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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 future drier and warmer climates. We therefore tested whether the effects of WTD variation on net ecosystem CO_2 exchange of a Western Canadian boreal fen peatland could be modelled through a process-level coupling of a prognostic WTD dynamic, 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 vascular and non-vascular plant water relations in an ecosystem model *ecosys*. *Ecosys* successfully simulated a May-October WTD drawdown by ~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 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

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35 seasonal and interannual variations in net ecosystem productivity (NEP). These modelled trends
36 were corroborated against eddy covariance hourly net CO_2 fluxes (modelled vs. measured:
37 R^2~0.8, slopes~1±0.1, intercepts~0.05 μmol m^{-2} s^{-1}), and against other automated chamber,
38 biometric, and laboratory measurements. Modelled drainage as an analog for climate change
39 showed that this boreal peatland would switch from a large carbon sink (NEP~160 g C m^{-2} yr^{-1})
40 to carbon neutrality (NEP~10 g C m^{-2} yr^{-1}) should water table deepened by a further ~0.5 m.
41 Therefore, representing the effects of interactions among hydrology, biogeochemistry and plant
42 physiological ecology on ecosystem carbon, water, and nutrient cycling in global carbon models
43 would improve our predictive capacity for changes in boreal peatland carbon sequestration under
44 changing climates.

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1. Introduction

Northern boreal peatlands have been accumulating carbon (C) at a rate of about 20-30 g 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, 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).

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

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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

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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 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 predict how boreal peatlands would behave under future drier and warmer climates, a peatland C model needs to have sufficient representation of 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 a continuous anaerobic zone below 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;

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

120 **1.1. Objective and rationale**

121 To overcome the inadequacies in peatland C models as discussed above, we represented a
122 prognostic and dynamic WTD, and a soil moisture retention scheme that are coupled with
123 microbial and root oxidation-reduction reactions, energy yields, growth, and uptake within a soil-
124 plant-microbe-atmosphere water, C and nutrient (nitrogen, phosphorus) scheme in a terrestrial
125 process model *ecosys*. Our objective was to test whether this coupling of hydrology with
126 biogeochemistry and plant physiological ecology in *ecosys* would enable successful simulation
127 of diurnal, seasonal and interannual variations in net CO_2 exchange as affected by variations in
128 WTD over a drying period from 2004 to 2009 in a western Canadian boreal fen peatland in
129 Alberta, Canada (will be termed as WPL hereafter) (Syed et al., 2006; Flanagan and Syed, 2011).
130 For this purpose, *ecosys* algorithms would first be fed by inputs for peat hydrological, biological,
131 chemical and physical properties, and plant physiology measured at the WPL or similar
132 peatlands. Then the modelled outputs for net ecosystem CO_2 exchange and WTD would be
133 tested against site measurements at the WPL. The tested modelled outputs would further be
134 examined to explain WTD effects on C processes at this northern boreal fen.

135 In the past, similar coupling of hydrological, biological and ecological feedbacks enabled
136 *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 a field study using eddy covariance (EC) micro-meteorological approach, Flanagan and Syed (2011) found no net effect of WTD drawdown from 2004-2009 caused by progressively drier and warmer weather on NEP of WPL. 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 hypothesize that 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 these effects of WTD drawdown on GPP and R_e and hence NEP at the WPL. For this purpose, we tested the following four modelling hypotheses while simulating WTD effects on R_e and GPP of WPL:

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181 (1) WTD drawdown would cause peat pore drainage and improve peat aeration that would
182 increase the energy yields from aerobic microbial decomposition and hence would increase R_e in
183 the modelled WPL ecosystem.

184 (2) Enhanced microbial activity due to WTD drawdown would also cause more rapid nutrient
185 mineralization and consequent greater root nutrient availability and uptake, greater leaf nutrient
186 concentrations and hence increased GPP.

187 (3) But when the WT falls below a certain threshold level, inadequate recharge of the near
188 surface peat layers through capillary rise would cause desiccation of those layers. Drying of near
189 surface peat layers and the surface residue can reduce near surface and surface peat respiration
190 that can partially offset the increase in deeper peat respiration due to aeration in hypothesis 1.

191 (4) Near surface peat desiccation would also reduce peat water potential and hydraulic
192 conductivity and hence vascular and non-vascular water uptake from desiccated near surface
193 layers. Since non-vascular mosses depend mainly on near surface peat layers for moisture
194 supply, reduction in moss water uptake would cause a reduction in moss water potential and
195 hence moss GPP. On the contrary, suppression of vascular root water uptake from desiccated
196 near surface layers under deeper WT would be offset by increased deeper root water uptake from
197 newly aerated deeper peat layers with higher water potentials that would sustain vascular canopy
198 water potential (ψ_c), canopy stomatal conductance (g_c) and GPP.

199 **2. Methods**

200 **2.1. Model development**

201 *Ecosys* is a process-based terrestrial ecosystem model that simulates 3D water, energy,
202 carbon and nutrient (nitrogen, phosphorus) cycles in different peatlands (Dimitrov et al., 2011;

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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. The equations that are cited within the text are listed in the sections S1-S4 in the supplementary material for further clarification.

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. 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 (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.

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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). 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) (Eqs. A1-A2, A4). Biomass (M) growth of each of the MFTs (Eq. A25a) is calculated from its DOC uptake (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 $[O_{2s}]$

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

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). Rapid M growth causes rapid mineralization (Eq. A26), and hence greater aqueous concentrations of NH_4^+, NO_3^- and $H_2PO_4^-$.

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

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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). Root N and P uptake under shallow WT is

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

315 **2.1.4. WTD effects on non-vascular gross primary productivity**

316 Effects of WTD drawdown on non-vascular (e.g., moss) GPP in *ecosys* is simulated from
317 peat moisture supplying capacity through capillary rise from the WT to adequately recharge

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318 shallow peat layers to sustain moss U_w. Tiny individuals of mosses with no stomatal regulation
319 are simulated in *ecosys* from intra-specific competition for light and nutrients (N, P) among large
320 moss populations. Simulated mosses in *ecosys* are mostly confined to near surface peat layers
321 that are frequently unsaturated. When WT deepens past a threshold level, inadequate capillary
322 rise (Eqs. D9, D12) causes near-surface peat desiccation, thereby reducing ψ_s and increasing Ω_s
323 (Eq. B9) of those layers. It causes a reduction in moss canopy water potential (ψ_c) while
324 equilibrating moss evaporation with moss U_w (Eq. B6). Reduced moss ψ_c causes a reduction in
325 moss carboxylation rate (Eqs. C3, C6a) and moss GPP (Eq. C1).

326 **2.2. Modelling experiment**

327 **2.2.1. Study site**

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

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339 **2.2.2. Field data sets**

340 *Ecosys* model inputs of half hourly weather variables i.e. incoming shortwave and
341 longwave radiation, air temperature (T_a), wind speed, precipitation and relative humidity during
342 2003-2009 were measured by Syed et al. (2006) and Flanagan and Syed (2011) at the
343 micrometeorological station installed at the WPL. To test the adequacy of WTD simulation in
344 *ecosys*, modelled outputs of hourly WTD were tested against WTD measured at the WPL with
345 respect to average hummock surface by Flanagan and Syed (2011). To examine how well *ecosys*
346 simulated net ecosystem CO_2 exchange at the WPL, we tested hourly modelled net ecosystem
347 CO_2 fluxes against those measured by using eddy covariance (EC) micro-meteorological
348 approach by Syed et al. (2006) and Flanagan and Syed (2011). Quality control, and gap-filling of
349 EC measured net CO_2 fluxes, and partitioning of EC-gap filled net CO_2 fluxes into GPP and R_e
350 were done by Syed et al. (2006) and Flanagan and Syed (2011).

351 Soil CO_2 fluxes measured by automated chambers can provide a valuable supplement to
352 EC CO_2 fluxes in testing modelled respiration by providing more continuous measurements than
353 EC. So, we also tested our modelled outputs against half-hourly automated chamber
354 measurements by Cai et al. (2010) at the WPL. These CO_2 flux measurements were carried out
355 over both hummocks and hollows by using a total of 9 steady-state transparent chambers (Cai et
356 al., 2010). Apart from soil respiration these chamber CO_2 fluxes thus included fixation and
357 autotrophic respiration from dwarf shrubs, herbs and mosses (Cai et al., 2010). Therefore we
358 compared modelled fixation and autotrophic respiration from understorey PFTs (e.g., shrub and
359 moss) combined with modelled soil respiration against these chamber net CO_2 fluxes measured
360 at the WPL. For this purpose net CO_2 flux measurements from all of those chambers were

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361 averaged and compared against average soil and understorey CO_2 fluxes modelled over the
362 hummock and the hollow.

363 **2.2.3. Model run**

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

371 Peat organic and chemical properties at different depths of the WPL were represented in
372 *ecosys* by inputs from measurements either at the site (e.g., Syed et al., 2006; Flanagan and Syed,
373 2011) or at similar nearby sites (e.g., Rippy and Nelson, 2007) (Fig. 1). However, we did not
374 have any site measurement for the nutrient gain through lateral water inflow which was observed
375 by Syed et al. (2006) during the field measurements. Instead, we used background wet deposition
376 rates of 0.5 mg ammonium-N, 0.25 mg nitrate-N and 0.075 mg phosphate-P per litre of
377 precipitation water to simulate an additional source of nutrient input.

378 *Ecosys* was run for a spin up period of 1961-2002 under repeating 7-year sequences of
379 hourly weather data (shortwave and longwave radiation, air temperature, wind speed, humidity
380 and precipitation) recorded at the site from 2003 to 2009. There was a drying trend observed
381 from 2003 to 2009 due to diminishing precipitation that caused WTD drawdown in the
382 watershed in which WPL is located, which lowered the WT of this fen peatland (Flanagan and

383 Syed, 2011). To accommodate the gradual drying effects of catchment hydrology on modelled
384 fen peatland WTD, we set the WTD_x at different levels based on the annual wetness of weather,
385 e.g., shallow, intermediate, and deep (WTD_x=0.19, 0.35 and 0.72 m below the hummock surface,
386 or 0.11 m above and 0.05 and 0.42 m below the hollow surface) (Fig. 1). There was no exchange
387 of water through lower model boundary to represent the presence of nearly impermeable clay
388 sediment underlying the peat (Syed et al., 2006) (Fig. 1). Variations in peat surface with WTD
389 variations, which is an important hydrologic self-regulation of boreal peatlands (Dise, 2009), was
390 not represented in this version of *ecosys*.
391 At the start of the spin up run, the hummock grid cell was seeded with an evergreen
392 needle leaf and a deciduous needle leaf over-storey plant functional types (PFT) to represent the
393 black spruce and tamarack trees at the WPL. The hollow grid cell was seeded with only the
394 deciduous needle leaf over-storey PFTs since the black spruce trees at the WPL only grew on the
395 raised areas. Each of the modelled hummock and the hollow was also seeded with a deciduous
396 broadleaved vascular (to represent dwarf birch) and a non-vascular (to represent mosses) under-
397 storey PFTs. The planting densities were such that the population densities of the black spruce,
398 tamarack, dwarf birch and moss PFTs were 0.16, 0.14, 0.3, and 500 m^{-2} respectively at the end of
399 the spin up run so as to best represent field vegetation (Syed et al., 2006; Mezbahuddin et al.,
400 2016). To include wetland adaptation, we used a root porosity (θ_{pr}) value of 0.1 for the two over-
401 storey PFTs and a higher θ_{pr} value of 0.3 for the under-storey vascular PFT to represent better
402 wetland adaptation in the under-storey than the over-storey PFTs. These θ_{pr} values were used in
403 calculating root O_2 transport through aerenchyma (Eq. D45) and did not change with
404 waterlogging throughout the model run. These θ_{pr} values were representatives of root porosities
405 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}. Model performance was evaluated from regression intercepts ($a \rightarrow 0$), slopes ($b \rightarrow 1$), coefficients of determination ($R^2 \rightarrow 1$), and root means squares for errors (RMSE$\rightarrow$0) for each study year to test whether there was any systematic divergence between the modelled and EC measured CO_2 fluxes. Similar regressions of modelled vs. gap-filled net CO_2 fluxes were also performed to test for any divergence between the modelled and gap-filled CO_2 fluxes. These regressions based tests are very important since any small

429 divergence between hourly modelled and EC measured as well as between hourly modelled and
430 gap-filled CO_2 fluxes can result in a large divergence between modelled and EC-gap filled
431 annual estimates.

432 **2.2.5. Sensitivity of modelled peatland CO_2 exchange to artificial drainage**

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

448 **3. Results**

449 **3.1. Model performance in simulating diurnal variations in ecosystem net CO_2 fluxes**

450 Variations in precipitation can cause change in WTD and consequent variation in diurnal
451 net CO_2 exchange across years. *Ecosys* simulated diurnal net CO_2 fluxes reasonably well which

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452 was measured each year from 2004 to 2008 with varying precipitation (Table 1). On a year-to-
453 year basis, regressions of hourly modelled vs. measured net ecosystem CO_2 fluxes gave
454 intercepts within 0.1 μmol m^{-2} s^{-1} of zero, and slopes within 0.1 of one, indicating minimal bias
455 in modelled outputs during each year from 2004-2008 (Table 1). On a growing season (May-
456 August) basis, regressions of modelled on measured hourly net CO_2 fluxes yielded larger
457 positive intercepts from 2004-2009 (Table 2). The larger intercepts were predominantly caused
458 by modelled overestimation of growing season day-time CO_2 fluxes. This overestimation was
459 offset by modelled overestimation of night-time CO_2 fluxes during the winter thus yielding
460 smaller intercepts from throughout-the-year regressions of modelled vs. EC measured fluxes
461 (Tables 1 vs. 2). We could not do a modelled vs. EC CO_2 regression for the entire year of 2009
462 due to the lack of flux measurements from September to December in that year. Values for
463 coefficients of determination (R^2) were ~ 0.8 ($P < 0.001$) for all years from both throughout-the-
464 year and growing season regressions (Tables 1 and 2). RMSEs were < 2.0 and ~2.5 μmol m^{-2} s^{-1}
465 for whole year regressions from 2004-2008 (Table 1) and for growing season regressions from
466 2004-2009 (Table 2) respectively. Much of the variations in EC measured CO_2 fluxes that was
467 not explained by the modelled fluxes could be attributed to a random error of ~20% in EC
468 methodology (Wesely and Hart, 1985). This attribution was further corroborated by root mean
469 squares for random errors (RMSRE) in EC measurements, calculated for forests with similar
470 CO_2 fluxes from Richardson et al. (2006) that were similar to RMSE (Table 1). The similar
471 values of RMSE and RMSRE also indicated that further constraint in model testing could not be
472 achieved without further precision in EC measurements.

473 Regressions of modelled vs. gap-filled CO_2 fluxes gave slopes and R^2 which were similar
474 to, and RMSEs which were smaller than those from modelled vs. EC-measured CO_2 fluxes for

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475 most of the years except for the throughout-the-year regressions in 2004 and 2006 when the
476 slopes were larger (Tables 1 and 2). The intercepts from modelled vs. gap filled CO_2 fluxes were
477 consistently more negative than those from modelled vs. EC measured fluxes for both whole
478 year (Table 1) and growing season (Table 2) regressions. It was mainly caused by larger
479 modelled than gap filled night-time CO_2 effluxes.

480 **3.2. Seasonality in WTD and net ecosystem CO_2 exchange**

481 Seasonality in WTD measured at the WPL showed interannual variation from 2004 to
482 2009 which was modelled reasonably well by *ecosys* (Figs. 2b, d, f, h, j, l). The interannual
483 variation in seasonality of WTD was modelled by adequate simulation of the balance between
484 vertical water fluxes i.e., precipitation vs. evapotranspiration and lateral water fluxes i.e.,
485 recharge vs. discharge. Larger precipitation to evapotranspiration ratio (*P/ET*) throughout 2004
486 caused the shallowest modelled WTD which remained above the hollow surface throughout most
487 of the year (Fig. 2b). WTD_x (=0.19 m) (Fig. 1) shallower than the modelled WTD in 2004
488 created a hydraulic gradient that caused net lateral recharge and hence further sustained the
489 shallow modelled WTD. A smaller *P/ET* in 2005 than in 2004 caused slightly deeper WTD that
490 remained at the hollow surface or within 0.1 m below the hollow surface (Fig. 2d). During this
491 year, WTD_x (=0.19 m) (Fig. 1) shallower than the modelled WTD caused net lateral recharge and
492 hence further sustained WTD close to the hollow surface. Declines in the *P/ET* over the growing
493 seasons of 2006 and 2007 caused modelled WTD drawdown to levels where the differences
494 between evapotranspiration and precipitation equilibrated with net lateral recharge caused by
495 hydraulic gradients yielded from WTD_x (=0.35 m) (Fig. 1) which was deeper than the modelled
496 WTD in both years (Figs. 2f, h). Continued declines in growing season *P/ET* in 2008 and 2009
497 caused further deepening of the WT (Figs. 2j, l). A WTD_x (=0.72 m) (Fig. 1) deeper than the

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498 modelled WTD in these growing seasons generated hydraulic gradients that caused net lateral
499 discharge which further deepened WT. Above mentioned modelled interannual variations in
500 seasonality of WTD from 2004 to 2009 were well corroborated by site measured half hourly
501 WTD at the WPL (Figs. 2b, d, f, h, j, l).

502 Seasonality in net CO_2 exchange at the WPL was predominantly governed by that in
503 temperature which controlled the seasonality in phenology and GPP as well as that in R_e. *Ecosys*
504 simulated the seasonality in phenology and hence GPP, and R_e reasonably well during a gradual
505 growing season WTD drawdown from 2004 to 2009 which was apparent by good agreements
506 between modelled vs. EC-gap filled daily NEP (Fig. 2) and hourly net CO_2 fluxes (Tables 1 and
507 2). Modelled NEP throughout the winters of most of the years were more negative than the EC-
508 gap filled NEP indicating larger modelled than EC-gap filled winter CO_2 effluxes (Fig. 2). This
509 trend was also indicated by negative intercepts from throughout-the-year regressions of modelled
510 vs. gap-filled CO_2 fluxes (Table 1). The onset of photosynthesis at the WPL varied interannually
511 depending upon spring temperature which was also modelled adequately by *ecosys*. For instance,
512 2004 with a cooler spring produced smaller early growing season (May) GPP and hence NEP
513 than 2005 with a warmer spring which was apparent in daily EC-gap filled and modelled NEP
514 (Figs. 2a vs. 2c).

515 **3.3. WTD effects on diurnal net ecosystem CO_2 exchange**

516 WTD variation can affect diurnal net CO_2 exchange by affecting peat O_2 status and
517 consequently root and microbial O_2 and nutrient availability, growth and uptake thereby
518 influencing CO_2 fixation and/or respiration. To examine modelled vs. measured WTD effects on
519 diurnal net CO_2 exchange at the WPL, we examined three 10-day periods with comparable
520 weather conditions (radiation and air temperature) that differed predominantly in their WTD

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521 during late growing seasons (August) of 2005, 2006 and 2008 (Fig. 3). A WTD drawdown from
522 late growing season of 2005 to that of 2006 in *ecosys* caused a reduction in peat water contents
523 and a consequent increase in O_2 influxes from atmosphere into the peat that eventually caused an
524 increase in modelled soil CO_2 effluxes (Fig. 4c). Increased modelled soil CO_2 effluxes in mid-
525 August of 2006 contributed to the larger modelled ecosystem CO_2 effluxes (R_e) as apparent in
526 larger modelled night-time fluxes in the late growing season of 2006 than in that of 2005 which
527 was well corroborated by night-time EC CO_2 fluxes during those periods (Fig. 4a). The
528 stimulation of R_e as a result of WTD drawdown was further corroborated by larger sums of
529 night-time soil CO_2 fluxes and understorey autotrophic respiration (R_a) as measured by Cai et al.
530 (2010) using automated chambers and modelled by *ecosys* in late growing season of 2006 with
531 deeper WTD than in that of 2005 with shallower WTD (Fig. 4b).

532 Further WTD drawdown into the late growing season of 2008 (Fig. 3c) caused improved
533 peat oxygenation and hence larger soil CO_2 effluxes in the model (Fig. 4c). It contributed to
534 similarly larger modelled night-time CO_2 fluxes in the late growing seasons of 2006 and 2008
535 than in 2005 that were also well corroborated by EC measured night-time fluxes during those
536 periods (Fig. 4a). Consequently, the sums of modelled night-time soil CO_2 fluxes and
537 understorey R_a in late growing season of 2008 were similarly larger as in 2006 with respect to
538 those in that period of 2005 (Fig. 4b). We did not have any chamber measurements available for
539 2008 to corroborate the modelled outputs. Despite larger night-time modelled and EC CO_2 fluxes
540 in the late growing season of 2008 than in 2005, the day-time influxes in 2008 were also similar
541 to those in 2005 (Fig. 4a). It indicated a greater late growing season CO_2 fixation with WTD
542 drawdown from 2005 to 2008. WTD drawdown thus stimulated both the night-time and the day-
543 time net CO_2 fluxes as apparent in both the modelled outputs and in EC flux measurements

544 during the three WTD conditions mentioned above thereby indicating increases in both R_e and
545 GPP with the deepening of WT.

546 Apart from WTD, temperature variation could also profoundly affect ecosystem net CO_2
547 exchange at the WPL. For a given WTD condition, warmer weather caused increases in R_e at the
548 WPL (Figs. 3b-c and 4a-b). Larger night-time modelled, EC-gap filled and chamber CO_2 fluxes
549 in warmer nights of day 214, 220 and 222 than the cooler nights of day 221, 224 and 218 in
550 2005, 2006 and 2008 respectively indicated the trend of increased R_e with warming under similar
551 WTD condition (Figs. 3b and 4a-b). However, at similar temperature conditions, modelled and
552 EC-gap filled night-time ecosystem CO_2 fluxes as well as modelled and chamber measured sums
553 of night-time soil CO_2 fluxes and understorey R_a under deeper WT in 2006 and 2008 were larger
554 than those in 2005 under shallower WT (denoted by the grey arrows in Figs. 3b and 4a-b). It
555 indicated R_e stimulation as a result of WTD drawdown at the WPL regardless of temperature
556 condition that further corroborated the net effects of WTD drawdown on R_e and hence on net
557 ecosystem CO_2 exchange.

558 The degree of stimulation in R_e at the WPL due to warming was also influenced by WT
559 conditions. To study this effect we further examined three 4-day warming events in late July and
560 early to mid-August of 2005, 2006 and 2008 with gradually deeper WT (Figs. 5a-f). The
561 warming events in early to mid-August of 2006 and 2008, when WT was deeper than in late July
562 of 2005, caused gradual increases in R_e as apparent from gradually larger modelled and EC-gap
563 filled night-time ecosystem CO_2 effluxes (Figs. 5h-i). Increases in R_e due to warming under
564 deeper WT were also apparent in gradually larger modelled and sums of chamber-measured
565 night-time soil CO_2 fluxes and understorey R_a in 2006 and modelled understorey and soil CO_2
566 fluxes in 2008 (Figs. 5k-l). This R_e stimulation due to warming under deeper WT contributed to

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567 declines in modelled and EC-gap filled July-August NEP in 2006 and 2008 (Figs. 2e, i). Unlike
568 in 2006 and 2008, a late-July warming event in 2005 with shallower WT did not yield a similarly
569 evident stimulation of either modelled or EC-gap filled R_e and either modelled or chamber
570 measured soil and understorey respiration (Figs. 5g, j). Lack of stimulation in R_e with warming
571 under shallower WT in 2005 resulted in the absence of decline in July-August NEP as occurred
572 in 2006 and 2008 (Figs. 2c vs. 2e, i). These findings thus showed that the stimulation of R_e due to
573 warming was greater with deeper WT thereby further indicating importance of WTD in
574 mediating potential future warming effects on NEP of northern boreal peatlands.

575 **3.4. Interannual variations in WTD and net ecosystem productivity**

576 The effects of WTD drawdown on modelled and EC-gap filled diurnal net ecosystem
577 CO_2 exchange also contributed to the effects of interannual variation in WTD on that of NEP.
578 *Ecosys* simulated a gradual drawdown of average growing season (May-August) WTD from
579 2004 to 2009 from gradually declining growing season *P/ET* and lateral water gain through
580 recharge (Fig. 6d). Simulated WTD drawdown was corroborated well by site measured WTD at
581 the WPL (Fig. 6d). Slightly deeper WT in 2005 than in 2004 caused larger growing season GPP
582 in *ecosys* that was corroborated by EC-derived GPP (Fig. 6b). The increase in GPP from 2004 to
583 2005 was also contributed by larger GPP in warmer May of 2005 than 2004. Slight WTD
584 drawdown from 2004 to 2005 did not raise either modelled or EC-derived growing season R_e
585 (Fig. 6c). It was because of June and July in 2005 being more than 2°C cooler than in 2004
586 thereby causing cooler soil which reduced R_e. Reduction in June and July R_e due to cooler soil
587 more than fully offset the increase in R_e due to slight WTD drawdown and resulted in decreased
588 growing season modelled and EC-derived R_e in 2005 than in 2004 (Fig. 6c). Larger GPP and
589 smaller R_e together caused a larger growing season NEP in 2005 than in 2004 (Fig. 6a).

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590 WTD drawdown in *ecosys* from 2005 to 2006 caused increases in both modelled growing
591 season GPP and R_e that was corroborated by EC-derived GPP and R_e (Figs. 6b-c). Increases in
592 GPP and in R_e with deepening of WT from 2005 to 2006 were also apparent in modelled vs. EC-
593 gap filled and chamber diurnal net CO_2 fluxes (Figs. 4-5). Warmer growing season in 2006 than
594 in 2005 (Fig. 6d) caused warmer soil that further contributed to the increase in modelled and EC-
595 derived growing season R_e from 2005 with shallower WT to 2006 with deeper WT (Figs. 4, 5
596 and 6c-d). A larger increase in growing season R_e than that in GPP caused modelled and EC-
597 derived growing season NEP to decrease from 2005 to 2006 (Fig. 6a). Continued growing season
598 WTD drawdown from 2006 to 2008 caused similar increases in modelled growing season GPP
599 and R_e that caused no significant changes in modelled growing season NEP (Figs. 6a-d). Like the
600 modelled estimates, EC-derived growing season GPP and R_e also increased with WTD
601 drawdown from 2006 to 2008 (Figs. 6a-d). However, the rate of increase in EC-derived growing
602 season R_e was smaller than that in modelled growing season R_e thereby contributing to a larger
603 growing season EC-gap filled NEP in 2008 than in 2006 which was not apparent in modelled
604 estimates (Figs. 6a-c). A further drawdown in WTD from the growing season of 2008 to 2009
605 caused reductions in both modelled and EC-derived growing season GPP and R_e (Figs. 6a-d).
606 Reductions in GPP and R_e from 2008 to 2009 could also be contributed by lower T_a in 2009 than
607 in 2008 that caused cooler canopies and soil (Figs. 6b-d). The reduction in EC-derived growing
608 season GPP was larger than that in EC-derived growing season R_e thereby causing a decrease in
609 growing season EC-gap filled NEP from 2008 to 2009 (Figs. 6a- c). On the contrary, the
610 reduction in modelled growing season GPP from 2008 to 2009 was less than that in the EC-
611 derived GPP thereby causing an increase in modelled growing season NEP from 2008 to 2009
612 (Figs. 6a-c).

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Despite the counteracting and offsetting effects of WTD and T_a on GPP and R_e, larger modelled and EC-derived estimates of growing season GPP and R_e in 2009 than in 2004 with similar mean T_a suggested that both modelled and EC-derived growing season GPP and R_e increased with the deepening of average growing season WT at the WPL (Figs. 6a-d). It was further corroborated by polynomial regressions of modelled growing season estimates of GPP and R_e on modelled average growing season WTD and similar regressions of EC-derived growing season GPP and R_e on measured average growing season WTD (Figs. 7a-c). The 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. 7b-c). Neither modelled nor EC-gap filled estimates of growing season NEP yielded significant regressions when regressed on modelled and measured growing season WTD respectively (Fig. 7a). 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. 6 and 7a).

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 modelled WTD averaged over the ice free periods (May-October) from 2004 to 2008 stimulated annual modelled and EC-derived GPP (Figs. 6f, h and 7e). 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 (Fig. 7d).

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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 though, 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 2004 to 2009 (Figs. 6-7).

Increased GPP with WTD drawdown (Figs. 6b, f and 7b, 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 PFT 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 ~0.05 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 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. 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. 6b, f and 7b, e). 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 drainage cycles 1 and 2 lowered growing season WT by ~0.5 m and ~0.55 m respectively from those in the real-time simulation in all the years from 2004 to 2009 (Fig. 8a).

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. 8c, f). The WTD drawdown affected modelled vascular and non-vascular growing season GPP quite differently. Modelled growing season

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682 vascular GPP increased with WTD drawdown before it plateaued and eventually decreased when
683 WTD fell below ~0.6 m from the hollow surface (~0.9 m below the hummock surface) (Figs. 9a,
684 c, e). On the contrary, modelled non-vascular growing season GPP continued to decrease with
685 WTD drawdown below ~0.1 m from the hollow surface (~0.4 m below the hummock surface)
686 (Figs. 9a-b, d).

687 WTD drawdown due to simulated drainage not only affected modelled growing season
688 GPP but also affected, and was affected by, the associated change in evapotranspiration. Deeper
689 WTD_x in drainage cycle 1 caused larger hydraulic gradients and greater lateral discharge thereby
690 deepening the WT with respect to that in the real-time simulation (Figs. 8a). Larger GPP
691 throughout the growing seasons of 2004-2007 in the drainage cycle 1 than in the real-time
692 simulation caused a greater vertical water loss through evapotranspiration that further
693 contributed to this deepening of WT (Fig. 8b). However, greater lateral water discharge in
694 drainage cycle 2 caused by deeper WTD_x did not deepen the modelled growing season WT much
695 below that in cycle 1 (Fig. 8a). The larger lateral water loss through discharge in drainage cycle 2
696 than in cycle 1 was mostly offset by slower vertical water losses through evapotranspiration as
697 indicated by smaller GPP in the drainage cycle 2 (Fig. 8b). The changing feedbacks between
698 WTD and GPP and hence evapotranspiration in *ecosys* also indicated the ability of the model to
699 simulate hydrological self-regulation which is an important characteristic of peatland eco-
700 hydrology (Dise, 2009).

701 Modelled growing season R_e continued to increase with deepening of modelled WT due
702 to drainage (Figs. 8d, g). Reductions in modelled growing season R_e from drainage cycle 1 to 2
703 during 2006-2009 indicated R_e inhibition due to desiccation of near surface peat layers and
704 surface residues (Fig. 8d). Overall larger increases in GPP than those in R_e with initial WTD

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drawdown in the drainage simulation slightly increased modelled growing season NEP (Figs. 8 b, e). Continued WTD drawdown 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. 8b-d). The 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

Modelled and EC-gap filled diurnal, seasonal and annual NEP, GPP and R_e vs. modelled and observed WTD suggested that WTD drawdown raised both GPP and R_e at the WPL (Figs. 2-7). 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. 6-7). 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 hypotheses that describe how *ecosys* would simulate above mentioned WTD effects on R_e, GPP and NEP at the WPL are discussed 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) (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 measurements at the WPL (Figs. 4-7). 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. 4c) (Eqs. D42-D43). Increased O_2 influxes enhanced [O_{2s}] and stimulated R_h (Eqs. A13, A20), soil respiration and hence R_e (Figs. 4-7). 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 (Figs. 4-7).

The modelling hypothesis of increased R_e stimulated by improved peat oxygenation due to WTD drawdown can be corroborated by other field, laboratory and modelling studies on similar peatlands. Automated chamber measurements by Cai et al. (2010) at our study site showed increased soil respiration with deeper WT thereby further corroborating our hypothesis

749 (Figs. 4b and 5j-l). Kotowska (2013) found through a combination of automated chamber
750 measurements and a laboratory incubation study that increases in aerobic microbial
751 decomposition stimulated by WTD drawdown contributed to higher R_e in a moderately rich fen
752 very close to our study site. Mäkiranta et al. (2009) also found increased rates of microbial
753 decomposition in a Finish peatland due to thicker aerobic zone and consequently larger amounts
754 of decomposable organic matter exposed to aerobic oxidation.

755 Modelled increase in R_e of 0.26 μmol CO_2 m^{-2} s^{-1} per 0.1 m of WTD drawdown was
756 greater than the EC-derived R_e increase of 0.16 μmol CO_2 m^{-2} s^{-1} per 0.1 m WTD drawdown
757 reported by Flanagan and Syed (2011) for WPL over the growing seasons of 2004-2009 (Figs.
758 6c-d). The modelled rate of increasing R_e was, however, comparable with that of ~0.3 μmol m^{-2}
759 s^{-1} per 0.1 m of WTD drawdown estimated by Peichl et al. (2014) from EC-derived R_e over the
760 growing seasons of 2001-2012 in a Swedish fen. Ballantyne et al. (2014) also reported an
761 increase in EC-derived R_e of ~0.33 μmol m^{-2} s^{-1} per 0.1 m of WTD drawdown from a WTD
762 manipulation study in a Michigan peatland thereby further corroborating our modelling
763 hypothesis of increased R_e due to WTD drawdown.

764 Apart from WTD, peat warming in *ecosys* also increased rates of decomposition (Eq. A1)
765 through an Arrhenius function (Eq. A6) and increased R_h and R_e (Figs. 3-6). Warming effect on
766 decomposition in *ecosys* was also modified by WTD. For a similar warming, greater thermal
767 diffusivity in peat with deeper WT and consequent smaller water contents caused greater peat
768 warming (Eqs. D34, D36). It enabled *ecosys* to simulate larger increases in R_e during warming
769 periods in 2006 and 2008 with deeper WT than in 2005 (Figs. 3-5). Increased stimulation of peat
770 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

WTD variations affected GPP in *ecosys* by affecting root and microbial O_2 availability, energy yields, root and microbial growth and decomposition, rates of mineralization and hence root nutrient availability and uptake. Wet soils under shallow WT caused low O_2 diffusion (Fig. 4c) (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 (Sect. 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 (Sect. 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. 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.

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793 WTD drawdown enhanced O_2 diffusion (Fig. 4c) (Eqs. D42-D44) and raised $[O_{2s}]$ so that
794 root O_2 demand in all the three vascular PFTs was almost entirely met by $[O_{2s}]$. Consequently
795 roots in all the PFTs could grow deeper which increased the root surface for nutrient uptake
796 (Sect. 3.4). Increase in modelled root growth due to WTD drawdown could be corroborated by
797 the increase in maximum rooting depth in black spruce and tamarack from 0.2-0.3 to 0.6 m with
798 a WTD drawdown from 0.14 to 0.9 m as a result of artificial drainage in a similar fen peatland in
799 Central Alberta as measured by Lieffers and Rothwell (1987). Murphy et al. (2009) also found a
800 significant increase in tree fine root production with WTD drawdown from ~0.1 to ~0.25 m
801 during a WTD manipulation study in a Finish peatland. Beside improved root growth, greater
802 $[O_{2s}]$ under deeper WT also enhanced rates of mineralization (Eq. A26) of DON and DOP (Eq.
803 A7) that raised aqueous concentrations of NH_4^+, NO_3^- and/or $H_2PO_4^-$ and hence facilitated root
804 nutrient availability and uptake. Enhanced root nutrient uptake increased foliar σ_N and/or σ_P with
805 respect to foliar σ_C (Eq. C11) that hastened the rates of carboxylation (Eq. C6) and hence raised
806 vascular GPP (Eq. C1) under deeper WT.

807 The three modelled vascular PFT were predominantly N limited as indicated by mass-
808 based modelled foliar N to P ratios of 6.6:1, 5.2:1 and 4.8:1 for black spruce, tamarack and dwarf
809 birch under shallow WT in the growing season of 2004. Modelled N to P ratios were
810 corroborated by mass-based foliar N to P ratios of 7.1:1 and 6.3:1 for black spruce and tamarack
811 measured by Syed et al. (2006) at our site during the summer of 2004. Mass-based foliar N to P
812 ratio less than 16:1 usually indicates that the particular vegetation is more N than P limited
813 (Aerts and Chapin III, 1999). Since the modelled PFTs were predominantly N limited, increases
814 in foliar N concentrations as a result of improved root nutrient availability, growth and nutrient
815 uptake with WTD drawdown enhanced modelled carboxylation rates and hence modelled GPP.

816 Choi et al. (2007) in a WT manipulation study found an increase in peat NO_3^--N due to enhanced
817 mineralization and nitrification stimulated by a WTD drawdown from 0.24 to 0.7 m below the
818 surface that caused increases in foliar N concentrations from ~21 to ~27 g kg^{-1} C (assuming 50%
819 of dry matter as organic C) in black spruce and ~41 to ~66 g kg^{-1} C in tamarack in a Central
820 Albertan fen peatland. Increases in foliar N concentrations due to enhanced root nutrient
821 availability and uptake with WTD drawdown in their study also caused significantly greater
822 radial tree growth. Macdonald and Lieffers (1990) in a WTD manipulation study also found that
823 WTD drawdown by ~0.45 m raised foliar N concentrations from ~19 to ~21 g kg^{-1} C (assuming
824 50% of dry matter as organic C) in black spruce and ~36 to ~42 g kg^{-1} C in tamarack trees that
825 enhanced net photosynthetic C assimilation rates by those tree species in an Albertan moderately
826 rich fen. The rates of increases in foliar N concentrations in black spruce and tamarack trees due
827 to WTD drawdown in similar peatlands are comparable with those in our modelled outputs (Sect.
828 3.4).

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

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836 **4.1.3. Hypothesis 3: Microbial water stress on R_e due to WT deepening below a threshold**
837 **WTD**

838 When WT in *ecosys* dropped below a threshold level of ~0.3 m from the hollow surface
839 (~0.6 m below the hummock surface), near surface peat desiccation reduced microbial access to
840 substrate for decomposition (Eq. A15) which enabled *ecosys* to simulate reduction in near
841 surface R_h. When reduction in near surface R_h more than fully offset the increase in deeper R_h,
842 net ecosystem R_h decreased. The offsetting effect on R_h partly contributed to simulated decrease
843 in growing season R_e (=R_h+R_a) from 2008 to 2009 with WTD drawdown that was corroborated
844 by a similar decrease in EC-derived R_e (Fig. 6c). Greater reductions in R_h in desiccated near
845 surface peat layers also caused the reductions in growing season R_e in drainage cycle 2 from
846 those in cycle 1 during 2007-2009 in the simulated drainage study (Fig. 8d). Similar to our study,
847 Peichl et al. (2014) found reductions in R_e when WTD fell below a threshold of ~0.3 m from the
848 peat surface in a Swedish fen which could be partially attributed to reduction in near surface R_h
849 due to desiccation. Mettrop et al. (2014) in a controlled incubation experiment found that the
850 rates of microbial respiration in a nutrient rich Dutch fen initially increased with peat drying and
851 consequent improved aeration. But excessive drying and consequent peat desiccation in their
852 study reduced microbial respiration efficiency, growth and biomass. Dimitrov et al. (2010a) in a
853 modelling study using *ecosys* also showed that a decrease in desiccated near surface peat
854 respiration partially offset increased deeper peat respiration when WT deepened below a
855 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 WT 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 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. 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 (Eqs. C1, C4). 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. 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. 6b and 9b-c). This modelled trend indicated increased vascular

879 dominance over moss with deepening of WT in the model. Several WTD manipulation studies
880 (e.g., Moore et al., 2006, Munir et al., 2014) in similar northern boreal peatlands reported
881 increased tree, shrub and herb growths over mosses with WTD drawdown that corroborates our
882 modelled trend. Gains in modelled vascular GPP halted and eventually vascular GPP started to
883 decline when WT fell below ~0.6 m from the hollow surface (~0.9 m below the hummock
884 surface) in our drainage simulation (Figs. 9c, e). It was because deeper root U_w (Eq. B6) could no
885 longer offset suppression of near-surface root U_w when WT fell below threshold WTD, thereby
886 causing lower ψ_c, ψ_t (Eq. B4), g_c (Eqs. B2, C4) and slower CO_2 fixation (Eq. C6).

887 Similar to our modelling study, Riutta et al. (2007) measured a reduction in moss
888 productivity due to water limitation when WTD fell below ~0.15 m from the surface in a Finish
889 fen peatland. However, vascular GPP during that period sustained in their study indicating no
890 vascular water stress (Riutta et al., 2007). Peichl et al. (2014) measured reduction in moss GPP
891 due to moss drying when WTD fell below ~0.3 m from the surface in a Swedish fen. They
892 inferred that the peat in their study did not have sufficient moisture supplying capacity through
893 capillary rise to sustain moss U_w when the WT fell below ~0.3 m from the surface. Reductions in
894 moss GPP due to decreased moss canopy water potentials were also modelled by Dimitrov et al.
895 (2011) using the same model *ecosys* when WTD fell below ~0.3 m from the hummock surface of
896 a Canadian bog. They, however, found no vascular plant water stress and hence no reduction in
897 vascular GPP during that period. Similarly, Kuiper et al. (2014) found reductions in moss
898 productivity with peat drying while vascular productivity sustained in a simulated drought
899 experiment on a Danish peat.

900 Continued deepening of WT can also cause vascular plant water stress and hence
901 reductions in vascular GPP as modelled in our study (Figs. 9c, e). It can also be corroborated by

902 field measurements across various northern boreal fen peatlands in Canada and Sweden.
903 Sonnentag et al. (2010) found a reduction in canopy stomatal conductance (g_c) and hence
904 vascular GPP when WT fell below ~0.4 m from the ridge surface at a fen peatland in
905 Saskatchewan. The dominant vascular vegetation in their study included tamarack and dwarf
906 birch, two of the three vascular PFTs in our modelling thereby further corroborating the
907 projected vascular water stress. Peichl et al. (2014) also found a reduction in vascular GPP due to
908 plant water stress when WTD fell below ~0.3 m from the surface in a Swedish fen peatland. The
909 WTD threshold for reductions in vascular GPP in those two field studies were shallower than
910 that in our modelled projection i.e. ~0.6 m from the hollow surface (~0.9 m below the hummock
911 surface) (Figs. 9a, c, e) thereby indicating different vertical rooting patterns determined by
912 specific interactions between hydrologic properties and rooting. Lafleur et al. (2005) and
913 Schwärzel et al. (2006) found much deeper WTD thresholds for reductions in vascular
914 transpiration that could negatively affect vascular GPP over a Canadian pristine peatland and a
915 German drained peatland. Those WTD thresholds were ~0.65 and ~0.9 m below the surface for
916 pristine and drained peatland respectively, further indicating the importance of root-hydrology
917 interactions and the resultant root adaptations, growth and uptake in determining WTD effects on
918 vascular GPP across peatlands.

919 **4.2. Divergences between modelled and EC-derived annual GPP, R_e and NEP**

920 Modelled annual GPP and R_e were consistently larger than EC-derived estimates of GPP
921 and R_e during 2005-2008 (Figs. 6f-g). Despite larger modelled vs. EC-derived GPP and R_e,
922 modelled annual NEP was consistently lower than the EC gap-filled annual NEP (Fig. 6e).
923 Smaller modelled NEP estimates were caused by larger modelled vs. EC-derived R_e than
924 modelled vs. EC-derived GPP (Figs. 6f-g). Larger deviation between modelled and EC-derived

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925 R_e estimates was mainly contributed by gap filled night-time CO_2 fluxes (=R_e) which was also
926 apparent in negative intercepts from modelled on gap-filled net CO_2 flux regressions (Table 1).
927 The gap-filling for night-time CO_2 fluxes was done by Syed et al. (2006) using empirical
928 relationships between EC CO_2 measurements and soil temperature (T_s) measured at 0.05 m depth
929 at the WPL. During night-time and the winter, peat at this shallow depth (0.05 m) could have
930 rapidly cooled down and thus yielded smaller night-time gap-filled CO_2 fluxes (Figs. 2, 4 and 5).
931 On the contrary, modelled CO_2 fluxes in those periods depended on the temperatures of not only
932 the shallow peat layers but also the deeper peat profiles that were warmer than the shallower
933 layers and hence simulated larger CO_2 effluxes than the gap-filled (e.g., Figs. 4a, 5h-i). CO_2
934 fluxes measured by automated chamber in cooler nights, however, did not decline as rapidly as
935 did the gap-filled CO_2 fluxes as night progressed further corroborating this reasoning for larger
936 modelled vs. gap-filled R_e during night-time and the winter (e.g., Figs. 4b vs. 4a, 5j-k vs. 5h-i).
937 Systematic uncertainties embedded in EC methodology could also contribute to larger
938 modelled vs. EC-derived annual and growing season R_e estimates (Figs. 6c, g). The major
939 uncertainty in the EC methodology is the possible underestimation of nighttime EC CO_2 flux
940 measurements due to poor turbulent mixing under stable air conditions (Goulden et al., 1997;
941 Miller et al., 2004). On the contrary, modelled biological production of CO_2 by plant and
942 microbial respiration was independent of turbulent mixing which would thus contribute to larger
943 modelled than EC-derived R_e estimates.
944 Larger modelled vs. gap-filled R_e might have also contributed to larger modelled vs. gap-
945 filled growing season and annual GPP (Figs. 6b, f). In EC datasets, GPP was derived from R_e.
946 Smaller gap-filled vs. modelled R_e would thus cause smaller EC-derived vs. modelled GPP.
947 Complete energy balance closure in the model vs. incomplete (~75%) energy balance closure in

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948 EC measurements would also cause a larger modelled than measured evapotranspiration
949 (Mezbahuddin et al., 2016) and possibly GPP (Figs. 6b, f). Unlike decoupled GPP and R_e during
950 gap-filling, modelled GPP influenced modelled R_e through root exudation and litter fall which
951 further contributed to deviation between modelled vs. EC-derived growing season and annual R_e
952 estimates (Figs. 6c, g). So, the uncertainties in the modelling that arose from discrepancies
953 between modelled and EC-derived R_e and GPP aggregates could not be resolved without
954 resolving the above mentioned uncertainties in EC methodology, and gap-filling, and
955 partitioning of EC-gap filled NEP into GPP and R_e.

956 **5. Conclusions**

957 Coupling of eco-hydrology and biogeochemistry algorithms in *ecosys* simulated increases
958 in R_e and GPP with deepening of WT from 2004 to 2009 in the boreal fen at the WPL. Similar
959 increases in R_e and GPP, however, left no net effect of WT deepening on modelled variations in
960 NEP. This modelled trend was corroborated by EC-derived NEP, R_e and GPP (Syed et al., 2006;
961 Flanagan and Syed, 2011) and automated chamber measured NEP and R_e (Cai et al., 2010) at the
962 WPL. The effects of WTD drawdown on R_e and GPP was modelled in *ecosys* by the algorithms
963 representing following processes:

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

(2) 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).

(3) 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).

(4) 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

993 drawdown would only sustain while WTD remained above a threshold level i.e. ~0.6 m below
994 the hollow surface (~0.9 m below the hummock surface). When WT fell below this threshold,
995 projected vascular GPP started to decrease with further WTD drawdown thereby causing
996 reductions in ecosystem GPP. Similar WTD threshold effects on vascular GPP were also found
997 in other studies in similar peatlands (Sect. 4.1.2).

998 Therefore, representing feedbacks between peatland hydrological and C processes in
999 *ecosys* enabled successful simulation of WTD effects on R_e, GPP and hence NEP of a northern
1000 boreal fen peatland. Projected drainage simulation in our study showed that continued WTD
1001 could alter ecosystem C balance of northern boreal peatlands by decreasing GPP and sustaining
1002 increased R_e thereby causing declines in NEP. These findings provide us with important insights
1003 into how northern boreal peatland C stocks would be affected by likely WTD drawdown under
1004 future drier and warmer climates. This study is also reproducible in other peatlands when the
1005 model is fed by required physical, hydrological, chemical, biological and ecological inputs those
1006 are measurable at the sites (Fig. 1) (Mezbahuddin et al., 2016). Successful simulation of
1007 hydrological effects on peatland C processes by *ecosys* for a northern boreal fen peatland in this
1008 study along with simulations of feedbacks between hydrology, biogeochemistry and ecology by
1009 the same model *ecosys* across other contrasting peatlands (e.g., Dimitrov et al., 2011; Grant et
1010 al., 2012; Mezbahuddin et al., 2014, 2015, 2016) would, therefore, provide us with a modelling
1011 framework for large scale (e.g., regional/continental/global) peatland C simulations, which
1012 currently is one of the most sought after in global terrestrial ecosystem carbon modelling
1013 community.

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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.

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1018 **Data availability**

1019 Field data that were used to validate model outputs are available at

1020 http://fluxnet.ornl.gov/site/292.

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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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1235 **Figure captions**

1236 **Fig. 1.** Layout for *ecosys* model run to represent biological, chemical and hydrological
1237 characteristics of a Western Canadian fen peatland. Figure is not drawn to scale. D_{humm} = depth
1238 to the bottom of a layer from the hummock surface; D_{holl} = depth to the bottom of a layer from
1239 the hollow surface; TOC = total organic C (Flanagan and Syed, 2011); TN = total nitrogen
1240 (Flanagan and Syed, 2011); TP = total phosphorus (Flanagan and Syed, 2011); CEC = Cation
1241 exchange capacity (Rippy and Nelson, 2007); the value for pH was obtained from Syed et al.
1242 (2006); WTD_x = external reference water table depth representing average water table depth of
1243 the adjacent ecosystem; L_t = distance from modelled grid cells to the adjacent watershed over
1244 which lateral discharge / recharge occurs

1245 **Fig. 2. (a, c, e, g, i, k)** 3-day moving averages of modelled and EC-gap filled net ecosystem
1246 productivity (NEP) (Flanagan and Syed, 2011), and **(b, d, f, h, j, l)** hourly modelled and half
1247 hourly measured water table depth (WTD) (Syed et al., 2006; Cai et al., 2010; Long et al., 2010;
1248 Flanagan and Syed, 2011) from 2004-2009 at a Western Canadian fen peatland. A positive NEP
1249 means the ecosystem is a carbon sink and a negative NEP means the ecosystem is a carbon
1250 source. A negative WTD represents a depth below hummock/hollow surface and a positive WTD
1251 represents a depth above hummock/hollow surface

1252 **Fig. 3.** Half hourly measured **(a)** incoming shortwave radiation, and **(b)** air temperature (T_a); and
1253 **(c)** hourly modelled and half hourly measured water table depth (WTD) (Syed et al., 2006; Cai et
1254 al.; 2010, Long et al.; 2010, Flanagan and Syed, 2011) during August 2005, 2006 and 2008 at a
1255 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. 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. 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. 3)

Fig. 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. 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. 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

Fig. 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. 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

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1301 **Fig. 9.** Real-time simulated and projected drainage simulated **(a)** average growing season (May-
1302 August) water table depth (WTD), **(b)** growing season sums of non-vascular (moss) gross
1303 primary productivity (GPP), and **(c)** growing season sums of vascular GPP; and regressions
1304 (P<0.001) of real-time simulated and projected drainage simulated sums of **(d)** non-vascular
1305 GPP, and **(e)** vascular GPP on real-time simulated and projected drainage simulated average
1306 growing season WTD during 2004-2009 at a Western Canadian fen peatland. A negative WTD
1307 represents a depth below hollow surface and a positive WTD represents a depth above hollow
1308 surface

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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		462	13600	400		
0.305	0.005					
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					

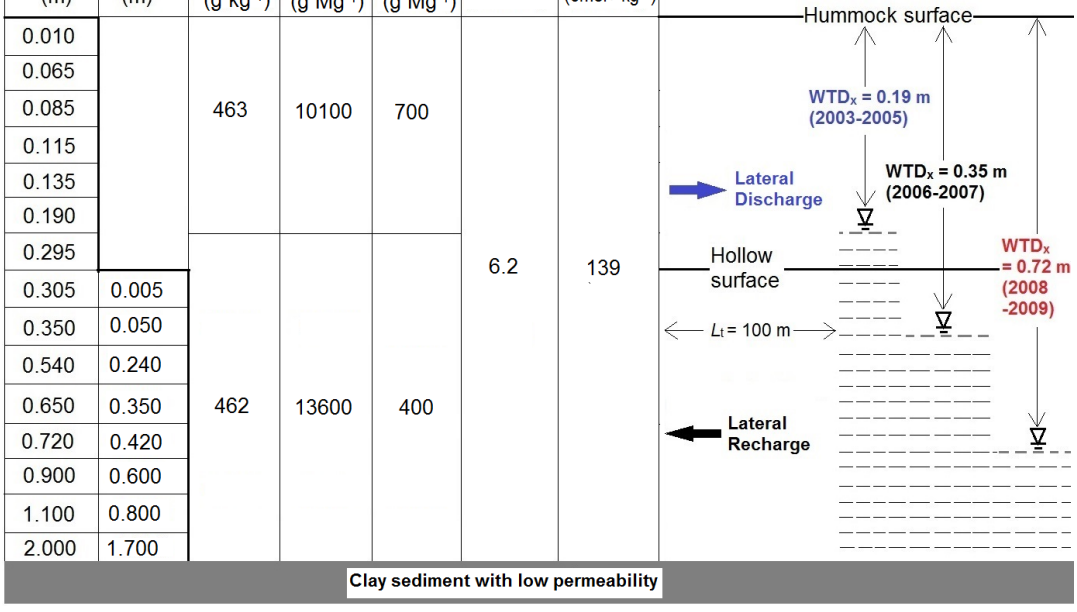

Fig. 1.

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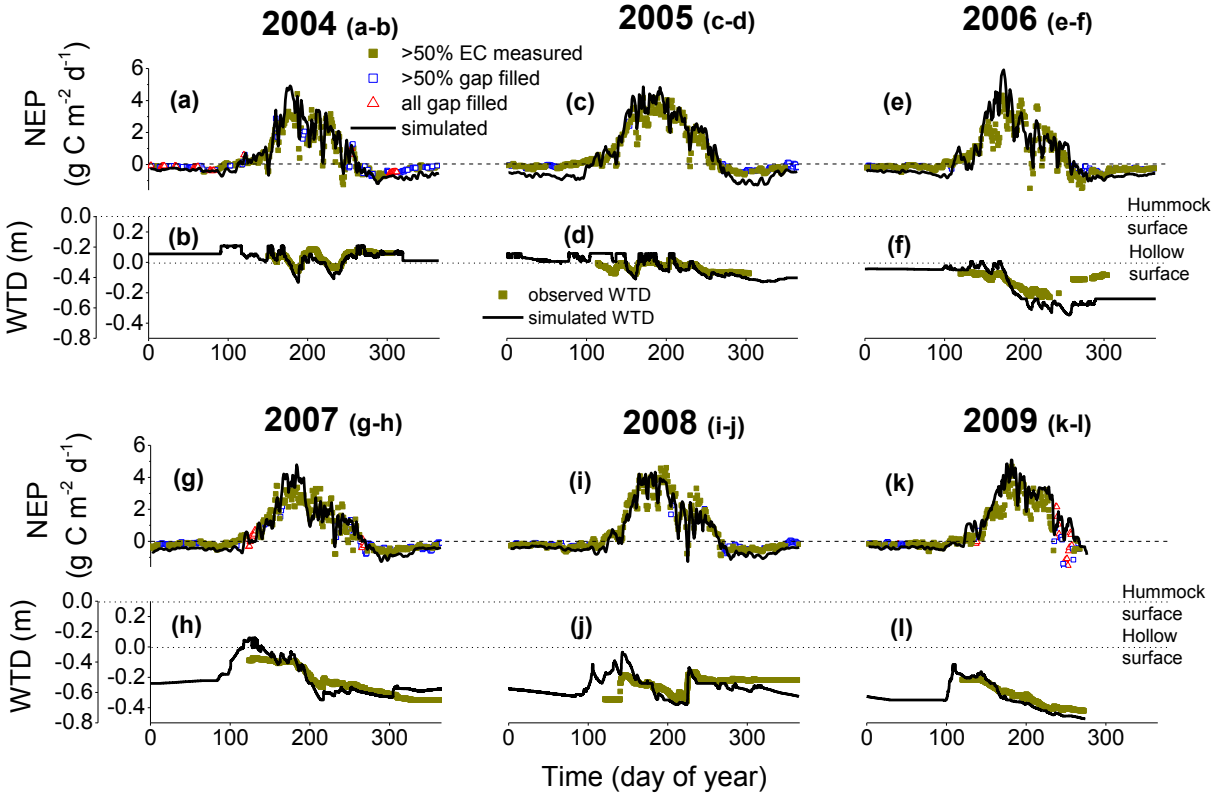

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1312 **Fig. 2.**

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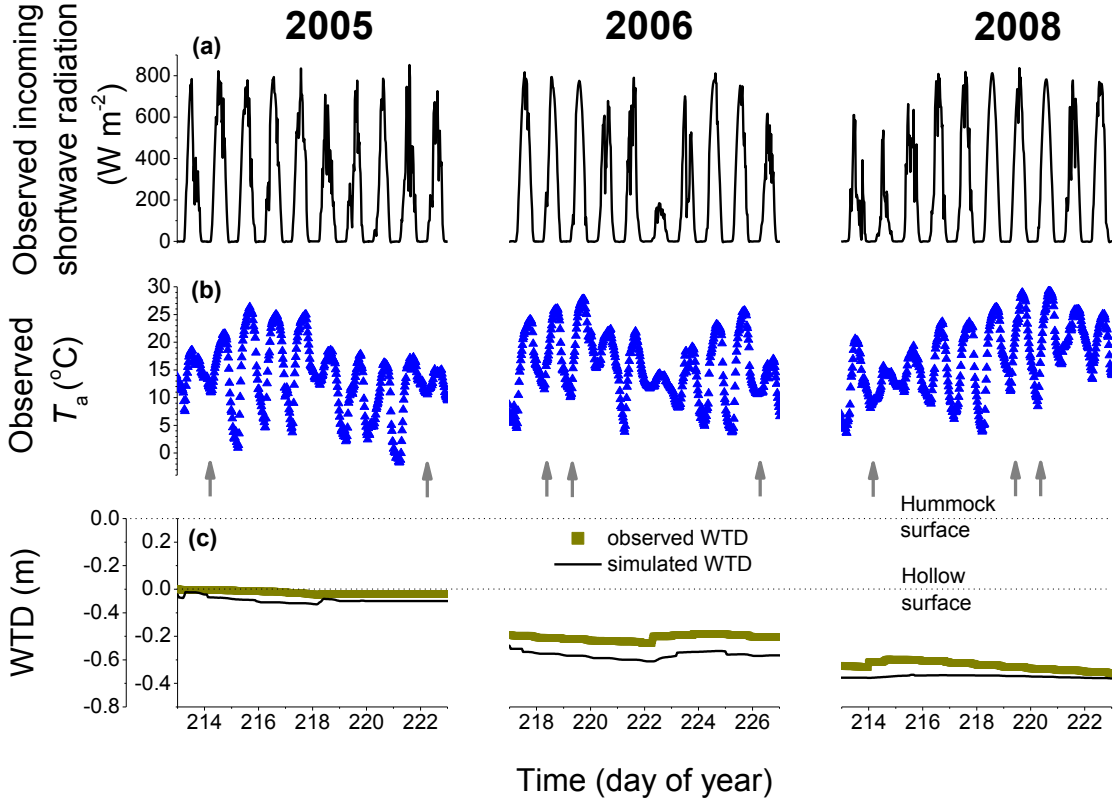

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1314 **Fig. 3.**

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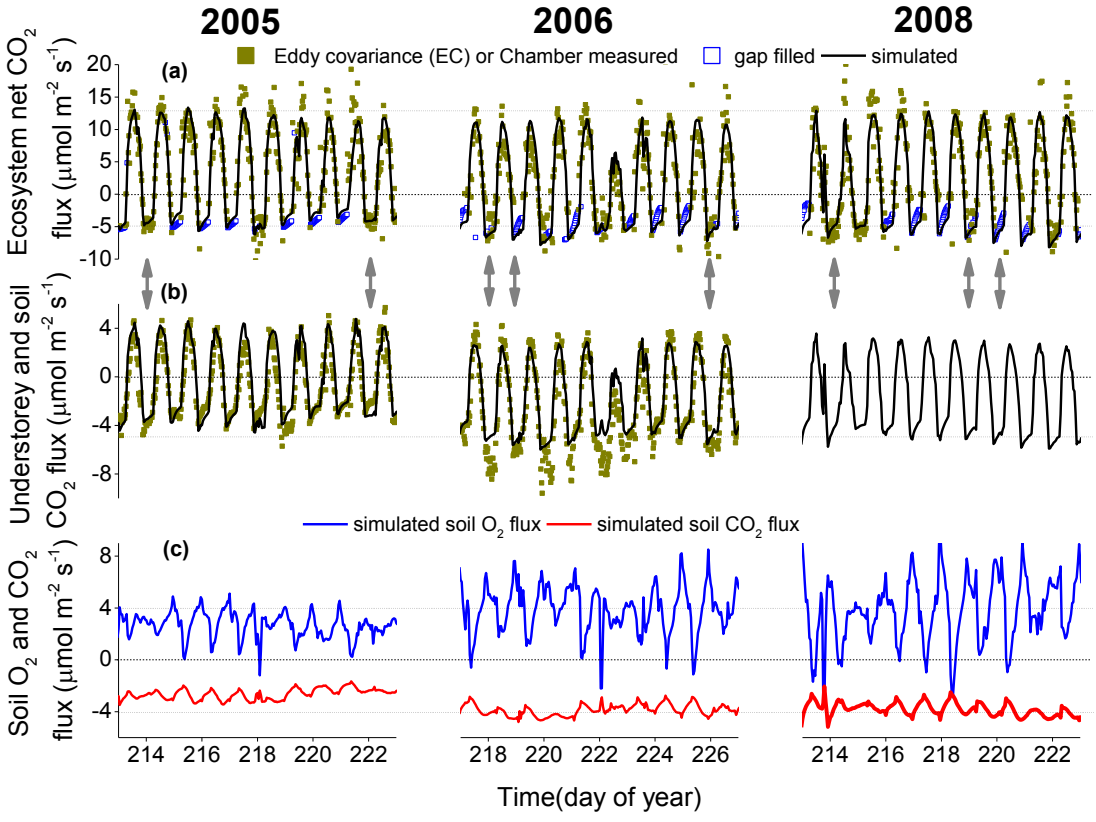

1315

1316 **Fig. 4.**

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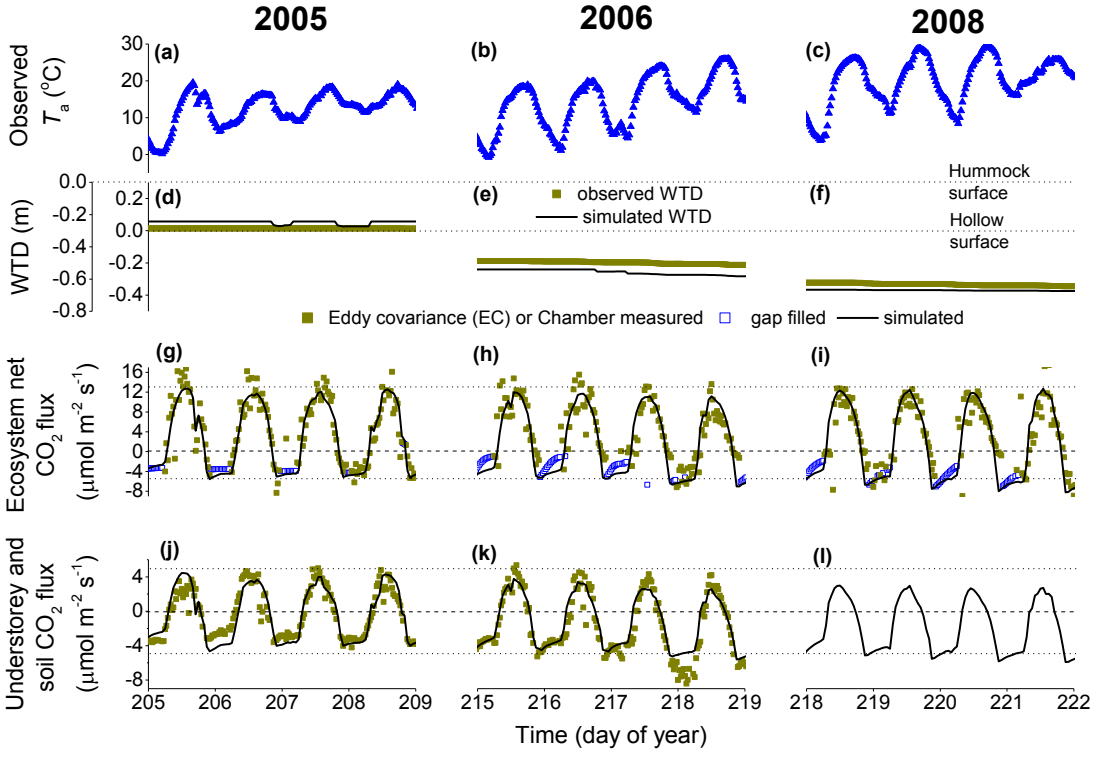

1317

1318 **Fig. 5.**

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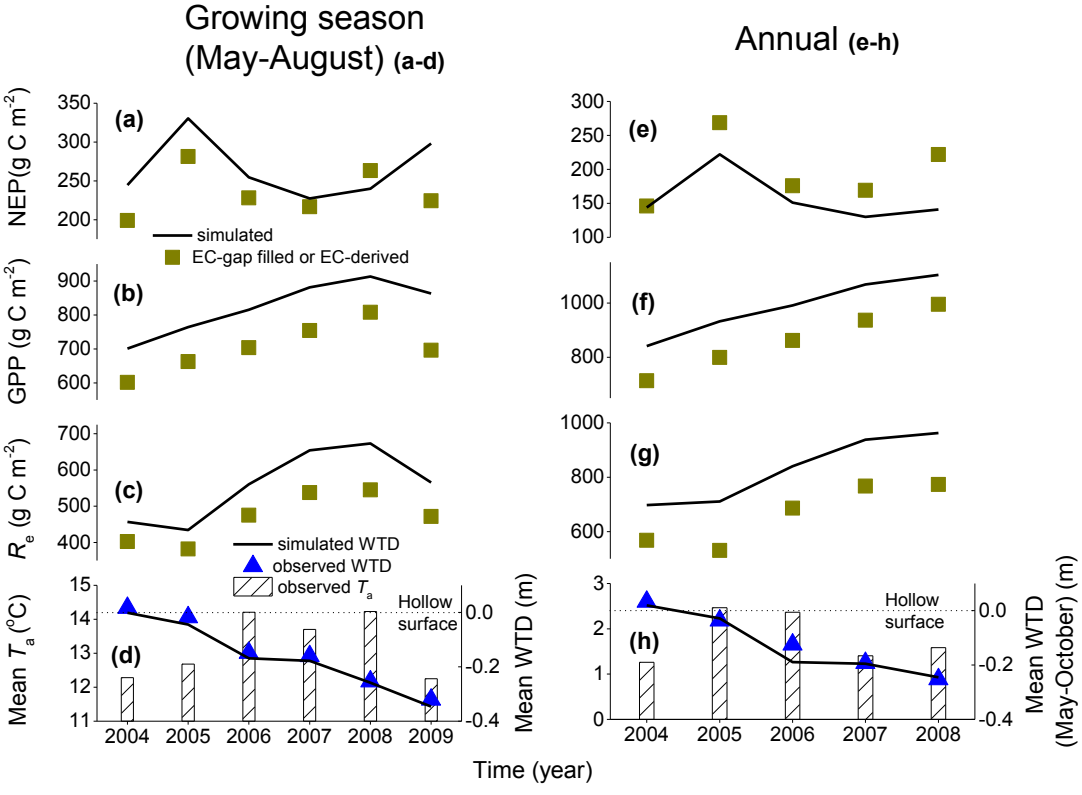

1319

1320 **Fig. 6.**

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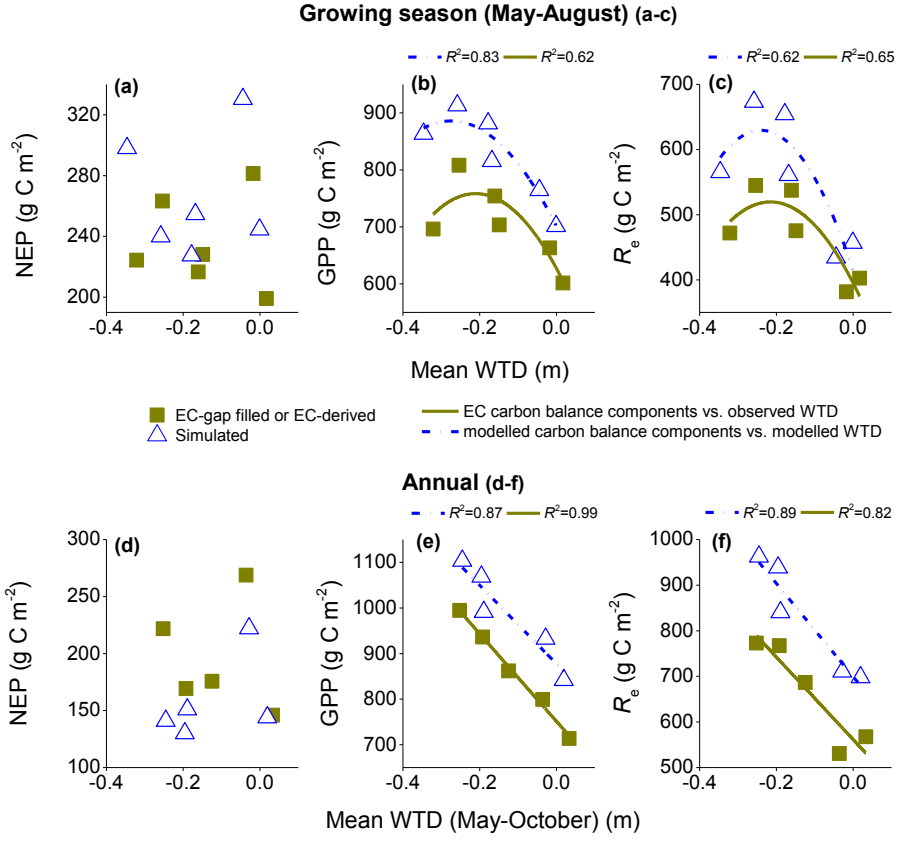

1321

1322 **Fig. 7.**

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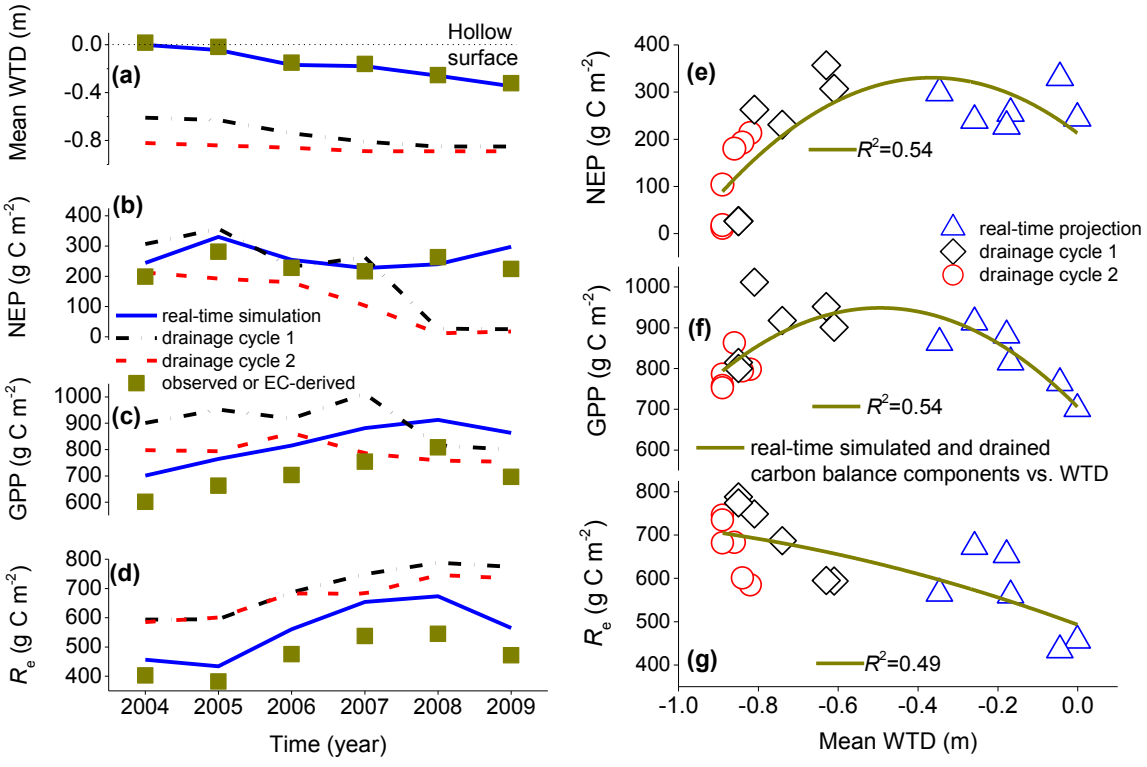

1323

1324 **Fig. 8.**

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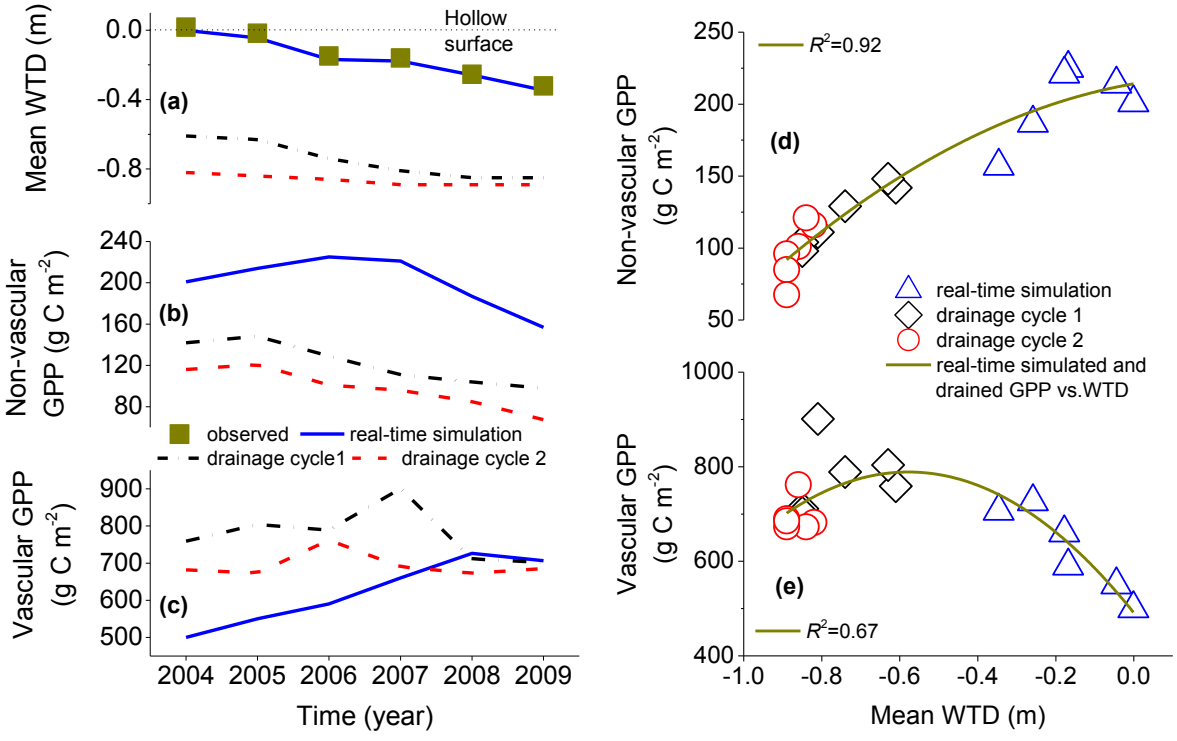

1325

1326 **Fig. 9.**

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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	

(*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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1335 **Table 2:** Statistics from regressions between modelled and EC-gap filled net ecosystem CO_2

1336 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	
2009	138	1010	-0.02	0.98	0.87	1.20	

1337 (*a, b*) from simple linear regressions of modelled on measured. R^2 = coefficient of determination
1338 and RMSE = root mean square for errors from simple linear regressions of measured on simulated.
1339 RMSRE= root mean square for random errors in eddy covariance (EC) measurements calculated
1340 by inputting EC CO_2 fluxes recorded at u^* (friction velocity) > 0.15 m s^{-1} into algorithms for
1341 estimation of random errors due to EC CO_2 measurements developed for forests by Richardson et
1342 al. (2006).