

INVITED RESEARCH REVIEW

Reducing model uncertainty of climate change impacts on high latitude carbon assimilation

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Abstract

The Arctic–Boreal Region (ABR) has a large impact on global vegetation–atmosphere interactions and is experiencing markedly greater warming than the rest of the planet, a trend that is projected to continue with anticipated future emissions of CO₂. The ABR is a significant source of uncertainty in estimates of carbon uptake in terrestrial biosphere models such that reducing this uncertainty is critical for more accurately estimating global carbon cycling and understanding the response of the region to global change. Process representation and parameterization associated with gross primary productivity (GPP) drives a large amount of this model uncertainty, particularly within the next 50 years, where the response of existing vegetation to climate change will dominate estimates of GPP for the region. Here we review our current understanding and model representation of GPP in northern latitudes, focusing on vegetation composition, phenology, and physiology, and consider how climate change alters these three components. We highlight challenges in the ABR for predicting GPP, but also focus on the unique opportunities for advancing knowledge and model representation, particularly through the combination of remote sensing and traditional boots-on-the-ground science.

KEYWORDS

arctic, boreal, forest, GPP, photosynthesis, remote sensing, taiga, tundra

1 | INTRODUCTION

High-latitude ecosystems, defined here as the Arctic–Boreal Region (ABR), mostly lie north of 55°N and occupy c. 17% of the global land area (Pan et al., 2013; Walker et al., 2005). The vegetated area of the Arctic (5.05×10^6 km²) and the boreal (18.8×10^6 km²) regions is typified by short growing seasons, cold mean annual temperatures, low nutrient cycling rates and availability, and low species diversity (Bobbink et al., 2010; Pan et al., 2013; Walker et al., 2005; Willig et al., 2003). Although these factors limit the biological activity of the ABR, northern regions have an enormous impact on global vegetation–atmosphere interactions and are a significant source of uncertainty in carbon uptake in terrestrial biosphere models (TBMs;

Fisher, Hayes, et al., 2018). Annual gross primary productivity (GPP) in the Arctic (1.6 Pg C year⁻¹) and boreal (8.3 Pg C year⁻¹) regions is small relative to global GPP (123 Pg C year⁻¹) but is also highly uncertain (Beer et al., 2010; Fisher, Hayes, et al., 2018; Fisher, Sikka, et al., 2014; Pan et al., 2013). In conjunction with an improved understanding of the processes that release CO₂ from the ABR, reducing uncertainty in CO₂ uptake is important for understanding whether the region will be a net source or sink for CO₂ in the future. Therefore, reducing uncertainty in GPP in the region is critical for more accurately estimating global carbon cycling, and understanding the response of the region to global change.

The planet has warmed by c. 1°C since the beginning of the Industrial Revolution, driven predominantly by a c. 50% increase in

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atmospheric carbon dioxide concentration ($[\text{CO}_2]$) (Ciais et al., 2013). Over the same period, the annual near-surface air temperature in the ABR has increased by more than twice the global mean (IPCC, 2014; USGCRP, 2017). Indeed, parts of Canada's Yukon region are already 3.5°C warmer than they were in the mid-20th century (Zhang et al., 2019). Under a scenario with continued high emissions of anthropogenic CO_2 , mean annual global temperatures are predicted to increase by ~4°C by 2100 (IPCC, 2014). However, the greatest degree of future warming is expected in high latitudes, where the Arctic is projected to warm by ~8°C by 2100 (Ciais et al., 2013) with enormous consequences for the functioning of arctic and boreal ecosystems (Euskirchen et al., 2009; Hinzman et al., 2005; Hugelius et al., 2020; Natali et al., 2012; Price et al., 2013; Schuur et al., 2015; Soja et al., 2007).

Climate change-carbon cycle feedbacks in these northern regions are complex and hold the potential to alter global carbon cycling. Global change can increase GPP through the direct effects of warming and rising $[\text{CO}_2]$ on photosynthesis and canopy growth, through an extended growing season, and increased rates of nutrient cycling and availability (Hinzman et al., 2005; Morison et al., 2018; Shaver & Chapin, 1980). These effects may underlie recent greening trends in this region (Arndt et al., 2019; Epstein et al., 2012; Reynolds et al., 2012). At the same time, increased thaw and degradation of permafrost is adding previously frozen and preserved carbon to the atmosphere, and dramatically altering hydrology and tree cover, and continued warming is expected change peatland regions from a net sink to a source of CO_2 (Carpino et al., 2018; Helbig et al., 2016; Hugelius et al., 2020; Jorgenson et al., 2006; Liljedahl et al., 2016; Schuur & Mack, 2018; Smith et al., 2005). Lastly, disturbance plays a critical role in this region, and many of the natural disturbance regimes which impact carbon cycling in the ABR (such as fires, drought, and insect damage) are prone to alterations via climate change (Seidl et al., 2017; Soja et al., 2007).

While disturbance can substantially alter the structure and function of northern ecosystems (Amiro et al., 2010; Bond-Lamberty et al., 2009; Mack et al., 2021), vegetation composition change across the ABR is spatially heterogeneous, and in the absence of disturbance is slow and often not observed (Arndt et al., 2019; Jorgenson et al., 2015; Tape et al., 2012). The slow change in community composition is partly because ABR vegetation is long-lived. Vegetative reproduction dominates in the Arctic where individual tussocks can be c. 150 years old, while sedge communities can be several thousand years old, and boreal hardwoods and conifers live 50–300 years (Burns & Honkala, 1990; Burns et al., 1990; Jónsdóttir et al., 2000; Mark et al., 1985). Thus, these existing communities have already experienced decades of global change and, by and large, are the same communities we need to understand and represent in TBMs to project the effects of the much greater changes anticipated for the next 50 years.

In the long term (>100 year), changes in vegetation composition and structure resulting from disturbance will play an increasingly dominant role in determining the response of the ABR to global change (Mack et al., 2021; Thom & Seidl, 2016). However, it is

uncertainty in the anthropogenic greenhouse gas emission scenario that dominates projections of global change on this timescale. In contrast, uncertainty in near-term (~50 year) projections of C uptake in the ABR are dominated by scientific uncertainty, that is, representation of the many processes that determine the response of ecosystems to global change (Fisher et al., 2014; Lovenduski & Bonan, 2017; USGCRP, 2017). Analyses of TBMs have consistently shown that model process representation and parametrization associated with photosynthesis and respiration drives a large fraction of the uncertainty in ecosystem fluxes and pools, including GPP, net primary productivity, leaf area index (LAI), latent heat flux, and soil organic matter carbon (Bonan et al., 2011; Booth et al., 2012; Ricciuto et al., 2018; Sargsyan et al., 2014). Therefore, a major advance needed to reduce near-term (~50 year) model uncertainty associated with carbon, water, and energy cycling and pools in the ABR is an improved representation of current vegetation, a robust understanding of the response and potential acclimation of current vegetation to projected global change, and an understanding of how global change will alter community composition following disturbance. Currently, a paucity of observational data in the ABR is limiting model improvement and evaluation (Fisher, Hayes, et al., 2018), in part due to the inherent remoteness of these ecosystems and the associated logistical challenges of carrying out in-situ measurements, particularly over large spatial and temporal scales.

Previous work has highlighted the primary drivers, impacts, and feedbacks of climate change on high-latitude ecosystems (AMAP, 2021; Gauthier et al., 2015; Price et al., 2013; Swann et al., 2010; Venäläinen et al., 2020) and the use of remote sensing to study vegetation and disturbance dynamics (Beamish et al., 2020; Gamon et al., 2004; Schimel et al., 2015), as well as new opportunities (Ustin & Middleton, 2021). Here, we specifically focus on the challenge of reducing the uncertainty associated with modeling GPP in the ABR. Within this framework, we consider the unique features, processes, and challenges of this region, and highlight the opportunities to improve model representation. We address four fundamental questions related to model representation of GPP in the region: (1) What is the current vegetation composition and distribution? (2) What are the current phenological patterns? (3) How can we best represent the physiological activity of the vegetation? (4) How will climate change alter vegetation composition, phenology, and physiology in ways that lead to changes in species composition?

2 | VEGETATION COMPOSITION AND DISTRIBUTION

Spatial and temporal variation in the uptake of carbon and associated fluxes of water and energy across the globe is determined by climate and the distribution of vegetation. In TBMs, the diversity of plant species and their traits are typically binned into groups known as plant functional types (PFTs), groupings that reflect plant size, life-history strategies, architecture, metabolism, and phenology (Wullschlegel et al., 2014). This simplification provides an intuitive

way to reduce ecological and model complexity by grouping functionally similar plant types while also balancing biological realism (Box, 1996; Fisher, Koven, et al., 2018; Woodward & Cramer, 1996). In most major climate models, the distribution of PFTs is determined by dynamic global vegetation models that provide an area-averaged representation of each PFT for each climatic grid cell (Fisher, Koven, et al., 2018; Fisher et al., 2015).

Understanding the composition of the ABR is a critical first step for modeling high-latitude GPP and resulting carbon stores. Much of the region is underlain by permafrost and the associated belowground carbon stocks are massive, accounting for about one-third of the world's stored carbon (Hugelius et al., 2020; Pan et al., 2013; Schuur et al., 2015; Tarnocai et al., 2009; Walker et al., 2005; Figure 1). While approximately 80% of the boreal zone is also underlain by permafrost, more than half of this area is discontinuous, sporadic, or isolated permafrost (Helbig et al., 2016; Tarnocai et al., 2009). Arctic land cover is dominated by graminoids and shrubs growing above a lichen or moss layer. The boreal region is dominated by extensive forests that account for 29% of the total global forested land area (Pan et al., 2013), but some areas also contain extensive wetland and peatland ecosystems (Gauthier et al., 2015; Hugelius et al., 2020; Tarnocai et al., 2002). Compared to other ecosystems, the ABR has a low plant biodiversity, with a small number of common species dominating regional communities. The relatively low plant diversity in the ABR and the long lifespans of northern plants makes wall-to-wall measurement of fractional cover of each PFT tractable and valuable. Despite this, high-latitude ecosystems

have been critically understudied, and existing observations and experiments are biased to small geographic regions, primarily located in North America and Scandinavia (Metcalf et al., 2018; Schimel et al., 2015). Our reliance on process knowledge and observational data from a small number of field sites raises questions about how effectively we can interpolate this knowledge about the vegetation composition of the ABR across the vast, heterogeneous spaces between them.

Our understanding of ecosystem and vegetation structure and composition across the ABR has been greatly advanced by the use of remote sensing (Peckham et al., 2008; Sulla-Menashe et al., 2018; e.g., Beamish et al., 2020; Jenkins et al., 2020). Importantly, remote sensing can help fill the significant spatial and temporal gaps in observational data for areas where ground-based measurements are difficult to obtain (Nelson et al., 2009; Schimel et al., 2015). The utility of remote sensing technologies to enhance the monitoring and measurement of high-latitude systems is rapidly growing, including the adoption of novel technologies and analysis techniques that can improve the accuracy of monitoring approaches (Assmann et al., 2019; Lara et al., 2019; Schimel et al., 2015; Sluijs et al., 2018; Yang, Meng, et al., 2020; Zhang et al., 2018). Remote sensing platforms, across many different spatiotemporal scales, can serve a wide range of purposes for studying this region (Langford et al., 2019; Lees et al., 2021; Shiklomanov et al., 2019; Table 1). Across the ABR, remote sensing has been used to monitor key biophysical properties, including LAI and the fraction of absorbed photosynthetically active radiation, as well as vegetation composition and albedo, and to infer

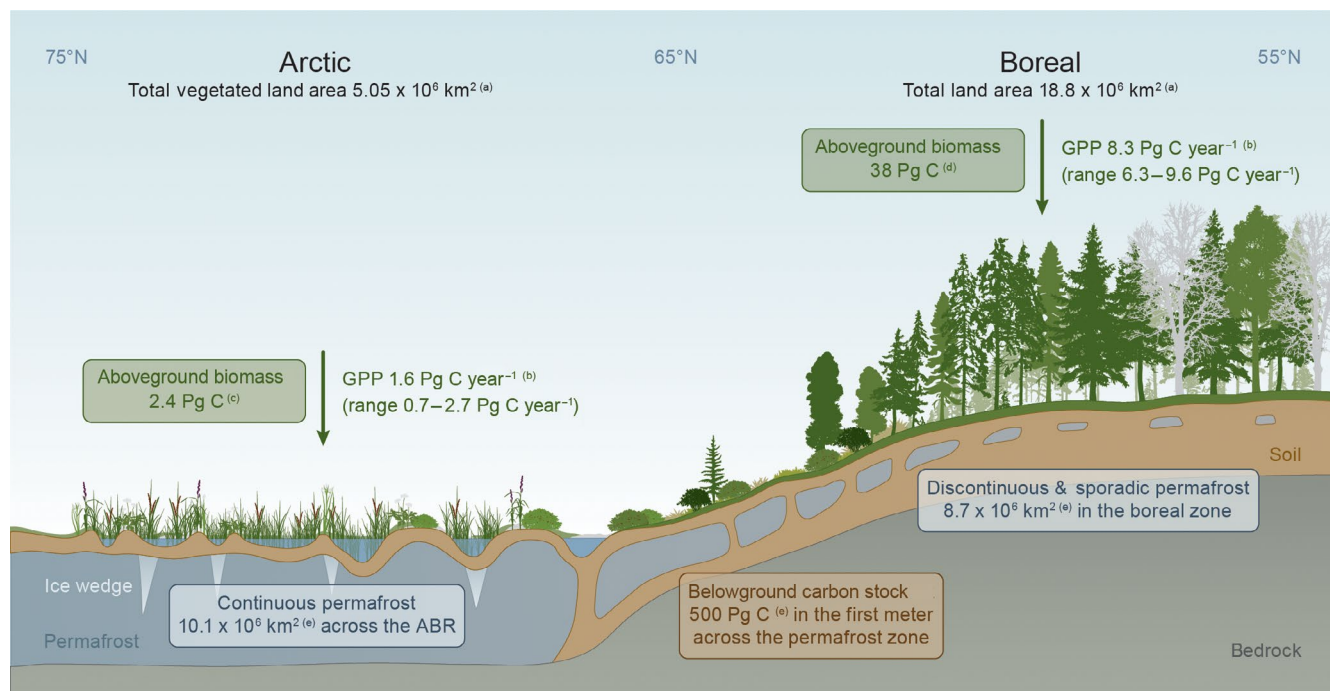


FIGURE 1 Conceptual diagram of the Arctic–Boreal Region (ABR). The latitude where the arctic ecosystem transitions to a boreal ecosystem, and the southern extent of the boreal region varies with longitude but can be broadly considered to range from 55 to 75°N. (a) (Walker et al., 2005), (b) (Beer et al., 2010), (c) (Epstein et al., 2012), (d) (Neigh et al., 2013), and (e) (Tarnocai et al., 2009) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Remote sensing technologies for monitoring and measuring high-latitude ecosystems

Remote sensing technology (key references)	How does it work	Data products and link to biological function	Example platforms
Imaging spectroscopy (IS) (Cawse-Nicholson et al., 2021; Serbin & Townsend, 2020; Ustin & Middleton, 2021; Ustin et al., 2004)	A passive optical remote sensing system that collects very high spectral resolution imagery between 350 and 2500 nm in a large number (e.g., >100) of narrow (<10 nm bandwidths) continuous spectral channels	Albedo, composition, plant traits, light-use efficiency	Airborne: AVIRIS, CASI Spaceborne: CHRIS, DESIS, Hyperion, PRISMA, Surface Biology and Geology (upcoming NASA mission)
Optical multispectral, multi-temporal, and very high-resolution imagery (Ustin & Middleton, 2021; Xie et al., 2008)	An optical multispectral imaging system captures image data within specific wavelength ranges across the electromagnetic spectrum. Common spectral coverage includes blue (~450–495 nm), green (~495–570 nm), red/red-edge (~620–750 nm), near infrared (~750–1100 nm), and sometimes shortwave-infrared (~1100–2500 nm)	Greenness, SVIs, albedo, LAI, land-use/land-cover, disturbance, land-surface phenology	AVHRR, Landsat, MODIS, QuickBird, Sentinel, SPOT, VIIRS, WoldView
Light detection and ranging (Lidar) (Cook et al., 2013; Lefsky et al., 2002; Lim et al., 2003)	An active remote sensing system that uses pulsed laser energy to very accurately measure the distance from the sensor to the target, based on elapsed time-of-flight of the light energy reflected from the surface	Three dimensional canopy structure, plant height, biomass, surface elevation	Airborne: LVIS, G-LiHT, NEON AOP Spaceborne: IceSat, GLAS, GEDI (poor coverage at high latitude)
Thermal Infrared (TIR) (Costa et al., 2013; Still et al., 2019)	A passive sensing system that measures energy emitted from objects in the mid-infrared (~8–14 μ m) region to calculate the temperature of the object using Planck's Law. Calculation of the surface temperature also requires the emissivity of the object, which for vegetation, is often assumed to be ~0.98	Land-surface temperature (LST), evapotranspiration (ET)	Landsat, MODIS, ECOSTRESS (poor coverage at high latitude)
Synthetic aperture Radio Detection and Ranging (Radar, SAR) (Harrell et al., 1995; Kimball et al., 2004; Saatchi & Moghaddam, 2000; Sinha et al., 2015; Zhou et al., 2019)	Radar systems operate in the microwave portion of the electromagnetic spectrum (c. 2–100 cm) with a frequency of 0.25–11 GHz. Active radar systems generate their own pulses that interact with surfaces and then measure the properties of the reflected radiation. Passive radar systems only measure radar signatures reflected from materials. Radar systems are generally "all weather" and can operate in different wavelengths and polarizations depending on the main purpose of the sensor. SAR systems create an artificially long antenna length by combining multiple measurements over a short time period into a single data stream allowing them to use a wide range of different frequencies	Canopy structure, canopy moisture, seasonality, surface elevation, soil freeze-thaw status, soil moisture, vegetation biomass, vegetation optical depth (VOD)	Airborne: AIRSAR, JERS-1, UAVSAR Spaceborne: NISAR (upcoming joint NASA ISRO mission), PALSAR, RADARSAT, SeaWinds, SRTM, TanDEM-X, TERRASar-X
Interferometric SAR (InSAR) (KelIndorfer et al., 2010; Qi & Dubayah, 2016; Yun et al., 2019)	InSAR combines the phase information of multiple SAR images of the same location into an "interferogram" to measure surface displacement or change	Canopy height, structure, and biomass, land-cover classification	Similar platforms as SAR but used to generate interferograms

TABLE 1 (Continued)

Remote sensing technology (key references)	How does it work	Data products and link to biological function	Example platforms
Solar-induced fluorescence (SIF) (Campbell et al., 2008; Meroni et al., 2009; Mohammed et al., 2019; Yang et al., 2015)	An optical, passive remote sensing approach that measures fluorescence (the re-emittance of absorbed light at red to far-red wavelengths) from plants in very narrow spectral regions. Vegetation absorbs sunlight to drive photosynthesis, but a fraction of this light is unused and is dissipated as fluorescence. Therefore, the SIF signatures relate to underlying photosynthetic status and can be used as a means to more directly infer GPP. However, SIF signals are only a very small fraction of the total reflectance signal (~2%) so sensors need to be very sensitive to the primary SIF wavelength ranges	SIF, GPP (through relationships derived between GPP from eddy covariance and SIF)	Airborne: CFIS Spaceborne: GOME, GOSAT, OCO-2/3, Tropomi

Abbreviations: AIRSAR, Airborne Synthetic Aperture Radar; AVHRR, Advanced Very High-Resolution Radiometer; AVIRIS, Airborne Visible/Infrared Imaging Spectrometer; CASI, Compact Airborne Imaging Spectrometer; CFIS, Chlorophyll Fluorescence Imaging Spectrometer; CHRIS, Compact High-Resolution Imaging Spectrometer; DESIS, DLR Earth Sensing Imaging Spectrometer; ECOSTRESS, ECOSystem Spaceborne Thermal Radiometer Experiment on Space Station; GEDI, Global Ecosystem Dynamics Investigation; GLAS, Geoscience Laser Altimeter System; GLiHT, Goddard's Lidar, Hyperspectral, and Thermal imager; GOME, Global Ozone Monitoring Experiment; GOSAT, Greenhouse Gases Observing Satellite; JERS-1, Japan Earth Resources Satellite-1; MODIS, MODerate resolution Imaging Spectrometer; NEON AOP, National Ecological Observatory Network Airborne Observatory Platform; NISAR, NASA-ISRO SAR Mission; OCO-2/3, Orbiting Carbon Observatory; PALSAR, Phased Array type L-band Synthetic Aperture Radar; PRISMA, PRecursoRe IperSpettrale della Missione Applicativa; RADARSAT, Radar Satellite Constellation; SPOT, Satellite Pour l'Observation de la Terre; SRTM, Shuttle Radar Topography Mission; TanDEM-X, TerraSAR-X add-on for Digital Elevation Measurement; UAVSAR, Unoccupied Aerial Vehicle Synthetic Aperture Radar; VIIRS, Visible Infrared Imaging Radiometer Suite.

vegetation productivity (Kimball et al., 2006; Langford et al., 2019; Serbin et al., 2013). Multi-temporal and multi-spectral platforms have provided regular characterization of vegetation composition across space and time (Potter et al., 1999; Reynolds et al., 2019; Wolter & Townsend, 2011), as well as characterizing canopy loss, change, or recovery from disturbance (Lees et al., 2021; Potapov et al., 2008; Schroeder et al., 2011; Wang, Sulla-Menashe, et al., 2020). In the North American region of the ABR, intensive field campaigns combined with airborne and satellite data have yielded detailed inventories of vegetation structure, functional status, and biomass using both passive and active radar platforms (Alonzo et al., 2020; Gamon et al., 2004; Saatchi & Rignot, 1997). Emerging remote sensing platforms and sensors offer excellent near-term opportunities to determine vegetation composition, enabling us to answer the key question of "what is out there?" but critical needs remain.

Remote sensing of the ABR has been historically limited by (1) poor data coverage outside of North America (Neigh et al., 2013; Nelson et al., 2009); (2) inconsistent coverage by key global imaging systems, including imaging spectroscopy (IS), thermal infrared (TIR), Lidar, and synthetic aperture radar (SAR)—as they are not available, have poor spatial coverage, coarse resolution, or have not regularly covered northern high latitudes; and (3) the fact that the low species diversity in the ABR is offset by high sub-pixel heterogeneity (Greaves et al., 2019; Riihimäki et al., 2019; Yang, Meng, et al., 2020). Critically, this sub-pixel heterogeneity in vegetation cover, distribution, composition, and structure is important to characterize as it is

a key driver of ecosystem-scale processes, including carbon fluxes and stores (Lara et al., 2020), yet is a significant challenge to account for in most satellite observations (Montesano et al., 2016; Siewert & Olofsson, 2020). Commercial high-resolution platforms could help to fill this gap (Davidson et al., 2016; Witharana et al., 2020), but are often more limited in their spectral and temporal coverage than other coarse-scale multispectral platforms, such as Landsat and MODIS (Table 1). Furthermore, the absence of ground truthing data for verifying high-latitude remote sensing observations is a major source of uncertainty in quantifying and monitoring vegetation changes across the Eurasian ABR (e.g., Neigh et al., 2013).

Despite these challenges, remote sensing has played a key role in providing regular accounting of high-latitude ecosystem composition, structure, and condition (Duncan et al., 2020). For example, the detailed circum-Arctic vegetation map (Reynolds et al., 2019), derived from both field surveys and remote sensing data, shows the distribution of primary land-cover types across the pan-Arctic region (Walker et al., 2005) and can be used with other data to connect land-cover patterns to ecosystem processes or to explore widespread changes in related properties, including permafrost-vegetation feedbacks (e.g., Nitze et al., 2018). Active remote sensing platforms, including SAR and Lidar (Table 1), have been used from local to larger scales to capture snapshots in time of vegetation structure, surface elevation, and aboveground biomass patterns (Kristensen et al., 2015; Neigh et al., 2013; Williams et al., 1999; e.g., Alonzo et al., 2020; Askne et al., 2017), as well as characterize

ecosystem resilience (Lees et al., 2021). From these remote sensing assessments, the circumboreal forest is estimated to contain ~38 Pg C in aboveground biomass. Using regression models between NDVI and aboveground phytomass (Epstein et al., 2012), total circumpolar Arctic biomass has been estimated to be ~2.4 Pg C (Figure 1). However, these assessments are often derived from a range of different datasets which are not continually available, are not available everywhere, or are validated on limited field observations, which results in significant uncertainty in estimates of vegetation cover and biomass (e.g., Saarela et al., 2020).

Overcoming the challenges outlined here requires new remote sensing platforms, novel use of existing platforms—including commercial high-resolution imagery to aid in calibration and validation—and paired field and airborne campaigns (e.g., the NASA Arctic/Boreal Vulnerability Experiment; Miller et al., 2019).

3 | THE IMPORTANCE OF PHENOLOGY FOR CAPTURING CARBON FLUXES

Understanding the composition of high-latitude vegetation is a prerequisite for modeling carbon uptake in the ABR. However, accurately representing the timing of bud burst (green-up), peak season productivity, and senescence and leaf fall (brown-down) for this region is also critical for estimating GPP because these processes are on-off switches for physiological activity. Measuring shifts in vegetation seasonality in response to climate extremes or long-term change is also critical to understand the impact of climate change on land-atmosphere feedbacks and carbon storage (Kross et al., 2014; Lindroth et al., 2020; Xia et al., 2015).

The growing season in the ABR is short compared to many other biomes, ranging from ~60 days in the high Arctic to ~260 days in the southern boreal region (Park et al., 2016). The short growing season typical of the region means that errors in estimation of green-up and brown-down have a more marked impact on GPP in the ABR than in temperate systems with longer growing seasons. Additionally, the dominance of evergreen species in portions of the ABR requires knowledge of the start and end of the primary photosynthetic period that may not be as clearly defined by seasonal "greenness" signals (Wong et al., 2020). A range of approaches are employed by TBMs to determine green-up and brown-down, including various metrics associated with air temperature, and the use of prescribed dates or photoperiod length (Fisher, Huntzinger, et al., 2014). In some cases, phenology also directly regulates leaf-level physiology through seasonal scalars on photosynthetic capacity (e.g., Medvigy et al., 2009). Approximately one-third of TBMs prescribe green-up and brown-down from spectral vegetation indices (SVIs) or other remotely sensed metrics (Fisher, Huntzinger, et al., 2014; MacBean et al., 2015).

Satellite remote sensing is ideally suited for characterizing global vegetation phenology, and in particular high-latitude phenology. For one, the increasing record of globally available, daily or near-daily observations from satellites covering the ABR has ushered in a new

era in the ability to quantify broad-scale annual phenology metrics, including the start and end of season, as well as other metrics including the rate of green-up and senescence, and seasonal amplitudes (Chen & Yang, 2020; Jeganathan et al., 2014; Peckham et al., 2008). Compared with other remote sensing products that often require models or transfer functions to convert the measured signal to the variable of interest (Myneni et al., 2002; Running et al., 2004), remote sensing of seasonal changes can be measured with simpler products like reflectance or SVIs, including NDVI. In addition, because they provide a synoptic view over multiple decades, satellite-derived phenology metrics can also be used to track changes in plant seasonality (Zeng et al., 2011), which allows us to determine the controls of plant seasonality on carbon cycling and storage (Pulliainen et al., 2017; Richardson et al., 2010; Zhu et al., 2013). More recently, the characterization of vegetation phenology has become more routine, particularly with the creation of standard data products (Ganguly et al., 2010), while novel platforms now enable higher temporal resolutions (Wheeler & Dietze, 2021). Similarly, biophysical products, including LAI, are often used to capture seasonality of plants, but also provide a more meaningful metric for evaluating carbon cycle models (Li et al., 2018; Viskari et al., 2015).

Optical remote sensing is particularly effective at capturing seasonal changes in broadleaf deciduous plants. Studies exploring seasonality in the ABR show that, in general, satellite observations provide good accuracy in characterizing start and end of season metrics of deciduous vegetation (Serbin et al., 2013). However, a large fraction of the ABR is composed of evergreen plants, which present additional challenges for the remote characterization of seasonality. The primary challenge is the much smaller spectral changes in SVIs of evergreen trees associated with seasonal transitions, coupled with a potentially strong signal from deciduous understory vegetation (Miller et al., 1997; Robin et al., 2008; Serbin et al., 2013), which limits the utility of traditional approaches that extract phenology from optical remote sensing data (Wang et al., 2018). Importantly, mischaracterization of evergreen phenology can then have significant impacts on monitoring and modeling of the ABR carbon cycle (Forkel et al., 2019; Richardson et al., 2012). Other background signal contamination, including contamination from snow cover, soil moisture change, shadows, and changing sun-sensor geometry during the spring and fall transition periods, can also reduce the performance of satellite-derived phenology (Wang et al., 2018). Furthermore, the longest satellite records often contain other artifacts stemming from changing platforms, orbital drift, and new sensor designs that also have to be accounted for, all of which may increase the uncertainties in derived seasonal metrics (Ji & Brown, 2017). However, surface phenology observation networks and approaches have matured (Seyednasrollah et al., 2019), providing critical new datasets for the assessment and improvement of tracking phenological signals in the ABR.

Despite these challenges, satellite phenology is widely used to study seasonality in the ABR. Remote sensing has revealed a general lengthening of the growing season as the climate warms, but also a potential stress-induced browning trend in later successional

vegetation (Bunn & Goetz, 2006; Dannenberg et al., 2020; Myneni et al., 1997; Park et al., 2016; Sulla-Menashe et al., 2018). The conflict between these two divergent patterns may, in part, be related to historical data artifacts, sensor mismatch or other scaling issues (Guay et al., 2014; Myers-Smith et al., 2020; Robin et al., 2008), but is likely reflecting a broader shift in seasonal greenness (either increasing or decreasing) in response to warmer, drier summer conditions or a general change in the surface moisture regime, which, in turn, impacts plant seasonality (Arndt et al., 2019; Myers-Smith et al., 2020). Disturbance also has a marked influence on phenology (Peckham et al., 2008; Serbin et al., 2009) which complicates the characterization of broad-scale NDVI patterns across the ABR (Figure 2). Recent evidence shows that the interpretation of greening and browning trends is strongly dependent on land cover and disturbance history, whereas areas of more stable land cover have much more muted trends (Wang & Friedl, 2019).

To address the challenges of accurately capturing evergreen seasonality and avoiding potential mischaracterization, new remote sensing observations combined with improved in-situ monitoring networks are needed (Tang et al., 2016). The consideration of additional information from TIR or solar-induced fluorescence (SIF) could be used to identify plant stress responses that may be confused with the phenological signals (greening vs browning) found in more commonly used, coarse-resolution NDVI data (Luus et al., 2017; Magney et al., 2019; Still et al., 2021). In addition, the increased coverage and availability of very high-resolution (<5 m) data allow for improved

characterization of fine-scale species composition and within-pixel phenological patterns (Arndt et al., 2019). By combining fine-resolution information with other long-term, coarse observations, it will become increasingly easy to identify whether satellite signals are related to underlying changes in vegetation physiology or stress, land-cover transition, or in response to disturbance (Figure 2). Lastly, while our discussion, and the majority of studies in the ABR, has focused on aboveground phenology, the belowground growing season length is markedly longer than that of the canopy, and understanding the relationship between subsurface dynamics and aboveground phenology will likely provide valuable insights into the carbon dynamics of high-latitude ecosystems and remains a critical research need for the region (Blume-Werry et al., 2016).

4 | REMOTE SENSING IS A VALUABLE TOOL FOR LINKING PHENOLOGY AND PHYSIOLOGY

Satellite remote sensing is an invaluable tool for characterizing vegetation across the ABR (Table 1). However, a key challenge is identifying the difference between the general “greenness” of vegetation, and the underlying physiology necessary to understand photosynthetic phenology (Wong et al., 2020; Wong & Gamon, 2015a). Observations have shown an increase in the seasonal cycle of CO₂ concentration (Graven et al., 2013), but we still lack

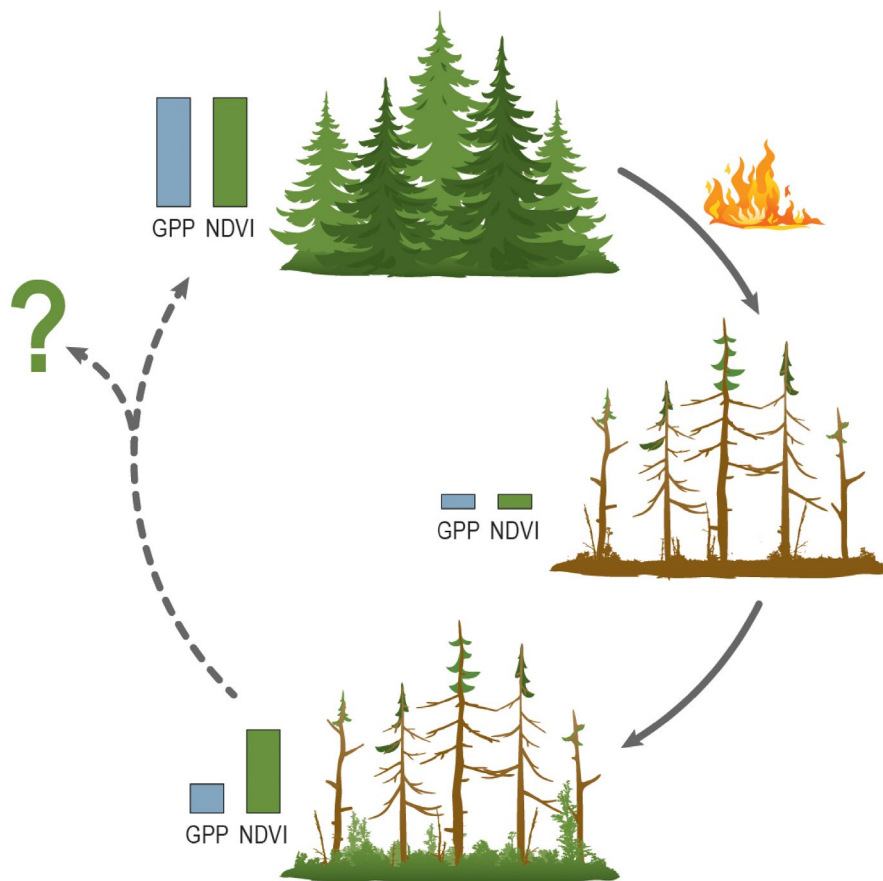


FIGURE 2 The potential mismatch between gross primary productivity (GPP) and forest greenness as estimated by normalized difference vegetation index (NDVI). Shortly after a disturbance event, such as a fire, understory vegetation can quickly develop and result in an NDVI signal that is not indicative of a return to the original, or an alternate, ecosystem state [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

an understanding of whether this can be attributed to a change in surface vegetation, growing season length, or a direct physiological response (Forkel et al., 2016; Piao et al., 2018; Thomas et al., 2016). While knowledge of the temporal and spatial variation in dominant plant types is critical for mapping and modeling carbon, water, and energy fluxes, these quasi-static maps do not account for the daily to seasonal changes in remote sensing signatures that relate to short-term environmental conditions and underlying plant physiology. A combination of long-term characterization of the changes in surface structure and composition and shorter-term (daily to seasonal) characterization of vegetation condition (as inferred from spectral signatures) is needed to better quantify short-term functional responses to weather conditions and longer-term changes in underlying physiology and GPP.

Historical analyses of satellite time-series data have related greenness to photosynthetic activity (e.g., Goetz et al., 2005), yet at the more local scale these connections can be more tenuous and may be impacted by leaf phenology, scale, vegetation composition, local environmental conditions, and canopy structure (e.g., La Puma et al., 2007; May et al., 2018). For example, in large portions of the ABR, satellite-derived NDVI can saturate early in the growing season or otherwise fail to track seasonal photosynthetic downregulation (Peñuelas et al., 2011), resulting in a disconnect between the general greenness signal and ecosystem productivity (Fiore et al., 2020; Ueyama et al., 2013). Other narrow-band SVIs that are sensitive to leaf pigment pools and fluxes, such as the photochemical reflectance index (PRI) and the chlorophyll/carotenoid index are far more sensitive to within-day and seasonal variation in underlying vegetation function and GPP (Gamon et al., 2016; Nichol et al., 2000; Peñuelas et al., 2011). During the NASA BOREal Ecosystem Atmosphere Study (BOREAS), field and airborne IS platforms, such as AVIRIS and CASI (Table 1), were used to demonstrate the capacity of spectroscopy to provide deeper insight into ABR leaf properties, canopy condition, and carbon fluxes, specifically to retrieve canopy light-use efficiency (Gamon et al., 2004; Rahman et al., 2001). Indices, including PRI, have since been used across the region to infer light use efficiency and GPP at seasonal and interannual timescales (Drolet et al., 2008; Nichol et al., 2002).

However, there remain additional challenges with specific attribution of the underlying plant conditions that are conveyed through reflectance signatures (Garbulsky et al., 2011). Historically, PRI was used to infer light-use efficiency or radiation-use efficiency of plants. However, the underlying drivers of PRI are complex, responding rapidly to changes in leaf physiology and pigment dynamics, particularly during spring and fall phenological transitions (Wong & Gamon, 2015b). Thus far, it is been challenging to transfer the specific derived relationships for any one study to new systems or locations given the many underlying drivers of variation in PRI (Garbulsky et al., 2011). Some of this mismatch is related to differences in measurement protocols, the multitude of challenges when scaling from leaves to canopies, potentially confounding seasonal changes in pigments not accounted for in these relationships, as well as canopy structural influences (Hilker et al., 2008; Peñuelas et al.,

2011). Given these issues, the widespread use of spectral index approaches like PRI to monitor carbon uptake across the ABR requires further development of measurement and scaling protocols (Gamon et al., 2019; Garbulsky et al., 2011), though the promise of these indices warrant further attention.

Together with SVI methods, other reflectance-based spectroscopic approaches could yield additional insights into the spatial and temporal variation of plant function across the ABR. In particular, since BOREAS, the capacity to map plant functional traits across space and time with IS has increased substantially (Gamon et al., 2019; Serbin & Townsend, 2020), including the retrieval of carbon fluxes and photosynthetic capacity (DuBois et al., 2018; Serbin et al., 2015). This is commonly achieved by developing empirical relationships between spectral reflectance and leaf traits at leaf, canopy, and landscape scales, using all the information provided by IS rather than selecting a single or small set of SVIs (Singh et al., 2015; Wang, Chlus, et al., 2020). In North America, the NASA ABoVE experiment (Miller et al., 2019) has generated a considerable amount of new airborne remote sensing data, including high spectral resolution AVIRIS imagery (Table 1), providing a new opportunity to characterize spatial and temporal variation in functional traits across a climate transect in the ABR. The use of additional airborne platforms, including the National Ecological Observatory Network (NEON) Airborne Observation Platform (AOP) and NASA Goddard's Lidar, Hyperspectral and Thermal Imager (G-LiHT) (Table 1) in portions of the ABR (Alonzo et al., 2020) could also enable retrieval of plant structural and functional properties (Kamoske et al., 2021). The potential use of these approaches to develop maps of plant traits in arctic and boreal vegetation should be explored in more detail and linked to both fieldwork and data from satellite platforms to develop relationships that can be used to retrieve plant traits throughout the ABR (e.g., Ma et al., 2020).

Other novel airborne and satellite observations may also provide more direct estimates of carbon fluxes in the ABR, including airborne flux measurements (Serafimovich et al., 2018) and SIF (Luus et al., 2017). SIF relates to GPP through the connection between photosynthesis and chlorophyll energy dissipation pathways; given this linkage, SIF observations have been used to estimate ecosystem- to global-scale plant GPP at daily, monthly, and seasonal scales across a range of plant types (Mohammed et al., 2019). However, issues remain as to the exact mechanisms driving this relationship across scales, which requires further development of the approach for widespread use (Chen et al., 2021). However, SIF closely tracks seasonal photosynthesis and GPP, including in evergreen conifer canopies (Magney et al., 2019) and arctic tundra (Luus et al., 2017). Given the increasing availability of airborne SIF observations through the ABoVE program (Table 1), including areas containing eddy covariance observations (Miller et al., 2019), it should be increasingly possible to improve linkages between vegetation productivity in the ABR and remote sensing of GPP, as well as improve the scaling of these relationships to satellite-derived SIF datasets.

Photosynthesis is strongly regulated by temperature (Yamori et al., 2014), making it critical to accurately estimate canopy

temperatures to accurately predict carbon uptake. Thermal infrared remote sensing (Table 1) can measure the land-surface temperature across space and time (Costa et al., 2013; Still et al., 2019, 2021). Steady improvements and availability of TIR remote sensing technologies have begun to enable remote sensing of plant function and stress, from leaves to whole ecosystems (Fisher et al., 2020; Yang, Meng, et al., 2020). The indirect remote sensing of photosynthetic capacity also requires knowledge of the thermal properties of vegetation (Serbin et al., 2015), while detection of plant stress responses is enhanced using TIR observations (Costa et al., 2013). In addition, TIR measurements allow for the indirect retrieval of surface water status and fluxes, including evapotranspiration (Chen & Liu, 2020; Fisher et al., 2020). Together with TIR observations (Table 1), it may also be possible to remotely sense ABR carbon, water, and energy cycling (Still et al., 2021). For example, Junttila et al. (2021) demonstrate the combined use of an optical and TIR approach to upscale both ecosystem-scale GPP and respiration across peatland sites in Sweden and Finland. However, some platforms do not currently provide data at high latitudes (Fisher et al., 2020). Moreover, the thermal regime in the ABR is complex, strongly tied to the cover and structure of vegetation (Kropp et al., 2020), and as a result, understanding the partitioning of energy across sensible, latent, and ground heat fluxes is essential for monitoring changes in ecosystem productivity to global change (Lorantý et al., 2018).

Linking physiological understanding of plants to their environment with remote sensing could transform the standard approach for model parameterization of PFTs (e.g., Serbin et al., 2015; Singh et al., 2015; Thomson et al., 2021). In addition, use of these data with models would also provide a means to constrain model process representation of albedo, evapotranspiration, LAI, and plant productivity (Shiklomanov et al., 2020; Smith et al., 2020; Viskari et al., 2015), evaluate model predictions or test new structural hypotheses (Collier et al., 2018; Forzieri et al., 2018; Kumar et al., 2012; Oleson & Bonan, 2000) and, importantly, scale up our functional understanding of ABR carbon dynamics and surface fluxes (Huemmrich et al., 2013; Pan et al., 2020).

5 | IMPROVING PHYSIOLOGICAL PARAMETERIZATION OF HIGH-LATITUDE PFTS OFFERS DISTINCT OPPORTUNITIES

While remote sensing can improve our knowledge of photosynthesis across broad spatial and temporal scales, our ability to reduce uncertainty in the modeling of high-latitude GPP can also benefit from incorporating a deeper understanding of the photosynthetic physiology within and among PFTs in the region. To give different PFTs their varying structural and functional properties, TBMs commonly prescribe static values of plant traits to each PFT (Wullschlegel et al., 2014). These traits then determine how a given PFT will respond to the environment, and in terms of GPP, determine what green “means” when linking phenology with physiological activity. Global-scale TBMs typically represent the ABR with ~5 PFTs

(Table 2). Furthermore, PFTs are often parameterized with identical, or nearly identical, values for key physiological processes connected to GPP, for example, quantum yield, the stomatal slope parameter (m , g_1), or the maximum carboxylation capacity of Rubisco (V_{cmax}) (Lin et al., 2015; Rogers, 2014; Rogers et al., 2019). Therefore, the PFT categories that are typically used to describe vegetation in the ABR lack important physiological diversity (Saccone et al., 2017) and, within a PFT, lack the plasticity of functional properties typically seen in a single species (Wullschlegel et al., 2014). For example, within the boreal evergreen needleleaf tree PFT, V_{cmax} can vary by at least 3.5-fold in the literature, and swapping between the highest and lowest V_{cmax} values reported within this PFT alters tree-level net carbon gain by 75% (Stinziano et al., 2018). Similarly, a recent study showed how Scots pine and Norway spruce, both in the evergreen needleleaf PFT, differ in their sensitivity to drought (Gutierrez Lopez et al., 2021).

The uncertainty around parameterizing PFTs was highlighted by Fisher, Hayes, et al. (2018), who found that climate modelers identified PFTs as one of the top six areas where more data are needed to improve the modeling of high-latitude terrestrial ecosystem dynamics. Dietze et al. (2014) demonstrated how including new observations of the stomatal slope parameter can lead to a reduction of uncertainty in modeled carbon gain, providing strong motivation for data collection and synthesis of traits that drive model uncertainty. The case for improving our spatial and temporal understanding of variation in key traits associated with model representation of GPP, such as V_{cmax} and g_1 , is clear and is also true for many biomes (Lin et al., 2015; Ricciuto et al., 2018; Rogers, 2014; Rogers et al., 2017). However, the low species diversity in the ABR makes this challenge theoretically tractable for this biome, and remote sensing offers exciting opportunities to retrieve these traits from airborne or satellite platforms (Cawse-Nicholson et al., 2021; Gamon et al., 2019). One opportunity to improve model representation of GPP that is particularly relevant for the ABR is improving our understanding and model representation of the low temperature sensitivity of quantum yield (Table 3).

5.1 | Quantum yield: A critical knowledge gap and a unique opportunity to improve model representation of GPP at high latitudes

High-latitude ecosystems experience high seasonality with regard to both temperature and irradiance. One of the greatest challenges for photosynthesis in these highly seasonal regions is photodamage (Ensminger et al., 2006). Low temperatures at high latitudes reduce the demand for ATP and NADPH in the Calvin–Benson cycle, but also the capacity for repair of photodamage and recovery from photoprotection mechanisms (Barber & Andersson, 1992; Bilger & Björkman, 1991). If low temperatures coincide with high to moderate irradiance conditions, the photosynthetic electron transport chain continues to absorb photons, since photochemistry is much less temperature sensitive than are enzymatic reactions (Ensminger et al., 2006; Groot

TABLE 2 Key physiological parameters associated with representation of photosynthesis and stomatal conductance in five major climate models

Terrestrial biosphere model (key references)	Plant functional types present in the Arctic–Boreal Region	Maximum rate of carboxylation, at the reference temperature 25°C ($V_{\text{cmax},25}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$)	Maximum quantum yield of electron transport of absorbed light ($\varphi_{\text{ET},a}$, mol electrons mol^{-1} absorbed quanta)	Key stomatal parameters associated with formulations used to represent water use efficiency	
				g_1 (unitless)	g_0 ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
CLM 5.0 (Lawrence et al., 2019)	NET boreal	55	0.425	2.35	100
	NDT boreal	52	0.425	2.35	100
	BDT boreal	50	0.425	4.45	100
	BDS boreal	44	0.425	4.7	100
	C ₃ Arctic grass	52	0.425	2.22	100
CTEM 2.0 (Melton & Arora, 2016)	NET	62	0.320	m (unitless)	b ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
	NDT	47	0.320	9	100
	BDT	57	0.320	9	100
	C ₃ grass	75	0.320	12	100
E3SM 1.0 (Golaz et al., 2019; Oleson et al., 2013)	NET boreal	63	0.425	m (unitless)	g_0 ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
	NDT boreal	39	0.425	9	10,000
	BDT boreal	58	0.425	9	10,000
	C ₃ Arctic grass	78	0.425	9	10,000
JULES 4.2 (Harper et al., 2016)	NET	54	0.320	F_0 (unitless)	D_{crit} (kg kg^{-1})
	NDT	51	0.320	0.875	0.06
	BDT	57	0.320	0.875	0.041
	BDS	50	0.320	0.875	0.06
	C ₃ grass	51	0.320	0.950	0.03
Orchidee 4.0 (Krinner et al., 2005; Naudts et al., 2015; Yin & Struik, 2009)	NET boreal	38	0.372	0.931	0.051
	NDT boreal	35	0.372	a_1, b_1 (unitless)	g_0 ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
	BDT boreal	38	0.372	0.85, 0.14	6.25
	C ₃ grass	70	0.372	0.85, 0.14	6.25

Note: * V_{cmax} at optimal growth temperature is variable and calculated as $27.5^\circ\text{C} + 0.25 \times$ the multiannual mean temperature, optimal growth temperature for the other PFTs in Orchidee is set at 25°C . Stomatal model formulations and descriptions of their parameters have been published previously.

Abbreviations: BDS, broad-leaved deciduous shrub; BDT, broad-leaved deciduous tree; CLM, The Community Land Model; CLM, Medlyn et al. (2011); CTEM, Canadian Terrestrial Ecosystem Model; CTEM, Leuning (1995); E3SM, Ball et al. (1987); E3SM, Energy, Exascale, Earth System Model; JULES, Jacobs (1994); JULES, Joint UK Land Environmental Simulator; NDT, needle-leaved deciduous tree; NET, needle-leaved evergreen tree; Orchidee, Organizing Carbon and Hydrology in Dynamic Ecosystems model; ORCIDEE, Yin and Struik (2009). For calculation of $\varphi_{\text{ET},a}$ see Rogers et al. (2019). Note that comparisons of stomatal parameters among models are not possible due to different model formulations.

TABLE 3 Current challenge and opportunities associated with improving estimation of gross primary productivity in the Arctic–Boreal Region

Challenge	Measurement need	Role of remote sensing	Opportunity	Outcome
What PFTs currently populate the ABR?	Improved estimates of fractional cover of PFTs	Identification of PFTs	High-resolution coverage maps	More accurate distribution for model initialization or evaluation
What is the current structure and stand biomass in the ABR?	Better estimates of standing biomass and canopy structure and in relation to disturbance and land-use history. Critical for model benchmarks	Characterize standing vegetation height, structure, and biomass properties	High-resolution maps of biomass and standing structure over space and time	Comprehensive characterization of the distribution of carbon stocks, historical patterns, and relationship with environmental drivers
Current PFT parameterization does not capture plasticity or variation	Measure key parameters currently in TBMs but poorly represented (e.g., V_{cmax} , g_1) and characterize their variation along climatic gradients	Linkage between traits and remote sensing can enable scaling of trait retrieval and establish links with environmental and climatic gradients	Wall-to-wall measurement of key traits critical to the modeling of GPP	Improved trait representation for the ABR. Development of climate-smart PFTs where the potential for acclimation is understood and represented in TBMs
Phenology is prescribed in TBMs	Link key environmental drivers to green-up and brown-down	Build in fine-scale topographic variation that can modulate phenological response	Improved understanding of environmental cues for green-up and brown-down	Emergent phenology in TBMs that is linked to environmental cues and constrained by physiological understanding
Green leaves do not always equate with full photosynthetic competency	Improved understanding of photosynthetic competency and stress tolerance including abiotic drivers, and biotic and temporal variation	High spectral resolution imagery, imaging spectroscopy, SIF, Thermal/ET, PRI, TIR	Add a missing component to TBMs that is particularly relevant for the ABR (variation in quantum yield)	New process understanding added to TBMs and improved model representation of GPP during the shoulder seasons

Abbreviations: g_1 , the stomatal slope parameter; GPP, gross primary productivity; PFTs, plant functional type; PRI, photochemical reflectance index; SIF, solar-induced fluorescence; TBMs, terrestrial biosphere models; TIR, thermal infrared; V_{cmax} , maximum carboxylation capacity of Rubisco.

et al., 1997; Oquist & Huner, 2003). The imbalance between the capacity to generate reductant and ATP through photochemistry and the capacity to use these products in the Calvin–Benson cycle can lead to the production of reactive oxygen species in the electron transport chain during cold, high light conditions, consequently damaging leaves (Ensminger et al., 2006; Murchie & Ruban, 2020; Oquist & Huner, 2003).

To prevent photodamage, some high-latitude evergreen conifers and arctic shrubs downregulate photosynthesis in the winter through a regulated inactivation of the photosystem II reaction center and a reorganization of the associated light harvesting complexes to reorient their activity towards light energy dissipation rather than light energy absorption (Ensminger et al., 2006; Oquist & Huner, 2003; Solanki et al., 2019). But there is considerable variation between species in the mechanisms used to prevent photodamage, with consequences for GPP. For example, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are co-occurring boreal evergreen needleleaf tree species that dominate Scandinavian forests, accounting for 91% of total forest cover in this region (Black et al., 2005). Scots pine actively downregulates its ability to fix CO₂ during the winter while upregulating electron sink capacity to prevent photodamage during cold, bright days (Saccone et al., 2017; Yang, Blanco, et al., 2020). This seasonal regulation allows Scots pine to reestablish photosynthetic CO₂ assimilation in the spring with minimal damage to the electron transport system. In contrast, Norway spruce lacks this mechanism, which results in repeated photodamage during spring and a suppression of photosynthesis (Yang, Blanco, et al., 2020). The differences in physiology between these two species therefore underlie differences in potential springtime GPP in these two common species, even though Norway spruce is in the same PFT, the same family (Pinaceae) and the same growing region as Scots pine.

The maximum quantum yield of photosynthesis reflects the ability of plants to use incident irradiance for CO₂ assimilation, and in unstressed plants is remarkably constant (Baker, 2008; Long et al., 1993). Therefore, most TBMs assume the same quantum yield for all PFTs and do not include any temperature sensitivity for this parameter (Dietze, 2014; Rogers et al., 2017). While this assumption is robust for many PFTs and biomes, it does not account for observations of low quantum yield that are associated with the typically cold growth temperatures experienced by arctic and boreal vegetation (Albert et al., 2012; Bokhorst et al., 2010; Kolari et al., 2014; Marchand et al., 2006; Rogers et al., 2019; Solanki et al., 2019; Wallin et al., 2013). Reductions in quantum yield and convexity (which determines the irradiance at which light saturation is reached), and slow recovery from photoprotection and photodamage reduce carbon gain by up to 32% in crop systems, and transgenic tobacco that had been bioengineered for a rapid recovery from photoprotection has a 15% increase in photosynthesis and yield (Kromdijk et al., 2016; Murchie & Ruban, 2020; Zhu et al., 2004). These studies in temperate systems strongly suggest that understanding known reductions in quantum yield in the ABR is an important area to consider. Seasonal hardening in evergreen species associated with long-lived quenching through

accumulation and retention of zeaxanthin dramatically reduces the quantum yield in the winter months and while the foliage appears green, the dehardening process can take weeks before quantum yield is restored, with clear implications for GPP (Murchie & Lawson, 2013; Murchie & Ruban, 2020). However, these phenomena are not currently represented in TBMs. A lack of understanding of the environmental cues, dynamics, and mechanisms of photodamage and photoprotection in the ABR is currently hindering potential implementation of a dynamic quantum yield in TBMs. Future field work focused on closing this knowledge gap could be enhanced if those efforts are coupled with remote sensing to maximize the potential to scale understanding and measurement approaches over space and time.

6 | HIGH-LATITUDE VEGETATION RESPONSES TO GLOBAL CHANGE WILL SHAPE LONG-TERM CHANGES IN CARBON UPTAKE

The impact of climate change on plants in northern latitudes is often assumed to be positive, since warming should allow for enhanced growth of highly productive species (Way & Oren, 2010), lengthen the growing season (Richardson et al., 2010, 2018), and alleviate low temperature inhibition of photosynthesis (Richardson et al., 2010; Stinziano & Way, 2014). Concurrently, high CO₂ concentrations can stimulate photosynthesis and growth (Ainsworth & Rogers, 2007). But the reality is more mixed. Under warming of up to 9°C imposed in the field on mature trees, tamarack (a deciduous conifer) had increased photosynthesis, which was correlated with higher stomatal conductance and lower leaf water potentials (Dusenge et al., 2020, 2021; Warren et al., 2021). In contrast, the evergreen conifer black spruce had lower stomatal conductance under warming, which allowed the trees to maintain a moderate stem water potential, but also constrained photosynthesis (Dusenge et al., 2021; Warren et al., 2021). This trade-off between prioritizing either water status or carbon uptake may become increasingly common in northern latitudes as the climate warms and the vapor pressure deficit (VPD) increases. For example, Van Herk et al. (2011) showed that sap flow increased significantly in black spruce trees under a simulated air warming treatment with VPD matching control, but lower rates in the warming and increased VPD treatment, illustrating a potentially strong constraint of VPD on the function of boreal tree species. Indeed, there are often negative effects of warming on boreal tree growth when soil moisture is low, but potential positive effects, especially in broad-leaved tree species, when soil water is abundant (D'Orangeville et al., 2018; Girardin et al., 2016; Reich et al., 2018).

Warming experiments and observations conducted over climatic gradients within the Arctic have demonstrated that shrubs, forbs, grasses, and sedges can all respond positively to warmer conditions, with increased biomass, plant height, leaf area, allocation to reproductive biomass, and earlier green-up (Arft et al., 1999; Bilger & Björkman, 1991; Björkman et al., 2018; Elmendorf, Henry,

Hollister, Björk, Boulanger-Lapointe, et al., 2012; Hudson et al., 2011; Klady et al., 2011; Wahren et al., 2005). However, the response of an individual species or PFT is strongly influenced by the presence or absence of permafrost, the climatic zone, and moisture regime, with notable differences between observations in Europe and North America (Bjorkman et al., 2018; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Myers-Smith et al., 2015; Wahren et al., 2005).

The changes in species composition, biomass, phenology, and photosynthetic physiology wrought by climate change will play an increasingly important role in determining the GPP of the ABR, yet our knowledge of how increasing temperature, $[CO_2]$, and VPD will affect high-latitude vegetation is lacking. The vast majority of experiments investigating temperature responses in the region have been passive warming experiments. While these experiments provide important understanding of how warming alters these communities (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012), the manipulations rarely elevate temperature by more than $\sim 1.5^\circ C$ (Marion et al., 1997), leaving critical uncertainty over the response to future projected temperature increases in the region (IPCC, 2014). There are even fewer examples of CO_2 manipulations in the ABR (Bridgman et al., 2020; Oechel et al., 1994) and, with some notable exceptions (Hanson et al., 2017; Lamba et al., 2018; Sigurdsson et al., 2013), manipulations of CO_2 and temperature that are aligned with projected temperature and $[CO_2]$ increases are rare.

6.1 | Composition

Global change-induced shifts in the composition of vegetation in the ABR are likely to occur via northwards migration of species, differential mortality rates between species, variation between species in their capacity to increase growth under warmer temperatures and higher $[CO_2]$, and variable responses to increased disturbance regimes (Figure 3).

While there is relatively little evidence for poleward migration of the northern treeline into Arctic tundra, increased recruitment of seedlings has been seen at many sites across Eurasia and North America (Gamache & Payette, 2005; MacDonald et al., 2008). This greater recruitment has led to a higher density of trees near the treeline, but the northern limit of the boreal tree line has yet to advance to the extent that it did during the Medieval Warm Period (~ 1000 – 1300 AD, Gamache & Payette, 2005; MacDonald et al., 2008). Thus, while large-scale shifts in the ecotone between the Arctic and boreal are likely over the next century, harsh tundra abiotic conditions and a lack of neighboring trees that modify local microclimates appear to currently limit seedling establishment beyond the treeline (Germino et al., 2002). The migration of temperate trees northwards could also significantly affect GPP, as many boreal evergreen species have low photosynthetic rates (Reich et al., 2018). However, the occurrence of boreal trees at a site impedes the establishment of temperate seedlings, mainly due to edaphic characteristics related to needle cover, the presence of dead wood, and

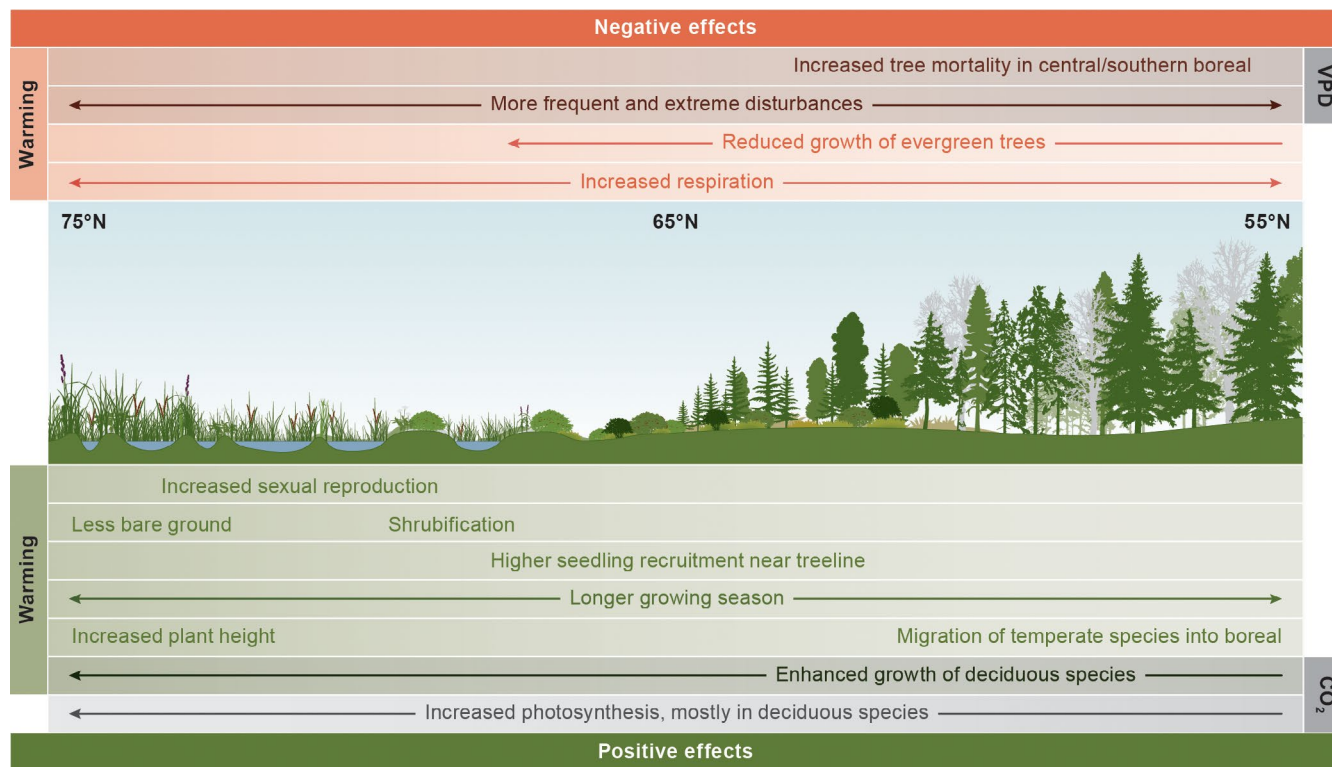


FIGURE 3 The individual, and combined, effects of the primary climate change drivers; rising CO_2 , temperature, and vapor pressure deficit (VPD) on processes and traits that will result in positive or negative impacts on gross primary productivity across the Arctic-Boreal Region [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

mycorrhizal abundance, which could cause lags between the climatic suitability of a site and the ability of temperate trees to migrate (Carteron et al., 2020; Johnstone et al., 2016; Solarik et al., 2020).

Changes in mortality and growth due to climate change will also alter the vegetation composition of the ABR. In the boreal forest, mortality rates are increasing in many tree species, particularly in North America (Luo & Chen, 2013, 2015; Peng et al., 2011). Tree mortality rates in a range of species increased 4.7% per year within the Canadian boreal region between 1963 and 2008, an effect attributed to climate change-induced drying (Peng et al., 2011). The stability of northern peatlands is strongly linked with moisture conditions, and prolonged drought can cause significant changes to peatland structure and composition, with important implications for carbon storage (Kokkonen et al., 2019; Lees et al., 2021; Zhong et al., 2020). However, greening trends are more evident in Eurasia than in North America as the climate warms (Jian et al., 2013), indicating key differences in how boreal ecosystems may respond to climate change. The cover of pioneer species, which mainly include deciduous trees and shrubs, is likely to increase in the boreal region as the climate warms, both because they often recover faster in disturbed areas where evergreen cover was previously dominant (Gauthier et al., 2014), but also because their growth tends to respond positively to increasing growth temperatures and CO₂ concentrations (Dusenge et al., 2020; Way & Oren, 2010). A broad range of evidence has indicated an increase in the growth and abundance of shrubs, and an advancing shrub line, across the Arctic. However, shrubification is not uniform across this region, with some areas showing no change, while others show marked increases. There are likely several factors leading to this heterogeneity and understanding the influence of disturbance, warming, nutrient cycling, topography, and hydrology will be key to identifying the drivers of shrub expansion (Mekonnen et al., 2021; Myers-Smith et al., 2020).

6.2 | Phenology

As the climate warms, earlier springs and extended warm temperatures in the autumn are prolonging the growing season (Garonna et al., 2014). The spring phenology of northern deciduous trees is more responsive to warming than that of evergreen species from the same range (Montgomery et al., 2020). While a longer growing season should increase GPP in the ABR, this change in phenology comes with risks. Earlier spring leaf-out due to warmer spring temperatures is correlated with increased risk of frost in northern latitudes (Liu et al., 2018; Richardson et al., 2018). In these conditions, variation in how species protect the photosynthetic apparatus during winter (as discussed above) is likely to translate into differences in the degree to which they can quickly upregulate photosynthesis in the spring. Indeed, the differences between winter photodamage defense strategies in Scandinavian boreal trees led to a suppression of spring carbon uptake in Norway spruce from repeated photodamage, but high photosynthetic rates in Scots pine (Saccone et al., 2017; Yang, Blanco, et al., 2020).

6.3 | Physiology

Model representation of leaf and canopy processes is central to projecting the response of plants and ecosystems to future global change and understanding the role plants play in determining the rate of climate change. Direct responses to rising CO₂ are limited to the increased carboxylation and reduced oxygenation reactions by Rubisco, and the reduction in stomatal conductance (Ainsworth & Rogers, 2007). The response of plants and ecosystems to increasing VPD is broader, including changes in leaf area and photosynthetic rate, but strongly mediated by the VPD response of stomatal conductance, which varies among PFTs (López et al., 2021). Although rising temperatures affect many ecosystem processes, there are direct responses of photosynthesis and stomatal conductance to warming (Dusenge et al., 2019). Plants also exhibit acclimation to these three environmental drivers in both rates and fluxes, via changes in their underlying physiology (Ainsworth & Rogers, 2007; Dusenge et al., 2019; Kumarathunge et al., 2019). In addition, key physiological traits underpin sensitivity to climate change, for example, the importance of minimum conductance (cuticular conductance+conductance through leaky stomata) in determining vulnerability to drought and subsequent increases in fire risk (Choat et al., 2018; Nolan et al., 2020). Therefore, accurate process representation and parameterization associated with model representation of CO₂ and water exchange is central to models' ability to project the impacts of global change.

While TBMs all represent these direct responses of photosynthesis to CO₂, temperature, and VPD (or relative humidity), model representation of acclimation to these principal drivers of global change is not as well developed (Rogers et al., 2017). Acclimation of photosynthesis to growth temperature is commonly represented by algorithms which adjust the parameters associated with the modified Arrhenius function (e.g., V_{cmax}) based on the growth temperature of a preceding time period (Kattge & Knorr, 2007). While the need to ensure that these formulations are appropriate for the cold conditions found in high latitudes has been raised (Stinziano et al., 2018), this approach is robust over an extended range of measurement temperatures, including the low growth temperatures of relevance to the ABR (Kumarathunge et al., 2019). The physiological acclimation of photosynthesis to rising [CO₂] (Ainsworth & Rogers, 2007) is largely absent from TBMs, with the exception of optimality approaches which enable well-documented reductions in V_{cmax} with rising [CO₂] (Smith et al., 2019). Lastly, the potential for physiological acclimation to rising VPD is largely unknown because very little work has isolated the physiological response and acclimation of rising VPD from rising temperature, and it is not yet possible to represent acclimation to VPD in TBMs (Grossiord et al., 2020; López et al., 2021). Therefore, the effects of global change on GPP in current TBMs are largely based upon model representations of direct physiological responses to global change, but not acclimation. When combined with static parameterization of PFTs, this lack of acclimation "bakes in" the response to global change and may not reflect important physiological changes that result from long-term exposure

to elevated temperature, [CO₂] and VPD (Ainsworth & Rogers, 2007; Dusenage et al., 2019; López et al., 2021).

Elevated CO₂ concentrations could boost photosynthesis and growth. However, studies that grew northern species under combined CO₂ and warming typically found weak effects of elevated CO₂ on photosynthesis and growth in high-latitude conifer species (Dusenage et al., 2020; Sigurdsson et al., 2013) or a downregulation of photosynthesis in response to high CO₂ (Dusenage et al., 2020; Lamba et al., 2018; Tjoelker et al., 1998), such that in many cases the effects of warming tend to predominate. While some of the variation we see in the response to these climate drivers may be related to differences between PFTs (Dusenage et al., 2020; Tjoelker et al., 1998), variation in the response to elevated [CO₂] within a PFT has also been found. Norway spruce and Scots pine, the Scandinavian boreal species discussed earlier, not only differ in how they deal with winter photodamage, but also in their ability to acclimate photosynthesis to elevated temperatures and atmospheric CO₂ concentrations (Kurepin et al., 2018). Under warming of up to 8°C and increased CO₂ concentrations, Scots pine maintains a similar photosynthetic rate as the control, cool-grown trees (Kurepin et al., 2018). Yet, elevated growth temperatures suppressed photosynthetic rates by 33%–50% in Norway spruce, a result that correlated with a diversion of reducing power from photosynthetic electron transport away from CO₂ fixation and toward alternate electron sinks (Kurepin et al., 2018).

7 | PATH FORWARD

Accurate characterization of the vegetation in the ABR is critical for improving the capacity of models to project the impact of global change on this important region and in turn to understand whether this region will continue to be a carbon sink in the future. The opportunity for improving process knowledge and parameterization in the ABR is ripe because the low species diversity, and the dominance of just a few species in many regions means that gaining knowledge and improving process representation in TBMs can realistically be achieved in the near term. Advancing our understanding will require field work to better understand and parameterize key processes for existing and potentially new classifications of PFTs. One critical tool to advance understanding, and to enable scaling across the ABR, will be the increased use of remote sensing. The biggest opportunities for scaling will be made by pairing ground-based field-studies of physiology and ecology with remote sensing. This synergy would provide invaluable opportunities to develop relationships between important physiological processes, the key plant traits that drive them, and remotely sensed signals; ultimately enabling retrieval of structural and functional parameters throughout the ABR (Serbin et al., 2015, 2019; Singh et al., 2015). An important bridge to enable scaling will be the increased use of unoccupied aerial systems which can capture fine-scale surface structural and functional diversity (Alonzo et al., 2020; Yang, Meng, et al., 2020), and, in combination with more coarse resolution data from airborne and satellite platforms,

inform our ability to scale and map key plant processes and traits. The increased availability of airborne datasets and upcoming spaceborne missions (Guanter et al., 2015; Miller et al., 2019; Kellogg et al., 2020; e.g., Cawse-Nicholson et al., 2021; Poulter, 2021) provides important new opportunities for increasing observations across the ABR.

Accurate representation of physiological processes is critical for capturing the response of plants and ecosystems to global change because these processes, and their parameterization, play a major role in determining the response of GPP to global change (Rogers et al., 2017). This is true globally, but process representation and parameterization of GPP in the ABR presents unique challenges and opportunities. For example, understanding of the low temperature sensitivity and temporal dynamics of reductions in quantum yield is a key knowledge gap that has the potential to have a marked impact on model estimates of GPP, yet is currently missing from models and is potentially important, but challenging to capture in the ABR.

Accurate model representation of the response of GPP to global change is also dependent upon understanding the acclimation of existing vegetation to the drivers of global change. Without a greater understanding of the acclimation response (and, by extension, the climate sensitivity) of a given PFT, the modelled response to climate change will be based on how those plants function in today's climate. In order to future-proof model representation of PFTs and enable accurate competition between PFTs in future climate scenarios, we need manipulative experiments to address key uncertainties surrounding the potential for acclimation and the possible climate sensitivity of plant productivity. Unfortunately, compared to temperate systems there have been relatively few manipulative experiments in the ABR that address physiological responses and acclimation to global change. Improving our understanding and model representation of acclimation is also critical if models are to accurately predict the outcome of competition between PFTs in novel climates, particularly following disturbance where the result of competition will determine the long-term response of the ABR to global change. Representation of climate-driven community composition changes will become increasingly important for long-term model projections.

We highlight that there is a growing need to categorize species not only by their current form and function, but also based on knowledge of their ability to acclimate, compete, and maintain physiological performance and growth under future climates scenarios, for example, climate-sensitive evergreen needleleaf trees and climate-resilient evergreen needleleaf trees. Our current definition and parameterization of PFTs are understandably based on our knowledge of the current structure and function of vegetation that comprises a given PFT. Therefore, our confidence in how a PFT will respond to global change does not account for the ability of species to acclimate and maintain physiological performance under future global change scenarios. This raises the question of whether we are currently parameterizing PFTs by looking in the rearview mirror. Building climate-smart PFTs that can represent the vegetation of the future is also essential for enabling proactive management of ecosystem services for anticipated global change (Overpeck & Breshears, 2021).

Understanding potential variation in how species respond to climate change presents us with the challenge of characterizing the climate change sensitivity of a large number of species and representing those species as PFTs in TBMs. However, it is important to consider the value of such an exercise in terms of the influence of a given species on regional carbon uptake. For some biomes, this is empirically and computationally daunting because the sheer number of species precludes us from capturing their physiological and structural diversity in any meaningful manner: for example, tropical forests are estimated to contain between 40,000 and 53,000 tree species (Slik et al., 2015). In contrast, the low plant biodiversity of arctic vegetation and the dominance of just a handful of tree species in boreal forests provides a unique opportunity for taking a deeper dive into modeling the species that define the carbon cycling of these regions. There are only six tree genera that comprise the majority of the entire global boreal forest canopy (*Abies*, *Betula*, *Larix*, *Picea*, *Pinus*, and *Populus*), making it feasible to parameterize models at the genus, or possibly even species level in these regions, and to understand the plasticity and climate sensitivity of these dominant species. The advantage of such an approach for high-latitude ecosystems would be to capture known differences between these genera in their photosynthetic physiology, as noted above, and their ability to respond to climate change.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

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

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