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LETTER

Shallow soils are warmer under trees and tall shrubs across Arctic and Boreal ecosystems

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Supplementary material for this article is available [online](#)

Abstract

Soils are warming as air temperatures rise across the Arctic and Boreal region concurrent with the expansion of tall-statured shrubs and trees in the tundra. Changes in vegetation structure and function are expected to alter soil thermal regimes, thereby modifying climate feedbacks related to permafrost thaw and carbon cycling. However, current understanding of vegetation impacts on soil temperature is limited to local or regional scales and lacks the generality necessary to predict soil warming and permafrost stability on a pan-Arctic scale. Here we synthesize shallow soil and air temperature observations with broad spatial and temporal coverage collected across 106 sites representing nine different vegetation types in the permafrost region. We showed ecosystems with tall-statured shrubs and trees (>40 cm) have warmer shallow soils than those with short-statured tundra vegetation when normalized to a constant air temperature. In tree and tall shrub vegetation types, cooler temperatures in the warm season do not lead to cooler mean annual soil temperature indicating that ground thermal regimes in the cold-season rather than the warm-season are most critical for predicting soil warming in ecosystems underlain by permafrost. Our results suggest that the expansion of tall shrubs and trees into tundra regions can amplify shallow soil warming, and could increase the potential for increased seasonal thaw depth and increase soil carbon cycling rates and lead to increased carbon dioxide loss and further permafrost thaw.

1. Introduction

Rapid increases in air temperature across the Arctic and Boreal region are associated with warming soils, thawing permafrost, and expanding tall-statured shrubs and trees in the tundra (Romanovsky *et al* 2003, Myers-smith *et al* 2011, Elmendorf *et al* 2012). Warming soils place the vast pool of carbon frozen in permafrost at risk of thawing and releasing greenhouse gases into the atmosphere (Schuur *et al* 2015, Biskaborn *et al* 2019). Warming soils also impact belowground plant function and root growth (Iversen *et al* 2015), modifying plant nutrient use, primary productivity, and transpiration (Cable *et al* 2014, Lafleur and Humphreys 2018, Hewitt *et al* 2019). Warmer soils and deeper seasonal thaw alter soil nutrient and carbon cycling (Keuper *et al* 2012, Salmon *et al* 2016, Finger *et al* 2016). Thus, quantifying the degree of soil warming is critical to understanding future ecosystem function and the

stability of underlying permafrost (Jorgenson *et al* 2001, Loranty *et al* 2018).

Vegetation change across the pan-Arctic is altering land surface energy dynamics with critical implications for soil thermal regimes in the permafrost region (Elmendorf *et al* 2012, Myers-Smith *et al* 2015, Martin *et al* 2017). Experimental manipulations of shrub cover in tundra ecosystems indicate that increasing shrub canopy ('shrubification') cover reduces summer soil temperatures and decreases the depth of seasonal thaw via canopy shading (Blok *et al* 2010, Myers-Smith and Hik 2013). In contrast, a recent study using eddy covariance measurements suggests that shrubs are associated with warmer summer soil temperatures (Lafleur and Humphreys 2018). Shrubs increase winter soil temperatures due to insulation by trapping snow (Myers-Smith *et al* 2015). The net effect on annual thermal regimes may depend on local and seasonal environmental conditions including microclimate, topography, and soil

properties (Zellweger *et al* 2020), and individual plot scale studies provide limited insight. The lack of consensus in plot scale observations creates uncertainty regarding potential feedbacks of shrubification in the tundra, and calls for a larger scale assessment of the impacts of vegetation on soil temperature.

Treeline advance may have similar soil temperature consequences to shrub expansion since observations indicate that greater tree leaf area is associated with decreased summer thaw depths (Fisher *et al* 2016). Associations between boreal forest cover and snow depth have also been related to warmer winter soil temperatures (Jean and Payette 2014). However, the effects of changing forest cover on soil temperatures has received considerably less attention compared to shrub expansion studies. This is an important knowledge gap as links between vegetation structure and soil thermal dynamics are critical for assessing the vulnerability of permafrost to ongoing climate warming and vegetation shifts (Lawrence *et al* 2012, Cable *et al* 2016).

The current understanding of boreal and tundra vegetation impacts on soil temperature is limited to local or regional scales (Blok *et al* 2010, Fisher *et al* 2016, Paradis *et al* 2016, Frost *et al* 2018) and lacks the generality necessary to predict soil warming and permafrost stability on a pan-Arctic scale. The net effects of vegetation on annual thermal regimes may also reflect local and seasonal meteorological and soil conditions. A synthesis of high-latitude studies with broader geographic coverage and greater variability in soil and site conditions can offer the potential to evaluate whether plot scale observations of vegetation impacts on soil temperature are consistent across studies within similar types of vegetation (Fidler *et al* 2017). Here we establish empirical linkages between observations of vegetation and air-soil temperatures using 106 sites located within nine common Arctic and Boreal vegetation types (Walker *et al* 2005) to address the following questions: (a) do shrubs and trees cool shallow soils during the warm season? (b) how does vegetation affect cold season soil temperatures? (c) does vegetation influence the seasonal dynamics of soil temperature on annual timescales?

2. Methods

2.1. Temperature data

Daily average soil and air temperature was compiled from 235 sites across the Arctic-boreal region that are underlain by permafrost and that include a vegetation description at the study locations. We compiled a total of 877 305 soil temperature observations and 304 492 air temperature observations. Figure 1 displays the pan-Arctic permafrost extent (Brown *et al* 2011) with study sites to provide context. Table 1 contains a full break down of the number of observations and sites for each

vegetation type and table S1 (is available online at <https://stacks.iop.org/ERL/16/015001/mmedia>) (electronic supplement) contains site descriptions for all sites used in analysis, and table S2 (electronic supplement) information for all 235 sites initially compiled.

Our analysis focused on a total of 106 sites with 305 973 soil and 169 362 air temperature observations that met the following considerations to achieve a harmonized analysis, and the remaining 129 sites originally compiled were not used in the analysis. The 106 sites used in the analysis were selected based on the criteria explained below. We focused only on soil temperature measured within the top 20 cm of the active layer, and sites without observations in the upper 20 cm were not included. We focus on the temperature in the upper 20 cm of the active layer has the closest coupling to the air temperature and influences the temperature of the soil below (Smith and Riseborough 1996, Hillel 1998). An initial analysis demonstrated that soil temperature varies nonlinearly at depths below 20 cm, and this nonlinear relationship can be highly variable between sites. Our sample size of sites with data below 20 cm was too limited to adequately characterize these deeper depths across the study domain, and thus any sites that did not make observations in the upper 20 cm of the soil were excluded. Air temperature measurements also needed to be taken from a minimum height of 1 m to avoid measurements within the snow during the winter. Sites with air temperature sensors mounted below 1 m in height above the ground were excluded. We use water years (October–September) rather than the calendar year to characterize annual temperature patterns since winter soil temperatures will be highly dependent on autumn soil temperature and snow accumulation. Sites needed at least 75% of a water year with observations to be included in the study. To avoid confusion with calendar year seasons and the ambiguity of defining transition periods, we define seasonality based on when site temperatures are below freezing (cold season) and above freezing (warm season).

2.2. Vegetation data

Each site was classified into a vegetation type based on the growth form of the dominant plant cover. We classified tundra plant communities similar to the broad physiognomic categories that vegetation communities are grouped in by Walker *et al* (2005) to allow for our results to be placed into broader geographical contexts. Boreal vegetation classes were classified by leaf functional type of the dominant tree cover including evergreen needleleaf boreal forest, deciduous needleleaf boreal forest, and mixed evergreen needleleaf and deciduous broadleaf boreal forest. Tundra vegetation types include herb barren, graminoid tundra (non-tussock forming), short shrub tundra (<40 cm in height), tussock tundra,

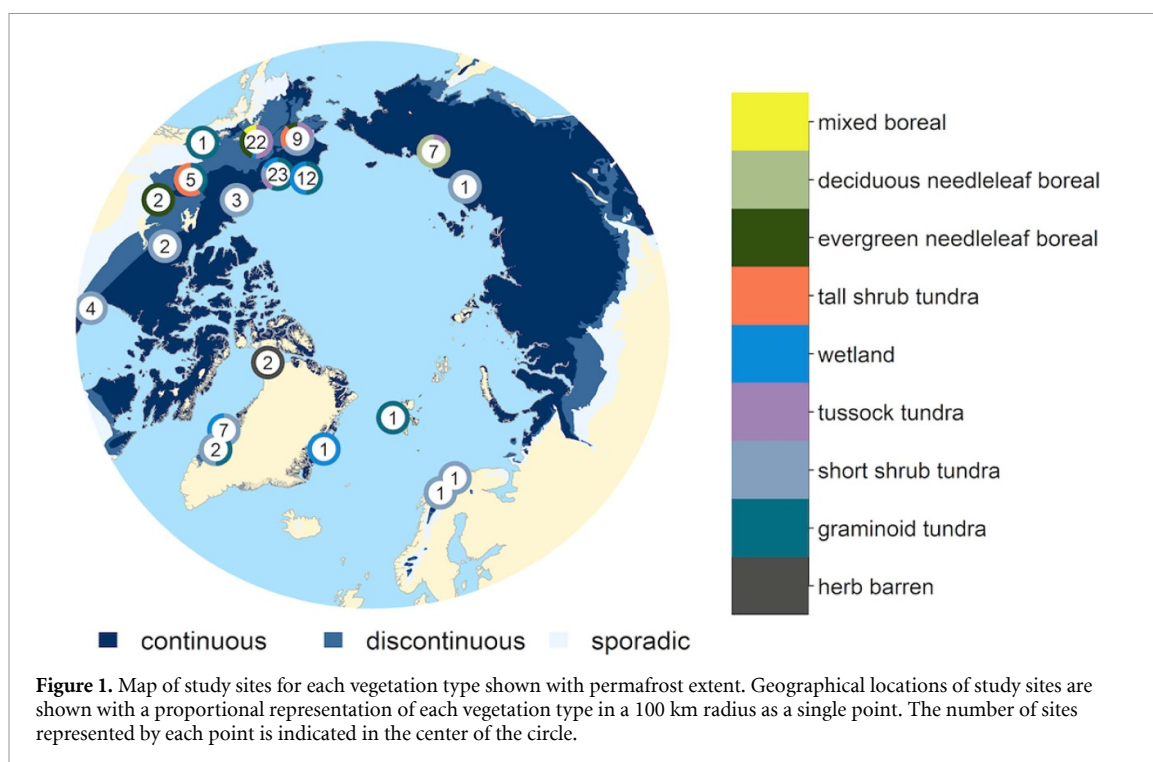


Table 1. Summary of site and temperature observations in analysis.

| Vegetation type | Number of Sites | Site \times years | Number of daily soil temperature observations | Number of daily air temperature observations |
|-----------------------------|-----------------|---------------------|---|--|
| Herb-barren | 2 | 9 | 5096 | 3193 |
| Graminoid tundra | 24 | 85 | 68 574 | 33 289 |
| Short shrub tundra | 24 | 109 | 54 520 | 43 476 |
| Tussock tundra | 17 | 77 | 58 520 | 33 609 |
| Wetland | 15 | 35 | 13 915 | 12 241 |
| Tall shrub tundra | 5 | 73 | 77 372 | 27 058 |
| Evergreen needleleaf boreal | 10 | 25 | 16 892 | 10 964 |
| Deciduous needleleaf boreal | 6 | 9 | 5760 | 3100 |
| Mixed boreal | 3 | 7 | 5111 | 2432 |
| Total | 106 | 429 | 305 973 | 169 362 |

tall shrub tundra (>40 cm in height), and wetland. Here we separated wetland as any vegetation type that experiences inundation throughout the duration of the warm season rather than a single plant functional type deviating from Walker *et al* (2005). We also simplified shrub categories from Walker *et al* (2005) including all dwarf and prostrate shrubs in our short shrub category and all tall shrubs defined as above >40 cm. Herb-barren and deciduous needleleaf have limited geographic scope with a few sites located in close proximity. We included these sites for comparison, but caution against broader geographic extrapolation.

2.3. Soil and air temperature models

Many sites have incomplete observations of air or soil temperature throughout a water year due to the timing of sensor deployment or sensor failure.

We implemented a phenomenological model of daily soil temperature in a Bayesian framework to account for missing observations. We used this model to gap fill missing temperature observations in the sites with 25% or less missing data in a water year. Using a statistical modelling approach allowed us to avoid bias in metrics such as mean annual, maximum, and minimum temperatures that can be heavily biased with missing observations and quantify uncertainty in these metrics. This modelling approach also provided a quantitative comparison of annual soil temperature patterns throughout a water year, and these parameters can be compared between sites in empirical models to better understand variabilities in air-soil temperature decoupling. A full description of the daily soil and air temperature model is included in the electronic supplement.

2.4. Empirical vegetation-temperature relationships

We implemented empirical models of air and soil annual temperature parameters (maximum, minimum, and mean annual soil temperature) to evaluate the influence of vegetation on air-soil temperature decoupling. We compared differences between the air and soil minimum and maximum temperature in a year and the number of days in the water year that were above zero across sites. We used a normalized measure of air and soil temperature decoupling to understand the cumulative decoupling of temperatures above and below freezing (Smith and Riseborough 1996, 2002). The n -factor for the freezing degree day soil:air ratio (n_f) was calculated from the degree days below freezing (FDD), and the thawing n factor (n_t) was calculated from the degree days above freezing (TDD):

$$n_f = \frac{\text{FDD}_{\text{soil}}}{\text{FDD}_{\text{air}}}$$

$$n_t = \frac{\text{TDD}_{\text{soil}}}{\text{TDD}_{\text{air}}}$$

We implemented multiple regressions in a Bayesian framework to evaluate empirical relationships between vegetation type and soil temperature parameters. We included the uncertainty from the air and soil temperature model in the empirical models of temperature parameters and n -factors that had missing observations using a Berkson error model to account for uncertainty in parameters. A multiple linear regression was conducted in a hierarchical Bayesian framework with the corresponding air temperature parameter and depth of measurement used as covariates and the vegetation type treated as fixed effects. This approach allowed us to compare soil temperature parameters between vegetation types while controlling for air temperature and sensor placement. Since we compare multiple soil temperature parameters between nine vegetation groups, we used a Bonferroni correction on credible intervals for any statistical inferences made between groups to help account for the many comparisons in this analysis (Ogle *et al* 2019).

3. Results

3.1. Soil and air temperature models

The daily soil temperature model had a model fit with R^2 of 0.95 (figure S1, electronic supplement). Soil temperature data were slightly over-predicted at low temperatures ($< -15^\circ\text{C}$) and under-predicted at higher temperatures with a least squares regression intercept of -0.09 at an observed temperature of 0°C and slope of 0.95°C per 1°C increase in observed soil temperature. The daily air temperature model fit had a R^2 of 0.83 (figure S1, electronic supplement). Air temperature data were slightly over-predicted at low temperatures ($< -10^\circ\text{C}$) and under-predicted at

higher temperatures with a least squares regression intercept of -1°C at an observed temperature of 0°C and slope of 0.83°C per 1°C increase in observed soil temperature. The empirical models of annual temperature measures with vegetation type, depth in soil, and annual air temperature measures had model fits with R^2 of 0.69 for minimum soil temperature, R^2 of 0.70 for maximum soil temperature, and R^2 of 0.72 for mean annual soil temperature (figure S2). Bivariate plots of the relationship between the air and soil temperatures in these empirical models are shown in figure S3. Models accounting for soil depth within each vegetation type for the n -factors, and the length of days above freezing had model fits with $R^2 = 0.51$, 0.69, and 0.28, respectively (figure S4).

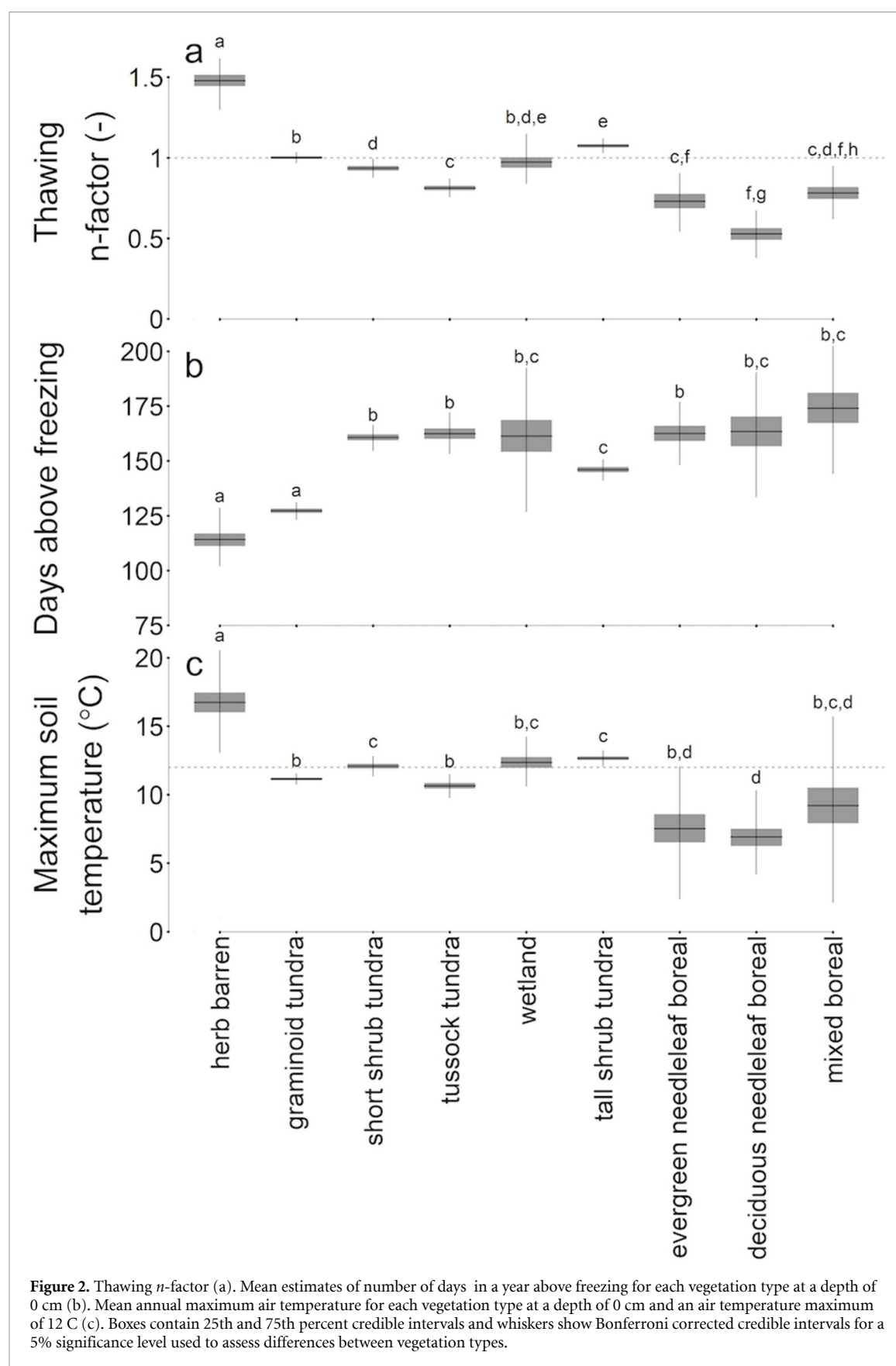
3.2. Warm season soil temperatures

Boreal forests and tussock tundra have lower soil temperatures in the warm season than other tundra vegetation types after accounting for air temperature and the depth of measurement. In above-freezing conditions, soil temperatures are highly decoupled from the air with a thawing n -factor at the soil surface (0 cm) far below one in boreal forests (figure 2(a)) with a ratio of 0.73 [Bonferroni adjusted 95% credible interval (CI): 0.54, 0.90] for evergreen needleleaf and 0.53 (CI: 0.38, 0.67) for deciduous needleleaf forests. Tussock tundra soil temperatures showed the greatest degree of decoupling from air temperatures compared to all other tundra types with a ratio of 0.81 (CI: 0.76, 0.87). Soils in herb-barren, graminoid tundra, and tall shrub tundra tended to be similar or warmer than the air with a thawing n -factor at or above one (figure 2(a)).

Soil temperatures remain above-freezing for the longest time period in boreal forests, wetlands, short shrub tundra, and tussock tundra with a statistically similar length of time ranging between 160 and 174 d on average (figure 2(b)). Under the same air temperature maximum of 12°C and at the soil surface (0 cm), deciduous needleleaf boreal forests had the lowest maximum soil temperatures that were roughly 5°C lower than the air (6.9; CI: 4.2, 10.3). Tall shrub tundra had slightly higher maximum soil temperatures than the air (12.7°C ; CI: 12.1, 13.2), and higher maximum soil temperatures than graminoid tundra (11.1°C ; CI: 10.8, 11.5). The similarity in the length of days above-freezing between different vegetation types suggests that differences in warm season soil temperature coupling to the air temperature is driven by magnitude of the maximum soil temperature rather than the length of time above freezing.

3.3. Cold season soil temperatures

Short shrub tundra, graminoid tundra, and herb-barren had the lowest soil temperatures in the cold season and all other vegetation types had similar soil temperatures despite broad differences in canopy height and characteristics between these vegetation



types. The freezing n -factors indicated that tall shrub, tussock, wetlands, and boreal forest soils were much warmer than the air with the highest decoupling from air temperatures (figure 3(a)), varying between 0.30

(CI: 0.12, 0.47) in deciduous needleleaf forests and 0.39 (CI: 0.35, 0.43) in tall shrub tundra. Short shrub and graminoid tundra had much closer coupling of freezing soil temperatures to the air with freezing

n -factors of 0.62 (CI: 0.57, 0.68) and 0.58 (CI: 0.55, 0.62), respectively. Herb-barren soils were colder than the air with a freezing n -factor of 1.2 (CI 1.11, 1.29).

Patterns in minimum soil temperature followed similar patterns as the freezing degree day ratios with herb barren, short shrub tundra, and graminoid tundra experiencing the lowest temperatures. Under a standardized air temperature of -22°C and at the soil surface (0 cm), minimum soil temperatures were -13.8°C (CI: -14.7 , -12.9) in graminoid tundra and -15°C (CI: -16.1 , -13.9). Soil temperatures were much higher than the air in boreal forests with evergreen needleleaf at -7.3°C (CI: -11.6 , -3.4) and deciduous needleleaf at -1.9°C (CI: -10.6 , 10). Tall shrub and tussock tundra had similar minimum soil temperatures of -8.8°C (CI: -9.7 , -7.9 and CI: -9.9 , -7.6 , respectively). Long-term patterns of winter precipitation derived from WorldClim data illustrate greater variability within than between vegetation types (figure S5), suggesting that geographic patterns in snowfall do not contribute to winter soil temperature patterns that we observe. We also found overlap in latitude and air temperatures (figures S6–S8) in most vegetation types indicating that potential differences between vegetation types likely do not reflect regional or climatic patterns for most vegetation types.

3.4. Annual soil temperature dynamics

Ecosystems with vegetation with very short canopies (<40 cm: herb barren, graminoid, and short shrub tundra) have the lowest mean annual soil temperatures compared to ecosystems characterized by trees or tall shrub vegetation types (figure 3(c)). Patterns in mean annual temperature closely followed patterns in minimum soil temperature (figures 3(b) and (c)). At a standardized mean annual air temperature of -6°C , mean annual soil temperatures in short shrub and graminoid tundra are -2.8°C (CI: -3.3 , -2.4) and -2.5°C (CI: -2.9 , -2.2), respectively, approximately two degrees lower than mean annual soil temperatures in evergreen needleleaf boreal forests and tall shrub tundra (figure 3(c)).

Variation in mean annual soil temperature is primarily driven by the minimum soil temperature in the cold season (figures 4(a) and (b)) in all vegetation types, and is likely linked to the latent heat exchange necessary for warming frozen soil. Surprisingly, summer maximum soil temperatures showed weak relationships (figures 4(c) and (d), tables S3 and S4), explaining 9%–50% of variability in mean annual temperature in most tundra vegetation types with the exception of herb-barren and tall shrub tundra. Mean annual soil temperature and maximum soil temperatures were closely related in ($R^2 = 0.80$) in herb-barren. There was no significant relationship in tall shrub tundra. Mean annual soil temperature was also not significantly related to maximum soil temperatures in all boreal forest types

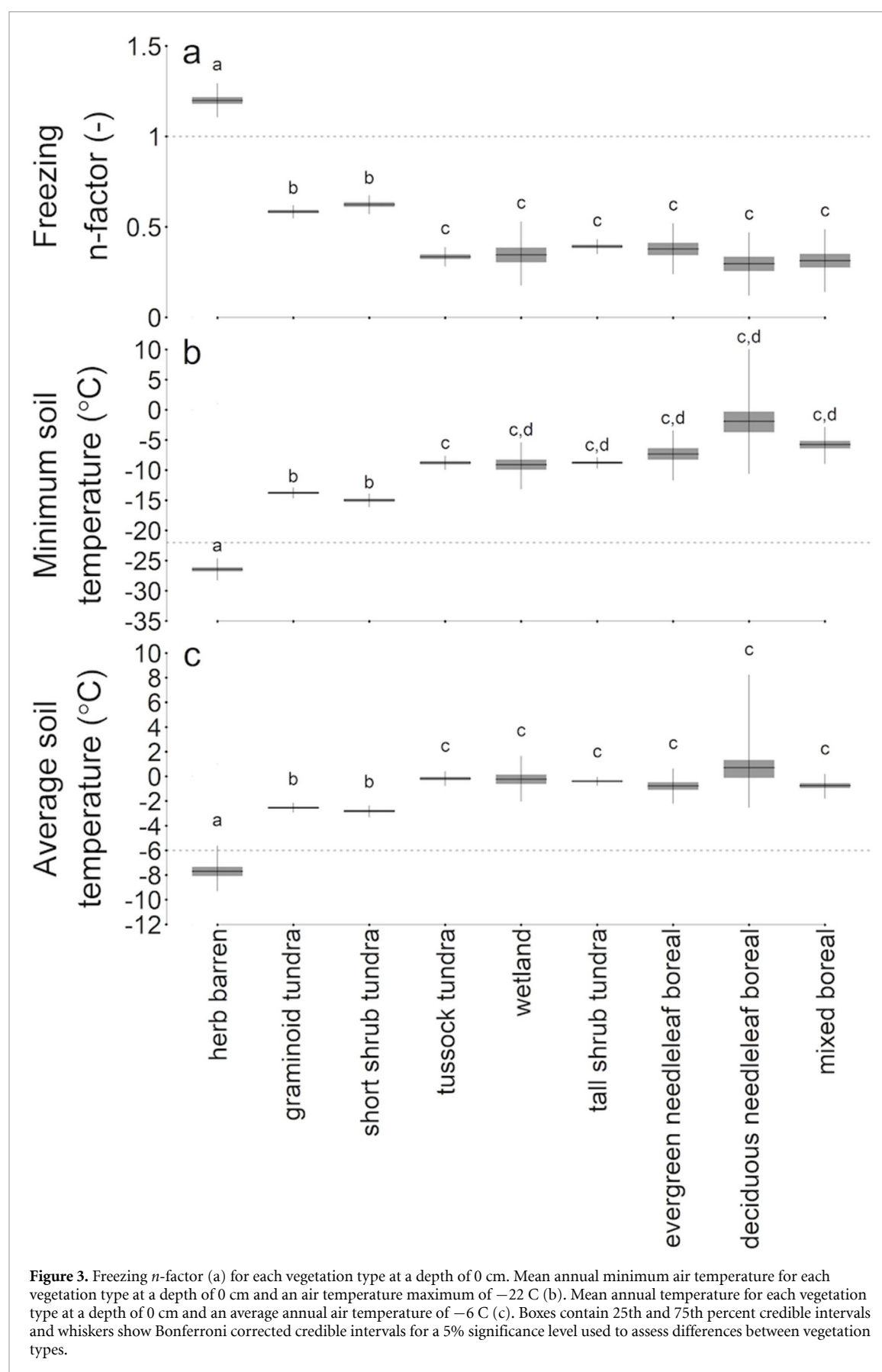
indicating that warmer summer conditions do not necessarily increase mean annual temperatures. Maximum soil temperature was not significantly related to minimum soil temperature with the exception of tall shrub tundra (electronic supplement, figure S9). Colder minimum temperatures were associated with warmer maximum temperatures in tall shrub tundra. This demonstrates that for many vegetation types, cold season conditions predominately drive mean annual soil temperatures, and there is not a strong coupling between cold season and warm season soil temperatures.

4. Discussion

4.1. Impacts of vegetation on cold- and warm-season soil temperature

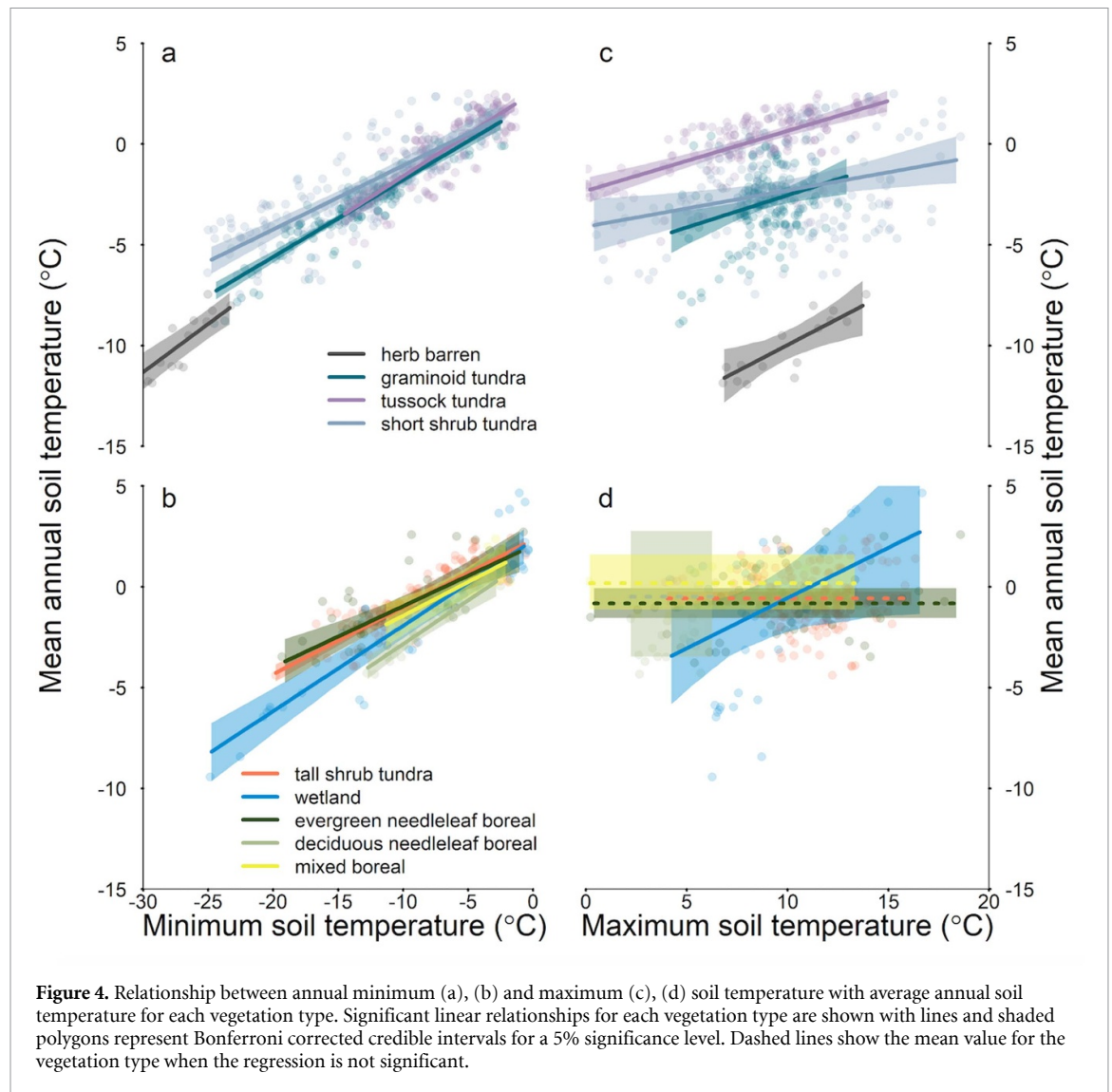
We found that tall shrub tundra had the highest soil temperatures after herb-barren during the warm season (figures 2(a)–(c)) when normalized by air temperature, contrary to observations of local soil cooling associated with shading from shrubs in the warm season (Blok *et al* 2010, Loranty *et al* 2018). Short shrub tundra also had higher temperatures than boreal forests and tussock tundra. Tall and short shrub ecosystems do not reflect the localized cooling effect of shading observed by other studies (Sturm *et al* 2001, Hinzman *et al* 2005, Myers-smith *et al* 2011), but rather exhibited relatively tight coupling with warm season air temperatures. Consequently, record high summer air temperatures across the Arctic (Serreze and Barry 2011, Overland *et al* 2017) may have a greater impact on warm season ecosystem processes such as plant phenology and productivity and nutrient dynamics in tundra ecosystems compared to boreal ecosystems (Loranty *et al* 2018, Post *et al* 2019). The cooling impact of shrubs during summer observed in manipulation experiments (Blok *et al* 2010, Myers-Smith and Hik 2013, Nauta *et al* 2015), likely describes a highly localized microclimate effect that is limited to directly below the shrub canopy (Lantz *et al* 2013). Our results indicate that such microclimate effects are awash in a larger dataset that includes a broader range of measurement probe locations within the ecosystem and varied meteorological conditions. As such, we acknowledge the limited geographic scope of herb-barren and deciduous needleleaf forest in this study are not necessarily representative of pan-Arctic wide patterns. Our results highlight that individual plot scale results in the warm season are highly localized results and measurements in localized regions are not suitable for broadly generalizing how vegetation can impact soil temperatures across the permafrost region.

We found that cold season soil temperatures were more consistent between vegetation types compared to the warm season, and vegetation types that are characterized by short canopies had the lowest temperatures after controlling for air temperature.



While we were unable to control for snow cover in our analyses, the broad geographic and climatological ranges captured by our sample sites

(figures S6–S9) indicate that our results do not reflect regional variation in snowfall. Vegetation affects cold season soil temperatures through impacts on snow



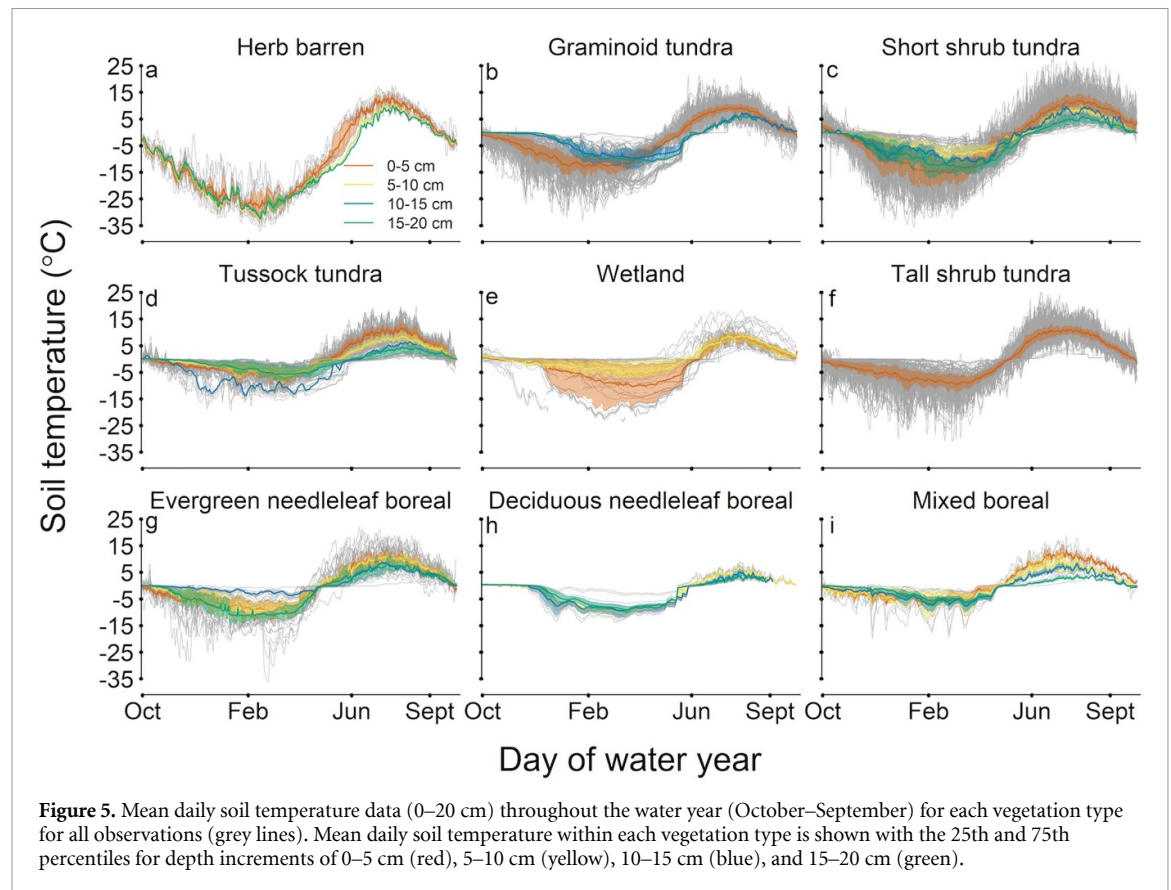
distribution and snowpack characteristics (Essery and Pomeroy 2004, Myers-smith *et al* 2011). Greater shrub height (Paradis *et al* 2016, Frost *et al* 2018) and higher forest cover (Jean and Payette 2014) are directly linked to higher winter soil temperatures, but we observe similarly high cold-season soil temperatures across all tall shrubs and trees. The insulating effect of snow on soil temperatures saturates at snow depths as low as 20 cm (Slater *et al* 2017), and thus geographic variation in snow cover or large differences in canopy height between the shrubs and trees in our study may have minimal influence across our broad geographical scope.

4.2. Vegetation and soil temperature on annual timescales

Overall, we found that annual soil thermal regimes in the permafrost region are dominated by cold season conditions likely due to physical processes associated with frozen soils such as higher thermal conductivity in frozen soils, the amount of latent heat necessary to thaw soils, the influence of snow meltwater in the

spring, and the release of latent heat in freezing soils (Shur and Jorgenson 2007, Throop *et al* 2012). Herb barren was the only vegetation type where both minimum and maximum temperatures were highly correlated with the mean annual soil temperatures as is typical for annual fluctuations in soil temperature (Hillel 1998). Annual patterns in soil temperature have a longer duration of the cold season than the warm season (figures 2(b) and 5) and soils in all vegetation types excluding herb-barren had some sites that experienced a zero curtain. The zero curtain is characterized by a prolonged time period (days–months) when temperatures linger near zero due to latent heat associated with freeze/thaw or the addition of snow meltwater into the soil (figure 5). Mean annual soil temperature did not significantly vary with warm season maximum temperatures in boreal and tall shrub tundra suggesting that mean annual conditions are more sensitive to temperature changes in the cold season.

Surprisingly, higher winter soil temperatures were not associated with higher summer soil temperatures



with no relationship between minimum and maximum temperatures in all vegetation types except for tall shrub tundra (figure S5). Sites with colder minimum temperatures tended to have warmer maximum temperatures in tall shrub tundra. It is likely that sites with warmer minimum temperatures and colder maximum temperatures could experience prolonged periods of freeze/thaw cycles due to high water content in the soil (Outcalt *et al* 1990, Romanovsky and Osterkamp 2000). This indicates that soil thermal characteristics and snow that influence coupling with air temperature are likely a driving factor in seasonal soil temperature amplitude (Nicholson 1979, Smith and Riseborough 1996). Further assessment of seasonal soil heat fluxes, soil moisture conditions, and vegetative traits and function would help elucidate the plot level seasonal drivers of temperature (Lorant *et al* 2018). In our synthesis, we found a paucity of data that simultaneously quantified vegetation composition and structure, soil moisture, soil, and snow properties. These inconsistencies are compounded by variation in duration of data availability, measurement height or depth in soil and air temperature measurements. While our modelling approach allowed us to overcome many of these issues, it is clear there is a continued need for better understanding the biological and physical drivers of soil-vegetation-atmosphere continuum coupling in the permafrost region, especially those related to interactions between vegetation canopies and snow cover.

4.3. Soil temperature and climate change

Our results indicate that ongoing vegetation change across the Arctic will alter relationships between air and soil temperatures with continued climate warming. Widespread tree and shrub expansion are among the most prominent changes, and will accelerate soil warming (Chapin *et al* 2000, Tape *et al* 2006, Pearson *et al* 2013, Frost and Epstein 2014). However, emerging evidence indicates that pan-Arctic vegetation change is not unidirectional (Phoenix and Bjerke 2016). Advances in long-term monitoring and remote sensing technologies have revealed heterogeneity in Arctic vegetation change typically inferred by time series analyses of satellite data (Myers-Smith *et al* 2020). In boreal forests, disturbances such as fire and permafrost thaw may lead to net declines in forest cover at the landscape scale (Helbig *et al* 2016, Sniderhan and Baltzer 2016). Consequently, accurate predictive understanding of future pan-Arctic soil temperature regimes, and associated impacts on permafrost and related climate feedbacks will require detailed understanding of vegetation dynamics. The contrary outcomes between some plot-scale shrub manipulations and our results demonstrates that small scale (meters—kilometers) spatial heterogeneity around plant canopies likely impacts soil temperatures (Palmer *et al* 2012). Our synthesis of plot scale observations demonstrates that there are clear differences between trees, tall shrubs, and short tundra vegetation at larger spatial scales, but we

cannot discern the causal mechanisms underlying these differences from our data alone. Our study suggests that a better understanding of the spatial heterogeneity in snow and soil conditions around plant canopies would lead to a better understanding of the impacts of vegetation on ground thermal regimes. Standardized and consistent methodological approaches that concurrently measure vegetation, snow, soil properties, and hydrologic conditions from plot to ecosystem scales with spatial coverage throughout the pan-Arctic and boreal regions would greatly enhance the causal understanding of vegetation impacts on soil temperature.

Permafrost temperatures are rising as the Arctic experiences increases in air temperature (Hinzman *et al* 2005, Romanovsky *et al* 2010), but rates of temperature increase vary with local hydrological conditions, soil thermal properties, and vegetation characteristics (Jorgenson *et al* 2001, Romanovsky *et al* 2010, Cable *et al* 2016). The mean annual temperature of the permafrost table is typically correlated with the mean annual temperature of the ground surface (Smith and Riseborough 1996, Romanovsky *et al* 2003). Our measures of mean annual surface soil temperature have implications for permafrost temperatures, but permafrost temperatures ultimately depend on both surface thermal dynamics and characteristics that affect heat transfer in the soil such as thermal conductivity and moisture content (Smith and Riseborough 1996, Cable *et al* 2016). Our work, for instance, does not quantify vegetation impacts on soil thermal conductivity (such as transpiration-driven soil drying that reduces conductivity), which might decouple the influence of warming surface soil temperatures on permafrost (Lorant *et al* 2018).

During the cold season, soil respiration is a significant source of carbon dioxide and can increase by a factor of 2.9–8.5 per 10 °C increase in winter soil temperature (Natali *et al* 2019). Our observations demonstrate that minimum soil temperatures are 4 °C–20 °C greater in tall shrub and tree vegetation types relative to short-statured vegetation types under the same air temperature. Though we cannot rule out the possibility that soil temperature increases preceded vegetation change, our results nonetheless imply that observed vegetation change across the Arctic may be associated with increased winter greenhouse gas emissions from soil respiration in recent decades. In the long term (centuries to millennia), soil warming that results in permafrost degradation and soil warming will alter carbon accumulation (Swanson *et al* 2000). Overall, continued increases in vegetation height associated with tall shrub and trees expansion over the next century (Myers-smith *et al* 2011, Elmendorf *et al* 2012) lead to warmer shallow soils and increase the potential for a permafrost carbon climate feedback.

Vegetation change across the Arctic has the potential to affect the coupling between air and soil

temperatures, with important implications for soil and carbon dynamics in permafrost regions. Numerous field studies have provided insights regarding the direction and magnitude of soil temperature changes associated with vegetation transitions, primarily at the seasonal timescale. Our pan-Arctic synthesis reveals that trees and shrubs promote warmer shallow soil temperatures at annual timescales, mainly due to warmer cold-season soil temperatures. Summer air temperatures do not have strong impacts on annual soil temperature dynamics, and so will primarily affect seasonal plant function and soil carbon dynamics in most tundra vegetation types. Tree and shrub expansion will amplify the effects of climate warming on soil temperature potentially leading to increases in winter carbon emissions and could increase permafrost temperature and thaw.

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Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: doi:10.18739/A2736M31X. Data will be available from 03 July 2020.

Author contributions

H K, M L, and S M N conceived the work. H K performed data analysis and generated figures. H K, M L, S M N, A R, I H M S, B A, J A, E B B, D B, G B W, J B, A B, S C, C T C, T A D, G V F, M G, T T H, S D M, J A O, D O, V G S, O S, L S V, M W, B E, L G, J H, P L, E S E, M H, T M J, I G, K Y, J L, M M, K T, M L and K L contributed unpublished data and site descriptions used in data analysis. All authors contributed to data interpretation and preparation of manuscript text.

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References

- Biskaborn B K *et al* 2019 Permafrost is warming at a global scale *Nat. Commun.* **10** 1–11
- Blok D, Heijmans P D, Schaepman-Strub G, Kononov A V, Maximov T C and Berendse F 2010 Shrub expansion may reduce summer permafrost thaw in Siberian tundra *Glob. Change. Biol.* **16** 1296–305
- Brown J, Ferrians O J J, Heginbottom J A and Melnikov E S 2011 *Circum-Arctic Map of Permafrost and Ground-ice Conditions* (Boulder, CO: National Snow and Ice Data Center/World Data Center for Glaciology. Digital Media)
- Cable J M, Ogle K, Bolton W R, Bentley L P, Romanovsky V, Iwata H, Harazono Y and Welker J 2014 Permafrost thaw affects boreal deciduous plant transpiration through increased soil water, deeper thaw, and warmer soils *Ecohydrology* **7** 982–97
- Cable W L, Romanovsky V E and Torre Jorgenson M 2016 Scaling-up permafrost thermal measurements in western Alaska using an ecotype approach *Cryosphere* **10** 2517–32
- Chapin F S III, Eugster W, Mcfadden J P, Lynch A H and Walker D A 2000 Summer differences among arctic ecosystems in regional climate forcing *J. Clim.* **13** 2002–10
- Elmendorf S C *et al* 2012 Plot-scale evidence of tundra vegetation change and links to recent summer warming *Nat. Clim. Change* **2** 453–7
- Essery R and Pomeroy J 2004 Vegetation and topographic control of wind-blown snow distributions in distributed and aggregated simulations for an Arctic Tundra basin *J. Hydrometeorol.* **5** 735–44
- Fidler F, Chee Y E N, Wintle B C, Burgman M A and McCarthy M A 2017 Metaresearch for evaluating reproducibility in ecology and evolution *BioScience* **67**
- Finger R A, Turetsky M R, Kielland K, Ruess R W and Mack M C 2016 Effects of permafrost thaw on nitrogen availability and plant—soil interactions in a boreal Alaskan lowland 1542–54
- Fisher J P *et al* 2016 The influence of vegetation and soil characteristics on active-layer thickness of permafrost soils in boreal forest *Glob. Change Biol.* **22** 3127–40
- Frost G V and Epstein H E 2014 Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s *Glob. Change. Biol.* **20** 1264–77
- Frost G V, Epstein H E, Walker D A, Matyshak G and Ermokhina K 2018 Seasonal and long-term changes to active-layer temperatures after tall shrubland expansion and succession in Arctic Tundra *Ecosystems* **21** 507–20

- Helbig M, Pappas C and Sonnentag O 2016 Permafrost thaw and wildfire: equally important drivers of boreal tree cover changes in the Taiga Plains, Canada *Geophys. Res. Lett.* **43** 1598–606
- Hewitt R E, Mack C, Taylor D L, Genet H and McGuire A D 2019 Below—ground plant traits influence tundra plant acquisition of newly thawed permafrost nitrogen *Journal of Ecology* **107** 950–62
- Hillel D 1998 Soil temperature and heat flow *Environmental Soil Physics* 2nd edn (San Diego, CA: Academic) pp 309–34
- Hinzman L D *et al* 2005 Evidence and implications of recent climate change in Northern Alaska and other Arctic regions *Clim. Change* **72** 251–98
- Iversen C M, Sloan V L, Sullivan P F, Euskirchen E S, McGuire A D, Norby R J, Walker A P, Warren J M and Wulfschlegel S D 2015 The unseen iceberg: plant roots in arctic tundra *New Phytol.* **205** 34–58
- Jean M and Payette S 2014 Effect of vegetation cover on the ground thermal regime of wooded and non-wooded palsas *Permafrost Periglacial Process.* **25** 281–94
- Jorgenson M T, Racine C H, Walters J C and Osterkamp T E 2001 Permafrost degradation and ecological changes associated with a warming climate in central Alaska *Clim. Change* **48** 551–79
- Keuper F, Bodegom P M V A N, Dorrepaal E and Weedon J T 2012 A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands *Glob. Change. Biol.* **18** 1998–2007
- Lafleur P and Humphreys E 2018 Tundra shrub effects on growing season energy and carbon dioxide exchange Tundra shrub effects on growing season energy and carbon dioxide exchange *Environ. Res. Lett.* **13** 055001
- Lantz T C, Marsh P and Kokelj S V 2013 Recent shrub proliferation in the Mackenzie Delta uplands and microclimatic implications *Ecosystems* **16** 47–59
- Lawrence D M, Slater A G and Swenson S C 2012 Simulation of present-day and future permafrost and seasonally frozen ground conditions in CCSM4 *J. Clim.* **25** 2207–25
- Lorant M M, Abbott B W, Blok D, Douglas T A, Epstein H E, Forbes B C and Mamet S D 2018 Reviews and syntheses: changing ecosystem influences on soil thermal regimes in northern high-latitude permafrost regions *Biogeosciences* **15** 5287–313
- Martin A C, Jeffers E S, Petrokofsky G, Myers-smith I and Macias M 2017 Shrub growth and expansion in the Arctic tundra: an assessment of controlling factors using an evidence-based approach *Environ. Res. Lett.* **12** 085007
- Myers-smith I H *et al* 2011 Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities *Environ. Res. Lett.* **6** 45509
- Myers-Smith I H *et al* 2015 Climate sensitivity of shrub growth across the tundra biome *Nat. Clim. Change* **5** 887–91
- Myers-Smith I H and Hik D S 2013 Shrub canopies influence soil temperatures but not nutrient dynamics: an experimental test of tundra snow-shrub interactions *Ecol. Evol.* **3** 3683–700
- Myers-Smith I H, Kerby J T and Phoenix G K *et al* 2020 Complexity revealed in the greening of the Arctic *Nat. Clim. Change* **10** 106–17
- Natali S M, Watts J D, Rogers B M, Potter S, Ludwig S M, Selbmann A-K and Sullivan P F 2019 Large loss of CO₂ in winter observed across pan-arctic permafrost region *Nat. Clim. Change* **9** 852–7
- Nauta A L *et al* 2015 Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source *Nat. Clim. Change* **5** 67–70
- Nicholson F 1979 Permafrost spatial and temporal variations near Schefferville, Nouveau-Québec *Geogr. Phys. Quat.* **33** 265–77
- Ogle K, Peltier D, Fell M, Guo J, Kropp H and Barber J 2019 Should we be concerned about multiple comparisons in hierarchical Bayesian models? *Methods Ecol. Evol.* **10** 553–64
- Outcalt S I, Arbor A, Nelson F E and Hinkel K M 1990 The zero curtain effect: heat and mass transfer across the isothermal region in freezing soil *Water Resour.* **26** 1509–16
- Overland J *et al* 2017 Surface air temperature *Arctic Report Card: Update for 2017*
- Palmer M J, Burn C R and Kokelj S V 2012 Factors influencing permafrost temperatures across tree line in the uplands east of the Mackenzie Delta, 2004–2010 *Can. J. Earth Sci.* **29** 877–94
- Paradis M, Lévesque E and Boudreau S 2016 Greater effect of increasing shrub height on winter versus summer soil temperature *Environ. Res. Lett.* **11**
- Pearson R G, Phillips S J, Lorant M M, Beck P S A, Damoulas T, Knight S J and Goetz S J 2013 Shifts in Arctic vegetation and associated feedbacks under climate change *Nat. Clim. Change* **3** 673–7
- Phoenix G K and Bjerke J W 2016 Arctic browning: extreme events and trends reversing arctic greening *Glob. Change. Biol.* **22** 2960–2
- Post E *et al* 2019 The polar regions in a 2C warmer world *Sci. Adv.* **5**.12 eaaw9883
- Romanovsky V E and Osterkamp T E 2000 Effects of unfrozen water on heat and mass transport processes in the active layer and permafrost *Permafrost Periglacial Process.* **11** 219–39
- Romanovsky V E, Sergueev D O and Osterkamp T E 2003 Temporal variations in the active layer and near-surface permafrost temperatures at the long-term observatories in Northern Alaska *Permafrost* **1** 989–94
- Romanovsky V E, Smith S L and Christiansen H H 2010 Permafrost thermal state in the polar Northern Hemisphere during the international polar year 2007–2009: a synthesis *Permafrost and Periglacial processes* **116** 106–16
- Salmon V G, Soucy P, Mauritz M, Celis G, Natali S M, Mack M C and Schuur E A 2016 Nitrogen availability increases in a tundra ecosystem during five years of experimental permafrost thaw *Glob. Change. Biol.* **22** 1927–41
- Schuur E A G *et al* 2015 Climate change and the permafrost carbon feedback *Nature* **520** 171–9
- Serreze M C and Barry R G 2011 Processes and impacts of Arctic amplification: a research synthesis *Glob. Planet. Change* **77** 85–96
- Shur Y L and Jorgenson M T 2007 Patterns of permafrost formation and degradation in relation to climate and ecosystems *Permafrost Periglacial Process.* **19** 7–19
- Slater A G, Lawrence D M and Koven C D 2017 Process-level model evaluation: a snow and heat transfer metric *Cryosphere* **11** 989–96
- Smith M W and Riseborough D W 1996 Permafrost monitoring and detection of climate change *Permafrost and Periglacial Processes* **7** 301–9
- Smith M W and Riseborough D W 2002 Climate and the limits of permafrost: a zonal analysis *Permafrost Periglacial Process.* **13** 1–15
- Sniderhan A E and Baltzer J L 2016 Growth dynamics of black spruce (*Picea mariana*) in a rapidly thawing discontinuous permafrost peatland *J. Geophys. Res. Biogeosci.* **121** 2988–3000
- Sturm M, Racine C and Tape K 2001 Increasing shrub abundance in the Arctic *Nature* **411** 546–7
- Swanson D K, Lacelle B and Tarnocai C 2000 Temperature and the boreal–subarctic maximum in soil organic carbon *Geogr. Phys. Quat.* **54** 157–67
- Tape K, Sturm M and Racine C 2006 The evidence for shrub expansion in Northern Alaska and the Pan-Arctic *Glob. Change. Biol.* **12** 686–702
- Throop J, Lewkowicz A G and Smith S L 2012 Climate and ground temperature relations at sites across the continuous and discontinuous permafrost zones, northern Canada *Can. J. Earth Sci.* **49** 865–76
- Walker D A, Raynolds M K and Daniëls F J A *et al* 2005 The circumpolar Arctic vegetation map *J. Veg. Sci.* **16** 267–82
- Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M and Van Calster H 2020 Forest microclimate dynamics drive plant responses to warming *Sci.* **368** 772–5