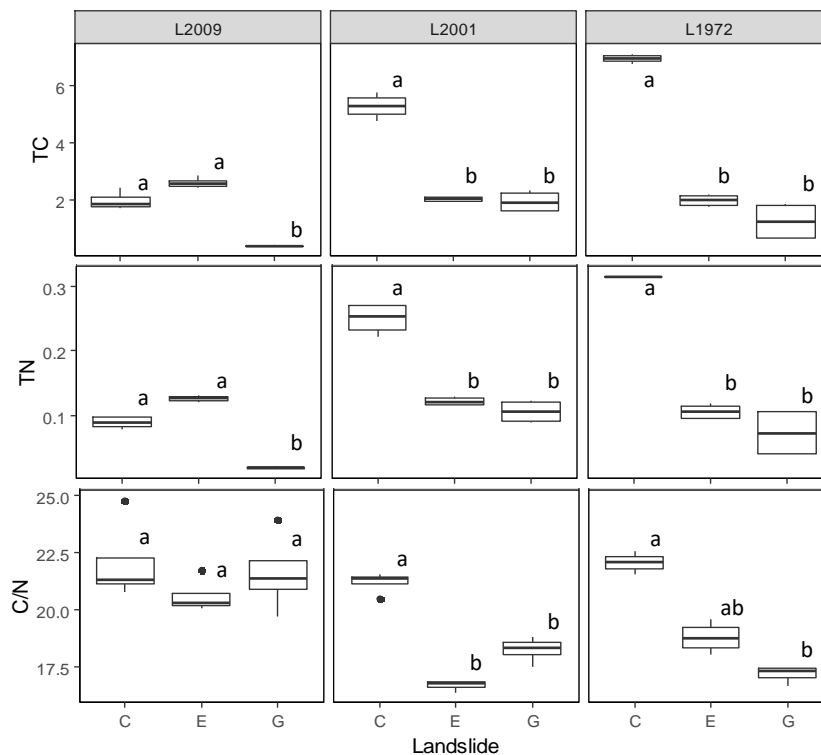


Fig. 4. The effect of landslide and its microsite type (E – right or left edge of landslide, G – ground) on total carbon content (TC, %), total nitrogen content (TN, %) and C/N values at 0-5 cm mineral soil horizon at landslides of different ages (L2009, L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates median, box boundaries indicate 25th and 75th percentiles, whiskers indicate highest and lowest values, dots above or below whiskers indicate outliers. Medians followed by different letters in the same curve are significantly different at $P < 0.05$ according to Tukey multiple comparisons of means analysis.

4.3. Influence on soil CO_2 emission and microbial activity

Soil respiration measurements conducted in the natural environment revealed slightly higher values at E-plots of all solifluction sites compare to adjacent control communities. Because of high variation of soil respiration values ($1.25-11.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$ at control sites, $0.37-14.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$ at E-plots, $0.53-18.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ sec}^{-1}$ at G-plots) caused by site microtopography, these differences were not statistically significant (Fig. 5). At L1972, we observed high variability of soil respiration at G-plots as well, which can be explained by developing of microtopography elements at G-plots environment during reforestation and successional processes (biological competition, niche formation etc.). While compare landslides of different age classes and successional stage, we found that soil respiration at young landslides

(L2009 and L2001) was not statistically differed, but soil CO₂ emission at old solifluction (L1972) was twice ($p < 0.0001$) higher than that at younger ones. For sake of justice, we have to admit that soil respiration at all studied intact stands was not equal. It was increasing ($p < 0.0015$) in a range of landslides L2009-L2001-L1972 demonstrating wide varieties of environment conditions and microtopography of studied region. At boreal ecosystems, microtopography is determined by cryoturbation processes and can be a source of high variability not only environmental factors (ST, MSWC) but biological parameters (e.g., soil microbial activity) as well.

Microbial respiration varied widely both at intact stands and sites disturbed by landslides as well as total soil respiration did according to the same reasons (Fig. 5). At 1-year old landslide (L2009) and adjacent intact stand, soil microbial respiration tended to be higher at E-plots but was not statistically differed. At L2001, we observed the same tendency as at L2009, and there was statistical difference between G- and E-plots, but not with control values due to its high variability. At L1972 site, there was statistically significant drop in MR values at G-plots compare to adjacent intact stand, likely it is connected to small soil microbial biomass (Fig. 5) and least number of microorganisms at trophic groups among microsites (Fig. 6). At control sites, contribution of microbial respiration to total soil CO₂ emission was almost the same – about 11-15% (Masyagina et al. 2013). At young landslide sites (L2009 and L2001), this value is two times higher than that of respective control sites, especially at E-plots. At the older landslide site (L1972), on the contrary, microbial respiration contribution was smaller than that of control site (Masyagina et al. 2013). Low contributions of microbial respiration at the older site was due to low soil microbial biomass (Fig. 5). The lowest contribution of microbial respiration was revealed at the G-plots where was revealed a successional recovery of vegetation resulted in increased root respiration contribution to total soil respiration.

In measurements of soil microbial biomass (MB) made on the basis of SIR values account, we consider heterotrophic bacteria of aerobic group. MB values in top 5 cm mineral soil layer did not reveal the difference among neither control stands nor landslide sites. However, MB values varied widely depending on the microenvironment: maximum variation was observed at E-plots and minimum at G-plots (Fig. 5). High variation of MB values revealed at E-plots resulted from high variation of ecological conditions and large amount of dead debris mixed with soil O- and mineral horizons after landslide disturbance. As it was already mentioned, at “young” landslides (L2009-L2001), minimal values of MB were registered at G-plots. In particular, at L2009, where, along with high variation of MB at E-plots, we observed significant declining of microbial biomass at G-plots likely due to critical deficit of soil nutrients and organic matter (Fig. 4) caused by nutrients runoff due to erosion processes following by landslide event. It goes well with low rates

of MR and SR at G-sites at L2009. Whereas, at L1972, soil microbial biomass at G-plots was comparable to MB values at E plots, which indicates gradual regeneration of microbiota in mineral soil.

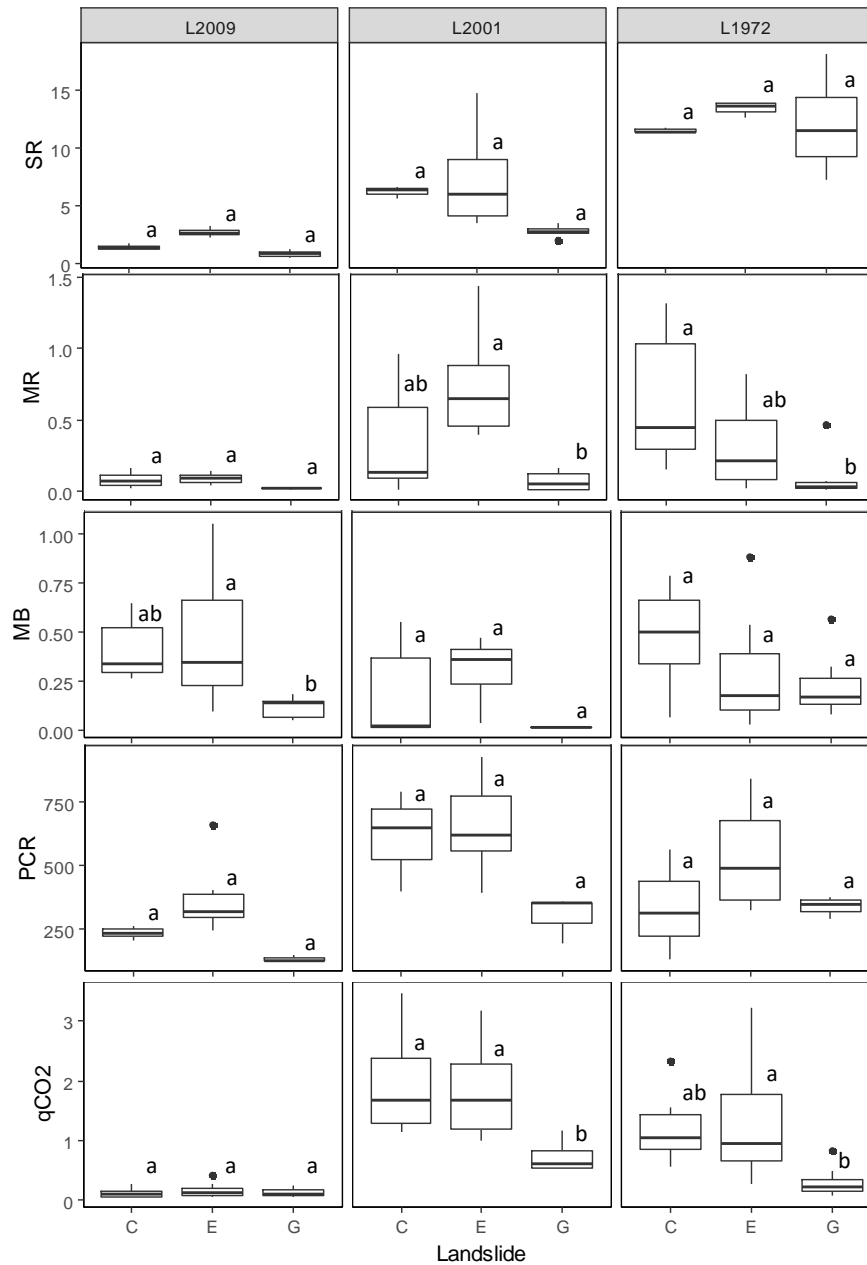


Fig. 5. The effect of landslide and its microsite type (C – control plot, E – right or left edge of landslide, G – ground) on soil respiration (SR, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), microbial respiration at 0-5 cm mineral soil horizon (MR, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), microbial biomass at 0-5 cm mineral soil horizon (MB, mg C g^{-1} dry soil), PCR (mln. fragment copies per g of dry soil) and qCO₂ values at 0-5 cm mineral soil horizon at landslides of different ages (L2009, L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates median, box boundaries indicate 25th and 75th percentiles, whiskers indicate

highest and lowest values, dots above or below whiskers indicate outliers. Medians followed by different letters in the same curve are significantly different at $P < 0.05$ according to Tukey multiple comparisons of means analysis.

DNA amount results will be here

Sustainability of soil system is mostly determined by sustainability of soil microbial community (Zvyagintsev, 1992). One of the important parameter of eco-physiological status of microbial population is the coefficient of microbiological activity, qCO_2 . Large deviation of qCO_2 value from “1” points to the disorder of normal functioning of soil microbiota due to some stress (Anderson and Domsch 1990). Analysis of coefficient of microbiological activity values shown intensive disturbance of microflora functioning at L2009 and L2001 sites, and less disturbance at L1972 sites (Fig. 5). Therefore, the restoration of eco-physiological status of soil microflora at sites damaged by landslides is very slow. In addition, there was disturbance of eco-physiological state of soil microbial communities at intact stands observed. At studied territories we are dealing with soil microbial coenosis developing at cryogenic soil which itself can influence eco-physiological state of soil microbiota.

4.4. Landslide influence on biotope composition (soil microbiota, plants)

Microbiota occupied permafrost soil or freezing soil substrate is mostly presented by so-called psychrophilic or psychrotrophic microorganisms. Their optimum temperature is $15^{\circ}C$; maximum is $20^{\circ}C$ and minimum at $0^{\circ}C$ and colder (Zvyagintsev et al., 1999). Among psychroactive soil microorganisms having low temperature adaptations there are different taxonomic groups: bacteria (oligotrophs, hydrolytic bacteria, copiotrophs, actinomycetes) and microscopic fungi (micromycetes). Bacteria prevail in permafrost soils due to its low temperature, periodical overwetting or drying of permafrost soil and subacid reaction of soil solution compare to fungi which are quiet sparse in these conditions (Marfenina 1994). Landslide disturbance essentially change environment and expected to influence structure of soil microbial community. The main contribution to permafrost soil microbiota structure oligotrophs make (Fig. 6). Oligotrophic bacteria are able to utilize nutrients and small amounts of nitrogen in soil, so they are essential for ecosystem functioning as far as this group prevents nitrogen loss from soil and accomplishes full mineralization cycle of organic matter (Sorokin, 1999). Therefore, oligotrophs prevail at control sites (350-24000 thous. $KOE\ g^{-1}$ of dry soil, Fig. 6) and at sites disturbed by landslides (900-8500 thous. $KOE\ g^{-1}$ of dry soil, Fig. 6) among other trophic groups. Soil

microbiota at landslide sites was presented mostly by copiotrophs (350-6000 thous. KOE g⁻¹ of dry soil) and oligotrophs due to low content of insoluble aromatic compounds (e.g., starch, cellulose or lignin) in soil and large amount of monomeric compounds and amino acids. Whereas at control sites, hydrolytic microbiota (700-6000 thous. KOE g⁻¹ of dry soil) prevails.

Contribution of microscopic fungi and actinomycetes changes depending on recovery succession stage. Thus, at “young” (L2001) landslide sites number of fungi (0-234 thous. KOE g⁻¹ of dry soil) and actinomycetes (0-130 thous. KOE g⁻¹ of dry soil) is lower than that of control (fungi: 250-600 thous. KOE g⁻¹ of dry soil, actinomycetes 170-420 thous. KOE g⁻¹ of dry soil, Fig. 6). Whereas, at “older” (L1972) landslide sites there is another pattern; the amount of fungi (40-4500 thous. KOE g⁻¹ of dry soil) and actinomycetes (30-180 thous. KOE g⁻¹ of dry soil) tend to be higher than that of control sites (fungi: 230-650 thous. KOE g⁻¹ of dry soil, actinomycetes 0-38 thous. KOE g⁻¹ of dry soil, Fig. 6), that points likely to recovery of microbiota community after landslide. The number of microscopic fungi as well as their variation is similar at control sites of two solifluctions. Low contribution of most trophic groups of soil microbiota after landslide results from critical changes occurred after disturbance (low C and N availability, lower MSWC, absence of vegetation etc.). After decades, we can expect that together with environment recovery and reforestation, soil microbial community will recover too.

Control stands represent relatively stable quasiclimax forest associations with well-developed tree layer comprised of *Larix gmelinii* (Rupr.) Rupr. with small amount of *Picea obovata* Ledeb. and *Pinus sibirica* Du Tour, and almost continuous moss-lichen ground cover (Table 2). Crop density varies from 0.4 to 0.7. The age of the stands varies from 90 to 200 years. The mean height of the larch trees ranges from 9 to 13 m and mean diameter ranges from 10 to 20 cm. The level of diversity is not very high with the number of species varying from 14 to 33. The forest understory generally consists of alder *Duschekia fruticosa* (Rupr.) Pouzar (15-30%), *Salix* spp., *Lonicera pallasii* Ledeb. (1-3%), *Juniperus sibirica* Burgsd., *Rosa acicularis* Lindley. Vascular species number is restricted due to the competition with moss species and niche limitations. The dominant species of ground vegetation at control plots of L2001 and L1972 are dwarf-shrubs *Ledum palustre* L. (10-30%), *Vaccinium vitis-idaea* L. (40-70%), *Vaccinium uliginosum* L. (3-5%) and grass species *Vicia megalotropis* Ledeb., *Festuca ovina* L. Ground cover generally consists of mosses *Pleurozium schreberi* (Brid.) Mitt. (40-60%), *Hylocomium splendens* (Hedw.) B. S. G. (20-40%), *Aulacomnium turgidum* (Wahlenb.) Schwaegr. (10-20%) and lichens *Cladina stellaris* (Opiz) Brodo (up to 20%), *Cladina rangiferina* (L.) Web. (10-60%), *Cetraria islandica* (L.) Ach. (1-5%), *Cetraria cucullata* (Bellardi) Ach. (1-3%), *Peltigera aphthosa* (L.)

Willd. (1-3%) and so on. A dry moss *Rhytidium rugosum* (Hedw.) Kindb. prevails with 90% of projecting cover of intact stand adjacent to L2009 site.

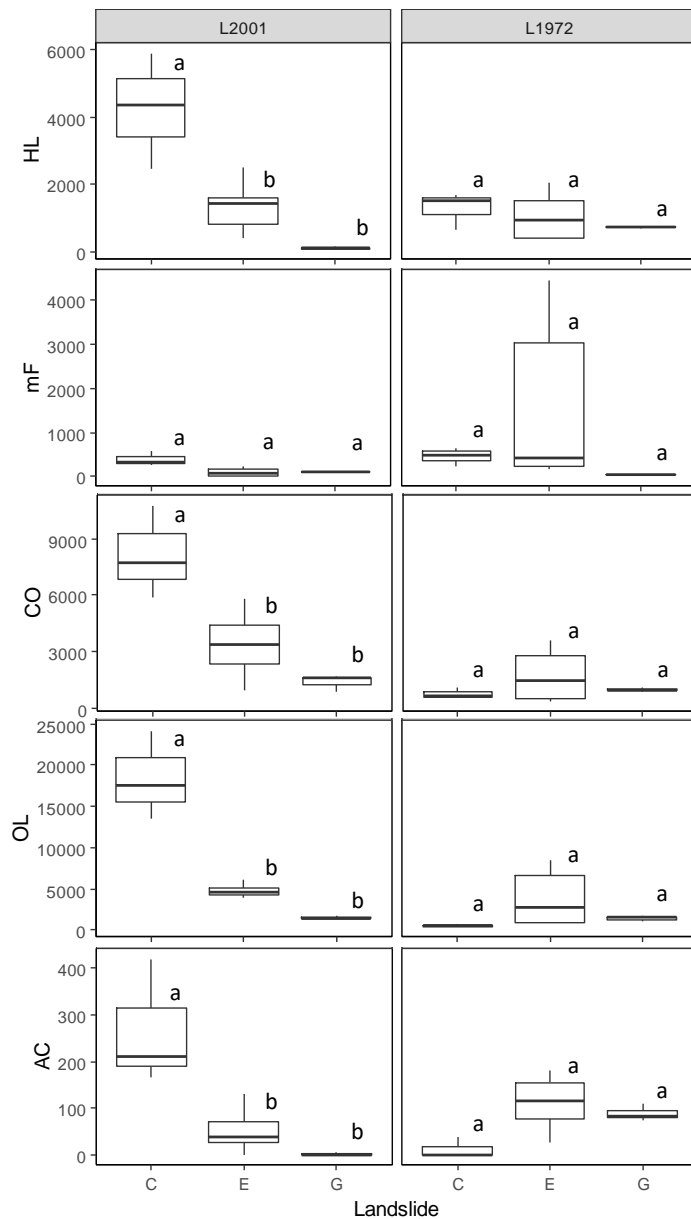


Fig. 6. The effect of landslide and its microsite type (C – control plot, E – right or left edge of landslide, G – ground) on number (thous. KOE g⁻¹ dry soil) of hydrolytic microflora (HL), microscopic fungi (MF), copiotrophs (CO), oligotrophs (OL) and actinomycetes(AC) colonies at 0-5 cm mineral soil horizon at landslides of different ages (L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates median, box boundaries (hinges) indicate 25th and 75th percentiles, whiskers indicate highest and lowest values, dots above or below whiskers indicate outliers. Medians followed by

different letters in the same curve are significantly different at $P < 0.05$ according to Tukey multiple comparisons of means analysis.

Landslides contribute significantly to transformation of stands, species composition and process of further reforestation and succession, and distinct vegetative difference between landslide site and neighboring forest is clearly observed (Geertsema and Pojar 2007). According to our study, total number of species at landslide sites of different successional stages varied from 48 to 52 species; that exceeds the number of species at adjacent control sites. The E-plots are disturbed areas, but there are a lot of survived plant species preserved as well as seed bank in soil. Therefore, at E-plots, usual species of intact forest communities are neighboring with invasive species (so-called “explerents”) intruded from other distant associations to the space released by landslide. About 25% of species at landslide sites do not occur in intact communities, they generally become established at the initial stages of restoration process. Invasive plant species appeared at E- and G-plots are more hygrophilous than that of adjacent control sites, for example *Calamagrostis Langsdorfii* (Link) Trin. and *Equisetum* sp. at L2001 and L1972. At E- and G-plots of L2009 we observed following invasive species: *Potentilla stipularis* L., *Potentilla inquinans* Turcz., *Rubus sachalinensis* H. Lev., *Viola biflora* L., *Polemonium boreale* Adams, *Poa sergievskajae* Prob., *Silene repens* Patrin, *Viola arenaria* DC. In the first years of restoration the portion of invasive species is 37%; after 33 years it is 11%. Also on the E-plots orchids *Cypripedium guttatum* Sw., *Dactylorhiza cruenta* (O.F. Mueller) are pretty abundant – up to 20% of cover.

Vascular plants contribute significantly (33-45 species) in biodiversity of landslide biotope. Thus, dominant species of dwarf shrub layer in intact communities *Ledum palustre*, *Vaccinium vitis-idea*, *Elymus kronokensis* (Kom.) Tzvelev, *Carex pediformis* subsp. *reventa* (V. Krecz.) Malysch. и *Festuca ovina* L., *Campanula rotundifolia* L. etc. remain at E-plots and actively develop at G-plots as well. According to Smith et al. (1986), the first colonizers at landslides in British Columbia are mostly shrubs and fern, which are following by tree species (spruce and alder). Lantz et al. (2009) revealed that during recovery, microenvironments in thermokarst favor shrub establishment. Vascular and moss species diversity at E-microsites tends to be higher than that of control stands in all age classes of landslide damaged larch stands (Fig. 7), excluding moss species amount in E-plots of L1972. Number of lichen species stay statistically lower compare to control sites after 30 years after landslide event. Highly likely, it caused by increased competition with vascular plants which succeeded due to higher growth rates in more favorable soil temperature conditions (Fig. 3) developed at E-plots after landslide disturbance. In future, we

expect recovery of lichen species amount as in L1972 due to accumulation of vast amount of dead wood ready to decompose which is a good substrate for lichen's associations.

G-plots located between edges of solifluction are characterized by an opened and mineralized substrate where succession goes as "primary succession", namely clear space without any plants or their germs in a substrate (Mirkin and Naumova 2012). Therefore, here, in absence of biological competition, any species of plant communities of studied region can intrude, and the number of species at G-plots is usually very high. This space is fast occupied by saplings of tree species (larch, alder, and willow) and sparse herbaceous vegetation like invasive *Carex media* R. Br., *Urtica dioica* L. and some species of ferns and equisetum. Amount of vascular species here is twice higher than that of control (Fig. 7) owing to invasive species. The young solifluction (L2009) is quite different from two others; here we observed decreasing of vascular species number at G-plots. This case can be explained by the absence of seed sources for successional associations disturbed by landslide. Two other (L2001 and L1972) landslide areas are located directly to Nizhnyaya Tunguska River valley where many species of petrophyte phytocenosis are placed including grassland mesophytes. Whereas, landslide area of L2009 is positioned at the valley of small stream that is tributary of Kochechum River, and this area is isolated from abundant valley of Kochechum River by natural forest communities and bare cliffs. Therefore, at E- and G-plots of L2009, a number of plant species (petrophyte species prevail, grassland species are sporadic) is limited compare to adjacent intact community. Mosses and lichens at G-plots are not as numerous by species as in control sites, and recovery of moss-lichen layer takes long time (more than 3 years). Possible reason of this trend is a substrate stability for occupation by lichens. Even though open surface of G-plot's substrate is a favorable place for colonization by lichens at primary stages of succession with no competition with vascular plants, lichens are having difficulties with fixation on substrate due to water erosion processes at snow thawing and summer rainfall. Lichen's thallome is very small, slowly growing and easy washes by thawing waters.

Regards to trophic (based on soil fertility) plant groups at landslides plots, we found that plant groups of mesotrophs and oligotrophs are dominated at primary stage of landslide succession (1-5 years after event) - *Diplazium sibiricum* (Turcz. ex G.Kunze) Kurata., *Duschekia fruticosa* (Rupr.) Pouzar., *Ribes rubrum* L., *Rosa acicularis* Lindl., *Rubus sachalinensis* Levl., *Sorbus sibirica* Hedl., *Ceratodon purpureus* (Hedw.) Brid. The same groups prevail in intact communities as well. In further recovery succession stages, the ratio of groups remains the same.

In the study, we also assess the impact of landslides of forest productivity. The intact (control) larch stands have a weak recovery potential – 500-2500 seedlings of larch per hectare, that is wide known characteristic of intact permafrost larch stands. Whereas *Larix gmelinii*

seedlings abundantly appear at E- and G-plots of area disturbed by landslide. Its amount at landslide plots exceeds the one at control plots by 10-30 times (Fig. 7). For comparison, after wildfires that are the main disturbing factor in boreal forests, on burnt areas of similar age, the natural regeneration of larch varies from 8 to 25 thousand per hectare (Prokushkin et al., 2000), that exceeds the number of seedlings in the intact communities by 5-17 times. The successful natural reforestation on solifluction plots occurs due to the availability of the extensive mineralized surface and a combination of different micro environmental conditions for seed germination. Some researches point to the radical changes in soil pH after landslide. Thus, Lambert (1972) found higher values of pH of soil disturbed by landslide compare to surrounding climax vegetation. Burn and Friele (1989) also found that soils of 43-year-old solifluction at Yukon had higher pH values (7.3–7.4), compared to 6.2 in soils under mature spruce forest. Moreover, according to study of Prokushkin et al. (2010), close to neutral soil acidity (pH 6.7-7.1), which was observed at landslides L2001 and L1972, is optimal for larch regeneration and functioning. All individuals observed on the sites were of seed-origin. Obviously, in the first years after disturbance there was a considerable reserve of larch seeds in the adjacent stands. It provided dense saplings formation. As far as *Larix* species are highly competitive species, especially in permafrost areas, we registered total prevalence of larch in tree level at E- and G-plots after 4-6 years or 35 years after landslide event. Alder and willow prevail in shrub layer at landslide plots because of interspecific competition. In the future, the intensification of root competition among the tree species will begin and the natural elimination of trees are expected.

Typically, in permafrost Siberian regions the process of stand formation after a fire takes 50-80 years (Bugaenko, 2002). Smith et al. (1986) revealed that tree cover recover after landslides more slowly compare to logged areas. According to Leibman (2009), at landslide-affected slopes at Yamal (Russia), bare surfaces are re-vegetating slowly with full regeneration of shrub-moss cover after several centuries. We assume a similar to Siberia burnt areas time interval for reforestation on solifluction plots. The recovery of damaged communities starts from the recovery of species of intact communities. At first years after landslide disturbance, hydrothermal conditions and light availability play the main role in recovery succession of forested ecosystems. Depending on these parameters and their heterogeneity in space and time, the biotope occupation occurs and there can be different types of microenvironment develop. Tree level – larch as a dominant, shrubs and dwarf shrubs reestablish quite successfully; moss and lichen cover recovers very slowly. Fallen trees become a substrate for local lichen-moss group formation. Mass accumulation of dead fallen wood on the margins (E-plots) of the sites later results in larch-lichen communities forming in bulging relief; on the bottom of washout gullies, larch-moss communities are forming. Alongside with this succession pattern, we observe numerous invasive species occupy

landslide plots. Thus, solifluction processes play an important role in the formation of vegetation cover structure in the cryolithic zone, especially on slopes under intensive insolation. All these facts show the restoration of the initial type of vegetation – boreal forest with *Larix gmelinii* as a dominant tree, since larch communities are characterized by the high capability for restoration under the harsh ecological conditions. However, global climate changes are continuing, and influence the future stability and recovery potential of plant communities of the permafrost zone.

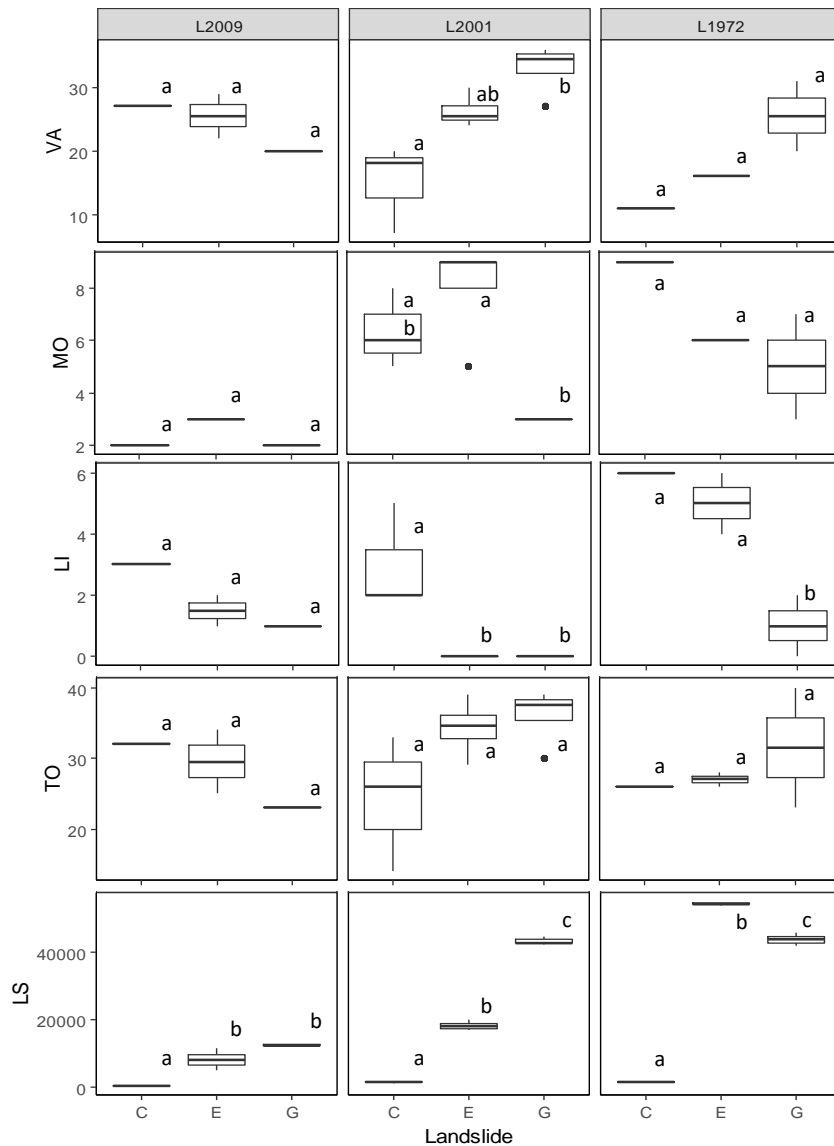


Fig. 7. The effect of landslide and its microsite type (C – control plot, E – right or left edge of landslide, G – ground) on number (pcs) of vascular (VA), moss (MO), lichen (LI) species, total number of species (TO), and *Larix* seedlings (LS, pcs ha⁻¹) amount at landslides of different ages (L2009, L2001, L1972). The values are arranged as boxplots (medians with confidence intervals, min, max). The horizontal line within the box indicates median, box boundaries indicate 25th and 75th percentiles, whiskers indicate highest and lowest values, dots above or below whiskers

indicate outliers. Medians followed by different letters in the same curve are significantly different at $P < 0.05$ according to Tukey multiple comparisons of means analysis.

5. Conclusions

Landslide processes are radically altered landscape, soil and biotope. Microecological conditions formed at the initial phase of regenerating succession after landslide disturbance are far different from those in control sites. Limited soil C and N availability at all landslide sites compare to control sites confirms that even “old” L1972 site is far from the state of the control site and C and N content did not recover after 35 years. “Young” landslide sites L2009 and L2001 are also spatially very heterogeneous with respect to ecological conditions. High variation of hydrothermal conditions and microenvironment at the “young” landslide sites resulted in increasing biodiversity of vascular plant, which resulted in high soil respiration variation. Similarly, at E-plots of “young” landslides, there was bigger soil microbial biomass and microbial respiration as compared to the control. At the “old” landslide site L1972, hydrothermal conditions were very close to the control sites. At the same time, analysis of microbial coenosis structure at intact and disturbed by landslides sites showed that oligotrophic microorganisms prevailed everywhere. Soil CO₂ emissions at L1972 which represents “old” stage of successional recovery were comparable to the control site and even tend to be higher and more variable spatially; however, soil microbial respiration and biomass was lower, both at E- and G-sites. The coefficient $q\text{CO}_2$ points to a stabilization of the microbial community at the L1972 site as it approached the value “1” and close to the control site state, except for G-plots.

Thus, ecological conditions of landslide sites were sharply different among types of microsites as well as control sites and were dependent on the age of landsliding disturbance event. Ecological conditions formed at landslide microsites affected regeneration processes of newly establishing forest in different ways. On the one hand, wood species (larch and *Dushekia*) regeneration occurred intensively during successional period. On the other hand, live vegetation cover (mostly vascular species), which is unrepresentative (or did not exist before) for these particular native larch stands, appeared. As we found, at landslides, total plant biodiversity is 1.5-2 times higher than that of the control site due to higher number of vascular plants. However, the number lichen species was significantly lower at the landslide sites than at the control. This goes well with considerations about landslides as a disturbance process, which increases site biological diversity through changing topography, soil and run-off conditions.

So, our results showed that in permafrost conditions of Siberia, after decades of a landslide disturbance, soil changes (like C and N content decreasing, microbial activity decreasing) may

persist for long time and may have great ecological impact, even if plant diversity and CO₂ fluxes are similar to the control site. Therefore, forested ecosystems in permafrost area disturbed after landsliding requires decades for final successful restoration. In addition, the degradation of permafrost due to landslides clearly hinders the accumulation of soil organic matter.

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Conflict of Interest: The authors declare that they have no conflict of interest.

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SUPPLEMENT

Table 4. Statistical results (F-values) of one-way ANOVAs for some physical, chemical and biological parameters at control plots of landslides and plots damaged by landslides in permafrost zone

	Control plots of landslides	Plots damaged by landslides
Source of variation	Landslide	Landslide
Soil temperature at 5 cm depth, °C	76.67**	242.8**
Mineral soil water content at 0-5 cm horizon, %	2.28	17.48**
Total soil C at 0-5 cm horizon, %	139.3**	0.52
Total soil N at 0-5 cm horizon, %	152.2**	2.35
C/N at 0-5 cm soil horizon	0.53	25.03**
Soil respiration, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	45.35**	28.81**
Microbial respiration at 0-5 cm mineral soil horizon, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	3.42*	11.34**
Microbial biomass at 0-5 cm mineral soil horizon, mg C g^{-1} dry soil	2.28	1.38
DNA amount, mln. fragment DNA copies per g^{-1} soil	3.97	3.37*
$q\text{CO}_2$	10.71**	18.8**
Number of hydrolytic microflora colonies, thous. KOE g^{-1} dry soil	8.19*	0
Number of microscopic fungi colonies, thous. KOE g^{-1} dry soil	0.16	2.74
Number of copiotrophs colonies, thous. KOE g^{-1} dry soil	26.54**	3.14
Number of oligotrophs colonies, thous. KOE g^{-1} dry soil	32.46**	0.35
Number of actinomycetes colonies, thous. KOE g^{-1} dry soil	10.29*	9.72**
Number of vascular plant species, pcs.	1.5	3.89*
Number moss species, pcs.	5.43	1.61
Number of lichen species, pcs.	1.2	7.05**
Total species number, pcs.	0.24	3.05
Larix seedlings, thous. pcs. ha^{-1}	107.5**	20.36**