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# Increased high-latitude photosynthetic carbon gain offset by respiration carbon loss during an anomalous warm winter to spring transition

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#### Abstract

Arctic and boreal ecosystems play an important role in the global carbon (C) budget, and whether they act as a future net C sink or source depends on climate and environmental change. Here, we used complementary in situ measurements, model simulations, and satellite observations to investigate the net carbon dioxide ( $CO_2$ ) seasonal cycle and its climatic and environmental controls across Alaska and northwestern Canada during the anomalously warm winter to spring conditions of 2015 and 2016 (relative to 2010–2014). In the warm spring, we found that photosynthesis was enhanced more than respiration, leading to greater  $CO_2$  uptake. However, photosynthetic enhancement from spring warming was partially offset by greater ecosystem respiration during the preceding anomalously warm winter, resulting in nearly neutral effects on the annual net  $CO_2$  balance. Eddy covariance  $CO_2$  flux measurements showed that air temperature has a primary influence on net  $CO_2$  exchange in winter and spring, while soil moisture has a primary control on net  $CO_2$  exchange in the fall. Funding information

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The net  $CO_2$  exchange was generally more moisture limited in the boreal region than in the Arctic tundra. Our analysis indicates complex seasonal interactions of underlying C cycle processes in response to changing climate and hydrology that may not manifest in changes in net annual  $CO_2$  exchange. Therefore, a better understanding of the seasonal response of C cycle processes may provide important insights for predicting future carbon-climate feedbacks and their consequences on atmospheric  $CO_2$ dynamics in the northern high latitudes.

#### KEYWORDS

ABoVE, boreal, carbon cycle, climate change, productivity, respiration, SMAP L4C, soil moisture, tundra

### 1 | INTRODUCTION

Arctic and boreal ecosystems play an important role in the global carbon budget, and whether they function as a future net carbon sink or source depends on seasonal climate variability and environmental change (Huemmrich et al., 2010; McGuire et al., 2012; Schuur et al., 2015). Increased warming and associated changes in the hydrologic cycle, land surface characteristics, and permafrost and snow conditions have already altered the biogeochemistry and biophysics of high-latitude ecosystems and their associated feedbacks to regional and global climate (Box et al., 2019; Koven et al., 2011). Climate warming has lengthened the growing season and contributed to high-latitude greening that has greatly enhanced photosynthetic carbon dioxide (CO<sub>2</sub>) uptake in the Northern Hemisphere over the past five decades (Ciais et al., 2019). However, high-latitude ecosystem warming also has the potential to enhance the decomposition of vast quantities of soil organic matter stored in permafrost soils, increasing soil carbon losses to the atmosphere, and reinforcing further climate warming (Commane et al., 2017; Jeong et al., 2018; Piao et al., 2008). The timing and magnitude of these photosynthetic and respiration responses to climate change have the potential to alter ecosystem carbon dynamics, and the magnitude and seasonality of atmospheric CO<sub>2</sub> concentrations (Anderegg et al., 2015; Graven et al., 2013). Since the future trajectory of the carbon cycle in highlatitude ecosystems has significant implications for Earth's climatecarbon feedback (Pearson et al., 2013; Winkler, Myneni, Alexandrov, & Brovkin, 2019), it is critical to gain a better understanding of climate sensitivity of the carbon cycle for projecting future climate change.

The net  $CO_2$  exchange depends on the balance between  $CO_2$  assimilation through vegetation productivity and  $CO_2$  release through ecosystem respiration (ER), which may respond differently to seasonal climate and environmental variations. High-latitude ecosystems are generally temperature or radiation limited, and therefore, warming has a primary control on the seasonal change in photosynthesis or respiration (Parazoo et al., 2018; Figure 1). Climate warming promotes earlier landscape thawing, a reduction in spring snow cover, earlier onset of vegetation productivity, and longer growing seasons (Box et al., 2019). These changes tend to benefit photosynthesis more than respiration (autotrophic and



**FIGURE 1** A conceptual framework showing the potential seasonal responses in net ecosystem carbon exchange to an anomalous warm spring in the high latitudes. Earlier landscape thawing from the warmer temperatures generally results in enhanced net carbon uptake in the spring. In contrast, a later fall freeze during an anomalous warm year can extend the growing season, which has the potential to enhance photosynthesis (a) or respiration (b) depending on soil moisture availability

heterotrophic) and therefore contribute to stronger net CO<sub>2</sub> uptake in the early growing season (Assmann et al., 2019; Myers-Smith et al., 2019). Temperature-controlled spring CO<sub>2</sub> uptake by plants is also the primary mechanism explaining year-to-year variations in atmospheric CO<sub>2</sub> concentration, although the temperature sensitivity of spring CO<sub>2</sub> uptake by plants at high latitudes appears to be weakening in recent decades (Piao et al., 2017). Stronger early season productivity also increases cumulative evapotranspiration (ET) demand, which can lead to lower soil moisture levels and drought stress later in the growing season (Barnett, Adam, & Lettenmaier, 2005; Buermann, Bikash, Jung, Burn, & Reichstein, 2013; Parida & Buermann, 2014; Yi, Kimball, & Reichle, 2014). Recent satellite observations over northern ecosystems have confirmed widespread moisture stress-induced decline in late growing season productivity offsetting productivity gains from warmer springs (Buermann et al., 2018), although uncertainty in the spatial pattern and magnitude of such seasonal compensations remains (Richardson et al., 2010). Late season respiration can either be enhanced due to increased labile organic matter availability (Commane et al., 2017) and higher soil organic carbon (SOC) turnover rate (Jeong et al., 2018), or reduced due

to soil moisture limitation. Depending on the sensitivity of productivity and respiration to climate and environmental change, net CO<sub>2</sub> uptake during the late growing season can either increase (Keenan et al., 2014) or decrease (Wolf et al., 2016). Cold season respiration has generally increased significantly with climate warming and may cause some high-latitude regions to switch from a net CO<sub>2</sub> sink to source in certain years (Commane et al., 2017). Better understanding of the response of net CO<sub>2</sub> exchange and its component fluxes (i.e., canopy photosynthesis and respiration) to underlying climate and environmental controls at seasonal timescales is needed to improve predictions of annual carbon budgets in northern ecosystems and their status as a terrestrial carbon sink or source for atmospheric  $CO_2$  in a warming climate.

A major obstacle to quantifying the northern carbon cycle is the scarcity of observational data over the region. In situ CO<sub>2</sub> flux measurements (eddy covariance [EC], chambers, and incubation experiments) and supporting meteorological and environmental measurements provide detailed field-level information to improve mechanistic understanding of the carbon cycle and its drivers. However, such measurements are often sparse, making it challenging to estimate the carbon-climate interactions in a spatially and temporally continuous manner based on observations alone. Scarcity of observational data also leads to insufficiently constrained and validated large-scale carbon flux estimates. As a result, there is large uncertainty in the sign and magnitude of the net annual carbon flux in high-latitude ecosystems estimated from atmospheric CO2 inversions and/or land surface models (Fisher, Huntzinger, Schwalm, & Sitch, 2014; McGuire et al., 2012, 2018). Remote sensing provides another tool to evaluate land surface conditions affecting net carbon exchange, either directly through photosynthetic activity derived from satellite vegetation indices or solar-induced chlorophyll fluorescence observations, or indirectly through satellite observed soil moisture and thermal conditions influencing ER (Schimel et al., 2015). However, satellite remote sensing retrievals are subject to observational errors, especially over the high northern latitudes where low solar illumination, frequent cloud cover, seasonal snow and ice cover, and heterogeneous land surface conditions can degrade sensor signalto-noise and result in significant data loss (Parazoo et al., 2018). To overcome limitations from any single dataset and method, we used complementary in situ measurements, model simulations, and remote sensing observations to untangle the effects of competing ecosystem processes and improve understanding of highlatitude climate-carbon feedbacks.

Here, we aim to understand the seasonal CO<sub>2</sub> dynamics and their climatic and environmental controls in high-latitude ecosystems during an anomalous warm winter to spring transition, using a suite of datasets across multiple spatial scales. We use the 2015/2016 El Niño event as a natural experiment within the National Aeronautics and Space Administration (NASA) Arctic Boreal Vulnerability Experiment (ABoVE) domain encompassing Alaska and northwestern Canada to assess how temperature anomalies affect seasonal CO2 exchange. We address three key research questions in this Global Change Biology -WILEY

study: (1) How does a warm spring affect seasonal CO<sub>2</sub> exchange in high-latitude ecosystems? (2) Are the seasonal dynamics of net CO<sub>2</sub> uptake (i.e., photosynthesis minus respiration) congruent with productivity? (3) How sensitive is net CO<sub>2</sub> exchange in northern high-latitude ecosystems to air temperature and soil moisture? We address these questions through our integrated observation and model-based analysis to clarify the seasonal carbon-climate interactions in high-latitude ecosystems.

#### 2 MATERIALS AND METHODS

#### 2.1 | Spatial domain

The ABoVE is a multiyear field campaign designed to increase understanding of the vulnerability and response of the Arctic-Boreal Region (ABR) to continued climate change. The ABR is warming at roughly twice the mean global rate due to Arctic amplification (Box et al., 2019; Loranty et al., 2016). Satellite observations show recent trends toward earlier and longer potential growing seasons, thawing permafrost and active layer deepening, and changes in snow cover conditions and hydrological budgets over the ABR coinciding with regional warming (Kim et al., 2014; Park, Kim, & Kimball, 2016; Watts, Kimball, Jones, Schroeder, & McDonald, 2012; Zhang, Kimball, Kim, & McDonald, 2011). Warming promotes longer growing seasons and stronger photosynthetic CO<sub>2</sub> uptake, but can also exacerbate drought-induced declines in vegetation productivity if available moisture becomes limiting (Zhang et al., 2008). Stronger photosynthetic CO<sub>2</sub> uptake from warming can also be offset by counterbalancing increases in shoulder season and winter CO<sub>2</sub> emissions (Box et al., 2019). The ABoVE campaign focuses on Alaska and western Canada, and encompasses approximately 22% (~6.4 million km<sup>2</sup>) of the northern (≥45°N) ABR. In this analysis, we divided the ABoVE domain into two major regions, tundra and boreal (including Taiga, Northern Forests, and Northwestern Forested Mountains), based on Environmental Protection Agency Level 1 North America ecoregion maps (https://www.epa.gov/eco-research/ ecoregions), to assess potential differences in seasonal CO<sub>2</sub> dynamics (Figure S1) between the two biomes. The tundra region is associated with a colder Arctic climate and is distributed at higher latitudes and alpine areas underlain by continuous (spatial extent >90%) permafrost (perennially frozen ground). However, recent warming is changing the ecosystem composition and structure through treeline migration and shrub encroachment in parts of the tundra region (Myers-Smith et al., 2011). The boreal forest region extends across sub-Arctic areas of central Alaska and northwestern Canada, and is underlain by isolated, sporadic, and discontinuous permafrost.

#### 2.2 Datasets

#### 2.2.1 | Carbon flux data

#### Eddy covariance measurements

We identified 18 EC flux towers across the ABoVE Core Study domain (Figure S1). Half-hourly estimates of net ecosystem CO<sub>2</sub> exchange -WILEY- Global Change Biology

(NEE) were quality controlled, filtered, gap-filled, and partitioned into their gross primary production (GPP) and ER components, and then aggregated to monthly averages. Towers in close proximity (within 9 km, to be consistent with model data) with each other were combined and averaged to represent a single site (Table 1). A total of 11 EC tower sites with at least 4 years of data (2013–2016) and representing the major boreal–Arctic ecosystem types and climate regimes within the ABoVE domain were used in this study. These sites were grouped into tundra (n = 6) and boreal (n = 5) biome types to validate the model carbon–flux estimates and to provide a mechanistic understanding of carbon–climate interactions. Brief tower site descriptions, including location, data availability, and references, are provided in Table 1.

#### Ensemble atmospheric CO<sub>2</sub> inversions

Atmospheric  $CO_2$  inversions (ACIs) provide regionally integrated estimates of net ecosystem-atmosphere carbon exchange based on atmospheric  $CO_2$  concentration measurements, a key observational component of the global carbon cycle (e.g., their observed temporal and spatial gradients). ACIs differ from each other mainly due to differences in the underlying number of atmospheric observations, transport models, spatial and temporal flux resolutions, land surface models used to predict prior fluxes, observation uncertainty and prior error assignment, and inversion methods (Peylin et al., 2013). A total of six ACI products, including Carbon-Tracker 2017 (CT2017; Peters et al., 2007), Carbon-Tracker Europe 2015 (CTE2015; Peters et al., 2010), Copernicus Atmosphere Monitoring Service (CAMS; Rayner, Enting, Francey, & Langenfelds,

Site name	Regions	Description	Latitude, longitude	Elevation (m)	Years analyzed	References
Bonanza Creek Experimental Forest (US-BON)	Boreal	Black Spruce forest	64.696N, 148.323W	100	2013-2016	Euskirchen, Edgar, Turetsky, Waldrop, and Harden (2014)
		Thermokarst col- lapse scar bog	64.695N, 148.321W	100	2013-2016	
		Rich Fen	64.703N, 148.313W	100	2013-2016	
Imnavait Creek Watershed (US-IMN)	Tundra	Wet sedge tundra (US-ICs)	68.606N, 149.311W	920	2010-2016	Euskirchen, Bret-Harte, Shaver, Edgar, and Romanovsky (2017)
		Moist acidic tussock tundra (US-ICt)	68.606N, 149.304W	930	2010-2016	
		Heath tundra (US-ICh)	68.607N, 149.296W	940	2010-2016	
Ivotuk (US-IVO)	Tundra	Tussock-sedge, dwarf shrub, moss	68.468N, 155.75W	543	2013-2016	Goodrich et al. (2016), Zona et al. (2016)
Atqasuk (US-ATQ)	Tundra	Sedge, grass, dwarf shub	70.469N, 157.109W	15	2013-2016	Goodrich et al. (2016), Zona et al. (2016)
Poker Flat Research Range (US-Prr)	Boreal	Black Spruce Forest	65.124N, 147.488W	210	2010-2016	Ikawa et al. (2015)
University of Alaska, Fairbanks (US-Uaf)	Boreal	Black Spruce Forest	64.866N, 147.856W	155	2010-2016	Ueyama et al. (2014)
Barrow	Tundra	Wet sedge tundra (US-BRW)	71.32N, 156.61W	1	2013-2016	
		Wet sedge tundra (US-Bes)	71.281N, 156.597W	4.6	2013-2016	
Poker Flat Research Range: Fire Scar (US-Rpf)	Boreal	Deciduous trees and shrubs are dominate at a burned black spruce forest	65.12N, 147.43W	491	2010-2016	Ueyama et al. (2019)
Eight Mile Lake (US-EML)	Tundra	Tundra on a degrad- ing permafrost	63.878N, 149.254W	700	2010-2016	Schuur et al. (2009)
Trail Valley Creek (CA-TVC)	Tundra	Low shrubs <40 cm on continuous permafrost	68.746N, 133.502W	85	2013-2016	Helbig et al. (2016)
Scotty Creek Landscape (CA-SCC)	Boreal	Forested perma- frost peat plateau- thermokarst bog landscape	61.308N, 121.299W	285	2013-2016	Helbig et al. (2017)

#### **TABLE 1** Site characteristics of eddy covariance flux towers for the study area

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1999), Jena CarboScope (versions s76\_v4.2 and s85\_v4.2; Rödenbeck, Conway, & Langenfelds, 2006; Rödenbeck, Houweling, Gloor, & Heimann, 2003), and JAMSTEC (Saeki & Patra, 2017), were obtained from 2010 to 2016, and resampled to a consistent 1° spatial resolution using a nearestneighbor approach at a monthly time step.

#### Ensemble of dynamic global vegetation models (TRENDY simulations)

The TRENDY intercomparison project compiles simulations from state-of-the-art dynamic global vegetation models (DGVMs) to evaluate terrestrial energy, water, and net  $CO_2$  exchanges (Le Quéré et al., 2018; Sitch et al., 2015). The DGVMs provide a bottom-up approach to evaluate terrestrial  $CO_2$  fluxes (i.e., net biome production [NBP]), and allow deeper insight into the mechanisms driving changes in C-stocks and fluxes. We used the ensemble mean NBP from eight TRENDY v6 DGVMs (Sitch et al., 2015), including CABLE, CLM4.5, JULES, LPJ, LPX, OCN, ORCHIDEE-MICT, and SDGVM, to investigate seasonal carbon dynamics over the ABoVE domain. Our analysis uses simulations from the "S3" simulations that includes time-varying atmospheric  $CO_2$  concentrations, climate, and land use. All simulations were based on climate forcing from the CRU-NCEPv4 climate variables at 6 hr resolution. The NBP outputs were summarized at 1° spatial resolution and monthly time step from 2010 to 2016.

#### Satellite data-driven carbon flux estimates (SMAP L4C)

To clarify the role of vegetation properties and environmental controls on seasonal CO<sub>2</sub> flux dynamics at high latitudes, we used the NASA Soil Moisture Active Passive (SMAP) mission Level 4 Carbon (L4C) product (Jones et al., 2017). The SMAP L4C provides global daily estimates of NEE, component carbon fluxes for GPP and ER, and surface SOC stocks. The L4C calculations are derived in a 9 km resolution global grid format using a satellite data-driven terrestrial carbon flux model informed by MODIS (MODerate resolution Imaging Spectroradiometer) vegetation and SMAP soil observations (Reichle et al., 2017). Other L4C meteorological inputs include surface minimum daily air temperature, atmospheric vapor pressure deficit (VPD), and incoming solar radiation provided from global reanalysis data. GPP is derived in the L4C framework using a light use efficiency (LUE) algorithm, where LUE is a spatially and temporally dynamic parameter sensitive to biome type and reduced for suboptimal environmental conditions, including cold temperatures, excessive VPD, low root-zone (0-100 cm) soil moisture levels, and frozen conditions. Heterotrophic respiration (Rh) is estimated using a three-pool soil decomposition model with cascading SOC quality and associated decomposition rates regulated by soil moisture and soil temperature. Autotrophic respiration (Ra) is defined as a daily proportion of GPP, while ER represents the daily sum of Rh and Ra. The influence of plant functional type and vegetation disturbance are partially represented in the model through satellite (MODIS) observed vegetation classification and fractional photosynthetic canopy cover inputs. The L4C model has been calibrated against FLUXNET tower CO<sub>2</sub> flux measurements and shows favorable global performance and accuracy (Jones et al., 2017). In this analysis, we use the L4C Nature Run (NR) record which extends over the entire study

period (2010–2016) relative to the shorter SMAP L4C operational (Ops) record (2015–present). The L4C NR record uses the same land model framework and MODIS vegetation inputs as the L4C Ops record except that the soil moisture and soil temperature inputs are not directly informed by SMAP observations. However, the SMAP L4C Ops and NR results show very similar spatial and temporal patterns over the domain from the overlapping records; whereby, the monthly difference between GPP, net ecosystem productivity [NEP], and Rh is generally less than 5% of the mean NR results (Figure S2).

#### GOME-SIF

Solar-induced chlorophyll fluorescence (SIF) is an electromagnetic signal emitted by plants during foliar light absorption by chlorophyll (Joiner et al., 2013; van der Tol, Berry, Campbell, & Rascher, 2014). SIF is directly proportional to photosynthetic activity (Porcar-Castell et al., 2014) and was shown to be an important indicator of photosynthetic activation and growing season duration throughout northern latitude ecosystems (Jeong et al., 2018; Parazoo et al., 2018). Spaceborne SIF is less sensitive to clouds, high albedo surfaces, and non-photosynthetic vegetation than reflectance-based vegetation indices. However, the SIF retrievals require a large sampling footprint and coarse temporal compositing of the data to enhance signal-to-noise that is exacerbated by lower solar illumination at higher latitudes. In this analysis, monthly SIF at 0.5° resolution was obtained from the GOME-2 sensor record for the 2010-2016 study period. The GOME-2 measurements onboard the Metop-A satellite are obtained at the 740 nm far-red peak in chlorophyll fluorescence emission (Kohler, Guanter, & Joiner, 2015). GOME-2 SIF values are additionally screened for solar zenith angles <60° and cloud fractions below 20% to increase signal-to-noise (Parazoo et al., 2018). Details of the retrieval of SIF from GOME-2 measurements can be found in Joiner et al. (2013).

The carbon flux in this analysis is defined with respect to the biosphere so that a positive value indicates that the biosphere is a net sink of CO<sub>2</sub> absorbed from the atmosphere. The different data products described above use different terminology (e.g., NBP, NEP, NEE) with slightly different meanings; however, they all provide estimates of net CO<sub>2</sub> exchange (Chapin et al., 2006), and are assumed to be similar (i.e., NEE≈NEP≈NBP) in the context of our study focus on the seasonal CO<sub>2</sub> cycle response to the 2015/2016 ENSO event. NEP is therefore represented in this study as the residual difference between vegetation GPP and ER.

#### 2.2.2 | Environmental and climate data

#### Freeze-thaw data

Daily 25 km resolution maps of landscape freeze/thaw status were obtained over the study domain from the global satellite Freeze-Thaw Earth System Data Record (FT-ESDR v4; Kim, Kimball, Glassy, & Du, 2017). The FT-ESDR is derived from calibrated 37 GHz brightness temperature ( $T_b$ ) retrievals from the Special Sensor Microwave Imager (SSM/I) and SSM/I Sounder (SSMIS) sensors. The satellite  $T_b$  retrievals are used to classify the predominant frozen or thawed condition of the land surface from morning (a.m.) and afternoon (p.m.) satellite -WILFY- Global Change Biology

overpasses to produce a composite daily (both a.m. and p.m.) record of landscape freeze-thaw (FT) status. The FT retrieval is obtained using a modified seasonal threshold algorithm that classifies daily  $T_{\rm b}$  variations in relation to grid cell-wise FT thresholds calibrated using surface air temperature data from global model reanalysis. The FT-ESDR has been validated against a variety of independent observations and shows favorable accuracy and performance (Kim et al., 2017).

#### Snow cover data

Daily 4 km resolution maps of snow cover were obtained from the National Snow and Ice Data Center Interactive Multisensor Snow and Ice Mapping System (IMS). Daily snow cover extent from the IMS is derived using a consortium of satellite geostationary visible imagery, polar orbiting multispectral sensors, passive microwave sensors, and ground observations (Helfrich, McNamara, Ramsay, Baldwin, & Kasheta, 2007). The IMS daily snow cover extent record is considered one of the best performing snow cover products available, due to the use of trained analysts and the inclusion of ground observations which decrease the contaminating influence of clouds during IMS production.

#### Climate data

Monthly gridded air temperature and precipitation at 0.5° spatial resolution from 2010 to 2016 were obtained from the Climate Research Unit (CRU TS v4.02) at the University of East Anglia (Harris, Jones, Osborn, & Lister, 2014).

#### 2.3 | Analysis approach

#### 2.3.1 | Frost-free season

Primary spring thaw was defined as the earliest calendar day of year (DOY) when a forward-looking, 14 day running window contains at least 13 days when the land surface was classified as thawed for both a.m. and p.m. satellite overpasses. The high threshold (13 of 14 days, or 93%) discriminates against early temporary thaw events and extended diurnal thaw-refreeze cycles characteristic of high-latitude springs (Kim, Kimball, Zhang, & McDonald, 2012). Similarly, the primary fall freeze-up date is defined as the first DOY when a forward-looking, 14 day running window contains at least 13 days when the land surface was classified as frozen (for both a.m. and p.m. satellite overpasses). The period between primary spring thaw and fall freeze-up dates defines the annual frost-free period for each calendar year over the study period (2010–2016).

#### 2.3.2 | Snow indicators

The last day of spring snow cover was defined as the first DOY with seven consecutive days of snow-free conditions indicated from the IMS record for each grid cell (Metsämäki et al., 2018; Wang et al., 2017). In a similar manner, fall snow cover onset was defined as the first DOY when a seven consecutive day moving window showed persistent snow cover. The period between the last day of spring snow cover and the first day of fall snow cover was defined as the annual snow free period for each grid cell.

#### 2.3.3 | Carbon uptake period

The SMAP L4C NR-derived daily GPP and NEP record was used to determine the (net) carbon uptake period (CUP), including spring GPP onset, fall GPP offset, and the seasonal start and end of NEP. The GPP onset was determined for each grid cell as the first DOY when a 7 day running window contained at least 5 days when the smoothed daily GPP reached 10% of the seasonal maximum (Wu et al., 2013). The GPP offset was determined in a similar manner when the smoothed daily GPP decreased below 10% of the seasonal maximum. The growing season length (CUP) was defined as the period between GPP onset and offset. The seasonal start of net carbon uptake was determined as the first DOY when a 7 day running window contained at least 5 days with smoothed daily NEP > 0 (Wu et al., 2013); whereas the net carbon uptake offset was determined as the first DOY when a 7 day running window contained at least 5 days with smoothed daily NEP < 0.

To address how a warm spring affects seasonal carbon dynamics in high-latitude ecosystems (research question 1), we compared the warm spring years (average for 2015 and 2016) to baseline average conditions (2010–2014) to investigate the seasonal carbon dynamics using multiple data at both site and regional scales. Site-level comparisons were made between EC observations and L4C model simulations at the tower site locations. Regional-scale aggregations representing the entire ABoVE domain and component boreal and tundra biomes were compared between the ACI ensemble, the TRENDY ensemble, and L4C simulations.

To determine the congruence of the seasonal dynamics of net carbon uptake (i.e., photosynthesis minus respiration) and productivity (research question 2), we compared the regional monthly anomaly between the net carbon uptake estimates (the ACI ensemble, the TRENDY ensemble, and L4C simulations) and productivity indicators (SMAP L4C GPP and GOME-2 SIF).

To identify the climatic and environmental sensitivity of carbon cycle dynamics (research question 3), we regressed NEP from the EC observations against air temperature and soil moisture. The slope of the regression line was interpreted as the climatic and environmental sensitivity of the carbon cycle. The simple linear regression was used here mainly due to weak collinearity among climatic (e.g., air temperature and precipitation) and environmental variables (e.g., soil temperature and soil water content) derived from the EC site observations (data not shown), as well as the availability of EC observations. Temperature sensitivity ( $\gamma$ : g C m<sup>-2</sup> day<sup>-1</sup> K<sup>-1</sup>) is the change in net carbon flux (g C m<sup>-2</sup> day<sup>-1</sup>) in response to a 1° temperature change, and soil moisture sensitivity ( $\theta$ : g C m<sup>-2</sup> day<sup>-1</sup> %<sup>-1</sup>) is the change in net carbon flux (g C m<sup>-2</sup> day<sup>-1</sup>) in response to a 1% change in degree of saturation. The degree of saturation is the ratio of the volume of water to the volume of voids in the soil, and ranges from 0% when the soil is absolutely dry to 100% when the soil is fully saturated. Climatic

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and environmental sensitivity was calculated for different seasons and regions (i.e., tundra and boreal), and only statistically significant (p < .05) results are reported.

## 3 | RESULTS

# 3.1 | Environmental and phenological anomaly in 2015 and 2016

The 2015/2016 El Niño year provided suitable conditions for a natural experiment to investigate the carbon cycle response to changes in temperature, and soil moisture availability at seasonal timescales in high-latitude ecosystems. The global 2015/2016 El Niño was one of the strongest ever recorded, beginning approximately in May 2015 and extending May 2016. The event caused positive anomalies of temperature ( $\Delta T = 2.13 \pm 2.06^{\circ}$ C; mean  $\pm$  SD, hereafter) and potential ET (3.85 ± 2.70 mm/month, 21% increase from baseline average: 18.5 mm/month) from January to May across the ABoVE domain (Figure S3). The anomalously warm spring conditions advanced the regional mean spring primary thaw date by  $7 \pm 6$  days and snow-off date by  $6 \pm 7$  days compared to the baseline conditions (DOY =  $137 \pm 14$  for primary thaw date;  $142 \pm 19$  for spring snow-off date; Figure 2; Figures S4 and S5). Consequently, anomalously early spring onset in L4C-derived GPP by 5 ± 5 days and CUP by 4 ± 10 days was also observed relative to baseline conditions (DOY 129 ± 16 for start of GPP, and 143 ± 18 for start of net carbon uptake; Figure 2; Figures S5 and S6), which is consistent with landscape thaw as a dominant control on the carbon cycle at high latitudes (Parazoo et al., 2018). The spatial patterns of these environmental and phenological anomalies largely mirrored the regional temperature anomaly (Figure S1), which provided additional evidence that the landscape transition from cold to warm seasons is mainly thermally regulated in high-latitude ecosystems. The June-December temperature and atmospheric water balance (potential ET minus precipitation) was not statistically different from the

baseline, and did not appear to have a significant influence on environmental and phenological anomalies during the fall of 2015 and 2016 (Figures S3–S6). The longer snow-free and frost-free seasons, and associated longer growing and carbon uptake season in 2015 and 2016, are mainly due to the spring environmental and phenological anomaly.

## 3.2 | Seasonal change in net carbon uptake and productivity

There was a strong increase in spring (May and June) net carbon uptake during the warm spring years (i.e., 2015–2016 relative to baseline condition from 2010 to 2014), which was consistent among datasets at varying spatial scales. Site-level comparisons indicate that spring NEP increased significantly in both the L4C simulations  $(0.42 \pm 0.05 \text{ g C m}^{-2} \text{ day}^{-1})$  and the EC observations  $(0.34 \pm 0.17 \text{ g C m}^{-2} \text{ day}^{-1})$  at the tower sites due to a relatively stronger increase in GPP than in ER (Figure 3). Similarly, spatial aggregation of the results over the ABoVE domain showed that spring NEP increased by  $60.29 \pm 15.73$  TgC for L4C and by  $25.97 \pm 4.06$  TgC for the TRENDY ensemble, although the L4C results showed an extension of anomalously high net C uptake into the fall (Figure 4).

Across the datasets of differing spatial scales, the stronger spring NEP was partially compensated by warming-induced ER enhancement in the preceding warm winter (January–March). The site-level comparisons suggest a significant NEP decrease in the preceding winter by about  $-0.11 \pm 0.11$  g C m<sup>-2</sup> day<sup>-1</sup> from the EC observations and  $-0.05 \pm 0.01$  g C m<sup>-2</sup> day<sup>-1</sup> from the L4C simulations, mainly due to an increase in ER (Figure 3). Regional aggregation showed that NEP decreased by  $-10.49 \pm 5.4$  TgC for L4C, by  $-9.64 \pm 7.84$  TgC for the ACI inversion, and by  $-4.48 \pm 3.02$  TgC for the TRENDY ensemble (Figure 4).

Changes in net C uptake were somewhat equivocal for the subsequent fall (September and October). The site-level comparison showed very small to insignificant changes in the NEP change and its



**FIGURE 2** Spatial patterns of anomalies in snow conditions (first column), freeze/thaw conditions (second column), and carbon uptake (third to fourth columns) during 2015–2016 relative to baseline conditions from 2010 to 2014 across the ABoVE domain. The first (a–d), second (e–h), and third (i–I) rows indicate spring, fall, and annual anomalies, respectively. CUP, carbon uptake period; GPP, gross primary productivity



**FIGURE 3** Site-level comparison in NEP between EC measurements (a) and L4C simulations (b, sampled at EC locations) between baseline years (2010–2014; black) and warm spring years (2015–2016; red). Shading denotes 1 standard deviation (*SD*) from the 11 EC site locations. Positive (negative) values indicate land as a carbon sink (source). EC, eddy covariance; ER, ecosystem respiration; GPP, gross primary production; L4C, Level 4 Carbon; NEP, net ecosystem production



component fluxes. The L4C results showed a slight increase in NEP due to a stronger decrease in ER relative to GPP, while the tower EC observations showed NEP enhancement due to a GPP increase and ER decrease. These results reflect complex interactions among carbon cycle, climate, and environmental controls (e.g., soil moisture) in the late growing season, while similar behavior was found from the regional aggregation results.

Month

Net carbon uptake and productivity showed different seasonal compensation behaviors in the warm spring (Figure 5). The enhancement of net carbon uptake during spring was offset by greater respiration response in the preceding anomalous warm winter (Figure 5a), while the increase in spring photosynthesis was counteracted by a subsequent decrease in the fall (Figure 5b). Our results showed similar seasonal compensation behavior over the ABoVE domain for both



FIGURE 5 Seasonal carbon cycle anomaly across the ABoVE domain for (a) net ecosystem production (NEP = GPP - ER). calculated as the difference between gross primary production (GPP) and terrestrial ecosystem respiration (TER); (b) satellite-based observations of ecosystem productivity represented by GPP from the NASA Soil Moisture Active Passive (SMAP) Level 4 Carbon (L4C) product, and solar-induced chlorophyll fluorescence (SIF) from the ESA GOME-2 sensor. The anomaly was calculated as the difference between warm spring (2015-2016) and baseline (2010-2014) conditions. The ACI ensemble includes CarbonTracker (CT2017), CarbonTracker Europe (CTE2016), CAMS, Jena CarboScope (s76\_v4.2 and s85\_v4.2), and JAMSTEC. TRENDY ensemble includes CABLE, CLM4.5, JULES, LPJ, LPX, OCN, ORCHIDEE-MICT, and SDGVM models. Shading denotes 1 spatial standard deviation (SD) from the regional monthly means within the ABoVE domain

L4C GPP and GOME-2 SIF observations (Figure 5; Figure S9), similar to previous studies (Buermann et al., 2018). The SIF record shows a temporal lag behind the spring GPP increase and temporal offset in advance of the fall GPP decrease indicated from the L4C record.

## 3.3 | Seasonal NEP change in tundra versus boreal regions

Tundra and boreal ecosystems showed different seasonal carbon dynamics in response to the anomalously warm spring, which may reflect different vegetation characteristics, soil conditions, and hydrological cycles. Both tundra and boreal ecosystems showed enhanced spring photosynthetic  $CO_2$  uptake during the warm spring (Figure 6). However, they differed in warming-induced winter respiration carbon losses. Enhanced winter respiration carbon losses from warmer temperatures (i.e.,  $-0.185 \pm 0.130$  g C m<sup>-2</sup> day<sup>-1</sup> for EC, and  $-0.038 \pm 0.029$  g C m<sup>-2</sup> day<sup>-1</sup> for L4C) were consistent among datasets in the boreal region, but not in the tundra region ( $-0.171 \pm 0.155$  g C m<sup>-2</sup> day<sup>-1</sup> for EC, and  $-0.011 \pm 0.029$  g C m<sup>-2</sup> day<sup>-1</sup> for L4C). Therefore, seasonal compensation in net carbon uptake was mainly driven by the boreal region.

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**FIGURE 6** Seasonal sensitivity of net ecosystem production (NEP) anomaly to the temperature anomaly in boreal and tundra ecoregions, using different datasets, for different seasons. Error bars denote 1 standard deviation (*SD*) from the seasonal estimate. The anomaly is calculated as the difference between warm spring years (2015 and 2016) and baseline years (2010–2014). EC, eddy covariance; L4C, Level 4 Carbon

# 3.4 | Climate and soil moisture sensitivity of carbon cycle

Using the EC observations and supporting biophysical measurements at the ABoVE tower sites, we found that temperature was the primary control on NEP during the cold season (January-March; Figure 7a) and spring (May and June; Figure 7b), while soil moisture was the primary control on NEP in the fall (September and October; Figure 7c). The temperature sensitivity of NEP ( $\gamma$ ) in spring ( $\gamma_{\rm spring}$  = 0.148 g C m<sup>-2</sup> day<sup>-1</sup> K<sup>-1</sup>, p < .05) is stronger than that in the cold season ( $\gamma_{winter}$  = -0.047 g C m<sup>-2</sup> day<sup>-1</sup> K<sup>-1</sup>, p < .05). The temperature sensitivity of NEP is also stronger in tundra ( $\gamma_{winter}^{tundra} = -0.123$ g C m<sup>-2</sup> day<sup>-1</sup> K<sup>-1</sup>, p = .31;  $\gamma_{\text{spring}}^{\text{tundra}} = 0.125$  g C m<sup>-2</sup> day<sup>-1</sup> K<sup>-1</sup>, p = .39) than that in boreal forest ( $y_{winter}^{boreal} = -0.035 \text{ g C m}^{-2} \text{ day}^{-1} \text{ K}^{-1}$ , p < .001 and .31;  $\gamma_{\text{spring}}^{\text{boreal}} = 0.076 \text{ g C m}^{-2} \text{ day}^{-1} \text{ K}^{-1}$ , p = .17). The L4C simulations and ACI inversions were consistent with the tower site results in showing lower NEP temperature sensitivity in winter and greater sensitivity in spring. The regional difference in NEP temperature sensitivity between tundra and boreal forest indicates seasonal and regional differences in climate-carbon interactions. In fall, the soil moisture sensitivity of NEP ( $\theta$ ) is 0.983 g C m<sup>-2</sup> day<sup>-1</sup> %<sup>-1</sup> (p < .01) over the entire ABoVE domain, and is higher in boreal forest ( $\theta_{fall}^{boreal} = 1.018$  $g C m^{-2} day^{-1} \%^{-1}$ , p < .01) than tundra ( $\theta_{fall}^{tundra} = 0.361 g C m^{-2} day^{-1} \%^{-1}$ , p = .7), suggesting a stronger moisture limitation on net carbon uptake in the boreal region.



FIGURE 7 Temperature and soil moisture influence on boreal-Arctic seasonal carbon dynamics using EC measurements for (a) winter (January-March), (b) spring (May and June), and (c) fall (September and October). Blue represents the tundra region and green represents the boreal region. Insets in (a) and (b) show the sensitivity of net ecosystem production (g C  $m^{-2} day^{-1}$ ) to the temperature anomaly (K), and inset in (c) shows the sensitivity of net ecosystem production (g C m<sup>-2</sup> day<sup>-1</sup>) to the soil moisture (ESA CCI) anomaly (degree of saturation) for the SMAP L4C simulation (blue) and the ACI ensemble (green)

#### DISCUSSION 4

The northern high latitudes are warming faster than the global average, with the highest rate of warming observed during the cold season (Box et al., 2019; Graham et al., 2017; Walsh et al., 2017). Such changes in temperature seasonality will have a stronger influence on shoulder season carbon exchange and thus play a major role in determining the future trajectory of northern high-latitude ecosystems as carbon sinks or sources to the atmosphere (Commane et al., 2017; Ueyama, Iwata, & Harazono, 2014). Using multiple data records at varying spatial scales, we demonstrated that seasonal compensation in the carbon cycle is widespread during an anomalously warm winter to spring transition in high-latitude ecosystems of North America. However, the seasonal compensation mechanism is different for productivity and net ecosystem carbon exchange, implying the importance of respiration in mediating productivity and carbon source/sink activity in the ABR. The different temperature and soil moisture sensitivity of net carbon exchange underscores the importance of untangling the effects of competing ecosystem processes at the seasonal scale to gain a better understanding of carbon-climate feedbacks at the regional scale and over longer periods.

#### 4.1 | Seasonal compensation for GPP and NEP

Numerous studies have used productivity as proxy to infer carbon sink/source activity, and found a widespread seasonal compensation in plant activity in northern ecosystems (Angert et al., 2005; Buermann et al., 2018). However, net carbon exchange depends on the balance between carbon uptake by plants and respired carbon losses from microbial and plant decomposition. The rates of these processes will increase with warming but it remains unclear which will dominate the net carbon balance in the future due to complex interactions among permafrost thaw-induced subsidence, hydrology, and nutrients, which leads to inconsistencies between model simulations and field data (Schadel et al., 2018). For example, paleo-records indicate

that the northern peatland carbon sink may increase under climate warming as plants assimilate more CO<sub>2</sub> than is lost through respiration (Gallego-Sala et al., 2018). Many model simulations, however, suggest that the northern ecosystem carbon sink is vulnerable to climate warming due to accelerated soil organic matter decomposition and permafrost degradation (McGuire et al., 2018; Schuur & Abbott, 2011; Walter Anthony et al., 2018). However, many knowledge gaps remain, including the major drivers and processes influencing the different seasonal compensation mechanisms between net carbon uptake and productivity. In particular, our results imply that seasonal change in the two component carbon fluxes (GPP and ER) and their response to climate and environmental change needs to be fully understood for more accurate prediction of carbon-climate interactions.

We found that the GOME-2 SIF record lags behind the spring GPP increase and is in advance of the fall GPP decrease indicated from the SMAP L4C record. This difference in temporal offset may reflect the different sensitivity of SIF-based photosynthetic activity and spectral reflectance-based LUE and GPP calculations to different environmental drivers. One possible explanation is that the SIF signal is generally weaker than satellite optically derived vegetation indices; thus, a stronger signal is needed for early/late season detection, with the strongest signals being close to peak photosynthetic activity. For example, Luus et al. (2017) show green-up and budburst to occur 1-2 weeks prior to SIF-based GPP onset in northern high-latitude deciduous tundra ecosystems. Another possible explanation is that plant physiology is more responsive to stress conditions than optical reflectance behavior.

#### 4.2 | Climate and environmental controls on season carbon cycle

Currently, we still have limited understanding of how the carbon cycle interacts with climate and the hydrological cycle at seasonal scales, leading to large uncertainties in the climate-carbon feedback at high latitudes (Winkler et al., 2019). Our analysis confirmed that temperature is a primary control on spring net carbon uptake in North American

boreal-Arctic ecosystems. The "warmer spring, bigger spring carbon sink" mechanism is still valid in many boreal-Arctic ecosystems because the productivity gains from earlier landscape thawing and reduced spring snow cover duration (Lawrence & Slater, 2010), earlier budburst (Badeck et al., 2004), and increased N availability (Salmon et al., 2016) outweigh carbon losses from warming-induced enhancement in ER. Such warming-induced enhancement of spring  $CO_2$  uptake by plants has been identified as the main mechanism explaining the increased seasonal  $CO_2$  amplitude (Forkel et al., 2016) and a stronger terrestrial carbon sink in the northern hemisphere in past decades (Ciais et al., 2019), although the temperature sensitivity of spring  $CO_2$  uptake appears to be weakening in recent decades (Piao et al., 2017).

Our results indicate that soil moisture may become an increasingly important environmental control on terrestrial carbon exchange in the late growing season, especially in boreal forests which tend to have relatively deep active layers and warmer, drier summer growing seasons. Satellite-based soil moisture data from ESA CCI showed an earlier depletion of soil moisture during the anomalously warm spring in the boreal region (Figure S10), which possibly contributed to a decrease in net carbon uptake (Figure 7c). The satellite-based findings are supported by tower data, which showed that the soil moisture sensitivity of NEP is higher in boreal forest than tundra (Figure 7c). These results indicate that the carbon cycle in high-latitude boreal ecosystems is at least seasonally constrained by low soil moisture availability, even though high-latitude ecosystems are still considered predominantly energy limited due to cold temperatures.

Our findings are consistent with previous studies indicating that spring hydrology has a strong influence on summer NEP in the boreal region (Yi et al., 2014) and that boreal forests may be increasingly vulnerable to drought (Dai, 2012) and more frequent and severe wildfires (Jolly et al., 2015) with continuing climate warming. Mounting evidence indicates that the effects of soil moisture on the carbon cycle are a major uncertainty in projecting future carbonclimate feedbacks (Green et al., 2019; Stocker et al., 2018; Trugman, Medvigy, Mankin, & Anderegg, 2018).

We were, however, unable to determine from observations which component carbon processes (i.e., productivity vs. respiration) predominantly control net ecosystem carbon exchange in the fall. One possible reason for this uncertainty is that the effects of soil moisture on productivity and respiration compensate each other and therefore dampen the resultant effect on NEP (Jung et al., 2017). In situ soil moisture measurement networks are extremely sparse at high latitudes, while soil moisture retrievals from operational satellite microwave sensors have a coarse (~25-40 km) sampling footprint, which is insufficient to resolve the large characteristic spatial heterogeneity in soil moisture conditions in permafrost landscapes. Sensitivity of carbon fluxes to climatic and environmental drivers also depends on plant functional types (Welp, Randerson, & Liu, 2007) and varies at different temporal scales (Mitra et al., 2019). Differential sensitivity of productivity and respiration to temperature and moisture availability increased uncertainty in net ecosystem carbon exchange during the late growing season in high-latitude ecosystems (Commane et al., 2017; Liu et al., 2018; Piao et al., 2008). Therefore, more work is needed to understand local to landscape level - Global Change Biology -WILEY

interactions among the carbon cycle, moisture availability, and climate, especially in the late season, to reduce uncertainty in estimating annual carbon sequestration. While the focus of this study emphasized the seasonal  $CO_2$  response to winter and spring warming anomalies, the ecological response to these relatively short-term climate anomalies is also influenced by a longer term legacy imposed from large-scale ecosystem disturbances, including wildfire and permafrost degradation, which appear to be intensifying in a warmer climate (Turetsky et al., 2017). The ongoing NASA ABoVE field campaign has a nested multiscale observational and modeling framework (Stofferahn et al., 2019) that is expected to continue to contribute to better understanding of carbon processes, disturbance, and climate feedbacks in the North American boreal–Arctic.

Similar to a previous analysis (Commane et al., 2017; Jeong et al., 2018), we also found warming significantly increased cold season respiration during the 2015/2016 El Niño year, which offset carbon uptake enhancement from earlier growing season onset and warmer temperatures during the subsequent spring within the ABoVE domain. If a faster rate of cold season warming unfolds as predicted, the magnitude and duration of cold season respiration carbon loss will be greatly enhanced (Natali et al., 2011; Webb et al., 2016; Zona et al., 2016), and potentially switch high-latitude ecosystems from a net carbon sink to a carbon source, thereby reinforcing a positive carbon-climate feedback in the Earth system (Huang et al., 2017; Koven et al., 2011; Schaefer, Lantuit, Romanovsky, Schuur, & Witt, 2014).

## 5 | CONCLUSIONS

The amplitude of the  $CO_2$  seasonal cycle has increased at high latitudes since the 1960s (Graven et al., 2013). Such change indicates significant alteration of the global carbon cycle, and has been attributed to increased plant photosynthetic uptake (Forkel et al., 2016; Wenzel, Cox, Eyring, & Friedlingstein, 2016), or increased respiration (Commane et al., 2017). Our results suggest that the seasonal differential response of photosynthesis and respiration to climate change during cold to warm transitions is a possible explanation for the increased  $CO_2$  seasonal cycle at high latitudes during the past decades, although with small influence on the aggregate annual carbon sink or source status in boreal-Arctic ecosystems.

A better understanding of the seasonal response of the carbon cycle to climate and environmental change provides important insights for future carbon-climate feedbacks and their consequences on atmospheric  $CO_2$  dynamics in the northern high latitudes. Based on in situ observations, model simulations, and atmospheric  $CO_2$  inversions, we found that seasonal compensation in the carbon cycle is widespread during a warm winter to spring transition, although the seasonal compensation mechanism is different for gross primary productivity and net ecosystem carbon exchange. The enhanced spring net carbon uptake was compensated by greater warming-induced respiration carbon losses during the preceding cold season. Despite a decline in productivity, the nearly neutral change in net carbon uptake in the

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late growing season implies the importance of respiration in mediating productivity and carbon source/sink activity in boreal-Arctic ecosystems. In a warmer climate, the carbon cycle in the boreal region may be increasingly controlled by hydrologic conditions and subject to much larger uncertainty due to poor understanding of future moisture conditions and large characteristic soil moisture spatial heterogeneity. The complex interactions among component carbon fluxes, climate, and environment underscore the importance of continued satellite monitoring of vegetation and soil conditions across the pan-Arctic (e.g., SMAP) to gain a better understanding of carbon-climate feedbacks in remote and climate sensitive regions.

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#### CONFLICT OF INTERESTS

The authors declare no conflict of interests.

#### DATA AVAILABILITY STATEMENT

All data analyzed in this study are publicly available. Carbon tracker is obtained from NOAA Earth System Research Laboratory (https:// www.esrl.noaa.gov/gmd/ccgg/carbontracker/), Carbon Tracker Europe from Wageningen University (http://www.carbontracker.eu/), Jena CarboScope is from MPG (http://www.bgc-jena.mpg.de/CarboScope/), and CAMS from ECMWF (http://apps.ecmwf.int/datasets/data/ cams-ghg-inversions/). SMAP L4C and freeze/thaw data are from the Numerical Terradynamic Simulation Group data portal (https://www. ntsg.umt.edu/) and the National Snow and Ice Data Center (https:// nsidc.org/). SIF by GOME2 is obtained from NASA Aura Validation Data Center (AVDC; https://avdc.gsfc.nasa.gov/pub/). TRENDY simulation is obtained from http://dgvm.ceh.ac.uk/index.html. Climate data are from Climate Research Unit (https://crudata.uea.ac.uk/cru/data/hrg/). Atmospheric CO<sub>2</sub> concentration data are from the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory (ESRL) archive (https://www.esrl.noaa.gov/). Snow cover data are from Interactive Multisensor Snow and Ice Mapping System (https://www.natice.noaa.gov/ims/).

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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