Dear Associate Editor Paul Stoy,

We are pleased to submit to Biogeosciences journal the revised version of the manuscript (bg-2016-265) **"**Species-specific temporal variation in photosynthesis as a moderator of peatland carbon sequestration**"** that was under review in the Biogeosciences Discussions forum. We found the comments of the Editor and the reviewers very useful in improving the manuscript. We have incorporated the comments to our manuscript and below, each of them are addressed separately. We would also like to thank for the interactive review process of the journal, since we found this conversational approach very fruitful.

The most substantial comment concerned the seasonal gap between eddy covariance-derived gross primary productivity estimate (GPP) and gross photosynthesis measurements upscaled to the ecosystem level (P_G). This issue was a matter of discussion when we were preparing our manuscript and we fully agree with the reviewers that it should be discussed more in depth, which now has been done. In addition to that we have modeled the temperature response of GPP to be able to calculate that for the growing season assuming similar temperature than during our laboratory measurements of photosynthesis. We believe this approach will further clarify the effect of temperature on the difference between GPP and P_G.

Associate Editor comments to the Author and our response:

Both referees provided insightful reviews and suggested that the manuscript is publishable in Biogeosciences after considering major suggested revisions. Please provide a detailed response to these comments and revise the manuscript accordingly and I will provide the referees the opportunity to decide if the revisions are sufficient to warrant publication in Biogeosciences.

> *We thank the Editor for offering us the change to resubmit our manuscript. We sincerely believe it was greatly improved after the revisions. Our detailed response to the specific comments is provided below.*

Answer to the comments by Anonymous Referee #1

General comments:

Korrensalo et al. presents one season of field measurements (eddy covariance), controlled laboratory experiments and modeled results of net and gross photosynthesis rates and/or gross primary production from a boreal bog in southern Finland and emphasizes the species specific contributions and the integration of plot to ecosystem scales. In particular, Korrensalo et al. differentiate between the vascular and bryophyte (moss) contributions, where the latter is oftentimes given a shadow-role in the literature of carbon and energy fluxes. Here, mosses are emphasized to play an important role in the overall wetland ecosystem-level flux. The two approaches in reaching the total system fluxes (eddy covariance and species-specific laboratory experiments) arrive at similar total seasonal fluxes. However, the figures suggest rather large seasonal differences (if I interpret them correctly). I would therefore appreciate increased attention to why that is. In fact, I think this difference is an interesting story (the story?) that emerged. Below are some thoughts that came to me as I reviewed.

> *We thank the reviewer for the time and effort used to our manuscript and for the thoughtful comments. We agree with the reviewer that the difference between the two methods should be discussed more clearly than it has been done before. We think the seasonal differences between the methods are mainly due to temperature. To clarify*

this, we have modeled the temperature response of GPP and simulated seasonal GPP in the same temperature than during our laboratory measurements. We hope the more detailed clarifications below explain the effect of temperature to the reader better than in the previous version of the manuscript.

Please define gross primary production (GPP), net (PN) and gross (PG) photosynthesis so reader who are not regularly working with these terms can follow your manuscript.

We have added the definitions of these terms on P2, L8-12 of the manuscript.

All figures: The graphs are presented with units, but there are no labels on the y-axises. Please include labels.

We have added the labels in addition to units.

Figure 1a: Why the discrepancy between the "total" and "eddy covariance" in Figure 1? It is unclear from the figure caption, but I think the two curves represent the laboratory derived estimate (total) and the eddy covariance estimate (eddy covariance) of the same variable? So why is the Total > EC in early season and EC > Total in later season?

First of all, the legend and caption of Figure 1 indeed needed some clarification. We have modified both of them so that it is easier to understand, which estimate came from which method.

After reading the comment we realized that our discussion on page 8, L18-40 about this matter is not clear enough. What we were trying to say there is that in the lab we measured potential photosynthesis of plants in their current conditions, i.e. under various light levels in 20°C and optimal moisture, but in the physiological state impacted by moisture conditions in the field. In the field gas exchange was measured under ambient conditions by the eddy covariance tower. The difference in spring between the two methods is likely due to the fact that both vascular plants and Sphagna had high photosynthetic potential (assessed as parameters k and Pmax that we measured in the lab), but were in the field limited by the low temperature. In the constant laboratory temperature of 20 °C this spring time potential was shown as high gross photosynthesis. In the end of the summer, a similar difference in temperature occurred between laboratory and field conditions. At this time, however, photosynthetic potential (again measured as k and Pmax) was low, and therefore the estimates of the two methods were similar. The higher mid-summer eddy covariance-derived GPP in comparison with laboratory measurements is something we cannot fully explain. The lack of vascular plant photosynthesis measurements in July cannot solely explain the deviation, which lasts for two months. We have clarified these points in the discussion on P8, L18-40.

Optimally we would have varied temperature as well as PAR while measuring photosynthesis of the 19 species in our study site to capture the photosynthesis response to T and PAR over the growing season but unfortunately that was not achievable. Varying two or more factors concurrently has been done in studies focusing on one or few species but in here our main focus was in differences between the species, therefore we were only able to cover potential in one temperature level. We added two sentences about this matter on P8, L20-23.

To point out more clearly the effect of temperature on the difference between the two methods used, we have added to the manuscript Eq. (4) describing the temperature response of eddy covariance-derived GPP. Using this model, we have simulated the seasonal GPP at constant temperature of 20 °C, same as in the laboratory measurements. This simulated GPP is now presented in the Fig. 1a and we hope the discussion in relation to that (P8, L18-40) clarifies the effect of temperature.

We thank you for the idea to point out in the manuscript that our results indicate that the ecosystem-level photosynthetic potential may peak at a different time than the ecosystem-level GPP (i.e. the "real" photosynthesis).

Figure 1d: What does "daily lawn surface water table" represent? I am confused by the word "lawn" (makes me think of a golf course). I suggest removing the smoothing curve and not include any line between dots unless the dots represents continuous daily measurements of water levels (there seems to be a larger data gap around Julian day 210).

Thank you for the comment! The term "lawn" is commonly used among peatland ecologists for a surface in peatland having an intermediate water table (in between hummocks and hollows). We as non-native speakers did not realize that this term could of course be quite confusing for someone not familiar with such use of that word, especially when it is only defined in the study site description. We added "intermediate peatland surface" to the figure legend.

We used available manual water table measurements to gap fill the larger data gap around Julian day 210. In addition, we removed the smoothing curve from the WT graph (Fig. 1d).

Figure 1b: I suggest plotting mean daily air temperature and then present the min and max daily air temperature as a shaded fill behind the mean daily air temperature line.

This is a good idea. We added daily minimum and maximum temperature in grey to the graph.

Figure 1 (figure caption): Why keeping the laboratory temperature at 20 C during the entire growing season if the mean daily air temperature only reached 20 C during a few days? What is the implication of this approach on the analyses? Can this partly explain the offsets in Fig 1a? We see a large drop in water tables in the field site following Julian day 120. The laboratory measurements tried to keep the temperature and moisture contents constant throughout the season, while the field measurements of air temperature and water table (ie moisture) present rather large variations. How does the limited moisture variability of the laboratory approach affect the overall conclusions stated by the authors? I am worried the authors may have over-stated their findings due to the complex relationships between water, air temperature and photosynthesis found in the field setting, especially considering the deviations in Figure 1a. In combination with Figure 2 (which I assume is based upon laboratory analyses, please clarify in figure text), it looks to me like the vascular plants may have been water-limited (too much water) in their photosynthesis in early season in the field (??)

It is a bit complicated that results and discussion are in separate chapters. Now in the results we show the different timing between the two estimates (laboratory and eddy covariance measurements) but we felt that we were fully allowed to discuss this only *later in the discussion section. We have added to Figure 1 seasonal GPP simulated at 20 °C, which we hope will more directly show the effect of temperature on the* P_G *and GPP. We also tried to work towards the discussion by adding daily temperature values as a sub-figure 1b below the comparison in Fig. 1a and by pointing out in Figure legend that lab measurements were conducted under constant 20°C temperature.*

We opened up a little the reasoning behind the choice to keep the temperature constant during the measurements in the section 2.2. (P3, L36-38). The core of our manuscript is to show the significance of seasonal and interspecific variations in potential photosynthetic light response for the ecosystem level processes. For this we needed to make the measured photosynthetic parameters comparable over the growing season. We could either choose constant temperature and moisture for all samples or measure temperature and moisture response of photosynthesis. Unfortunately, the latter was not possible due to the limitations of time. Temperature of 20 °C was selected simply because that is close to the room temperature and also realistic for the field conditions. Photosynthesis measurement devices have a limited capability of regulating the temperature and this temperature was possible to maintain in the laboratory. In our opinion the offsets in Fig. 1a are definitely a result of the constant temperature during the measurements. See also our revisions under your question related to Figure 1a, which intend to clarify the discussion section.

We do agree that the effect of moisture on Sphagnum photosynthesis should be better discussed in this manuscript, which has now been done on P9, L15-18. However, we think the constant moisture of the samples during the measurements is not as severe problem as it may seem. The physiological state of mosses is responding to prevailing moisture conditions in the field as shown by Hájek at al. (2009): Sphagnum samples showed physiological differences related to site conditions over two weeks after sampling. Also in this earlier study, samples collected from the field were wetted before measurements. We think the low vascular plant photosynthesis in spring (Fig. 2) is mainly due to low vascular leaf area during that period. However, suffering from excess moisture is an interesting further explanation for this.

Finally, we have clarified all of the figure captions to make it clear, which data is based on laboratory or field measurements.

Figure 3b. Why the decreasing response of the Sphagnum species throughout the study period? The total seasonal gross photosynthesis is similar between the two methods, but the distribution of those fluxes over the season is rather different between the two methods (laboratory versus eddy covariance). This observation is currently not discussed in the manuscript and I think this is the most interesting piece of the results. I would like to see the text in the results section to address the seasonal variability that we see in the figures. The results section is currently focusing on the total seasonal values, while the figures show some rather interesting seasonal variations (in time and between methods).

We think that the decreasing photosynthetic potential of Sphagna reflects the decreasing trend of water table over the growing season. Please see on P9, L15-18 the suggested additional sentences for the discussion to point this out.

We agree with the reviewer that our discussion regarding the differences between the two methods should be clarified. Please see section 4.1, which now has been modified to meet this demand.

The results regarding seasonal variations of photosynthesis have now been presented more in depth in section 3.1.

Please refer to specific figures in the discussion.

We went through the discussion section and added appropriate references to figures.

Page 7, Line 33: The sentence is odd. Remove "when" perhaps?

You are quite right, removing the word "when" clarified the sentence.

The discussion refers to time by naming the month. I suggest all graphs use months instead of Julian day.

We have now added the months as well.

The discussion or literature does not address the impact on hydrology to the photosynthesis, which, especially for mosses, can have a major impact.

Thank you for the good point, we should definitely address hydrology in discussion. We have added some discussion about this matter on P9, L15-18.

Answer to the comments by Anonymous Referee #2

General comments

Korrensalo et al. have produced a detailed study with species level in vivo CO2 exchange measurements, produced models of net (PN) and gross photosynthesis (PG) for the measured species, and compare the reconstructed PG's, extrapolated to the ecosystem, with ecosystem gross photosynthesis (GPP) derived from EC tower measurements. The comparison of such different materials are astonishingly good, and show the potential of the methods to contribute to ecosystems models. Not only limited to systems models, the results can be used to test ecological hypotheses as well. I agree with Referee #1 that one of the most interesting issues revealed is the seasonal gap (June-July) between the PG and GPP, GPP showing higher values. The Supplement contains the estimated parameter values of the species specific, monthly light response functions. Those values somewhat considered in the discussion, but could perhaps be more utilized to inspect the species the live aggregated in the specific microforms with largest changes in LAI and coverage over the season? The topic is highly relevant to BG, the manuscript offers good data, sound methods, and novel ideas, reaching to conclusions that nicely build on the previous work of the authors I am familiar with. There are some open questions, posed in the specific comments, that may need more work. The manuscript should be publishable after a moderate (major) revision. The issues raised by Referee #1 earlier have already been agreed by the authors in AC1.

We would like to thank the reviewer for the overall positive comment on our manuscript and for making the effort to read the comments of the previous reviewer as well as our interactive comment on that. We fully agree with the general comment that the values presented in the supplementary data should be discussed more in depth. This has been done in another manuscript, which was recently accepted to another journal, but has not yet been published. In addition, we are currently preparing a manuscript where the differences in CO_2 balance among vegetation communities *growing on different microforms are studied. We have addressed the comments by the reviewer separately below.*

Specific comments

1/26-27

The last inference on that "functional diversity may increase the stability of C sink of boreal bogs" comes fro thin air, bacause the concept "functional diversity" was not opened earlier in the abstract. Please modify so that the relationship between the vascular plants and Sphagna that were used in the analyses, and functional diversity becomes clear. Alternatively, use the earlier mentioned study units instead to avoid a hop from species or growth form level to more abstract functional diversity.

You are right, we clearly lost some essential information when trying to reduce the word count of the abstract. Please see the new version of the abstract, where functional diversity is better defined.

2/22-29

One apparent factor may be changes in shading of moss layer due to light extinction under devoloping LAI and coverage. Thus the interaction with the community structure may have imortance.

We understand this concern well, but, knowing the site very well, we do not think the shading of the moss layer plays a large role in Siikaneva site. We would like to point out the low maximum LAI at the site (Fig. 1c) and demonstrate the very sparse vascular layer with the photograph below. On P8, L4-7 we added a sentence: "Although the shading of the moss layer by vascular plants may figure as a potential error source of P_G upscaled with PPFD measured above the vegetation, it is not likely to be caused by the sparse cover of vascular plants at the site (Supplementary information, Fig. S3) with low seasonal maximum LAI (Fig. 1c)." We have also added the site photograph to the supplementary information.

4/17
This is the critical period when the GPP and PG most differ.

> *Thank you for bringing this up. We have now discussed the effect of lacking measurements on P8, L29-32.*

5/4
Were the irradiation data used logged by the EC? Was any attempts made to estimate light extinction below the changing coverage and LAI of the vasculars? If not, the irradiation seen by the Sphagna living under vasculars may be an overestimate. Could this be significant?

> *On P5, L9-10 it is told that the source of the light data is a measurement station close to the site. To clarify the height were light was measured, we also added word "above-canopy" to those lines. Because of the sparse vascular vegetation at our site, we did not attempt to estimate the difference in light level above and below the canopy. We have assumed that shading has only a negligible effect on the moss photosynthesis estimate, but of course, it would have been a good idea to quantify this. Please see also our answer to the comment regarding P2, L22-29 and the attached photograph where the sparseness of vascular vegetation is demonstrated.*

7/25
Alm et al (1999) reported on dry-out of mosses that did not recover in terms of photosynthetic capacity after the drought period. Comparison with this may not be valid in all communities?

> *This is true, and we have now noted that on P8, L12-13. In this study we did not compare the vegetation communities, so we would like to limit the comparison with the article by Alm et al. (1999) to the ecosystem-level estimate of cumulative growing season gross photosynthesis. However, in our future work we will concentrate on the differences among plant communities in CO_2 balance.*

7/31
Language: ...likely to be largely due to ... Uncertainty indicators twise?

> *Thank you for noticing the mistake. The sentence is now rewritten: "The shape of P_G and GPP development differed over the growing season, especially at the beginning of the summer, which is largely due to the constant temperature of 20 °C in our laboratory measurements (Fig. 1b)."*

7/37-38
Heterotropgic respiration is part of GPP and peaks in field just during the period with highest difference between Pg and GPP. Both WT and temperature control the oxic decomposition. WT is not in the respiration model (Eq. 2). Also perhaps shading of Sphagna. Any comments on these?

> *The residuals of Eq. (2) did not correlate with WT level, and we therefore did not include WT in the model. However, this can be partly due to the limited WT range of the nighttime data to which the respiration model was fitted. If requested by the reviewer, we are happy to add a sentence about this to the Method section.*
>
> *Above we visualized the low coverage of vascular plants with a photograph (found also in Supplementary information, Fig. S3). Because of this, we do not think that the shading of Sphagna plays a large role at our site.*

9/9

Do you refer here to the concept of functional diversity? I think you need be specific on what aspect of diversity is actually in focus here.

> *Thank you for pointing this out. We have now clarified the paragraph and hope the changes on P10, L11-15 make it sufficiently specific.*

9/13-14

The vegetation structure with sparse or dense field layer may also affect the photosynthesis dynamics due to differences in light extinction over the growing season. Any commnets on the basis of S1 table of light response parameters? Another issue is the solar declination that is latitude specific. That could affect the shaded moss assemblages?

> *We agree with the reviewer, that in many ecosystems shading of the mosses by vascular plants would indeed be an important issue, possible also having an effect of the seasonal changes in light response parameters of photosynthesis. We added above a photograph, which we think shows that our site is an exception to that because of the low coverage of vascular plants, which also can be seen as low maximum LAI (Fig. 1c).*

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 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 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, 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, i.e. the presence of plant groups with different seasonal timing and efficiency of photosynthesis, may increase the stability of C sink of boreal bogs.~~Results imply that functional diversity may increase the stability of C sink of boreal bogs.~~

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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 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). The rate by which CO_2 enters the ecosystem through photosynthesis of all of the individual plants together is the definition of gross primary production (GPP). When ecosystem respiration (R_{eco}) is subtracted from GPP, the result is net ecosystem exchange (NEE) of CO_2 between the ecosystem and the atmosphere. On the scale of individual plants, the same processes are called gross photosynthesis (P_G), plant respiration (R) and net photosynthesis (P_N), respectively (Chapin et al. 2011).

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Boreal bogs are ecosystems with low species diversity but high diversity of growth forms due to the large 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 growth forms have differential responses to warming and water table level manipulation, which can help to 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~~NEE and GPP~~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 type (Small, 1972) and between phases of growing season (Korrensalo et al., ~~unpublished data~~2016). 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 potential 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 photosynthetic~~sis~~ properties, and the properties vary over the growing season, we expect their importance for the ecosystem carbon sequestration also 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.

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, 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 flux~~)~~ 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. Only PPFD was varied during the measurements, while we kept a~~A~~ir temperature ~~was~~ at constant~~set to~~ 20 °C, the flow rate at~~to~~ 600 µmol s^{-1} and the CO_2 concentration in the incoming air at~~to~~ 400 ppm to be able to compare the seasonal changes in photosynthetic potential among species. The relative humidity inside the cuvette was kept at 50% for the vascular plants and below 90% for the *Sphagna*. The measured ~~Net~~

~~photosynthesis (~~P_N value~~)~~ 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 saturation curve of P_N (Larcher, 2003)~~ (Eq. (1))~~:

$$PN_{si} = R_s + \frac{Pmax_s\, PPFDsi}{k_s + PPFDsi} + e_{si} \qquad (1)$$

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 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 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. Then, ~~so~~ light response curves for these two 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 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 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 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 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, above-canopy PPFD data from SMEAR II measurement 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. Growing season ~~net and gross photosynthesis estimates —~~P_N and P_G~~—~~ of the whole study site were calculated as a sum of their 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 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 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 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 elevation angle was lower than 5°~~ below the horizon~~. Peat temperature at 5cm depth was used as the driver of R_{eco}, ~~yielding~~ in the following relationship~~ Eq. (2)~~:

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

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 night time NEE data were R_{ref}, the reference respiration at the temperature of 12 °C, and Q_{10}, ~~is~~ the temperature sensitivity coefficient.

The GPP estimates were~~as~~ calculated by subtracting the modeled R_{eco} from the EC-derived NEE values. 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)~~:

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

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.

Since laboratory measurements of P_G were conducted at a constant temperature of 20 °C and EC measurements at the air temperatures present at the field site, the temperature limitation of GPP was studied by fitting to the GPP data a model similar to Eq. (3), but complemented with a Gaussian type temperature response (Maanavilja et al. 2011):

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$$GPP = \frac{Pmax\ PPFD}{k + PPFD}(LAI + b)\exp\left(\frac{-0.5\,(T_a - T_{opt})^2}{T_{tol}^2}\right) \qquad (4)$$

where T_a is the air temperature, T_{opt} is the temperature optimum of GPP and T_{tol} is the temperature tolerance of GPP (deviation from the optimum at which GPP is 60% of the maximum). Using Eq. (4), GPP at 20°C and at ambient PAR and LAI was simulated for the study site over the growing season.

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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}. In the GPP model fit complemented with temperature response (Eq. (4)), *Pmax* was 1852 mg(CO_2) m^{-2} h^{-1}, k was 170.3 µmol m^{-2} s^{-1}, b was 0.1, T_{opt} was 22.6 °C and T_{tol} was 20.9 °C.

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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 and~~,~~ lower in the middle of the summer ~~and quite similar in the autumn~~ (Fig. 1a). The GPP simulated at 20 °C, the same temperature as during the laboratory measurements, was similar than upscaled P_G in spring but closer to the measured GPP in the middle of the summer (Fig. 1a). In the autumn, all of the three estimates showed rather similar levels (Fig. 1a).

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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. Otherwise, *Sphagnum* P_G decreased steadily over the growing season (Fig. 2). Seasonal changes in vascular P_G showed similar patterns than vascular LAI development, although the maximum P_G was reached slightly earlier in the season than maximum LAI (Fig. 1a, Ic and 2).

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. 2 and 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 15.1~~9~~, 9.1 and 8.4 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 7.4, 6.8~~.7~~ and 2.8~~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 production~~vity~~ 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~~EC measurements (Fig. 1a), 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

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balances from ~~eddy-covariance~~EC 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. Although the shading of the moss layer by vascular plants may figure as a potential error source of P_G, upscaled with PPFD measured above the vegetation, it is not likely to be caused by the sparse cover of vascular plants at the site (Supplementary information, Fig. S3) with low seasonal maximum LAI (Fig. 1c). ~~–~~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 where the exceptionally dry conditions during the measured season reduced photosynthetic capacity of many *Sphagnum* species. Our growing season P_G was 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. 1a~~b~~). Constant temperature allowed us to investigate the change in photosynthetic parameters of the species affected by the seasonal changes in moisture conditions in the field. Since the large number of species studied made it unachievable to measure temperature response of species-specific P_G, we instead chose to model the temperature dependence of EC-derived GPP (Eq. (4), Fig. 1a). Our upscaled P_G values were higher than GPP in May when vascular plants had a high capacity to use low light levels (low k value) and *Sphagna* had high Pmax (Fig. 1a) (Supplementary information, Table S1), but this was the case when temperatures in the field remained mostly below 20 °C and limited the measured GPP (Fig. 1b). The temperature limitation of measured GPP is demonstrated by the lower spring-time measured GPP in comparison with GPP simulated at 20 °C (Eq, (4), Fig. 1a). Both measured GPP and GPP simulated at 20 °C show higher levels than P_G in July and August (Fig. 1a), for which the reason remains partly unclear. Because the difference between GPP and P_G lasted for two months, the lack of vascular plant P_G measurements in July can only partly explain this midsummer deviation between the two methods. In September, when *Sphagnum* Pmax values and k values of both vascular plants and *Sphagna* were at their lowest, P_G, ~~and~~ measured GPP and GPP at 20 °C were all similar despite the difference between air and laboratory temperatures (Fig. 1a). ~~However, temperature might not explain the large midsummer GPP values in comparison to P_G.~~ According to our results peatland photosynthesis is temperature limited, especially in spring; *Sphagna* had a high photosynthetic potential due to favourable moisture conditions at that time (Fig. 2), but the low field temperatures limited ecosystem-level GPP (Fig. 1a and b). Temperature limitation of spring-time photosynthesis is well known for boreal forests (Tanja et al. 2003; Ensminger et al. 2004), as well as for bog *Sphagna* (Moore et al. 2006). ~~More accurate estimates of P_G would require accounting for the temperature dependence of photosynthesis.~~ Mean annual temperature together with PPFD during the growing season are the most important factors explaining *Sphagnum* productivity at the global scale (Gunnarsson, 2005; Loisel et al.,

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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., 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 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 September (Supplementary information, Table S2) resulted in an almost linear decrease in ecosystem-scale *Sphagnum* P_G over the growing season (Fig. 2). The seasonally decreasing *Sphagnum* P_G is likely to reflect the change in the moisture conditions. Water table depth, which, together with precipitation, is known to be the most important moderator of *Sphagnum* photosynthesis (Hayward and Clymo 1983; Backéus 1988; Lindholm 1990; Nijp et al. 2014), decreased at the study site over the growing season (Fig. 1d).

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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), occurring slightly earlier in the season than maximum vascular LAI (Fig. 1c). Evergreen shrubs have been observed to be the second group to start photosynthesizing after *Sphagna* in spring (Moore et al., 2006). Similarly, the vascular plants with highest upscaled P_G ~~at our site at the ecosystem scale~~ in May were the evergreen shrubs *A. polifolia* and *C. vulgaris* (Fig. 3a). The contributions of different species to total *Sphagnum* P_G did not differ over the growing season (Fig. 4). Based on these observations, phenology and areal cover, 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.

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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 (Table 1). 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 (Table 1). *S. rubellum* has earlier found to have lower light saturated photosynthesis and higher respiration than most of the other *Sphagnum* species (Supplementary information, Table S1, Korrensalo et al., ~~unpublished data~~2016). 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 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 at~~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).

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; Cardinale et al. 2011; Morin et al., 2014). In addition to species and genotype diversity (Hughes et al. 2008), the functional diversity, i.e. the presence of species and plant functional types with different physiology, morphology, resource requirements, seasonal growth patterns and life history may increase the productivity of an ecosystem (Tilman et al. 1997; Cadotte et al. 2008). Although this study did not directly test the insurance hypothesis, our results also indicate that functional diversity, especially in regard of differences in phenology and seasonal changes in photosynthetic parameters,~~ of species~~ decreased the temporal 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 (Fig. 3a). 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 the sedge *R. alba* (Fig. 3 a and b). Especially ecosystem-level *Sphagnum* P_G was modified by the seasonal decrease in photosynthetic potential (Supplementary information, Table S1). This suggests that the growing season P_G of our study site is not only more stable, but it is also larger than it would be with a more functionally homogenous assemblage of species. 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.

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Based on small-scale experimental studies, bog species and growth forms are known to vary in terms of their 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 species in the timing of their maximum P_G (Fig. 3a and b). 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 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 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. In spring, potential ecosystem-level gross photosynthesis was much higher than measured gross primary production, which appeared to be due to temperature limitation of 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.

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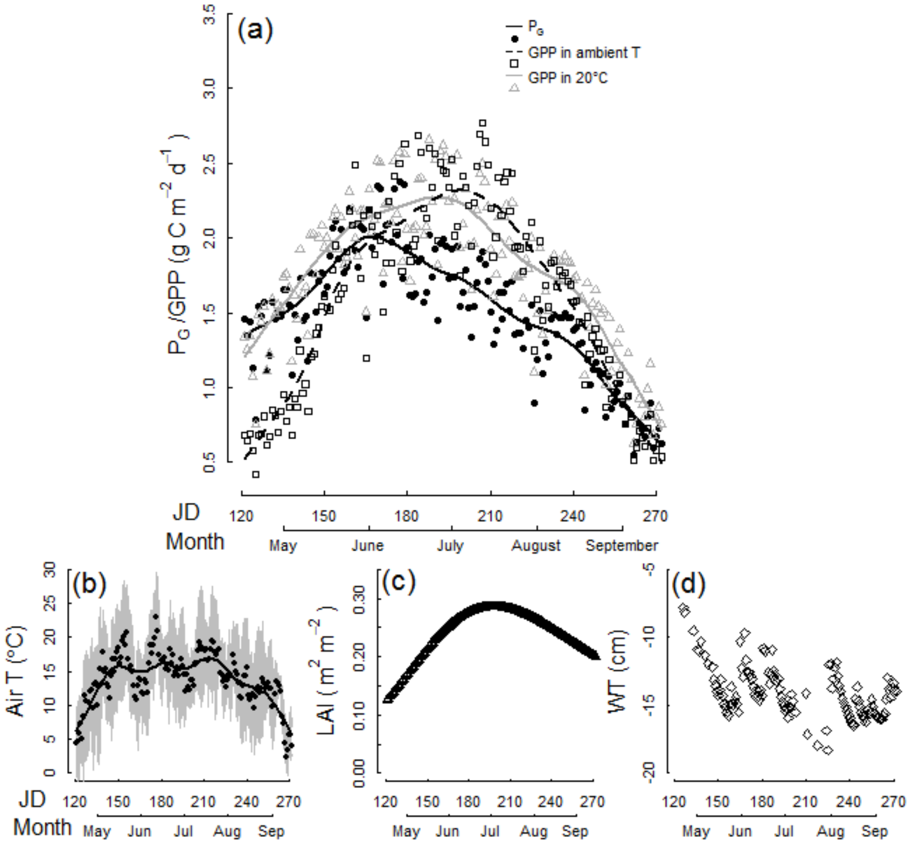
Tables

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


(a)
P_G
GPP in ambient T
GPP in 20°C
P_G /GPP (g C m^{-2} d^{-1})
0.5
1.0
1.5
2.0
2.5
3.0
3.5
JD
120
150
180
210
240
270
Month
May
June
July
August
September
(b)
Air T (°C)
0
5
10
15
20
25
30
JD
120
150
180
210
240
270
Month
May
Jun
Jul
Aug
Sep
(c)
LAI (m^2 m^{-2})
0.00
0.10
0.20
0.30
120
150
180
210
240
270
May
Jun
Jul
Aug
Sep
(d)
WT (cm)
-5
-10
-15
-20
120
150
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210
240
270
May
Jun
Jul
Aug
Sep

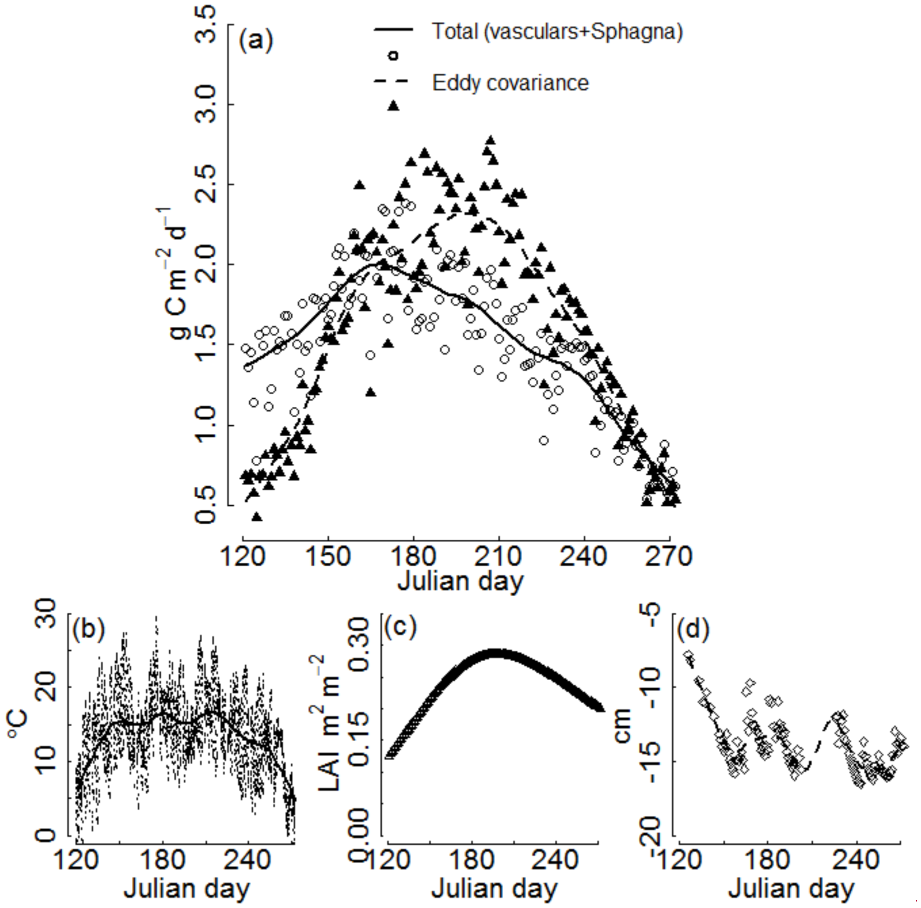

Figure 1: a) Comparison of total daily ecosystem-level gross photosynthesis estimate of all plants (P_G) derived from laboratory measurements with GPP estimates derived directly from the eddy covariance measurements and with GPP simulated at constant temperature of 20°C. The temperature in laboratory photosynthesis measurements was kept constant at 20 °C during the whole growing season. b) Daily m~~M~~ean air temperature (in black) and daily temperature variation (in grey fill) ~~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 (i.e. intermediate) 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.~~

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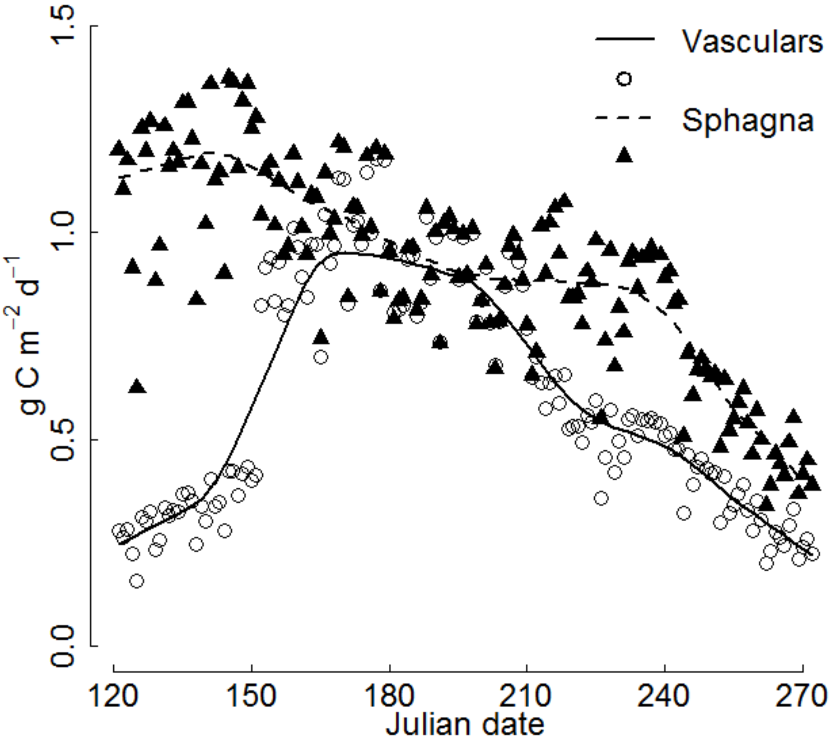

Vasculars
○
Sphagna
▲
g C m^{-2} d^{-1}
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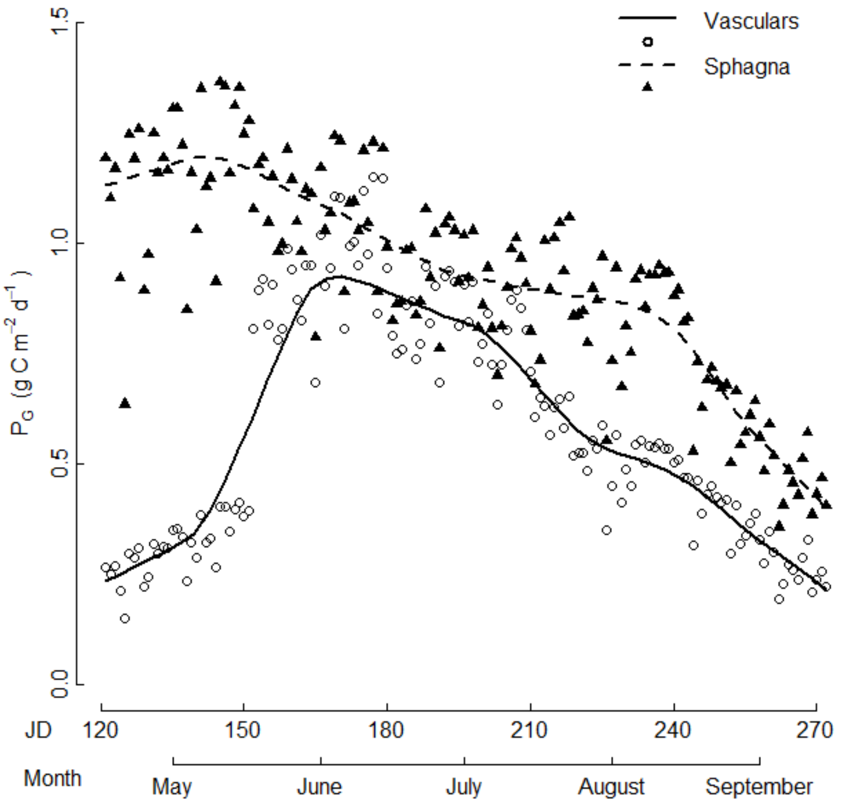
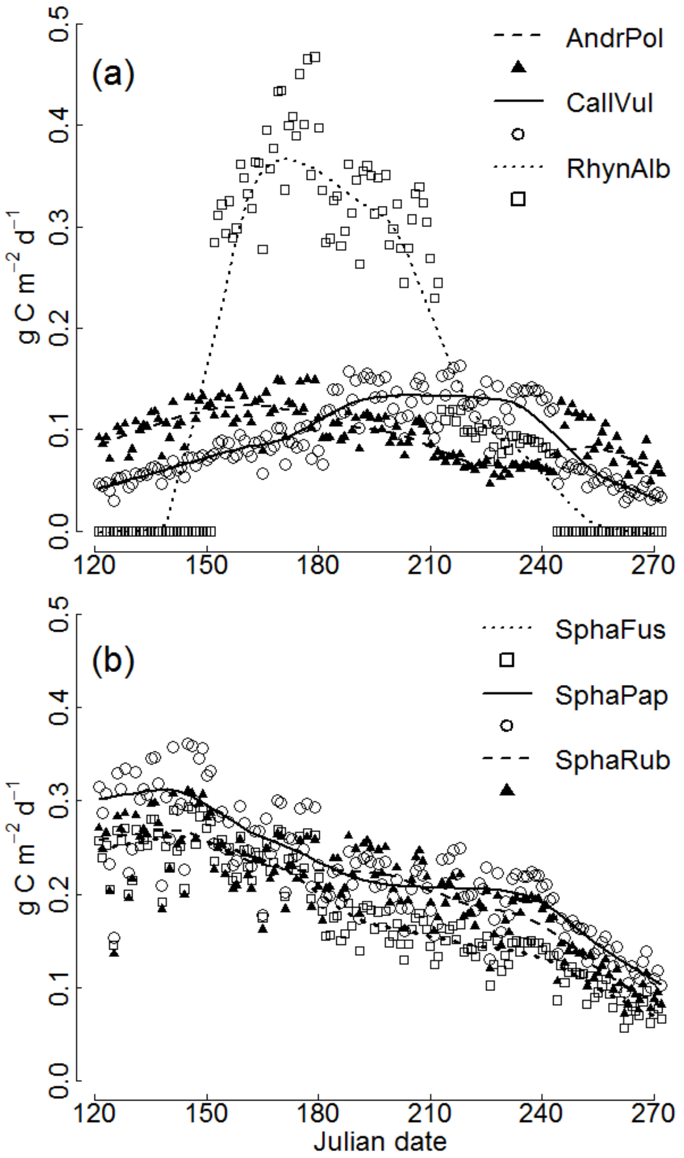


Figure 2: Daily gross photosynthesis estimates (g C m^{-2} d^{-1}) of vascular plants and *Sphagna* upscaled to ecosystem-level using the species-specific, monthly light response curves derived from laboratory measurements ~~gross photosynthesis estimates (g C m^{-2} d^{-1}) of vascular plants and *Sphagna*~~. Lines represent Loess averaging (smoothing parameter=0.25)


(a)
AndrPol
CallVul
RhynAlb
g C m^-2 d^-1
0.0
0.1
0.2
0.3
0.4
0.5
120
150
180
210
240
270
(b)
SphaFus
SphaPap
SphaRub
g C m^-2 d^-1
0.0
0.1
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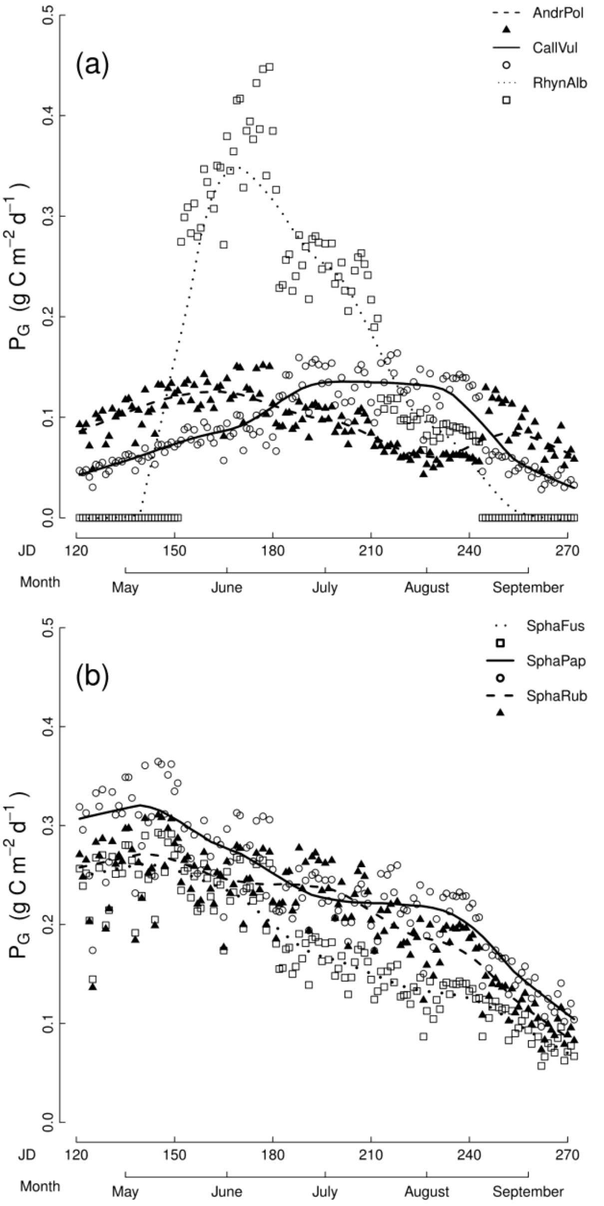
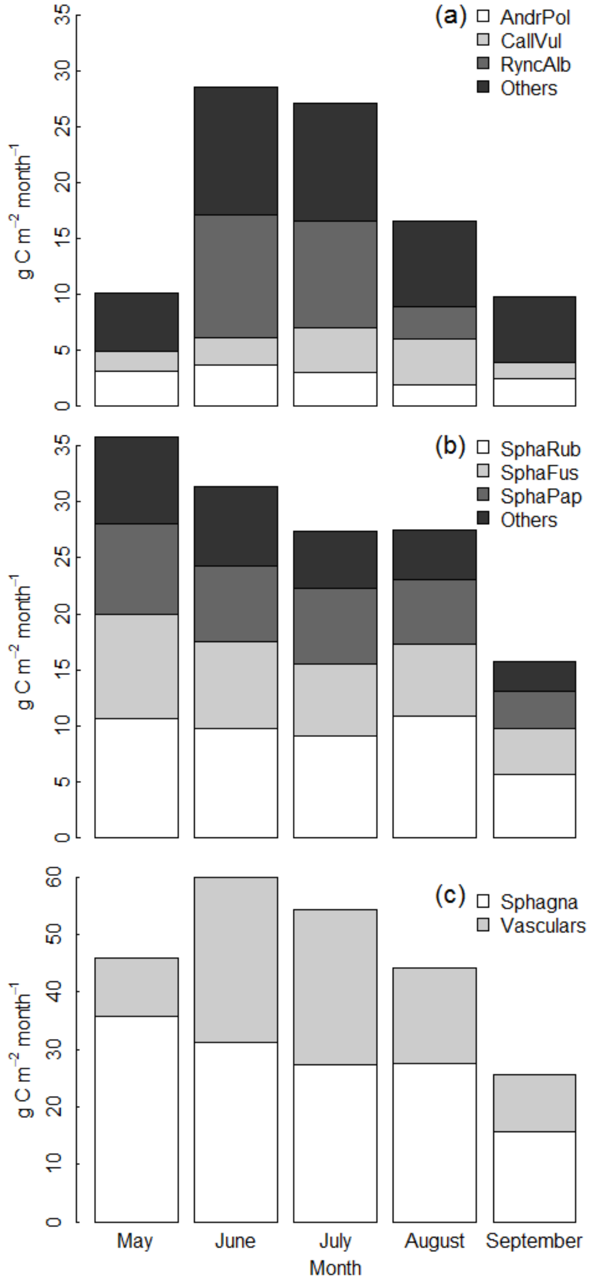


Figure 3: ~~Ecosystem-level D~~daily gross photosynthesis estimates (g C m^{-2} d^{-1}) of the three most productive a) vascular and b) *Sphagnum* species upscaled to ecosystem-level using the species-specific, monthly light response curves derived from laboratory measurements. Lines represent Loess 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*.


(a)
AndrPol
CallVul
RyncAlb
Others
(b)
SphaRub
SphaFus
SphaPap
Others
(c)
Sphagna
Vasculars
g C m^{-2} month^{-1}
0
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May
June
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Month

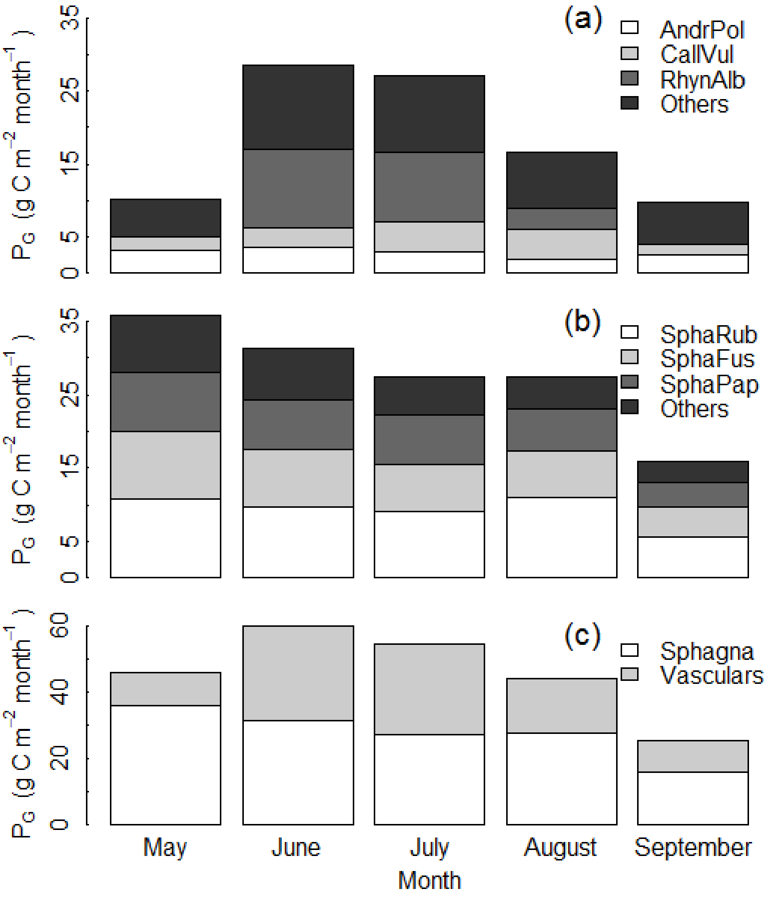

Figure 4: Species' proportions of monthly ecosystem-scale gross photosynthesis (P_G) of a) vascular plants, b) *Sphagnum* mosses and c) the contribution of those two groups to total monthly ecosystem scale P_G.- Ecosystem-level P_G was calculated using the species-specific, monthly light response curves derived from laboratory measurements. For abbreviations of the species' names see Figure 3.

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