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The net ecosystem carbon balance (NECB) at catchment scales in the Arctic

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The Net Ecosystem Carbon Balance (NECB) is a crucial metric for understanding integrated carbon dynamics in Arctic and boreal regions, which are vital to the global carbon cycle. These areas are associated with significant uncertainties and rapid climate change, potentially leading to unpredictable alterations in carbon dynamics. This mini-review examines key components of NECB, including carbon sequestration, methane emissions, lateral carbon transport, herbivore interactions, and disturbances, while integrating insights from recent permafrost region greenhouse gas budget syntheses. We emphasize the need for a holistic approach to quantify the NECB, incorporating all components and their uncertainties. The review highlights recent methodological advances in flux measurements, including improvements in eddy covariance and automatic chamber techniques, as well as progress in modeling approaches and data assimilation. Key research priorities are identified, such as improving the representation of inland waters in process-based models, expanding monitoring networks, and enhancing integration of long-term field observations with modeling approaches. These efforts are essential for accurately quantifying current and future greenhouse gas budgets in rapidly changing northern landscapes, ultimately informing more effective climate change mitigation strategies and ecosystem management practices. The review aligns with the goals of the Arctic Monitoring and Assessment Program (AMAP) and Conservation of Arctic Flora and Fauna (CAFF), providing important insights for policymakers, researchers, and stakeholders working to understand and protect these sensitive ecosystems.

KEYWORDS

net ecosystem carbon balance, high Arctic, boreal zone, permafrost region, carbon sequestration, methane emissions, lateral transport, herbivore interactions

1 Importance of understanding NECB in high arctic and northern boreal catchments

The delicate balance of carbon (C) exchange within ecosystems, particularly in Arctic and northern boreal catchments, holds significant implications for understanding and mitigating the impacts of climate change. The Net Ecosystem Carbon Balance (NECB) considers all carbon fluxes, including both vertical net exchange of C between ecosystems and the atmosphere and lateral C transfer downstream. The NECB integrates processes such as photosynthesis and autotrophic and heterotrophic respiration (López-Blanco et al., 2019; See et al., 2024), methane emissions (McNicol et al., 2023; Parmentier et al., 2024; Yuan et al., 2024), and lateral C transport (Rocher-Ros et al., 2019; Casas-Ruiz et al., 2023). Only few studies so far have included all components (Roulet et al., 2007; Nilsson et al., 2008; Jutinen et al., 2013; Pumpanen et al., 2014). Most often land-atmosphere exchanges, lateral dissolved organic C (DOC) fluxes, and their links to hydrological pathways or the impacts of grazing and environmental disturbances are studied in isolation. Addressing all flux components, i.e., compiling NECB, provides a comprehensive measure of an ecosystem's capacity at the landscape level to act as either a C sink or a source. This is essential for evaluating ecosystem health—referring to its resilience and functional stability—and its role in climate regulation (Schuur et al., 2015).

Understanding the regulation of all flux components is pivotal now when the Arctic and boreal ecosystems are undergoing some of the fastest warming on the planet, with temperatures increasing three to four times faster than the global average (AMAP, 2022; Rantanen et al., 2022). Recent climate models project Arctic temperature increases of 3°C–4°C by mid-century, far outpacing global averages due to Arctic amplification (Box et al., 2019). This phenomenon, driven by feedback mechanisms such as albedo changes from sea ice and snow loss, shifts in atmospheric and oceanic circulation, and variations in cloud cover and water vapor, has profound implications for C cycling in these regions (Serreze and Barry, 2011).

Arctic amplification alters precipitation patterns and form (Bintanja and Andry, 2017; Bintanja et al., 2020), disrupts permafrost stability (Koven et al., 2011; Turetsky et al., 2020), and accelerates greenhouse gas (GHG) emissions (Natali et al., 2019; Hugelius et al., 2024; Ramage et al., 2024). While extended growing seasons may enhance plant productivity, increased soil respiration can counteract these gains by releasing stored C (Natali et al., 2019). The overall intensification of biogeochemical activities in soil and water bodies further amplifies this dynamic. Moreover, permafrost destabilization risks releasing vast amounts of stored C, altering hydrological regimes and affecting CO₂ and CH₄ emissions and lateral C transport (Schuur et al., 2009; Vonk et al., 2023). Additionally, warming increases the likelihood of extreme events (Walsh et al., 2020), such as droughts or heavy precipitation, which can exacerbate ecosystem instability and further disrupt C and water cycles (Frank et al., 2015).

The NECB in Arctic-boreal systems plays a central role in global climate change projections due to the enormous C stocks stored in these regions and their sensitivity to warming (McGuire et al., 2009;

Schuur et al., 2015). Permafrost regions store approximately 1,000 ± 200 Pg of organic C within the upper 3 m (Hugelius et al., 2014; Mishra et al., 2021; Palmtag et al., 2022)—almost double the C present in the atmosphere. Understanding the NECB responses to warming is crucial for predicting potential carbon-climate feedbacks, which can significantly impact global climate trajectories (Vonk and Gustafsson, 2013; Turetsky et al., 2020). These feedback effects represent a significant challenge for maintaining the stability of the Earth's climate system (Vonk and Gustafsson, 2013; Schuur et al., 2015; Turetsky et al., 2020).

Recent studies (Hugelius et al., 2024; Ramage et al., 2024) have underscored the critical role of permafrost regions in the global C cycle, providing pan-Arctic insights into GHG dynamics from 2000 to 2020. For example, GHG flux upscaling estimates indicate the permafrost region is a net CO₂ sink but a significant source of CH₄ and N₂O emissions (Ramage et al., 2024). Modeling approaches reveal a weak CO₂ sink and substantial CH₄ and N₂O emissions, with a net warming effect over short timescales (20 years) but a neutral effect over 100 years (Hugelius et al., 2024). These findings highlight substantial uncertainties and mismatches between field observations and models, emphasizing the need for localized investigations to better understand site-specific dynamics and interactions affecting NECB across diverse Arctic ecosystems. Watts et al. (2023) estimated the terrestrial domain of Arctic-Boreal zone be a C sink as a whole, but if accounting the aquatic ecosystems, the sink decreased notably and there were substantial differences in the C sink strength across the boreal-arctic domain.

2 Components contributing to the NECB

Understanding the components of the NECB is key to comprehending how Arctic and boreal ecosystems operate and adapt to environmental changes. These components encompass net ecosystem CO₂ exchange, methane emissions, lateral C transport, interactions with herbivores, and ecosystem disturbances. Below, we delve into each component in detail to explore their individual and collective roles in shaping NECB.

2.1 Net ecosystem exchange (NEE) of CO₂

NEE is the balance between gross primary production (GPP) and ecosystem respiration (ER), and both are fundamental components of the NECB. GPP represents the total CO₂ assimilated by plants through photosynthesis, while ER encompasses the release of CO₂ from organisms and decaying matter, including both autotrophic (plant) and heterotrophic (microbial) respiration (López-Blanco et al., 2019). The balance between these two processes determines whether an ecosystem acts as an atmospheric CO₂ sink or source (McGuire et al., 2009; See et al., 2024).

In Arctic regions, GPP is typically constrained by short growing seasons, low temperatures, snow cover, and limited nutrient availability (Chapin III et al., 2000). However, climate change alters these limitations, potentially enhancing GPP by extending the growing season, increasing temperatures in air, soil and water

bodies, and augmenting nutrient availability through permafrost thaw (Natali et al., 2015; López-Blanco et al., 2020). Studies have shown that GPP in tundra ecosystems is highly sensitive to temperature fluctuations and can significantly influence NECB (Euskirchen et al., 2006). Longer-term changes in plant community composition, such as shrub expansion, can alter photosynthetic rates and GPP across different landscapes (Myers-Smith et al., 2011; Bjorkman et al., 2018). The NEE is highly sensitive to annual variations in water table levels and temperature. For instance, dry summers or periods with atmospheric drought can shift peatlands, typically net CO₂ sinks, into net CO₂ sources, primarily due to reductions in GPP (Alm et al., 1999; Aurela et al., 2007; Rinne et al., 2020). Historically, peatlands have functioned as C sinks in most years, facilitating peat accumulation over time, which has cooled the climate due to the stored C (Frolking and Roulet, 2007).

In high latitudes, ER, on the other hand, is expected to increase with warming temperatures, potentially offsetting gains in GPP (Schuur et al., 2009; Commane et al., 2017). Soil respiration, a major component of ER, is particularly sensitive to temperature changes in permafrost regions (Bond-Lamberty and Thomson, 2010). Recent research has highlighted the importance of winter respiration, which can significantly contribute to annual C budgets (Natali et al., 2019). Helbig et al. (2022) analyzed multiyear eddy covariance data from boreal-Arctic peatland sites and found that warm anomalies increased CO₂ uptake relative to average conditions when warming occurred in early summer, whereas late-summer warming resulted in increased CO₂ release. These anomalies were linked to earlier vegetation development during early summer and typically lower water levels in late summer, possibly suppressing GPP and increasing ER.

The Arctic-boreal zone exhibits substantial variability in CO₂ fluxes, with observed annual NEE ranging from $-27.9 \text{ g C m}^{-2} \text{ yr}^{-1}$ (net CO₂ uptake) to net release of CO₂ in certain years. Seasonal dynamics are pronounced, with monthly GPP varying from -2 to -516 g C m^{-2} and ER from 0 to 550 g C m^{-2} (Virkkala et al., 2022; See et al., 2024). Notably, more than 30% of the region functions as a net CO₂ source, and when fire emissions are included, the permafrost region approaches a net zero CO₂ balance, highlighting the critical role of fire in shaping regional C dynamics (Virkkala et al., 2025). The complex interplay between GPP and ER under changing climate conditions underscores the need for continued monitoring and improved modeling of these processes to accurately predict future C dynamics in Arctic-boreal ecosystems (Virkkala et al., 2022). Respiratory outputs (particularly heterotrophic respiration), and C turnover and decomposition processes remain highly uncertain and poorly constrained in models (Carvalhais et al., 2014; López-Blanco et al., 2019). Precipitation and soil moisture have been highlighted as the key drivers of heterotrophic respiration interannual variability (Yao et al., 2021; Guenet et al., 2024). Such uncertainties ultimately propagate over the rate and magnitude of C accumulation.

2.2 Methane emissions (CH₄)

CH₄ emissions play a crucial role in the NECB of Arctic-boreal ecosystems, particularly in wetlands and peatlands, and areas

affected by permafrost thaw. Methane is produced by microbes under anaerobic conditions and has a much higher global warming potential than CO₂ over short time scales (Turetsky et al., 2014; Kuhn et al., 2021). Even without considering the global warming potential, methane emissions in wet ecosystems also form a significant component of the mass transfer of C and may account for 20% of the total C turnover (Christensen et al., 2007). In many, if not all, wetlands CH₄-C losses decrease substantially the C gain of NEE (Juutinen et al., 2013; Rinne et al., 2020). Recent studies have shown that methane emissions in the Arctic are higher than previously estimated, especially during the cold season (Zona et al., 2016). Treat et al. (2018a) estimated that methane emissions from freshwater bodies (observationally measured) contribute 4%–17% of the total annual methane emissions for the circumpolar Arctic region, corresponding to $6.1 \pm 1.5 \text{ Tg CH}_4/\text{year}$ north of 40° latitude. This is also the case in results obtained from ecosystems models for which the calibration is mainly driven by growing season datasets and for which cold season processes may be missing or may not be well accounted for (Ito et al., 2023). CH₄ emissions from lakes and streams are crucial components to consider in the boreal-Arctic region, especially as part of catchment-scale assessments. Some studies even identify freshwater bodies as the largest CH₄ source in the boreal-Arctic area (Wik et al., 2016).

Arctic-boreal wetlands, including peatlands, are significant sources of methane, with emissions modulated by warming and vegetation activity. Wetlands emit in the order of 48.7 (13.3 – 86.9) $\text{Tg CH}_4 \text{ yr}^{-1}$, while freshwater systems contribute approximately $12.5 \text{ Tg CH}_4 \text{ yr}^{-1}$ (Parmentier et al., 2024). These emissions are influenced by temperature, vegetation activity, and permafrost thaw. For instance, a recent study found that temperature explains 52.3% of the increasing CH₄ emission trend, followed by GPP (40.7%) (Yuan et al., 2024). Thawing permafrost can lead to the formation of thermokarst lakes and extend wetland areas, potentially releasing large amounts of previously frozen organic matter and increasing methane production (Treat et al., 2018b; Turetsky et al., 2020; Parmentier et al., 2024).

The spatial and temporal variability of methane emissions across Arctic-boreal landscapes presents significant challenges for accurate quantification and prediction. Recent efforts, such as the BAWLD-CH₄ dataset, have advanced our understanding of methane flux patterns across diverse boreal and Arctic ecosystems (Kuhn et al., 2021). However, uncertainties remain, particularly regarding the fate of methane in the water column and its transport through soil, surface runoff and snow (Saunois et al., 2020). For instance, non-growing seasons, particularly in autumn and spring, remain difficult periods for maintaining continuous methane flux measurements (Jentsch et al., 2024). Vegetation composition and the presence or absence of specific vascular plant species also significantly influence methane emissions, making the impacts of climate change on future vegetation composition a critical area for further study (AMAP, 2015). Uncertainties surrounding lateral methane transport from wet tundra and peatlands are compounded by limited understanding of dissolved methane dynamics—how much is oxidized versus emitted from streams and ponds (Oh et al., 2020). These processes, currently underrepresented in ecosystem models, demand further investigation across diverse Arctic landscapes. Challenges persist in both experimental and

observational approaches to accurately measure methane emissions on an annual scale in the context of NECB. Addressing these gaps is essential for improving the parameterizations used in process models. Ultimately, enhancing our understanding of methane dynamics is key to accurately assessing the greenhouse gas budget of Arctic-boreal regions and predicting their feedback to global climate change (Hugelius et al., 2024).

2.3 Lateral C transport

Lateral C transport, the movement of DOC, particulate organic C (POC), and dissolved inorganic C (DIC), plays a crucial role in the Arctic-boreal C balance, yet it remains underrepresented in NECB assessments (Dean et al., 2020). Carbon moves from terrestrial ecosystems to aquatic systems via groundwater leaching, runoff, streams, and rivers, contributing to substantial C losses from terrestrial ecosystems, influencing both local and regional C budgets (Tank et al., 2012; Tank et al., 2018; Vonk et al., 2023). A significant portion of this C is either emitted as CO₂ and CH₄ from freshwater systems or transported to the ocean, with global fluxes estimated at 5.1 Pg C yr⁻¹—of which 0.9–1.3 Pg C yr⁻¹ reaches the ocean, 2.1–2.9 Pg C yr⁻¹ is released as CO₂, and 0.6–1.5 Pg C yr⁻¹ is buried in sediments (Tank et al., 2018). Globally, lateral C fluxes have been estimated to be comparable to the terrestrial CO₂ sink, approximately 3.1 Pg C yr⁻¹ (Le Quéré et al., 2016), ranging from 1.1 Pg C yr⁻¹ to 5.1 Pg C yr⁻¹ (Drake et al., 2018). In Arctic-boreal ecosystems, studies suggest that lateral C fluxes represent 0.2%–1.4% of the terrestrial C stock, depending on the region and landscape characteristics (Martens et al., 2022), and nearly 20% of the net terrestrial C uptake (Kling et al., 1991).

Recent high-resolution studies have revealed complex seasonal and interannual variations in DOC transport processes in subarctic headwater catchments (Croghan et al., 2024) and indicated complex variations between C sources at the landscape level. Climate change is altering these transport mechanisms, with spring snowmelt floods and summer/autumn storm events becoming increasingly important for DOC export (Rawlins and Karmalkar, 2024), and also winter runoff in southern Arctic sites. The thawing of permafrost is expected to enhance the mobilization and transport of previously frozen organic matter, potentially leading to increased DOC and DIC fluxes to aquatic systems (Vonk and Gustafsson, 2013).

The fate of this laterally transported C is crucial for understanding its impact on the global C cycle. While some of the C may be deposited in sediments or transported to the ocean, a significant portion can be evaded directly to the atmosphere or processed within inland waters, leading to CO₂ and CH₄ emissions (Casas-Ruiz et al., 2023; Mustonen et al., 2024). Recent research has highlighted that small watersheds and water bodies including streams, ponds and lakes may play a disproportionate role in Arctic land-ocean fluxes, emphasizing the need for better representation of these systems in C budget assessments (Vonk et al., 2023). However, the lack of watershed-scale studies across Arctic limit our ability to identify the main controlling factors and key locations at the landscape level.

Integrating aquatic C fluxes and the ecosystem-atmosphere exchange of C remain a challenge due to the high spatial and

temporal variability of these processes. Improved monitoring networks including high-resolution sensors, coupled with advanced modeling approaches, are necessary to better constrain estimates of lateral C transport and its contribution to NECB in Arctic-boreal ecosystems (Rocher-Ros et al., 2019; Olefeldt et al., 2021).

2.4 Herbivore interactions

The role of herbivores in C cycling within high-latitude ecosystems has gained increasing recognition in recent years (Schmitz et al., 2014). Both large herbivores, such as reindeer/caribou (Ylänne et al., 2018), muskox (Falk et al., 2015) and small mammals (Tuomi et al., 2019), significantly influence C cycling in Arctic and boreal ecosystems through grazing, trampling, and nutrient deposition (Koltz et al., 2022), also during the snowy seasons. Their trampling and cratering in search of food under the snow can damage the vegetation, potentially hindering treeline expansion (Heggenes et al., 2017). Additionally, tree girdling caused by reindeer rubbing against young trees (“buck rub”) can further inhibit forest regeneration (Roturier and Bergsten, 2006). Their interactions can alter vegetation dynamics, soil properties, hydrology, energy balances, and C and nutrient cycling, ultimately affecting the NECB (Ylänne et al., 2015; Schmitz et al., 2023; Schmidt et al., 2024). In the Arctic, grazing and trampling activities compact snow reducing insulation, which consequently prevents permafrost thawing, thereby reducing CH₄ emissions. For example, increasing herbivore densities in Arctic regions could protect up to 80% of the Yedoma permafrost domain, which stores around 500 Gt of organic C (Schmitz et al., 2023). However, herbivory can also have mixed effects on C dynamics, with some studies showing reductions in C uptake by 15%–70% due to changes in plant community composition and ecosystem respiration rates (Schmitz et al., 2018).

Large herbivores are known to influence plant community structure, often reducing shrub and moss abundance and promoting graminoid-dominated vegetation (Olofsson et al., 2009), or reducing overall plant biomass (Olofsson et al., 2014). This shift can have cascading effects on ecosystem processes, including C sequestration, soil respiration (Väisänen et al., 2014), and methane emissions (Falk et al., 2015), as well as on ecosystem energy balance via changes in, e.g., evapotranspiration (Zimov et al., 1995), albedo (te Beest et al., 2016), soil thermal regimes, and thaw depth (Windirsch et al., 2022). Recent studies have highlighted the substantial impacts of herbivores on C fluxes and stocks; for example, muskox and lemming herbivory can reduce net CO₂ uptake in the short term, though vegetation often recovers quickly (Falk et al., 2015; Plein et al., 2022), while different types of large animals can increase the C storage in permafrost soils (Zimov, 2005; Windirsch et al., 2022). Further research is needed however to disentangle whether increased C content results from reduced decomposition or higher C input. Herbivory-induced changes in plant communities not only impact NECB directly but also indirectly through various belowground alterations, such as changes in the quantity and quality of litter (Francini et al., 2014) and soil organic matter (Väisänen et al., 2015). Additionally, herbivores can induce shifts in soil faunal (Sørensen et al., 2009)

and microbial communities (Ahonen et al., 2021). Herbivores also influence their environment through the redistribution of nutrients, contributing to local fertilization (Van Der Wal et al., 2004) and physical disturbances, such as trampling (Mosbacher et al., 2019).

The overall strength and direction of herbivore effects on NECB can vary spatially and temporally, influenced by factors such as herbivore traits and density, plant community composition, and climate conditions (Schmitz and Leroux, 2020). Understanding these complex herbivore-ecosystem interactions is essential for accurately assessing and predicting C dynamics in rapidly changing Arctic and boreal regions (Koltz et al., 2022).

2.5 Disturbances

Disturbances can significantly impact the NECB of tundra and boreal ecosystems (Foster et al., 2022) by altering C storage and fluxes (Phoenix and Bjerke, 2016). Climate change is intensifying various disturbance regimes in the Arctic, including extreme weather events (Christensen et al., 2020; van Beest et al., 2022), thermokarst formation (Lewkowicz and Way, 2019; Turetsky et al., 2020), wildfires (Mack et al., 2011; Byrne et al., 2024), and insect outbreaks (Heliasz et al., 2011; Lund et al., 2017).

These natural disturbances, combined with anthropogenic activities like resource extraction (mining, land use and settlements) and infrastructure development (Raynolds et al., 2014), are reshaping tundra landscapes and C dynamics. Extreme weather events disrupt vegetation growth and soil processes (Phoenix and Bjerke, 2016), while thermokarst formation mobilizes frozen soil C (Turetsky et al., 2020). Increasingly frequent wildfires consume surface vegetation and alter post-fire succession (Mack et al., 2011), and expanding insect outbreaks can reduce productivity and increase shrub and tree mortality (Heliasz et al., 2011; López-Blanco et al., 2017; Lund et al., 2017). The northward expansion of beavers into Arctic tundra ecosystems is emerging as a significant disturbance regime, profoundly altering hydrological patterns, accelerating permafrost thawing and enhancing methane emissions (Tape et al., 2022; Clark et al., 2023). The complex interplay between these disturbances creates feedbacks that amplify climate change impacts in tundra and boreal ecosystems (Raynolds et al., 2014; Phoenix and Bjerke, 2016), highlighting the need for comprehensive monitoring and modeling of Arctic C balance.

Understanding and quantifying these components together provides a comprehensive view of the key ecosystem processes influencing NECB in Arctic and boreal ecosystems. Future research should focus on integrating these components to better predict ecosystem responses to ongoing climate change.

3 Methodological advances

Recent years have seen significant advancements in our understanding of high-latitude C dynamics, driven by improvements in both observational techniques and modeling approaches. These advances have enhanced our ability to understand, quantify, and predict NECB in Arctic and boreal ecosystems.

3.1 Eddy covariance flux measurements

Eddy covariance (EC) has become the gold standard for measuring ecosystem-scale greenhouse gas fluxes (Baldocchi, 2003), and recent years have seen significant advancements in this technique. High-frequency open-path and closed-path gas analyzers have improved, allowing for more precise measurements of CO₂, CH₄, and H₂O fluxes (Burba, 2013). The development of low-power, low-maintenance EC systems has enabled year-round measurements in remote Arctic and boreal locations, addressing critical data gaps during the non-growing season (Oechel et al., 2014). Additionally, novel approaches such as the use of unmanned aerial vehicles (UAVs) equipped with miniaturized EC systems (Bolek et al., 2024) or connected with high-resolution portable GHG analysers (Scheller et al., 2022) have emerged, allowing for spatial mapping of fluxes and concentration hot spots over heterogeneous landscapes.

Recent studies have also focused on improving flux gap-filling and partitioning methods. Vekuri et al. (2023) have recently shown that the commonly used marginal distribution sampling (MDS) method produces significant systematic error for data sets collected from northern (>60°N) sites, and should be replaced by machine learning methods which avoid this error. The partitioning methods, which are typically used after gap-filling the NEE time series, separate NEE into its component fluxes of GPP and ER. There are novel machine learning approaches that have been developed to improve the accuracy of flux partitioning, particularly in Arctic ecosystems where traditional methods may fall short (Tramontana et al., 2020). Furthermore, advances in CH₄ isotope measurement techniques have provided new insights into the sources and sinks of C in these ecosystems, revealing significant spatial variations in δ¹³C-CH₄ values and highlighting the importance of substrate availability for methanogenesis in driving CH₄ emissions patterns (Rinne et al., 2022).

3.2 Automatic chambers flux measurements

Automatic chamber systems have become increasingly important for measuring GHG fluxes in Arctic-boreal ecosystems, particularly during the challenging non-growing season (Koskinen et al., 2014) and in aquatic systems (Thanh Duc et al., 2020). These systems allow for continuous, high-frequency measurements of CO₂ and CH₄ fluxes, providing crucial data on temporal and spatial variability (Pirk et al., 2017; Natali et al., 2019), also documenting surprising seasonal dynamics and episodic events (Mastepanov et al., 2008). Recent advancements in automatic chamber design have improved their reliability in harsh Arctic conditions, with better insulation and heating systems to prevent snow and ice accumulation (Mastepanov et al., 2013; Korriakoski et al., 2017).

Multi-chamber systems have been developed to capture spatial heterogeneity in flux patterns, especially important in ecosystems with high microtopographic variability (Mastepanov et al., 2013; Pirk et al., 2017). Additionally, the integration of soil temperature and moisture sensors within chamber systems has enhanced our understanding of the environmental drivers of flux variability (Göckede et al., 2019). These systems can now be coupled with

real-time gas analyzers, allowing for immediate data processing and quality control (Korkiakoski et al., 2020). This advancement enables researchers to obtain and analyze high-quality greenhouse gas flux data in near real-time, improving the efficiency and accuracy of field measurements in Arctic and boreal ecosystems.

3.3 Lateral C transport measurements

Lateral transport of C, with particular focus on understanding the speciation of the C pool, has gained attention as a crucial component of the NECB in Arctic-boreal systems (Tank et al., 2018). Recent methodological advances have improved our ability to quantify these fluxes. High-frequency *in situ* sensors for DOC and POC using optical sensors have been deployed in river systems, allowing for continuous monitoring of C export from terrestrial to aquatic ecosystems (Shogren et al., 2021; Rawlins and Karmalkar, 2024). Coupling high-frequency dissolved C concentrations with discharge (e.g., concentration-discharge relationships) provides a tool to identify processes that control C export (Gómez-Gener et al., 2021; Speir et al., 2024). To understand the fate of this C export, there is a need to couple these measurements with *in-situ* aquatic flux measurements, especially given the spatial variability of these fluxes (Bretz et al., 2021).

Tracer techniques, using both stable and radioactive isotopes, have been refined to better understand the sources and ages of water and laterally transported C. These methods have revealed the importance of old C mobilisation from thawing permafrost in lateral fluxes (Serikova et al., 2018), novel approaches combining hydrological measurements with C concentration data have improved estimates of annual C export, particularly during the critical spring freshet period (Beel et al., 2021). Further, recent studies using ^{222}Rn have provided estimations of methane transport in groundwater (Olid et al., 2022).

There has been a recent call for more spatially resolute sampling to identify landscape control points that influence lateral C transport and, consequently, emissions from land-water systems (Bernhardt et al., 2017). To accurately scale these fluxes to the catchment level, it is essential to account for both the landscape features that supply C to freshwater systems (e.g., wetlands, thaw slumps) and *in-situ* controls such as gas transfer velocity (Kokelj et al., 2013; Rocher-Ros et al., 2019; Shogren et al., 2019).

3.4 Enclosure experiments to understand the herbivory component

Fences that either exclude or enclose herbivores are an essential tool for quantifying the impact of herbivory on NECB in Arctic-boreal ecosystems. Long-term enclosure studies, spanning several decades to over a century, have provided valuable insights into the cumulative effects of herbivores on vegetation structure, soil C stocks, and greenhouse gas fluxes (Ylänne et al., 2018). Moreover, enclosure designs that selectively exclude different herbivore guilds (e.g., large, small mammals, and geese) help the disentanglement of their specific impacts (Köster et al., 2017; Petit Bon et al., 2023), which is particularly relevant in the context of shifting tundra herbivory communities (Barbero-Palacios et al., 2024).

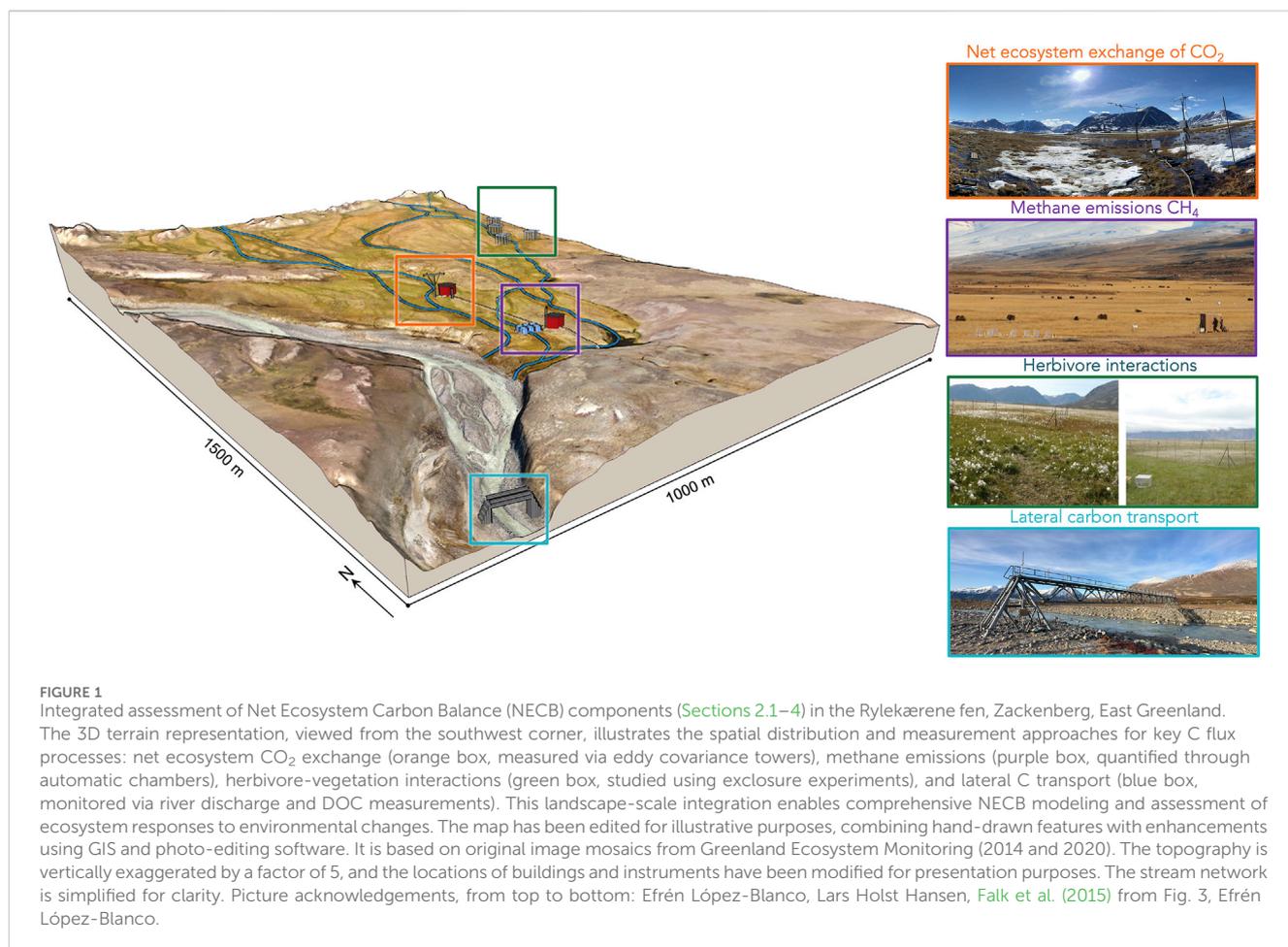
The integration of flux measurement techniques with enclosure and enclosure experiments has significantly improved our understanding of herbivory effects on C cycling. For instance, portable flux chambers have been used to compare CO_2 and CH_4 fluxes inside and outside enclosures, revealing how herbivores influence both primary productivity and soil respiration (Cahoon et al., 2012; Lara et al., 2017; Silfver et al., 2020), and how plant abundance, phenology, and nitrogen dynamics change (Mosbacher et al., 2019). Some studies have combined enclosures with manipulative experiments (e.g., warming, fertilization) to investigate how herbivory interacts with other environmental changes to affect NECB (Sjögersten et al., 2012; Väisänen et al., 2014), and to provide crucial data on potential feedbacks between climate change and herbivore impacts on C cycling (Post et al., 2021).

3.5 Long-term monitoring networks and data-model synthesis efforts

Long-term monitoring networks have become increasingly crucial for understanding the complex dynamics of Arctic-boreal C cycling. The FLUXNET network, for example, and its regional counterparts (e.g., ICOS in Europe, AmeriFlux and NEON in North America), has been instrumental to provide continuous, multi-year datasets of C, water, and energy fluxes from numerous sites in high-latitude regions (Pastorello et al., 2020). Specifically, the FLUXNET- CH_4 community network has greatly enhanced our understanding of methane dynamics in wetland ecosystems across the Arctic-boreal zone (Knox et al., 2019). The Greenland Ecosystem Monitoring (GEM) program (Christensen et al., 2017), established in 1995, provides a unique integrated and interdisciplinary approach to understanding Arctic ecosystems and climate change effects, by measuring a wide range of cross-cutting variables across a catchment scale, from glaciers to marine systems within a 20 km range. GEM serves as example of coordinated observational data gathering across meteorological, hydrological, terrestrial and limnic ecosystem domains in a confined catchment area providing the opportunity for true data-based NECB budgeting (Figure 1). This may in turn serve as pivotal data for NECB model calibration and validation.

These networks not only provide essential data for understanding current C dynamics but also serve as early warning systems for detecting ecosystem changes. For instance, the International Tundra Experiment (ITEX) network (Henry et al., 2022), established in the early 1990s, continues to provide valuable long-term data on the impacts of experimental warming on tundra vegetation and associated C fluxes (Bjorkman et al., 2018). Likewise, the Back to the Future project reveals multi-decadal changes in vegetation and soil C stocks (Callaghan et al., 2011).

In-situ GHG budget synthesis efforts have been instrumental in integrating diverse datasets to derive comprehensive insights across the pan-Arctic region. For example, the recent second phase of the Regional Carbon Cycle Assessment and Processes project (RECCAP2) (Ciais et al., 2022) has specifically focused on the permafrost region (Hugelius et al., 2024; Ramage et al., 2024), synthesizing multiple lines of evidence to deliver thorough assessments of current C dynamics in these critical areas. This budgeting initiative includes three extensive compilations of



GHG flux datasets for CO₂ (Virkkala et al., 2022), CH₄ (Kuhn et al., 2021), and nitrous oxide, N₂O (Voigt et al., 2020), all derived from valuable *in-situ* observations. These collective efforts have not only advanced our understanding of existing C cycling patterns but have also underscored the numerous unresolved uncertainties that persist in this field.

3.6 Modeling approaches and data assimilation

Since the 1970s, Earth System Models (ESM) have been used to study the NECB by accounting for biophysical processes. However, it is only in the 2000s that these models began to incorporate the full complexity of the C cycle and its interactions with the other biophysical components (Fisher and Koven, 2020). Since then, significant progress has been made in modeling approaches and data assimilation techniques to improve Arctic-boreal C cycling representation. The development of more sophisticated ESM that incorporate permafrost dynamics, coupled carbon-nitrogen cycles, and improved representations of Arctic vegetation has enhanced our ability to project future changes in the NECB. Specifically, ESM have been refined to explicitly represent key processes specific to high-latitude ecosystems, such as permafrost dynamics (Guimberteau et al., 2018; Chaudhary et al., 2020), snow insulation effects (Wang

et al., 2013; Pongracz et al., 2021; Charbit et al., 2024), *Sphagnum* dominated peatland ecosystems (Qiu et al., 2022), vegetation shifts (van den Hurk et al., 2016) and lateral transfer of C from land to rivers (Bowring et al., 2019; Bowring et al., 2020). The incorporation of microbial dynamics and soil organic matter decomposition models has improved simulations of soil C responses to warming (Huang et al., 2021).

Data assimilation techniques have evolved to better integrate diverse observational datasets with model simulations and ultimately allowing for better constraints on regional and pan-Arctic C budgets. For example, the Carbon data model Framework (CARDAMOM) (López-Blanco et al., 2019; Hugelius et al., 2024) or the Carbon Cycle Data Assimilation System (CCDAS) (Kemp et al., 2014; Scholze et al., 2019) now incorporate a wide range of observations, including atmospheric CO₂ concentrations, satellite-derived vegetation indices, soil organic C, plant biomass, burned area, and forest loss to provide more accurate estimates of C fluxes, stocks, and transit times and quantify their uncertainties.

Moreover, machine learning approaches, such as neural networks and random forests, have been increasingly used to upscale site-level flux measurements to regional and pan-Arctic scales, providing new insights into spatial patterns and drivers of C fluxes (Väisänen et al., 2014; Peltola et al., 2019; Virkkala et al., 2021; Yao et al., 2021; McNicol et al., 2023; Nelson et al., 2024).

Additionally, the development of benchmarking systems that use multiple observational constraints has enhanced our ability to evaluate and improve Earth System Models for high-latitude regions (Collier et al., 2018; Hou et al., 2023).

In situ data are also crucial for the calibration and validation of process-based models (Le Noë et al., 2023). Specifics of Arctic regions promoted sensitivity model analysis studies assessing models' capacity in simulating Arctic ecosystems (Dantec-Nédélec et al., 2017; Pongracz et al., 2021). Today, more and more models are employing harmonized monitoring databases with statistical optimisation approaches such Bayesian methods and history matching (Salmon et al., 2022; Bacour et al., 2023; McNeill et al., 2024), among others, to calibrate model parameters at regional or global scales and to pinpoint model weaknesses. Additionally, *in situ* data synthesis and meta-analysis are guiding modellers to assess model development priority that aims to reduce model uncertainty or to enhance physical process representation.

4 Remaining uncertainties

Despite the recent advancements in our understanding of C cycling dynamics, significant uncertainties persist, particularly in permafrost regions. The release of CO₂, CH₄, and N₂O, and also lateral DOC transport from thawing permafrost represents a critical yet poorly constrained component of the global C budget. Climate change hydrologically activates different layers of Arctic soils, potentially triggering new C processes. The recently published permafrost RECCAP2 update, following an initial budgeting effort (McGuire et al., 2012), aimed to address these uncertainties by synthesizing two decades of observations and modeling efforts (Hugelius et al., 2024; Ramage et al., 2024). Insights from RECCAP2 highlight the complexity of permafrost region GHG dynamics and underscore the need for improved monitoring and modeling approaches to accurately quantify their contribution to atmospheric GHG concentrations. Two important take-home messages have been found: First, there are large discrepancies between bottom-up and top-down estimates (Hugelius et al., 2024) - Bottom-up approaches (data-driven upscaling and process-based models) generally estimate higher land-to-atmosphere fluxes for all GHGs compared to top-down approaches (atmospheric inversions). This points to fundamental differences in methodologies that need to be reconciled. From a modeling perspective, priorities for future research include improved representation of inland water ecosystems including rivers, lakes, reservoirs and materials lateral transfer, and disturbances like fire dynamics and abrupt permafrost thaw in process-based models, and the compilation of process-based model ensembles for CH₄ and N₂O (Hugelius et al., 2024). The increased complexity of models, driven by the explicit representation of processes, is both challenging and essential to accurately capture the spatial heterogeneity and temporal dynamics of NECB. Second, there is a need for more and better well-distributed *in-situ* data coverage - there are significant gaps in spatial and temporal coverage of *in situ* GHG measurements, especially for winter and shoulder seasons (Ramage et al., 2024). On a related note, the ongoing geopolitical conflict and war between Russia and Ukraine have severely deteriorated our ability to study

and understand not only current but also future pan-Arctic changes (López-Blanco et al., 2024).

The northward advancement of the tree- (Harsch et al., 2009) and shrub- (Myers-Smith and Hik, 2018) lines in the boreal-Arctic transition zone represents two significant ecological processes driven by climate warming, with implications for vegetation composition, surface albedo, and C dynamics. These shifts can enhance aboveground C storage but may also reduce surface albedo, as darker canopies replace tundra vegetation, thereby amplifying regional warming through feedback mechanisms (Sturm et al., 2005; Bjorkman et al., 2018; Schmidt et al., 2024). However, the advancement of tree and shrub lines is neither uniform nor as rapid as anticipated (Myers-Smith et al., 2011; Rees et al., 2020), due to local factors such as nutrient availability, soil conditions, and herbivory, which further modulate these processes. For example, nitrogen limitation in Arctic soils has been shown to constrain tree growth despite warming (Körner and Paulsen, 2004). Moreover, shifts in vegetation composition can alter soil organic C dynamics and decomposition rates, influencing net C balance (Natali et al., 2019). Herbivory also plays a significant role by altering vegetation structure and soil properties; for example, reindeer grazing can reduce shrub density and limit C uptake, further effecting ecosystem C storage (Koltz et al., 2022).

At a local-to-regional scale, addressing these uncertainties will require expanded and comparable long-term monitoring measurements, continued data synthesis efforts for CO₂, CH₄ and N₂O (e.g., , improved resolution in upscaling techniques (Ramage et al., 2024), and ultimately advancing integration between field observations, remote sensing data, and numerical models to more effectively constrain previously unconstrained ecosystem processes (Hugelius et al., 2024). Reducing these uncertainties is critical for accurately quantifying the contemporary and future GHG budgets of the permafrost region.

5 Future perspective

This paper highlights the critical importance of Arctic and boreal ecosystems in the global C cycle and their vulnerability to rapid climate change. Our review of the key NECB components, methodological advances, and remaining uncertainties, emphasizes the critical need to address and quantify uncertainties in GHG budgeting for permafrost regions and provides several key insights for future research and policy directions:

1. Integrated monitoring approaches: There is a pressing need for more comprehensive, year-round monitoring networks that integrate multiple NECB components, including CO₂ and CH₄ fluxes, lateral C transport, and disturbance impacts. Long-term, catchment-scale studies like the one flagged in Zackenberg Valley offer valuable models for future research efforts.
2. Focus on understudied components: Greater attention should be given to quantifying and understanding the roles of winter fluxes, lateral transport of C, disturbance regimes, and herbivore interactions in the NECB of Arctic-boreal

ecosystems. This will likely help reduce discrepancies between bottom-up and top-down GHG estimates.

3. Advancing methodologies: Reducing uncertainties in NECB assessments requires the adoption of state-of-the-art technologies and methods. For example, this includes deploying high-resolution GHG analyzers that can operate in extreme Arctic winters and remote areas with limited power supply, using high-resolution remote sensing tools to improve upscaling capabilities, and integrating isotopic/radioactive tracing techniques to better understand the sources and ages of transported C. Additionally, heavily data-constrained modeling approaches and innovative field experiments are crucial to quantifying and disentangling the individual processes shaping the Arctic-boreal C budget.
4. Interdisciplinary collaboration: Addressing the complex challenges of Arctic C cycling requires increased collaboration across disciplines, including ecology, biogeochemistry, hydrology, and climate science and across approaches, including measurements, remote sensing and modeling. This interdisciplinary approach is essential for developing a holistic understanding of NECB dynamics.
5. Policy and collaboration frameworks: Strengthening NECB research within the context of the Arctic Council, integrating the AMAP and CAFF agendas, is vital. This includes fostering collaboration between local data-model initiatives and pan-Arctic networks, encouraging the development of holistic, site-specific programs with broader regional relevance, and aligning these efforts with international climate goals.

By addressing these key areas, researchers can significantly enhance our ability to predict and mitigate the impacts of climate change on Arctic and boreal C cycles. This improved understanding will be crucial for informing effective climate policy, ecosystem management strategies, and global climate change mitigation efforts in these rapidly changing northern landscapes.

Author contributions

EL-B: Conceptualization, Methodology, Visualization, Writing – original draft, Writing – review and editing. MV: Writing – review and editing, Investigation, Resources. ES: Writing – review and editing, Investigation, Resources. CJ: Writing – review and editing, Investigation, Resources. NS: Writing – review and editing, Investigation, Resources. HM: Writing – review and editing, Investigation, Resources. AL: Writing – review and editing, Investigation, Resources. SJ: Writing – review and editing, Investigation, Resources. JS: Visualization, Writing – review and editing, Investigation, Resources. TC: Conceptualization, Writing – review and editing, Investigation, Resources.

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Conflict of interest

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