GAME CHANGER

Invited Contribution for the 2022 Anniversary Edition



Will accelerated soil development be a driver of Arctic Greening in the late 21st century?#

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Take-Home Message

Climate warming is transforming the Arctic at an unprecedented rate with previously barren and sparsely vegetated landscapes undergoing "greening". We postulate that the observed vegetation changes throughout the Arctic are not only tied to warming, but to changes in soil properties and their impacts on plants and soil microbial communities. A key to understanding extent and patterns of greening of formerly sparsely vegetated Arctic environments will be to unravel the interactions between the biosphere and the role of soil genesis.

KEYWORDS

Arctic Greening, Arctic warming, high Arctic, plant-soil Interactions, polar environments, soil development

1 | MODERN ARCTIC WARMING AND THE ROLE OF SOILS

The disappearance of Arctic permafrost due to climate warming (Christiansen et al., 2020) and the rapid decomposition of carbon (C) in organic soil layers accumulated for millennia have drawn much attention in recent years within the soil science community (Hugelius et al., 2014; Jobbágy & Jackson, 2000; Schuur & Mack, 2018). There is a risk of a large soil carbon–atmosphere climate feedback, but large uncertainties exist about the magnitude of this feedback (Bradford et al., 2016; Friedlingstein et al., 2014; García-Palacios et al., 2021). For example, warming of Arctic tundra has been shown to restructure soil food webs, C input and soil organic carbon (SOC) stocks. Little to no net losses of the overall tundra C stocks were observed upon soil warming. Net gains in plant biomass compensated for net losses in soil C, with the

fate of SOC stocks in deeper mineral horizons remaining highly uncertain (Sistla et al., 2013).

Arctic soil C research has largely concentrated on the changes of C cycling in soils with thick organic layers that are vulnerable to decomposition, or on sediments and deposits that became ice-free after glacial retreat (Bruhwiler et al., 2021). However, despite their vast spatial extent, mineral soils in high Arctic regions, with sparsely distributed vegetation and shallow soils without prior accumulation of thick organic layers, have not yet been considered a central element to understanding future C cycling in a warming Arctic. Likewise, the development of these soils has not been considered a major force in explaining changing vegetation patterns and ecosystem functioning in the Arctic thus far. In this Game Changer article for the 100-year anniversary edition of JPNSS, the authors argue that including knowledge gained on the role of soil formation will be key to understanding the complex

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feedback loops between climate and vegetation in the Arctic. Pedogenesis in high latitudes could potentially create extensive soil systems that can function as C sinks over a timespan of centuries.

High Arctic tundra ecosystems are traditionally characterized by short vegetation periods, thin soils and complex patches of barren and vegetated landscapes on the edge of polar deserts and oceans. These ecosystems are experiencing rapid and severe climate change and are warming at a rate of approximately twice the global average (Pachauri et al., 2014; Post et al., 2019). At the same time, an increase in plant net primary productivity, increasing diversity, abundance and range expansion of potentially more productive plant species has been observed throughout the high Arctic (Harrison, 2020; Myers-Smith et al., 2020; Post et al., 2009; Wasowicz et al., 2020). The consequences of these changing conditions are shifts in the distribution patterns of native vegetation as well as the establishment of new plant species, which include alien vascular plant species from lower latitudes that are better adapted to a warmer climate. Collectively, these climatic-primary productivity feedbacks are often referred to as 'Arctic Greening' (Myers-Smith et al., 2020). However, recent observations have shown that vegetation across the Arctic is not responding uniformly to warming. Certain areas are 'browning' due to the dieback of native lichen and moss tundra vegetation, while other regions remain unchanged (Berner et al., 2020). The different trajectories of these high Arctic ecosystems can be partially explained by climatic factors such as changes in temperature, precipitation and wildfires, and by the ability of plant populations to respond to novel environmental conditions and recover from extreme climatic events (Bjorkman et al., 2017). Moreover, there is growing evidence that the variation in the pace of Arctic vegetation change - especially in the high Arctic - can also be explained by changes in abiotic and (micro)biotic soil properties as well as topographic factors (Aerts, 2006; Gries et al., 2020; Sarneel et al., 2020). In fact, warming-induced development of soil chemical, physical and microbial properties to support plant life might be key to understanding patterns and the extent of Arctic Greening in many regions.

2 | SOIL DEVELOPMENT IN A WARMING ARCTIC

In the Arctic, climatic limitations with low rates of (bio-)chemical weathering hamper the release of nutrients from minerals and slow the formation of thicker, richer soils. Under a cold and dry climate, the development of just a few centimetres thick soils can take several hundreds or even thousands of years (Bölter et al., 2006; Voroney & Heck, 2015). Thus, soil weathering and development, including interrelations between abiotic factors and soil biota, is typically assumed to play-out over much longer time scales, and is therefore not rapid enough to contribute to Arctic Greening over a period of years to decades. However, geochemically young soils and sediments in the Arctic might react much more rapidly than expected under warmer conditions than more weathered systems in mid and lower latitude, directly affecting microbial and vegetation dynamics. These interactions will proceed in the following manner: First, since Arctic soils are shallow, the weathering front will be very close to the surface, and thus located within those layers that will warm the strongest during summer months (Kropp et al.,

2020: Lemke et al., 2007). Second, weathering under Arctic conditions is highly biased towards physical processes such as freeze-thawing cycles and the deterioration of rocks into smaller fragments, increasing mineral surface area (Hall et al., 2002). Under warmer and wetter conditions, exposed mineral surfaces are then prone to stronger (bio-)chemical weathering processes (Hall et al., 2002). Similarly, large amounts of unconsolidated sediment, transported and deposited along freely meandering rivers, provide excellent pre-conditions under a warmer climate for plant growth (Clarke, 2002). Third, the degree of chemical alteration of soils and sediments in the Arctic through weathering is still low. A large amount of primary minerals are present in topsoils, which, depending on local geochemistry of soil parent material, can weather much more quickly than soils predominantly consisting of more weathered minerals (Blacker, 2018; Wilson, 2004) or minerals with lower intrinsic susceptibility to chemical weathering. Finally, Arctic Greening itself will be another factor further accelerating soil development (Figure 1). For instance, higher amounts of root exudates will contribute to soil acidification and mineral weathering (Kleber et al., 2021). Due to its generally darker colour, higher organic matter input to soil can significantly impact soil thermal dynamics and accelerate soil warming (Zhu et al., 2019).

In conclusion, and in contrast to common understanding, soil development in geochemically young but warming Arctic soils could be rapid and therefore govern changes in ecological networks (Bradley et al., 2014; Carlson et al., 2017; Hornig, 2018). Once climatic barriers for chemical weathering are overcome, the development of the capacity of Arctic soils to release rock-derived nutrients for plant growth, as well as the degree and speed of the formation of reactive mineral surfaces (clay minerals and paedogenic oxides), will govern the quality and quantity of vegetation C inputs to soil and its capacity to stabilize C against decomposition (Grosse et al., 2011). In turn, increasing plantderived metabolites will positively feedback the speed of this process. Accelerated (bio-)chemical weathering, higher reactivity and release of nutrients into the soil solution (Bradley et al., 2014; Carlson et al., 2017) will potentially boost Arctic Greening to an extent that has not been seen since the onset of the Holocene and is likely not comparable to any warming responses that occurred throughout the Pleistocene. While soil development could potentially lead to binding more C in soils to minerals in areas where soils are currently underdeveloped, plant range expansions in the Arctic could create a positive feedback to changing surface albedo and alter the terrestrial C cycle (Swann et al., 2010). Thus, with the growing influence of developing mineral soils in the high Arctic on nutrient and water fluxes, strong responses and potential feedback effects to pedogenesis can be expected within the Arctic biosphere.

3 | FEEDBACK BETWEEN BIOSPHERE RESPONSES AND SOIL DEVELOPMENT IN A WARMING ARCTIC

The distinct differences in the seasonality of solar radiation, as well as the speed and extent of today's anthropogenic warming of high Arctic environments compared to prior events in the Pleistocene, make



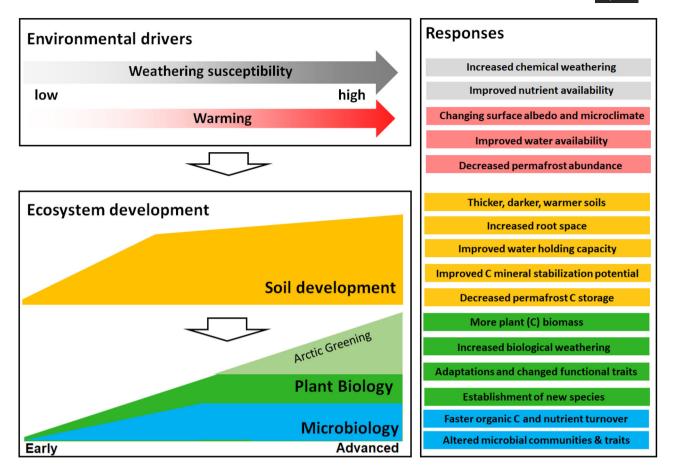


FIGURE 1 Schematic representation of soil development in response to environmental change, indicating the associated (delayed) responses of biological processes that can be expected once soil formation has created an environment that supports them

it hard, if not impossible, to find proper (mid-latitude) equivalents to study and estimate the direction of Arctic soil and ecosystem development. Denser vegetation coverage could lead to a positive feedback, resulting in improved soil microclimatic conditions and water storage (Aalto et al., 2013; Ge et al., 2017) with microorganisms facilitating the transfer of nutrients between soil and plants. Plant-associated and free-living soil bacteria, archaea and fungi will then be major determinants of how plant biomass becomes incorporated into soil C stocks and for the availability of soil nutrients to plants (e.g., Dubey et al., 2021; Liang et al., 2017). Near-neutral or alkaline soils developing towards more acidity, driven for example by root exudates, can then in turn lead to higher nutrient release and further improve soil conditions for plant growth (Blacker, 2018). Similarly, if Arctic Greening results in changing plant-driven organic C inputs or P-availability in soil, we will likely see changes in soil microbial community composition and structure, as C and P are often identified as important controls on (Arctic) bacterial and fungal richness (Gray et al., 2014; Siciliano et al., 2014). Changes in the soil microbial community structure may, in turn, influence plant and soil properties and the cycling of nutrients such as N, P and base cations as well as soil organic matter decomposition. These expectations build largely on our knowledge from boreal and alpine systems. However, drivers of spatial patterns and the speed of C build-up in soil and vegetation in the Arctic are poorly understood.

Moreover, we still do not have a complete picture of which microorganisms are carrying out critical C transformations in High-Arctic tundra soils, let alone under different temperature and soil moisture conditions. Hillslopes and exposed hilltops might remain predominantly water and temperature limited for much longer periods of time, due to the unfavourable conditions for soil formation and plant growth. Since climate change impacts are expected to be uneven across the Arctic (Westergaard-Nielsen et al., 2017), it is uncertain which mechanisms and processes become dominant (and important enough) to affect C fluxes across Arctic landscape units. C cycling in valleys and along rivers, where water and sediments accumulate and chemical weathering accelerates, might become increasingly controlled by soil and vegetation processes.

4 | CONCLUSIONS

As Arctic soil landscapes continue to change, we need to understand potential biological and physico-chemical feedback associated with the Arctic's transition into a novel state. Undoubtedly, through the mineralization of SOC that was previously protected through cold temperatures, Arctic environments will be one of the largest sources for greenhouse gas emissions in the 21st century creating a feedback



towards even more warming in the future. However, the development of Arctic soils will not stop with the loss of C and the disappearance of permafrost over large areas. Mineral weathering may hold the key to store more SOC over the coming centuries in Arctic soils, thereby at least partly compensating for C losses from thawing permafrost areas. Thus, constraining the timescale and spatial extent of Arctic Greening may require a better understanding of Arctic soil weathering and development, a key process that has not received much attention. Characterizing local patterns of soil formation in sediments and bedrock, their drivers and underlying mechanisms in relation to plant succession, will therefore be cornerstones for the prediction of soil functioning and C and nutrient cycling during warming of the highestlatitude environments. Furthermore, Arctic plant community dynamics and soil development are often perceived as independent processes that occur at different time scales. While it is clear that warming is already affecting large areas of polar environments, soil development and the geochemical alterations that come along with it through weathering are generally perceived to take decades to centuries. Soil development is likely to contribute substantially to the changes of plant community composition (Alexander et al., 2018; Hagedorn et al., 2019). However, the point at which it becomes the dominant factor for Arctic Greening remains unknown. Therefore, Arctic climate change calls for more interdisciplinary approaches to develop a deeper understanding of the eco-evolutionary aspects underlying Arctic Greening and soil development. We need novel experimental approaches that can simulate plausible future combinations of soils, climate, microbial communities and plants. Studies across biogeoclimatic gradients could therefore constitute a major step forward in the understanding of how soil-vegetation-microbial interactions will govern the pace and shape of greening in the warming higher Arctic.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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