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Variation in CO_2 and CH_4 Fluxes Among Land Cover Types in Heterogeneous Arctic Tundra in Northeastern Siberia

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Abstract

Arctic tundra is facing unprecedented warming, resulting in shifts in the vegetation, thaw regimes, and potentially in the ecosystem-atmosphere exchange of carbon (C). The estimates of regional carbon dioxide (CO_2) and methane (CH_4) budgets, however, are highly uncertain. We measured CO_2 and CH_4 fluxes, vegetation composition and leaf area index (LAI), thaw depth, and soil wetness in Tiksi (71° N, 128° E), a heterogeneous site located within the prostrate dwarf-shrub tundra zone in northeastern Siberia. Using the closed chamber method, we determined net ecosystem exchange (NEE) of CO_2, dark ecosystem respiration (ER), ecosystem gross photosynthesis (Pg), and CH_4 fluxes during the growing season. We applied a previously developed high-spatial-resolution land-cover map over an m area of 35.8 km^2. Among the land-cover types varying from barrens to dwarf-shrub tundra and tundra wetlands, the light-saturated NEE and Pg scaled with the LAI of vascular plants. Thus, the graminoid-dominated tundra wetlands, with high LAI and the deepest thaw depth, had the highest light-saturated NEE and Pg (up to -21 (uptake) and 28 mmol m^{-2} h^{-1}, respectively) and were disproportionately important for the summertime CO_2 sequestration on a landscape scale. Dry tundra, including the dwarf-shrub-dominated vegetation and only sparsely vegetated lichen tundra, had only small CO_2 exchange rates. While tundra wetlands were sources of CH_4, lichen tundra, including bare ground habitats, consumed atmospheric CH_4 at a substantial rate. On a landscape scale, the consumption by lichen tundra and barrens could offset *ca.* 10% of the CH_4 emissions. We acknowledge the uncertainty involved in spatial extrapolations due to a small number of replicates per land-cover type. This study, however, highlights the need for distinguishing different land-cover types including the dry tundra habitats to account for their consumption of the atmospheric CH_4 when estimating tundra C-exchange on a larger spatial scale.

1 Introduction

It is uncertain whether the Arctic tundra is a sink or a source of atmospheric carbon (C). The current estimates suggest a sink of 13–110 Tg C yr^{-1}, but their uncertainty range crosses the zero balance (McGuire et al. 2012, Virkkala et al. 2020). Improving these estimates is vital, because the Arctic tundra covers a vast area of 7.6 million km^2 (Walker 2000) that is experiencing substantial warming (IPCC 2013, Chen et al. 2021). Warming can alter C exchange, either amplifying or mitigating climate change through ecosystem–atmosphere interactions. Some local-scale studies suggest that the Arctic tundra is shifting from a small sink to a source of C (Webb et al. 2016, Euskirchen et al. 2017). It is likely that the climate change response of the ecosystem carbon dioxide (CO_2) sink strength and methane (CH_4) emissions, whether an increase or a decrease, depends on site-specific changes in thawing, wetness, and vegetation (McGuire et al. 2018). C dynamics of different tundra habitats need to be quantified across the Arctic to improve the upscaling of arctic CO_2 and CH_4 balances and to monitor how ecosystems respond to environmental changes.

The uncertainty in the arctic C balance estimates arises from the sparse and uneven observation network, which provides poor support for model-based spatial extrapolation (*cf.* McGuire et al. 2018, Virkkala et al. 2021). On a local scale, landscape heterogeneity and the related difficulty of mapping the spatial distribution of habitats and their C fluxes add to this uncertainty (McGuire et al. 2012, Treat et al. 2018, Saunois et al. 2020). In addition, year-to-year variations in seasonal features, particularly the timing of spring, summer temperatures, and snow depth have been found to cause substantial variation in the annual net CO_2 and CH_4 balances (Aurela et al. 2004, Humphreys and Lafleur 2011, Zhang et al. 2019).

Fine-scale spatial heterogeneity in soil water saturation, thaw depth, vegetation characteristics, and soil organic content is typical of the tundra landscape (*e.g.*, Virtanen and Ek 2014, Mikola et al. 2018, Lara et al. 2020). These factors control CO_2 and CH_4 exchange, and on an annual scale, tundra wetlands typically act as net CO_2 sinks while upland tundra areas have a close-

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

Biogeosciences Discussions

to-neutral C balance (*e.g.*, Marushchak et al. 2013, Virkkala et al. 2021). While tundra wetlands are substantial sources of CH_4, dry tundra act as a small sink of atmospheric CH_4. Particularly, the tundra barrens show high consumption rates of atmospheric CH_4 due to the high-affinity methane oxidizing bacteria (Jørgensen et al. 2014, Lau et al. 2015, D'Imperio et al. 2017, Oh et al. 2020). Thus, distinguishing dry and wet tundra with their moisture and vegetation characteristics is crucial when mapping C exchange within the tundra biome. Treat et al. (2018) tested spatial resolution requirements for such mapping on a landscape level and found that a 20-m pixel size captured the spatial variation in a reasonable manner, while a coarser resolution resulted in underestimation of both the landscape-scale CO_2 uptake and CH_4 emissions. In addition, understanding the spatial heterogeneity of ecosystem C exchange substantially enhances analyses of micrometeorological measurements that, while in principle representing spatially integrated fluxes, may provide biased balances in a highly heterogeneous environment (*e.g.*, Tuovinen et al. 2019). Thus, plot-scale data, allowing studies of the local relationship between gas exchange and soil and vegetation properties, are necessary for improving and validating upscaling methods.

The aim of this study was to assess the spatial patterns and magnitudes of CO_2 and CH_4 fluxes within heterogenous prostrate dwarf-shrub tundra in Tiksi, located in northeastern Russia. Growing season fluxes of CO_2 (ecosystem net exchange, photosynthesis, and respiration) and CH_4 were determined using the chamber method to answer the questions: (i) what is the magnitude of these fluxes in different land-cover types? And (ii) how do they depend on vegetation characteristics and soil wetness? In addition, to test the spatial representativeness of the chamber data, we extrapolated the habitat-level measurements in space to compare them with the ecosystem-level data measured with the micrometeorological eddy covariance (EC) technique.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

2 Materials and Methods

2.1 Study site

The study site is located near the Tiksi Observatory (see Uttal et al. 2016) in Yakutia, northeastern Russia (71.5943 N, 128.8878 E), 500 m inland off the Laptev Sea coast and, on average, 7 m above sea level (Fig. 1). The area belongs to the middle-arctic prostrate dwarf-shrub tundra subzone (Walker, 2000) and has continuous permafrost. In the end of the growing season, the maximum thaw depth is 40 cm (Mikola et al. 2018). Climate in Tiksi is defined by cold winters and cool summers. The long-term mean annual temperature and mean annual precipitation were -12.7 °C and 232 mm, respectively, during the normal period 1981–2010. Growing season lasts about 3 months, and the soils typically freeze in the end of September and the permanent snow falls in October and thaws in June (AARI 2018).

Soil organic content varies from negligible in lichen covered and bare graveled areas to *ca.* 40% in tundra wetlands (Mikola et al. 2018). Bedrock and soils are alkaline, resulting in high plant species richness. Vegetation consists of mosses, lichens, grasses, sedges, prostrate dwarf-shrubs such as willows (*Salix* spp.), dwarf birch (*Betula nana*), and *Diapensia lapponica*, and forb species (Fig. 1, Table 1). The average heights of dwarf-shrub species are 4–6 cm and the leaf area index (LAI) of vascular plants reaches up to 1 m^2 m^{-2} in the wetland and meadow habitats with graminoid vegetation (Juutinen et al. 2017). The land cover at the site has been classified *a priori* and mapped based on a combination of field inventories and high-spatial resolution satellite images (Mikola et al. 2018). The *a priori* land-cover types (LCT) consist of wet fen, dry fen, graminoid tundra, bog, meadow at the stream bank, dwarf-shrub tundra, and lichen tundra (includes bare ground with vegetation patches) (Table 1). A section of the wet and dry fen within the EC footprint area is disturbed by vehicle tracks that create open water surfaces, and there is also an area of eroded bare-peat surface on a dry fen.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

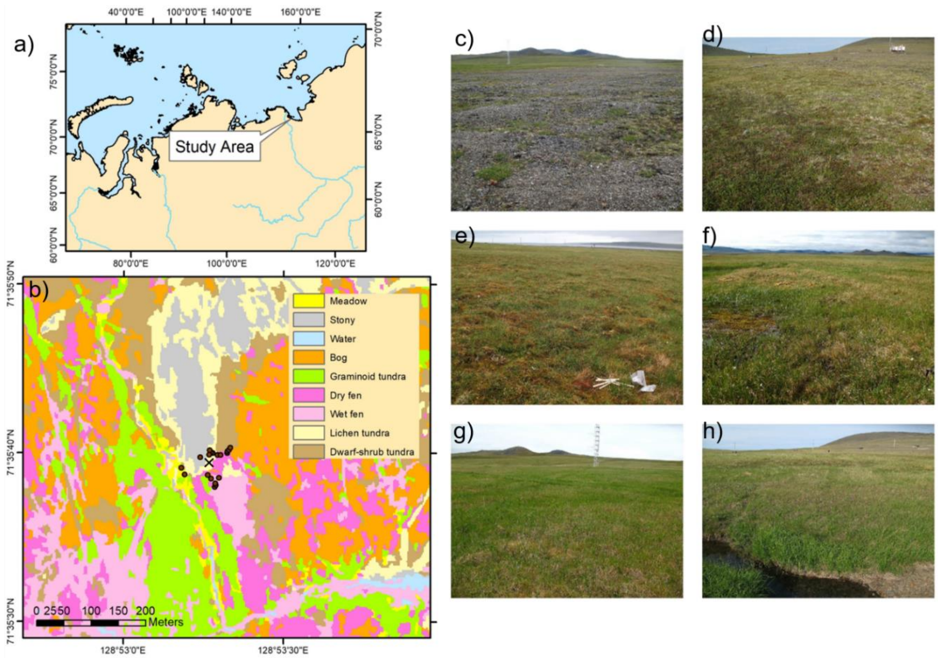

Fig. 1. a) Location of the study area in Tiksi, Yakutia, Russia, **b**) Land-cover map and the chamber flux measurement points (dots) and the EC mast (×) on the map, and photos of the LC types: **c**) lichen tundra with barrens, lichens, and patches of vegetation, **d**) dwarf-shrub tundra, **e**) bog, **f**) wet and dry fen, **g**) graminoid tundra, and **h**) meadow by the stream.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

Table 1. Soil and vegetation characteristics of the land cover types (LCT) and their proportions in the EC impact area (90% of the cumulative footprint).

LCT	Soil properties and plant taxa	Proportion (%)[2]
Lichen tundra[1]	Mixture of vegetated patches, stones, and bare ground. Lichens, *Dryas octopetala, Vaccinium vitis-ideae, Salix polaris, Diapensia lapponica, Oxytropis* spp, *Astragalus* spp., *Pedicularis* spp., *Artemisia* spp., *Minuartia* sp.,	8 (barren), 11 (sparse vegetation)
Dwarf-shrub tundra	Shallow organic layer on mineral soil ground Feather mosses, lichens, *Salix polaris, Vaccinium vitis-ideae, Vaccinium uliginosum, Dryas octopetala, Cassiope tetragona, Betula nana, Polygonum viviparum, Pedicularis* spp., *Carex* spp.	18
Meadow	Shallow organic layer on mineral soil ground *Calamagrostis* sp., *Festuca* sp, *Salix* spp. *Polygonum viviparum, Bistorta major, Polemonium* sp., *Valeriana* sp.	1.4
Graminoid tundra	Shallow peat layer on mineral soil ground Feather mosses, *Sphagnum* spp., *Carex* spp., *Eriophorum* spp., *Calamagrostis* spp., *Salix* spp., *B. nana, Saxifraga* spp., *Ranunculus* spp., *Bistorta major, Stellaria* sp., *Valeriana* sp., *Polemonium* sp., *Comarum palustre* .	13
Bog	Dry hummock habitat at the tundra peatland *Sphagnum* spp., feather mosses, *Salix* spp., *Vaccinium uliginosum, Vaccinium vitis-idaea, Betula nana, Rhodendron tomentosum, Cassiope tetragona, Carex* spp., *Polygonum viviparum., Stellaria* sp.	23
Dry fen	Intermediate wet tundra peatland habitat *Sphagnum* spp., *Carex* spp., *Salix* spp, *Saxifraga* spp., *Comarum palustre, Epilobium* spp., *Ranunculus* spp., *Pedicularis* spp., *Stellaria* sp.	10
Wet fen	Wet tundra peatland habitat with open pools *Brown mosses, Carex* spp., *Eriophorum* spp., *Ranunculus* sp., *Caltha palustris, Pedicularis* sp., *Saxifraga* sp.	15

[1)] Combined land-cover types bare and lichen tundra in Juutinen et al. (2017), Mikola et al. (2018), Tuovinen et al. (2019), [2)] Proportion within the 90% coverage of the mean EC footprint area during the growing season of 2014 (Tuovinen et al. 2019).

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

2.2 CO_2 and CH_4 flux measurements

Fluxes of CO_2 and CH_4 were measured using static chambers set on 12 pre-installed collars of 50 cm × 50 cm. The measurement points (collars) were set to cover the heterogeneity in land cover, and in each study year, there were 1–4 measurement points per each LCT (Table 2). Most of the data were collected during a study campaign in July 15 – August 16, 2014. The growing season had started earlier due to a warm period and daily mean air temperature stayed over 5 °C since July 5 (Fig. 2) (Tuovinen et al. 2019). Net ecosystem exchange of CO_2 (NEE) and ecosystem respiration of CO_2 in dark (ER) were measured using transparent and opaque chambers (transparent chamber covered with a hood), respectively, allowing the estimation of ecosystem gross photosynthesis (Pg) as difference of NEE and ER. Fluxes of CH_4 were determined from closures of both transparent and opaque chambers, but because there was no difference between them when performed consecutively, the data from transparent chamber measurements were used for flux calculations. In addition, CH_4 fluxes were measured during shorter campaigns in 2012, 2013, 2016, and 2019 (Table 2). These data also included vehicle track disturbance plots and an eroded bare-peat surface, which were measured in 2019.

Table 2. Measurement periods, measured fluxes (CH_4, ER, NEE), and number of measurement points and observations (points, observations) in each land cover type (LCT) across the study years.

LCT	2012 Jul 18–21 CH_4	2013 Jul 5–Sep 3 CH_4	2014 Jul 15–Aug 16 ER, NEE, CH_4	2016 May 30, Aug 4–5, Sep 13–14 CH_4	2019 Aug 28–Sep 1 CH_4
Wet fen	4, 4	6, 22	3, 107	3, 27	5, 72
Vehicle track					2, 30
Dry fen	2, 2	4, 11	3, 107	3, 14	2, 26
Bare peat					1, 15
Bog	2, 2	3, 7	1, 36		1, 13
Meadow	1, 1	2, 6	2, 62		
Dwarf-shrub tundra	1, 1		1, 36	1,1	
Lichen tundra		1, 3	2, 67	2, 18	2, 29
Snow and ice[1]				2, 2	

[1]Measured only on May 30, 2016.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

In 2012 and 2013, CH_4 concentrations inside the chamber were analyzed from samples stored in glass vials using a gas chromatograph equipped with a flame ionization detector in the laboratory of the Voeikov Main Geophysical Observatory. Four samples per each 20-min chamber closure were collected. Since July 2014, CH_4 and CO_2 concentrations inside the chambers were recorded every second during closures of about 5-min using a gas analyzer (Los Gatos Research, DLT-100). Gas fluxes between the ecosystem and the atmosphere were calculated from the phase of linear concentration change in the chamber head space over time accounting for temperature, volume, and atmospheric pressure. Concentration change during each chamber closure was evaluated visually for determining the closure start time and to remove cases showing nonlinearity due to leaks, ebullition, or saturation. There were a few ebullition cases at the vehicle track measurement points that had only sparse or no vegetation cover.

The fluxes of CO_2 and CH_4 were also measured by the micrometeorological EC method, which provides continuous data of the atmosphere-biosphere fluxes averaged on an ecosystem scale. The EC system consisted of a three-dimensional sonic anemometer (USA-1, METEK Gmbh, Elmshorn, Germany), a closed-path CH_4 analyzer (RMT-200, LGR, Inc., CA, USA), and a closed-path CO_2/H_2O analyzer (LI-COR LI-7000, Inc., Lincoln, NE, USA). The fluxes were calculated as 30-min averages and processed using standard methods (Aubinet et al. 2012). The EC measurement system and the post-processing procedures have been presented in more detail by Tuovinen et al. (2019).

Supporting meteorological measurements including air temperature (Tair) (Vaisala, HMP), soil temperature (Tsoil) (IKES, Nokeval), photosynthetic photon flux density (PPFD) (Kipp & Zonen, PQS1), and water table level relative to the ground surface (WT) (8438.66.2646, Trafag) were collected by a Vaisala QML datalogger as 30-min averages. We also present meteorological data for the period 2011–2019 to relate the conditions during the measurement campaign in Jul 15-

Aug 16, 2014, and the CH_4 flux campaigns in 2012, 2013, 2014, 2016, and 2019, to the nine-year overall.

2.3 Vegetation and Topographic Wetness Index

On a site level, vegetation and soil characteristics were inventoried in plots assigned into a systematic grid outside the area covered by the gas flux measurement points in 2014 (see Juutinen et al. 2017; Mikola et al. 2018). The projection cover (%) of plant species and species groups, and the mean canopy height of each species group were recorded. Seven species groups were included in the inventory: *Sphagnum* mosses, feather mosses, brown mosses, dwarf shrubs, *Betula nana*, *Salix* species, forbs, and graminoids. A subset of the plots was harvested, and vascular plant leaves were scanned to determine the one-sided LAI to estimate empirical relationships between LAI and %-cover and canopy height to estimate LAI in the collars (see Juutinen et al. 2017). In the collars, cover (%) and height (cm) of each species group were recorded weekly during the gas flux measurement campaign July 15–August 16, 2014. Because there were no observational vegetation data for the other years than 2014, the green chromatic coordinate (GCC) was used as a proxy for the amount of green above-ground vascular plants (*e.g.* Richardson 2019). GCC was calculated from the digital numbers of red (R), green (G), and blue (B) color channels as the ratio of green in the images (GCC= G/(R+G+B)) from digital RGB photos of the vegetation inside the collars. The photos were taken at the time of measurements. We determined an empirical relationship between LAI and GCC by using a data set of harvested plots with digital RGB photographs and measured LAI data (n=91). Data distributions varied among the LCTs due to the intrinsic differences and amount of vegetation. For the LAI estimation, we used a linear relationship (R^2 = 0.46, p<0.001) between LAI and GCC determined using the entire data set (see appendix Fig. 1 for the data and equation).

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

To quantify potential soil wetness at each measurement point, we calculated the mean topographic wetness index (TWI) value based on a 2 m spatial resolution digital elevation model (Mikola et al. 2018). To characterize differences between growing seasons as manifested by vegetation greenness, MODIS Normalized Difference Vegetation Index (NDVI) with 16-day temporal and 500 m spatial resolution was calculated for a circular area with 300 m radius from the flux tower using Google Earth Engine (Gorelick et al. 2017). NDVI was derived for 2011–2019 to place the measurement years in the context of year-to-year variation in weather.

2.4 Data analyses

When examining the role of the habitat types in CO_2 and CH_4 exchange, we applied the land cover classification presented in Mikola et al. (2018). The data collected in July 15 – August 16, 2014 were used for examining gas exchange in relation to the variation in LAI, GCC, WT, and TWI among the collars. Utilizing the ER and NEE fluxes measured with opaque and transparent chambers, respectively, we assessed the light response of Pg and NEE with a hyperbolic function

$$\mathrm{NEE} = ER - Pg_{max} \times \mathrm{PPFD}/(\beta+\mathrm{PPFD}), \qquad \text{eq. 1.}$$

where Pg_{max} is the asymptotic maximum of photosynthesis, and β is the half-saturation PPFD. To ensure comparability between different measurement days in relatively low light conditions, we determined the light-normalized Pg_{800}, *i.e.*, Pg at PPFD = 800 µmol m^{-2} s^{-1}. The corresponding NEE, *i.e.*, NEE_{800}, is then obtained as a sum of Pg_{800} and ER. Fluxes of CH_4 are expressed as collar means. We used a sign convention where a positive value means net release to the atmosphere and a negative value denotes net uptake by the ecosystem.

To find the main factors and gradients in the plant community, gas flux, and environmental variables data measured in the flux collars in 2014, we performed a detrended correspondence analysis (DCA) of the species group data with post-hoc fit of environmental

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

variables, including gas fluxes, WT, LAI, GCC, elevation, and thaw depth as supplementary variables. The DCA was performed on logarithmically transformed, centered species data (species as species groups) using Canoco 5 (Ter Braak and Šmilauer 2012). Regression analyses were used to test the relationships between gas flux estimates and vascular LAI, GCC, WT, and TWI. All CH_4 flux data from the years 2012–14, 2016, and 2019 were used to quantify the mean growing season CH_4 flux for each LCT and examine the relationship between CH_4 and GCC and TWI.

We compared the LCT-specific flux estimates based on the chamber measurements with the estimates based on EC measurements over the same period. Partitioning of the EC-based CO_2 fluxes to Pg and ER and estimates of Pg_{800} and NEE_{800} were calculated similarly to that of chamber data using Eq. (1). The EC flux data were classified into five wind sectors (30–125°, 125–185°, 185–239°, 239–310°, 310–360° based on the mean EC flux footprint, modeled for the growing of 2014 by Tuovinen et al. (2019). The sectors distinguished areas dominated by different LCTs, especially tundra heaths and wetlands, and, similarly, sectors with large and small vascular LAI. For each sector, the footprint-weighted areal proportions of LCTs and mean vascular LAI were derived from the high spatial resolution land-cover and LAI maps (Mikola et al. 2018). For this comparison, sector averages of Pg_{800}, ER, NEE_{800}, and CH_4 flux were calculated from the chamber data by weighting the LCT-specific flux estimates with the above-mentioned LCT proportions in each sector. Because there were no measurement points within graminoid tundra, we applied wet fen (for CO_2) and dry fen (for CH_4) flux estimates for the graminoid tundra based on the observed similarities in LAI and soil wetness, respectively. Overall, graminoid tundra can be considered part of the fen continuum in terms of soil characteristics (high organic content) and CH_4 exchange (Mikola et al. 2018, Tuovinen et al. 2019).

Finally, to synthesize the CO_2 and CH_4 exchange variability across the tundra, we upscaled the LCT-specific average NEE_{800}, Pg_{800}, ER, and CH_4 flux to the 35.8 km^2 area surrounding our study site, for which a LCT map was produced by Mikola et al. (2018).

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

3 Results

3.1 Meteorology

In 2014, when we collected most of the flux data, temperature sum accumulation (with a 0 °C T_{air} threshold) was near-average during the thaw period (the period when soil surface temperature was continuously above 0°C), but the spring and mid-growing season were warmer than on average (Fig. 2a). The average air temperature was 15°C during the gas flux measurements. Accordingly, the MODIS NDVI showed an early start of greening (Fig. 2b-d), and vegetation development had already started at the beginning of the measurement period. In 2010–2019, which included the other CH_4 measurement years, the thaw period lasted for 74–124 days, creating a temperature sum range of 642–1003 °C days (Fig. 2a). Surface soils thawed between May 28 and July 9 and froze again between September 21 and October 1. Among the observation years, the years 2012 and 2019 had notably longer and warmer thaw periods than the other years. The driest habitat, lichen tundra, thawed 10–15 days earlier than the other habitats, and had ca. 3 °C higher soil temperature than the wet fen at the depth of 5 cm (Fig. 2b–c). Water table depth, measured at a wet fen location, showed only subtle interannual variation (Fig. 2e). In 2014, the active layer depth, measured over the measurement period close to the collars, was deepest in the end of August, reaching 30–40 cm in the wetland and meadow habitats, and remained < 30 cm in the dry dwarf-shrub tundra (Fig. 2f). Lichen tundra had rocks underneath the loose surface layer, which made it impossible to measure the actual thaw depth.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

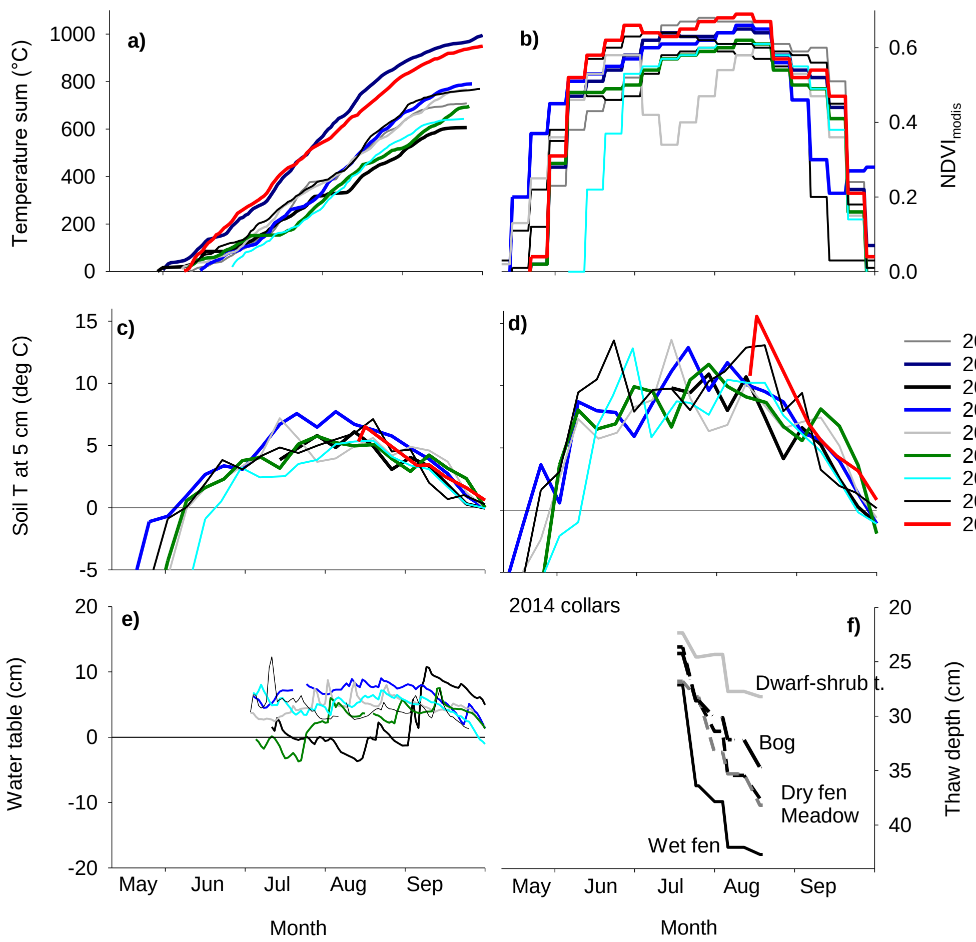

Fig. 2. Meteorology in May to September in years 2011–2019. **(a)** Air temperature accumulation with threshold values soil surface > 0 °C and air T > 0 °C, **b)** seasonal dynamics of NDVI in the study area, 16 d aggregated MODIS data, **c)** weekly means of soil temperature at depth of 5 cm in wet fen and **d)** in dry tundra, **e)** water table relative to the ground surface in wet fen, and **f)** LCT means of thaw depth in the measurement collars in 2014.

3.2 *Multivariate analysis*

DCA axes 1 and 2, which explained 49% and 14% of the variation in the grouped species data (Fig. 3). Lichen tundra and wet fen plots differed most from each other along the axis 1. Accordingly, the supplementary variables WT, vascular plant LAI, thaw depth, TWI, GCC, Pg_{800}, NEE_{800}, and CH_4

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

Biogeosciences
Discussions
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fluxes correlated positively with the axis 1 with post-hoc correlations (r) of 0.6–0.9, as derived from the DCA weighted correlation matrix. Elevation had a positive correlation with the axis 2 (r = 0.8), along which there were gradients in moss abundance and soil organic content.

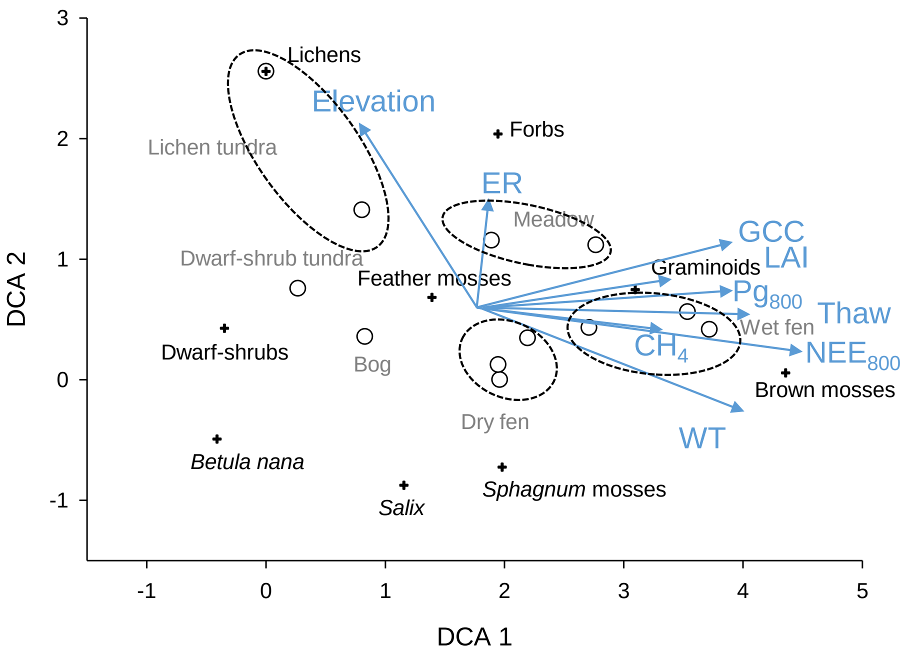

Fig. 3. DCA ordination diagram based on species (species groups) data from the measurement collars in 2014. In the plot, the scores of species groups (cross), sample plots (open symbols), and post-hoc fits of supplementary variables (arrows, blue type) mean CH_4, Pg_{800}, ER, NEE_{800}, thaw depth (Thaw), water table relative to the ground surface (WT), green chromatic coordinate (GCC), vascular plant LAI, and elevation above sea level (Elevation). Land-cover types of the sample plots are indicated (grey type) and plots assigned to same LCTs are circled. Eigenvalues for axis 1 and 2 are 0.597 and 0.171, respectively, and axis 1 and 2 explain cumulatively 63% of the variation in the species group data.

3.3 *Exchange of CO_2 and CH_4*

Among different LCTs, the light-normalized photosynthesis (Pg_{800}) varied from about 5 mmol m^{-2} h^{-1} in the lichen tundra to about 22 and 27 mmol m^{-2} h^{-1} in the wet fen and meadow, respectively.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

Pg_{800} was strongly and positively related to the vascular plant LAI and the greenness index GCC (Fig. 4). There was also a positive correlation between Pg_{800} and WT and TWI, possibly because the highest LAI occurred at the wet fen and meadow plots. However, the TWI values for the two meadow plots located on an elevated bank of the stream were disproportionately high in relation to the WT at the plots, probably because of insufficient locational accuracy or an artefact in the digital elevation model. Ecosystem respiration was higher in the two meadow plots, on average 18 mmol m^{-2} h^{-1} than in other plots. The relationship between ER and LAI was weaker than that of Pg_{800} and LAI (Fig. 4). The net exchange, NEE_{800}, varied from about zero in the lichen tundra plots to a net CO_2 uptake of 16 mmol m^{-2} h^{-1} in the meadow and wet fen plots. NEE_{800} was more tightly linked to Pg_{800} than ER and was correlated with LAI, GCC, WT, and TWI (Fig. 4).

There was substantial consumption of the atmospheric CH_4 in the lichen tundra plots (mean -0.02 mmol m^{-2} h^{-1}, Fig. 5). Minor consumption occurred in the meadow, dwarf-shrub tundra, and bog plots (mean <-0.002 mmol m^{-2} h^{-1}), and efflux to the atmosphere was observed in the dry fen and wet fen plots (means 0.05 and 0.16 mmol m^{-2} h^{-1}, respectively, Fig. 5). The eroded bare-peat plot within the dry fen habitat and the vehicle-track plots in wet fen had large emissions (up to 0.2 mmol m^{-2} h^{-1}), which were of the same magnitude as in the undisturbed dry and wet fen habitats. Variation among the plot means (Fig. 4, year 2014 data) was positively correlated with WT. Large CH_4 emissions occurred when TWI was > 4, except the two meadow plots, which showed net consumption of CH_4 but had an unrealistically high TWI (see above and Figs. 4 and 6). Variation in CH_4 fluxes was not related to variation in LAI or GCC.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

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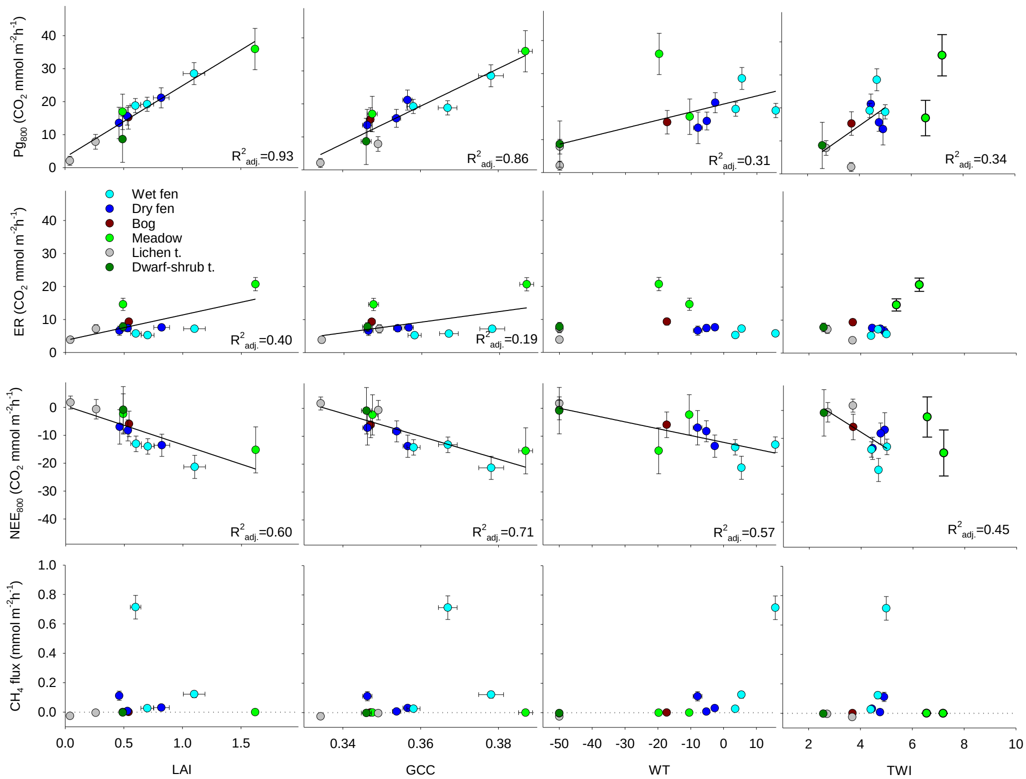

Fig. 4. Variation in estimates of Pg_{800}, ER, NEE_{800} (Eq. 1) and collar means of CH_4 fluxes in relation to variation in collar means of LAI, GCC, WT and TWI on July 6–August 16, 2014. Error bars denote the standard error of estimate. Fitted regression lines and adjusted coefficients of determination ($R^2_{adj.}$) are included for significant linear relationships. The two meadow plots were not included in the TWI regressions.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

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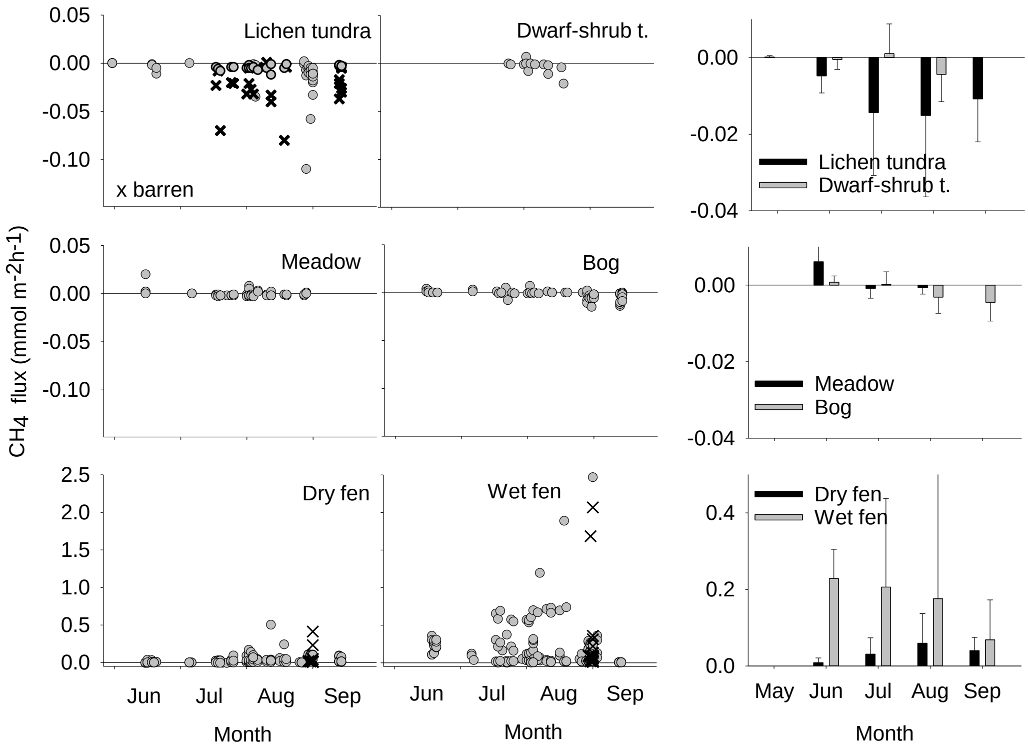

Fig. 5. Instantaneous (left panels) and monthly mean (right panels, with ±SD error bars) CH_4 fluxes in each LTC. The data are a composite of all study years. Barren surfaces are indicated among the lichen tundra data. The eroded bare-peat and vehicle-track plots are plotted as part of the dry fen and wet fen data (×), respectively, but these data are not included in the monthly means. Note that the panel groups have different y-axis scales.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

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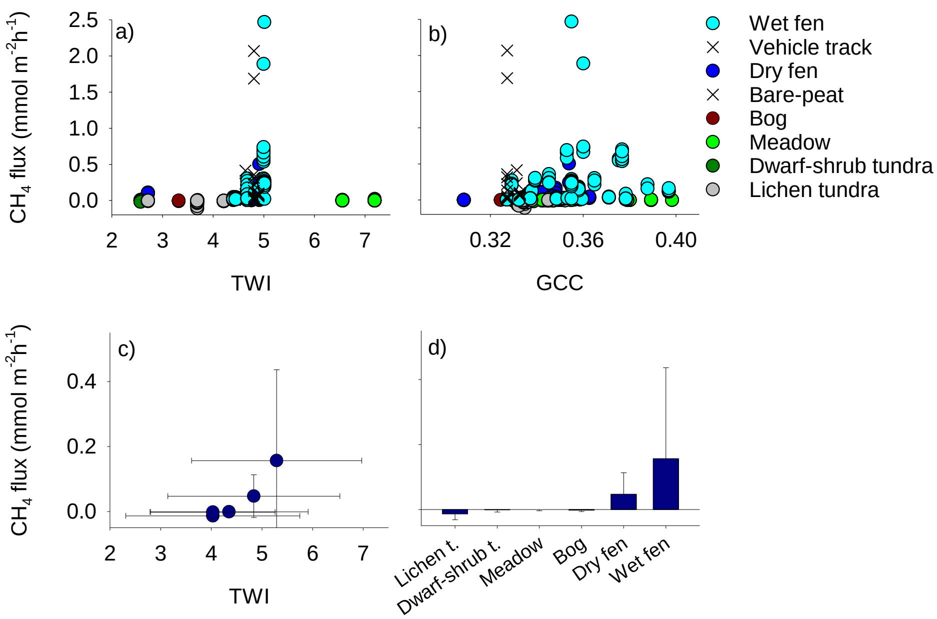

Fig. 6. Instantaneous CH_4 fluxes in the LCTs in relation to **a)** plot specific TWI and **b)** GCC and **c)** LCT mean (±SD) CH4 fluxes in relation to LCT mean (±SD) TWI (excluding the meadow plots with erroneous TWI) and **d)** LCT mean CH_4 fluxes (±SD). Data from years 2014, 2016, and 2019.

To compare the chamber-based flux data with those derived from the EC measurements, the EC data were classified based on wind direction, which reflects the varying domination of different LCTs within the EC source area. In both the southern and south-western wind sectors (125–185° and 185–239°), wet fen and graminoid tundra together contributed *ca.* 40% of the footprint-weighted LCT areas (Fig. 7a). In these directions, vegetation mainly consisted of graminoids, as dry fen, wet fen, graminoid tundra, and meadow contributed 80% in total. The northern sector (310–360°) was characterized by the abundance of lichen tundra and bare ground that accounted for 68% of the footprint-weighted LCT areas, while all the other LCTs covered less than 18% in total. The other wind direction sectors had more even LCT distributions. The differences between the sectors were similar in the EC-based and spatially weighted chamber-based averages of CO_2 exchange (Fig. 7). Both Pg_{800} and NEE_{800} were largest in the southern and south–

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

western sectors and clearly smallest in the barren–lichen tundra-dominated sector in the north. The chamber-based estimates of CO_2 exchange were, however, lower: Pg_{800} was 57%, ER was 93%, and NEE_{800} was 44% of the EC-based estimate.

The southern and south-western wind sectors with abundant dry and wet fens and graminoid tundra had clearly the largest CH_4 fluxes (Fig. 7). The estimate based on chamber measurements was 30% and 50% larger than the EC-based estimate for the east sector (dominated by dry fen and bog) and south sector (dominated by dry and wet fen), respectively. In contrast, the chamber-based estimate was 56–67% of the EC-based estimate for the other sectors, dominated by graminoid tundra and lichen tundra.

Within the extended study area of 35.8 km^2, the LCT-weighted mean NEE_{800}, corresponding to the LCT-specific chamber-based fluxes that were upscaled with the footprint-weighted LCT areas, was -6 mmol m^{-2} h^{-1} (uptake relative to the atmosphere). The corresponding mean Pg_{800} was 12 mmol m^{-2} h^{-1}, and CH_4 flux 0.05 mmol m^{-2} h^{-1} (Table 3). Relative to their spatial cover (28% in total), wet and dry fens were disproportionally important for the landscape-level net exchange of CO_2, photosynthesis, and CH_4, contributing 74%, 47%, and 99% of the net landscape totals (Table 3). Consumption of CH_4 by lichen tundra (including barrens), dwarf-shrub tundra, and meadow tundra soils was 10% of the CH_4 emission. Particularly, the barrens contributed to the consumption of CH_4 due to their large area and high consumption rate. Note, however, that the EC-based estimates for the wind direction sectors suggested about two times as high NEE_{800} and *ca.* 30% smaller CH_4 emissions for the wet fens, and 30% larger consumption for the barrens and lichen tundra.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

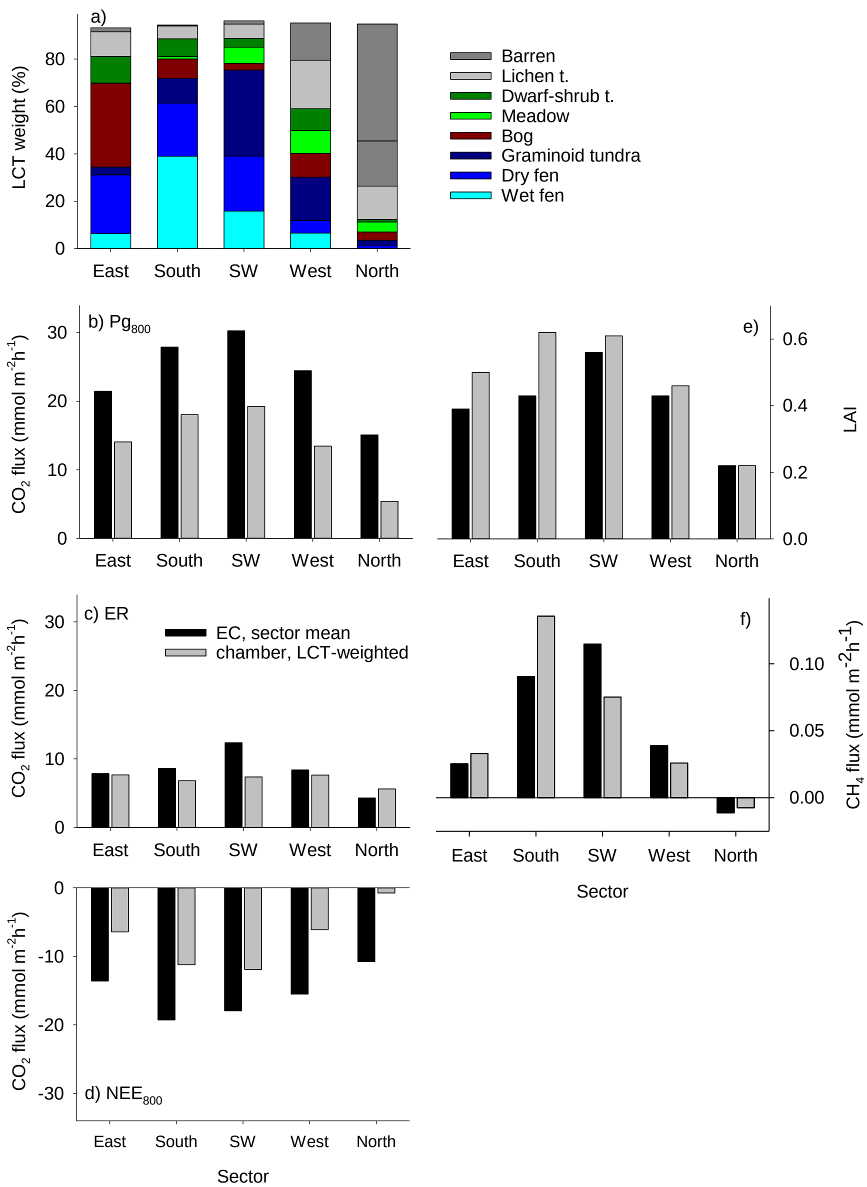

Fig. 7. a) Footprint-weighted mean contribution of each LCT to the EC measurements divided into wind direction sectors, and comparison of EC and chamber-based sector means of **b-d)** CO_2 exchange (Pg_{800}, ER, and NEE_{800}) **e)** vascular plant LAI, and **f)** CH_4 fluxes. The chamber-based data are weighted by the LCT proportions shown in panel a. Map of LAI (Tuovinen et al., 2019) and the LAI measured in the collars were used to estimate the EC- and chamber-related sector means, respectively.

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

Biogeosciences Discussions

Table 3. Land-cover type distribution in the mapped 35.8 km^2 area, means and standard errors (se) calculated from the collar-specific estimates of Pg_{800}, ER, NEE_{800} and CH_4 based on the 2014 data, and proportional (%) landscape budgets.

LCT	Area (%)	Pg_{800} (mmol $m^{-2}h^{-1}$)		ER (mmol $m^{-2}h^{-1}$)		NEE_{800} (mmol $m^{-2}h^{-1}$)		CH_4 flux (mmol $m^{-2}h^{-1}$)		NEE_{800} (%)	Pg_{800} (%)	CH_4 flux (%)
Mean[1]		11.21		6.60		-4.61		0.053				
		mean	sd	mean	sd	mean	sd	mean	sd			
Wet fen	16.4	21.93	-3.91	6.44	0.98	-15.49	3.39	0.223	0.286	55.1	32.1	88.66
Dry fen	11.6	14.60	1.02	6.99	0.39	-7.61	0.64	0.059	0.052	19.1	15.1	10.80
Gram. t.	3.4	21.93	3.91	6.44	0.98	-15.49	3.39	0.059	0.052	11.4	6.7	10.77
Bog	9.1	15.27		9.34		-5.93		0.000		11.7	12.4	0.03
Meadow	0.4	26.45	9.51	17.66	3.06	-8.79	6.45	-0.001	<0.001	0.8	0.9	-0.01
Dwarf-s. t.	27.4	8.64		7.80		-0.85		-0.003		5.0	21.1	-1.65
Lichen t.	11.1	4.98	2.87	5.53	1.68	0.55	1.20	-0.005		-1.3	4.9	-1.05
Barren	15.3	4.98	2.87	5.53	1.68	0.55	1.20	-0.026		-1.8	6.8	-7.56
Water	5.3	NA		NA		NA		NA				

[1] Spatial LCT area-weighted mean, [2]Graminoid tundra fluxes estimated using values for wet fen (CO_2) and dry fen (CH_4)

4 Discussion

The studied tundra site in Tiksi in northeastern Siberia has heterogeneous land cover, which is reflected as equally heterogeneous CO_2 and CH_4 exchange. On the one hand, we found that the tundra wetlands have a disproportional role: dry and wet fens and meadow had the highest CO_2 uptake capacity and particularly the wet fen showed high CH_4 emissions. On the other hand, our results highlight the high consumption of atmospheric CH_4 by lichen tundra (barrens and small vegetated patches). This CH_4 consumption is high compared to other non-wetland tundra habitats and, on the landscape scale, could offset 9 of the CH_4 emissions. These data augment the knowledge on the functional diversity, namely distribution of different land-cover types, and their emission factors across the vast arctic tundra and will lend support to bottom-up and top-down extrapolations across the Arctic.

Within this tundra landscape, the graminoid-dominated wetlands with organic-rich soils constitute an important part of the ecosystem-atmosphere exchange of CO_2 and CH_4. Within an area of 35.8 km^2 mapped around our study site (Mikola et al. 2018), wet and dry fens and the fen-like graminoid tundra covered 31% of the area but contributed as much as 73% to the potential light-saturated CO_2 sink during the peak growing season. These wetlands are also the sites having high soil organic matter content and C pools (Mikola et al. 2018) and CH_4 emissions to the atmosphere (see also Tuovinen et al. 2019).

The spatial extrapolation of fluxes is clearly sensitive to a small number of chamber measurement points as there is large within-LCT variation e.g., in the wet fen and meadow data. For this reason, it is neither possible to conclude which LCTs differ significantly from each other in the CO_2 or CH_4 fluxes. Our conclusions made from the chamber data are, however, corroborated by the temporally matching section of EC data, categorized by wind direction to reflect the main LCT patterns around the EC mast, which show similarity to the chamber data. Instead of categorical LCT classification, maps of those variables, LAI, and WT, for instance, that drive CO_2 and CH_4 exchange would be preferable for spatial modeling of these ecosystem functions (Räsänen et al. 2021). Mikola et al. (2018) found, however, that distinguishing, for instance, soil organic content based on remote sensing and using the same LCT classification was a challenge in the same site.

The spatial pattern of the growing season light-saturated photosynthesis and net CO_2 exchange was strongly related to the corresponding pattern of the LAI of vascular plants (Fig. 3, 4). Hence, the abundance of graminoid (Cyperaceae and Poaceae) vegetation predicted a large NEE_{800}, which varied from near zero in lichen tundra up to 25 mmol m^{-2} h^{-1} in wet fen. Ecosystem respiration had a smaller role than Pg in determining NEE, but we note that our data cover only a section of the growing season with warmer temperatures and half to full-grown vegetation. The importance of ER is likely to be different when considering the full annual balance (*e.g.*, Hashemi et al. 2021). While our data represent only the growing season, a similar relationship has also been found between the annual NEE and LAI at a tundra site with a mixture of wet and dry tundra in northeastern Europe (Marushchak et al. 2013), in a multi-site EC study in Alaskan tundra

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

(McFadden et al. 2003), in Canadian low arctic tundra wetlands (Lafleur et al. 2012), and across tundra sites (Street et al. 2007; Shaver et al. 2007).

The magnitude of Pg_{800} and NEE_{800} in the fen and meadow plots of this study were similar to the maximum Pg and NEE found in tundra wetland in Seida in northeastern Europe (Marushchak et al. 2013), at low tundra wetland sites in eastern Canada (Lafleur et al. 2012), and at a wetland-dominated but more continental site (with an equal growing season length) in northeastern Siberia (van der Molen et al. 2007). The vegetation and Pg_{800} of lichen tundra and dwarf-shrub tundra in our study resembled those observed within the polygon rim habitat of the polygon tundra in the Lena River delta, while those of meadow, dry fen, and wet fen resembled the wet polygon center habitats (Eckhardt et al. 2019). In our study, the variation of ecosystem respiration resulted from the variation in vascular plant LAI, soil organic content, and water saturation: the highest ER occurred in mineral soil meadow with high LAI suggesting substantial autotrophic respiration and likely deep rooting and large root biomass contributing to the ecosystem respiration (Fig. 4). In wetlands, respiration may be attenuated by the soil water saturation.

Our chamber-based estimate of the average CH_4 flux within the 35.8 km^2 upscaling area was 0.05 mmol m^{-2} h^{-1}, which is close to 0.04 mmol m^{-2} h^{-1} obtained by Tuovinen et al. (2019) who combined EC data with footprint modeling to statistically determine LCT group-specific CH_4 fluxes. Within this upscaling area, 28% of the area emitted CH_4, while the other habitats either consumed atmospheric CH_4 (lichen tundra including barrens, coverage 26%) or were close to neutral relative to the atmosphere (Figs. 4, 5, Table 3). The wettest spots were the sites having the highest CH_4 emissions (Fig. 4). We observed no clear relationship between vegetation and CH_4 flux in plot level, which could partly be due to the small size of data. At a LCT level, high LAI and high CH_4 emissions co-occurred if WT was high enough (Fig. 3). The sites showing the highest emissions had a high soil organic matter content, an indication of slow decomposition in anoxic conditions, and we also found that the eroded bare-peat surface of dry fen and the disturbed vehicle

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

tracks had high CH_4 emissions. In the case of eroding surfaces, gas efflux may be enhanced by transport pathways emerging from changes in soil structure. Wet depressions, like the vehicle tracks in this study, have in turn been found to have high CH_4 emissions relative to their surroundings in permafrost, which results from the abundance of graminoids producing easily degradable litter compared to dwarf-shrubs, and the potentially increasing nutrients from seasonal permafrost degradation (*e.g.*, Bubier et al. 1995, McCalley et al. 2014, Wickland et al. 2020). All in all, our data encourage applying indicators of wetness together with vegetation parameters as a means of CH_4 flux upscaling in tundra environment. While the topographic wetness index in general was a reasonable surrogate for WT, distinguishing the dry and wet soils, erroneous TWI values were estimated for the streamside meadow, possibly due to insufficient locational accuracy, because the plots were located right next to the stream, but on an elevated bank.

The recognition of CH_4 consuming tundra habitats is important for accurately estimating the net CH_4 balance of tundra. The substantial uptake of atmospheric CH_4 by lichen tundra (here a mixture of bare ground and sparse vegetation) in Tiksi was inferred by Tuovinen et al. (2019) based on a source allocation analysis of EC data: the average flux of the consuming area was estimated at -0.03 mmol m^{-2} h^{-1}, which corresponds to -21.6% of the total upscaled CH_4 flux. In this study, the average growing season CH_4 uptake was -0.02 mmol m^{-2} h^{-1} in the lichen tundra plots and an order of magnitude lower in graminoid tundra, dwarf-shrub tundra, and bog. Our upscaling exercise resulted in a CH_4 sink that counterbalanced about -10% of the CH_4 emission, which likely is an underestimate due to an overestimation of the emissions from the wet fens. High consumption of atmospheric CH_4 in barrens is associated with the high affinity methanotrophs (Jørgensen et al. 2014; Lau et al. 2015; D'Imperio et al. 2017, St Pierre et al. 2019). For instance, on Disko Island, Greenland, which consists of similar land cover types to Tiksi, uptake of CH_4 by bare ground was -0.005–0.01 mmol m^{-2} h^{-1} during the growing season, while a mean flux of -0.003–-0.004 mmol m^{-2} h^{-1} was observed in dry tundra heath (D'Imperio et al. 2017). These consumption rates associated

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

with tundra barrens and high-affinity methanotrophs can be high relative to consumption rates measured on north-boreal forest soils (for instance, -0.01 mmol $m^{-2}h^{-1}$, Lohila et al. 2016).

5 Conclusions

Our results provide new observations of carbon exchange for the prostrate dwarf shrub tundra sub-zone, which covers an area of 2.3 million km^2 of the Arctic (Walker 2000). Graminoid vegetation favored the wet and moist habitats, such as wet fens and the streamside meadow, which were characterized by large CO_2 uptake and CH_4 emissions. The heterogeneity of landscape and the related large spatial variability of CO_2 and CH_4 fluxes observed in this study encourage to monitor the Arctic sites for changes in habitat type distribution. Such changes can include the forming of meadows and appearance of new vegetation communities, such as erect shrubs, that benefit of warming-induced changes in thaw depth and soil wetness. The spatial extrapolation based on a small number of measurement points involves inherent uncertainty but still allowed us to identify key relationships between CO_2 and CH_4 fluxes and vegetation and moisture features, which can be utilized in more robust upscaling experiments that make use of EC measurements.

Data availability. The flux data used in this study can be accessed via the Zenodo data repository: Juutinen, Sari. (2022). Dataset for a manuscript entitled Variation in CO2 and CH4 Fluxes Among Land Cover Types in Heterogeneous Arctic Tundra in Northeastern Siberia [Data set]. Zenodo. https://doi.org/10.5281/zenodo.5825705

https://doi.org/10.5194/bg-2022-5
Preprint. Discussion started: 26 January 2022

Author contributions

TL, MA, and SJ designed the study. TL, MA, and AM took care of the overall site governance and maintenance. VI, ML, TL, JM, JN, EV, TL, TV, and MA conceived the field measurements of CO_2 and CH_4, vegetation, and environmental variables. In addition, ML calculated green chromatic coordinates, and MA and J-PT postprocessed the EC data and J-PT modeled the footprint and estimated footprint LCT fractions. AR and TV processed and modelled the landcover data and estimated TWI and NDVI for the plots and area. SJ compiled the chamber flux data and conducted the data analyses and spatial extrapolations and wrote the manuscript with contributions from all co-authors.

Competing interests

The authors declare that they have no conflict of interest.

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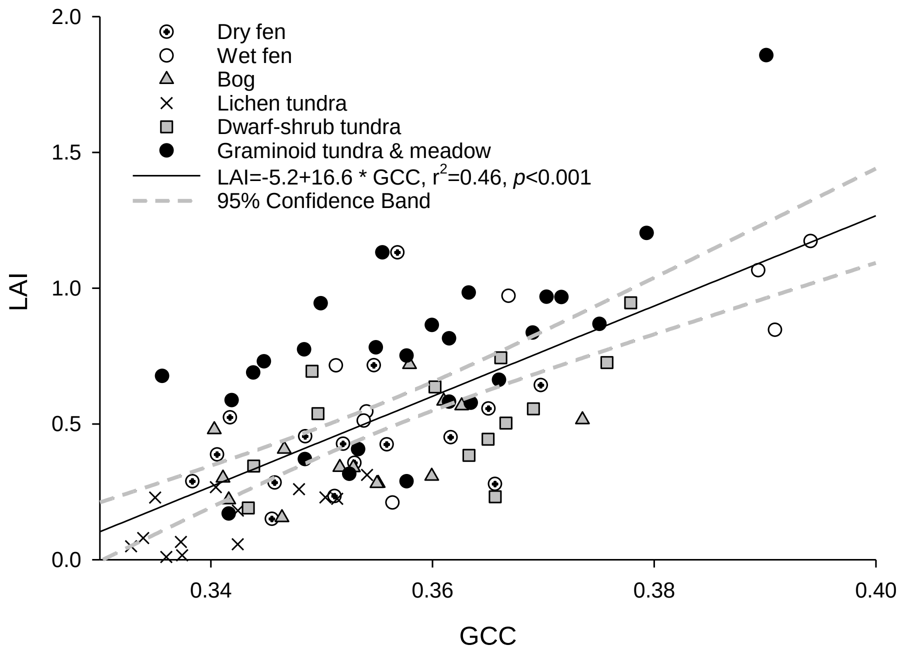
Biogeosciences Discussions

Appendix



Appendix Figure 1. Relationship between GCC and vascular plant LAI in the harvested plots. LCTs are indicated with symbols. In the LCT-specific regressions (not shown), the coefficient of determination ($R^2_{adj.}$) was lowest for dry fen (0.06) and highest for wet fen (0.54). Regression slopes varied from 8.3 for dry fen to 17.8 for the combined graminoid tundra and meadow LC