We have now finished the revision of the paper. The review comments were very helpful and we trust that considering them greatly improved the manuscript. Please find below a list with all comments and our detailed responses, including a description of the changes in the manuscript.

Anonymous Referee #1

- < − >

  → **The first section is quite similar in approach and objectives to a handful of papers that have been published over the last 5 or 6 years, including work by Janssens, Del Grosso, and Richardson; results of the present study should, I think, be put in the context of this earlier work.**

  Janssens, I.A. et al. 2003. Climatic influences on seasonal and spatial differences in soil CO2 efflux. In: Valentini, R. (Ed.), Fluxes of Carbon, Water and Energy of European Forests. Springer, Berlin, pp. 233-253.

  Del Grosso, S.J. et al. 2005. Modeling soil CO2 emissions from ecosystems. Biogeochemistry 73: 71–91.

  Richardson, A.D. et al. 2006. Comparing simple respiration models for eddy flux and dynamic chamber data. Ag & Forest Met 141: 219-234.

  ← We now refer to those in the discussion section (p. 8, l. 683) (p. 8, l. 684).

  done

- < − >

  → **The second section does not seem to follow logically from the first, especially since there is no overlap between the sites with measurements and the site that is modeled.**

  ← We agree that this was not explained well. We have added the reasoning to the methods (p. 2, l. 146).

  The idea of a dynamic vegetation model like LPJ-GUESS is to have a model with one fix implementation of all the biogeochemical and vegetation dynamics. By providing the model with a given set of plant functional types, the model can be applied to different forest ecosystems, e.g. over whole Europe. Ideally, the model therefore should be calibrated just once and then is run in differing ecosystems. We conducted our study on an elevation gradient to account for different temperature regimes. By running the simulations along an elevation gradient, the weather drivers are gradually changing, whereas the precipitation and temperature pattern at the calibration sites did not differ systematically, which makes comparison more difficult compared to a gradient study within one valley. The difference of the sites along the Ticino elevation gradient therefore are only reflected by the given temperature and precipitation regimes but underlying the same broad-scale weather regime. And this in turn makes a comparison more meaningful. The interpretation of the study results does not depend on the location of the modeling study, as long as the same climatic region is used. As other studies have been conducted in the Ticino catchment in our group, the choice of the Ticino catchment as a study site stood to reason.

done

- **< 1 >**

→ **The introduction highlights some of the challenges of modeling soil respiratory processes. On P8131 L15, it is stated that a consensus has not yet emerged on the climate sensitivity of soil carbon decomposition, then on L23+, decomposition of SOM is highly complex, as it is driven by a combination of factors. However, the authors then resort to evaluating simple, well-known models that effectively contain no pools, do not incorporate moisture (or other environmental driver) effects, lump together autotrophic and heterotrophic R, and are driven by a single soil temperature (of questionable representativeness). So the approach taken seems at odds with the motivation for the study.**

← We acknowledge this issue. The motivation for the study has been clarified in the abstract (p. 1, l. 16) and in the introduction (p. 2, l. 74), (p. 2, l. 99).

The motivation for the study was an uncertainty analysis of temperature dependence of the soil carbon dynamics. We wanted to be able to systematically quantify the uncertainty and therefore used just one model implementation as-is to exclude further uncertainties of model inter-comparisons. We therefore calibrated different potential temperature-response functions to experimental datasets of total soil respiration and replaced the standard function in the three pool soil carbon model in LPJ-GUESS. The model itself was kept as-is, we introduced parameter uncertainties and looked at the uncertainties propagation of model projections of heterotrophic soil respiration and soil carbon stocks.

done

- **< 2 >**

→ **Re: P8132 L11. Since the soil R data are a combination of autotrophic and heterotrophic processes, it is not clear to me how the analysis performed really provides insight into**

heterotrophic respiration specifically; related to this, I find it very strange that later (P8135 L15+), that in the LPJ analysis, the L&T function is used for autotrophic respiration, but the five different candidate models are used for heterotrophic respiration.

← We agree that this was not clear. We have clarified this issue in the methods section (p. 3, l. 237).

We use the total soil respiration to estimate the overall temperature response of soil respiration, as more data set were available for total soil respiration. In the model LPJ-GUESS, the root respiration is modeled as part of the autotrophic respiration and does therefore influence plant net primary production (NPP). As the amount of litter produced depends on NPP, a change in root respiration would change litter input. To avoid this indirect impact of temperature, we did not change the implementation of autotrophic respiration to guarantee comparable litter inputs for all simulations on a given elevation level.

done

- < **3** >

→ **The motivation for focusing on the Ticino catchment in the southern Alps is not clear, especially given that none of respiration datasets are from this region. Why not conduct the LPJ modeling for the eight sites used in the model selection part of the manuscript?**

← See the comment above (p. 1, l. 28), where we clarified the reasons for choosing the Ticino catchment.

done

- < **4** >

→ **Sec. 2.1.2. It is not at all clear to me how the response functions were parameterized when included in the LPJ model. The section in the manuscript that appears to describe this (P8136 L22+) is quite cryptic and this needs to be improved. How were confidence intervals of turnover times estimated? I cannot find this in the manuscript.**

← Yes, this was not very clear. In the revised version, the paragraph describing the usage of the SIMLAB software has been moved upwards to clarify how the functions were parameterized (p. 4, l. 292).

The confidence interval for the turnover times could not be estimated with the given experimental datasets, we therefore took the values by Parton et al. (1987) as stated in the text (p. 4, l. 316).

done

- **< 5 >**

→ **P8136 L4+, L18. The way in which the parameter uncertainties were estimated needs to be documented (Monte Carlo methods or otherwise?). Furthermore, on L13 of this page it is reported that nonlinear OLS was used to fit model parameters, however, subsequently (P8145 L15) the increased scatter of model residuals at higher temperatures is mentioned; this indicates heteroscedasticity (non-constant error variance), which means that OLS assumptions are violated, and a weighted least squares approach should be used instead. Whether or not the error distribution is normal is not even discussed. Finally, on P8143, L18, there are comments about the need to consider parameter uncertainties (rather than an individual value), but it seems as if the authors treat the parameters as independent of one another (although on P8136 L19 the correlation matrix is mentioned).**

← We have improved the manuscript to explain these points better. We used the method of expected-value parameters (Ratkowsky, 1990) to linearize all functions in order to get parameter uncertainties based on nonlinear regression. We have described this in the methods (p. 3, l. 260) and have added a short summary of the method for clarification (p. 3, l. 264).

The scatter of the data points at higher temperatures does not necessarily imply heteroscedasticity. The authors who compiled the dataset (Hibbard et al., 2006) used an ordinary least squares approach to fit the function of Lloyd and Taylor (1994). Additionally, heteroscedasticity does not cause OLS coefficient estimates to be biased nor inconsistent, but it can cause the variance of the parameters to be underestimated. Based on these considerations, we decided not to change the text.

Lastly, the parameters of the temperature-response functions are not treated as independent in our analysis. The correlation matrix from the non-linear function fits is considered based on the the method of Iman and Conover (1982) upon generation of parameter samples in the SIMLAB software (p. 4, l. 292).

done

- **< 6 >**

→ **The Gaussian and van't Hoff functions reach maxima before declining. This fine, but as in no instance are there data to constrain the declining portion of the curve (as acknowledged on P8145 L10+), and so I find the decision to show the decline (i.e. Fig 1), or to draw any inferences from this (e.g. P8144 L25), surprising. Also, in light of this, I would**

be very hesitant about using these functions under climate change scenarios where the model is being used to make predictions well outside the domain used for parameterization. (Related to this: for at least one of the sites in Fig 1, it would be nice to see the confidence intervals on model predictions shown graphically).

← We are aware of these issues and show and discuss them (p. 7, l. 621), (p. 7, l. 653) and (p. 9, l. 795). Furthermore, the main conclusions of our study are not altered, that there is a higher uncertainty in low-temperature regimes and a possible overestimation of high-temperature regimes.

To illustrate the issue even more, we added a new figure (Fig. 2) which shows the confidence intervals for the five candidate functions for one of the calibration sites (HOW).

done

- < **7** >

→ **Overall I find the discussion (which is repetitive and wandering) to be in need of reorganization and better editing.**

← We have restructured the discussion and carefully removed repetitions (p. 7, l. 613) (p. 8, l. 694) (p. 8, l. 745) (p. 8, l. 744) (p. 8, l. 702). Furthermore, we have now four paragraphs in the discussion, dealing with "fit of the functions", "short-term carbon flux under present climate", "long-term carbon stock under present climate" and "long-term carbon stock under future climate". We hope that this is sufficient to tidy up the discussion and make it easily comprehensible for the reader (p. 8, l. 696) (p. 8, l. 781) (p. 8, l. 707) (p. 8, l. 724) (p. 8, l. 751).

done

- < **8** >

→ **The modeling is conducted over a narrow elevational range but then conclusions are drawn about warm vs. cold climates, high vs. low latitudes, etc (sec. 4.4). While I understand the need to present the results in a way that emphasizes their broad importance, I think this is a stretch, as there are many ways in which boreal/subarctic ecosystems are dissimilar from subalpine ecosystems.**

← The elevation gradient spans over 2000 m, which we do not believe to be "narrow", as it results in a large range of annual mean temperatures (11.5-1.0° C). To clarify this, we have edited this in the methods part (p. 4, l. 328).

We acknowledge that the alpine ecosystems are not identical to e.g. boreal/subarctic ecosystems. However, the model LPJ-GUESS, like other ecosystem models uses only climatic factors, $CO_2$and soil properties as drivers to predict vegetation. We have added a comment to the conclusions, that the higher latitudes are taken as an analog to higher elevations, because of the low-temperature regime (p. 9, l. 809).

done

- < **9** >

  $\rightarrow$ **It would have been nice to see the providers of the data (to the Hibbard database) acknowledged for their efforts.**

  $\leftarrow$ We apologize and have corrected this deficiency (p. 9, l. 818).

done

Anonymous Referee #2

- < **1** >

  $\rightarrow$ **First, there are some minor points of confusion regarding naming of soil C pools. In section 2.1.1, the authors refer to 2.85y, 33y, and 1000y, respectively, but it is not clear which pools are associated with these respective turnover times. The only list that I could find was at the beginning of that section, where the 3 pools are listed in the following order: litter, slow SOM and fast SOM. However, that order doesn't make sense. I presume that the correct order is litter, fast SOM, and slow SOM, but that is also confusing, because the fast SOM should have turnover times of years, not decades.**

  $\leftarrow$ The order of the soil carbon pool names and their associated turnover times have been corrected and clarified in the text (p. 2, l. 162) (p. 3, l. 178). According to our sources (see refs in the manuscript), fast SOM does have turnover times of decades rather than years, hence we did not change this.

done

- < **2** >

  $\rightarrow$ **At the end of section 2.2, the Century model pools are described as having turnover times of 1-5y, 20-24y, and 200-1500y for litter, fast and slow SOM decomposition." This is incorrect for the Century model. Both litter layer pools and the fast pool in the mineral soil have turnover times on the order of years in the Century model, not decades. The slow pool has turnover times on the order of decades, not centuries or millennia. Only the passive pool has turnover**

times as long as 200-1500y. This confusion about the Century model leads me to wonder if there is similar confusion about identifying pools in the LPJ-GUESS model in section 2.1.1.

← We worked exclusively with the ecosystem model LPJ-GUESS here, and did not use any parts of the Century model. To avoid this confusion, we clarified this in the introduction (p. 2, l. 104) and in the method parts (p. 2, l. 138).

done

- < **3** >

→ **More important than this confusion about pool names and their respective turnover times, is the more basic question of whether a model fit to short-term CO2 efflux rates, such as the fitting done in this manuscript with the database compiled by Hibbard et al. (2006), to address questions of long term soil C storage over decades and centuries. There are at least two problems with this approach. First, short-term CO2 efflux rates include the temperature sensitivity of root growth and root respiration over seasons as well as decomposition of SOM. The apparent temperature sensitivity across seasons may be inflated due to plant phenology compared to the actual temperature sensitivity of decomposition processes. Second, the long-term soil C storage is affected by stabilization processes, such as formation and destruction of soil aggregates and sorption and desorption of C substrates on mineral surfaces, but these are not captured in simple models of temperature sensitivity of respiration. The concept of a slow pool with a turnover time of several decades is useful, but the reaction constant (k) is not really the reaction rate of a single process, but rather an indicator of the net effect of several stabilization and destabilization processes and decomposition processes. The temperature sensitivities of these various processes probably cannot be inferred from fitting a model to contemporary measurements of soil CO2 efflux. On what basis do the authors think that this could be legitimate?**

← Thank you for stressing these issues; we have clarified them in the manuscript, as follows. We built upon LPJ-GUESS and analyzed its uncertainty by using the model as-is, i.e. without any changes or modifications, except for the temperature response functions as described in the paper. This is a simple procedure from the modeling perspective, as the only thing we did is to replace the original temperature response function and associated parameters with the alternative functions and parameters.

There are no long-term experiments of soil carbon dynamics (decades to centuries). The model LPJ-GUESS uses a simplified soil dynamics module, but it has been validated at several sites (Smith et al., 2001; Morales et al., 2007; Hickler et al., 2004). We have now clarified this point in the introduction (p. 2, l. 99).

We have also added a clarification in the introduction, that in spite of all the complexity present in reality, simple models have been developed and yielded legitimate projections of soil carbon fluxes and long-term carbon storage (p. 2, l. 74).

done

- $<$ **4** $>$

  → **Assuming that the decomposition of the slow pool should respond to temperature in the same manner as contemporary CO2 efflux measurements suggests that the turnover times are simply functions of temperature in the same way that root respiration and decomposition of the fast pool are sensitive to temperature. However, the factors that stabilize soil C into the slow pool could be more or less sensitive to temperature. Moreover, the turnover times of these pools could vary with climate for a number of reasons, including direct responses of decomposition of SOM within aggregates to temperature, but also including formation and breakdown of aggregates and sorption and desorption processes. There is no discussion in this manuscript of the various processes that might affect turnover times in soils, and how those processes are affected by temperature.**

  ← We have added an explicit clarification in the methods section (p. 4, l. 308) were we address this issue. We acknowledge that these processes are not taken into account in the soil dynamics of the model LPJ-GUESS; rather, we conducted an uncertainty study with the model "as-is", and propose that the additional uncertainty mentioned by the reviewer is covered by the uncertainty in turnover times, which we considered explicitly (case $w\tau$).

  done

- $<$ **5** $>$

  → **The model assumes that 0.45% of litter inputs is transformed to the slow pool and 29.55% to the fast pool, apparently under all climate scenarios. Why would one assume that these transfer functions are constant with climate? The relative fractions that are decomposed within the litter layer and that are stabilized in mineral soils may also be temperature dependent, but this possibility does not seem to be considered.**

← We acknowledge the problems implied by this concern. We let the transfer fractions from the litter pool to the two SOM pools constant because there is no knowledge how they will respond to a changing climate. The transfer fractions have a direct effect on the size of the specific carbon pools, i.e. a higher fraction would result in a larger pool. The changes in pools with climate change however, are less influenced by this fraction and more by the temperature response itself. The higher uncertainties at lower temperatures are a result of the generally larger carbon pools, due to the slower turnover time at lower temperatures and the larger accumulation of carbon due to slow decomposition. This larger accumulation of carbon will still be found if the transfer fractions were varied somewhat with climate.

done

- < **6** >

→ **In summary, I have no qualms with comparing the efficacy of various temperature models to see how well they simulate measured fluxes, but the conceptual link to simulating long-term soil C storage is not sufficiently well developed for the results to be useful.**

← We took up this issue of short-term vs. long-term soil carbon dynamics and refer to the comment by reviewer #2 (p. 8, l. 290): The idea of ecosystem models is to be able to estimate long-term responses after being calibrated and validated against short-term data.

done

Anonymous Referee #3

- < − >

→ **In general, much effort has been put on the fit of the functions to the data and the evaluation of the fit and the statistical methods (calibration). Finally, the equations are used in a biosphere model to project soil carbon stocks. This part is described in less detail but would actually be very important in order to get the whole picture of the "story". I wonder if it would have been of interest to conduct a sensitivity analysis for all the parameters used in the LPJ-GUESS soil module (e.g. turnover times, autotrophic respiration). Personally, I would have been also interested in how good the vegetation was represented e.g. in the Ticino catchment, because I would guess that this is important for the estimation of the soil carbon stocks. The uncertainty for the soil carbon stocks in the Ticino catchment were estimated but not**

compared to observed data. The link between short-term and long-term carbon stocks is not clear. How can you conclude from estimating the response functions for short-term carbon stocks to long-term carbon stocks?

← We are aware that our analysis does not provide a complete sensitivity analysis of the model, but this would have been clearly beyond the scope of our analysis. Still, the turnover times have been included in our uncertainty analysis in the case $w\tau$ (p. 4, l. 303).

Autotrophic respiration has no direct effect on the soil carbon pools in LPJ-GUESS, as it contributes to vegetation biomass but not to the soil carbon pools. For further explanations, see our response to reviewer #1 (p. 3, l. 88).

It has been argued that the uncertainty in soil respiration will lead to high uncertainty in estimations of future soil carbon stocks, especially in warmer regions, where the uncertainty in the parameters of the temperature response function is very high. This is why we conducted a study specifically aimed to investigate this hypothesis. We did not want to replicate other studies that have addressed other aspects of the sensitivity of LPJ-GUESS. For example, Wramneby et al. (2008) studied the uncertainty of LPJ-GUESS to variations in 9 parameters, but focused on vegetation dynamics and its influence on NEE and tree community structure.

Zaehle et al. (2005) conducted a sensitivity analysis of the LPJ-DGVM (Dynamic Global Vegetation Model), which the LPJ-GUESS model builds upon, we now cite them in the methods section (p. 3, l. 185).

The vegetation is simulated well in the Ticino catchment, but the exact species distribution is not of major importance, as (in LPJ-GUESS) soil dynamics are driven by litter input solely without taking into account litter quality. Still, we have added information on the vegetation cover to the results section (p. 5, l. 459).

A comparison with observed data would be interesting. However, such a comparison was not needed for our study, as we did not conduct a model validation, but an uncertainty analysis along this elevation gradient

Lastly, the issue of short-term vs. long-term soil carbon dynamics is addressed in our response to reviewer #2 (p. 8, l. 290).

done

- < **1** >

→ **p. 8130, l. 12 and throughout the manuscript: The terms short-term soil carbon dynamics, short-term carbon flux are used. Do they always refer to heterotrophic respiration?**

← Thank you for mentioning this difficulty for the reader. Yes they do refer to the same, as we focus on the heterotrophic soil carbon process in our model. We clarified this in the introduction (p. 1, l. 62) and the methods (p. 3, l. 192) that these terms are used as synonyms.

done

- < **2** >

  → **p. 8131, l. 27/28: Could you give some examples of the models?**

  ← We have added references to a set of widely used vegetation and biogeochemistry models.(p. 2, l. 82) Prominent models specific for the soil carbon dynamics are the Century (Parton et al., 1987) and the RothC (Jenkinson, 1990) models.

  done

- < **3** >

  → **p. 8133, l. 19/20: Is the model able to predict vegetation in the (rather small-scale) Ticino catchment? Does it simulate the tree-line at the right position? How much does the simulated vegetation influence the soil carbon stocks?**

  ← We agree that the above-ground vegetation should not be neglected altogether in the results. The model is able to predict the potential natural vegetation correctly.

  We have added a paragraph in the results (p. 5, l. 459) covering the estimates of tree line and vegetation composition along the elevation gradient.

  The direct influence of vegetation on soil carbon dynamics is equal for all simulations we have done, as we varied only the temperature response function for SOM decomposition. Vegetation influences soil carbon pools via litter input, which differs between plant functional types, but this input was exactly the same in all simulation runs for a given elevation level, as there is no feedback from litter decomposition to vegetation dynamics in LPJ-GUESS.

  done

- < **4** >

  → **p. 8133, l. 22: litter, slow SOM, fast SOM, does not correspond with p.8134, l. 7 turnover times. Later on p. 8136 it is described that it has been sampled over a different timescale. Please explain.**

  ← The order of these lists was completely garbled. This has been corrected and clarified at (p. 2, l. 162) and (p. 3, l. 178). For details, see our response to reviewer #2 (p. 6, l. 233).

The decay rates cannot be inferred from short-term soil carbon flux measurements. Instead, we adopted the uncertainty bound suggested by Parton et al. (1987) to investigate the importance of uncertainties in the decay rates themselves, as these may change in future. The standard model parameters lay well within the uncertainty bounds by Parton et al. (1987). Please see also our resopnse to reviewer #2 (p. 8, l. 315).

done

- < **5** >

  → **p. 8134, l. 21: Please insert (Table 1) after C=B=0.**

  ← "(Table 1)" has been inserted (p. 3, l. 209).

  done

- < **6** >

  → **p. 8136, l.5-6: The method could be explained better. E.g. what is the method of expected-value parameters?**

  ← We have clarified this part of the method description and have added a short description of the method of "expected-value parameters" (p. 3, l. 264).

  done

- < **7** >

  → **p.8136, l. 26-28: The methods are not clearly described. It is unclear why these two cases have been discriminated.**

  ← We have now clarified this in the text (p. 4, l. 308): the case $w\tau$ includes the uncertainty of the turn-over times of the soil carbon pools. This uncertainty combines the uncertainty of the current value of the parameter as well as the uncertainty in the future development of the value.

  done

- < **8** >

  → **p. 8137, l.15: Did you run the simulations for these 11 sites? Later the results are only shown for 3 sites. Later (p. 8138, l.19) you state that simulations were run for 30 independent ... patches. Are these the sites?**

  ← We have improved this paragraph for clarity. The simulations were run on 11 elevation levels along the elevation gradient. All these sites can be recognized in figure 5. For figures 3 and 4, we only show three elevations out of these 11 to avoid overloading the figures with information. The results of elevations between the presented sites lay, as expected, in between those shown.

The “30 independent patches” refer to the configuration of the model. As the model includes stochastic processes such as disturbances and vegetation dynamics, each modelled site is simulated several times (here N=30) and afterwards averaged to take into account this stochasticity.

We have clarified the issue with the patches in the methods part (p. 5, l. 377).

done

- **< 9 >**

  → **p. 8138, l. 1: The description of how you have derived the set of daily values from randomly selected years and monthly values of the CRU dataset is not clear.**

  ← We have clarified the derivation of the set of daily values in the methods part (p. 4, l. 342) (p. 4, l. 360) (p. 4, l. 370).

  done

- **< 10 >**

  → **p. 8138, l. 20: Does the length of the model spin-up influence the soil carbon stocks? If yes, what would be the effects on your uncertainty analysis?**

  ← (p. 5, l. 386)The length of the model spin-up has no influence on the steady-state soil carbon stock, because the sizes of the steady-state soil carbon pools are solved analytically, as mentioned in the methods part. After vegetation has reached the equilibrium with the spinup climate (in simulation-year 700), the average litter input is estimated for 200 years (i.e. from the simulation-years 700 to 900); from these values, the average temperature response coefficient are calculated. Afterwards, the steady-state soil carbon pools of the three-pool system is solved analytically. Thus, a longer spin-up period would have no effect on soil carbon stocks.

  done

- **< 11 >**

  → **The results would be easier to understand if you would place section 3.3 before section 3.2. Also section 4.3 should be moved before section 4.2**

  ← We have adopted this suggestion, and have switched the sections of “short-term responses” and “long-term responses” both in the results and the discussion (p. 6, l. 472) (p. 6, l. 510) (p. 8, l. 696) (p. 8, l. 718).

done

- < **12** >

  → **The parameters for the temperature response functions were estimated for low altitudes but then applied to high altitudes, is that problematic?**

  ← No, this is not problematic, as the temperature range is more important than altitude itself. The elevation range we used in our simulations covers the range observed in the measured data for the warm temperatures. The simulated gradient extends into higher elevations, but as the temperatures there are quite low, this is not a problem, because the uncertainty in model estimations is generally low for the low temperature range. We decided not to change the text in this regard.

done

- < **13** >

  → **p. 8143, l. 15: reliability instead of explanatory power?**

  ← We have replaced "explanatory power" by "reliability" at (p. 7, l. 575) and (p. 7, l. 651).

done

- < **14** >

  → **p. 8145, l. 28: "in regions where soil temperature normally does not exceed values of 20° C, for instance in forests at high elevations and high latitudes"... but this is expected to change under future climate conditions?**

  ← Yes, this is expected to change under future climate and we take it up in the discussion section (p. 8, l. 774). We mainly express the concern in using the temperature functions without new parameter estimations using larger temperature ranges (p. 7, l. 621). In our study, the largest changes in carbon storage and the highest uncertainty occur at higher elevations (low temperatures). At these elevations we do usually not expect soil temperatures above 20° C, even under climatic change. We therefore believe that our conclusions are valid and not influenced by the limits in two of the temperature functions.

done

- < **15** >

  → **Figure 1: The legend is hard to read, please change boxes to line types.**

  ← The boxes in the legend have been changed to colored lines instead.

done

- < **16** >

  → **p. 8149, l.14: The last two sentences are too long, please rewrite.**

  ← We agree and have rewritten them (p. 8, l. 774).

done

Interactive Comment

- < − >

  → **I would just like to remind the authors of two papers with a very similar approach.**

  Rodrigo et al. (1997) analytically compared several temperature sensitivity functions, whereas Bauer et al. (2008) also used a carbon turnover model to investigate the sensitivity towards six different temperature reduction functions. It probably makes sense to refer to those papers in the introduction and the discussion.

  Bauer, J., Herbst, M., Huisman, J.A., Weihermüller, L., Vereecken, H.: Sensitivity of simulated soil heterotrophic respiration to temperature and moisture reduction functions. Geoderma, 145, 17-27, 2008.

  Rodrigo, A., Recous, S., Neel, C., Mary, B.: Modelling temperature and moisture effects on C-N transformation in soils: comparison of nine models. Ecological Modelling, 102, 325-339, 1997.

  ← Thank you for the valuable references, we have incorporated them in the discussion (p. 8, l. 712) (p. 7, l. 672).

done

References

Hibbard, K., Hudiburg, T., Law, B., Reichstein, M., and Sulzman, J.: Northern Hemisphere Temperate Ecosystem Annual Soil Respiration Data (from Hibbard et al. 2005. An analysis of soil respiration across northern hemisphere temperate ecosystems. Biogeochemistry 73:29-70), Tech. rep., 2006.

Hickler, T., Smith, B., Sykes, M. T., Davis, M. B., and Sugita, S.: Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA, Ecology, 85, 519, 2004.

Iman, R. L. and Conover, W. J.: A distribution-free approach to inducing rank correlation among input variables, Communications in Statistics - Simulation and Computation, 11, 311–334, 1982.

Jenkinson, D. S.: The Turnover of Organic Carbon and Nitrogen in Soil, Royal Society of London Philosophical Transactions Series B, 329, 361–367, 1990.

Lloyd, J. and Taylor, J. A.: On the Temperature Dependence of Soil Respiration, Functional Ecology, 8, 315–323, 1994.

Morales, P., Hickler, T., Rowell, D. P., Smith, B., and Sykes, M. T.: Changes in European Ecosystem Productivity and Carbon Balance Driven by Regional Climate Model Output, Global Change Biology, 13, 108–122, 2007.

Parton, W. J., Schimel, D. S., Cole, C. V., and Ojima, D. S.: Analysis of factors controlling soil organic matter levels in Great Plains grasslands, Soil Science Society of America Journal, 51, 1173–1179, 1987.

Ratkowsky, D. A.: Handbook of Nonlinear Regression Models, in: Statistics: Textbooks and Monographs, Marcel Dekker, Inc., New York, 1990.

Smith, B., Prentice, I. C., and Sykes, M. T.: Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space, Global Ecology and Biogeography, 10, 621–637, 2001.

Wramneby, A., Smith, B., Zaehle, S., and Sykes, M. T.: Parameter uncertainties in the modelling of vegetation dynamics–Effects on tree community structure and ecosystem functioning in European forest biomes, Ecological Modelling, 216, 277–290, 2008.

Zaehle, S., Sitch, S., Smith, B., and Hatterman, F.: Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics, Global Biogeochemical Cycles, 19, GB3020, 2005.

Manuscript prepared for Biogeosciences
with version 3.0 of the LaTeX class copernicus.cls.
Date: 14 January 2010

Temperature response functions introduce high uncertainty in modelled carbon stocks in cold temperature regimes

Portner Hanspeter, Bugmann Harald, and Wolf Annett

Forest Ecology, Institute of Terrestrial Ecosystems, Department of Environmental Sciences, ETH Zürich, 8092 Zürich

Abstract. Models of carbon cycling in terrestrial ecosystems contain formulations for the dependence of respiration on temperature, but the sensitivity of predicted carbon pools and fluxes to these formulations and their parameterization is not well understood. Thus, we made an uncertainty analysis of soil organic matter decomposition with respect to its temperature dependency using the ecosystem model LPJ-GUESS.

We used five temperature response functions (Exponential, Arrhenius, Lloyd-Taylor, Gaussian, Van't Hoff). We determined the parameter uncertainty ranges of the functions by nonlinear regression analysis based on eight experimental datasets from northern hemisphere ecosystems. We sampled over the uncertainty bounds of the parameters and run simulations for each pair of temperature response function and calibration site. The uncertainty in both long-term and short-term heterotrophic soil carbon dynamics was analyzed over an elevation gradient in southern Switzerland.

The function of Lloyd-Taylor turned out to be adequate for modelling the temperature dependency of soil organic matter decomposition, whereas the other functions either resulted in poor fits (Exponential, Arrhenius) or were not applicable for all datasets (Gaussian, Van't Hoff). There were two main sources of uncertainty for model simulations: (1) the uncertainty in the parameter estimates of the response functions, which increased with increasing temperature and (2) the uncertainty in the simulated size of the soil carbon pools, which increased with elevation, as slower turn-over times lead to higher carbon stocks and higher associated uncertainties. The higher uncertainty in carbon pools with slow turn-over rates has important implications for the uncertainty in the projection of the change of soil carbon stocks driven by climate change, which turned out to be more uncertain for higher elevations and hence higher latitudes, which are of key importance for the global terrestrial carbon budget.

Correspondence to: Portner Hanspeter (hanspeter.portner@env.ethz.ch)

1 Introduction

Anthropogenic CO_2 emissions from fossil fuel consumption, cement-manufacturing and deforestation are leading to an increase in atmospheric CO_2 concentrations, thus inducing considerable changes of the climate at global, regional and local scales (Solomon et al., 2007). Atmospheric CO_2 concentrations are also strongly affected by changes in the major global natural carbon reservoirs. For example, at present significantly more carbon is stored in the world's soils than in the atmosphere (Schlesinger, 1997). Climatic changes have a direct impact on global soil carbon stocks, but their quantification is subject to considerable debate and disagreement (Davidson and Janssens, 2006; Kirschbaum, 2006; Hakkenberg et al., 2008). If significant amounts of carbon currently stored as organic matter belowground are transferred to the atmosphere by a warming-induced acceleration of decomposition, a positive feedback to climate change may occur (Bronson et al., 2008). Conversely, if increases of plant-derived carbon inputs to soils exceed increases in decomposition, the feedback would be negative. Despite much research, a consensus has not yet emerged on the climate sensitivity of soil carbon decomposition.

Soil respiration is commonly divided into two components: root respiration with associated mycorrhizal respiration and soil organic matter (SOM) decomposition. We focus on SOM decomposition here which is also known under the terms of heterotrophic or microbial soil respiration. SOM has turnover times ranging from years to decades and even centuries. It is often conceptualised as several distinct pools with increasing residence times (Knorr et al., 2005; Kirschbaum, 2004; Eliasson et al., 2005) or as continuous with gradual decay rates (Ågren and Bosatta, 1987; Bosatta and Ågren, 1999). Decomposition of SOM is highly complex, as it is driven by a combination of factors such as temperature (Berg and Laskowski, 2005a), moisture conditions (Cisneros-Dozal et al., 2006) and its chemical quality (Berg and Laskowski, 2005b; Weedon et al., 2009; Cornwell et al., 2008).

In spite of all this complexity, relatively simple models have been developed and shown to be useful; therefore, we focus on soil dynamics as they were implemented in a widely used biosphere model, LPJ-GUESS (Smith et al., 2001)

Many biogeochemical models have been developed and applied to study the response of the carbon cycle to past, current and future changes in climate. While the process of carbon uptake (photosynthesis) is represented in a fairly detailed manner in these models (e.g. BiomeBGC (Thornton et al., 2002), IBIS (Kucharik et al., 2000), LPJ-DGVM (Sitch et al., 2003), LPJ-GUESS (Smith et al., 2001), CLM (Oleson et al., 2004) or Triffid (Foley et al., 1996)), the equally important process of carbon release by soil respiration is represented in a comparatively simple manner (Cramer et al., 2001; Friedlingstein et al., 2006). Although some models have been specifically developed to study soil carbon dynamics, their representation of aboveground productivity and hence litter input is usually highly simplified (Parton et al., 1987; Jenkinson, 1990). Interestingly, there is no agreement on the choice of the form of the response function that is used to describe the sensitivity of soil carbon decomposition to temperature.

In this study, we focus on the sensitivity of LPJ-GUESS (Smith et al., 2001), to a range of possible formulations for the temperature dependency of soil organic matter decomposition, in order to evaluate their assets and drawbacks. We use the model without any further changes to provide consistent estimates of above- and belowground litter production, but we vary the temperature response functions of heterotrophic (i.e., soil) decomposition.

Thus, we assess the impact of uncertainty in the formulation of the temperature response of heterotrophic soil respiration on estimates of present and future carbon storage in ecosystems and hence on the CO_2 feedback to the atmosphere. We specifically investigate the relative importance of the model formulation versus the uncertainty introduced by using different parameterization data sets in LPJ-GUESS. We quantify the resulting impacts with regard to both short-term soil carbon fluxes and long-term soil carbon storage along a large elevation gradient in southern Switzerland.

2 Methods

We chose a holistic approach and considered not only the raw fits of candidate functions to calibration datasets, but also the number of parameters, the uncertainty in parameter estimates and the uncertainty in model output variables. We placed a special focus on the identification of a suitable model formulation that not only fitted well to experimental data, but also led to acceptable uncertainty in the output variables when employed in LPJ-GUESS.

In biogeochemical models, the relationship between SOM decomposition and soil temperature is often described by one out of a set of related functions. We tested five candidate functions: a simple Exponential function with a constant Q_{10}, the Arrhenius function, the Gaussian function, the Van't Hoff function and the Lloyd-Taylor function. The Exponential and Arrhenius functions are simplifications of the function proposed by Van't Hoff (1901). Lloyd and Taylor (1994) proposed a modified Arrhenius function and Tuomi et al. (2008) and O'Connell (1990) suggested a Gaussian function. The details of the five functions are described below.

We built upon the well-established LPJ-GUESS model (Smith et al., 2001) and soil respiration data from different Ameriflux and CarboEuropeIP sites (Hibbard et al., 2005, 2006). We used only one ecosystem model, LPJ-GUESS, to avoid further uncertainties introduced by different representations of other vegetation processes which typically arise in model inter-comparisons (Cramer et al., 2001; Morales et al., 2005). The Ticino catchment in southern Switzerland with its large climate gradient was used as a case study to evaluate the sensitivity of the model to the uncertainty in model parameters with respect to different process formulations and calibration datasets with varying temperature regimes. We used the Ticino catchment as our study site instead of modelling the calibration sites directly, in order to reduce the influence of specific weather patterns , which differed greatly between the calibration sites.

2.1 The LPJ-GUESS model

We used the dynamic ecosystem model LPJ-GUESS (Smith et al., 2001; Sitch et al., 2003). The model framework incorporates process-based representations of plant physiology, establishment, competition, mortality and ecosystem biogeochemistry. LPJ-GUESS has been successful in predicting vegetation distribution, net primary production and net ecosystem exchange in many different ecosystems (Smith et al., 2001; Morales et al., 2007).

2.1.1 LPJ-GUESS soil module

Soil carbon in LPJ-GUESS is divided into three distinct pools: litter, fast SOM and slow SOM. The temporal dynamics of the carbon stock (C_i) of each individual pool (i) are modeled on a daily basis and follow first-order kinetics with a decay rate k_i (Eq. 1). The decay rate itself depends on soil temperature and soil moisture, expressed as the product of the decay rate $k_{i,T_{ref}}$ at a given reference temperature T_{ref}, the temperature response function R_T and the moisture response function R_M (Eq. 2). The decay rate $k_{i,T_{ref}}$ is the reciprocal of turnover time $\tau_{i,T_{ref}}$.

$$\frac{\Delta C_i}{\Delta t} = -k_i \times C_i \tag{1}$$

$$k_i = k_{i,T_{ref}} \times R_T \times R_M \tag{2}$$

Litter from leaves, roots and tree stems is added to the litter pool at the end of each simulation year. Each of the three carbon pools, i.e. litter, fast and slow SOM, has its own specific turnover time ($\tau_{i,T_{ref}}$) at reference temperature T_{ref}=10°C and ample soil moisture: 2.85 y, 33 y and 1000 y for the litter, fast SOM and slow SOM pools, respectively (Meentemeyer, 1978; Foley, 1995). The mineralized litter is divided into three parts, 70% are respired, whereas 0.45% are transferred to the slow and 29.55% to the fast SOM pool (Foley, 1995). Both SOM pools then undergo decomposition independently, i.e. without feedbacks to the other pools. In a previous study it has been shown that soil carbon pools were sensitive to the transfer fractions (Zaehle et al., 2005), as they influence the input into the system of soil carbon pools. In our study we focus instead on the response of the soil carbon pools and fluxes on the temperature response and turnover times directly, without confounding the results with variable amounts of litter input. We therefore treated the transfer fractions as constants.

Throughout the paper, we always refer to the heterotrophic soil respiration when talking about soil carbon dynamics and soil carbon fluxes.

2.1.2 Temperature response functions implemented in LPJ-GUESS

Five potential response functions were implemented in the model (Tab. 1). The Exponential response function (E) features a constant Q_{10} value. It is motivated by Van't Hoffs rule, stating that the rate of a reaction increases two- to threefold for an increase in temperature by 10°C (Van't Hoff, 1901). The Arrhenius function (A) is based on the concept of an activation energy for chemical and biological reactions. However, realizing that the change of the rate is not constant over temperatures, Van't Hoff therefore suggested a more complex formula (V). Importantly, the Exponential and Arrhenius formulations are direct derivatives of the Van't Hoff formulation, obtained by setting the parameters $A = B = 0$ and $C = B = 0$ (Tab. 1), respectively. The response function in the standard implementation of LPJ-GUESS is based on Lloyd and Taylor (1994) (L). It is a variant of the Arrhenius function, suggested by Lloyd and Taylor (1994), because it often leads to better fits against empirical data by allowing for a decrease in activation energy with increasing energy. It must meet the condition $T > T_0$. The Gaussian function (G) in turn is based on Lloyd-Taylor, by taking into account the first three terms of the Taylor series expansion of the exponent of the Lloyd-Taylor function (Tuomi et al., 2008; O'Connell, 1990). Note that the Exponential, Arrhenius and Lloyd-Taylor functions are monotonically rising functions, whereas the Gaussian and the Van't Hoff functions have a maximum.

As the decay constant $k_{i,T_{ref}}$ is valid only at the reference temperature T_{ref}, the response functions were expressed relative to this temperature (Tab. 1). We thus reparameterized the functions by combining Eqs. 3-4, leading to the general scheme of Eq. 5, where f_{abs}, f_{rel} and $R_{T_{ref}}$ refer to the absolute and the relative response functions and to the reference respiration at a given reference temperature T_{ref}, respectively.

$$R_T = f_{abs}(T) \times Const \tag{3}$$

$$R_{T_{ref}} = f_{abs}(T_{ref}) \times Const \tag{4}$$

$$R_T = R_{T_{ref}} \times f_{rel}(T, T_{ref}) \tag{5}$$

In the default version of LPJ-GUESS, autotrophic (root and mycorrhiza) and heterotrophic soil respiration (SOM decomposition) are modelled using the same response function. As we focused on SOM decomposition here, only the heterotrophic soil respiration was varied using the five alternative formulations introduced above. The autotrophic soil respiration (root respiration and stem respiration) was in all simulations modeled with the standard response function of Lloyd-Taylor. We did not change the response function for the autotrophic respiration as it is used in the calculation of net primary production, which determines growth, but also litter production. As we wanted to ensure that litter input does not vary between simulations, the autotrophic respiration was kept in its default implementation.

2.2 Fitting of the temperature response functions

We used the database compiled by Hibbard et al. (2006), which contains datasets of soil respiration from different experimental sites of the northern hemisphere in Europe and America. Eight sites were selected for calibration (Tab. 2) to reflect forest vegetation types that are significant for our research area (evergreen-needleleaf, mixed deciduous-evergreen, deciduous-broadleaf); we only used datasets that provided more than 30 measurements of temperature and soil respiration. Measurements were made on a daily basis, distributed over the whole year for time periods ranging from 1995 to 2002, depending on the site.

In nonlinear regression, the usual parameter confidence intervals cannot be used because the parameters show nonlinear behavior. Therefore, we first linearized all five standardized functions using the method of expected-value parameters (Ratkowsky, 1990). Models in expected-value parameterization are close to linear models in terms of the statistical properties of their parameter estimates, i.e. the confidence intervals of the parameters are comparable, and thus a follow-up uncertainty analysis will yield unbiased results.

The functions were linearized by replacing the initial parameters with a set of new parameters, whereby the new parameters reflect the expected-value of the function output at a given position of the curve. We linearized for all parameters but $R_{T_{ref}}$: the confidence intervals are provided in the appendix (Tab. A1). In order to make response functions across the different sites comparable, they were normalized ($R_{T_{norm}}$) in such a way that the reference respiration $\overline{R_{T_{ref}}}$ at reference temperature T_{ref}=10°C is equal to 1 for each site and equation (Eq. 6).

$$R_{T_{norm}} = (\overline{R_{T_{ref}}})^{-1} \times R_T \quad (6)$$

We used all five response functions at all eight sites and performed nonlinear fits for each dataset-function pair using nonlinear least-squares estimates in the statistics software package R (R Development Core Team, 2008).

To fit the Van't Hoff function, we introduced an additional data point in each data set at (-40°C, 0μmol C $m^{-2}s^{1}$) to ensure that the function converges to zero when approaching the absolute zero temperature (0 K). We determined the 99% confidence intervals for each parameter of each function and the correlation matrix of the parameters for each individual fit. The goodness of each fit was quantified by the Bayesian information criterion (BIC) introduced by Schwarz (1978).

We used the SIMLAB software from the European Joint Research Center (Saltelli et al., 2004) to generate the parameter sample sets. For each fit, we generated a latin hypercube sample (N=20). We sampled uniformly over the confidence intervals of the parameters and included the parameter dependencies through the correlation matrix obtained in the fitting procedure based on the method of Iman and Conover (1982).

We used the 99% confidence intervals of the parameters, we created a sample of parameter sets over their corresponding confidence range for each response function-site pair. We further discriminated between two cases: In the case woτ (without τ), we sampled over the confidence intervals of the response function parameters only. In the case wτ (with τ), we additionally sampled over the confidence intervals of the turnover times for the litter, fast and slow soil carbon pools τ_l, τ_f and τ_s. Including the uncertainty of turnover times, enables us to investigate how important the uncertainties in the estimations of current turnover times are for the results. By using variable rather than fixed turnover times, we account for the additional uncertainty induced by the fact that future turnover times may change with the climate. The turnover times for the three carbon pools for the case wτ had a range of 1-5y for the litter pool, 20-40y for the fast SOM and 200-1500y for the slow SOM as suggested by Parton et al. (1987). We thus assumed implicitly that the turnover times depended neither on each other nor on the other parameters of the response functions.

2.3 Simulations with LPJ-GUESS

2.3.1 Interpolation of climate data

LPJ-GUESS is driven by daily weather input, including mean temperature, precipitation sum, percentage sun-shine and atmospheric CO_2 concentration. The climate data were compiled for a large elevation transect in the Ticino catchment in the Southern Swiss Alps ranging from 300 to 2300 m a.s.l., sampled at 200 m intervals, resulting in a total of 11 individual sites. The mean annual temperatures varied widely, ranging from -1 to 11.5°C along this gradient.

Climate data for the period of 1901-2006 were compiled from different sources. Daily mean temperatures and daily precipitation sums for the period of 1960-2006 were obtained from a spatially explicit climate data set of Switzerland with a spatial resolution of 1 ha. The data were derived using the DAYMET model (Thornton et al., 1997), which was developed specifically for complex terrain such as mountain ranges (data source: Land Use Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research, Switzerland). For each elevation level we calculated the mean daily temperature and precipitation of 100 adjacent grid points (using a 10x10 grid) at a south-facing slope.

Temperature and precipitation data for the period of 1935-1959 were based on the nearest automated meteorological station Locarno-Monti (distance 24 km), which served as a reference to derive the daily anomalies relative to the long-term climatology of this station. The daily anomalies of the Locarno-Monti station for the years 1935-1959 were applied to the climatology of the years 1960-1970 of each elevation site. This prolonged the climate input for each elevation level back to the year 1935. Lastly, the climate for the period 1901-1934 was based on monthly data from the Climate Research Unit (CRU TS 1.2, Mitchell et al. (2003)). For this period, the daily climate anomalies were taken from 35 randomly chosen years out of the Locarno-Monti dataset. The CRU dataset was sampled along the elevation gradient and the daily anomalies were applied to the samples.

The dataset for percentage sunshine was based on the reference station Locarno-Monti (1960-2006) and the CRU TS 1.2 dataset for the period of 1901-1959. The same dataset was used for all elevation levels, assuming that mean daily cloud cover did not differ within the valley.

For the future projections, i.e. from 2007 to 2106, we chose the SRES A2 scenario data from the PRUDENCE project (Christensen et al., 2007), as provided to us by the Institute of Atmosphere and Climate of ETH Zurich. As LPJ-GUESS requires a continuous time series, we performed a linear interpolation of the anomalies between the future and the control runs of the climate model with respect to mean annual temperature and annual precipitation sum. We assumed percentage sunshine to not change. For each elevation site, the interpolated differences were then then added to randomly chosen years of the period of 1961-1990. Lastly, a dataset for annual global atmospheric CO_2 concentration was compiled based on the PRUDENCE data set.

2.3.2 Simulation experiments

Simulations were run for the 11 sites for a total of 1206 years. Each site was modelled with 30 independent replicate patches to account for stochastic processes in the vegetation dynamics, like establishment and growth. We analysed the mean of all 30 patches for each site. The first 1000 years were used for a model spin-up, whereas the subsequent 206 years corresponded to the calendar years 1901-2106. The spin-up period was based on a constant long-term climate, but considering interannual variations; this is adequate for estimating the equilibria for both soil carbon pools and vegetation composition (Sitch et al., 2003). During the spin-up period, the long-term equilibria of the litter, fast and slow SOM pools were estimated by analytically solving the differential flux equations assuming that the annual litter inputs from the years 700 to 900 are representing the steady state litter inputs; this is ligitimate because vegetation composition and productivity have reached their equilibrium by the simulation year 700.

Uncertainty analysis was performed for each pair of response function and site separately. As the key variable to assess uncertainty, we chose the sum of the three carbon pool sizes at the beginning of August 2006 as a proxy for mean annual pool size. The summed soil carbon pool fluxes were also evaluated as monthly sums. We used the month of August, because soil respiration was generally highest at that time within the year.

To provide a better overview, we report our results referring not to each pair of response function and site separately, but grouped them by the given response functions.

3 Results

3.1 Fit of the functions

We divided the response functions into three groups sharing similar curve characteristics: (1) Exponential&Arrhenius, (2) Gaussian&Van't Hoff and (3) Lloyd-Taylor.

The Exponential and Arrhenius equations overestimated soil respiration at temperatures below 10°C in all datasets (Fig. 1). Lloyd-Taylor generally performed better not showing an overestimation at lower temperatures. At five sites, the Gaussian and Van't Hoff equations yielded a maximum in the temperature range of 15-25°C , but they provided the best estimates below 10°C because the maximum was located at rather low temperatures, they tended to underestimate respiration at high temperatures (Fig. 1).

All parameter estimates and their corresponding 99% confidence intervals were significant ($P < 0.05$) except for the first parameter of the Van't Hoff equation (Appendix Tab. A2). The only parameter estimate directly comparable between the different response functions was the reference respiration, which ranged from 1.06-1.15 $\mu\mathrm{mol\,C\,m^{-2}\,s^{-1}}$ at the site BEP to 3.49-3.63 $\mu\mathrm{mol\,C\,m^{-2}\,s^{-1}}$ at the site THA, respectively (cf. Appendix Tab. A3; site acronyms are provided in Tab. 2).

The ranking of the performance of the response functions depended on the criterion used: When the sum of squared residuals was used (Tab. 3), Van't Hoff performed best (7/8), Gaussian dominated the second rank (5/8) and Lloyd-Taylor dominated the third rank (5/8), but it showed the best fit at the site MEO. When the data for all sites were combined, thus comprising a larger variability of environmental conditions than any site-specific dataset, Lloyd-Taylor showed the best overall fit. The Exponential and Arrhenius formulations generally showed an inferior fit compared to any of the other three equations.

Based on the Bayesian information criterion, i.e. when considering also the number of parameters employed in a given formulation, the performance of the Van't Hoff equation was lower as it features the largest number of parameters (Tab. 4). It now was ranked the second best model at four sites. Best were the Gaussian model at five sites, the Lloyd-Taylor model at two sites and the Arrhenius model at one site. As for the case of the sum of squared residuals, Lloyd-Taylor showed the best performance when all the data were analyzed together, and it was best at two sites, second best at another two sites and third best at the remaining four sites (Tab. 4).

The uncertainty in the response function according to the sampled parameters showed an increase with increasing temperature (Fig. 2). As expected, uncertainties increased with the number of parameters used: the Exponential and Arrhenius formulations had the lowest uncertainty ranges, Gaussian and Van't Hoff the highest, and Lloyd-Taylor was characterized by intermediate uncertainty ranges.

3.2 Tree line and vegetation distribution

Gehrig-Fasel et al. (2007) have estimated the potential regional tree line elevations for whole Switzerland. The regional tree line was derived from highest forest patches in a rectangular 10 km x 10 km moving search window. For the Ticino catchment they report that potential tree line reaches up to 2300 m. The simulated tree line along the elevation gradient is close to this value, although a bit higher, i.e. at 2400 m. The simulated vegetation distribution corresponds well to the observed southern Swiss alpine vegetation (Körner, 2003), changing from deciduous-dominated forests at low elevation to evergreen-dominated forests starting at 1300 m to grass-dominated vegetation above the tree line.

3.3 Short-term carbon flux under present climate

The results for the Exponential and Arrhenius response functions are combined and referred to as E&A. The results for the Lloyd-Taylor function are reported separately (L) and the functions of Gaussian and Van't Hoff are combined and referred to as G&V.

The total carbon fluxes to the atmosphere for case wτ do not directly depend on the turn-over times of the carbon pools, but instead on the size of the carbon pools (results not shown), we therefore report only for the case woτ. If not differently stated, units of monthly carbon fluxes in August are given in $\mathrm{kg\,C\,m^{-2}\,month^{-1}}$.

Elevation 300 m: Soil carbon fluxes for all response functions ranged between 0.06 and 0.11 (Fig. 3), whereby the range was somewhat smaller for the E&A functions. The uncertainty ranges of G&V and Lloyd-Taylor were 1.4 and 1.5 times larger relative to the range of E&A.

Elevation 1300 m: On 1300 m elevation the median values were rather similar ranging from 0.087 to 0.161 (Fig. 3), although the uncertainty range was larger for the Gaussian and the Lloyd-Taylor function.

Elevation 2300 m: While carbon fluxes increased from 300 to 1300 m, they decreased again up to 2300 m and three distinct subgroups were identifiable: E&A with a range of 0.076-0.105, G&V with a range of 0.082-0.159, and Lloyd-Taylor with a range of 0.078-0.145 (Fig. 3). This resulted in uncertainty ranges for G&V and Lloyd-Taylor that were 2.7 and 2.3 times the range of E&A.

Changes with elevation: The medians of monthly respiration showed a bell-shaped curve over the elevation gradient, starting with low values at 300 m, inflecting at around 1300 m and then decreasing again up to 2300 m. Although the means always were in the range of $0.1\pm0.02\ \mathrm{kg\,C\,m^{-2}\,month^{-1}}$, the uncertainty ranges increased steadily with elevation, particularly for the response functions G&V and Lloyd-Taylor, leading to uncertainty ranges at 2300 m that were 1.5 and 1.7 times larger than the range at 300 m.

3.4 Long-term carbon stock under present climate

Looking at the carbon stock estimates in 2006, the response functions could be divided into the same groups as found in the regression analysis, both according to their median and the magnitude of their uncertainty range (Fig. 4). If not stated otherwise, the units of carbon pools are $\mathrm{kg\,C\,m^{-2}}$.

Elevation 300 m: Soil carbon stock estimates for E&A ranged from 9.2-13, for Gaussian&Vant't Hoff from 6-15.7 and for Lloyd-Taylor from 8-14.1 when the uncertainty in turnover times was not included. The uncertainty ranges of G&V and Lloyd-Taylor were a factor 2.5 and 1.6 higher than those of the E&A formulations (Fig. 4). When the uncertainty in turnover times ($w\tau$) was considered as well (Fig. 4), uncertainty ranges generally increased. The differences between the groups decreased, however, as the medians were more similar. In addition, the uncertainty range differed less between the groups G&V vs. Lloyd-Taylor, amounting to 1.4 and 1.2 times the uncertainty range of the E&A formulations, respectively (Fig. 4). The response functions E&A showed a strong increase in the uncertainty when the uncertainty in the turnover times of the carbon pools was considered in the analysis.

Elevation 1300 m: The E&A formulations yielded soil carbon stocks in the range of 14.8-20.2, whereas G&V as well as Lloyd-Taylor showed a larger range of 14.1-23.7 and 15-21.5, respectively (Fig. 4). The uncertainty ranges of G&V and Lloyd-Taylor amounted to 1.8 and 1.2 times the range of E&A. When the uncertainty in turnover times was considered additionally, median values differed only little (0.35 $\mathrm{kg\,C\,m^{-2}}$), but the uncertainty ranges were much larger (2.1, 1.4 and 2.0 times) for E&A, Gaussian&Van't Hoff and Lloyd-Taylor, respectively (Fig. 4).

Elevation 2300 m: At the highest elevation, soil carbon stocks were generally largest and showed a much larger range compared to lower elevation sites. Projections ranged from 17.7-38, from 21.4-80.4 and from 18.5-64.6 for E&A, G&V and Lloyd-Taylor, respectively (Fig. 4). For the case wτ we found ranges of 13.6-37.7, 15.8-75.8 and 15.1-59.7, respectively (Fig. 4). When the uncertainty in turnover times was considered, the median carbon stock was 1.6 $\mathrm{kg\,C\,m^{-2}}$ lower. In contrast to the other two elevations, the range of carbon stock predictions was almost unaffected by the uncertainty in turnover times.

Changes with elevation: The uncertainty range increased with increasing elevation for all three subgroups, whereby the largest uncertainties were found at the 2300 m elevation site for all model formulations.

3.5 Long-term carbon stock under future climate

The uncertainty in potential loss of soil carbon due to climate warming (SRES A2 scenario, difference between values from 2106 and 2006) was most pronounced at higher elevations (Fig. 5). The same patterns as under current climate were evident for all candidate functions, and hence they are not shown separately.

The standard implementation of LPJ-GUESS (with the Lloyd-Taylor formulation) projects a loss of up to 5 $\mathrm{kg\,C\,m^{-2}}$ due to climate change over the whole elevation gradient. Accounting for the overall uncertainty in response function, site and turn-over times, the uncertainty in loss of carbon readily increased with elevation, ranging from 1.9 $\mathrm{kg\,C\,m^{-2}}$ at 300 m up to 15.3 $\mathrm{kg\,C\,m^{-2}}$ at 2300 m, thus leading to highly uncertain projections at higher elevations. The uncertainty ranges in the projection of soil carbon loss at 1300 m and 2300 m amounted to 3.1 and 8 times the range at 300 m, respectively.

4 Discussion

The reliability of model outputs heavily depends on the associated uncertainty. Models often consist of many functions whose parameters are estimated e.g. using regression analysis based on experimental data. The parameters thus do not have one 'true' value, but they are characterized by an uncertainty band. The error based on the uncertainty will propagate through the model and lead to a corresponding uncertainty in model output (Jones et al., 2003). Different process formulations and different parameter sets of the SOM decomposition dynamics may lead to different model results and therefore may have consequences for the applicability of model projections.

4.1 Fit of the functions

The response functions could be assigned into three groups: Exponential&Arrhenius, Gaussian&Van't Hoff and Lloyd-Taylor. Both Exponential and Arrhenius overestimated the temperature response at low ($<10^{\circ}$C) temperatures, which resulted in an overall insufficient fit, thus corroborating the results of earlier research (Lloyd and Taylor, 1994). The Exponential function, which is based on a constant Q_{10} value is not adequate as the Q_{10} value has been shown to decrease with increasing temperature (Kirschbaum, 1995). Nevertheless, the Exponential function was included in the analysis because the usage of Q_{10} values is still common.

For the other three functions, the rankings differed depending on the criterion employed. As expected, the Van't Hoff function ranked best when considering the summed square residuals, as it has the largest number of parameters. When we used the Bayesian information criterion, which evaluates the model fit relative to the number of parameters, the Gaussian and Lloyd-Taylor functions performed better. The good performance of the Gaussian function is in line with results from agricultural and forest soils in Finland and Sitka spruce plantations in Scotland (Tuomi et al., 2008). The Lloyd-Taylor function has been reported to give good results for a variety of soil types (Lloyd and Taylor, 1994) and it is widely used in soil and ecosystem models (Adair et al., 2008; Kucharik et al., 2000; Thornton et al., 2002).

Although the Gaussian and Lloyd-Taylor functions feature the same number of parameters, the Gaussian formulation outperformed the Lloyd-Taylor function by matching more of the eight datasets used in this study, which is in line with findings by Tuomi et al. (2008). Importantly, when all individual sites were combined, Lloyd-Taylor outperformed both Gaussian and Van't Hoff with respect to a ranking based on both the summed-squared-residuals and the Bayesian information criterion. As we found that both Gaussian and Van't Hoff underestimate the response at higher temperatures, we conclude that the decrease of respiration rates at high temperatures was mainly an artefact of model parameterisation. A decline in respiration rates would be expected at considerably higher temperatures due to microbial protein denaturation, but the modeled declines found for our datasets were starting at too low temperatures (Larcher, 2001). Especially at sites in a colder temperature regime, Gaussian and Van't Hoff inflect too early and therefore are not suitable as candidate response functions if the function is to be applied over a broad temperature spectrum (Friedlingstein et al., 2006). Functions that do not have this decline at high temperatures, such as Exponential, Arrhenius or Lloyd-Taylor, would have to be complemented by an additional function at very high temperatures to cover respiration decline due to protein denaturation. However, based on our data sets there are not enough data points to provide a good estimate of the maximum point, we therefore neither have a reliable estimation of the decline of Van't Hoff and Gaussian directly nor of an additional declining function for Exponential, Arrhenius or Lloyd-Taylor.

The higher the number of parameters there were in a given function, the more increased the uncertainty range of the overall parameter space. Although each additional parameter improved the curve fit significantly, it also contributed up to the total uncertainty for the given response function.

Generally, the uncertainty of the response functions increased with higher temperatures, because most data points of the eight study sites were highly scattered at higher temperatures. Due to their better reliability, one would be tempted to choose the Gaussian or Van't Hoff response function. However, as the functions were optimized using a dataset that comprises temperate test sites only, they would need to be verified over a larger temperature range. Hence, when applying such functions particularly for warmer conditions (subtropical and tropical) in the context of global vegetation modelling efforts, they are likely to have an unsatisfactory performance. In our test region, even the site with the highest annual mean temperature (at 300 m on our elevation gradient), soil temperatures of 20°C were exceeded on average on only 10% of the days per year. For sites at higher elevations and hence lower temperatures, soil temperatures never reached the values where the response function had the highest uncertainty. Hence, the high uncertainty at higher temperatures has only small or no consequences at all for the uncertainty in model output in regions where soil temperature normally does not exceed values of 20°C, for instance in forests at high elevations and high latitudes.

We have to bear in mind however, that measured data at each individual site may be influenced by additional factors, such as soil moisture conditions (Rodrigo et al., 1997; Cisneros-Dozal et al., 2006), litter chemistry (Berg and Laskowski, 2005b) and soil quality (Conant et al., 2008). Still, the regression analysis based on the compound data set shows, that the default response function of Lloyd-Taylor in LPJ-GUESS is worth considering for further work. These findings are in agreement with those by Adair et al. (2008), which found that the function of Lloyd-Taylor performed best with a three-pool model on the Long-term Intersite

Decomposition Experiment Team (LIDET) data set. The good performance of Llloyd-Taylor, when short-term carbon fluxes are considered, was also shown by Del Grosso et al. (2005) for range land sites and by Richardson et al. (2006) who tested different response functions for the short-term carbon fluxes at flux towers. Our findings, however, are in contrast to those by Tuomi et al. (2008), which found the Gaussian function to be best on incubation measurements from different sources. Gaussian functions might be the best functions to use, but they require calibration across a broad range of temperatures as we could show that the uncertainty of the flexing point at higher temperatures will determine the reliability of the long-term results.

4.2 Short-term carbon flux under present climate

The short-term soil carbon fluxes in the month of August 2006 showed a diverse picture along the elevation gradient for both the response function and the size of the soil carbon stock. The medians of the projections under all response functions showed a bell-shaped behavior along the elevation gradient, the highest values being found at 1300 m.

The fact that the soil carbon fluxes increased up to middle and higher elevations and then started to decrease again lead to the conclusion that the sensitivity of the soil carbon fluxes changed from being more sensitive to carbon pool size at low elevations to being more sensitive to the rate of decomposition (i.e. the response function itself) at high elevations. This is analogous to Atkin and Tjoelker (2003), who found that the temperature dependence of plant respiration is limited by by the turnover rate (enzyme activity) at low temperatures and by substrate availability (pool size) at high temperatures.

We could show in our study that the choice of soil temperature functions is crucial for the short-term carbon turnover (Bauer et al., 2008). Moreover, the interaction of carbon pool size and decomposition rates determines the size of the soil carbon pools as well as the short-term carbon fluxes.

4.3 Long-term carbon stock under present climate

At low elevations and high temperatures, carbon pools turned over relatively quickly and therefore large carbon stocks did not accumulate. Carbon pools at higher elevations tend to be higher, due to the slower turnover rates; this is reflected in our simulation results, and it also agrees with experimental findings by Rodeghiero and Cescatti (2005); Zinke and Stangenberger (2000), but not with Perruchoud et al. (2000) who found little evidence for a significant influence of climate on soil carbon stocks in Swiss forests.

The uncertainty bounds of total soil carbon stocks generally increased with elevation, i.e. they decreased with increasing mean temperature for all response functions and sites. At first sight, this may appear counter-intuitive as the uncertainty of the response function itself was found to increase with temperature. This apparent paradox is caused by the fact that the high uncertainty of the response function at high temperatures does not result in a high uncertainty of the long-term carbon stocks, because the carbon is readily decomposed and no large soil carbon pools are formed. It is important to take into account that the accumulation of uncertainty was larger as the average decomposition rate became slower. This was illustrated by the result that the influence of the uncertainty in turnover times diminished with increasing elevations. An additional change in an already very low decomposition rate did have only minor effects on the estimations of carbon storage.

At higher temperatures and thus at lower elevations, uncertainty in long-term soil carbon stocks resulted from the uncertainties in temperature response functions itself. Due to high turnover rates, only little carbon accumulated and therefore uncertainty in carbon stock estimations was comparatively low. This may nevertheless be important when comparing ecosystems within the tropics and subtropics. Holland et al. (2000) showed with the Century model that a low temperature sensitivity lead to lower soil carbon decomposition but also to higher soil carbon pools.

4.4 Long-term carbon stock under future climate

With a climate warming scenario, the carbon pools on all elevation levels turned over faster, and carbon stocks therefore were projected to diminish in the next 100 years, as suggested by Jones et al. (2005) and Friedlingstein et al. (2006). However, the high uncertainty in the size of soil carbon pools at higher elevations (i.e. in colder areas) resulted in highly uncertain projections on the net release of carbon from these areas. Therefore, the uncertainty in potential carbon loss from soils in temperate and cold climates is higher than for warmer regions. The higher uncertainty regarding the carbon storage potential of high altitude and high latitude soils adds up to the higher temperature sensitivity of the non-labile soil organic matter pools, as reported by Knorr et al. (2005).

According to Townsend et al. (1992) soil respiration in tropical ecosystems will be more sensitive to increasing temperature in future. They also suggested that soil respiration in boreal and tundra ecosystems should be less sensitive to increasing temperatures. This is likely to be true for the response of the decomposition process to temperature itself. We showed, however, that due to the higher uncertainties in soil carbon pool size in temperate and boreal regions, the relative importance of carbon released from soil in a changing climate should be reconsidered regarding to the tropics vs. high-latitude and high-altitude ecosystems.

Taking into account that high-latitude soils contain large amounts of carbon whose respiration could cause a significant positive feedback to climate change (Davidson and Janssens, 2006), the uncertainty we found for the projections from LPJ-GUESS for exactly these conditions calls for caution in the interpretation of earlier modeling studies (Friedlingstein et al., 2006), and it clearly calls for further research in this regard.

5 Conclusions

The function of Lloyd-Taylor turned out to be adequate for modelling the temperature dependency of soil organic matter decomposition in LPJ-GUESS, as the alternative functions where not as favorable, because they either resulted in poor fits (Exponential, Arrhenius) or were not applicable when extrapolating beyond the given datasets (Gaussian, Van't Hoff).

We investigated the two main sources of uncertainty for model simulations: On one hand, the uncertainty in the parameter estimates of the response functions, which increased with decreasing elevation. On the other hand, we evaluated the resulting uncertainty in the simulation of carbon pools and fluxes and found an increase with elevation. The soil carbon at low elevations was readily degraded due to faster turnover times, whereas at higher elevations, the slower turnover times lead to higher carbon stocks and as a consequence higher associated uncertainties. This increased uncertainty in the size of carbon pools with slow turn-over rates has implications for the uncertainty in the projection of the change of soil carbon stocks driven by climate change. The increased uncertainty for higher elevations and, when taken as an analog for the higher latitudes, contributes to a high uncertainty when estimating the global carbon budget.

Acknowledgements. This work was supported by grant no. TH-14 07-1 of ETH Zürich and by the National Centre of Competence in Climate Research (NCCR Climate), Switzerland.

Climate and CO_2 data were provided through the PRUDENCE data archive, funded by the EU through contract EVK2-CT2001-00132.

We would like to thank the researchers which contributed to the compound dataset of Hibbard et al. (2006) for making their datasets freely available to anybody.

References

Adair, E. C., Parton, W. J., Del Grosso, S. J., Silver, W. L., Harmon, M. E., Hall, S. A., Burke, I. C., and Hart, S. C.: Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates, Global Change Biology, 14, 2636–2660, 2008.

Ågren, G. I. and Bosatta, N.: Theoretical analysis of the long-term dynamics of carbon and nitrogen in soils, Ecology, 68, 1181–1189, 1987.

Atkin, O. K. and Tjoelker, M. G.: Thermal acclimation and the dynamic response of plant respiration to temperature, Trends in Plant Science, 8, 343–351, 2003.

Bauer, J., Herbst, M., Huisman, J., Weihermüller, L., and Vereecken, H.: Sensitivity of simulated soil heterotrophic respiration to temperature and moisture reduction functions, Geoderma, 145, 17–27, 2008.

Berg, B. and Laskowski, R.: Anthropogenic impacts on litter decomposition and soil organic matter, Advances in Ecological Research, 38, 263–290, 2005a.

Berg, B. and Laskowski, R.: Climatic and Geographic Patterns in Decomposition, Advances in Ecological Research, 38, 227–261, 2005b.

Bosatta, E. and Ågren, G. I.: Soil organic matter quality interpreted thermodynamically, Soil Biology & Biochemistry, 31, 1889–1891, 1999.

Bronson, D. R., Gower, S. T., Tanner, M., Linder, S., and Herk, I. V.: Response of soil surface CO2 flux in a boreal forest to ecosystem warming, Global Change Biology, 14, 856–867, 2008.

Christensen, J., Carter, T., Rummukainen, M., and Amanatidis, G.: Evaluating the performance and utility of regional climate models: the PRUDENCE project, Climatic Change, 81, 1–6, 2007.

Cisneros-Dozal, L. M., Trumbore, S., and Hanson, P. J.: Partitioning sources of soil-respired CO2 and their seasonal variation using a unique radiocarbon tracer, Global Change Biology, 12, 194–204, 2006.

Conant, R. T., Drijiber, R. A., Haddix, M. L., Parton, W. J., Paul, E. A., Plante, A. F., Six, J., and Steinweg, J. M.: Sensitivity of organic matter decomposition to warming varies with its quality, Global Change Biology, 14, 868–877, 2008.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Dìaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V., and Westoby, M.: Plant species traits are the predominant control on litter decomposition rates within biomes worldwide, Ecology Letters, 11, 1065–1071, 2008.

Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. A., Brovkin, V., Cox, P. M., Fisher, V., Foley, J. A., Friend, A. D., Kucharik, C., Lomas, M. R., Ramankutty, N., Sitch, S., Smith, B., White, A., and Young-Molling, C.: Global response of terrestrial ecosystem structure and function to CO2 and climate change: results from six dynamic global vegetation models, Global Change Biology, 7, 357–373, 2001.

Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165–173, 2006.

Del Grosso, S., Parton, W., Mosier, A., Holland, E., Pendall, E., Schimel, D., and Ojima, D.: Modeling soil CO2 emissions from ecosystems, Biogeochemistry, 73, 71–91, 2005.

Eliasson, P. E., McMurtrie, R. E., Pepper, D. A., Stromgren, M., Linder, S., and Ågren, G. I.: The response of heterotrophic CO2 flux to soil warming, Global Change Biology, 11, 167–181, 2005.

Foley, J. A.: Numerical Models of the Terrestrial Biosphere, Journal of Biogeography, 22, 837–842, 1995.

Foley, J. A., Prentice, I. C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., and Haxeltine, A.: An Integrated Biosphere Model of Land Surface Processes, Terrestrial Carbon Balance, and Vegetation Dynamics, Global Biogeochemical Cycles, 10, 603–628, 1996.

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K., Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N.: Climate–Carbon Cycle Feedback Analysis: Results from the C4MIP Model Intercomparison, Journal of Climate, 19, 3337–3353, 2006.

Gehrig-Fasel, J., Guisan, A., and Zimmermann, N. E.: Tree line shifts in the Swiss Alps: Climate change or land abandonment?, Journal of Vegetation Science, 18, 571–582, 2007.

Hakkenberg, R., Churkina, G., Rodeghiero, M., Börner, A., Steinhof, A., and Cescatti, A.: Temperature sensitivity of the turnover times of soil organic matter in forests, Ecological Applications, 18, 119–31, 2008.

Hibbard, K., Law, B., Reichstein, M., and Sulzman, J.: An analysis of soil respiration across northern hemisphere temperate ecosystems, Biogeochemistry, 73, 29–70, 2005.

Hibbard, K., Hudiburg, T., Law, B., Reichstein, M., and Sulzman, J.: Northern Hemisphere Temperate Ecosystem Annual Soil Respiration Data (from Hibbard et al. 2005. An analysis of soil respiration across northern hemisphere temperate ecosystems. Biogeochemistry 73:29-70), Tech. rep., 2006.

Holland, E. A., Neff, J. C., Townsend, A. R., and McKeown, B.: Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: Implications for models, Global Biogeochemical Cycles, 14, 1137–1151, 2000.

Iman, R. L. and Conover, W. J.: A distribution-free approach to inducing rank correlation among input variables, Communications in Statistics - Simulation and Computation, 11, 311–334, 1982.

Jenkinson, D. S.: The Turnover of Organic Carbon and Nitrogen in Soil, Royal Society of London Philosophical Transactions Series B, 329, 361–367, 1990.

Jones, C., McConnell, C., Coleman, K., Cox, P., Falloon, P., Jenkinson, D., and Powlson, D.: Global climate change and soil carbon stocks; predictions from two contrasting models for the turnover of organic carbon in soil, Global Change Biology, 11, 154–166, 2005.

Jones, C. D., Cox, P., and Huntington, C.: Uncertainty in climate carbon-cycle projections associated with the sensitivity of soil respiration to temperature, Tellus B, 55, 642–648, 2003.

Kirschbaum, M. U. F.: The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage, Soil Biology and Biochemistry, 27, 753–760, 1995.

Kirschbaum, M. U. F.: Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss?, Global Change Biology, 10, 1870–1877, 2004.

Kirschbaum, M. U. F.: The temperature dependence of organic-matter decomposition–still a topic of debate, Soil Biology and Biochemistry, 38, 2510–2518, 2006.

Knorr, W., Prentice, C. I., House, J. I., and Holland, E. A.: Long-term sensitivity of soil carbon turnover to warming, Nature, 433, 298–301, 2005.

Körner, C.: Alpine plant life: functional plant ecology of high mountain ecosystems, Springer, Berlin, 2 edn., 2003.

Kucharik, C. J., Foley, J. A., Delire, C., Fisher, V. A., Coe, M. T., Lenters, J. D., Young-Molling, C., Ramankutty, N., Norman, J. M., and Gower, S. T.: Testing the Performance of a Dynamic Global Ecosystem Model: Water Balance, Carbon Balance, and Vegetation Structure, Global Biogeochemical Cycles, 14, 795–825, 2000.

Larcher, W.: Ökophysiologie der Pflanzen, Verlag Eugen Ulmer, Stuttgart, 6. neubearbeitete auflage edn., 2001.

Lloyd, J. and Taylor, J. A.: On the Temperature Dependence of Soil Respiration, Functional Ecology, 8, 315–323, 1994.

Meentemeyer, V.: Macroclimate the Lignin Control of Litter Decomposition Rates, Ecology, 59, 465–472, 1978.

Mitchell, T. D., Mitchell, T. D., Carter, T. R., Jones, P. D., Hulme, M., and New, M.: A comprehensive set of climate scenarios for Europe and the globe., Tyndall Centre for Climate Change Research Working Paper, 2003.

Morales, P., Sykes, M. T., Prentice, I. C., Smith, P., Smith, B., Bugmann, H., Zierl, B., Friedlingstein, P., Viovy, N., and Sabate, S.: Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes, Global Change Biology, 11, 2211–2233, 2005.

Morales, P., Hickler, T., Rowell, D. P., Smith, B., and Sykes, M. T.: Changes in European Ecosystem Productivity and Carbon Balance Driven by Regional Climate Model Output, Global Change Biology, 13, 108–122, 2007.

O'Connell, A. M.: Microbial decomposition (respiration) of litter in eucalypt forests of South-Western Australia: An empirical model based on laboratory incubations, Soil Biology and Biochemistry, 22, 153–160, 1990.

Oleson, K., Dai, Y., Bonan, G., Bosilovich, M., Dickinson, R., Dirmeyer, P., Hoffman, F., Houser, P., Levis, S., Niu, G. Y., et al.: Technical description of the community land model "(CLM)". Technical Note "NCAR/TN-461+" "STR", National Center for Atmospheric Research, Boulder, Colo, 2004.

Parton, W. J., Schimel, D. S., Cole, C. V., and Ojima, D. S.: Analysis of factors controlling soil organic matter levels in Great Plains grasslands, Soil Science Society of America Journal, 51, 1173–1179, 1987.

Perruchoud, D., Walthert, L., Zimmermann, S., and Lüscher, P.: Contemporary carbon stocks of mineral forest soils in the Swiss Alps, Biogeochemistry, 50, 111–136, 2000.

R Development Core Team: R: A Language and Environment for Statistical Computing, Vienna, Austria, 2008.

Ratkowsky, D. A.: Handbook of Nonlinear Regression Models, in: Statistics: Textbooks and Monographs, Marcel Dekker, Inc., New York, 1990.

Richardson, A. D., Braswell, B. H., Hollinger, D. Y., Burman, P., Davidson, E. A., Evans, R. S., Flanagan, L. B., Munger, J. W., Savage, K., Urbanski, S. P., and Wofsy, S. C.: Comparing simple respiration models for eddy flux and dynamic chamber data, Agricultural and Forest Meteorology, 141, 219–234, 2006.

Rodeghiero, M. and Cescatti, A.: Main determinants of forest soil respiration along an elevation/temperature gradient in the Italian Alps, Global Change Biology, 11, 1024–1041, 2005.

Rodrigo, A., Recous, S., Neel, C., and Mary, B.: Modelling temperature and moisture effects on C-N transformations in soils: comparison of nine models, Ecological Modelling, 102, 325–339, 1997.

Saltelli, A., Tarantola, S., Campolongo, F., and Ratto, M.: Sensitivity analysis in practice - a guide to assessing scientific models, John Wiley & Sons, Ltd., Chichester, 2004.

Schlesinger, W. H.: Biogeochemistry: an Analysis of Global Change, Academic Press, San Diego, second edn., 1997.

Schwarz, G.: Estimating the Dimension of a Model, The Annals of Statistics, 6, 461–464, 1978.

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, Global Change Biology, 9, 161–185, 2003.

Smith, B., Prentice, I. C., and Sykes, M. T.: Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space, Global Ecology and Biogeography, 10, 621–637, 2001.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., M.Tignor, and Miller, H.: IPCC, 2007: Summary for Policymakers, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2007.

Thornton, P. E., Running, S. W., and White, M. A.: Generating surfaces of daily meteorological variables over large regions of complex terrain, Journal of Hydrology, 190, 214–251, 1997.

Thornton, P. E., Law, B. E., Gholz, H. L., Clark, K. L., Falge, E., Ellsworth, D. S., Goldstein, A. H., Monson, R. K., Hollinger, D., Falk, M., Chen, J., and Sparks, J. P.: Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests, Agricultural and Forest Meteorology, 113, 185–222, 2002.

Townsend, A. R., Vitousek, P. M., and Holland, E. A.: Tropical soils could dominate the short-term carbon cycle feedbacks to increased global temperatures, Climatic Change, 22, 293–303, 1992.

Tuomi, M., Vanhala, P., Karhu, K., Fritze, H., and Liski, J.: Heterotrophic soil respiration–Comparison of different models describing its temperature dependence, Ecological Modelling, 211, 182–190, 2008.

Van't Hoff, J. H.: Vorlesungen über theoretische und physicalische Chemie. Erstes Heft: Die chemische Dynamik, Druck und Verlag von Friedrich Vieweg und Sohn, Braunschweig, 1901.

Weedon, J. T., Cornwell, W. K., Cornelissen, J. H., Zanne, A. E., Wirth, C., and Coomes, D. A.: Global meta-analysis of wood decomposition rates: a role for trait variation among tree species?, Ecology Letters, 12, 45–56, 2009.

Zaehle, S., Sitch, S., Smith, B., and Hatterman, F.: Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics, Global Biogeochemical Cycles, 19, GB3020, 2005.

Zinke, P. J. and Stangenberger, A. G.: Elemental storage of forest soil from local to global scales, Forest Ecology and Management, 138, 159–165, 2000.

Table 1. Temperature response functions

Id	Differential equation	Absolute function	Relative function[a]
E[b]	$\frac{dlnR_T}{dT} = C$	$R_T = e^{C\times T} \times Const$	$R_T = R_{T_{ref}} \times e^{C\times(T-T_{ref})}$
A	$\frac{dlnR_T}{dT} = \frac{A}{T^2}$	$R_T = e^{-\frac{A}{T}} \times Const$	$R_T = R_{T_{ref}} \times e^{A\times(\frac{1}{T_{ref}}-\frac{1}{T})}$
G	$\frac{dlnR_T}{dT} = a + 2bT$	$R_T = e^{aT+bT^2} \times Const$	$R_T = R_{T_{ref}} \times e^{a\times(T-T_{ref})+b\times(T^2-T_{ref}^2)}$
V	$\frac{dlnR_T}{dT} = \frac{A}{T^2} + \frac{B}{T} + C$	$R_T = e^{-\frac{A}{T}} \times T^B \times e^{C\times T} \times Const$	$R_T = R_{T_{ref}} \times e^{A\times(\frac{1}{T_{ref}}-\frac{1}{T})+B\times log(\frac{T}{T_{ref}})+C\times(T-T_{ref})}$
L	$\frac{dlnR_T}{dT} = \frac{A}{(T-T_0)^2}$	$R_T = e^{-\frac{A}{T-T_0}} \times Const$	$R_T = R_{T_{ref}} \times e^{A\times(\frac{1}{T_{ref}-T_0}-\frac{1}{T-T_0})}$

[a] Functions expressed relative to reference temperature $T_{ref} = 10°\mathrm{C}$ with reference respiration $R_{T_{ref}}$ normalized to 1 at mean reference respiration $\overline{R_{T_{ref}}}$. [b] The candiate functions are: Exponential (E), Arrhenius (A), Gaussian (G), Van't Hoff (V) and Lloyd-Taylor (L).

Table 2. Site characteristics

Site	Description	Location		Elevation (m)	MAT[a]	N[b]	Forest vegetation type
BEP	Belgium de Inslag Pine	51.31N	4.31E	16	10	41	Evergreen-needleleaf
DUK	Duke FACE	35.97N	79.1W	120-163	15.5	47	Evergreen-needleleaf
HAR	Harvard	42.54N	72.17W	180-490	7.85	197	Mixed Deciduous-evergreen
HES	Hesse	48.67N	7.08E	300	9.7	39	Deciduous-broadleaf
HOW	Howland	45.2N	68.7W	60	5.69	164	Evergreen-neddleleaf
MEO	Metolius old site	44.5N	121.62W	915-1141	8.5	316	Evergreen-needleleaf
THA	Tharandt	50.96N	13.75E	380	7.6	279	Evergreen-needleleaf
UMB	Univ. of Michigan Biological Station	45.56N	84.71W	234	6.2	78	Mixed Deciduous-evergreen

Characteristics of the sites providing the soil respiration data. Adapted from Hibbard et al. (2006). [a]MAT: Mean annual temperature in $°\mathrm{C}$. [b]N: Number of data points.

Table 3. Summed squared residuals of nonlinear model fits

Site	SSR[a]				
	E	A	G	V	L
BEP	2.6	2.5	1.72	**1.69**	2.1
DUK	81.1	79.7	72.2	**71.8**	73.7
HAR	249.7	246.4	216.9	**215.3**	229.3
HES	23.3	23.0	19.22	**19.17**	21.1
HOW	88.4	84.9	53.9	**53.4**	65.6
MEO	110.9	110.2	108.4	108.4	**108.3**
THA	248.9	247.7	243.4	**240.8**	242.5
UMB	53.3	52.5	51.5	**49.9**	51.2
All	184.4	182.0	212.9	218.4	**176.0**

[a] SSR: Summed Squared Residuals. Best (lowest) values for each site shown in bold numbers. *All* is the compound dataset consisting of all eight individual datasets.

Table 4. Ranking of nonlinear model fits

Site	BIC[a]				
	E	A	G	V	L
BEP	5.0	3.9	**-9.4**	-8.9	-1.2
DUK	161.1	160.3	**157.9**	162.5	158.9
HAR	576.2	573.7	**552.8**	556.0	562.9
HES	92.7	92.2	**87.5**	91.0	91.1
HOW	347.1	341.1	**275.8**	277.6	304.9
MEO	556.6	554.6	551.9	555.2	**551.8**
THA	760.3	758.9	756.3	757.6	**755.3**
UMB	193.7	**192.6**	193.4	194.8	192.9
All	1159.6	1145.4	1322.6	1353.7	**1110.0**

[a] BIC: Bayesian information criterion (Schwarz, 1978). Best (lowest) values for each site shown in bold numbers. *All* is the compound dataset consisting of all eight individual datasets.

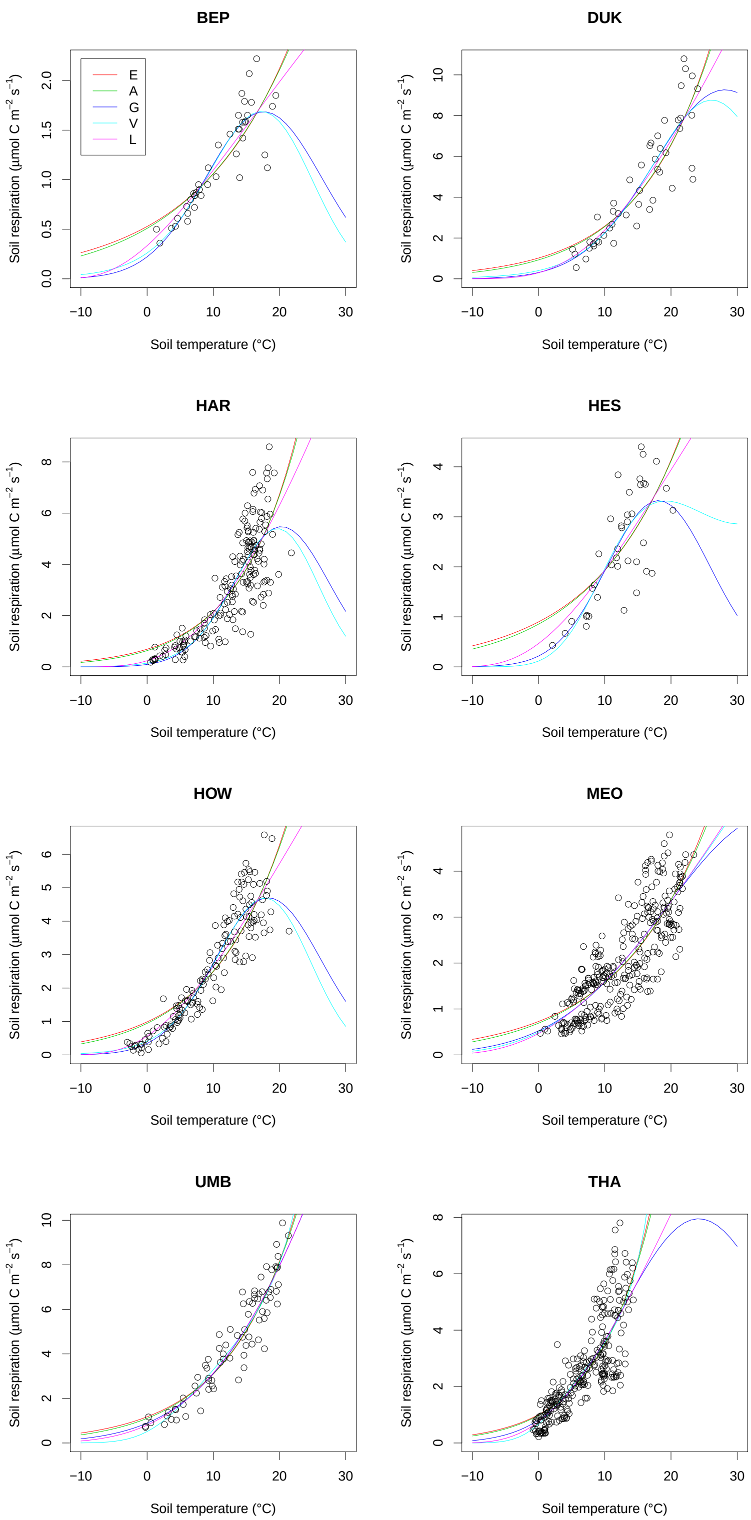

Fig. 1. Best non-linear fit for the soil respiration as a function of soil temperature for all sites are shown (E: Exponential, A: Arrhenius, G: Gaussian, V: Van't Hoff, L: Lloyd-Taylor). The abbreviations of the sites are explained in Tab. 2.

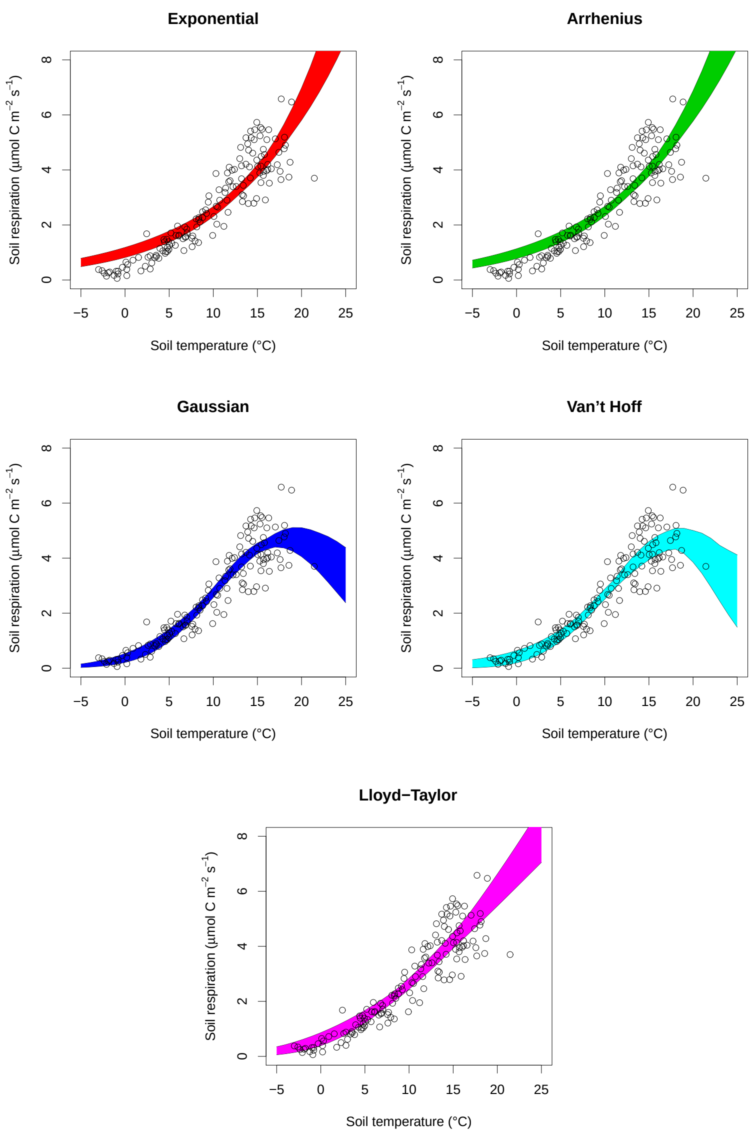

Fig. 2. Uncertainty bound for each candidate temperature response function spanned out by the sampled function parameter range sets for the site HOW. The abbreviation of the site is esplained in Tab. 2.

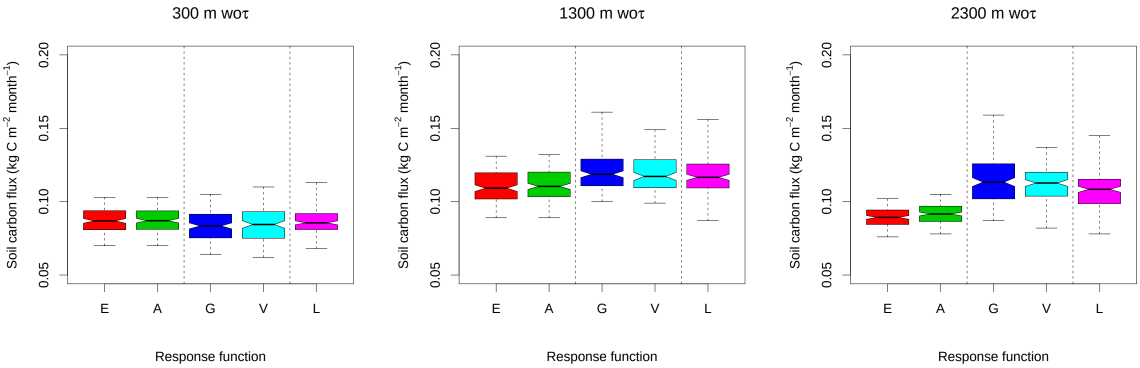

Fig. 3. Uncertainty in short-term soil carbon flux in August 2006 on 300 m, 1300 m and 2300 m of elevation. Pairs of response functions and sites have been grouped according to the response function used. The box plots span over the 95% confidence interval. Models are separated by the dashed lines into groups with similar means and uncertainty ranges. Abbrevations as in Fig. 1.

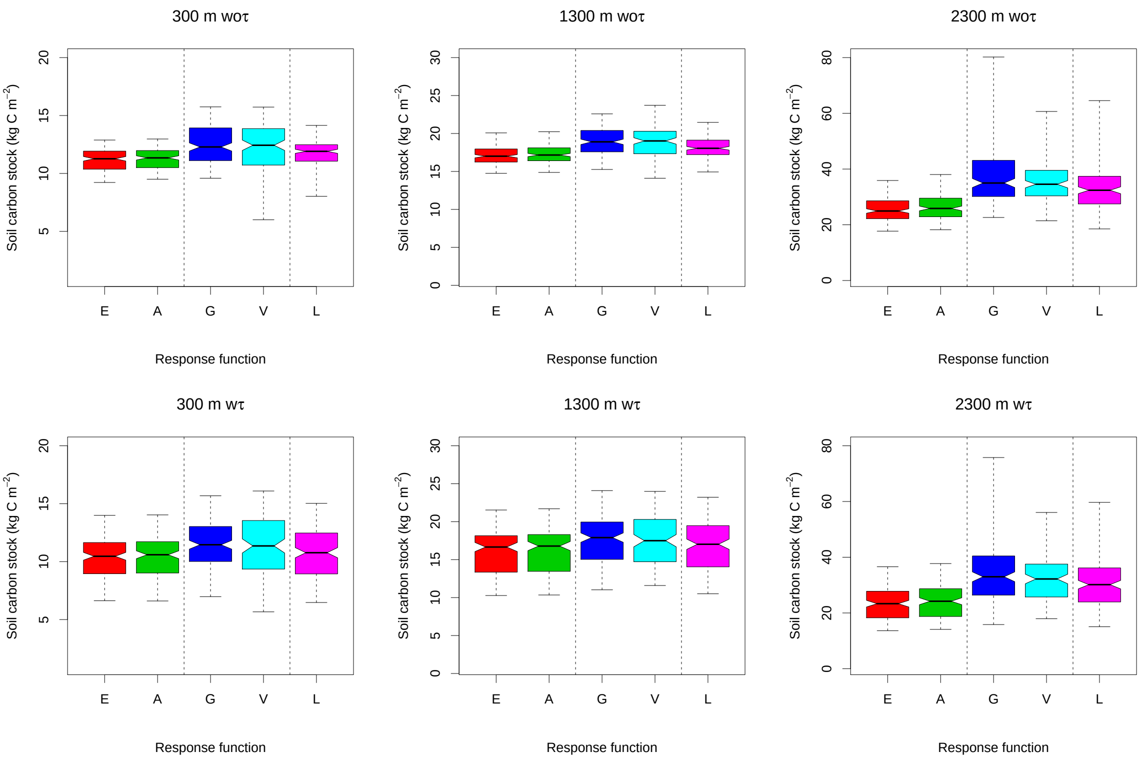

Fig. 4. Uncertainty in long-term soil carbon stocks in August 2006 with varying (case wτ) and fixed (woτ) turnover times on 300 m, 1300 m and 2300 m of elevation. Pairs of response functions and sites have been grouped according to the response function used. The box plots span over the 95% confidence interval. Models are separated by the dashed lines into three distinct groups with similar means and uncertainty ranges. Abbrevations as in Fig. 1.

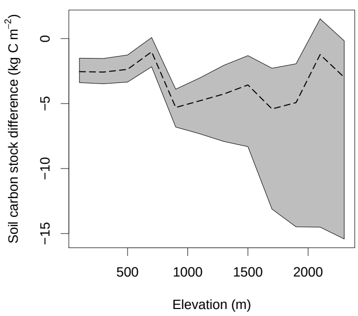

Fig. 5. Uncertainty in future projections of the difference of the long-term soil carbon stocks between 2006 and 2106, based on a SRES A2 climate scenario over all response functions and all sites with varying turnover times.

Table A1. Linearized temperature response functions

Id	Linearized function[a]
E[b]	$R_T = (\overline{R_{T_{ref}}})^{-1} \times \mathbf{R_{T_{ref}}}^{\frac{x1-T}{x1-T_{ref}}} \times \mathbf{E_1}^{\frac{T-T_{ref}}{x1-T_{ref}}}$
A	$R_T = (\overline{R_{T_{ref}}})^{-1} \times \mathbf{R_{T_{ref}}}^{\frac{T_{ref}\times(T-x1)}{T\times(T_{ref}-x1)}} \times \mathbf{A_1}^{\frac{x1\times(T_{ref}-T)}{T\times(T_{ref}-x1)}}$
G	$R_T = (\overline{R_{T_{ref}}})^{-1} \times \mathbf{R_{T_{ref}}}^{\frac{(T-x1)(T-x2)}{(T_{ref}-x1)(T_{ref}-x2)}} \times \mathbf{G_1}^{-\frac{(T-T_{ref})(T-x2)}{(T_{ref}-x1)(x1-x2)}} \times \mathbf{G_2}^{\frac{(T-T_{ref})(T-x1)}{(T_{ref}-x2)(x1-x2)}}$
V	$R_T = (\overline{R_{T_{ref}}})^{-1} \times \mathbf{R_{T_{ref}}}^{P_{01}+P_{02}\times T^{-1}+P_{03}\times T+P_{04}\times ln(T)} \times \mathbf{V_1}^{P_{11}+P_{12}\times T^{-1}+P_{13}\times T+P_{14}\times ln(T)}$ $\times \mathbf{V_2}^{P_{21}+P_{22}\times T^{-1}+P_{23}\times T+P_{24}\times ln(T)} \times \mathbf{V_3}^{P_{31}+P_{32}\times T^{-1}+P_{33}\times T+P_{34}\times ln(T)}$
L	$R_T = (\overline{R_{T_{ref}}})^{-1} \times \mathbf{R_{T_{ref}}} \times (\frac{\mathbf{L_1}}{\mathbf{R_{T_{ref}}}})^{\frac{(T_{ref}-T)(\mathbf{L_2}-x1)}{(\mathbf{L_2}-T)(T_{ref}-x1)}}$

[a]Temperature response functions linearized with the method of expected-value parameters (Ratkowsky, 1990). T_{ref}=283.15K, x0=268.15K (for V only), x1=280.15K, x2=292.15K. [b] The candiate functions are: Exponential (E), Arrhenius (A), Gaussian (G), Van't Hoff (V) and Lloyd-Taylor (L).

Table A2. Significance levels

Site	P-Value[a]													
	$R_{T_{ref}}$	E_1	$R_{T_{ref}}$	A_1	$R_{T_{ref}}$	G_1	G_2	$R_{T_{ref}}$	V_1	V_2	V_3	$R_{T_{ref}}$	L_1	L_2
BEP	***	***	***	***	***	***	***	***	**	***	***	***	***	***
DUK	***	***	***	***	***	***	***	***	++	***	***	***	***	***
HAR	***	***	***	***	***	***	***	***	++	***	***	***	***	***
HES	***	***	***	***	***	***	***	***	++	***	***	***	***	***
HOW	***	***	***	***	***	***	***	***	***	***	***	***	***	***
MEO	***	***	***	***	***	***	***	***	++	***	***	***	***	***
THA	***	***	***	***	***	***	***	***	++	***	*	***	***	***
UMB	***	***	***	***	***	***	***	***	++	***	***	***	***	***

Significance levels are given in P-Values for all the parameters of nonlinear model fits for each pair of temperature response function (as given in Appendix Tab. A1) and calibration site. [a] Significance codes for P-values: 0 *** 0.001 ** 0.01 * 0.05 $^{+}$ 0.1 $^{++}$ 1.

Table A3. Model parameter ranges

Site	$R^a_{T_{ref}}$	E_1	$R_{T_{ref}}$	A_1	$R_{T_{ref}}$	G_1	G_2
BEP	1.06[0.94:1.18]	0.86[0.72:0.99]	1.06[0.94:1.18]	0.86[0.72:0.99]	1. 15[1.03:1.28]	0.81[0.68:0.93]	1.66[1.39:1.94]
DUK	2.58[1.94:3.23]	1.96[1.34:2.57]	2.56[1.92:3.20]	1.90[1.29:2.51]	2. 25[1.50:3.00]	1.36[0.56:2.16]	6.46[5.67:7.26]
HAR	2.15[1.84:2.46]	1.53[1.22:1.84]	2.15[1.84:2.46]	1.50[1.19:1.82]	1. 92[1.54:2.31]	0.96[0.56:1.36]	5.38[4.75:6.01]
HES	1.93[1.52:2.34]	1.53[1.06:2.01]	1.93[1.52:2.34]	1.52[1.04:1.99]	1. 92[1.49:2.36]	1.19[0.62:1.76]	3.30[2.41:4.20]
HOW	2.49[2.30:2.68]	1.89[1.68:2.09]	2.50[2.31:2.69]	1.88[1.68:2.09]	2. 75[2.56:2.94]	1.74[1.53:1.94]	4.68[4.22:5.14]
MEO	1.57[1.46:1.68]	1.25[1.13:1.36]	1.57[1.46:1.68]	1.24[1.12:1.35]	1. 59[1.47:1.70]	1.18[1.05:1.32]	3.16[3.01:3.30]
THA	3.49[3.32:3.67]	2.40[2.23:2.58]	3.51[3.33:3.68]	2.42[2.24:2.59]	3. 63[3.40:3.86]	2.52[2.31:2.73]	7.16[3.92:10.39]
UMB	3.10[2.77:3.43]	2.32[1.98:2.65]	3.10[2.77:3.43]	2.29[1.96:2.63]	3. 12[2.78:3.45]	2.21[1.82:2.61]	7.35[6.93:7.77]

Site	$R_{T_{ref}}$	V_1	V_2	V_3	$R_{T_{ref}}$	L_1	L_2
BEP	1.14[1.02:1.26]	0.10[0.01:0.20]	0.80[0.68:0. 92]	1.65[1.37:1.93]	1.10[0.96:1.24]	0.84[0.71: 0.97]	253.15[202.12:304.18]
DUK	2.23[1.49:2.98]	0.17[-0.18:0.52]	1.39[0.61:2 .16]	6.50[5.69:7.31]	2.39[1.69:3.10]	1.51[0.55: 2.46]	253.15[194.46:311.84]
HAR	1.90[1.53:2.28]	0.03[-0.03:0.09]	0.98[0.59:1 .36]	5.37[4.73:6.00]	2.12[1.79:2.45]	1.30[0.92: 1.69]	253.15[217.07:289.23]
HES	1.96[1.43:2.50]	0.01[-0.08:0.10]	1.16[0.55:1 .78]	3.32[2.43:4.21]	1.93[1.50:2.36]	1.41[0.87: 1.96]	253.15[162.56:343.74]
HOW	2.71[2.52:2.90]	0.13[0.04:0.22]	1.71[1.51:1. 91]	4.62[4.15:5.09]	2.64[2.43:2.86]	1.88[1.67: 2.08]	253.15[234.22:272.08]
MEO	1.59[1.44:1.74]	0.22[-0.30:0.74]	1.18[1.05:1 .32]	3.15[2.98:3.31]	1.60[1.48:1.72]	1.19[1.05: 1.32]	243.07[201.39:284.74]
THA	3.57[3.32:3.81]	0.07[-0.10:0.24]	2.61[2.35: 2.88]	14.8[-2.7:32.4]	3.63[3.43:3.84]	2.55[2.32 :2.78]	252.26[226.98:277.53]
UMB	3.29[2.85:3.73]	0.07[-0.16:0.31]	2.28[1.84:2 .72]	7.30[6.88:7.71]	3.14[2.79:3.48]	2.21[1.83: 2.59]	230.29[153.06:307.52]

Model parameter estimates for nonlinear fits of each pair of temperature response function (as given in Appendix Tab. A1) and calibration site with their corresponding 99% confidence interval in square brackets. [a] $R_{T_{ref}}$: Reference respiration at reference temperature $T_{ref} = 283.15K$.