Species-specific temporal variation in photosynthesis as a moderator of peatland carbon sequestration

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Abstract. In boreal bogs plant species are low in number, but they differ greatly in their growth forms and photosynthetic properties. We assessed how ecosystem carbon (C) sink dynamics were affected by seasonal variations in photosynthetic rate and leaf area of different species. Photosynthetic properties (light-response

15 parameters), leaf area development and areal cover (abundance) of the species were used to quantify species-specific net and gross photosynthesis rates (P_N and P_G, respectively), which were summed to express ecosystem-level P_N and P_G. The ecosystem-level P_G was compared with a gross primary production (GPP) estimate derived from eddy covariance measurements (EC).

Species areal cover rather than differences in photosynthetic properties determined the species with the highest P_G

20 of both vascular plants and *Sphagna*. Species-specific contributions to the ecosystem P_G varied over the growing season, which in turn determined the seasonal variation in ecosystem P_G. The upscaled growing-season P_G estimate, 230 g C m^{-2}, agreed well with the GPP estimated by the EC, 243 g C m^{-2}.

Sphagna were superior to vascular plants in ecosystem-level P_G throughout the growing season but had a lower P_N. P_N results indicated that areal cover of the species together with their differences in photosynthetic parameters

25 shape the ecosystem-level C balance. Species with low areal cover but high photosynthetic efficiency appear to be potentially important for the ecosystem C sink. Results imply that functional diversity may increase the stability of C sink of boreal bogs.

Key-words

CO_2, ecosystem stability, insurance hypothesis, vascular plant, *Sphagnum*

1 Introduction

Northern peatlands are a globally important carbon (C) sink and storage of approximately 500 gigatons of C (Gorham, 1991; Yu et al., 2012) as a result of an imbalance between photosynthesis and decomposition. Boreal bogs are peatland ecosystems where photosynthetic productivity is limited by mid-summer dry periods, light

5   induced stress and, in particular, low nutrient availability (Frolking et al., 1998; Moore et al., 2002; Hájek et al., 2009). Due to the low rate of photosynthesis, the annual C sink of boreal bogs is weak and sensitive to changes; even a small change in the environmental conditions that regulate the C cycle can turn the ecosystem into a C source (Waddington and Roulet, 2000; Lund et al., 2012).

Boreal bogs are ecosystems with low species diversity but high diversity of growth forms due to the large

10   microtopographical variation and associated diversity of habitats along the water table gradient (Turetsky et al., 2012). Several studies (e.g. Weltzin et al., 2000; Moore et al., 2002; Leppälä et al., 2008) have reported that patterned bogs produce more biomass and have less variation in gross photosynthesis over the growing season than fens, which receive additional nutrients from the surrounding mineral soil and generally have more homogenous, sedge-dominated vegetation (Weltzin et al., 2000). Experimental studies have shown that bog plant

15   growth forms have differential responses to warming and water table level manipulation, which can help maintain the level of total ecosystem productivity under changing environmental conditions (Weltzin et al., 2000; Breeuwer et al., 2009). Short-term plant removal experiments have shown the differential roles of plant functional types for the peatland ecosystem net and gross carbon exchange (Ward et al., 2009; Kuiper et al., 2014; Robroek et al., 2015). Photosynthetic properties of bog plants are known to differ widely between species of the same functional

20   type (Small, 1972) and between phases of growing season (Korrensalo et al., unpublished data). So far, the role of species-level differences in temporal variation of bog ecosystem photosynthesis has not been studied.

Here, we aim to solve the linkage between the temporal pattern of bog carbon balance and the development of species-specific photosynthesis and leaf area. For this purpose, we quantified the contribution of different plant species to ecosystem-level photosynthesis over a growing season. As species differ in their photosynthesis

25   properties and the properties vary over the growing season we expect their importance for ecosystem carbon sequestration vary over the season. To reach our aim we estimate net and gross photosynthesis (P_N and P_G) for the whole study site based on the monthly species-level light response of photosynthesis and species-specific leaf area development over a growing season. To validate the upscaling approach, the sum of species-level P_G is compared to the gross primary production (GPP) derived from eddy covariance (EC) measurements at the study site.

30   ## 2 Methods

2.1 Study site

The study site (61° 50.179' N, 24° 10.145' E) is situated in an ombrotrophic bog, which is a part of the Siikaneva peatland complex in Southern Finland, located in the southern boreal vegetation zone. The annual temperature sum in the area (base temperature 5 °C) is 1318 degree days, annual rainfall is 707 mm and the average annual,

35   January and July temperatures are 4.2, -7.2 and 17.1 °C, respectively (30 year averages from Juupajoki-Hyytiälä weather station). The study site has a surface topography typical of raised bogs that varies from open water pools

and mud surfaces to hollows, lawns and hummocks. An eddy covariance (EC) tower is mounted on a raft in the center of the site.

The vegetation is mainly composed of 11 vascular plant and eight *Sphagnum* species (Table 1), the abundance of which varies markedly along the microtopographical gradient. A continuous *Sphagnum* carpet covers the surfaces from hummocks to hollows, although no *Sphagna* are present on the mud and water surfaces. *Sphagnum cuspidatum* and *S. majus* are dominant in hollows, *S. papillosum, S. rubellum, S. balticum* and *S. magellanicum* in lawns, and *S. fuscum*, *S. rubellum* and *S. angustifolium* cover the hummocks. Vascular plant species composition includes *Rhynchospora alba*, *Scheuchzeria palustris* and *Carex limosa* vegetation on mud and hollow surfaces, dwarf shrubs (*Andromeda polifolia*, *Vaccinium oxycoccos*) and *Eriophorum vaginatum* on lawn surfaces, and a thick shrub layer of *Calluna vulgaris*, *Betula nana*, *Empetrum nigrum*, and sedges *Eriophorum vaginatum* and *Trichophorum cespitosum* on hummocks.

2.2 Plant level photosynthesis measurements

To quantify the role of plant species in ecosystem-level photosynthesis over the growing season, we conducted net photosynthesis (P_N) measurements of 19 most common species at the study site. Over the growing season 2013, we measured CO_2 exchange of 3–5 samples of each species per month at three light levels with two open, flow-through gas exchange measurement devices (GFS-3000, Walz, Germany and LI-6400, LI-COR, USA). Samples were collected from several locations inside the study area a maximum of 30 hours prior to measurement; *Sphagna* were collected into small plastic bags and vascular plants into plastic boxes with an ample amount of roots and peat. These were kept moist until measured. Vascular plants were kept in shaded conditions and *Sphagna* were stored in the dark at 5 °C. The moss cuvettes were filled with *Sphagnum* capitula imitating their natural shoot density of each species in the field, resulting in a total number of 6–16 capitula inside a cuvette depending on the species. Before placing the capitula into the cuvettes, they were first wetted and then lightly dried of excess water with pulp paper. The cuvette was then placed under a photosynthetic photon flux density (PPFD) of approximately 1000 µmol m^{-2} s^{-1} to acclimate to light for 20 min. The measured light levels were 2000, 25 and 0 µmol m^{-2} s^{-1} for vascular plants and 2000, 35 and 0 µmol m^{-2} s^{-1} for *Sphagna*. Light levels were designed to both catch the linear, light-limited beginning and the light-saturated maximum of the light response curve without causing photoinhibitory reduction of photosynthetic rate (Laine et al., 2015). Vascular plants were measured with a standard cuvette, but for *Sphagna* we used a moss cuvette of our own construction with internal dimensions of 3 × 2 × 1 cm (Hájek et al., 2009) with a net bottom to allow airflow above and below the sample reducing the aerodynamic resistance. After changing the light level, we waited for the P_N to reach steady state before recording the CO_2 exchange. Air temperature was set to 20 °C, the flow rate to 600 µmol s^{-1} and the CO_2 concentration in the incoming air to 400 ppm. The relative humidity inside the cuvette was kept at 50% for the vascular plants and below 90% for the *Sphagna*. Net photosynthesis (P_N) of each sample at the three light levels was expressed per photosynthesizing leaf area (mg CO_2 m^{-2} (LA) h^{-1}), which was the leaf area inside the cuvette measured with a scanner for vascular plants and assumed to be the cuvette area for *Sphagna*. Two of the species, namely *Rhynchospora alba* and *Rubus chamaemorus*, were not yet of measurable size in May; *R. alba* had already mostly senesced in September and therefore were not measured in those months. Altogether, the data consisted of 720 measurements.

2.3 Net photosynthesis model

To obtain a species-wise flux reconstruction of P_N and P_G, we fitted a nonlinear mixed-effects model separately for each combination of species and month. Mixed-effects modeling approach allowed us to take into account the variation between samples, of which each was measured at three light levels. We used the hyperbolic light

5   saturation curve of P_N (Larcher, 2003) (Eq. (1)):

$$PN_{si} = R_s + \frac{Pmax_s\ PPFDsi}{k_s + PPFDsi} + e_{si} \tag{1}$$

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 parameters to be estimated are 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), and were assumed to be constant for each combination of species and month. e_{si} is the normally distributed residual

10   variance of the model with a mean of zero. Normally distributed random effect of the sample was included in one to three of the parameters depending on the model. The random effect structure was selected based on the Akaike information criterion (AIC) values of the alternative models with random effects included in a different combination of parameters. The random effects for the sub-models of each nonlinear model form a vector of random effect with non-zero correlation. Parameter values for the 87 P_N models are presented in Supplementary

15   information (Table S1). All models were fitted using the functions *nlme* of the R program package *nlme* (Pinheiro and Bates, 2000).

Sphagna were not measured in June nor were vascular plants in July due to technical failures of the devices so light response curves for these months were fitted by combining the data from the previous and following month for each species. In 5 of the 95 species–month combinations only one sample of the species had an acceptable

20   measurement. The parameters for these months were estimated separately without the mixed model structure (Supplementary information, Table S1).

2.4 Upscaling

To upscale species-level photosynthesis to the ecosystem level, the cover of each species was estimated within the study site with a systematic vegetation inventory conducted in July 2013. We estimated the relative cover of each

25   plant species in 121 0.071 m^2 plots (Table 1), which were arranged in a regular grid in a 30 m radius circle around the EC tower. To link net photosynthesis measured per leaf area to species cover, we converted species cover in the study area to leaf area index (LAI) using linear relationships between the two (Supplementary information, Table S2). Relationships were based on an inventory made in July 2012 over a 200 m radius circle where species cover was estimated and then all living aboveground vegetation was harvested from 65 0.071 m^2 inventory plots

30   for LAI measurements. The vascular plant LAI of these samples was measured in the laboratory.

We monitored LAI development of each vascular plant species over the growing season in 18 permanent sampling plots (0.36 m^2) that represented all the vegetation communities (n=3 in each vegetation community) along the microtopographical gradient in the study site. LAI was estimated every third week according to method described by Wilson et al., (2007). Continuous LAI development of each species was then estimated by fitting a log-linear

35   response to the observations. The shape of the log-linear LAI development was taken from this fitting and the

growing season LAI maximum for each species was taken from the converted average cover (Table 1). *Sphagnum* leaf area was assumed to stay constant over the whole growing season and was obtained using the average cover from the 2013 inventory.

Using the light response curves, estimated daily LAI, and half-hourly PPFD data from SMEAR II measurement
5 station (61° 50.845' N, 24° 17.686' E), we calculated P_N and P_G for each half hour period (mg CO_2 m^{-2} 30 min^{-1}) over the growing season (Julian days 121–273) with the species-wise and monthly light response curves. P_G was calculated with the same model without the R parameter, i.e. assuming that respiration is zero. Model predictions were not meaningfully changed by using marginal prediction, i.e. averaging the predictions over the distribution random effects (e.g. de-Miguel et al., 2012) and were therefore computed using the fixed part of the model only.
10 Growing season net and gross photosynthesis estimates – P_N and P_G – of the whole study site were calculated as a sum of the daily values.

2.5 Ecosystem-level CO_2 exchange measurements and estimation of gross primary production

To validate the measured levels of photosynthesis, the calculated values were compared with the GPP estimates obtained by EC measurements, which offer an independent estimate of the ecosystem-level CO_2 exchange
15 measured directly as turbulent vertical fluxes (e.g. Baldocchi, 2003; Aubinet et al., 2012). The EC system comprised 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 EC sensors were mounted on the mast 2.5 m above the peat surface. EddyUH software was used to process the raw data and produce the 30-min average fluxes of latent heat, sensible heat, and CO_2 (Mammarella et al., 2015). Standard EC data checks based on
20 the widely accepted quality criteria (e.g. Aubinet et al., 2012) were applied partly automatically by the software and partly manually; the EC data at friction velocity (u_*) less than 0.1 m s^{-1} were rejected. The resulting EC fluxes represent the exchange over a quasi-elliptical source area (footprint) located within about 30 m upwind of the EC mast, as suggested by footprint calculations using the model by Kormann and Meixner, (2001).

Net ecosystem exchange (NEE) measured by the EC method was then partitioned into ecosystem gross primary
25 production (GPP) and ecosystem respiration (R_{eco}). The daytime R_{eco} estimates were obtained from the Q_{10}-type temperature response curve fitted to the nighttime EC data, when respiration is the only component of NEE. Nighttime was defined as all the periods when the sun was lower than 5° below the horizon. Peat temperature at 5cm depth was used as the driver of R_{eco}, yielding the relationship Eq. (2):

$$R_{eco} = R_{ref} Q_{10}^{\left(\frac{T_p - T_{ref}}{10}\right)}$$
(2)

30 where T_p is the peat temperature at a 5cm depth (°C) and T_{ref} is the peat reference temperature of 12°C. Parameters to be estimated from the fit of the model (Eq. (2)) to all available nighttime data were R_{ref}, the reference respiration at the temperature of 12 °C, and Q_{10} is the temperature sensitivity coefficient.

The GPP estimate was calculated by subtracting the modeled R_{eco} from the EC-derived NEE. Finally, in order to gap-fill the GPP time series, a model using PPFD (from the SMEAR II measurement station) and the footprint-scale LAI was fitted to the data following Eq. (3):

$$GPP = \frac{Pmax\ PPFD}{k + PPFD}(LAI + b) \tag{3}$$

where GPP is expressed in mg (CO_2) m^{-2} h^{-1}. LAI is the modeled daily vascular leaf area index described above, while b represents the temporally constant contribution of the *Sphagnum* to total LAI.

3 Results

3.1 Cumulative growing season gross photosynthesis

Fitting the temperature response curve of respiration (R_{eco}, Eq. (2)) into the nighttime eddy covariance data yielded a reference respiration (R_{ref}) of 123 mg(CO_2) m^{-2} h^{-1} and Q_{10} of 3.5, which were then used for partitioning the eddy covariance net ecosystem exchange (NEE) into gross primary productivity (GPP) and respiration (R_{eco}). In the GPP model (Eq. (3)) fit, *Pmax* was 1721.8 mg CO_2 m^{-2} h^{-1}, k was 128.3 μmol CO_2 m^{-2} s^{-1} and b was 0.08. After gap-filling the GPP data (Eq. (3)), the resulting cumulative growing season GPP estimate was 243 g C m^{-2}.

Cumulative growing season gross photosynthesis (P_G) upscaled to the ecosystem level using the separate light response curves for species and months (Eq. (1)) was 230 g C m^{-2} (Julian days 121–273). Daily P_G estimates were higher than GPP values from the EC tower in spring, lower in the middle of the summer and quite similar in the autumn (Fig. 1).

Sphagna at the study site had higher cumulative growing season P_G value (138 g C m^{-2}) than vascular plants (92 g C m^{-2}). *Sphagna* had higher daily P_G than vascular plants in spring and autumn but were almost at the same level in the middle of the summer (Fig. 2). A small increase in *Sphagnum* photosynthesis was observed during May (Fig. 2 and 3b) due to increment of daily PPFD towards midsummer.

The three vascular plant species having the highest P_G in the ecosystem were *C. vulgaris*, *R. alba* and *A. polifolia*. *A. polifolia* was the most productive species in May and September, *R. alba* in June and July and *C. vulgaris* in August (Fig. 3a and 4a). With 13% cover altogether (Table 1), they formed 22% of the seasonal ecosystem P_G and 56% of the vascular plant P_G (Fig. 4). The three *Sphagnum* species with highest P_G at the ecosystem level were *S. papillosum*, *S. fuscum* and *S. rubellum* (Fig. 3b and 4b). As with all of the *Sphagnum* species, their P_G per ground area decreased steadily over the growing season (Fig. 3b). With 42% cover altogether (Table 1), they formed 40% of the seasonal ecosystem P_G, 67% of the P_G of *Sphagnum* mosses (Fig. 4).

3.2 Cumulative growing season net photosynthesis

The aboveground vegetation of the study site was a carbon sink of 77 g C m^{-2} over the growing season as estimated by P_N value upscaled to ecosystem level using the species- and month-wise light response curves. P_N results for *Sphagna* and vascular plants were reversed in comparison to P_G estimates; P_N of *Sphagna* was 20 g C m^{-2} and vascular P_N was 57 g C m^{-2}.

The same vascular plant species had the highest growing season P_N and P_G; *R. alba, C. vulgaris* and *A. polifolia* had the highest P_N estimates of 15.9 and 8 g C m^{-2}, respectively (Table 1). These three species made up 57% of the total vascular P_N and 42% of the whole ecosystem-level P_N.

S. fuscum, *S. papillosum*, and *S. majus* had the highest seasonal P_N of *Sphagnum* species 7.7 and 3 g C m^{-2}, respectively (Table 1). The P_N of these three species was 85% of the total *Sphagnum* P_N and 22% of the seasonal ecosystem P_N. Although having a one of the highest coverage and P_G, *S. rubellum* was not among the three most productive species in terms of P_N.

4 Discussion

4.1 Comparison of upscaled gross photosynthesis values with eddy covariance gross primary productivity estimates

Accounting for the differences in photosynthetic parameters between species and between phases of the growing season appeared to accurately estimate ecosystem P_G when upscaling species level measurements. *Sphagnum* mosses especially showed a large seasonal variation in their photosynthetic light response, which could be accounted for in this upscaling approach. The similarity of the P_G estimates calculated with species-wise and monthly light response curves and GPP estimates derived from eddy covariance measurements adds credibility to the methods used and indicates that the photosynthetic parameters measured under laboratory conditions are comparable with field measurements. Both methods carry their error sources. Annual CO_2 flux balances from eddy-covariance measurements are prone to significant systematic bias, sometimes in excess of 30%, but usually between 10–30% of the cumulative flux (e.g. Baldocchi, 2003; Rannik et al., 2006). Our P_G estimates include errors related to the LAI development measurements, visual species cover estimation, the conversion from cover to LAI, and the laboratory measurements of photosynthetic parameters. By taking into account the variation between samples in the 87 P_N models (Eq. (1)) we aimed at more accurate estimation of the light response parameters. Nevertheless, our ecosystem-level P_G estimate may contain bias caused by not accounting for the random effects of the 87 models in the upscaling procedure. The cumulative growing season P_G of 230 g C m^{-2} is very similar to the 205 g C m^{-2} obtained by Alm et al., (1999) at an ombrotrophic bog site under similar climatic conditions and comparable water levels but considerably lower than the 500 g C m^{-2} obtained by Moore et al., (2002) and Roulet et al., (2007) at a temperate ombrotrophic bog with much lower water table levels. While our value only covers the period from May until September, it falls just below the large range of annual GPP values (250 to 900 g C m^{-2}) measured with the EC method from seven northern peatland sites (Lund et al., 2010).

The shape of P_G and GPP development differed over the growing season, especially at the beginning of the summer, which is likely to be largely due to the constant temperature of 20 °C in our laboratory measurements (Fig. 1b). Our P_G values were higher than GPP in May when vascular plants had a high capacity to use low light levels (k) and *Sphagna* had high Pmax (Supplementary information, Table S1), but when temperatures in the field remained mostly below 20 °C and limited the measured GPP. In September, when *Sphagnum* Pmax values and k values of both vascular plants and *Sphagna* were lowest, P_G and GPP were similar despite the difference between air and laboratory temperatures. However, temperature might not explain the large midsummer GPP values in comparison to P_G. More accurate estimates of P_G would require accounting for the temperature dependence of photosynthesis. Mean annual temperature together with PPFD during growing season are the most important

factors explaining *Sphagnum* productivity at the global scale (Gunnarsson, 2005; Loisel et al., 2012), and the temperature optimum of *Sphagnum* photosynthesis is known to change over the growing season (Gaberščik and Martinčič, 1987). However, the temperature dependence and acclimatization of species-level photosynthesis in peatlands has been studied only with a few *Sphagnum* species (Gaberščik and Martinčič, 1987; Robroek et al.,

5   2007).

4.2 The contribution of plant species to ecosystem-level gross photosynthesis

Among both *Sphagna* and vascular plants, the species with the highest seasonal upscaled P_G (g C per m^{-2} of ground area) – and hence the most productive species at the ecosystem scale – were also the ones with the highest areal cover. Neither for vascular plants nor for *Sphagna* could this order be changed by the differences in photosynthetic

10   properties between species. At the ecosystem scale, *Sphagna* covering on average 63% of the ground area had higher upscaled daily P_G values for the whole summer than vascular plants covering only 24% despite the lower Pmax values of *Sphagna* (Supplementary information, Table S1). In ombrotrophic bogs, *Sphagna* are known to be the first group to start photosynthesizing in early spring (Moore et al., 2006), which was also evident at our site (Fig. 2). Combination of low Pmax values in July and September and high respiration rates in August and

15   September (Supplementary information, Table S2) resulted in an almost linear decrease in ecosystem-scale *Sphagnum* P_G over the growing season (Fig. 2).

Despite low Pmax values, *R. alba* was among the three vascular plant species with highest P_G at the ecosystem scale due to its high cover at the site (Table 1). It also had a very sharp but short-lived LAI and P_G peak at the end of June (Fig. 3a), which was largely the reason for the peak in vascular plant P_G (Fig. 2). Evergreen shrubs have

20   been observed to be the second group to start photosynthesizing after *Sphagna* in spring (Moore et al., 2006). Similarly, the vascular plants with highest P_G at our site at the ecosystem scale in May were the evergreen shrubs *A. polifolia* and *C. vulgaris*. The contributions of different species to total *Sphagnum* P_G did not differ over the growing season (Fig. 4). Based on these observations, phenology rather than differences in photosynthetic parameters among species seems to be the key factor in determining the species with highest P_G of a bog ecosystem.

25   **4.3 Ecosystem-level net photosynthesis**

The variation in photosynthetic properties changed the roles of the plant species in seasonal ecosystem-level carbon sink. Although *Sphagna* had more than twice the cover of vascular plants, seasonal P_N was much lower than vascular plants. The seasonal P_N of *Sphagnum* species was not in relation with their areal cover; for example the species with highest cover, *S. rubellum*, had a small seasonal P_N. *S. rubellum* has earlier found to have lower

30   light saturated photosynthesis and higher respiration than most of the other *Sphagnum* species (Supplementary information, Table S1, Korrensalo et al., unpublished data). The differences in photosynthetic parameters of *Sphagnum* species seem to become much more visible in ecosystem-level P_N than of vascular plant species, since the leaf area of *Sphagna* stays similar over the growing season. The vascular plants most important for the ecosystem-level P_N were the same as the species with greatest cover. However, *T. cespitosum* with only 1% of

35   areal cover made up 12% of the seasonal vascular P_N.

Our results indicate that in addition to areal cover of the species, differences in photosynthetic parameters between species shape the ecosystem-level carbon sink of a bog. Species with low areal cover may be important for the

ecosystem carbon sink because of their high photosynthetic efficiency. However, the P_N results have to be interpreted with care, since they contain the R parameter estimated based on respiration measurements done in 20 °C, which is higher than field temperature for most of the growing season. This general overestimation of respiration may be the reason behind slightly negative seasonal P_N of *S. balticum* (Table 1).

5   **4.4 The role of functional diversity for peatland carbon sink**

According to the insurance hypothesis, species diversity both enhances productivity and decreases the temporal variance of productivity of a plant community (Yachi and Loreau, 1999). This hypothesis has gained support from testing in several ecosystem types, especially in grasslands (Hector et al., 2010; Morin et al., 2014). Although this study did not directly test the hypothesis, our results also indicate that diversity of species decreased the temporal

10   variation of ecosystem-level P_G and could therefore decrease the variation of the ecosystem C sink. Vascular plant species of different phenology had the highest ecosystem-level photosynthesis at distinct phases of the growing season. In addition, *Sphagna* and evergreen shrubs formed two stable baselines of ecosystem P_G, which was further increased by the mid-summer P_G peak of *R. alba*. This suggests that the growing season P_G of our study site is not only more stable but is also larger than it would be with a more functionally homogenous assemblage of species.

15   Several studies have suggested that the C sink function of bogs is more stable over the growing season than that of fens, which have more homogenous and sedge dominated vegetation (Bubier et al., 1998; Leppälä et al., 2008). Hence, our results should be compared with the patterns of photosynthetic productivity of a peatland site with a more homogenous plant assemblage.

Based on small-scale experimental studies, bog species and growth forms are known to vary in terms of their

20   contribution to ecosystem productivity and to differ in their responses to manipulations of environmental conditions (Weltzin et al., 2000; Ward et al., 2009; Kuiper et al., 2014). In this study, the laboratory measurements of species photosynthetic parameters were for the first time upscaled to ecosystem level over a whole growing season and verified by the comparison with EC measurements. The diversity of vegetation was found to make the photosynthetic productivity of a boreal bog more stable over a growing season as seen by the differences within

25   species in the timing of their maximum P_G. Diversity in species responses to environmental factors is hypothesized to make a plant community more resilient towards changing conditions (Yachi and Loreau, 1999; Gunderson, 2000). In addition to species diversity, plant community diversity within an ecosystem has been shown to increase ecosystem stability during a severe drought in grasslands (Frank and McNaughton, 1991). In boreal bogs, *Sphagnum* mosses create microtopographic variations that – according to model simulations – increase resilience

30   towards environmental perturbations both through the diversity of growth forms it supports and by variation in physical properties between microforms (Turetsky et al., 2012). To find out about the effect of bog spatial heterogeneity on ecosystem resilience, studies extending over several growing seasons are needed. As demonstrated in an arctic sedge fen, the impact of extreme weather conditions on ecosystem C sink may occur with a lag of one growing season (Zona et al., 2014). Our study provides tools to empirically study the role of

35   species and community diversity at the ecosystem scale. The combination of laboratory measurements of photosynthetic parameters, phenological monitoring and EC measurements opens up the possibility of long-term and experimental ecosystem-level studies on the effect of functional diversity on the peatland ecosystem carbon sink. The long-term measurements would permit the inclusion of a wider range of environmental conditions. In

particular, the EC method would allow for a comparison of the effect of diversity at sites with different plant assemblages.

4.5 Conclusions

The areal cover of the species determined the species with the highest gross photosynthesis while phenology in leaf area and photosynthetic activity drove the variation in ecosystem-level gross photosynthesis. Ecosystem-level net photosynthesis was more of a combination of the differences in (i) photosynthetic parameters, which were important in *Sphagna*, (ii) phenology, which largely defined vascular productivity, and (iii) areal coverage, which acted in both vascular plants and *Sphagna*.

The different growth strategies of the plant species present at our study site appeared to increase the ecosystem-level photosynthesis and decrease it's variation within a growing season. We are looking forward for the future studies finding out, if the diversity of growth forms has the same stabilizing effect on the interannual variation of ecosystem-level photosynthesis.

Data availability

The data associated with the manuscript will be published in PANGAEA repository. Upon request, the data can also be obtained from the corresponding author.

Author contribution

EST formulated the idea. AK, TH and EST designed the measurements, which were done by AK and TH. AK, TH and EST were responsible for the primary photosynthesis data processing. Eddy covariance data collection and analysis was done by PA, JR, TV and IM. The mixed-effects models were developed by LM and AK. AK, PA and EST wrote the manuscript, which was commented by all the other authors.

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Conflict of Interest

The authors declare that they have no conflict of interest.

References

Alm, J., Schulman, L., Walden, J., Nykänen, H., Martikainen, P. J. and Silvola, J.: Carbon balance of a boreal bog during a year with an exceptionally dry summer, Ecology, 80(1), 161–174, doi:10.1890/0012-9658(1999)080[0161:CBOABB]2.0.CO;2, 1999.

Aubinet, M., Vesala, T. and Papale, D.: Eddy Covariance: A Practical Guide to Measurement and Data Analysis, Springer Netherlands, 2012.

Baldocchi, D. D.: Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future, Global Change Biology, 9(4), 479–492, 2003.

5 Breeuwer, A., Robroek, B. J. M., Limpens, J., Heijmans, M. M. P. D., Schouten, M. G. C. and Berendse, F.: Decreased summer water table depth affects peatland vegetation, Basic and Applied Ecology, 10(4), 330–339, doi:10.1016/j.baae.2008.05.005, 2009.

Bubier, J., Crill, P., Moore, T., Savage, K. and Varner, R.: Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex, Global Biogeochemical Cycles, 12, 703–714, doi: 10.1029/98GB02426,
10 1998.

Frank, D. A. and McNaughton, S. J.: Stability Increases with Diversity in Plant Communities: Empirical Evidence from the 1988 Yellowstone Drought, Oikos, 62(3), 360–362, doi:10.2307/3545501, 1991.

Frolking, S. E., Bubier, J. L., Moore, T. R., Ball, T., Bellisario, L. M., Bhardwaj, A., Carroll, P., Crill, P. M., Lafleur, P. M., McCaughey, J. H., Roulet, N. T., Suyker, A. E., Verma, S. B., Waddington, J. M. and Whiting, G.
15 J.: Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands, Global Biogeochemical Cycles, 12, 115–126, doi: 10.1029/97GB03367, 1998

Gaberščik, A. and Martinčič, A.: Seasonal dynamics of net photosynthesis and productivity of Sphagnum papillosum, Lindbergia, 105–110, 1987.

20 Gorham, E.: Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming, Ecological Applications, 1(2), 182, doi:10.2307/1941811, 1991.

Gunderson, L. H.: Ecological resilience–in theory and application, Annual review of ecology and systematics, 425–439, 2000.

Gunnarsson, U.: Global patterns of *Sphagnum* productivity, Journal of Bryology, 27(3), 269–279,
25 doi:10.1179/174328205X70029, 2005.

Hájek, T., Tuittila, E.-S., Ilomets, M. and Laiho, R.: Light responses of mire mosses - a key to survival after water-level drawdown?, Oikos, 118(2), 240–250, doi:10.1111/j.1600-0706.2008.16528.x, 2009.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. and Uotila, P. (eds.): Retkeilykasvio (Field Flora of Finland), Ed. 4. Finnish Museum of Natural History, Helsinki, 1998.

30 Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E. M., Bazeley-White, E., Weilenmann, M. and others: General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding, Ecology, 91(8), 2213–2220, 2010.

Kormann, R. and Meixner, F. X.: An analytical footprint model for non-neutral stratification, Boundary-Layer Meteorology, 99(2), 207–224, 2001.

Kuiper, J. J., Mooij, W. M., Bragazza, L. and Robroek, B. J.: Plant functional types define magnitude of drought response in peatland CO2 exchange, Ecology, 95(1), 123–131, 2014.

Laine, A. M., Ehonen, S., Juurola, E., Mehtätalo, L. and Tuittila, E.-S.: Performance of late succession species along a chronosequence: Environment does not exclude *Sphagnum fuscum* from the early stages of mire development, edited by M. Zobel, Journal of Vegetation Science, 26(2), 291–301, doi:10.1111/jvs.12231, 2015.

Laine, J.: The intricate beauty of "Sphagnum" mosses: a Finnish guide to identification, University of Helsinki Department of Forest Ecology, 2009.

Larcher, W.: Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups, Springer, 2003.

Leppälä, M., Kukko-Oja, K., Laine, J. and Tuittila, E.-S.: Seasonal dynamics of CO_2 exchange during primary succession of boreal mires as controlled by phenology of plants, Ecoscience, 15(4), 460–471, doi:10.2980/15-4-3142, 2008.

Loisel, J., Gallego-Sala, A. V. and Yu, Z.: Global-scale pattern of peatland *Sphagnum* growth driven by photosynthetically active radiation and growing season length, Biogeosciences, 9(7), 2737–2746, doi:10.5194/bg-9-2737-2012, 2012.

Lund, M., Lafleur, P. M., Roulet, N. T., Lindroth, A., Christensen, T. R., Aurela, M., Chojnicki, B. H., Flanagan, L. B., Humphreys, E. R., Laurila, T., Oechel, W. C., Olejnik, J., Rinne, J., Schubert, P. and Nilsson, M. B.: Variability in exchange of CO2 across 12 northern peatland and tundra sites: exchange of CO_2 in wetlands, Global Change Biology, 16(9), 2436-2448, doi:10.1111/j.1365-2486.2009.02104.x, 2009.

Lund, M., Christensen, T. R., Lindroth, A. and Schubert, P.: Effects of drought conditions on the carbon dioxide dynamics in a temperate peatland, Environmental Research Letters, 7(4), 45704, doi:10.1088/1748-9326/7/4/045704, 2012.

Mammarella, I., Peltola, O., Nordbo, A., Järvi, L. and Rannik, ü.: EddyUH: an advanced software package for eddy covariance flux calculation for a wide range of instrumentation and ecosystems, Atmospheric Measurement Techniques Discussions, 1–33, doi:10.5194/amt-2015-323, 2016.

de Miguel, S., Mehtätalo, L., Shater, Z., Kraid, B. and Pukkala, T.: Evaluating marginal and conditional predictions of taper models in the absence of calibration data, Canadian Journal of Forest research, 42(7), 1383-1394, doi: 10.1139/x2012-090, 2012.

Moore, T. R., Bubier, J. L., Frolking, S. E., Lafleur, P. M. and Roulet, N. T.: Plant biomass and production and CO2 exchange in an ombrotrophic bog, Journal of Ecology, 90(1), 25–36, doi:10.1046/j.0022-0477.2001.00633.x, 2002.

Moore, T. R., Lafleur, P. M., Poon, D. M. I., Heumann, B. W., Seaquist, J. W. and Roulet, N. T.: Spring photosynthesis in a cool temperate bog, Global Change Biology, 12(12), 2323–2335, doi:10.1111/j.1365-2486.2006.01247.x, 2006.

Morin, X., Fahse, L., de Mazancourt, C., Scherer-Lorenzen, M. and Bugmann, H.: Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics, edited by M. Rejmanek, Ecology Letters, 17(12), 1526–1535, doi:10.1111/ele.12357, 2014.

Pinheiro, J. and Bates, D.: Mixed-Effects Models in S and S-PLUS, Springer New York, 2000.

5   Rannik, Ü., Kolari, P., Vesala, T. and Hari, P.: Uncertainties in measurement and modelling of net ecosystem exchange of a forest, Agricultural and Forest Meteorology, 138(1–4), 244–257, doi:10.1016/j.agrformet.2006.05.007, 2006.

Robroek, B. J. M., Limpens, J., Breeuwer, A. and Schouten, M. G. C.: Effects of water level and temperature on performance of four Sphagnum mosses, Plant Ecology, 190(1), 97–107, doi:10.1007/s11258-006-9193-5, 2007.

10   Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R. and Bubier, J.: Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, Global Change Biology, 13(2), 397–411, doi:10.1111/j.1365-2486.2006.01292.x, 2007.

Rydin, H. and Jeglum, J. K.: The Biology of Peatlands, OUP Oxford, 2013.

Small, E.: Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat

15   bog plants, Canadian Journal of Botany, 50(11), 2227–2233, 1972.

Turetsky, M. R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A. D. and Tuittila, E.-S.: The resilience and functional role of moss in boreal and arctic ecosystems: Tansley review, New Phytologist, 196(1), 49–67, doi:10.1111/j.1469-8137.2012.04254.x, 2012.

Waddington, J. M. and Roulet, N. T.: Carbon balance of a boreal patterned peatland, Global Change Biology,

20   6(1), 87–97, doi:10.1046/j.1365-2486.2000.00283.x, 2000.

Ward, S. E., Bardgett, R. D., McNamara, N. P. and Ostle, N. J.: Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment, Functional Ecology, 23(2), 454–462, doi:10.1111/j.1365-2435.2008.01521.x, 2009.

Weltzin, J. F., Pastor, J., Harth, C., Bridgham, S. D., Updegraff, K. and Chapin, C. T.: Response of bog and fen

25   plant communities to warming and water-table manipulations, Ecology, 81(12), 3464–3478, doi:10.1890/0012-9658(2000)081[3464:ROBAFP]2.0.CO;2, 2000.

Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K. A., Farrell, E. P. and Tuittila, E.-S.: A high resolution green area index for modelling the seasonal dynamics of CO2 exchange in peatland vascular plant communities, Plant Ecology, 190(1), 37–51, doi:10.1007/s11258-006-9189-1, 2007.

30   Yachi, S. and Loreau, M.: Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis, Proceedings of the National Academy of Sciences, 96(4), 1463–1468, 1999.

Yu, Z. C.: Northern peatland carbon stocks and dynamics: a review, Biogeosciences, 9(10), 4071–4085, doi:10.5194/bg-9-4071-2012, 2012.

Zona, D., Lipson, D. A., Richards, J. H., Phoenix, G. K., Liljedahl, A. K., Ueyama, M., Sturtevant, C. S. and Oechel, W. C.: Delayed responses of an Arctic ecosystem to an extreme summer: impacts on net ecosystem exchange and vegetation functioning, Biogeosciences, 11(20), 5877–5888, doi:10.5194/bg-11-5877-2014, 2014.

Tables

Table 1 Average projection cover of the most common plant species at the study site, maximum leaf area index (LAI) values, and cumulative seasonal gross and net photosynthesis (P_G, P_N) of the species measured in this study. The cover values are based on a vegetation inventory conducted in 2013 at the study site within the 30 m radius footprint of the eddy covariance tower (N=121). LAI values of vascular plants are seasonal maxima of each species calculated by converting the cover values into LAI using species-wise linear relationships (Supplementary information, Table S2). *Sphagnum* LAI is assumed to stay similar over the growing season and is simply the coverage expressed as LAI. *Sphagnum* and vascular species nomenclature according to Laine et al., (2009) and Hämet-Ahti (1998), respectively.

Species	Cover mean ± S.E. (%)	LAI ($m^2\ m^{-2}$)	Seasonal P_G (g C m^{-2})	Seasonal P_N (g C m^{-2})
Vascular total	24.2 ± 1.9	0.29	92.2	57.3
Rhynchospora alba	6.9 ± 0.8	0.10	23.3	15.1
Andromeda polifolia	3.7 ± 0.4	0.03	14.4	8.4
Calluna vulgaris	2.8 ± 0.9	0.04	13.8	9.1
Rubus chamaemorus	2.5 ± 0.6	0.03	6.9	4.5
Eriophorum vaginatum	1.5 ± 0.3	0.02	6.0	3.8
Vaccinium oxycoccos	1.2 ± 0.2	0.01	5.3	3.2
Drosera rotundifolia	1.1 ± 0.1			
Empetrum nigrum	1.0 ± 0.5	0.01	2.3	1.2
Trichophorum cespitosum	1.0 ± 0.5	0.02	11.5	6.7
Drosera longifolia	0.8 ± 0.4			
Scheuchzeria palustris	0.8 ± 0.1	0.02	5.1	3.0
Betula nana	0.4 ± 0.2	0.004	1.1	0.5
Carex limosa	0.4 ± 0.1	0.005	2.4	1.8
Sphagnum total	63.8 ± 3.7	0.65	137.8	19.9
Sphagnum rubellum	18.3 ± 2.6	0.18	30.7	0.8
S. papillosum	12.9 ± 2.3	0.13	33.9	6.8
S. fuscum	11.0 ± 2.3	0.11	27.1	7.4
S. balticum	8.3 ± 1.5	0.08	15.7	-0.5
S. cuspidatum	4.8 ± 1.3	0.05	13.4	1.7
S. majus	4.7 ± 1.2	0.05	12.7	2.8
S. angustifolium	1.3 ± 0.5	0.01	3.6	0.6
S. lindbergii	0.8 ± 0.8			
S. magellanicum	0.3 ± 0.1	0.003	0.7	0.1
Other mosses and lichens				
Pleurozium schreberi	0.8 ± 0.5			
Mylia anomala	0.2 ± 0.1			
Cladina rangiferina	0.4 ± 0.2			

Figures
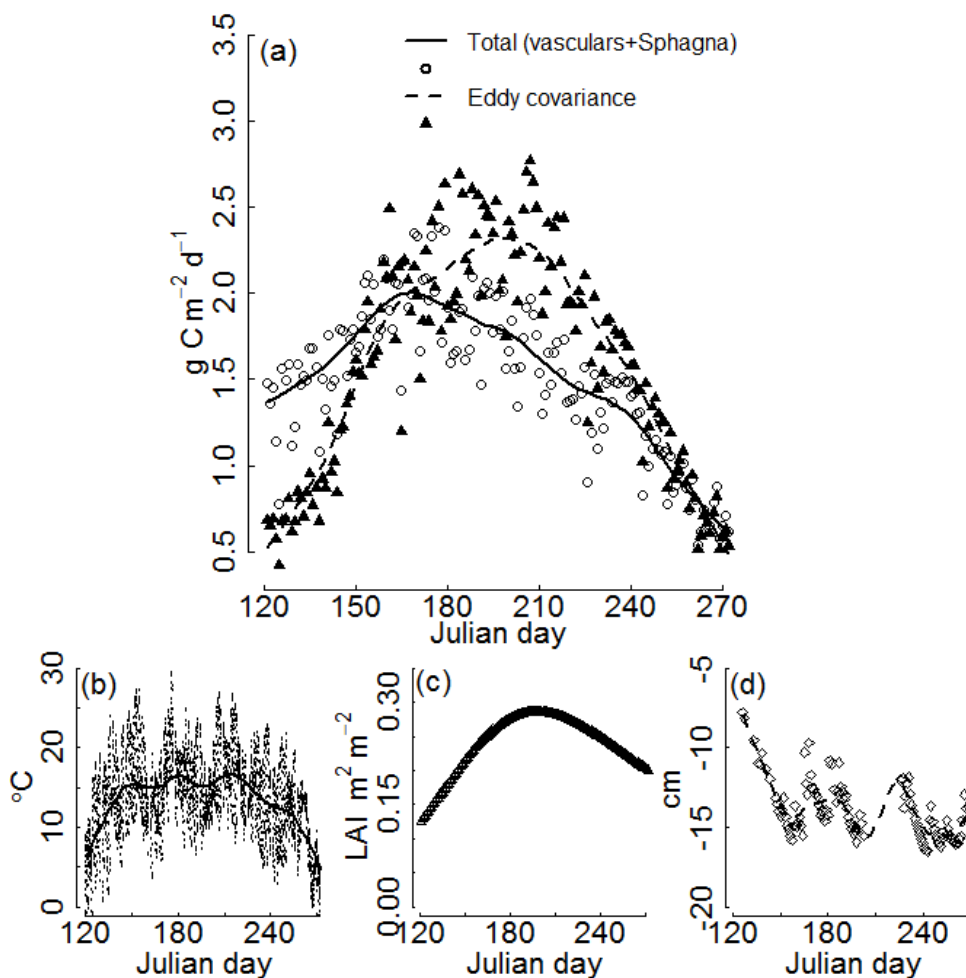
Figure 1: a) Comparison of daily ecosystem-level gross photosynthesis estimate of all plants with GPP estimates from the eddy covariance measurements. b) Mean hourly air temperature (Hyytiälä Forest Research Station 10 km from the study site, Finnish Meteorological Institute, 2016), c) sum of modeled vascular leaf area during the growing season 2013 and d) average daily lawn surface water table (WT) at the study site. Lines represent locally weighted scatterplot smoothing (Loess, smoothing parameter=0.25) curves. The temperature in laboratory photosynthesis measurements was kept constant at 20 °C during the whole growing season.
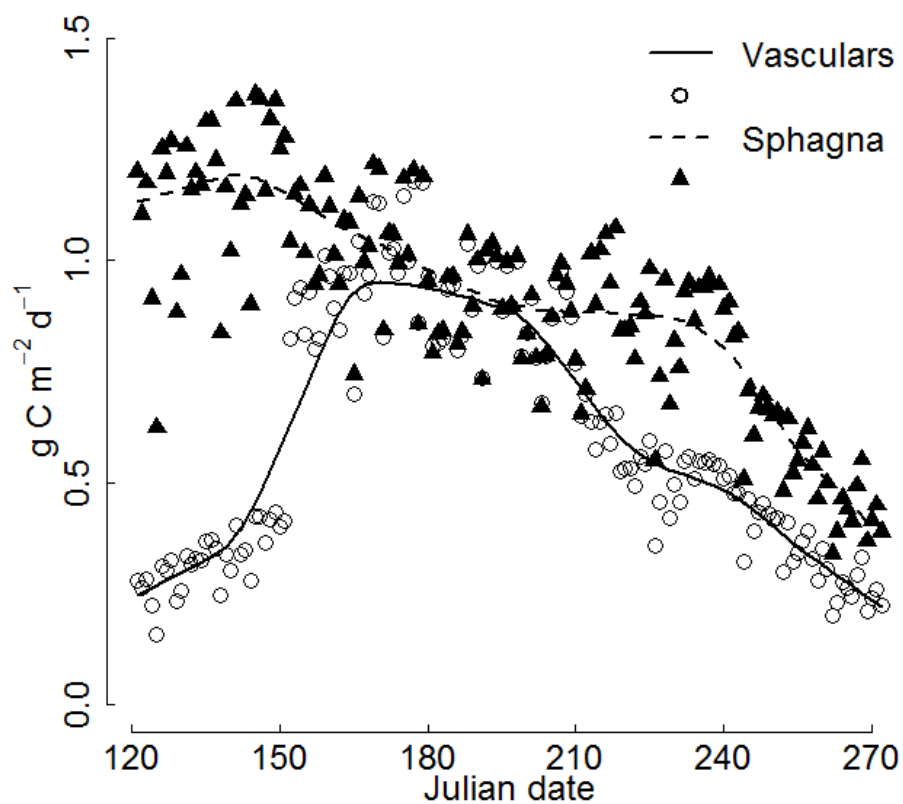
Figure 2: Daily ecosystem-level gross photosynthesis estimates (g C m^{-2} d^{-1}) of vascular plants and *Sphagna*.
Lines represent Loess averaging (smoothing parameter=0.25)
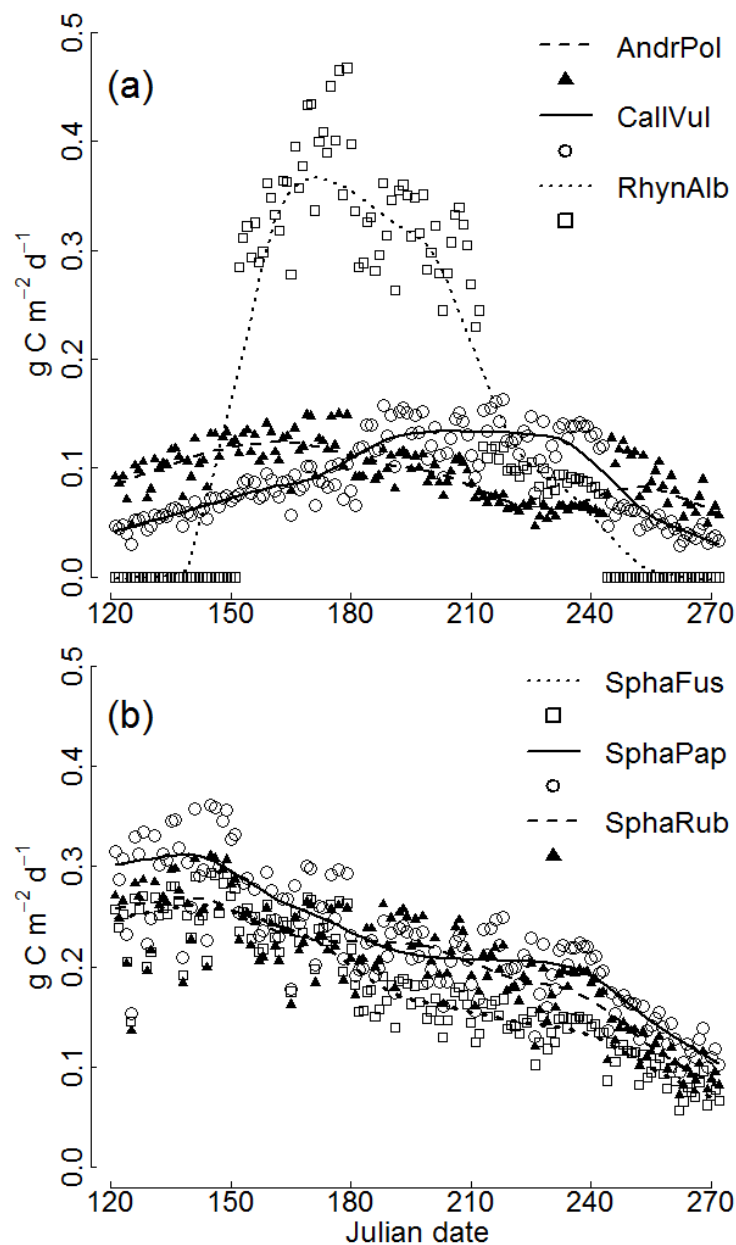
Figure 3: Ecosystem-level daily gross photosynthesis estimates (g C m^{-2} d^{-1}) of the three most productive a) vascular and b) *Sphagnum* species. Lines represent Loess averaging (smoothing parameter=0.25). The species cover within the study site (EC footprint) is given in Table 1. Abbreviations of the species' names are: AndrPol=*Andromeda polifolia*, CallVul=*Calluna vulgaris*, RhynAlb=*Rhynchospora alba*, SphaFusc=*Sphagnum fuscum*, SphaPapi=*Sphagnum papillosum*, SphaRube=*Sphagnum rubellum*.
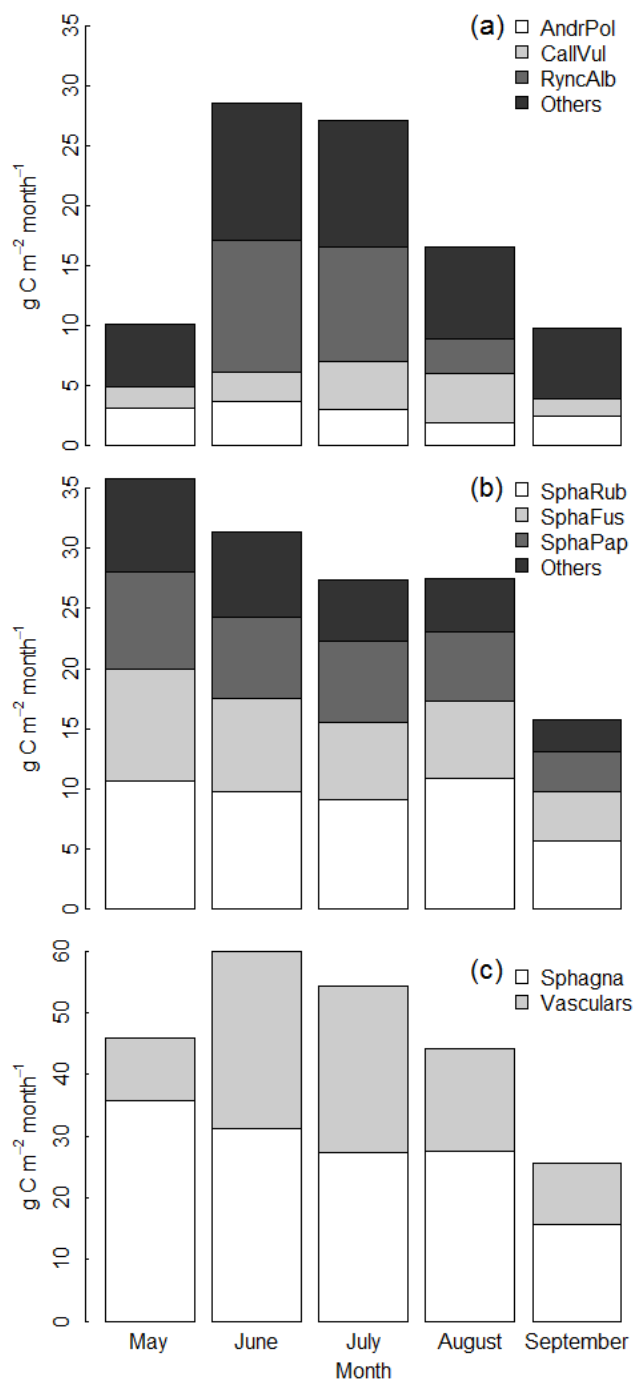
Figure 4: Species' proportions of monthly ecosystem-scale gross photosynthesis (P$_G$) of a) vascular plants, b) *Sphagnum* mosses and c) the contribution of those two groups to total monthly ecosystem scale P$_G$. For abbreviations of the species' names see Figure 3.