

Arctic soil microbial diversity in a changing world

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Abstract

The Arctic region is a unique environment, subject to extreme environmental conditions, shaping life therein and contributing to its sensitivity to environmental change. The Arctic is under increasing environmental pressure from anthropogenic activity and global warming. The unique microbial diversity of Arctic regions, that has a critical role in biogeochemical cycling and in the production of greenhouse gases, will be directly affected by and affect, global changes. This article reviews current knowledge and understanding of microbial taxonomic and functional diversity in Arctic soils, the contributions of microbial diversity to ecosystem processes and their responses to environmental change.

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1. Specificity of Arctic soils and ecosystems

1.1. Arctic region

The Arctic region includes terrestrial, freshwater and marine environments across northern Asia, Europe and North America. The boundary of the Arctic region is often defined by the Arctic Circle (66°32'N), but the boundary can be drawn far below this, when based on climate, marine or terrestrial environments [1]. When based on temperature, the Arctic is often delimited by the 10 °C July isotherm. However, the Arctic exhibits considerable variation in temperature, precipitation and soil characteristics both spatially and temporally. Arctic terrestrial ecosystems are often divided into three different biogeographical zones with a gradient in environmental conditions from north to south: the High Arctic, Low Arctic and Subarctic (Table 1, Fig. 1a) [1], although various alternative classifications exist. The High Arctic is the northern part of the Arctic region including Greenland, Nunavut

Canadian islands (i.e. Baffin Island, Parry Islands, Queen Elizabeth Islands and Ellsmere Islands), Russian islands (i.e. Franz Josef Land, New Siberia Islands and part of Novaya Zemlya), Severnaya Zemlya and Svalbard (Fig. 1a). The Low Arctic extends mainly from the Arctic continental coastline to the treeline, while the Subarctic boundary starts from the treeline to the closed-canopy of the boreal forest and the southern limits of permafrost (Fig. 1a) [1]. The difference between these zones is seen in the gradient from the High Arctic to Subarctic with changes in temperature, precipitation and plant cover (Table 1). Hence, the growing season increase from the High Arctic to Subarctic as well the size of plants and plant cover, from bare soil and discontinuous cover to continuous (Table 1). The High Arctic is characterised by Polar deserts, corresponding to areas where annual precipitation is <150 mm and the mean temperature of the warmest month is <10 °C (Polar semi-desert is also used for areas with annual precipitation of 150–250 mm) [2].

The Arctic is characterised by cold temperatures, as low as –40 °C in winter (sometimes lower in Siberia) rising to 15 °C (and higher in continental Asia) in summer across the southern Arctic regions [1]. Annual precipitation is low in the Arctic,

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Table 1

Description of the three main Arctic regions: High Arctic, Low Arctic and Subarctic (based on Jones et al. [2]).

	High Arctic	Low Arctic	Subarctic
Limit	Northern part of Arctic region	Arctic continental coastline to the treeline	From the treeline to the upper latitudinal limit of the boreal forest
Growing season	1–2.5 months	3–4 months	3.5–12 months
Temperature	Annual <−15 °C Mean July 4–8 °C	Annual −15 to −10 °C Mean July 4–11 °C	Large fluctuations Annual −20 to 5 °C (even below −20 °C in Siberia, where the average in January is −50 °C)
Precipitation	<250 mm or between 250 and 500 mm (only Greenland ice cap receives >1000 mm)	<500 mm and often <250 mm	Large variations with annual precipitation varying from <250 mm, up to 750 mm
Plant cover	Large areas of bare soil Discontinuous plant cover Bryophyte and lichen 50–80%, vascular plant 0–20%	Plant cover increases to 80–100% Decrease in bryophyte and lichen density	Increase in vegetation height due to shrub dominance. Plant cover 100%
Ecosystems	Polar desert ^a and polar semi-desert ^b , tundra,	Increase of tundra area and peatland; decrease in polar semi-desert area	Transition zone between Arctic tundra and boreal forest; large areas of wetland

^a Polar deserts are areas where annual precipitation is <150 mm and the mean temperature of the warmest month is <10 °C [2].

^b Polar semi-desert is also used for areas with annual precipitation of 150–250 mm [2].

with less than 500 mm for most of the Arctic with precipitation occurring mostly in the form of snow, increasing from the High Arctic to Subarctic, although the Greenland ice caps (High Arctic) receives precipitation >1000 mm (Table 1). Annual solar radiation received in the Arctic represents a third to a half of the radiation received in temperate and equatorial zones [1], although during at least some of the summer period there is 24 h sunlight within the Arctic Circle but also 24 h darkness in some of the winter period. The growing season, which corresponds to the period of growth of plants, varies between 1 and 2.5 months in the High Arctic, while it can last up to a year in the Subarctic [1].

1.2. Arctic soils

Arctic regions harbour a high diversity of soils. Indeed, 75% of the soil groups defined by the World Reference Base (WRB) [2] are present in the Arctic region. From these soils, about 60% represent cold soils (i.e. soils affected by permafrost). Cryosols are the dominant soil group (27%) and are defined as soils in cold regions where permafrost is present, where water occurs mainly in a frozen form, and cryosols are formed under cryogenic processes (e.g. frost heave, freeze-thaw cycles, cryoturbation) [2]. Permafrost is defined as ground (including soil, rocks, ice and organic material) that remains at or below 0 °C for at least two consecutive years. Permafrost comprises 24% of exposed land in the northern hemisphere (excluding areas beneath ice sheets; Fig. 1b) [2]. Most of the permafrost was formed during the past ice ages and is divided into four types: continuous, discontinuous, sporadic and isolated patches. Permafrost is found on land but can also be found below the sea (Fig. 1b). The continuous permafrost corresponds to permafrost occurring everywhere

throughout an entire region, while discontinuous permafrost covers between 50 and 90% of area, sporadic permafrost covers 10–50% of area and is surrounded by unfrozen soil, and isolated permafrost covers only 0–10% [2]. Moving from the High Arctic to the Subarctic, the distribution of continuous permafrost decreases, while discontinuous permafrost increases to finish as sporadic and isolated patches (Fig. 1b). The upper part of Arctic soil, named the “active layer”, thaws during summer to a depth of between 20 cm and 150 cm and refreezes each winter, but is not part of the permafrost by definition. The thickness of the active layer in summer depends upon local temperature, ground material, soil water content and plant cover, and generally increases in depth from the High Arctic to the Subarctic.

Arctic soils are characterised by a number of key features: multiple soil horizons are often found; low temperatures influenced by air temperature but also by permafrost, snow and plant cover; and soil water contents varying from saturated to dry depending on precipitation, soil drainage characteristics and permafrost (Table 2). Arctic soils are also characterised by large amounts of organic C, which to 3 m depth are estimated to be more than twice the atmospheric C pool [2–4]. Organic C accumulates because plant material is only partially decomposed in Arctic soils due to the low soil temperatures, short periods for biological (microbial) activity and sometimes acidic and/or anoxic conditions [2]. Carbon is accumulated near the surface as plant materials are deposited as litter and in deeper soil horizons due to cryogenic processes that move plant material and soluble compounds down toward the permafrost, where a horizon rich in organic matter can be formed. The migration of organic matter can take thousands of years and enable long-term storage of C [2]. Soils affected by permafrost contain potentially ~50% of the global organic C

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