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CO₂ fluxes and ecosystem dynamics at five European treeless peatlands – merging data and process oriented modelling

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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 to what extent CO_2 fluxes measured at different sites, can be explained by common processes and parameters implemented in the model. The CoupModel 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.

The model, utilizing a site independent configuration for most of the parameters, captured seasonal variability in the major fluxes well. 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, heterotrophic respiration rates 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.

Applying common parameter values for the timing of plant shooting and senescence, and a minimum temperature for photosynthesis, had only a minor effect on model performance, even though the gradient in site latitude ranged from 48° N (South-Germany) to 68° N (northern Finland). This was also true for common parameters defining the moisture and temperature response for decomposition.

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CoupModel is able to describe measured fluxes at different sites or under different conditions, providing that the rate of soil organic decomposition, photosynthetic efficiency, and the regulation of the mobile carbon (C) pool are estimated from available information on specific soil conditions, vegetation and management of the ecosystems.

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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 different characteristics with respect to climate, hydrology, 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.

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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 5 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 typically 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 CO₂ from forest sites has shown that dynamics of CO₂ 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 CO₂ 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).

Many carbon ecosystem models have been run on site scale such as Biome-BC (Feng et al., 2011), DNDC (Li et al., 1992a, b; Dietiker et al., 2010), PaSim (Calanca et al., 2007), PIXGRO (Adiku et al., 2006), CANDY (Franko et al., 1997), DAYCENT

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(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 model was designed for a wide range of soil types and different ecosystems and applications (see Jansson, 2012 for review). It is capable of simulating CO₂ (Klemedtsson et al., 2008), nitrous oxide (N₂O) (Norman et al., 2008) and methane (CH₄) fluxes (Ravina, 2007). The CoupModel combines the advantages of an hourly time step, necessary for analysing e.g. chamber flux data and detailed sub modules for predicting plant growth and respiration, soil nitrogen (N) and C processes, energy and heat fluxes, soil temperature, soil frost and snow depth. The CoupModel also allows the user to select between different sub models and access all parameters via a user interface. An extensive model description can be found in Jansson and Karlberg (2010).

The main aim of this study was to extend the knowledge on ecosystem modelling of peatlands by applying and calibrating the process oriented CoupModel to five data rich European flux measurement sites. Specific objectives were:

- I. to identify differences and similarities in CO₂ related processes between various sites which largely differ in their forcing data.
- II. to identify problems related to the model representation of the different ecosystem processes for peatlands.
- III. to identify and discuss the impact of available data for estimating CO₂ fluxes from peatlands in general.

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 (Table 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 ($R_{\rm eco}$) and different amounts of biomass. This is reflected in the annual accumulated NEE based on measurements, ranging from $-364\,{\rm g\,C\,m^{-2}\,a^{-1}}$ to $592\,{\rm g\,C\,m^{-2}\,a^{-1}}$ (Fig. 1).

Dynamic forcing data for model input (water table and meteorology) was available from measurements at all sites (Table S1 in the Supplement). Data used for model parameter constraint included measurements of LAI, soil temperature and NEE (Table S2 in the Supplement). Measured NEE was partitioned into $R_{\rm eco}$ and GPP by the use of empirical models based $R_{\rm eco}$ from night time NEE or opaque chambers. Though this will be called measured data in the following.

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 $-1.4\,^{\circ}$ 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

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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, CO₂ 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. (2014), 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. CO₂ fluxes were measured half hourly by EC and biweekly with opaque chambers between 2004 and 2010. A detailed description of the sites 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 $-20\,\mathrm{cm}$ compared to $-25\,\mathrm{cm}$ 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 $R_{\rm eco}$ 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 12 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.

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. Vapour pressure deficit was calculated from the relative humidity and cloud fraction from global radiation input and latitude. Snow fall was simulated from precipitation and air temperature, snow melt from global radiation, air temperature and simulated soil heat flux.

Data was gap filled by simple linear interpolation for gaps < 6 h. 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 h 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

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independent of initial values. Data from the available years was copied to previous years if not available from an adjacent climate station.

The lower boundary condition for heat conduction was assumed to be constant and equal to the parameter $T_{\rm amean}$ (a list of symbols and abbreviations can be found in Table 2).

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

2.2.2 Water table

To create the best possible representation of ground water level we used the measured ground water level in hourly or highest available resolution to be used as a dynamic forcing data of the ground water level in the model.

In addition to the water in the soil profile a surface water pool was simulated with a storage capacity of 10 mm and runoff characteristics for generation of surface runoff. Drainage or optionally inflow to the simulated profile was simulated by the drainage equation.

2.2.3 Carbon and nitrogen

For each soil layer the organic substrate was represented by two pools, one with a slow and one with a high turnover rate. The initial conditions of both pools were estimated from measured soil data as described in Sect. 2.2.5 and Table 3. To avoid effects from the decomposition rate in the fast pool which was calibrated, the decomposition rate in the slow pool (k_h) was set constant to $2 \times 10^{-8} \, d^{-1}$ as decomposition of resistant carbon is less responsible for the variation in soil respiration (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.

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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 and vegetation height were simulated. Permanent, perennial vegetation was configured with maximal plant height of 0.6 m and lowest root depth of -0.6 m. 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, including aerenchyma to tolerate water saturated soil conditions. 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 ($T_{\rm EmergeTth}$) reached the value of $T_{\rm EmergeSum}$. Both parameters were calibrated (Table S4, in the Supplement). The accumulation of temperatures started when the day length exceeds 10 h. Snow cover hindered shooting by reducing the radiation passing through to the plant, while low soil temperatures reduced plant water uptake. Five consecutive days in the autumn with day lengths shorter than 10 h and with temperatures below $T_{\rm DormTth}$ terminated the growing season and plants went to dormancy.

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

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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 for 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 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.

The soil profile was divided into several layers with different depths. To each layer water retention, hydraulic conductivity, initial organic N, C:N and pH parameters were assigned according to soil data from each site. Total soil organic carbon (SOC) per layer was attributed to SOC pools on the basis of their C:N ratio whereas C:N ratio of the slow decomposing pool was assumed to be 10, while for the fast pool 27.5 was chosen according to measured C:N of leaf tissues at FsA and FsB (Table 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

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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 5 in Fig. 2, details on the calibration procedures are presented as Supplement.

For the basic calibration (step I, Fig. 2) 350 000 to 700 000 runs were performed for each site, using 45 selected parameters with assumed uniform random range (Table S4 in the Supplement). Parameter ranges were then constrained based on selected runs (step I and II, Fig. 2), showing acceptable performance to multiple variables (Table 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. 2). A number of simulations were also made by single value representations of parameters (step IV, Fig. 2) 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 Table 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-Sutcliffe 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).

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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 (Table 4). Figure 3 shows the differences between measurements and model C1.

3.1.1 Fluxes

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

In respect to $R_{\rm eco}$ 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 $|0.1| \, {\rm g} \, {\rm C} \, {\rm m}^{-2} \, {\rm day}^{-1}$. 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 $R_{\rm eco}$ 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 $2.11\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$ for the single runs at FsA and FsB, respectively, and a weaker overestimation for the accepted runs. The overestimation was less pronounced at Amo $(0.13\,\mathrm{g\,C\,m^{-2}\,day^{-1}})$ and Lom $(0.01\,\mathrm{g\,C\,m^{-2}\,day^{-1}})$. At Hor winter fluxes were underestimated with a ME of $-0.26\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$. This was reflected in the accumulated NEE (Fig. 3) leading to a much higher $\mathrm{CO_2}$ loss compared to the $\mathrm{CO_2}$ 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

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nearly compensated due to the underestimated spring $R_{\rm eco}$, 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. 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 m² m⁻². An exception was Hor, where LAI was underestimated by ME of -0.61 and 1.49 m² 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 $R_{\rm eco}$ R^2 to 0.66 compared to 0.75 in C1 and led to an overestimation of winter $R_{\rm eco}$ 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 pool (k_l) and radiation use efficiency (ε_L) .

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Activity under saturated conditions ($p_{\theta \text{Satact}}$), 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 $R_{\rm eco}$ 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 and therefore constrained independently: $p_{\rm ck}$ covaried with the extinction coefficient in the Beer law $(k_{\rm rn})$ which is used to calculate the partitioning of net radiation between canopy and soil surface. Strong linear negative correlation between coefficients for growth $(k_{\rm gresp})$ and maintenance respiration $(k_{\rm mrespleaf})$ was detected.

The effect of the different parameter in the water response function $p_{\theta \rm Satact}$, $p_{\theta \rm Upp}$ and p_{θ} 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 $p_{\theta \rm Upp}$ and p_{θ} were set to default values and $p_{\theta \rm Satact}$ constrained by additional multiple runs together with $k_{\rm I}$. Differences between sites in $k_{\rm I}$ are reduced with higher $p_{\theta \rm Satact}$ (Fig. 4), however, higher $p_{\theta \rm Satact}$ increase overestimation of winter $p_{\theta \rm Satact}$ at FsA and FsB (Figs. 5 and 6d). A wider range of $p_{\theta \rm Satact}$ was acceptable for summer $p_{\theta \rm Satact}$ (Fig. 5).

Beside moisture response, decomposition rate (k_{\parallel}) and temperature response $(t_{\rm Q10}, t_{\rm Q10bas})$ control soil respiration. The effect on $R_{\rm eco}$ was cofounded by plant respiration.

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Different patterns for different sites and variables for each of the parameters were even more pronounced when only $k_{\rm l}$, $t_{\rm Q10}$ and $k_{\rm mrespleaf}$ were in calibration (Fig. 5).

Single runs with different configurations (Fig. 6) revealed that higher plant respiration as well as steeper temperature response can lead to less overestimation of respiration in winter (Fig. 6d) but lead to reduced performance (Fig. 6c). In all single runs, despite the different configurations, FsA always showed the highest k_{\parallel} while Amo had the lowest (Fig. 6a). A higher saturation activity reduces the difference in k_{\parallel} values, but leads to higher overestimation of winter fluxes.

4 Discussion

4.1 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 $R_{\rm eco}$ 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. 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. Furthermore, GPP cannot be measured directly neither by the chamber nor the EC method. Instead it was derived from NEE and $R_{\rm eco}$ or night time NEE, including the uncertainty of two different measurements and empirical modelling.

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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 5 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. 3). Overestimation of winter $R_{\rm eco}$ 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 $R_{\rm eco}$ was overestimated in the selected single run. For FsB and especially FsA, this was also true for all multiple runs. As Reco 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 Sects. 4.7-4.9. 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. 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.

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 **BGD**

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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. 5a). Setting $p_{\rm ck}$ to a common value of 100% reduced the differences in $\varepsilon_{\rm L}$ between the sites C7 (Fig. 5e), 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.

Start of senescence

Site specific calibration was needed for the temperature sum initiating the start of senescence ($T_{\text{MatureSum}}$). However, if the resulting day of the year was plotted instead, the differences between sites became small (Fig. 5) 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.

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 9267

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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 $m_{\rm retain}$ 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 $m_{\rm retain}$ 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 gramnoides 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.

4.6 Radiation use efficiency

As plants were not nutrient limited in the model setup, lowest values for $\varepsilon_{\rm L}$ 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 $p_{\rm ck}$. However, a common value for $p_{\rm ck}$ reduced the differences in $\varepsilon_{\rm L}$ and led to low $\varepsilon_{\rm L}$ at the ombrotrophic Amo site, but to an even lower value at the minerotrophic Lom. The assumption of plants being well adapted to water stress might not be true for the restored Hor site and might explain the low productivity. Additionally, $\varepsilon_{\rm L}$ is known to be species specific (Sinclair and Horie, 1989; Reich et al., 1998; Wohlfahrt et al., 1999).

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Radiation use efficiency is an important parameter needing site specific calibration. If common values were used for $\varepsilon_{\rm L}$, $\rho_{\rm ck}$ and $m_{\rm retain}$, 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 $\rho_{\rm ck}$ and $m_{\rm retain}$ the discrepancy would be even higher. However $\varepsilon_{\rm L}$ can easily be fitted if either GPP, biomass or LAI is known.

4.7 The control of decomposition and plant respiration by soil temperature

The whole year $R_{\rm eco}$, which was dominated by summer $R_{\rm eco}$ 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 $R_{\rm eco}$, using the same $t_{\rm Q10}$ value. Higher $t_{\rm Q10}$ would decrease overestimation of winter $R_{\rm eco}$ especially at the southern sites FsA and FsB, but also reduce model performance for whole year $R_{\rm eco}$. 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 $t_{\rm Q10}$ 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 $R_{\rm eco}$ includes autotrophic and heterotrophic respiration, while winter $R_{\rm eco}$ is strongly dominated by heterotrophic respiration.

4.8 The control of decomposition by soil moisture

The activity under saturated conditions in respect to unsaturated conditions is described by $p_{\theta \text{Satact}}$ and was strongly negative correlated with decomposition rate k_{I} . Patterns for $p_{\theta \text{Satact}}$ 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

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values did not reduce the performance except at FsB. At Lom only winter $R_{\rm eco}$ was considered, as conditions were always saturated during summer. For acceptable winter $R_{\rm eco}$, $p_{\theta \rm Satact}$ 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 $p_{\theta \text{Satact}}$ would decrease overestimation of winter fluxes. However it would also reduce model performance at all sites and increase the site specific differences in k_1 (Fig. 6).

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 $p_{\theta \text{Satact}}$ would be justified for wetter sites. If k_{\parallel} was constant between sites and instead $p_{\theta \text{Satact}}$ fitted, this would lead to the value of $p_{\theta \text{Satact}}$ to decrease in the order FsB > FsA > Lom > Hor > Amo (Fig. 4) which cannot be justified by the differences in water levels which increase in FsA < FsB \ll Amo < Hor \ll Lom. Therefore a different $p_{\theta \text{Satact}}$ 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.

4.9 The control of decomposition by substrate

The largest differences of parameters between sites appeared for the maximum decay rate of the fast C pool k_1 . 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, $k_{\rm l}$ values at FsA and FsB are substantially higher than at Amo (Fig. 4 and Fig. 6). Higher $t_{\rm Q10}$

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values lead to two groups of k_1 values: similar high ones for Lom, FsA and FsB and substantially lower ones for Hor and Amo (Fig. 6).

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. 7). 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 pool (Fig. 6, 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 $k_{\rm l}$ 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, $k_{\rm l}$ 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 pool was almost inert. A higher decay rate for the slow pool would result in a lower k_{\parallel} for sites with high C stock in the slow pool (cf. Table 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;

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Smith, 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).

The highest decomposition rates occurred at sites with highest biomass production. 5 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_1 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_1 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 (Table 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.

Conclusions

Differences between sites in respect to CO₂ fluxes could be explained if beside air temperature, water table and soil C- and N- stocks, also site specific plant productivity

and decomposition rates were taken into account. Substrate quality, litter input, as well as pH values were likely explanations for the differences in decomposition rates.

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 O₂ in the soil.

The model parameters which strongly affected model performance were successfully constrained by the available long term measurement data on NEE, partitioned into GPP and $R_{\rm eco}$, LAI and biomass, including 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.

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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.

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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 [m²] | 120 000 | 250 000 | 120 000 | 400 |
| Latitude; | 67°59′83″ N; | 55°47′34″ N; | 52°14′25″ N | 48°22′50" N |
| longitude | 24°12′55″ E | 3°14′35″ W | 5°4′17″ E | 11°41′12″ E |
| Peatland type | fen | bog | fen | fen |
| Dominant vegeta- tion | 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 | -1.4/-15-13 | 10/4–15 | 9.8/3-17 | 7.5/-2-17 |
| temperature/range ^a [°C] | | | | |
| Mean water table [cm] | +1.2 | -12.5 | ~ -10 | -25 (A) -20 (B) |
| Annual precipita- tion [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 |
| рН | 5.5-6.0 | 4.4 | 4.8–6.0 | 5.5–6.7 |

^a Annual range of mean monthly temperatures.

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Table 2. Abbreviations and symbols.

| Abbreviation | Description |
|------------------------|--|
| С | 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 pool |
| k_{l} | rate coefficient for the decay of the fast C pool |
| k _{mrespleaf} | maintenance respiration coefficient for leaves |
| $k_{\rm rn}$ | extinction coefficient in the Beer law used to calculate the partitioning of net radiation be- |
| | tween plant canopy and soil surface |
| LAI | leaf area index |
| ME | mean error |
| $m_{ m retain}$ | coefficient for determining allocation to mobile internal storage pool |
| N | nitrogen |
| NSE | Nash–Sutcliffe efficiency |
| $ ho_{ck}$ | speed at which the maximum surface cover of plants is reached |
| $p_{	hetaLow}$ | water content interval in the soil moisture response function for microbial activity, mineralisation-immobilisation, nitrification and denitrification |
| $p_{	heta Upp}$ | 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 conduc- |
| ' amean | tion |
| $T_{MatureSum}$ | temperature sum beginning from grain filling stage for plant reaching maturity stage |
| T_{DormTh} | 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 |
| $T_{EmergeTh}$ | 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 |
| $arepsilon_{L}$ | radiation use efficiency |

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

| | depth [m] | Lom | Amo | Hor | FsA | FsB |
|-----------------------|-----------|-------------------|-------------------|------|------|------|
| C Fast pool | 0-0.1 | 23 | 136 | 13 | 4 | 8 |
| [kg m ⁻³] | 0.1-0.3 | 17 | 137 | 16 | 20 | 14 |
| | > 0.3 | 28 | 119 | 98 | 24 | 25 |
| C Slow pool | 0-0.1 | 1 | 54 | 59 | 103 | 80 |
| [kg m ⁻³] | 0.1-0.3 | 13 | 50 | 63 | 84 | 76 |
| | > 0.3 | 23 | 56 | 58 | 46 | 36 |
| Fast pool: | 0-0.1 | 95 % | 72% | 18% | 3% | 9% |
| Total C | 0.1-0.3 | 56% | 73% | 20% | 20% | 16% |
| | > 0.3 | 55% | 68% | 62% | 35 % | 41% |
| C:N | 0-0.1 | 27 | 23 | 13 | 11 | 12 |
| | 0.1-0.3 | 20 | 22 | 13 | 14 | 13 |
| | > 0.3 | 20 | 21 | 22 | 17 | 17 |
| Dry bulk density | 0-0.1 | 0.06 ^a | 0.39 | 0.35 | 0.59 | 0.33 |
| [g cm ⁻³] | 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.

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Table 4. Highest achieved values for selected performance indices.

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

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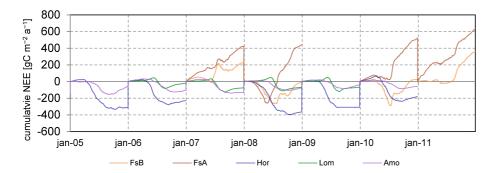


Figure 1. Measured NEE from gapfilled time series. Positive values indicate CO₂ emission, negative CO₂ uptake by the ecosystem.

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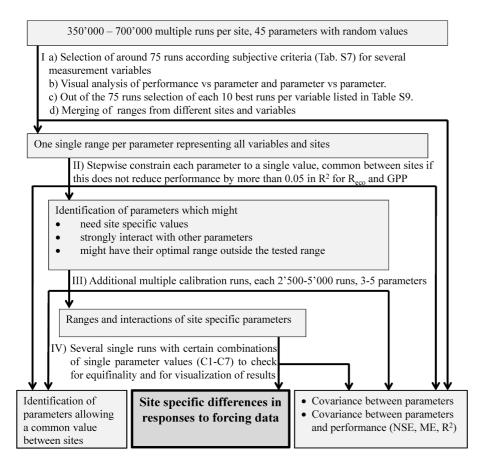


Figure 2. Stepwise parameter calibration. Boxes show the outcome of each step. Description for scenarios C1-C7 can be found in Table S8 in the Supplement.

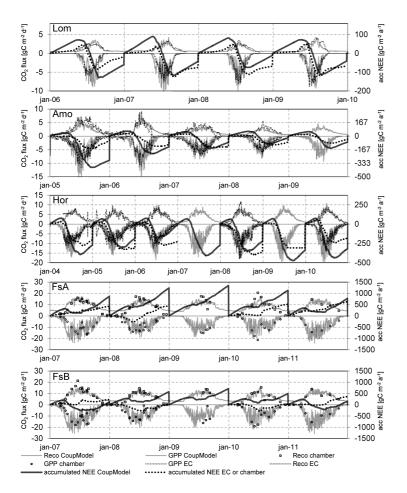


Figure 3. Simulated and measured $R_{\rm eco}$ (positive) and GPP (negative) fluxes and accumulated NEE for one selected set of parameter values (C1) common between all sites. Note the different scales.

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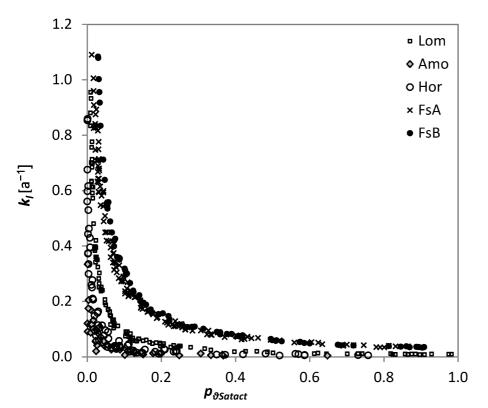


Figure 4. Dependencies between the parameters for decomposition rate and saturation activity for the different sites, based on additional multiple runs.

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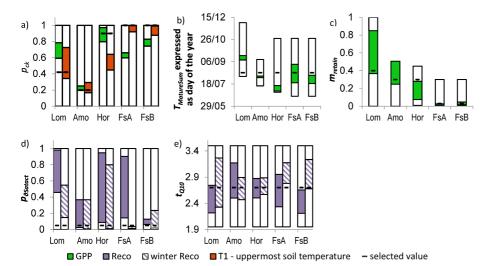


Figure 5. Obtained distributions of parameter values as constrained by additional multiple runs (calibration step III). Ranges for $k_{\rm I1}$ and $\varepsilon_{\rm L}$ are not shown due to their interactions with several parameters. Coloured bars show the range of the 10 runs with the best performance 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.

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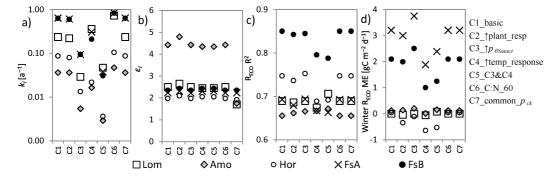


Figure 6. Values for the parameters decomposition rate (a) and light use efficiency (b) and resulting model performance (c, d) when applying various single value representations of parameters (C1-C7, see Table S8 in the Supplement).

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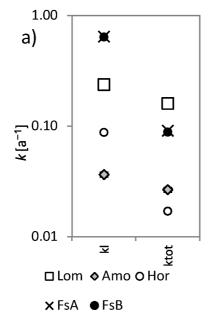


Figure 7. Decomposition rates of fast pool (k_{\parallel}) and calculated rate of total organic matter if only one pool was used (k_{tot}) .