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Review Article

Seasonal dynamics of Arctic soils: Capturing year-round processes in measurements and soil biogeochemical models

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ABSTRACT

The Arctic is undergoing rapid changes in climate, altering the status and functioning of high-latitude soils and permafrost. The vast majority of studies on Arctic soils and permafrost are conducted during the summer period due to ease of accessibility, sampling, instrument operation, and making measurements, in comparison to during winter and transition seasons. However, there is increasing evidence that microbial activity continues in Arctic soils outside of the summer period. Moreover, it is becoming clear that understanding the seasonal dynamics of Arctic soils is of critical importance, especially considering that the under-studied winter is the period that is most sensitive to climate warming. Soil biogeochemical models have advanced our understanding of the functioning and fate of soils in the Arctic, however it is vital that seasonality in biotic and abiotic processes is accurately captured in these models. Here we synthesize recent investigations and observations of the year-round functioning of Arctic soils, review soil biogeochemical modelling frameworks, and highlight certain processes and behaviors that are shaped by seasonality and thus warrant particular consideration within these models. More attention to seasonal processes will be critical to improving datasets and soil biogeochemical models that can be used to understand the year-round functioning of soils and the fate of the soil carbon reservoir in the Arctic.

1. Introduction

The Arctic has undergone rapid changes in climate during recent decades, including widespread increases in air temperature and overall increases in annual precipitation (as rainfall and snowfall) (Box et al., 2019; Meredith et al., 2019; Kalnay et al., 1996; Rapaić et al., 2015; Rawlins et al., 2010). In particular, the winter period is experiencing the highest rates of human-induced climate warming (Graham et al., 2017; Post et al., 2019): from 1971 to 2017, Arctic air temperatures have increased on average by 3.1 °C during the winter months (October–May), compared with a 1.8 °C increase during the summer period (June–September) (Box et al., 2019). Concurrently, snow cover and permafrost area are generally in decline across most regions of the Arctic (except for some parts of Siberia which have recorded increased prevalence and persistence of seasonal snow cover) (Bormann et al., 2018; Bulygina et al., 2009; Lemke et al., 2007; Schindler and Donahue, 2006; Tomczyk et al., 2021). Changes in air temperature and precipitation have induced a series of alterations to soil and permafrost, including

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increases in soil temperature, changes to soil moisture regimes, deepening of permafrost active-layer depths, reductions in the spatial extent of permafrost, prolonging of the vegetation growing season, and shortening durations of snow cover (Box et al., 2019; Brown et al., 2018; Lund et al., 2012, 2014; Meredith et al., 2019; Nicolsky et al., 2017; Parmentier et al., 2011; Romanovsky et al., 2017). There is mounting evidence that feedback processes are already affecting Arctic soils, including increased primary production and growing season carbon uptake, as well as elevated soil respiration during the non-growing season, resulting in significant changes to the net carbon fluxes between the land and atmosphere (Chapin III et al., 2005; Lemke et al., 2007; López-Blanco et al., 2017; Lund et al., 2010; Lund, 2018; Rößger et al., 2022).

The Arctic region contains large quantities of soil organic carbon. Hugelius et al. (2014) estimated that ~1300 Pg C is stored in Arctic soils, with 472 ± 27 Pg C in the upper-most 1 m, accounting for close to half of the total organic carbon stored in soils globally (Batjes, 2014; Jobbágy and Jackson, 2000). This enormous carbon pool is largely stored in soils with mean annual temperatures below freezing (< 0 °C) (Hugelius et al., 2014). These soils are highly vulnerable to climate warming, which causes thawing of permafrost that accelerates carbon mobilization and decomposition processes, elevating rates of carbon exchange between soil and the atmosphere. Both long-term records and process-based models have confirmed an increase in the net flux of soil carbon into the atmosphere due to warming of the Arctic over the past two decades (Euskirchen et al., 2017; McGuire et al., 2012).

Soils in high latitudes exhibit distinct seasonality in biotic and abiotic characteristics. Summers of perpetual daylight are punctuated by extended periods of 24-h darkness, snow cover and sub-zero temperatures (Fig. 1). Microbial respiration rates during wintertime in Arctic soils have typically been assumed to be low, limited largely by below-freezing temperatures and therefore reduced liquid water availability to soil microorganisms (Mazur, 1980; Arndt et al., 2020; Dunfield et al., 1993). However, recent studies have observed continuous soil respiration fluxes from Arctic soils during winter periods (Arndt et al., 2020; Natali et al., 2019) as well as bursts of carbon emitted from soils following early spring thawing (Nielsen et al., 2001; Raz-Yaseef et al., 2017; Teepe and Ludwig, 2004), substantially increasing the annual carbon efflux of arctic tundra ecosystems (Fahnestock et al., 1999). In fact, winter-time soil emissions are now known to be a significant regulator of the net ecosystem carbon balance in the Arctic because of the disproportionate rate of warming in the Arctic during winter, as well as the alterations to the timing of the transition periods between summer and winter seasons (i.e. spring thaw and fall freeze-up). Records have also captured considerable carbon dioxide (CO_2) emissions from Arctic soils during the 'shoulder seasons' (i.e., during fall freezing and springtime thawing) (Commane et al., 2017; Zona et al., 2016). Similarly, methane (CH_4) fluxes from Arctic soils during wintertime are considered to make up a significant portion (15–50%) of the annual methane fluxes to the atmosphere in the Arctic region (Flessa et al., 2008; Zona et al., 2016; Treat et al., 2018). Given the high global warming potential of methane (28–34times that of CO_2 over a 100 year period (GWP-100)) and the prevalence of methane-producing thermokarsts in the Arctic (Turetsky et al., 2020), understanding the seasonal changes in methane production and consumption is crucial to better establish current and future global carbon budgets. The timing, magnitude and nature by which greenhouse gasses are produced and released from high-latitude soils is also strongly shaped by variation in transport processes, linked to seasonal changes in the extent of freezing, saturation and snow-cover (Chuvilin et al., 2021; Heinze, 2021; Lange et al., 2016).

A wealth of new observations and experiments on shoulder-season and wintertime Arctic soil dynamics provide insights into better understanding and predicting the seasonality of microbial activity and carbon dynamics in Arctic soils. The emergence of year-round data (e.g., Pedron et al., 2022) will undoubtedly enable an improved understanding and prediction of the fate of Arctic soils under future warming scenarios, as well as the development and application of more robust and accurate mechanistically-based soil biogeochemical models. Numerical models are powerful tools enabling future predictions of feedbacks between the changing climate and the terrestrial carbon cycle, which can help to provide valuable information for policymaking. It may be necessary to consider microbial activity explicitly in soil carbon models

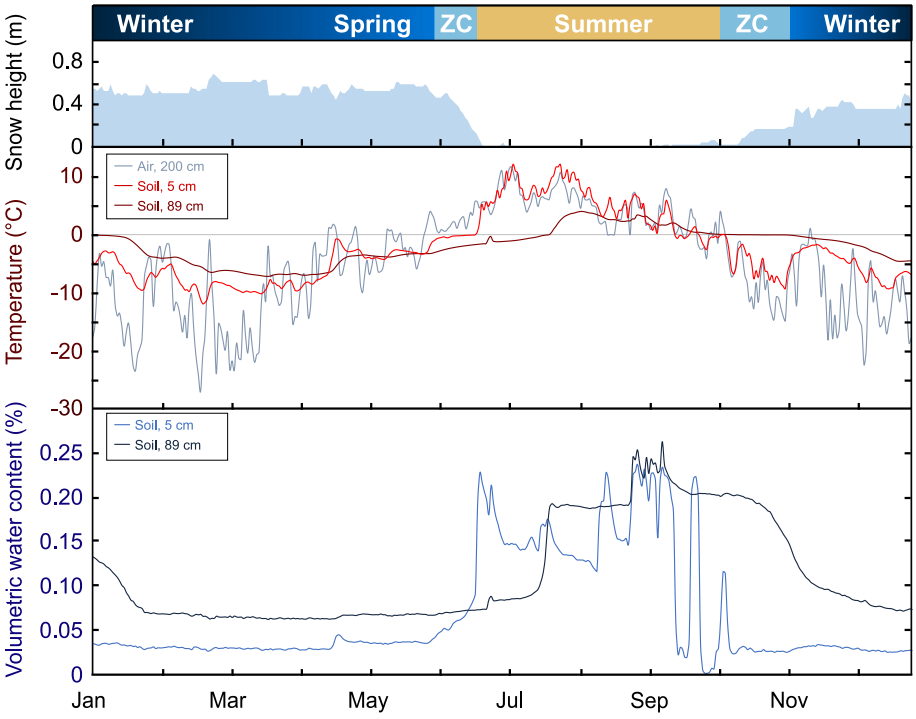

Fig. 1. Time-series of soil properties at the Bayelva permafrost monitoring site in Svalbard for the year 2019. The zero-curtain period (Table 1) is marked by 'ZC'. The data is a continuation of the data record published in Boike et al. (2018).

because microbes drive a large fraction, if not the majority, of soil carbon turnover in the Arctic, and respond dynamically to environmental and climate change. However, there are large discrepancies between the formulations and outputs of different model simulations, as well as between model simulations and observations (Fisher et al., 2014; McGuire et al., 2016; Webb et al., 2016; Meredith et al., 2019). For example, model-intercomparison studies demonstrate that there is high variability in predicted carbon fluxes from Arctic tundra soils, and that the magnitude of discrepancies between models and observations can be as large as the observed fluxes themselves (Fisher et al., 2014; McGuire et al., 2016; Shirley et al., 2022; Ito et al., 2023). The nature, timing, magnitude and causes of observed discrepancies between both the formulations and the outputs of model simulations are numerous and complex. In particular, winter-time carbon fluxes are poorly simulated by many process-based models (McGuire et al., 2016, 2018a), however can be adequately captured and accounted for in empirical models (Natali et al., 2019).

As evidence for Arctic climate change is mounting, the effects of these changes on the carbon cycle can start to be observed (Bruhwiler et al., 2021). Nevertheless, looking forward, there are major discrepancies (i.e. divergent signs and magnitudes of changes) in the modeled predictions of global soil carbon changes by the end of the century, mainly driven by differences in the assumptions regarding soil carbon persistence, especially in the Arctic (Wieder et al., 2019).

To improve our understanding of Arctic soil carbon cycling, and make better predictions of the fate of these systems under future warming scenarios, it is necessary to simulate soil biogeochemical dynamics not just during summer periods, but year-round, and to include the microbial mechanisms that modulate soil carbon responses to climate. Here, we first synthesize new observations, measurements and experiments capturing winter, shoulder-season, or all-year-round Arctic soil dynamics. Second, we review soil microbial and biogeochemical modelling frameworks and highlight important factors to consider when applying models year-round to bridge gaps in resolving seasonal processes and improving the simulation of microbial activity and carbon fluxes in Arctic terrestrial ecosystems. The term “soil” encompasses diverse landforms and ecosystems, spanning mineral and organic soils to wetlands. Whilst wetlands and seasonally inundated areas are noted as critical hotspots for CH_4production and emission (Wik et al., 2016; Comyn-Platt et al., 2018), we focus this review primarily on Arctic upland, tundra, mineral and organic soils and cryosols.

2. Seasonality of microbial processes and carbon cycling in Arctic soils

2.1. Soil microbial dynamics and the interplay with soil physical processes

2.1.1. Microbial activity

Soil microorganisms play a crucial role in regulating carbon emissions from Arctic soils (Hopple et al., 2020; Natali et al., 2019; Schuur et al., 2015; Pedron et al., 2022), and are highly temperature and moisture sensitive (Brooks et al., 1997; Clein and Schimel, 1995; Elberling and Brandt, 2003). Indeed, microbial respiration in Arctic soil changes dynamically across seasons (Raz-Yaseef et al., 2017), and with climatic variables such as snow cover (Yi et al., 2020). Similarly, the exchange of greenhouse gases between permafrost soils and the atmosphere are further regulated by above-ground vegetation, through both direct uptake of CO_2 by primary production of plants (Wei et al., 2021), and vegetation-driven changes to the hydrological regime (Keuschnig et al., 2022).

It is now well established that liquid water may persist in frozen peatlands where temperature drops well below the freezing point of water (Pavlova, 1970), and that soil microorganisms continue to actively decompose organic matter at relatively high rates at temperatures well below 0 °C, and at measurable rates down to −18 °C (Elberling and Brandt, 2003) – thus potentially producing a considerable amount of CO_2 during the snow-covered winter periods lasting many months. Indeed, soil microbes likely remain sensitive to changes in soil temperature and moisture regimes at temperatures below 0 °C (Brooks et al., 1997; Elberling and Brandt, 2003; Monson et al., 2006; Schmidt et al., 2009).

Whilst the upper-most layers of soils may be frozen during winter and shoulder-season periods, deeper layers of soils (Fig. 1) (Boike et al., 2018; Keuschnig et al., 2022) and taliks (Parazoo et al., 2018; Farquharson et al., 2022) may remain thawed, and microorganisms in these deep layers continue to respire, producing CO_2 and CH_4. It is estimated that 14 to 80% of the CO_2 that is produced in snow-covered soils remains trapped in the snow and soil column (Elberling and Brandt, 2003). The amount of CO_2 trapping is highly dependent on soil moisture levels and microbial community dynamics (Keuschnig et al., 2022). The trapping of CO_2 in snow-covered soils implies a substantial decoupling in time between the CO_2 being produced in the soil over winter, and CO_2 emissions that can be measured from the snow/soil surface. High rates of CO_2 emissions typically measured during spring may be partially attributed to trapped CO_2 that is released following changes to soil moisture regimes due to thawing events (Goulden et al., 1998; Zimov et al., 1996). However, more recent evidence shows that the majority of CO_2 production under the snow takes place during late winter (Liptzin et al., 2009; Monson et al., 2006) when soil temperatures are near 0 °C and microbial biomass (especially fungi) reach their maximum population sizes (Schmidt et al., 2009) and CO_2 fluxes are more synchronized with production of CO_2. A recent study by Arndt et al. (2020) indicates that bursts of respiration caused by infiltration of the soil by O_2-rich snow melt water are partially responsible for late-winter fluxes of CO_2 (rather than just arising from bursts of stored gases). Importantly, methane produced by methanogens in thawed deeper layers may escape to the atmosphere largely without being oxidized by methanotrophs if near-surface layers containing methanotrophs remain frozen (Zona et al., 2016).

2.1.2. Microbial biomass, community structure, and function

Shifts in bacterial and fungal community composition of Arctic tundra soils are apparent between early and late summer periods (Männistö and Häggblom, 2006; Wallenstein et al., 2007), and across seasons (i.e. summer and winter) (Buckeridge et al., 2013; Lipson and Schmidt, 2004; Pold et al., 2021; Schadt et al., 2003). Recently, Poppeliers et al. (2022) revealed that Arctic soil microbial biomass and community structure undergo seasonal, with the most dynamic period being the transition between winter and spring, although they stress that the fall to winter transition is relatively unstudied. In addition, Bardgett et al. (2005) and Buckeridge et al. (2013) suggested that Arctic soil microbial communities tend to be bacteria-dominated in summer, and fungal-dominated in winter. Accordingly, shifts in fungal-bacteria (F:B) ratio are predicted during summer-to-winter and winter-to-summer transitions – most notably a spike in F:B ratio during the winter and early spring under the snow (Aanderud et al., 2013; Buckeridge and Grogan, 2008; Lipson et al., 2009; Schadt et al., 2003; Waring et al., 2013; Zinger et al., 2009), potentially leading to functional differences and thus alteration to biogeochemical fluxes (e.g. soil respiration) during the winter season (Monson et al., 2006; Schmidt et al., 2009).

Experimental studies have suggested that microbial communities may be able to respond rapidly to seasonal shifts in substrate availability (Schimel and Mikan, 2005; Sturm et al., 2005). This may be linked to the apparent differences in fungal and bacterial biomass, since fungi and bacteria are known to have different enzymatic degradation potentials. For example, cellulose and lignin are the two most abundant input carbon sources in soil, and studies have found that fungi are more capable of degrading lignin than bacteria under the same environmental conditions (Datta et al., 2017). Lipson et al. (2002) showed that cellulose activity and breakdown of phenolic compounds were highest in the winter in tundra soils corresponding to the highest activity and biomass of fungi in the same soils, and several studies (Finestone et al., 2022;

Schmidt et al., 2008; Singh et al., 2012) have shown that many fungal isolates from cold soils have high extracellular cellulase activity. "Snow mold" fungi are very common and active in snow-covered ecosystems throughout the world, including high-Arctic and Antarctic soils (Tojo and Newsham, 2012; Liptzin et al., 2015). It has been postulated that the filamentous growth form and rapid doubling time of these snow molds allow them to access plant litter on the soil surface during the snow-covered season. These traits give snow molds an advantage over bacteria since most bacteria depend on mobility through an aqueous phase to colonize organic matter (Schmidt et al., 2009).

2.1.3. Physiological changes and dormancy

As well as structural and functional changes, physiological changes can be expected among soil microbial communities across different seasons (Table 1). Many microorganisms are known to transition into a reversible state of dormancy when confronted with unfavorable conditions, subsisting in a state of comparatively lower metabolic activity until environmental conditions become more favorable – upon which they can resume a higher level of activity (Lennon and Jones, 2011). The metabolic activities of dormant vegetative microorganisms are largely limited to essential maintenance processes such as biomolecular repair and replacement, and the allocation of energy towards new biomass growth is minimal. Many bacteria and most fungi also produce spores that exhibit virtually no metabolic activity until they are activated in response to environmental stimuli. Many spore producers are opportunistic fungi that persist during stressful periods as spores and then grow rapidly during times when environmental conditions are favorable to them. For example, some rapidly growing psychrophilic snow-mold fungi such as those related to *Mortierella alpina* become active in the fall and winter and grow rapidly as secondary colonists of decaying organic matter in cold ecosystems including Arctic tundra, and produce both asexual spores and thick-walled meiospores (zygospores) that allow them to survive during the summer (Geml et al., 2021; Schmidt et al., 2008, 2009; Thormann et al., 2003). Dormancy therefore serves an ecologically important role throughout the year in polar environments – in particular, by enhancing the persistence of seasonal microbial communities and maintaining ecosystem diversity and functioning until the onset of conditions that are conducive to growth for seasonally active microbial populations.

2.2. Carbon fluxes

Carbon cycling in Arctic soils is a distinctly seasonal process that is strongly shaped by multiple varying and compounding environmental factors. Arctic soils are generally considered as a CO_2 source during the snow-covered winter season, and as a net-neutral to CO_2 sink during the summer due to higher photosynthesis and respiration (Fisher et al., 2014; Oechel et al., 1993; Ravn et al., 2020). For CH_4, Arctic soils are considered to be a net source on an annual basis with net emissions of CH_4 during the summer (Bruhwiler et al., 2021). However, recent studies have highlighted geographical differences in annual carbon budgets (see Lau et al., 2015), as well as across the transitional and winter seasons (Lüers et al., 2014; Waldrop et al., 2021; Zhang et al., 2019).

Alaska contains a range of different permafrost landforms, that are typically characterized by deep layers of carbon-rich soil. In recent years, as the depth of seasonal thawing deepens and the annual duration of the thawed period lengthens, this deep carbon is becoming more accessible to soil microorganisms and is increasingly vulnerable to degradation. Previous data synthesis efforts have reported the Alaskan tundra permafrost region as a carbon source to the atmosphere over the past 40 years (Belshe et al., 2013), while other synthesis and modelling studies have recognized the region as either a carbon sink or carbon neutral (Fisher et al., 2014; McGuire et al., 2012). Uncertainties in Alaskan soil carbon budgets largely arise due to the inherent difficulties in establishing long-term continuous measurements of soil carbon fluxes

Table 1
Characteristics and seasonal variations in physical and biological properties of Arctic tundra and upland soils.

Type of change	Property	Typical seasonal characteristics
Physical	Thermal properties	*Summer:* Soil temperatures generally above 0 °C throughout the soil active layer (until the upper-most limit of the permafrost layer). *Fall:* Zero-curtain phenomenon: soil temperature is de-coupled from air temperature and maintained at 0 °C due to latent heat. Upper-most layers freeze (<0 °C) earliest due to sub-zero air temperatures. The freezing front propagates downwards over time. *Winter:* The entire soil depth profile (i.e. the active layer and the permafrost layer) is predominantly frozen (<0 °C). *Spring:* Upper-most layers warm earlier than deeper layers. Zero-curtain phenomenon where soil temperature is de-coupled from air temperature and maintained at 0 °C due to latent heat (less pronounced than fall period).
	Water availability	*Summer*: Water available in liquid form (>0 °C). *Fall*: Liquid water begins to freeze. *Winter*: Majority of soil water is in frozen state, yet limited liquid water may persist in thin films, lenses or pockets. *Spring*: Frozen soil water begins to melt.
	Snow dynamics	*Summer:* Summers in the Arctic are generally snow-free. *Fall:* Thin temporary snow cover. *Winter:* Snowpack accumulates. Periodic melting and rain-on-snow events possible. *Spring:* Periods of accumulation and periods melting and rain-on-snow events. Snow may persist until early summer.
	Gas exchange	*Summer*: Active exchange of gases between soil and atmosphere, and within soil pores. *Fall*: Generally active gas exchange between soil and atmosphere, and within the soil. *Winter*: Snowpack and frozen soil restricts gas exchange. *Spring*: Bursts of gas exchange between soil and atmosphere as the snowpack melts and soil thaws.
Biological	Microbial community structure	Changes to microbial community structure (both bacterial and fungal) observed across seasons.
	Microbial community activity	*Summer:* Highest rates of activity. *Fall:* Microbial activity rates begin to reduce as microorganisms are limited by temperature and moisture availability. Many non-psychrophilic microbes may become dormant, whilst psychrophilic snow mold fungi may remain active. *Winter:* Limited data. Microbial activity restricted but may persist in limited capacity and area. Majority of microorganisms may be dormant. *Spring:* Microbial activity resumes as soil thaws and microbes transition out of dormancy.
	Microbial community function	Seasonal dynamics vary with site factors and do not seem to have a consistent pattern (see Section 3.2.3). Seasonally-driven changes to the soil hydrological regime affect redox state of the soil and likely drives changes in the dominance between aerobic SOC decomposition (producing CO_2) and anaerobic SOC decomposition (producing CH_4).

(*continued on next page*)

Table 1 (*continued*)

Type of change	Property	Typical seasonal characteristics
	Fungal to bacterial ratio	Higher fungal:bacterial (F:B) ratios during the winter and early spring hypothesized based on available information, potentially leading to shift in dominant functional characteristics and biochemical fluxes.
	Above-ground vegetation	*Summer:* Fixation of CO_2 by plants during periods of high primary productivity. Elevated plant respiration. *Shoulder seasons and winter*: Minimal to no primary productivity, basal plant respiration.
	Greenhouse gas production and exchange	CO_2 produced in aerobic soil layers and transported upward and downward via diffusion; CH_4 produced in (often water-saturated) anaerobic soil layers, transported upward and downward via diffusion and advection, and may be oxidized during transport through adjacent layers (particularly if those layers are oxygenated). Influence of above-ground vegetation on CO_2 fluxes as described above and vegetation-driven changes to soil hydrological regime.

over appropriate timescales and spatial scales. Indeed, carbon flux measurements from eddy covariance towers provide valuable year-round continuous measurements that can shed light on soil carbon budgets on a seasonal basis, but these fluxes might not always be synchronous with soil microbial respiration (especially during periods of snow-cover).

Data from continuously monitored heath and wet sedge tundra (2008–2015) and tussock tundra (2013–2014) in Alaska suggest that these sites were all net carbon sources on an annual basis, with considerable interannual variability. A substantial amount of carbon was released from the soil to the atmosphere during winter periods (Euskirchen et al., 2017), whilst during the growing season (June–August), these sites were a net carbon sink - with gross primary productivity (GPP) offsetting ecosystem respiration. During the observation periods, both the heath tundra and tussock tundra sites exhibited elevated carbon uptake associated with warming summer temperatures, suggesting that the regional growing-season carbon sink could be enhanced under a warming climate. Nevertheless, despite interannual and seasonal variability, carbon that had accumulated during the growing season was subsequently lost during the snow-covered cold season (from September to May) via soil respiration– indicating that soil microbes were still active during winter, and that active-layer carbon remains available for microbial degradation year-round. The observation of continuous microbial respiration in carbon-rich Arctic Alaskan soils over winter is further supported by CARVE aircraft data collected over Alaskan tundra from 2012 to 2014 (Commane et al., 2017), strengthening the case that Alaskan tundra soils were a net source of carbon to the atmosphere during winter. Both studies also highlighted the early winter (October to December) as a period of significant carbon release - emphasizing the importance of the zero-curtain period (the period during which soil active layer temperature stays near the freezing point of water due to latent heat transfer during the freezing or thawing process, despite substantially different temperatures of the adjacent air, Fig. 1) on the annual carbon balance. In both studies, peak daily net carbon emissions were found to occur in the transitional fall period (late September to early November) – coinciding with the period when plant GPP dropped dramatically while soil microorganisms remained active in the non-frozen soil. Both studies also showed that the net carbon balance turned from carbon loss (winter) to carbon accumulation (summer) around June, coinciding with the beginning of the snow-free period and the onset of plant primary productivity. The net carbon accumulation peaked in July to August, associated with rising GPP from greening vegetation during the growing season.

For Alaskan wetlands, enhanced summer methanogenesis may be counteracted by high summer CH_4 oxidation, especially in younger bogs where available carbon and nitrogen are comparatively rich. Observations showed that young Alaskan lowlands with collapse-scar bogs from permafrost thawing are a carbon sink in summer and a carbon source in winter, while older peatland plateaus act as a carbon source both in winter and summer (Waldrop et al., 2021).

Studies conducted in the permafrost-affected Siberian Arctic also provide valuable insight into the seasonal dynamics of high-latitude soil carbon fluxes. Continuous eddy covariance measurements on polygonal tundra and river terraces at the Samoylov research site in the Lena River delta, northeastern Siberia, indicate that despite a general accumulation of carbon during the period of measurement (2010 to 2017), the growing season carbon sink is largely offset by low but continuous cold-season soil respiration (Holl et al., 2019). Continuous year-round eddy covariance measurements at this site suggest that whilst 39% of the total annual methane released occurs during the cold season, recent increases in summer air temperature correspond to earlier and intensified summer methane emissions (Rößger et al., 2022). Another study has further suggested that the increased cold season respiration in response to warming might, in the future, outpace the increase in plant carbon uptake during the growing season (Runkle et al., 2013), transforming the Siberian tundra into a carbon source.

Similar patterns in the seasonality of soil carbon fluxes have been observed in west Greenland in recent years, where warming has stimulated both growing season carbon uptake and annual soil carbon loss. A five-year eddy covariance measurement (Zhang et al., 2019) showed that west Greenland heath tundra was a carbon sink of -35 ± 15 g C m^{-2} yr^{-1}, with rapid transitions in the carbon exchange during the beginning and the end of the growing season. The annual budget was strongly affected by the balance between the growing season carbon accumulation encouraged by warming and the carbon that is released from underneath snow-covered but non-frozen soil. In fact, it has been shown that elevated cold-season CO_2 emissions have reduced the regional carbon sink noticeably (Zhang et al., 2019). Net carbon release from west Greenland heath tundra was highest during the transitional spring-to-summer period, around mid to late June, before the rapid increase in plant GPP, though similar in magnitude to the carbon emitted during the transition from summer to fall. At this site, plant GPP continued to increase during the summer period and the net carbon sink peaked in late August before switching back to a carbon source as temperature and photosynthetically-active radiation decreased. During the five-year measurement period, warmer years (2015 and 2016) were associated with significant increases in both growing season GPP and non-growing season carbon emissions, and the total overall net carbon accumulation was lowest. Considering areas with moist tundra, ice-free west and northeast Greenland tundra were also observed to be a methane sink, consuming 1.4 to 18.3 times more CH_4 than the amount being emitted to the atmosphere from wetlands (D'Imperio et al., 2017; Juncher Jørgensen et al., 2015). These findings further underscore the importance of understanding how different components of the diverse Arctic permafrost ecosystems (upland and lowland tundra, river terraces, heath, wetlands, etc.) respond to the changing climate and together shape the regional seasonality and carbon balance.

Long-term and year-round carbon flux measurements are scarce for far north archipelagos such as Svalbard. In contrast to many other high-latitude permafrost regions, the Svalbard archipelago is semi-desert and the soil is not as carbon rich as many other high-latitude environments such as in North America and Siberia (Sipes et al., 2022; Schuur et al., 2015; Nakatsubo et al., 2005). Soil carbon cycling is mostly driven by local processes that result in highly heterogeneous soil ecosystems (Sipes et al., 2022). Nitrogen, labile carbon, and soil moisture limit microbial activity and plant productivity, especially in the forefield of retreating glaciers (Yoshitake et al., 2007; Nakatsubo et al., 2005; Bradley et al.,

2014), but potential for phosphorus limititation has not been adequately tested. During summer, tundra ecosystems across the Svalbard archipelago are usually observed to be weak carbon sinks (Magnani et al., 2022; Pirk et al., 2017). Soil microbial activity is thought to persist during winter periods as continuous carbon emissions have been captured for at least some part of the cold season (Lüers et al., 2014). A single year eddy covariance observation conducted at a permafrost site in north-west Spitsbergen found that the annual carbon budget was close to neutral from spring 2008 to spring 2009 (Lüers et al., 2014). Low-level but sustained winter carbon emissions were observed until late January, and net carbon fluxes varied positively and negatively between February and June. Carbon taken up during the growing season (June–September) by plants was almost entirely offset by respiration during fall and winter. Similar patterns were observed from January 2015 to January 2016 at the same site, despite the annual carbon balance strongly depending on CO_2 flux peaks of debated origin (Jentzsch et al., 2021). During the transition seasons the net carbon balance is generally dominated by emissions, but fall season soil respiration can be higher (Lüers et al., 2014) or lower (Cannone et al., 2016, 2019) during spring, depending on the site and year of measurement. This variability can be explained by the combined effect of active layer thaw depth and surface temperature that limited the emissions during the shoulder seasons (Cannone et al., 2019). Also, seasonal variations of the emissions potentially mirror changes in the structure of soil bacterial communities, as shown at an active-layer site (Schostag et al., 2015). On top of seasonal changes, the size and composition of the microbial community in Svalbard tundra soils has been observed to change after a four-year warming treatment during which 1 °C soil warming was induced, resulting in a 44% increase in summertime emissions (Newsham et al., 2022). Hence, microbial shifts induced by climate change effects may change the balance of natural carbon cycles, which further support the need for in-depth modelling of the complex microbial dynamics.

3. Soil biogeochemical modelling

In this section, we review current process-based soil biogeochemical model formulations and provide recommendations for future developments, specifically considering the need to capture seasonal processes in Arctic soil biogeochemical models. We focus on conventional process-based modelling approaches (reviewed by Chandel et al., 2023) – i.e. those that usually distinguish various components of the system (microbial biomass, organic carbon, etc.) in multiple distinct 'pools', linked by a system of coupled ordinary differential equations and parameter values that describe biological and other processes leading to transformations of and transfers between these pools. These equations are then numerically solved over a defined time-period to provide a time-series of model outputs including the size of various reservoirs/pools and the rates/magnitudes of fluxes between them. Alternative modelling approaches such as statistically/empirically based modelling, structural equation modelling, generalized linear mixed models, and individual-based modelling are not considered in this review (Schnecker et al., 2014; Bradley et al., 2016a; Hellweger and Bucci, 2009).

3.1. Soil organic carbon and biomass: Pools, transformations and fluxes

3.1.1. Soil Carbon Pools

In order to simulate the transformation of carbon and other elements from one form to another, it is necessary to distinguish different pools (chemical and biological fractions) of carbon within the model framework.

Most extant soil biogeochemical models, such as the CENTURY and ROTH-C models, characterize soil carbon decomposition by its mean residence time or turnover rate through different carbon pools (Parton et al., 1987; Jenkinson, 1990) and simulate microbial dynamics and microbially driven soil organic carbon decomposition implicitly using first order kinetics (i.e., carbon pool turnover rate; Todd-Brown et al., 2012) based on a linear relationship with the total soil carbon stock (Jenkinson et al., 1987; Parton et al., 1988). These models typically define soil organic carbon (SOC) in one or more carbon pools and use first-order linear decay rates modified by environmental factors to simulate the biogeochemical reactions between the pools and the fluxes to the atmosphere (Fig. 2A). These models therefore do not explicitly resolve the microbial dynamics that ultimately regulate and drive soil carbon cycling (Allison et al., 2010; Conant et al., 2011; Cotrufo et al., 2013; Schmidt et al., 2011; Six et al., 2006; Treseder et al., 2012).

In these first-order kinetics models, prescribed parameters are used to describe environmental sensitivities of SOC decomposition processes – such as using a fixed Q_{10} (temperature sensitivity) factor, where a Q_{10} value of 2.0 is used to prescribe a doubling of SOC decomposition with every 10 °C rise in soil temperature (Davidson and Janssens, 2006). Such prescribed environmental dependencies imply that the simulated biogeochemical processes are assumed to function optimally with available substrates and a fixed concentration of microbial enzymes (i.e. a non-growing biomass). However, in nature, soil physical and biological conditions are heterogeneous and change with time and between environments - leading to deviations from such prescribed relationships. Soil microbial respiration changes dynamically across seasons (Raz-Yaseef et al., 2017), and with climatic variables such as snow cover (Yi et al., 2020), making respiration poorly approximated by the steady loss rates often included in biogeochemical models to represent pools of soil microbial carbon (e.g., Li et al., 1992, 1994; Wang et al., 2010). Measurement techniques that accompanied the earlier versions of soil biogeochemical models provided valuable knowledge and validation data on total soil carbon stocks and soil carbon fluxes. The emergence of molecular tools including gene sequencing now enable more detailed information, including microbial biomass content, function, and enzymatic activity to be coupled with model simulations (Schneegurt et al., 2003; Frey et al., 2008; Bradley et al., 2016b; Guo et al., 2020).

3.1.2. Soil Microbial Community Dynamics

The next generation of soil biogeochemical models specifically address the simplification of first-order-decay models by explicitly introducing microbial carbon into the set of defined carbon pools (Fig. 2B). Microbially-explicit models define microbial biomass as one or more explicit pools whose dynamics (growth, death, dormancy etc.) may be sensitive to a continuum of biotic and abiotic factors. Some microbially-explicit soil biogeochemical models have been tested for applications at global scales, such as the MIcrobial-MIneral Carbon Stabilization (MIMICS) model (Wieder et al., 2015), the Carbon, Organisms, Rhizosphere, and Protection in the Soil Environment (CORPSE) model (Sulman et al., 2014), and CLM-Microbe model (He et al., 2021). These models have, in general, performed well when compared with contemporary observations. Yet, importantly, very few microbially-explicit soil models have been applied specifically to the Arctic region. A previous application of MIC-TEM in the Arctic (Zha and Zhuang, 2018) with and without an explicit microbial formulation, showed that simulations with an explicit description of microbial biomass predicted more carbon to be released from soils during the 21st century compared to those with a microbially-implicit description.

In 'microbially-explicit' model structures, the microbial biomass carbon pool constitutes a rate-limiting factor in the SOC decomposition process, and thus both biotic and abiotic factors together strongly influence the simulated soil respiration behavior (Sierra et al., 2011; Zha and Zhuang, 2018). However, even among models that include explicit representation of one or more microbial biomass pools, such as the DAYCENT (Wang et al., 2010), MOMOS (Pansu et al., 2004, 2010) and DNDC (Li et al., 1992, 1994) models, microbial biomass pools are often not used to drive decomposition reaction rates; rather, they are defined as simply another organic carbon pool (distinct from non-living organic carbon) with an independently prescribed loss rate. These models thus may lack important and climatologically-sensitive biogeochemical

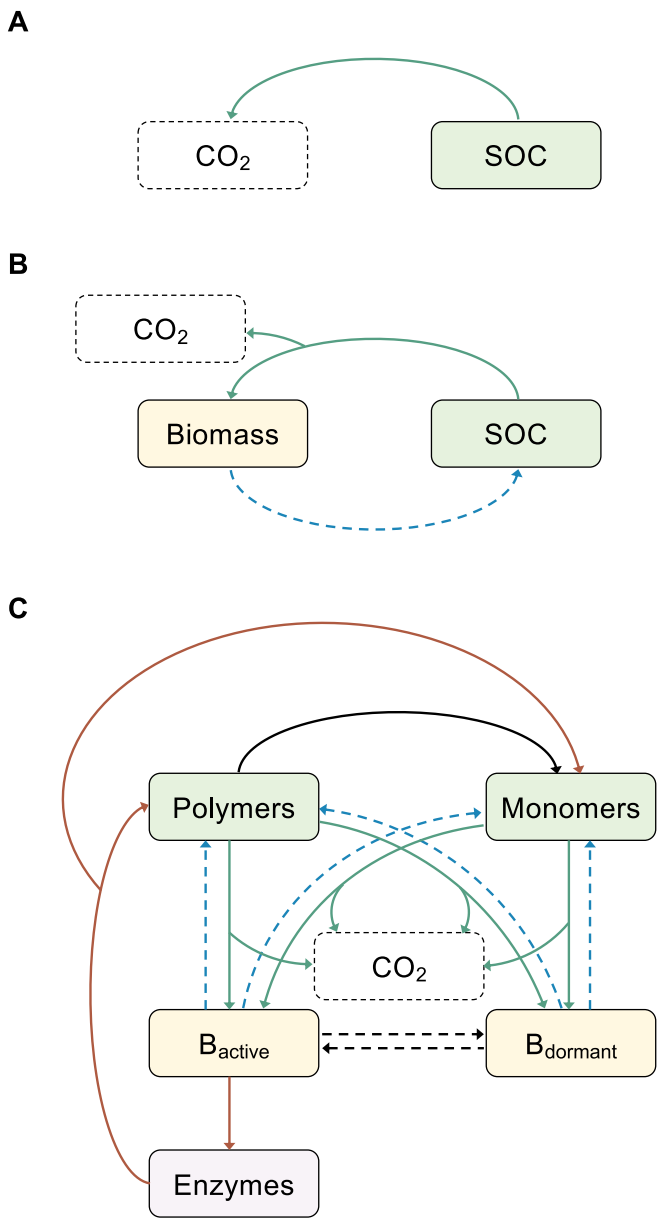

Fig. 2. Diagrams for the formulation of microbial soil carbon models. (A) A microbially-implicit soil organic carbon (SOC) degradation model; (B) A microbially-explicit model; (C) A microbially-explicit model where microbial biomass is represented in distinct pools for active and dormant biomass (B_{active} and $B_{dormant}$ respectively), SOC is divided into polymers and monomers, and enzyme production and consumption processes are explicitly resolved. State variables are represented by solid-border shapes and derived variables (i.e. CO_2 production) are represented by a dashed-border shapes. The consumption/degradation of organic carbon (to microbial biomass and CO_2) is represented by solid green arrows. The contribution of necromass (i.e. dead microbial biomass) to SOC is represented by dashed blue arrows. Enzyme production and consumption is represented by solid red arrows. The transformation of polymers into monomers is represented by the solid black arrow. The transfer of microbial biomass between active and dormant states (i.e. transition into and out of dormancy) is represented by dashed black arrows. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mechanisms that might be centrally involved in climate feedbacks.

Extant microbial soil models often define carbon pools along the reaction chain:

1. Input carbon pool(s). Input carbon represents the fresh substrate source for soil microbial decomposition from above-ground and surface environments, and usually consists of vegetation litter-fall and exudates. These inputs can be further divided depending on their reactivity (e.g. labile, refractory), and/or their molecular complexity (e.g. monomers, polymers) (Fig. 2C) (Allison, 2012; Tang and Riley, 2015; Wieder et al., 2015);
2. Microbial biomass pool(s). Some soil models include microbial biomass as a defined pool and thus it is explicitly resolved within the soil biogeochemical reaction framework. Here, the fraction of soil carbon comprised by microbial biomass is defined within one or more state variables (i.e. stores): simulated as one pool in some models (Allison et al., 2010), or in several discrete pools, for instance, divided according to function (Wieder et al., 2015; Bradley et al., 2015), and/or according to carbon assimilation strategy (e.g. structural microbial biomass and reserve microbial biomass pools) (Tang and Riley, 2015; Zha and Zhuang, 2018);
3. Extracellular enzyme pool(s). Extracellular enzymes play a vital role as catalyst in carbon decomposition process (Allison et al., 2010; Grant et al., 2001; He et al., 2014; Parton et al., 1987; Tang and Riley, 2015, 2019), can show distinct seasonal patterns in cold environments (Weintraub et al., 2007), and can be explicitly resolved in models of soil carbon in order to more accurately represent how soil carbon cycling and microbial-enzymatic decomposition is affected by environmental factors – including those that vary seasonally. Where enzymes are explicitly resolved within soil biogeochemical models, the abundance of enzymes depends on microbial biomass (a portion of microbial carbon uptake is allocated to enzyme production) and environmental conditions (Schimel and Weintraub, 2003); therefore enzyme-explicit models typically apply an empirical relationship between microbial biomass and enzyme production. Enzyme production rates are also constrained by physical factors to simulate litter decomposition at each time step (Allison et al., 2010; He et al., 2014; Tang and Riley, 2015).

Soil models compute the reactions between these carbon pools, including the depolymerization (i.e. degradation) of SOC, the uptake of substrates (i.e., microbial C assimilation), microbial growth and turnover, and the production and turnover of enzymes. Inputs and outputs are also computed, including litter carbon (polymeric compounds including cellulose, hemicellulose, lignin, monomers including intracellular material, easily-leached monomeric compounds and root exudates). Some soil biogeochemical models distinguish different molecular weights of input carbon, so that monomers are assimilated by microbes (part of which is respired, the rest goes into reserve microbial pool that supports maintenance, enzyme production, and microbial growth), and polymers are degraded by enzymes to lower molecular weight carbon (Tang and Riley, 2015, 2019). Other soil biogeochemical models distinguish input carbon by their chemical quality (e.g., metabolic versus structural litter inputs) (Wieder et al., 2015).

Carbon pools must be sufficiently represented in models so that model behavior can adequately capture both the steady-state and the dynamic nature of biogeochemical processes occurring in the natural environment. Thus, as factors such as carbon quality, microbial biomass, and enzyme activity change over seasonal cycles, the simulated soil carbon and microbial dynamics will be reliably captured.

3.2. Modelling microbial dynamics in Arctic soils and considerations for year-round simulations

Certain applications of microbially-explicit models to year-round studies of Arctic soils may require consideration of dynamic processes that are not currently resolved or poorly resolved in existing soil biogeochemical model frameworks. Current soil biogeochemical models, for example, are known to poorly constrain methane emissions, in particular during the shoulder and winter seasons (Treat et al., 2018).

As new data and understanding of the year-round processes occurring in Arctic soils emerges, as well as the recognition of previously unknown sensitivities to changes in climate, it is important to revisit soil biogeochemical modelling frameworks to assess where developments and improvements can be made.

3.2.1. *Microbial Growth, Maintenance, and turnover*

Soil microbial dynamics are intricate and complex; however, various fundamental biological processes are recognized by most existing microbially-explicit soil biogeochemical models, including microbial growth, maintenance (i.e., energy/substrate use for processes other than growth) and turnover (i.e. death/mortality). Conceptual and numerical representations for microbial growth and maintenance are, in general, built on two distinct steps: (1) substrate uptake and (2) substrate assimilation.

Microbially-explicit modelling approaches must first define rules to determine how and at what rates microorganisms take up and assimilate SOC. There are three general categories of mathematical expressions for uptake and assimilation of SOC in extant models: (1) Michaelis–Menten kinetics (MM, Michaelis and Menten, 1913), or Monod kinetics (Monod, 1949), (2) reverse Michaelis–Menten kinetics (r-MM, Schimel and Weintraub, 2003), and (3) a combination or generalization of the original and the reverse MM kinetics. Conceptual diagrams representing MM and r-MM kinetics are displayed in Fig. 3.

The original MM kinetics assumes that substrate (SOC) concentration exerts a limitation on substrate uptake, and thus on growth rate. The rate of substrate uptake is calculated according to:

$$v = \frac{V_{max} \cdot S}{K_S + S} \tag{1}$$

where v is the actual substrate uptake rate, V_{max} denotes the maximum substrate uptake rate, K_S represents the half saturation constant, and S is the substrate concentration.

The r-MM kinetics, alternatively, assumes that enzyme concentration exerts a limit on substrate uptake rate, and the rate of substrate uptake is calculated as:

$$v = \frac{V_{max} \cdot E}{K_E + E} \tag{2}$$

where E is the enzyme concentration, K_E represents the half saturation constant for enzyme concentration and V_{max} is the same of Eq. (1).

MM and r-MM kinetics have been applied to improve soil biogeochemical models with reasonable results (Allison et al., 2010; Drake et al., 2013; Schimel and Weintraub, 2003; Sulman et al., 2014; Wieder et al., 2015). However, it is important to note that in the natural environment, substrate and enzyme conditions can be highly heterogeneous across the various temporal and spatial scales of observation, measurement, and model application. Moreover, discrepancies still exist among and between model simulations, as well as between model simulations and observations.

Microbial growth efficiency (the ratio of growth to assimilation) and carbon use efficiency (CUE, the ratio between carbon retained by microbes in the microbial biomass pool and enzyme production, and the carbon taken up by the microbes) are often used to describe microbial assimilation of carbon substrate (Manzoni et al., 2012; Tang and Riley, 2015). These terms are essentially synonymous among many soil numerical models. As substrate transits through the soil and is captured by a microorganism, a fraction of the substrate that is assimilated is utilized to support the microbial maintenance requirement - usually calculated as proportional to the microbial biomass pool and scaled by microbial turnover and growth rates. Model simulations often assume that respiration loss is only due to carbon released during the assimilation process. More dynamic models consider respiration loss during the assimilation and maintenance processes (Grant et al., 2001; Petersen et al., 2005; Sitch et al., 2003; Tang and Riley, 2015). One commonly used approach

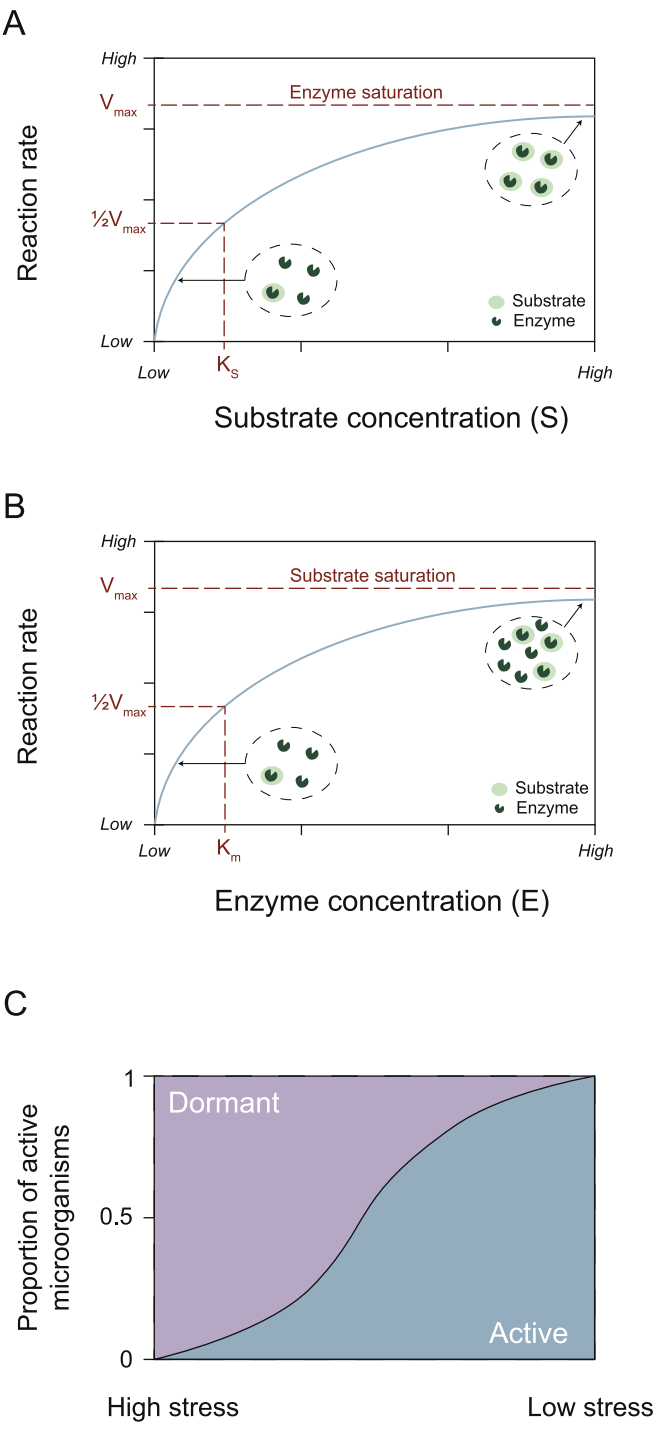

Fig. 3. Conceptual diagram of the mechanisms described for soil microbially explicit modelling. (A) MM-kinetics, (B) reverse MM-kinetics, and (C) dormancy switch.

considers maintenance as an additional consumption of substrate aside from the substrate that is consumed by microbial growth (Pirt, 1965), whereas another approach considers maintenance as a catabolic process (i.e. derived from respiration/consumption of cell biomass carbon stores) (Herbert, 1959). After maintenance activities, the residual substrate may then be partitioned into growth and enzyme production, computed as being proportional to their maximum potential rates (see Fig. 2).

Most microbially explicit models capture the entire microbial community within a single basic unit – the microbial carbon pool, while

some models further distinguish explicit pools for structural microbial biomass and reserve microbial biomass (Tang and Riley, 2015). Major advantages of the structural/reserve representation are that it allows for (i) an explicit representation of the allocation of carbon between maintenance and growth within simulated microbial communities, and (ii) a storage mechanism that becomes important in regulating microbial activity when carbon supply changes. This description of microbial biomass may be particularly influential to microbial growth and carbon fluxes considering seasonal changes in carbon availability in Arctic soils arising from biotic (e.g. litter input) and abiotic (e.g. freeze-thaw) changes. Many Arctic soil ecosystems, however, such as tundra, are not typically rich in soil litter carbon supplies from upper layers of vegetation (i.e. from mosses and short vascular plants), and thus a significant microbial reserve would not ordinarily be predicted in these systems (Elmendorf et al., 2012; Lloyd, 2001; Meentemeyer et al., 1982; Uchida et al., 2010; Villarreal et al., 2012).

Rates of microbial maintenance, growth, and turnover are expected to vary depending on seasonal changes in major environmental characteristics. Maintenance respiration is relatively commonly considered in microbially explicit models. It is usually prescribed in a linear relation to total active microbial biomass, but can also be empirically determined and/or scaled with environmental factors such as temperature and soil moisture (Moorhead and Sinsabaugh, 2006; Petersen et al., 2005; Schimel and Weintraub, 2003; Wang et al., 2014). Growth respiration is another commonly considered loss flux in many models and is generally presented as being proportional to the soil carbon decomposition flux (Moorhead and Sinsabaugh, 2006; Pansu et al., 2004; Tang and Riley, 2015). Similar to descriptions of maintenance cost, some models assume that this respiration flux is influenced by environmental factors (temperature, soil moisture, etc.) and scaled according to certain relationships with these variables (Tang and Riley, 2015). A turnover rate is usually prescribed to microbial pools in soil biogeochemical models to simulate microbial mortality. This mortality term is often dependent on microbial density or population size (Tang and Riley, 2015; Wieder et al., 2015). Microbial necromass (i.e. dead microbial biomass) will typically be cycled back into SOC pools – making this carbon available as substrates for decomposition. Microbial growth, maintenance and turnover are explicitly described in many soil biogeochemical models, and process rates are commonly linked to factors such as temperature, moisture availability, and light. Seasonal variation in these factors thus drives responses in the microbial community dynamics and resulting transformations of carbon pools (including organic carbon degradation and greenhouse gas production). Therefore, accurate representation of these processes and their dependencies on environmental variables (constrained, for example, by empirical measurements) will be critical in accurately simulating soil carbon cycling in Arctic soils on a seasonal basis.

3.2.2. Traits of soil microorganisms

The traits of soil microorganisms are typically described numerically by assigning various sets of parameters to each defined biomass pool (e.g. bacteria, fungi), and the values of these parameters can be adjusted to represent sensitivities to different environmental factors. Manzoni and Porporato (2007), for instance, demonstrated that bacteria and fungi respond differently to soil moisture availability: fungi are better suited to cope with water stress, while bacteria are more sensitive to changes in soil moisture. Other studies have shown that rates of methanogenesis are more sensitive to temperature ($Q_{10} \approx 4$) than methanotrophy ($Q_{10} \approx 2$) (Segers, 1998; Le Mer and Roger, 2001), although high-affinity methanotrophs in Arctic soils are strongly temperature sensitivite at temperatures lower than 5.6 °C ($Q_{10} \approx 8$) (Lau et al., 2015). In models, these behaviors can be shaped by specific algorithms and parameter values that are prescribed to groups of biomass (which are often represented by distinct state-variables/groups/pools). Given the distinct physiological and functional responses of different microbial groups to the various compounding and fluctuating environmental stresses (low temperatures, frequent freeze-thaw cycles, low or fluctuating water availability) experienced by Arctic soil microorganisms, representation of distinct microbial pools in soil models to simulate community composition might enable more accurate simulation of activity, resistance and function of Arctic soil microbes to seasonal and other environmental changes.

Similarly, a dual-microbial biomass pool structure – which would comprise of distinct groups of biomasses with different growth and adaption strategies – may be used to capture observed seasonal changes in Arctic soil respiration rates. Models can explicitly resolve microbial community composition by representing bacterial and fungal pools that respond differently to the changing environment. Such approaches have been applied to describe the priming effect in soil – whereby soil organic matter turnover changes due to substrate addition in the short term (Kuzyakov et al., 2000), effectively enabling the simulation of two microbial groups with different traits that compete for substrate with different growth strategies: r-strategists that grow quicker using more easily accessible substrates, and k-strategists that grow slower using resources more efficiently (Fontaine and Barot, 2005; Pianka, 1970). Ultimately, considering the high degrees of seasonal change in Arctic soils, models should capture variability in the traits of organisms to seasonal changes in environmental conditions, and in the biomass stock of organisms with different traits across seasons.

3.2.3. Functional groups

Some soil biogeochemical models distinguish distinct microbial functional groups. In such a 'functionally-explicit' model, microorganisms are classified into distinct biomass pools (represented numerically by separate state-variables) based on their metabolic function.

A common example among soil biogeochemical models is the distinction between CO_2 producing aerobic heterotrophs, and CH_4 generating anaerobes (i.e. methanogens). Methane dynamics are simulated in some soil biogeochemical models – in particular for wetlands (Cao et al., 1995; Christensen et al., 1996; Fan et al., 2013; Grant, 1998; Riley et al., 2011; Treat et al., 2018; Wania et al., 2010). Some numerical soil biogeochemical models treat CH_4 implicitly – where processes such as methane production are simulated as a portion of total heterotrophic respiration (Xu et al., 2016; Wania et al., 2010), or as a proportion of litter/SOC decomposition (Cao et al., 1995; Zhuang et al., 2004). Alternatively, some models treat methane dynamics explicitly, for example, in Segers' model (Segers and Kengen, 1998) and the 'ecosys' model (Grant, 1998), where CH_4 production is captured as anaerobic carbon mineralization of acetate (in saturated environments). Methane production in anaerobic soils is generally simulated as a function of an ecosystem-specific maximum potential production rate and limited by substrate availability, soil temperature, pH, and soil redox state (Xu et al., 2016). CH_4 produced in soil may be oxidized as it diffuses through the soil profile (Zhuang et al., 2004; Oh et al., 2020). This process can be captured in models using specific algorithms for aerobic methanotrophy which generally fall into two categories (both of which use dual Monod Michaelis-Menten-like equations): (1) CH_4 oxidation as a function of soil CH_4 concentration, temperature, and soil moisture (Tian et al., 2010; Xu and Tian, 2012; Zhu et al., 2014); and (2) CH_4 oxidation as a function of soil CH_4 and O_2 concentration, temperature, and soil moisture (Arah and Stephen, 1998; Riley et al., 2011). Models that explicitly simulate methane dynamics often show large discrepenses between model predictions and empirical data (Bohn et al., 2015; Melton et al., 2013; Treat et al., 2018).

It is well established that the hydrological regime of Arctic soils, including the prevalence of water-logged conditions in thawed soil layers, varies on a seasonal basis (Hodson et al., 2019; Joabsson and Christensen, 2001), with implications for soil redox status and domiant carbon degradation pathways including CO_2 and CH_4 production (see Section 3.3.3). A study in a seasonal lagoon in Svalbard showed that methane concentrations vary from over 10 mg/L in the transitional spring period to below 0.005 mg/L in summer (Hodson et al., 2019).

Another study in a seasonal wetland in Greenland showed that CO_2 and CH_4 fluxes change significantly during the summer thawed period (Joabsson and Christensen, 2001). For certain modelling applications, therefore, it is important that soil redox states (including transitions between oxic and anoxic conditions) and the corresponding dominance of microbial groups (e.g. aerobic versus anaerobic heterotrophs) and decomposition products (e.g. CO_2 versus CH_4) are captured by soil biogeochemical models - potentially necessitating the explicit consideration of different functional groups in soil biogeochemical models.

The majority of microbially explicit soil models do not explicitly simulate nutrient cycling (Allison et al., 2010; Tang and Riley, 2015; Wieder et al., 2015), although N and P cycling processes are included in some more recent model applications (Huang et al., 2021; Yu et al., 2020), and nutrient availability may be important to capture year-round considering the role of seasonal changes in nutrients (arising from litter inputs, precipitation and hydrological pathways, weathering, and other factors) on microbial activity and carbon cycling.

3.2.4. *Microbial Dormancy*

Dormancy – despite its ecological significance, is often overlooked in soil modelling studies (Lennon and Jones, 2011). Most microbially-explicit models assume a single pool representing total microbial biomass, and sensitivities to environmental conditions are prescribed by variations in the growth and mortality terms. Typical soil models therefore consider microbial cells to be either alive and active, or dead. However, as has been described in Section 2.1, a large fraction of the microorganisms in natural soils may be in a metabolically inactive state, and the proportion of active versus inactive (i.e. dormant) microorganisms is subject to change depending on environmental conditions. Thus, incorporating dormancy into microbial models may lead to more accurate and realistic simulations of microbial activity, respiration, and carbon and nutrient cycling – especially in settings where environmental harshness fluctuates, such as with seasonality in Arctic soils and other high latitude systems.

There are two general approaches for capturing the different physiological states of microbial biomass in numerical models.

The first approach is to regard the 'fraction of active biomass' (i.e. the ratio of active biomass to total living biomass, Fig. 2C) as a state variable (e.g., Panikov, 1995; Blagodatsky and Richter, 1998; Ingwersen et al., 2008). The value of this state variable can be influenced by environmental conditions – enabling a dynamic response of the active/dorman fraction of microbial biomass to factors such as substrate limitation and temperature.

The second approach is to separate the total live biomass into two (or more) explicit pools, considering active biomass and dormant biomass as distinct state variables (e.g. Bär et al., 2002; He et al., 2015; Stolpovsky et al., 2011). Like the first approach, this second approach also enables microbial biomass to respond dynamically to changes in the environment, but it requires more parameters to describe it. He et al. (2015) explicitly simulated active and dormant microbial biomass pools, calculating the transition between the two states by introducing a parameter representing substrate availability to microbes, which is controlled by substrate diffusivity and soil moisture content. A general formulation of the second approach, i.e. the explicit representation of active and dormant microbial pools, is:

$$\frac{dB_A}{dt} = F_D - R_G - R_M + R_{DA} - R_{AD} - M_A \quad (3)$$

$$\frac{dB_D}{dt} = R_{AD} - R_{DA} - M_D \quad (4)$$

where B_A and B_D represent active and dormant microbial biomass, respectively, F_D is monomer uptake, R_G and R_M are growth and maintenance rates, M_A and M_D represent cell mortality, and R_{AD} and R_{DA} represent the transitions between active and dormant microbial pools. Here, only the active microbes take up monomers from litter inputs and allocate carbon for growth, maintenance, and enzyme production. Dormant microorganisms take up and also allocate carbon towards maintenance activities. Studies suggest that the maintenance coefficient of dormant microbes can be two to three orders of magnitude lower than that of the active fraction (Anderson and Domsch, 1985a, 1985b). In most models that explicitly resolve active and dormant microbial biomass, both biomass pools (active and dormant), as well as enzymes (if they are explicitly resolved), decay due to mortality and natural breakdown processes, returning carbon to monomer and polymer pools (Fig. 2). In the "explicit pools" approach, rates for the reversible processes of activation and deactivation can be prescribed (Locey, 2010; Ayati, 2012), or calculated based on sensitivity to environmental factors - a phenomenon known as 'responsive' switching (Lennon and Jones, 2011; Bär et al., 2002). The model of Manzoni et al. (2014) prescribed a dormancy-dependance based on osmoregulation – suggesting that increases in osmolyte concentration (that are described numerically by a water potential parameter) trigger a transition to dormancy (Manzoni et al., 2014). As well as 'responsive switching', microorganisms may also transition into and out of dormancy by 'spontaneous' switching, even under stable environments (Kussell and Leibler, 2005; Lennon and Jones, 2011; Piggot and Hilbert, 2004).

For model applications to high latitude Arctic soils, the 'responsive' dormancy strategy might be most suitable to realistically capture the variability in microbial activity and associated biogeochemical processes on a seasonal basis – considering the fluctuating environmental conditions (i.e. moisture, temperature, light, substrate inputs) encountered by soil microorganisms across seasonal (as well as shorter and longer) timescales. The freezing of soils not only produces 'harsh' or stressful conditions to soil microorganisms, but also limits the physical transport of substrate (and thus energy sources to microorganisms) into the soil. Seasonal patterns in microbial state-switching may be critical in shaping year-round soil carbon decomposition processes and thus the overall carbon budget of the Arctic. Resolving the effects of environmental factors (such as temperature and soil moisture) on triggering the transitions of soil microorganisms between active and dormant states, as well as imposing physical limitations to substrate transport, likely will lead to improvements in the general understanding and simulation of year-round microbial processes in Arctic soils.

3.2.5. *Extracellular enzymes*

Enzyme production is explicitly calculated in some microbially-explicit models as being proportional to the size of the microbial biomass pool. Enzyme production rates can be prescribed as a function of the magnitude of the total or active microbial biomass pools. Enzyme loss rates can similarly be prescribed as a turnover rate (He et al., 2015; Zha and Zhuang, 2018). Enzyme-catalyzed SOC decomposition can be viewed from the perspective of Langmuir adsorption, and reaction rates can be described as a maximum reaction rate scaled by temperature dependence, such as an Arrhenius equation (Davidson et al., 2012). This approach results in enzyme-catalyzed SOC decomposition rates that are more sensitive to environmental factors than the fixed Q_{10}-equation approach used by models assuming first-order kinetics. Prescribing sensitivities of enzyme production and loss to seasonally-variable environmental factors will be important to accurately capture year-round dynamics in enzyme-explicit models.

3.3. *Incorporating physical properties and processes into soil biogeochemical models*

The dynamics of the active layer and therefore, the activity of soil microorganisms and associated carbon transformations in permafrost are strongly shaped by soil physical properties, and influenced by snowpack and vegetation dynamics, which, in Arctic systems in particular, vary considerably on a seasonal basis (Rasmussen et al., 2018; Wei et al., 2021; Jin et al., 2022; Keuschnig et al., 2022). Here, we describe some of the most important physical characteristics that can be

incorporated into soil biogeochemical models to enable year-round simulations of microbial and biogeochemical processes in the Arctic. The long-term goal is to use continuous soil- and geophysical observations as input data to inform more realistic soil biogeochemical modelling.

3.3.1. Soil temperature distribution and effects on microbial activity

Thermal conductivity in permafrost determines the speed of heat transfer through the soil, and thus, governs temperature distribution with depth and the rate of thawing. For numerical models to capture the thermal conductivity of frozen soils, they need to account for:

(i) Soil porosity, bulk density and compaction. Soils with higher porosity tend to have lower thermal conductivity because the pores act as insulating voids, hindering heat flow. Hence, soil compaction with depth generally leads to increased thermal conductivity (Angelopoulos et al., 2020).
(ii) Particle size and distribution (i.e. soil texture), and mineral composition: coarse-grained soils, such as sand and gravel, generally have higher thermal conductivity due to better heat conduction between larger particles compared to fine-grained soils. Additionally, different minerals have different thermal conductivities and heat capacities. For example, soils with high quartz content generally have higher thermal conductivity than those with higher clay content (Ye et al., 2022).
(iii) Gas and liquid content: dry or water un-saturated soils have lower thermal conductivity than water-saturated ones because of the higher thermal conductivity of water compare to air (Dong et al., 2015).
(iv) Salinity: pure water has relatively low thermal conductivity compared to saltwater.
(v) Ice and organic matter content: increasing ice and organic matter content within the soil structure have opposite effects on its thermal conductivity. While ice content increases the thermal conductivity of the composite soil (Chuvilin et al., 2021), organic matter acts as an insulating material (Bruin et al., 2023). This thermal coupling is thought to be critical for projecting future permafrost dynamics, since the response of soil temperature to rising air temperature would be significantly impacted by changes in organic matter content related to microbial activity (Zhu et al., 2019).

Soil temperature has long been recognized to exert a significant control on microbial activity and carbon cycling – including affecting microbial enzyme activity, organic matter decomposition rates, growth rates, maintenance costs, and in fact, most biogeochemical reactions in soil ecosystems (Burns et al., 2013; Davidson and Janssens, 2006; Mu et al., 2016). Considering the limitation that temperature imposes on Arctic soil microbial activities, including the impact of freeze-thaw processes and substrate transport, a realistic representation of temperature sensitivity is especially important for achieving robust and accurate estimates of seasonal carbon dynamics in Arctic soils.

One of the simplest formulations used to explain the temperature dependence of biochemical reactions in numerical modelling is a linear relationship with parameters extracted from linear regression on temperatures, as used in DAYCENT and LPJ models (Del Grosso et al., 2002; Wania, 2007). Another earlier formulation used is the Q_{10} temperature coefficient. This method applies an empirical coefficient to prescribe an exponential relationship between reaction rates and temperature. Q_{10} values typically vary between 1.3 and 3.3 – effectively prescribing an increase in reaction rates by a factor of 1.3 to 3.3 per 10 °C rise in temperature (Bekku et al., 2003; Raich and Schlesinger, 1992). A later commonly used metric describing the sensitivity of microbial and enzyme activity to temperature is the Arrhenius equation. Whilst the Q_{10} method is based on a single parameter that prescribes the slope between rates and temperature, the Arrhenius equation requires both an activation energy and an exponential factor (Arrhenius, 1889). Both temperature sensitivity metrics are, in effect, first derivatives of the temperature (Singh and Gupta, 1977), and assume that the activation energy needed for biochemical reactions is constant within a given temperature range (Allison et al., 2018). In fact, in the Michaelis-Menten formulation of decomposition, temperature sensitivity is already established in rate constants: V_{max} depends on temperature following the Arrhenius equation, and K_S, K_E depend on temperature following a linear relationship (Todd-Brown et al., 2012). This assumption has been questioned by recent studies providing evidence that enzymatic heat capacity might change with temperature (Hobbs et al., 2013). New theories such as macromolecular rate theory (MMRT) have been proposed to explain the varying activation energy with temperature (Alster et al., 2016; Hobbs et al., 2013). Nevertheless, it has been suggested that when temperatures are close to zero, both Arrhenius theory and MMRT yield very similar Q_{10} values (Allison et al., 2018). Therefore, it may be more important to consider applying the more complex MMRT to ecosystems with higher and more variable temperature ranges. These theories can be formulated mathematically as:

$$\text{Linear}: r = r_0 \cdot (aT + b) \tag{5}$$

$$Q_{10}: r = r_0 \cdot Q_{10}^{(T-T_0)/10} \tag{6}$$

$$\text{Arrhenius}: r = Ae^{-E_a/R \cdot T} \tag{7}$$

$$\text{MMRT}: ln(r) = ln\left(\frac{k_B \cdot T}{h}\right) - \frac{\Delta H_{T_0} + \Delta C_p(T - T_0)}{R \cdot T} + \frac{\Delta S_{T_0} + \Delta C_p(lnT - lnT_0)}{R} \tag{8}$$

where r is the reaction rate, T denotes the temperature, T_0 is the reference temperature, E_a represents the activation energy, k_B is Boltzmann's constant, h is Planck's constant, R is the universal gas constant, H denotes enthalpy, and S stands for entropy.

3.3.2. Hydraulic conductivity and soil moisture effects on microbial activity

Hydraulic conductivity in permafrost refers to how easily fluids (i.e., liquid and gas/air) can flow through the porous media and existing fractures, thus, governing water infiltration, soil moisture content, and gas diffusion and transport (Huang et al., 2016; Heinze, 2021; Jiang et al., 2021). To capture the hydraulic conductivity of frozen soils it is important that models account for soil properties, such as pore connectivity, bulk density, organic matter content, and soil texture, which exert first-order controls on the soil's ability to store and transport fluids (Huang et al., 2016). For certain applications, models may track variations in ice content through time, as well as the consequent geomechanical response of the soil. For instance, the presence of ice can partially or entirely fill the soil's pore spaces, significantly reducing its connectivity and restricting fluid flow and infiltration (Larsbo et al., 2019). In contrast, thawing increases the soil's hydraulic conductivity by removing ice from pores (e.g., Watanabe and Kugisaki, 2017; Jiang et al., 2021). Yet, such an effect can be masked by soil volumetric consolidation or collapse that is expected upon thawing (De La Fuente et al., 2020; Shastri et al., 2021). Moreover, models that account for the occurrence of fractures (induced either by pore-overpressure or freeze–thaw cycles and that might act as preferential permeable paths), the formation of taliks (which generally act as preferential flow paths for water), or the effects of vegeation on soil structure (the root systems of plants can create channels and pores in the soil, which can either enhance or reduce hydraulic conductivity, depending on the type of vegetation and the depth and density of the roots) and exposure to rain (plants may act as a natural mulch, reducing erosion and increasing water infiltration) are more suitable to capture preferential pathways for fluid flow, which can dramatically increase the hydraulic conductivity of the system (Watanabe and Kugisaki, 2017; Jin et al., 2022).

Soil moisture is also known to exert a significant control on microbial activity, respiration and carbon assimilation. This is firstly due to the intrinsic nature by which soil microbes and enzymes require moisture and therefore are affected by moisture stress, and secondly, the consideration that physical transport of substrates through the soil medium, for instance active and passive movement of chemical species through pores in the soil column, affects substrate availability by limiting supply via active transport (Harris, 1981; Manzoni et al., 2014).

Most numerical models that explicitly consider soil moisture prescribe a non-linear relationship between microbial activity and moisture availability. A widely used algorithm uses water potential, which can be calculated from volumetric water content, to prescribe the empirical relationship $A(\psi)$ (Andren and Paustian, 1987; Rodrigo et al., 1997):

$$A(\psi) = \frac{log(-\psi) - log(-\psi_{min})}{log(-\psi_{opt}) - log(-\psi_{min})} \quad (9)$$

where ψ is water potential, ψ_{opt} is the water potential that yields the optimal decomposition rate and ψ_{min} represents the water potential at which microbial activities cease. A similar equation can be written as (Manzoni et al., 2012):

$$A(\psi) = 1 - \left(\frac{log(\psi/\psi_{fc})}{log(\psi_{th}/\psi_{fc})}\right)^{\alpha} \quad (10)$$

where α represents a shape parameter, ψ_{th} denotes a water stress threshold and ψ_{fc} is a reference water potential corresponds to the soil field capacity. The equation allows respiration to decrease gradually as water potential becomes increasingly negative, and empirical values of $\psi_{th}$and α determine the sensitivity of microbial activity to changes in soil moisture.

Some models use water content instead of water potential to describe the relationship between microbial activities and soil moisture, as shown below (Myers et al., 1982; Rodrigo et al., 1997):

$$g(\theta) = m\frac{(\theta - \theta_{ref})}{(\theta_{opt} - \theta_{ref})} + c \quad (11)$$

where θ is volumetric water content, $g(\theta)$ describes microbial sensitivity in response to soil moisture, θ_{opt} is the optimal water content for microbial activities, θ_{ref} is a reference parameter, and m and c are empirical coefficients.

Few soil models also account for the effect of water limitation on substrate diffusion and binding. However, those that do generally prescribe an effective affinity parameter to match Michaelis-Menten-type substrate uptake by microbes (Tang and Riley, 2019):

$$K_{s,w} = K_{s,w,0}\left(\frac{\nu_m \cdot \delta}{4 \cdot \pi \cdot D_{s,w,0} \cdot r_m (r_m + \delta)} + \frac{\nu_m}{4 \cdot \pi \cdot D_s (r_m + \delta)}\right) k_{s,w,1} \frac{N_{cell}}{N_A \cdot \nu_m} \quad (12)$$

where $K_{s,w,0}$ is the reference substrate affinity parameter, $k_{s,w,1}$ denotes the unicellular substrate interception coefficient, δ represents the thickness of the water film formed over the microsite of a cluster of particles, microbes and substrates, ν_m is the mean microsite volume size, N_{cell} is the number of cells per microsite, r_m represents the microbial cell size, D_s is bulk diffusivity for substrate, $D_{s,w,0}$is aqueous diffusivity for substrate and N_A is Avogadro's number.

3.3.3. Freeze-thaw dynamics

Determining the freezing point in soils is vital to comprehend permafrost dynamics (freeze–thaw behavior) and quantify ice and unfrozen water content within the porous media (Thomas et al., 2009; Yokohata et al., 2020). Experimental tests and field observations have evidenced the effects of pore capillary pressure in narrow pores on inhibiting ice formation (De La Fuente et al., 2021). Water in frozen soils is proven to remain unfrozen at temperatures well below 0 °C due to such capillary forces, which lower the activity of the water, and, consequently, its freezing point (Zhou et al., 2018). This is important not only because of the impact of the pore-filling species on soil's thermal and hydraulic properties, but because in permafrost, access to nutrients and the ability to eliminate waste materials are limited by the thickness of the unfrozen water films (Rivkina et al., 2000). Thus, models should not assume that soils are fully frozen below 0 °C. Instead, they should account for the dependency of the water freezing point on the soil's pore size distribution and solute content of the liquid phase (Kozlowski, 2009).

The freeze-thaw dynamics of permafrost are also pivotal in determining the thickness of both saturated and unsaturated sediment layers, thereby influencing the penetration of oxygen vertically within the soil. This dynamic control establishes a depth-equilibrium between aerobic and anaerobic oxidation processes, shaping the redox conditions and biogeochemical processes occurring within the soil (Patrick et al., 1996; Fiedler et al., 2007; Vepraskas and Faulkner, 2001). The resultant redox conditions directly impact soil carbon storage by influencing the rates and pathways of organic matter decomposition. Additionally, soil redox conditions exert an indirect effect on organic matter remineralization by affecting the bioavailability of organic molecules and nutrients in the soil (Herndon et al., 2020).

3.3.4. Snowpack dynamics

Observations indicate that the timing of snow onset and changes in snowpack depth may result in prolonged periods of unfrozen soil despite soil temperatures close to or slightly below 0 °C – thus maintaining an active un-frozen layer in which microbial activity can continue (Box et al., 2019; Outcalt et al., 1990; Zona et al., 2016). Snow has a dual effect on the soil beneath it: a short period of cooling during early onset of snow accumulation, and a long period of warming as the snow provides insulation from dropping air temperatures. The insulating properties of the snowpack may bring about different effects on soil thermal and carbon dynamics in the short-term (depending on temperature and corresponding snowpack depth), but on a longer annual basis, the warming effect due to snowpack insulation is dominant (Zhang, 2005).

Snowpacks also act as a buffer between the air and the soil - altering the soil thermal conditions and contributing to attenuated soil temperature variation as compared with near-surface air temperature (Lawrence and Slater, 2010; Osterkamp, 2007; Stieglitz et al., 2003; Rixen et al., 2022). Lawrence and Slater (2010) estimated that during the latter half of the last century, >50% of the alteration to Arctic soil temperatures may be attributed to impacts from snow variability. Multiple characteristics of the snowpack affect insulation effects and therefore soil microbial activities, including: the timing and duration of snowfall, the density, thickness, and structure of the snowpack, as well as local topography and wind conditions (Zhang, 2005; Rixen et al., 2022). In the Terrestrial Ecosystem Model (TEM), snowpack thickness is changing over the simulation time and is estimated from snow water equivalent data and empirical snow density. The thermal heat flux within snow and soil layers were calculated and iterated until the heat flux from the snowpack side balances that from the ground side (Lyu and Zhuang, 2018). This insulation effect resulted in 6.4 $^{\circ}C$ warmer soil (top 5 cm) during the non-growing season in the Arctic, and a slower transition of freeze-thaw in early spring and later fall, as compared to the model where insulation is not simulated.

Although the effect of the snowpack as an insulator to soils is considered in many land-surface models, the dynamic development of the snowpack over the cold season is often neglected (Bormann et al., 2013; Chadburn et al., 2017; De Michele et al., 2013; Ekici et al., 2015; Lyu and Zhuang, 2018). Even studies focused on the improvement of snow and soil thermal dynamics schemes seldom assess the effect of snowpack dynamics on heterotrophic respiration or microbial activity (e.g., Chadburn et al., 2015). The accumulation and densification of a snowpack alters its thermal conductivity, and together with environmental factors such as wind, could be an important control on soil microbial activity and associated biogeochemical cycles. Incorporating the

effect of a dynamic snowpack in Arctic microbially-explicit models thus may enable improved simulations of seasonal patterns of microbial activity and carbon emissions in high latitude soils – particular during the early winter and spring thawing, when the typical burst emissions are observed.

3.3.5. Latent heat and zero-curtain phenomena

The zero-curtain effect refers to the phenomenon of soils maintaining temperatures near $0^{\circ}C$ over extended periods of freezing or thawing due to the release and uptake of latent heat by water. This phenomenon can be observed in the active layer of permafrost soils during transition seasons (Fig. 1). During the fall transitional to winter, when soil liquid water is about to freeze, latent heat released during the freezing process may offset heat loss by conduction towards the surface layer and keep the subsurface temperature around 0 °C for some extended period of time. Latent heat also plays an important role during the spring snowmelt period, when energy from solar radiation and rising ambient temperatures is absorbed by the snowpack. Early snowmelt may keep the soil surface temperature lower than the air temperature due to latent heat energy lost from the soil to snowmelt. As the snowmelt continues and snowpack temperature stays around the 0 °C isotherm, refreezing of the meltwater (from snowmelt) releases latent heat that subsequently warms the snowpack and the soil (Zhang, 2005). The overall effect of this process on soil temperature and microbial activity is complex and still requires further investigation.

During the zero-curtain period, water contained within freezing soils may be forced to the top and bottom of the freezing fronts forming segregated ice (Fu et al., 2022), meanwhile leaving air pockets in the active layer (Arndt et al., 2020). During this period, CO_2 production may remain relatively high and can account for a substantial portion of the annual carbon balance: fall time net carbon balance can be 15.9 ± 0.7g C m^{-2}, contributing about 42% of the total annual non-summer net carbon emission (Commane et al., 2017; Oechel et al., 2014). Throughout the zero-curtain period, microbial activity may continue in unfrozen soils whilst the diffusion and advection of the produced CO_2 may be obstructed by the freezing fronts and overlying snowpack, which act as barriers. This can result in periodic bursts of carbon released as CO_2 after the spring thaw eliminates these barriers (Elberling and Brandt, 2003; Koponen and Martikainen, 2004). Importantly, zero-curtain phenomena (1) allow microbes to remain active in soils during winter, (2) change the diffusion, advection and microbial status in response to seasonal transitions, and (3) may de-couple the timing of CO_2 that is produced in soils from CO_2 fluxes measured above ground.

In order to simulate the zero-curtain phenomena observed in the Arctic, accurate representation of soil physical parameters, especially temperature, moisture, and latent heat, is likely to be necessary. Currently, many land surface models tend to underestimate soil temperature during the freezing period due to possible inadequate estimation of the effect of snow cover insulation and latent heat, which subsequently introduces freezing of soil water and inhibition of microbial activity and respiration in the model simulations that are not representative of the natural system (which may remain at least partially thawed) (Dankers et al., 2011; Nicolsky et al., 2017; Yang et al., 2018). Accurate representation of the zero-curtain phenomenon is therefore critical for improving simulations of seasonal changes in Arctic soil carbon cycling – especially since inaccurate estimates of soil temperature and freeze-thaw processes may lead to an underestimation of seasonal CO_2 emissions and inaccuracies in the overall carbon balance. A phase-change scheme incorporating latent heat could help improve the simulation of freeze-thaw processes in the cold season and year-round.

3.3.6. Multiphase transport

The permafrost is a dynamic multiphasic environment, encompassing both solid (i.e., soil, organic matter, and ice) and mobile fluid phases (i.e., gas and liquid). As indicated in previous sections, tracking the evolution of liquid-gas content within the active layer may be crucial for certain model applications. Firstly, gas within pores serves as an insulator that contributes to the long-term preservation of ice for instance warming such as during spring/summer transitions (see section 3.3.1). Secondly, its occurrence in pores is linked to the soil water content, thus influencing microbial activity, and potentially triggering sediment fractures (see section 3.3.2) Thirdly, gas content and soil permeability (which can be affected seasonally by freezing and thawing cycles) affects gas exchange between soil and atmosphere, thus, having important implications on carbon cycling (Lange et al., 2016).

Models that incorporate multiphase transport may be particularly suitable for assessing the fate of microbially-produced CO_2 and CH_4 and, thus their ultimate impact on carbon cycling and climate (De La Fuente et al., 2022). Multiphase transport models are also capable to account for additional sources of gases to the system, which may include injection via filtration along faults from depth (Khimenkov and Stanilovskaya, 2022) or due to destabilization of permafrost-associated hydrates (Ruppel and Kessler, 2017).

3.4. Model implementation

The application of soil biogeochemical models to the simulation of year-round dynamics of Arctic soils will require certain implementation considerations, including the spatial and temporal dimensions to be covered, the resolution to be achieved, and the types and characteristics of data that are used to initialize and validate model simulations. Here, we briefly discuss implementation issues to consider specifically for year-round applications of soil biogeochemical models.

3.4.1. Temporal resolution and time step

The temporal resolution of model output can generally be adjusted depending on the timescale of the particular processes of interest – down to a minimum time step that is commensurate with the numerical implementation of the mathematical solver used to execute the model. Most existing soil biogeochemical models are run at hourly or daily time steps, and provide output of simulated fluxes at hourly, daily or monthly intervals (Allison et al., 2010; Tang and Riley, 2015; Sulman et al., 2014; Wieder et al., 2015; Zhuang et al., 2001).

A timescale of hours or days is likely suitable to allow model simulations to capture responses to diurnal and seasonal changes, including during the zero-curtain period, when soil conditions transition between frozen and thawed states in a matter of days (Belokopytova et al., 2021; Boike et al., 2018; Hinkel et al., 2001). Data collected at the Bayelva permafrost monitoring site in western Svalbard indicates that variability in surface soil temperature largely correspond to air temperature. At this site, temperature variation in near-surface soils is relatively minor during the summer (constant light) and winter (constant dark) periods, but hourly variability and diurnal cycles are pronounced during transitional seasons (Boike et al., 2018), where the temperature of uppermost soil layers can fluctuate above and below freezing during day and night respectively (Boike et al., 2018). Thus, models with hourly temporal resolution may capture the rapid freezing and thawing and accordingly trigger microbial growth, turnover and dormancy responses. Coarser time-steps (such has with daily or monthly averages) would not capture fluctuations in environmental conditions (such as freeze-thaw) occurring on shorter timescales, and therefore responses in the microbial activity and associated carbon transformations may be innaccurate. Thus, an hourly temporal resolution may suit the model equilibrium assumption whilst also allowing for the model to capture short and longer-term variability in the carbon flux observed at various monitoring sites. Daily time intervals, whilst not fully capturing diurnal oscillations in temperature or associated soil carbon fluxes (in particular during transition seasons) may nevertheless be suitable to capture major seasonal patterns.

The temporal resolution of available forcing data in the study area is also an important factor to consider. When finer-resolution temporal forcing data are not available, it is common practice to interpolate

coarser-resolution data as forcing data to drive a model. For example, linear interpolation methods were used to transform the monthly CRU climate dataset into daily intervals to study the carbon dynamics of Alaska wetlands (Lyu et al., 2018). The Arctic region generally lacks year-round field observations, in particular due to logistical and practical difficulties in making continuous measurements during the snow-covered/winter period. Interpolated meteorological data may be the only available data for the cold season, and importantly, interpolations may not capture rapid responses to abrupt environmental changes. Year-round meteorological data (with hourly to daily resolution) are now increasingly available at high-latitude sites (Belokopytova et al., 2021; Boike et al., 2018, 2019; Hartl et al., 2020), providing suitable forcing data to models. This improved forcing data, combined with suitably fine temporal resolution in models, will likely bring about improvements to modelling seasonal changes in carbon and microbial activity.

As a word of caution, it is important to note that imposing a higher temporal resolution in modelling incurs a higher computational cost, and thus the trade-offs between model resolution and computational cost must also be considered.

3.4.2. Spatial dimensions: Vertical

Many soil-biogeochemical models are 0-D (i.e. not spatially resolved), with a box-model structure that does not discern any vertical structure or differences (Koven et al., 2013). Some simplified and earlier soil biogeochemical models consider only the top organic layer as a single fixed SOC profile and assume that the deeper mineral layer does not significantly impact biogeochemical reactions (Baudena et al., 2007; Brandes and Den Hollander, 1996; Klepper and den Hollander, 1999). Beyond single layer box models, discrete layers of soil may be represented in multi-layer box models, where each vertically-stacked box contains prescribed initial conditions and the reactions unfold without any vertical exchange of carbon (Kuc, 2005). Vertical heterogeneity in soil characteristics and resulting carbon cycling is considered in the Community Land Model (CLM, Koven et al., 2013; Lawrence et al., 2011) and RothC model (Coleman and Jenkinson, 1996; Jenkinson and Coleman, 2008), capturing vertical advection and diffusion to at least 3 m depth (Koven et al., 2013; Tang and Riley, 2015). Currently, vertical SOC distribution is generally defined according to the root distribution, and trade-offs between the vertical allocation and root nutrient uptake are not considered (Fisher et al., 2012; Koven et al., 2013).

The vertical characteristics of Arctic soils are physically, chemically and biologically heterogeneous, both at discrete timepoints and also considering seasonal and long-term change. For example, deeper layers of some permafrost soils may contain vast quantities of SOC which are largely buffered from seasonal temperature changes, but may become more dynamic and play an active role in soil biogeochemical cycling under future climate warming as permafrost thaw depth increases (Koarashi et al., 2012; Tarnocai et al., 2009). Past vertically resolved applications of microbially-implicit soil models to the Arctic have assessed how changes in simulated soil temperature affected the active-layer depth, and have predicted variations in overall soil carbon stores and fluxes as a result of built-in SOC-temperature sensitivities (Genet et al., 2013; Burke et al., 2017; Lyu et al., 2018; Lyu and Zhuang, 2018).

Vertically-resolved model schemes will enable seasonal changes in the depth of the active layer, the thawing and/or freezing fronts, and subsequent changes to microbial activity in the soil depth-profile to be captured. Since the upper-most layers of soil profiles are typically the most biologically active (due to the abundant microorganisms and substrates) and responsive to environmental variation, it might be advantageous to apply a finer vertical resolution in the uppermost layers and a relatively coarser vertical resolution beneath these layers to the bottom mineral layer, in order to reduce computational costs.

3.4.3. Spatial dimensions: Horizontal

Heterogeneity in soil biological, physical and chemical characteristics occurs across a landscape (i.e. laterally/horizontally) across a range of scales from individual soil particles to plots and landscapes. These heterogeneities arise due to numerous interacting factors including geomorphological, climatological, hydrological, chemical and biological processes, often mediated by the soil, that have occurred in the past and are presently shaping the environment. Seasonal processes affecting Arctic soils may also manifest differently across spatial scales, for instance due to (micro-)topographic features, local hydrological processes including variations in the depth of the water table, and snow cover. For instance, hydrological heterogeneities are highly pronounced at the Samoylov research site in the Lena River delta, northeast Siberia, where 58% of the land area is classified as dry tundra and 17% is classified as wet tundra (Boike et al., 2019; Nitzbon et al., 2019). Seasonal permafrost thawing further contributes to horizontal hydrological heterogeneities through its dual impact on ground permeability. The increased permeability resulting from permafrost thaw facilitates lateral water movement across the landscape, influencing lateral flow patterns and fostering the creation of features such as thaw ponds and channels (Bense et al., 2012). Changes in lateral water movement impacts hydrological connectivity, enhancing the transport of suspended sediment and particulate organic matter (Lafrenière and Lamoureux, 2019; Walvoord and Striegl, 2021). On the other hand, water released from thawing can strengthen surface or deep runoff rather than storage, causing alterations to seasonal runoff patterns (Bring et al., 2016). Both of these processes can ultimately affect microbial community dynamics and biogeochemical processes (Blaud et al., 2015).

When applying a model to a regional scale and beyond, the spatial resolution of the model simulation may be limited to a large extent by the spatial coverage and resolution of the available forcing data, particularly in regions which are highly heterogeneous in soil characteristics, hydrology, and topography. Meteorological and geo-hydrological data are usually available either through reanalysis or remote sensing data collected by airborne platforms or satellites. These data are generally gridded at 1.0 km or 0.5° resolution, with some products available at a finer resolution of 250 m (Justice et al., 1998; Shao et al., 2011). Therefore, these are also the most common spatial resolutions used by regional soil biogeochemical models. Nevertheless, considering the horizontal scale and resolution that is resolved in soil biogeochemical models is especially important when extrapolating parameters that are calibrated at the site-level to regional scales and beyond.

Differences in the spatial resolution of soil biogeochemical models can result in different output characteristics. For example, 11 different Earth system models were driven with the same set of meteorological data and run to compare the SOC change between the end and the beginning of the 21st century in the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Todd-Brown et al., 2013, 2014). These models are originally designed with different modelling grid resolution for different geographies and ecosystems, and were extrapolated to be applied to the global scale. The different models produced a wide range of simulated SOC changes ranging from carbon loss of 72 Pg C over a century, to carbon gain of 253 Pg C. In particular, high-latitude regions were subject to large discrepancies between model outputs, from carbon loss of 37 Pg C to carbon gain of 146 Pg C (Todd-Brown et al., 2014). This indicates that many models especially lack accurate simulation of high-latitude soil processes, and poorly represent heterogenous permafrost dynamics across the northernmost land masses.

3.4.4. Validation data

The application of land surface models is critically reliant on data: used both as forcing data for model initialization and utilization, and for calibration and validation. The quantity and quality of data that is available may greatly influence the design, behavior, and performance of numerical models, and the confidence entrusted in their outputs. Both in situ and remotely sensed data may be used for forcing, calibration and validation purposes (Liu et al., 2016; Lyu and Zhuang, 2018; Tan et al., 2016; Chadburn et al., 2017). For instance, climatic data collected on-

site was combined with remotely-sensed data on snow prevalence (of the same temporal and spatial resolution) to run a biogeochemical model to quantify northern high latitude region carbon responses to soil thermal changes (Lyu and Zhuang, 2018). In NASA's ABoVE project, an array of 18 land surface models guided the identification of target variables, as well as the spatial and temporal resolution of monitoring trough a suite of field, airborne and satellite measurements (Fisher et al., 2018). Interpolation or downscaling methods can also be used to accommodate the integration of multiple data types of different resolutions for model applications (Lyu et al., 2018; McGuire et al., 2018b).

Future applications of soil biogeochemical models must, in particular, consider how data can be effectively collected and used year-round to calibrate model simulations. Consideration must be given not only to which variables might be critical to measure, but also to the timespan and temporal resolution of this data. For model applications to Arctic soils, continuous vertically-resolved data on soil temperature and water content will be especially important in order to predict soil microbial activity and carbon degradation year-round. In addition, records of snow depth and snow characteristics would benefit the representation of both soil temperature and emission timing. When incorporating meteorological data, consideration should be given to seasonal variability but also inter-annual variability, including extreme weather conditions such as periodic winter-warming, or summer drought (Zhu and Zhuang, 2013). For Arctic regions, extreme events could greatly affect the soil thermal and hydrological conditions, driving subsequent changes to soil microbial activities and carbon fluxes. The use of forcing and validation datasets of past extreme events may enable a better constraint of model parameters and sensitivity.

4. Conclusions and recommendations

A better understanding of longer-term interactions between Arctic soils and permafrost, climate, microorganisms, vegetation, soil organic matter and nutrients, and snow cover, alongside a refined model depiction of subsurface conditions such as ground ice, will contribute significantly to improved modelling of soil biogeochemical processes. Here we describe the seasonal changes in Arctic soil microbiology and biogeochemistry, and the various factors that should be considered for the development and application of soil biogeochemical models year-round in Arctic settings to improve understanding of processes in Arctic soils and permafrost, and reduce uncertainty regarding the thermo-hydraulic state of permafrost and its future climate feedbacks. Ultimately, model complexity and structure should be guided by available knowledge, data, and the overarching research questions. Therefore, in practice, model development may need to be largely bespoke to each specific application. The most complex model, whilst potentially more closely resembling the complexities of the natural environment, is not necessarily the most useful. In general, a model should be as simple as possible, but not any simpler than that – a simple model may produce equally beneficial and constructive results (e.g. Manzoni and Porporato, 2009). Simple mechanistic models applied to different locations with high temporal and spatial resolution may help in the identification of the most relevant processes to be implemented and tested in global models (e.g. Todd-Brown et al., 2012), as well as explore the importance of representing interspecies and interkingdom (plant-microbe) interactions (Naylor et al., 2020). These simple mechanistic models are promising for bridging the gap between data-driven models aimed at identifying the drivers of carbon dynamics in field studies, and complex land surface models, which often fail at accurately representing practical observations despite being process-oriented. With a simpler model, the opportunity to learn about microbiome-climate feedbacks and their role on shaping seasonal dynamics may be limited. The application of any model should be viewed as a work in progress, to be constantly re-evaluated and tested in the context of the evolving data availability and mechanistic understanding. Over time, these tools will be incrementally improved and better constrained such that they become more useful in analytically testing hypotheses, extrapolating, interpolating and constructing budgets of processes and rates, and enabling predictive capabilities.

The emergence of year-round data and the integration of this data and understanding of seasonal processes into soil biogeochemical models will be critical to understand and predict the year-round functioning and fate of Arctic soil biology and biogeochemistry, particularly under a changing climate. Year-round measurements of microbial activity rates, organic carbon uptake and remineralization, carbon dioxide and methane production and consumption, and soil thermal and hydrological characteristics will particularly help to constrain the understanding of seasonal processes and simulations of microbially-explicit models. Moreover, improvements to models and understanding rely especially on consideration of how the carbon pool magnitude, fate and cycling dynamics varies with the microbial community's taxonomic and functional trait composition, and ways in which the carbon dynamics depart from idealized models due to spatial and temporal heterogeneity of biological, geological, physical and geochemical factors. Incorporating this complexity into models, over temporal and spatial scales that are appropriate to resolve potentially important abiotic constraints on biological processes (such as the zero-curtain effect and the progression of thawing and freezing fronts with soil depth) is a formidable but vital challenge, which, if overcome, will yield vast improvements in the understanding and predictive capabilities of the year-round functioning of Arctic soils and carbon stocks.

CRediT authorship contribution statement

Zhou Lyu: Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Pacifica Sommers:** Writing – review & editing, Funding acquisition. **Steven K. Schmidt:** Writing – review & editing, Funding acquisition. **Marta Magnani:** Writing – review & editing. **Mihai Cimpoiasu:** Writing – review & editing. **Oliver Kuras:** Writing – review & editing, Funding acquisition. **Qianlai Zhuang:** Writing – review & editing. **Youmi Oh:** Writing – review & editing. **Maria De La Fuente:** Writing – review & editing. **Margaret Cramm:** Writing – review & editing. **James A. Bradley:** Conceptualization, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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