Authors' responses to the comments of anonymous Referee #1

[All the references to the line numbers, figures and tables in authors' responses are of revised version of the manuscript unless otherwise stated]

Referee's comment: This paper compares the results of the ecosystem biophysical model ecosys against field measurements of environmental variables (primarily water table depth – WTD) and carbon fluxes measured by eddy covariance (EC) at a treed peatland in western Canada over a 5 year time frame when WT was decreasing at the site. The model, ecosys, is a very sophisticated tool and has been widely applied in the past against many different ecosystem types, with success. It is fair to say that is among the top ranked platforms for simulating ecosystem functioning. With that said, the purpose of this particular paper is a bit foggy. The EC flux measurements from this site, including the time series over which the WTD had declined, have been clearly reported in previous literature, as has been cited in this study. Therefore, is the purpose of this study 1) to simply to test if ecosys can simulate the trend in measured EC fluxes over the study period, or 2) to use ecosys to explain the behaviour of the EC-fluxes, which cannot be obtained from most common EC and environmental measurements? The paper seems to do a bit of both, but the main objective is not clear. However, given the extensive testing of ecosys at other peatlands and other ecosystems, the former seems to be quite a weak objective. The latter is more scientifically interesting, but that is not the way the paper is set out.

Authors' response:

The objective of this paper was to test whether a coupling of algorithms from independent published research that describe feedbacks among peat biogeochemistry, peatland hydrology and peat forming vegetation would be able to simulate and explain WTD effects on peatland CO_2 *exchange in a boreal peatland. This testing of algorithms representing interactions between peatland biogeochemistry and hydrology help reconcile our current understanding based on inferences drawn numerically from relationships among EC-gap filled partitioned NEP, GPP,* R_e *and WTD. However, given the non-linearity and peatland-specific responses of WTD-C cycle feedbacks, testing these algorithms in peatlands with contrasting peat type, vegetation, hydrology, climate and weather conditions also have important scientific and practical implications. Current predictive capacity of water table depth (WTD) effects on peat carbon (C) accumulation and degradation is limited by poor representation of peatland biogeochemistry in the peatland C models. So testing ecosys algorithms against measurements in a boreal fen, which is very different from the earlier peatlands where ecosys was tested in terms of climate, hydrology, peat forming substrates and vegetation, should complement those in earlier papers in examining the adequacy and robustness of our predictive capacity of these feedbacks.*

The objective and rationale section (lines 122-139) are now heavily edited to clearly lay out the objective, purpose and the implications of the study to remove any confusion.

Referee's comment: There are 4 operating hypotheses (not repeated here). These are not stated in terms of what is reflected in the EC-derived measurements, which seems to be the main thrust of the paper from the rest of the introduction, but rather in terms of biophysical processes that will take place in the model. Hence, it is a source of some of the confusion about the purpose of this paper. It would be nice to see an attempt to improve the introduction with a clearer purpose.

Authors' response:

Perhaps the best way to present the model hypotheses is to state the physical and biological processes affected by WTD and how they are modelled, as we have done in the current manuscript. These processes, if accurately modelled, should manifest themselves as increased CO_2 effluxes from increased R_h with increasing WTD, offset by increased CO_2 influxes with increased N uptake. At some point, further increases in WTD will manifest itself as decreased CO_2 effluxes and influxes with greater water stress. These manifestations should then be corroborated by observations by EC and flux chambers and by other eco-physiological measurements such as N status as has been done in the manuscript. The reflection of those hypotheses in EC-measurements was also somewhat stated in lines 171-175 of the previous version of the manuscript. However, the objective and rationale (lines 122-139) and hypotheses (lines 141-172) sub-sections within the introduction section are now heavily edited to clearly lay out the objective, purpose and hypotheses so as to remove any confusion upfront as suggested.

Referee's comment: Another concern about the present manuscript is that there is a lot of attention to how ecosys performs in simulating the WTD. It seems to me that this topic was adequately covered in the previous paper, Mezbahuddin et al. (2016), so why do we need the emphasis here.

Authors' response:

The contents in lines 481-501 of the previous version of the manuscript are now removed to eliminate the overlap with Mezbahuddin et al. (2016) (lines 482-483).

Referee's comment: I have a small worry about the comparison of ecosys modelled fluxes against gap-filled data (especially nighttime (Re) fluxes – section 3.3). Since the gap-filling is a model itself – now we are comparing one model against another. I realize there is a discussion of how this may have affected the comparison, but that does little to convince readers that the comparison of modelled and measured data is sound. Why not just compare half hours where measured data were available to test ecosys, if that is the point of the paper (see above).

Authors' response:

The real test of modelled outputs of hourly net CO_2 fluxes was against EC-measured hourly net CO_2 fluxes excluding any gap-filled flux. Since the model is hourly time-step, we averaged two half-hourly measured EC net CO_2 fluxes (no gap-filled fluxes) to test the modelled *fluxes against. If any or both of the two half-hourly fluxes was gap-filled, the average hourly net CO_2 fluxes were termed as "gap-filled".*

Daily, growing season and annual aggregates of EC NEPs include number of gap-filled net CO_2 fluxes. The sole reason of regressing modelled results against gap-filled CO_2 fluxes was to examine how much of the deviation between modelled and EC gap-filled estimates of growing season and annual NEP, and between modelled and EC-partitioned GPP and R_e were contributed by the gap-filled fluxes. However, since it created confusion, we now moved those regression results for gap-filled vs. modelled net CO_2 fluxes to a separate table in the supplementary material and edited the texts accordingly (lines 404-414, 447-467, 840-858) (Table S1 in page 43 of supplementary material).

<u>Referee's comment:</u> Section 4.2 Divergence between modeled and EC-derived fluxes makes some interesting points, but as it stands very little of this has been tested or analyzed in any detail, so we really don't know what the source of the discrepancy is. It would be nice to see some attempt or suggestions as to how to hone in on the most likely causes of the discrepancy. You seem to suggest the EC-derived measurements are wrong, which may well be, but I am not sure that the model is not without fault.

<u>Authors' response:</u>

The likely contribution of uncertainties due to modelling into the divergence between modelled and EC-derived seasonal and annual GPP and R_e estimates are now included in lines 873-897 (the texts in those lines are not repeated here).

<u>Referee's comment:</u> The Conclusion section is not really a conclusion. First, much of it is simply a re-statement of the main findings. Second, it suffers the same problems as the objective of the study namely, not really being clear. The final statements about the value and application of the ecosys model, while possibly true, seem a little self-serving.

<u>Authors' response:</u>

The conclusions section is now heavily edited to remove most of the re-statements, and to link it better with the revised statements of objectives. The final statements are now rephrased to remove any confusion (lines 899-941).

<u>Referee's comment:</u> Finally, the manuscript needs a good editing, although the writing is such that it is understandable, there are many awkward statements/phrases, issues with tense, or grammatical errors that could be addressed to improve the manuscripts readability. I have pointed out some of these in the minor points below, but there are several others. Overall, this could be quite a useful contribution, especially if cast in the role of using ecosys to help understand the pattern and responses of EC-derived fluxes over time, something that is hard to

get from just EC and environmental measurements, rather than just another test of the ecosys algorithms at another peatland site.

<u>Authors' response:</u>

The manuscript is now thoroughly revised and edited to remove any sentence or grammatical errors (e.g., lines 118-120, 498-539, 543-568, 571-580, 583-591, 593-594, 614-617, 627-629, 631-640, 643-649, 655-662, 840-858 etc.). The objective and rationale section (lines 122-139) is now revised to clearly represent the focus of the study which was to examine the underlying processes affecting WTD – peatland C cycle feedbacks. This will also serve as a reconciliation of the inferences drawn on WTD-C feedbacks in this peatland by using EC-gap filled and partitioned aggregates.

<u>Referee's comment:</u> Minor Issues: 1. Line 81-82 & line 87, Lafleur et al. (2005) reference is inappropriate here, they discuss Re not GPP. Also relevant on lines 908-911. 2. Lines 95-97, as above this reference does not discuss a threshold for WTD and GPP, perhaps another reference by this author?

<u>Authors' response:</u>

The correct reference is now inserted (lines 1027-1029).

<u>Referee's comment:</u> 3. Lines 98-107, the start of this paragraph is poorly worded. First one does not start a new paragraph with the word 'therefore". The sentence beginning "So, to adequately predict : : :" is awkward and doesn't quite read right. As with the next sentence – the phrase "do not have prognostic WTD dynamics that prevent simulation" is confusing and awkward.

<u>Authors' response:</u>

All of the three sentences are now rephrased (lines 103-109).

<u>Referee's comment:</u> 4. Lines 314-317, these two sentences that describe the simulated mosses are very difficult to understand, some revision for clarity is needed. Should be put in terms of what a real moss is and where it grows.

<u>Authors' response:</u>

Those sentences are now edited to describe more specifically how moss is simulated in ecosys (lines 299-305).

<u>Referee's comment:</u> 5. Line 447, the word diurnal here is incorrect; Table 1 compares instantaneous half hour fluxes. Diurnal suggests some course of measurements over the daytime.

<u>Authors' response:</u>

Edited (line 448).

<u>Referee's comment:</u> 6. Line 457-58, the sentence here about 2009 is not needed here; simply add it as a foot note to the Table.

<u>Authors' response:</u>

The line is now removed from the text and is added as a footnote to the Table 1.

<u>Referee's comment:</u> 7. Line 478-81, this sentence is somewhat heuristic; the Figure certainly does not show these components. I think it is adequate just to say the model simulated measured WTD well.

<u>Authors' response:</u>

Edited (lines 482-483).

<u>Referee's comment:</u> 8. Line 536, word 'also' is not needed.

<u>Authors' response:</u>

Removed (line 512).

<u>Referee's comment:</u> 9. Line 537, what does 'It' refer to?

<u>Authors' response:</u>

'It' referred to 'similar day-time fluxes in 2005 and 2008 despite larger night-time fluxes in 2008 than in 2005', now revised (lines 516-517).

<u>Referee's comment:</u> 10. Line 538-41, this long sentence is somewhat awkward and doesn't really say anything new.

<u>Authors' response:</u>

The sentence is now removed.

<u>Referee's comment:</u> 11. Lines 559-61, the sentence here seems to be missing a word or words, does not read well.

<u>Authors' response:</u>

The sentence is now rephrased (lines 529-532).

<u>Referee's comment:</u> 12. Lines 55-570, you seem to miss an opportunity here. You describe how warming does not stimulate Re when water table was high in 2005, and how it is stimulated by warming in low WT years (2006 and 2008), yet given the sophistication in ecosys there is not real explanation of why this works the way it does, what is the biogeochemical functioning that

does or does not stimulate Re under low and high WTs respectively? Further down you describe the mechanisms associated with GPP, why not the same with Re?

Authors' response:

The mechanisms describing how warming affected R_e in shallow vs. deeper WT conditions is discussed in lines 697-702.

Referee's comment: 13. Line 632-33, this was mentioned above (#6), no need to repeat it here.

Authors' response:

Deleted.

Referee's comment: 14. Lines 664-69 Section 3.5, You state this drainage experiment ": : : would 667 also serve as a climate change analog in providing us insight into how potential WTD drawdown 668 under future drier and warmer climates would affect boreal peatland GPP, Re and hence NEP." I don't see how, as the atmospheric changes of higher temperatures and perhaps higher VPD are not included. I think it is fair to say this simulation represents the effects of WT drawdown only.

Authors' response:

We did not include rise in temperature and consequent VPD effects in our drainage simulation. Those sentences are now edited as suggested to remove the confusion (lines 38-39, 911-912).

Referee's comment: 15. Lines 673-74, I don't think you need this sentence, it is rather obvious that changes would occur and you have a lot of words following to describe them.

Authors' response:

Deleted.

Referee's comment: 16. Lines 683-696, is this enhanced evapotranspiration coming from the tree cover or ground vegetation or both?

Authors' response:

The enhanced evapotranspiration was coming from the tree cover. Now explicitly mentioned in the text (lines 628, 632).

Referee's comment: 17. Lines 848-51, should note here that his Dimitrov et al. 2010 study was on a temperate bog not a fen.

Authors' response:

It is now mentioned within the text (line 774).

Authors' responses to the comments of anonymous Referee #2

General Comments

Referee's comment: The manuscript addresses impacts on CO_2 fluxes from changes in water table depth by using the ecosys model. The model is tested with eddy covariance and chamber CO_2 fluxes from a boreal peatland field site. The manuscript is dense throughout and requires very careful attention on the part of the reader to follow along. While the ecosys model is complex, how this paper is written exacerbates the complexity of the model. Right now, this paper would be an incredibly useful guide to someone wanting to run the ecosys model themselves, but lacks a clear and story that is supported by the results of this work. The major issue I have with this work is the relative complexity of the ecosys model next to the small amount of observed data that the model is compared with. Since ecosys has so many moving parts "under the hood", I can't say that I'm surprised at all to see it match data as well as it does. A good fit to observed data is not a new finding itself, and in a broader sense, the research questions aren't new. In fact, there is a good amount of overlap with Mezbahuddin et al. (2016), as brought up by Referee 1. So, I'm stuck reading through a dense description of a complex model, and at the end, it's compared with limited amounts of data that itself is modeled. The main conclusions seem to be focused on internal modeled variables within the ecosys model that have zero comparison to data. The major conclusions are changes in modeled O_2 diffusion, N mineralization rates, nutrient availability, microbial concentrations, plant functional type GPP. These results, as currently presented, are simply not supported by comparing to net CO_2 fluxes. The authors state in the conclusions that "These modelling hypotheses were also corroborated by various field, laboratory and modelling studies over similar peatlands (Sect. 4.1)" but the reader is left to dig out bits of information through the entire discussion section. At a bare minimum, for me to trust the conclusions of this work, the authors must provide a clear and succinct comparison of their model parameters to literature values in a table/graph, including error analysis. Also, asking the reader to trust your conclusions because they match literature is fine, but there is a major issue when the story of the paper is that inter-site variation of peatland sites is high.

Authors' response: To facilitate point-by-point responses, we addressed the general comments by separating and re-organizing those into smaller segments under the following points:

(1) The manuscript is dense throughout and requires very careful attention on the part of the reader to follow along.

Authors' response:

Significant editing of the manuscript is done to simplify the story as much as possible (e.g., lines 118-120, 122-172, 498-539, 543-568, 571-580, 583-591, 593-594, 614-617, 627-629, 631-640, 643-649, 655-662, 840-858, 899-941 etc.). The main body of the revised version of the manuscript is about 700 words smaller than the earlier version of the manuscript.

(2) Right now, this paper would be an incredibly useful guide to someone wanting to run the ecosys model themselves, but lacks a clear and story that is supported by the results of this work….The major issue I have with this work is the relative complexity of the ecosys model next to the small amount of observed data that the model is compared with. Since ecosys has so many moving parts "under the hood", I can't say that I'm surprised at all to see it match data as well as it does…. So, I'm stuck reading through a dense description of a complex model, and at the end, it's compared with limited amounts of data that itself is modeled…. These results, as currently presented, are simply not supported by comparing to net CO_2 fluxes.

<u>*Authors' response:*</u>

Hourly modelled outputs of net ecosystem CO_2 fluxes have already been tested against hourly net CO_2 fluxes measured (excluding the gap-filled values) by eddy covariance (EC) approach over a gradually drying weather period from 2004 to 2009 (Tables 1a, b). Modelled hourly understorey vegetation and soil CO_2 fluxes are also tested against hourly automated chamber measured CO_2 fluxes over two years with contrasting WTD conditions i.e., 2005 with shallower WTD vs. 2006 with deeper WTD (Table 1c). To further constrain and explain modelled WTD effects on GPP and R_e, modelled daytime and nighttime net CO_2 exchange have already been examined closely for shorter periods (e.g. 10-day) with contrasting WTD along with EC-measured net ecosystem CO_2 fluxes, and chamber measured net understory vegetation and soil CO_2 fluxes (Figs. 4-6). The examination of modelled WTD effects on CO_2 exchange have already been extended to daily, growing season, and annual time-scales along with EC-gap filled NEP and partitioned GPP and R_e (Figs. 3, 7,8).

The internal peat biogeochemistry and peatland nutrient cycling modelled in ecosys are now tested against leaf nitrogen concentrations, N mineralization, rooting depth, GPP, and R_e measured/estimated at either our site or at sites that had similar peat substrates, hydrology and/or plant functional types (Table 2) (lines 744-749). So, the testing of the modelled results should be as robust as it could be within the best availability of measurements.

(3) A good fit to observed data is not a new finding itself, and in a broader sense, the research questions aren't new.

<u>*Authors' response:*</u>

Northern peatlands are likely to be important in future carbon cycle-climate feedbacks due to their large carbon pools and vulnerability to hydrological change. Current predictive capacity on water table depth (WTD) effects on peat carbon (C) accumulation and degradation is limited by poor representation of peatland biogeochemistry in the peatland C models. So, the novelty of this research lies upon its effort to test whether a coupling of algorithms from independent published research that describe feedbacks among peat biogeochemistry, peatland hydrology and peat forming vegetation would be able to simulate and explain WTD effects on peatland CO_2 exchange in a boreal peatland. This testing of algorithms representing interactions between *peatland biogeochemistry and hydrology not only improves our predictive capacity of WTD effects on peatland CO_2 exchange, but also help reconcile our current understanding based on inferences drawn numerically from relationships among EC-gap filled partitioned NEP, GPP, R_e and WTD.*

Previous model inter-comparison studies showed the need for representing interactions among peat biogeochemistry, hydrology and peat vegetation physiology to improve predictive capacity of WTD –C process feedbacks without peatland-specific parameterization of model algorithms (lines 103-120). So, the objective of this study was to examine whether a coupling of site-independent model algorithms describing peatland carbon, nitrogen, oxygen, and water cycling which was fed by site-specific measurable inputs with physical meanings would simulate and explain WTD effects on peatland CO_2 exchange for the boreal peatland. The objective and rationale section is now heavily edited to more clearly state the research objective (lines 122-139).

(4) In fact, there is a good amount of overlap with Mezbahuddin et al. (2016), as brought up by Referee 1.

Authors' response:

The contents in lines 481-501 of the previous version of the manuscript are now removed to eliminate the overlap with Mezbahuddin et al. (2016) (lines 482-483).

(5) The main conclusions seem to be focused on internal modeled variables within the ecosys model that have zero comparison to data. The major conclusions are changes in modeled O_2 diffusion, N mineralization rates, nutrient availability, microbial concentrations, plant functional type GPP……. The authors state in the conclusions that "These modelling hypotheses were also corroborated by various field, laboratory and modelling studies over similar peatlands (Sect. 4.1)" but the reader is left to dig out bits of information through the entire discussion section. At a bare minimum, for me to trust the conclusions of this work, the authors must provide a clear and succinct comparison of their model parameters to literature values in a table/graph, including error analysis.

Authors' response:

The comparison of above mentioned modelled outputs are now formally and succinctly done in table 2 against corresponding measurements at the site or at peatlands that had similar peat substrates, hydrology and/or plant functional types.

(6) Also, asking the reader to trust your conclusions because they match literature is fine, but there is a major issue when the story of the paper is that inter-site variation of peatland sites is high.

Authors' response:

Our main tests of the modelled outputs have been against EC, chamber and biometric measurements at the site (Figs. 3-7) (Tables 1, 2). Since the inter-site variations of feedbacks between WTD and peatland C cycle are mediated by the interactions among peat forming climate and vegetation, peatland hydrology, and peat type (lines 60-104), we have always made sure that the sites we are comparing our modelled processes against are similar to our sites in any combination of those characteristics (e.g., footnotes in table 2). However, we have also discussed our results against some contrasting peatlands so as to highlight the underlying mechanisms that lead to inter-site variations in these feedbacks (e.g., lines 832-837). The conclusion section is heavily edited to remove any confusion related to inter-site variation of these feedbacks (lines 921-940).

<u>Specific Comments:</u>

<u>Referee's comment:</u> Specific Comments to expand on the above general comment, the eddy covariance and chamber data is not explained well enough in this paper. Let me be clear, that doesn't mean that I have issues with the data itself, just how it is presented and used here. Referee 1 brought up the issue of comparing model output to gap filled data, which is comparing a model to another model. That is absolutely an issue in this work, and I second what Referee 1 highlights as a major issue, but I'll go further. There needs to be more discussion of the data, how it was gap-filled, possible sources of error and what that means when compared to the model results. I know this is a modeling work, but with very limited observational data to compare the model results with, simply saying in two sentences "To examine how well ecosys simulated net ecosystem CO_2 exchange at the WPL, we tested hourly modelled net ecosystem CO_2 fluxes against those measured by using eddy covariance (EC) micro-meteorological approach by Syed et al. (2006) and Flanagan and Syed (2011). Quality control, and gap-filling of EC measured net CO_2 fluxes, and partitioning of EC-gap filled net CO_2 fluxes into GPP and Re were done by Syed et al. (2006) and Flanagan and Syed (2011)" is not enough when the first line says "we used observational data" and the second says "please read those other papers for their methods". Now, when we get to the details of the chamber fluxes, there are slightly more details, but again, not nearly enough. Again, you partition net CO_2 using a model, but don't explain anything beyond that.

<u>Authors' response:</u>

Daily, growing season and annual aggregates of EC NEP includes number of gap-filled net CO_2 fluxes. The sole reason of regressing modelled results against gap-filled CO_2 fluxes was to examine how much of the deviation between modelled and EC gap-filled estimates of growing season and annual NEP, and between modelled and EC-partitioned GPP and R_e were contributed by the gap-filled fluxes. However, since it created confusion, we have moved any comparison between modelled and gap-filled fluxes to a separate table in supplementary *materials (Table S1 in page 43 of supplementary material) and edited the texts accordingly (lines 402-412, 445-465, 845-857). Tables 1a and 1b in the revised version of the manuscript now only include tests between modelled and EC-measured (excluding gap-filled fluxes) net ecosystem CO_2 fluxes (lines 402-412, 445-465).*

Methods for screening, gap-filling, and partitioning of EC datasets are now comprehensively discussed (lines 334-343).

Referee's comment: You average over 9 chambers, but don't say why or what that means? How much error is introduced here? What is the range of observed fluxes? The reader doesn't know, so again going back to my main issue, with very limited observational data, ecosys modeled results look good at the surface, but the work is limited in how much the reader can trust the results of an over-parameterized and under-tested model.

Authors' response:

Those 9 chambers were in place to cover spatial variation due to peatland micro-topography while measuring the net CO_2 fluxes from understorey vegetation and soil. We averaged fluxes from those chambers to include overall hummock-hollow variations into the averaged CO_2 fluxes. Chamber flux measurements are now discussed in sufficient details (lines 344-351, 413-426). Figures 4 and 5 in the previous version of the manuscript (Figs. 5b and 6j,k in the revised version of the manuscript) are now redone to include standard error of means of spatially averaged chamber fluxes to represent flux variations among the chambers. Moreover, a separate regression test with error analysis between modelled understory and soil CO_2 fluxes, and the chamber CO_2 fluxes are now included for 2005 and 2006 with contrasting WTD (Table 1c) (lines 413-426, 681-687). This test further strengthens the robustness of the modelled outputs.

Referee's comment: Once we move past the issue of how the observational data is described, we move through a lot of model descriptions and results that are very, very dense. I'm very happy to see what looks like the full set of equations that go into ecosys in the appendixes, but the reader is left with only very dense blocks of text to try to figure out what parts of the model are important and why. I would suggest keeping the entire set of equations in the appendix, but moving the main equations used here into the text of the manuscript. Then, the reader doesn't have to dig out the equations for context and, more importantly, it would be easier to focus the story around those few equations.

Authors' response:

The model development section describes the key equations that are related to the four operating hypotheses. The respective equations that are listed in the appendices are also cited within the text. The current model description is self-explanatory and a reader does not have to always go back to the appendices to understand the processes. However, the citation of the *equation within the text makes sure that a reader can go back to the appendices at any time to see details of a particular equation. Few key equations from the appendices could be pasted into and described in this section as suggested. However, we have felt that it would either make the section even denser or the story could be incomplete if roamed around only a few equations. So, instead of bringing equations into the model development section, we have preferred to include a visualization in the form of a flow chart summarizing those key processes and linking the flow chart with the description as suggested by reviewer 3 (Fig. 1) (lines 204, 207, 209, 215, 216, 233, 237, 240, 241, 248, 250, 277, 279, 286, 291, 297, 309, 311, 672, 683, 711, 723, 735, 786, 788, 793, 807 and 870).*

<u>Referee's comment:</u> As the reader is starting to get a handle of the main story presented, a major issue comes up again. There isn't enough data to support the conclusions. Even the highlighted results in the abstract are heavily focused on things like nitrogen dynamics, nutrient mineralization, GPP of plant functional types, all of which are 100 percent internal to the model without any space in the manuscript devoted to why the read should trust the internal model equations.

<u>Authors' response:</u>

The internal peat biogeochemistry and peatland nutrient cycling modelled in ecosys are tested against leaf nitrogen concentrations, N mineralization, rooting depth, GPP, and R_e measured/estimated at either our site or at sites that had similar peat substrates, hydrology and/or plant functional types. Those comparisons are summarized in a table (Table 2) and are described in the texts (e.g., lines 689-694, 737-753 etc.). WTD effects on modelled vascular vs. non-vascular plant water relations and hence productivities were tested against site measured hourly latent heat fluxes, sensible heat fluxes and Bowen ratios, and daily soil moisture contents at different depths. These tests of modelled vascular vs. non-vascular plant water relations which were described in Mezbahuddin et al. (2016) are now briefly cited (806-809). The model equations were derived from independent research which were rigorously tested in other published studies. The sources of each of those equations are listed in the supplementary material. However, sources and the significance of the model equations and the novelty of the modelled process interpretations are now briefly discussed (179-188, 900-903).

<u>Referee's comment:</u> Finally, the conclusions presented are simply changes in variables that are internal to the model, without anything to compare them with other than literature values from other studies. As mentioned in the general comment above, the literature values could be a valid check if done well, but as this manuscript is currently written, that needs to be done more formally and not in the discussion. With the suggestion of strengthening the comparison of the modeled conclusions to literature as well as the authors pinning a lot of the trust in their conclusions on said literature values, when the ending of the introduction/justification section is as follows: "Moreover, since hydrological feedbacks to key peatland C processes are highly non-linear and site-specific, testing of ecosys algorithms across contrasting peatlands would also

facilitate formation of a modelling platform for scaling up simulations of those feedbacks across peatlands at larger spatial scales i.e., national, regional, continental or global as also recommended by Waddington et al. (2015)" the reader is going to be confused. On one hand, you compare your conclusions to literature and say "look, these results fit with other studies" but the entire paper was setup with the story of "there are lots of variations across peatland sites" throughout the introduction. So, I'm confused and this needs to be cleared up either by heavy editing of the story.

Authors' response:

The conclusion section is now heavily edited to include general conclusions, and the implications of those conclusions (lines 898-940). A formal succinct comparison between the modelled outputs and measurements from the same site, and similar sites from earlier studies is done in a separate table (Table 2). The mentioned sentence within the quote is now rephrased to remove any confusion and contradiction with earlier description (932-938).

Authors' responses to the comments of anonymous Referee #3

<u>Referee's comment:</u> This manuscript describes simulations of peatland biogeochemistry using the ecosys model, and compares the results to observations from a flux tower, chambers, and water table observations. The model is used to support a detailed analysis of interactions among soil microbial processes, mosses, vascular plants, and hydrology under different water table regimes. The model does a very good job of replicating measured hydrology and carbon cycling at the site, and the analysis produces some very interesting insights about the peatland response to changes in water table. The explanation of how different components of the peatland (vascular plants, non-vascular plants, aerobic decomposition, etc) interact differently under saturated, unsaturated, and deep water table conditions was especially interesting, and I think this has great promise to be a useful framework for future analyses in this field. Overall, I think this was a really nice paper, with novel insights, an impressive model, and clearly written (though dense) presentation.

<u>Referee's comment:</u> My only major suggestion in that a visualization of the interactions at different water table levels might help to summarize the results in a way that's easier for readers to grasp. Sections 2.1.2 and 2.1.3 lay out a lot of competing responses to water table depth (oxygen availability, decomposition, root growth, nitrogen availability, : : :). While the description is pretty clear, I think a visualization would be really helpful. This could be as simple as a table or text box with columns for vascular plants, non-vascular plants, aerobic microbes, etc and rows for different hydrological regimes with the key processes affecting each ecosystem component.

<u>Authors' response:</u>

A flow chart is now added as figure 1 in the revised version of the manuscript to depict the key biogeochemical and physiological effects on plant and microbial functional types (e.g., aerobic vs. anaerobic microbial processes, nitrogen and water uptake etc.) as mediated by different water table depth regimes that are modelled in ecosys. This figure are also adequately linked to the text (lines 204, 207, 209, 215, 216, 233, 237, 240, 241, 248, 250, 277, 279, 286, 291, 297, 309, 311, 672, 683, 711, 723, 735, 786, 788, 793, 807 and 870).

<u>Referee's comment:</u> Also, there are a lot of interesting mechanistic explanations in the Discussion, but I think there's an opportunity to tie these to the existing literature a little better. Are these new insights about process interactions that have not been discussed in the past? Or are these known interactions that have not been successfully modeled before? A little discussion of the novelty of the process interpretations and general framework of the results versus the novelty of the model itself might help place the results in a better context.

<u>Authors' response:</u>

The mechanistic explanations in the discussion is now summarized in table 2 of the revised version of the manuscript to facilitate the comparison between modelled processes and existing literature. The intention of the mechanistic discussion was to test the adequacy of existing knowledge of our process interpretation to reproduce WTD-C feedbacks in a northern boreal fen which has not been done before. The novelty of the process interpretations vs. modelled processes are now discussed (179-188, 900-903).

<u>Referee's comment:</u> Specific comments: Lines 17-22: This sentence is really long and hard to follow. I would suggest rewriting it.

<u>*Authors' response:*</u>

The sentence is now rephrased (lines 17-22).

<u>Referee's comment:</u> Lines 38-40: This is an important result, and it might help to also briefly explain the process behind it (e.g. more drainage eventually leads to limitation of GPP due to water limitation).

<u>*Authors' response:*</u>

Done (lines 42-43).

<u>Referee's comment:</u> Line 46: The units of g/yr don't seem right.

<u>*Authors' response:*</u>

Corrected (line 49).

<u>Referee's comment:</u> Lines 316-318: This sentence has some grammatical issues. I suggest rewriting it.

<u>*Authors' response:*</u>

The sentence is no longer needed due to rephrasing of the whole paragraph (lines 299-309), and so it has been removed.

<u>Referee's comment:</u> Lines 642-666: These root responses were very interesting. I don't think I've seen this process represented in ecosystem models in the past. Lines 682-686: It's very interesting how vascular plants have an optimum at an intermediate water depth while non-vascular plants don't. Very interesting implications for changes in relative biomass under different conditions.

<u>*Authors' response:*</u>

Yes, it is very interesting and another unique contribution of this study. We have also cited field studies that reported relative domination of vascular over non-vascular species with WTD drawdown in nearby similar peatlands (lines 798-799).

Coupled eco-hydrology and biogeochemistry algorithms enable simulation of water table depth effects on boreal peatland net CO_2 exchange

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Abstract

Water table depth (WTD) effects on net ecosystem CO_2 exchange of boreal peatlands are largely mediated by hydrological effects on peat biogeochemistry, and eco-physiology of peatland vegetation. Lack of representation of these effects in carbon models currently limits our predictive capacity for changes in boreal peatland carbon deposits under potential future drier and warmer climates. We ~~therefore tested~~examined whether ~~whether the effects of WTD variation on~~ a process-based ecosystem model *ecosys* could simulate net ecosystem CO_2 exchange of a Western Canadian boreal fen peatland over a gradually deepening water table due to drier weather from 2004 to 2009. The goal was to test whether a process-level ~~could be modelled through a process-level~~ coupling of a prognostic WTD with ~~dynamic~~1) ~~, which arises from equilibrium between vertical and lateral water fluxes, with~~ oxygen transport~~,~~ which controls energy yields from microbial and root oxidation-reduction reactions, and 2) vascular and non-vascular plant water relations ~~in an ecosystem model *ecosys*~~could explain mechanisms that control variations in net CO_2 exchange of a boreal fen under contrasting WTD conditions i.e. shallow vs. deep WTD. ~~*Ecosys* successfully simulated~~ A~~a~~ May-October WTD drawdown ~~by~~ of ~0.25 m ~~measured in the fen from 2004 to 2008, which was attributed to reduced precipitation relative to evapotranspiration, and reduced lateral recharge relative to discharge. This WTD drawdown~~ hastened oxygen transport to microbial and root surfaces, enabling greater microbial and root energy yields, and peat and litter decomposition, which raised modelled ecosystem respiration (R_e) by ~0.26 µmol CO_2 m^{-2} s^{-1} per 0.1 m of WTD drawdown. It also augmented nutrient mineralization, and hence root nutrient availability and uptake, which resulted in improved leaf nutrient (nitrogen) status that facilitated carboxylation, and raised modelled vascular gross primary productivity (GPP) and plant growth. The increase in modelled vascular

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GPP exceeded declines in modelled non-vascular (moss) GPP due to greater shading from increased vascular plant growth, and moss drying from near surface peat desiccation, thereby causing a net increase in modelled growing season GPP by ~0.39 µmol CO_2 m^{-2} s^{-1} per 0.1 m of WTD drawdown. Similar increases in GPP and R_e left no significant WTD effects on modelled seasonal and interannual variations in net ecosystem productivity (NEP). These modelled trends were corroborated well ~~against~~ by eddy covariance measured hourly net CO_2 fluxes (modelled vs. measured: R^2~0.8, slopes~1±0.1, intercepts~0.05 µmol m^{-2} s^{-1}), ~~and against other~~ hourly measured automated ~~-~~chamber net CO_2 fluxes (modelled vs. measured: R^2~0.7, slopes~1±0.1, intercepts~0.4 µmol m^{-2} s^{-1}), and other biometric~~,~~ and laboratory measurements. Modelled drainage as an analog for WTD drawdown induced by climate change driven drying showed that this boreal peatland would switch from a large carbon sink (NEP~160 g C m^{-2} yr^{-1}) to carbon neutrality (NEP~10 g C m^{-2} yr^{-1}) should water table deepened by a further ~0.5 m. This decline in projected NEP indicated that a further WTD drawdown at this fen would eventually lead to a decline in GPP due to water limitation. Therefore, representing the effects of interactions among hydrology, biogeochemistry and plant physiological ecology on ecosystem carbon, water, and nutrient cycling in global carbon models would improve our predictive capacity for changes in boreal peatland carbon sequestration under changing climates.

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1. Introduction

Northern boreal peatlands have been accumulating carbon (C) at a rate of about 20-30 g m^{-2} yr^{-1} over several thousand years (Gorham, 1991; Turunen et al., 2002). Drier and warmer future climates can affect the resilience of long-term boreal peatland C stocks by lowering water table (WT) that can halt or even reverse the C accumulation in boreal peatlands (Limpens et al., 2008; Dise, 2009; Frolking et al., 2011). To maintain and protect the C sequestration potentials of boreal peatlands we need an improved predictive capacity of how these C stocks would behave under future drier and warmer climates. ~~Despite the need~~However, boreal peatland C processes are currently under-represented in global C models largely due to inadequate simulation of hydrologic feedbacks to C cycles (St-Hilaire et al., 2010; Sulman et al., 2012). This ~~shortfall~~ can be overcome by integrating interactions between eco-hydrology of peatland vegetation, and peat biogeochemistry into finer resolution process models that can eventually be scaled up into larger spatial and temporal scale C models (Waddington et al., 2015).

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The hydrologic feedbacks to boreal peatland C processes are largely mediated by water table depth (WTD) variation and its effects on peat-microbe-plant-atmosphere exchanges of C, energy, water and nutrients (Grant et al., 2012). WTD drawdown can affect net ecosystem productivity (NEP) of boreal peatlands through its effects on ecosystem respiration (R_e) and gross primary productivity (GPP). Receding WT can cause peat pore drainage that enhances microbial O_2 availability, energy yields, growth and decomposition and hence increases R_e (Sulman et al., 2009, 2010; Cai et al., 2010; Flanagan and Syed, 2011; Peichl et al., 2014). The rate of increase in R_e due to the WTD drawdown may vary with peat moisture retention and quality of peat forming substrates (Preston et al., 2012). For instance, peats with low moisture retention exhibit more rapid pore drainage than those with high moisture retention thus causing more increase in R_e for similar WTD drawdowns (Parmentier et al., 2009; Sulman et al., 2009, 2010; Cai et al., 2010). Peats formed from *Sphagnum* mosses degrade at rates slower than those formed from remains of vascular plants (Moore and Basiliko, 2006). So for similar WTD drawdowns, moss peats would generate less increase in microbial decomposition and hence R_e than would sedge, reed or woody peats (Updegraff et al., 1995). Continued WTD drawdown can also cause near surface peat desiccation from inadequate recharge through capillary rise from deeper WT. Desiccation of near surface or shallow peat layers can cause a reduction in microbial decomposition that can partially or fully offset the increased decomposition in the deeper peat layers thereby yielding indistinct net effects of WTD drawdown on R_e (Dimitrov et al., 2010a).

The interactions between WTD and GPP vary across peatlands depending upon peat forming vegetation. For instance, increased aeration due to WTD drawdown enhances root O_2 availability and growth in vascular plants (Lieffers and Rothwell, 1987; Murphy et al., 2009). Enhanced root growth is also associated with greater root nutrient availability and uptake from more rapid mineralization facilitated by greater microbial energy yields, growth and decomposition under deeper WT (Choi et al., 2007). Greater root nutrient uptake in turns increases the rate of vascular CO_2 fixation and hence GPP (Sulman et al., 2009, 2010; Cai et al., 2010; Flanagan and Syed, 2011; Peichl et al., 2014). WTD drawdown, however, does not affect the non-vascular (e.g., moss) GPP in the same way it does the vascular GPP (Lafleur et al., 2005). Non-vascular plants mostly depend upon the water available for uptake in the near surface or shallow peat layers (Dimitrov et al., 2011). These layers can drain quickly with receding WT and thus have to depend on moisture supply through capillary rise from deeper WT (Dimitrov et al., 2011; Peichl et al., 2014). If recharge through the capillary rise is not adequate, near surface peat desiccation occurs which slows moss water uptake, causes eventual drying of mosses and reduces moss GPP (Lafleur et al., 2005; Riutta 2008; Sonnentag et al., 2010; Sulman et al., 2010; Dimitrov et al., 2011; Kuiper et al., 2014; Peichl et al., 2014). Near surface peat desiccation also suppresses vascular root water uptake from the desiccated layers (Lafleur et al., 2005; Dimitrov et al., 2011). But enhanced root growth and elongation facilitated by improved O_2 status in the newly aerated deeper peat layers under deeper WT enables vascular roots to take up water from wetter deeper layers (Dimitrov et al., 2011). If deeper root water uptake offsets the reduction in water uptake from desiccated near surface layers, vascular transpiration (T), canopy stomatal conductance (g_c) and hence GPP are sustained under deeper WT (Dimitrov et al., 2011). But if the WT falls below certain threshold level under which deeper root water uptake can no longer sustain vascular T, g_c and hence vascular GPP declines (Lafleur et al., 2005; Wu et al., 2010).

~~Therefore,~~ WTD variation can thus affect boreal peatland NEP through its effects on peat moisture and aeration and consequent root and microbial oxidation-reduction reactions and energy yields. ~~So, to adequately~~To predict how boreal peatlands would behave under future drier and warmer climates, a peatland C model thus needs to ~~have sufficient representation of~~simulate WTD dynamics that determine the boundary between aerobic and anaerobic zones and controls peat biogeochemistry. However, most of the current process-based peatland C models either do not ~~have a prognostic WTD dynamic that prevent simulation of~~simulate a continuous anaerobic zone below a prognostic WT (e.g., Baker et al., 2008; Schaefer et al., 2008; Tian et al., 2010), or do not simulate peat saturation since any water in excess of field capacity is drained in those models (e.g., Gerten et al., 2004; Krinner et al., 2005; Weng and Luo, 2008). Moreover, instead of explicitly simulating the above-described hydrological and biological interactions between peat aeration and biogeochemistry, most of those models use scalar functions of soil moisture contents to inhibit R_e and GPP under low or high moisture conditions (e.g., Frolking et al., 2002;

Zhang et al., 2002; Bond-Lamberty et al., 2007; St-Hilaire et al., 2010; Sulman et al., 2012). Consequently, those peatland C models could not simulate declines in GPP and R_e due to shallow WT while simulating WTD effects on CO_2 exchange of peatlands across northern US and Canada (Sulman et al., 2012). Furthermore, the approach of using scalar functions to simulate moisture limitations to GPP and R_e requires site-specific parameterization of ~~the scalar functions~~model algorithms which ~~makes this approach less suitable when scaling up across different peatlands~~reduces scalabitiy of those peatland C models.

1.1. Objective and rationale

~~To overcome the inadequacies in peatland C models as discussed above~~In this study, we tested a process-based terrestrial ecosystem model *ecosys* against eddy covariance (EC) net CO_2 fluxes measured over a drying period from 2004 to 2009 in a western Canadian boreal fen peatland in Alberta, Canada (will be termed as WPL hereafter) (Syed et al., 2006; Flanagan and Syed, 2011). The objective was to test whether the coupling of ~~represented~~ a ~~prognostic and~~ dynamic WTD that arises from vertical and lateral water fluxes as a function of~~, and a~~ a soil moisture retention scheme ~~that are coupled~~ with 1) oxygen transport, 2) microbial and root oxidation-reduction reactions and ~~,~~ energy yields, and 3) root, microbial and plant growth ~~,~~ and uptake within a soil-plant-microbe-atmosphere water, C and nutrient (nitrogen, phosphorus) scheme ~~in a terrestrial process model *ecosys*~~in an ecosystem process model could explain underlying processes that govern hydrological effects on net CO_2 exchange of a northern boreal fen under contrasting WTD conditions (e.g., shallower vs. deeper WTD). This study would reconcile our knowledge on the feedback mechanisms among hydrology, eco-physiology, and biogeochemistry of peatlands which are predominantly based upon inferences drawn from EC-gap filled values that include empirically modelled estimates. It would also provide us with a

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better insight and improved predictive capacity on how carbon deposits in northern boreal peatlands would behave under changing climates. Rigorous site-scale testing of coupled eco-hydrology and biogeochemistry algorithms in ecosystem process models such as *ecosys* would provide us with important insights to improve large-scale representation of these processes into next generation land surface models. ~~Our objective was to test whether this coupling of hydrology with biogeochemistry and plant physiological ecology in *ecosys* would enable successful simulation of diurnal, seasonal and interannual variations in net CO$_2$ exchange as affected by variations in WTD over a drying period from 2004 to 2009 in a western Canadian boreal fen peatland in Alberta, Canada (will be termed as WPL hereafter) (Syed et al., 2006; Flanagan and Syed, 2011). For this purpose, *ecosys* algorithms would first be fed by inputs for peat hydrological, biological, chemical and physical properties, and plant physiology measured at the WPL or similar peatlands. Then the modelled outputs for net ecosystem CO$_2$ exchange and WTD would be tested against site measurements at the WPL. The tested modelled outputs would further be examined to explain WTD effects on C processes at this northern boreal fen.~~

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~~In the past, similar coupling of hydrological, biological and ecological feedbacks enabled *ecosys* to successfully simulate WTD effects on net ecosystem CO$_2$ exchange of two contrasting bog peatlands e.g., (1) a northern shrub-moss peat bog at Mer Bleue, Ontario, Canada (Dimitrov et al., 2011), and (2) a tropical woody peat bog at Palangkaraya, Central Kalimantan, Indonesia (Mezbahuddin et al., 2014); and a northern shrub-sedge fen peatland at Lost Creek, Wisconsin, USA (Grant et al., 2012). But the mixture of moss and woody peats in the boreal fen peatland under current study had a moisture retention characteristic that differed significantly from all the peatlands in those previous studies (Mezbahuddin et al., 2016). Peats in those previous studies drained as soon as the matric water potential (ψ_m) fell below zero. On the contrary, peats under~~

~~current study held moisture content close to saturation and did not drain until ψ_m fell below ~-0.004 MPa (Mezbahuddin et al., 2016). Consequently, the Campbell type (Campbell, 1974) power function in *ecosys*, that was used to simulate peat moisture retention scheme in those previous simulations, significantly underestimated peat moisture content in this boreal fen (Mezbahuddin et al., 2016). However, substitution of the existing power function in *ecosys* with a sigmoidal logistic function (van Genuchten, 1980) significantly improved simulation of peat moisture retention over a wide range of moisture conditions in this boreal fen peatland (Mezbahuddin et al., 2016). Since peat moisture retention largely mediates peat oxygenation and hence peatland biogeochemistry, plant water relations, and CO_2 fixation, testing of *ecosys* algorithms with the inclusion of the improved moisture retention scheme against the measurements at the WPL would offer a further test of robustness of process level modelling of hydrological feedbacks to peatland CO_2 exchange. Moreover, WPL differed from those other peatlands, where *ecosys* algorithms of eco-hydrological and biogeochemical feedbacks were previously tested, either in climate (e.g., boreal vs. temperate vs. tropical), or hydrology (e.g., fen vs. bog), or peatland vegetation (e.g., non-vascular vs. vascular), or peat forming substrates (e.g., moss vs. sedge vs. woody peats), or depth of peat deposits, or in any combination of these peatland characteristics (Dimitrov et al., 2011; Grant et al., 2012; Mezbahuddin et al., 2014, 2015, 2016). Since these peatland characteristics predominantly govern hydrological regulations to peatland C processes, further testing of *ecosys* algorithms at the WPL would thus test the versatility and robustness of coupled ecology, hydrology and biogeochemistry algorithms in simulating and explaining WTD effects on net ecosystem CO_2 exchange across contrasting peatlands. Moreover, since hydrological feedbacks to key peatland C processes are highly non-linear and site-specific, testing of *ecosys* algorithms across contrasting peatlands would also~~

~~facilitate formation of a modelling platform for scaling up simulations of those feedbacks across peatlands at larger spatial scales i.e., national, regional, continental or global as also recommended by Waddington et al. (2015).~~

1.2. Hypotheses

In an ~~field study using~~ eddy covariance (EC) study ~~micro-meteorological approach~~, Flanagan and Syed (2011) found no net effect of a weather driven WTD drawdown ~~from 2004-2009 caused by progressively drier and warmer weather~~ on NEP of WPL over 2004-2009. From the regressions of EC-derived GPP and R_e on site measured WTD, they inferred that the absence of a net effect on NEP was caused by similar increases in GPP and R_e with WTD drawdown. We hypothesized that coupled eco-hydrology and biogeochemistry algorithms ~~a prognostic, dynamic WTD driven by equilibrium between vertical and lateral water fluxes that determines root and microbial redox reactions and energy yields, microbial decomposition, root and microbial growth and uptake~~ in *ecosys* would be able to simulate and explain underlying mechanisms of these effects of WTD drawdown on GPP and R_e and hence NEP at the WPL. ~~For this purpose, w~~We tested the following four ~~modelling~~ central hypotheses ~~while simulating WTD effects on R_e and GPP of WPL~~:

(1) WTD drawdown would increase R_e of the northern fen at the WPL. This effect of WTD drawdown on R_e could be modelled by simulation of ~~cause~~ peat pore drainage and improved peat aeration that would increase the energy yields from aerobic microbial decomposition and hence would increase R_e ~~in the modelled WPL ecosystem~~.

(2) WTD drawdown would increase GPP of the northern fen at the WPL. This effect of WTD drawdown on GPP could be modelled by simulating ~~E~~enhanced microbial activity due to WTD

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drawdown that would ~~also~~ cause more rapid nutrient mineralization and ~~consequent~~ greater root nutrient availability and uptake, greater leaf nutrient concentrations and hence increased GPP.

(3) Increase in R_e with WTD drawdown (hypothesis 1) would cease should WTD fall below a threshold depth. ~~But when the WT falls below a certain threshold level,~~ This threshold WTD effect on R_e could be modelled by simulating inadequate recharge of the near surface peat layers through capillary rise from the deeper WTD below the threshold level that would cause desiccation of those layers. Drying of near surface peat layers and the surface residue could~~an~~ reduce near surface and surface peat respiration that ~~can~~ would partially offset the increase in deeper peat respiration due to aeration ~~in hypothesis 1~~.

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(4) Net effect of threshold WTD on GPP would be driven by the balance between how WTD would affect vascular vs. non-vascular GPP. This threshold WTD effect on GPP would be modelled by simulating vascular vs. non-vascular water relations under deeper WTD below the threshold level. Near surface peat desiccation in hypothesis 3 would ~~also~~ reduce peat water potential and hydraulic conductivity and hence vascular and non-vascular water uptake from desiccated near surface layers. Since non-vascular mosses depend mainly on near surface peat layers for moisture supply, reduction in moss water uptake would cause a reduction in moss water potential and hence moss GPP. On the contrary, suppression of vascular root water uptake from desiccated near surface layers under deeper WT would be offset by increased deeper root water uptake from newly aerated deeper peat layers with higher water potentials that would sustain vascular canopy water potential (ψ_c), canopy stomatal conductance (g_c) and GPP.

2. Methods

2.1. Model development

Ecosys is a process-based terrestrial ecosystem model that simulates 3D water, energy, carbon and nutrient (nitrogen, phosphorus) cycles in different peatlands (Dimitrov et al., 2011; Grant et al., 2012; Sulman et al., 2012; Mezbahuddin et al., 2014, 2015, 2016). *Ecosys* algorithms that govern the effects of WTD variations on ecosystem net CO_2 exchange which are related to our hypotheses are described below. These algorithms in *ecosys* are derived from published independent basic research which describe eco-hydrological and biogeochemical mechanisms that govern carbon, nutrient (N, P), water, and energy balance of terrestrial ecosystems. E~~e~~quations representing *ecosys* algorithms related to our hypotheses ~~that~~ are cited within the text, and are listed in the sections S1-S4 in the supplementary material with references to their sources for further clarification. These site-independent basic terrestrial ecosystem process algorithms in *ecosys* are thus not parameterized for each peatland site. Instead the coupled algorithms are fed with peatland-specific measurable soil, weather, vegetation and management inputs to simulate C, nutrient (N, P), water and energy balance of that particular peatland ecosystem.

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2.1.1. Water table depth (WTD)

The WTD in *ecosys* is calculated at the end of each time step as the depth to the top of the saturated zone below which air-filled porosity is zero (Eq. D32). It is the depth at which lateral water flux is in equilibrium with the difference between vertical influxes (precipitation) and effluxes (evapotranspiration). Lateral water transfer between modelled grid cells in *ecosys* and the adjacent ecosystem occurs to and from a set external WTD (WTD$_x$) over a set distance (L_t) (Fig. 2~~1~~). The WTD$_x$ represents average watershed WTD with reference to average hummock surface. The WTD in *ecosys* is thus not prescribed, but rather controls, and is controlled by lateral and vertical surface and subsurface water fluxes (Eqs. D1-D31). More detail about how peatland WTD, vertical and lateral soil water flow, and soil moisture retention are modelled in *ecosys* can be found in Dimitrov et al. (2010b) and Mezbahuddin et al. (2015, 2016).

2.1.2. Heterotrophic respiration and WTD

WTD fluctuation in *ecosys* ~~, which arises from variations in the balance between vertical and lateral fluxes,~~ determines the boundary between and the extent of aerobic vs. anaerobic soil zones. So WTD fluctuation affects *ecosys*'s algorithms of organic oxidation-reduction transformations and microbial energy yields, which drive microbial growth, substrate decomposition and uptake (Fig. 1) (Eqs. A1-A30). Organic transformations in *ecosys* occur in a residue layer and in each of the user defined soil layers within five organic matter-microbe complexes i.e., coarse woody litter, fine non-woody litter, animal manure, particulate organic C and humus (Fig. 1). Each of the complexes has three decomposition substrates i.e., solid organic C, sorbed organic C and microbial residue C; the decomposition agent i.e., microbial biomass; and the decomposition product i.e., dissolved organic C (DOC) (Fig. 1). Rates of the decomposition and resulting DOC production in each of the complexes is a first-order function of the fraction of substrate colonized by active biomasses (M) of diverse microbial functional types (MFTs). The MFTs in *ecosys* are obligate aerobes (bacteria and fungi), facultative anaerobes (denitrifiers), obligate anaerobes (fermenters), heterotrophic (acetotrophic) and autotrophic (hydrogenotrophic) methanogens, and aerobic and anaerobic heterotrophic diazotrophs (non-symbiotic N_2 fixers) (Fig. 1) (Eqs. A1-A2, A4). Biomass (M) growth of each of the MFTs (Eq. A25a) is calculated from its DOC uptake (Fig. 1) (Eq. A21). The rate of M growth is driven by energy yield from growth respiration (R_g) (Eq. A20) that is calculated by subtracting maintenance respiration (R_m) (Eq. A18) from heterotrophic respiration (R_h) (Eq. A11). The values of R_h are driven by oxidation of DOC (Eq. A13). DOC oxidation may be limited by microbial O_2 reduction (Eq. A14) driven by microbial O_2 demand (Eq. A16) and constrained by O_2 diffusion calculated from aqueous O_2 concentrations in soil ([O_{2s}]) (Eq. A17). Values of [O_{2s}] are maintained by convective-dispersive transport of O_2 from the atmosphere to gaseous and aqueous phases of the soil surface layer (Eq. D41), by convective-dispersive transport of O_2 through gaseous and aqueous phases in adjacent soil layers (Eqs. D42, D44), and by dissolution of O_2 from gaseous to aqueous phases within each soil layer (Eq. D39).

Shallow WTD in *ecosys* can cause lower air-filled porosity (θ_g) in the wetter peat layers above the WT. Lower θ_g reduces O_2 diffusivity in the gaseous phase (D_g) (Eq. D44) and gaseous O_2 transport (Eqs. D41-D42) in these layers. Peat layers below the WT have zero θ_g that prevents gaseous O_2 transport in these layers. So, under shallow WT, [O_{2s}] relies more on O_2 transport through the slower aqueous phase (Eq. D42) which causes a decline in [O_{2s}]. Decline in [O_{2s}] slows O_2 uptake (Eq. A17) and hence R_h (Eq. A14), R_g (Eq. A20) and growth of M (Eq. A25). Lower M slows decomposition of organic C (Eqs. A1-A2) and production of DOC which further slows R_h (Eq. A13), R_g and growth of M (Fig. 1). Although some MFTs can sustain DOC oxidation by reducing alternative electron acceptors (e.g., methanogens reducing acetate or CO_2 to CH_4, and denitrifiers reducing NO_x to N_2O or N_2), lower energy yields from these reactions reduce R_g (Eq. A21), and hence M growth, organic C decomposition and subsequent DOC production (Fig. 1). Slower decomposition of organic C under low [O_{2s}] also causes slower decomposition of organic nitrogen (N) and phosphorus (P) (Eq. A7) and production of dissolved organic nitrogen (DON) and phosphorus (DOP), which causes slower uptake of microbial N and

P (Eq. A22) and growth of *M* (Eq. A29) (Fig. 1). Slower *M* growth causes slower mineralization (Eq. A26), and hence lowers aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (Fig. 1).

WTD drawdown can increase θ_g that results in greater D_g (Eq. D44) and more rapid gaseous O_2 transport. A consequent rise in [O_{2s}] increases O_2 uptake (Eq. A17) and R_h (Eq. A14), R_g (Eq. A20) and growth of *M* (Eq. A25). Larger *M* hastens decomposition of organic C (Eqs. A1-A2) and production of DOC which further hastens R_h (Eq. A13), R_g and growth of *M*. More rapid decomposition of organic C under adequate [O_{2s}] in this period also causes more rapid decomposition of organic N and P (Eq. A7) and production of DON and DOP, which increases uptake of microbial N and P (Eq. A22) and growth of *M* (Eq. A29) (Fig. 1). Rapid *M* growth causes rapid mineralization (Eq. A26), and hence greater aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (Fig. 1).

When WTD recedes below a certain threshold level, capillary rise from the WT can no longer support adequate recharge of the near surface peat layers and the surface litter (Eqs. D9, D12). It causes desiccation of the residue and the near surface peat layers thereby causing a reduction in water potential (ψ_s) and an increase in aqueous microbial concentrations ([M]) in each of these layers (Eq. A15). Increased [M] caused by the peat desiccation reduces microbial access to the substrate for decomposition in each of the desiccated layers and reduces R_h (Eq. A13). Reduction in R_h is calculated in *ecosys* from competitive inhibition of microbial exo-enzymes with increasing concentrations (Eq. A4) (Lizama and Suzuki, 1991).

2.1.3. WTD effects on vascular gross primary productivity

Ecosys simulates effects of WTD variation on vascular GPP from WTD variation effects on root O_2 and nutrient availability and root growth and uptake. Root O_2 and nutrient uptake in *ecosys* are coupled with a hydraulically driven soil-plant-atmosphere water scheme. Root growth in each vascular plant population in *ecosys* is calculated from its assimilation of the non-structural C product of CO_2 fixation (σ_C) (Eq. C20). Assimilation is driven by R_g (Eq. C17) remaining after subtracting R_m (Eq. C16) from autotrophic respiration (R_a) (Eq. C13) driven by oxidation of σ_C (Eq. C14). Oxidation in roots may be limited by root O_2 reduction (Eq. C14b) which is driven by root O_2 demand to sustain C oxidation and nutrient uptake (Eq. C14e), and constrained by O_2 uptake controlled by concentrations of aqueous O_2 in the soil ($[O_{2s}]$) and roots ($[O_{2r}]$) (Eq. C14d). Values of $[O_{2s}]$ and $[O_{2r}]$ are maintained by convective-dispersive transport of O_2 through soil gaseous and aqueous phases and root gaseous phase (aerenchyma) respectively and by dissolution of O_2 from soil and root gaseous to aqueous phases (Eqs. D39-D45). O_2 transport through root aerenchyma depends on species-specific values used for root air-filled porosity (θ_{pr}) (Eq. D45). Shallow WTD and resultant high peat moisture content in *ecosys* can cause low θ_g that reduces soil O_2 transport, forcing root O_2 uptake to rely more on $[O_{2r}]$ and hence on root O_2 transport determined by θ_{pr}. If this transport is inadequate, decline in $[O_{2r}]$ slows root O_2 uptake (Eqs. C14c-d) and hence R_a (Eq. C14b), R_g (Eq. C17) and root growth (Eq. C20b) and root N and P uptake (Eqs. C23b, d, f) (Fig. 1). Root N and P uptake under shallow WT is further slowed by reductions in aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (Eqs. C23a, c, e) from slower mineralization of organic N and P (Fig. 1). Slower root N and P uptake reduces concentrations of non-structural N and P products of root uptake (σ_N and σ_P) with respect to that of σ_C in leaves (Eq. C11), thereby slowing CO_2 fixation (Eq. C6) and GPP.

WTD drawdown facilitates rapid D_g which allows root O_2 demand to be almost entirely met from $[O_{2s}]$ (Eqs. C14c-d) and so enables more rapid root growth and N and P uptake (Eqs. C23b, d, f). Increased root growth and nutrient uptake is further stimulated by increased aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (Eqs. C23a, c, e) from more rapid mineralization of organic N and P during deeper WT (Fig. 1). Greater root N and P uptake increases concentrations of σ_N and σ_P with respect to σ_C in leaves (Eq. C11), thereby facilitating rapid CO_2 fixation (Eq. C6) and GPP. When WT falls below a certain threshold, inadequate capillary rise (Eqs. A9, A12) from deeper WT causes near-surface peat desiccation that reduces soil water potential (ψ_s) and raises soil hydraulic resistance (Ω_s) (Eq. B9), thereby forcing lower root water uptake (U_w) from desiccated layers (Fig. 1) (Eq. B6). However, deeper rooting facilitated by increased [O_{2s}] under deeper WT can sustain U_w (Eq. B6) from wetter deeper peat layers with higher ψ_s and lower Ω_s (Eq. B9). If U_w from the deeper wetter layers cannot offset the suppression in U_w from desiccated near surface layers, the resultant net decrease in U_w causes a reduction in root, canopy and turgor potentials (ψ_r, ψ_c and ψ_t) (Eq. B4) and hence g_c (Eq. B2b) in *ecosys* when equilibrating U_w with transpiration (T) (Eq. B14). Lower g_c reduces CO_2 diffusion into the leaves thereby reducing CO_2 fixation (Eq. C6) and GPP (Eq. C1) (Fig. 1).

2.1.4. WTD effects on non-vascular gross primary productivity

Ecosys simulates non-vascular plants (e.g., mosses) as tiny plants with no stomatal regulations that grow on modelled hummock and hollow grid cells (Dimitrov et al., 2011). Model input for moss population is usually larger and hence intra-specific competition for lights and nutrients is greater so that individual moss plant and moss belowground growth (i.e. root like structures for water and nutrient uptake) are smaller (Eq. C21b). Shallower belowground growth of simulated mosses in *ecosys* means the water uptake of mosses are mostly confined to the near surface peat layers. ~~Effects of WTD drawdown on non-vascular (e.g., moss) GPP in *ecosys* is simulated from peat moisture supplying capacity through capillary rise from the WT to adequately recharge shallow peat layers to sustain moss U_w. Tiny individuals of mosses with no stomatal regulation are simulated in *ecosys* from intra-specific competition for light and nutrients~~

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~~(N, P) among large moss populations. Simulated mosses in *ecosys* are mostly confined to near surface peat layers that are frequently unsaturated.~~ When WT deepens past a threshold level, inadequate capillary rise (Eqs. D9, D12) causes near-surface peat desiccation, thereby reducing ψ_s and increasing Ω_s (Eq. B9) of those layers (Fig. 1). It causes a reduction in moss canopy water potential (ψ_c) while equilibrating moss evaporation with moss U_w (Eq. B6). Reduced moss ψ_c causes a reduction in moss carboxylation rate (Eqs. C3, C6a) and moss GPP (Fig. 1) (Eq. C1).

2.2. Modelling experiment

2.2.1. Study site

The peatland eco-hydrology and biogeochemistry algorithms ~~for effects of WTD variations on ecosystem net CO_2 exchange~~ in *ecosys* were tested in this study against measurements of WTD and ecosystem net CO_2 fluxes at a flux station of the Fluxnet-Canada Research Network established at the WPL (latitude: 54.95°N, longitude: 112.47°W). The study site is a moderately nutrient-rich treed fen peatland within the Central Mixed-wood Sub-region of Boreal Alberta, Canada. Peat depth around the flux station was about 2 m. This peatland is dominated by stunted trees of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) with an average canopy height of 3 m. High abundance of a shrub species *Betula pumila* (dwarf birch), and the presence of a wide range of mosses e.g., *Sphagnum* spp., feather moss, and brown moss characterize the under-storey vegetation of WPL. The topographic, climatic, edaphic and vegetative characteristics of this site were described in more details by Syed et al. (2006).

2.2.2. Field data sets

Ecosys model inputs of half hourly weather variables i.e. incoming shortwave and longwave radiation, air temperature (T_a), wind speed, precipitation and relative humidity during 2003-2009 were measured by Syed et al. (2006) and Flanagan and Syed (2011) at the micrometeorological station installed at the WPL. To test the adequacy of WTD simulation in *ecosys*, modelled outputs of hourly WTD were tested against WTD measured at the WPL with respect to average hummock surface by Flanagan and Syed (2011). To examine how well *ecosys* simulated net ecosystem CO_2 exchange at the WPL, we tested hourly modelled net ecosystem CO_2 fluxes against hourly accumulated measurements~~those measured~~ (average of two half-hourly) collected by~~ using eddy covariance (EC) micro-meteorological approach by~~ Syed et al. (2006) and Flanagan and Syed (2011) by using eddy covariance (EC) micro-meteorological approach. Each of these EC-measured net CO_2 fluxes consisted of an eddy flux and a storage flux (Syed et al. 2006). Erroneous flux measurements due to stable air conditions were screened out with the use of a minimum friction velocity (u*) threshold of 0.15 m s^{-1} (Syed et al. 2006). The net CO_2 fluxes that survived the quality control were used to derive half hourly R_e (=nighttime net CO_2 fluxes) and GPP (=daytime net CO_2 fluxes – R_e) (Barr et al., 2004; Syed et al., 2006). To derive daily, seasonal and annual estimates of GPP, and R_e, the data gaps resulting from the quality control were filled based on empirical relationships between soil temperature at a shallow depth (0.05 m) and measured half hourly R_e, and between incoming shortwave radiation and measured half hourly GPP using 15-days moving windows. The gap-filled R_e and GPP were then summed up for each half hour to fill NEP data gaps to derive daily, seasonal and annual estimates of EC-gap filled NEP (Barr et al., 2004; Syed et al., 2006).~~Quality control, and gap-filling of EC measured net CO_2 fluxes, and partitioning of EC-gap filled net CO_2 fluxes into GPP and R_e were done by Syed et al. (2006) and Flanagan and Syed (2011).~~

Soil CO_2 fluxes measured by automated chambers can provide a valuable supplement to EC CO_2 fluxes in testing modelled respiration by providing more continuous measurements than EC. So, we also tested our modelled outputs against half-hourly automated chamber

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measurements by Cai et al. (2010) at the WPL. These CO_2 flux measurements were carried out during ice-free periods (May-October) of 2005 and 2006 over both hummocks and hollows by using a total of 9 non-steady -state automatic transparent chambers (Cai et al., 2010). A~~part~~ ~~from~~long with soil respiration these chamber CO_2 fluxes ~~thus~~ included fixation and autotrophic respiration from dwarf shrubs, herbs and mosses (Cai et al., 2010). ~~Therefore we compared modelled fixation and autotrophic respiration from understorey PFTs (e.g., shrub and moss) combined with modelled soil respiration against these chamber net~~ ~~CO_2~~ ~~fluxes measured at the WPL. For this purpose net~~ ~~CO_2~~ ~~flux measurements from all of those chambers were averaged and compared against average soil and understorey~~ ~~CO_2~~ ~~fluxes modelled over the hummock and the hollow.~~

2.2.3. Model run

Ecosys model run to simulate WTD effects on net CO_2 exchange of WPL had a hummock and a hollow grid cell that exchanged water, heat, carbon and nutrients (N, P) between them and with surrounding vertical and lateral boundaries (Fig. 2~~1~~). The hollow grid cell had near surface peat layer that was 0.3 m thinner than the hummock cell representing a hummock-hollow surface difference of 0.3 m observed in the field (Long, 2008) (Fig. 2~~1~~). Any depth with respect to the modelled hollow surface would thus be 0.3 m shallower than the depth with respect to the modelled hummock surface.

Peat organic and chemical properties at different depths of the WPL were represented in *ecosys* by inputs from measurements either at the site (e.g., Syed et al., 2006; Flanagan and Syed, 2011) or at similar nearby sites (e.g., Rippy and Nelson, 2007) (Fig. 2~~1~~).~~ However, we did not have any site measurement for the nutrient gain through lateral water inflow which was observed by Syed et al. (2006) during the field measurements. Instead, we used background wet deposition~~

~~rates of 0.5 mg ammonium-N, 0.25 mg nitrate-N and 0.075 mg phosphate-P per litre of precipitation water to simulate an additional source of nutrient input.~~

Ecosys was run for a spin up period of 1961-2002 under repeating 7-year sequences of hourly weather data (shortwave and longwave radiation, air temperature, wind speed, humidity and precipitation) recorded at the site from 2003 to 2009. There was a drying trend observed from 2003 to 2009 due to diminishing precipitation that caused WTD drawdown in the watershed in which WPL is located, which lowered the WT of this fen peatland (Flanagan and Syed, 2011). To accommodate the gradual drying effects of catchment hydrology on modelled fen peatland WTD, we set the WTD_x at different levels based on the annual wetness of weather, e.g., shallow, intermediate, and deep (WTD_x=0.19, 0.35 and 0.72 m below the hummock surface, or 0.11 m above and 0.05 and 0.42 m below the hollow surface) (Fig. 2~~1~~). There was no exchange of water through lower model boundary to represent the presence of nearly impermeable clay sediment underlying the peat (Syed et al., 2006) (Fig. 2~~1~~). Variations in peat surface with WTD variations, which is an important hydrologic self-regulation of boreal peatlands (Dise, 2009), was not represented in this version of *ecosys*.

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At the start of the spin up run, the hummock grid cell was seeded with an evergreen needle leaf and a deciduous needle leaf over-storey plant functional types (PFT) to represent the black spruce and tamarack trees at the WPL. The hollow grid cell was seeded with only the deciduous needle leaf over-storey PFTs since the black spruce trees at the WPL only grew on the raised areas. Each of the modelled hummock and the hollow was also seeded with a deciduous broadleaved vascular (to represent dwarf birch) and a non-vascular (to represent mosses) under-storey PFTs. The planting densities were such that the population densities of the black spruce, tamarack, dwarf birch and moss PFTs were 0.16, 0.14, 0.3, and 500 m^{-2} respectively at the end of the spin up run so as to best represent field vegetation (Syed et al., 2006; Mezbahuddin et al., 2016). To include wetland adaptation, we used a root porosity (θ_{pr}) value of 0.1 for the two over-storey PFTs and a higher θ_{pr} value of 0.3 for the under-storey vascular PFT to represent better wetland adaptation in the under-storey than the over-storey PFTs. These θ_{pr} values were used in calculating root O_2 transport through aerenchyma (Eq. D45) and did not change with waterlogging throughout the model run. These θ_{pr} values were representatives of root porosities measured for various northern boreal peatland plant species (Cronk and Fennessy, 2001). Non-symbiotic N_2 fixation through association of cyanobacteria and mosses are also reported for Canadian boreal forests (Markham, 2009). This was represented in *ecosys* as N_2 fixation by non-symbiotic heterotrophic diazotrophs (Eq. A27) in the moss canopy. Further details about *ecosys* model set up to represent the hydrological, physical and ecological characteristics of WPL can be found in Mezbahuddin et al. (2016).

When the modelled ecosystem attained stable values of net ecosystem CO_2 exchange at the end of the spin-up run, we continued the spin up run into a simulation run from 2003 to 2009 by using a real-time weather sequence. We tested our outputs from 2004-2009 of the simulation run against the available site measurements of WTD, net EC CO_2 fluxes and net chamber CO_2 fluxes over those years.

2.2.4. Model validation

To examine the adequacy of modelling WTD effects on canopy, root and soil CO_2 fluxes which were summed for net ecosystem CO_2 exchange at the WPL, we spatially averaged hourly net CO_2 fluxes modelled over the hummock and the hollow to represent a 50:50 hummock-hollow ratio and then regressed against hourly EC measured net ecosystem CO_2 fluxes for each year from 2004-2009 with varying WTD. Each of these hourly EC measured net ecosystem CO_2

fluxes used in these regressions is an average of two half-hourly net CO_2 fluxes measured at a friction velocity (u*) greater than 0.15 m s^{-1} that survived quality control procedure (Sec. 2.2.2). Model performance was evaluated from regression intercepts (a→0), slopes (b→1), coefficients of determination (R^2→1), and root means squares for errors (RMSE→0) for each study year to test whether there was any systematic divergence between the modelled and EC measured CO_2 fluxes.

Similar regressions were performed between ~~Therefore we compared~~ modelled and automated chamber measured net CO_2 fluxes for ice free periods (May-October) of 2005 and 2006 to further test the robustness of modelled soil respiration under contrasting WTD conditions. Each of the half-hourly measured chamber net CO_2 fluxes included soil respiration, and fixation and autotrophic respiration from understorey vegetation (e.g., shrubs, herbs and mosses)~~from understorey PFTs (e.g., shrub and moss)~~. So, we combined ~~with~~ modelled soil respiration with modelled fixation and autotrophic respiration from understorey PFTs for comparison against these chamber measured net CO_2 fluxes~~ measured at the WPL~~. ~~For this purpose~~We also averaged net CO_2 flux measurements from all of the~~ose~~ 9 chambers ~~were averaged~~ for each half hour to accommodate the variations in those fluxes due to microtopography (e.g., hummock vs. hollow). Two half hourly averaged values of net CO_2 fluxes were then averaged again to get hourly mean net chamber CO_2 fluxes for comparison against modelled hourly sums of soil and understorey fluxes averaged over modelled hummock and hollow. Model performance was evaluated from regression intercepts (a→0), slopes (b→1), coefficients of determination (R^2→1), and root means squares for errors (RMSE→0) for each of 2005 and 2006.~~and compared against average soil and understorey CO_2 fluxes modelled over the hummock and the hollow.~~~~of modelled vs. gap-filled net CO_2 fluxes were also performed to test~~

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~~for any divergence between the modelled and gap-filled CO_2 fluxes. These regressions based tests are very important since any small divergence between hourly modelled and EC measured as well as between hourly modelled and gap-filled CO_2 fluxes can result in a large divergence between modelled and EC-gap filled annual estimates.~~

2.2.5. Sensitivity of modelled peatland CO_2 exchange to artificial drainage

Large areas of northern boreal peatlands in Canada have been drained primarily for increased forest and agricultural production since plant productivity in pristine peatlands are known to be constrained by shallow WTD (Choi et al., 2007). Drainage and resultant WTD drawdown can affect both GPP and R_e on a short-term basis and the vegetation composition on a longer time scale thereby changing overall net CO_2 exchange trajectories of a peatland. To predict short-term effects of drainage on WTD and hence ecosystem net CO_2 exchange of WPL, we extended our simulation run into a projection run consisting two 7-yr cycles by using repeated weather sequences of 2003-2009. While doing so, we forced a stepwise drawdown in WTD_x by 1.0 and 2.0 m from that used in spin-up and simulation runs (Fig. 2~~1~~) in the first (drainage cycle 1) and the second cycle (drainage cycle 2) respectively. This projection run would give us a further insight about how the northern boreal peatland of Western Canada would be affected by further WTD drawdown as a result of drier and warmer weather as well as a disturbance such as drainage. It would also provide us with a test of how sensitive the modelled C processes were to the changes in model lateral boundary condition as defined by WTD_x in *ecosys*.

3. Results

3.1. Model performance in simulating diurnal variations in ecosystem net CO_2 fluxes

Variations in precipitation can cause change in WTD and consequent variation in diurnal net CO_2 exchange across years. *Ecosys* simulated ~~diurnal~~ hourly EC-measured net CO_2 fluxes ~~reasonably~~ well ~~which was measured each year from~~over 2004-~~ to ~~2008 with varying precipitation (Table 1a). On a year-to-year basis, regressions of hourly modelled vs. EC-measured net ecosystem CO_2 fluxes gave intercepts within 0.1 μmol m^{-2} s^{-1} of zero, and slopes within 0.1 of one, indicating minimal bias in modelled outputs during each year from 2004-2008 (Table 1a). On a growing season (May-August) basis, regressions of modelled on measured hourly net CO_2 fluxes yielded larger positive intercepts from 2004-2009 (Table 1b~~2~~). The larger intercepts were predominantly caused by modelled overestimation of growing season day-time CO_2 fluxes. This overestimation was offset by modelled overestimation of night-time CO_2 fluxes during the winter thus yielding smaller intercepts from throughout-the-year regressions of modelled vs. EC measured fluxes (Tables 1a vs. b~~2~~). ~~We could not do a modelled vs. EC CO_2 regression for the entire year of 2009 due to the lack of flux measurements from September to December in that year.~~ Values for coefficients of determination (R^2) were ~ 0.8 ($P < 0.001$) for all years from both throughout-the-year and growing season regressions (Tables 1~~ and 2~~a, b). RMSEs were < 2.0 and ~2.5 μmol m^{-2} s^{-1} for whole year regressions from 2004-2008 (Table 1a) and for growing season regressions from 2004-2009 (Table 1b~~2~~) respectively. Much of the variations in EC measured CO_2 fluxes that was not explained by the modelled fluxes could be attributed to a random error of ~20% in EC methodology (Wesely and Hart, 1985). This attribution was further corroborated by root mean squares for random errors (RMSRE) in EC measurements, calculated for forests with similar CO_2 fluxes from Richardson et al. (2006) that were similar to RMSE (Tables 1a, b). The similar values of RMSE and RMSRE also indicated that further constraint in model testing could not be achieved without further precision in EC measurements.

Regressions of modelled vs. ~~gap-filled~~chamber measured net CO_2 fluxes gave ~~slopes and~~ R^2 of $\sim$0.7 for ice-free periods (May-October) of 2005 and 2006 indicated that the variations in soil respiration, and the fixation and aboveground autotrophic respiration due to WTD drawdown were modelled well (Table 1c). Smaller intercepts from those regressions meant lower model biases in simulating soil and understorey CO_2 fluxes under deepening WT (Table 1c). Although the slope was within 0.1 of one in 2005, it was a bit smaller in 2006 indicating lower modelled vs. chamber measured soil and understorey net CO_2 fluxes in 2006 (Table 1c). It was because some of the nighttime chamber fluxes in warmer nights of summer 2006 were as large as the EC measured ecosystem net CO_2 fluxes corresponding to those same hours which could not be modelled to their full extent. RMSE lower than RMSRE meant the errors in modelling soil and understorey CO_2 fluxes were within the limit of random errors due to chamber measurements (Table 1c). It further indicated the robustness of modelled outputs for soil and understorey CO_2 fluxes under different WTD conditions (e.g., shallower in 2005 vs. deeper in 2006) (Table 1c). ~~which were similar to, and RMSEs which were smaller than those from modelled vs. EC-measured CO_2 fluxes for most of the years except for the throughout-the-year regressions in 2004 and 2006 when the slopes were larger (Tables 1 and 2). The intercepts from modelled vs. gap filled CO_2 fluxes were consistently more negative than those from modelled vs. EC measured fluxes for both whole year (Table 1) and growing season (Table 2) regressions. It was mainly caused by larger modelled than gap filled night-time CO_2 effluxes.~~

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3.2. Seasonality in WTD and net ecosystem CO_2 exchange

Ecosys simulated the seasonal and interannual variations in WTD from 2004 to 2009 well at the WPL ~~Seasonality in WTD measured at the WPL showed interannual variation from 2004 to 2009 which was modelled reasonably well by *ecosys* (Figs. 2b, d, f, h, j, l). The interannual variation in seasonality of WTD was modelled by adequate simulation of the balance between vertical water fluxes i.e., precipitation vs. evapotranspiration and lateral water fluxes i.e., recharge vs. discharge. Larger precipitation to evapotranspiration ratio (*P/ET*) throughout 2004 caused the shallowest modelled WTD which remained above the hollow surface throughout most of the year (Fig. 2b). WTD$_x$ (=0.19 m) (Fig. 1) shallower than the modelled WTD in 2004 created a hydraulic gradient that caused net lateral recharge and hence further sustained the shallow modelled WTD. A smaller *P/ET* in 2005 than in 2004 caused slightly deeper WTD that remained at the hollow surface or within 0.1 m below the hollow surface (Fig. 2d). During this year, WTD$_x$ (=0.19 m) (Fig. 1) shallower than the modelled WTD caused net lateral recharge and hence further sustained WTD close to the hollow surface. Declines in the *P/ET* over the growing seasons of 2006 and 2007 caused modelled WTD drawdown to levels where the differences between evapotranspiration and precipitation equilibrated with net lateral recharge caused by hydraulic gradients yielded from WTD$_x$ (=0.35 m) (Fig. 1) which was deeper than the modelled WTD in both years (Figs. 2f, h). Continued declines in growing season *P/ET* in 2008 and 2009 caused further deepening of the WT (Figs. 2j, l). A WTD$_x$ (=0.72 m) (Fig. 1) deeper than the modelled WTD in these growing seasons generated hydraulic gradients that caused net lateral discharge which further deepened WT. Above mentioned modelled interannual variations in seasonality of WTD from 2004 to 2009 were well corroborated by site measured half hourly WTD at the WPL~~ (Figs. 3~~2~~b, d, f, h, j, l) (Mezbahuddin et al., 2016).

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Seasonality in net CO_2 exchange at the WPL was predominantly governed by that in temperature which controlled the seasonality in phenology and GPP as well as that in R_e. *Ecosys* simulated the seasonality in phenology and hence GPP, and R_e ~~reasonably~~ well during a gradual growing season WTD drawdown from 2004 to 2009 which was apparent by good agreements between modelled vs. EC-gap filled daily NEP (Fig. 3~~2~~) and modelled vs. EC-measured hourly net CO_2 fluxes (Table~~s~~ 1~~ and 2~~). Modelled NEP throughout the winters of most of the years were more negative than the EC-gap filled NEP indicating larger modelled ~~than EC-gap filled winter~~ CO_2 effluxes than EC-gap filled fluxes during the winter (Fig. 3~~2~~). ~~This trend was also indicated by negative intercepts from throughout-the-year regressions of modelled vs. gap-filled CO_2 fluxes (Table 1).~~ The onset of photosynthesis at the WPL varied interannually depending upon spring temperature which was also modelled ~~adequately~~ well by *ecosys*. For instance, *ecosys* modelled ~~2004 with a cooler spring produced~~ a smaller early growing season (May) GPP and hence NEP in 2004 with a cooler spring than 2005 ~~with a warmer spring~~ which was also apparent in daily EC-gap filled ~~and modelled~~ NEP (Figs. ~~2~~3a vs. ~~2~~c).

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3.3. WTD effects on diurnal net ecosystem CO_2 exchange

WTD variation can affect diurnal net CO_2 exchange by affecting peat O_2 status and consequently root and microbial O_2 and nutrient availability, growth and uptake thereby influencing CO_2 fixation and~~/or~~ respiration. ~~*To examine modelled vs. measured*~~*Ecosys* simulated WTD effects on diurnal net CO_2 exchange at the WPL well over~~, we examined~~ three 10-day periods with comparable weather conditions (radiation and air temperature) during late growing seasons (August) of 2005, 2006 and 2008 ~~that differed predominantly in their WTD during late growing seasons (August) of 2005, 2006 and 2008~~ (Fig. 4~~3~~). A WTD drawdown from August ~~late growing season of~~ 2005 to ~~that of~~August 2006 in *ecosys* caused a reduction in peat water

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contents and a consequent increase in O_2 influxes from atmosphere into the peat that eventually caused an increase in modelled soil CO_2 effluxes (Fig. 5~~4~~c). This stimulation of soil respiration was corroborated by modelled vs. chamber measured (Cai et al., 2010) night-time soil CO_2 fluxes and understorey autotrophic respiration (R_a) in August 2006 with deeper WTD which were larger than those in 2005 with shallower WTD (Fig. 5b). ~~Increased~~ Larger modelled soil CO_2 effluxes in~~ mid-August of~~ 2006 contributed to the larger modelled ecosystem CO_2 effluxes (R_e) ~~as apparent in larger modelled night-time fluxes in the late growing season of 2006 than in that of 2005 which~~that was ~~well corroborated~~ also apparent in ~~by~~ night-time EC CO_2 fluxes in 2006 which were larger than those in 2005 ~~during those periods~~ (Fig. 5~~4~~a). ~~The stimulation of R_e as a result of WTD drawdown was further corroborated by larger sums of night-time soil CO_2 fluxes and understorey autotrophic respiration (R_a) as measured by Cai et al. (2010) using automated chambers and modelled by *ecosys* in late growing season of 2006 with deeper WTD than in that of 2005 with shallower WTD (Fig. 4b).~~

~~Further~~ Continued WTD drawdown into the late growing season of 2008 (Fig. 4~~3~~c) ~~caused~~ sustained improved peat oxygenation and hence larger modelled soil CO_2 effluxes ~~in the model~~ (Fig. 5~~4~~c). ~~It contributed to similarly larger~~Consequently, modelled night-time net ecosystem CO_2 fluxes, and soil and understorey CO_2 fluxes in ~~the late growing seasons of~~ 2006 and in 2008 were similarly larger than those in 2005 ~~that~~ which was ~~were also well~~ corroborated well by EC measured night-time fluxes during ~~those periods~~2006 and 2008 vs. 2005 (Figs. 5~~4~~a-b). Although ~~Consequently, the sums of modelled night-time soil CO_2 fluxes and understorey R_a in late growing season of 2008 were similarly larger as in 2006 with respect to those in that period of 2005 (Fig. 4b). We did not have any chamber measurements available for 2008 to corroborate the modelled outputs. Despite larger~~ night-time modelled and EC measured net

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ecosystem CO_2 fluxes in ~~the late growing season of~~ 2008 were larger than those in 2005, the day-time modelled and EC measured ~~influxes~~ CO_2 fluxes in 2008 ~~were also similar to those in 2005~~did not decline with respect to those in 2005 (Fig. 5~~4~~a). Similar day-time fluxes in 2005 and 2008 despite larger night-time fluxes in 2008 than in 2005~~It~~ indicated a greater late growing season CO_2 fixation in 2008 with deeper ~~with~~ WTD ~~drawdown from 2005 to 2008~~than in 2005 with shallower WTD. ~~WTD drawdown thus stimulated both the night-time and the day-time net CO_2 fluxes as apparent in both the modelled outputs and in EC flux measurements during the three WTD conditions mentioned above thereby indicating increases in both R_e and GPP with the deepening of WT.~~

~~Apart from~~Beside WTD, temperature variation ~~could~~ also profoundly affected ecosystem net CO_2 exchange at the WPL. For a given WTD condition~~,~~ warmer weather caused increases in R_e at the WPL (Figs. ~~3~~4b-c and 5~~4~~a-b). ~~Larger n~~Night-time modelled, and EC~~-gap filled~~ and chamber measured ecosystem, soil, and understorey CO_2 fluxes, in warmer nights of day 214, 220 and 222 were larger than those in ~~the~~ cooler nights of day 221, 224 and 218 in 2005, 2006 and 2008 respectively ~~indicated the trend of increased R_e with warming under similar WTD condition~~ (Figs. 4~~3~~b and 3~~4~~a-b). However, ~~at~~ for a ~~similar~~ given temperature ~~conditions,~~ modelled and EC-gap filled night-time ecosystem CO_2 fluxes, ~~as well as~~and modelled and chamber measured ~~sums of~~ night-time soil and understorey CO_2 fluxes were larger ~~and understorey R_a~~ under deeper WT conditions in 2006 and 2008 ~~were larger~~ than ~~those in 2005~~ under shallower WT condition in 2005 (denoted by the grey arrows in Figs. 4~~3~~b and 5~~4~~a-b). It~~It indicated R_e stimulation as a result of WTD drawdown at the WPL regardless of temperature condition that further corroborated the net effects of WTD drawdown~~showed net WTD

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drawdown effect on R_e (separated from temperature effect) and hence on ~~net ecosystem CO_2 exchange~~NEP.

The degree of R_e stimulation ~~in R_e at the WPL~~ due to warming was also influenced by WTD at the WPL ~~conditions~~. ~~To study this effect we further examined three 4-day warming events in late July and early to mid-August of 2005, 2006 and 2008 with gradually deeper WT (Figs. 5a-f).~~ The warming events in early to mid-August of 2006 and 2008, when WT was deeper than in late July of 2005, caused gradual increases in ~~R_e as apparent from gradually larger~~ modelled, and ~~and~~ EC~~-gap filled~~ and chamber measured night-time ecosystem, soil and understorey CO_2 effluxes (=R_e) (Figs. 6~~5~~h, ~~-i~~i, k, l). ~~Increases in R_e due to warming under deeper WT were also apparent in gradually larger modelled and sums of chamber-measured night-time soil CO_2 fluxes and understorey R_a in 2006 and modelled understorey and soil CO_2 fluxes in 2008 (Figs. 5k-l).~~ This R_e stimulation due to warming under deeper WT contributed to declines in modelled and EC-gap filled July-August NEP in 2006 and 2008 (Figs. 3~~2~~e, i). ~~Unlike in 2006 and 2008, a late-July warming event in 2005 with shallower WT did not yield a similarly evident stimulation of either modelled or EC-gap filled R_e and either modelled or chamber measured soil and understorey respiration (Figs. 5g, j).~~ Lack of similar stimulation in R_e with warming under shallower WT in 2005 did not yield a similarly evident stimulation of either modelled or EC or chamber measured ecosystem, soil and understorey night-time CO_2 effluxes (Figs. 6g, j vs. h, i, k, l) which resulted in the absence of decline in July-August NEP as occurred in 2006 and 2008 (Figs. 3~~2~~c vs. ~~2~~e, i). ~~These findings thus showed that the~~Greater warming driven R_e stimulation ~~of R_e due to warming was greater with~~under deeper WT ~~thereby further indicating~~further indicated the importance of WTD in mediating potential ~~future warming~~ effects of future warmer climates on ~~NEP of northern~~ boreal peatland NEP~~s~~.

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3.4. Interannual variations in WTD and net ecosystem productivity

The effects of WTD drawdown on modelled and EC-gap filled diurnal net ecosystem CO_2 exchange also contributed to the effects of interannual variation in WTD on that of NEP. *Ecosys* simulated a site measured gradual drawdown of average growing season (May-August) WTD well from 2004 to 2009 ~~from gradually declining growing season *P/ET* and lateral water gain through recharge (Fig.~~ 7~~6d). Simulated WTD drawdown was corroborated well by site measured WTD at the WPL~~ (Fig. 7~~6~~d) (Mezbahuddin et al., 2016). ~~Slightly~~ A small WTD drawdown ~~deeper WT in 2005 than in 2004 caused~~simulated a large ~~larger~~ increase in growing season GPP from 2004 to 2005 ~~in *ecosys* that~~~~which was also corroborated by~~~~apparent~~as corroborated by similar increase in~~in~~ EC-derived GPP (Fig. 7~~6~~b). Th~~e increase in GPP from 2004 to 2005~~is increase in GPP was also contributed by a larger GPP in ~~warmer~~ May ~~of~~ 2005 which was warmer than May 2004 ~~than 2004~~. This small ~~Slight~~ WTD drawdown, however, ~~from 2004 to 2005~~ did not raise either modelled or EC-derived growing season R_e from 2004 to 2005 (Fig. ~~6~~7c). ~~It was because of~~ June and July of~~in~~ 2005 ~~being~~ was ~~more than~~cooler than 2004 by over ~~-~~2°C ~~cooler~~ which ~~than in 2004 thereby causing~~caused cooler soil ~~which~~ that reduced R_e in 2005. Reduction in R_e in June~~ and ~~-July ~~R_e in~~ 2005 due to cooler soil more than fully offset the increase in R_e due to ~~slight~~ the small WTD drawdown and resulted in ~~decreased growing season~~ modelled and EC-derived R_e ~~in 2005~~ that were smaller in the growing season of 2005 than in 2004 (Fig. 7~~6~~c). Larger GPP and smaller R_e ~~together~~ gave rise to modelled and EC-gap filled ~~caused a larger~~ growing season NEP estimates ~~in 2005 which~~that were larger in 2005 than those in 2004 (Fig. 7~~6~~a).

WTD drawdown ~~in *ecosys*~~ from 2005 to 2006 ~~caused increases~~~~increased~~raised both ~~in both~~ modelled and EC-derived growing season GPP and R_e ~~that was corroborated by EC-derived~~

~~GPP and R_e~~ (Figs. 7~~6~~b-c)~~. Increases in GPP and in R_e with deepening of WT from 2005 to 2006 were also apparent in modelled vs. EC-gap filled and chamber diurnal net CO_2 fluxes (Figs. 54 65)~~. Warmer growing season in 2006 ~~than in 2005 (Fig. 76d)~~ caused warmer soil that further contributed to the increase in modelled and EC-derived growing season R_e from 2005 with shallower WT to 2006 with deeper WT (Figs. 5~~4~~, 6~~5~~ and 7~~6~~c-d). A~~ larger~~n increase in growing season R_e that was ~~than~~ greater than ~~an~~the increase in ~~that in~~growing season GPP ~~from 2005 to 2006~~ ~~caused~~ caused a decline in modelled and EC-derived growing season NEP from 2005 to 2006 ~~to decrease from 2005 to 2006~~ (Fig. 7~~6~~a). Continued growing season WTD drawdown from 2006 to 2008 caused similar increases in modelled growing season GPP and R_e ~~that caused~~ and hence no significant change~~s~~ in modelled growing season NEP (Figs. ~~6~~7a-d). ~~Like the modelled estimates, EC-derived growing season GPP and R_e also increased with WTD drawdown from 2006 to 2008 (Figs. 6a-d). However~~W~~,~~ith this continued WTD drawdown from 2006 to 2008, however, ~~the rate of increase in~~ EC-derived growing season GPP ~~R_e~~ increased more than EC-derived growing season R_e ~~was smaller than that in modelled growing season R_e thereby contributing to a larger growing season EC-gap filled NEP estimate in 2008 that was larger than that in 2006~~that resulted a larger EC-derived NEP in the growing season of 2008 than in 2006 ~~which was not apparent in modelled estimates~~ (Figs. 7~~6~~a-d~~e~~). A further drawdown in WTD from the growing season of 2008 to that of 2009 caused reductions in both modelled and EC-derived growing season GPP and R_e (Figs. 7~~6~~a-d). Reductions in GPP and R_e from 2008 to 2009 ~~could also be~~was also contributed by lower T_a in 2009 than in 2008 that caused cooler canopies and soil (Figs. 7~~6~~b-d). The reduction in EC-derived growing season GPP was larger than that in EC-derived growing season R_e thereby causing a decrease in growing season EC-gap filled NEP from 2008 to 2009 (Figs. 7~~6~~a- c). On the contrary, the reduction in modelled growing season

GPP ~~from 2008 to 2009~~ was ~~less~~ smaller than ~~that~~ the reduction in ~~the EC-derived~~modelled R_e ~~GPP thereby~~that ~~causing~~ yielded an increase in modelled growing season NEP from 2008 to 2009 (Figs. 7~~6~~a-c).

~~Despite the counteracting and offsetting effects of WTD and T_a on GPP and R_e, larger m~~Modelled and EC-derived estimates of growing season GPP and R_e in 2009 were larger than those in 2004 ~~with~~ despite similar mean T_a in those years (Figs. 7a-d). It suggested that ~~both modelled and EC-derived growing season GPP and R_e increased~~increases in growing season GPP and R_e ~~with the deepening of average growing season WT~~ from 2004 to 2009 was a net effect of the deepening of average growing season WT ~~at the WPL~~ (Figs. 7~~6~~a-d). It was further corroborated by polynomial regressions of modelled growing season estimates of GPP and R_e ~~on~~ against modelled average growing season WTD, and similar regressions of EC-derived growing season GPP and R_e ~~on~~ against site measured average growing season WTD (Figs. 8~~7~~a-c). These relationships showed that there were increases in modelled and EC-derived growing season GPP and R_e with deepening of the growing season WT from 2004 to 2008 after which further WTD drawdown in 2009 started to cause slight declines in both GPP and R_e (Figs. 8~~7~~b-c). Neither modelled nor EC-gap filled estimates of growing season NEP yielded significant regressions when regressed ~~on~~ against modelled and measured growing season WTD respectively (Fig. 8~~7~~a). It indicated that similar increases in modelled and EC-derived growing season estimates of GPP and R_e with deepening of WT ~~along with some counteracting effects of T_a~~ left no net effects of WTD drawdown on either modelled or EC-derived growing season NEP (Figs. 7~~6~~ and 8~~7~~a).

~~WTD effects on growing season GPP and R_e and hence NEP from 2004 to 2009 as measured at the WPL and modelled by *ecosys* were also consistent at an annual time scale from 2004 to 2008 (Figs. 6e-h).~~ Similar to the growing season trend, drawdown of both measured and

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modelled WTD averaged over the ice free periods (May-October) from 2004 to 2008 generally stimulated annual modelled and EC-derived GPP and R_e (Figs. 7~~6~~f, g, h and 8~~7~~e, f).~~ The deepening of WT also raised modelled and EC-derived annual R_e from 2005 to 2008 as was in the case of growing season R_e (Figs. 6g-h and 7f). ~~ Similar increases in both modelled and EC-derived annual GPP and R_e with WTD drawdown left no net WTD effects on modelled and EC-gap filled annual NEP (Figs. 7e, 8~~7~~d).~~ We did not include the year 2009 while examining the effects of WTD drawdown on interannual variation of GPP, R_e and NEP due to the lack of EC CO_2 flux measurements from September to December in 2009 (Figs. 6e-h and 7d-f). Even~~ Although~~,~~ modelled WTD effects on GPP, R_e and hence NEP ~~were~~ corroborated well by EC-derived GPP, R_e and EC-gap filled NEP, the modelled growing season and annual GPP and R_e were consistently higher than the EC-derived estimates of those ~~from~~ throughout ~~2004 to 2009~~the study period (Figs. ~~6~~7-8~~7~~).

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Increased GPP with WTD drawdown (Figs. ~~6~~7b, f and 8~~7~~b, e) was modelled ~~by *ecosys*~~ predominantly through increased root growth and uptake of nutrients and consequently improved leaf nutrient status and hence more rapid CO_2 fixation in vascular PFTs. Under shallow WT during the growing season of 2004, roots in modelled black spruce and tamarack PFTs hardly grew below 0.35 m from the hummock surface~~ (black spruce was not planted in the hollow) and the roots of modelled tamarack PFT were mostly confined within 0.35 m below the hummock surface and 0.05 m below the hollow surface~~. Modelled root densities of both black spruce and tamarack were higher by 2-3 orders of magnitude in the top 0.19 m of the hummock (data not shown). A WTD drawdown ~~from~~ by ~0.~~05~~ 4 m ~~above the hollow surface (~0.25 m below the hummock surface) in the growing season of 2004 to ~0.35 m below the hollow surface (~0.65 m below the hummock surface) in the growing season of 2009~~from the growing season of 2004 to that of 2009 caused ~~an~~ increase in maximum modelled rooting depth ~~from 0.35 to 0.65 m below the hummock surface in black spruce and from 0.35 to 0.65 m below the hummock and from 0.05 to 0.35 m below the hollow surface in the tamarack PFT~~in both PFTs (Table 2). Increased root growth in modelled vascular PFTs augmented root surface area for nutrient uptake under deeper WT in the growing season of 2009 than in 2004. Increased root surface area along with increased nutrient availability due to more rapid mineralization with improved aeration as a result of WTD drawdown from 2004 to 2009 caused improved root nutrient uptake in modelled vascular PFTs. Increased root growth, nutrient availability and hence uptake due to WTD drawdown from the growing season of 2004 to that of 2009 ~~in *ecosys*~~ caused an increase in modelled foliar N concentrations in black spruce, tamarack and dwarf birch PFTs ~~from 14, 32, and 37 g N kg^{-1} C to 17, 37 and 45 g N kg^{-1} C respectively,~~ driving the increases in GPP modelled over this period (Figs. 7~~6~~b, f and 8~~7~~b, e) (Table 2)~~. The modelled foliar N concentrations in the growing season of 2004 were well corroborated by the foliar N concentrations of 12, 33 and 41 g N kg^{-1} C for black spruce, tamarack and dwarf birch as measured by Syed et al. (2006) during summer 2004 at our study site~~.

3.5. Simulated drainage effects on WTD and NEP

Artificial drainage can drastically alter ~~the~~ WTD in a peatland that can cause dramatic changes in peatland NEP by shifting the balance between GPP and R_e. ~~To predict drainage effects on WTD and hence C balance of WPL, we performed a projected drainage simulation in *ecosys* with two additional 7-year weather cycles (Sect. 2.2.5). This drainage simulation would also serve as a climate change analog in providing us insight into how potential WTD drawdown under future drier and warmer climates would affect boreal peatland GPP,~~ ~~R_e and hence NEP. Forcing WTD$_x$ deeper by 1 and 2 m in the~~Projected ~~drainage cycles 1 and 2 lowered~~ growing season WT was deeper by ~~by~~ ~0.5 m and ~0.55 m respectively from those in the real-time simulation in drainage cycles 1 and 2 in all the years from 2004 to 2009 (Fig. 9~~8~~a).

~~The projected drawdown of growing season WTD in *ecosys* caused changes in modelled growing season NEP, GPP and R_e.~~ Modelled growing season GPP increased with drainage-induced WTD drawdown up to ~0.5 m below the hollow surface (~0.8 m below the hummock surface) below which GPP decreased (Figs. 9~~8~~c, f). The WTD drawdown affected modelled vascular and non-vascular growing season GPP quite differently. Modelled growing season vascular GPP increased with WTD drawdown before it plateaued and eventually decreased when WTD fell below ~0.6 m from the hollow surface (~0.9 m below the hummock surface) (Figs. 10~~9~~a, c, e). On the contrary, modelled non-vascular growing season GPP continued to decrease with WTD drawdown below ~0.1 m from the hollow surface (~0.4 m below the hummock surface) (Figs. 10~~9~~a-b, d).

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WTD drawdown due to simulated drainage not only affected modelled growing season GPP but also affected, and was affected by, the associated change in ~~evapo~~transpiration from vascular canopies. Deeper WTD$_x$ in drainage cycle 1 caused larger hydraulic gradients and greater lateral discharge thereby deepening the WT with respect to that in the real-time simulation (Figs. ~~8~~10a). Larger GPP throughout the growing seasons of 2004-2007 in the drainage cycle 1 than in the real-time simulation caused a greater vertical water loss through ~~evapotranspiration~~ rapid transpiration from vascular canopies that further contributed to this deepening of WT (Fig. 9~~8~~b). However, greater lateral water discharge in drainage cycle 2 caused by deeper WTD$_x$ did not deepen the modelled growing season WT much below that in cycle 1 (Fig. 9~~8~~a). The larger lateral water loss through discharge in drainage cycle 2 than in cycle 1 was mostly offset by slower vertical water losses ~~through evapotranspiration~~due to vascular plant water stress as indicated by smaller GPP in the drainage cycle 2 (Fig. 9~~8~~b). The changing feedbacks between WTD, and GPP and ~~hence evapotranspiration~~plant water relations in *ecosys* also indicated the ability of the model to simulate hydrological self-regulation which is an important characteristic of peatland eco-hydrology (Dise, 2009).

Modelled growing season R_e continued to increase with projected ~~deepening of modelled~~ drainage driven WTD drawdown~~ due to drainage~~ (Figs. 9~~8~~d, g). Reductions in modelled growing season R_e from drainage cycle 1 to 2 during 2006-2009 indicated R_e inhibition due to desiccation of near surface peat layers and surface residues (Fig. 9~~8~~d). Overall ~~larger increases in~~ GPP increased more than ~~those in~~ R_e with drainage driven initial WTD drawdown ~~in the drainage simulation~~ that caused a small~~slightly~~ increase in~~d~~ modelled growing season NEP (Figs. ~~8~~9 b, e). Continued drainage driven WTD drawdown, however, ~~in the drainage simulation~~ caused declines in GPP particularly in model years of 2008 and 2009 ~~while causing greater R_e or a smaller decline in R_e than in GPP, thereby causing declines in NEP~~ (Figs~~s~~. 9c~~8b-d~~). This decrease in GPP was also accompanied by increased R_e thereby causing a decrease in NEP when WT fell below a threshold of about ~0.45 m from the hollow surface, particularly during the drier years (Figs. 9b-g). This~~e~~ projected drainage ~~simulation~~ effect on WTD and NEP ~~in *ecosys* may reflect short-term drainage effects and hence~~ may be transient. Long-term manipulation of WTD ~~through drainage~~ may produce different trajectories of WTD effects on C processes and plant water relations in northern boreal peatlands via vegetation adaptation and succession (Strack et al., 2006; Munir et al., 2014).

4. Discussion

4.1. Modelling WTD effects on northern boreal peatland NEP

Hourly ~~M~~modelled, ~~and~~ EC measured, and ~~gap~~chamber measured net ecosystem, and soil and understorey CO_2 fluxes, and modelled and EC-derived ~~filled diurnal,~~ seasonal and annual NEP, GPP and R_e estimates ~~vs. modelled and observed WTD suggested~~showed that WTD drawdown raised both GPP and R_e at the WPL (Figs. ~~2~~3-8~~7~~). Similar increases in GPP and R_e with WTD drawdown ~~along with some offsetting effects of T_a~~ yielded no net effect of WTD drawdown on NEP at the WPL during 2004-2009 (Figs. 7~~6~~-~~7~~8). Four ~~The simulated drainage experiment in *ecosys* suggested that the increase in GPP would diminish and eventually shift to a decrease in GPP should WT fall further below a threshold of about ~0.45 m from the hollow surface, particularly during drier years (Figs. 8c, f and 9). The decrease in GPP would also be accompanied by increased R_e thereby causing a decrease in NEP should the deepening of WT continue at the WPL (Figs. 8b, d-e, g). Our~~ central hypotheses that ~~describe~~ outlined how coupled eco-hydrology and biogeochemistry algorithms in *ecosys* would simulate and explain the mechanism of these ~~above mentioned~~ WTD effects on R_e, GPP and NEP at the ~~WPL~~ boreal fen peatland under study are ~~discussed~~ examined in details in the following sections of 4.1.1 to 4.1.4.

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4.1.1. Hypothesis 1: Increase in R_e with WTD drawdown

Shallow WTD in *ecosys* caused shallow aerobic zone above WT and thicker anaerobic zone below the WT. In the shallow aerobic zone, peat O_2 concentration $[O_{2s}]$ was well above the Michaelis-Menten constant for O_2 reduction (K_m=0.064 g m^{-3}) and hence DOC oxidation and consequent microbial uptake and growth in *ecosys* was not much limited by $[O_{2s}]$ (Eqs. A17a, C14c). On the contrary, $[O_{2s}]$ in the thicker anaerobic zone below the WT was well below K_m so that DOC oxidation was coupled with DOC reduction by anaerobic heterotrophic fermenters, which yielded much less energy (4.4 kJ g^{-1} C) than did DOC oxidation coupled with O_2 reduction (37.5 kJ g^{-1} C) (Fig. 1) (Eq. A21). Lower energy yields in the thicker anaerobic zone resulted in slower microbial growth (Eq. A25) and R_h (Eq. A13). Since the anaerobic zone in *ecosys* was thicker than the aerobic zone under shallow WT, lower modelled R_h in the anaerobic zone contributed to reduced modelled soil respiration and hence R_e that was corroborated by EC and chamber measurements at the WPL (Figs. 5~~4~~-8~~7~~) (Tables 1 and 2).

WTD drawdown in *ecosys* caused peat pore drainage and increased θ_g thereby deepening of the aerobic zone. It raised D_g (Eq. D44) and increased O_2 influxes into the peat (Fig. ~~4~~5c) (Eqs. D42-D43). Increased O_2 influxes enhanced $[O_{2s}]$ and stimulated R_h (Eqs. A13, A20), soil respiration and hence R_e (Figs. ~~4~~5-8~~7~~). Rapid mineralization of DON and DOP due to improved $[O_{2s}]$ under deeper WT also raised aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (Eqs. C23a, c, e) that increased microbial nutrient availability, uptake (Eq. A22) and growth (Eq. A29) and further enhanced R_e (Fig. 1) (Figs. 5~~4~~-8~~7~~). Modelled

~~The modelling hypothesis of increased~~ R_e ~~stimulated~~ stimulation by improved peat oxygenation due to WTD drawdown ~~can be~~was corroborated well by ~~other field, laboratory and modelling studies on similar peatlands~~EC and chamber measurements at the site (Figs. 5-8) (Tables 1 and 2). However, the chamber measured nighttime net CO_2 fluxes during warmer nights of 2006 with deeper WT were sometimes as large as corresponding EC-measured net ecosystem CO_2 fluxes (Figs. 5-6). Those very large chamber CO_2 effluxes could not be modelled to their full extent and consequently modelled vs. chamber CO_2 flux regression yielded a slope lower than 1±0.1 in 2006 (Table 1c). Although modelled rate of increase in R_e with each 0.1 m of WTD drawdown was larger than EC-derived rate, it is still comparable with rates reported for

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other similar peatlands (Table 2). ~~Automated chamber measurements by Cai et al. (2010) at our study site showed increased soil respiration with deeper WT thereby further corroborating our hypothesis (Figs. 4b and 5j-l).~~ Kotowska (2013)~~ found through~~ carried out chamber based field measurements and laboratory incubation experiments in a moderately rich fen very close to our study site which~~ a~~ ~~combination of automated chamber measurements and a laboratory incubation study~~reported that a WTD drawdown driven ~~that increases in~~stimulation of aerobic microbial decomposition ~~stimulated by WTD drawdown~~ contributed to ~~higher~~ increased R_e~~ in a moderately rich fen very close to our study site~~. Mäkiranta et al. (2009) also found ~~increased~~ rapid ~~rates of~~ microbial decomposition in a Finish peatland due to thicker aerobic zone and consequently larger amounts of decomposable organic matter exposed to aerobic oxidation.

~~Modelled increase in R_e of 0.26 µmol CO_2 m^{-2} s^{-1} per 0.1 m of WTD drawdown was greater than the EC-derived R_e increase of 0.16 µmol CO_2 m^{-2} s^{-1} per 0.1 m WTD drawdown reported by Flanagan and Syed (2011) for WPL over the growing seasons of 2004-2009 (Figs. 6c-d). The modelled rate of increasing R_e was, however, comparable with that of ~0.3 µmol m^{-2} s^{-1} per 0.1 m of WTD drawdown estimated by Peichl et al. (2014) from EC-derived R_e over the growing seasons of 2001-2012 in a Swedish fen. Ballantyne et al. (2014) also reported an increase in EC-derived R_e of ~0.33 µmol m^{-2} s^{-1} per 0.1 m of WTD drawdown from a WTD manipulation study in a Michigan peatland thereby further corroborating our modelling hypothesis of increased R_e due to WTD drawdown.~~

Apart from WTD, peat warming in *ecosys* also increased rates of decomposition (Eq. A1) through an Arrhenius function (Eq. A6) and increased R_h and R_e (Figs. ~~3~~4-7~~6~~). Warming effect on decomposition in *ecosys* was also modified by WTD. For a similar warming, greater thermal diffusivity in peat with deeper WT and consequent smaller water contents caused greater peat warming (Eqs. D34, D36). It enabled larger ~~*ecosys* to~~ simulation of ~~e larger increases in~~ R_e during warming periods in 2006 and 2008 with deeper WT than in 2005 (Figs. 4~~3~~-6~~5~~). Increased stimulation of peat decomposition by warming under deeper WT was also modelled by Grant et al. (2012) using the same model *ecosys* over a northern fen peatland at Wisconsin, USA and by Ise et al. (2008) using a land surface scheme named ED-RAMS (Ecosystem Demography Model version 2 integrated with the Regional Atmospheric Modeling System) coupled with a soil biogeochemical model across several shallow and deep peat deposits in Manitoba, Canada.

4.1.2. Hypothesis 2: Increase in GPP with WTD drawdown

Modelled WTD variations ~~affected~~ influenced GPP ~~in *ecosys*~~ by ~~affecting~~ controlling root and microbial O_2 availability, energy yields, root and microbial growth and decomposition, rates of mineralization and hence root nutrient availability and uptake (Fig. 1). Wet soils under shallow WT caused low O_2 diffusion (Fig. 5~~4~~c) (Eqs. D42-D44) into the peat and consequent low $[O_{2s}]$ meant that root O_2 demand had to be mostly met by $[O_{2r}]$. *Ecosys* inputs for root porosity ($\theta_{pr} = 0.1$) that governed O_2 transport through aerenchyma (Eq. D45) and hence maintained $[O_{2r}]$ was not enough to meet the root O_2 demand in saturated soil by the two over-storey tree PFTs i.e. black spruce and tamarack, causing shallow root systems to be simulated in these two tree PFTs under shallow WTD (Sec~~t~~. 3.4). The under-storey shrub PFT (dwarf birch) had a higher root porosity (θ_{pr}=0.3) and hence had deeper rooting under shallow WT than the two tree PFTs (Sec~~t~~. 3.4). Shallow rooting in the tree PFTs reduced root surface area for nutrient uptake. Root nutrient uptake (Eqs. C23b, d, f) in all the PFTs was also constrained by low nutrient availability due to smaller aqueous concentrations of NH_4^+, NO_3^- and/or $H_2PO_4^-$ (Eqs. C23a, c, e) resulting from slower mineralization (Eq. A26) of DON and DOP (Eq. A7) because of low [O_{2s}] in the wet soils under shallow WT (Fig. 1). Slower root growth and nutrient uptake caused lower foliar σ_N and/or σ_P with respect to foliar σ_C (Eq. C11) that slowed the rates of carboxylation (Eq. C6) and hence reduced vascular GPP (Eq. C1) under shallow WT.

WTD drawdown enhanced O_2 diffusion (Fig. 5~~4~~c) (Eqs. D42-D44) and raised [O_{2s}] so that root O_2 demand in all the three vascular PFTs was almost entirely met by [O_{2s}]. Consequently roots in all the PFTs could grow deeper which increased the root surface for nutrient uptake (Table 2) (Sec~~t~~. 3.4). Increase in modelled rooting d~~growth~~ epth due to WTD drawdown ~~could be corroborated by the increase in maximum rooting depth in black spruce and tamarack from 0.2-0.3 to 0.6 m with a WTD drawdown from 0.14 to 0.9 m as a result of artificial drainage in a similar fen peatland in Central Alberta as measured by Lieffers and Rothwell (1987).~~was corroborated well by studies on same PFTs as in our study grown on similar peatlands very close to the study site (Table 2). Murphy et al. (2009) ~~also~~ found a significant increase in tree fine root production with WTD drawdown from ~0.1 to ~0.25 m during a WTD manipulation study in a Finish peatland. Beside improved root growth, greater [O_{2s}] under deeper WT also enhanced rates of mineralization (Eq. A26) of DON and DOP (Eq. A7) that raised aqueous concentrations of NH_4^+, NO_3^- and/or $H_2PO_4^-$ and hence facilitated root nutrient availability and uptake (Fig. 1). Enhanced root nutrient uptake increased foliar σ_N and/or σ_P with respect to foliar σ_C (Eq. C11) that hastened the rates of carboxylation (Eq. C6) and hence raised vascular GPP (Eq. C1) under deeper WT.

The three modelled vascular PFT were predominantly N limited as indicated by mass-based modelled foliar N to P ratios ~~of 6.6:1, 5.2:1 and 4.8:1 for black spruce, tamarack and dwarf birch under shallow WT in the growing season of 2004. Modelled N to P ratios were~~ that ~~corroborated~~ matched well ~~by~~ with site-measured mass-based foliar N to P ratios~~-~~ (Table 2)~~of~~

~~7.1:1 and 6.3:1 for black spruce and tamarack measured by Syed et al. (2006) at our site during the summer of 2004~~. Mass-based modelled and measured foliar N to P ratio in all the PFTs were less than 16:1 ~~usually indicates that~~indicating that the ~~particular~~ vegetation at the WPL ~~is~~ was~~more~~ N ~~than P~~ limited (Aerts and Chapin III, 1999). Since the modelled PFTs were predominantly N limited, increases in foliar N concentrations as a result of improved root nutrient availability, growth and nutrient uptake with WTD drawdown enhanced modelled carboxylation rates and hence modelled GPP. In a similar fen peatland close to our study site, Choi et al. (2007) ~~in a WT manipulation study~~ found an increase in peat NO$_3^-$-N due to enhanced mineralization and nitrification stimulated by a WTD drawdown ~~from 0.24 to 0.7 m below the surface that caused increases in foliar N concentrations from ~21 to ~27 g kg^{-1} C (assuming 50% of dry matter as organic C) in black spruce and ~41 to ~66 g kg^{-1} C in tamarack in a Central Albertan fen peatland~~which improved foliar N status, and hence increased radial tree growth of black spruce and tamarack (Table 2). ~~Increases in foliar N concentrations due to enhanced root nutrient availability and uptake with WTD drawdown in their study also caused significantly greater radial tree growth.~~ Macdonald and Lieffers (1990) ~~in a WTD manipulation study~~ also found ~~that WTD drawdown by ~0.45 m raised~~improved foliar N concentrations ~~from ~19 to ~21 g kg^{-1} C (assuming 50% of dry matter as organic C)~~ in black spruce and ~~~36 to ~42 g kg^{-1} C in~~ tamarack trees that enhanced net photosynthetic C assimilation rates by those tree species in a northern~~n~~ Alberta~~n~~ moderately rich fen (Table 2). The rates of increases in foliar N concentrations in black spruce and tamarack trees due to WTD drawdown as reported in those studies ~~in similar peatlands~~ are comparable with those in our modelled outputs (~~Sect. 3.4~~Table 2). Although modelled rate of increase in GPP with each 0.1 m of WTD drawdown was larger

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than EC-derived rate, it is still comparable with rates reported for other similar peatlands (Table 2).

~~Modelled growing season GPP increased by 0.39 µmol CO_2 m^{-2} s^{-1} per 0.1 m WTD drawdown which was greater than the EC-derived GPP increase of 0.22 µmol CO_2 m^{-2} s^{-1} per 0.1 m WTD drawdown as reported by Flanagan and Syed (2011) for the WPL over the growing seasons of 2004-2009. However, the modelled GPP increase with WTD drawdown was comparable with the range of 0.28 to 0.4 µmol CO_2 m^{-2} s^{-1} per 0.1 m WTD drawdown reported by Peichl et al. (2014) and Ballantyne et al. (2014) for northern boreal fen peatlands in Michigan and Sweden.~~

4.1.3. Hypothesis 3: Microbial water stress on R_e due to WT deepening below a threshold WTD

When modelled WTD ~~in *ecosys* dropped~~fell below a threshold ~~level~~ of ~0.3 m from the hollow surface (~0.6 m below the hummock surface), ~~near surface peat~~ desiccation of the surface residue layer and near surface shallow peat layers reduced microbial access to substrate for decomposition (Eq. A15) which enabled ~~*ecosys* to simulate~~simulation of ~~reduction~~ reduced ~~in near surface~~ R_h in those layers. When reduction in surface residue and near~~-~~surface R_h more than fully offset the increase in deeper R_h, net ecosystem R_h decreased. The offsetting effect on R_h partly contributed to simulated decrease in growing season R_e (=R_h+R_a) from 2008 to 2009 with WTD drawdown that was corroborated by a similar decrease in EC-derived R_e (Fig. 7~~6~~c). Greater reductions in R_h in desiccated surface residue and near surface peat layers also caused the reductions in growing season R_e in drainage cycle 2 from those in cycle 1 during 2007-2009 in the simulated drainage study (Fig. 9~~8~~d). Similar to our study, Peichl et al. (2014) found reductions in R_e when WTD fell below a threshold of ~0.3 m from the peat surface in a Swedish fen which could be partially attributed to reduction in near surface R_h due to desiccation. Mettrop et al. (2014) in a controlled incubation experiment found that the rates of microbial respiration in a nutrient rich Dutch fen initially increased with peat drying and consequent improved aeration. But excessive drying and consequent peat desiccation in their study reduced microbial respiration efficiency, growth and biomass. Dimitrov et al. (2010a) ~~in a~~while modelling CO$_2$ exchange of a northern temperate bog~~study~~ using *ecosys* ~~also~~ showed that a decrease in desiccated near surface peat respiration partially offset increased deeper peat respiration when WT deepened below a threshold of ~0.6-0.7 m from the hummock surface.

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4.1.4. Hypothesis 4: Plant water stress on GPP due to WT deepening below a threshold WTD

~~Deepening of~~Modelled WTD drawdown below a threshold level also caused rapid peat pore drainage and low moisture contents in the near surface peat layers which were colonized by most of the vascular root systems and all of the ~~ll of~~belowground biomasses of ~~the~~ non-vascular mosses (Eqs. D9-D29). When WTD fell below ~0.1 m from the hollow surface (~0.4 m below the hummock surface), vertical recharge through capillary rise from the WT was not adequate to maintain near surface peat moisture. It reduced peat water potential (ψ_s) and raised peat hydraulic resistance (Ω_s) (Eq. B9) that supressed root and moss water uptake (U_w) (Eq. B6) from desiccated near surface peat layers (Fig. 1). Since moss U_w entirely depended upon moisture supply from the near surface layers, reduction in U_w from desiccation of these layers caused reduction in moss canopy water potential (ψ_c) ~~(Mezbahuddin et al., 2016)~~ and hence moss GPP (Fig. 1) (Eqs. C1, C4) (Mezbahuddin et al., 2016). Reduction in root U_w from desiccated near surface layers, however, was offset by increased root U_w (Eq. B6) from deeper wetter layers, which had higher ψ_s and lower Ω_s, due to deeper root growth facilitated by enhanced aeration. It enabled the vascular PFTs in *ecosys* to sustain ψ_c, canopy turgor potential (ψ_t) (Eq. B4), stomatal conductance (g_c) ~~(Mezbahuddin et al., 2016)~~ (Eqs. B2, C4) and hence to sustain increased GPP (Eq. C1) due to higher root nutrient availability and uptake (Fig. 1) (Mezbahuddin et al., 2016). Increased vascular GPP and consequent greater vascular plant growth further imposed limitations of water, nutrient and light to the modelled non-vascular PFTs due to interspecific competition and greater shading from the overstorey vascular PFTs. However, increases in vascular GPP due to enhanced plant nutrient status more than fully offset the suppression in moss GPP due to moss drying, and greater shading and competition from the overstorey, thereby causing a net increase in modelled GPP with WTD drawdown (Figs. 7~~6~~b and 10~~9~~b-c). ~~This modelled trend~~This~~ indicated~~ simulation of increased vascular dominance over moss with deepening of WT~~ in the model~~ was corroborated by ~~. S~~several WTD manipulation studies (e.g., Moore et al., 2006, Munir et al., 2014) in similar ~~northern boreal~~ peatlands in Alberta that reported increased tree, shrub and herb growths over mosses with WTD drawdown~~ that corroborates our modelled trend~~. However, ~~Gains in~~increase in ~~modelled~~ projected vascular GPP eventually ~~halted~~ plateaued and it ~~eventually vascular GPP~~ started to decline when WT fell below ~0.6 m from the hollow surface (~0.9 m below the hummock surface) ~~in our drainage simulation~~ (Figs. 10~~9~~c, e). It was because deeper root U_w (Eq. B6) could no longer offset suppression of near-surface root U_w when WT fell below threshold WTD, thereby causing lower ψ_c, ψ_t (Eq. B4), g_c (Eqs. B2, C4) and slower CO_2 fixation (Eq. C6) (Fig. 1).

These threshold WTD effects on modelled vascular and non-vascular plant water relations were validated well by testing modelled vs. site measured hourly energy fluxes (latent and sensible heat) and Bowen ratios, and modelled vs. site measured daily soil moisture at different depths throughout 2004-2009 as described in Mezbahuddin et al. (2016).~~Similar to our~~

~~modelling study,~~ Riutta et al. (2007) measured a reduction in moss productivity due to water limitation when WTD fell below ~0.15 m from the surface in a Finish fen peatland. However, they reported a sustained vascular GPP during that period ~~sustained in their study~~ indicating no vascular water stress (Riutta et al., 2007). Peichl et al. (2014) ~~measured~~ measured a reduction in moss GPP due to moss drying caused by insufficient moisture supply through capillary rise when WTD fell below ~0.3 m from the surface in a Swedish fen. ~~They inferred that the peat in their study did not have sufficient moisture supplying capacity through capillary rise to sustain moss U_{w} when the WT fell below ~ 0.3 m from the surface.~~ Reductions in moss GPP due to decreased moss canopy water potentials were also modelled by Dimitrov et al. (2011) using the same model *ecosys* when WTD fell below ~0.3 m from the hummock surface of a Canadian temperate bog. They, however, found no vascular plant water stress and hence no reduction in vascular GPP during that period. Similarly, Kuiper et al. (2014) found reductions in moss productivity with peat drying while vascular productivity sustained in a simulated drought experiment on a Danish peat.

Continued deepening of WT can also cause vascular plant water stress and hence reductions in vascular GPP as ~~modelled~~ projected in our ~~study~~ drainage simulation (Figs. 10~~9~~c, e). It can also be corroborated by field measurements across various northern boreal fen peatlands in Canada and Sweden. Sonnentag et al. (2010) found a reduction in ~~canopy~~ stomatal conductance (g_{c}) of a canopy that included tamarack and dwarf birch and ~~hence~~ a consequent decline in ~~vascular~~ GPP when WT fell below ~0.4 m from the ridge surface at a fen peatland in Saskatchewan. ~~The dominant vascular vegetation in their study included tamarack and dwarf birch, two of the three vascular PFTs in our modelling thereby further corroborating the projected vascular water stress.~~ Peichl et al. (2014) also found a reduction in vascular GPP due to plant water stress when WTD fell below ~0.3 m from the surface in a Swedish fen~~ peatland~~. The WTD threshold for reductions in vascular GPP in those two field studies were shallower than that in our modelled projection i.e. ~0.6 m from the hollow surface (~0.9 m below the hummock surface) (Figs. ~~9~~10a, c, e) thereby indicating different vertical rooting patterns determined by specific interactions between hydrologic properties and rooting. Lafleur et al. (2005) and Schwärzel et al. (2006) found much deeper WTD thresholds for reductions in vascular transpiration that could negatively affect vascular GPP over a Canadian pristine ~~peatland~~ bog and a German drained fen respectively~~peatland~~. Those WTD thresholds were ~0.65 and ~0.9 m below the surface for the pristine and drained peatland respectively, further indicating the importance of root-hydrology interactions and the resultant root adaptations, growth and uptake in determining WTD effects on vascular GPP across peatlands.

4.2. Divergences between modelled and EC-derived annual GPP, R_e and NEP

Modelled seasonal and annual GPP and R_e were consistently larger than EC-derived estimates of GPP and R_e during 2004~~5~~-2009~~8~~ (Figs. ~~6~~7b, c, f, -g). Although modelled annual ~~Despite larger modelled vs. EC-derived~~ GPP and R_e were larger than the EC-derived estimates,~~,~~ modelled annual NEP were~~as~~ consistently lower than the EC gap-filled annual NEP (Fig. ~~6~~7e). M~~Smaller m~~Modelled annual NEP were smaller than EC-derived estimates because ~~smaller than EC-derived estimates were caused by~~due to ~~larger differences in larger modelled and~~modelled R_e were larger than EC-derived ~~vs.~~estimatesR_e ~~than~~~~EC-derived R_e than differences beween~~by margins bigger- than by what modelled GPP were larger than ~~vs.~~~~and~~ EC-derived ~~GPP~~ estimates (Figs. 7~~6~~f-g). ~~Larger deviation between m~~Modelled R_e ~~and~~ were larger than EC-derived R_e estimates ~~was~~ mainly ~~contributed by~~due to the presence of gap filled night-time CO_2 fluxes (=R_e) in EC-derived estimates which were smaller than corresponding modelled values. ~~which~~ It was

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~~also~~ apparent in negative intercepts that resulted from regressions of modelled ~~on~~ vs. gap-filled net CO_2 fluxes ~~regressions~~ (Table S1 in supplementary material). G~~The g~~ap -fill~~ing for night-time CO_2 fluxes was done by Syed et al. (2006) using empirical relationships between EC CO_2 measurements and~~ed R_e fluxes ~~were dependent on~~were calculated from ~~changes in~~ soil temperature (T_s) ~~measured~~ at a shallow depth (0.05 m)~~ depth~~ (Sec. 2.2.2)~~ at the WPL~~. During night-time and in the winter, peat at this shallow depth ~~(0.05 m)~~ ~~could have~~ rapidly cooled down and ~~thus~~ yielded smaller night-time gap-filled CO_2 fluxes (Figs. 3~~2~~, 5~~4~~ and 6~~5~~). On the contrary, corresponding modelled CO_2 effluxes ~~in those periods depended~~ were affected by ~~on~~ the temperatures of not only the shallow peat layers but also the deeper peat profile~~s~~ that were warmer than the shallower layers and thus ~~s and hence simulated~~ were larger ~~CO_2 effluxes~~ than the gap-filled fluxes (e.g., Figs. 5~~4~~a, 6~~5~~h-i). Like modelled CO_2 effluxes, chamber measured CO_2 effluxes ~~measured by automated chamber~~ in cooler nights~~, however,~~ also did not decline as rapidly as did the corresponding gap-filled CO_2 fluxes as night progressed which further indicated the likely contribution of gap-filling ~~artifeat~~artifact to CO_2 effluxes that were smaller than corresponding modelled fluxes ~~further corroborating this reasoning for larger modelled vs. gap-filled R_e being smaller than the modelled R_e during night-time and in the winter~~ (e.g., Figs. 5~~4~~b vs. 4a, 6~~5~~j-k vs. ~~5~~h-i).

Systematic uncertainties embedded in EC methodology could also have contributed to ~~larger modelled vs.~~ EC-derived annual and growing season R_e estimates which were smaller than the modelled values (Figs. 7~~6~~c, g). The major uncertainty in the EC methodology is the possible underestimation of nighttime EC CO_2 flux measurements due to poor turbulent mixing under stable air conditions (Goulden et al., 1997; Miller et al., 2004). On the contrary, modelled biological production of CO_2 by plant and microbial respiration was independent of turbulent

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mixing which would thus contribute to ~~larger~~ modelled R_e that were larger than EC-derived ~~R_e~~ estimates.

~~Larger Modelled modelled vs. gap-filled R_e which were larger than gap filled R_e might have also o contributed to larger modelled seasonal and annual GPP that were vs. gap-filledlarger than EC-derived growing season and annual GPP (Figs. 76b, f). In EC datasets, GPP wereas derived from R_e. Smaller gap-filled vs. modelled R_e would thus cause smaller EC-derived vs. modelled GPP.~~ Complete energy balance closure in the model ~~vs.~~as opposed to incomplete (~75%) energy balance closure in EC measurements would also give rise to ~~cause a larger~~ modelled ~~than measured~~ evapotranspiration ~~(Mezbahuddin et al., 2016)~~ and ~~possibly~~ GPP values that were larger than EC-derived estimates (Figs. 7~~6~~b, f) (Mezbahuddin et al., 2016). M~~Unlike decoupled GPP and R_e during gap-filling, m~~odelled GPP influenced modelled R_e through root exudation and litter fall (Fig. 1). ~~which~~ Therefore, modelled GPP that were larger than EC-derived estimates would have further contributed to ~~deviation between~~ modelled ~~vs. EC-derived~~ growing season and annual R_e estimates that were larger than EC-derived estimates (Figs. 7~~6~~c, g).

Modelled GPP and hence R_e can also be larger than EC-derived estimates due to uncertainties in model inputs for soil organic N, N ~~wet or dry~~ deposition, N_2 fixation and any other sources of N inputs into the modelled ecosystem. In *ecosys*, plant productivity ~~of a PFT~~ is governed by ~~leaf~~foliar N status which is constrained by root N availability and uptake. Our ~~Modelled plant productivity also influences modelled R_e through litter fall and root exudation. Our~~ input for organic N into each modelled peat layer was measured for corresponding depth at the site (Fig. 2). To simulate N deposition, ~~The~~ background wet deposition rates of 0.5 mg

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ammonium-N, and 0.25 mg nitrate-N per litre of precipitation that were reported for the study area ~~as reported for the site area~~ were used as model inputs~~ to simulate N deposition~~. However, from visual field observations, it was evident that there was a significant amount of nutrient inflow with the lateral water influxes into this fen peatland from the surrounding upland forests which was not quantified. To mimic this lateral nutrient inflow, we doubled the background wet deposition of NH_4^+ and NO_3^- as reported for the area and used these as a surrogates of lateral nutrient inflow into the modelled ecosystem. ~~*We*~~*Ecosys* also ~~used~~included a N_2 fixing algorithm which simulated symbiotic N_2 fixation in moss canopies~~mechanism~~ ~~by lichens which~~that was reported for the boreal forests (Sec. 2.2.3). We tested the adequacy of these N inputs into the model by comparing modelled leaf N concentrations against those measured in the field. The modelled foliar N concentrations for black spruce and tamarack PFTs corroborated well against site measurements (Table 2). To further examine the contribution of uncertainty due to model inputs towards the divergence between modelled and~~vs.~~ EC-derived seasonal and annual GPP and R_e, we performed a sensitivity test where we had a parallel run without doubling the background N wet deposition rates in the model, hence simulating no lateral N influx into the modelled ecosystem. Unlike the current run with lateral N inflow, ~~This~~the parallel run ~~(~~without lateral N inflow~~)~~ simulated GPP and R_e which were ~~that matched better with the~~very close to the EC-derived ~~GPP and R_e as opposed to the current run (with lateral N inflow)~~estimates. However, the regressions between hourly ~~the~~ modelled net CO_2 fluxes from the parallel run and ~~the~~ EC-measured hourly net CO_2 fluxes ~~(excluding gap-filled fluxes)~~ gave slopes of ~0.8 indicating under-simulation of the EC-measured fluxes in the parallel run with ~~(~~no lateral N inflow~~) despite better matching EC-derived GPP and R_e aggregates~~. ~~So, the uncertainties in the modelling that arose from discrepancies between modelled and EC-derived R_e and GPP aggregates could not be~~

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~~resolved without resolving the above mentioned uncertainties in EC methodology, and gap-filling, and partitioning of EC-gap filled NEP into GPP and R_e.~~

5. Conclusions

Our modelling study showed that, when adequately coupled in algorithms of a process-based ecosystem model, the existing knowledge of peatland eco-hydrological and peat biogeochemical processes could explain underlying mechanisms that governed WTD effects on net ecosystem CO_2 exchange of a boreal fen. Testing of our hypotheses against EC-measured net CO_2 fluxes, automated chamber fluxes and other biometric measurements at the site revealed that a drier weather driven WTD drawdown at this boreal fen raised both R_e and GPP due to improved aeration that facilitated 1) microbial and root O_2 availability, energy yields, growth and decomposition which raised microbial and root respiration; and 2) rapid nitrogen mineralization, and consequently increased root nitrogen availability and uptake that improved leaf nitrogen status and hence raised carboxylation (Figs. 1, 7-8) (Table 2). Similar increases in R_e and GPP with WTD drawdown to a certain depth caused no net WTD drawdown effect on NEP (Fig. 8). Modelled drainage projection, however, showed that further WTD drawdown caused by either drainage or climate change induced drying could cause plant water stress and reduce GPP and hence NEP of this boreal fen (Figs. 9-10). This study further reconciled and mechanistically explained the WTD effects on seasonal and annual GPP, R_e and hence NEP of this boreal fen which was previously speculated from EC-derived estimates. However, although modelled CO_2 fluxes were validated well by the EC and chamber measured net CO_2 fluxes, modelled values of annual and seasonal GPP and R_e were consistently larger than the EC-derived estimates (Table 1) (Figs. 7-8) (Sec. 4.2). These discrepancies between modelled and EC-derived GPP and R_e estimates also raised a potential research question of whether or not to use more

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robust process-based estimates of these peatland C balance components instead of empirically modelled EC-derived estimates that might not include some of the above discussed offsetting feedbacks in peatland eco-hydrology and biogeochemistry.

The model algorithms that were used in this study represented coupled feedbacks among ecosystem processes that governed carbon, water, energy, and nutrient (N, P) cycling in a terrestrial ecosystem. These feedbacks were thus not parameterized for this particular boreal fen peatland site. Instead, the modelled boreal fen was simulated from peatland specific model inputs for weather, soil, and vegetation properties that had physical meaning and were quantifiable at the site (Fig. 2). These modelled process level interactions were also validated by corroborating modelled outputs against site measurements. On the contrary, most of the current peatland C models uses scalar functions to represent these feedbacks and so those model algorithms have to be parameterized for each peatland site. Therefore, the modelling approach as described in this study should be more robust than the scalar feedback approach while assessing WTD effects on peatland C balance under contrasting peat types, climates and hydrology, or under unknown future climates. These process level feedbacks are also scalable once the peatlands of interest are defined within the modelled landscapes by scalable model inputs for weather; peat hydrological, physical, and biological properties; and plant functional types (Sec. 2.2.3). Current global land surface models either lack or have very poor representation of these feedbacks which is thus far limiting our large scale predictive capacity on WTD effects on boreal peatland C stocks. This modelling exercise would thus provide valuable information to improve representation of these feedbacks into next generation land surface models. Therefore, the insights gained from this modelling study should be a significant contribution to our understanding and apprehension of how peatlands would behave with changing hydrology under future drier and warmer

Formatted: Indent: First line: 1.27 cm, Space After: 10 pt, Adjust space between Latin and Asian text, Adjust space between Asian text and numbers climates.~~Coupling of eco-hydrology and biogeochemistry algorithms in *ecosys* simulated increases in R_e and GPP with deepening of WT from 2004 to 2009 in the boreal fen at the WPL. Similar increases in R_e and GPP, however, left no net effect of WT deepening on modelled variations in NEP. This modelled trend was corroborated by EC-derived NEP, R_e and GPP (Syed et al., 2006; Flanagan and Syed, 2011) and automated chamber measured NEP and R_e (Cai et al., 2010) at the WPL. The effects of WTD drawdown on R_e and GPP was modelled in *ecosys* by the algorithms representing following processes:~~

~~Improved [O_{2s}] facilitated by rapid O_2 diffusion (Eqs. D42-D44) under deeper WT raised microbial energy yields while oxidizing DOC coupled with O_2 reduction (Eq. A21) and hence caused increases in R_e. Increased mineralization rates of DON and DOP due to improved [O_{2s}] also increased aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$ (Eqs. C23a, c, e) that facilitated microbial nutrient availability, uptake (Eq. A22) and growth (Eq. A29) and hence further enhanced R_e.~~

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~~Increased nutrient availability due to rapid mineralization with WTD drawdown as mentioned above hastened root nutrient (mainly N) availability and uptake (Eqs. C23b, d, f). Root nutrient availability and uptake in *ecosys* were further facilitated by increased root growth stimulated by improved [O_{2s}] under deeper WT. Greater root growth and uptake thus caused improved foliar σ_N with respect to σ_C thereby enhancing CO_2 fixation (Eq. C6) and vascular GPP (Eq. C1).~~

~~When WT in *ecosys* dropped below ~0.3 m from the hollow surface (~0.6 m below the hummock surface), inadequate capillary recharge from WT caused desiccation of near surface peat layers and surface residues (Eqs. D9, D12). Surface and near surface peat desiccation raised microbial concentrations and reduced microbial access to substrate for decomposition in these~~

~~desiccated layers (Eq. A15). It enabled *ecosys* to simulate reduction in R_h in the desiccated peats from competitive inhibition of microbial exo-enzymes with increasing concentrations (Figs. 6c, 8d) (Eq. A4).~~

~~When WT fell below ~0.1 m from the hollow surface (~0.4 m below the hummock surface) vertical recharge of near surface peat layers through capillary rise from WT was not enough to sustain moss water uptake thereby causing moss drying and consequent reduced moss GPP (Eqs. C1, C4). However, sustained increases in vascular GPP due to root water uptake from deeper wetter layers more than fully offset the suppression of moss GPP thereby causing a net increase in GPP with WTD drawdown (Figs. 6b and 9b-c).~~

~~These modelling hypotheses were also corroborated by various field, laboratory and modelling studies over similar peatlands (Sect. 4.1). Moreover, the projected drainage simulation showed that the increase in vascular GPP due to improved plant nutrient status caused by WTD drawdown would only sustain while WTD remained above a threshold level i.e. ~0.6 m below the hollow surface (~0.9 m below the hummock surface). When WT fell below this threshold, projected vascular GPP started to decrease with further WTD drawdown thereby causing reductions in ecosystem GPP. Similar WTD threshold effects on vascular GPP were also found in other studies in similar peatlands (Sect. 4.1.2).~~

~~Therefore, representing feedbacks between peatland hydrological and C processes in *ecosys* enabled successful simulation of WTD effects on R_e, GPP and hence NEP of a northern boreal fen peatland. Projected drainage simulation in our study showed that continued WTD could alter ecosystem C balance of northern boreal peatlands by decreasing GPP and sustaining increased R_e thereby causing declines in NEP. These findings provide us with important insights into how northern boreal peatland C stocks would be affected by likely WTD drawdown under~~

~~future drier and warmer climates. This study is also reproducible in other peatlands when the model is fed by required physical, hydrological, chemical, biological and ecological inputs those are measurable at the sites (Fig. 1) (Mezbahuddin et al., 2016). Successful simulation of hydrological effects on peatland C processes by *ecosys* for a northern boreal fen peatland in this study along with simulations of feedbacks between hydrology, biogeochemistry and ecology by the same model *ecosys* across other contrasting peatlands (e.g., Dimitrov et al., 2011; Grant et al., 2012; Mezbahuddin et al., 2014, 2015, 2016) would, therefore, provide us with a modelling framework for large scale (e.g., regional/continental/global) peatland C simulations, which currently is one of the most sought after in global terrestrial ecosystem carbon modelling community.~~

Code availability

The *ecosys* model codes are listed in equation forms and sufficiently described in the supplementary material. The model codes that were written in FORTRAN will also be available on request from either symon.mezbahuddin@gov.ab.ca or rgrant@ualberta.ca.

Data availability

Field data that were used to validate model outputs are available at http://fluxnet.ornl.gov/site/292.

Author contribution

M. Mezbahuddin contributed to the model code modification and development, designing modelling experiment, simulation, validation, and analyses of modelled outputs. R. F. Grant is the original developer of the model *ecosys* and also contributed into simulation design and model runs. L. B. Flanagan was site principal investigator who led the collection, and quality control of the field data that were used to validate model outputs. M. Mezbahuddin wrote the manuscript with significant contributions from R. F. Grant and L. B. Flanagan.

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Figure captions

Fig. 1. Schematic ~~representation~~diagram of *ecosys* al~~o~~gorithms representing~~of~~ coupled key eco-physiological and biogeochemical (aerobic and anaerobic) processes, and plant water relations of a typical boreal fen peatland ecosystem that are affected by water table depth (WTD) fluctuation. Ψ_a, Ψ_c, and Ψ_s =atmospheric, canopy and soil water potentials; Ψ_r=vascular root or non-vascular belowground water potential; r_c=canopy stomatal resistance (=1/canopy stomatal conductance (g_c)); Ω_s=soil hydraulic resistance; Ω_r=hydraulic resistance to water flow through plants; OM=organic matter; DOC, DON, DOP=dissolved organic carbon, nitrogen, and phosphorus; POC = particulate organic C; and POM = particulate organic matter

Fig. ~~1~~2. Layout for *ecosys* model run to represent biological, chemical and hydrological characteristics of a Western Canadian fen peatland. Figure is not drawn to scale. D_{humm} = depth to the bottom of a layer from the hummock surface; D_{holl} = depth to the bottom of a layer from the hollow surface; TOC = total organic C (Flanagan and Syed, 2011); TN = total nitrogen (Flanagan and Syed, 2011); TP = total phosphorus (Flanagan and Syed, 2011); CEC = Cation exchange capacity (Rippy and Nelson, 2007); the value for pH was obtained from Syed et al. (2006); WTD_x = external reference water table depth representing average water table depth of the adjacent ecosystem; L_t = distance from modelled grid cells to the adjacent watershed over which lateral discharge / recharge occurs

Fig. 3~~2~~. (a, c, e, g, i, k) 3-day moving averages of modelled and EC-gap filled net ecosystem productivity (NEP) (Flanagan and Syed, 2011), and **(b, d, f, h, j, l)** hourly modelled and half hourly measured water table depth (WTD) (Syed et al., 2006; Cai et al., 2010; Long et al., 2010; Flanagan and Syed, 2011) from 2004-2009 at a Western Canadian fen peatland. A positive NEP

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means the ecosystem is a carbon sink and a negative NEP means the ecosystem is a carbon source. A negative WTD represents a depth below hummock/hollow surface and a positive WTD represents a depth above hummock/hollow surface

Fig. 4~~3~~. Half hourly measured **(a)** incoming shortwave radiation, and **(b)** air temperature (T_a); and **(c)** hourly modelled and half hourly measured water table depth (WTD) (Syed et al., 2006; Cai et al.; 2010, Long et al.; 2010, Flanagan and Syed, 2011) during August 2005, 2006 and 2008 at a Western Canadian fen peatland. A negative WTD represents a depth below hummock/hollow surface and a positive WTD represents a depth above hummock/hollow surface. Grey arrows indicate nights with similar temperatures

Fig. 5~~4~~. (a) Half hourly EC-gap filled (Flanagan and Syed, 2011) and hourly modelled ecosystem net CO_2 fluxes, **(b)** half hourly automated chamber measured (Cai et al., 2010) and hourly modelled understorey and soil CO_2 fluxes, and **(c)** hourly modelled soil CO_2 and O_2 fluxes during August 2005, 2006 and 2008 at a Western Canadian fen peatland. No chamber CO_2 flux measurement was available for 2008. A negative flux represents an upward flux or a flux out of the ecosystem and a positive flux represents a downward flux or a flux into the ecosystem. Grey arrows indicate nights with similar temperatures (Fig. 4~~3~~)

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Fig. 6~~5~~. (a-c) Half hourly observed air temperature (T_a), **(d-f)** hourly modelled and half hourly observed water table depth (WTD) (Syed et al., 2006; Cai et al., 2010; Long et al., 2010; Flanagan and Syed, 2011), **(g-i)** half hourly EC-gap filled (Flanagan and Syed, 2011) and hourly modelled ecosystem net CO_2 fluxes, **(j-l)** half hourly automated chamber measured (Cai et al., 2010) and hourly modelled understorey and soil CO_2 fluxes during July-August 2005, 2006 and 2008 at a Western Canadian fen peatland. No chamber CO_2 flux measurement was available for

2008. A negative flux represents an upward flux or a flux out of the ecosystem and a positive flux represents a downward flux or a flux into the ecosystem. A negative WTD represents a depth below hummock/hollow surface and a positive WTD represents a depth above hummock/hollow surface

Fig. 7~~6~~. Modelled and EC-derived (Flanagan and Syed, 2011) growing season (May-August) sums of **(a)** net ecosystem productivity (NEP), **(b)** gross primary productivity (GPP), and **(c)** ecosystem respiration (R_e) during 2004-2009; **(d)** observed mean growing season air temperature (T_a) and measured and modelled average growing season water table depth (WTD) during 2004-2009; Modelled and EC-derived (Flanagan and Syed, 2011) annual sums of **(e)** NEP, **(f)** GPP, and **(g)** R_e during 2004-2008; and **(h)** observed mean annual T_a and measured and modelled average WTD during ice free periods (May-October) of 2004-2008 at a Western Canadian fen peatland. A negative WTD represents a depth below hollow surface and a positive WTD represents a depth above hollow surface. A positive NEP means the ecosystem is a carbon sink. Annual modelled vs. EC-gap filled NEP, GPP, R_e estimates for 2009 was not compared due to the lack of flux measurements from September to December in that year.

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Fig. 8~~7~~. Regressions ($P<0.001$) of growing season (May-August) sums of modelled and EC-derived (Flanagan and Syed, 2011) **(a)** net ecosystem productivity (NEP), **(b)** gross primary productivity (GPP), and **(c)** ecosystem respiration (R_e) on growing season averages of modelled and observed water table depth (WTD) during 2004-2009; and regressions ($P<0.001$) of annual sums of modelled and EC-derived (Flanagan and Syed, 2011) **(d)** NEP, **(e)** GPP and **(f)** R_e on average modelled and measured WTD during ice free periods (May-October) of 2004-2008 at a Western Canadian fen peatland. A negative WTD represents a depth below hollow surface and a positive WTD represents a depth above hollow surface. A positive NEP means the ecosystem is a carbon sink

Fig. 9~~8~~. (a) Observed, real-time simulated and projected drainage simulated average growing season (May-August) water table depth (WTD); EC-derived, real-time simulated and projected drainage simulated growing season sums of **(b)** net ecosystem productivity (NEP), **(c)** gross primary productivity (GPP), and **(d)** ecosystem respiration (R_e); and regressions ($P<0.001$) of real-time simulated and projected drainage simulated sums of **(e)** NEP, **(f)** GPP, and **(g)** R_e on real-time simulated and projected drainage simulated average growing season WTD during 2004-2009 at a Western Canadian fen peatland. A negative WTD represents a depth below hollow surface and a positive WTD represents a depth above hollow surface. A positive NEP means the ecosystem is a C sink

Fig. 10~~9~~. Real-time simulated and projected drainage simulated **(a)** average growing season (May-August) water table depth (WTD), **(b)** growing season sums of non-vascular (moss) gross primary productivity (GPP), and **(c)** growing season sums of vascular GPP; and regressions ($P<0.001$) of real-time simulated and projected drainage simulated sums of **(d)** non-vascular GPP, and **(e)** vascular GPP on real-time simulated and projected drainage simulated average growing season WTD during 2004-2009 at a Western Canadian fen peatland. A negative WTD represents a depth below hollow surface and a positive WTD represents a depth above hollow surface

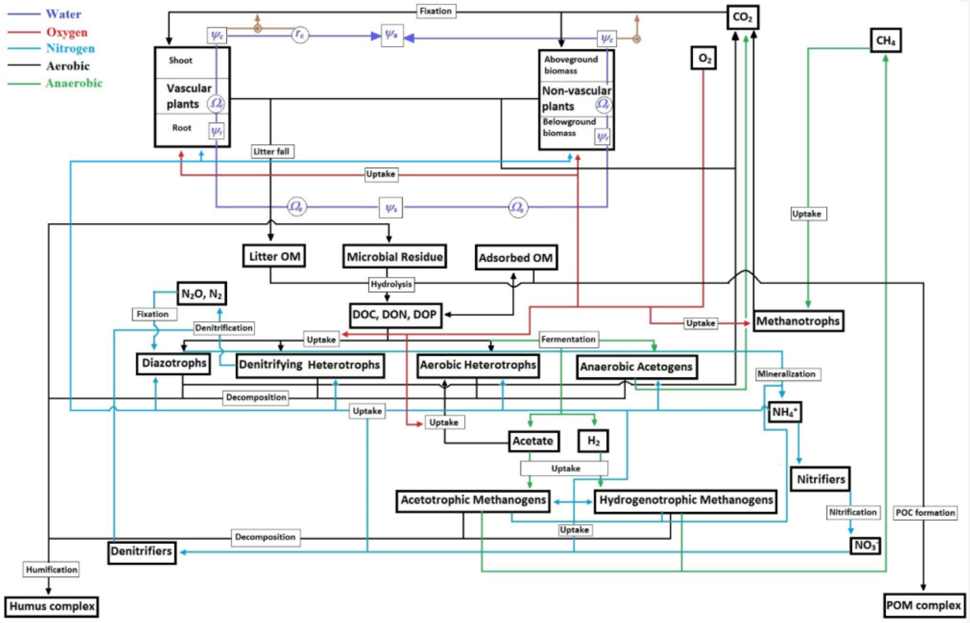

Fig. 1.

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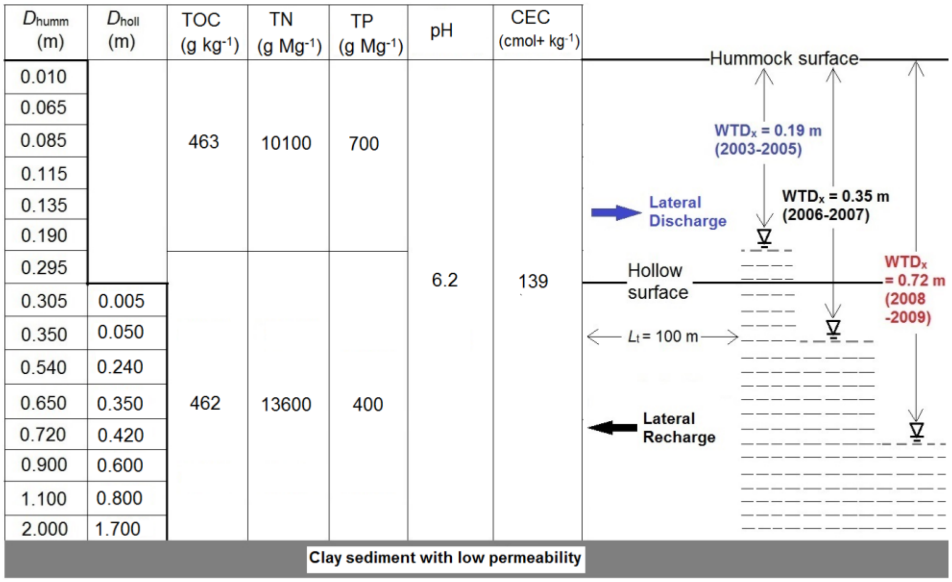


D_{humm} (m)	D_{holl} (m)	TOC (g kg^{-1})	TN (g Mg^{-1})	TP (g Mg^{-1})	pH	CEC (cmol+ kg^{-1})
0.010		463	10100	700	6.2	139
0.065						
0.085						
0.115						
0.135						
0.190						
0.295						
0.305	0.005	462	13600	400		
0.350	0.050					
0.540	0.240					
0.650	0.350					
0.720	0.420					
0.900	0.600					
1.100	0.800					
2.000	1.700					

Fig. 2~~1~~.

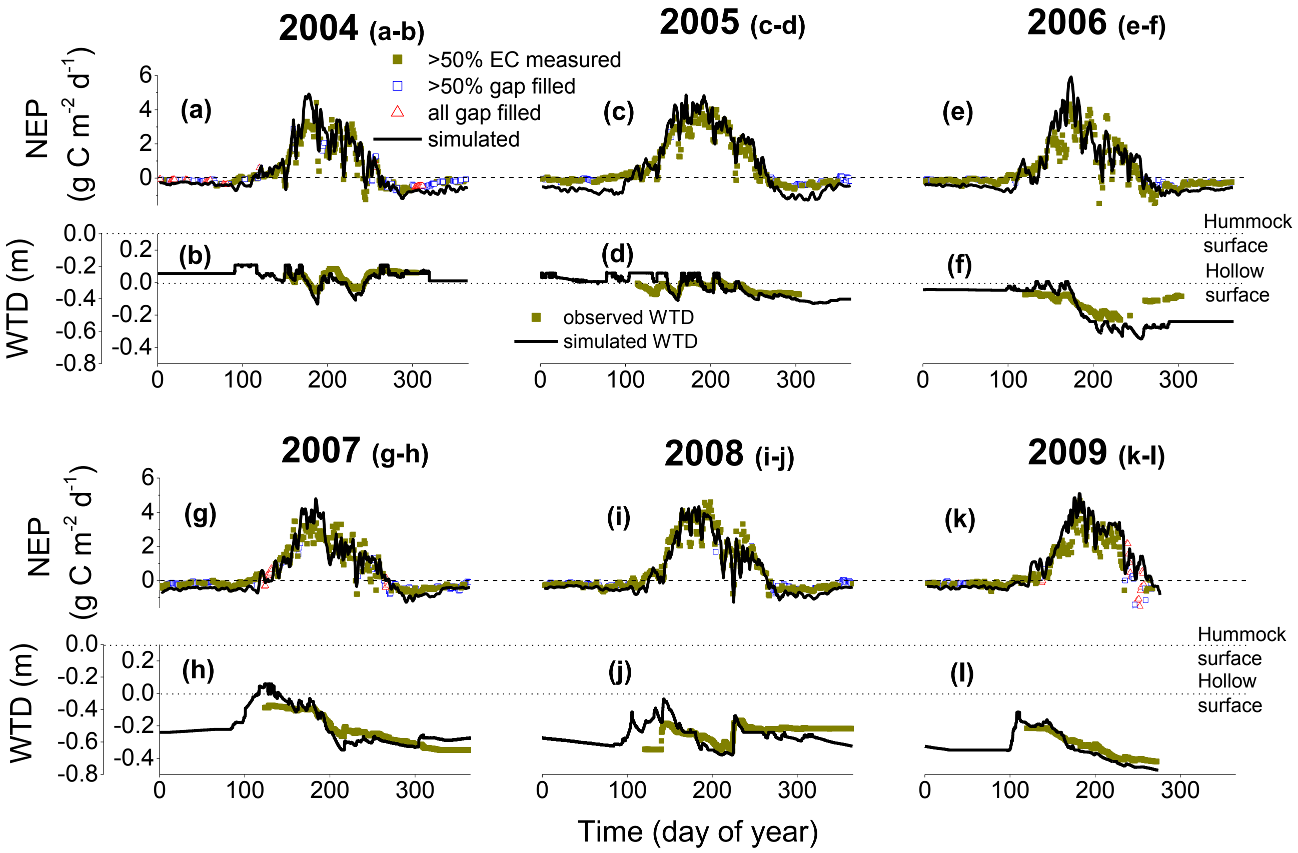

2004 (a-b)
2005 (c-d)
2006 (e-f)
2007 (g-h)
2008 (i-j)
2009 (k-l)
■ >50% EC measured
□ >50% gap filled
△ all gap filled
simulated
NEP (g C m-2 d-1)
(a)
(c)
(e)
(g)
(i)
(k)
6
4
2
0
WTD (m)
0.0
-0.2
-0.4
-0.6
-0.8
0.2
0.0
-0.2
-0.4
(b)
(d)
(f)
(h)
(j)
(l)
■ observed WTD
simulated WTD
Hummock surface
Hollow surface
0
100
200
300
Time (day of year)

Fig. ~~2~~3.

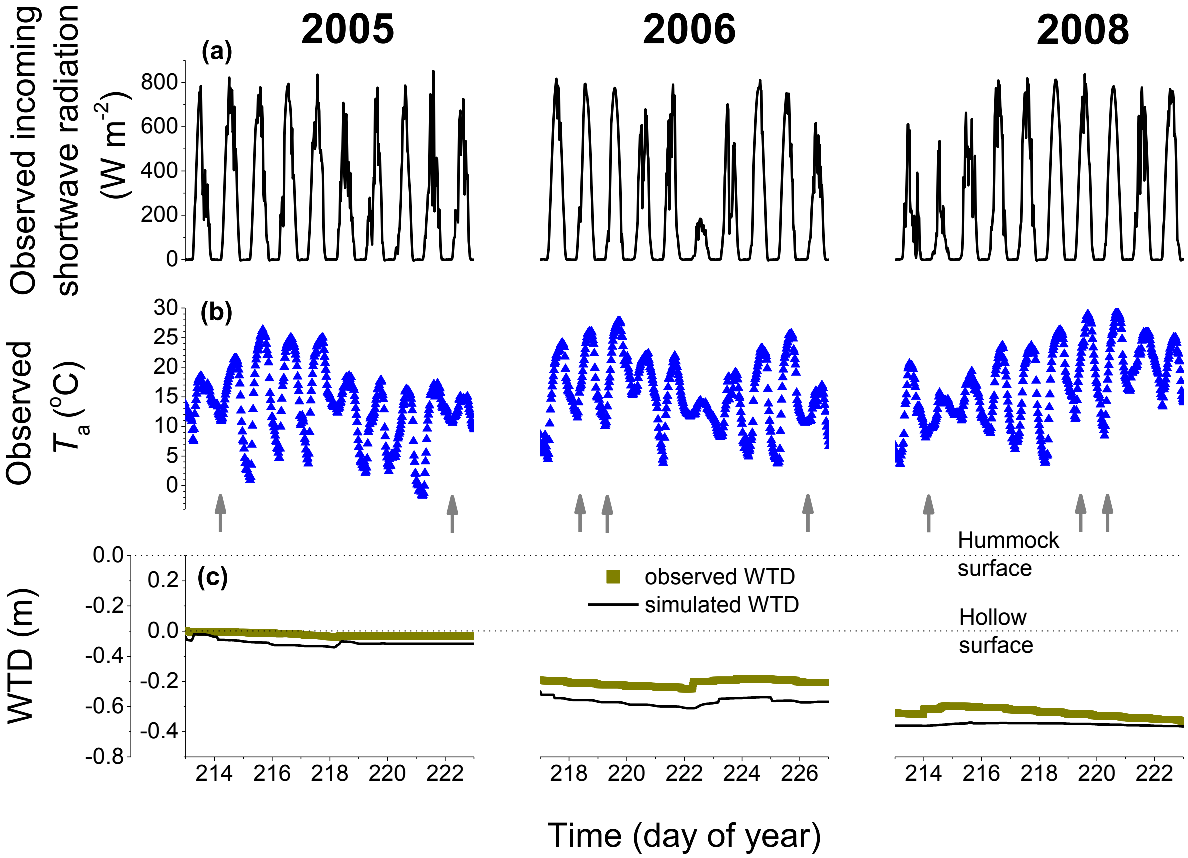
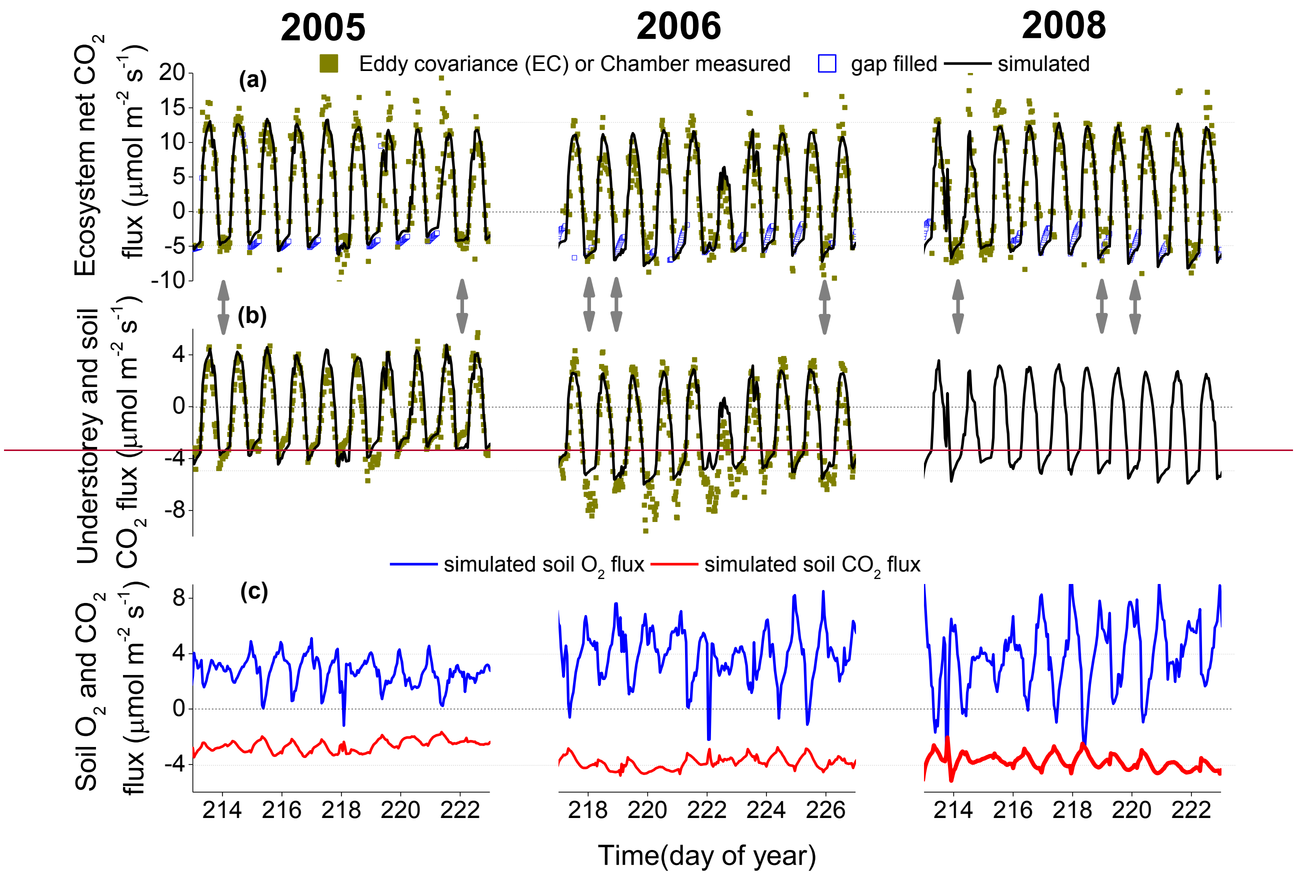

2005
2006
2008
(a)
Observed incoming shortwave radiation (W m^{-2})
800
600
400
200
0
(b)
Observed T_a (°C)
30
25
20
15
10
5
0
Hummock surface
Hollow surface
(c)
observed WTD
simulated WTD
WTD (m)
0.0
-0.2
-0.4
-0.6
-0.8
0.2
0.0
-0.2
-0.4
214
216
218
220
222
218
220
222
224
226
214
216
218
220
222
Time (day of year)

Fig. 4~~3~~.


2005
2006
2008
Eddy covariance (EC) or Chamber measured
gap filled
simulated
(a)
Ecosystem net CO2 flux (µmol m-2 s-1)
20
15
10
5
0
-5
-10
(b)
Understorey and soil CO2 flux (µmol m-2 s-1)
4
0
-4
-8
simulated soil O2 flux
simulated soil CO2 flux
(c)
Soil O2 and CO2 flux (µmol m-2 s-1)
8
4
0
-4
214
216
218
220
222
218
220
222
224
226
214
216
218
220
222
Time(day of year)

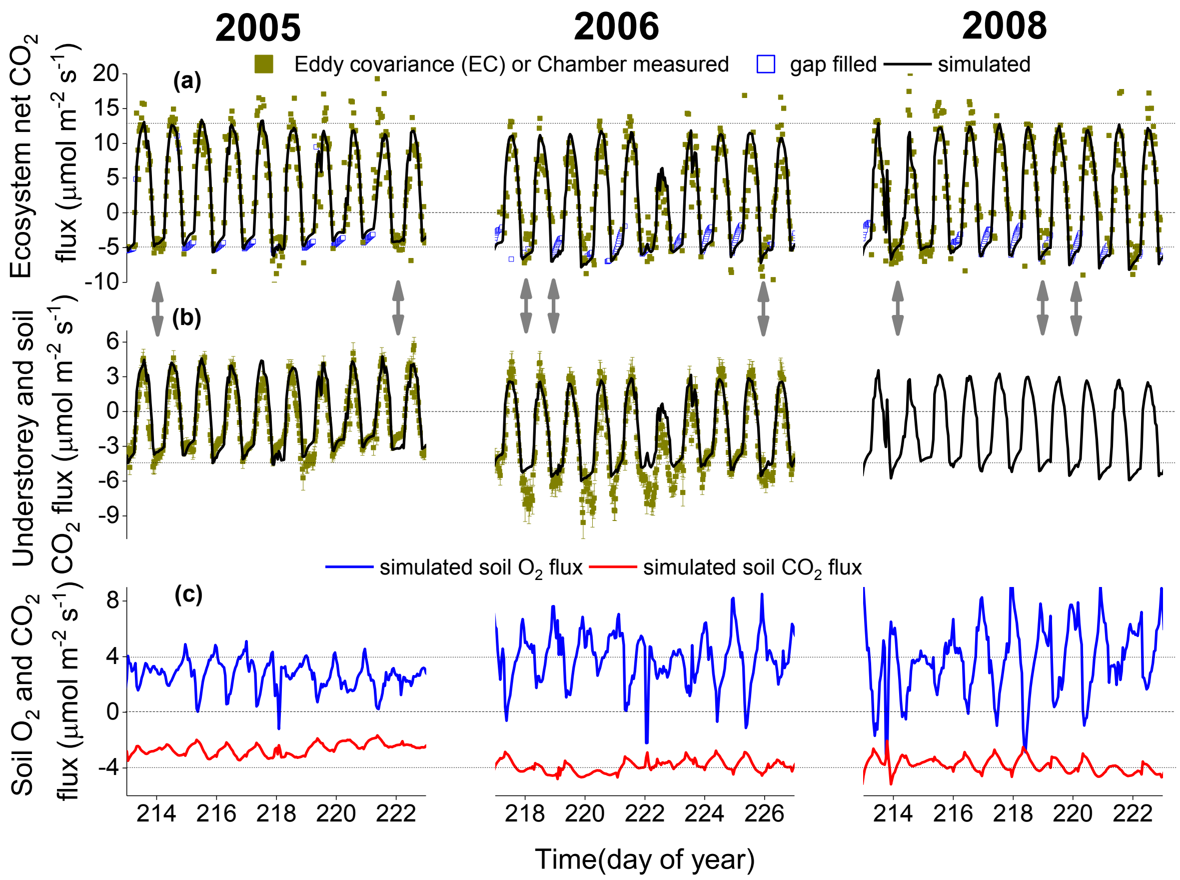
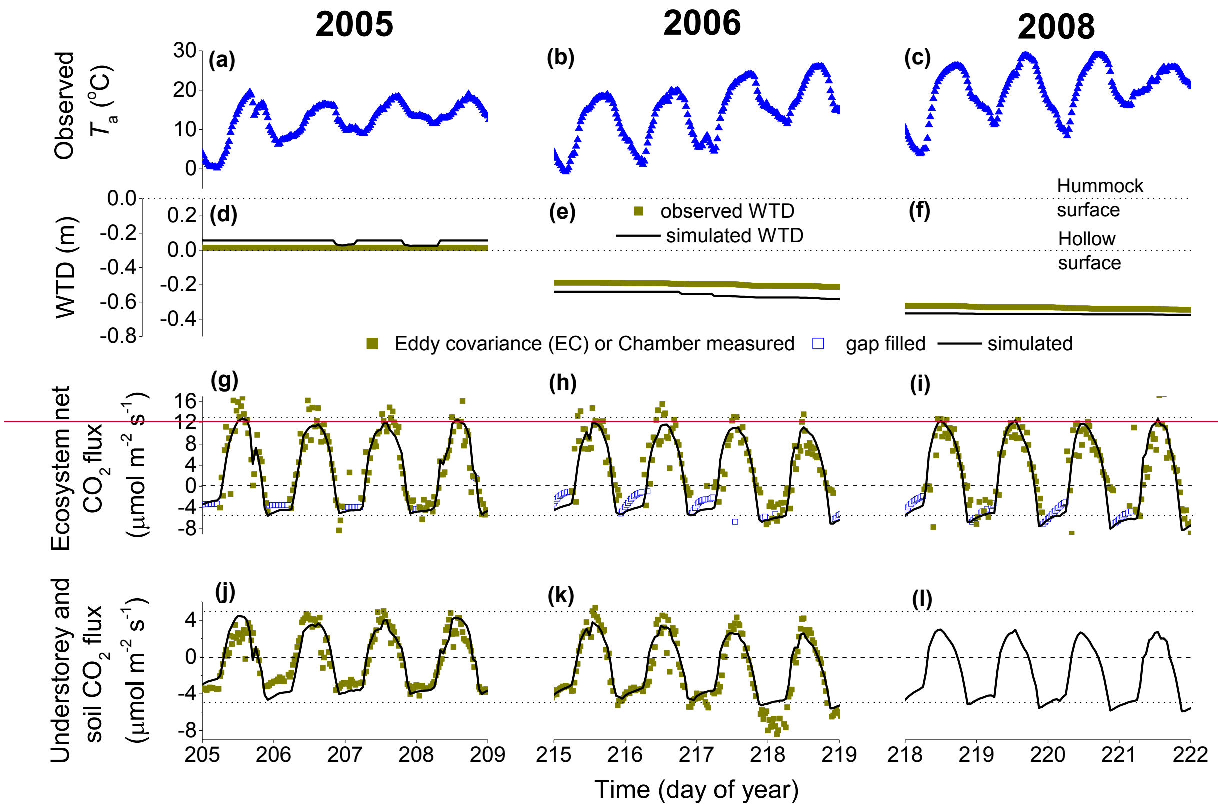


Fig. 54.

Field Code Changed


2005
2006
2008
Observed T_a (°C)
30
20
10
0
(a)
(b)
(c)
WTD (m)
0.0
-0.2
-0.4
-0.6
-0.8
0.2
0.0
-0.2
-0.4
(d)
(e)
(f)
observed WTD
simulated WTD
Hummock surface
Hollow surface
Eddy covariance (EC) or Chamber measured
gap filled
simulated
Ecosystem net CO_2 flux (μmol m^{-2} s^{-1})
16
12
8
4
0
-4
-8
(g)
(h)
(i)
Understorey and soil CO_2 flux (μmol m^{-2} s^{-1})
4
0
-4
-8
(j)
(k)
(l)
205
206
207
208
209
215
216
217
218
219
218
219
220
221
222
Time (day of year)

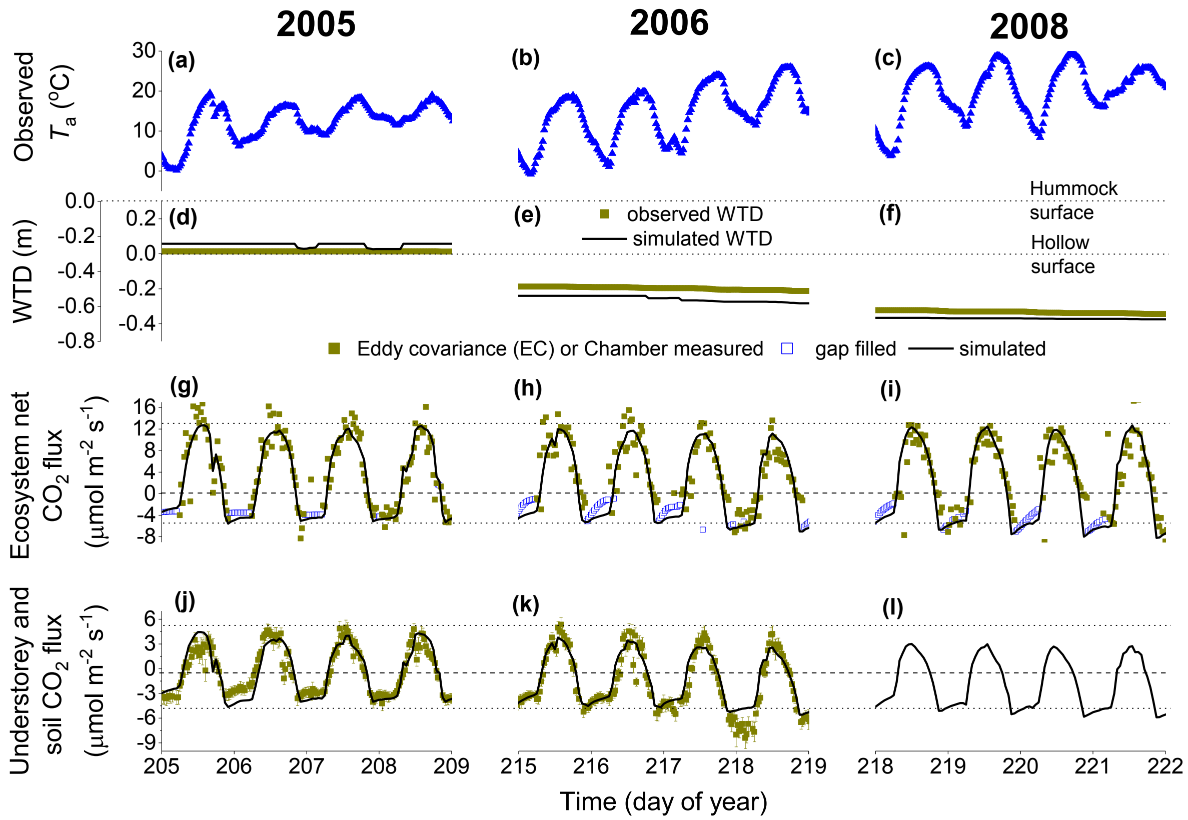


Fig. 6~~5~~.

Field Code Changed

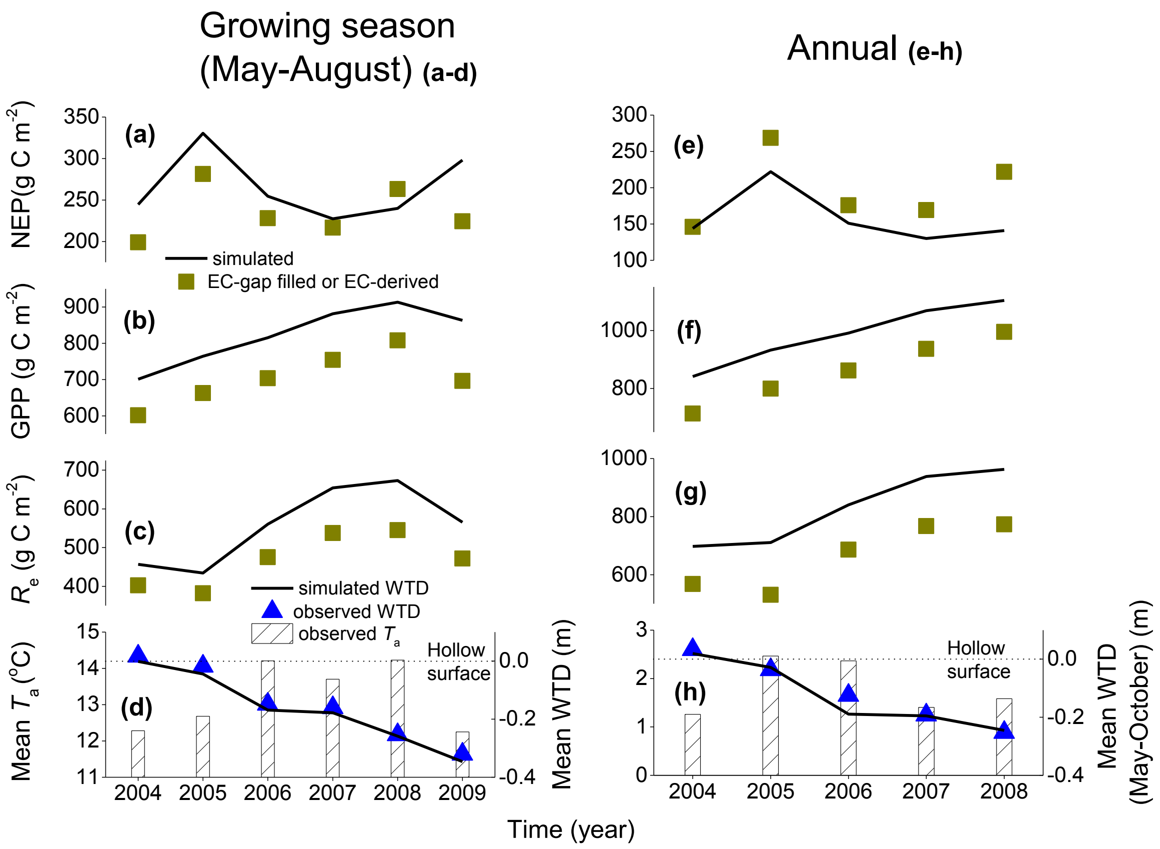

Growing season
(May-August) (a-d)
Annual (e-h)
NEP(g C m^{-2})
350
300
250
200
(a)
simulated
EC-gap filled or EC-derived
GPP (g C m^{-2})
900
800
700
600
(b)
R_e (g C m^{-2})
700
600
500
400
(c)
simulated WTD
observed WTD
observed T_a
Mean T_a (°C)
15
14
13
12
11
(d)
Hollow
surface
0.0
-0.2
-0.4
Mean WTD (m)
2004
2005
2006
2007
2008
2009
300
250
200
150
100
(e)
1000
800
(f)
1000
800
600
(g)
3
2
1
0
(h)
Hollow
surface
0.0
-0.2
-0.4
Mean WTD
(May-October) (m)
2004
2005
2006
2007
2008
Time (year)

Fig. 7~~6~~.

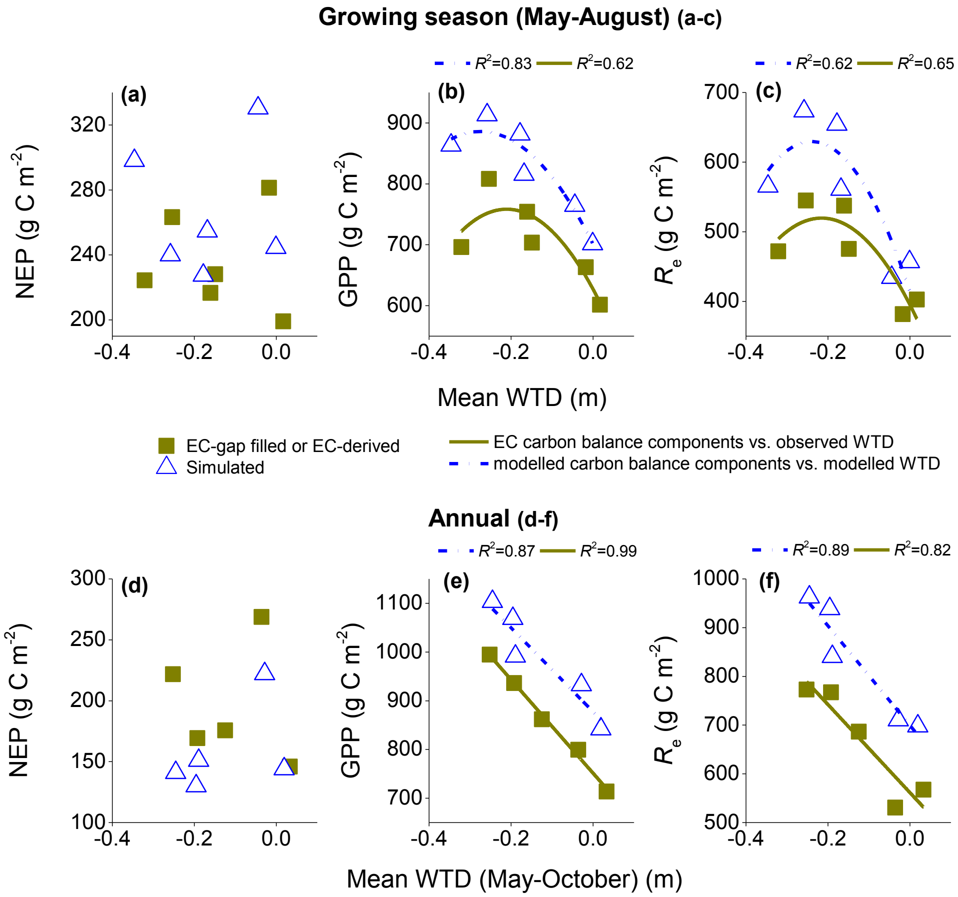

Growing season (May-August) (a-c)
R²=0.83
R²=0.62
R²=0.62
R²=0.65
(a)
(b)
(c)
NEP (g C m-2)
GPP (g C m-2)
Re (g C m-2)
320
280
240
200
900
800
700
600
700
600
500
400
-0.4
-0.2
0.0
Mean WTD (m)
EC-gap filled or EC-derived
Simulated
EC carbon balance components vs. observed WTD
modelled carbon balance components vs. modelled WTD
Annual (d-f)
R²=0.87
R²=0.99
R²=0.89
R²=0.82
(d)
(e)
(f)
300
250
200
150
100
1100
1000
900
800
700
1000
900
800
700
600
500
Mean WTD (May-October) (m)

Fig. 8~~7~~.

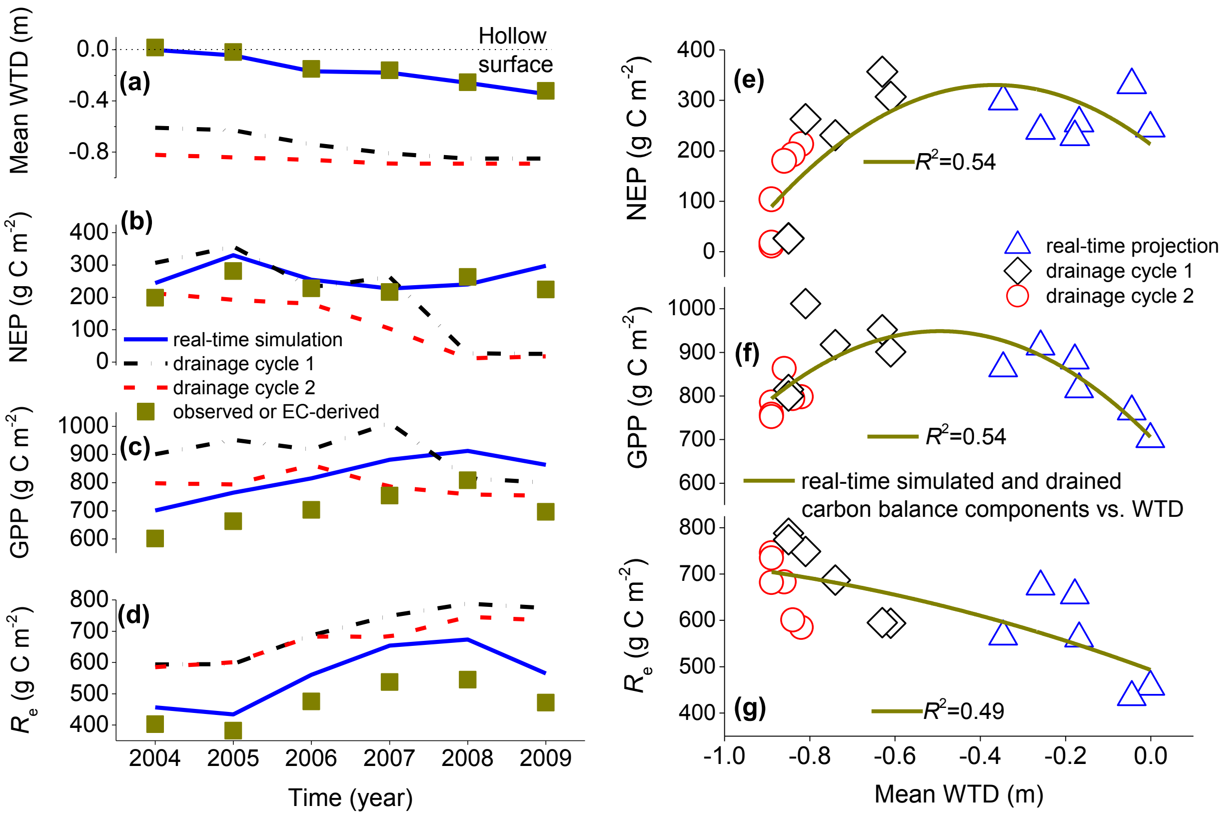

Mean WTD (m)
0.0
-0.4
-0.8
Hollow surface
(a)
NEP (g C m^{-2})
400
300
200
100
0
(b)
real-time simulation
drainage cycle 1
drainage cycle 2
observed or EC-derived
GPP (g C m^{-2})
1000
900
800
700
600
(c)
R_e (g C m^{-2})
800
700
600
500
400
(d)
2004
2005
2006
2007
2008
2009
Time (year)
NEP (g C m^{-2})
(e)
R^2=0.54
real-time projection
drainage cycle 1
drainage cycle 2
GPP (g C m^{-2})
(f)
R^2=0.54
real-time simulated and drained carbon balance components vs. WTD
R_e (g C m^{-2})
(g)
R^2=0.49
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
Mean WTD (m)

Fig. 9~~8~~.

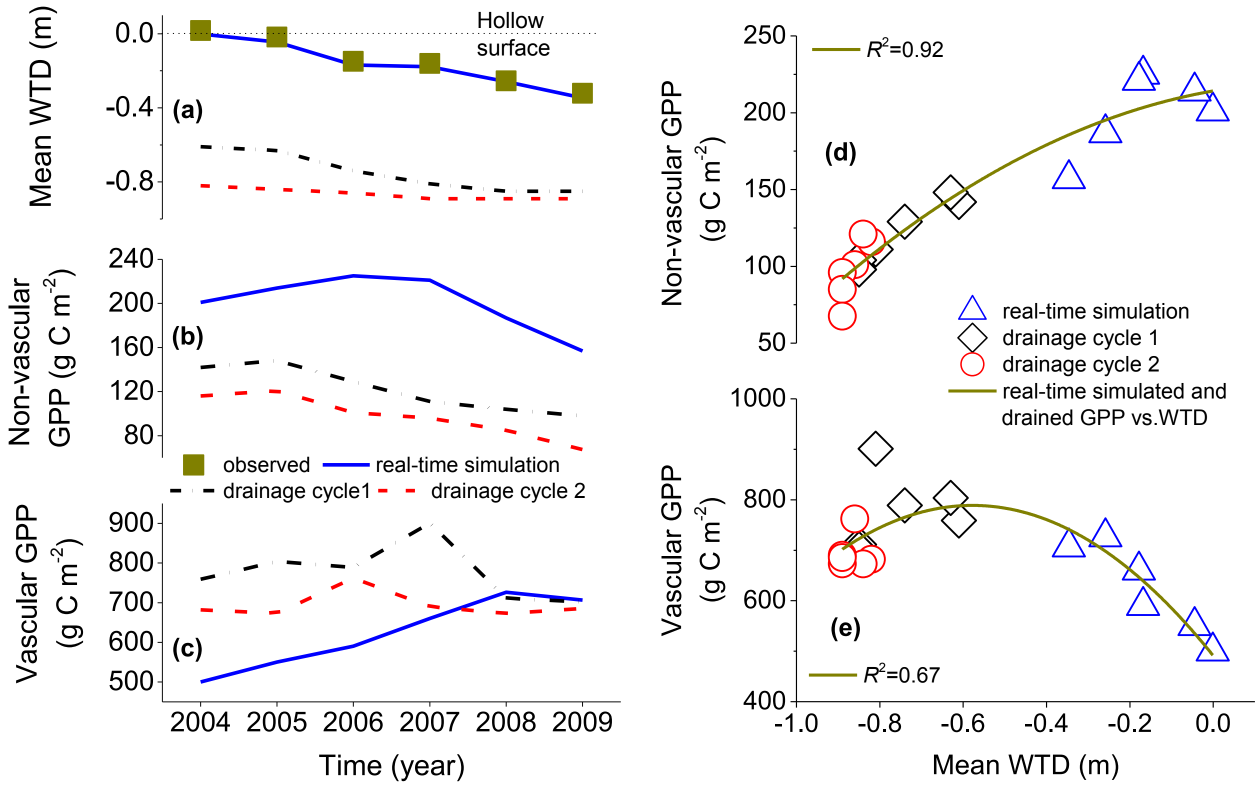

Mean WTD (m)
0.0
-0.4
-0.8
(a)
Hollow
surface
Non-vascular
GPP (g C m^{-2})
240
200
160
120
80
(b)
observed
real-time simulation
drainage cycle1
drainage cycle 2
Vascular GPP
(g C m^{-2})
900
800
700
600
500
(c)
2004
2005
2006
2007
2008
2009
Time (year)
Non-vascular GPP
(g C m^{-2})
250
200
150
100
50
(d)
R^2=0.92
real-time simulation
drainage cycle 1
drainage cycle 2
real-time simulated and
drained GPP vs.WTD
Vascular GPP
(g C m^{-2})
1000
800
600
400
(e)
R^2=0.67
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
Mean WTD (m)

Fig. 10~~9~~.

~~**Table 1:** Statistics from regressions between modelled and EC gap-filled net ecosystem CO_2 fluxes throughout the years of 2004-2008 at a Western Canadian fen peatland~~

~~**Year**~~	~~**Total annual precipitation (mm)**~~	~~***n***~~	~~***a***~~	~~***b***~~	~~R^2~~	~~**RMSE (µmol m^{-2} s^{-1})**~~	~~**RMSRE (µmol m^{-2} s^{-1})**~~
~~**Modelled vs. eddy covariance CO_2 fluxes measured at $u^* > 0.15$ ms^{-1}**~~							
~~**2004**~~	~~**553**~~	~~**5034**~~	~~**0.08**~~	~~**1.10**~~	~~**0.81**~~	~~**1.58**~~	~~**1.92**~~
~~**2005**~~	~~**387**~~	~~**5953**~~	~~**0.07**~~	~~**1.03**~~	~~**0.82**~~	~~**1.68**~~	~~**1.99**~~
~~**2006**~~	~~**465**~~	~~**6012**~~	~~**0.07**~~	~~**1.08**~~	~~**0.79**~~	~~**1.68**~~	~~**1.98**~~
~~**2007**~~	~~**431**~~	~~**5385**~~	~~**0.06**~~	~~**0.99**~~	~~**0.79**~~	~~**1.83**~~	~~**2.09**~~
~~**2008**~~	~~**494**~~	~~**5843**~~	~~**-0.01**~~	~~**0.98**~~	~~**0.84**~~	~~**1.63**~~	~~**2.02**~~
~~**Modelled vs. gap-filled CO_2 fluxes**~~							
~~**2004**~~	~~**553**~~	~~**3750**~~	~~**-0.13**~~	~~**1.20**~~	~~**0.89**~~	~~**0.64**~~	
~~**2005**~~	~~**387**~~	~~**2807**~~	~~**-0.49**~~	~~**1.03**~~	~~**0.76**~~	~~**0.82**~~	
~~**2006**~~	~~**465**~~	~~**2748**~~	~~**-0.48**~~	~~**1.15**~~	~~**0.81**~~	~~**0.58**~~	
~~**2007**~~	~~**431**~~	~~**3375**~~	~~**-0.36**~~	~~**0.97**~~	~~**0.74**~~	~~**1.23**~~	
~~**2008**~~	~~**494**~~	~~**2941**~~	~~**-0.54**~~	~~**1.05**~~	~~**0.79**~~	~~**0.95**~~	

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~~(*a*, *b*) from simple linear regressions of modelled on measured. R^2 = coefficient of determination and RMSE = root mean square for errors from simple linear regressions of measured on simulated. RMSRE= root mean square for random errors in eddy covariance (EC) measurements calculated by inputting EC CO_2 fluxes recorded at *u** (friction velocity) > 0.15 m s^{-1} into algorithms for estimation of random errors due to EC CO_2 measurements developed for forests by Richardson et al. (2006).~~

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~~**Table 2:** Statistics from regressions between modelled and EC-gap filled net ecosystem CO_2 fluxes during the growing seasons of 2004-2009 at a Western Canadian fen peatland~~

~~Year~~	~~Total growing season precipitation (mm)~~	~~*n*~~	~~*a*~~	~~*b*~~	~~R^2~~	~~RMSE (µmol m^{-2} s^{-1})~~	~~RMSRE (µmol m^{-2} s^{-1})~~
~~Modelled vs. eddy covariance CO_2 fluxes measured at *u** > 0.15 ms^{-1}~~							
~~2004~~	~~287~~	~~2043~~	~~0.55~~	~~1.05~~	~~0.78~~	~~2.27~~	~~2.55~~
~~2005~~	~~276~~	~~2200~~	~~0.82~~	~~0.98~~	~~0.79~~	~~2.50~~	~~2.74~~
~~2006~~	~~253~~	~~2107~~	~~0.48~~	~~1.06~~	~~0.78~~	~~2.36~~	~~2.76~~
~~2007~~	~~237~~	~~1822~~	~~0.65~~	~~0.93~~	~~0.75~~	~~2.91~~	~~3.06~~
~~2008~~	~~276~~	~~2070~~	~~0.32~~	~~0.96~~	~~0.82~~	~~2.45~~	~~2.85~~
~~2009~~	~~138~~	~~1870~~	~~0.76~~	~~1.01~~	~~0.81~~	~~2.27~~	~~2.83~~
~~Modelled vs. gap filled CO_2 fluxes~~							
~~2004~~	~~287~~	~~837~~	~~-0.01~~	~~1.21~~	~~0.87~~	~~1.22~~	
~~2005~~	~~276~~	~~680~~	~~-0.57~~	~~1.07~~	~~0.75~~	~~1.26~~	
~~2006~~	~~253~~	~~773~~	~~-1.70~~	~~0.95~~	~~0.73~~	~~0.78~~	
~~2007~~	~~237~~	~~1058~~	~~-0.51~~	~~0.98~~	~~0.76~~	~~1.88~~	
~~2008~~	~~276~~	~~810~~	~~-1.04~~	~~1.02~~	~~0.79~~	~~1.62~~	

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~~**2009 138 1010 -0.02 0.98 0.87 1.20**~~

~~(*a, b*) from simple linear regressions of modelled on measured. R^2 = coefficient of determination and RMSE = root mean square for errors from simple linear regressions of measured on simulated. RMSRE= root mean square for random errors in eddy covariance (EC) measurements calculated by inputting EC CO_2 fluxes recorded at *u** (friction velocity) > 0.15 m s^{-1} into algorithms for estimation of random errors due to EC CO_2 measurements developed for forests by Richardson et al. (2006).~~**Table 1.** Statistics from regressions between hourly modelled and measured net CO_2 fluxes from 2004-2009 at a Western Canadian fen peatland

(a) Regressions of modelled vs. EC measured (recorded at $u^* > 0.15$ m s^{-1}) net ecosystem CO_2 fluxes over whole years of 2004-2008[a]

Year	Total annual precipitation (mm)	*n*	*a*	*b*	R^2	RMSE (μmol m^{-2} s^{-1})	RMSRE (μmol m^{-2} s^{-1})
2004	553	5034	0.08	1.10	0.81	1.58	1.92
2005	387	5953	0.07	1.03	0.82	1.68	1.99
2006	465	6012	0.07	1.08	0.79	1.68	1.98
2007	431	5385	0.06	0.99	0.79	1.83	2.09
2008	494	5843	-0.01	0.98	0.84	1.63	2.02

(b) Regressions of modelled vs. EC measured (recorded at $u^* > 0.15$ m s^{-1}) net ecosystem CO_2 fluxes over growing seasons (May-August) of 2004-2009

Year	Total growing season precipitation (mm)	*n*	*a*	*b*	R^2	RMSE (μmol m^{-2} s^{-1})	RMSRE (μmol m^{-2} s^{-1})
2004	287	2043	0.55	1.05	0.78	2.27	2.55
2005	276	2200	0.82	0.98	0.79	2.50	2.74
2006	253	2107	0.48	1.06	0.78	2.36	2.76

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2007	237	1822	0.65	0.93	0.75	2.91	3.06
2008	276	2070	0.32	0.96	0.82	2.45	2.85
2009	138	1870	0.76	1.01	0.81	2.27	2.83

(c) Regressions of modelled vs. measured chamber net CO_2 fluxes (understorey vegetation and soil CO_2 fluxes) over ice free periods (May-October) of 2005-2006

Year	Mean May-October WTD (m)		*n*	*a*	*b*	R^2	RMSE (µmol m^{-2} s^{-1})	RMSRE (µmol m^{-2} s^{-1})
	Measured	Modelled						
2005	0.34	0.33	3285	0.43	1.05	0.68	1.19	2.38
2006	0.42	0.48	3855	0.31	0.85	0.71	1.44	3.25

WTD = water table depth below the hummock surface; (*a, b*) from simple linear regressions of modelled on measured, and R^2 = coefficient of determination; RMSE = root mean square for errors from simple linear regressions of measured on simulated; RMSRE= root mean square for random errors in measurements from simple linear regressions of simulated on measured. RMSRE for eddy covariance (EC) measurements were calculated by inputting EC CO_2 fluxes recorded at u^* (friction velocity) > 0.15 m s^{-1} into algorithms for estimation of random errors due to EC CO_2 measurements developed for forests by Richardson et al. (2006).

[a] whole year modelled vs. EC net CO_2 flux regression for 2009 could not be done due to the lack of flux measurements from September to December in that year.

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Table 2. Effects of water table depth (WTD) drawdown on components of ecosystem carbon and nutrient cycles of a Western Canadian fen peatland

		Modelled	Eddy covariance-derived/biometrically measured at the site [a]	Values from other studies in similar peatlands
Rate of increase in R_e with each 0.1 m of WTD drawdown		0.26 µmol CO_2 m^{-2} s^{-1}	0.16 µmol CO_2 m^{-2} s^{-1}	(1) ~0.3 µmol CO_2 m^{-2} s^{-1} [b] (2) ~0.33 µmol CO_2 m^{-2} s^{-1} [c]
Rate of increase in GPP with each 0.1 m of WTD drawdown		0.39 µmol CO_2 m^{-2} s^{-1}	0.22 µmol CO_2 m^{-2} s^{-1}	(1) ~0.28 µmol CO_2 m^{-2} s^{-1} [b] (2) ~0.44 µmol CO_2 m^{-2} s^{-1} [c]
Leaf nitrogen concentration (July 2004)	Black Spruce	14 g N kg^{-1} C	12 g N kg^{-1} C	
	Tamarack	32 g N kg^{-1} C	33 g N kg^{-1} C	
	Dwarf Birch	37 g N kg^{-1} C	41 g N kg^{-1} C	
Leaf nitrogen (N) to phosphorus (P) ratio (July 2004)	Black Spruce	6.6:1	7.1:1	
	Tamarack	5.2:1	6.3:1	

	Dwarf Birch	4.8:1	
Increase in foliar nitrogen concentrations with WTD drawdown	Black Spruce	from 14 to 17 g N kg^{-1} C with a WTD drawdown from ~0.25 to ~0.65 m below the hummock surface over the growing seasons of 2004-2009	(1) from ~21 to ~27 g N kg^{-1} C with a WTD drawdown from 0.24 to 0.7 m below peat surface [d] (2) from ~19 to ~21 g N kg^{-1} C for a WTD drawdown by ~0.45 m [e]
	Tamarack	from 32 to 37 g N kg^{-1} C with a WTD drawdown from ~0.25 to ~0.65 m below the hummock surface over the growing seasons of 2004-2009	(1) from ~41 to ~66 g N kg^{-1} C for a WTD drawdown from 0.24 to 0.7 m below peat surface [d] (2) from ~36 to ~42 for a WTD drawdown by ~0.45 m [e]
	Dwarf Birch	from 37 to 45 g N kg^{-1} C with a WTD drawdown from ~0.25 to ~0.65 m below the hummock	

		surface over the growing seasons of 2004-2009		
Increase in maximum rooting depth with WTD drawdown	Black spruce	from 0.35 to 0.65 m below the hummock surface with a WTD drawdown from ~0.25 to ~0.65 m over the growing seasons of 2004-2009		from 0.1 to 0.6 m below peat surface with a WTD drawdown from 0.1 to 0.7 m below hummock surface [f]
	Tamarack	from 0.35 to 0.65 m below the hummock surface with a WTD drawdown from ~0.25 to ~0.65 m over the growing seasons of 2004-2009		from 0.2 to 0.6 m below peat surface with a WTD drawdown from 0.1 to 0.6 m below hummock surface [f]

GPP=gross primary productivity; R_e = ecosystem respiration; [a] Syed et al. (2006), Flanagan and Syed (2011); [b] Peichl et al. (2012) for a Swedish fen; [c] Ballantyne et al. (2014) for a Michigan fen peatland complex that has similar peat and plant functional types as our study site; [d] Choi et al. (2007) for a central Alberta fen peatland located ~350 km to the southwest of the study site; [e] Macdonald and Lieffers (1990) for a northern Alberta fen peatland located ~250 km to the northwest of the study site; [f] Lieffers and Rothwell (1987) for a northern Alberta fen peatland located ~250 km to the northwest of the study site.

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