

Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source

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Arctic tundra ecosystems are warming almost twice as fast as the global average¹. Permafrost thaw and the resulting release of greenhouse gases from decomposing soil organic carbon have the potential to accelerate climate warming^{2,3}. In recent decades, Arctic tundra ecosystems have changed rapidly⁴, including expansion of woody vegetation^{5,6}, in response to changing climate conditions. How such vegetation changes contribute to stabilization or destabilization of the permafrost is unknown. Here we present six years of field observations in a shrub removal experiment at a Siberian tundra site. Removing the shrub part of the vegetation initiated thawing of ice-rich permafrost, resulting in collapse of the originally elevated shrub patches into waterlogged depressions within five years. This thaw pond development shifted the plots from a methane sink into a methane source. The results of our field experiment demonstrate the importance of the vegetation cover for protection of the massive carbon reservoirs stored in the permafrost and illustrate the strong vulnerability of these tundra ecosystems to perturbations. If permafrost thawing can more frequently trigger such local permafrost collapse, methane-emitting wet depressions could become more abundant in the lowland tundra landscape, at the cost of permafrost-stabilizing low shrub vegetation.

Arctic tundra ecosystems are characterized by permanently frozen ground (permafrost) covered by a soil layer, named the active layer, which thaws and refreezes every year. Permafrost thaw and the resulting release of carbon dioxide and methane by microbial decomposition of previously frozen organic carbon is considered one of the most significant potential feedbacks from terrestrial ecosystems to the climate system^{1,2}. Warming and thawing of permafrost have been observed in many locations in recent decades⁷. Although thawing depth is controlled to a large extent by the regional climate, non-climatic factors, such as changes in vegetation and hydrology, can strongly modify the response of permafrost to global warming^{8,9}.

For a better understanding of the response of permafrost to climate change, it is important to determine how observed vegetation changes, for example, deciduous shrub expansion^{5,6}, contribute to stabilization or destabilization of the permafrost. We set up a shrub removal experiment at a Northeast-Siberian tundra site in 2007¹⁰. The study site represents poorly drained lowland tundra underlain by thick continuous permafrost in the Low Arctic climate zone. We clipped off all aboveground

biomass of the dominant deciduous shrub species *Betula nana* (dwarf birch) in five 10-m-diameter plots, leaving a few other shrubs, graminoids (grasses and sedges), mosses and lichens. The five control plots consisted of undisturbed *B. nana*-dominated vegetation. *B. nana* is a common tundra shrub species and is expected to benefit from climate warming¹¹. The control and *B. nana*-removal plots were very similar at the start of the experiment (Supplementary Table 1). Here, we report on our field observations over six years during which the removal plots have undergone major changes.

Shrub removal increased the thawing depth (active layer thickness) within one year (Fig. 1). This was consistent with larger ground heat fluxes in the removal plots¹⁰. In the following years the difference in active layer thickness between control and removal plots increased further, from a difference of 5 cm on average in 2008 to 15 cm in 2012 (Fig. 1; 2012: control = 25.8 ± 0.8 cm (mean \pm s.e.m., $n = 5$ plots), removal = 40.8 ± 1.8 cm; $F_{1,8} = 30.1$, $P = 0.001$). In the control plots, active layer thickness was largest in 2011 (Fig. 1), which experienced an exceptionally wet and warm summer (Supplementary Table 2).

By the fourth year (summer 2010) we noticed that parts of the removal plots were subsiding and became almost water saturated. The following summers, surface elevation and water table measurements revealed significant differences between the two treatments. The control plots were found to have an elevated convex shape, whereas the removal plots had mostly collapsed into concave depressions (Fig. 2). Over five years (2007–2012), the surface in the removal plots had subsided on average by 16.3 cm ($F_{1,8} = 20.0$, $P = 0.002$; Fig. 3a). This implies an average sinking of 3.3 cm yr^{-1} . As a consequence of the soil subsidence, snow thickness in winter and water table depth in summer changed. The concave depressions could store a thicker snow pack (Fig. 3b). In April 2012 snow thickness was 24.8 ± 1.7 cm in control plots compared to 35.0 ± 4.4 cm in removal plots ($F_{1,8} = 4.8$, $P = 0.060$). During the first years of the experiment (2008 and 2009), when soil subsidence was not yet obvious, snow thickness was not significantly different between control and removal plots (2008: $F_{1,8} = 2.8$, $P = 0.134$; 2009: $F_{1,8} = 2.1$, $P = 0.184$). During summer, the removal plots became visibly wetter than the control plots. This is expressed in near-surface water tables in the removal plots (Fig. 3c; $F_{1,8} = 8.3$, $P = 0.020$), the appearance of (permanent) pools in two removal plots and temporary ponding of water in four out of five removal plots (Supplementary Fig. 1).

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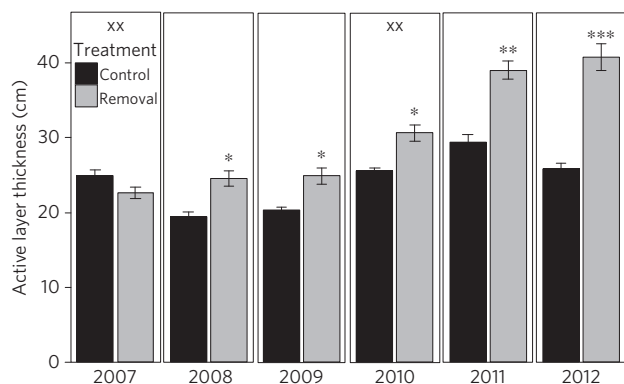


Figure 1 | Late-July active layer thickness in control and *B. nana* removal plots from 2007 to 2012. Data are mean values \pm s.e.m., $n=5$ plots. xx indicate years of *B. nana* removal. *, ** and *** indicate significant differences between the two treatments ($p < 0.05$, $p < 0.01$, $p < 0.001$, respectively).

Vegetation composition in the removal plots changed after the *B. nana* removal and wetting of the plots, whereas the vegetation composition in the control plots remained stable (Supplementary Fig. 2). The most striking development was the strong increase in graminoid cover in the removal plots over the period 2007–2012, with the difference between control and removal plots increasing over the years (Supplementary Fig. 2). In particular, *Arctagrostis latifolia*, a grass species that was already sparsely growing between the shrubs before the removal, expanded strongly (Supplementary Table 3). From 2010 onwards, wet sedge species *Eriophorum angustifolium* colonized the removal plots, probably spreading from nearby wet depressions.

Measured methane fluxes indicate a net release of methane from removal plots and a net uptake in control plots (Fig. 3d; $F_{1,7.99} = 13.4$, $P = 0.006$). This was consistent with earlier measured negative methane fluxes in similar *B. nana* shrub patches and positive fluxes (net emission) in wet depressions¹². The increased methane emissions in the removal plots were positively related to active layer thickness, soil moisture content and graminoid cover (Supplementary Fig. 3). It is well established that water tables close to the surface enhance methane emission as a result of decreased oxygen availability within the active layer, thereby stimulating methane production and depressing methane oxidation¹³.

Removal of aboveground biomass of *B. nana* shrubs in 10-m diameter experimental plots induced small-scale permafrost collapse, resulting in thaw pond development within five years (Fig. 4a). This illustrates the protective role of the low shrub vegetation cover. *B. nana* was the dominant vascular plant species in all ten plots at the start of the experiment and the removal of its aboveground biomass in summer 2007 meant a large reduction in total aboveground vascular plant biomass. The 4–5 cm thick ground cover of mostly mosses and some lichens was left behind and was not affected by the removal treatment (Supplementary Fig. 2). In addition, the organic top soil layer of 10–15 cm thickness was left intact, as the shrubs were clipped off at the moss surface. Mosses and organic soil layers are well-known good insulators but apparently not sufficient to prevent the active layer thickness increasing in the removal plots. The *B. nana* canopy was on average only 20 cm tall, but the low shrubs were strongly branched, thereby providing shading of the ground¹⁴.

The initial increased thawing after removal of the shrubs probably resulted in melting of ice within the top of the permafrost, leading to soil subsidence (Fig. 4b). Permafrost can contain large proportions of pure ice—when this ice melts the soil on top of it subsides. Lowland tundra is generally underlain by ice-rich permafrost, with ice contents as high as 80% by volume in the top

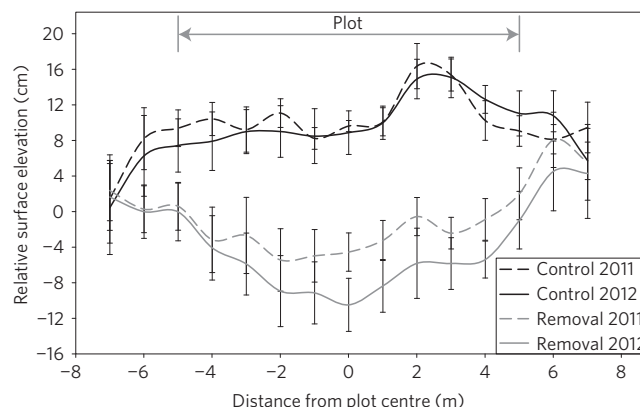


Figure 2 | Relative surface elevation in control and *B. nana* removal plots.

Relative surface elevation was measured across the 10-m diameter plot and 2 m beyond in 2011 (dashed lines) and 2012 (solid lines). Data are mean values \pm s.e.m., $n=5$ plots. Relative surface elevation was calculated as elevation at each distance within plot minus average elevation outside plot.

of the permafrost¹⁵. The changes in surface elevation contributed to further thawing by effectively trapping snow and water in the depressions that evolved from the soil subsidence (Fig. 4b). The control plots with shrub vegetation had a thinner snow pack than the concave removal plots, which is in contrast to thicker snow packs in shrub patches measured elsewhere¹⁶. This can be explained by the overall low vegetation height at our experimental site. Therefore, the top of the snow pack is rather flat and snow thickness is determined by the microtopography of the soil surface below the snow. A thicker insulating snow pack keeps the soil warmer in winter, which can increase active layer thickness in summer¹⁷. The subsidence of the removal plots also led to ponding of water in the new depressions—particularly in 2011, when July precipitation was very high. Sub-surface drainage of water is limited owing to the shallow active layer and barriers to lateral water flow due to microrelief in the permafrost table¹⁸. Surface water has a low albedo, causing increased absorption of solar energy, through which it may have contributed to further thawing from 2011 onwards^{9,19}.

Thus the initial increased thawing after removal of the shrubs triggered a positive feedback loop of thawing \rightarrow soil subsidence \rightarrow trapping of snow and water \rightarrow more thawing (Fig. 4b). This feedback is supported by the time series of active layer thickness data (Fig. 1). The strong active layer thickness increase in removal plots relative to control plots observed in the fifth year after removal (2012) can no longer be attributed to direct effects of shrub removal and is probably the result of continued sinking and trapping of snow and water in the removal plots. A prerequisite for soil subsidence on increased thawing is a high ice content of the permafrost. The strong feedback mechanisms can therefore be expected to be most pronounced in ice-rich permafrost regions. Of the total permafrost area, 20% can be characterized as ice-rich²⁰. Most of the tundra zone around the Arctic Ocean in Siberia, Alaska and Canada is considered at high risk of thaw subsidence²¹. In our study, 16 cm of soil subsidence was accompanied by a further 15 cm of increased thaw depth. As active layer thickness is measured relative to the surface this means that the permafrost table lowered on average by 31 cm in the removal plots over five years. This permafrost collapse occurred despite a mean annual temperature of -13.4°C . The substantial lowering of the permafrost table probably made earlier-frozen old organic carbon available for microbial decomposition²².

The rapid transition from slightly elevated shrub patches to water-saturated depressions observed in our field experiment illustrates the vulnerability of the tundra ecosystem to perturbations. The strong linkages between permafrost, vegetation

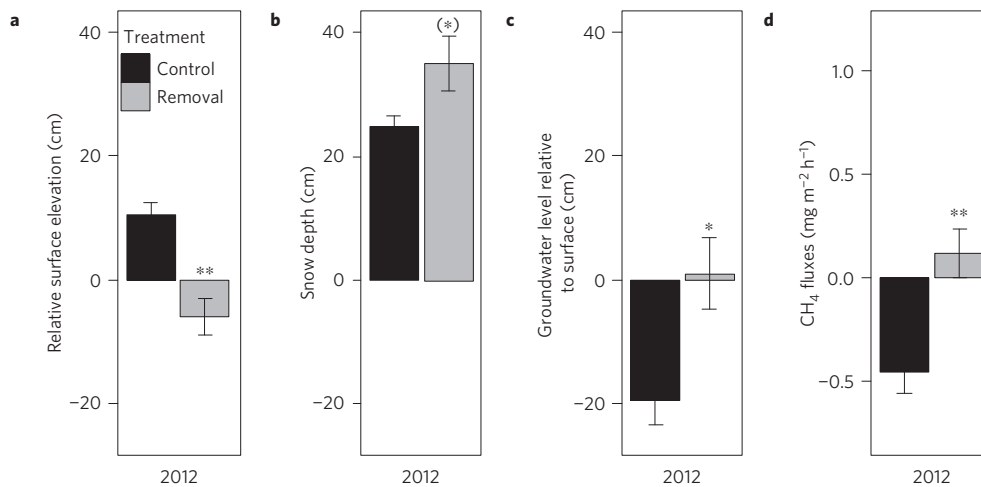


Figure 3 | Relative surface elevation, snow depth, groundwater level and methane flux in control and *B. nana* removal plots in 2012. **a–d**, Data are mean values \pm s.e.m., $n=5$ plots for relative surface elevation (**a**), snow depth in April (**b**), groundwater level in mid-July (**c**) and methane flux in early August (**d**). The legend in **a** applies to all panels. (*), * and ** indicate significant differences between the two treatments ($p < 0.10$, $p < 0.05$, $p < 0.01$, respectively). Positive methane (CH_4) fluxes indicate net emissions of methane to the atmosphere; negative values indicate net uptake of methane from the atmosphere.

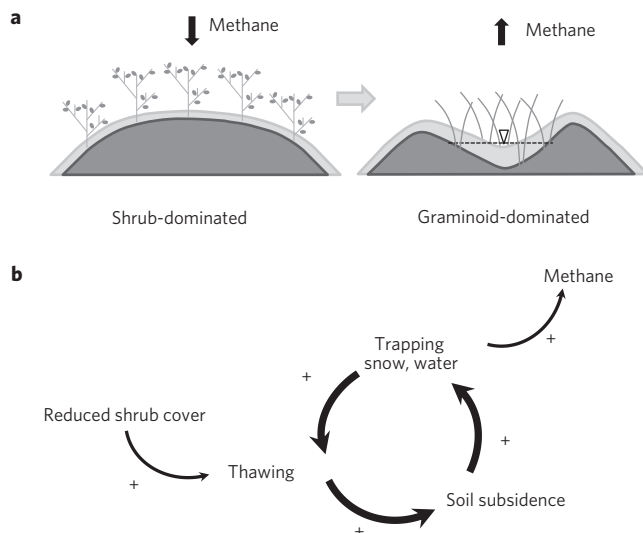


Figure 4 | How elevated shrub patches turned into graminoid-dominated wet depressions after removal of *B. nana* shrubs. **a**, Schematic representation of the permafrost collapse that took place in the *B. nana* removal plots. **b**, The positive feedback loop triggered by reduced shrub cover and the implications for the methane balance, all measured in the field experiment.

composition, microtopography, snow and hydrology, shown in this study, are prominent features of the lowland tundra landscape, which help protect the permafrost but also make the tundra vulnerable to disturbance^{9,23,24}. It was not only within our experimental plots that the permafrost collapsed. We observed several thaw ponds with drowning *B. nana* shrubs in the study area. The trigger for the small-scale permafrost collapse in these 'natural' thaw ponds was often unclear. Perhaps a gap in the protective shrub cover due to ageing of shrub plants or increases in plant pathogen pressure²⁵ could initiate the positive feedback loop. Climate warming, flooding and destruction of vegetation have also been suggested as triggers causing permafrost collapse features^{26–28}.

Observations from all over the Arctic suggest increased shrub growth coinciding with summer warming during recent decades²⁹. However, if increased permafrost thawing can more frequently trigger small-scale permafrost collapse, methane-emitting wet sedge

depressions might become more abundant in the landscape, at the cost of permafrost-stabilizing low shrub vegetation, at least in poorly drained ice-rich permafrost regions. Increasing wetland extent due to increased small-scale permafrost collapse in the Arctic tundra region seems an underestimated trajectory in response to climate warming^{4,30}. Our findings show that even disturbance of part of the vegetation can trigger feedback loops that cause permafrost collapse and an ecosystem shifting from being a methane sink to a source. They have far reaching implications for all human activities in the Arctic, for example, oil and gas field development, which may destroy the vegetation, and for the Arctic greenhouse gas balance, with potential feedbacks to global climate warming.

Methods

Study site. The study was conducted at the Chokurdakh Scientific Tundra Station (70° 49' N, 147° 29' E, 10 m above sea level) located in the Kytalyk (Siberian crane) Wildlife Reserve in the Indigirka lowlands in north-eastern Yakutia, Russian Federation. Chokurdakh mean annual air temperature is -13.4°C (1981–2010), with -34.0°C mean January temperature and 10.3°C mean July temperature. Mean annual precipitation is 196 mm (1981–2010), of which 76 mm (39%) falls in the summer months (June to August). The study area is underlain by thick continuous permafrost with a high ice content ($>20\%$ by volume)³⁰, which reaches more than 300 m depth. The field experiment was set up in a drained lake basin, which consists mostly of elevated shrub patches dominated by *Betula nana* L. (dwarf birch) shrubs surrounded by a diffuse drainage network of wet depressions dominated by the graminoid species *Eriophorum angustifolium* Honck. See Supplementary Methods for a more extensive site description.

Experimental design. We established ten circular plots of 10 m diameter in the elevated *B. nana* patches within the drained thaw lake basin in summer 2007¹⁰. Plots were selected pairwise, on the basis of proximity and similarity in vegetation composition and shrub density. Subsequently, the two treatments were randomly assigned to the plots within each pair: a control treatment (no shrub removal) and a removal treatment. Aboveground biomass of *B. nana* was removed by clipping stems at the moss surface to minimize disturbance. To maintain the *B. nana* removal treatment, regrowth of *B. nana* was removed in summer 2010. It was not necessary to remove the regrowth every year. One year after removal there was very limited regrowth, but by the third year regrowth was substantial in all removal plots and therefore removed. Regrowth could occur as the stems were clipped off at the moss surface, so new shoots could develop from remaining belowground resources in coarse roots. Only permanently wet conditions seemed to prevent recolonization.

Measurements. At the start of the experiment before manipulation, plant species abundance measurements and aboveground biomass harvests have been made for all ten plots. In addition, soil thawing depth, soil moisture and soil temperatures were measured during experiment establishment in mid-July 2007. Active layer thickness, using a bluntly tipped metal probe, and plant species abundances,

using the point-intercept method, have been measured every summer since the start of the experiment. Relative surface elevation and water table depth were measured in summer 2011 and 2012. Methane fluxes were measured in summer 2012 using a closed chamber of 29 cm diameter connected to an INNOVA 1312 photo-acoustic field gas monitor. See Supplementary Methods for details of the measurements.

Data analysis. The effect of the *B. nana* removal treatment on active layer thickness, relative surface elevation, water level, snow depth and vegetation cover was assessed using a repeated measures analysis of variance (RM-ANOVA) with treatment (control, removal) as between-subject factor and year as within-subject factor. Subsequently, differences between control and removal treatment in specific years were analysed using one-way ANOVA. As plot pair generally had no effect on the measured variables, it was not included in the ANOVA. All data were tested for a normal distribution and equality of variance. These statistical analyses were performed using SPSS 19. See Supplementary Methods for methane flux calculations and data analysis.

Received 12 May 2014; accepted 21 October 2014;
published online 24 November 2014

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Acknowledgements

We thank T. Strukova, S. Ianygin, A. Kononov, D. Suzdalov and S. Karsanaev for logistic support and assistance at the field site. We acknowledge support by Darwin Center for Biogeosciences (projects 1043 and 3052), The Netherlands Organisation for Scientific Research (Vidi-project 864.09.014), Wageningen Institute for Environment and Climate Research (WIMEK), Danish National Research Foundation (CENPERM DNR100) and the EU Seventh Framework Programme (FP7/2007–2013).

Author contributions

F.B., M.M.P.D.H., D.B. and A.L.N. conceived the project; all authors contributed to the field work; A.L.N. and D.B. analysed the data; M.M.P.D.H., A.L.N., D.B. and J.L. wrote the manuscript with contributions from B.E., F.B. and J.v.H.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.M.P.D.H.

Competing financial interests

The authors declare no competing financial interests.