Statistical upscaling of ecosystem CO₂ fluxes across the terrestrial tundra and boreal domain: Regional patterns and uncertainties

Anna-Maria Virkkala¹,² | Juha Aalto¹,³ | Brendan M. Rogers² | Torbern Tagesson⁴,⁵ | Claire C. Treat⁶ | Susan M. Natali² | Jennifer D. Watts² | Stefano Potter² | Aleks Lehtonen⁷ | Marguerite Mauritz⁸ | Edward A. G. Schuur⁹ | John Kochendorfer¹⁰ | Donatella Zona¹¹,¹² | Walter Oechel¹¹,¹³ | Hideki Kobayashi¹⁴ | Elyn Humphreys¹⁵ | Mathias Goeckede¹⁶ | Hiroki Iwata¹⁷ | Peter M. Lafleur¹⁸ | Eugenie S. Euskirchen¹⁹ | Stef Bokhorst¹⁰ | Maija Marushchak²¹,²² | Perti J. Martikainen²² | Bo Elberling²³ | Carolina Voigt²²,²⁴ | Christina Biasi²² | Oliver Sonnentag²⁴ | Frans-Jan W. Parmentier⁴,²⁵ | Masahito Ueyama²⁶ | Gerardo Celis²⁷ | Vincent L. St.Louis²⁸ | Craig A. Emmerton²⁸ | Matthias Peichl²⁹ | Jinshu Chi²⁹ | Järvi Järveoja²⁹ | Mats B. Nilsson²⁹ | Steven F. Oberbauer³⁰ | Margaret S. Torn³¹ | Sang-Jong Park³² | Han Dolman³³ | Ivan Mammarella³⁴ | Namyi Chae³⁵ | Rafael Poyatos³⁶,³⁷ | Efrén López-Blanco³⁸,³⁹ | Torben Rojle Christensen³⁹ | Min Jung Kwon⁴⁰,⁴¹ | Torsten Sachs⁴² | David Holl⁴³ | Miska Luoto¹

¹Department of Geosciences and Geography, Faculty of Science, University of Helsinki, Helsinki, Finland
²Woodwell Climate Research Center, Falmouth, MA, USA
³Weather and Climate Change Impact Research, Finnish Meteorological Institute, Helsinki, Finland
⁴Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden
⁵Department of Geosciences and Natural Resource Management, Copenhagen University, Copenhagen, Denmark
⁶Alfred Wegener Institute Helmholtz Center for Polar and Marine Research, Potsdam, Germany
⁷Natural Resources Institute Finland, Helsinki, Finland
⁸University of Texas at El Paso, El Paso, TX, USA
⁹Center for Ecosystem Science and Society, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, USA
¹⁰Atmospheric Turbulence and Diffusion Division of NOAA’s Air Resources Laboratory, Oak Ridge, TN, USA
¹¹San Diego State University, San Diego, CA, USA
¹²University of Sheffield, Sheffield, UK
¹³University of Exeter, Exeter, UK
¹⁴Research Institute for Global Change, Japan Agency for Marine-Earth Science and Technology, Yokoama, Japan
¹⁵Carleton University, Ottawa, ON, Canada
¹⁶Dept. Biogeochemical Signals, Max Planck Institute for Biogeochemistry, Jena, Germany
¹⁷Department of Environmental Science, Shinshu University, Matsumoto, Japan
¹⁸School of the Environment, Trent University, Peterborough, ON, Canada

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The regional variability in tundra and boreal carbon dioxide (CO$_2$) fluxes can be high, complicating efforts to quantify sink-source patterns across the entire region. Statistical models are increasingly used to predict (i.e., upscale) CO$_2$ fluxes across large spatial domains, but the reliability of different modeling techniques, each with different specifications and assumptions, has not been assessed in detail. Here, we compile eddy covariance and chamber measurements of annual and growing season CO$_2$ fluxes of gross primary productivity (GPP), ecosystem respiration (ER), and net ecosystem exchange (NEE) during 1990–2015 from 148 terrestrial high-latitude (i.e., tundra and boreal) sites to analyze the spatial patterns and drivers of CO$_2$ fluxes and test the accuracy and uncertainty of different statistical models. CO$_2$ fluxes were up-scaled at relatively high spatial resolution (1 km$^2$) across the high-latitude region using five commonly used statistical models and their ensemble, that is, the median of all five models, using climatic, vegetation, and soil predictors. We found the performance of machine learning and ensemble predictions to outperform traditional regression methods. We also found the predictive performance of NEE-focused models to be low, relative to models predicting GPP and ER. Our data compilation and ensemble predictions showed that CO$_2$ sink strength was larger in the boreal biome (observed and predicted average annual NEE $-46$ and $-29$ g C m$^{-2}$ yr$^{-1}$, respectively) compared to tundra (average annual NEE $+10$ and $-2$ g C m$^{-2}$ yr$^{-1}$). This pattern was associated with large spatial variability, reflecting local heterogeneity in soil organic carbon stocks, climate, and vegetation productivity. The terrestrial ecosystem CO$_2$ budget, estimated...
using the annual NEE ensemble prediction, suggests the high-latitude region was on average an annual CO$_2$ sink during 1990–2015, although uncertainty remains high.

**KEYWORDS**
Arctic, CO$_2$ balance, empirical, greenhouse gas, land, permafrost, remote sensing

1 | **INTRODUCTION**

The terrestrial ecosystem carbon dioxide (CO$_2$) balance is one of the largest uncertainties in the global carbon budget (Friedlingstein et al., 2020), with high latitudes (i.e., tundra and boreal biomes) representing one of the least-constrained budgets (López-Blanco et al., 2019; Schuur et al., 2015; Zscheischler et al., 2017). Moreover, due to polar amplification and large carbon stocks, the high latitudes have the potential for substantial positive feedbacks to climate warming (Abbott et al., 2016; Gasser et al., 2018; Schuur et al., 2008; Turetsky et al., 2020). Currently, in the absence of major disturbances (e.g., fire), boreal forests are generally CO$_2$ sinks (Bradshaw & Warkentin, 2015; Pan et al., 2011), while regional estimates of tundra vary from sinks (McGuire et al., 2009, 2012, 2016) to sources (Belshé et al., 2013). Both the growing and non-growing seasons are important for these annual budget estimates. A recent synthesis found that non-growing season soil CO$_2$ emissions from the northern permafrost region are larger than previously estimated (Natali et al., 2019). However, CO$_2$ uptake by plants over the growing season can be substantial and is often the dominant component of the annual CO$_2$ budget (Alekseychik et al., 2017; Kolari et al., 2009; Lafleur et al., 2012). The current state of the annual terrestrial high-latitude CO$_2$ budget (net sink or source) remains highly uncertain. A key research priority is to develop robust data-driven quantitative frameworks to constrain regional boreal and tundra CO$_2$ budgets at annual and seasonal time scales.

Estimating high-latitude CO$_2$ fluxes across large areas and over long timescales is challenging due to their high spatiotemporal variability (Ai et al., 2018; Wilkman et al., 2018) that is controlled by a range of environmental variables (Camps-Valls et al., 2015; Lund et al., 2010). The ecosystem CO$_2$ balance (i.e., net ecosystem CO$_2$ exchange; NEE) is the relatively small difference between the two large CO$_2$ fluxes of photosynthesis (gross primary production; GPP) and ecosystem respiration (ER; comprising autotrophic and heterotrophic respiration). Although NEE can be measured with the eddy covariance (EC) and chamber techniques (Baldocchi et al., 1988; Lundegårdh, 1927), GPP and ER are estimated indirectly using environmental light and temperature measurements for EC sites (Lasslop et al., 2010; Reichstein et al., 2005) and dark chamber measurements for chamber sites (Shaver et al., 2007). Field studies have shown that GPP, ER, and NEE depend on climatic conditions (e.g., temperature, precipitation, and radiation) (López-Blanco et al., 2017; Nobrega & Grogan, 2008; Zhang et al., 2018), vegetation (Cahoon et al., 2012; Fox et al., 2008; Järveoja et al., 2018),
and soil properties (e.g., soil nutrients and moisture) (Arens et al., 2008; Dagg & Lafleur, 2011; Lund et al., 2009). However, our understanding of the influence of these drivers on GPP and ER, and particularly on NEE, across the entire high-latitude region remains limited (see e.g., Belshé et al., 2013; Lund et al., 2010).

Knowledge of the contemporary high-latitude terrestrial CO\textsubscript{2} budget is further limited by an increasing, but still relatively sparse, flux measurement network (Alton, 2020; Chu et al., 2017; Virkkala et al., 2018). The majority of flux sites are concentrated within a few intensively studied regions, particularly Alaska and Fennoscandia (Metcalfe et al., 2018; Pastorello et al., 2020; Virkkala et al., 2019), with just a few sites in other large regions such as Siberia and northern Canada. Consequently, issues related to the temporal, geographical and environmental representativeness of the measurements need to be considered to accurately estimate high-latitude carbon budgets and their uncertainties. Previous studies have used a variety of synthesis approaches (Belshé et al., 2013; McGuire et al., 2012), and statistical (Natali et al., 2019), process-based (López-Blanco et al., 2019; McGuire et al., 2018; Rawlins et al., 2015; Wania et al., 2009) and atmospheric inversion models (McGuire et al., 2012), yielding highly different CO\textsubscript{2} budgets. Most of these modeling studies have been conducted at coarse spatial resolutions (25–100 km; Natali et al., 2019; Rawlins et al., 2015; López-Blanco et al., 2019) that do not fully capture the heterogeneity in high-latitude environments despite their importance for the regional CO\textsubscript{2} budgets (Raynolds et al., 2019; Treat et al., 2018). New efforts synthesizing the current distribution of flux data and developing models at high spatial resolution are required to improve our understanding on the spatial patterns and magnitudes of CO\textsubscript{2} fluxes.

Models that rely on the statistical relationships between CO\textsubscript{2} flux and predictor variables have been increasingly employed to constrain global and high-latitude CO\textsubscript{2} budgets (e.g., Jung et al., 2020; Natali et al., 2019; Warner et al., 2019). These statistical models are useful for predicting fluxes across larger areas (i.e., upscaling) because they directly draw upon relationships between fluxes and environmental variables, can account for environmental variability across space and time at high resolutions, and are able to handle biases in the geographic representation of the data (Jung et al., 2020; Natali et al., 2019; Warner et al., 2019). A broad range of statistical models and data sources are available for upscaling, but not all of these have been fully utilized. For example, many past studies have upcaled high-latitude fluxes using a single model (Natali et al., 2019; Peltola et al., 2019; Ueyama, Ichii, et al., 2013), but how different models compare with each other is not well known (with exception of Jung et al., 2017 and Tramontana et al., 2016). Further, most of these studies have primarily used machine learning models due to their ability to capture non-linear relationships and interactions in data (Elith et al., 2008). However, traditional regression methods can be a powerful tool in upscaling high-latitude ground conditions due to their ability to extrapolate beyond the range of data used for training, and due to their generalizability and ease of interpretation (Aalto et al., 2018). Finally, many of the recent upscaling studies have relied on EC flux measurements only, neglecting chamber measurements despite their importance as additional data sources (with exception of Natali et al., 2019). Chambers are useful especially in remote, sparsely measured treeless tundra where they can capture the entire ecosystem CO\textsubscript{2} balance and directly measure NEE and ER (Sørensen et al., 2019). Thus, a compilation of both EC and chamber flux measurements and the comparison of available modeling techniques is clearly required to ensure accurate CO\textsubscript{2} flux estimates from existing data and models.

Here, we synthesize annual and growing season CO\textsubscript{2} fluxes from EC and chamber measurements across the high-latitude terrestrial tundra and boreal region. We then use this new database to upscale annual average ecosystem CO\textsubscript{2} fluxes at relatively high spatial resolution (1 km\textsuperscript{2}) across the high-latitude domain using several statistical models. We compare our new database of in situ CO\textsubscript{2} fluxes to past tundra syntheses (Belshé et al., 2013; McGuire et al., 2012), provide a detailed assessment of model performance, analyze the spatial patterns and drivers of CO\textsubscript{2} fluxes, and discuss the resulting CO\textsubscript{2} budget estimates and recommendations for future work. We focus on understanding the spatial variability in average CO\textsubscript{2} fluxes instead of a temporal analysis of CO\textsubscript{2} flux change; however, our modeling framework also considers the interannual variability in fluxes.

2 | MATERIAL AND METHODS

2.1 | Data collection

2.1.1 | Collection of CO\textsubscript{2} flux data

Our study area was defined by the high-latitude tundra and boreal biomes (>45°N) based on global ecoregions (20.6 × 10\textsuperscript{6} km\textsuperscript{2}; Figure 1; Dinerstein et al., 2017). We first conducted a literature survey to identify existing EC and chamber-based terrestrial CO\textsubscript{2} flux observations of GPP, ER, and NEE over annual and growing season periods across the domain. Potential sites were identified from previous studies (Ichii et al., 2017; Marushchak et al., 2013; McCallum et al., 2013; Watts et al., 2014) and prior synthesis efforts (Belshé et al., 2013; McGuire et al., 2012; Virkkala et al., 2018). We augmented the resulting site list using a Web of Science search with key words (“tundra” or “boreal” or “arctic”) and ("CO\textsubscript{2} flux" or "CO\textsubscript{2} exchange" or "CO\textsubscript{2} budget"). Additionally, a community call was solicited through a CO\textsubscript{2} flux synthesis workshop (Parmentier et al., 2019), whereby investigators contributed their most current unpublished data. Additional EC data were downloaded from FLUXNET2015 (Pastorello et al., 2020). The compiled dataset represents all natural terrestrial vegetation types (categorized by needle- or broadleaf forest, shrubland, grassland, wetland, and sparse vegetation) present in the high-latitude region.

We included studies and sites with NEE, GPP, and ER estimates over a full growing season or calendar year (i.e., cumulative flux). Growing season flux measurements are provided by EC and chambers. Non-growing season flux measurements include a variety of methods in addition to EC and chambers (e.g., a gas diffusion method by Björkman et al., 2010, soda lime by Welker et al., 2004, or an
Growing season length and measurement period were defined in multiple ways at individual sites. To allow inter-site comparison, we filtered out measurements that did not represent the entire growing season and standardized the remaining measurements (see Supplementary Text Section 1.1 and a similar approach in Belshe et al., 2013). From this filtered dataset, we calculated average growing season daily flux rates based on the reported measurement length and standardized the fluxes based on a common growing season length. The final list of sites having representative annual or growing season measurements is provided in Table S1, sites that were excluded from our analysis are in Table S2.

The resulting dataset included 148 sites with CO$_2$ fluxes from 1990 to 2015 from variable measurement periods (Figure 1). We compiled 1448 cumulative annual and growing season flux values (when chamber measurements were aggregated per site; Figure 1); 82% of the aggregated observations are from EC and 18% are from chambers. Annual and growing season NEE were the most widely reported fluxes in the dataset (Figure 1). Unlike McGuire et al. (2012)
and Belshe et al. (2013) we also included data from the boreal biome, additional tundra sites, and wetlands (not synthesized in Belshe et al., 2013; Figure S1). Similar to McGuire et al. (2012) and Belshe et al. (2013), our database primarily represents undisturbed environments. However, it also includes measurements from ca. 10 sites that have experienced high natural, anthropogenic or anthropogenically induced disturbances, such as permafrost thaw (Bäckstrand et al., 2010; Cassidy et al., 2016; Trucco et al., 2012), fires (Iwata et al., 2011; Ueyama et al., 2019), insect outbreaks (Heliasz et al., 2011; López-Blanco et al., 2017; Lund et al., 2017), or extensive harvesting practices (Coursolle et al., 2012; Machimura et al., 2005). Throughout the text, positive numbers for NEE indicate net CO$_2$ loss to the atmosphere (i.e., CO$_2$ source) and negative numbers indicate net CO$_2$ gain (i.e., CO$_2$ sink). GPP and ER are always given as positive numbers.

2.1.2 Gridded predictors and reference flux data

We acquired 10 eco-physiologically relevant predictors at 1-km$^2$ resolution (0.0083°) representing climate, vegetation, topographic, and soil conditions: growing degree days (GDD3; °C), freezing degree days (FDD; °C), water balance (WAB; mm), maximum growing season normalized difference vegetation index (NDVI), topographic wetness index (TWI), potential incoming direct annual solar radiation (RAD; MJ cm$^{-2}$ yr$^{-1}$), soil organic carbon stocks in the upper 2 meters (SOC; tons per ha), topsoil (0–5 cm) pH, topsoil clay content (CLAY; %), and land cover (LC; classes were mixed or broadleaved forest, needle-leaved forest, grassland and shrubland, wetland, sparse vegetation; see Supplementary Text Section 1.2 and Figure S2 for more information about the predictors). These predictors characterize previously identified key relationships between CO$_2$ fluxes and summer and winter temperatures, radiation, precipitation, local hydrology and soil conditions, soil carbon stocks, and vegetation properties (i.e., see Beer et al., 2010; Belshe et al., 2013; Lund et al., 2010; Natali et al., 2019; Ueyama, Iwata, et al., 2013). NDVI further reflects disturbances as it can show spectral browning signals related to drought, harvesting, or fires (Myers-Smith et al., 2020; Figure S3; Supplementary Text Section 2.5). We recognize that GPP and ER partitioning and gap filling rely on supporting environmental data (e.g., temperature and radiation), and consequently these fluxes already include some information about variables that we also used as predictors in our statistical models. We used annual (1990–2015) data for GDD3, FDD, WAB, and NDVI; the remaining predictors were considered to be static. All predictor datasets were masked to only include high-latitude tundra and boreal biomes (Dinerstein et al., 2017), and to exclude permanent water bodies, urban areas, and croplands based on a land cover dataset developed by ESA (2017).

We compared our annual ecosystem NEE predictions and budgets (see Section 2.2.1) with FLUXCOM, a global product derived from FLUXNET EC towers and machine learning at 0.5° resolution (Baldocchi et al., 2001; Jung et al., 2017; Tramontana et al., 2016) and an ensemble of global Earth system models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) at 1.92 × 1.5° resolution (Taylor et al., 2012) (Supplementary Text Section 1.3).

2.2 Data analysis

2.2.1 Statistical modeling

Our main response variables were annual and growing season cumulative GPP, ER, and NEE, but we also modeled daily average GPP, ER, and NEE during the growing season. Annual and growing season CO$_2$ fluxes were linked to the environmental predictors using a range of different statistical modeling methods (Figure S4). We used five statistical models; two were extensions of linear regression models, and three were based on machine-learning. All of these models have been widely used in empirical CO$_2$ flux upscaling studies (Bond-Lamberty & Thomson, 2010; Hursh et al., 2016; Tramontana et al., 2016; Ueyama, Ichii, et al., 2013). Specifically, we examined generalized linear models (GLMs); generalized additive models (GAMs); generalized boosted regression trees (GBMs); random forest (RF models); and support vector machines (SVMs).

We used several model approaches because individual models have inherent strengths and weaknesses (Supplementary Text Section 2). For example, machine learning methods might suffer from overfitting, whereas regression methods might result in unrealistic values when extrapolated outside the model data range. Further, individual models may detect different patterns in the data, and the best performing models are not always the same for different response variables (Segurado & Araújo, 2004). We also produced an ensemble prediction by calculating a median prediction over the five predictions from the individual modeling methods (see also Tramontana et al., 2016). We used the median instead of the mean to avoid extreme predicted values inflating the ensemble prediction. In this procedure, the uncertainty of the ensemble is expected to be lower than the uncertainty of a single model (Aalto et al., 2018). Consequently, we produced six model predictions for each of our response variables.

To determine the main drivers of the spatial patterns of response variables, the relative contribution of predictors in the models was assessed using a prediction re-shuffling approach (Nittynen & Luoto, 2018). We first fit the model and developed predictions using the original data, and then repeated this procedure with the values for one predictor randomly permuted. The contribution of a variable was calculated as a correlation between these two predictions (i.e., original model and the model with a shuffled predictor) subtracted from one:

$$\text{Relative contribution} = 1 - \text{correlation} \left( \frac{\text{Prediction}_{\text{original data}} - \text{Prediction}_{\text{randomly permuted data}}}{\text{Prediction}_{\text{original data}}} \right)$$

Values close to 1 indicate that the two predictions were different, indicating high variable importance of the predictor variable.
Each predictor was randomly permuted 100 times for each flux with each of the modelling methods, and an ensemble contribution was derived by taking a mean of the values. To visualize a predictor’s effect on a response variable after controlling for the effects of other predictors, partial dependence plots were derived from the random forest model. For both variable importance and partial dependence plot analyses, we used daily average growing season fluxes because the growing season length estimates that were used to calculate growing season fluxes are not independent from GDD3. We found that the daily average fluxes correlated strongly with the growing season fluxes (Pearson’s correlation 0.93–0.94), so they can be assumed to reflect the same relationships with the predictors.

To extrapolate across the study domain, we fit the models using the entire dataset to produce annual flux predictions and their ensembles that were subsequently averaged to 1990–2015 mean values. Because the ensemble predictions were among the most accurate and least uncertain predictions across all response variables, and because their use is generally recommended in predictive efforts (Araújo & New, 2007), our final flux maps and budgets were based on the flux ensemble. In addition to annual and growing season budgets, we also calculated a non-growing season budget (see Table S4). We had different numbers of observations and sites available for each flux and model, and consequently observed and predicted ER and GPP fluxes and budgets do not sum up to NEE.

2.2.2 Model fit, predictive performance and uncertainty

To evaluate model fit, we predicted fluxes over the entire model training data. To assess the predictive performance of the models, we used a leave-one-site-out cross validation scheme in which each site was iteratively left out from the dataset, and the remaining data were used to predict fluxes for the excluded site (Bodesheim et al., 2018). For both model fit and predictive performance, we calculated bias as an average of the absolute error between prediction and actual observations, Pearson correlation (r) to determine the strength of the linear relationship between the observed and predicted fluxes, and root mean squared error (RMSE) to estimate the model error. We use the terms “observed” and “predicted” to distinguish between field measurements and model predictions but acknowledge that some of these observed values represent indirect estimates of fluxes (e.g., GPP).

We evaluated the prediction uncertainty of all flux models and the budget uncertainty of annual and growing season NEE models using a repeated random resampling procedure (Aalto et al., 2018). Prediction uncertainty was calculated to characterize the spatial variability in flux predictions across the high-latitude region, whereas budget uncertainty quantified the range of potential NEE budget values. We used bootstrapping (fractional resampling with replacement based on LC classes) to subset the model training data into 200 different datasets, all of which had the same number of observations as the original flux data itself. These 200 datasets were then used to produce 200 individual predictions with all five statistical models and their ensemble for each flux and for each year from 1990 to 2015 to assess prediction uncertainty which was summarized using the prediction interval (PI: 95th percentile - 5th percentile). Uncertainty for annual and growing season NEE budgets was estimated by calculating the range of budgets from the 50 first ensemble predictions out of the 200 predictions for each year from 1990 to 2015, due to computational constraints. For more details, see Supplementary Text Section 2.4 and Figure S5.

3 RESULTS

3.1 Observed flux variation

Flux measurements showed considerable variation in magnitudes and signs (CO2 sink vs source) across the high-latitude environments (Figure 1 and Table 1). Observed annual NEE (no upscaling) was on average a small source of CO2 in the most northern parts of the study domain (tundra: +10 g C m−2 yr−1, 42 sites; northern permafrost region: +6 g C m−2 yr−1, 63 sites) and in drier environments (tundra upland: +16 g C m−2 yr−1, 36 sites), whereas the boreal biome (−46 g C m−2 yr−1, 41 sites), and in particular boreal uplands (−47 C m−2 yr−1, 34 sites), and non-permafrost regions (−90 g C m−2 yr−1, 20 sites) were net ecosystem CO2 sinks. All environmental categories were, on average, net CO2 sinks during the growing season, with the average NEE ranging from −37 to −115 g C m−2 period−1 (Table 1). Tundra upland and non-permafrost regions had the lowest average growing season sink strength. The non-permafrost region sink was greatly reduced by one disturbed site that had large source values up to +600 g C m−2 period−1 (Petrone et al., 2014), but this was not apparent in the annual averages because the same site did not report annual fluxes. Although the environmental conditions at the sites were fairly representative of the entire high-latitude region (Figure S6), colder environments with low NDVI and GDD3 as well as high FDD were less well represented (e.g., large areas of Siberia; Figure 1). Some chamber sites were located in conditions that would have otherwise remained undersampled (Figure S6). These included sites with relatively high soil organic carbon stocks in Hudson Bay Lowland and northwestern Canada, and wet climates in Greenland and northern Fennoscandia.

3.2 Predictive performance of the models

The model fit and predictive performance analyses indicated that the GBM, RF and SVM (machine learning) methods outperformed the GLM and GAM (regression model) approaches across most of the response variables (in particular with NEE, but also with GPP and ER; model fit of annual machine learning models: r = 0.69–0.99 vs. regression models: r = 0.6–0.92; predictive performance of annual machine learning methods: r = 0.2–0.73 vs. regression models:
r = 0.12–0.72; Figure 2g-i). We found that the machine learning-based methods were less uncertain (Figure S7) and predicted values within the range of the observed fluxes as opposed to regression models. However, the machine learning method that performed best and had the least uncertainties varied depending on the flux response variable.

Ensemble predictions were among the best performing models (model fit of annual and growing season ensemble models: r = 0.68–0.94; predictive performance of annual and growing season ensemble models: r = 0.21–0.73; Figure 2 and Figure S8). However, similar to the individual models, model fit and predictive performance was lower for annual and growing season NEE compared to GPP and ER (model fit for GPP and ER: r = 0.89–0.94 vs. NEE: r = 0.68–0.77; predictive performance for GPP and ER: r = 0.53–0.71 vs. NEE: r = 0.21–0.27; Figure 2 and Figure S8). Annual models for ER and NEE exhibited a better fit and predictive performance than the growing season models (based on r), whereas the opposite was true for GPP (Figure 2 and Figure S8). The growing season GPP model fit and predictive performance was higher than that of the ER models, but annual GPP and ER models performed equally well. Model fit and predictive performance were similar in models trained with and without chambers (Table S3). In most predictive performance analyses, the lowest and highest observed fluxes were over- and underestimated, respectively, indicating overall poor predictive performance at the extremes (Figures S9 and S10).

Average predicted and observed fluxes were of similar magnitude (Table 1). However, there was a tendency for the average predicted values to have slightly larger GPP and ER values (e.g., observed and predicted annual NEE in the tundra: 250 g C m⁻² yr⁻¹ and −90 g C m⁻² yr⁻¹, respectively) and stronger net CO₂ sink. Note that ER and GPP do not sum up to NEE as different numbers of observations and sites were available for each flux and model. Moreover, some plant uptake occurs outside of our defined growing season, and consequently growing season GPP and annual GPP do not equal to each other. The average fluxes were calculated based on the extent of the high-latitude tundra and boreal biomes (Dinerstein et al., 2017), permafrost zones (Brown et al., 2002), and land cover (i.e., wetlands, and everything else is upland; ESA, 2017). The confidence intervals for the observed fluxes and the uncertainty ranges for the predicted fluxes can be found in the Table S6.
Predicted fluxes showed high spatial variability across the region with a general trend towards decreasing fluxes and sink strength with increasing latitude for GPP, ER, and NEE (Figure 3 and Figure S11). The variability was related to differences in climate (GDD3 and FDD), solar radiation (RAD) and vegetation greenness (NDVI), which had the strongest influence on most of the fluxes (Figure 4). Moreover, SOC, CLAY, and LC were important variables for annual NEE; CLAY and SOC both had a positive yet saturating relationship (Figure S12). The relationship between LC and NEE suggested that the annual and growing season net sink strength was largest in wetlands and smallest in sparse vegetation (Figures S12 and S13). Some variables had a very low variable importance for most of the fluxes (e.g., TWI, soil pH).

Our predictions revealed regional hot spots in annual and growing season NEE, GPP, and ER. Strong annual and growing season CO₂ sinks, having low ER and high GPP, were found in forested regions with high GDD3, NDVI, RAD, and low FDD across Fennoscandia and European Russia, southern Canada, and southern Siberia (Figure 3 and Figure S11). Annual CO₂ sources were identified within northern and central Siberia, Greenland, northern and central Alaska, as well as
as northern Canada. These regions were located mainly in the tundra, characterized by high FDD, and low GDD3 and NDVI. Growing season CO$_2$ sources were located in southeastern Siberia, northern Siberia and some parts of southern and northern Canada. Largest uncertainties in flux predictions were found in areas with relatively strong CO$_2$ sinks in the boreal biome, such as in Fennoscandia and eastern Canada, but also in the tundra (e.g., Canadian Arctic Archipelago; Figure 3 and Figure S11). The largest differences across our annual NEE, and CMIP5 and FLUXCOM predictions were found in European Russia, Fennoscandia, and southeastern Canada (Table 2).

### 3.4 Terrestrial ecosystem NEE budget for the high-latitude region

Our ensemble predictions showed that the high-latitude tundra and boreal region was on average an annual terrestrial ecosystem CO$_2$ sink over the 26-year (1990–2015) study period (Table 2). The annual NEE budget (based on upscaled NEE data) averaged −419 Tg C yr⁻¹ (90% uncertainty range: −559 to −189 Tg C yr⁻¹; range of budgets across the study period: −449 to −366 Tg C yr⁻¹). When estimating annual NEE according to the separately modeled annual GPP (11,344 Tg C yr⁻¹) and ER (10,397 Tg C yr⁻¹) budgets, we obtain an NEE budget of −948 Tg C yr⁻¹. The average high-latitude growing season NEE budget over the period of 1990–2015 was −1018 Tg C yr⁻¹ (−1332 to −455 Tg C yr⁻¹, 90% uncertainty range), which was supported by the difference between the average growing season ER (5800 Tg C yr⁻¹) and GPP (7016 Tg C yr⁻¹) budgets. For the regional budgets, see Table 2.

The average annual NEE budgets over the study period from CMIP5 and FLUXCOM were −488 and −1056 Tg C yr⁻¹, respectively (Table S5). In the boreal biome, average annual GPP in our study was 8850 compared to 8561 Tg C yr⁻¹ in FLUXCOM. In the tundra biome, the average annual GPP in this study was twice as high as in FLUXCOM (2495 and 1267 Tg C yr⁻¹, respectively). Differences were larger for annual ER. Our annual ER budget for the boreal and tundra biomes was 8241 and 2156 Tg C yr⁻¹, respectively, but the same budgets were only 6363 and 1200 Tg C yr⁻¹ in FLUXCOM. For the regional NEE budgets estimated with CMIP5 and FLUXCOM, see Table S5.

### 4 DISCUSSION

This study provides a conceptual and methodological framework to bridge the gap between local, regional, and high-latitude scales in
statistical flux upscaling. Our framework is unique in that it (a) compiles a new dataset of growing season and annual fluxes using EC and chamber data and investigates the drivers of these fluxes; (b) quantifies the performance of different statistical models; and (c) provides the first spatially continuous high-latitude maps of CO$_2$ fluxes and their uncertainties at high spatial resolution, capturing the inherent spatial heterogeneity in predictors and fluxes and minimizing biases in upscaling compared to coarser scale models (Figure 5e). The better geographical and environmental coverage of the flux measurements compared to past efforts improves our understanding of the spatial patterns and regional budgets of terrestrial ecosystem CO$_2$ fluxes, however, uncertainties in our direct model estimates of NEE remained rather high.

4.1 Drivers and spatial patterns of GPP, ER, and NEE

Our results suggest that climatic, vegetation, and soil variables were all important predictors for terrestrial ecosystem CO$_2$ fluxes. However, almost all CO$_2$ fluxes were strongly driven by the broad climatic gradients and spatiotemporal variability in solar radiation, growing and non-growing season climatic conditions, water balance, and the resulting vegetation greenness patterns, supporting the findings of previous syntheses (Belshe et al., 2013; Lund et al., 2010; Natali et al., 2019). Even though these climatic variables are not independent of our GPP and ER estimates (see Section 4.2), confidence in these results can be drawn from the underlying mechanistic relationships between the climate drivers and fluxes. For example, GPP across large scales is dependent on growing season temperatures, length of season, and radiation, which regulate and provide resources for plant growth (López-Blanco et al., 2017; Lund et al., 2010), and ER is largely driven by enzymatic processes, which are tightly linked with temperatures (Davidson et al., 2006) as well as plant growth (La Puma et al., 2007). In general, we found that warmer, moderately wet, and greener conditions (i.e., environments of higher biomass as indicated by NDVI) increased the magnitude of annual GPP and ER. However, our results also indicate that the overall net sink strength increases with larger greenness, warmer and shorter winters, and wetter climate. These results suggest that GPP and ER respond rather similarly to changes in climate and vegetation conditions across the high-latitude region, although GPP might increase even more due to
increases in vegetation greenness (Berner et al., 2020) and changing climate (Lund et al., 2010). However, differences in these relationships might occur in different regions and land cover types (Baldocchi et al., 2018; Belshe et al., 2013; Lafleur et al., 2012).

In addition to the climate and greenness variables operating mostly at large scales, other more local-scale variables such as soil organic carbon stock and land cover helped explain CO$_2$ fluxes. Soil organic carbon stock was the most important predictor for annual NEE, and it had a positive relationship with it, demonstrating that areas with high carbon stocks might lose more CO$_2$ to the atmosphere. However, this result was not supported by the annual ER models, which would represent the main process behind this positive relationship (i.e., larger carbon stocks have more potential for increased CO$_2$ emissions, particularly in dry conditions (Voigt et al., 2019)). The lack of this relationship might be due to annual ER models not covering the full range of conditions represented by the annual NEE models, or spurious causal relationships being identified by the relatively poorly performing NEE models. The importance of land

| Category        | Annual GPP | Annual ER | Annual NEE | Growing season GPP | Growing season ER | Growing season NEE | Area ×10$^6$ km$^2$ |
|-----------------|------------|-----------|------------|--------------------|-------------------|--------------------|---------------------|
| High-latitude   | 11,344     | 10,397    | -419 (-559 to -189) | 7016               | 5800              | -1018 (-1332 to -455) | 20.6               |
| Boreal          | 8850       | 8241      | -406 (-499 to -239) | 5496               | 4531              | -715 (-1037 to -224) | 13.9               |
| Tundra          | 2495       | 2156      | -13 (-81 to 62)    | 1520               | 1269              | -303 (-338 to -224) | 6.7                |
| Boreal upland   | 8437       | 7808      | -17 (-475 to -226) | 5158               | 4245              | -655 (-973 to -196) | 12.9               |
| Boreal wetland  | 412        | 433       | -17 (-28 to -10)   | 338                | 287               | -60 (-70 to -29)    | 0.9                |
| Tundra upland   | 2451       | 2115      | -9 (-78 to 64)     | 1486               | 1240              | -294 (-330 to -218) | 6.6                |
| Tundra wetland  | 44         | 41        | -4 (-3 to -1)      | 34                 | 29                | -8 (-9 to -6)       | 0.1                |
| No permafrost   | 3407       | 3116      | -238 (-288 to -185) | 1895               | 1587              | -223 (-353 to -45)  | 4.2                |
| Permafrost      | 7924       | 7269      | -181 (-305 to 32)  | 5114               | 4207              | -793 (-1000 to -414) | 16.3               |
cover was expected as it summarizes many key processes related to carbon cycling (e.g., the carbon uptake capacity, temperature sensitivity, as well as quantity and quality of carbon inputs into the soil; Sørensen et al., 2019) and other environmental characteristics (e.g., soil moisture is likely higher in wetlands than in sparse vegetation).

Our ensemble prediction suggested that most of the southern portion of the high-latitude terrestrial region was an annual net ecosystem CO$_2$ sink while the central and northern regions were neutral or small net CO$_2$ sources. Observed and predicted spatial patterns in fluxes were similar to those described by most previous studies. For example, our compiled field observations and predictions are consistent with the majority of Alaskan tundra being an annual ecosystem CO$_2$ source on average, similar to the average observed fluxes in McGuire et al. (2012) or the prediction in Ueyama, Ichii, et al. (2013). The strongest annual ecosystem CO$_2$ sinks in our study were located in southern European Russia, Fennoscandia, and southern Canada, as also observed in the FLUXCOM product (Jung et al., 2017). Studies were located in southern European Russia, Fennoscandia, and southern Canada, which were not covered by the FLUXCOM model training data. Some of the sites in these regions were annual net CO$_2$ sources on some years (Emmerton et al., 2016; Karelin et al., 2013). A similar disagreement was found between an Asia-focused statistical upscaling analysis by Ichii et al. (2017) which suggested stronger sink strength across large parts of Siberia, likely due to a limited number of northern eddy covariance sites used to train their models. The largest regional differences between our predictions, CMIP5, and FLUXCOM occurred in central Siberia, Fennoscandia, and eastern Canada and the Canadian Arctic Archipelago, and these differences were primarily driven by the fact that CMIP5 showed these regions to be sources whereas they were sinks in FLUXCOM and our analysis (Figure 5). These regional differences demonstrate that these particular areas should be studied further to understand the sink-source patterns more accurately in the future.

Our uncertainty estimation suggests that CO$_2$ flux predictions should be interpreted carefully in areas that lack sampling locations or have large variability in fluxes that cannot be captured by the predictor variables. Such areas are particularly concentrated in European Russia, eastern Canada, and the Canadian Arctic Archipelago. As the accuracy of the predictions can usually be improved with increases in the quantity and quality of data, new measurements in these regions or better predictors would likely improve the performance of high-latitude CO$_2$ flux models.

### 4.2 Key sources of uncertainty in our modeling approach

No single best model could be identified across the five modeling methods. However, the three machine learning methods outperformed the two regression models, particularly for NEE, as demonstrated by the improved model performance, lower uncertainty, and the lack of unrealistically high or low flux values in predictions. The better performance of the machine learning methods was likely related to their flexibility and capability to find complex structures in the flux data (Elith et al., 2008). Our results demonstrate that several machine learning methods should be tested to produce the most accurate high-latitude flux predictions and that ensemble methods provide robust predictions (Araújo & New, 2007). Our results also indicate that an ensemble prediction based on machine learning methods alone would likely lead to higher model accuracy and transferability (see also Tramontana et al., 2016).

Our models performed well when predicting to the same data that the models were trained with, but the models had challenges when tested against independent validation data. The predictive performance of our ensemble predictions was comparable to (annual GPP and ER) or less than (growing season GPP, ER, NEE, and annual NEE) that of other global and regional upscaling studies (Ichii et al., 2017; Natali et al., 2019; Peltola et al., 2019; Tramontana et al., 2016; Ueyama, Ichii, et al., 2013). However, comparisons of cross-validation results are hampered by different cross-validation techniques used in studies, with some of the studies including observations from the same site both in the model training and validation data, therefore providing overly optimistic accuracy estimates based on non-independent data. Moreover, these other studies primarily focused on a smaller area and/or shorter time period (with the exception of Tramontana et al., 2016), and used a different set of predictors, further complicating this comparison. In these other studies, the correlation ($r$) between observed and predicted fluxes (derived with cross validation), measured mostly throughout the year as daily-to-monthly fluxes, was roughly 0.65–0.7 for NEE and 0.7–0.8 for GPP and ER. There are several reasons for why some of our models performed more poorly than these previous studies, which we explain below.

The lower quantity of measurements and weaker comparability of fluxes derived with EC and chamber techniques and with variable measurement lengths might explain the lower predictive performance in our study compared to the other upscaling studies. As we used aggregated fluxes over the growing season and annual time scales, the sample size in our models was smaller than in other efforts which all used daily or monthly fluxes (a few hundred observations versus thousands of observations). A larger sample size usually increases the predictive performance of the models, particularly when these measurements cover variable environmental conditions that can be captured by the predictors. For example, FLUXCOM models (Jung et al., 2017, 2020; Tramontana et al., 2016) might have had a higher predictive performance than our models because they use a global FLUXNET database (Pastorello et al., 2020), which covers broad environmental gradients. However, FLUXNET data originates mostly from lower latitudes (e.g., only five sites from the Arctic and 34 from the boreal out of 224 global sites in total used in Tramontana et al., 2016). This could explain the larger net sink strength in FLUXCOM compared to our predictions. The higher
predictive performance of FLUXCOM compared to our prediction might also be explained by the fact that FLUXNET is based on a single flux measurement technique (EC) with standardized filtering, gap-filling, and partitioning procedures. We included chambers to our analysis as they covered conditions that were not covered by the EC network even though we acknowledge that using both chamber and EC measurements, and different partitioning methods for EC, increased the number of different flux measurement techniques and study designs, and may have made the comparison of fluxes across sites more uncertain (Fox et al., 2008; Tramontana et al., 2016). However, we observed no significant differences in fluxes estimated with the two approaches indicative of these mismatches (Figure S6d), and the performance of models did not change when chambers were excluded from model training data. These results suggest that the relatively low performance of some models is related to the high variability in both EC and chamber-derived CO₂ flux estimates that is not captured by our predictors. Further, it demonstrates that including chamber measurements, despite operating at different spatial and temporal resolutions than the EC technique, did not decrease the model performance. It is also possible that the lower predictive performance of growing season models compared to annual models was related to the variable growing season measurement periods used across the studies. We accepted this variability because our goal was to use as many published fluxes as possible to improve the geographical and environmental coverage of sites.

The accuracy of our ensemble predictions varied depending on the flux, with the predictive performance being lowest for NEE models (r = 0.21–0.27). The predictive performance of our GPP and ER models was higher (r = 0.53–0.73) and is comparable to past efforts (Ichii et al., 2017; Natali et al., 2019; Tramontana et al., 2016; Ueyama, Ichii, et al., 2013) because these fluxes represent the ecophysiological and biogeochemical processes describing CO₂ uptake and loss, respectively. GPP and ER also already included some information about temperature and radiation variables that we used as predictors in our statistical models, which may introduce some circularity and artificially inflate the model performance. Our NEE models over- and underestimated low and high (i.e., large negative and positive) values, respectively, by approximately 100–200 g C m⁻² yr⁻¹, which has also been demonstrated with NEE and other fluxes in previous upscaling studies (Ichii et al., 2017; Tramontana et al., 2016; Warner et al., 2019). These extreme values were often from disturbed sites experiencing for example, permafrost thaw or extreme forest management practices, or represented an observation that was notably different from the site mean. Based on the cross validation results of the individually modeled annual NEE, a substantial fraction (53%) of annual source observations were predicted to be sinks (similar to the pattern observed in Ichii et al., 2017; Figure 3b), but some sink observations (24%) were also predicted as sources. We also discovered that the observed average annual NEE was often larger (more positive) than the individually predicted average NEE, which was either a result of the model not being able to predict sources accurately, or of the distribution of flux sites being biased towards environments with larger CO₂ source observations than the entire region on average (see the large number of sites with source observations originating primarily only from Alaska in Figure 1). These results demonstrate that the predictors included in our analyses did not fully represent the spatial gradients and dynamic temporal variability in environmental conditions that influence carbon cycle processes, and particularly the high and low NEE conditions. Further research should explore improvements offered by other current and potential future predictors related to the disturbance and permafrost conditions, snow cover duration and snow depth, soil moisture and nutrient availability, and phenology, root properties, and microbial communities (Illeris et al., 2003; Järveoja et al., 2018; Nobrega & Grogan, 2007).

Even though the geographical and environmental coverage of the flux sites was improved in our study compared to previous efforts, our models included only ca. 10 sites from heavily disturbed conditions (see Section 2.1.1). Consequently, our sites did not cover the full range of disturbance and post-disturbance recovery conditions and the associated impacts on CO₂ fluxes. For example, rapidly thawing permafrost and burned landscapes remained largely under-sampled across Siberia. These disturbances have a substantial impact on carbon cycling in high-latitude ecosystems (Abbott et al., 2016; Walker et al., 2019), including direct emissions from the disturbance (not estimated with our models) and typically increased net CO₂ emissions for several years to decades after the disturbance (Cousolle et al., 2012; Kittler et al., 2017; Lund et al., 2017; Turetsky et al., 2020) which should ideally be captured by our models. The lack of flux data representing disturbed and post-disturbance recovery conditions likely leads to underestimations in net ecosystem CO₂ emissions, and is generally thought as one of the key limitations in statistical upscaling efforts (Jung et al., 2020; Zscheischler et al., 2017).

### 4.3 Terrestrial ecosystem CO₂ budget and its uncertainty

Although our models may be biased towards sinks, our results suggest that high-latitude terrestrial ecosystems were on average an annual net CO₂ sink during 1990–2015. The uncertainty of this budget was high, as demonstrated by the low predictive performance of the annual NEE model, and the fact that budgets derived from different predictions (individual NEE predictions and ER-GPP predictions) differed by ca. 500 Tg C yr⁻¹ – the latter most likely being linked to the different numbers of observations and sites available for each flux and model (Figure 1). Nevertheless, the annual NEE budget was of similar magnitude to the one estimated by CMIP5 models and larger (less negative) than the one estimated by FLUXCOM (Table S5). The boreal biome was responsible for most of this sink strength (~406 Tg C yr⁻¹, from ~499 to ~239 Tg C yr⁻¹; 13.9 × 10⁶ km²). In contrast, the tundra biome was on average a small sink (~13 Tg C yr⁻¹, from ~81 to +62 Tg C yr⁻¹; 6.7 × 10⁶ km²) or a small source (~10 g C m⁻² yr⁻¹), based on our predictions and observations. This suggests that the tundra biome was on average close to CO₂ neutral even though the large soil organic carbon stocks of this region would indicate larger historical CO₂ sink strength (Hugelius et al.,
Our tundra budget is within the range (though on average more positive, indicating stronger source) of the one comprising process and inversion models, and field-based estimates by McGuire et al. (2012) (−103 Tg C yr⁻¹, from −297 to +89 Tg C yr⁻¹). However, it differs from the source budget (+462 Tg C yr⁻¹, from +94 to +840 Tg C yr⁻¹; 10.5 × 10⁶ km²; wetlands not included) estimated by Belshe et al. (2013). The divergence of average annual NEE across our and Belshe et al. (2013) study is likely explained by our inclusion of fluxes from wetlands, which were on average annual net ecosystem CO₂ sinks (Table 1). The discrepancy between our and the McGuire et al. (2012) study can be explained by a 50% increase in new annual tundra source observations in our dataset (see e.g., Celis et al., 2017; Euskirchen et al., 2014), which were not included in the McGuire et al. (2012) analysis. Further, there are some differences in the study domain boundaries (e.g., the tundra domain in Belshe et al., 2013 was larger than in this study) which might explain some of the discrepancies between these studies, although the general patterns of these boundaries were rather similar (see e.g., Figure I in McGuire et al., 2012 vs. our tundra domain in Figure 1).

Our findings suggest that both the boreal and tundra biomes were relatively strong CO₂ sinks during the growing season. Our growing season CO₂ budgets estimated for the same seasons as in previous studies (see Supplementary Text Section 2.3), derived both by predicting NEE as well as subtracting GPP from ER suggest that the growing season net uptake is stronger than or similar to the estimates in Belshe et al. (2013) and Natali et al. (2019). The growing season NEE budget calculated for 100 days in the tundra was −296 Tg C yr⁻¹ in this study, compared to −137 ± 80 Tg C yr⁻¹ in Belshe et al. (2013). The growing season NEE budget estimated for 153 days in the northern permafrost region in this study was −1122 Tg C yr⁻¹, whereas the process model estimates varied between −687 and −1647 Tg C yr⁻¹ in Natali et al. (2019). Further, the observed daily average growing season NEE in tundra demonstrated a stronger sink strength than the average growing season NEE reported in McGuire et al. (2012) and Belshe et al. (2013) (−0.6, −0.3, and −0.2 g C m⁻² d⁻¹, respectively). Even though we acknowledge that some plant uptake and CO₂ emissions occur outside of our defined growing season (i.e., our growing season estimates did not capture the spring and autumn seasons), our results demonstrate that growing season CO₂ uptake might be larger than previously thought.

4.4 | Summary and next steps in high-latitude CO₂ flux upscaling

Overall, our findings suggest that statistical predictions aimed at describing high-latitude CO₂ flux patterns provide new insights into the understanding of broad GPP and ER patterns but have uncertainty with NEE. Furthermore, this study demonstrates that machine learning models are a robust and accurate empirical approach to predicting high-latitude terrestrial CO₂ fluxes, and that no individual machine learning model outperformed the others. This therefore supports the use of ensemble predictions to reduce uncertainties associated with a single method and to produce more robust predictions. Nevertheless, the building of better models with an improved flux measurement network remains the highest research priority. Our results suggest that the next steps for future high-latitude upscaling efforts are to (a) measure fluxes over the entire year in as many sites as possible, (b) establish new sites in data-poor regions and regions where CO₂ predictions were most uncertain, such as in Europe, Russia, Siberia, eastern Canada, and Canadian Arctic Archipelago, and specifically in disturbed and high-Arctic conditions, (c) develop better geospatial predictors (e.g., describing soil moisture and nutrients or permafrost thaw) to explain fluxes, (d) conduct detailed sensitivity tests of the importance of the flux measurement method, data distribution, and different predictor datasets influencing the budgets, and (e) build models at a finer temporal resolution than annual and growing season, to capture rapidly changing transition periods and bypass issues associated with temporal aggregation and varying definitions of seasons. High-latitude specific models are needed to more accurately monitor current emissions and improve understanding of the role of high-latitude regions in the global carbon cycle, as large changes in carbon cycling are likely in the near future.

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AUTHOR CONTRIBUTIONS

AMV and ML designed the study. AMV extracted the flux data from the literature and the community call was designed and gathered by MM, TS et al. AMV, JA, and SP prepared the gridded datasets. ML, JA, and AMV developed the modeling framework. TT, CT, BR, JDW, and SMN commented on the analysis and AMV, with the help of JA and ML, conducted the analysis. Other authors contributed data and all authors were involved in the writing.

DATA AVAILABILITY STATEMENT

Data are archived and freely available at Zenodo. The synthesis dataset is available at http://doi.org/10.5281/zenodo.4519583. Annual and averaged flux predictions are available at http://doi.org/10.5281/zenodo.4521852. The codes to run the statistical models and predictions together with the uncertainty estimation can be found in an R Markdown file as a supplement (Virkkalaetal_CO2flux_upscaling.pdf).

ORCID

Anna-Maria Virkkala https://orcid.org/0000-0003-4877-2918
Juha Aalto https://orcid.org/0000-0001-6819-4911
Brendan M. Rogers https://orcid.org/0000-0003-6711-8466
Torbern Tagesson https://orcid.org/0000-0003-3011-1775
Claire C. Treat https://orcid.org/0000-0002-1225-8178
Susan M. Natali https://orcid.org/0000-0002-3010-2994
Alessi Lehtonen https://orcid.org/0000-0003-1388-0388
Marguerite Mauritz https://orcid.org/0000-0001-8733-9119
Edward A. G. Schuur https://orcid.org/0000-0002-1096-2436
Mathias Goeckede https://orcid.org/0000-0003-2833-8401
Hiroki Iwata https://orcid.org/0000-0002-8962-8982
Peter M. Lafleur https://orcid.org/0000-0003-0347-9128
Stef Bokhorst https://orcid.org/0000-0003-0184-1162
Maija Marushchak https://orcid.org/0000-0002-2308-5049
Perri J. Martikainen https://orcid.org/0000-0003-0415-8449
Bo Elberling https://orcid.org/0000-0002-6023-885X
Carolina Voigt https://orcid.org/0000-0001-8589-1428
Christina Biasi https://orcid.org/0000-0002-7413-3354
Oliver Sonnentag https://orcid.org/0000-0001-9333-9721
Frans-Jan W. Parmentier https://orcid.org/0000-0003-2952-7706
Masahito Ueyama https://orcid.org/0000-0002-4000-4888
Vincent L. St.Louis https://orcid.org/0000-0001-5405-1522
Craig A. Emmerton https://orcid.org/0000-0001-9511-9191
Matthias Peichl https://orcid.org/0000-0002-9940-5846
Jinshu Chi https://orcid.org/0000-0001-5688-8895
Järvi Järveoja https://orcid.org/0000-0001-6317-660X
 Mats B. Nilsson https://orcid.org/0000-0003-3765-6399
 Sang-Jong Park https://orcid.org/0000-0002-6944-6962
Ivan Mammarella https://orcid.org/0000-0002-8516-3356
Rafael Poyatos https://orcid.org/0000-0003-0521-2523
Efrén López-Blanco https://orcid.org/0000-0002-3796-8408
Torben Raile Christensen https://orcid.org/0000-0002-4917-148X
Min Jung Kwon https://orcid.org/0000-0002-7330-2320
Torsten Sachs https://orcid.org/0000-0002-9959-4771
David Holl https://orcid.org/0000-0002-9269-7030
Miska Luoto https://orcid.org/0000-0001-6203-5143

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**SUPPORTING INFORMATION**

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

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Statistical upscaling of ecosystem CO2 fluxes across the terrestrial tundra and boreal domain: Regional patterns and uncertainties

Anna-Maria Virkkala1,2 | Juha Aalto1,3 | Brendan M. Rogers2 | Torbern Tagesson4,5 | Claire C. Treat6 | Jennifer D. Watts2 | Stefano Potter2 | Aleks Lehtonen7 | Marguerite Mauritz8 | Edward A. G. Schuur9 | John Kochendorfer10 | Donatella Zona11,12 | Walter Oechel11,13 | Hideki Kobayashi14 | Elyn Humphreys15 | Mathias Goeckede16 | Hiroki Iwata17 | Peter M. Lafleur18 | Eugenie S. Euskirchen19 | Stef Bokhorst20 | Maija Marushchak21,22 | Pertti J. Martikainen22 | Bo Elberling23 | Carolina Voigt22,24 | Christina Biasi22 | Oliver Sonnentag24 | Frans-Jan W. Parmentier4,25 | Masahito Ueyama26 | Gerardo Celis27 | Vincent L. St.Louis28 | Craig A. Emmerton28 | Matthias Peichi29 | Jinhui Chi29 | Järvi Järveoja29 | Mats B. Nilsson29 | Steven F. Oberbauer30 | Margaret S. Torn31 | Sang-Jong Park32 | Han Dolman33 | Ivan Mammarrella34 | Namyi Chae35 | Rafael Poyatos36,37 | Efrén López-Blanco38,39 | Torben Rojle Christensen39 | Min Jung Kwon40 | Torsten Sachs41 | David Holl42 | Miska Luoto1

1Department of Geosciences and Geography, Faculty of Science, University of Helsinki, Helsinki, Finland
2Woodwell Climate Research Center, Falmouth, MA, USA
3Weather and Climate Change Impact Research, Finnish Meteorological Institute, Helsinki, Finland
4Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden
5Department of Geosciences and Natural Resource Management, Copenhagen University, Copenhagen, Denmark
6Alfred Wegener Institute Helmholtz Center for Polar and Marine Research, Potsdam, Germany
7Natural Resources Institute Finland, Helsinki, Finland
8University of Texas at El Paso, El Paso, TX, USA
9Center for Ecosystem Science and Society, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ, USA
10Atmospheric Turbulence and Diffusion Division of NOAA’s Air Resources Laboratory, Oak Ridge, TN, USA
11San Diego State University, San Diego, CA, USA
12University of Sheffield, Sheffield, UK
13University of Exeter, Exeter, UK
14Research Institute for Global Change, Japan Agency for Marine-Earth Science and Technology, Yokoama, Japan
15Carleton University, Ottawa, ON, Canada
16Dept. Biogeochemical Signals, Max Planck Institute for Biogeochemistry, Jena, Germany
17Department of Environmental Science, Shinshu University, Matsumoto, Japan
18School of the Environment, Trent University, Peterborough, ON, Canada

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