# Ground ice melt in the high Arctic leads to greater ecological heterogeneity

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## Summary

**1.** The polar desert biome of the Canadian high Arctic Archipelago is currently experiencing some of the greatest mean annual air temperature increases on the planet, threatening the stability of ecosystems residing above temperature-sensitive permafrost.

**2.** Ice wedges are the most widespread form of ground ice, occurring in up to 25% of the world's terrestrial near-surface, and their melting (thermokarst) may catalyse a suite of biotic and ecological changes, facilitating major ecosystem shifts.

**3.** These unknown ecosystem shifts raise serious questions as to how permafrost stability, vegetation diversity and edaphic conditions will change with a warming high Arctic. Ecosystem and thermokarst processes tend to be examined independently, limiting our understanding of a coupled system whereby the effect of climate change on one will affect the outcome of the other.

**4.** Using in-depth, comprehensive field observations and a space-for-time approach, we investigate the highly structured landscape that has emerged due to the thermokarst-induced partitioning of microhabitats. We examine differences in vegetation diversity, community composition and soil conditions on the Fosheim Peninsula, Ellesmere Island, Nunavut. We hypothesize that (i) greater ice wedge subsidence results in increased vegetation cover due to elevated soil moisture, thereby decreasing the seasonal depth of thaw and restricting groundwater outflow; (ii) thermokarst processes result in altered vegetation richness, turnover and dispersion, with greater microhabitat diversity at the landscape scale; and (iii) shifts in hydrology and plant community structure alter soil chemistry.

**5.** We found that the disturbance caused by melting ice wedges catalysed a suite of environmental and biotic effects: topographical changes, a new hydrological balance, significant species richness and turnover changes, and distinct soil chemistries. Thermokarst areas favour a subset of species unique from the polar desert and are characterized by greater species turnover (β-diversity) across the landscape.

**6.** *Synthesis.* Our findings suggest that projected increases of thermokarst in the polar desert will lead to the increased partitioning of microhabitats, creating a more heterogeneous high arctic landscape through diverging vegetation communities and edaphic conditions, resulting in a wetland-like biome in the high Arctic that could replace much of the ice-rich polar desert.

**Key-words:** biodiversity, climate change, determinants of plant community diversity and structure, ice wedges, permafrost, plant–climate interactions, polar desert, species richness, thermokarst

## Introduction

The high Arctic biome is warming at double the global rate (IPCC 2013), which has led to warmer ground surface temperatures (Allison *et al.* 2011), shifts in surface hydrology (Smith *et al.* 2005), increases in active layer depth (Åkerman & Johansson 2008; Schuur *et al.* 2008) and changes in vegetation cover (Sturm *et al.* 2005). Indeed, in the high

Arctic, the first effects of warming air temperatures on plant communities are becoming evident (Hill & Henry 2011), and a warming climate has been linked to changes in the dynamics of permafrost, microtopography and vegetation (Jonasson, Michelsen & Schmidt 1999; Shaver *et al.* 2001; Van Wijk *et al.* 2003; Walker *et al.* 2006). Less well understood is how melting ground ice, contained within permafrost and particularly sensitive to a warming climate, may directly and indirectly catalyse ecological changes across the high Arctic.

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Permafrost underlies more than 25% of the Earth's land surface (Zhang *et al.* 1999) and one particularly common type of ground ice, known as ice wedges, occurs wherever continuous permafrost exists (French 2007) and may constitute over 50% of the volume of the top 3 m of ground (Pollard & French 1980). An ice wedge is a v-shaped body of ice that extends downwards for three to four metres and is formed by repeated thermal contraction cracking of the ground during winter months that is infilled by surface waters during the spring melt period. Ice wedges in the polar desert create a network of high-centred polygon tops, surrounded by low-relief polygon troughs under which the ice wedges lay. Given their ubiquity, mass and sensitivity to warming temperatures, the melting of ice wedges plays an important role in changing moisture regimes throughout this water-scarce region (Edlund, Woo & Young 1990), as high Arctic polar deserts receive 80% of their annual precipitation in the form of low-density snow, with little liquid precipitation during summer months (Rydén 1977).

Thermokarst is the climate-induced process of ice-rich permafrost melt, and its effects resonate through the geomorphology, ecology and biota of the Arctic (Billings & Peterson 1980). Two primary effects of thermokarst are the groundwater contributions made by melting ground ice during hot years (Edlund, Woo & Young 1990) and changes in local relief. Changes in landscape topography (subsidence) occur due to the volumetric loss of excess ice during melt, causing linear depressions in the ground known as troughs. These troughs are localized low points that promote the collection and transmission of water either directly from greater snow accumulation during winter months or from surface run-off during the snowmelt period. The enlargement of troughs through thermokarst-induced subsidence increases snowpack and surface run-off collection and should amplify local accumulation of water.

The presence of ice wedge polygon systems also creates biotic heterogeneity within the arctic landscape, as many environmental characteristics vary significantly over the metre or decimetre scale (Zona *et al.* 2011). Small differences in elevation (less than 10 cm) can lead to significant variations in pH, soil nutrients and soil moisture. The net effect is a highly structured landscape with microsite variation in vegetation cover and composition within the ice wedge polygon system. The general climate features of permafrost, precipitation and solar regime transform these microtopographic differentiations into steep environmental gradients along which vegetation communities change dramatically (Billings & Peterson 1980; Bliss, Svoboda & Bliss 1984; Engstrom *et al.* 2008; Huemmrich *et al.* 2010). Thermokarst, which amplifies differences in microtopography, is thus predicted to further increase biotic heterogeneity.

The harsh conditions of dry polar deserts have left the high Arctic with a relatively homogenous vegetation cover of low diversity (Edlund & Alt 1989). However, we suggest that the amplification of microtopographic differences through thermokarst likely results in greater environmental heterogeneity and thus greater community composition change among

thermokarst areas compared to the surrounding polar desert. Further, these changing community patterns and abundances are likely to alter soil chemistry of thermokarst areas through increased plant growth and associated microbial activity. While microbial nitrogen fixation – a process that requires sufficient soil moisture (Mengel *et al.* 2001) is likely to increase in thermokarst areas, increased plant growth may deplete soil nitrogen, phosphorus and potassium, and decrease soil pH (through selective ion uptake at their roots) while increasing organic matter build-up through the deposition of dead material.

With the breadth of possible ecosystem and landscape alterations due to thermokarst, it is surprising that ecosystem change and landscape change have been researched relatively independent of one another. Climate change is predicted to be the largest driver of Arctic biodiversity loss (Sala *et al.* 2000), yet significant gaps remain in our understanding of the underlying landscape processes that structure Arctic biodiversity. Changes in thermokarst rate and magnitude may resonate through the ecosystem at all levels – potentially intensifying predicted and documented changes to edaphic conditions (Lang *et al.* 2012), vegetation primary productivity (Elmendorf *et al.* 2012) and carbon sink/source dynamics (Abnizova *et al.* 2012) that may be expressed regionally and globally. A clear need exists to examine ecosystem and geomorphic processes as a coupled system in the light of a warming climate. Thermally sensitive ice wedges, the most ubiquitous yet ecologically overlooked periglacial feature, may be the canary in the coalmine for widespread high Arctic change.

Using a space-for-time approach, we examined the ecological effects of thermokarst in the Fosheim Peninsula, Ellesmere Island, Nunavut, within the Canadian high Arctic. This region is characteristic of a polar desert environment with little precipitation, nutrient poor soils, an extremely short growing season and a homogenous vegetation cover comprised primarily of dry dwarf-shrub tundra with pockets of sedge communities (Edlund, Woo & Young 1990). Within a hypothesis validation framework, we evaluate whether (i) greater ice wedge subsidence results in increased vegetation cover due to elevated soil moisture, thereby decreasing the seasonal depth of thaw (active layer) and restricting groundwater outflow; (ii) thermokarst processes result in altered vegetation richness (alpha diversity, Shannon's H), turnover (beta diversity) and dispersion (NRI, NTI), and whether amplified differences in relief between polygon tops and troughs drive greater microhabitat diversity at the landscape scale; and (iii) shifts in plant community structure alter soil chemistry, elevating organic matter, $NH_4+$ and $NO_3-$, and decreasing P, K and soil pH.

## Materials and methods

### STUDY SITE

Data were collected from a thermokarst site within a flat plateau region of the Fosheim Peninsula near Eureka, Ellesmere Island, Nunavut, Canada. This area was chosen for our study because it is representative of both the periglacial and biotic polar desert conditions found across the high Arctic, the accessibility of nearby logistical

support, the relatively lengthy (for the region) historical record of previous environmental study and the authors' field experience within the region. Permafrost in the area exceeds 500 m thickness (Taylor 1991) with a relatively thin mean active layer thickness of 57 cm that varies considerably depending on microclimatic conditions (Couture & Pollard 1998). The largely flat topography has, in geologic timescales, recently risen from the sea due to isostatic rebound (2000–9000 years before present depending on elevation: Hodgson 1985; Bell 1996). The resulting landforms are comparatively new, with relatively minor effects from biological processes given the slow rate of community succession in cold environments. In the Fosheim Peninsula alone, there is an estimated 1456.8 $km^2$ of ground ice, of which ~700 $km^2$ is probably wedge ice (Couture & Pollard 1998).

To select our study site, we first examined remote sensing data for the region (coarse-resolution Google Earth imagery) and identified 14 sites across the Fosheim Peninsula for aerial survey. During the survey, half were scouted with on the ground visual assessment, and the site selected for intensive fieldwork needed to be both representative of processes of interest and able to provide the basics for logistical operation. The study site (79.84574° N, 85.37028° W), a 200 m × 100 m area containing both polar desert and thermokarst plant communities, is representative of the broader area. There are no major landscape features in the immediately surrounding area, and the site is not drainage for regional snowmelt or rainfall catchment (Fig. 1). Thus, geomorphic differences in the site represent localized thermokarst processes affecting the ice wedge/vegetation system. At 101 m elevation, the area lies below the Holocene marine limit (Hodgson 1985; Bell 1996) and soils consist of fine-grained marine clay sediments.

## DATA COLLECTION

All data were collected during June and July 2013. Plant community composition was measured by visually estimating percentage cover within 0.5 $m^2$ quadrats placed at alternating polygon tops and troughs (between 5 and 10 m apart) along five transects running 200 m east to west, spaced 25 m apart north to south. We followed a stratified random sampling approach, recording compositional data within 80

quadrats with 20 samples in each of the following microtopography subunits: polar desert (control) tops, polar desert (control) troughs, thermokarst tops and thermokarst troughs. Five thermokarst trough quadrats were excluded due to standing water that remained throughout the study season. All vascular vegetation was identified to the species level, with vouchers submitted to the Marie-Victorin Herbarium in Montreal, QC (Table S1 in Supporting Information). Vascular plant nomenclature in this paper follows Saarela *et al.* (2013). Percentage cover of moss, lichen, leaf litter and bare ground was also noted.

Microtopographical subunits were initially classified by visual inspection of the dominant plant community and later verified using ground penetrating radar (GPR). Assigning the category of polygon top or trough is straightforward as troughs delineate the edges of tops. The GPR was used to create a near-surface hydrological map along each transect, and thermokarst/polar desert quadrats were easily separated by their distinct hydrological conditions. GPR data were collected using a Sensors & Software GPR unit with 500 MHz range sensors with a 0.25 m step size (Annan 2004). A detailed digital elevation model (DEM) of the site was created in ArcGIS (ESRI 2011) using 2000 elevation points collected by Trimble dGPS throughout the site and at each quadrat. GPR data transects were corrected for relief using interpolated dGPS elevation points from the DEM in EKKO View Deluxe software (Sensors & Software Inc. 2003). Polygon trough subsidence was calculated by taking the difference between trough elevation and the average elevation of immediately neighbouring polygons tops.

## PHYLOGENY RECONSTRUCTION

A molecular phylogeny of vascular plants was reconstructed using GenBank sequences for *rbcL* and *matK* from Saarela *et al.* (2013) (Table S1). These two genes have by far the best taxonomic coverage for species in the region. For one species, *Papaver radicatum* var. *radicatum*, there was no exact match in GenBank. In this instance, we used *Papaver dahlianum* as a placeholder as this most likely represents the closest taxonomic relative in the region. No other representatives from the *Papaver* genus were present at our site.
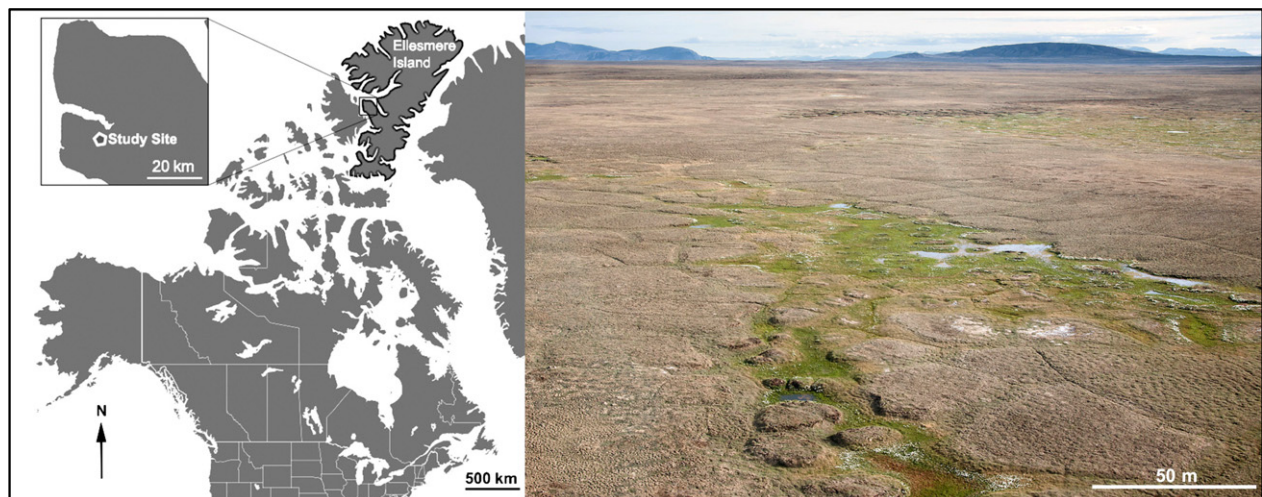


**Fig. 1.** Thermokarst study site on the Fosheim Peninsula, Ellesmere Island, Canada (79.84574° N, 85.37028° W). The area is an exceptionally flat plateau of marine sediments having recently (~9000 years ago) been exposed from the sea through isostatic rebound. The thermokarst zone is clearly visible with bright green vegetation and marked subsidence and geomorphic expression of ice wedge troughs. (Map created from GeoCommons).

Sequences were aligned with MAFFT version 7 (Katoh & Standley 2013) and checked manually in MacClade (Maddison & Maddison 2005). The modelTest function from the *phangorn* R package (Schliep 2011) was used to determine the best fit evolutionary model for each gene region (for *rbcL,* this was the HKY + G + I, and for *matK,* the GTR + G model was selected). A partitioned analysis was then run in MrBayes 3.2 (Ronquist *et al.* 2012) for 4 million generations, which was sufficient for model convergence, defined as average standard deviation of chain split frequencies of 0.01. The phylogeny was dated using the *chronopl* function from the *ape* package (Paradis, Claude & Strimmer 2004) with the following calibration points: Monilophytes 354mya (Bateman 1991), Eudicots 124mya (Hughes & McDougall 1990) and Saxifragales 91mya (Hermsen *et al.* 2003), and rooted using *Equisetum arvense* as an out-group.

## SOILS

At each quadrat, we collected data on soil chemistry and physical properties. Active layer depth was ascertained by pounding a permafrost probe into the four corners of the quadrat and calculating the average depth of penetrance. Ground temperature was taken at 12 cm soil depth as this represents general maximum rooting depth. Soil samples were collected by taking 12 cm deep slices from the four corners of the quadrat. Samples were homogenized, air-dried for several days and then pulverized. Wet/dry weight ratios were taken in the field for %$H_2O$.

Soil chemistry was analysed as follows: pH using a 1:2 soil-to-solution ratio using $H_2O$, then measured by pH meter (Hendershot, Lalande & Duquette 1993). Extractable $NO_3-$ and $NH_4+$ were obtained using a 2 M KCl extraction ratio of 1:10 soil to solution and shaken for 1 h. The filtrate was analysed by colorimetry for the determination of N on a multichannel Lachat Quikchem auto-analyser (Lachat Instruments 13-107-06-1-A, 10-107-06-2-C, 13-107-06-2-B; Maynard & Kalra 1993). Available P and K were determined by a multi-element extraction using Mehlich III solution and then measured by flow injection analysis (Lachat Instruments 13-115-01-1-B; Tran & Simard 1993). Percentage of organic matter was measured by loss-on-ignition of a (previously heated to 105 °C for 24 h) sample burned at 360 °C for 4 h. The difference in weight between the two steps is attributed to loss of organic matter expressed as a percentage (Schulte, Kaufmann & Peter 1991).

## STATISTICAL ANALYSIS OF VEGETATION AND SOIL DATA

First, spatial structure in vegetation abundance and soil moisture was evaluated using Moran's I, for which positive values indicate positive spatial autocorrelation and negative values indicate negative autocorrelation. Values around zero signify spatially independent data. Computed distances were binned into distance classes to smooth out stochastic effects. Significance was assessed by randomizations (*n* = 1000). Secondly, we evaluated spatial structure in the residuals from a linear regression run on total plot vegetation abundance explained by soil moisture.

We examined plant community differences of the four microtopographies by ordinating each plot's species composition and abundance using non-metric multidimensional scaling (NMDS) of a Bray–Curtis distance matrix calculated from percentage cover in the r-library *vegan* (Oksanen *et al.* 2013). Differences among groups were calculated using a permutational multivariate analysis of variance (PERMANOVA) on a Bray–Curtis distance matrix and 1000

randomizations. Species richness (alpha diversity) was measured as number of species per plot, and evenness was measured using the Shannon diversity index H′. Phylogenetic structure in plant community composition was assessed using two metrics, the net relatedness index (NRI) and mean nearest taxon index (NTI) in the r-library *picante* (Kembel *et al.* 2010), weighting by abundance to take into account the relative dominance of each species within a given quadrat. These metrics quantify the phylogenetic clustering of taxa relative to a null expectation that species composition is a random draw from the regional species pool (999 randomizations). Positive NRI and NTI values point towards phylogenetic clustering (closely related species tend to co-occur), whereas negative values indicate phylogenetic overdispersion (closely related species tend not to co-occur).

Means testing for richness, percentage cover, evenness, NRI and NTI were assessed using two-way, type III ANOVAs for imbalanced designs to account for the unequal number of samples (due to five plots being dropped from thermokarst troughs because of standing water) followed by Tukey tests for post hoc significance testing. The explanatory variables were location (control or thermokarst) and type (top or trough). We used type III ANOVAs as they are less dependent (than type I) on the ordering of explanatory variables and more accurate for analyses with unequal sample sizes. Finally, the turnover of plant species composition among plots (β-diversity) was quantified using the *raup-crick* function from Chase *et al.* (2011). β-diversity values of −1 indicate that plots are more similar to each other than expected by random chance and values of 1 indicate dissimilarity. Differences in β-diversity distributions between groups were tested using a two-tailed Kolmogorov–Smirnov test.

For means testing soil chemistries between microtopographies, two-way, type III ANOVAs for imbalanced designs were run followed by Tukey tests for post hoc analysis. All analyses were conducted in R version 3.0.2 (R Core Team 2014).

# Results

## MICROTOPOGRAPHY

dGPS and GPR transects were successful in generating a subsurface hydrological map of the site that easily delineated thermokarst (Figs S1 and S2), ground-truthed with soil moisture results. Strong contact signals (the boundary between different subsurface materials) were detected at the season's current depth of thaw within the thermokarst area where soil moisture was high (confirmed by soil moisture analysis Fig. 2) and showed a much weaker signal in control plots (Fig. S2). Subsidence of troughs within the thermokarst area (31 cm) was significantly greater than in non-thermokarst areas (18 cm) ($F_{1,33} = 25.17$, $P < 0.001$). Further, it is likely that mean thermokarst trough subsidence was even greater than reported here, as troughs that had standing water (and thus lower relief) were excluded from analysis.

Thermokarst plots had significantly shallower active layer depths ($F_{1,71} = 79.83$, $P < 0.001$) than control plots (Fig. 2) with troughs significantly shallower than tops ($F_{1,71} = 51.20$, $P < 0.001$), with a significant interaction effect ($F_{1,71} = 13.88$, $P < 0.001$) indicating that thermokarst effects were greater in troughs. Ground temperature at 12 cm depth (measured at 4 pm) within thermokarst plots was markedly colder ($F_{1,71} = 41.38$, $P < 0.001$) than control plots with troughs

significantly colder than tops ($F_{1,71} = 29.61$, $P < 0.001$), with a non-significant interaction effect. Post hoc tests were all significant ($P < 0.001$).

## PLANT COMMUNITY COMPOSITION

The study site included 22 species (Table S1) out of the estimated 140 species indigenous to the Fosheim Peninsula (Edlund, Woo & Young 1990), with control and thermokarst zones both having a gamma diversity (pooled species richness) of 17. The polar desert top and trough included 16 and 17 species, respectively, with *Salix arctica* and *Poa pratensis* dominating. *Pedicularis hirsuta* was found in tops but not troughs. Five species, *Cerastium arcticum*, *Saxifraga tricuspidata*, *P. radicatum*, *P. hirsuta* and *Dryas integrifolia*, were

found in polar desert but were completely absent from thermokarst.

Thermokarst top had the smallest species pool (13 species) and was dominated by *S. arctica* and *Dupontia fisheri*. Thermokarst trough contained 16 species and was the only microhabitat not dominated by *S. arctica*, instead being dominated by *D. fisheri* and *C. aquatilus*. Five species, *D. fisheri*, *C. aquatilus*, *S. cernua*, *E. triste* and *E. scheuchzeri,* were unique to thermokarst areas, being absent from the surrounding polar desert.

Vegetation cover shows strong spatial autocorrelation (Fig. S3), shifting from positive to negative over a distance of 100 m, with plots >150 m apart showing positive autocorrelation. However, the residuals extracted from a linear regression of abundance explained by %H$_2$O show no significant spatial autocorrelation.

A best-solution NMDS ordination of plot community composition was reached after 18 runs with a resulting stress of 0.14, indicating a good fit in 2D space (Fig. 3). Tops and troughs overlapped within each of polar desert and thermokarst; however, there was little overlap between polar desert and thermokarst. Additionally, thermokarst had a greater spread in ordination space indicating greater variance in species composition and abundance. PERMANOVA results show that thermokarst communities are significantly distinct from control ($P < 0.001$); however, tops do not differ significantly from troughs. Importantly, the significant interaction ($P = 0.02$) of location (control or thermokarst) and type (top or trough) indicates a differing response in community com-
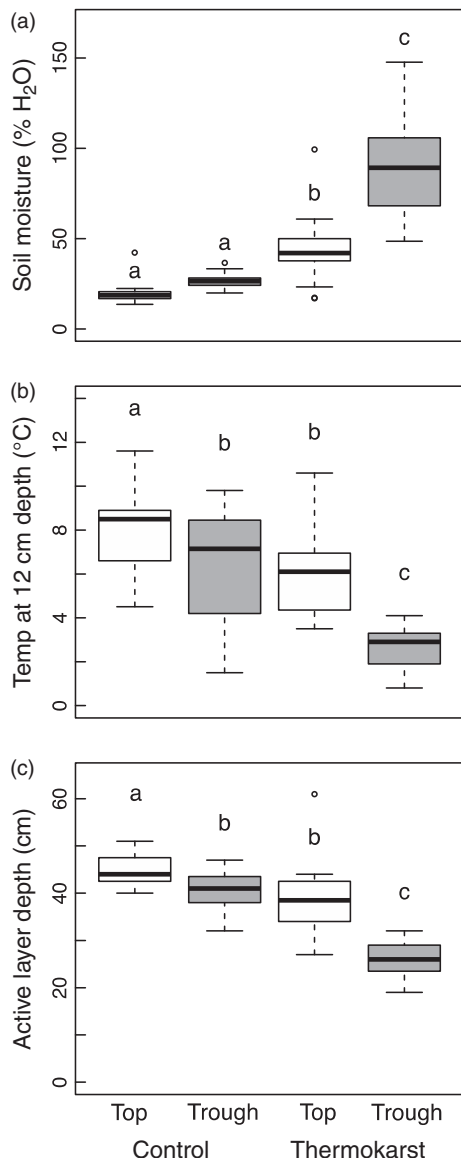


**Fig. 2.** Soil abiotic variables measured at the four different microtopographies. Box whiskers represent 1.5 interquartile range (IQR) boundaries. Letters above boxes represent significantly different values ($P < 0.01$, ANOVA and Tukey post hoc test).
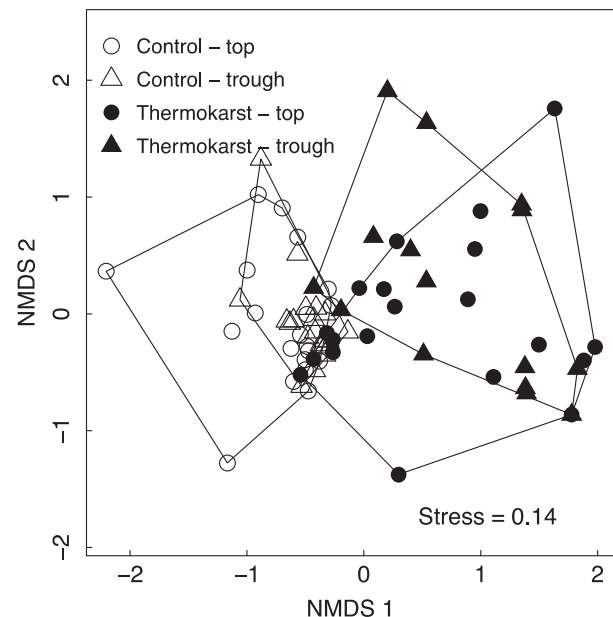


**Fig. 3.** NMDS ordination using a Bray–Curtis dissimilarity matrix generated from plant community composition. Hulls connect the outermost points of each microtopography to show spread of the data. The control and thermokarst groups show clear separation from one another, but top and trough compositions do not significantly differ. Thermokarst microtopographies also show more variance in community structure than control groups.

position change depending on whether thermokarst occurs to a polygon top or trough (Table S2).

### RICHNESS, TURNOVER, AND DISPERSION

Thermokarst plots had significantly lower species richness ($F_{1,71} = 37.82$ $P < 0.001$) than control plots, but there were no significant differences between tops and troughs (Fig. 4). Percentage cover was significantly greater in thermokarst plots than control plots ($F_{1,71} = 47.21$ $P < 0.001$), with troughs having significantly greater percentage cover than tops ($F_{1,71} = 10.43$ $P < 0.01$); interaction effects were non-significant. Evenness results showed similar patterns to species richness, with thermokarst plots significantly less even than control plots ($F_{1,71} = 27.79$ $P < 0.001$), with no signifi-

cant differences between tops and troughs. We note that contrast in richness and percentage cover should, however, be interpreted cautiously as plots do not represent fully independent sampling units.

The distribution of β-diversity values between thermokarst and polar desert was significantly different for both tops ($D = 0.1785$, $P = 0.005$ from Kolmogorov–Smirnov test) and troughs ($D = 0.1682$, $P = 0.01$ from Kolmogorov–Smirnov test). For polar desert tops and troughs, there is a distinct left-ward skew of β-diversity, indicating greater relatedness of species composition within microtopographic classifications (Fig. 5). In contrast, for thermokarst tops and troughs, the distribution of β-diversity values shifts right, indicating a greater dissimilarity of vegetation within thermokarst. For both tops and troughs, thermokarst plots are significantly more dissimilar in their community composition than polar desert.

There were no significant differences in NRI or NTI between thermokarst and control plots, or between tops and troughs (Fig. S4).

### SOIL CHEMISTRY

Soil chemistry differed significantly between thermokarst and control plots. P, K and pH values were lower in thermokarst for both tops and troughs, with K and pH significantly lower in thermokarst troughs than thermokarst tops (Fig. 6). Organic matter content was significantly higher in thermokarst consistent with the deposition and build-up of plant material in thermokarst soils, but there was no discernable difference for $NO_3-$, and most results were below laboratory detection limit. However, there was a trend for higher $NH_4+$ in thermokarst, significantly so for thermokarst tops.

## Discussion

A suite of biotic and abiotic differences are apparent in the area of thermokarst-induced subsidence of ice wedges. Most notably, subsidence alters surface hydrology (Edlund, Woo & Young 1990) such that plant growth is promoted, giving rise to new, wetland-like plant communities in the high Arctic. Thermokarst plant communities are distinct in species composition, have altered microtopographical soil chemistries and result in an increased microhabitat divergence of tops and troughs in ice wedge polygon systems (Zona *et al.* 2011). As a consequence of these changes, a highly structured landscape has emerged that is distinct from polar desert. Due to the abundance of ice wedges in this environment, we predict local ecosystem heterogeneity to generally increase across the high Arctic with further climate warming. A key question is whether such changes will exacerbate or ameliorate current warming trends. Our results suggest that increased graminoid/ sedge vegetation growth insulates the ground from further thermal change, likely through increased albedo (Blok *et al.* 2011) and retention of soil moisture (Woo & Young 2006), thereby reducing active layer depth and promoting system resiliency.
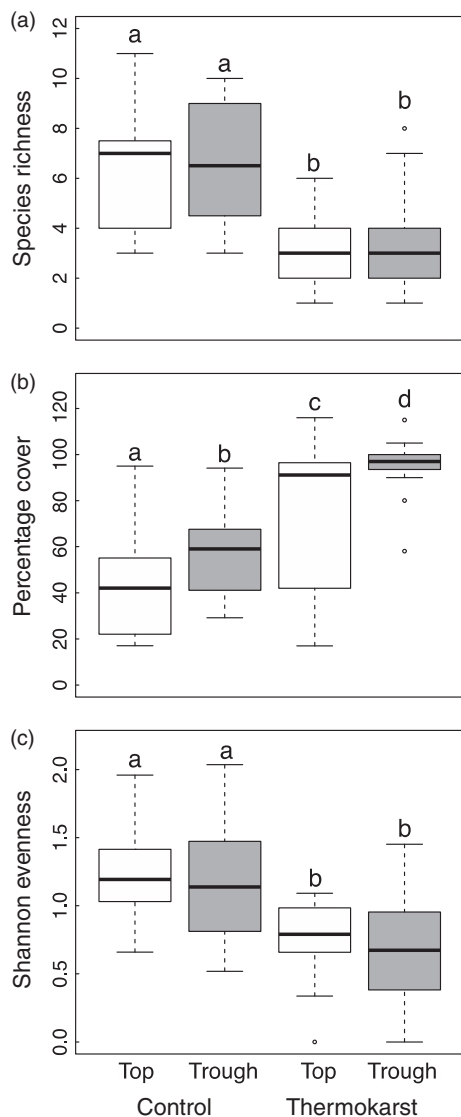


**Fig. 4.** Measures of plant species richness (alpha diversity) (a), percentage cover (b) and evenness (c) of the four microtopographies. Box whiskers represent 1.5 interquartile range (IQR) boundaries. Letters above boxes represent significantly different values ($P < 0.01$, ANOVA and Tukey post hoc test).
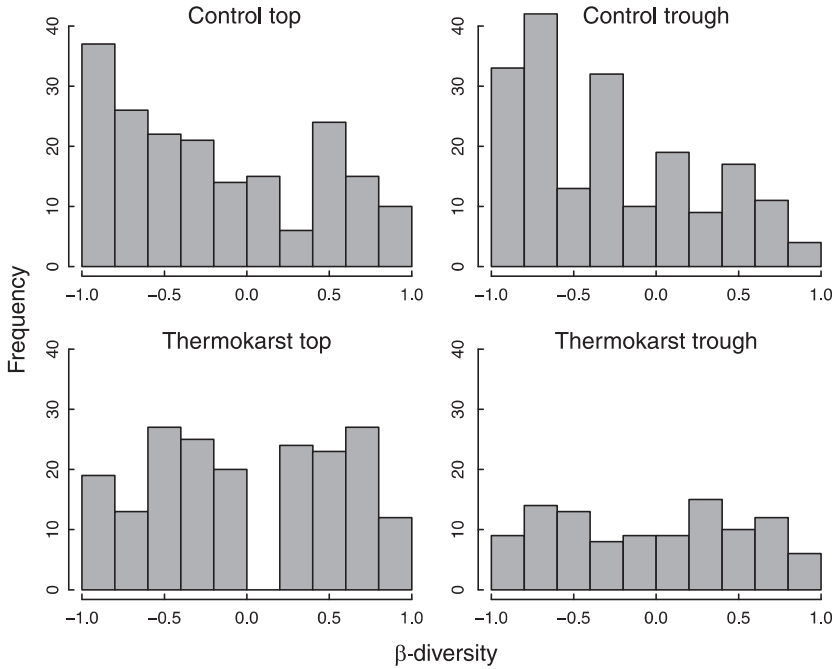
**Fig. 5.** β-diversity of plots within each of the four microtopographies. This calculation used a modification (Chase *et al.* 2011) of the Raup-Crick metric of β-diversity (Raup & Crick 1979). It calculates all pairwise comparisons of sites to see whether local communities are more dissimilar (approaching +1), as dissimilar (approaching 0) or less dissimilar (approaching −1), than expected by random chance. By splitting the calculation into the different microtopographies, we can see how the relatedness of plots within each group changes. Control areas are distinctly left-skewed – they tend to be less dissimilar (more similar) than expected by chance, whereas both thermokarst groups are more evenly distributed. Therefore, as a region of tops and troughs experience thermokarst, they become less similar to one another in species composition. Frequencies in thermokarst trough group are lower overall because there were less plots to compare than the other three groups (15 as opposed to 20).
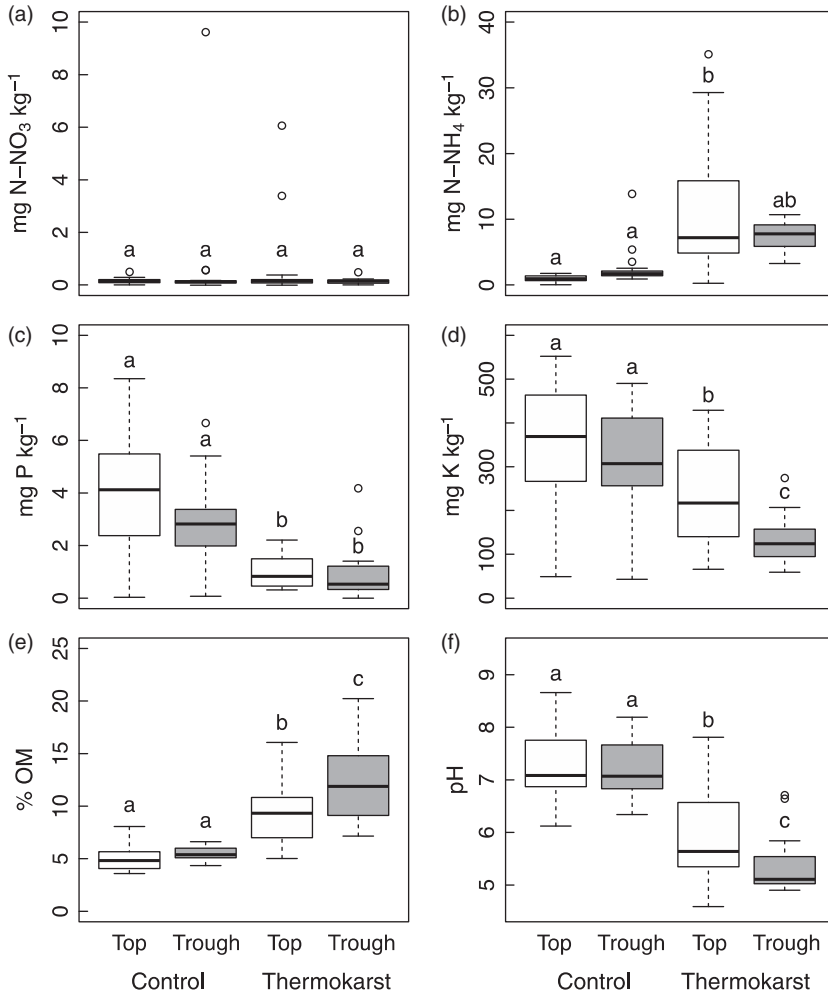


**Fig. 6.** Soil chemistry variables measured at plots on control tops, control troughs, thermokarst tops and thermokarst troughs: (a) plant available nitrate, (b) plant available ammonium, (c) phosphorus, (d) potassium, (e) per cent organic matter of loss-on-ignition and (f) pH. Box whiskers represent 1.5 interquartile range (IQR) boundaries; dots are outliers beyond the 1.5 IQR. Letters above boxes represent significantly different values ($P < 0.01$, ANOVA and Tukey post hoc test).

## MICROTOPOGRAPHY

We show that ground penetrating radar (GPR), ground-truthed with soil moisture data, accurately characterizes thermokarst subsurface moisture conditions and may be able to identify areas sensitive to thermokarst but that do not yet show ground surface evidence. The tops and troughs of thermokarst represent the same top and trough features found in non-thermokarst sites (i.e. the ice wedges occur in both areas) – but the relief change (subsidence) caused by thermokarst amplifies the expression of these features and induces hydrological change. Importantly, our results reveal that thermokarst areas have *shallower* active layers, meaning that the seasonal depth of thaw does not penetrate as deeply. This finding may appear counter-intuitive; however, we suggest that vegetation growth, stimulated by increased water collection, provides an insulating layer that reduces active layer depth (Shur & Jorgenson 2007) and thereby limits further groundwater seepage. We further suggest that thermokarst may induce a negative feedback cycle that stabilizes the ground to thermal change from high Arctic warming, as noted in long-term remote observation analysis (Jorgenson, Shur & Pullman 2006). The link between stabilizing vegetation growth and permafrost thaw is of great importance globally and needs further examination as potential negative feedbacks would greatly alter projections of permafrost thaw extent.

## NOVEL PLANT COMMUNITIES

The altered hydrology within thermokarst plots results in novel plant communities distinct from the vegetation of the polar desert. For example, thermokarst troughs were the only microtopographic feature not dominated by *Salix arctica* (Fig. S5). This willow species, which dominates across the other three microtopographies, appears to be an ecological generalist capable of tolerating a broad range of hydrological conditions (Dawson & Bliss 1989). However, the waterlogged soils in thermokarst troughs appear to fall outside its natural tolerance (Dawson & Bliss 1989), and this microtopography may reflect a tipping point of abiotic change – where thermokarst has pushed the community from polar desert into wetland conditions. Indeed, we show that spatial structure in vegetation cover is almost entirely explained by soil moisture, demonstrating the large effect of altered hydrological patterns on plant growth.

With the exception of thermokarst troughs, dominant species were similar among microtopographies, likely reflecting the broad water tolerance of these species (Ehleringer & Miller 1975; Shaver, Chapin & Billings 1979; Grulke & Bliss 1988). Five species were unique to polar desert and five different species were unique to thermokarst areas. Distinct vegetation succession patterns of polygonal tundra vary greatly as thermokarst features evolve through time (Billings & Peterson 1980), and as a thermokarst feature stabilizes, so should its resident vegetation. The broader implication of diverging communities is that with increasing thermokarst, and over time, we should expect to see polar desert communities transition to wetland communities with distinct assemblages.

## NOVEL SOIL CHEMISTRY

Mirroring the patterns we observed for plant communities, we also found a significant divergence in soil chemistry between thermokarst and polar desert. Most striking was the increase in soil moisture content within thermokarst, likely through the collection of melt run-off and increased snow accumulation as a consequence of altered microtopography through subsidence (Edlund, Woo & Young 1990). While we might have expected leaching to elevate soil nutrient content in thermokarst troughs, we found that P and K values were lower in thermokarst than in the surrounding polar desert. P and K are depositional and would have been laid down when this area was still sea floor. We therefore suggest their depletion in thermokarst reflects consumption of these resources through increased plant growth. Increased plant activity also explains the lower soil pH values in thermokarst, as acidification of soil occurs through selective ion uptake at the roots (Mengel *et al.* 2001). Elevated plant growth also increases the organic matter content of thermokarst soils, resulting in soils that are significantly more carbon-rich than surrounding polar desert. As the area has only relatively recently (in geologic time-scales) emerged from the sea (2000–9000 years before present) and northern ecosystem processes are notoriously slow, the development of carbon-rich thermokarst soils should be regarded as a new feature resulting from biotic development (Edlund & Alt 1989). However, whether thermokarst areas will function as carbon sinks will ultimately depend on rates of microbial soil respiration relative to rates of carbon sequestration through vegetative growth (Soegaard & Nordstroem 1999).

In contrast to P and K, soil nitrogen is not depositional; instead, it accumulates through the conversion of atmospheric $N_2$ to ammonium and nitrate mediated by aerobic bacterial action. We find a weak but significant trend for higher ammonia accumulation in thermokarst soils, but no matching trend for soil nitrate. Low soil nitrate is not entirely surprising for two reasons. First, the second step in the oxidation reaction, the conversion of ammonia to nitrate, is slowed down by cold temperature and waterlogged soils. Secondly, plants in this area may be nitrogen deprived such that they take up $NH_4+$ as soon as it becomes available in the soil, leaving less available for the second oxidation stage.

Our results suggest that thermokarst soils may be N-limited, rather than P-limited (Haag 1974). However, we predict this to change over time, as nitrogen can be replenished through continual, slow microbial input, whereas there is little depositional input of phosphorus (Gordon, Wynn & Woodin 2002). Thus, with increased moisture and microbial–plant associations to facilitate nitrogen fixation in thermokarst areas, we may see a gradual shift from a nitrogen- to phosphorus-limited system. The consequences of such a shift on arctic vegetation are not yet clear, but our analysis already shows

that thermokarst soil is increasingly divergent from the soil of the polar desert.

### INCREASING ECOLOGICAL HETEROGENEITY

We initially predicted that thermokarst processes would induce changes to richness, turnover and dispersion among plant communities. Thermokarst was found to have lower alpha diversity at the plot level, but the species pool (gamma diversity) of thermokarst was equally as rich as the non-thermokarst control. We propose that as thermokarst changes microhabitat conditions, polygon top and trough differences are amplified, creating new hydrological niche space for colonization. Incoming (wetland) species dominate this niche, as indicated by decreased species evenness, resulting in lower species richness per plot but increased turnover between plots.

However, we found the lack of difference in phylogenetic dispersion between plant communities between control and thermokarst areas surprising given the strongly divergent soil conditions, particularly the strong soil moisture gradient. It is possible that after initial colonization of thermokarst, competitive interactions dominate for later-successional species (Cargill & Chapin 1987), removing any signal of phylogenetic clustering. Alternatively, water tolerance might demonstrate only weak phylogenetic conservatism. A wide range of water tolerance has been documented within many different arctic species, often through ecotypic differentiation (Teeri 1973; Shaver, Chapin & Billings 1979; Grulke & Bliss 1988). In this landscape, hydrological conditions vary from water-saturated conditions of the spring snowmelt to desert conditions during dry summers. It might therefore be unsurprising if water tolerance is an evolutionary labile trait that is not strongly structured on the phylogeny. Such evolutionary plasticity would explain how it is possible for vegetation communities to differentiate significantly between microtopographies, yet demonstrate little phylogenetic structure (Fig. S5).

Importantly, not only does the composition of thermokarst vegetation diverge from that of the polar desert, there is also greater heterogeneity at the site scale. Thus, while plot-level alpha diversity and evenness are lowered, there is greater compositional turnover in thermokarst communities across the site, particularly within troughs. This shift is driven by changes in the dominant species within thermokarst and is mirrored by shifts in soil nutrients. We posit that the amplified relief change between tops and troughs promotes the divergence of microhabitats, resulting in a greater diversity of habitats. While we observe heterogeneity increasing locally, we suggest that due to the large spatial coverage of polygons across the high Arctic that this is likely repeated across the region. However, regional heterogeneity may not necessarily increase, since other locales may increase heterogeneity in a similar way. Given that ice wedges are ubiquitous across the continuous permafrost region, and they occupy enormous ground volume across the arctic zones of North America, Europe and Asia, we believe they will be a catalyst for widespread ecosystem change in light of a warming Arctic.

## SUMMARY

Climate change is predicted to be the largest driver of future biodiversity loss in the Arctic (Sala *et al.* 2000). Our study suggests that in the near future, it is likely that further geomorphic partitioning of habitats due to thermokarst will facilitate community restructuring drawn from local species pools. This restructuring may lead to an increasing shift of polar desert towards a more heterogeneous landscape comprised of a mosaic of different habitat types. Contrary to studies suggesting loss of biodiversity with climate change, our results indicate that ecosystem changes in the high Arctic might result in a wider range of habitat types supporting a greater diversity of plant species. In addition, increasing arctic primary productivity (Elmendorf *et al.* 2012) may provide greater nesting habitats for migratory birds and richer foraging for ungulates, and in general better support the needs of higher trophic levels. However, increased thermokarst and ponding of water may lead to elevated permafrost carbon emission. Polygonal tundra thermokarst ponds release carbon at an order of magnitude higher than dry polar desert (Abnizova *et al.* 2012), and the expansion of thaw lakes in neighbouring Siberia has been linked to a 54% increase in methane emissions (Walter *et al.* 2006). The shrinking of polar desert therefore represents the gradual loss of one of Earth's most extreme biomes and disadvantageous carbon dynamics, while favouring the expansion of a novel and perhaps more biotically diverse wetland system.

## Data accessibility

Data on vegetation composition, soil chemistry and abiotic variables are available from the Dryad Digital Repository at doi: 10.5061/dryad.5n628 (Becker, Davies & Pollard 2015).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Species list and sequence information used for phylogenetic trees.

**Table S2.** PERMANOVA results testing differences in community structure.

**Figure S1.** Digital Elevation Model (DEM) of site thermokarst.

**Figure S2.** 500 MHz GPR transects.

**Figure S3.** Moran's I and spatial autocorrelation results.

**Figure S4.** Phylogenetic NRI and NTI results of the four microtopography types.

**Figure S5.** Averaged phylogenetic trees of the four microtopography types.