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Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem

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ABSTRACT

The aim of this study was to asses how the variability in carbon gas exchange at the plant community scale affected the C gas exchange estimates at the ecosystem scale in a fen that was homogeneous in a micrometeorological sense, that is, had an even surface topography and plant cover. CO_2 and CH_4 exchange was measured at the plant community scale with chambers and at the ecosystem scale with the eddy covariance (EC) technique. Community-scale measurements were upscaled to the ecosystem scale by weighting the community-specific estimates by the area of the community. All communities were net CO_2 sinks and CH_4 sources during the growing season, but net ecosystem production (NEP) and CH_4 emissions ranged from 21 to 190 g CO_2-C m^{-2} and from 4.3 to 13 g CH_4-C m^{-2}, respectively, between the communities. The seasonal estimates of NEP and CH_4, upscaled to the 200 m radius from the EC tower, were 82 and 7.9 g CH_4-C m^{-2}, which agreed well with the EC measurements. As the communities differed markedly in their C gas dynamics, their proportions controlled the ecosystem scale estimates. Successful upscaling required detailed knowledge on the proportions and leaf area of the communities.

1. Introduction

In natural ecosystems, environmental conditions vary, forming different habitats that support different plant communities. In boreal peatlands, raised bogs and northern aapa fens typically have a mosaic surface pattern of dry and wet microforms (Ruuhijärvi, 1983; Couwenberg and Joosten, 2005), and these microforms support specialized plant communities (Malmer et al., 1994; Heikkinen et al., 2002b). In contrast, aapa fens in the southern part of the boreal zone typically have less pronounced variation in microtopography and plant community composition (Ruuhijärvi, 1983; Sjörs, 1983).

Northern peatlands are globally important carbon reservoirs (Gorham, 1991). They are, in general, net sinks of atmospheric CO_2 and sources of CH_4. However, spatial variation in carbon gas dynamics between peatland sites and even between plant communities within a site is considerable. Within a peatland site, one of the adjacent plant communities may act as a CO_2 sink while, simultaneously, another is a source (Waddington and Roulet, 2000; Heikkinen et al., 2002a) and their CH_4 emissions may vary more than six-fold (Moore and Knowles, 1990; Kutzbach et al., 2004). Therefore, ecosystem scale CO_2 and CH_4 dynamics depend strongly on the plant community composition and on the proportion of the different communities in the ecosystem.

Plant community scale variation in carbon gas fluxes can be captured with chamber measurements, on condition that the sample plots cover the spatial variation in vegetation. The advantage of the chamber measurements is that the source area is well defined and fluxes can thus be attributed to specific plant communities. However, upscaling the estimates for the whole site requires information on how big an area fraction each measured plot represents. The eddy covariance method is a micrometeorological, non-intrusive technique that integrates the fluxes originating from a larger area and thus measures the C gas dynamics at the ecosystem scale. Nevertheless, as the source area of the eddy covariance measurements varies with atmospheric stability and wind direction, the knowledge on the degree of spatial variation in the ecosystem is important for the interpretation of the results, as discussed by Laine et al. (2006).

In this study we aimed, first, to quantify the spatial variation in vegetation and carbon gas dynamics at the plant community (enclosure) scale in a boreal fen that, when observed at the

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ecosystem (micrometeorological) scale, had a relatively even surface topography and plant cover. Even a site with horizontally heterogeneous source distribution can be assumed homogeneous in the micrometeorological sense if the horizontal length scale of the heterogeneities is small enough. In that case the effect of these heterogeneities would be smeared by turbulence below the measurement height. Secondly, we aimed to assess how the spatial variation regulates the ecosystem scale carbon gas dynamics. To achieve the aims, we described the plant communities and their distribution within the study site and quantified the CO_2 and CH_4 dynamics in the different communities with chamber measurements. Then, we combined the community-specific C gas exchange estimates and knowledge of the area proportion of the communities to upscale the estimates from the plant community scale to the ecosystem scale. These upscaled estimates were compared with the ecosystem scale (eddy covariance) measurements to evaluate our upscaling procedure.

2. Methods

2.1. Study site

The study was carried out in Siikaneva fen in southern Finland (61°49.961′N, 24°11.567′E, 160 m a.s.l.) on the border of the southern and middle boreal vegetation zones (Ahti et al., 1968). The annual rainfall of the region is 713 mm, of which about one-third falls as snow, and the average temperatures for January and July are −7.4 and 15.5 °C, respectively (Juupajoki-Hyytiälä weather station, Drebs et al., 2002). Aurela et al. (2007) provide a detailed description of the weather conditions in the study area. The study site is a nutrient poor, that is, oligotrophic, open fen with a relatively uniform surface topography. The field layer is quite scarce and dominated by sedges (*Eriophorum vaginatum*, *Carex rostrata*, *C. limosa*). The moss layer is a continuous *Sphagnum* carpet dominated by *S. balticum*, *S. majus* and *S. papillosum*. Species nomenclature follows Hämet-Ahti et al. (1998) for vascular plants and Koponen et al. (1977) for mosses. Peat depth in the site ranges from 2 to 4 m.

Permanent gas exchange sample plots of 56 × 56 cm (n = 18) and the eddy covariance measurement tower were located in the centre of the site (Fig. 1). The open fen area extends to about 200 m North and South of the tower and several hundreds of metres to the East and West. We established the sample plots and built boardwalks that were supported by poles going all the way to the mineral soil 6 months prior to the study to minimize disturbance. The study period was from May 2004 to February 2006.

2.2. Field measurements

2.2.1. Vegetation. To describe the spatial variation in vegetation, we conducted a systematic vegetation inventory in 2005, extending to 200 m radius from the centre of the site (Fig. 1). A 30-m sampling grid was laid out. In addition to the plots in the basic grid, every second grid plot consisted of a cluster of six supplementary plots. The projection cover of each species was visually estimated in a total of 341 sample plots using a circular frame of 0.071 m^2.

To relate the CO_2 and CH_4 fluxes to the temporal variation in vegetation, green area of vascular plants (VGA) was monitored in 18 permanent gas exchange sample plots every 4 weeks during the snow-free season. We estimated the VGA of each species as a product of the number of green leaves in the plot and the average green leaf size. To describe the seasonal development continuously, we fitted a log-normal curve to the monthly VGA observations, separately for each species in each plot. Evergreen shrubs did not show this clear seasonal rhythm and their VGAs were linearly interpolated between the measurement days. The method is described in detail by Wilson et al. (2007).

2.2.2. CO_2 and CH_4 exchange in plant community scale. During the snow-free seasons 2004 and 2005, CO_2 and CH_4 exchange measurements with closed chambers were carried out weekly or biweekly, starting from 17 May 2004. The gas exchange sample plots were surrounded by stainless steel collars inserted to a depth of 30 cm. The collars had a water groove that allowed chamber placement and air-tight sealing of the measurement system.

Instantaneous net CO_2 exchange in each plot was measured with a transparent plastic chamber (60 × 60 × 31 cm) equipped with a battery-operated fan, a cooling system that maintained the temperature within 2 °C of the ambient temperature, and a portable infrared gas analyser (EGM-3 and EGM-4, PP Systems, UK). Measurements lasting 90–180 s were carried out in full light and under one or two different shades that reduced the amount of incoming light by 40–50% and 75–90%. During the measurements, CO_2 concentration in the chamber headspace, photosynthetic photon flux density (PPFD) under the chamber roof, and chamber temperature were recorded at 15-s intervals. After the measurements in light, the chamber was covered with an opaque hood and the CO_2 exchange in the dark was measured. The chamber was removed from the plot between measurements to restore the ambient gas concentration. Water level in a perforated tube next to each plot, and peat temperatures at 5, 10 and 20 cm below the moss surface were measured simultaneously with the CO_2 exchange measurements in order to relate the fluxes to the prevailing environmental conditions.

CH_4 exchange was measured with an opaque aluminium chamber of 60 × 60 × 30 cm equipped with a battery-operated fan. After placing the chamber on the water groove of the collar, it was sealed with a septum plug that had a 30 cm long tube of 1 mm diameter, fitted with a three-way stopcock. A 40-ml air sample was drawn to a polypropylene syringe at 5, 15, 25 and 35 min after closing the chamber. Chamber temperature was measured at the sampling occasions. Peat temperatures at 5, 10, 20 and 30 cm below the moss surface and water level were measured once during the CH_4 exchange measurement. Gas samples

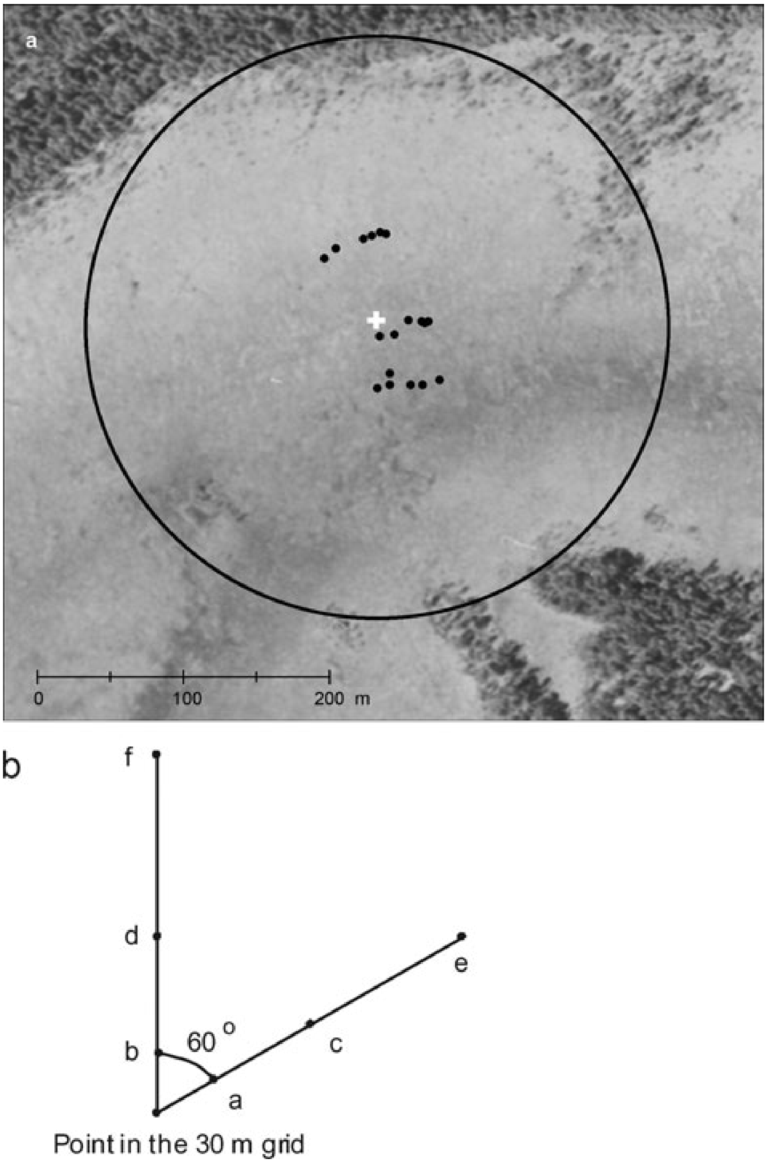

Fig. 1. (a) Aerial photograph of the study site, location of the eddy covariance measurement tower (white cross), permanent gas exchange sample plots (black circles) and the extent of the vegetation inventory, 200 m radius from the measurement tower. (b) In the 30-m vegetation inventory grid, every second grid point consisted of a cluster of additional sample plots at 1 m (points a and b), 5 m (points c and d) and 10 m (points e and f) distance from the basic grid point.

were stored in coolers at +4 °C before analysis, which was carried out within 36 h. Samples were analysed with a HP-5890A gas chromatograph (Hewlett-Packard, USA) with 1-ml loop, 6 × 1/8 inches packed column and flame ionization detector (GC-fid).

During the snow-covered season (November–March), CO_2 and CH_4 exchange was measured by the static chamber or snowpack diffusion method (Alm et al., 1999), approximately every 7 weeks. Chambers were used when the snow depth was <20 cm, otherwise the snowpack diffusion method was applied. The chamber method was the same as in the CH_4 measurements during the snow-free season. In the snowpack diffusion method, gas samples from the top of the snow pack and from the moss surface were drawn into 40-ml syringes using a metal pipe of 1-mm diameter. Average porosity of the snow was simultaneously determined at each sampling point by weighting a volumetric snow sample and calculated using the density of pure ice (0.92 g cm^{-3}). CH_4 concentrations in the samples were analysed with the GC-fid and CO_2 concentrations with EGM-4 in the laboratory.

Flux rates in the chamber measurements were calculated from the linear rate of change in CO_2 or CH_4 concentration inside the chamber headspace. CO_2 exchange measurements in the dark represented total (autotrophic and heterotrophic) respiration (R_{TOT}). An estimate for gross photosynthesis (P_G) was calculated by subtracting the CO_2 exchange rate in the light conditions from the exchange rate in the subsequent dark measurement. The flux in the snowpack diffusion method was calculated from the concentration difference between the top and the bottom layer as a function of layer depth, porosity and snow temperature by applying Fick's first law of diffusion through porous media and using the diffusion coefficients of 0.139 and 0.22 $cm^2\ s^{-1}$ for CO_2 and CH_4, respectively (Sommerfeld et al. 1993). We state P_G, R_{TOT} and CH_4 emission values as positive.

2.2.3. CO_2 and CH_4 exchange at ecosystem scale. In addition to the chamber method, CO_2 and CH_4 fluxes were measured using the eddy covariance (EC) technique. In the EC method, the areally averaged flux at the ecosystem scale is obtained as the covariance of the vertical wind speed and the constituent in question. Three dimensional wind vector was measured at the rate of 10 Hz by an acoustic anemometer (USA-1, METEK, Germany) that was placed 3 m above the peat surface. CO_2 concentration was measured with a closed path infrared gas analyser (IRGA, LI-7000, Li-Cor Inc., USA) and CH_4 concentration with a tunable diode laser absorption spectrometer (TDL, TGA-100, Campbell Scientific Inc., USA), at a rate of 10 Hz. The air inlet of the IRGA and TDL were located 20 cm below the anemometer measurement path. The EC data acquisition was carried out by an in-house Python program BARFLUX (Finnish Meteorological Institute). The fluxes were calculated as half-hourly covariances using block averaging. Gap filling was carried out with regressions models and interpolation (see Aurela et al., 2007, for CO_2 and Rinne et al., 2007, for CH_4). The measurement system and the data post-processing procedures are presented in more detail in Aurela et al. (2007).

2.3. Data analysis

2.3.1. Defining vegetation communities. We classified vegetation into communities with TWINSPAN cluster analysis (Hill, 1979), using TWINSPAN for Windows 2.3. To study the compositional difference between plant communities, we ordered the vegetation data with detrended correspondence analysis (DCA), using Canoco for Windows 4.52 (Ter Braak and Šmilauer, 2002). We used segment detrending and log-transformation of species data.

2.3.2. Quantifying C gas dynamics at plant community scale. To obtain seasonal and annual C gas exchange estimates for different plant communities, we reconstructed CO_2 and CH_4 exchange for the growing season (June–September) 2004 and for the whole year 2005.

CO_2 exchange rate changes rapidly along with the environmental conditions and, therefore, CO_2 exchange measurements by chambers reflect only a momentary situation. To reconstruct the CO_2 gas exchange under different environmental conditions we developed process-based non-linear regression models for P_G (eqs 1–4) and R_{TOT} (eqs 5 and 6), with PPFD, air temperature in the chamber, water level and VGA as independent variables. Data from the snow-free season was used in modelling. The models were parametrized separately for each plant community. Because the communities differed in their responses, we needed to adapt the models accordingly. eq. (1) is the P_G model in its basic form and eqs (2)–(4) are modified versions of the P_G model. Similarly, eq. (5) is the basic form of the R_{TOT} model and eq. (6) is a modification. Models are adapted from and the response functions are discussed in more detail in Tuittila et al. (2004).

$$P_{G\_EV,HO} = b_1 \frac{I}{k_I + I} \exp\left[-0.5\left(\frac{T - T_{opt}}{T_{tol}}\right)^2\right] \times \exp\left[-0.5\left(\frac{W - W_{opt}}{W_{tol}}\right)^2\right](s + V), \quad (1)$$

$$P_{G\_HU} = b_1 \frac{I}{k_I + I} \exp\left[-0.5\left(\frac{T - T_{opt}}{T_{tol}}\right)^2\right] \times \exp\left[-0.5\left(\frac{W - W_{opt}}{W_{tol}}\right)^2\right] V, \quad (2)$$

$$P_{G\_CR} = b_1 \frac{I}{k_I + I} \exp\left[-0.5\left(\frac{T - T_{opt}}{T_{tol}}\right)^2\right](s + V), \quad (3)$$

$$P_{G\_CL} = b_1 \frac{I}{k_I + I} \exp\left[-0.5\left(\frac{T - T_{opt}}{T_{tol}}\right)^2\right]\frac{V}{k_v + V}, \quad (4)$$

In eqs (1)–(4), I is the photosynthetic photon flux density, T is air temperature, W is water level and V is vascular green area. eq. (1) describes the photosynthetic response of *Eriophorum vaginatum* lawns (EV) and hollows (HO). In eq. (1), the photosynthetic response to PPFD is saturating, the response to T and water level is Gaussian and the response to VGA is linear. Parameter k_I is the level of PPFD at which half of the maximum P_G rate is reached. Parameter T_{opt} denotes the temperature optimum for photosynthesis and T_{tol} denotes the temperature tolerance (deviation from the optimum at which P_G is 60% of its maximum). Similarly, W_{opt} and W_{tol} denote the water level optimum and tolerance. Parameter s denotes the modelled proportion of *Sphagnum* P_G of the total P_G in such way that $s/V = P_{G\_Sphagnum}/P_{G\_Vasculars}$. Equation (2) describes the photosynthetic response of hummocks (HU). It is similar to eq. (1) but lacks the parameter s. Equations (3) and (4) describe the photosynthetic response of *Carex rostrata* lawns (CR) and *C. lasiocarpa* (CL) lawns, respectively, both which lack the water level response. In addition, eq. (4) lacks the parameter s and the response to VGA is saturating, parameter k_V denoting the VGA at which half of the maximum P_G rate is reached. Model parameters for different plant communities are shown in Table 1.

$$R_{TOT\_HU,EV,CR,HO} = b_2 \exp\left[b_3\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)\right] \times \frac{1}{1 + \exp\left(-\frac{W - b4}{b5}\right)} + (b_7 V) \quad (5)$$

Table 1. Gross photosynthesis model (eqs 1–4) parameter values (and their standard errors), coeffifient of determination (R^2) and standard error of the estimate (S.E.E.) in different plant communities. HU – hummocks (eq. 2), EV – *Eriophorum vaginatum* lawns (eq. 1), CL – *Carex lasiocarpa* lawns (eq. 4), CR – *C. rostrata* lawns (eq. 3), HO – hollows (eq. 1)

	HU	EV	CL	CR	HO
b_1 (mg CO_2-C m^{-2} h^{-1})	709.6 (58.70)	336.8 (23.00)	557.3 (99.28)	445.0 (32.27)	557.2 (49.95)
k_I (μmol m^{-2} s^{-1})	199.6 (49.99)	126.0 (16.33)	318.5 (72.8)	180.0 (25.25)	183.2 (39.41)
T_{opt} (°C)	20.76 (0.8679)	25.55 (1.119)	23.55 (14.41)	23.41 (0.721)	26.15 (4.474)
T_{tol} (°C)	11.52 (1.776)	13.67 (1.279)	18.81 (6.331)	11.49 (0.8898)	17.25 (5.633)
W_{opt} (cm)	−24.46 (1.339)	−14.61 (0.6681)			−8.122 (1.062)
W_{tol} (cm)	15.88 (2.078)	16.79 (1.199)			10.42 (0.8783)
s		0.3282 (0.0374)		0.2216 (0.0318)	0.102 (0.0192)
k_V (m^2 m^{-2})			0.4111 (0.1479)		
R^2	0.60	0.74	0.80	0.79	0.73
S.E.E. (mg CO_2-C m^2 h^{-1})	42.3	27.3	42.8	30.8	22.8

$$R_{TOT\_CL} = b_2 \exp\left[b_3\left(\frac{1}{T_{ref} - T_0} - \frac{1}{T - T_0}\right)\right] \times \exp(-b_6 W) + (b_7 V). \quad (6)$$

In eq. (5), T is air temperature, W is water level and V is vascular green area. The respiratory response to temperature is described with exponential function from Lloyd and Taylor (1994), the response to water level is sigmoidal and the response to VGA is linear. Parameter b_3 is the activation energy divided by the gas constant, T_{ref} is a reference temperature, set at 283.15 K, T_0 is the temperature minimum at which respiration reaches zero, set at 227.13 K (Lloyd and Taylor, 1994), b_4 is the slope determining the speed and direction of change in R_{TOT} along the water level range and b_5 denotes the water level at the centre of the fastest change along the water level range. Parameter b_7 denotes the change in respiration per a VGA unit. In eq. (6), the water level response is described as negative exponential function. The difference between the two water level responses is that the sigmoidal form starts to show saturation in deep water levels (no further increase in respiration after a certain water level threshold). However, there were not enough data points for this two-parameter sigmoidal water level function in *Carex lasiocarpa* (CL) lawns. We confirmed that simulating the respiration with either model resulted in a similar respiration estimate (difference in the seasonal respiration <2%) in the other communities for which we were able to fit the sigmoidal response. However, the sigmoidal response is ecologically more realistic and the models can thus be extrapolated for deeper water levels than those observed in this study. Model parameters for different plant communities are shown in Table 2.

The growing season CO_2 exchange of each sample plot was reconstructed with the P_G and R_{TOT} models eqs (1)–(6), with 1-h time step. Continuous air temperature and PPFD data were obtained from the weather station at the site. Continuous VGA was derived from the VGA models. Water level in each plot was linearly interpolated between measurement days. Hourly net ecosystem production (NEP) was calculated by subtracting R_{TOT} from P_G. NEP is positive when the plant community is a net CO_2 sink. Seasonal estimates for the CO_2 exchange were derived by integrating the reconstructed hourly values.

Table 2. Total respiration model (eqs 5 and 6) parameter values (and their standard errors), coefficient of determination (R^2) and standard error of the estimate (S.E.E.) in different plant communities. HU – hummocks (eq. 5), EV – *Eriophorum vaginatum* lawns (eq. 5), CL – *Carex lasiocarpa* lawns (eq. 6), CR – *C. rostrata* lawns (eq. 5) and HO – hollows (eq. 5)

	HU	EV	CL	CR	HO
b_2 (mg CO_2-C m^{-2} h^{-1})	25.23 (7.013)	31.49 (3.419)	17.79 (3.179)	32.31 (5.775)	73.06 (37.61)
b_3 (K)	351.3 (47.99)	284.6 (20.95)	253.2 (37.62)	287.0 (28.00)	196.9 (43.46)
b_4 (cm)	−5.808 (2.386)	−6.212 (1.192)		−8.089 (2.439)	−7.414 (1.557)
b_5 (mg m^{-2} cm^{-1})	−10.6 (2.133)	−3.847 (0.9847)		−5.698 (2.167)	−11.64 (6.308)
b_6 (mg m^{-2} cm^{-1})			0.0305 (0.0084)		
b_7 (mg CO_2-C m^{-2} h^{-1})	49.09 (17.12)	18.58 (7.720)	18.83 (7.783)	61.1 (11.48)	60.67 (9.431)
R^2	0.82	0.71	0.84	0.80	0.74
S.E.E. (CO_2-C mg m^{-2} h^{-1})	13.6	13.9	13.3	13.9	10.6

The growing season CH_4 emissions were reconstructed by linearly interpolating the fluxes in each sample plot between measurement days. CH_4 measurement data was divided into two categories: measurements with a linear change in concentration and those that showed a non-linear increase, which is likely due to ebullition. Results were calculated separately for the first category, representing diffusive CH_4 flux and for the whole data set, representing both diffusive flux and ebullition. Seasonal estimates for the CH_4 exchange were derived by integrating the daily values.

To estimate the annual CO_2 and CH_4 balances, fluxes were reconstructed for the snow-covered period by calculating the mean flux for each measurement day and linearly interpolating the mean fluxes between the measurement days. The mean flux in each measurement day represented the whole study site and the differences between the plant communities during the snow-covered period were not studied. The last measurement at the end of and the first measurement in the beginning of the snow-free season were used as a starting and end values for the interpolation. For the snow-free period, the CO_2 fluxes were reconstructed with P_G and R_{TOT} models and CH_4 fluxes were linearly interpolated between measurement days.

2.4. *Upscaling from plant community scale to ecosystem scale*

To study the effect of the delineation of the ecosystem on the C gas exchange estimates, upscaling was carried out separately for three observation radii: 200, 120 and 90 m from the centre of the study site (EC tower). 200 m radius is the maximum radius of the open peatland in the shortest (N and S) directions, representing 75% footprint. The 120 and 90 m radii represent approximately 50 and 33% footprints, respectively. The extent of the footprints were estimated with the footprint calculator available at http://footprint.kljun.net (method by Kljun et al., 2004), using standard deviation of vertical velocity fluctuations of 0.1 m s^{-1}, surface friction velocity of 0.25 m s^{-1}, surface roughness of 0.07 m and boundary layer height of 1500 m as inputs, which are the average conditions in the study site. We did not aim to make a footprint climatology, that is, to calculate an individual footprint for each 30-min period.

As the plant cover of the communities varied across the study site, VGAs in the gas exchange sample plots were not representative for the entire site. Therefore, we calculated the mean cover of each species in each plant community, separately for the different observation radii. We converted plant cover to VGA using the data from the gas exchange sample plots. The conversion was done separately for thin-leaved, erect plants, that is, sedges and *Scheuchzeria palustris* (VGA = 0.6858 × cover/(8.8968 + cover), $r^2 = 0.63$), for plants with more horizontally oriented leaves, i.e. dwarf shrubs (VGA = 0.0207 × cover, $r^2 = 0.53$) and for flat and large-leaved *Menyanthes trifoliata* and *Rubus chamaemorus* (VGA = 0.0066 × cover, $r^2 = 0.73$). This converted mean VGA represented the maximum (peak season) VGA. The seasonal rhythm of the VGA development of each species was adopted from the gas exchange sample plot, calculated for each day as a proportion of the maximum VGA.

CO_2 reconstruction for the growing season for different plant communities in 200, 120 and 90 m observation radii was carried out by rerunning the P_G and R_{TOT} models eqs (1)–(6) for June–September 2005, using the scaled VGAs.

CH_4 exchange for each plant community was calculated as the average of the CH_4 exchange in the gas exchange sample plots belonging to the same plant community. After normalizing the CH_4 fluxes by soil temperature at 35 cm depth that was the strongest controlling factor of the CH_4 fluxes in the study site (Rinne et al., 2007), plotwise CH_4 fluxes were neither correlated with total VGA in the plot ($r = -0.29$ to 0.20, $p > 0.05$) nor with VGA of aerenchymatous plants ($r = -0.18$ to 0.21, $p >$ 0.05). Therefore, no VGA scaling was necessary.

To upscale the NEP and CH_4 emission from the plant community scale to the ecosystem scale, the community specific NEP and CH_4 emission estimates for each observation radius were weighted by the area of the community in the radius.

2.5. *Uncertainty analysis*

To assess the uncertainty in the seasonal upscaled NEP and CH_4 estimates measured by the chamber method, errors were divided into two categories: errors related to the flux estimates and errors related to the estimates of the area proportions of the plant communities. The uncertainty analysis was carried out separately for each observation radius.

The errors related to the NEP estimates consisted of the modelling errors and of the spatial variation within each plant community, resulting from the variability in VGA (Table 3). To assess the errors related to the variability in VGA, we ran the P_G and R_{TOT} simulations for each plant community with the whole range of VGAs observed in the vegetation inventory plots and calculated the standard error of the mean of these simulations.

For CH_4, uncertainty in the chamber derived flux estimates that resulted from the low measurement frequency and linear interpolation between measurement days was evaluated using the EC data. From the EC data, CH_4 flux of every seventh day was selected, and the seasonal flux was calculated by linearly interpolating the fluxes between the days. This procedure was repeated using each weekday at the time as the starting point for the interpolation. The interpolated estimates were compared with the actual seasonal CH_4 emission estimate obtained with the continuous EC measurements (Table 3). Uncertainty related to the spatial variation in CH_4 emissions within the plant communities was estimated using the standard error in the seasonal CH_4 emission estimates within each community. In hummocks and *Carex lasiocarpa* lawns, the number of sample plots (2 and 1, respectively) was not sufficient for estimating the standard error of the mean. Therefore, we used the largest standard error, that

Table 3. Uncertainties in the upscaled net ecosystem production (NEP) and CH_4 emission estimates, measured by the chamber method, in different observation radii. Standard error of the gross photosynthesis (P_G) and total respiration (R_{TOT}) models relative to the mean measured values; standard error of the seasonal NEP, simulated with all observed vascular green areas (VGA) in different observation radii; standard error associated with the CH_4 interpolation; standard error in the CH_4 emissions within each plant community, representing spatial variation within the community; standard error of the NEP and CH_4 emissions calculated with alternative community proportions in different observation radii; and all uncertainties combined (eqs 7 and 8). All values are percentages. HU – hummocks, EV – *Eriophorum vaginatum* lawns, CL – *Carex lasiocarpa* lawns, CR – *C. rostrata* lawns, HO – hollows

	All	HU	EV	CL	CR	HO
Δ P_G		31	25	26	25	39
Δ R_{TOT}		19	27	20	24	28
Δ VGA 200 m		14	6.0	17	9.2	16
Δ VGA 120 m		20	7.7	21	6.8	27
Δ VGA 90 m		45	8.3	24	10	27
Δ CH_4 interpolation	3.8					
Δ CH_4 spatial variation		15	13	15	7.7	15
Δ NEP, community proportions (200 m/120 m/90 m)	1.3/1.5/3.7					
Δ CH_4, community proportions (200 m/120 m/90 m)	2.4/1.2/2.4					
Total Δ NEP (200 m/120 m/90 m)	39/41/44					
Total Δ CH_4 (200 m/120 m/90 m)	14/14/15					

of the hollows, as the standard error of the hummocks and the *Carex lasiocarpa* lawns.

Uncertainty in the area proportion of the plant communities was evaluated by calculating the community proportions in three alternative grids consisting of (1) basic grid plots with 60 m sampling interval, (2) 'e' plots and (3) 'f' plots (Fig. 1). Seasonal NEP and CH_4 emissions were upscaled to the ecosystem scale using these alternative proportions and compared with the actual estimates (Table 3).

The total uncertainty in the upscaled NEP estimate was calculated by combining the uncertainties using the error propagation principle eq. (7):

$$\Delta\mathrm{NEP} = \sqrt{(\Delta A)^2 + \sum Ai\left[(\Delta P_{\mathrm{G}i})^2 + (\Delta R_{\mathrm{TOT}i})^2 + (\Delta V_i)^2\right]}, \tag{7}$$

where ΔA, ΔP_{Gi}, ΔR_{TOTi} and ΔV_i are the uncertainties associated with the area proportion of the communities, P_G models, R_{TOT} models and VGA within each community, respectively. The community-specific errors were weighted by the area of the community (Ai).

Similarly, the uncertainty in the upscaled CH_4 emission estimate was derived from eq. (8):

$$\Delta\mathrm{CH}_4 = \sqrt{(\Delta A)^2 + (\Delta I)^2 + \sum Ai(\Delta \mathrm{S}i)^2}, \tag{8}$$

where Δ_I and $\Delta_S i$ are the uncertainties associated with the linear interpolation and spatial variation in CH_4 emissions within each plant community.

This resulted in a total uncertainty of 39, 41 and 44% in NEP during the growing season 2005 in 200, 120 and 90 m observation radius, respectively (Table 3). The corresponding uncertainties in seasonal CH_4 emissions were 14, 14 and 15%. This uncertainty analysis in not conclusive and there are other sources of error such as measurement errors, uncertainty in the representativeness of the gas exchange sample plots and classification errors of the vegetation communities that were not considered here. Therefore, these uncertainty estimates are indicative estimates of the magnitude of the uncertainty.

Uncertainty estimates for the seasonal NEP and CH_4 emissions measured by the EC method were 25 and 3%, respectively (Aurela et al., 2007; Rinne et al., 2007).

3. Results

3.1. Vegetation

Vegetation in the site was classified into hollows, three types of lawns and three types of hummocks. As there were no gas exchange sample plots in minerotrophic hummocks or ombrotrophic hummocks that were small in area, those plant communities were combined with *Carex lasiocarpa* lawns and low hummocks, respectively, based on their similar community composition. Species composition of the communities is shown in Table 4.

The main variation in the vegetation was related to moisture conditions; the first DCA-axis (eigenvalue 0.42) ordered the communities from hollows to hummocks (Fig. 2). Hollows were distinct from the other communities.

VGA was highest in *Carex lasiocarpa* lawns and lowest in hollows (Fig. 3). Hummocks had less pronounced seasonality than the other communities, owing to the greatest proportion of evergreen shrubs. The VGA pattern was similar in both study years. Peak season VGA in gas exchange sample plots was quite similar to the peak season VGAs in the whole study site except in *Carex lasiocarpa* lawns, where the VGA in the gas exchange

Table 4. Plant communities, their dominant vascular and moss species, and mean water level (WL) during growing season 2005. The species shown in each case make up at least 75% of the total vascular or moss cover. Nomenclature follows Hämet-Ahti et al. (1998) for vascular plants and Koponen et al. (1977) for mosses. WL data is from the permanent gas exchange sample plots. WL is measured relative to the moss surface of the community and WL below the moss surface is expressed as negative. HU – hummocks, EV – *Eriophorum vaginatum* lawns, CL – *Carex lasiocarpa* lawns, CR – *C. rostrata* lawns, HO – hollows

Community	Dominant species	WL (cm)
HU	*Eriophorum vaginatum, Andromeda polifolia, Betula nana, Rubus chamaemorus*	−22
	Sphagnum balticum, S. magellanicum, S. papillosum	
EV	*Eriophorum vaginatum, Andromeda polifolia, Vaccinium oxycoccos, Betula nana*	−11
	Sphagnum papillosum, S. balticum	
CL	*Carex lasiocarpa, Betula nana, Andromeda polifolia,*	−14
	Menyanthes trifoliata	
	Sphagnum papillosum, S. balticum	
CR	*Carex rostrata, Andromeda polifolia, Scheuchzeria palustris,*	−12
	Vaccinium oxycoccos, Betula nana	
	Sphagnum papillosum, S. balticum	
HO	*Scheuchzeria palustris, Carex rostrata, C. limosa*	2
	Sphagnum majus, S. balticum	

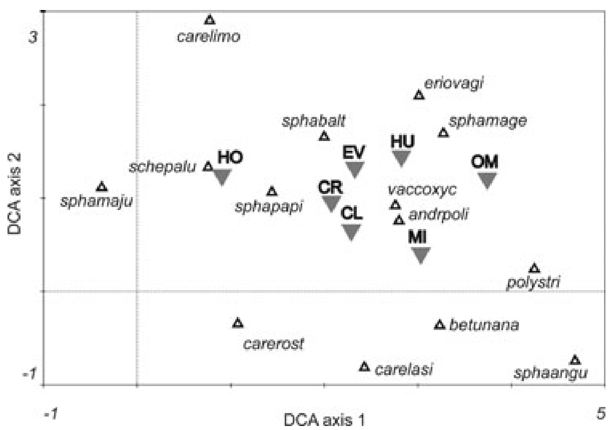

Fig. 2. DCA ordination of the plant communities in the study site. Only species the variation of which ≥10% is explained are shown. Plant communities (grey triangles): CL – *Carex lasiocarpa* lawns, CR – *C. rostrata* lawns, EV – *Eriophorum vaginatum* lawns, HO – hollows, HU – low hummocks, MI – minerotrophic hummocks, OM – ombrotrophic hummocks. Species (open triangles): andrpoli – *Andromeda polifolia*, betunana – *Betula nana*, carelasi – *Carex lasiocarpa,* carelimo – *Carex limosa*, carerost – *Carex rostrata,* eriovagi – *Eriophorum vaginatum*, polystri – *Polytrichum strictum*, schepalu – *Scheuchzeria palustris*, spahbalt – *Sphagnum balticum*, sphaangu – *S. angustifolium*, sphamage – *S. magellanicum*, sphamaju – *S. majus*, sphapapi – *S. papillosum* and vaccoxyc – *Vaccinium oxycoccos*.

sample plot was much higher than in the whole study site (Fig. 4). Peak season VGAs were slightly lower in the 90 m observation radius than in the other radii.

Plant communities were not uniformly distributed within the study site but their proportions varied in different observation radii (Fig. 5). Lawns were the dominant category regardless of the observation radius. Hummocks were most abundant on the edges and hollows were most abundant in the centre of the study site.

3.2. C gas exchange at plant community scale

During the snow-free season, measured P_G values ranged from −23 to 359 mg CO_2-C m^{-2} h^{-1}, measured R_{TOT} values from −2.5 to 153 mg CO_2-C m^{-2} h^{-1} and measured CH_4 exchange from −0.02 to 17.7 mg CH_4-C m^{-2} h^{-1} (Fig. 6). All fluxes showed a seasonal pattern. The monthly mean light saturated P_G (PPFD > 500 μmol m^{-2} s^{-1}) was highest in *Carex lasiocarpa* lawns and lowest in hollows. Monthly R_{TOT} was highest in *Carex lasiocarpa* lawns and hummocks and lowest in hollows. Monthly CH_4 emissions were highest in hollows and *Carex lasiocarpa* lawns and lowest in hummocks. Measured P_G values were similar in both years, R_{TOT} values were higher during midsummer in 2005 than in 2004 and CH_4 values were higher in 2004 than in 2005. The average wintertime CO_2 and CH_4 emission was 6.6 mg CO_2-C m^{-2} h^{-1} and 0.43 g CH_4-C m^{-2} h^{-1}, respectively. The 2004 growing season was colder and considerably wetter than the 2005 growing season. In 2004, the water level stayed close to the moss surface during the entire growing season while in 2005 the water level decreased steadily from May to mid-July and after which it rose close to the surface again.

Plant communities differed in their photosynthetic responses (eqs 1–4, Table 1). Low hummocks, *Eriophorum vaginatum* lawns and hollows had their optimum water level for photosynthesis at −25, −15 and −8 cm, respectively (parameter W_{opt}). The water level tolerance, however, was wide in all three communities (parameter W_{tol}). Photosynthesis of *Carex lasiocarpa* and *C. rostrata* lawns was not sensitive to water level (no parameters W_{opt} and W_{tol}). Contrary to the other communities, in *C. lasiocarpa* lawns where the peak season VGA was the highest, photosynthetic response to VGA started to show saturation (parameter k_V). In hummocks the contribution of vascular plants and *Sphagna* to the community photosynthesis could not be

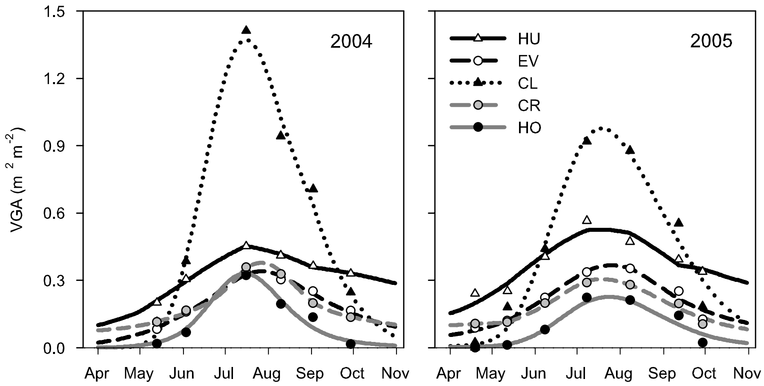

Fig. 3. Vascular green area (VGA) development in different plant communities in 2004 and 2005, monitored in the gas exchange sample plots. Points are VGAs on the VGA measurement days and curves are the modelled seasonal VGA development (see text). Average values of the gas exchange sample plots belonging to the same plant community are shown. HU – hummocks, EV – *Eriophorum vaginatum* lawns, CL – *Carex lasiocarpa* lawns, CR – *C. rostrata* lawns and HO – hollows.

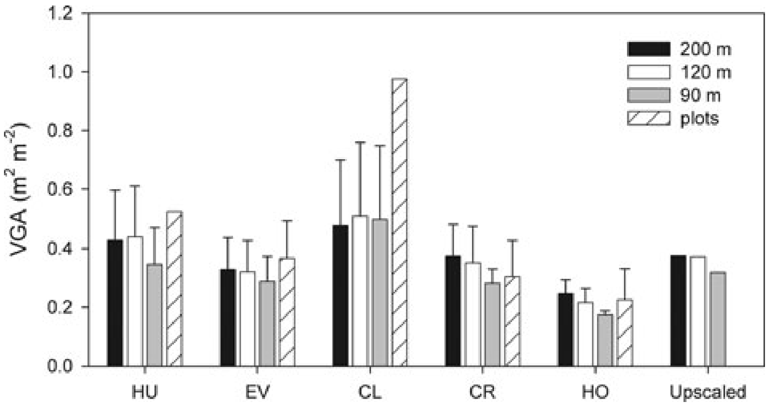

Fig. 4. Peak season vascular green area (VGA) in 2005 in different plant communities within 200 m 120 m and 90 m radius from the centre of the study site and in the gas exchange sample plots. VGA was upscaled from the plant community scale to the ecosystem scale of different radii by weighting the community-specific VGAs by the area of the plant community in each radius. HU – hummocks, EV – *Eriophorum vaginatum* lawns, CL – *Carex lasiocarpa* lawns, CR – *C. rostrata* lawns and HO – hollows.

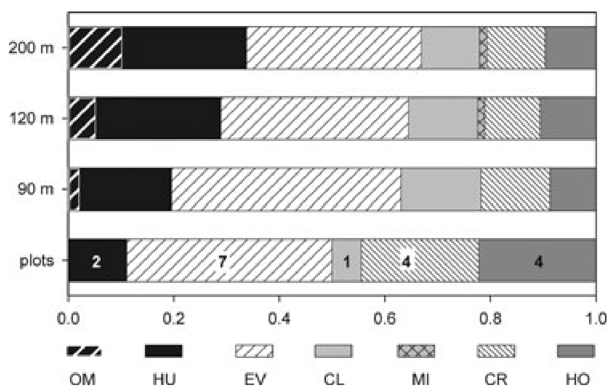

Fig. 5. Proportion of the plant communities within 200 m, 120 m and 90 m radius from the centre of the study site and the number of gas exchange sample plots in different plant communities. Plant communities: OM – ombrotrophic hummocks, HU – low hummocks, EV – *Eriophorum vaginatum* lawns, CL – *Carex lasiocarpa* lawns, MI – minerotrophic hummocks, CR – *C. rostrata* lawns and HO – hollows. Ombrotrophic hummocks are combined with low hummocks and minerotrophic hummocks with *C. lasiocarpa* lawns in subsequent analyses.

separated (no parameter *s*), because in hummocks the VGA was quite high also in the beginning and the end of the growing season.

Seasonal P_G was highest in *Carex lasiocarpa* lawns and hummocks and lowest in hollows (Fig. 7). Seasonal R_{TOT} was lowest in hollows and similar in the other plant communities. Seasonal NEP was positive in all plant communities. However, the variation was considerable, from 21 g C m^{-2} (hollows) to 190 g C m^{-2} (*C. lasiocarpa* lawns). The variation in NEP between the communities was mostly related to the variation in P_G. Methane emissions were highest in *C. lasiocarpa* lawns and hollows and lowest in hummocks. In 2004, ebullition was observed in all communities except in hummocks, but in 2005 ebullition was negligible in all communities except in hollows. CH_4 emissions were higher in 2004 than in 2005 in all plant communities. However, the pattern in C gas exchange between the plant communities was similar in both study years.

3.3. *Upscaled net ecosystem production (NEP) and CH_4 emissions*

The upscaled seasonal (June–September 2005) NEP was 83 g CO_2-C m^{-2} in the 200 and 120 m observation radii and 64 g CO_2-C m^{-2} in the 90 m observation radius (Fig. 8a). The NEP estimates were 20–30% higher when calculated using the VGA of the gas exchange sample plots directly, without scaling it to represent the VGA in each observation radius. The scaling had the biggest effect on the NEP of hummocks and *Carex lasiocarpa* lawns. The VGA-scaled estimates agreed well with the ecosystem scale (eddy covariance) estimate, which was slightly lower (8%) than the estimates for 200 and 120 m radii but higher (16%) than the estimate for the 90 m radius.

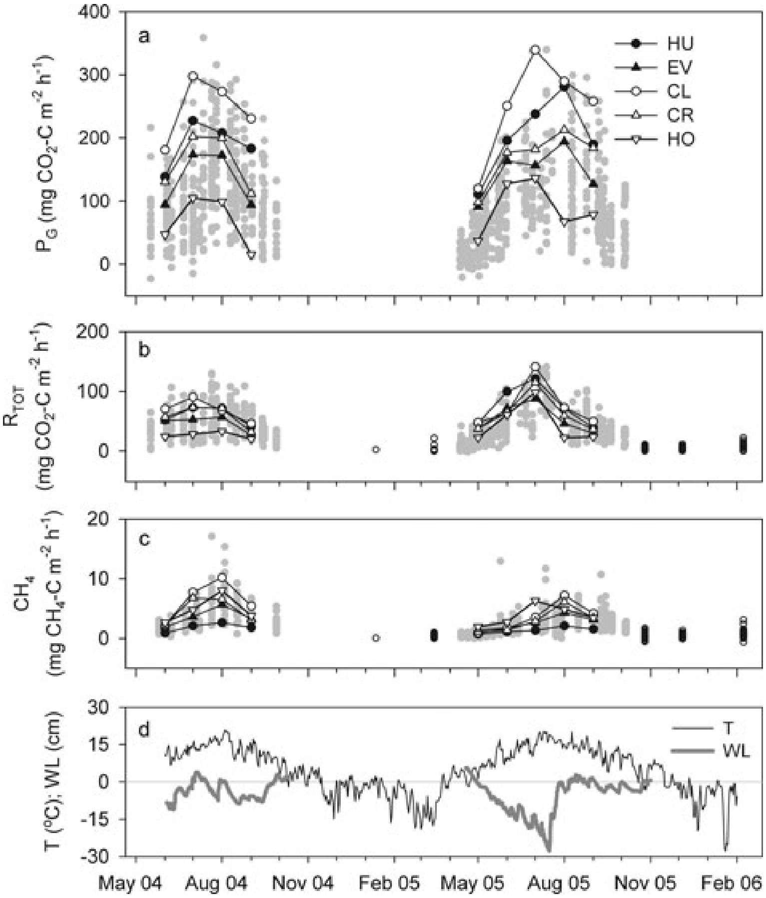

Fig. 6. (a) Measured gross photosynthesis (P_G), (b) total respiration (R_{TOT}) and (c) CH_4 emissions during snow-free (grey dots) and snow-covered (open dots) seasons. Lines are monthly average fluxes of the plant communities. Monthly average P_Gs are calculated from light-saturated (PPFD > 500 μmol m^{-2} s^{-1}) measurements. During the snow-covered season, fluxes represent the entire study site instead of different plant communities. (d) Daily mean temperature (T) in the study site and water level (WL) in the continuous monitoring spot (lawn level). WL is negative when below the moss surface. HU – hummocks, EV – *Eriophorum vaginatum* lawns, CL – *Carex lasiocarpa* lawns, CR – *C. rostrata* lawns and HO – hollows.

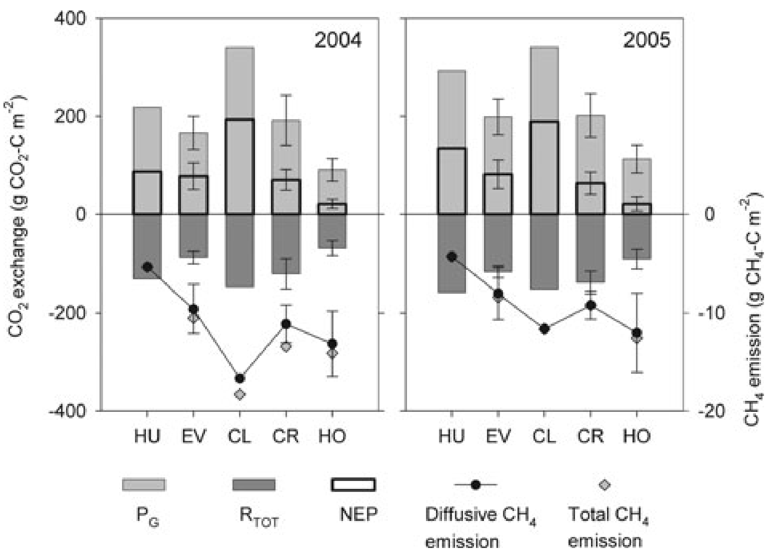

Fig. 7. Gross photosynthesis (P_G), total respiration (R_{TOT}), net ecosystem production (NEP), and diffusive and total (diffusive flux + ebullition) CH_4 emissions in different plant communities during growing seasons (June–September) 2004 and 2005. Values are averages of the gas exchange sample plots belonging to the same plant community and error bars are standard deviations within the community. Positive values indicate uptake to the ecosystem and negative values emissions to the atmosphere. HU – hummocks, EV – *Eriophorum vaginatum* lawns, CL – *Carex lasiocarpa* lawns, CR – *C. rostrata* lawns and HO – hollows. Note the scale for CH_4 emissions in the right axis.

The upscaled total (diffusive + ebullition) seasonal CH_4 emissions were 7.9, 8.2 and 8.6 g CH_4-C m^{-2} in 200, 120 and 90 m observation radius, respectively. The ecosystem scale measurements showed 16–26% lower CH_4 emissions.

The annual carbon balance was 77, 75 and 33 g C m^{-2} in the 200, 120 and 90 m observation radius, respectively (Table 5). Of the CO_2 uptake (NEP) during the snow-free season, approximately 27% was emitted as CO_2 during the snow-covered

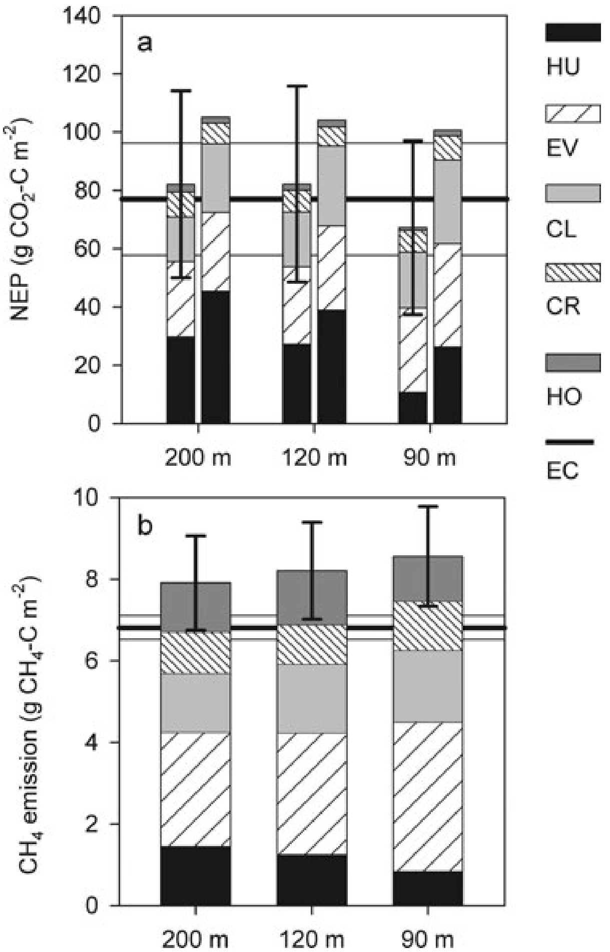

Fig. 8. Seasonal (June-September 2005) (a) net ecosystem production (NEP) and (b) CH_4 emission (diffusive flux + ebullition), upscaled from the plant community level to the ecosystem level of different observation radii by weighting the community-specific estimates by the area of the community in each radius (see Fig. 5). The columns indicate the ecosystem level NEP and CH_4 emission and the fills in the columns indicate the contribution of each plant community. NEP is upscaled both with vascular green area (VGA) that is representative for each radius (left columns) and with VGAs in the gas exchange sample plots (right columns) (see Fig. 4 and models for gross photosynthesis and total respiration, eqs 1–6). Error bars show the uncertainty in the upscaled estimates. Thick horizontal lines mark the ecosystem level NEP and CH_4 emission measured by the eddy covariance (EC) technique and thin horizontal lines show the uncertainty. NEP is positive when the community/ecosystem is a net CO_2 sink. HU – hummocks, EV – *Eriophorum vaginatum* lawns, CL – *Carex lasiocarpa* lawns, CR – *C. rostrata* lawns and HO – hollows.

season, and 10 and 2% as CH_4 during the snow-free and snow-covered seasons, respectively, in the 200 and 120 m observation radii. In the 90 m observation radius, the corresponding figures were 37, 14 and 3%. It is to be noted, however, that the emission estimates for the snow-covered season were averaged for the entire study site and do not take the spatial variation within the study site into account.

3.4. *Sensitivity of the ecosystem scale C exchange estimates to the plant community proportions*

The sensitivity of the seasonal C gas exchange estimates, upscaled from the plant community scale to the ecosystem scale (200 m radius), to the plant community proportions was studied by varying the proportion of each community from 0 to 1, while the remaining proportion was divided between the other communities relative to their original proportions. This hypothetical examination showed that the ecosystem scale NEP estimate was most sensitive to the proportions of *C. lasiocarpa* lawns and hollows (Fig. 9a), which had considerably higher and lower the seasonal NEP, respectively, than the entire ecosystem. In a hypothetical situation in which the study site would consist solely of *Carex lasiocarpa* lawns, the seasonal NEP would be 125 g CO_2-C m^{-2}, and in a situation in which the study site would consists solely of hollows, 25 g CO_2-C m^{-2}, while estimate with the actual plant community proportions is 83 g CO_2-C m^{-2}.

CH_4 emissions would increase if the proportions of *Carex lasiocarpa* lawns or hollows increased, and decrease if the proportion of hummocks increased (Fig. 9b). The sensitivity of the seasonal carbon balance to the proportion of the plant communities was very similar to the sensitivity of NEP (Fig. 9c). The global warming potential (GWP) balance over a 100-yr time horizon was most sensitive to the proportion of hollows; even a small increase in their proportion would turn the modest net cooling effect into net warming effect (Fig. 9d). Both the NEP and CH_4 emissions of *Eriophorum vaginatum* lawns and *Carex rostrata* lawns were close to the estimates for the entire ecosystem. Therefore, the ecosystem scale estimates are not sensitive to the changes in their proportions.

4. Discussion

4.1. *CO_2 and CH_4 dynamics in different plant communities*

The Siikaneva fen had only moderate variability in the surface topography and plant cover. The dominant vascular and moss species in each community were also common in at least two other communities. The multivariate analysis confirmed that even the two most different plant communities in terms of the species composition shared on average 25% of their species. In contrast, in patterned peatlands the species composition in the microforms can be completely different (Waddington and Roulet, 2000; Heikkinen et al., 2002b). However, despite the relatively uniform vegetation composition, plant communities in the Siikaneva site differed in their carbon gas dynamics. P_G varied more between the communities than $R_{TOT,}$ thus explaining most of the variation in NEP. Of the communities, *Carex*

Table 5. Annual carbon gas balance and its components: net ecosystem production (NEP), CO_2 exchange during snow-covered season and CH_4 exchange during snow-free and snow-covered season, upscaled from the plant community scale to the ecosystem scale of different observation radii. Positive values indicate uptake and negative values emission to the atmosphere. Unit in the table is g C m^{-2} a^{-1}

	200 m	120 m	90 m
Annual carbon gas balance	56	56	40
NEP, snow-free season	93	94	78
CO_2 emissions, snow-covered season	−26	−26	−26
CH_4 emissions, snow-free season	−9.3	−9.6	−10
CH_4 emissions, snow-covered season	−2.2	−2.2	−2.2

lasiocarpa lawns had the largest seasonal P_G, as a result of the highest VGA. Hummocks had the second highest peak season VGA and the seasonal variation in VGA was smaller in hummocks than in the other plant communities, owing to the greatest proportion of evergreen shrubs. Consequently, hummocks were efficient photosynthesizers even in the beginning and at the end of the growing season.

Hollows, with the lowest VGA and also the sparsest moss cover, had the smallest seasonal NEP. In other studies as well, hollows had the smallest NEP among the communities studied (Waddington and Roulet, 2000; Laine et al., 2006; Strack et al., 2006). We found a response of P_G to water level in three of our five plant communities. In hummocks and in *Eriophorum vaginatum* lawns, the measured growing season mean water level was within a few centimetres from the modelled water level optimum. In contrast, in hollows the average water level during the growing season was 2 cm above the moss surface whereas the modelled water level optimum for the photosynthesis was 8 cm below the moss surface. These suboptimal conditions may partly explain the low seasonal photosynthesis in hollows, as a very high water content in *Sphagnum* mosses slows down the CO_2 and O_2 exchange in chloroplasts (Wallén et al., 1988).

Methane was an important component of the carbon balance of the plant communities, especially in hollows, where the NEP was small and CH_4 emissions were high. Hummocks had the smallest CH_4 emissions, which is consistent with other studies (Moore and Knowles, 1990; Bubier et al., 1993; Alm et al., 1997; Heikkinen et al., 2002a,b). However, in Siikaneva the CH_4 emissions were similar in lawns and hollows, as observed also by Alm et al. (1997), whereas in some other fens, CH_4 emissions from hollows or pools are considerably higher than from lawns (Moore and Knowles, 1990; Bubier et al., 1993; Heikkinen et al., 2002a). In Siikaneva, similar fluxes from lawns and hollows were probably a result of a higher green area of sedges in lawns than in hollows, providing more substrate for the methanogenic microbes (e.g. Chanton et al., 1995) and more transport routes for CH_4 from the soil to the atmosphere through the aerenchymatous tissue in sedges (e.g. Ding et al., 2004).

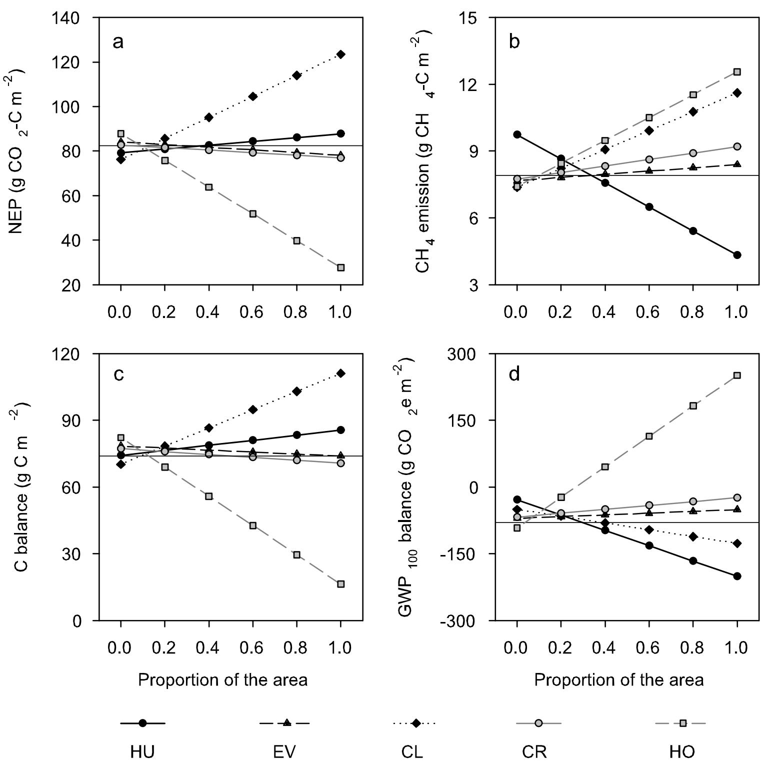

Fig. 9. Sensitivity of the seasonal (June-September 2005) ecosystem scale (a) net ecosystem production (NEP), (b) CH_4 emission, (c) carbon balance, and (d) global warming potential balance over a 100-yr time horizon (GWP_{100}), expressed as CO_2 equivalents (CO_2e), to the proportion of the plant communities. In the figures, the area proportion of each plant community at the time is varied from 0 to 1 and the remaining proportion is divided between the other communities relative to their original area in the 200 m observation radius. Horizontal black lines indicate the situation with the actual plant community proportions. (a and c) Positive values indicate uptake to the ecosystem. (d) Positive values indicate a net warming effect. HU – hummocks, EV – *Eriophorum vaginatum* lawns, CL – *Carex lasiocarpa* lawns, CR – *C. rostrata* lawns and HO – hollows.

4.2. *Upscaling from the plant community scale to the ecosystem scale*

4.2.1. Importance of the plant community distribution. Because of the considerable variation in NEP and CH_4 emissions between the plant communities, upscaling from the plant community level to the ecosystem level required knowledge on the plant community proportions within the study area. As plant communities were not evenly distributed within the site, the upscaled results varied depending on the observation radius.

The upscaled seasonal NEP estimates were similar for 200 and 120 m observation radii and lower for 90 m radius. In the 90 m radius, both the smaller proportion of hummocks and lower VGAs contributed to the lower NEP. Taking the variation in VGA into account had a big impact on the NEP upscaling. The gas exchange sample plot in *Carex lasiocarpa* lawn, especially, was unrepresentative in terms of VGA. CH_4 emission estimates were the biggest in the 90 m radius, intermediate in the 120 m radius and the lowest in the 200 m radius, which was mostly controlled by the proportion of hummocks, which had markedly lower CH_4 emissions than the other communities.

The hypothetical examination of the sensitivity of the C gas dynamics on the proportion of the plant communities showed that hollows, although quite small in area, had a disproportionately large role in ecosystem scale C gas dynamics. It is evident that the sensitivity of the ecosystem scale C gas dynamics to the proportion of different plant communities depends on how similar or dissimilar the communities in the ecosystem are in respect to their C gas dynamics.

4.2.2. Comparison of the upscaled and ecosystem scale estimates. The purpose of the comparison between the upscaled estimates from the plant community scale and the direct measurements at the ecosystem scale was to evaluate our upscaling procedure, rather than to provide a thorough methodological comparison. The agreement between the upscaled chamber measurements and EC measurements was quite good for NEP and CH_4. The upscaled estimates in the 200 m observation radius corresponded best with the EC measurement. This result was expected because approximately only 50 and 33% of the fluxes measured by the EC method originate from the 120 and 90 m observation radii. However, the upscaled NEP estimates in each radius and the EC derived NEP estimate were within the uncertainty range of one another. The upscaled CH_4 emissions estimates in the 200 and 120 m radii were within the uncertainty range of the EC derived estimate while the estimate in the 90 m radius was larger.

Owing to the numerous error sources, the uncertainty in the upscaled chamber derived NEP and CH_4 emissions estimates were larger than the uncertainty in the EC derived estimates. Both measurement methods had larger uncertainty for NEP than for CH_4. The largest components in the NEP uncertainty, both in the chamber and EC methods, were the CO_2 exchange models. The uncertainties are of a similar magnitude as in a Canadian poor fen (Bubier et al., 1999). The uncertainty related to CH_4 interpolation was quite small. It is encouraging that seasonal CH_4 fluxes can be accurately estimated by the chamber method even with relatively low measurement frequency, at least in a site where episodic fluxes do not play a major role. CO_2 fluxes respond to environmental conditions in a much shorter timescale than CH_4 fluxes which partly explains the greater uncertainty in NEP estimates.

The range of the seasonal NEP estimates for different sedge dominated fens is wide, seasonal NEPs ranging from -21 to 161 g CO_2-C m^{-2} (Alm et al., 1997; Lafleur et al., 1997; Soegaard and Nordstroem, 1999; Griffis et al, 2000; Aurela et al., 2002; Heikkinen et al., 2002a; Heikkinen et al., 2004) and annual CO_2 balances from -3 to 98 g CO_2-C m^{-2} (Alm et al., 1997; Heikkinen et al., 2002a; Aurela et al., 2004). Similarly, annual CH_4 emissions vary greatly between different fens, from 2.2 to 22 g CH_4-C m^{-2} (Moore and Knowles, 1990; Alm et al., 1997, Hargreaves et al., 2001) and the within-site variation can be almost as large (Moore and Knowles, 1990; Alm et al., 1997; Heikkinen et al., 2002a). The upscaled ecosystem estimates obtained in this study were within the range of those reported for other sedge dominated fens.

Even during the wintertime, the fluxes may vary between plant communities (Alm et al., 1997; Heikkinen et al., 2002a), although this aspect was not taken into account in this study. However, compared with the variation during the growing season, the spatial variation during wintertime is small. During the snow-covered season, measurements with the chamber or the snowpack diffusion method were conducted only sporadically. CO_2 and CH_4 emissions measured by chamber and snowpack diffusion methods were of similar magnitude but slightly lower and higher, respectively, than those measured by the EC method (Aurela et al., 2007; Rinne et al., 2007). Because of the smaller wintertime CO_2 emissions measured by the chamber and snowpack diffusion methods, the estimate for the annual CO_2 balance was bigger (i.e. the fen was a stronger sink) than that estimated by the EC method (Aurela et al., 2007). Also the annual CH_4 emission estimate by the chamber and snowpack diffusion method was higher than by the EC method (Rinne et al., 2007).

4.3. *Representativeness of the gas exchange sample plots*

In this study, the gas exchange sample plots were chosen subjectively, after a thorough visual inspection of the site. The goal was to choose plots that would cover the spatial variation in the study site, would be situated close to the measurement tower and would not be unnecessarily far away from each other, which is a definite advantage when conducting measurements with heavy, bulky and sensitive equipment. After conducting the vegetation inventory, it could be seen that despite the careful selection, two plant communities present in the 200 m observation radius were not selected for gas exchange measurements and the plant cover in the subjectively chosen plots was higher than on the study site in general. The two missing communities were small in area, especially in the 90 m observation radius, as they were mostly situated on the edges of our 200 m inventory radius. The plant communities with which the missing communities were combined were quite similar in species composition and we consider that their carbon gas dynamics estimates serve as good surrogates. However, as can be seen from the case of the hollows, even a plant community with minor area proportion can play an important role in the ecosystem scale carbon gas dynamics, if its dynamics are very different from those of the other communities. Therefore, our estimates for the 90 m observation radius where the proportion of the missing communities is negligible are the most reliable of the three observation radii. However, the agreement between the upscaled estimates and the EC estimates is good for the 200 m observation radius, which indicates that the C gas dynamics of the missing communities can be estimated with the other communities.

5. Conclusions

Our results showed that even in a fen with a relatively even surface topography and uniform vegetation composition, carbon gas dynamics differed markedly between plant communities. Therefore, the community proportions were a fundamental controller of the ecosystem scale C gas exchange. The communities were not uniformly distributed within the study site. Consequently, the ecosystem scale C gas exchange estimates depended also on the delineation of the ecosystem boundaries. Hollows were the most different plant community in terms of species composition and C gas dynamics, which made the ecosystem scale estimates especially sensitive to the area proportion of hollows. The C gas exchange estimates that were upscaled from the plant community scale to the ecosystem scale agreed well with the simultaneous ecosystem scale (eddy covariance) measurements. Successful upscaling required detailed knowledge on the plant community proportions and on the amount of vegetation.

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