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Min Jung Kwon¹ , Ashley Ballantyne^{1,2}, Philippe Ciais¹ , Ana Bastos³ , Frédéric Chevallier¹ , Zhihua Liu² , Julia K Green^{1,5} , Chunjing Qiu^{1,4} and John S Kimball²¹ Laboratoire des Sciences du Climat et de l'Environnement, CEA-CNRS-UVSQ, Gif-sur-Yvette, France² Department of Ecosystem and Conservation Science, University of Montana, Missoula, MT, United States of America³ Department Biogeochemical Integration, Max Planck Institute for Biogeochemistry, Jena, Germany⁴ UMR MIA 518, Université Paris-Saclay, INRAE, AgroParisTech, Paris, France⁵ Department of Environmental Science, Policy and Management, University of California at Berkeley, Berkeley, CA, United States of AmericaE-mail: minjung.kwon86@gmail.com**Keywords:** high latitudes, extreme temperatures, CO₂ flux, seasonal transitionsSupplementary material for this article is available [online](#)**Abstract**

Siberia experienced an unprecedented strong and persistent heatwave in winter to spring of 2020. Using bottom-up and top-down approaches, we evaluated seasonal and annual CO₂ fluxes of 2020 in the northern hemisphere (north of 30 °N), focusing on Siberia where the pronounced heatwave occurred. We found that, over Siberia, CO₂ respiration loss in response to the pronounced positive winter temperature anomaly was greater than in previous years. However, continued warming in the spring enhanced photosynthetic CO₂ uptake, resulting in the largest seasonal transition in net ecosystem CO₂ exchange; that is, the largest magnitude of the switch from the net CO₂ loss in winter to net CO₂ uptake in spring until June. However, this exceptional transition was followed by the largest reduction in CO₂ uptake in late summer due to multiple environmental constraints, including a soil moisture deficit. Despite a substantial increase of CO₂ uptake by 22 ± 9 gC m⁻² in the spring in response to the heatwave, the mean annual CO₂ uptake over Siberia was slightly lower (3 ± 13 gC m⁻² yr⁻¹) than the average of the previous five years. These results highlight the highly dynamic response of seasonal carbon fluxes to extreme temperature anomalies at high latitudes, indicating a seasonal compensation between abnormal uptake and release of CO₂ in response to extreme warmth that may limit carbon sink capacity in high northern latitudes.

1. Introduction

Global surface air temperature has increased rapidly since the beginning of the 20th century (0.08 °C per decade; Hartmann *et al* (2013)), but almost twice as fast in the Arctic (Serreze *et al* 2009, Cohen *et al* 2014). Extremely warm and persistent temperature anomalies have also increased significantly (Barriopedro *et al* 2011, Perkins-Kirkpatrick and Lewis 2020). By the end of this century, temperatures are predicted to increase by up to 11.4 °C in the Arctic (Collins *et al* 2013), in addition to more frequent and intense temperature extreme events.

Warming influences net CO₂ fluxes by altering the balance between photosynthesis and respiration throughout the year, and the magnitude of this response differs by season due to associated shifts in the prevailing limiting factors. In northern high

latitudes, temperature is one of the dominant limiting factors of CO₂ uptake in spring. Seasonal thawing and the arrival of persistent warm temperatures in spring trigger leaf bud burst and flowering (Arft *et al* 1999, Aerts *et al* 2006, Ernakovich *et al* 2014), and can induce early onset of photosynthesis (gross primary production; GPP) and net CO₂ uptake (negative values of net ecosystem CO₂ exchange; NEE) by terrestrial ecosystems (Piao *et al* 2008, 2020, Park *et al* 2016, Li *et al* 2018, Parazoo *et al* 2018, Liu *et al* 2020). Yet an early onset of the growing season increases the chance of frost damage and a reduction in photosynthesis (Richardson *et al* 2018, Treharne *et al* 2019). In fall, ecosystem respiration (R_{eco}) is more responsive to warming than GPP (Piao *et al* 2008), which can be attributed to constraints on photosynthesis such as photoperiod, moisture, nutrient availability, and genetic or physiological controls linked to sink

limitations in plants (Arft *et al* 1999, Aerts *et al* 2006, Ernakovich *et al* 2014, Liu *et al* 2020, Zani *et al* 2020, Zhang *et al* 2020). In contrast, soil and root respiration continue in thawed soil (Blume-Werry *et al* 2016, Hicks Pries *et al* 2016). When the intensity of warming is high, as in the case of heatwaves, warming can either substantially increase CO₂ uptake in the absence of water stress (Wolf *et al* 2016, Bastos *et al* 2020a) or decrease it if soils become too dry (Ciais *et al* 2005, Reichstein *et al* 2013, Zscheischler *et al* 2014). The response to warming may also differ by ecosystem (Welp *et al* 2007, Bastos *et al* 2020a, Flach *et al* 2021) and species (Babst *et al* 2012, Niu *et al* 2014).

Siberia experienced an unprecedented heatwave in 2020 (Ciavarella *et al* 2021, Overland and Wang 2021): temperatures were 4.6 °C warmer than average from January to March (relative to 1981–2010) with extremely high temperatures persisting even longer in northern Siberia regions. Such sustained high temperature anomalies have probably not been observed in this area in the last 3 million years (Haywood *et al* 2020), but are expected to occur more frequently by the end of this century (Fan *et al* 2020). Although heatwaves often coincide with drought due to strong land-atmosphere coupling (Miralles *et al* 2019), the heatwave event over Siberia in 2020 did not coincide with drought, likely due to snow cover at the time of the heatwave and weak land-atmosphere coupling in high latitudes (Humphrey *et al* 2021). Here, we use the Siberian winter heatwave as an extreme event ‘natural experiment’ to evaluate its impact on the seasonal CO₂ balance at northern high latitudes. We compare NEE from several independent estimates over Siberia (>50 °N), and over Eurasia and North America (>30 °N; in the supplementary material). Specifically, we (a) quantify the changes in seasonal CO₂ fluxes of 2020 in response to the winter-to-spring warmth event, and (b) investigate whether changes in CO₂ fluxes during this early season influenced those in the later seasons, and the net annual CO₂ balance.

2. Methods

2.1. Seasonal variations and anomalies of climate and thaw date

We obtained climate data (ERA5 reanalysis)—air temperature, precipitation, and soil moisture—from 1979 through 2020 from the European Center for Medium-Range Weather Forecasts (ECMWF). We calculated the (linearly) detrended anomalies in climate variables for each grid cell relative to 1979–2019. We also used other climate variables as inputs for the simulation of a land surface model (LSM) and a multivariate Granger causality (MVGCC) analysis. The spring thaw date of surface soil was calculated from the daily Freeze-Thaw Earth System Data Record v5.0 based on satellite microwave measurements (ESDR; Kim *et al* (2017, 2021)). The spring thaw date was defined annually as the earliest calendar day of the

year when a forward-looking, 14-day running window contained at least 13 days when the land surface was classified as thawed, following Liu *et al* (2020). The ESDR data is available from www.ntsug.umt.edu/freeze-thaw/.

2.1.1. Estimates of net ecosystem CO₂ exchange

We compared NEE estimates from three independent approaches: an LSM with high-latitude processes (Organizing Carbon and Hydrology in Dynamic Ecosystems-aMeliorated Interactions between Carbon and Temperature; ORCHIDEE-MICT), a carbon flux model that integrates remote-sensing observations (Soil Moisture Active Passive—Level 4 Carbon; SMAP-L4C), and an atmospheric inversion system (Copernicus Atmosphere Monitoring Service combined with the second Orbiting Carbon Observatory; CAMS-OCO2). All of these estimates use different input data and methods, and each has its own strengths and weaknesses for detecting flux patterns (Schimel *et al* 2015, Bastos *et al* 2020c). The advantage of comparing them is that they are largely independent of each other, which enables us to better quantify uncertainties in seasonal CO₂ fluxes in response to the northern hemisphere heatwave event in 2020.

2.2. ORCHIDEE-MICT land surface model simulations

LSMs simulate physical, hydrological, and biogeochemical processes based on deterministic equations, with parameters usually calibrated from site observations. Although they may over- or underestimate fluxes under extreme climate conditions if the model is not well constrained (Schewe *et al* 2019, Bastos *et al* 2020b), they capture the magnitude and variability of CO₂ fluxes quite well for non-extreme climate conditions. Furthermore, LSMs allow us to diagnose the underlying processes (e.g. R_{eco}, GPP, and fires) contributing to patterns of anomalous net CO₂ fluxes and their potential environmental drivers. We used ORCHIDEE-MICT, which includes high-latitude processes such as permafrost, soil temperature, and soil carbon interactions, and a detailed calibration against multiple datasets (Guimberteau *et al* 2018). This model estimates global CO₂ fluxes close to the averages of LSM ensembles (Kondo *et al* 2020).

The ORCHIDEE-MICT (v8.7.1) LSM simulates energy, hydrologic, and carbon cycles, including processes that influence CO₂ exchange between the land and atmosphere on a 30 min to daily time-step. ERA5 reanalysis data (air temperature, humidity, pressure, shortwave and longwave incoming radiation, wind vectors, and precipitation) were used for performing a model simulation from 1979 to 2020 at 1° × 1° resolution, with a fixed land cover map for the year 2010 (HYDE3.2; Klein Goldewijk *et al* (2017)). Daily flux rates were aggregated into monthly fluxes.

The model was run for 150 years looping (randomly mixing) the years from 1979 to 1990 to reach

equilibrium. Then, a soil accumulating spin-up submodule was run for 10,000 years to approximate soil carbon stock equilibrium at the start of the simulation. The full model was run for another 150 years to reach the equilibrium of physical variables and carbon pools and, finally, a transient run was conducted from 1979 to the end of 2020 following the same protocol as in Bastos *et al* (2020a). The global annual atmospheric CO₂ concentration for the model transient run was prescribed from the Mauna Loa Observatory record (NOAA, Earth System Research Laboratories).

2.3. Satellite data-driven carbon flux estimates (SMAP-L4C)

Satellite data-driven models estimate CO₂ fluxes and are forced by observations, such as phenology and soil moisture, to constrain gross CO₂ fluxes. They produce CO₂ fluxes with quite good performance (Luus and Lin 2015, Jones *et al* 2017); however, they can miss some nonlinear soil feedback, such as permafrost carbon decomposition. We used the daily CO₂ flux record from the NASA SMAP L4C product (Jones *et al* 2017), which is calibrated against global tower CO₂ flux measurements (FLUXNET; <https://fluxnet.org/>) and shows favorable performance and accuracy in high-latitude regions (Liu *et al* 2020).

Daily CO₂ fluxes from L4C cover a shorter period (2015–2020) than the LSM because the SMAP data are only available from 2015. The L4C product is a satellite data-driven carbon flux model using SMAP assimilation enhanced (level 4) surface (0–5 cm depth) and root zone (0–1 m depth) soil moisture and temperature (Reichle *et al* 2017), and MODIS (MODerate resolution Imaging Spectroradiometer) vegetation observations as key drivers. Other L4C meteorological inputs include surface daily minimum air temperature, atmospheric vapor pressure deficit, and incoming solar radiation provided from global reanalysis data. SMAP-L4C provides global daily estimates of NEE and component CO₂ fluxes for GPP and heterotrophic respiration (Rh) since March 31, 2015. The L4C calculations are processed at 1 km resolution and posted to a 9 km resolution global grid format. Daily rates of GPP, Rh, and NEE were aggregated into monthly, gridded carbon fluxes at 0.25° × 0.25° resolution. We calculated NPP by subtracting NEE from Rh. The SMAP-L4C data is available from the National Snow and Ice Data Center (<https://nsidc.org/data/spl4cmdl>).

2.4. CAMS atmospheric inversion based on satellite column-average CO₂ retrievals

Atmospheric inversion models use atmospheric CO₂ observations and transport models to estimate the source and sink magnitudes of the land and ocean. Because of the usage of actual CO₂ concentrations, CO₂ flux estimates from inversions aggregate emissions and absorptions from all processes between

the Earth's surface and the atmosphere (fire, land use change, etc; fossil fuel emissions are usually prescribed in atmospheric inversions). We used inversions of the CAMS, which show similar estimates of the inversion ensemble means (Peylin *et al* 2013, Kondo *et al* 2020).

Sources and sinks of CO₂ fluxes are diagnosed using releases FT20r3 (called CAMS-OCO2 hereafter; 2015–2020) and, to a lesser extent here, v20r1 (called CAMS-surface hereafter; 1979–2019) of the CAMS global atmospheric inversion (Chevallier *et al* 2019). CAMS-OCO2 assimilated the column-average CO₂ dry air-mole fraction (XCO₂) retrieved from the OCO-2 radiance measurements. Version 10r of NASA's Atmospheric CO₂ Observations from Space OCO-2 retrievals was used. CAMS-OCO2 covers the period between September 2014 and December 2020. The advantage of this OCO-2-driven inversion compared to the CAMS-surface inversion, which assimilates measurements of surface air samples, is its closer to real-time update, enabled by the rapid delivery of XCO₂ retrievals. However, CAMS-surface covers a much longer period, from 1979 until June 2020, thereby allowing a broader climatic perspective. Both CAMS inversions also used a full set of prior estimates of the CO₂ surface fluxes (including a climatology of natural fluxes over land simulated by the ORCHIDEE model) and represent atmospheric transport with the general circulation model of the Laboratoire de Météorologie Dynamique (LMDz), nudged towards ERA5 horizontal winds. The inversion itself relies on a variational formulation of Bayes theorem. For this study, we used monthly averages of the net land-atmosphere fluxes of CO₂ at 1.89° latitude × 3.75° longitude resolution for both inversions.

2.5. Flux anomalies and transitions between quarters

After linearly detrending the monthly time series of CO₂ fluxes, we calculated 2020 anomalies compared to the averages of 2015–2019 for each quarter. We also quantified the seasonal 'transitions' of these CO₂ fluxes, defined as flux differences between successive quarters of the calendar year. We hypothesized that a strong CO₂ uptake in the early growing season will reduce CO₂ uptake in the late growing season due to the depletion of resources, e.g. soil moisture or nitrogen, and would make the transition in CO₂ fluxes between consecutive seasons stronger than usual. In order to quantify the transitions, we calculated the seasonal sum of fluxes by quarter (gC m⁻² quarter⁻¹ over each region; Q1: January–March; Q2: April–June; Q3: July–September; Q4: October–December) and their first order differences between successive quarters, following Yue *et al* (2017), providing a time series of transitions denoted as e.g. NEE_{Q2-Q1} for NEE_{Q2}–NEE_{Q1}. Because negative NEE indicates net CO₂ uptake by land, more negative values of NEE_{Q2-Q1} represent a larger change between NEE_{Q1}

(usually positive due to net CO₂ emission in Q1) and NEE_{Q2} (usually negative due to net CO₂ uptake in the spring-centered Q2 period); i.e. a large CO₂ emission in Q1 and/or a large CO₂ uptake in Q2. NEE_{Q1-Q4[-1]} refers to the NEE transition between Q1 of the current and Q4 of the previous year. To quantify the relationships between seasonal NEE transitions during the growing season, we performed a regression analysis between NEE_{Q2-Q1} and NEE_{Q3-Q2} by pooling all years. If more negative NEE_{Q2-Q1} (switch to a stronger CO₂ uptake from Q1 to Q2) is followed by less negative NEE_{Q3-Q2} (switch to a weaker CO₂ uptake from Q2 to Q3) due to environmental constraint in the later growing season, this transitional relationship will be shown as a negative slope in the regression. We performed all analyses over Siberia (>50°N, 40–180°E), and additionally over Eurasia (>30°N, 25°W–180°E) and North America (>30°N, 25–180°W), the results of which are shown in the supplementary material.

2.6. Granger causality analysis

To infer the causal impact of monthly air temperature, precipitation, soil moisture, and snow (SWE; predictor variables *X*) on NEE (response variable *Y*), we performed a MVGC analysis (Granger 1980) for each pixel location within the study region using data from 1979 to 2020. MVGC is a statistical technique that utilizes vector autoregressive models to determine whether the history of *X* (from the current and previous *N* months) adds information useful for the prediction of *Y* (if so, *X* is said to Granger-cause *Y*). For each 1° × 1° grid cell, first both predictor and response variables were linearly detrended, deseasonalized, and then normalized by their local mean and standard deviation for 1979–2020. Then an MVGC toolbox was used to generate a vector autoregressive model predicting the normalized NEE anomalies (Barnett and Seth 2014). Only the ORCHIDEE-MICT simulation was used for this analysis because the shorter time periods for SMAP-L4C and CAMS-OCO2 were not sufficient for robust results using MVGC.

Using each pixel's model output, normalized NEE anomalies were predicted for the full time period using all predictor variables that were deemed significant at a *P* value of 0.1 based on an F-test with a null-hypothesis of 0-Granger causality (NEE_{predicted,all}). Then, NEE anomalies were again predicted, this time with one predictor variable *X* set to 0 (NEE_{predicted,withoutX}). The overall fraction of variability explained by each predictor variable could then be quantified using equation (1), a sample equation of the fraction of variability in NEE explained by *X*:

$$\frac{\text{var}(\text{NEE}_{\text{predicted,all}}) - \text{var}(\text{NEE}_{\text{predicted,withoutX}})}{\text{var}(\text{NEE}_{\text{normalized}})} \quad (1)$$

To generate the fraction of variability in NEE explained by each predictor variable *X* per quarter, equation (1) was again used, but only for time-steps from the time series that fell during the quarter of interest.

In order to understand whether a predictor variable *X* had a positive or negative impact on NEE, the time series of NEE predicted with one predictor variable *X* removed (NEE_{predicted,withoutX}) was subtracted from the time series of NEE estimated using all predictor variables (NEE_{predicted,all}). These time series were again separated by quarter, and then the average values of each of the seasonal time series were calculated. Should the resulting predictor coefficient be positive (negative), then it can be inferred that the predictor variable has a positive (negative) influence on NEE anomalies.

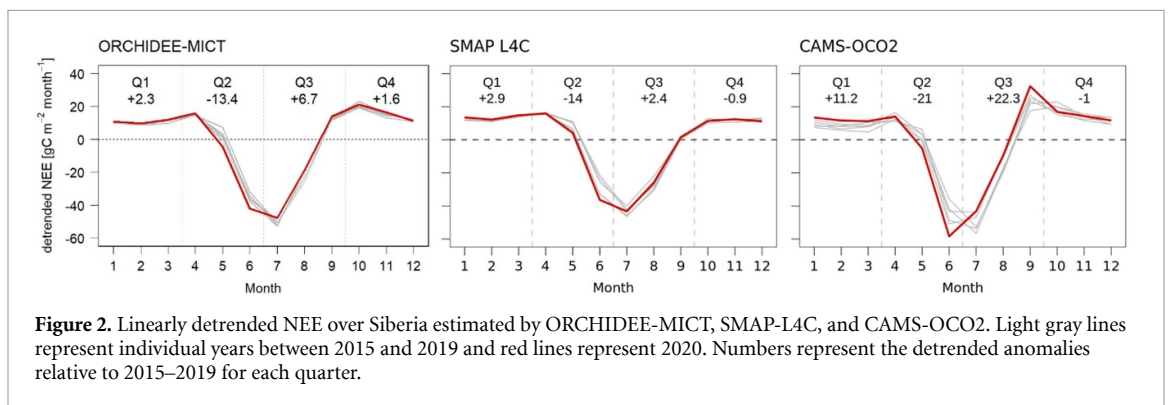
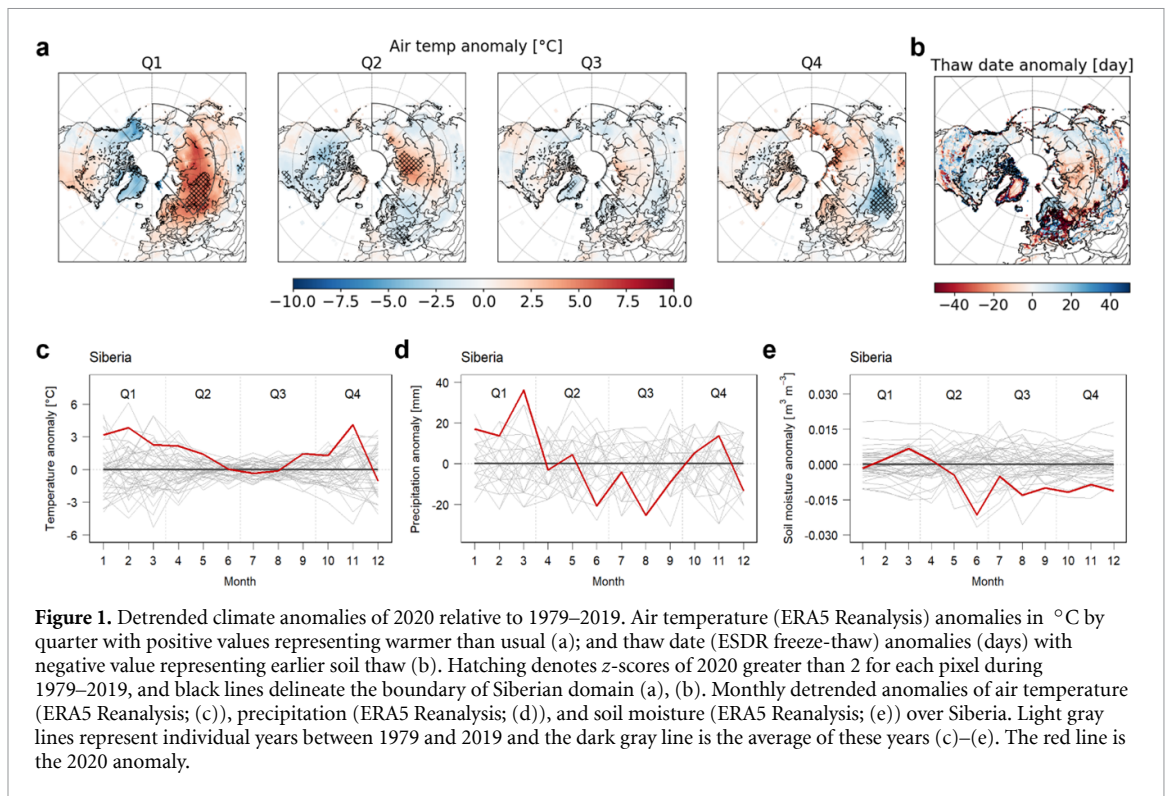
3. Results

3.1. Climate anomalies

Air temperature was extremely high throughout the year 2020 over Siberia (figures 1(a), (c), and S1(a)) (available online at stacks.iop.org/ERL/16/124030/mmedia) for the years 2015–2020), with some spatial and temporal (seasonal) variation. The heatwave had its largest extent from eastern Europe to eastern Siberia in Q1, and persisted in Q2 with an epicenter in northern central Siberia. Then, it further continued in the north of the Arctic circle in Q3 and Q4 (figure 1(a)). From exposure to an average 3.1 °C warmer air temperature in Q1 compared to the years 1979–2019 (over land, detrended anomaly), soil thawed *ca.* 5 days earlier relative to 1979–2019 across Siberia, with central Siberia showing the largest anomaly since the start of the observation period in 1979 (figure 1(b)). The precipitation anomaly of 2020 was at or above average until May but turned to below average from June onwards (figure 1(d)), with large spatial variation (figures S1(b) and S2(a)). The resulting soil moisture anomaly was comparable to the previous years until May but lower from June until the end of the year (figure 1(e)), especially in central and eastern Siberia (figures S1(c) and S2(b)). Higher air temperature anomalies coincided with greater precipitation (figure S3(a)), as well as with slight increases in soil moisture during Q1, but with slight decreases in soil moisture during Q3 (figure S3(b)). Increases in soil moisture were correlated spatially with positive precipitation anomalies in Q2 and Q3 (figure S3(c)).

3.2. Seasonal NEE anomalies

With positive temperature anomalies in Q1 and Q2, higher NEE_{Q1} (larger emission) and lower NEE_{Q2} (stronger uptake) were observed in 2020 compared to those of the previous five years (figures 2, 3, S4 and S5). The larger CO₂ uptake and an earlier shift from source to sink in Q2 was attributed to a large



increase in NPP_{Q2} , despite increased Rh_{Q2} in 2020 that partially offset the NEE changes (figures S5–S7). Less negative NEE_{Q3} values and an earlier shift from net CO_2 uptake to net CO_2 emission were found in Q3 of 2020, and they were related to stronger decreases in NPP_{Q3} than in previous years (figures S5–S7). The three estimates showed similar seasonal patterns until the peak of the growing season, with a transition from net CO_2 source to sink around May. However, SMAP-L4C showed a longer growing season with near-neutral CO_2 fluxes in September, while ORCHIDEE-MICT and CAMS-OCO2 indicated net CO_2 sources in the same month. In particular, CAMS-OCO2 showed large CO_2 emission peaks in September.

From the MVGC analysis based on 1979–2020, these seasonal NEE anomalies were explained largely by snow in Q1 and Q2 over Siberia (28.0% and 10.8% during Q1 and Q2, respectively), with more snow generally reducing CO_2 emissions or increasing

CO_2 uptake, especially in the high latitudes (figure S8). Other predictor variables locally explained NEE anomalies; for instance, warmer air temperature enhanced CO_2 uptake in Q2 but CO_2 emission in Q3 over central Siberia (figure S8).

3.3. Seasonal transitions in NEE

The NEE_{Q2-Q1} transition during 2020 was the most negative (switch to the strongest CO_2 uptake) of the recent record, with a difference of $15.7\text{--}32.3\text{ gC m}^{-2}$ (32.7%–60.0%) compared to the average of 2015–2019 (table S1 and figures 3(a) and (b)). In contrast, the NEE_{Q3-Q2} transition in 2020 was the most positive or the least negative (switch to the weakest CO_2 uptake), being $15.0\text{--}20.2\text{ gC m}^{-2}$ (24.2%–306.2%) more positive than during any year since 2015 (table S1 and figures 3(a) and (b)). These enhanced and reduced uptake transitions were due to more CO_2 release (larger Rh) than average for NEE_{Q1} , more CO_2 uptake (larger NPP) than average for NEE_{Q2} , and less

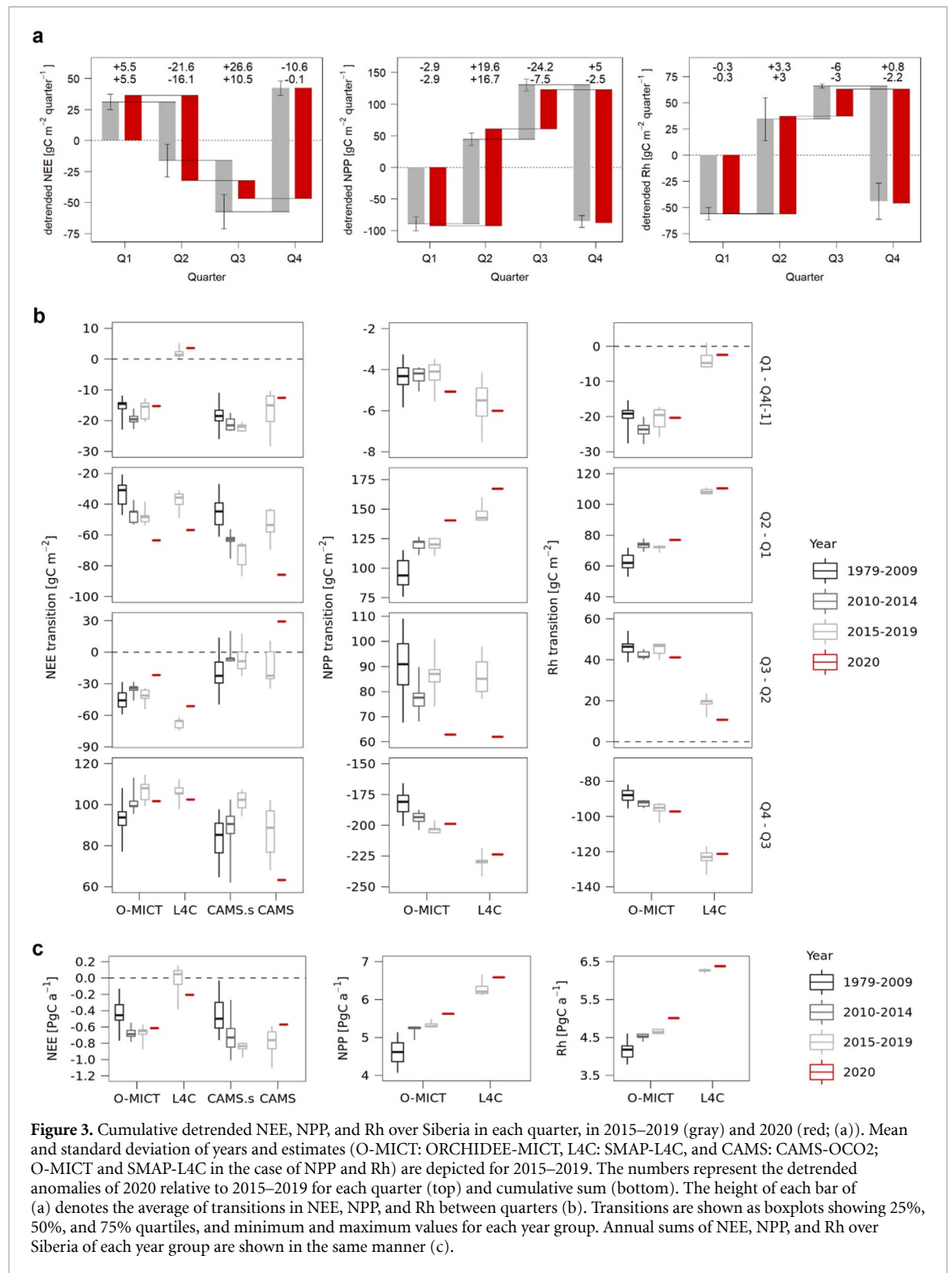


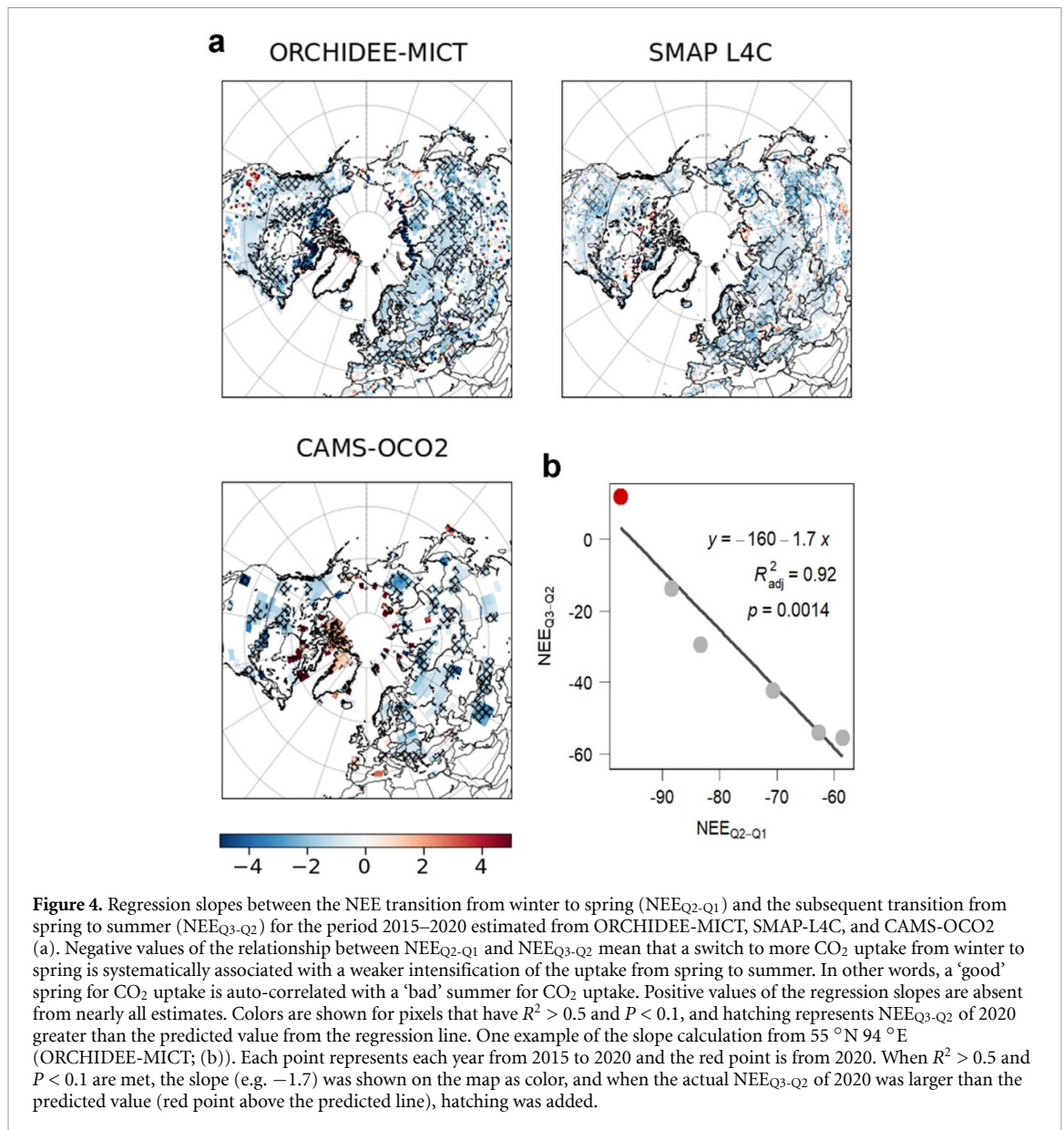
Figure 3. Cumulative detrended NEE, NPP, and Rh over Siberia in each quarter, in 2015–2019 (gray) and 2020 (red); (a). Mean and standard deviation of years and estimates (O-MICT: ORCHIDEE-MICT, L4C: SMAP-L4C, and CAMS: CAMS-OCO2; O-MICT and SMAP-L4C in the case of NPP and Rh) are depicted for 2015–2019. The numbers represent the detrended anomalies of 2020 relative to 2015–2019 for each quarter (top) and cumulative sum (bottom). The height of each bar of (a) denotes the average of transitions in NEE, NPP, and Rh between quarters (b). Transitions are shown as boxplots showing 25%, 50%, and 75% quartiles, and minimum and maximum values for each year group. Annual sums of NEE, NPP, and Rh over Siberia of each year group are shown in the same manner (c).

CO₂ uptake than average for NEE_{Q3} (figure 3(a)). This sequence of transition anomalies (NEE_{Q2-Q1} then NEE_{Q3-Q2}) was largely driven by the abnormal increase in NPP_{Q2-Q1} and decrease in NPP_{Q3-Q2}, despite concurrent changes in Rh, which partially offset the magnitudes of the large NPP swings (figure 3(b)). In summary, earlier and stronger onset of net CO₂ uptake (more negative NEE_{Q2-Q1}) was followed by an earlier decrease in the net CO₂ uptake and return to a CO₂ source in the late season (less negative

NEE_{Q3-Q2}). This compensation in the transitions is clearly indicated by negative relationships between NEE_{Q2-Q1} and NEE_{Q3-Q2} not only in Siberia but in most regions north of 30 °N (figures 4 and S9), and from both NPP and Rh (figure S9).

3.4. Annual CO₂ balance

We found a higher CO₂ uptake in Q2 (more negative NEE_{Q2}) due to extensive warming, but it was followed by a subsequent decrease in CO₂ uptake or



increase in CO_2 release in Q3 (less negative NEE_{Q3}), offsetting the large spring CO_2 uptake. This strong seasonal compensation resulted in a slightly smaller annual sink by 0.1–0.2 PgC in 2020 (10.3%–28.4%) compared to the mean of 2015–2019 in ORCHIDEE-MICT and CAMS-OCO2 but a slightly larger annual sink by 0.2 PgC in SMAP-L4C compared to previous years (table S2 and figure 3(c)). In addition to the more negative NEE_{Q2} and less negative NEE_{Q3} , more positive NEE_{Q1} was consistently shown in the three estimates (figure 2) when the highest temperature anomalies were observed (figures 1(a) and (c)).

3.5. The year 2020 compared to previous decades

We also evaluated how the year 2020 behaved in the context of long-term trends based on the records of ORCHIDEE-MICT and CAMS-surface since 1979. Over the period of 1979–2019, ORCHIDEE-MICT and CAMS-surface long-term trends consistently

showed more negative NEE_{Q2-Q1} (switch to a larger spring CO_2 uptake) and less negative NEE_{Q3-Q2} (switch to a smaller CO_2 uptake or a larger CO_2 release after the peak growing season) over time (figure 3(b)). The year 2020 showed general decreasing NEE_{Q2-Q1} and increasing NEE_{Q3-Q2} trends concurrent with the heatwave over Siberia (figure 3(b)); however, these strong transitions were abrupt considering the difference in seasonality between 2020 and 2010–2019 was as large as the decadal change from 1979–2009 to 2010–2019. Annually, Siberia showed larger CO_2 sinks from 2010 to 2014 compared to 1979–2009, and this increase was followed by a slight change in 2015–2019; i.e. a larger (CAMSSurface) or smaller (ORCHIDEE-MICT) CO_2 sink, followed by a slight reduction in net CO_2 uptake in 2020 (figure 3(c)), with continuous warming trends over time and the heatwave event in 2020 (figure S10).

4. Discussion

4.1. Heatwave effects on CO₂ seasonality and net annual carbon balance

The high northern latitude heatwave of 2020 was extremely widespread and persisted from winter to spring over Siberia, resulting in an earlier start of summer. Unlike the usual concurrence of heatwave and drought, the heatwave over Siberia in 2020 occurred in the presence of snow cover and higher than average precipitation until May. Although tight feedback processes among high temperature, dry soil, and increased vapor pressure deficit are often found in the mid-latitudes (Miralles *et al* 2019), this land-atmosphere coupling (feedback) tends to be weaker at high latitudes (Humphrey *et al* 2021). Abundant snowmelt water and precipitation maintained sufficient soil moisture until May; thus, strong CO₂ uptake was dominant in the absence of soil moisture deficits. This increased CO₂ uptake in response to the heatwave is different from the reduced CO₂ uptake that has been observed during other concurrent heatwave and drought events, e.g. in Europe (Ciais *et al* 2005, Zscheischler *et al* 2014, Bastos *et al* 2020a). Although specific plant functional types can alleviate the reduction in CO₂ uptake in response to heatwave and drought events (Flach *et al* 2018, 2021), strong CO₂ uptake over Siberia in 2020 emphasizes the role of sufficient soil moisture in sustaining photosynthesis. It is also supported by the MVGC analysis indicating negative influence of snow (SWE) on NEE anomalies; i.e. more snow results in relatively larger net CO₂ uptake in the early growing season. Soil moisture did little to explain the NEE anomalies, possibly due to mixed effects of increasing soil moisture during snowmelt and decreasing soil moisture during photosynthesis over multiple months.

The strong CO₂ uptake in early summer, however, could not persist over the whole growing season despite continuing positive temperature anomalies, possibly due to one or more environmental constraints: (a) increased photosynthesis and evapotranspiration activity coincided with a negative precipitation anomaly from June to September. Soil moisture was depleted more quickly because of the increased evapotranspiration demand, and was not replenished by precipitation during the growing season. The resulting increase in dry soil conditions reduced photosynthesis and CO₂ uptake later in the summer, as seen by Buermann *et al* (2018), Lian *et al* (2020), and Zhang *et al* (2020) in the mid-latitudes. (b) The depletion of nitrogen availability in the late growing season (Haddad *et al* 2002, van Wijk *et al* 2003, Reich and Hobbie 2013) and a reduction in plant access to soil nutrients (figure 1(e); Moyano *et al* (2013)) may have limited further CO₂ uptake in the late growing season. (c) Limited carbon sink capacity of plants, e.g. carbohydrate accumulation suppressing photosynthesis, could have contributed to earlier

senescence following enhanced spring photosynthesis (Paul and Foyer 2001, Keenan and Richardson 2015, Zani *et al* 2020). All of these factors (or combinations of them) could have ceased further active CO₂ sequestration in the late summer over Siberia. In addition, active photosynthesis in the early growing season may have fueled CO₂ release in later seasons (Brooks *et al* 2004, Jeong *et al* 2018). The emerging relationship of greater NPP in Q2 and increased NEE (reduced CO₂ uptake or increased CO₂ emission) in Q3 and Q4 supports this explanation. Overall, early onset of net CO₂ uptake or strong net CO₂ uptake in the early growing season did not necessarily enhance the net annual CO₂ sink, and even led to a smaller CO₂ sink in 2020 when estimated by the inversion and the process-based model (figure 3(c)).

4.2. Discrepancies among estimates

While the extreme seasonal transitions of 2020 in comparison to previous years were consistent for each model estimate (interannual variations within each estimate), there were some discrepancies among model estimates. Annual sums of both NPP and Rh over Siberia in 2020 were the highest or second highest compared to those of 2015–2019, and ORCHIDEE-MICT simulated a smaller NEE sink than the mean of 2015–2019, whereas SMAP-L4C simulated a larger sink. This discrepancy can be attributed to the different underlying processes and varying sensitivity of NPP and Rh in response to the extreme climate condition. For example, SMAP-L4C showed a noticeable decrease in Rh in June 2020, which could be attributed to stronger sensitivity of respiration to soil moisture depletion. (a) The underrepresentation of SOC contributions to Rh from deeper soil layers (Endsley *et al* 2020, Yi *et al* 2020), which can underestimate respiration during fall when surface soils freeze and deeper soil layers remain thawed, and (b) near-neutral CO₂ balances of SMAP-L4C, which are associated with the relatively short operational record, may also contribute to the discrepancy. Differences in model inputs and underlying model algorithms and assumptions may have further contributed to differences in the timing and magnitudes of seasonal transitions between ORCHIDEE-MICT and SMAP-L4C.

One of the limitations for direct comparison between bottom-up estimates and inverse modeling is the CO₂ fluxes that they include. Biogenic NEE of inverse modeling includes all CO₂ fluxes in addition to photosynthesis and respiration, such as CO₂ emissions from wildfire, land use change, and lateral transport. The largest wildfire activities and CO₂ emission were observed in June–August 2020 in the Arctic Circle (CAMS 2021), and annually 173–205 TgC was emitted by fire over Siberia in 2020 when estimated by ORCHIDEE-MICT, Global Fire Assimilation System v1.2 and the Global Fire Emissions Database (GFED) v4.1 (figure S11; note that

GFED fire emissions for 2020 are preliminary). These fire emissions over Siberia were higher than the average of previous years. However, including fire CO₂ emissions does not change the interannual NEE patterns and anomalies of 2020 as shown in this study (figure S12). Adding fire CO₂ emissions did not bring the three estimates closer (figure S12), as other processes, such as land use change and lateral transport, are not included in bottom-up estimates, which can be sources of discrepancy between bottom-up estimates and inversions (e.g. Jung *et al* (2020), Kondo *et al* (2020)).

4.3. Implications for the long-term carbon balance at high latitudes

In this study, we found that extremely warm spring temperatures over Siberia in 2020 significantly enhanced spring CO₂ uptake by the land surface. However, although warmer than usual temperatures persisted until the end of the year, potential environmental constraints reduced CO₂ uptake in the summer, and Siberia ended up as a smaller annual CO₂ sink in 2020 than in previous, less warm years. Our results indicate that the responses of terrestrial ecosystems to extreme climate events can be both immediate (due to near-term responses to climate forcings) and lagged (due to accumulating environmental constraints), and that an enhancement in CO₂ uptake during an extended growing season will not necessarily lead to a large net annual CO₂ sink. The ecosystem carbon response can be lagged even by years, e.g. suppression of CO₂ uptake can occur in subsequent years through accelerated soil respiration (Arnone III *et al* 2008, Babst *et al* 2012) and increased insect outbreaks (Bjerke *et al* 2014), or fire CO₂ emission can increase after warm summers (Scholten *et al* 2021); thus, multi-year observations would be needed to fully quantify the heatwave impacts on important CO₂ cycle processes and their legacy effects on the high-latitude carbon budget.

Warming has increased land CO₂ uptake over the last five decades (Ciais *et al* 2019b, Piao *et al* 2020), and stronger thermal optimality of photosynthesis compared to respiration to warming implies that future warming in the Arctic may further enhance carbon uptake (Saxe *et al* 2001, Niu *et al* 2012). However, carbon uptake sensitivity to warming has decreased in the last few decades, especially in high latitudes (Piao *et al* 2017, Yin *et al* 2018, Bastos *et al* 2019). Our findings also show that the increasing carbon uptake rate paused in recent years, and the year 2020, which experienced a record warming, was a slightly smaller carbon sink in Siberia, as shown in the ORCHIDEE-MICT and CAMS-OCO2 results. The different magnitudes of acclimation of photosynthesis and respiration to warming may change this trend (Lombardozi *et al* 2015, Reich *et al* 2016), and further observation and analysis would be needed to fully explain the relationship between net carbon

uptake and warming. Nonetheless, our results imply that, despite the enhanced seasonal CO₂ uptake by land due to a heatwave with no concurrent drought, extremely warm temperatures do not necessarily result in significantly greater net annual carbon sink activity in the northern high latitudes due to compensating seasonal responses in ecosystem productivity and respiration. The timing and duration of heatwaves and other environmental constraints all play a role in the seasonal and annual carbon cycle. Considering substantial decreases in CO₂ uptake with concurrent drought (Ciais *et al* 2005, Zscheischler *et al* 2014) and slight decreases in the annual CO₂ uptake without drought, as shown in this study, more frequent and intense heatwave events in the high latitudes are likely to reduce land carbon uptake in the future.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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Conflict of interest

The authors declare no conflict of interest.

ORCID iDs

Min Jung Kwon  <https://orcid.org/0000-0002-7330-2320>

Philippe Ciais  <https://orcid.org/0000-0001-8560-4943>

Ana Bastos  <https://orcid.org/0000-0002-7368-7806>

Frédéric Chevallier  <https://orcid.org/0000-0002-4327-3813>

Zhihua Liu  <https://orcid.org/0000-0002-0086-5659>

Julia K Green  <https://orcid.org/0000-0002-8466-2313>

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