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). However, the estimates of regional carbon dioxide (CO_2) and methane (CH_4) budgets 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 area of 35.8 km^2 for spatial extrapolation. Among the land-cover types varying from barren to dwarf-shrub tundra and tundra wetlands, the NEE and Pg at the photosynthetically active photon flux density of 800 µmol m^{-2} h^{-1} (NEE_{800} and Pg_{800}) were greatest in the graminoid-dominated habitats, i.e., streamside meadow and fens, with NEE_{800} and Pg_{800} of up to -21 (uptake) and 28 mmol m^{-2} h^{-1}, respectively. Vascular LAI was a robust predictor of both NEE_{800} and Pg_{800} and, on a landscape scale, the fens were disproportionately important for the summertime CO_2 sequestration. Dry tundra, including the dwarf-shrub-dominated vegetation and barren, had smaller CO_2 exchange rates. The fens were the dominant source of CH_4, while the dry mineral soil tundra consumed atmospheric CH_4, which on a landscape scale amounted to -9 % of the total CH_4 balance. The largest seasonal mean CH_4 consumption rate of 0.02 mmol m^{-2} h^{-1} occurred in sand- and stone-covered barren. The high consumption rate agrees with the estimate based on the eddy covariance measurements at the same site. We acknowledge the uncertainty involved in spatial extrapolations due to a small number of replicates per land-cover type. This study highlights the need to distinguish different land-cover types including the dry tundra habitats to account for their different CO_2 and CH_4 flux patterns, especially the consumption of 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, and either amplify or mitigate 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, temperature, and vegetation (McGuire et al. 2018). Dynamics of C exchange need to be quantified across the Arctic habitats 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, Kuhn 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-to-neutral CO_2 balance (*e.g.*, Marushchak et al. 2013, Virkkala et al. 2021). While tundra wetlands are substantial sources of CH_4, dry tundra acts as a small sink or small source of atmospheric CH_4 (Bartlett and Harriss 1993, Kuhn et al. 2021).

Mineral soil tundra barrens, however, have been found to have high consumption rates of atmospheric CH_4 which is due to the high-affinity methane oxidizing bacteria (Emmerton et al. 2014, Jørgensen et al. 2014, D'Imperio et al. 2017, Oh et al. 2020). These bacteria can utilize atmospheric CH_4 as energy source at low atmospheric concentrations, opposite to the low-affinity methane oxidizers that require higher CH_4 concentrations and occur in wetlands (*e.g.*, Oh et al. 2020). A modeling exercise that introduced the high-affinity methanotrophy for mineral-rich soils resulted in a doubling of the circumpolar soil CH_4 sink above 50° N compared to previous estimates (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 improves analyses of eddy covariance (EC) measurements that, while in principle representing spatially integrated fluxes, may provide biased gas flux balances in a highly heterogeneous source/sink environment, as the spatial integration of EC involves non-uniform weighting of the surface elements that contribute to the measured flux (Tuovinen et al. 2019).

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, we extrapolated the plot-level measurements in space and compared them with the ecosystem-level data measured with the EC technique.

2 Materials and Methods

2.1 Study site

The study site is located near the Tiksi Observatory in Sakha (Yakutia) (see Uttal et al. 2016), 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. 1a). 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 *ca.* 40 cm (Mikola et al. 2018). The 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 climate 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).

Bedrock is 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 (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 fen 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 (LCTs) consist of wet fen, dry fen, graminoid tundra, bog, meadow at the stream bank, dwarf-shrub tundra, and lichen tundra that consists of barren ground with rocks and sand and patches of vegetation (Table 1, Fig. 1 c–h, for a closer view see Fig. A1). Organic layer depth is negligible in lichen tundra and a few centimeters in dwarf-shrub tundra, meadow, and graminoid tundra. In bog, dry fen, and wet fen, the organic layer depth is at least the maximum depth of the active layer, *ca.* 30–40 cm. Soil organic content reach *ca.* 40 % in tundra wetlands (Mikola et al. 2018). 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.

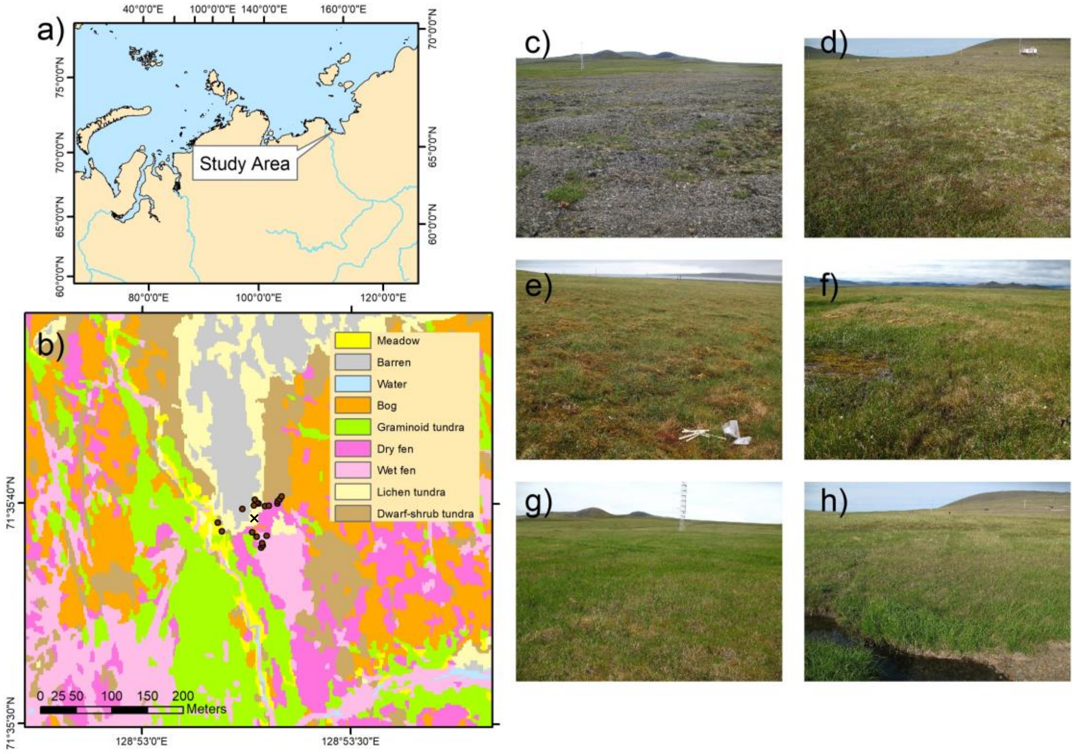

Fig. 1. a) Location of the study area in Tiksi, Yakutia, Russia, **b**) Land-cover map with the chamber flux measurement points (dots) and the EC mast (×), and photos of the land-cover types: **c**) lichen tundra with barren ground and patches of vegetation, **d**) dwarf-shrub tundra, **e**) bog, **f**) wet and dry fen, **g**) graminoid tundra, and **h**) meadow by the stream. See Tuovinen et al. (2019) for the EC footprint climatology.

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,* e.g. genera *Thamnolia, Flavocetraria, Alectoria, Stereocaulon,* dwarf shrubs *Dryas octopetala, Vaccinium vitis-ideae, Salix polaris, Diapensia lapponica,* and forbs *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).

2.2 CO_2 and CH_4 flux measurements

Fluxes of CO_2 and CH_4 were measured using static chambers equipped with a fan and set on 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 (12 collars). 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 and 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 partitioning of ecosystem gross photosynthesis (Pg) 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 opaque 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.

	2012	2013	2014	2016	2019
LCT	Jul 18–21	Jul 5–Sep 3	Jul 15–Aug 16	May 30, Aug 4–5, Sep 13–14	Aug 28–Sep 1
	CH_4	CH_4	ER, NEE, CH_4	CH_4	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.

In 2012 and 2013, four air samples were taken from the chambers using syringes. The samples were stored in glass vials prior to the analysis. First, a vial was flushed with the sample and then filled to over-pressure. The samples were analyzed for CH_4 concentration using a TSVET 500-M gas chromatograph (Chromatek, Russia) with a flame ionization detector at the laboratory of the Voeikov Main Geophysical Observatory within a month from sampling. Each measurement was accompanied by calibration using standard gas mixtures with the NOAA2004 scale. The vials were tested prior to the field sampling using a standard gas: after two weeks, the vials were still over-pressurized and sample CH_4 concentrations were within ±3 ppb of the initial standard gas concentration. 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 (DLT-100, Los Gatos Research, Inc., San Jose, CA, USA) (see Fig. A2 for examples). Gas fluxes between the ecosystem and the atmosphere were calculated from the phase of linear concentration change in the chamber head space over time and 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. The first data points were generally neglected when determining the slope of concentration change over time, and the cases with a linear concentration change had a coefficient of determination (R^2) > 0.9. For near zero flux cases smaller R^2 values were accepted to not ignore those cases. There were a few ebullition cases at the vehicle track measurement points that had only sparse or no vegetation cover, and those measurements were included in the final data. When determining NEE fluxes measured using the transparent chamber, the data were screened for variation in photosynthetically active photon flux density (PPFD), measured during the chamber closure, and rejected if the PPFD variation exceeded 100 µmol m^{-2} s^{-1} during the measurement.

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, Los Gatos Research, Inc., San Jose, CA, USA), and a closed-path CO_2/H_2O analyzer (LI-7000, LI-COR, 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 (T_{air}) (HMP, Vaisala), soil temperature (T_{soil}) (IKES, Nokeval), PPFD (PQS1, Kipp & Zonen), 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 July 15 - August 16, 2014, and the CH_4 flux campaigns in 2012, 2013, 2014, 2016, and 2019, to longer-term variations.

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 find an empirical relationships between LAI and %-cover and canopy height to estimate the LAI in the collars (see Juutinen et al. 2017). In the collars, the projection cover and canopy height of each species group were recorded weekly during the gas flux measurement campaign in 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 proportion of green in the RGB images, GCC = G/(R+G+B), of the vegetation inside the collars. The photographs 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 photographs and measured LAI data (n=91). 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 Fig. A3 for the data and equation).

To quantify the 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, the MODIS Normalized Difference Vegetation Index (NDVI) with 16-day temporal and 500 m spatial resolution was calculated for a circular area with a 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 LCTs 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. The light-normalized Pg and NEE at PPFD = 800 µmol m^{-2} s^{-1} (Pg_{800} and NEE_{800}, respectively), were estimated by fitting a hyperbolic response function of CO_2 vs PPFD utilizing the ER and NEE flux data:

$$NEE = ER - Pg_{max} \times PPFD/(\beta+PPFD), \quad (1)$$

where Pg_{max} is the asymptotic maximum of photosynthesis, and β is the half-saturation PPFD. Fluxes of CH_4 are expressed as temporally averaged per each collar. 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. Fluxes of CH_4 measured over all study years, 2012–2019, were averaged for each LCT.

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. 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 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 or species groups) using Canoco 5 (Ter Braak and Šmilauer 2012).

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 those with a 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 LCT 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 chamber 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 (2014 data) to the 35.8 km^2 area surrounding our study site, for which a LCT map was produced by Mikola et al. (2018).

3 Results

3.1 Environmental conditions

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), and vegetation development had already started at the beginning of the measurement period. In 2011–2019, 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, with least snow accumulation, thawed 10–15 days earlier than the other habitats, and had a ca. 3 °C higher soil temperature than the wet fen at the depth of 5 cm (Fig. 2c–d). Water table level, 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 *ca.* 40 cm in wet fen, 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.

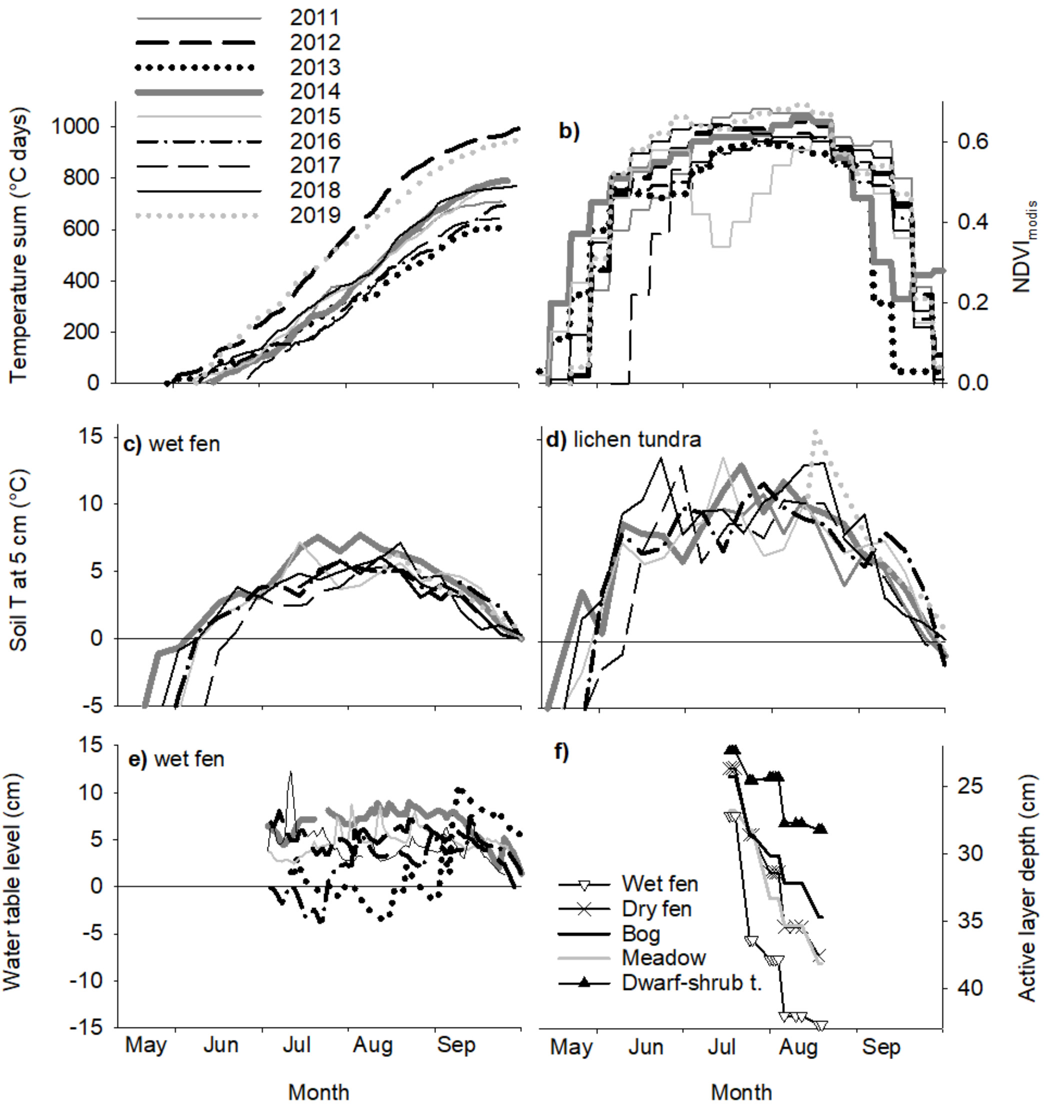

Fig. 2. **(a)** Air temperature accumulation with the threshold surface T_{soil} and T_{air} of 0 °C, **b)** seasonal dynamics of NDVI in the study area, 16 d MODIS data, **c)** weekly means of soil temperature at depth of 5 cm in wet fen and **d)** in lichen tundra, **e)** water-table level relative to the ground surface in wet fen, and **f)** LCT means of thaw depth in the measurement collars in 2014. Rocks in the ground prevented detecting the thaw depth of lichen tundra.

3.2 Exchange of CO_2 and CH_4

Among different LCTs, Pg_{800} varied from about 5 mmol m^{-2} h^{-1} in the lichen tundra to 22 and 27 mmol m^{-2} h^{-1} in the wet fen and meadow, respectively. Pg_{800} was strongly and positively correlated with the vascular plant LAI and the greenness index GCC (Fig. 3). There was also a positive correlation between Pg_{800} and both 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 highest in the two meadow plots, on average 18 mmol $m^{-2} h^{-1}$. The relationship between ER and LAI was weaker than between Pg_{800} and LAI (Fig. 3). 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 to ER and was correlated with LAI, GCC, WT, and TWI (Fig. 3).

There was substantial consumption of the atmospheric CH_4 in the barren tundra (mean -0.018 ± standard error 0.002 mmol $m^{-2} h^{-1}$) and in vegetated lichen tundra (-0.006 ± 0.002 mmol $m^{-2} h^{-1}$) (Figs. 4 and 5). Minor consumption occurred in the bog, meadow, and dwarf-shrub tundra plots (mean -0.001 ± standard error 0.0008 mmol $m^{-2} h^{-1}$), while 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; Figs. 4 and 5). The eroded bare-peat plot within the dry fen habitat and the vehicle-track plots in wet fen had equally high emissions as the fens (up to 0.2 mmol $m^{-2} h^{-1}$). Variation among the plot means of CH_4 flux (Fig. 3 for 2014, Fig. 5 for all years) was related to WT, and CH_4 emissions occurred when TWI was > 4. The two meadow plots that showed net consumption of CH_4 had an unrealistically high TWI relative to their WT (see above and Figs. 3 and 5). Variation in CH_4 fluxes was incoherently related to variation in LAI and GCC because of the high emission cases in plots with little vegetation, including the wettest wet fen plot, vehicle-track, and bare-peat plots (Fig. 5).

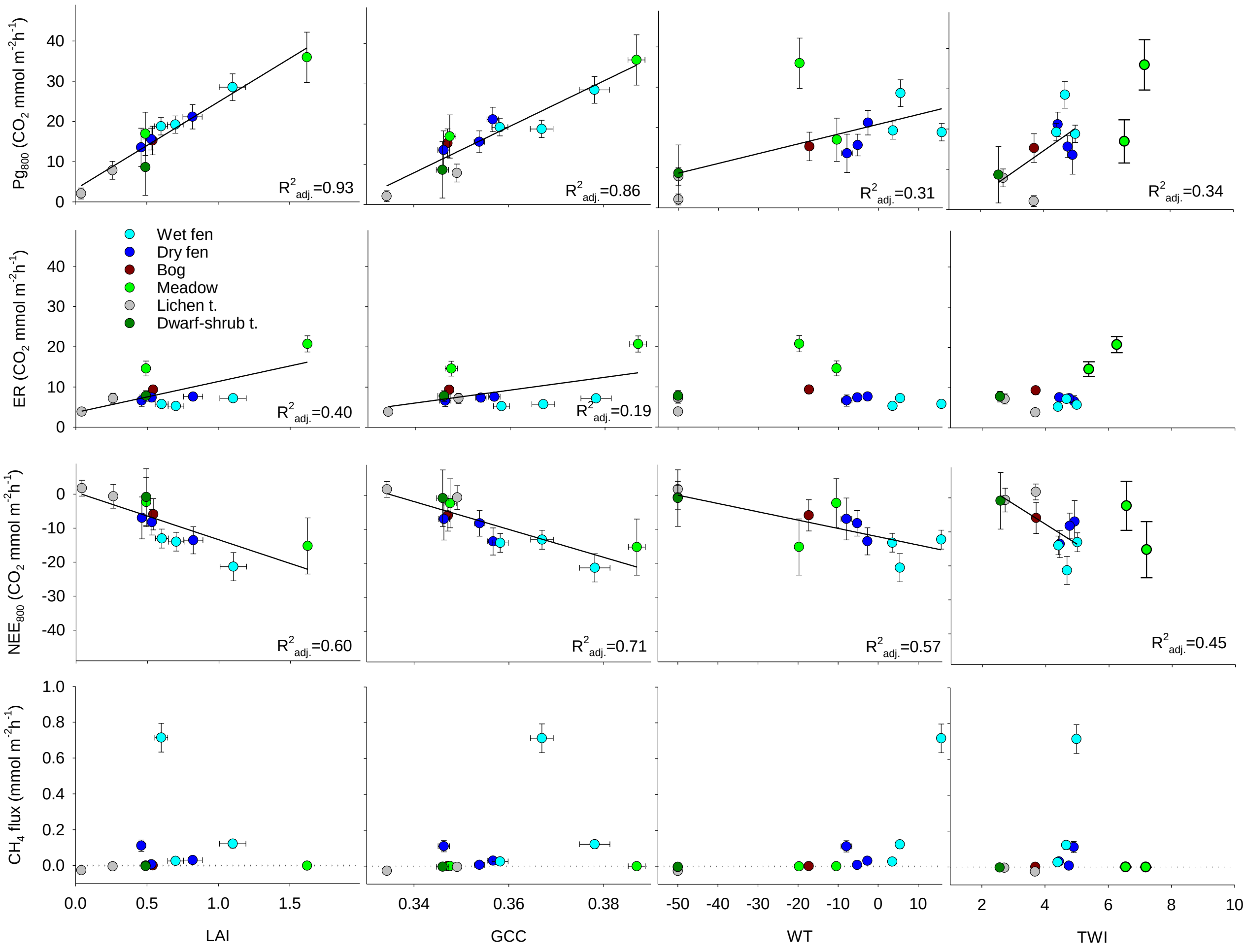

Fig. 3. Variation in estimates of Pg_{800}, ER, NEE_{800} (Eq. 1) and collar means of CH_4 fluxes in relation to variation in collar means of LAI, GCC, WT, and TWI in July 6–August 16, 2014. Error bars denote the standard error of estimate. Fitted regression lines and adjusted coefficients of determination ($R^2_{adj.}$) are included for the significant linear relationships. The two meadow plots were not included in the TWI regressions.

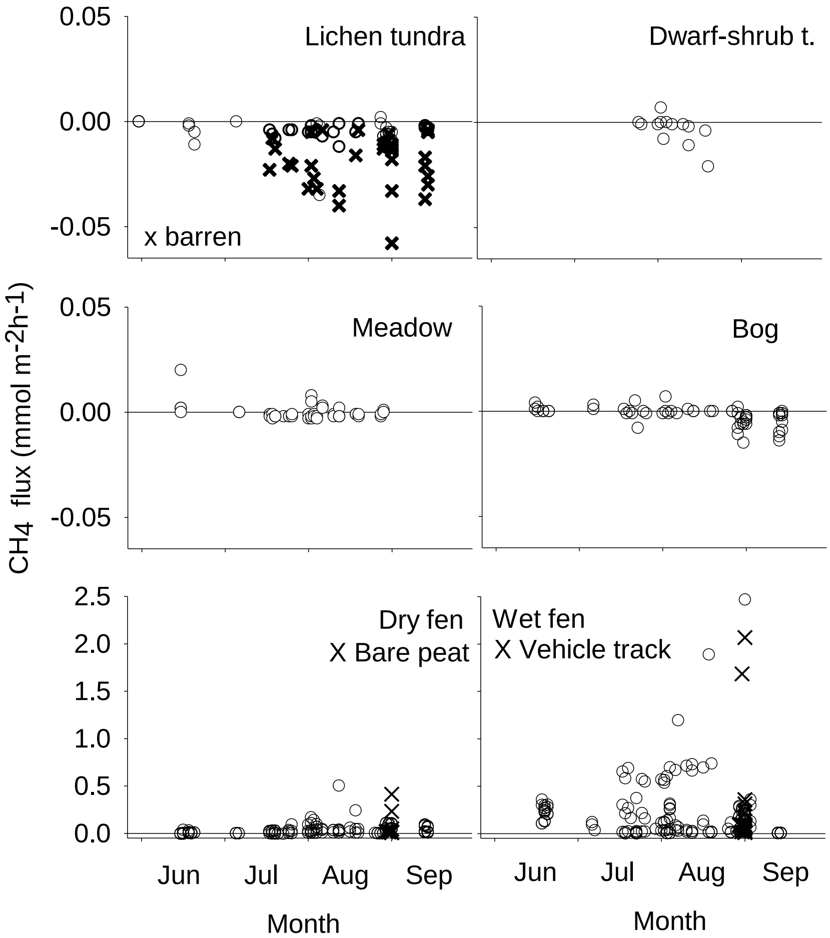

Fig. 4. Instantaneous CH_4 fluxes in each LCT. The data are a composite of all study years. Barren surfaces are indicated among the lichen tundra data. The eroded bare-peat and vehicle-track plots (×) are plotted as part of the dry fen and wet fen data, respectively. Note that the panel groups have different y-axis scales.

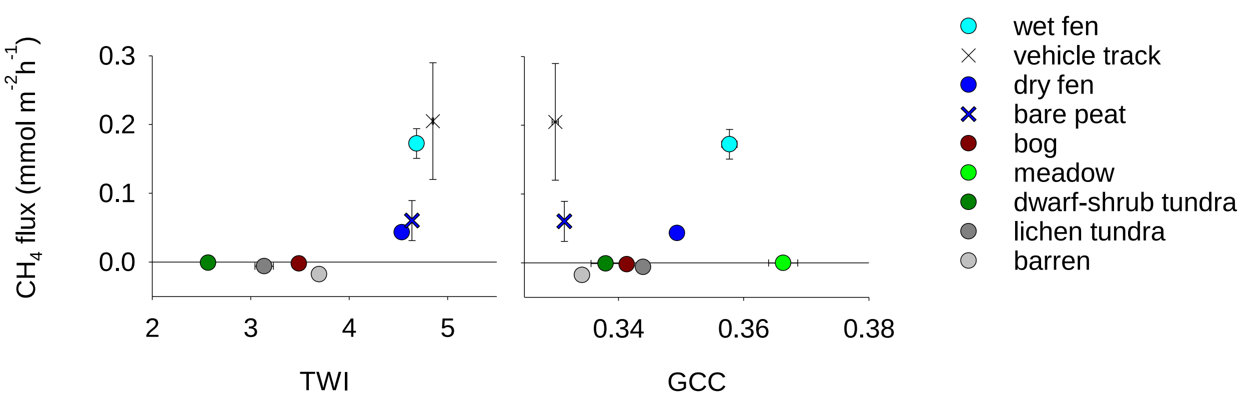

Fig. 5. LCT mean (±SE) CH_4 fluxes in relation to LCT mean (±SE) TWI (excluding the meadow) and GCC. Data from years 2012–2019.

The DCA ordination of species groups with a post-hoc fit of environmental variables (elevation, WT, thaw depth, LAI, GCC, and CO_2 and CH_4 exchange) showed that species distributed along a moisture gradient. Axis 1 explained 49 % of the variation in the species data and distinguished the wet and dry LCTs from wet fen to lichen tundra (Fig. 6). Graminoids and brown mosses occurred in the wet end of the gradient, while dwarf-shrubs, *Betula nana*, and lichens occurred in the dry end of it. The barren plot (the other lichen tundra plot) with its negligible vegetation differed most from the other plots. Axis 2 explained additional 14 % of the variation in the species data (Fig. 6). The supplementary variables WT, vascular plant LAI, thaw depth, GCC, Pg_{800}, NEE_{800}, and CH_4 fluxes correlated positively with Axis 1 having post-hoc correlations (r) of 0.6–0.9, as derived from the DCA-weighted correlation matrix. In turn, plot's elevation and ER had positive correlations with Axis 2 (r = 0.8 and 0.4, respectively).

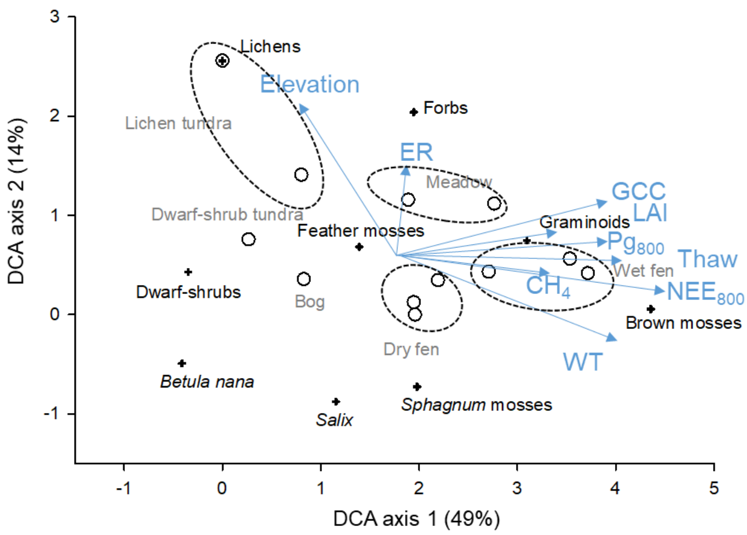

Fig. 6. DCA ordination diagram based on species (species groups) data from the measurement collars in 2014. The explained variation in the species data is indicated for the axes. In the plot, the scores of species groups (cross), sample plots (open symbols), and post-hoc fits of the supplementary variables (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 the same LCTs are circled.

In both the southern and south-western wind sectors (125–185° and 185–239°), vegetation mainly consisted of graminoids, as the LCTs dry fen, wet fen, graminoid tundra, and meadow comprised 80 % of the total EC footprint-weighted area (Fig. 7a). The northern sector (310–360°) was characterized by 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. 7b–d). Both Pg_{800} and NEE_{800} were largest in the southern and south-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: on average, Pg_{800} was 57 %, ER 93 %, and NEE_{800} 44 % of the mean EC-based fluxes among the wind direction sectors.

The southern and south-western wind sectors with abundant dry and wet fens and graminoid tundra had clearly the largest CH_4 fluxes (Fig. 7f). The estimate based on chamber measurements was 30 % and 50 % larger than the mean EC-based flux in 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 smaller than the EC flux for the other sectors, which were dominated by graminoid tundra, lichen tundra, and barren ground. Both the EC- and chamber-based measurements showed consumption of atmospheric CH_4 in the northernmost sector, of which barren ground and lichen tundra covered 50 % and 20 %, respectively. The mean EC flux was three times the chamber-based estimate.

Within the extended study area of 35.8 km^2, the LCT-weighted mean NEE_{800} was -4.6 mmol m^{-2} h^{-1} (uptake relative to the atmosphere). The corresponding mean Pg_{800} was 11 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 Pg_{800}, NEE_{800}, and CH_4 emissions, because the fens contributed 47 % of total Pg_{800} and 74 % of NEE_{800}, and were the dominant source of CH_4 emission (Table 3). Consumption of CH_4 by barren and lichen tundra, dwarf-shrub tundra, and meadow tundra soils contributed -9 % of the CH_4 balance, and the barren ground dominated the sink.

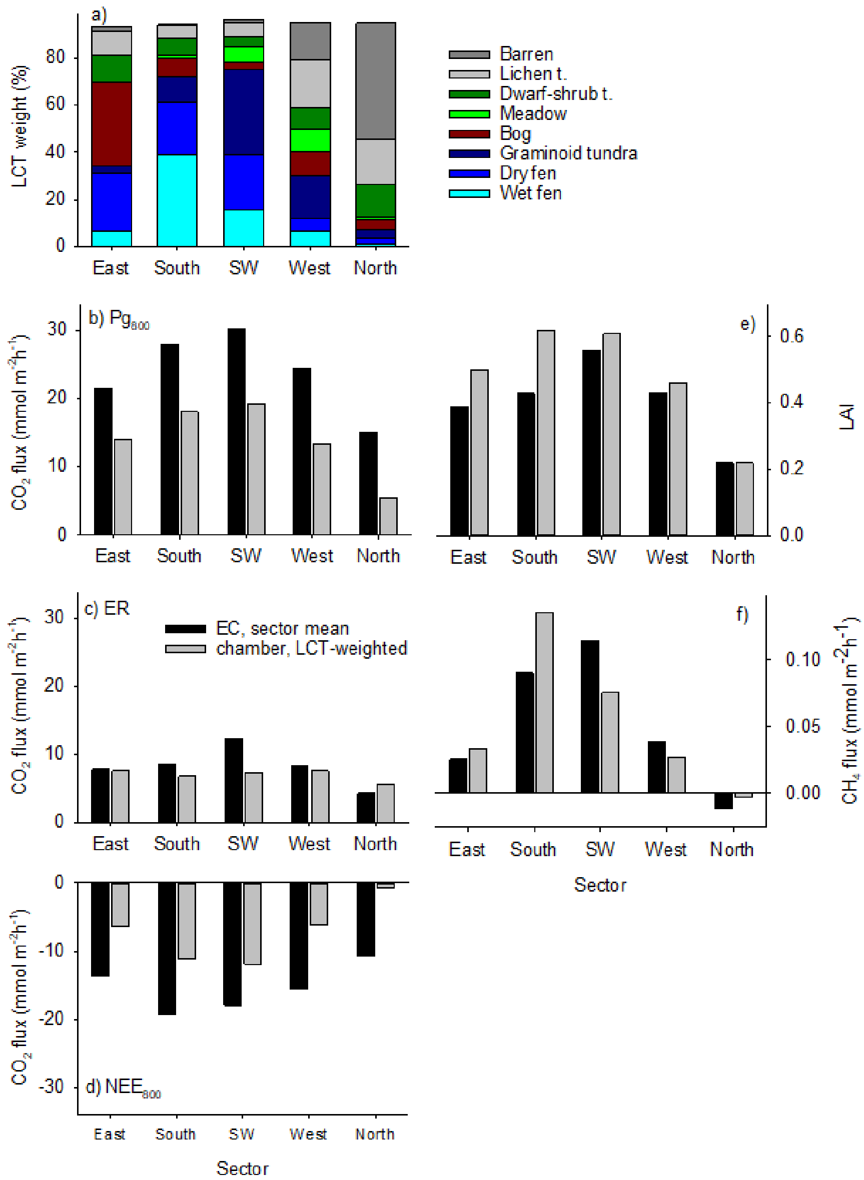

Fig. 7. Footprint-weighted mean contribution of each LCT to the EC measurements divided into wind direction sectors (**a**), and comparison of EC and chamber-based sector means of CO_2 exchange (Pg_{800}, ER, and NEE_{800}) **(b-d)** vascular plant LAI **(e)**, and CH_4 fluxes **(f)**. The chamber-based data are weighted by the LCT proportions shown in panel a. All data were measured in 2014. 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, in panel e.

Table 3. Land-cover type distribution in the mapped 35.8 km^2 area (Mikola et al. 2018), spatially weighted and LCT-specific means of Pg_{800}, ER, NEE_{800}, and CH_4, and proportions of LCTs in landscape totals of Pg_{800}, NEE_{800}, and CH_4fluxes . Standard error of mean (SE) is shown for the LCT-specific estimates. Data period: July 15 – August 16, 2014.

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})		Pg_{800} (%)	NEE_{800} (%)	CH_4 flux (%)
Mean[1]		11.2		6.6		-4.6		0.05				
		mean	SE	mean	SE	mean	SE	mean	SE			
Wet fen	16.4	21.9	2.5	6.4	0.7	-15.5	3.2	0.29	0.05	32.1	55.1	94.5
Dry fen	11.6	14.6	3.5	7.0	1.1	-7.6	4.6	0.05	0.01	15.1	19.1	11.2
Gram. t.[2]	3.4	21.9	2.5	6.4	0.7	-15.5	3.2	0.05	0.01	6.7	11.4	3.3
Bog	9.1	15.3	3.6	9.3	1.0	-5.9	4.6	0.0001	0.0005	12.4	11.7	0.03
Meadow	0.4	26.4	5.8	17.7	1.9	-8.8	7.7	-0.001	0.0004	0.9	0.8	-0.01
Dwarf-s. t.	27.4	8.6	7.0	7.8	1.3	-0.8	8.3	-0.003	0.0015	21.1	5.0	-1.8
Lichen t.	11.1	5.0	2.2	5.5	1.3	0.5	3.5	-0.005	0.001	4.9	-1.3	-1.1
Barren	15.3	5.0	1.4	5.5	1.0	0.5	2.3	-0.020	0.003	6.8	-1.8	-6.1
Water	5.3	NA		NA		NA		NA				

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

2 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. We found that the LAI of vascular plants was a robust predictor of Pg_{800} and NEE_{800} across the LCTs. On the one hand, due to the distribution of species and LAI, the tundra wetlands had a disproportionate role in the landscape-level CO_2 uptake capacity. The fens also dominated the landscape's CH_4 emissions. On the other hand, our results highlight the high CH_4 consumption rates within the dry tundra areas. The consumption of the atmospheric CH_4 by dry tundra was -9 % of the total CH_4 balance within this landscape, and the consumption rate of the barren was much higher that in other dry tundra habitats. This finding is in agreement with other studies and suggest distinguishing non-vegetated dry tundra habitats when upscling CH_4 fluxes (Table 4). In Tiksi, the barren was characterized by sand and rocks underlain by chists (Fig. A1). The consumption of CH_4 was smaller if the sand and stones were partly covered with vegetation and, in lichen tundra, with a thin organic layer (Figs. 5 and A1).

The land-cover categorical approach serves to distinguish the basic features of spatial variation in CO_2 and CH_4 fluxes. The extreme ends of the moisture and vegetation gradients from barren to wet fen are clearly distinguishable, also in terms of CO_2 and CH_4 exchange (Fig. 6). Overall, microrelief, moisture gradient, vegetation types and ecosystem functions are connected. Barren areas are wind swept having minimal snow accumulation, while in wet depressions snow accumulation further increases soil moisture (Fig. 6, Callaghan et al. 2011). Nevertheless, the spatial extrapolation of fluxes is clearly sensitive to a small number of chamber measurement points as there is large within-LCT variation, as observed in the wet fen and meadow data, which originates from the plot-to-plot variation in LAI. The LCTs share common features and form a continuum as shown by the DCA ordination (Fig. 6). Mikola et al. (2018) used a larger data set from Tiksi and also found that the neighboring LCTs overlapped in terms of soil properties and vegetation. Despite the limited number of observations, our conclusions drawn from the chamber data are, corroborated by the temporally matching section of EC data, which show similarity to the chamber data (Fig. 7). Furthermore, the statistical analysis of EC data by Tuovinen et al. (2019) showed that it is possible to find significant differences between different LCT categories representing high and low CH_4 emitters and CH_4 sinks. However, for spatial modeling of ecosystem functions, maps of key variables, such as LAI and WT, that drive CO_2 and CH_4 exchange would be preferable to categorical LCT classification (Räsänen et al. 2021).

The spatial pattern of the growing season Pg_{800} and NEE_{800} was strongly related to the corresponding pattern of the LAI of vascular plants (Figs. 3 and 4). Hence, the abundance of graminoid (Cyperaceae and Poaceae) vegetation was associated with 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 (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 equally long growing season) 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. 3).

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, we estimate that 28 % of the area emitted CH_4, while the other habitats either consumed atmospheric CH_4 (barren and lichen tundra, dwarf-shrub tundra, meadow) or were close to neutral relative to the atmosphere (Fig. 4, Table 3). The relationship between vascular plant LAI and CH_4 flux was confused by the occurrence of large CH_4 fluxes in plots with little or no vegetation. Those cases occurred at the wettest fen plot and bare-peat and vehicle track plots (Figs. 3–5). High LAI, high WT and high CH_4 emissions systematically co-occurred in wet fen (Fig. 6). The eroded bare-peat surface of dry fen and the disturbed vehicle tracks had high CH_4 emissions, where erosion or disturbance may have created CH_4 flux hotspots due co-occurrence of permafrost scars, water saturation, and recently thawed organic matter (*e.g.*, Bubier et al. 1995, McCalley et al. 2014, Wickland et al. 2020). These are small-scale landscape features, while in a larger scale, our data encourage applying indices of wetness and vegetation as a means of CH_4 flux upscaling in a tundra environment.

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 corresponded to -22 % of the total upscaled CH_4 flux. In this study, the average seasonal CH_4 uptake was -0.02 mmol m^{-2} h^{-1} in the barren tundra and an order of magnitude lower in meadow, dwarf-shrub tundra,. Our upscaling exercise suggested a CH_4 sink that corresponded -9 % of the regional CH_4 balance. This difference may originate from the LCT-weighting and the small sample of the chamber-based estimate and, in general, demonstrates the inherent sensitivity involved in upscaling of fluxes of opposite direction.

High consumption of atmospheric CH_4 in barrens is associated with the high affinity methanotrophs (Emmerton et al. 2014, Jørgensen et al. 2014, D'Imperio et al. 2017, St Pierre et al. 2019). In our summary of CH_4 fluxes in mineral-rich dry tundra (Table 4), the consumption values of this study and Tuovinen et al. (2019) are the highest, but similar rates have been observed in other dry tundra sites with little or no vegetation. 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 with tundra barrens and high-affinity methanotrophs can be even higher than those measured on north-boreal forest soils (for instance, -0.01 mmol m^{-2} h^{-1}, Lohila et al. 2016).

Table 4. Summary of reported consumption rates of atmospheric CH_4 in mineralsoil dry tundra.

Location	Habitat type	Mean	Min	Max	Reference
		(μmol m^{-2} h^{-1})			
Narsarsuaq, Greenland	low elevation heath vegetation	-1.2	-4.0	-0.2	St Pierre et al. 2019
Narsarsuaq, Greenland	high elevation heath vegetation	-2.6	-11.9	3.6	St Pierre et al. 2019
Disko Island, Greenland	low elevation heath vegetation	-3.8	-12.1	-1.1	St Pierre et al. 2019
Disko Island, Greenland	high elevation heath vegetation	-3.5	-12.1	-1.3	St Pierre et al. 2019
Tierra del Fuego, Argentina	alpine tundra	0.5	-16.6	10.3	Sá et al. 2019
Disko Island, Greenland	dry tundra heath[1]	-4.0	-4.4	-2.5	D'Imperio et al. 2017
Disko Island, Greenland	bare ground[1]	-9.0	-15.0	-3.8	D'Imperio et al. 2017
Disko Island, Greenland	Betula nana and Salix sp. heath	-4.0			Christiansen et al. 2014
Axel Heiberg Island, CA	vegetated ice-wedge polygon		-2.7	-0.3	Lau et al. 2015
Lake Hazen, Ellesmere I., CA	polar desert[2]	-3.6	-7.0	0.0	Emmerton et al. 2014
Zackenberg Valley, Greenland	moist tundra	-3.1	-7.0	-2.0	Jørgensen et al. 2014
Zackenberg Valley, Greenland	dry tundra & barren ground	-7.0	-16.0	-4.0	Jørgensen et al. 2015
Zackenberg Valley, Greenland	tundra heath	-1.3	-6.0	0.0	Christensen et al. 2000
Okse Bay, Ellesmere I., CA	polar desert[3]	-0.5			Brummel et al. 2014
Petterson R., Ellesmere I., CA	polar desert[3]	-0.04			Brummel et al. 2014
Dome, Ellesmere I., CA	polar desert[3]	-0.5			Brummel et al. 2014
BAWLD-CH_4 Synthesis	dry tundra		-2.9	5.2	Kuhn et al. 2021
BAWLD-CH_4 Synthesis	boreal forest		-2.6	-0.5	Kuhn et al. 2021
Tiksi, RU	Barren & lichen tundra[4]	-29			Tuovinen et al. 2019
Tiksi, RU	lichen tundra mean	-11.3	-57.9	-0.4	This study
Tiksi, RU	barren	-18.1	-57.9	-3.0	This study
Tiksi, RU	vegetated	-6.0	-34.7	-0.4	This study
Tiksi, RU	meadow	-1.0	-21.1	24.5	This study
Tiksi, RU	dwarf-shrub tundra	-0.2	-2.9	20.3	This study
Tiksi, RU	bog	-2.1	-14.8	6.6	This study

1) mean estimated from a figure, 2) min and max estimated from a figure, 3) one-three day measurement, 4) estimated from EC measurements with a statistical model.

5 Conclusions

Our results provide new observations of carbon exchange for the prostrate dwarf shrub tundra sub-zone, which covers a substantial area of the Arctic. These data augment the knowledge on the functional diversity, namely the 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. Graminoid vegetation that favored the wet and moist habitats, such as wet fens, was characterized by large CO_2 uptake and CH_4 emissions. In addition, our data support the observation of notable consumption of atmospheric CH_4 in barren tundra that has substantial coverage across the Arctic. 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 wet fens 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 studies 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

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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Appendix A

Fig. A1. Examples of the barren (left) and lichen tundra (right) plots with close views (bottom). Vegetation consists of lichens *Flavocetraria* sp., *Thamnolia* sp., *Alectoria* sp., dwarf-shrubs *Dryas octopetala*, *Vaccinium vitis-idaea*, *Cassiope tetragona*, and graminoids and forbs such as *Carex spp. and Polygonum viviparum*.

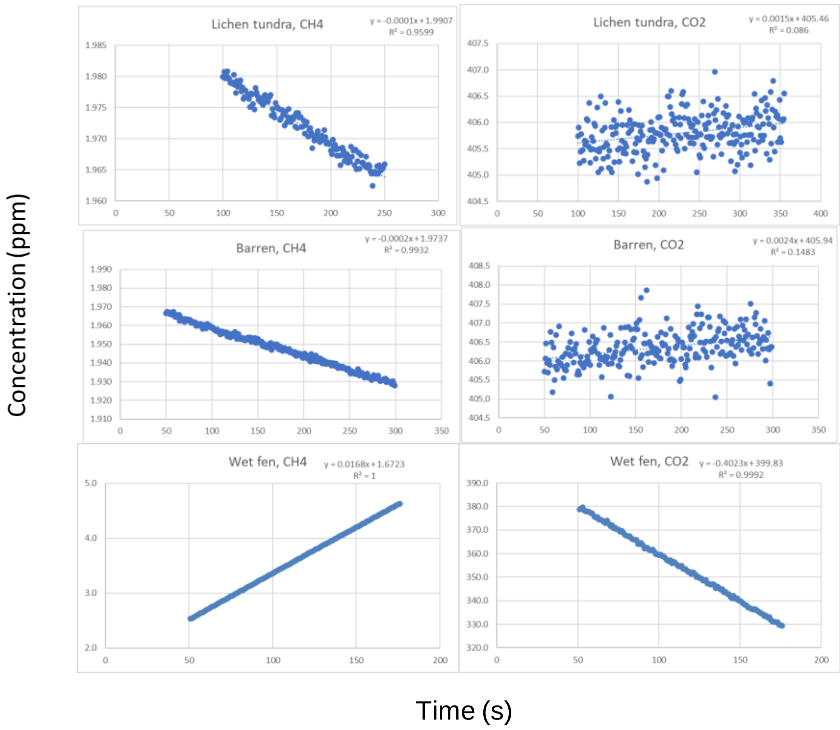

Fig. A2. Examples of gas concentrations in chambers measured using the LRG analyzer (DLT-100, Los Gatos Research, Inc., San Jose, CA, USA). The examples represent lichen tundra, barren, and wet fen.

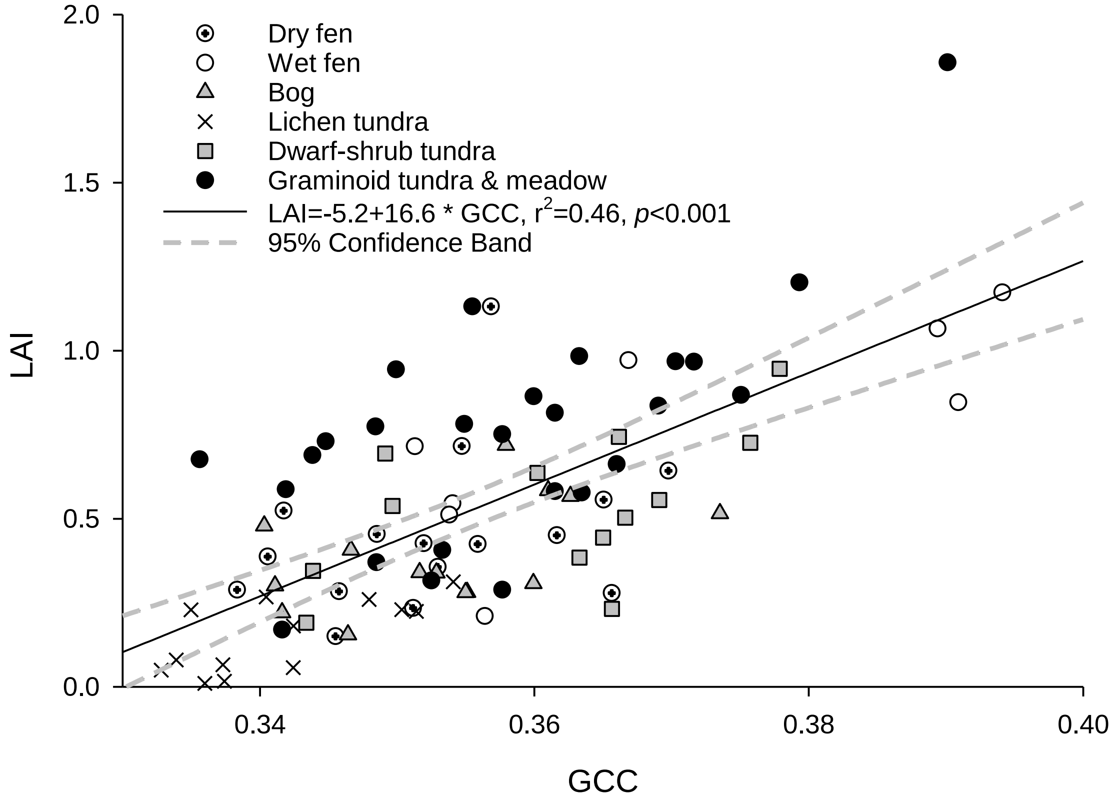

Fig. A3. Relationship between GCC and vascular plant LAI in the harvested plots. LCTs are indicated with symbols. In the LCT-specific regressions (not shown), the coefficient of determination ($R^2_{adj.}$) was lowest for dry fen (0.06) and highest for wet fen (0.54). Regression slopes varied from 8.3 for dry fen to 17.8 for the combined graminoid tundra and meadow LCT.