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Interactive comment on "Modelling the habitat preference of two key *Sphagnum* species in a poor fen as controlled by capitulum water retention" *by* Jinnan Gong et al.

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We are grateful to two anonymous reviewers that had put a lot of effort to improve our manuscript. Accordingly, we did our best to follow the suggestions. In those few cases where we disagreed or were not able to do that, we explain why. Please find our responses to each comment below.

Referee 1

General comments

1. Please provide a list of abbreviations! It was hard work trying to follow the methods

and results without one.

R: We now provide a list of symbols and abbreviations as suggested (new Table 1).

2. A discussion of some literature very relevant to this study, exploring the same ideas though without using a formal model, is missing: (Titus, et al. 1983, Titus and Wagner 1984). One of the interesting results of these studies is that there is a seasonal dynamic in the water-content response of photosynthesis. This may be very relevant to your model, if the model is sensitive to these 0water-stress0 responses. (Rydin 1986, 1993a, b, 1997, Rydin and Barber 2001) And more: check the publications by Hakan Rydin, he has been working on competition between Sphagna for along time.

Another important source, which, however, has not yet been fully published (but a relevant summary with numbers to compare yours against is available in the thesis summary: http://www.diva-portal.org/smash/get/diva2:1282760/FULLTEXT01.pdf), is the recent PhD thesis by Fia Bengtsson (Uppsala), in particular chapters 4 and 5. This paper (Hájek 2014) is also very relevant, among other things for some methodological issues.

R: Thank you for pointing out missing references to relevant literature. Indeed we were missing quite a number of classics and new ones that are now used to deepen Intro and Discussion. Originally, we presented model development and empirical measurements in two separate manuscripts; In the merging we had accidentally lost a big part of references but now they are included again.

3. Model structure: The abstract promises a very wide scope (0dynamic feedback between plant community structure and the environment0), but there is no feedback from the species composition (Modules 1 and 2) on the hydrology (module 3) in the model. Therefore: how does this model really address the feedback you mention?

R: Our model lacks the feedback to hydrology as the referee pointed out. We now removed the parts of Abstract and Introduction that give reader a reason to expect otherwise.

In the discussion, you could also be more explicit about the implications of the species composition on biogeochemical processes, see e.g. (Bengtsson, et al. 2016, Cornelissen, et al. 2007). Alternatively, do not suggest this focus on feedbacks in the abstract and introduction.

R: In the discussion we now describe the implications of the species composition on biogeochemical processes via their traits.

The vertical water transport is implemented in detail, but in the detailed modules 1 and 2 there does not seem to be horizontal water exchange between neighbours, although this may play an important role in maintaining Sf in hummocks, supported by the water held in Sm (Rydin 1985 ; Rydin and McDonald 1985 ; Robroek et al. 2007a). In your experiments, basing the drying speed on single capitula, the capitulum density, i.e. facilitation between neighbours in retaining water, could not affect the drying speed, thereby possibly missing part of the difference between the lawn and the hummock species (i.e. under-estimating the difference).

R: Our model also lacks horizontal water transport that has found to allow individuals of lawn species to be present in dried habitats. The pattern is interesting and may play a role in speeding up the spreading of lawn species when conditions become wetter. Unfortunately, in this first attempt to mechanistically model Sphagnum community dynamics we were only able focus getting the general distribution pattern realistic and leave perfection for later. In this stage essential data for parameter values not yet exist for quantifying horizontal water transport among neighboring individuals such as hydraulic conductivity. The model can be improved further when the parameterization could be supported by experimental studies.

In our drying experiment a layer of capitula, with same density as in field was placed on the cuvette, therefor the neighbours do to some extend affect the drying process, yet, the stems are lacking and it surely does not truly reflect the field conditions.

Speed as such was not yet our focus but the response of photosynthesis to water content, and we do think our approach catches the between species differences in this process.

4. Model parameters / results L487 & L520-522 Please also explain why Sf has an advantage over Sm in the lawns. Why does Sf have faster growth? This is not clear to me at all. According to your photosynthesis measurements, Sf has a lower Amax (which seems strange, usually indeed lawn species have higher rates) and the same respiration rate as Sm. Therefore, at high water content and high light, Sm and not Sf should have a benefit in terms of NSC production. As the conversion from NSC to biomass is the same for both species, the only way to explain the higher length growth of Sf in the lawn environment is the higher Hspc (higher height growth per unit biomass). Correct?

R: The explanation suggested by the Refree 1 is correct. We have now written out that the bigger height growth of S. fallax per biomass production rate is because of its looser structure. Like us, Bengtson et al. (2016) measured similar photosynthesis rate for the two species, but clearly higher height growth for S. fallax. (Bengtsson, F., Granath, G., & Rydin, H. (2016). Photosynthesis, growth, and decay traits in Sphagnum – a multispecies comparison. Ecology and Evolution, 6(10), 3325-3341.)

5. Ecophysiological measurements / model parameters: L1017 You state here that A tended to increase with time and that it peaked at water contents below the maximum, as indeed shown by the theoretical figure 1B, but not by the measured curves in Fig 2C. Indeed I would have expected such a peak. Can you explain the absence of diffusion limitation in your experiment? Good ventilation..? Is it realistic to measure one capitulum in isolation? Lots of air all around it compared to a capitulum immerged in a (wet) Sphagnum mat: : : Consequently, also, how homogenously will the capitula have dried out in the GFS compared to in a Sphagnum mat?

R: The expected peak was actually there, see redrawn figure B2C. For some reason (not clear to us anymore) we had earlier cut the X-axis (capitulum water content) shorter in panel C than in the other panels.

We did not measure single capitulum in isolation but a layer of capitula was placed on cuvette (see Fig. B1A). We rewrote the related methods section to make them clearer.

It has been shown that the speed of drying during gas exchange measurements can strongly affect the conclusions about optimum water content and water compensation point (Hájek 2014). Under quick drying, as in your experiments, it seems typical to get the type of curves you present. However, under slower drying, as would be typical in the field, the optimum WC would be lower and the depression at high WC stronger. In particular the high compensation point you found, at water contents of up to 600%, seems to be a typical artefact of such fast drying, related to the inhomogenous drying within the capitula.

R: In slow drying (Hájek 2014), environmental vapor pressure remains constant and evaportation rate decreases with time. In such experimental conditions water movement could be sufficiently rebalanced between internal and external tissues, so that the water potential becomes equilibrized among different parts of capitulum. However, in field conditions, evaporation demand could be more strongly driven by radiation than vapor pressure deficit, particularly during a hot clear summer day. Thus, it could be much faster than in a dessication chamber and consequently, the water content may not rebalance fast enough to reach equalibrium. Moreover, the branch leaves in the outer part of capitula could be more photosynthetically active than the internal core parts. As the drying is heterogenous, photosynthesis rate could be largely reduced just by the drying of outer tissues, even though the internal core part could be wetter. This is also supported by our measurement, which showed a higher compensation point for photosynthesis than that from the slow drying experiment (Hájek 2014). Therefore, we believe the fast drying could be a better imitation of field processes.

Also, a field water content of 1470 and 809% water per dry mass seems extremely low for Sphagnum in general and for these species. For S magellanicum I have seen max WC values reported between 2000 and 3000%, and for S. fallax of about 1500% (or 1100%, equivalent to 12 gFM/gDM (Titus, et al. 1983)). You even state yourself (Line270) that it is known that Wmax is around 25-30 g g-1. So I do not understand why you started you experiment at 14,7 and 8,09 g g-1 or where you use these values, as opposed to the values in L277.

R: The reason for the low field water contents compared to earlier published values lies in the measurement method we used (as explained in supplementary material). We measured the capitulum and stem section WC separately and allowed the external water on Sphagnum surfaces to dry out before weighing the fresh weight. We started the experiment on the water content levels where excess water does not limit photosynthesis. This optimal WC is now shown in redrawn Figure B2C, which now starts already in a higher water content. We have now tried to explain this better in Methods.

If the light curves took up to 120 minutes to complete (why? That is a very long time especially if you only measured at 4 light levels, which seems very little to determine a reliable curve: : :), and drying down to the compensation point took 120-180 minutes, this implies that during the light response measurements you measured a combination of reduced light and reduced water content, so that the curves probably do not reflect only the light response. For determining the Amax this should be no problem, as you started at the highest light level, i.e. at Amax. Are you sure there was no photoinhibition at these high light levels? This may be a problem when starting light response measurements at the high end, as it would affect the rest of the measurements.

R: It is true that the light response curve cannot exclude the impact of drying. To mitigate the impact, we have measured the photosynthesis at highest light level from the beginning of each measurement, then decreased the light level sequentially (as respiration could be less sensitive to drying).

We have added more details on the measurement protocol and choice of light levels.

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The cuvette relative humidity was kept at 80% to slow down the drying process, but not to cause damage to the devise. The maximum light level 1500 PPFD was chosen based on our earlier studies with more light levels (Laine 2011, 2015) where we had not observed any photoinhibition until PPFD 2000, and A were often still increasing between PPFD 800 and 1500. Laine, A. M., Juurola, E., Hájek, T., & Tuittila, E. S.: Sphagnum growth and ecophysiology during mire succession. Oecologia, 167(4), 1115-1125, 2011. Laine, A. M., Ehonen, S., Juurola, E., Mehtätalo, L., & Tuittila, E. S.: Performance of late succession species along a chronosequence: Environment does not exclude Sphagnum fuscum from the early stages of mire development. Journal of vegetation science, 26(2), 291-301, 2015.

6. Model tests: As an important difference between your and previous models lies in the coupling to environmental fluctuations and stochasticity (L97-98), it would make sense to present a test of the importance of these processes to the model output. Would a simpler model provide similarly good results?

R: We believe that the main purpose of modelling is to illustrate the reality and serve as a tool for systematic assessment of the processes. Simple community models without individual-based processes implicitly weigh on generality and forgive outliers. However, environmental fluctuation and extremes are becoming more frequent and intensive with climate change, and this is likely to give advantage to an otherwise unlikely change in peatland community. To help with this situation, our modelling is able to populate outputs along a probability distribution and allows assessing individuals with different trait combinations as a part of the probabilities. As these models are fundamentally different in focuses and underlying mechanisms, simply comparing the goodness of results seems pointless.

I would also be interested in seeing the effects of the water retention and photosynthetic water-response parameters separately. Especially since the parameters for the latter may suffer from some measurement artefacts.

R: This is a very appreciated comment. Our future goal is also to make the picture clearer and understanding the factorial effects is a very important aspect. At the moment, our data and techniques are insufficient to separate the different effects. Therefore, model testing based on the parameters quantified by the “mixed” information could be less informative, unless we have had improved measurement data.

In addition, S. fallax and S. magellanicum are largely different in both water retention and photosynthetic response to water stress. Further testing on species either with similar water retention, or with similar photosynthetic response would be more informative to this question.

7. Presentation: L279-352 are all about module 3, which seems a bit unbalanced, seeing that modules 1 and 2 seem more important for the competition results. Model 3 is not tested in this paper:

R: Module 3 is about environment and it was not tested here because it was not in the focus of this paper. However, to bridge environmental fluctuation to community processed, our center of the focus, we needed to set up the environment first.

Specific comments

L20 In the introduction it could be explained more clearly why a mechanistic model I needed to predict species compositions under changing water levels. Is a prediction based on known habitat preferences not good enough?

R: The species known preference along the prevailing moisture gradient might not directly serve as a reliable predictor for future species compositions as water table fluctuation is likely to increase. This is now added in Introduction.

L60-61 how does the species composition affect these processes? In particular (for discussion), how do your species / ecological types affect these processes?

R: through interspecific variability in species traits such as photosynthetic potential and litter quality

L381 it would be interesting to see the effects of water retention and water stress separately

R: See above the response to 6

L471 to me it does not look like photosynthesis of S. fallax is more sensitive to changes in the water content, as Amax lies at lower water contents than for S magellanicum, suggesting that it can handle dry conditions better.

R: In this study, we use the term sensitivity to represent the dependency of photosynthesis changes to water content changes in capitula. Although S. fallax has greater tolerance to relatively low water content, the water content change for photosynthesis to drop from maximum to zero was much smaller than S. magellanicum (B2C). This is why we claim that photosynthesis of S. fallax is more sensitive to changes in the water content. This is now better pointed out in the text.

L552 how exactly may it serve?

R: we have removed the sentence

L561 Similarly, how could it be used in DVM development? If you can, please try to be more explicit here.

R: We introduced a mechanism to include competition based on growth rates that could be used in building dynamic community structure into DVMs.

Table 1: Rs20 was not significantly different between the species, then why use different values here? How large is the effect on the results?

R: These values are measured from field experiments and reported here. Although the means are not significantly different, we cannot judge that the probability distributions are the same, based on only several samples. Therefore, we used the measured means and standard deviations to generate probability distributions for each species.

Technical corrections:

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L24 employs

R: corrected

L50 why “during decadal timeframe”?

R: not within few years but faster than a hundred yeas

L57 have

R: corrected

L66 remove “community”

R: removed

L69 I do not think that this modelling can be considered a “space-for-time” approach. The processes are different in space than in time.

R: removed

L90 : : :that is covered: : :, : : :As competition occurs: : :

R: modified as suggested

L100 within the peatland moss layer

R: added

L102 whose competitiveness?

R: clarified

L106 positions a long a

R: corrected

L113 modelled is located

R: modified as suggested

L119 with a sparse cover of vascular plants

R: modified as suggested

L125 The Peatland: : :

R: added

L126 explain “water-energy conditions”

R: clarified

L128 consisting

R: modified

L132 are driven

R: modified

L142-143 A is not directly controlled by CWR, please rephrase

R: rephrased

L145 These were not really random variables, but variables randomly selected from a distribution

R: corrected

Eq5: what are the rules for the timing of growth? Any relation to WC?

R: Timing of growth is controlled by a temperature threshold and NSC availability. Growth occurs when T > 5 °C and NSC is above zero. The dynamics of NSC storage is related to WC through net photosynthesis.

L191 explain where Kimm is based on

R: Reference added to Asaeda, T. and Karunaratne (2000)

Asaeda, T. and Karunaratne, S.: Dynamic modelling of the growth of Phragmites australis: model description, Aquatic Botany, 67, 301-318, 2000.

L204 ii) biomass, or NSC?

R: NSC; corrected

L212 This order of sentences suggests that an exhaustion of NSC storage would be due to lateral growth, which would not make sense, as lateral growth should not take place if NSC supplies are not enough to sustain both new capitula

R: Indeed, it does not make sense. Removed

L217 why suddenly “moss parameters‘ - better use the same terms all the time

R: reformulated

L227 how does shoot density vary in the model, if you model one capitulum per grid cell?

R: Ds is BM per grid cell, not the number of capitula. The (suggested) table of abbreviations with their units will clary this.

L235 where is the centre of the moss layer?

R: removed

L239 what is the 0capacity of water0?

R: corrected to “water uptake capacity”

L264 0where Wopt is the optimal water: : :

R: reformulated

L270-278 It is not clear to me why this equation was needed.

R: In Eq. 11 we evaluated the water stress effect at high Wcap conditions, which are beyond the upper boundary of our drying experiment. Therefore in Eq. 12 we used a brief method to estimate the capitula Wcap from volumetric water content of moss carpet.

L277 Is the same W max used for both species..? An how about the values in Table B1

R: Yes, same value is used for both species. This is a theoretical maximum for high water-content restrictions on photosynthesis (Frolking et al., 2002), which is needed but not our focus in the modelling.

L294 are listed

R: changed

L295-313 Why are snow dynamics important for the model?

R: Snow dynamics impact environmental conditions in the early growing season. As they are currently under change due to climate change, we considered important to include them for better predictions.

L318 What are “periodic lateral boundary conditions”?

R: rewritten

L323 of the model

R: added

L346-347 WTs is the multi-year mean of weekly water table?

R: clarified

L474 insert return

R: I was not able to find were to insert

L487 This would be a good place to explain why Sf overgrowsn Sm in the lawns.

R: Explanation included. Basically, the looser structure of S. fallax allows its faster height growth.

L495 in other hydraulic R: added

L513 Explain the 0this could be because0, this is not obvious

R: the text was quite unclear, now clarified

L520 As Amax was lower in Sf, and Rs20 was the same, it seems that only Hspec would explain the result. You could repeat the test adjusting only Hspec to test this.

R: Hspec is a very powerful trait but our focus here was not to discuss each trait. Also, we don't have a species that would have lower in Hspec but resembles S. fallax in other traits. Therefore, we don't understand why this test would be meaningful.

L527 dominated

R: modified

L544 This would be a good place to explain how these impacts work and what your model thus implies (or could imply when tested under climate-change conditions) for peatland stability and functioning

R: Explained

Table 1: I would recommend adding the units inside the table

R: added

Table 1 & Table B1: A in bryophytes is usually expressed in nmol g-1 s-1, to avoid to many 0 before significant digits start.

R: we prefer to use the current version

Table 2 and 3: please explain abbreviations

R: explanation added

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Appendix L 150 at one hertz?

R: Changed to every second.

L209 The software is R, R Studio is just an interface

R: corrected

Fig B2: it is impossible to distinguish the models form the data especially in C. See comments above about the curves in C.

R: The lines have now been redrawn. Fig B2 shows only measured values.

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