CO_2 fluxes and ecosystem dynamics at five European treeless peatlands – Merging data and process oriented modelling

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Abstract

The carbon dioxide (CO_2) exchange of five different peatland systems across Europe with a wide gradient in landuse intensity, water table depth, soil fertility and climate was simulated with the process oriented CoupModel. The aim of the study was to find out whether CO_2 fluxes, measured at different sites, can be explained by common processes and parameters or to what extend a site specific configuration is needed. The model was calibrated to fit measured CO_2 fluxes, soil temperature, snow depth and leaf area index (LAI) and resulting differences in model parameters were analysed. Finding site independent model parameters would mean that differences in the measured fluxes could be explained solely by model input data: water table, meteorological data, management and soil inventory data.

Seasonal variability in the major fluxes was well captured, when a site independent configuration was utilized for most of the parameters. Parameters that differed between sites included the rate of soil organic decomposition, photosynthetic efficiency, and regulation of the mobile carbon (C) pool from senescence to shooting in the next year.

The largest difference between sites was the rate coefficient for heterotrophic respiration. Setting it to a common value would lead to underestimation of mean total respiration by a factor of 2.8 up to an overestimation by a factor of 4. Despite testing a wide range of different responses to soil water and temperature, rate coefficients for heterotrophic respiration were consistently lowest on formerly drained sites and highest on the managed sites. Substrate decomposability, pH and vegetation characteristics are possible explanations for the differences in decomposition rates.

Specific parameter values for the timing of plant shooting and senescence, the photosynthesis response to temperature, litter fall and plant respiration rates, leaf morphology and allocation fractions of new assimilates, were not needed, even though the gradient in site latitude ranged from 48°N (South-Germany) to 68°N (northern Finland) differed largely in their vegetation. This was also true for common parameters defining the moisture and temperature response for decomposition, leading to the conclusion, that a site specific interpretation of these processes is not necessary. In contrast, the rate of soil organic decomposition, photosynthetic efficiency, and the regulation of the mobile carbon (C) pool need to be estimated from available information on specific soil conditions, vegetation and management of the ecosystems, to be able to describe CO_2 fluxes under different conditions.

1 Introduction

In recent years, many datasets have been collected from a number of sites and across multiple years, containing detailed and high resolution measurements of carbon (C) fluxes, plant and soil characteristics, meteorological and water table data (Baldocchi et al., 2001; Baldocchi, 2007). Several of the measured sites are peatlands, which have accumulated vast amount of C since the last deglaciation. Under drained conditions, peatlands have a high carbon dioxide (CO_2) emission potential (e.g. van den Bos, 2003; Lohila, 2004; Drösler et al., 2008;

Maljanen et al., 2010). Understanding the processes driving CO_2 emissions is essential in the development of management practices to reduce greenhouse gas emissions.

Direct comparison of measured data can be used to explore the effect of single variables if the site conditions are similar or differ only in few variables, e.g. in manipulation experiments (Chivers et al., 2009; Ward et al., 2013) or different vegetation types at the same site (e.g. Chojnicki et al., 2010). However, the sites in this study have very different characteristics with respect to climate, hydrology, current and former land management, vegetation and soils. Direct site comparisons of measured flux data (e.g. Alm et al., 1999; Humphreys et al., 2006; Lund et al., 2009; Drewer et al., 2010) are often uninformative when trying to distinguish between responses of several individual factors. Typically, multiple factors are linked and interact with each other complicating the analysis. Therefore, important drivers at one site might not play a significant role on another site (e.g. Lafleur et al., 2005). Process oriented modelling provides a method to identify to what extent observations at different sites can be described by the same processes, while accounting for such interactions.

Process oriented modelling requires (1) that the model can describe the observations and (2) that the parameters used in the model to describe the observations can be estimated from available data. Typically, studies focus on demonstrating how well the model can describe a certain set of data (e.g. van Huissteden et al., 2009; Calanca et al., 2007; Frolking et al., 2001; St-Hilaire et al., 2010). In contrast, the focus of this study was exploring differences between the sites while model performance was subordinate. Process oriented models often require a large number of input parameters which are usually difficult to estimate based on available data from less intensively investigated sites (Juston et al., 2010). Parameters may interact with each other and the available information does not allow a single or unambiguous mathematical solution (Beven and Freer; 2001, Beven, 2006; van Oijen et al., 2013). However, for all sites in this study, accurate gas flux measurements in combination with detailed measurements of soil and plant conditions were available. Such extensive measurements have been demonstrated to be useful in identifying the governing properties for specific sites. For example the modelling of CO_2 from forest sites has shown that dynamics of CO_2 fluxes are restricted to a certain range of parameter values (Wu and Jansson, 2013; Wu et al., 2013).

A systematic evaluation of one model against data from multiple sites with a common set of parameters will allow a better understanding of processes not only at the individual sites but also on the site-specific differences which control the resulting fluxes (e.g. Calanca et al., 2007; van Huissteden et al., 2006; van Huissteden et al., 2009). This is a necessary precondition for accurate predictions of CO_2 fluxes under different climate scenarios or at different locations. On peatlands, some attempts have been made to consider site differences using simplified process models on national (e.g. ECOSSE, Bell et al., 2012) and global scales (e.g. InTec, Ju and Chen, 2005; McGill, St-Hilaire et al., 2010) and up to millennial timescale (Schuldt et al., 2013). However we are not aware of any studies comparing differences in parameter distributions of CO_2 related processes between treeless peatland sites, using an uncertainty based approach and a detailed process oriented model running on site scale.

Many carbon ecosystem models are available for site scale application such as Biome-BC (Feng et al., 2011), DNDC (Li et al., 1992a; Li et al., 1992b; Dietiker et al., 2010), PaSim (Calanca et al., 2007), PIXGRO (Adiku et al., 2006), CANDY (Franko et al., 1997), or DAYCENT (CENTURY) (Del Grosso et al., 2005). Some models were explicitly created or adapted to peatlands such as PDM (Frolking et al., 2001), PCARS (Frolking et al., 2002), CASA (Potter et al., 2001), NASA-CASA (Del Grosso et al., 2005), *ecosys* (Grant et al., 2012), wetland-DNDC (Zhang et al., 2002), peatland DOS-TEM (Fan et al., 2013), PEATLAND-VU (van Huissteden et al., 2006) or GUESS-ROMUL (Yurova et al., 2007).

In this work the CoupModel was used, which is a detailed process oriented model coupling heat and mass transfer for soil-plant-atmosphere systems (Jansson and Karlberg, 2010). The CoupModel was chosen for the following reasons: The model was designed for a wide range of soil types and different ecosystems and applications (see Jansson, 2012 for review) which might be useful as some of the sites in this study are already quite degraded and might not respond like a typical, intact peatland anymore. The model has been shown to be capable of simulating all three main greenhouse gases from peatlands: CO_2 (Klemedtsson et al., 2008), nitrous oxide (N_2O) (Norman et al., 2008) and methane (CH_4) (Ravina, 2007). Further, the CoupModel includes detailed sub modules for the most relevant processes in the carbon cycle: It predicts plant growth, plant transpiration and autotrophic respiration, soil nitrogen (N) and C processes, energy and heat fluxes, soil temperature, soil frost and snow depth. It supports an hourly time step for input and output data and can run in even finer time resolution, which is necessary for analysing e.g. chamber flux data. The user can select between different sub models, different equations and different complexities and easily access all parameters via a user interface. Calibration procedures with randomized parameter values and methods for visualisation and detailed analysis of the model output are supported. An extensive model description can be found in Jansson and Karlberg (2010). The model and its documentation as well as several tutorials for its application can be downloaded from the CoupModel homepage (CoupModel, 2014).

The main aim of this study was to find out to what extend the large differences in measured CO_2 fluxes between five data rich European flux measurement sites can be solely explained by the differences in meteorology, water table and management. Therefore the process oriented CoupModel was applied using an uncertainty based Monte Carlo approach. Specific objectives were:

(I) to identify differences and similarities between various sites in CO_2 related processes, corresponding parameters and responses to forcing data.

(II) to identify and discuss the impact of available data for estimating key parameters in CO_2 flux models in general.

(III) to identify problems related to the model representation of the different ecosystem processes for open peatlands.

2 Methods

2.1 Description of sites and investigations

The CoupModel was applied to five treeless peatland sites with a wide gradient in land use intensity, water level, soil nutrient status and mean annual temperature (Tab. 1). Together with the climatic gradient from North-Finland to South-Germany and a different growing season, this leads to great differences in amplitude and dynamics of gross primary productivity (GPP), ecosystem respiration (R_{eco}) and different amounts of biomass. This is reflected in the annual accumulated net ecosystem exchange (NEE) based on measurements, ranging from −395 g C m^{-2} to 636 g C m^{-2} (Fig. 1).

Dynamic forcing data for model input (water table and meteorology) was available from measurements at all sites (Tab. S1 in the supplement). Data used for model parameter constraint included measurements of LAI, soil temperature and NEE (Tab. S2 in the supplement). Measured NEE was partitioned into R_{eco} and GPP by the use of empirical models based on R_{eco} from night time NEE respectively opaque chambers at FsA and FsB. The empirical R_{eco} models are based on temperature (Lloyd and Taylor, 1994), while light level based functions were used for GPP according Falge et al. (2001). Corrections and gap filling at flux tower sites was done according the methods described in Reichstein et al. (2005). A detailed description is given in the references listed in Table S2 in the supplement. Though R_{eco} and GPP are not explicitly measured, this will be called measured data in the following for simple distinction from the simulated fluxes by the CoupModel.

The northernmost site, Lompolojänkkä fen (Lom), located in Finland is a nutrient rich natural mire with sedges, shrubs and mosses. Mean air temperature from 2006 to 2010 was −1.4 °C and the mean groundwater table during the snow-free season was close to the peat surface. Data for model calibration were available from 2006 to 2010 and consisted of eddy covariance (EC) and automatic chamber data of CO_2 fluxes, snow depth and leaf area index (LAI) measurements. A detailed description of the site and measurement methods can be found in Aurela et al. (2009), Drewer et al. (2010) and Lohila et al. (2010).

The Scottish site, Auchencorth Moss (Amo) is an ombrotrophic bog, with vegetation consisting of grasses, sedges and soft rushes, covering a primarily Sphagnum base layer. The site is managed for low intensity sheep grazing with less than one livestock unit per hectare, but this was not accounted for in the model. Amo encompasses a small area of peat extraction in the south west of the catchment, which is unlikely to fall within the flux footprint of the EC system. The site was drained over a century ago, however, the drains are no longer considered to be in operation. The mean water table was −12.5 cm between 2006 and 2010. Mean temperature during this period was 10 °C, CO_2 data from EC during the same period was used for model calibration. A detailed description of the site and measurements can be found in Helfter et al. (in review), Drewer et al. (2010) and Dinsmore et al. (2010).

Horstermeer fen (Hor) is located in the Netherlands in a drained natural lake. It used to be agricultural land, but was abandoned more than 15 years ago. The water table was raised during restoration leading to a mean value of −10 cm during the simulation period from 2004 to 2010. It became a semi-natural grassland, a nature reserve without any mowing management. The vegetation is very heterogeneous with reed, grass and small shrubs (Hendriks, 2009). The mean temperature during the simulation period was 10 °C. CO_2 fluxes were measured half hourly by EC and biweekly with opaque chambers between 2004 and 2010. A detailed description of the site and measurements methods can be found in Hendriks et al. (2007).

Freisinger Moos (FsA and FsB) is a drained nutrient rich fen in the south of Germany. The two sites FsA and FsB lie next to each other in a drained sedge meadow which was cut once per year. The mean annual hay yield was 4.19 or 4.07 t dry weight ha^{-1} a^{-1} for FsA and 5.67 or 6.17 t dry weight ha^{-1} a^{-1} for FsB for the years 2010 and 2011, respectively. FsB is located in a small depression with a mean water level of −20 cm compared to −25 cm for FsA during the years 2007 to 2011. Mean temperature during this period was 7.5 °C. FsB contains mainly tall sedges with little reed while FsA is vegetated by a mixture of sedges, grasses and herbs. Manual transparent and opaque chamber data of CO_2 fluxes (n=3 for each plot), measured several times a day every 3 to 4 weeks and half hourly meteorological data were available for the time period of 2007 to 2011. A detailed description of chamber configuration, measurement technique and empirical model approach were given in Drösler (2005), Beetz et al. (2013) and Leiber-Sauheitl et al. (2014). Measured R_{eco} and empirical modelled GPP during measurement period of each measurement day were used for parameter constraint, empirically modelled values between measurement days were only used for visualisation and comparison.

2.2 Model description

CoupModel v4 from 12th April 2013 was used for simulations. The current version can be downloaded from KTH, 2014. A detailed description can be found in Jansson and Karlberg (2010). The model represents the ecosystem by a description of C and N fluxes in the soil and in the plant. It includes all main abiotic fluxes, such as soil heat and water fluxes that represent the major drivers for regulation of the biological components of the ecosystem. The most important equations with the corresponding parameters and switches differing from the default setup in the used version can be found in Tables S3, S4, S5 and S6 in the supplement. The major model assumptions relating to the model application to peatlands are described below. Figure 2 shows a scheme of the main carbon fluxes and pools in the current CoupModel setup.

2.2.1 Meteorological driving variables and integration time step of the model

Hourly values of global radiation, relative humidity, precipitation, wind speed, and air temperature, measured at each site were used as input. Data was gap filled by simple linear interpolation for gaps < 6 hours. Larger gaps were filled by values from other adjacent climate stations. At Hor the station used for gap filling provided only daily values. Hourly values were retrieved assuming uniform distribution over 24 hours for precipitation, wind speed and relative humidity and sinusoidal distribution for temperature and global radiation.

Model performance was only evaluated for the years when meteorological data was available. The simulations were started two years prior to the evaluation period, so the system (in particular the plant) could adapt to the site conditions and become more independent of initial values. Data from the available years was copied to previous years if not available from an adjacent climate station.

The model internal time step was half-hourly for abiotic processes and hourly for nitrogen and carbon related processes.

2.2.2 Dynamic coupled heat and water model for above soil surface conditions

An interception model for both, radiation and precipitation, a snow model and a surface pool model was used to provide boundary conditions at the soil surface. Interception and plant evaporation was dependent on the simulated leaf area index of the plant as well as the degree of coverage, while transpiration depended additionally on the simulated water uptake of the plant. Cloud fraction was calculated from global radiation input and latitude. Incoming radiation was partitioned between one part, which was absorbed by the plant canopy and another part, which reached the soil. Surface temperature was simulated based on an energy balance approach, where the radiation reaching the soil equals the sum of sensible and latent heat flux to the air and heat flux to the soil. Soil evaporation was derived from an iterative solution of the soil surface energy balance of the soil surface, using an empirical parameter for estimating the vapour pressure and temperature at the soil surface. Vapour pressure deficit was calculated from the relative humidity input. Snow fall was simulated from precipitation and air temperature, snow melt from global radiation, air temperature and simulated soil heat flux. Surface runoff was controlled by a surface pool of water that covers various fractions of the soil surface. Under over saturated periods the flow of water in the upper soil compartment could be directed up-wards, towards the surface pool. Surface runoff was calculated as a function of the amount of water in the surface pool.

2.2.3 Dynamic heat and water model for the soil

The soil profiles were divided into 12 layers with an increasing layer depth from 5 cm for the upper layer to 100 cm in the lowest layer. Heat flow between adjacent soil layers were calculated based on thermal conductivity functions accounting for the content of ice and water. The heat flow equation is based on a coupled equation accounting for the freezing and thawing in the soil (Jansson and Halldin, 1979). Convection was not accounted for. The lower boundary was calculated as temperature based on a sine variation at the soil surface and a damping depth for the whole soil profile as well as a parameter for the annual mean temperature T_{amean} and annual amplitude of temperature T_{aamp} at the site (a list of symbols and abbreviations can be found in Table 2).

Soil water depended on infiltration to the soil, soil evaporation, water uptake by plant roots and ground water flow. Soil moisture represented as liquid water content, was calculated based on the water storage and temperature. Water flows between adjacent soil layers were calculated according Richards equation (1931), considering hydraulic conductivity, water potential gradient and vapour diffusion. Soil water characteristics were described by the Brooks & Corey (1964) equation between two threshold water tensions, while a log linear expression was applied at higher water tensions and a linear expression at water contents close to saturation. Unsaturated conductivity was simulated according Mualem (1976) with additionally accounting for the conductivity in macro pores. The ground water level was defined by assuming a continuous zone of saturation from water table level down to the lower boundary of the considered soil profile. To force saturation at the measured ground water level, water was added to or removed from the corresponding layer.

2.2.4 Vegetation

Vegetation was simulated according to the explicit big leaves concept (e.g. Dai et al., 2004) but only one plant canopy layer, representing the complete plant community was defined. Albedo, LAI, vegetation height and vegetation cover were simulated. Permanent, perennial vegetation was configured with maximal plant height of 0.6 m, a lowest root depth of −0.6 m and a maximal plant cover of 100%. Grain development was assumed to play a minor role and was therefore disabled. Plant respiration was assumed to be depended on growth and maintenance (e.g. Hansen and Jensen, 1977).

For leaf assimilation, the light use efficiency approach (Monteith, 1972; Monteith and Moss, 1977, see e.g. Hilker et al., 2008 for review) was used, at which total plant growth is proportional to the global radiation absorbed by canopy but limited by unfavourable temperature and limited soil water. For simplicity plant assimilation was simulated independent of dynamics in N availability. This might be justified as none of the sites was fertilized in the recent years and the vegetation community was assumed to be adapted to the nutrient conditions at each site. Differences in N availability between sites are included in the radiation efficiency (ε_L). Plants were assumed to be well adapted to wet conditions (Keddy 1992, Steed et al. 2002), including aerenchyma to tolerate water saturated soil conditions (Jackson & Armstrong 1999). Plant stress due to high water saturation was therefore disabled.

Plant development started every spring when the accumulated sum of air temperatures above a threshold value ($T_{EmergeTth}$) reached the value of $T_{EmergeSum}$. Both parameters were calibrated (Tab. S4, in the supplement). The accumulation of temperatures started when the day length exceeds 10 hours. Snow cover hindered shooting by reducing the radiation passing through to the plant, while low soil temperatures reduced plant water uptake.

Beside a small amount of litter fall occurring during the whole plant growth period (Robson, 1973; Duru and Ducrocq, 2000; Fulkerson and Donaghy, 2001), senescence was assumed to start after the plant reached maturity and therefore depended on growth stage (e.g. Thomas and Stoddart, 1980) and temperature sums (e.g. Davidson and Campbell, 1983). As this was not yet directly supported by the model, the stem pool was used for brown, senescent, standing biomass. Therefore new assimilates were constantly allocated to roots and leaf only, while existing leaf biomass was reallocated after maturity to the stem pool. A third stage of litter fall was configured depending on a minimum threshold temperature sum: Five consecutive days in the autumn with day lengths shorter than 10 hours and with temperatures below $T_{DormTth}$ terminated the growing season and plants went to dormancy.

During litter fall part of the C is stored in a mobile pool, which can be then reused for shooting in the next year (e.g. White, 1973; Wingler, 2005).

Harvest took place at FsA and FsB. Based on observations in the field, 85% of the above ground plant material was removed at harvest. Harvest dates were known and implemented in the model. After harvest the growth stage was allowed to be reset to a lower value (e.g. Thomas and Stoddart, 1980). Reallocation of C from root to leaves could take place like reported for e.g. *Festuca pratensis* (Johansson, 1992; 1993).

2.2.5 Soil carbon and nitrogen

The organic substrate was represented by two C and N pools for each of the 12 soil layers: one with a slow and one with a high turnover rate coefficient. Decomposition products from the fast pools are partitioned into CO_2 which is released to the atmosphere and C which is partly moved to the slow pools and partly returned to the fast pools. Decomposition products from the slow pools are partly released as CO_2 and partly returned to the slow pools. The initial values for the amount of C and N per layer was given by measurements and partitioned into the two pools for each layer according the measured C:N ratio as described in section 2.2.5 and Table 3. Beside the turnover rate coefficients and amount of substrate in each pool per layer, decomposition rates depended on the response to soil moisture and temperature in the corresponding layer.

As the rate coefficients for decomposition were expected to strongly affect each other, only the coefficient for the fast decomposition pools were calibrated. The coefficient for the slow pools (k_h) was kept constant at a low value of $2 \cdot 10^{-8}$ d^{-1} during the calibration runs which might be justified as decomposition of resistant carbon is less responsible for the variation in soil respiration (e.g. Whalen et al., 2000).

Nitrogen and methane related processes were considered by a model including the most important pathways and fluxes. However no emphasize on the calibration of these processes were made in this study since the current objective was on CO_2 fluxes from the peatlands.

2.2.6 Independent approach to find values of site specific parameters

Dry and wet N deposition, latitude and thickness of the organic layer were used as constant site specific input.

Water retention parameters were assigned to each soil layer according to soil data from each site. However, at Amo and Lom, water retention and at all sites unsaturated conductivity was assigned from the CoupModel soil database as suggested by Lundmark, (2008) for peat soils. Measured total soil organic carbon (SOC) per layer was partitioned to the two SOC pools per layer on the basis of the measured total C:N ratio per layer whereas the initial C:N ratios of the slow decomposing pools were assumed to be 10, while for the fast pools 27.5 was chosen according to measured C:N of leaf tissues at FsA and FsB (Tab. 3).

2.3 Parameter calibration approach

The aim of the calibration was to find out to what extent the same parameter values could be used for all sites compared to a site specific representation. A stepwise approach was carried out starting with finding the best site specific parameter representations and then trying to merge them to common values valid for all sites. Finally the common representation was revised to some few parameters showing great site specific effect on model performance. An overview of the different steps can be found in Figure 3, details on the calibration procedures are presented as supplementary material.

For the basic calibration (step I, Fig. 3) 350’000 to 700’000 runs were performed for each site. 45 parameters which were suspicious of eventually being site specific were selected and calibrated with an assumed uniform random range (Tab. S4 in the supplement). Parameter ranges were then constrained based on selected runs (step I and II, Fig. 3), showing acceptable performance to multiple variables (Tab. S7 in the supplement), measured at the sites.

Several additional multiple calibration runs were performed, with few selected parameters each, to unravel parameter interactions (step III, Fig. 3). A number of simulations were also made by single value representations of parameters (step IV, Fig. 3) to visualize the impact of certain parameter values on interacting parameters and on performance. These runs are called single runs in the following, numbered with C1 to C7 and described in Tab. S8 in the supplement.

Selection of runs and evaluation of performance was based on three indices: coefficient of determination (R^2) asses how well the dynamics in the measurement derived values are represented by the model. Mean error (ME), also called y-intercept (Willmott, 1982) indicates a lag or lead between model predictions and measured data (Moriasi et al., 2007). Nash-Sutcliff efficiency (NSE) (Nash and Sutcliffe, 1970) accounts for both, deviation of dynamics and magnitude. It ranges from $-\infty$ to 1, whereas 1 means the best fit of modelled to measured data and values < 0 indicate that the mean measured value is a better predictor than the simulated value, which indicates an unacceptable performance (Moriasi et al., 2007).

3 Results

3.1 Model performance – results of basic calibration and selected common configuration

Model performance showed distinct differences between the sites, depending on the investigated variable and on the number of considered runs (Tab. 4). Figure 4 shows the differences between measurements and model C1.

3.1.1 Fluxes

At all sites dynamics in R_{eco} fluxes were simulated considerably better than GPP (Tab. 4). Performances for NEE were worse as simulation errors in GPP and R_{eco} are summed up.

In respect to R_{eco} and GPP the selected single runs represent a parameter configuration close to the best ones possible in the tested range: their R^2 value did not differ more than 0.05 from the best result achieved in the multiple calibration, while ME values were smaller |0.1| g C m^{-2} day^{-1}. Clearly lower R^2 and higher ME values in single runs for biomass and LAI simulation, indicates that none of the runs could give best results for all variables at the same time. E.g., best values for GPP can only be achieved if poorer performance would have been accepted for other parameters like winter R_{eco} or LAI (see criteria for accepted runs in Table S7 in the supplement).

The ME values in Table 4 show a clear overestimation of winter fluxes by 3.21 and 2.11 g C m^{-2} day^{-1} for the single runs at FsA and FsB, respectively, and a weaker overestimation for the accepted runs. The overestimation was less pronounced at Amo (0.13 g C m^{-2} day^{-1}) and Lom (0.01 g C m^{-2} day^{-1}). At Hor winter fluxes were underestimated with a ME of −0.26 g C

m^{-2} day^{-1}. This was reflected in the accumulated NEE (Fig. 4) leading to a much higher CO_2 loss compared to the CO_2 balance estimated by the empirical model approach at FsA and FsB. At Lom higher accumulated NEE due to the overestimation of winter R_{eco} was visible in the first months of each year. It was nearly compensated due to the underestimated spring R_{eco}, or overcompensated due to GPP overestimation, as e.g. in summer 2006, which was very dry.

3.1.2 Explanatory variables

Of all variables, the highest R^2 values were achieved for soil temperature at all sites. Temperatures in deeper soil layers (−50 or −60 cm) had better fits than in upper layers with R^2 values close to 0.9 or higher and maximum mean deviation of 0.15 °C. The fit of modelled vs. measured snow depth, which was only available at Lom, had a R^2 value of 0.75 with a mean error of less than 10 cm.

Simulation of LAI represented the measurements quite well with R^2 values between 0.53 and 0.76 and mean error of maximum 0.12 m^2 m^{-2}. An exception was Hor, where LAI was underestimated by ME of −0.61 and 1.49 m^2 m^{-2} in the accepted 75 runs and in the selected single run C1, respectively. At Hor, root biomass was underestimated in the single run by ME of −281 g C m^{-2} and living leaf biomass by −122 g C m^{-2}.

In most of the runs of the basic calibration at Hor, either GPP was overestimated or leaf biomass and LAI was underestimated. Therefore, beside the common configuration C1, a different configuration was tested where plant respiration and litter fall parameters for Hor were set to much lower values than in the tested range to fit to GPP and LAI at the same time. However, this reduced performance for R_{eco} R^2 to 0.66 compared to 0.75 in C1 and led to an overestimation of winter R_{eco} with a ME of 0.75 g C m^{-2} day^{-1}.

3.2 Parameter constraint

Site specific calibration was needed for the speed at which the maximum surface cover is reached (p_{ck}), the mean value in the analytical air temperature function (T_{amean}), temperature sum for reaching plant maturity ($T_{MatureSum}$), coefficient for determining allocation to mobile internal storage pool (m_{retain}), decomposition rate of the fast SOC pools (k_l) and radiation use efficiency (ε_L).

Activity under saturated conditions ($p_{\theta Satact}$), threshold temperature for plant dormancy (T_{DormTh}), response to a 10 °C soil temperature change on the microbial activity (t_{Q10}) and base temperature for the microbial activity (t_{Q10bas}) covary with performance indices but showed different patterns for different validation variables and for different sites.

Most of the parameters did not show any influence on performance indices within the tested range (Fig. S1 in the supplement), demonstrating that either the relatively low effect of the parameter was overcompensated by the effect of more sensitive parameters, or the range used for calibration is sufficiently constraining. Each of these parameters did not reduce model performance indicated by R^2 by more than 0.05 for GPP or R_{eco} after setting them to a common value.

3.3 Correlations between parameters

In the basic calibration, the following parameters were identified to interact with other parameters: p_{ck} covaried with the extinction coefficient in the Beer law (k_{rn}) which is used to calculate the partitioning of net radiation between canopy and soil surface. Strong linear negative correlation between coefficients for growth (k_{gresp}) and maintenance respiration ($k_{mrespleaf}$) was detected.

The effect of the different parameter in the water response function $p_{\theta Satact}$, $p_{\theta Upp}$ and $p_{\theta p}$ compensated each other. They could not be constrained without a very high measurement resolution of fluxes and water table combined with high water table fluctuation at the same time. Therefore $p_{\theta Upp}$ and $p_{\theta p}$ were set to default values and $p_{\theta Satact}$ constrained by additional multiple runs together with k_l. Differences between sites in k_l are reduced with higher $p_{\theta Satact}$ (Fig. 5), however, higher $p_{\theta Satact}$ increase overestimation of winter R_{eco} at FsA and FsB (Fig. 6 and Fig. 7 d). A wider range of $p_{\theta Satact}$ was acceptable for summer R_{eco} (Fig. 6).

Beside moisture response, decomposition rate (k_l) and temperature response (t_{Q10}, t_{Q10bas}) control soil respiration. The effect on R_{eco} was cofounded by plant respiration. Different patterns for different sites and variables for each of the parameters were even more pronounced when only k_l, t_{Q10} and $k_{mrespleaf}$ were in calibration (Fig. 6).

Single runs with different configurations (Fig. 7) revealed that higher plant respiration as well as steeper temperature response can lead to less overestimation of respiration in winter (Fig. 7 d) but lead to reduced performance (Fig. 7 c). In all single runs, despite the different configurations, FsA always showed the highest k_l while Amo had the lowest (Fig. 7 a). A higher saturation activity reduces the difference in k_l values, but leads to higher overestimation of winter fluxes.

4 Discussion

Despite not being specifically developed for peatland CoupModel was able to simulate measured fluxes quite well. The model was run in a simple configuration with only two SOC pools per layer, no explicit representation of microbes, and only one plant layer. Even though, CoupModel was capable to adequately reproduce the measurements. Several points were identified, where further, peatland specific processes or more detailed representations might improve the model. Those are discussed in the following subsections.

From the 45 calibrated parameters, 8 parameters could be identified to actually need a site specific representation to achieve acceptable performance. Those parameters are discussed in section 4.3 to 4.10. The remaining 37 parameters were not sensitive in the tested ranges, even though site specific values could have been expected: For example, it is known that grassland species differ in their assimilation and growth response to temperatures (Billings et al., 1978; Wohlfahrt et al., 1999). Plant respiration rates in graminoids differ between species (Poorter et al., 1991; Scheurwater et al., 1998; van der Werf et al., 1988) and depend among others on light (Rovira, 1969; Bahn et al., 2013) nutrient (Paterson and Sim, 2000) and moisture conditions (Crow and Wieder, 2005) as well as on cutting regime (Bokhari, 1977). Allocation fractions to different plant parts differ between species and depend on nutrients conditions (Aerts et al., 1991; Gong et al., 2014) as well as shading (Bahn et al., 2013). Values for specific leaf area are species specific (e.g. Poorter et al., 1990; Reich et al., 1998) and differ in response to nutrient availability (Meziane and Shipley, 1999). Leaf life time (e.g. Ryser and Urbas, 2000) as well as leaf and root turnover rates (Schläpfer and Ryer, 1996) vary between graminoid species.

The five peatland sites largely differed in their vegetation composition, plant life-forms and species. Nevertheless common values for all sites could be applied for parameters related to these processes, without reducing model performance on R_{eco} and GPP in R^2 values by more than 0.05. That shows that either the studied sites on a vegetation community level did not differ much in these processes, or that the impact of those parameters is subordinate compared to the impact of other parameters, meteorological input and other site conditions.

Models with a focus on multiple year carbon fluxes do therefore not need a site specific interpretation of these processes.

4.1 Model initialisation

Many models use spin-up routines of many years until SOC pools reach a steady state (e.g. Dimitrov et al., 2010; Smith et al., 2010; Thornton and Rosenbloom, 2005). Here, measured C:N values were used to partition the SOC between pools, while ranges for parameter values were chosen in a way, that the amount of carbon in the soil pools did not change very drastically. However no further effort was made to force the pools to be in equilibrium. It was assumed that this might not be the case in the real world either: Drainage ditches at FsA and FsB are still maintained, leading to high carbon losses and changes in substrate quality. Land use at Hor was quite recently changed from a fertilized and deeply drained crop land to a nature reserve with restored water table. Also Amo used to be more intensively managed and drained, but the drainage system was not maintained. Land use history was not known and SOC measurements were available from only one date per site. The measured carbon fluxes were therefore the only indication about carbon loss or addition to the complete system, while changes in relative pool sizes were not known. The partitioning of the SOC has implications on the parameter distribution for the rate coefficient for decomposition, which is discussed in section 4.10.

4.2 Model performance

The best achieved performance highly differed between the different validation variables and between the different sites. This was not only caused by the models ability to simulate the different output parameters but also due to measurement quality, measurement uncertainty, measurement methods (temporal and spatial resolution) and heterogeneity of the sites.

GPP was simulated markedly poorer as compared to R_{eco} at all sites and not only in the single runs, but also in the complete set of performed multiple runs. An explanation might be that in the model the whole plant community consisting of different individuals, species and even functional types, with different life cycles and adaptations to light availability and temperature was simplified to only one plant. Especially mosses differ largely from vascular plants in respect to their ecology and response to water, temperature and light conditions (Gaberščik and Martinčič, 1987; Harley et al., 1989; Murray et al., 1993; Turetsky, 2003), which might be important at the moss rich Lom and Amo. The vegetation at Hor consists of species with very different strategies and requirements for nutrient and water. At FsB, reed, which is known for a late emerge, was well present in some of the years while it did hardly appear in other years. FsA is relatively species rich and several of these species are abundant only during parts of the vegetation period. Also, using a more complex photosynthesis model like e.g. Farquhar et al. (1980, 2001) and testing a wider range of parameters might lead to a better fit. Including plant stress due to high water levels and nutrient limitation might improve the performance on some sites. E.g. Sagerfors et al. found 2008 photosynthesis to be limited also by too high water levels, so that the McGill wetland model assumes reduced photosynthesis outside a water level range of −10 to −20 cm (Wu et al., 2013). Furthermore, GPP cannot be measured directly neither by the chamber nor the EC method. Instead it was derived from NEE and R_{eco} or night time NEE, including the uncertainty of two different measurements and empirical modelling.

Heterogeneity of vegetation was very distinct at Hor, which might explain the difficulties to simulate the right amounts of GPP and biomass at the same time. The biomass and LAI taken into account for this study might not be fully representative of the whole EC fetch for all wind directions. Hor is also a site which deviates strongly with respect to other sites, with recent large changes in management. It is in successional transition from intensively used dairy farming meadow (approximately 20 years ago) towards reed fen with willow thickets. Soil and vegetation still show the imprint of high nutrient level derived from manuring practices (e.g. patches with abundant *Urtica dioca*). This likely still affects GPP. These features could be a better explanation of the deviating GPP than the additionally tested configuration with strongly reduced litter fall and plant respiration rates.

Even though the winter fluxes are small compared to the summer fluxes they have a marked role in the annual NEE balances (Fig. 4). Overestimation of winter R_{eco} in combination with slightly underestimated winter GPP lead to high overestimation of annual accumulated NEE, emphasising the importance of winter flux dynamics in the annual balances. At all sites except Hor, winter R_{eco} was overestimated in the selected single run. For FsB and especially FsA, this was also true for all multiple runs. As R_{eco} at Lom and Amo are typically relative low, the effect was less pronounced.

Several different reasons for the winter R_{eco} overestimation are possible: explanations due to model setup and parameterisation are discussed in the sections 4.7, 4.8 and 4.9. Additionally, gases might be trapped within the snow and under the ice (Bubier et al., 2002; Maljanen et al., 2010) and therefore be seen by the measurement instruments only in spring time, when they are released. A gastight ice cover was not realised in the current model setup. Frozen or ice covered soils are quite common at the boreal Lom, but also at FsA and FsB which have a more continental climate than the other sites.

The ability of the model in simulating soil moisture could not be evaluated, as this variable was measured only at Lom, where the soil was close to saturation throughout the year. Therefore, and as ground water level was used as input, hydraulic properties could not be constraint. Further, swelling, shrinking and hysteresis effect which are important factors in hydraulic characteristics of peat soils (Kellner & Halldin 2002) were not accounted for. This could have an effect on model performance and parameter values, especially those related to the soil moisture response.

4.3 Soil temperature dynamics

Due to the isolating impact of the snow cover (e.g. Zhang, 2005), the value of mean annual soil temperature (T_{amean}) was expected to be slightly higher than the mean annual air temperature. Constrained values of soil temperature were 1.5 to 5 °C higher than the mean annual air temperature at all sites. If the model was run under different conditions without further fitting, factors causing differences between mean annual soil temperatures and corresponding air temperature need to be considered.

4.4 The role of soil temperature and GPP to constrain the plant cover

Accepted fits for soil temperature in the uppermost measured soil layer led to p_{ck} values, close to the measured coverage of vascular plants for each sites. Therefore the measured coverage could directly be used in the configuration C1 (Fig. 6 a). Setting p_{ck} to a common value of 100% reduced the differences in ε_L between the sites C7 (Fig. 6 e), but led to underestimation of soil temperature in the uppermost soil layer by at most −0.45 °C in ME at Amo. An explanation could be that mosses are contributing to the plant coverage in respect to GPP but not to temperature, especially at sites where they are the main peat forming material.

4.5 Start of senescence

Site specific calibration was needed for the temperature sum initiating the start of senescence ($T_{MatureSum}$). However, if the resulting day of the year was plotted instead, the differences between sites became small (Fig. 6) and setting it to the mean value of all sites did not reduce model performance in GPP R^2 by more than 0.05. Induction of senescence with graminoids is known to depend on both, temperature and day length (Nuttonson, 1958; Proebsting et al., 1976; Thomas and Stoddart, 1980; Davidson and Campbell, 1983). However the differences between the sites in this study could be explained solely by the relative day length.

4.6 Seasonal and management control of mobile plant pool for regrowth

The proportion of C in the plant which does not become litter, but instead is stored for shooting in the next year (m_{retain}), differed largely between sites. At Lom, a value of at least 40% led to accepted performance while a maximum of 3% was found for FsA and FsB; a mean value of 20% would reduce R^2 of GPP by at least 0.04 for these sites. At Amo and Hor neither a value of 3% nor 40% reduced R^2 of GPP by more than 0.01. An explanation for low m_{retain} at FsA and FsB could be that the same pool is used for regrowth after cut and therefore not available for shooting anymore, as the regrowth rate in both early spring and after cut depend on carbohydrate reserve (White, 1973; Davies, 1988; Klimeš and Klimešová, 2002). Steele et al. (1984) conclude that defoliation late in the year will affect spring regrowth.

At Lom high m_{retain} might be an adaption to the short vegetation period (Kistritz et al., 1983). Evergreen parts of the vegetation like dwarf shrubs, lower leaf parts of graminoides and mosses were not accounted for which also affects regrowth in spring. Saarinen (1998) found that 60-70% of shoots and 20% of green biomass in a *Carex rostrata* fen survived the winter and hypothesised based on comparison with other studies that the proportion increase with increasing latitude.

The storage pool is an important parameter needing site specific calibration but can be fitted if several measurements during spring and early summer of either GPP, biomass or LAI are available.

4.7 Radiation use efficiency

As plants were not nutrient limited in the model setup, lowest values for ε_L were expected under the most nutrient poor conditions (Longstreth and Nobel, 1980; Reich et al., 1994;

Haxeltine and Prentice, 1996; Gamon et al., 1997; Wohlfahrt et al., 1999). The opposite was true if site specific values were used for p_{ck}. However, a common value for p_{ck} reduced the differences in ε_L and led to low ε_L at the ombrotrophic Amo site, but to an even lower value at the minerotrophic Lom. Nutrient status of the soil can therefore not explain the differences in ε_L. The assumption of plants being well adapted to nutrient and water stress might not be true for the restored Hor site, where parts of the vegetation still consists of species which are not typical for wetlands. This might explain the low productivity at that site, but could only be covered by a model, if site specific plant responses to high water levels would be applied. Additionally, ε_L is known to be species specific (Sinclair and Horie, 1989; Reich et al., 1998; Wohlfahrt et al., 1999).

Radiation use efficiency is an important parameter needing site specific calibration. If common values were used for ε_L, p_{ck} and m_{retain}, mean GPP would be underestimated by a factor of 2.4 (FsB) or overestimated by a factor of 3 (Lom). If site specific values were used for p_{ck} and m_{retain} the discrepancy would be even higher. However ε_L can easily be fitted if either GPP, biomass or LAI is known.

4.8 The control of decomposition and plant respiration by soil temperature

The whole year R_{eco}, which was dominated by summer R_{eco} could be described by a single temperature response function at all sites. However, it was not possible to find an equal good fit to both summer and winter R_{eco}, using the same t_{Q10} value. Higher t_{Q10} would decrease overestimation of winter R_{eco} especially at the southern sites FsA and FsB, but also reduce model performance for whole year R_{eco}. Different temperature responses for different sites (e.g. Jacobs et al., 2007), seasons (e.g. Lipson et al., 2002) and temperature ranges (e.g. Lloyd and Taylor, 1994; Paul, 2001; Atkin et al., 2003) are reported in the literature. This is partly explained by multiplicative effects of several temperature sensitive processes (Davidson et al., 2006; Kirschbaum, 2006) but still, a constant t_{Q10} might be a wrong assumption (Atkin et al., 2005).

More sophisticated temperature responses like the Ratkowsky-function (Ratkowsky et al., 1982) might improve the performance for individual sites. This might also be true for separate temperature response functions for plant and soil, as summer R_{eco} includes autotrophic and heterotrophic respiration, while winter R_{eco} is strongly dominated by heterotrophic respiration.

4.9 The control of decomposition by soil moisture

The activity under saturated conditions in respect to unsaturated conditions is described by $p_{\theta Satact}$ and was strongly negative correlated with decomposition rate k_l. Patterns for $p_{\theta Satact}$ differed between sites and variables. At all sites a minimum value of around 5% led to acceptable performance in whole year R_{eco}, while also quite high values did not reduce the performance except at FsB. At Lom only winter R_{eco} was considered, as conditions were always saturated during summer. For acceptable winter R_{eco}, $p_{\theta Satact}$ needed to be very low. This was not true for Lom, where water in the upper soil layer partly froze in the model and led to high winter respiration.

As the soil at FsA and FsB was saturated during winter, a common lower value for $p_{\theta Satact}$ would decrease overestimation of winter fluxes. However it would also reduce model performance at all sites and increase the site specific differences in k_l (Fig. 7).

Permanently saturated soils contain less O_2 than temporally saturated ones (e.g. Kettunen et al., 1999), which effects decomposition (e.g. Reddy and Patrick, 1975; DeLaune et al., 1981; Holden et al., 2004). Therefore lower $p_{\theta Satact}$ would be justified for wetter sites. If k_l was constant between sites and instead $p_{\theta Satact}$ fitted, this would lead to the value of $p_{\theta Satact}$ to decrease in the order FsB > FsA > Lom > Hor > Amo (Fig. 5) which cannot be justified by the differences in water levels which increase in FsA < FsB << Amo < Hor << Lom. Therefore a different $p_{\theta Satact}$ cannot explain differences in soil respiration between sites. However, amount of aerenchymous plants, leading to soil aeration (e.g. Armstrong, 1980; Bendix et al., 1994; Grosse et al., 1996) were not taken into account. They reach the highest coverage at FsB (90%), followed by FsA (62%), Hor (50%), Lom (around 10%) and Amo (around 6%). Modelling water response depending on soil O_2 and redox potential, including O_2 conductance from plants, might help to analyse the differences in decomposition rate and reduce winter overestimation. E.g. in the Wetland-DNDC model, the water response function depends on redox potential: decomposition under saturated condition is reduced by a factor of 0.6 if redox potential is high, but by a factor of 0.2 if redox potential is low (Zhang et al., 2002).

4.10 The control of decomposition by substrate

The largest differences of parameters between sites appeared for the maximum decay rate of the fast C pools k_l. Setting it to a common value would lead to an underestimation of mean R_{eco} by a factor of 2.8 at FsB or an overestimation by a factor of 4 at Amo.

Despite different temperature and water response curves being tested, k_l values at FsA and FsB are substantially higher than at Amo (Fig. 5 and Fig. 7). Higher t_{Q10} values lead to two groups of k_l values: similar high ones for Lom, FsA and FsB and substantially lower ones for Hor and Amo (Fig. 7).

The partitioning into SOC pools strongly effects the differences, as can be shown by calculating decomposition rates for the total SOC (k_{tot}) based on k_l, k_h and SOC in the pools of the upper 30 cm as used in the C1 scenario (Fig. 8). However, FsB and FsA still have much higher rates than Amo. Resulted values and ranges of k_{tot} (0.02-0.16 a^{-1}) are comparable with reported values from laboratory incubation studies of peat cores (0.03-1.66 a^{-1}, Moore and Dalva, 1997; 0.01-0.35 a^{-1}, Glatzel et al., 2004; 0.008 a^{-1}, Kechavarzi et al., 2010; a SOC content of 30% was assumed for conversion from dry mass).

Lower decomposability is often associated with higher C:N ratios (e.g. Zeitz and Velty, 2002; Limpens and Berendse, 2003; Bragazza et al., 2006; Zhang et al., 2008), which might be important especially for the moss rich Amo and Lom. Assuming a C:N ratio of 60 for the fast pools (Fig. 7, C6) leads to a decomposition rate at Lom which is close to those at FsA and FsB, while those of Hor and Amo remain substantially lower.

Low pH might be one reason for the low k_l at Amo (e.g. DeLaune et al., 1981; Bergman et al., 1999). Despite being nutrient rich and having a high pH and high biomass production, leading to large amounts of labile carbon added to the soil, k_l values at Hor were very low. This might be connected to land use history and the origin of the peat from partly clayey-lake sediment. Most of the labile C in the parent peat in the upper, formerly drained soil layers might have been decomposed before and therefore stabilised.

In the current setup the slow pools were almost inert. A higher decay rate for the slow pools would result in a lower k_l for sites with high C stock in the slow pools (cf Tab. 3). This would decrease the differences between FsA and FsB compared to Lom and Amo, but increase the differences between FsA compared to FsB and compared to Hor.

Substrate quality is known to effect decomposition rates (e.g. Raich and Schleisinger, 1992; Belyea, 1996; Fang and Moncrieff, 2005; Yeloff and Mauquoy, 2006). Therefore, many other SOC models use several different SOC pools (e.g. Franko et al., 1997; Smith et al., 1997; Cui et al., 2005; Del Grosso et al., 2005; van Huissteden et al., 2006) to account for differences in substrate quality. This leads to the problem of partitioning total SOC into the pools (e.g. Helfrich et al., 2007; Zimmermann et al., 2007). In some models, the various SOC pools differ also in their response functions (e.g. Smith et. al, 2010).

The highest decomposition rates occurred at sites with highest biomass production. A correlation of productivity with soil respiration was found in several comparison studies (e.g. Janssens et al., 2001; Reichstein et al., 2003). Fresh material provided by the plants might lead to higher microbial activity and priming effect (e.g. Kuzyakov, 2002; Fontaine et al., 2007). Higher plant to soil respiration ratio reduced the differences in k_l between the sites and lowered winter R_{eco}, especially at the highly productive FsA and FsB, but also reduced the model performance at all sites except Amo.

Vegetation at Amo and Lom consist largely of mosses which are more resistant to decomposition then vascular plants (Rudolph and Samland, 1985; Verhoeven and Toth, 1995; Limpens and Berendse, 2003; Moore et al., 2007) and might further explain the low k_l value at Amo. Despite the lower biomass production, higher moss cover and higher C:N ratio compared to Hor, FsA or FsB, Lom has a relative high decomposition rate. This can be explained by the very low dry bulk density, resulting in low amount of C in the upper soil layers (Tab. 3) which are most exposed to decomposition (e.g. Fang and Moncrieff, 2005). Also, a low dry bulk density accompanies with low degree of degradation and therefore high amounts of labile carbon (e.g. Grosse-Brauckmann, 1990).

Despite the large differences in accumulated NEE (Fig. 1) between FsA and FsB, they almost do not differ in their decomposition rates. This confirms the expectations that the differences in NEE between FsA and FsB can be fully explained by the differences in water table, biomass and carbon stocks.

5 Conclusions

Differences between sites in respect to CO_2 fluxes could be explained if beside air temperature, water table and soil C- & N- stocks, also site specific plant productivity and decomposition rates were taken into account. Differences in nutrients availability and soil wetness could not explain the differences in plant productivity between the sites. Substrate quality, litter input, as well as pH values were likely explanations for the differences in decomposition rates. A site specific interpretation was not needed for processes related to plant phenology, their response to temperature, allocation of new assimilates and plant respiration and litter fall rates.

The model parameters which strongly affected model performance were successfully constrained by the available long term measurement data on NEE, partitioned into GPP and R_{eco}, LAI and biomass, including rooting depth and root biomass at one site, water table, soil temperature and soil C and N stocks as well as meteorological data and snow data at one site. It would have been useful if additional information was available about root biomass at all sites, root litter fall and soil water content to validate the model performance in the corresponding processes. A second measurement of C and N stocks, several years after the first, as well as information about the degree of decomposition on all sites would have been very helpful to constrain decomposition rates and partitioning between SOM pools.

Some improvements in the model and its configuration were identified to obtain a better performance for simulations of GHG fluxes from treeless peatlands. Examples include separate temperature responses for plant and soil heterotrophic respiration. The static response to water saturated conditions needs to be replaced by a function that considers the change of O_2 in the soil.

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The simulation files with the setup according the common configuration together with the according version of CoupModel can be provided upon request.

Appendix A:

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Tables

Table 1. Site characteristics

Code	Lom	Amo	Hor	FsA and FsB
Country	Finland	UK	Netherlands	Germany
Site name	Lompolojänkkä	Auchencorth moss	Horstermeer	Freisinger Moos
Area [m^2]	120000	250000	120000	400
Latitude; longitude	67°59'83"N; 24°12'55"E	55°47'34"N; 3°14'35"W	52°14'25"N 5°4'17"E	48°22'50"N 11°41'12"E
Peatland type	fen	bog	fen	fen
Dominant vegetation	mosses, sedges, shrubs	grasses, sedges, soft rush, mosses	grass, reeds, small shrubs	sedges, herbs, grasses (A), tall sedges (B)
Landuse and management	natural mire	restored; grazed	restored; nature reserve	drained, 1 cut a^{-1}
Mean temperature / range[a] [°C]	−1.4/−15-13	10/4-15	9.8/3-17	7.5/−2-17
Mean water table [cm]	+ 1.2	−12.5	~ −10	−25 (A) −20 (B)
Annual precipitation [mm]	484	1155	797	788
N deposition [kg ha^{-1} a^{-1}]	8.13	1.59		7.1
Peat depth [m]	2-3	0.5-5	2	3
pH	5.5-6.0	4.4	4.8-6.0	5.5-6.7

[a] annual range of mean monthly temperatures

Table 2. Abbreviations and symbols

Abbreviation	Description
C	carbon
CO_2	carbon dioxide
EC	eddy covariance
GHG	greenhouse gas
GPP	gross primary production
k_{gresp}	growth respiration coefficient
k_h	rate coefficient for the decay of the slow C pools
k_l	rate coefficient for the decay of the fast C pools
k_{tot}	Total rate of decomposition calculated from k_h, k_l and SOC of the corresponding pools in the upper 30 cm
$k_{mrespleaf}$	maintenance respiration coefficient for leaves
k_{rn}	extinction coefficient in the Beer law used to calculate the partitioning of net radiation between plant canopy and soil surface
LAI	leaf area index
ME	mean error
m_{retain}	coefficient for determining allocation to mobile internal storage pool
N	nitrogen
NSE	Nash-Sutcliff efficiency
p_{ck}	speed at which the maximum surface cover of plants is reached
$p_{\theta p}$	power coefficient in the response function of microbial activity in dependency of soil moisture
$p_{\theta Satact}$	activity under saturated conditions in the soil moisture response function for microbial activity, mineralisation-immobilisation, nitrification and denitrification
$p_{\theta Upp}$	water content interval in the soil moisture response function for microbial activity, mineralisation-immobilisation, nitrification and denitrification
R^2	coefficient of determination
R_{eco}	ecosystem respiration
SOC	soil organic carbon
T_{amean}	assumed value of mean air temperature for the lower boundary condition for heat conduction
T_{aamp}	assumed value of the amplitude of the sine curve , representing the lower boundary condition for heat conduction
$T_{MatureSum}$	temperature sum beginning from grain filling stage for plant reaching maturity stage
$T_{DormTth}$	critical air temperature that must be undershoot for temperature sum calculation
$T_{EmergeSum}$	air temperature sum that is the threshold for start of plant development
$T_{EmergeTth}$	critical air temperature that must be exceeded for temperature sum calculation
t_{Q10}	response to a 10 °C soil temperature change on the microbial activity, mineralisation-immobilisation, nitrification, denitrification and plant respiration
t_{Q10bas}	base temperature for the microbial activity, mineralisation-immobilisation, nitrification and denitrification at which the response is 1
ε_L	radiation use efficiency

Table 3. Partitioning of measured SOC to the pools. The data in the table is aggregated into 3 soil layers, however 12 layers were used in the model

	depth [m]	Lom	Amo	Hor	FsA	FsB
Measured total C [kg m^{-3}]	0-0.1	24	190	72	107	88
	0.1-0.3	30	187	79	104	90
	> 0.3	51	175	156	70	61
Measured C:N [kg m^{-3}]	0-0.1	27	23	13	11	12
	0.1-0.3	20	22	13	14	13
	> 0.3	20	21	22	17	17
Estimated fraction of fast pool / total C	0-0.1	95%	72%	18%	3%	9%
	0.1-0.3	56%	73%	20%	20%	16%
	> 0.3	55%	68%	62%	35%	41%
Dry bulk density [g cm^{-3}]	0-0.1	0.06[a]	0.39	0.35	0.59	0.33
	0.1-0.3	0.06	0.37	0.48	0.29	0.52
	> 0.3	0.10	0.37[b]	0.50	0.18	0.17

[a] no data available, value from lower layer used

[b] no data available, value from upper layer used

Table 4. Highest achieved values for selected performance indices

Variable	Index	Lom		Amo		Hor		FsA		FsB	
		all/selected runs	single run	all/selected runs	single run	all/selected runs	single run	all/selected runs	single run	all/selected runs	single run
NEE	R^2	0.61/0.60	0.59	0.59/0.58	0.55	0.53/0.51	0.48	0.20/0.16	0.15	0.25/0.21	0.19
	ME	0.00	0.05	0.00	0.04	0.00	0.02	0.00	1.43	0.00	−0.05
GPP	R^2	0.66/0.66	0.65	0.68/0.68	0.66	0.58/0.57	0.55	0.38/0.35	0.34	0.40/0.39	0.35
	ME	0.00	0.05	0.00	−0.09	0.00	0.04	0.00	0.06	0.00	−0.03
R_{eco} EC	R^2	0.79/0.74	0.69	0.71/0.71	0.66	0.78/0.77	0.75	n.a.	n.a.	n.a.	n.a.
	ME	0.00	0.00	0.00	−0.05	0.00	−0.06	n.a.	n.a.	n.a.	n.a.
R_{eco} chamber	R^2	0.73/0.71	0.64	0.67/0.57	0.38	0.52/0.48	0.45	0.73/0.66	0.69	0.87/0.81	0.85
	ME	0.00	−0.06	0.00	0.04	0.00/−4.74	−5.38	0.00	−0.01	0.00	−0.08
R_{eco} winter	R^2	0.67/0.63	0.63	0.14/0.08	0.06	0.28	0.28	0.51/0.43	0.32	0.92/0.89	0.89
	ME	0.00	0.01	0/0.04	0.13	0.00	−0.26	0/1.60	3.21	0.00/0.73	2.11
upper soil temperature	R^2	0.88/0.87	0.87	0.86	0.84	0.92	0.91	0.88/0.86	0.84	0.88/0.86	0.84
	ME	0.00	−0.01	−0.03	−0.08	−1.37/−1.51	−1.77	0.00/0.58	0.35	0/1.20	0.35
lower soil temperature	R^2	0.95	0.95	0.90	0.89	0.89	0.89	0.97/0.96	0.94	0.92/0.91	0.94
	ME	0.00	−0.03	0.00	0.02	0.00	−0.08	0.00	−0.15	0.00	−0.15
Snow depth	R^2	0.75	0.75	n.a.	n.a	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
	ME	-0.1	-0.06	n.a.	n.a	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
LAI	R^2	0.65/0.51	0.53	n.a.	n.a	0.36/0.31	0.33	0.75/0.69	0.61	0.82/0.76	0.61
	ME	0.00	0.11	n.a.	n.a	0.00/−0.61	−1.49	0.00	0.12	0.00	0.05
Above ground living biomass	R^2	n.a.	n.a.	n.a.	n.a	0.02/0.00	0.00	0.31/0.26	0.24	0.47/0.43	0.32
	ME	n.a.	n.a.	n.a.	n.a	0	−112	0/−20	−21	0/−36	−48
Root biomass	R^2	n.a.	n.a.	n.a.	n.a	0.28/0.07	0.01	n.a.	n.a.	n.a.	n.a.
	ME	n.a.	n.a.	n.a.	n.a	0.00	−282	n.a.	n.a.	n.a.	n.a.

n.a. not available

Figures

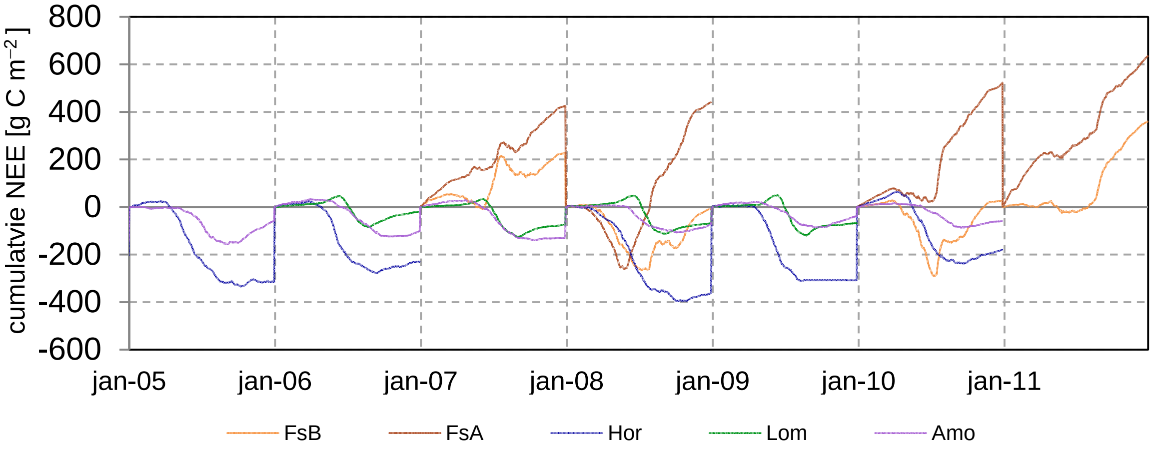

Figure 1. Measured NEE from gapfilled time series. Positive values indicate CO_2 emission, negative CO_2 uptake by the ecosystem.

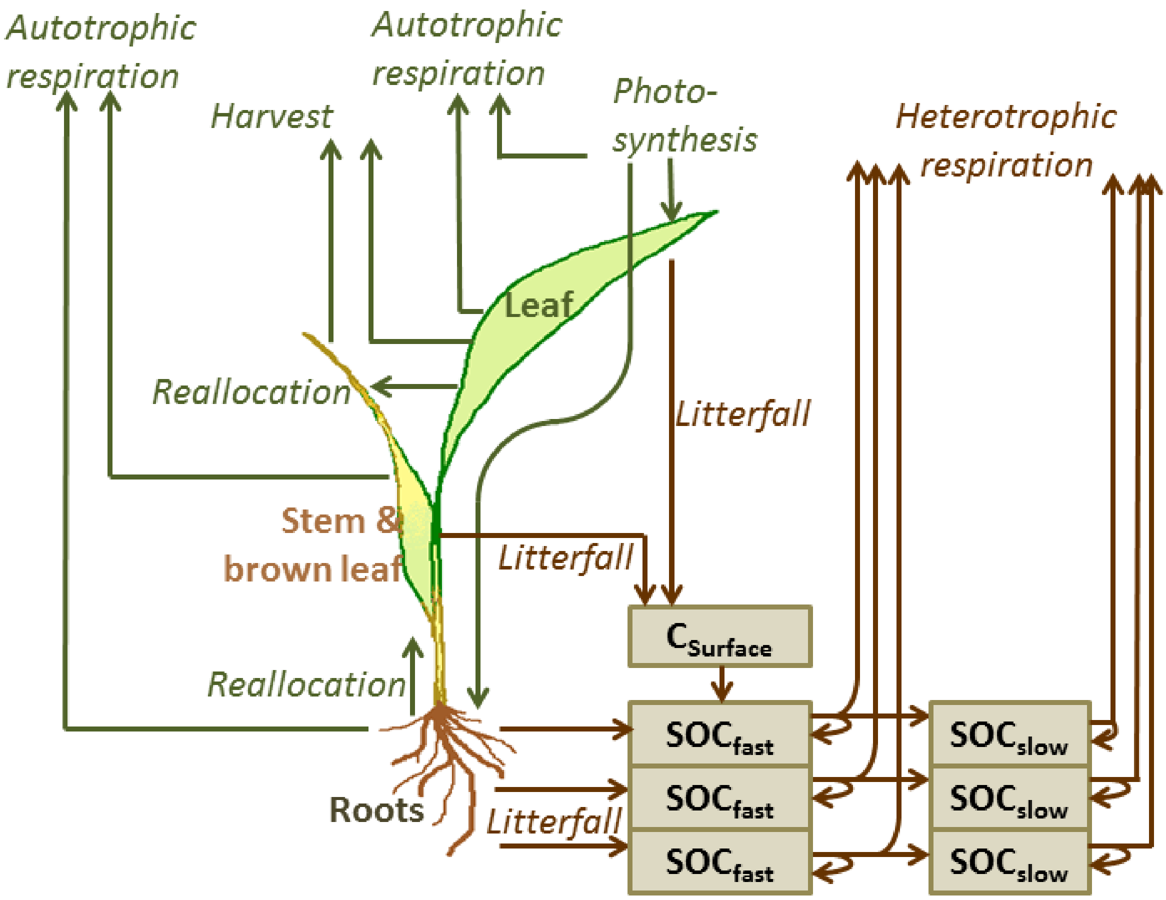

Figure 2: Scheme of carbon fluxes and pools in the current CoupModel setup

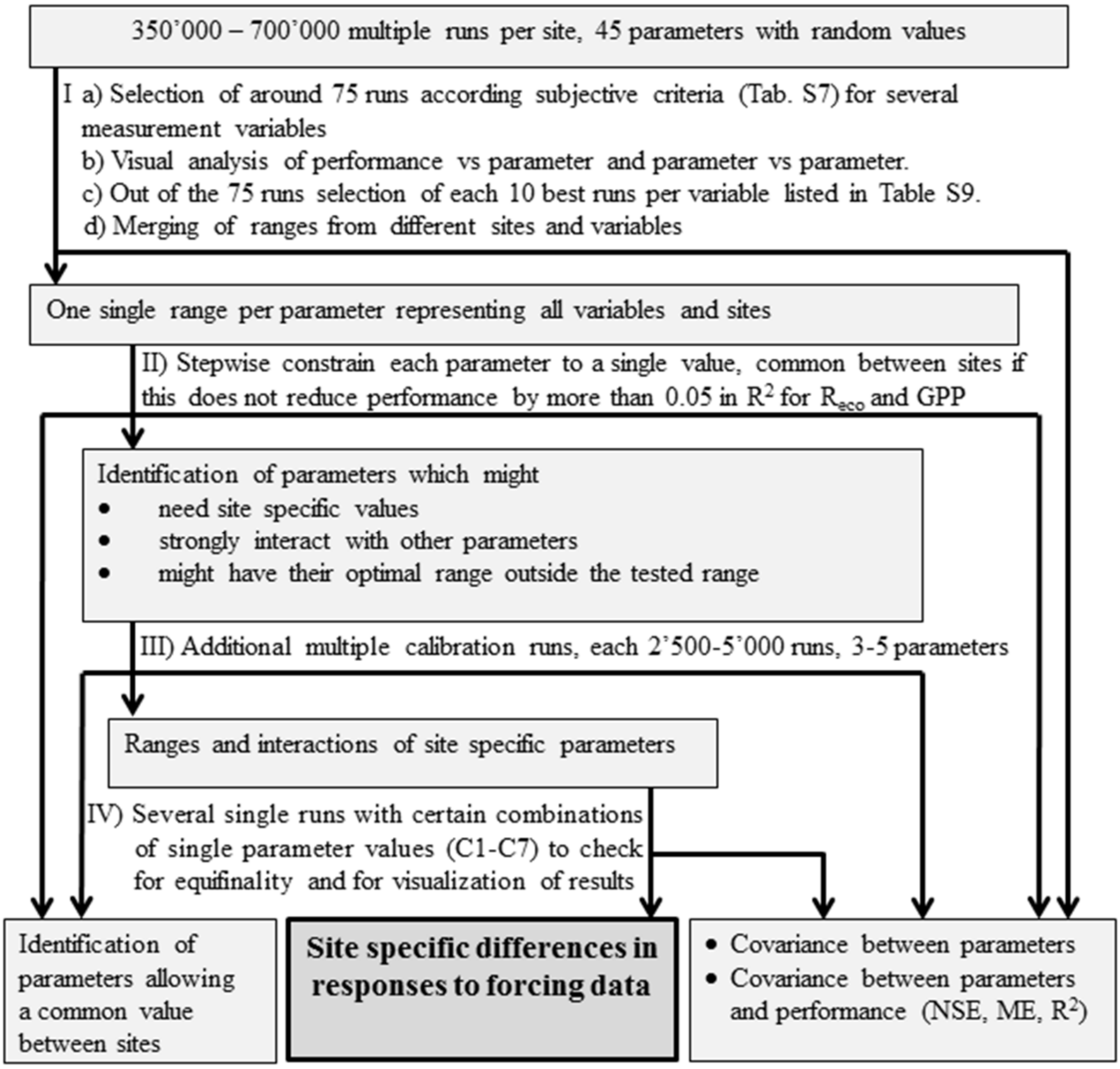

Figure 3. Stepwise parameter calibration. Boxes show the outcome of each step. Description for scenarios C1-C7 can be found in Table S8 in the supplement.

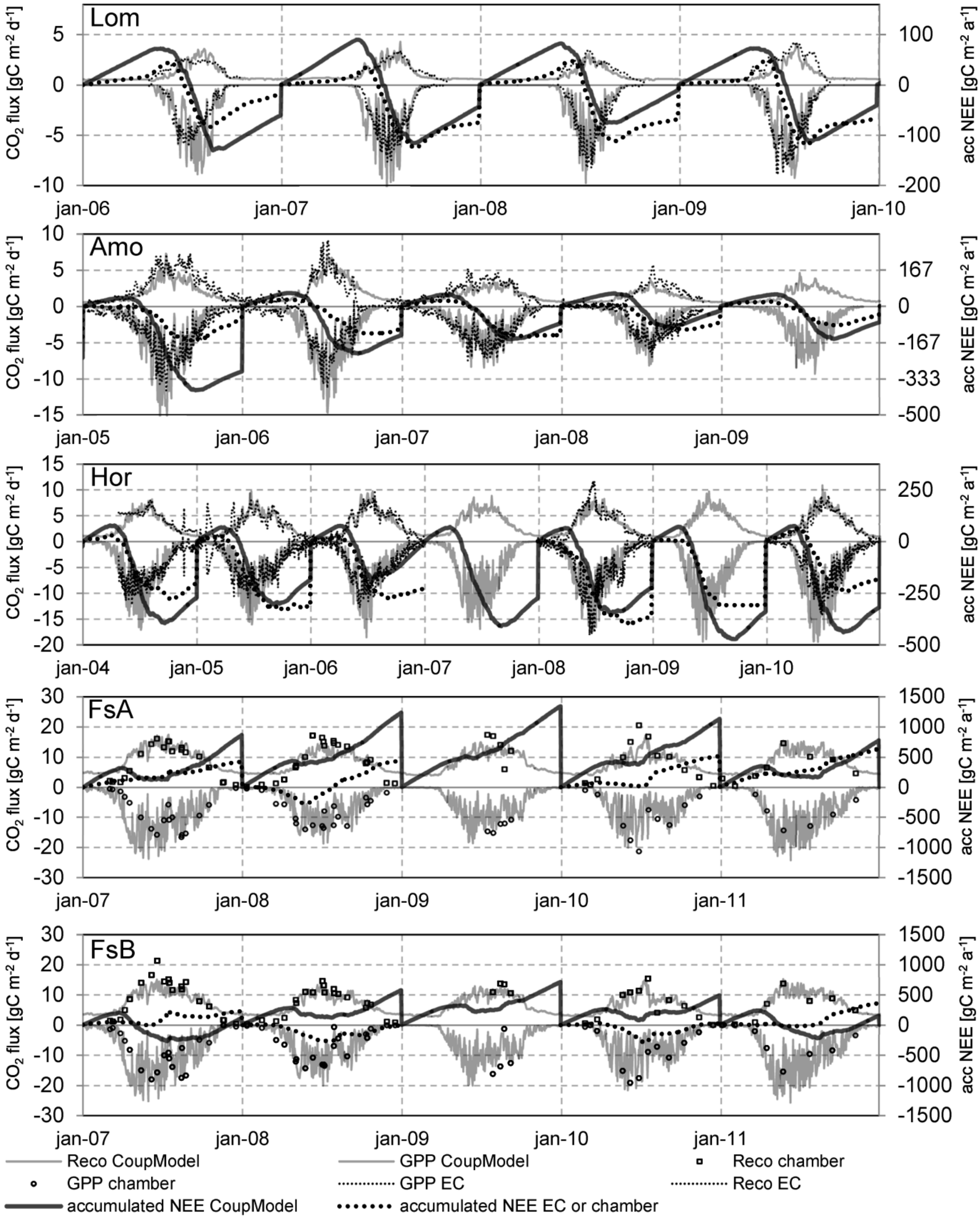

Figure 4. Simulated and measured R$_{eco}$ (positive) and GPP (negative) fluxes and accumulated NEE for one selected set of parameter values (C1) common between all sites. Note the different scales.

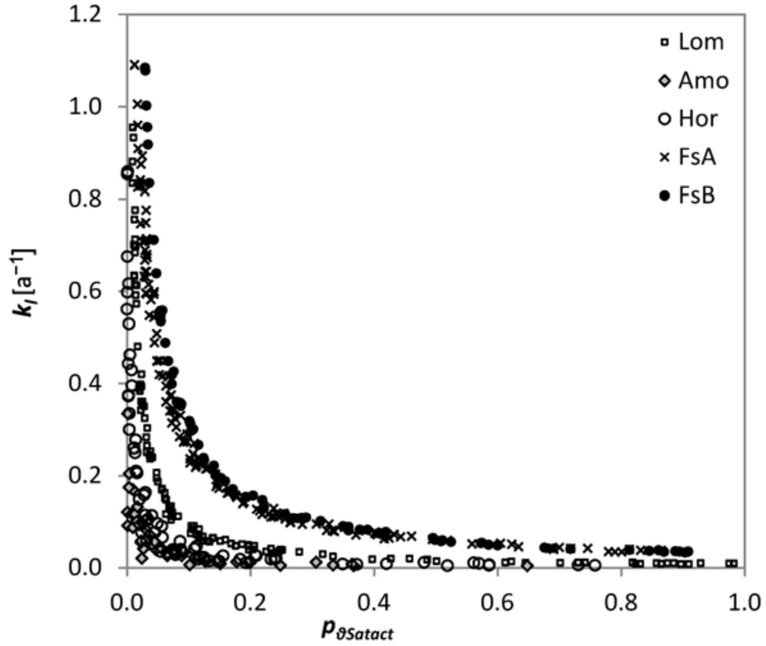

Figure 5. Dependencies between the parameters for decomposition rate and saturation activity for the different sites, based on additional multiple runs.

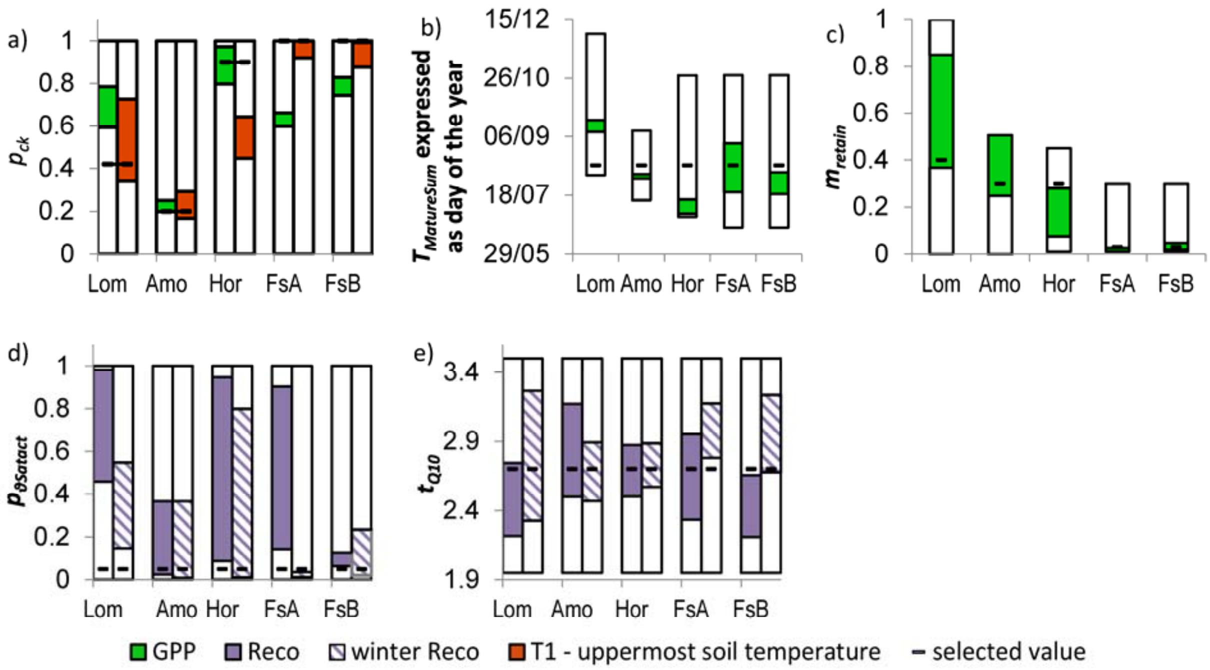

Figure 6. Obtained distributions of parameter values as constrained by additional multiple runs (calibration step III). Ranges for k_{l1} and ε_L are not shown due to their interactions with several parameters. Coloured bars show the range of the 10 runs with the best performance for

each validation variable. Prior ranges are indicated by the frame around the bar. Black dash is the value chosen for the common configuration C1.

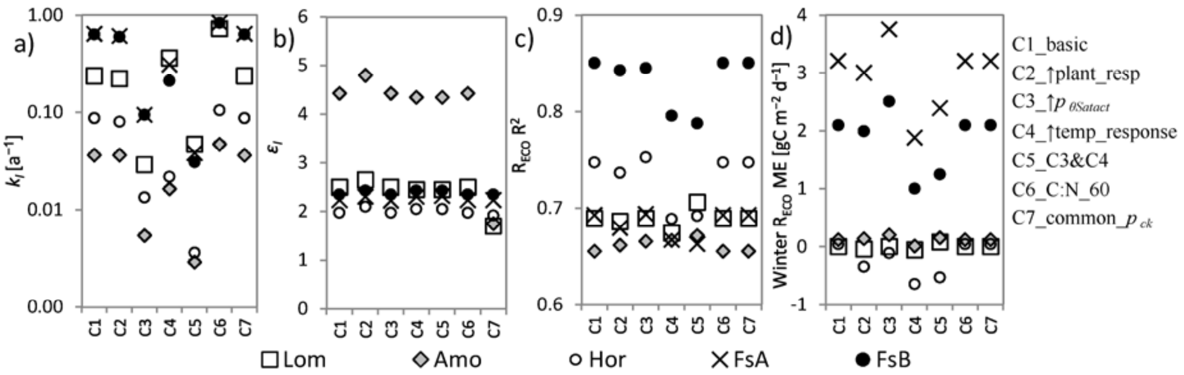

Figure 7. Values for the parameters decomposition rate (a) and light use efficiency (b) and resulting model performance (c, d) when applying various single value representations of parameters (C1-C7, see Tab. S8 in the supplement).

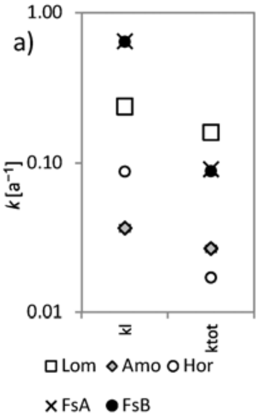

Figure 8. Decomposition rates of fast pools (k_l) and calculated rates of total organic matter decomposition if only one pool was used (k_{tot}) for each site and each layer