Dissertationes Forestales 240

Behind the stability of boreal bog carbon sink: Compositional and functional variation of vegetation across temporal and spatial scales

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Academic dissertation

To be presented, with the permission of the Faculty of Science and Forestry of the University of Eastern Finland, for public criticism in lecture room AG100, Agora building (Joensuu campus, Yliopistokatu 4, Joensuu) on June 19th 2017, at 12 o'clock noon.

Title of dissertation: Behind the stability of boreal bog carbon sink: Compositional and functional variation of vegetation across temporal and spatial scales

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Dissertationes Forestales 240

https://doi.org/10.14214/df.240

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ISSN 1795-7389 (online)
ISBN 978-951-651-570-3 (pdf)

ISSN 2323-9220 (print)
ISBN 978-951-651-571-0 (paperback)

Publishers:
Finnish Society of Forest Science
Faculty of Agriculture and Forestry of the University of Helsinki
School of Forest Sciences of the University of Eastern Finland

Editorial Office:
Finnish Society of Forest Science
Viikinkaari 6, FI-00790 Helsinki, Finland
http://www.dissertationesforestales.fi

Korrensalo, A. (2017). Behind the stability of boreal bog carbon sink: Compositional and functional variation of vegetation across temporal and spatial scales. Dissertationes Forestales 240. 35 p. https://doi.org/10.14214/df.240

ABSTRACT

This study aims to quantify how the spatially varying vegetation modifies the carbon sink of a boreal bog. Photosynthesis, respiration, biomass composition, biomass production and net ecosystem exchange were studied on three levels: plant species, community and ecosystem.

There was a clear plant species turnover and a strong decrease in standing biomassfrom dry to wet plant communities. Biomass production was even along the water table gradient due to higher biomass turnover rate of wet habitat species than hummock species. Both respiration and gross photosynthesis were the highest in dry plant communities, but their symmetrical water table responses resulted in no differences in net ecosystem exchange among plant communities. However, this evenness did not hold in the absence of *Sphagna*; sparsely vegetated bare peat surfaces were mostly carbon sources. The small difference in water table between *Sphagnum*-covered hollows and bare peat surfaces suggests that even a small change in water table could induce shifts between them.

The observed spatially-even carbon sink contradicts earlier studies. However, the components behind that spatial evenness showed high variability and responded to environmental conditions as previously observed. The site-specific relative abundances of functionally varied species appeared to have a larger effect on the overall carbon sink than anticipated.

Different plant species and communities had the highest photosynthesis and carbon sink at distinct times of the growing season, decreasing the ecosystem-level seasonal variation. Over the three studied years, the roles of plant communities in the ecosystem-level carbon sink changed. This indicates that the presence of species with different seasonal growth patterns and responses to environmental conditions could increase ecosystem resiliency in changing conditions. To verify this, the responses of functionally different components to environment, either based on natural variation or experimentally defined, should be included in process-models predicting the fate of bog carbon sink in changing climate.

Keywords: carbon balance, peatland, ecosystem resiliency, net ecosystem exchange, biomass production, *Sphagnum*

ACKNOWLEDGEMENTS

The years of working with this thesis have been full of learning to think and growing up to do science. I was fortunate not to do all that alone, but in a wonderful company of intelligent and kind people, who shared their skills and knowledge with me. My first supervisor, Eeva-Stiina Tuittila, is to be warmly thanked for all the discussions, insightful advice and her tremendous amount of support. My second supervisor, Lauri Mehtätalo, is to be thanked for being my guide in the world of mixed-effects modeling and showing such a patience along that road.

I would like to thank the Helsinki side of our Siikaneva team, Timo Vesala, Pavel Alekseychik, Ivan Mammarella and Janne Rinne for providing the micrometeorological data and for the excellent contribution to all of my manuscripts. I thank Raija Laiho for her wise guidance in biomass matters and Tomas Hájek for the irreplaceable advice in measuring photosynthesis and analyzing the data.

I am deeply grateful for all those who helped me with the field and laboratory work: Antonio Cestelo, María Gutierrez, Eva-Stina Kerner, Laura Kettunen, Diana Neuhauser, Janne Sormunen and Salli Uljas – the two field seasons with you were unforgettable. I still wonder how it was possible to have so much fun and still get so much done. I warmly thank the staff at Hyytiälä Forestry Field Station for all the help and support and all of the other Hyytiälä residents with whom I shared thoughts in the sauna or at lunch table.

This work was funded by the Faculty of Science and Forestry, University of Eastern Finland and Finnish Cultural Foundation, which are greatly acknowledged for their financial support. I would also like to thank the pre-examiners of my thesis, Professor Martin Heimann and Docent A. Lauren for their wise comments. I thank all of my co-workers at the School of Forest Sciences in Joensuu for creating such a friendly and supportive working environment. I also thank the members of our soil and peatland research group; Dmitrii, Elisa, Jinnan, Mihailis and Nicola for the help and everyday sharing of ideas.

Thank you, my friends outside of natural sciences, for offering me a different point of view and keeping my horizon wide. I am deeply grateful for my family for the unconditional love and support. Finally, to Matti, my great gratitude for taking me out to adventure, sharing with me both the moments of joy and confusion and all the love.

In Hyytiälä, May 2017

LIST OF ORIGINAL PAPERS

This thesis is based on the following articles, which are referred to in the text by the Roman numerals. The articles **II** and **III** are reprinted with the kind permission of the publisher or with the rights retained as author. The articles **I** and **IV** are author versions of manuscripts.

I Korrensalo, A., Kettunen, L., Laiho, R., Alekseychik, P., Vesala, T., Mammarella, I., Tuittila, E-S. (2017). Boreal bog plant communities along a water-table gradient differ by their standing biomass but not by their biomass production. Submitted manuscript.

II Korrensalo, A., Hájek, T., Vesala, T., Mehtätalo, L., Tuittila, E.-S. (2016). Variation in photosynthetic properties among bog plants. Botany 94(12): 1127–1139. http://dx.doi.org/10.1139/cjb-2016-0117

III Korrensalo, A., Alekseychik, P., Hájek, T., Rinne, J., Vesala, T., Mehtätalo, L., Mammarella, I., Tuittila, E.-S. (2017). Species-specific temporal variation in photosynthesis as a moderator of peatland carbon sequestration. Biogeosciences 14(2): 257–269. http://dx.doi.org/10.5194/bg-14-257-2017

IV Korrensalo, A., Mehtätalo, L., Alekseychik, P., Uljas, S., Mammarella, I., Vesala, T., Tuittila, E-S. (2017). The role of vegetation in the temporal and spatial variation of carbon sink in a boreal bog based on chamber and eddy-covariance measurements. Manuscript.

Aino Korrensalo is fully responsible for the summary of this doctoral thesis.

I A. Korrensalo participated in conducting the biomass measurements and data analysis. She served as the main author of the manuscript with contributions from all other authors.
II A. Korrensalo participated in planning of the study, photosynthesis measurements and data analysis. In cooperation with other authors, A. Korrensalo acted as the first author of the manuscript.
III A. Korrensalo participated in planning of the study, photosynthesis measurements and data analysis. A. Korrensalo coordinated writing of the manuscript as the first author, with contributions from all other authors.
IV A. Korrensalo participated in conducting the chamber measurements, data processing and statistical analysis. She served as the main author of the manuscript with contributions from all other authors.

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1. INTRODUCTION

Peatlands are ecosystems characterized by a high water level and the accumulation of organic matter into peat. Most of the world's peatlands, 3.46 x 10^6 km^2 or 87 %, are found in boreal and subarctic vegetation zones of North America, Russia, and Fennoscandia (Joosten and Clarke 2002). Because of the organic matter accumulating function, they are extremely important carbon storage and estimated to store between 250 and 455 Pg of carbon, which is about a half of the carbon present as CO_2 in the atmosphere (Gorham 1991, Turunen et al. 2002; Yu 2011). Due to the high water level and poor substrate quality, they produce organic matter faster than it can decompose. This excess of organic matter is stored as peat, which can form layers up to several meters of depth (Rydin and Jeglum 2013). Peatlands can be divided into two main categories: minerotrophic and ombrotrophic. Minerotrophic fens receive water and nutrients from the surrounding areas as runoff whereas ombrotrophic bogs have atmospheric deposition as their only source of water and nutrients (Vitt 2006).

Generally, peatlands act as small but persistent sinks for atmospheric carbon, i.e. their CO_2 uptake is greater than release with positive net ecosystem exchange (NEE) (Yu 2012). Atmospheric CO_2 is captured by autotrophic peatland plants in photosynthesis and used in growth, storage, respiration, root exudates or mychorriza function. About 40-70 % of this fixed carbon is directly released back to the atmosphere as plant root and shoot respiration (Gifford 2003, Litton et al. 2007). The remaining part of the carbon eventually ends up in the decomposition process. Above the water table oxygen-demanding microbes decompose dead plant material aerobically producing CO_2. Below the water table anoxic conditions prevail, and CH_4 is produced by the anaerobic decomposers. As a result of decomposition, most of the carbon in soil organic matter is released back to the atmosphere in heterotrophic respiration as CO_2 and CH_4. The rest of the carbon, up to 15 % of the original autotrophic C fixation, remains undecomposed and is stored below the water table and becomes peat (Clymo 1984, Gorham 1991, Francez and Vasander 1995).

The components of peatland carbon cycle are dependent on several environmental factors. The amount of CO_2 fixed in photosynthesis depends on photosynthetically active radiation (photosynthetic photon flux density, PPFD), CO_2 concentration, temperature, water conditions and quality and quantity of photosynthesizing plant biomass. Aerobic decomposition and therefore the amount of heterotrophic CO_2 release is regulated by temperature, moisture, volume of aerobic peat layer, decomposer community, nutrient conditions and substrate quality (Chapman and Thurlow 1998, Laiho 2006). Water table level controls the proportion of carbon released as CO_2 or CH_4 (Updegraff et al. 2001). The lower the water table, the larger proportion of the readily decomposable fresh plant litter is decomposed in aerobic conditions. Having different photosynthesis rate (Leppälä et al. 2008) and litter quality (Strákova et al. 2011), plant species composition has an effect on both autotrophic and heterotrophic parts of the carbon cycle. The species of same growth form can be expected to demand similar conditions and respond similarly to changes in environment (Chapin et al. 1996). Therefore, species are often divided into plant functional groups to detect patterns in the response of vegetation to changing conditions and the distribution of plant functional types along prevailing environmental gradients (e.g. Frolking et al. 2010).

1.1. Spatial variation in the boreal bog carbon sink

Boreal bogs are peatland ecosystems that are often characterized by an uneven surface topography, varying from hummocks rising up to 50 cm above the mean water table to intermediate lawn surfaces, hollows and open water pools (Rydin and Jeglum 2013). Water table refers here to the ecologically relevant relative distance from the moss surface, instead of the absolute water table position in relation to mineral soil below. *Sphagnum* mosses, a genus dominating boreal bog ground layer, is in a key role in shaping the surface formations by creating acidic, nutrient-poor environment of slow decomposition, which is unfavorable for many other plant species (van Breemen 1995; Verhoeven and Liefveld 1997). Hummock *Sphagna* have higher capillarity, are better able to retain water in their capitula and have higher productivity in nutrient poor conditions allowing the hummocks to rise above the mean water table (Hayward and Clymo 1982; van Breemen 1995). Lawn *Sphagnum* structural tissues are stimulated by CO_2 originating from the decomposition below, which allows them to rise above hollow species and outcompete them (Smolders et al. 2001). Hollow *Sphagna* are more productive in terms of biomass increment and photosynthesis rate (Gunnarsson 2005; Granath et al. 2009; Laine et al. 2011), but their lower drought resistance limits their habitat to the wet surfaces (van Breemen 1995; Väliranta et al. 2007). These habitats created by *Sphagnum* mosses favor different composition of vascular plant species. Dry hummocks have a thick enough aerobic layer for the roots of dwarf-shrubs, which on their part have higher water potential and photosynthesis in drought conditions (Small 1972a; Small 1972b). Sedges have a lower drought tolerance (Busch and Losch 1999), but also aerenchymatic tissue that allow them to transport oxygen to their roots in the wet hollow conditions (Wiessner et al. 2002).

The described water table gradient among the spatial formations regulates not only plant species composition, but also the processes of net ecosystem CO_2 exchange; photosynthesis and respiration, which is further separated into autotrophic respiration by plants and heterotrophic respiration of organic material decomposing micro-organisms. In this context, water table gradient is an abstract concept referring to a gradual change in plant species composition in relation to moisture instead of an actual, physical gradient. Plant species typical for the dry end of the water table gradient, hummock *Sphagna* and dwarf-shrubs, are known to have lower photosynthesis rate than sedges or lawn and hollow *Sphagna* (Leppälä et al. 2008; Laine et al. 2011). Despite this, hummocks are known to often have higher photosynthesis than the wetter plant communities due to their generally higher photosynthesizing leaf area (Laine et al. 2007; Munir et al. 2014). Since plant biomass usually decreases from the dry end of the water table gradient towards hollows (Vasander 1982; Moore et al. 2002), also autotrophic respiration can be expected to follow the same pattern. Although the litter formed in the dry plant communities is more resistant to decomposition

(Turetsky et al. 2008; Strákova et al. 2011), heterotrophic respiration is stimulated by a thicker aerobic layer (Silvola et al. 1996), and the decomposition of the less recalcitrant litter of hollow species is hindered by high water table (Bengtsson et al. 2016). As a result, also the total respiration has been found to be higher in hummocks (Alm et al. 1999; Laine et al. 2006; Laine et al. 2007; Strack et al. 2006). However, the existing information on the spatial variability of net ecosystem exchange is not straightforward; the dry peatland communities have been reported to have either larger (Waddington and Roulet 2000; Strack et al. 2006; Laine et al. 2006; Laine et al. 2007; Riutta et al 2007) or similar (Alm et al. 1999; Moore et al. 2002; Bubier et al. 2003a) carbon sink than the wet ones. This discrepancy is likely to be a result of differences in vegetation structure among studied bog sites; almost solely dwarf-shrub dominated, generally drier bog sites (Moore et al. 2002) are likely to function in a different way than wetter sites having also a substantial proportion of sedge-covered plant communities (Laine et al. 2007).

1.2. Temporal variation in the boreal bog carbon sink

Seasonal variations

Both photosynthesis and respiration are dependent on the seasonally changing temperature, moisture conditions, light level, and naturally, the amount of leaf area. Since the photosynthesizing area of *Sphagna* is not varying seasonally, they are able to photosynthesize also in early spring and late autumn, followed then by evergreen vascular plants when they no longer are dormant after winter, and finally, deciduous species when bud burst has taken place (Moore et al. 2006; Leppälä et al. 2008). The seasonal changes in respiration are found to be controlled by water table (Fenner and Freeman 2011) and temperature (Lafleur et al. 2005), which differ in their importance in dry and wet community types (Maanavilja et al. 2011).

Interannual variations

In the scale of several years, bogs are known to have a small but persistent carbon sink, which, however, can be altered or even turned into a carbon source due to variations in temperature, moisture (Alm et al., 1999; Waddington and Roulet, 2000; Lund et al. 2012) and light conditions (Nijp et al. 2015). When moisture and temperature regimes change between years, plant communities differ in their responses; for example in a dry year, R, P_G and NEE of some plant communities may decrease, while decreasing or staying similar in other communities (Bubier et al. 2003b). The seasonal timing and magnitude of changes in temperature and precipitation has been found to be an important control for the interannual variation of bog C sink (Waddington and Roulet 2000; Lund et al. 2012). However, there is so far very little research about the interannual variability in bogs with diverse vegetation structure.

Bogs respond to long-term changes in climatic conditions with a change in the relative abundance of the different plant communities (Belyea and Baird 2006; Mathijssen et al. 2016); drier conditions increase the cover of hummocks and increase in moisture causes expansion of hollows. The predicted climate change has been estimated to increase temperature and fluctuations in moisture conditions during the next centuries in the boreal region (IPCC 2013). These changes have been predicted to decrease the water table of bogs and increase dwarf-shrub cover, which in turn may enhance the productivity (Laine et al. 1995; Breeuwer et al. 2009; Holmgren et al. 2015). On the other hand, enhanced respiration in warmer climate and lower photosynthesis due to increasing cloudiness may act against that change. To reveal the consequences of changing climate to the carbon sink and storage of bogs, there has lately been a number of studies attempting to predict the responses of plant community composition to changing climate, and consequently, the responses of carbon sink processes regulated by the spatially varying vegetation (Frolking et al. 2010; Saint-Hilaire et al. 2010; Wu et al. 2011; Gong et al. 2013; Holmgren et al. 2015). For this purpose, it is essential to know, how the spatial variation in vegetation regulates the carbon sink processes in bogs with different magnitudes of spatial heterogeneities and species compositions.

1.3 Aims of the study

The aim of this study is to quantify how the spatially varying vegetation structure and changing weather conditions modify the carbon sink of a boreal bog. The hypothesis was that the variation in vegetation composition along the water table gradient regulates and decreases the temporal and spatial variation in the carbon sink of a boreal bog. This study is a cross-section of carbon sink processes in a single bog site in the scale of a single plant, plant community and ecosystem (Fig. 1). These processes include I) vegetation structure and biomass production, II) the differences among plant species and plant functional types in their photosynthetic efficiency, III) the seasonal variation in photosynthesis of plant species and plant functional groups and IV) the spatial, seasonal and interannual variation in the net ecosystem exchange.

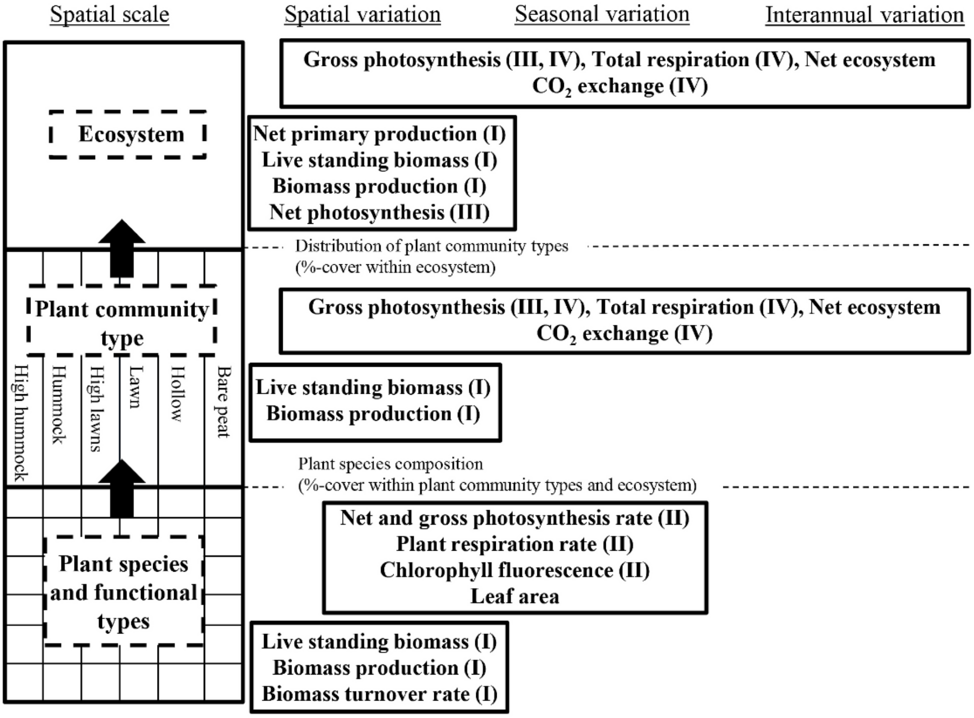

Figure 1. A schematic presentation of the studied carbon sink components at different spatial and temporal scales.

2. MATERIALS AND METHODS

2.1. Site description and placement of the permanent measurement plots

The study site is a nutrient poor (ombrotrophic) bog, which is a part of Siikaneva – a large peatland complex in Southern Finland (61° 50.179'N, 24° 10.145'E), located in the southern boreal vegetation zone (Fig. 2, Ahti et al. 1968). The annual temperature sum (base temperature 5 °C) is 1318 d.d., annual rainfall is 707 mm and yearly, January and July average temperatures are 4,2, -7,2 and 17,1 °C, respectively (30 year averages of the period 1982-2011 from Juupajoki-Hyytiälä weather station). The site has a surface topography typical for raised bogs varying from open water pools and bare peat surfaces to *Sphagnum* moss-covered lawns and hummocks. The vegetation differs markedly in relation to water table. In bare peat surfaces vegetation consists only of a scarce cover of *Rhynchospora alba* (L.) Vahl.. Hollows are covered by *Sphagnum cuspidatum* Ehrh. ex Hoffm., *S. majus* (Russow) C.E.O. Jensen, *Rhynchospora alba* and *Scheuchzeria palustris* L.. In lawns a continuous *Sphagnum* moss carpet (*S. papillosum* Lindb., *S. rubellum* Wils. and *S.*

magellanicum Brid.) is combined with dwarf-shrubs (*Andromeda polifolia* L., *Vaccinium oxycoccos* L.) and *Eriophorum vaginatum* L., whereas hummocks have a moss carpet of *S. fuscum* (Schimp.) H. Klinggr., *S. angustifolium* (C.E.O. Jensen ex Russow) C.E.O. Jensen and *S. rubellum* and a dwarf-shrub layer of *Calluna vulgaris* (L.) Hull, *Betula nana* L. and *Empetrum nigrum* L..

An eddy covariance measurement tower was placed in the centre of the bog, and the study area was set up as a circle around that point having a radius of 30 meters, which is based on the area where the majority of the flux measured by eddy covariance tower was estimated to be coming from in most conditions. The variation in vegetation along water table gradient was divided into seven classes based on their species composition (Table 1 in I). Around the eddy covariance tower, 18 permanent measurement plots were located in three groups to cover the spatial variation in vegetation composition (Fig. 3). In each of the three plot groups, there were six plots, representing the six plant community types with vegetation cover (excluding open water pools); high hummock (HHU), hummock (HU), high lawn (HL), lawn (L), hollow (HO) and bare peat (BP). Boardwalks were built close to the sample plots and the tower to avoid disturbance to the peat and vegetation during the measurements.

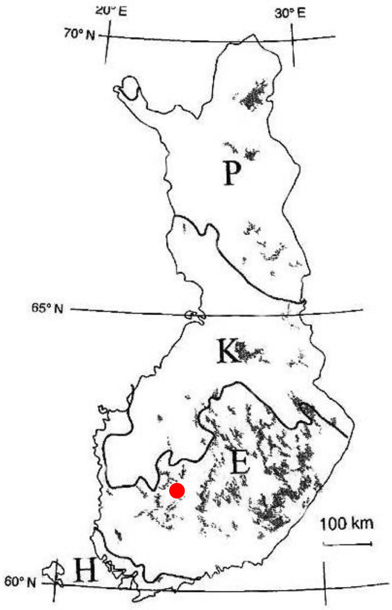

Figure 2. The location of the study site in red and vegetation zones: P = Northern boreal, K = Middle boreal, E = Southern boreal and H = Hemiboreal (Map: Ministry of the Environment).

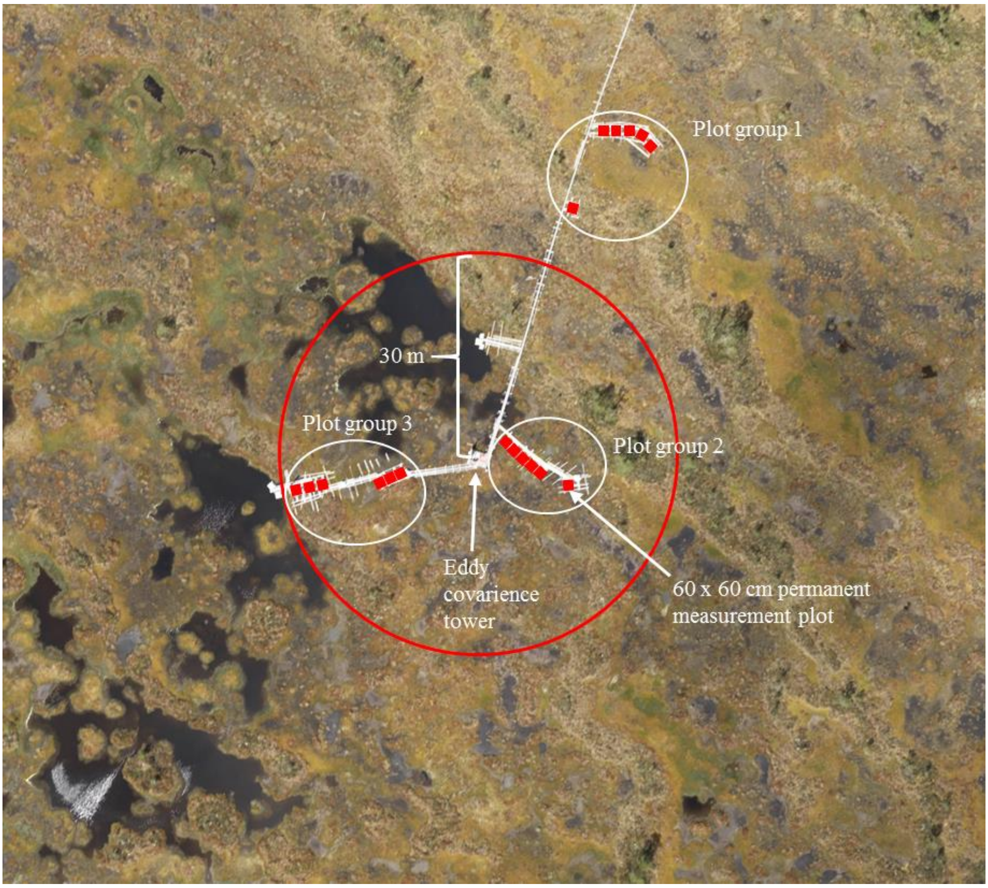

Figure 3. The placement of measurement plots around eddy covariance tower. (Photograph: Ilkka Korpela)

2.2. Quantifying the variation in vegetation

To estimate the role of each plant community type for the ecosystem-level carbon sink based on measurement data, the areal cover of each plant species and community type were recorded over the whole 30 m radius study area with two types of vegetation inventories made in July 2012 and 2013.

The first vegetation inventory, made in 2012, was extended to an area within 200 m from the eddy covariance tower as a sampling grid of 542 inventory plots (Fig. 4) to quantify the variation in vegetation also in the surroundings of the study area. In every plot the projection cover of each species was estimated inside a circular frame of 0,071 m^2. The surface type was recorded based on the species composition. At every fourth plot of the grid, six so-called satellite plots were included to the inventory 1, 5 and 10 meters from the main grid plot (Fig. 4). Aboveground parts of vascular plants were harvested at every second grid plot and

Sphagnum capitula at every fourth plot from the area of the circular frame after the projection cover had been estimated (Fig. 4).

The second vegetation inventory was made in 2013 to describe the covers of species and vegetation communities in relation to water table within the main flux footprint of the eddy covariance tower. A grid of 122 inventory plots was laid out within 30 m radius from the eddy covariance tower with five meter distances between each plot (Fig. 5). Species' projection covers were estimated at each plot, and based on that information, the plant community types of the plots were also recorded. Water table of every inventory plot was measured from a perforated plastic tube, which was installed into the depth of 50 cm.

A detrended correspondence analysis (DCA) of the vegetation inventory data from summer 2013 was used to examine how the plant species composition is structured and related to water table. Species' covers at the 18 permanent measurement plots were also estimated and included in this analysis to find out how well the permanent plots represent the variation in vegetation observed within the whole study area. The analysis was made with Canoco 5 software (ter Braak and Šmilauer 2012).

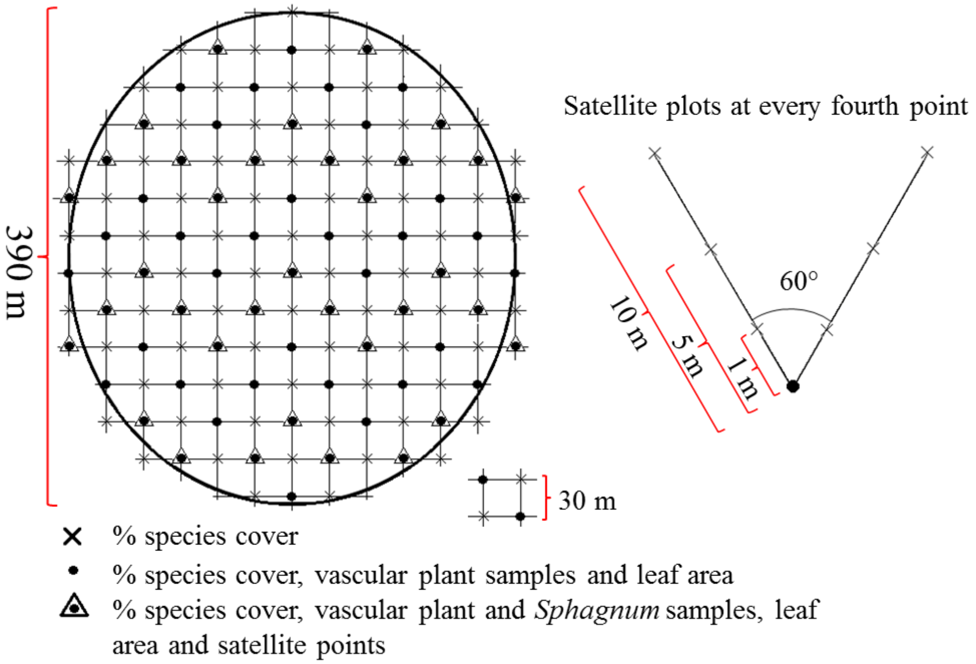

Figure 4. Sampling grid in the vegetation inventory in 2012: measured variables and the placement of satellite plots.

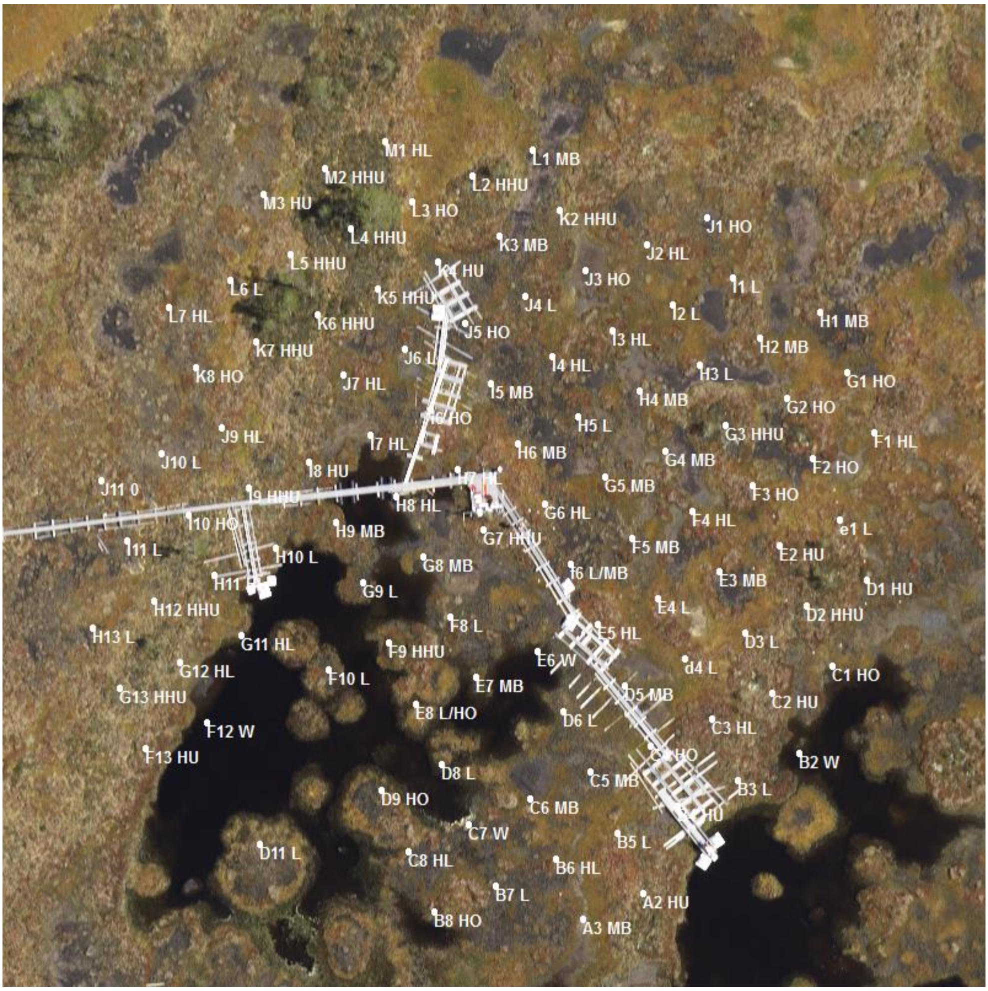

Figure 5. Sampling grid in the vegetation inventory in 2013. 14 inventory plots are not visible in the figure due to missing coordinates, but the information from the plots was used in the analysis. The abbreviations of the plant community types are explained in section 2.1. (Photograph: Ilkka Korpela)

2.3. Species level measurements

Vascular green area measurements (I, III and IV)

Seasonal development of vascular green area of each vascular plant species at the 18 permanent sample plots was measured following Wilson et al. (2007) from May to September in 2012-2015. The number of leaves of each vascular plant species in each sample plot was calculated biweekly and multiplied by the size (m^2) of an average leaf on each measurement day, defined by measuring the area of 10−15 leaves collected close to the sample plots with a scanner, which was divided by their number. For certain dwarf-shrubs, the length (cm) of stem containing green leaves within each sample plot was measured instead of the number of leaves and the average leaf area (m^2) per one centimeter of stem instead of average leaf size.

Measuring Sphagnum moss biomass production (I)

To define the biomass increment of each *Sphagnum* species the cranked wire method (Clymo 1970) was used. A total of 66 wires were installed into patches of each of the eight species to be measured. The length growth in each of the 66 patches was measured between May 19 and September 7 of 2014. The shoot density and weight of one centimeter of stem were defined for each species from samples taken next to the 66 wires. The biomass production in dry mass g m^{-2} growing season^{-1} was calculated for each of the cranked wire patches using these values. Biomass production of each *Sphagnum* species in the 18 sample plots was calculated using species-wise averages of biomass production per m^2 and the relative cover of each species inside the plots.

Conversion among species cover, vascular green area and live standing biomass (I)

The aboveground vegetation was harvested in part of the plots during the vegetation inventory made in 2012 (Fig. 4). The vascular green area of harvested vascular plants was defined and leaves and stems were separated. Dry biomass of each plant species in the samples was weighed after drying. The correlations were established for each species among vascular green area, areal cover defined in the inventory and live standing biomass. These correlations were used to convert the seasonal vascular green area increment of each plant species at the 18 permanent sample plots into aboveground biomass production (including stems, branches and leaves). The correlations were also utilized to convert the cover of each *Sphagnum* species and the seasonal maximum vascular green area of each vascular plant species at the 18 permanent sample plots to live standing biomass (capitulum biomass for *Sphagna*).

Belowground live standing biomass and biomass production (I)

Belowground biomass was measured in August 2015 from 18 peat cores taken close to the permanent measurement plots. Cores were cut into 10 cm layers and live roots were separated from these layers. The roots were then divided into dwarf-shrub and sedge roots, which were dried before weighing.

To obtain an estimate of the belowground biomass production for each community type we used the root ingrowth core method (Laiho et al. 2014). Cylinder-shaped mesh bags of 3 cm diameter and 50 cm effective length were filled with commercial non-fertilized *Sphagnum* peat and installed into each of the 18 sample plots in October 2012 and removed in October 2014. The cores were then cut into 10 cm layers and the ingrown roots were separated, classified into sedges and dwarf-shrubs, dried and weighed. The sum of live and dead roots in the cores was divided by two to get an annual biomass production estimate.

Physiological measurements (II and III)

Monthly measurements of the photosynthesis light response parameters and chlorophyll fluorescence (F_v/F_m) were conducted over the growing season (May-September) 2013 of 11 vascular plant and 8 *Sphagnum* species on the study site (Table 2 in II). Light response parameters describe the photosynthetic efficiency of the plant, while F_v/F_m is an indirect measure of stress related to light inhibition and lack of moisture or nutrients (Maxwell and

Johnson 2000). An open, flow-through gas exchange measurement system (GFS-3000, Walz, Germany and LI-6400, LI-COR, USA) was used to measure CO_2 exchange in the plants sampled within the study area and brought to laboratory. Net CO_2 assimilation rate at three different levels of PPFD was measured. After photosynthesis measurement, samples were dark-acclimated for 45 min and F_v/F_m was measured using a pulse-modulated chlorophyll fluorometer (FMS-1, Hansatech, UK).

Net and gross photosynthesis, and respiration of each measured sample were expressed per photosynthesizing area (mg CO_2 m^{-2} LA h^{-1}) and per unit of dry mass (mg CO_2 g^{-1} h^{-1}). For each sample, the maximum quantum yield of CO_2 assimilation (α in mg CO_2 μmol^{-1}) and light compensation point (LCP, the PPFD level required for net photosynthesis to reach zero) were calculated. Principal component analysis (PCA) was applied to explore the main trends in photosynthetic parameters, namely net and gross photosynthesis at three light levels, LCP, α and F_v/F_m. To quantify how much variation in photosynthetic parameters is explained by the difference between vascular plants and *Sphagna*, PFTs, species and months, partial redundancy analysis (pRDA) was applied. These analyses were made with Canoco 5 software (ter Braak and Šmilauer 2012).

Differences in net photosynthesis light response parameters among species, PFTs and months were quantified similarly to Kangas et al. (2014) by applying a hyperbolic light saturation curve (Larcher 2003):

$$PN_{si}=\frac{Pmax_s\ PPFDsi}{k_s+PPFDsi}-R_s+e_{si} \qquad \text{(Eq. 1)}$$

where PN_{si} is the observed net CO_2 exchange (mg CO_2 m^{-2} LA h^{-1}) and $PPFD_{si}$ is the photosynthetic photon flux density for measurement i of sample s. The three estimated parameters were the maximum rate of light-saturated net photosynthesis ($Pmax_s$), the PPFD level where half of Pmax was reached (k_s) and respiration (R_s). Log link was used for $Pmax_s$, k_s and R_s to restrict them to be positive. The three parameters were further written as a linear function of fixed predictors and normally distributed random effects (Eq. 2a-e in II). Finally, the differences in clorophyll fluorescence F_v/F_m among species, PFTs and months were quantified using linear mixed effects models (Eq. 3-7 in II). These analyses were made using the function nlme and lme of the R program package nlme (Pinheiro and Bates 2000).

2.4. Community-level measurements

Net ecosystem exchange measurements (IV)

The exchange of CO_2 between the vegetation community and the atmosphere was measured with the closed chamber method (e.g. Riutta et al. 2007) in different environmental conditions. The measurements were conducted during the snow-free period in 2012−2015. A transparent plexiglass chamber (56 x 56 x 30 cm) was placed onto an aluminium collar that was installed to each of the 18 permanent sample plots. Photosynthetic photon flux density (PPFD), temperature inside the chamber and the change in CO_2 concentration were recorded using radiation and temperature sensors inside the chamber and an infrared gas analyzer (EGM-4, PP-systems, UK) connected to the chamber. At every plot, 3−4 measurements were conducted on each measurement day; first in full light, then one or two times under PPFD level reduced by 40-90%, and finally in the dark. Water table at each plot was recorded simultaneously with the measurements. Net ecosystem exchange during a measurement was calculated as a linear change in CO_2 concentration in the chamber headspace. CO_2 exchange measured in the dark represented the sum of autotrophic and heterotrophic respiration.

To reconstruct net ecosystem exchange flux of the six measured vegetation community types over the growing seasons 2012−2014 and to quantify their responses to environmental variables, we used a non-linear mixed-effects model with similar hyperbolic light saturation curve than in Eq. (1) (Larcher et al. 2003):

$$NEE_{trsij} = \frac{Pmax_{trsi} PPFD_{trsij}}{k_{trsi} + PPFD_{trsij}} - R_{trsi} + e_{trsi} \qquad \text{(Eq. 2)}$$

where NEE_{trsij} is the observed net CO_2 exchange per square meter and the predictor $PPFD_{trsij}$ is the photosynthetic photon flux density (µmol m^{-2} s^{-1}) for measurement j on week i on plot s in plot group r on year t. The parameters to be estimated are respiration (R_{trsi}), maximum rate of light saturated photosynthesis ($Pmax_{trsi}$) and the level of PPFD were half of Pmax was reached (k_{trsi}). The residual (e_{trsi}) is normally distributed with mean zero and constant variance.

In the full model, the parameters R_{trsi}, $Pmax_{trsi}$ and k_{trsi} were written as linear functions of fixed predictors and random effects. For R_{trsi} and $Pmax_{trsi}$ the included fixed predictors were plant community type (six levels), air temperature as second degree polynomial and vascular green area (VGA) transformed according to Boolean model VGA_B=1-exp(-VGA) to account for the effect of self-shading on photosynthesis at high leaf areas. Since none of the possible fixed predictors seemed to explain the variation in k_{trsi}, it was assumed to be constant with the appropriate combination of random effects. Since random variation occurred at all of the four possible levels (year, plot group, plot, week), they were all included as random effects of the three parameters. The model was fitted using the function nlme of the R program package nlme (Pinheiro and Bates, 2000). For realistic prediction of annual fluxes, the dependence of random effects over time were analyzed using the predicted weekly random effects for each permanent measurement plot.

Using the nonlinear mixed-effects model (Eq. (2)) and the temporal correlations of the random effects within a growing season, daily (g CO_2 m^{-2} d^{-1}) and yearly (g CO_2 m^{-2} growing $season^{-1}$) cumulative gross photosynthesis, respiration and net ecosystem exchange at each of the 18 measurement plots during growing seasons 2012−2014 were reconstructed. For the reconstruction, continuous PPFD and air temperature data recorded at 30 min intervals and daily VGA of each measurement plot calculated using a log-linear VGA development model (Wilson et al. 2007) were used. To validate the fixed part of the model (Eq. (1)), the NEE measurements of growing season 2015 were used as an external validation data set, which was not used for model construction.

2.5. Upscaling of measurements to the ecosystem level

Ecosystem-level live standing biomass, biomass production (I) and daily or seasonal net ecosystem exchange (IV) were estimated by first calculating an average value of the three replicate plots representing each plant community type (Fig. 3). Then, the areal covers of each plant community type from the vegetation inventory of 2013 were used as weights to calculate an ecosystem-level weighed average of these values.

To upscale the species level photosynthesis measurements to ecosystem scale (III), a similar light response model to Eq. (1) was fitted separately for each of the 19 plant species in the five months of the growing season. These monthly light response curves were used together with seasonal vascular green area development of each species and half-hourly

PPFD data to calculate an ecosystem-level gross photosynthesis estimate for each day of growing season 2013.

2.6. Ecosystem-level gas exchange measurements (I, III, IV)

To validate the carbon sink measurements conducted in the species or plant community scale, eddy covariance method was used. Continuous micrometeorological flux measurements of the 2.5 m high eddy covariance tower in the center of the study area (Fig. 3) provided an independent estimate of ecosystem-level CO_2 exchange. Vertical wind velocity and a respective scalar variable (such as CO_2 concentration) were measured at high frequency during the growing seasons 2012-2015 by the eddy covariance system, comprising of a 3-D ultrasonic anemometer (USA-1, METEK Meteorologische Messtechnik GmbH, Germany) and an enclosed H_2O/CO_2 gas analyzer (LI-7200, LI-COR Biosciences, USA). The turbulent flux rates were based on the covariance between vertical wind velocity and CO_2 concentration. EddyUH software was used to process the raw data and average the fluxes of latent heat, sensible heat, and CO_2 over 30 min periods (Mammarella et al., 2015). The resulting eddy covariance fluxes represent the exchange over a quasi-elliptical source area (footprint), which is estimated to be located within approximately 30 m upwind of the tower using the footprint calculations model by Kormann and Meixner (2001).

Net ecosystem exchange of CO_2 (NEE) measured by the eddy covariance tower was partitioned into ecosystem gross primary production (GPP) and ecosystem respiration (R_{eco}). To obtain R_{eco}, a Q_{10}-type temperature response curve was fitted to the nighttime eddy covariance data, when respiration is the only component of NEE. For this, the temperature in the depth of 5 cm in the peat was used. The GPP estimates were calculated by subtracting the modeled R_{eco} from the measured NEE. To fill the gaps in GPP, a similar light response model than Eqs. (1)-(2) was fitted following:

$$GPP = \frac{Pmax\ PPFD}{k + PPFD}(VGA + b) \qquad \text{(Eq. 3)}$$

where GPP is expressed in mg (CO_2) m^{-2} h^{-1}. *VGA* is the modeled daily vascular green area described above, while *b* represents the temporally constant contribution of the *Sphagnum* to total photosynthesizing leaf area. An ecosystem-level net primary production (NPP) estimate was derived from eddy covariance measurements in 2014 to compare that with biomass production estimate as NPP = NEE – R_h. Heterotrophic respiration (R_h) was estimated using the proportion of R_h from R_{eco} derived from literature, which falls within the range of 43-65% (Crow and Wieder 2005).

3. RESULTS

The results of this thesis are presented following the logic described in Figure 1. The first chapter shows the results regarding the spatial variation in vegetation and carbon sink processes at the studied bog site. I first describe the variation in species composition of plant community types and the distribution of plant community types along the water table gradient. After that, I show, how this spatial variation in vegetation is reflected in the carbon sink functions. The second chapter of the results describes the seasonal and interannual variations in the carbon cycling functions. The third chapter of the results presents the ecosystem-scale carbon sink processes upscaled from measurements at species and plant community type scale and compares these with the estimates derived from eddy covariance measurements.

3.1. Spatial variation in vegetation structure and carbon sink

The vegetation within the study area (30 metres from the eddy covariance tower) consisted of 22 plant species, of which 9 were mosses and 13 were vascular plants. The most important gradient in the species composition was related to moisture (DCA axis 1, eigenvalue = 0.639); the order of the plots along the axis is relative to their water table (Fig. 6a and b). Along this gradient, vegetation was a continuum from high hummocks, characterized by dwarf-shrubs (*Calluna vulgaris, Betula nana, Empetrum nigrum*) and hummock *Sphagna* (*S. angustifolium, S. fuscum*), towards the wet end of the gradient dominated by sedges (*Carex limosa, Rhynchospora alba*) and hollow *Sphagn*a (*S. cuspidatum, S. majus*). In the wet end of the moisture gradient, there was more variation also along a second gradient (DCA axis 2, eigenvalue = 0.196), which was related to *Sphagnum* moss cover and moss species composition. The second gradient separated bare peat surfaces without any *Sphagnum* cover from lawns and hollows with almost 100 % *Sphagnum* cover.

The same two gradients than in species composition were also found in the carbon sink properties among the 18 permanent sample plots. The main gradient (PCA axis 1, eigenvalue = 0.46) was related to moisture, as shown by the strong correlation between the first axis and mean water table, and the ordering of plant community types from high hummocks to hollows and bare peat surfaces along the axis (Fig. 7). The first gradient was heavily correlated with e.g. total live standing biomass, net and gross photosynthesis, respiration, as well as live standing biomass and biomass production of hummock *Sphagna* and dwarf-shrubs (Fig. 7).

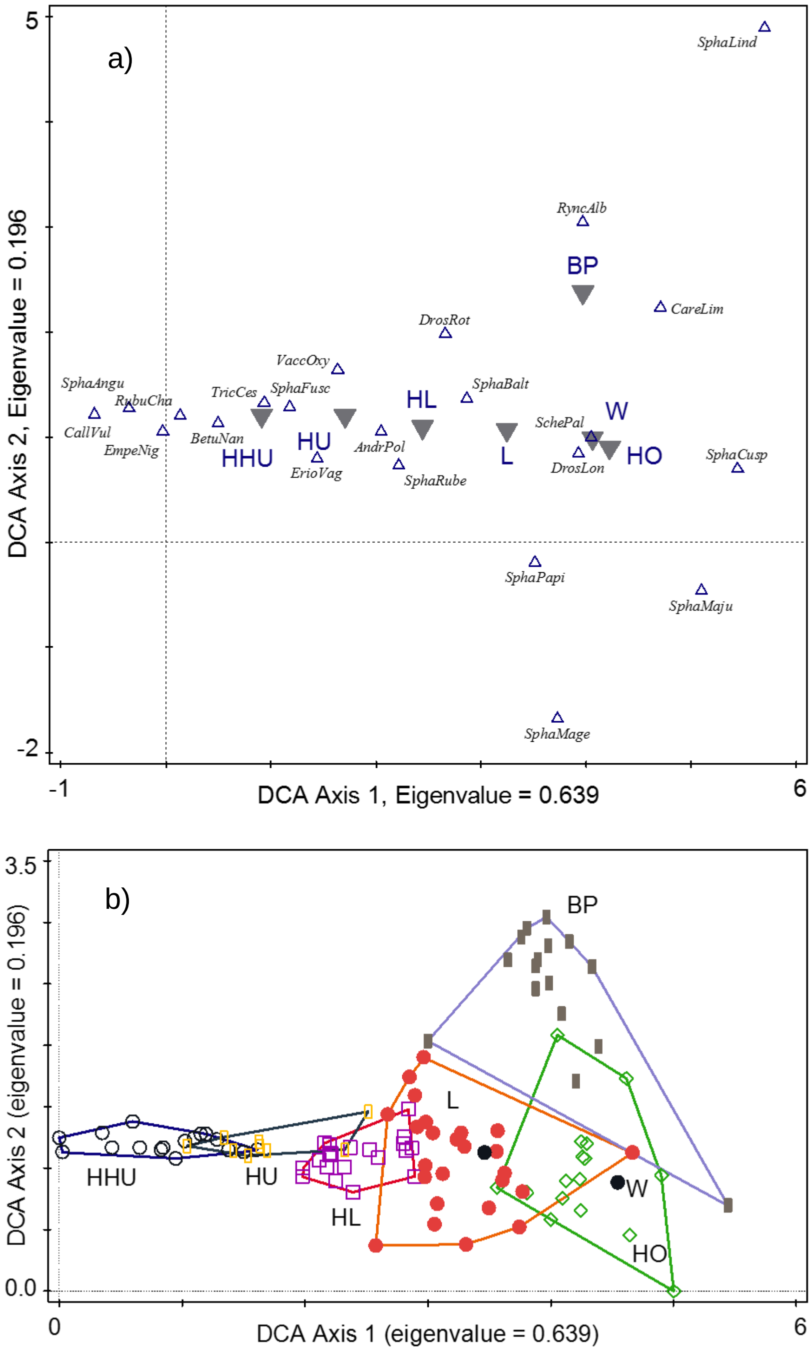

Figure 6. Detrended correspondence analysis (DCA) of 122 sample plots describing the two main gradients in variation of vegetation (DCA axis 1 and 2), with a) showing the variation in plant species composition among the plant community types and b) showing, how the sample plots belonging to a certain plant community type are separated based on their species composition. Abbreviations of plant community types are explained in section 2.1.

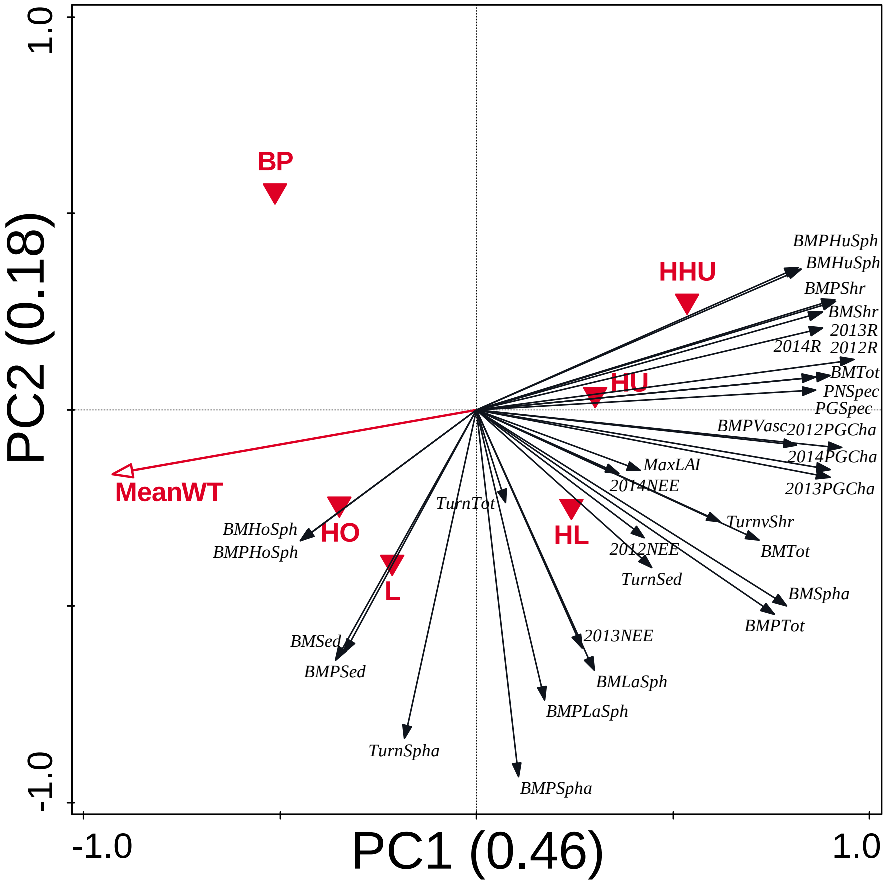

Figure 7. Principal component analysis (PCA) describing the two main gradients in carbon sink properties among the 18 permanent sample plots (PCA axis 1 and 2). The abbreviations of these properties are: MaxLAI = seasonal leaf area index maximum; BM = live standing biomass; BMP = biomass production; Turn=biomass turnover rate (BMP:BM); HuSph, LaSph, HoSph = hummock, lawn and hollow *Sphagna*; Shr and Sed = dwarf-shrubs and sedges; Spha and Vasc = sum of *Sphagnum* and vascular species; PNSpec and PGSpec = species scale net and gross photosynthesis measurements upscaled to plot level using the areal covers of the species within the plots; 2012PGCha, 2013PGCha and 2014PGCha = chamber-based gross photosynthesis in different years; 2012R, 2013R and 2014R = chamber-based respiration in different years; 2012NEE, 2013NEE and 2014NEE = chamber-based net ecosystem exchange in different years. Mean water table and plant community type of the plots are included as supplementary variables (in red). The eigenvalues of the axis are given in parenthesis.

In paper I, live standing plant biomass (g m^{-2}) in Siikaneva was found to decrease gradually from dry to wet community types both above- and belowground (Fig. 1a in I). This relation was mainly shaped by the water table response of above- and belowground dwarf-shrub standing biomass, likewise concentrated on the dry end of the water table gradient (Fig. 1e and 3a-b in I).

In paper II, differences in photosynthetic properties among species were found to divide *Sphagna* into their traditional plant functional types based on the preferred habitat along the water table gradient; hollow and lawn *Sphagna* with higher gross photosynthesis rate than in hummock *Sphagna*. *Sphagnum* mosses had in general lower photosynthesis rate than vascular plants. However, the differences in photosynthetic properties among vascular plant species did not follow the traditional plant functional type division into evergreen and deciduous dwarf-shrubs with lower photosynthesis rate in comparison with sedges. The differences were neither correlated with the wetness of the preferred habitat by the species.

In paper III, it was observed that the differences in gross photosynthesis rates among species were of minor importance when upscaled to ecosystem-level. For both vascular plants and *Sphagna*, the magnitude of ecosystem-level gross photosynthesis was shaped by the species cover and leaf area. *Sphagnum* mosses with lower photosynthesis rate but a higher cover at the site had higher ecosystem-level gross photosynthesis than vascular plants. However, ecosystem-level net photosynthesis was observed to be shaped by the combination of areal covers and species-specific photosynthesis rates. Species with low cover at the site but high photosynthesis rate (e.g. *Trichophorum cespitosum*, *Sphagnum majus*) were more important for the ecosystem-scale carbon sink than implied by their areal cover (Table 2 in III). In Figure 7, species level gross and net photosynthesis measurements upscaled to measurement plot level (PGSpec and PNSpec in Fig. 7) followed the same trend than standing biomass and leaf area, which were the highest in dry end of the water table gradient (Fig. 7).

In paper IV, plant community-scale gross photosynthesis and respiration were found to have high spatial variation and to be the largest in high hummocks, with a decrease towards the wet plant communities (Fig. 5 in IV).

As with species composition, there was a second, weaker gradient (PCA axis 2, eigenvalue = 0.18) in the variation of carbon sink properties, which ordered the sample plots based on their *Sphagnum* cover (Fig. 7). It separated bare peat surfaces from other plant community types, and to a lesser extent, high hummocks with a slightly smaller *Sphagnum* cover, from the solely *Sphagnum*-dominated communities. In line with this, the second gradient was correlated with carbon sink properties related to *Sphagna*; biomass production of lawn *Sphagna*, total *Sphagnum* biomass production and *Sphagnum* biomass turnover rate.

In paper I, *Sphagnum* mosses of the wet plant communities were found to have higher biomass turnover rate than hummock species (Fig. 4 in I). Due to this difference in turnover, standing *Sphagnum* biomass was the largest in hummocks and high lawns, but *Sphagnum* biomass production was the largest in lawns (Figs. 1b and 2b in I). Also sedges, growing mainly in the wet end of the moisture gradient, had a higher biomass turnover rate than dwarf-shrubs (Fig. 4 in I). Although total standing biomass was concentrated to the dry plant communities (Fig. 6, Fig. 1a in I), this higher productivity and water table optima observed for sedges and *Sphagna* of wet habitats were able to balance out the opposite water table response of dwarf-shrubs (Fig. 2a-f in I). As a result, the only clear difference among plant community types in biomass production was found between bare peat surfaces and all other communities (Fig. 2a in I), a pattern also seen in Figure 7.

In paper IV, the only difference among plant community types in net ecosystem exchange was observed between bare peat surfaces and the other five communities (Fig. 5 in IV), again also seen in Figure 7. The reconstructed seasonal fluxes showed that lawns and hollows accounted for a larger proportion of the seasonal net ecosystem exchange in 2013, which was the warmest of the three growing seasons (Table 2 and Fig. 3 in IV). The seasonal net ecosystem exchange of high hummocks was the largest in 2014 (Fig. 5 in IV), which was the year with the most fluctuations in temperature and light levels (Fig. 3 in IV). In Figure 7, net ecosystem exchange was more correlated with second axis in 2013 and with first axis in 2014.

3.2. Temporal variation in carbon sink processes

In paper II, the seasonal changes in photosynthetic efficiency of *Sphagna*, i.e. the parameters of photosynthetic light response, were more important than the differences among plant functional types or species (Fig. 1b in II). In vascular plants, there was more variation in photosynthetic efficiency among species than among plant functional types or months of growing season (Fig. 1a in II).

In paper III, the seasonal changes in photosynthetic efficiency of *Sphagna* were seen as a gradual decline in the upscaled *Sphagnum* gross photosynthesis from May to September (Fig. 2 in III), following the seasonal decline in water table within the site (Fig. 1 in III). The seasonal course of upscaled vascular plant gross photosynthesis followed the leaf area development of plant functional types. Evergreen shrubs regulated the level of vascular plant gross photosynthesis in the early and late growing season, although also acting as a stable baseline of photosynthesis in the middle of the summer, when sedges took the leading role (Fig. 3a in III).

In paper IV, respiration and gross photosynthesis of plant community types were found to have the same order of magnitude throughout the growing seasons 2012-2014 (Fig. 6 in IV). In net ecosystem exchange, this was not the case, and different plant community types had the highest net ecosystem exchange at distinct times during the three growing seasons. The persisting pattern over the three years was that lawns had the highest net ecosystem exchange in almost every spring and autumn (Fig. 6 in IV). Wet plant community types had the highest interannual variation in the reconstructed respiration and gross photosynthesis. Net ecosystem exchange of any community type did not show any significant interannual variation (Fig. 5 in IV).

3.3. Ecosystem-level carbon sink

Paper I: **live standing biomass** estimate for the whole site was 587 ± 119 dry mass g m^{-2}, consisting of 14 %, 63 %, 22 % and 1 % of *Sphagna*, dwarf-shrubs, sedges and other vasculars, respectively. **The biomass production** of Siikaneva bog was 132 ± 15 dry mass g m^{-2} during growing season 2014, which converted from dry mass to carbon falls between **58-95 g C m^{2}**. It was evenly divided among the main plant functional types at the site; the proportions of *Sphagna*, dwarf-shrubs and sedges were 31, 32 and 32 % of the total biomass production, respectively. The biomass production of other vascular plants was only 4 % of the total. However, the eddy covariance derived **net primary production** of the site for growing season 2014 was much higher than biomass production estimate, ranging **from 166 to 202 g C m^{-2}**.

Paper III: The cumulative **gross photosynthesis** for the growing season **2013**, i.e. the upscaled species-wise and monthly gross photosynthesis estimates summed up, was **230 g C m^{-2}**. The estimate was fairly similar to **the gross primary production estimate** derived from eddy covariance measurements, which was **243 g C m^{-2}**. The seasonal course of these two estimates differed to some extent, especially in spring, due to the difference between the temperature where photosynthesis measurement was conducted and the field temperature. Of the total ecosystem-level gross photosynthesis, *Sphagna*, dwarf-shrubs, sedges and other vascular plants accounted for 60 %, 16 %, 19 % and 5 %, respectively. **The cumulative net photosynthesis** for the growing season 2013, i.e., respiration subtracted from gross photosynthesis in the species-wise and monthly estimates when upscaling, was **77 g C m^{-2} growing season^{-1}**. The proportions of *Sphagna*, dwarf-shrubs, sedges and other vascular plants of this were 26 %, 29 % and 35 % and 10 %, respectively. Net photosynthesis estimate corresponded well with the range of biomass production, and the division among plant functional types is rather similar.

Paper IV: **Net ecosystem exchange** reconstructed for growing seasons **2012**, **2013** and **2014** using the chamber measurements were **61**, **67** and **66 g C m^{-2}** growing season^{-1}, respectively. Of these years, 2012 was the coldest, wettest and cloudiest, 2013 was the warmest and 2014 had the most fluctuating temperature and amount of light (Fig. 3 in IV). Lawns are the plant community with highest cover within the site, and they account for the largest share of net ecosystem exchange in every growing season (Table 2 in IV). Net ecosystem exchanges measured by the eddy covariance tower were **47**, **109** and **97 g C m^{-2}** growing season^{-1}, for years 2012, 2013 and 2014, respectively.

4. DISCUSSION

Water table gradient defines the spatial variability of carbon sink processes in bog ecosystems by altering the physical peat properties and supporting different plant functional types at distinct points (Rydin and Jeglum 2013). Live standing biomass in bogs is concentrated on the dry end of the water table gradient, where dwarf-shrubs dominate the vascular plant vegetation (I: Moore et al. 2002; Vasander et al. 1982). Sedge biomass grows towards the wet end of the water table gradient, but remains generally lower than dwarf-shrub biomass (I: Moore et al. 2002; Vasander et al. 1982). *Sphagnum* mosses form a continuum of species adapted to distinct points along the water table gradient (Hayward and Clymo 1982; Rydin 1993), but due to the higher capitulum density of hummock and high lawn species, also the live standing biomass of *Sphagnum* mosses decreases towards hollows (I).

In this study, the same main plant functional types formed the standing biomass than in earlier research (Vasander 1982; Moore et al. 2002), but due to the relative wetness of the studied bog, the proportions of the species typical of wet habitats were higher (I). The plant functional types with higher water table optimum, namely sedges, lawn *Sphagna* and hollow *Sphagna*, are known to have higher photosynthesis and biomass turnover rate than dwarf shrubs and hummock *Sphagna* (Forrest, 1971; Gunnarsson 2005; Leppälä et al. 2008; Granath et al. 2009; Laine et al. 2011). Biomass production of bogs has been reported to decrease from the dry communities towards the wet ones, hand in hand with standing biomass (Kosykh et al. 2008). However, in the case of the bog site studied here, the “biomass stoichiometry” in the proportions of plant functional groups with different functioning led to an outcome, where biomass production was spatially even (I).

In bogs, spatial variation is known to be high in processes regulating net ecosystem exchange; respiration and gross photosynthesis. The thicker aerobic layer in the dry end of the water table gradient is known to enhance respiration (IV, Alm et al. 1999; Laine et al. 2006; Laine et al. 2007; Strack et al. 2006), and photosynthesis seems to be the highest in plant communities that support the highest amount of plant biomass and photosynthesizing leaf area (Fig. 7; I; IV; Laine et al. 2006). The most usual spatial pattern in net ecosystem exchange seems to be higher carbon sink in the dry plant communities (Waddington and Roulet 2000; Laine et al. 2006; Riutta et al 2007). However, it seems that if respiration and photosynthesis have a rather symmetrical relationship to water table (Bubier et al. 1998), it can result in a spatially even net ecosystem exchange (IV).

Despite all the spatial evenness in biomass production and net ecosystem exchange between most of the plant community types, it has to be recalled, that 27 % of the bog is not that well-off, consisting of bare peat surfaces and open water pools. In both biomass production and net ecosystem exchange, the only spatial difference was the lower values in bare peat surfaces than in other community types (I; IV). During two out of three measured growing seasons, bare peat surfaces acted as carbon sources to the atmosphere (IV). Although we did not measure CO_2 fluxes of open water pools, they are known to act as carbon sources, even in cases where they have small cover of vegetation (Waddington and Roulet 2000).

According to insurance hypothesis, functional diversity, i.e. the presence of species and plant functional types with different physiology, morphology, resource requirements, seasonal growth patterns and life history, increases the productivity of an ecosystem and makes it temporally more stable (Tilman et al., 1997; Yachi and Loreau 1999; Gunderson 2000; Cadotte et al., 2008). Within the studied bog, the amplitude of habitats along the water table gradient gave rise to functional diversity, i.e. the presence of morphologically and phenologically different plant functional types with varying water table optima and biomass turnover rate. This functional diversity made the carbon sink functions spatially more stable (I; IV). This, however, was only the case in plant communities covered by *Sphagna* and the vascular plants associated with the habitats created by them.

Functional diversity also seems to make the bog carbon sink processes more stable within a growing season, when compared to fens with more homogeneous, sedge-dominated vegetation (Bubier et al. 1998; Leppälä et al. 2008). Different bog plant functional types have the highest gross photosynthesis at distinct times of the growing season due to their seasonal rhythms of leaf area development (III; Leppälä et al. 2008). In gross photosynthesis of bogs, *Sphagnum* mosses and evergreen dwarf-shrubs form a seasonally rather stable baseline for gross photosynthesis already starting in spring (III, Moore et al. 2006) in contrast to sedges, which have a high peak in leaf area and gross photosynthesis in midsummer (III, Leppälä et al. 2008). In the plant community scale the same is seen as the dry plant communities dominated by evergreen dwarf-shrubs and hummock *Sphagna* start photosynthesizing in spring (IV; Bubier; Leppälä et al. 2008), and sedge dominated wet communities have a sharper midsummer photosynthesis peak (IV; Leppälä et al. 2008). Seasonal changes in temperature and water table seem to be more visible in *Sphagnum* photosynthesis (III), because their photosynthesizing area does not change to a large extent seasonally and they respond more readily to changes in moisture due to the lack of vascular tissue. The seasonal changes caused by abiotic factors to photosynthesis and respiration were observed to be smaller in community-level net ecosystem exchange (IV). Further, different plant communities had the highest net ecosystem exchange at distinct times of the growing season (IV). As a result of these, the ecosystem-level flux was seasonally more stable than in any of the plant community types (IV). This gives some support for the insurance hypothesis in terms of stabilizing the seasonal variation. However, it remains questionable, whether the functional diversity of bogs would also increase their productivity or carbon sink in comparison with more homogeneous peatlands. Although such differences among bogs and fens have been reported in the long-term carbon accumulation rate (Turunen et al. 2002), in the short term carbon sink this does not seem to be the case (Bubier et al. 1998; Leppälä et al. 2008).

The process-based models predicting the fate of peatland carbon sink and storage in the changing climate are currently attempting to take into account the effect of spatial variation of vegetation in regulating the carbon sink processes (e.g. Frolking et al. 2010; Saint-Hilaire et al. 2010; Wu et al. 2011; Gong et al. 2013). In addition to carbon sequestration, plant species composition also has a far-reaching effect on the carbon release through decomposition. Although the differences in decomposition caused by species are greater than the climate-driven or site-specific differences (Cornwell et al. 2008; Strákova et al. 2011), the research has so far focused more on studying the effects of abiotic factors on these processes. Even if the vegetation community changes, the peat properties it has created can be expected to remain long after (Belyea and Baird 2006). In this study, the similar amount of biomass production in different plant communities was made of completely different elements (I). In dry plant communities, there is larger belowground input of fresh carbon for decomposition in the form of root litter (I), but on the other hand, both below- and aboveground it has larger proportion of lignin-rich woody tissues and *Sphagnum fuscum*, which are resilient to decomposition. In wet communities, the litter produced by sedges and hollow *Sphagna* is more readily decomposable (Strákova et al. 2011), and the root production extends deeper into the peat (I; Murphy and Moore 2010). Moreover, peatland plants affect their belowground surroundings by producing root exudates (Ström et al. 2005), yet another source of fresh carbon for the decomposer community, but which only very few studies have tried to quantify.

Photosynthesis and respiration were most varying in the wet plant community types due to interannual variations in weather conditions (IV). Lawns and hollows have a very small difference in water table with bare peat surfaces (Fig. 6), but this statistically insignificant difference appears to mark the line between *Sphagnum* dominated surfaces with spatially even carbon sink and the almost non-vegetated surfaces acting as carbon sources. It seems possible, that even a rather small, long-term change in water table could cause fluctuations in the cover among these plant community types, or that a drastic dry period that leads to critical desiccation of hollow *Sphagna* could shift *Sphagnum* communities to bare peat surfaces (Karofeld et al. 2015). On the other hand, drier conditions could also favor the more competitive hummock species (Robroek et al. 2007). Therefore, it seems crucial to find out, what triggers the transformation between vegetated surfaces, bare peat surfaces without *Sphagna* and open water pools, and include these processes into predictive ecosystem models.

Peatlands are currently considered as complex adaptive systems, which are resilient to environmental changes to some degree, but capable of rapid transformation to an alternative stable state at higher level of perturbation (Belyea and Baird, 2006; Dise, 2009; Heijmans et al. 2013). The spatial surface patterning typical for bog state emerges as a result of self-organizing process (Belyea and Baird, 2006). Model simulations suggest, that these microtopographic variations created by *Sphagnum* mosses increase resilience towards environmental perturbations both through the diversity of plant growth forms they support and by variation in physical properties between microforms (Turetsky et al., 2012). These features give support to the insurance hypothesis, which states that the diversity in species responses to environmental factors makes a plant community more resilient towards changing conditions (Yachi and Loreau, 1999; Gunderson, 2000; Loreau and de Mazancourt, 2013). In addition to species diversity, plant community diversity within an ecosystem has been shown to increase ecosystem stability during disturbances (Frank and McNaughton, 1991). The results of this study indicate a spatial (I, IV) and within season (III, IV) homeostasis of carbon sink in *Sphagnum* dominated surfaces, regulated by the diverse responses of the species and plant community types to environmental factors. However, from the point of view of predicting the effects of climate change on carbon sink of bog ecosystems, the essential question is, how the spatial variation in vegetation will affect their carbon sink over long periods of time. According to the reconstructed chamber fluxes during three growing seasons with slightly varying weather conditions, the proportions of plant community types of the ecosystem-level carbon sink changed (IV). This gives an implication, that the different responses of plant community types could provide a mechanism of resilience towards environmental variations even over longer timescales. However, to empirically confirm this, it is necessary to conduct long-term comparisons of sites with similar climate but different vegetation structure to include the effects of a wider variety of environmental conditions on the carbon sink.

Currently, long-term changes in carbon sink processes are widely studied using eddy covariance measurements (e.g. Helfter et al. 2013; Peichl et al. 2014; Lund et al. 2015). This methodology provides an excellent way to compare multiyear time series along wide climatic gradients, but it is not able to catch the components of the ecosystem-level CO_2 fluxes, which in this context are not only gross photosynthesis and respiration, but the contributions of different plant species and species groups to the ecosystem functioning. The results presented here suggest, that it is hard to say much at all about the stability of bog carbon sink without knowing, where the formed new plant material is located and from which species it consists of. Without accounting for the spatially varying vegetation, it may be difficult to fully understand the underlying reasons for the seasonal and interannual variations in bog carbon sink detected by the long-term eddy covariance measurements. Therefore, it seems important for the future studies to continue combining eddy covariance measurements with ecological measurements at different spatial scales as done here.

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