



**QUEEN'S
UNIVERSITY
BELFAST**

Pathways for Ecological Change in Canadian High Arctic Wetlands Under Rapid Twentieth Century Warming

Sim, T. G., Swindles, G. T., Morris, P. J., Galka, M., Mullan, D., & Galloway, J. M. (2019). Pathways for Ecological Change in Canadian High Arctic Wetlands Under Rapid Twentieth Century Warming. *Geophysical Research Letters*, 46(9), 4726-4737. <https://doi.org/10.1029/2019GL082611>

Published in:
Geophysical Research Letters

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights

©2019. American Geophysical Union. All Rights Reserved. This work is made available online in accordance with the publisher's policies. Please refer to any applicable terms of use of the publisher.

General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Open Access

This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. – Share your feedback with us: <http://go.qub.ac.uk/oa-feedback>

Sim Thomas, George (Orcid ID: 0000-0001-8604-9996)

Swindles Graeme, Thomas (Orcid ID: 0000-0001-8039-1790)

Morris Paul J. (Orcid ID: 0000-0002-1145-1478)

Galloway Jennifer (Orcid ID: 0000-0002-4548-6396)

Pathways for ecological change in Canadian High Arctic wetlands under rapid twentieth century warming

T. G. Sim¹, G. T. Swindles^{1, 2}, P. J. Morris¹, M. Galka³, D. Mullan⁴, J. M. Galloway^{5, 6}

¹School of Geography, University of Leeds, LS2 9JT, UK

²Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa, Ontario, Canada

³Department of Geobotany and Plant Ecology, Faculty of Biology and Environmental Protection, University of Lodz, 12/16 Banacha Str., Lodz, Poland

⁴School of Natural and Built Environment, Queen's University Belfast, Belfast, N. Ireland, UK

⁵Aarhus Institute of Advanced Studies (AIAS), Aarhus University, 8000 Aarhus C, Denmark

⁶Natural Resources Canada/Ressources naturelles Canada, Geological Survey of Canada/Commission géologique du Canada, Calgary, Alberta, T2L 2A7, Canada

Corresponding author: Thomas Sim (gy12tgs@leeds.ac.uk)

Key Points:

- The ecological, hydrological and C accumulation responses of Arctic wetlands to climate warming may be strongly influenced by wetland type;
- Contrasting site-specific responses to an increase in growing degree days include increased moss diversity and a shift to shrub-dominance;
- Intensive grazing from Arctic geese may be an important driver for recent vegetation change in High Arctic coastal wetlands.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1029/2019GL082611

Abstract

We use paleoecological techniques to investigate how Canadian High Arctic wetlands responded to a mid-twentieth century increase in growing degree days (GDD_0). We observe an increase in wetness, moss diversity and carbon accumulation in a polygon mire trough, likely related to ice-wedge thaw. Contrastingly, the raised center of the polygon mire showed no clear response. Wet and dry-indicator testate amoebae increased concomitantly in a valley fen, possibly relating to greater inundation from snowmelt followed by increasing evapotranspiration. This occurred alongside the appearance of generalist hummock mosses. A coastal fen underwent a shift from sedge to shrub-dominance. The valley and coastal fens transitioned from minerogenic to organic-rich wetlands prior to the GDD_0 increase. A subsequent shift to moss-dominance in the coastal fen may relate to intensive grazing from Arctic geese. Our findings highlight the complex response of Arctic wetlands to warming and have implications for understanding their future carbon sink potential.

Plain Language Summary

The response of Arctic wetland ecosystems and carbon stores to climate change is uncertain. We investigate the response of wetland ecosystems in the Canadian High Arctic to twentieth century climate warming. We use proxies for changes in vegetation (plant macrofossils) and wetness (testate amoebae) preserved in the wetland soil in combination with radiocarbon dating to reconstruct the past ecology of these wetlands. This approach allows us to explore beyond the timeframe of monitoring studies. Our results suggest that wetland type is an important determinant of the response of ecological, hydrological and soil carbon accumulation to climate warming. Our findings highlight the clear, but complex response of Arctic wetlands to twentieth century warming. This has important implications for understanding the future carbon sink potential of these ecosystems.

Keywords

Permafrost Peatlands; Climate Change; Growing Degree Days; Testate Amoebae; Shrubification; Arctic Geese Grazing.

1 Introduction

Climate warming over the last century has been greatest in the Arctic and is projected to continue in the twenty-first century at a rate above the global average [Christensen *et al.*, 2013]. Arctic warming is causing widespread permafrost thaw [Jorgenson *et al.*, 2006; Payette *et al.*, 2004] and alteration of terrestrial ecosystem hydrology [Smith *et al.*, 2007], vegetation [Myers-Smith *et al.*, 2011] and wildfire regimes [Gibson *et al.*, 2018; Myers-Smith *et al.*, 2008]. Changes to high-latitude ecosystems are likely to influence their carbon budgets, including global warming through enhanced carbon emissions [Dorrepaal *et al.*, 2009]. Permafrost soils in general could become carbon sources with warming through greater aerobic (CO₂) and anaerobic (CH₄) decomposition rates [Natali *et al.*, 2015; Schuur *et al.*, 2015]. However, longer, warmer growing seasons and changes in Arctic precipitation regimes [Bintanja & Selten, 2014; Kattsov *et al.*, 2007; Kopec *et al.*, 2016] may stimulate carbon capture through enhanced plant productivity in peatlands, and the transition of minerotrophic wetlands into organic peatlands [Charman *et al.*, 2013; 2015; Gallego-Sala *et al.*, 2018; Morris *et al.*, 2018]. Recent evidence shows an inconsistent response of Arctic and sub-Arctic peatlands to warming in terms of carbon accumulation [Zhang *et al.*, 2018a].

In the Arctic, wetlands occupy ~8% of the non-glaciated land area [Walker *et al.*, 2005] and – although high-latitude carbon stocks are poorly constrained – wetlands store a disproportionate amount of carbon for their extent [Tarnocai *et al.*, 2009]. Arctic wetlands exemplify the complexity of landscapes underlain by permafrost and typically occur in three locales: on ground affected by ice-wedge formations (polygon mires); on previously-glaciated terrain with favorable topographic depressions (known as patchy wetlands); and in coastal zones of isostatic uplift (coastal wetlands) [Glenn & Woo, 1997; Woo & Young, 2006]. Across Arctic wetlands, warming has been linked to greater plant biomass [Hill & Henry, 2011], vegetation composition changes and desiccation [Woo & Young, 2006, 2014; Zhang *et al.*, 2018b]. Ice-wedge polygon mires specifically are complex and dynamic systems [de Klerk *et al.*, 2011; Fritz *et al.*, 2016], and degradation in response to recent warming has led to changes in vegetation and drainage [Fraser *et al.*, 2018; Jorgenson *et al.*, 2015; Liljedahl *et al.*, 2016; Perreault *et al.*, 2017]. Similarly, vegetation in some sub-Arctic and Arctic coastal wetlands has been altered by increasing bird grazing pressures in recent decades [Jefferies & Rockwell, 2002; Peterson *et al.*, 2013].

Future hydrological changes, vegetation shifts and degradation of permafrost have been identified as key areas of uncertainty in the prediction of permafrost carbon dynamics [Abbott *et al.*, 2016]. There is limited information on the response of Arctic wetlands to climate change and their potential to transition into productive peatlands on centennial timescales. For the first time in the Canadian High Arctic, we use a high-resolution paleoecological approach (testate amoebae and plant macrofossils) to reconstruct past moisture conditions and vegetation histories in peat-forming wetlands. We aim to investigate the ecological response to twentieth century climate warming in the three main types of High Arctic wetland: (i) a polygon mire; (ii) a valley fen (a type of patchy wetland); and (iii) a coastal fen.

2 Study sites, materials and method

The study region is in the continuous permafrost zone of the western Canadian Arctic tundra, between the latitudes 68.5 and 74.5°N [Figure 1]. We study two wetlands on northern Banks Island, Northwest Territories: a polygon mire (74.459°N, 121.04°E) and a valley fen (74.05°N, 118.429°E). The distinctive topography of the polygon mire was captured by extracting a monolith from a raised center mound and from a surrounding trough. Our third

site is a coastal fen (68.65°N, 105.455°E) located on an island ~50 km south of Cambridge Bay, Nunavut, where two monoliths <10 m apart were collected as replicate paleo-records.

Monoliths were sampled to the base of the active layer and subsampled in the laboratory at 1-cm depth intervals. Bulk density and organic matter content were calculated in accordance with *Chambers et al.* [2011]. Testate amoebae were prepared for analysis using the method outlined by *Booth et al.* [2010]. In the absence of an appropriate transfer function, testate amoebae were grouped into categories of hydrological preference based on a detailed literature review (Table S2). Plant macrofossils were prepared in accordance with *Galka, et al.* [2017a]. Above-ground plant macrofossils and bulk peat (where reliable plant macrofossils were not present) were radiocarbon dated (Table S1). Radiocarbon dates were calibrated using Clam 2.2 [Blaauw, 2010] in R 3.4.3 [R Core Team, 2018]. The IntCal13 [Reimer et al., 2013] calibration curve for pre-bomb dates and *Hua et al.* [2013] for post-bomb dates were used. When post-bomb dates demonstrated multiple probability distributions during calibration, we applied the principle of superposition to determine the most likely probability distribution. Chronological uncertainty can be introduced by cryoturbation in permafrost soils, particularly towards to base of the active layer [Bockheim & Tarnocai, 1998; Ping et al., 2008]. These factors are considered in our interpretation and are comprehensively discussed in the supplementary materials (Table S1 and Text S3). The most appropriate age-depth model for each chronology was selected including linear interpolation, cubic spline and polynomial regression. Growing degree days above 0°C (GDD₀) were calculated for each site from monthly climate re-analysis data spanning the period AD 1851–2011 [Compo et al., 2011]. Change point analysis [Killick & Eckley, 2014] was conducted in R 3.4.3 [R Core Team, 2018] on GDD₀ time series data for each site. See full methods and study site information in supplementary material [Figures S1 to S6; Tables S1 to S2; Text S1 to S3].

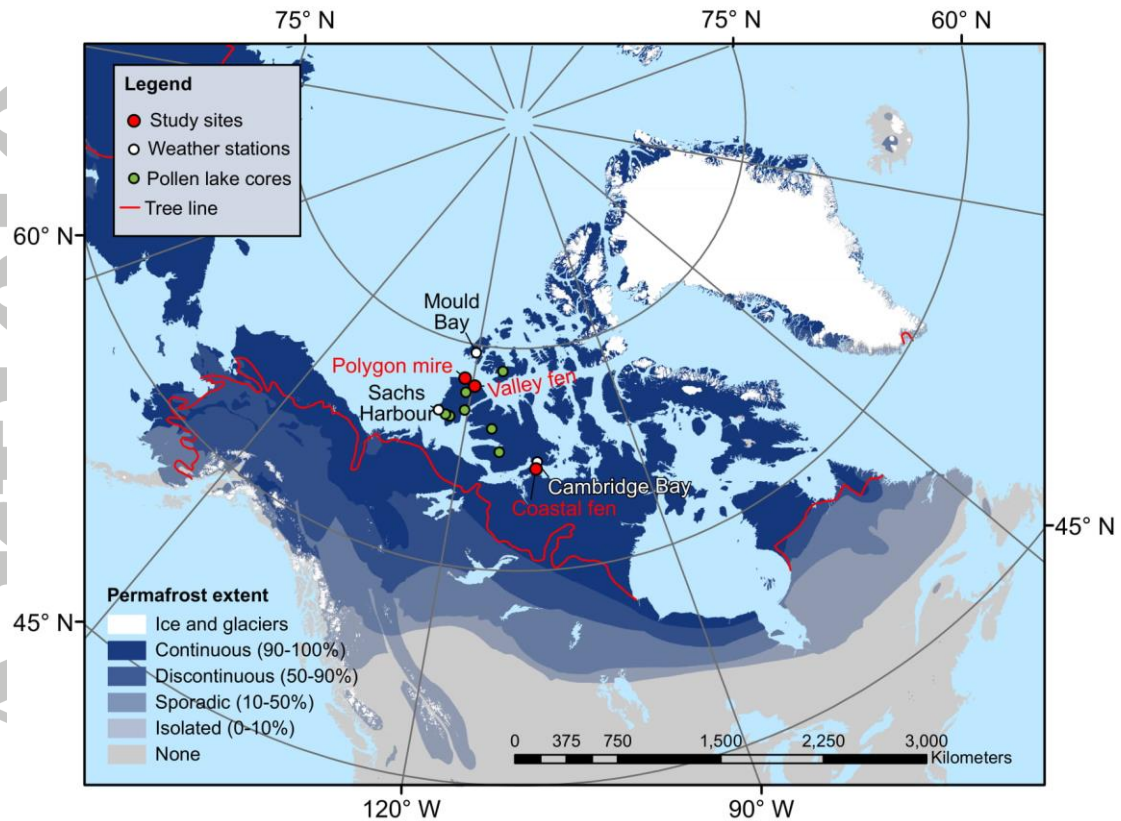


Figure 1. Study sites, nearby weather stations and lake cores used for pollen-based temperature reconstruction [Gajewski, 2015]. Permafrost and the tree line data from Brown *et al.* [2002].

3 Results

3.1 Twentieth century warming and lengthening growing seasons in the western Arctic

In the western Arctic following a warm period from ~10–7.5 Ka BP there was general cooling throughout the Holocene [Gajewski, 2015; Figure 2c]. Weather station records beginning ~AD 1950 document twentieth century climatic warming near to our sites [Figure 1], and across the Arctic [Hassol *et al.*, 2004]. The Cambridge Bay and Sachs Harbour stations show pronounced warming rates of 0.3°C per decade and 0.5°C per decade respectively, contrasted to 0.1°C per decade at Mould Bay, the highest latitude station [Figure 2a]. Re-analysis data [Compo *et al.*, 2011] demonstrated a pronounced increase in GDD₀ across all wetland sites with changepoints detected between 1931 and 1940 [Figure 2b]. Following respective changepoints, mean GDD₀ at the polygon mire increased from 49 ± 50 °C days yr⁻¹ to 152 ± 46 °C days yr⁻¹ (changepoint: 1940) and at the valley fen, from 105 ± 76 to 260 ± 6 °C days yr⁻¹ (changepoint: 1936) (error terms indicate standard deviation). After the 1931 changepoint, mean GDD₀ at the coastal fen increased from 400 ± 132 to 605 ± 68.3 °C days yr⁻¹.

The rise in GDD₀ in the 1930s [Figure 2b] is consistent with a well-documented climatic fluctuation (~1920-1940) around the North Atlantic. This event began in the 1920s and resulted in positive Arctic-wide average temperature anomalies for most of the 1930s

[Johannessen *et al.*, 2004; Polyakov *et al.*, 2003]. Causes of the climatic fluctuation remain open to debate, with internal atmospheric variability, anthropogenic greenhouse gas forcing, solar variability, volcanic forcing and regional dynamic feedbacks proposed in the literature [Wood & Overland, 2010]. Bengtsson *et al.* [2004] suggested natural variability was the likely cause, as reduced sea ice cover was critical in initiating warming of $\sim 1.7^{\circ}\text{C}$ during the peak period between 1930 and 1940 at $60\text{--}90^{\circ}\text{N}$. However, Wood & Overland [2010] interpreted the event as an intrinsically-forced albeit essentially random climatic phenomenon, superimposed on rising temperatures associated with anthropogenic forcing. GDD_0 have remained high following this event [Figure 2b] and increased elsewhere in the Canadian High Arctic in the past few decades [Woo & Young, 2014].

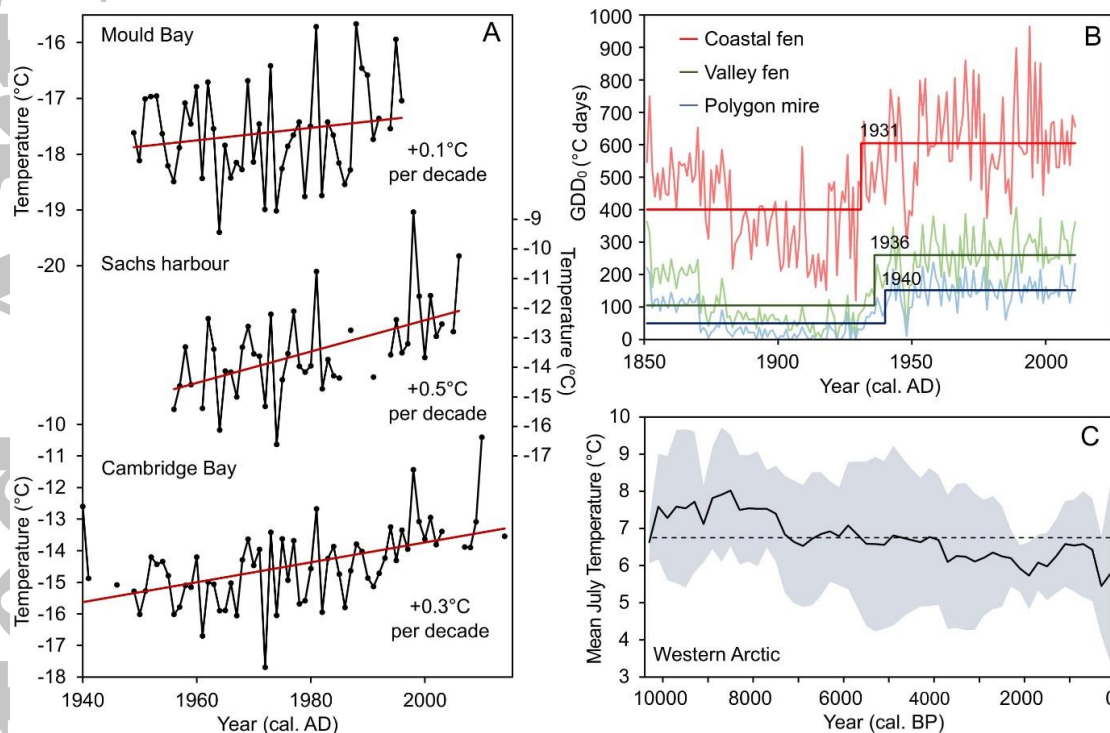


Figure 2. Recent warming in western Canadian Arctic. **a)** Annual temperature data from nearby weather stations. **b)** GDD_0 modelled for each site from climate re-analysis data [Compo *et al.*, 2011]. Stepped lines indicate changepoints. **c)** Reconstructed mean July temperature for western Arctic during the Holocene [Gajewski, 2015]. Shading indicates one standard deviation.

3.2 Paleoeological results

3.2.1 Polygon mire

The polygon mire demonstrates contrasting responses to recent warming between the raised center and the trough. The raised center monolith [11 cm; Figure 3a] is mainly composed of partially-decomposed *Scorpidium cossonii* (80–90.5%), bulk density is relatively high ($0.36 \pm 0.1 \text{ g cm}^{-3}$), while organic matter is relatively low ($29.8 \pm 9.4\%$), and carbon accumulation increases towards the top of the profile. The trough monolith [17 cm; Figure 3b] is more dynamic by comparison, recording multiple vegetation shifts. The lower phase (17–7 cm) consists of a light-brown, peaty soil undergoing a gradual transition ($\sim \text{AD } 750\text{--}1800$) from *S. cossonii* (40–85%) and *Warnstorfia sarmentosa* (0–35%) moss to a more

sedge (Cyperaceae) and herb-dominated wetland. During this phase carbon accumulation is low ($6.2 \pm 2.1 \text{ g m}^{-2} \text{ yr}^{-1}$), organic matter is low ($27.8 \pm 8.7\%$) and there is relatively high bulk density ($0.51 \pm 0.16 \text{ g cm}^{-3}$). In the upper phase (0–7 cm) organic matter increases (max: 77.4%) and bulk density decreases (min: 0.04 g cm^{-3}). A sedge and herb-dominated ecosystem is present from ~AD 1800 before an increase in moss diversity at ~AD 2000, including the presence of *S. cossonii* (20–70%), *Calliergon* spp. (10–30%) and *Campyllum* cf. *stellatum* (10–20%). Coincident with this ~AD 2000 is a shift in hydrological conditions, with wet-indicator testate amoeba taxa increasing dramatically ($68.8 \pm 17.9\%$) and carbon accumulation increasing to between $45.7\text{--}102.8 \text{ g m}^{-2} \text{ yr}^{-1}$.

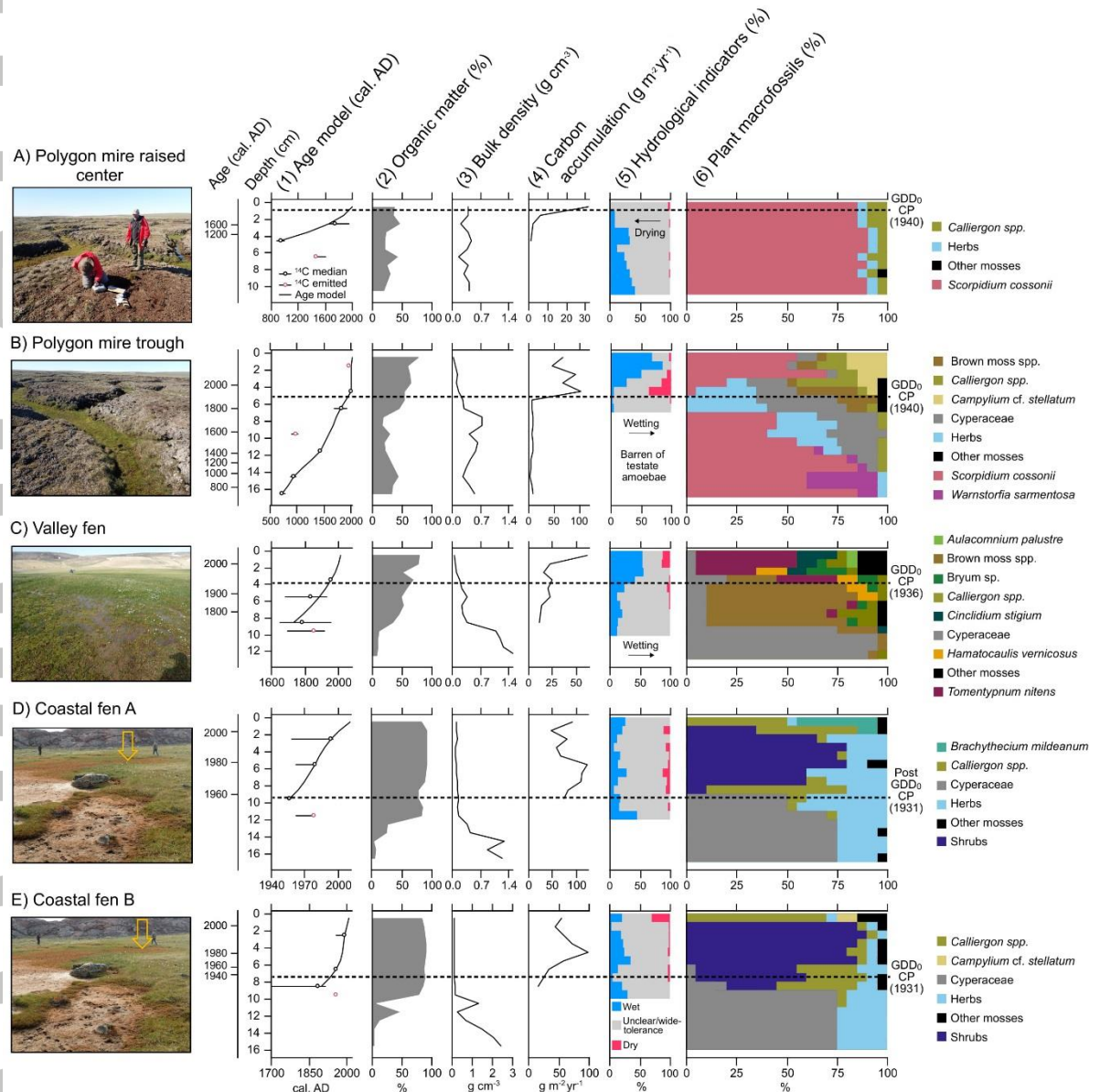


Figure 3. Summary stratigraphic diagram of paleoecological variables from polygon mire raised center (a), polygon mire trough (b), valley fen (c) and coastal fen (d and e; yellow arrows indicate sampling locations). GDD₀ CP is changepoint in GDD₀. For detailed stratigraphic diagrams see Figures S7-S21.

3.2.2 Valley fen

The valley fen monolith [13 cm; Figure 3c] is composed of three main phases. Notwithstanding chronological uncertainty, our age-depth model suggests that the base of the record (13–9 cm) accumulated before ~AD 1780. The base phase is characterized by a pale-colored mineral layer of low organic matter content (7.2–11.6%), high bulk density (1.08–1.52 g cm⁻³) and sedge-dominated vegetation (>75%). At ~7 cm (~AD 1800) there is a sharp increase in organic matter (11.6–33.4%) and a decrease in bulk density (1.08–0.38 g cm⁻³). Throughout the middle section of the profile (9–4 cm) there is a gradual increase in organic matter to 56.5% and decrease in bulk density to 0.23 g cm⁻³ (~AD 1950). This change represents the development of a more productive intermediate or rich fen system dominated by Brown moss spp. (60–75%), *Calliergon* spp. (<20%) and *Hamatocaulis vernicosus* (<10%), with increasing carbon accumulation (10.9–20.1 g m⁻² yr⁻¹). In the top 4 cm (~AD 1950 onwards), the wetland demonstrates properties more characteristic of a peatland. Organic matter continues to increase to 78.8% and bulk density decreases further to 0.06 g cm⁻³. *Tomentypnum nitens* (30–50%), *Cinclidium stygium* (0–20%) now dominate the valley fen record alongside other mosses. These mosses (including *T. nitens* and *C. stygium*) may have been present under the Brown moss spp. classification, however decomposition made species identification impossible.

3.2.3 Coastal fen

The peat monoliths analyzed from coastal fen A (CFA) and coastal fen B (CFB) demonstrate highly similar responses, each recording two distinct phases [Figure 3d and 3e]. Notwithstanding chronological uncertainty, our age-depth model suggests the lower phase (CFA 17–12 cm, CFB 16–10 cm) accumulated before ~AD 1950. This lower phase is characterized by a pale-colored minerogenic layer dominated by sedges and herbs, with low organic matter (mostly 2–26%), and a high bulk density (max: 2.44 g cm⁻³), which decreases up the succession (min: 0.38 g cm⁻³). The upper phase (CFA 12–0 cm, CFB 10–0 cm) is characterized by a darker-colored peaty layer of poorly-decomposed plant material and a sharp rise in organic matter that remains consistently high (average of upper phases in both monoliths = 87 ± 4.8%) alongside a relatively low bulk density (average of upper phases in both monoliths = 0.12 ± 0.02 g cm⁻³). The vegetation in the upper phase initially changes from sedge and herb-dominance, to a transitional phase dominated by the moss *Calliergon richardsonii* (CFA 9–8 cm, CFB 9–8 cm). Shrubs then dominate (CFA 8–2 cm, CFB 8–1 cm), before a return to a dominance of *C. richardsonii* (>50%) alongside the appearance of *Brachythecium mildeanum* (in CFA) (<40%). At the coastal fen site, the ecosystem shift to shrub-dominance is coincident with fast carbon accumulation rates (~AD 1980) of >100 g m⁻² yr⁻¹.

4 Discussion

Under twenty-first century warming and in the presence of adequate moisture, Arctic wetlands such as our study sites may become more productive and transition into peatlands – this could to some extent mitigate carbon losses from degrading peatlands further south [Charman *et al.*, 2015; Gallego-Sala *et al.*, 2018]. The Arctic wetlands we studied did demonstrate ecological responses to a mid-twentieth century increase in GDD₀. However, the pathway of these responses varied between wetland types and therefore their future carbon balance is likely to be complex and may vary between wetland types. In particular, our results highlight the importance of ground-ice dynamics, changing seasonal hydrological regimes and herbivory.

Ground-ice dynamics and permafrost feedbacks:

Ground-ice dynamics and feedbacks in permafrost regions are a key uncertainty in understanding the carbon cycling response of these systems to warming [Grosse *et al.*, 2016; Schuur *et al.*, 2015]. We believe our polygon mire site exemplifies the influence ground-ice dynamics can have upon wetland structure and ecology with warming. A changepoint increase in GDD_0 was detected at the polygon mire in 1940 [Figure 2b]. A further increase in GDD_0 from 1956–2016 at Sach Harbour has been documented and linked to increasing active layer depth [Fraser *et al.*, 2018]. At the polygon mire, the raised center monolith showed no response to recent warming, perhaps because permafrost thaw has not yet induced the collapse of the raised center structure, as may be the case in some Siberian peatlands (c.f. Telteuwskoï *et al.*, 2016). In contrast, the trough demonstrates high sedge abundance from ~AD 1800, consistent with stable or initially degrading ice-wedges, while the shift to dominance of hydrophilic moss (*S. cossonii*) from ~AD 2000, is characteristic of advanced ice-wedge degradation [Figure 3.6b; Jorgenson *et al.*, 2015]. Recent ice-wedge degradation is further supported by an increase in wet-indicator testate amoeba from ~AD 2000 [Figure 3.5b]. This decadal or sub-decadal timescale of trough wetting is supported by observations from across the Arctic since the mid-twentieth century [Fraser *et al.*, 2018; Jorgensen *et al.*, 2015; Liljedahl *et al.*, 2016]. The previous periods of sedge and herb-dominance and moss-dominance in the record [Figure 3.6b] may relate to previous ice-wedge degradation and stabilization cycles. However, accurate interpretation of these previous trough vegetation shifts is limited by the absence of a testate amoeba hydrological record (barren below 7 cm). Local geomorphological and autogenic vegetation processes are key in the formation and variability of polygon mires, but climate change may modify these patterns [Ellis & Rochefort, 2004]. We suggest the magnitude of recent warming [Figure 2] alongside background autogenic processes caused a threshold of ice-wedge thaw to be reached ~AD 2000 in the polygon mire.

Under advanced ice-wedge degradation and the establishment of hydrological connectivity between troughs, landscape-scale drainage can be initiated [Liljedahl *et al.*, 2016]. Drainage could threaten wetland persistence and expose partially-decomposed carbon to increased aerobic decomposition – elevating CO₂ emissions [Schädel *et al.*, 2016]. However, the establishment of moss vegetation ~AD 2000, under wetter conditions [Figure 3b], may represent a negative ecological feedback to ice-wedge thaw in troughs. The accumulated layer of moss since ~AD 2000 may act as an insulating layer alongside slumped material from trough banks to retard further thaw [Jorgenson *et al.*, 2006; 2015]. The slumping process was observed onsite [Figure S2] and may explain an older bulk peat date (1–2 cm; AD 1956 ± 1) stratigraphically above a reliable plant macrofossil date (4–5 cm; AD 1998 ± 2; Table S1). The negative ecological and geomorphological (slumping) feedbacks could contribute to the deceleration of ice-wedge degradation. Our results highlight the importance of ground-ice dynamics and autogenic factors in polygon mires with warming [c.f. Fritz *et al.*, 2016; Vardy *et al.*, 2005].

Changing hydrological regime and precipitation with warming:

The short growing season of around two months in the High Arctic creates a highly seasonal hydrological regime, which our results suggest is being influenced by warming. When temperatures rise above 0°C there is an influx of water to catchments from the thaw of ground-ice and snowbanks that have accumulated over the winter [Glenn & Woo, 1997] – this is particularly relevant at our valley fen site. An increase in GDD_0 at the valley fen from AD 1936 [Figure 2b] is followed at ~AD 1950 by a marked increase in wet-indicator testate amoeba taxa and slight increase in dry-indicator taxa [Figure 3.5c]. The apparent increase in

wetness is likely as a result of increased catchment thaw under warming conditions – a process that has been observed in other Arctic and alpine regions [Fontana *et al.*, 2010; Woo & Young, 2014]. The increase in dry-indicator testate amoeba taxa may represent increasingly dry conditions towards the end of the growing season as a result of increased evapotranspiration over a longer and warmer summer [Oechel *et al.*, 1998; Woo & Young, 2014; Zhang *et al.*, 2018b]. This increased variability in hydrological conditions from ~AD 1950 is further supported by the presence of the hummock mosses *T. nitens* (30–50%) and *Aulacomnium palustre* (<5%). These mosses have broad climatic and ecological ranges [Minke *et al.*, 2009; Nicholson & Gignac, 1995] making them suitable for the increasingly variable moisture conditions. *T. nitens* specifically has been observed in both wet High Arctic [Steere & Scotter, 1979] and dry Boreal fens [Gignac *et al.*, 1991], suggesting a certain resilience to warming temperatures alongside more variable hydrology.

Under the likely scenario of further Arctic warming [Christensen *et al.*, 2013], alterations to the hydrology of the valley fen may threaten future persistence. Greater summer snowmelt may increase inundation in the short term. However, there may come a point where snowbanks become sufficiently depleted by increased evapotranspiration and no longer have the capacity to sustain wetlands [Woo & Young, 2006]. Possible increases in twenty-first century Arctic late-autumn and winter precipitation [Bintanja & Selten, 2014; Kattsov *et al.*, 2007] may counteract increased evaporative losses to some extent. However, large uncertainties remain in predicting future precipitation patterns. Since ~AD 1950 there has been no clear shift in precipitation at the closest weather stations to our sites [Figure S1]. Furthermore, increased future permafrost thaw and active layer thickening could increase permeability and thus drainage [Avis *et al.*, 2011]. Under the scenario of drying, CO₂ emissions from aerobic decomposition are likely to increase and the wetland may become a carbon source [Oechel *et al.*, 1998]. Carbon accumulation rates since ~AD 1950 remain consistent around 20 g m⁻² yr⁻¹ before a recent increase to 61.3 g m⁻² yr⁻¹ [Figure 3.4c]. This increase hints at improved productivity with increased GDD₀, indicating that the wetland ecosystem has not reached a moisture-limited point where carbon loss to decomposition outweighs input from litter. However, this carbon accumulation rate should be treated with caution because incomplete decomposition of recently accumulated organic matter was not accounted for. Our results demonstrate a clear ecosystem shift in response to recent warming, linked to a changing hydrological regime. The balance of possible increases in twenty-first century precipitation against summer evapotranspiration losses - alongside potential changes to drainage with permafrost thaw - are likely to determine the future sustainability and carbon accumulation capacity of this valley fen and potentially similar Arctic wetlands.

Potential impact of herbivory on Arctic coastal wetlands:

The timing and magnitude of the ecosystem shift from sedges to shrubs is well established in both coastal fen records by ~AD 1950 and is likely linked to warming. The subsequent shift to moss dominance in both records since ~AD 2000 is likely linked to changes in avian grazing pressures. The increased dominance of shrubs in this coastal wetland ~AD 1950 follows an increase in GDD₀ at AD 1931 [Figure 2b]. Northward expansion of shrub communities and increased productivity in response to recent warming has been widely documented across the tundra [Elmendorf *et al.*, 2012; Myers-Smith *et al.*, 2011; Tape *et al.*, 2006] and directly linked to increased shrub and decreased sedge abundance in an Alaskan coastal wetland [Carlson *et al.*, 2018]. Isostatic uplift can lead to a drop in relative sea-level and lowering of the water table, increasing dryness to facilitate sedge to shrub succession [Klinger & Short, 1996]. However, any hydrological shift associated with an increased abundance of shrubs is unclear in our testate amoeba data.

Furthermore, the projected range of sea-level change for nearby Cambridge Bay by 2100 relative to 2010 is between a 15 cm fall and 30 cm rise, depending upon future emissions scenarios [James *et al.*, 2011]. Therefore, isostatic uplift is likely to be more relevant in regions where uplift outpaces global eustasy, such as Hudson Bay and the Northwest Passage [James *et al.*, 2015]. We suggest the increase in GDD_0 is the most plausible mechanism driving this shift to shrub-dominance at our site. The role of climate is further supported by evidence of a recent increase in shrub taxa in sub-Arctic permafrost peatlands in Sweden [Galka, *et al.*, 2017b] and Alaska [Galka *et al.*, 2018] - areas of limited isostatic uplift [Geruo *et al.*, 2013; Peltier, 2004].

The contemporary wetland ecosystem demonstrates minimal shrub cover and contains large sections of bare substrate and patches of dead moss [Figure S4]. Both coastal fen monoliths demonstrate a recent shift to mosses ~AD 2000 [Figure 3d and 3e]. Wildfire has reduced shrub cover in similar environments [Higuera *et al.*, 2008; Mack *et al.*, 2011], but the absence of macro-charcoal at our site rules this out. An alternative possibility for the reappearance of moss is increased grazing by Arctic geese, e.g. lesser snow geese (*Chen caerulescens*) and Ross's geese (*Anser rossii*). Snow geese have demonstrated a preference for herbivory of vascular plants and therefore across the coastal wetlands of northern Canada, areas that have been subjected to destructive grazing often experience an increase in moss vegetation abundance [Abraham & Jefferies, 1997; Alisauskas *et al.*, 2006]. In areas of more intense grazing, replacement of moss by bare peat has been documented [Conkin & Alisauskas, 2017]. Similarly, the recolonization of mosses towards the edge of the wetland [Figure S4] is typical of disturbed wetlands [Speed *et al.*, 2010].

Arctic geese populations are being driven up by improved food availability from agricultural production (via artificial fertilizers and subsidy policies) in the wintering grounds of the southern United States [Fox *et al.*, 2005; Jefferies *et al.*, 2004]. Our coastal fen site is located ~20 km northwest of Queen Maud Gulf Migratory Bird Sanctuary (QMBS), a major summer nesting site for Arctic geese [Cooch *et al.*, 2001] and bird presence can be confirmed unambiguously at our coastal fen site by an abundance of tracks and excrement [Figure S4]. The QMBS has seen Arctic geese nesting populations rise from ~44,300 in 1965 to ~2,251,900 in 2006, with over 50% of this increase occurring since 1998 [Kerbes *et al.*, 2014]. The likely recent intensification of grazing in established summer nesting sites may have caused snow geese to seek out more pristine habitats further north as they warm, such as our site, and begin to degrade them. Therefore, we suggest either edge recolonization following snow geese disturbance or selective snow geese herbivory provides a plausible explanation for the dramatic shift from a shrub to moss-dominated ecosystem ~AD 2000. It remains unclear what implications this shift from shrub to moss-dominance will have upon long-term carbon accumulation rates, however our findings highlight the potential importance of avian grazing (substantially influenced by non-climate factors) in the context of future Arctic carbon cycling.

5 Conclusions

Warming of the western Canadian Arctic has caused a mid-twentieth century increase in growing degree days above 0°C (GDD_0). In the absence of long-term monitoring data our high-resolution multiproxy paleoecological approach – the first of its kind in the Canadian High Arctic – allowed us to identify alternate pathways for ecological responses to recent warming in three wetlands. The main findings of our study are:

- 1) An increase in moss diversity, decrease in sedges and herbs, and an increase in carbon accumulation rate occurred in the trough of a high centered polygon mire following the shift

in GDD₀. Testate amoeba data suggest increased wetness at this time which may be related to ice-wedge thaw driven by recent climate warming. In comparison, the raised center of the polygon mire showed no clear response to recent warming.

2) In a valley fen, the appearance of generalist mosses coincides with the shift in GDD₀. This occurs alongside an increase in both dry- and wet-indicator testate amoebae that may suggest increased seasonality in hydrological conditions (wetter conditions during snowmelt, and drier conditions in the late summer owing to increased evapotranspiration). This site shifted from a minerogenic to an organic-rich wetland sometime prior to the shift in GDD₀.

3) A coastal fen site experienced an ecosystem shift coincident with an increase in GDD₀ from a sedge-dominated fen to a shrub-dominated fen with a high carbon accumulation rate. This site shifted from a minerogenic wetland to an organic-rich peatland sometime before the shift in GDD₀. The results from this site have important implications for understanding the expansion of shrub communities in the Arctic.

4) A subsequent reduction in shrub cover in the coastal fen since ~AD 2000 and recolonization by mosses may be related to an increase in destructive grazing by Arctic snow geese. This may affect long-term carbon accumulation rates.

5) Our results show clear, albeit complex ecological responses to warming in these Arctic wetlands. These complexities have important implications for understanding of the future carbon sink potential of these ecosystems under climate warming and are important areas for future research.

Acknowledgments, Samples, and Data

TGS is funded by the Leeds-York Natural Environment Research Council Doctoral Training Partnership (NE/L002574/1). We acknowledge the generous support of Natural Resources Canada, Geological Survey of Canada in funding our radiocarbon dating and thank the André E. Lalonde AMS Laboratory, University of Ottawa, for the rapid analysis. This paper represents NRCan Contribution number / Numéro de contribution de RNCAN: 20180298. For the Banks Island sample collection, we thank Rod Smith of Geological Survey Canada, René Gysler of Great Slave Helicopters and Andrew Durbano. Sample collection occurred during a Geological Survey of Canada Geo-Mapping for Energy and Minerals Program (GEM Western Arctic) field program. For the Elu Inlet sample collection, we thank Thomas Hadlari, Attima Hadlari, Elisabeth Jansen-Hadlari, Francis Emingak, Braden Gregory, and Nawaf Nasser. Funding for field logistics was provided by a Polar Knowledge Canada/Savoir polaire Canada Grant #1516-149 to Jennifer Galloway and Timothy Patterson and from the Geological Survey of Canada Environmental Geoscience Program. For the helpful discussion and comments regarding the identification and classification of the ciliate Vaginicolidae (included alongside testate amoebae as a paleohydrological indicator) we thank Matthew Amesbury, Anatoly Bobrov, Louis Beyens, Dan Charman, Clément Duckert, Diego Fontaneto, Anna Kosakyan, Mariusz Lamentowicz, Michelle McKeown, Edward Mitchell, Thomas Roland, Ferry Siemensma, and Dave Wilkinson. We thank Lars Hedenäs for help in the identification of brown-moss species in the plant macrofossil analysis. We thank the contributors to the Climate Explorer site for the re-analysis and station data used in this paper and are grateful to Environment Canada for the extended temperature records for the Sachs Harbour station. We acknowledge receiving isostatic uplift data from <http://grace.jpl.nasa.gov>. We also thank Konrad Gajewski for his advice on interpretation of past temperature reconstructions and for directing us to pollen temperature reconstruction datafiles. All paleoecological data is available in the supplementary files.

References

- Abbott, B. W., Jones, J. B., Schuur, E. A. G., Chapin III, F. S., Bowden, W. B., Bret-Harte, M. S., et al. (2016). Biomass offsets little or none of permafrost carbon release from soils, streams, and wildfire: an expert assessment. *Environmental Research Letters*, 11(3), 034014. <https://doi.org/10.1088/1748-9326/11/3/034014>
- Abraham, K. F., & Jefferies, R. L. (1997). *High goose populations: Causes, impacts and implications*. In B. D. J. Batt (Ed.), Arctic ecosystems in peril: Report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture Special Publication (pp. 7–72). Ottawa, Ontario: Canadian Wildlife Service.
- Alisauskas, R. T., Charlwood, J. W., & Kellett, D. K. (2006). *Vegetation Correlates of the History and Density of Nesting by Ross's Geese and Lesser Snow Geese at Karrak Lake, Nunavut*. Arctic. Arctic Institute of North America. <https://doi.org/10.2307/40512794>
- Amesbury, M. J., Mallon, G., Charman, D. J., Hughes, P. D. M., Booth, R. K., Daley, T. J., & Garneau, M. (2013). Statistical testing of a new testate amoeba-based transfer function for water-table depth reconstruction on ombrotrophic peatlands in north-eastern Canada and Maine, United States. *Journal of Quaternary Science*, 28(1), 27–39. <https://doi.org/10.1002/jqs.2584>
- Amesbury, M. J., Roland, T. P., Royles, J., Hodgson, D. A., Convey, P., Griffiths, H., & Charman, D. J. (2017). Widespread Biological Response to Rapid Warming on the Antarctic Peninsula. *Current Biology*, 27(11), 1616–1622. <https://doi.org/10.1016/j.cub.2017.04.034>
- Avis, C. A., Weaver, A. J., & Meissner, K. J. (2011). Reduction in areal extent of high-latitude wetlands in response to permafrost thaw. *Nature Geoscience*, 4(7), 444–448. <https://doi.org/10.1038/ngeo1160>
- Bengtsson, L., Semenov, V. A., & Johannessen, O. M. (2004). The Early Twentieth-Century Warming in the Arctic—A Possible Mechanism. *Journal of Climate*, 17(20), 4045–4057. [https://doi.org/10.1175/1520-0442\(2004\)017<4045:TETWIT>2.0.CO;2](https://doi.org/10.1175/1520-0442(2004)017<4045:TETWIT>2.0.CO;2)
- Beyens, L., & Chardez, D. (1995). An Annotated List of Testate Amoebae Observed in the Arctic between the Longitudes 27° E and 168° W. *Archiv Für Protistenkunde*, 146(2), 219–233. [https://doi.org/10.1016/S0003-9365\(11\)80114-4](https://doi.org/10.1016/S0003-9365(11)80114-4)
- Beyens, L., Chardez, D., de Baere, D., de Bock, P., & Jaques, E. (1990). Ecology of terrestrial testate amoebae assemblages from coastal Lowlands on Devon Island (NWT, Canadian Arctic). *Polar Biology*, 10(6), 431–440. <https://doi.org/10.1007/BF00233691>
- Bick, H. 1972. Ciliated Protozoa: *An illustrated guide to the species used as biological indicators in freshwater biology*. Geneva, Switzerland: World Health Organization.
- Bintanja, R., & Selten, F. M. (2014). Future increases in Arctic precipitation linked to local evaporation and sea-ice retreat. *Nature*, 509(7501), 479–482. <https://doi.org/10.1038/nature13259>
- Blaauw, M. (2010). Methods and code for ‘classical’ age-modelling of radiocarbon sequences. *Quaternary Geochronology*, 5(5), 512–518. <https://doi.org/10.1016/J.QUAGEO.2010.01.002>
- Bobrov, A. A., Charman, D. J., & Warner, B. G. (1999). Ecology of Testate Amoebae

- (Protozoa: Rhizopoda) on Peatlands in Western Russia with Special Attention to Niche Separation in Closely Related Taxa. *Protist*, 150(2), 125–136. [https://doi.org/10.1016/S1434-4610\(99\)70016-7](https://doi.org/10.1016/S1434-4610(99)70016-7)
- Booth, R. K. (2008). Testate amoebae as proxies for mean annual water-table depth in Sphagnum-dominated peatlands of North America. *Journal of Quaternary Science*, 23(1), 43–57. <https://doi.org/10.1002/jqs.1114>
- Booth, R. K., Lamentowicz, M., & Charman, D. J. (2010). Preparation and analysis of testate amoebae in peatland palaeoenvironmental studies. *Mires and Peat*, 7(02), 1–7.
- Bockheim, J., & Tarnocai, C. (1998). Recognition of cryoturbation for classifying permafrost-affected soils. *Geoderma*, 81(3–4), 281–293. [https://doi.org/10.1016/S0016-7061\(97\)00115-8](https://doi.org/10.1016/S0016-7061(97)00115-8)
- Brown, J., Ferrians, O., Heginbottom, J. A., & Melnikov, E. (2002). Circum-Arctic Map of Permafrost and Ground-Ice Conditions, Version 2. Boulder, Colorado USA: National Snow and Ice Data Center.
- Carlson, L. G., Beard, K. H., & Adler, P. B. (2018). Direct effects of warming increase woody plant abundance in a subarctic wetland. *Ecology and Evolution*, 8(5), 2868–2879. <https://doi.org/10.1002/ece3.3902>
- Chambers, F. M., Beilman, D. W., & Yu, Z. (2011). Methods for determining peat humification and for quantifying peat bulk density, organic matter and carbon content for palaeostudies of climate and peatland carbon dynamics. *Mires and Peat*, 7(07), 1–10.
- Charman, D. J., Hendon, D., & Woodland, W. A. (2000). *The identification of testate amoebae (Protozoa: Rhizopoda) in peats: QRA Technical Guide No. 9. Quaternary Research Association*. London: Quaternary Research Association. <https://doi.org/10.1016/j.quascirev.2004.02.012>
- Charman, D. J., Blundell, A., & Abrupt Climate Change Over the European Land Mass project members. (2007). A new European testate amoebae transfer function for palaeohydrological reconstruction on ombrotrophic peatlands. *Journal of Quaternary Science*, 22(3), 209–221. <https://doi.org/10.1002/jqs.1026>
- Charman, D. J., Beilman, D. W., Blaauw, M., Booth, R. K., Brewer, S., Chambers, F. M., et al. (2013). Climate-related changes in peatland carbon accumulation during the last millennium. *Biogeosciences*, 10(2), 929–944. <https://doi.org/10.5194/bg-10-929-2013>
- Charman, D. J., Amesbury, M. J., Hinchliffe, W., Hughes, P. D. M., Mallon, G., Blake, W. H., et al. (2015). Drivers of Holocene peatland carbon accumulation across a climate gradient in northeastern North America. *Quaternary Science Reviews*, 121, 110–119. <https://doi.org/10.1016/J.QUASCIREV.2015.05.012>
- Christensen, J. H., Kumar, K. K., Aldrian, E., An, S.-I., Cavalcanti, I. F. A., de Castro, M., et al. (2013). Climate Phenomena and their Relevance for Future Regional Climate Change. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, et al. (Eds.), *The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1217–1310). Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

- Compo, G. P., Whitaker, J. S., Sardeshmukh, P. D., Matsui, N., Allan, R. J., Yin, X., et al. (2011). The Twentieth Century Reanalysis Project. *Quarterly Journal of the Royal Meteorological Society*, 137(654), 1–28. <https://doi.org/10.1002/qj.776>
- Conkin, J., & Alisauskas, R. T. (2017). Conversion of tundra to exposed peat habitat by snow geese (*Chen caerulescens caerulescens*) and Ross's geese (*C. rossii*) in the central Canadian Arctic. *Polar Biology*, 40(3), 563–576. <https://doi.org/10.1007/s00300-016-1979-x>
- Cooch, E., Rockwell, R. F., & Brault, S. (2001). Retrospective Analysis of Demographic Responses to Environmental Change : a Lesser Snow Goose Example. *Ecological Monographs*, 71(3), 377–400. [https://doi.org/10.1890/0012-9615\(2001\)071\[0377:RAODRT\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2001)071[0377:RAODRT]2.0.CO;2)
- Corliss, J. O. (1979). *The Ciliated Protozoa : Characterization, Classification and Guide to the Literature*. (2nd ed.). Oxford, United Kingdom: Pergamon Press.
- Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., & Aerts, R. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature*, 460(7255), 616–619. <https://doi.org/10.1038/nature08216>
- Ellis, C. J., & Rochefort, L. (2004). Century-scale development of polygon-patterned tundra wetland, Bylot Island (73° N, 80° W). *Ecology*, 85(4), 963–978. <https://doi.org/10.1890/02-0614>
- Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., et al. (2012). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, 2(6), 453–457. <https://doi.org/10.1038/nclimate1465>
- Flora of North America Editorial Committee. (2007). *Flora of North America North of Mexico, Volume 27: Bryophytes, Part 1: Mosses*. Oxford, United Kingdom: Oxford University Press.
- Fontana, F. M. A., Trishchenko, A. P., Luo, Y., Khlopenkov, K. V, Nussbaumer, S. U., & Wunderle, S. (2010). Perennial snow and ice variations (2000–2008) in the Arctic circumpolar land area from satellite observations. *Journal of Geophysical Research*, 115, 4020. <https://doi.org/10.1029/2010JF001664>
- Fox, A. D., Madsen, J., Boyd, H., Kuijken, E., Norriss, D. W., Tombre, I. M., & Stroud, D. A. (2005). Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. *Global Change Biology*, 11(6), 881–893. <https://doi.org/10.1111/j.1365-2486.2005.00941.x>
- Fraser, R., Kokelj, S., Lantz, T., McFarlane-Winchester, M., Olthof, I., & Lacelle, D. (2018). Climate Sensitivity of High Arctic Permafrost Terrain Demonstrated by Widespread Ice-Wedge Thermokarst on Banks Island. *Remote Sensing*, 10(6), 954. <https://doi.org/10.3390/rs10060954>
- Fritz, M., Wolter, J., Rudaya, N., Palagushkina, O., Nazarova, L., Obu, J., et al. (2016). Holocene ice-wedge polygon development in northern Yukon permafrost peatlands (Canada). *Quaternary Science Reviews*, 147, 279–297. <https://doi.org/10.1016/J.QUASCIREV.2016.02.008>

- Gajewski, K. (2015). Quantitative reconstruction of Holocene temperatures across the Canadian Arctic and Greenland. *Global and Planetary Change*, 128, 14–23. <https://doi.org/10.1016/J.GLOPLACHA.2015.02.003>
- Galka, M., Tobolski, K., Lamentowicz, Ł., Ersek, V., Jassey, V. E. J., van der Knaap, W. O., & Lamentowicz, M. (2017a). Unveiling exceptional Baltic bog ecohydrology, autogenic succession and climate change during the last 2000 years in CE Europe using replicate cores, multi-proxy data and functional traits of testate amoebae. *Quaternary Science Reviews*, 156, 90–106. <https://doi.org/10.1016/J.QUASCIREV.2016.11.034>
- Galka, M., Szal, M., Watson, E. J., Gallego-Sala, A., Amesbury, M. J., Charman, D. J., et al. (2017b). Vegetation Succession, Carbon Accumulation and Hydrological Change in Subarctic Peatlands, Abisko, Northern Sweden. *Permafrost and Periglacial Processes*, 28(4), 589–604. <https://doi.org/10.1002/ppp.1945>
- Galka, M., Swindles, G. T., Szal, M., Fulweber, R., & Feurdean, A. (2018). Response of plant communities to climate change during the late Holocene: Palaeoecological insights from peatlands in the Alaskan Arctic. *Ecological Indicators*, 85, 525–536. <https://doi.org/10.1016/J.ECOLIND.2017.10.062>
- Gallego-Sala, A. V., Charman, D. J., Brewer, S., Page, S. E., Prentice, I. C., Friedlingstein, P., et al. (2018). Latitudinal limits to the predicted increase of the peatland carbon sink with warming. *Nature Climate Change*, 1. <https://doi.org/10.1038/s41558-018-0271-1>
- Geruo, A., Wahr, J., & Zhong, S. (2013). Computations of the viscoelastic response of a 3-D compressible Earth to surface loading: an application to Glacial Isostatic Adjustment in Antarctica and Canada. *Geophysical Journal International*, 192(2), 557–572. <https://doi.org/10.1093/gji/ggs030>
- Gibson, C. M., Chasmer, L. E., Thompson, D. K., Quinton, W. L., Flannigan, M. D., & Olefeldt, D. (2018). Wildfire as a major driver of recent permafrost thaw in boreal peatlands. *Nature Communications*, 9(1), 3041. <https://doi.org/10.1038/s41467-018-05457-1>
- Gignac, L. D., Vitt, D. H., Zoltai, S. C., & Bayley, S. E. (1991). Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada. *Nova Hedwigia*, 53, 27–71.
- Glenn, M. S., & Woo, M. (1997). Spring and summer hydrology of a valley-bottom wetland, Ellesmere Island, Northwest Territories, Canada. *Wetlands*, 17(2), 321–329. <https://doi.org/10.1007/BF03161420>
- Grosse, G., Goetz, S., McGuire, A. D., Romanovsky, V. E., & Schuur, E. A. G. (2016). Changing permafrost in a warming world and feedbacks to the Earth system. *Environmental Research Letters*, 11(4), 040201. <https://doi.org/10.1088/1748-9326/11/4/040201>
- Grimm, E. C. (1987). CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences*, 13(1), 13–35. [https://doi.org/10.1016/0098-3004\(87\)90022-7](https://doi.org/10.1016/0098-3004(87)90022-7)
- Hadenäs, L. (2003). The European species of the Calliergon–Scorpidium–Drepanocladus complex, including some related or similar species. *Meylania*, (28), 1–116.

- Hammer, Ø., Harper, D. A. ., & Ryan, P. D. (2001). PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4(1), 9.
- Hassol, S., Arctic Climate Impact Assessment: Arctic Monitoring and Assessment Programme, Program for the Conservation of Arctic Flora and Fauna & International Arctic Science Committee. (2004). *Impacts of a warming Arctic : Arctic Climate Impact Assessment*. Cambridge, United Kingdom: Cambridge University Press.
- Higuera, P. E., Brubaker, L. B., Anderson, P. M., Brown, T. A., Kennedy, A. T., & Hu, F. S. (2008). Frequent Fires in Ancient Shrub Tundra: Implications of Paleorecords for Arctic Environmental Change. *PLoS ONE*, 3(3), e0001744. <https://doi.org/10.1371/journal.pone.0001744>
- Hill, G. B., & Henry, G. H. R. (2011). Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology*, 17(1), 276–287. <https://doi.org/10.1111/j.1365-2486.2010.02244.x>
- Hua, Q., Barbetti, M., & Rakowski, A. Z. (2013). Atmospheric Radiocarbon for the Period 1950–2010. *Radiocarbon*, 55(04), 2059–2072. https://doi.org/10.2458/azu_js_rc.v55i2.16177
- James, T.S., Henton, J.A., Leonard, L.J., Darlington, A., Forbes, D.L., & Craymer, M., (2015). Tabulated values of relative sea-level projections in Canada and the adjacent mainland United States; Geological Survey of Canada, Open File 7942, 81. <https://doi.org/10.4095/297048>
- James, T.S., Simon, K.M., Forbes, D.L., Dyke, A.S., and Mate, D.J., (2011). Sea-level Projections for Five Pilot Communities of the Nunavut Climate Change Partnership; Geological Survey of Canada, Open File 6715, 23. <https://doi.org/10.4095/288019>
- Jefferies, R. L., & Rockwell, R. F. (2002). Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science*, 5(1), 7–16. <https://doi.org/10.1111/j.1654-109X.2002.tb00531.x>
- Jefferies, R. L., Rockwell, R. F., & Abraham, K. F. (2004). The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of Arctic wetlands – a continuing saga. *Environmental Reviews*, 11(4), 193–232. <https://doi.org/10.1139/a04-002>
- Johannessen, O. M., Bengtsson, L., Miles, M. W., Kuzmina, S. I., Semenov, V. A., Alekseev, G. V., et al. (2004). Arctic climate change: observed and modelled temperature and sea-ice variability. *Tellus A: Dynamic Meteorology and Oceanography*, 56(4), 328–341. <https://doi.org/10.3402/tellusa.v56i4.14418>
- Jorgenson, M. T., Shur, Y. L., & Pullman, E. R. (2006). Abrupt increase in permafrost degradation in Arctic Alaska. *Geophysical Research Letters*, 33(2), L02503. <https://doi.org/10.1029/2005GL024960>
- Jorgenson, M. T., Kanevskiy, M., Shur, Y., Moskalenko, N., Brown, D. R. N., Wickland, K., et al. (2015). Role of ground ice dynamics and ecological feedbacks in recent ice wedge degradation and stabilization. *Journal of Geophysical Research: Earth Surface*, 120(11), 2280–2297. <https://doi.org/10.1002/2015JF003602>
- Juggins, S. (2007). C2 Version 1.5 User guide. Software for ecological and palaeoecological data analysis and visualisation. Newcastle upon Tyne, UK: Newcastle University.

- Juggins, S. (2018). Rioja: Analysis of Quaternary Science Data. R package version 0.9-15.1. Retrieved from <https://cran.r-project.org/package=rioja>
- Kattsov, V. M., Walsh, J. E., Chapman, W. L., Govorkova, V. A., Pavlova, T. V., Zhang, X., et al. (2007). Simulation and Projection of Arctic Freshwater Budget Components by the IPCC AR4 Global Climate Models. *Journal of Hydrometeorology*, 8(3), 571–589. <https://doi.org/10.1175/JHM575.1>
- Kerbes, R. H., Meeres, K. M., & Alisauskas, R. T. (2014). *Surveys of nesting lesser snow geese and ross's geese in Arctic Canada, 2002 - 2009. Arctic Goose Joint Venture Special Publication*. U.S. Fish and Wildlife Service, Washington, D.C. and Canadian Wildlife Service, Ottawa, Ontario.
- Killick, R., & Eckley, I. A. (2014). changepoint : An R Package for Changepoint Analysis. *Journal of Statistical Software*, 58(3), 1–19. <https://doi.org/10.18637/jss.v058.i03>
- de Klerk, P., Donner, N., Karpov, N. S., Minke, M., & Joosten, H. (2011). Short-term dynamics of a low-centred ice-wedge polygon near Chokurdakh (NE Yakutia, NE Siberia) and climate change during the last ca 1250 years. *Quaternary Science Reviews*, 30(21–22), 3013–3031. <https://doi.org/10.1016/J.QUASCIREV.2011.06.016>
- Klinger, L. F., & Short, S. K. (1996). Succession in the Hudson Bay Lowland, Northern Ontario, Canada. *Arctic and Alpine Research*, 28(2), 172–183. <https://doi.org/10.1080/00040851.1996.12003163>
- Kopeck, B. G., Feng, X., Michel, F. A., & Posmentier, E. S. (2016). Influence of sea ice on Arctic precipitation. *Proceedings of the National Academy of Sciences of the United States of America*, 113(1), 46–51. <https://doi.org/10.1073/pnas.1504633113>
- Kralik, U. (1961). Ein Beitrag zur Biologie von loricierten peritrichen Ziliaten, insbesondere von *Platycola truncata* Fromentel 1874. *Arch. Protistenk.*, 105, 201–258.
- Lamarre, A., Magnan, G., Garneau, M., & Boucher, É. (2013). A testate amoeba-based transfer function for paleohydrological reconstruction from boreal and subarctic peatlands in northeastern Canada. *Quaternary International*, 306, 88–96. <https://doi.org/10.1016/J.QUAINT.2013.05.054>
- Lamentowicz, Ł., Lamentowicz, M., & Gąbka, M. (2008). Testate amoebae ecology and a local transfer function from a peatland in western Poland. *Wetlands*, 28(1), 164–175. <https://doi.org/10.1672/07-92.1>
- Liljedahl, A. K., Boike, J., Daanen, R. P., Fedorov, A. N., Frost, G. V., Grosse, G., et al. (2016). Pan-Arctic ice-wedge degradation in warming permafrost and its influence on tundra hydrology. *Nature Geoscience*, 9(4), 312–318. <https://doi.org/10.1038/ngeo2674>
- Mack, M. C., Bret-Harte, M. S., Hollingsworth, T. N., Jandt, R. R., Schuur, E. A. G., Shaver, G. R., & Verbyla, D. L. (2011). Carbon loss from an unprecedented Arctic tundra wildfire. *Nature*, 475(7357), 489–492. <https://doi.org/10.1038/nature10283>
- Mauquoy, D., & van Geel, B. (2007). Mire and peat macros. In S. A. Elias (Ed.), *Encyclopedia of Quaternary Science* (pp. 2315–2336). Amsterdam, Netherlands: Elsevier.
- Microworld. (2018). Microworld: world of amoeboid organisms. Retrieved from <https://www.arcella.nl/>

- Minke, M., Donner, N., Karpov, N., de Klerk, P., & Joosten, H. (2009). Patterns in vegetation composition, surface height and thaw depth in polygon mires in the Yakutian Arctic (NE Siberia): a microtopographical characterisation of the active layer. *Permafrost and Periglacial Processes*, 20(4), 357–368. <https://doi.org/10.1002/ppp.663>
- Mitchell, E. A. D., Buttler, A. J., Warner, B. G., & Gobat, J.-M. (1999). Ecology of testate amoebae (Protozoa: Rhizopoda) in *Sphagnum* peatlands in the Jura mountains, Switzerland and France. *Écoscience*, 6(4), 565–576. <https://doi.org/10.1080/11956860.1999.11682555>
- Morris, P. J., Swindles, G. T., Valdes, P. J., Ivanovic, R. F., Gregoire, L. J., Smith, M. W., et al. (2018). Global peatland initiation driven by regionally asynchronous warming. *Proceedings of the National Academy of Sciences of the United States of America*, 115(19), 4851–4856. <https://doi.org/10.1073/pnas.1717838115>
- Myers-Smith, I. H., Harden, J. W., Wilmking, M., Fuller, C. C., McGuire, A. D., & Chapin, F. S. I. (2008). Wetland succession in a permafrost collapse: interactions between fire and thermokarst. *Biogeosciences*, 5(12), 1273–1286.
- Myers-Smith, I. H., Forbes, B. C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., et al. (2011). Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4), 045509. <https://doi.org/10.1088/1748-9326/6/4/045509>
- Nacken, M., & Reise, K. (2000). Effects of herbivorous birds on intertidal seagrass beds in the northern Wadden Sea. *Helgoland Marine Research*, 54(2–3), 87–94. <https://doi.org/10.1007/s101520050006>
- Natali, S. M., Schuur, E. A. G., Mauritz, M., Schade, J. D., Celis, G., Crummer, K. G., et al. (2015). Permafrost thaw and soil moisture driving CO₂ and CH₄ release from upland tundra. *Journal of Geophysical Research: Biogeosciences*, 120(3). <https://doi.org/10.1002/2014JG002872>
- Nicholson, B. J., & Gignac, L. D. (1995). Ecotope Dimensions of Peatland Bryophyte Indicator Species along Gradients in the Mackenzie River Basin, Canada. *The Bryologist*, 98(4), 437. <https://doi.org/10.2307/3243583>
- Oechel, W. C., Vourlitis, G. L., Hastings, S. J., Ault, R. P., & Bryant, P. (1998). The effects of water table manipulation and elevated temperature on the net CO₂ flux of wet sedge tundra ecosystems. *Global Change Biology*, 4(1), 77–90. <https://doi.org/10.1046/j.1365-2486.1998.00110.x>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2017). vegan: Community Ecology Package. Retrieved from <https://cran.r-project.org/package=vegan>
- Payette, S., Delwaide, A., Caccianiga, M., & Beauchemin, M. (2004). Accelerated thawing of subarctic peatland permafrost over the last 50 years. *Geophysical Research Letters*, 31(18), L18208. <https://doi.org/10.1029/2004GL020358>
- Peltier, W. R. (2004). Global glacial isostasy and the surface of the ice-age Earth: the ICE-5G (VM2) model and GRACE. *Annual Review of Earth and Planetary Sciences*, 32(1), 111–149. <https://doi.org/10.1146/annurev.earth.32.082503.144359>
- Perreault, N., Lévesque, E., Fortier, D., Gratton, D., Lamarque, L. J., Perreault, N., et al. (2017). Remote sensing evaluation of High Arctic wetland depletion following

- permafrost disturbance by thermo-erosion gully processes. *Arctic Science*, 3, 237–253. <https://doi.org/10.1139/as-2016-0047>
- Peterson, S. L., Rockwell, R. F., Witte, C. R., & Koons, D. N. (2013). The Legacy of Destructive Snow Goose Foraging on Supratidal Marsh Habitat in the Hudson Bay Lowlands. *Arctic, Antarctic, and Alpine Research*, 45(4), 575–583. <https://doi.org/10.1657/1938-4246.45.4.575>
- Ping, C. L., Michaelson, G. J., Kimble, J. M., Romanovsky, V. E., Shur, Y. L., Swanson, D. K., & Walker, D. A. (2008). Cryogenesis and soil formation along a bioclimate gradient in Arctic North America. *Journal of Geophysical Research*, 113(G3), G03S12. <https://doi.org/10.1029/2008JG000744>
- Polyakov, I. V., Bekryaev, R. V., Alekseev, G. V., Bhatt, U. S., Colony, R. L., Johnson, M. A., et al. (2003). Variability and Trends of Air Temperature and Pressure in the Maritime Arctic, 1875–2000. *Journal of Climate*, 16(12), 2067–2077. [https://doi.org/10.1175/1520-0442\(2003\)016<2067:VATOAT>2.0.CO;2](https://doi.org/10.1175/1520-0442(2003)016<2067:VATOAT>2.0.CO;2)
- Qin, Y., Mitchell, E. A. D., Lamentowicz, M., Payne, R. J., Lara, E., Gu, Y., et al. (2013). Ecology of testate amoebae in peatlands of central China and development of a transfer function for paleohydrological reconstruction. *Journal of Paleolimnology*, 50(3), 319–330. <https://doi.org/10.1007/s10933-013-9726-6>
- R Core Team. (2018). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org>
- Reimer, P. J., Brown, T. A., & Reimer, R. W. (2004). Discussion: Reporting and Calibration of Post-Bomb ^{14}C Data. *Radiocarbon*, 46(03), 1299–1304. <https://doi.org/10.1017/S0033822200033154>
- Reimer, P. J., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Ramsey, C. B., et al. (2013). IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. *Radiocarbon*, 55(04), 1869–1887. https://doi.org/10.2458/azu_js_rc.55.16947
- Schädel, C., Bader, M. K.-F., Schuur, E. A. G., Biasi, C., Bracho, R., Čapek, P., et al. (2016). Potential carbon emissions dominated by carbon dioxide from thawed permafrost soils. *Nature Climate Change*, 6(10), 950–953. <https://doi.org/10.1038/nclimate3054>
- Schuur, E. A. G., McGuire, A. D., Schädel, C., Grosse, G., Harden, J. W., Hayes, D. J., et al. (2015). Climate change and the permafrost carbon feedback. *Nature*, 520(7546), 171–179. <https://doi.org/10.1038/nature14338>
- Smith, A. J. E. (2004). *The Moss Flora of Britain and Ireland* (2nd ed.). Cambridge, United Kingdom: Cambridge University Press.
- Smith, L. C., Sheng, Y., & MacDonald, G. M. (2007). A first pan-Arctic assessment of the influence of glaciation, permafrost, topography and peatlands on northern hemisphere lake distribution. *Permafrost and Periglacial Processes*, 18(2), 201–208. <https://doi.org/10.1002/ppp.581>
- Smith, H. G. (1992). Distribution and ecology of the testate rhizopod fauna of the continental Antarctic zone. *Polar Biology*, 12(6–7), 629–634.
- Speed, J. D. M., Cooper, E. J., Jónsdóttir, I. S., Van Der Wal, R., & Woodin, S. J. (2010). Plant community properties predict vegetation resilience to herbivore disturbance in

- the Arctic. *Journal of Ecology*, 98(5), 1002–1013. <https://doi.org/10.1111/j.1365-2745.2010.01685.x>
- Steere, W. C., & Scotter, G. W. (1979). Bryophytes of Banks Island, Northwest Territories, Canada. *Canadian Journal of Botany*, 57(10), 1136–1149. <https://doi.org/10.1139/b79-137>
- Swindles, G. T., Amesbury, M. J., Turner, T. E., Carrivick, J. L., Woulds, C., Raby, C., et al. (2015). Evaluating the use of testate amoebae for palaeohydrological reconstruction in permafrost peatlands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 424, 111–122. <https://doi.org/10.1016/J.PALAEO.2015.02.004>
- Tape, K., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, 12(4), 686–702. <https://doi.org/10.1111/j.1365-2486.2006.01128.x>
- Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., & Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, 23(2), GB2023. <https://doi.org/10.1029/2008GB003327>
- Taylor, L. S., Swindles, G. T., Morris, P. J., & Gałka, M. (2019). Ecology of peatland testate amoebae in the Alaskan continuous permafrost zone. *Ecological Indicators*, 96, 153–162. <https://doi.org/10.1016/J.ECOLIND.2018.08.049>
- Teltewskoi, A., Beermann, F., Beil, I., Bobrov, A., De Klerk, P., Lorenz, S., et al. (2016). 4000 Years of Changing Wetness in a Permafrost Polygon Peatland (Kytalyk, NE Siberia): A Comparative High-Resolution Multi-Proxy Study. *Permafrost and Periglacial Processes*, 27(1), 76–95. <https://doi.org/10.1002/ppp.1869>
- Vardy, S. R., Warner, B. G., Turunen, J., & Aravena, R. (2000). Carbon accumulation in permafrost peatlands in the Northwest Territories and Nunavut, Canada. *The Holocene*, 10(2), 273–280. <https://doi.org/10.1191/095968300671749538>
- Vardy, S. R., Warner, B. G., & Asada, T. (2005). Holocene environmental change in two polygonal peatlands, south-central Nunavut, Canada. *Boreas*, 34(3), 324–334. <https://doi.org/10.1111/j.1502-3885.2005.tb01104.x>
- de Vleeschouwer, F., Chambers, F. M., & Swindles, G. T. (2010). Coring and sub-sampling of peatlands for palaeoenvironmental research. *Mires and Peat*, 7, 1–10.
- Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., et al. (2005). The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, 16(3), 267–282. <https://doi.org/10.1111/j.1654-1103.2005.tb02365.x>
- Warner, B. G., & Charman, D. J. (1994). Holocene changes on a peatland in northwestern Ontario interpreted from testate amoebae (Protozoa) analysis. *Boreas*, 23(3), 270–279. <https://doi.org/10.1111/j.1502-3885.1994.tb00949.x>
- Warner, B. G., & Chengalath, R. (1991). *Habrotrocha angusticollis* (Bdelloidea, Rotifera): A new paleoecological indicator in Holocene peat deposits in Canada. *SIL Proceedings, 1922-2010*, 24(5), 2738–2740. <https://doi.org/10.1080/03680770.1989.11899146>
- Woo, M., & Young, K. L. (2006). High Arctic wetlands: Their occurrence, hydrological characteristics and sustainability. *Journal of Hydrology*, 320(3–4), 432–450. <https://doi.org/10.1016/J.JHYDROL.2005.07.025>

- Woo, M., & Young, K. L. (2014). Disappearing semi-permanent snow in the High Arctic and its consequences. *Journal of Glaciology*, 60(219), 192–200.
<https://doi.org/10.3189/2014JoG13J150>
- Wood, K. R., & Overland, J. E. (2010). Early 20th century Arctic warming in retrospect. *International Journal of Climatology*, 30(9), 1269–1279.
<https://doi.org/10.1002/joc.1973>
- Zhang, H., Gallego-Sala, A. V., Amesbury, M. J., Charman, D. J., Piilo, S. R., Välranta, M. M., & Zhang, H. (2018a). Inconsistent response of Arctic permafrost peatland carbon accumulation to warm climate phases. *Global Biogeochemical Cycles*.
<https://doi.org/10.1029/2018GB005980>
- Zhang, H., Piilo, S. R., Amesbury, M. J., Charman, D. J., Gallego-Sala, A. V., & Välranta, M. M. (2018b). The role of climate change in regulating Arctic permafrost peatland hydrological and vegetation change over the last millennium. *Quaternary Science Reviews*, 182, 121–130. <https://doi.org/10.1016/J.QUASCIREV.2018.01.00>