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Temperature dependence of soil respiration modulated by thresholds in soil water availability across European shrubland ecosystems

Page heading: Temperature dependence of soil respiration

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Abstract

Soil respiration (SR) is a major component of the global carbon cycle and plays a fundamental role in ecosystem feedback to climate change. Empirical modelling is an essential tool for predicting ecosystem responses to environmental change, and also provides important data for calibrating and corroborating process-based models. In this study, we evaluated the performance of three empirical temperature-SR response functions (Exponential, Lloyd-Taylor and Gaussian) at seven shrublands located within three climatic regions (Atlantic, Mediterranean and Continental) across Europe. We investigated the performance of SR models by including interaction between soil moisture and soil temperature. We found that the best fit for the temperature functions depended on the site specific climatic conditions. Including soil moisture we identified thresholds in the three different response functions that improved the model fit in all cases. The direct soil moisture effect on SR, however, was weak at the annual time scale. We conclude that the exponential soil temperature function may only be a good predictor for SR in a narrow temperature range, and that extrapolating predictions for future climate based on this function should be treated with caution as modelled outputs may underestimate SR. The addition of soil moisture thresholds improved the model fit at all sites, but had a far greater ecological significance in the wet Atlantic shrubland where a fundamental change in the soil CO_2 efflux would likely have an impact on the whole carbon budget.

Keywords: annual soil respiration, empirical soil respiration models, soil moisture threshold, shrubland, temperature dependence, temperature sensitivity

Introduction

Soil respiration (SR) is a dominant component of the terrestrial carbon cycle and has a significant influence on global radiative forcing (*IPCC 2013*). In terrestrial ecosystems atmospheric CO_2 is assimilated during photosynthesis, and then released either via autotrophic respiration or through heterotrophic decomposition of carbon compounds differing in recalcitrance and sensitivity to temperature (*Davidson & Janssens, 2006*). Both soil moisture availability and temperature may alter with a changing climate, and this will affect decomposition processes and root activity, potentially changing rates of CO_2 efflux from soils. However, it is poorly understood how altered temperature and soil moisture availability will affect soil CO_2 efflux across multiple ecosystems. In fact, because of the interaction of multiple environmental processes often occurring simultaneously it is hard to make predictions beyond empirical data bounds (*Vicca et al., 2014*). SR response functions derived from empirical data collected at different temporal and spatial scales could be useful for improving the predicted impact of future climate on ecosystem processes (*Kirschbaum, 2004; Vicca et al., 2014*).

Temperature is often a predominant factor controlling biological metabolic processes and a broad spectrum of relationships between temperature and SR has been tested (*Subke & Bahn, 2010; Wu et al., 2011; Shen et al., 2013*). Most commonly, the exponential function has been used to model the temperature-respiration relationship (*Davidson & Janssens, 2006; Beier et al., 2009; Vicca et al., 2014*). In these cases, however, exponential models were usually applied in a relatively narrow temperature range not exceeding 30°C. *In situ* SR studies covering a wide range of temperature and moisture conditions are rare and the limited availability of such data affects the ability of modellers to fit SR functions to empirical data (*Vicca et al., 2014*). Consequently, to study SR on a wide range of ecosystems and climatic conditions, the Arrhenius, Lloyd-Taylor, Gaussian, and Quadratic functions have been used

(*Lloyd & Taylor, 1994; Tuomi et al., 2008; Reichstein & Beer, 2008; Lellei-Kovács et al., 2011; González-Ubierna et al., 2014*).

Occasionally, to improve on the fit of a simple exponential model, a wider environmental range has been incorporated by fitting separate functions to subranges of temperature (*Murthy et al., 2003, Bradford et al., 2008*) and soil depth (*Pavelka et al., 2007*) or to Mediterranean wet versus dry seasons (*de Dato et al., 2010*). Other studies have used additional parameters to account for factors other than temperature like soil moisture content (*Suseela et al., 2012; Kopittke et al., 2013; Wang et al., 2014*), soil physical and chemical properties (*Wang et al., 2003; Balogh et al., 2011; Kotroczó et al., 2014*), different substrate availability (*Davidson et al., 2006*), or different SOM content and quality (*Curiel Yuste et al., 2010*). Other studies have also attempted to provide mechanistic explanations for the temperature dependence of SR (*Davidson et al., 2006; von Lützow & Kögel-Knabner, 2009*). In a review, *Billings & Ballantyne* (*2013*) examined the mechanisms that are linked to SR, and reported that temperature induced changes in microbial community structure, microbial metabolic rates and catalytic rate of exo-enzymes may lead to a decline of SR as a response to an increase in the soil temperature.

The relationship between soil moisture and SR has been modelled using many different functions that include linear (*Leirós et al., 1999*), exponential (*Rodrigo et al., 1997*), second-order exponential, i.e. Gaussian (*Howard & Howard, 1993; Mielnick & Dugas, 2000; Vicca et al., 2014*) and reverse exponential (*Zhou et al., 2007*) relationships. Limitation of SR by soil moisture has been observed when substrate diffusion is limited by low soil water availability (*Howard & Howard, 1993*), but also when the diffusion of O_2 is restricted by high soil water content (*Skopp et al., 1990*). Mechanistic studies of the relationship between soil moisture and SR conducted by *Davidson et al.* (*2006*) revealed that CO_2 efflux is not only influenced by moisture induced changes in soil physical properties, but also, autotrophic root respiration and heterotrophic microbial decomposition are directly impacted by changes in soil moisture. Evaluation of the impact of soil moisture is more difficult than that of temperature because the efficiency of water uptake is influenced by various soil physical properties and also by physiological processes of the organisms. At any given soil moisture content water uptake may differ for numerous reasons such as soil texture (sand or clay), plant water use efficiency, stress tolerance and soil microbial composition (e.g. fungal to baterial ratio) (*Moyano et al., 2013*).

The approaches to study the combined impact of temperature and moisture on SR modelling differ in two fundamental ways: 1. additive versus interactive (*Mielnick & Dugas, 2000; Reichstein et al., 2002; Qi et al., 2002; Xu et al., 2004; Zhou et al., 2006*); 2. continuous versus threshold (*Davidson et al., 1998; Reichstein et al., 2002; Rey et al., 2002; Fernandez et al., 2006; Yan et al., 2011*). Moisture thresholds that alter SR activities significantly may be very important in modelling carbon fluxes, not only in arid and semiarid, but also in mesic ecosystems (*Suseela et al., 2012*).

In a coordinated network of climate change experiments (EU projects CLIMOOR, VULCAN and INCREASE) along a natural temperature and precipitation gradient across European shrublands, whole ecosystem manipulations of warming and summer drought conditions were conducted. The experiments resulted in a trend of increased SR in response to the warming treatments and significant reduction in SR in response to the drought treatments (*Emmett et al., 2004; Koppitke et al., 2014*). However, some of the ecosystems also had an individual response to warming and drought that makes general conclusions difficult to draw. In the longer term, repeated summer drought resulted in an increased SR in the hydric ericaceous shrubland in Wales. *Sowerby et al.* (*2008*) suggested that the year-round reduction in soil moisture content of the organic-rich podzol soil resulted in a year-round stimulation of SR. *Lellei-Kovács et al.* (*2008*) found that in the semiarid Hungarian shrubland, warming and drought reduced the rate of SR. In the Italian Mediterranean shrubland *de Dato et al.* (*2010*) observed a temporary decrease in SR as a short-term response to the warming and drought treatments.

In a previous study, we investigated the mechanisms that control SR in the semiarid Hungarian shrubland with extreme temperature and soil moisture regimes, by empirical modelling SR as a response function of temperature and moisture (*Lellei-Kovács et al., 2011*). Applying the same approaches, here we expand this work by modelling SR using two- or three-years of empirical data collected from seven different shrubland ecosystems across Europe with markedly different natural temperature and moisture regimes. We compared the performance of three empirical SR models, the exponential, the Lloyd-Taylor and the Gaussian functions, and integrated moisture into the models using additive and interactive approaches. The aims were to (i) investigate the effect of soil temperature and soil moisture content on SR in the different soils, and (ii) improve model predictions of SR under future climate change scenarios. We hypothesised, that: (i) the exponential model performs appropriately only in a relative narrow temperature range, (ii) the Gaussian temperature dependence function would be the best predictive SR model in ecosystems exposed to a relatively large temperature range, and (iii) inclusion of soil moisture thresholds would improve the predictive power of the models at sites where moisture is an obvious controlling factor (e.g. xeric or hydric ecosystems), whilst in mesic ecosystems the inclusion of moisture would have a smaller impact.

Material and methods

Characteristics of the studied shrubland ecosystems

The study was conducted along natural temperature and precipitation gradients across Europe (*Beier et al., 2009*), in seven different shrubland ecosystems (see Table 1, 2), that included four Atlantic heathlands at two sites in Denmark (Mols, DK-M, and Brandbjerg, DK-B), one site in the Netherlands (Oldebroek, NL), and one site in the United Kingdom (Clocaenog, UK) (*Sowerby et al., 2008*), two Mediterranean garrigues, one in Spain (Garraf, ES) (*Sardans et al., 2008*) and one in Italy (Capo Caccia, IT) (*de Dato et al., 2010*), and one shrubland in the Pannonian sandy forest steppe region in Hungary (Kiskunság, HU) (*Lellei-Kovács et al., 2011*). Meteorological data between 2001 and 2012 (except ES between 2002 and 2003 and DK-B between 2006 and 2012) were recorded either directly at the sites, or at standard meteorological stations located nearby (Table 1). Mean annual temperature ranges from 8.0 at the DK-B site to 16.8 at the IT site. Mean annual precipitation varies between 549 mm in IT and 1345 mm at the UK site. The variability of climate among sites could be expressed by the modified Gaussen-index (mean annual precipitation / 2 x mean annual temperature, *Peñuelas et al., 2007*) with higher aridity at its lower values (Table 1).

Field experiments and measurements

Plot-sized climate manipulation experiments were established in the seven shrubland ecosystems (see above). The experimental plots were subjected to either year-round passive night-time warming by insulating reflective curtains, extended drought periods by rain-activated transparent polyethylene roofs or an un-treated control since 1999 (ES, UK, NL, DK-M), since 2001 (HU, IT) or since 2005 (DK-B) (for detailed description of the experimental design and the effects on soil temperature and moisture, see at *Beier et al.,* *2004; Lellei-Kovács et al., 2008; Mikkelsen et al., 2008; de Dato et al., 2010*). In this study, we used data from different treatments together with data from control plots, i.e. a response surface approach, where treatments are seen as a widening of the natural range of environmental variables (see also *Lellei-Kovács et al., 2011, and Table S1 for data of the treatment effects on soil temperature, soil moisture and SR*).

Two or three years of SR measurements were conducted biweekly or monthly in the experimental plots, with exception of periods with snow cover and when the soil surface was frozen. Measurements were done between 2010 and 2012, but in ES between 2002 and 2003. SR data presented are the sum of autotrophic (root respiration) and heterotrophic (microbial respiration) soil processes. SR rates were measured by infrared gas exchange systems equipped with SR chambers: LI-6400XT with LI-6400-09 chamber (LICOR Biosciences, Lincoln, NE USA) in the NL and DK sites; LI-8100 with 8100-102 chamber (LICOR Biosciences, Lincoln, NE USA) in the UK and IT sites; EGM-3 (PP Systems, Hertfordshire, UK) in manual mode to analyze air samples from a closed-type, custom-built PVC chamber in ES; ADC Leaf Chamber Analyzer 4 with PLC & 2250 Soil hood (ADC BioScientific, Hoddesdon, UK) in HU. Three permanent subplots were used within each plot to capture within-plot heterogeneity, and plot means were used in the subsequent analyses. (For further details see: *Beier et al., 2009*; *de Dato et al., 2010; Lellei-Kovács et al., 2011; Kopittke et al., 2013*.) Micrometeorological variables were recorded in every plot continuously by automated instruments (Table 3): soil temperature at 5 cm below the soil surface, and volumetric soil moisture content at the defined soil depths (Table 2).

Soil properties including soil texture (mechanical and Pipet Method), soil organic matter content (Tyurin method or dry combustion) and soil pH (by potentiometer with glass electrode) were measured at each site at the given soil depths (Table 2) before starting the treatments. Wilting point and field capacity were determined from the soil moisture retention curve (pF curve) using soil samples from the sites (Table 5) at the defined soil depths (Table 2). An exception was IT, where soil texture data were used to determine wilting point and field capacity (*Saxton & Rawls, 2006*).

Empirical model of the temperature and moisture sensitivity of SR

For statistical evaluation, we followed the methodology used by *Lellei-Kovács et al. (2011)* and treated the datasets of the seven sites independently. Separate analyses for each site were necessary to account for differences in biota, organic matter content, texture, and moisture content (Table 2, 3).

We first fit three different temperature dependence models (see Equations 1-3). Each of the three response functions represents a possible relationship between increasing soil temperature and SR. Specifically: (i) the exponential function assumes that the logarithm of respiration is a linear function of temperature, thus the Q_{10} temperature coefficient is constant (Eq. 1); (ii) the Lloyd-Taylor function assumes that the influence of temperature change is higher at lower than at higher temperatures, thus the logarithm of respiration is a saturating function of temperature, and Q_{10} decreases with increasing temperature and its asymptote is one (i.e. at extremely high temperature there is no further change in respiration) (Eq. 2); and (iii) the Gaussian function presumes that there is an optimal temperature for SR. Above this optimum an increase in temperature causes a decline in SR. In this case Q_{10} is also a decreasing function of temperature, but it can fall below one (Eq. 3).

Equations 1-3. The models used to fit soil temperature and SR field data, where SR = soil respiration; T = soil temperature in Kelvin; a, b, and c are parameters of the models:

Eq. 1. Exponential: $SR = exp\,(a + bT)$;

Eq. 2. Lloyd-Taylor: $SR = exp\,(a + b\,/\,(T - c))$;

Eq. 3. Gaussian: $SR = \exp(a + bT + cT^2)$

After a log transformation of SR data, the exponential and the Gaussian functions (Eq. 1, 3) could be fit using linear regression. The Lloyd-Taylor function (Eq. 2) was fit by non-linear least squares regression also using log-transformed SR as a dependent variable to make the models statistically comparable, as discussed further below. To initialize the parameters of non-linear fit, parameter c was set to zero, while starting values of a and b were calculated by linear regression using $1/T$ as an independent variable.

In some cases, to preserve the expected shape of the fit curve, we had to apply constraints on the parameters of Equations 1-3. These constraints for the functions were:

Exponential: $b \geq 0$;
Gaussian: $c \leq 0$;
Lloyd-Taylor: $b \leq 0, c \geq 0$.

The potential effect of soil moisture content on SR was analysed comparing three different soil moisture inclusion methods in the temperature dependence models:

1. there is no inclusion of soil moisture content,
2. the effects of soil moisture content and soil temperature are additive (i.e. only parameter a depends on soil moisture content),
3. the effects of soil moisture content and soil temperature are interactive.

Combining the three temperature dependence functions and the three soil moisture effects resulted in nine models for each site. We treated the soil moisture effect as a categorical variable as we did not have any *a priori* knowledge of its functional form. Additive effect means that soil moisture influences only the parameter a, thus, within one model, temperature dependence curves of logSR are parallel at different moisture levels, while interaction means that soil moisture influences parameters b and c too resulting non-parallel temperature dependence curves of logSR.

In many cases, arbitrarily chosen cut-off points are used for transforming continuous variables into categories that introduces subjectivity into the modelling process. To avoid this problem, our categorizations were created by fitting decision tree models using a conditional inference framework that resulted in different soil moisture cut-off points depending on the applied temperature functions. When testing for additive effects, the residuals of the temperature functions were the dependent functions of the conditional inference trees (*Hothorn et al., 2006*) that searches for homogeneous groups of residuals (and thus parameter *a*) according to moisture values. We applied model-based recursive partitioning (*Zeileis et al., 2005*) to search for categories in soil moisture that were homogeneous in the parameters of temperature dependence. Because model-based partitioning can handle linear models only, we assumed that the parameter *c* of the Lloyd-Taylor function was independent of soil moisture, and equal to the value estimated in the first approach (no soil moisture effect). Based on this assumption, we fit the Lloyd-Taylor function by linear regression using $1/(T-c)$ as independent variable.

To compare the performance of SR models with different number of parameters, we used corrected Akaike Information Criteria (AICc) that combines fit and complexity of models; its smaller value indicates a better model (*Johnson & Omland, 2004*). Because log-transformed SR values were used as dependent variables in all models, AICc values calculated for different models were comparable (*Burnham & Anderson, 2002*). For statistical comparison of the models we calculated the Akaike weights (*Johnson & Omland, 2004*) of the models in two ways: (i) models that considered only soil temperature; (ii) all the nine models of the three temperature functions combined with the three ways of soil moisture inclusions. Akaike weights were calculated for each site and in each of aforementioned methods separately (see in Table 4). As the sum of Akaike weights calculated in one intercomparison is 1, the model with an Akaike weight above 0.9 was considered unequivocally the best, and all the others were not interpreted. In case of more models having Akaike weights above 0.1, all these models were accepted with approximately a similar level of support in the data (*Johnson & Omland, 2004*).

All statistical analyses were conducted in R statistical environment (*R Development Core Team, 2008*), tree models were fit using the *party* package (*Hothorn et al., 2006*).

Calculations of annual SR rates by the empirical models of SR

Based on the soil temperature and moisture models of SR demonstrated above, we calculated the annual SR using the daily measured soil temperature and soil moisture meteorological data for years 2010, 2011 and 2012 in the control plots at all but the ES site. For the ES site year-round daily soil moisture data were not available for the calculations. We estimated the median and the 90% confidence interval of the estimated annual SR using the Monte Carlo simulation: predicted values were calculated with parameters randomly chosen from a multivariate normal distribution with means and co-variances estimated by fitting 10,000 times. Because of the collinearity of partial derivatives with respect to the parameter *b* and *c* in the Lloyd-Taylor model, these parameters were associated with large values in the variance-covariance matrix, leading to extremely wide confidence intervals. Because the wide confidence intervals were an artefact of the non-linear regression, in the case of the Lloyd-Taylor model we decided to use only the predicted values.

Results

Variability of environmental factors and SR during the study

Soil texture varied among sites, with high sand content at HU, NL, DK-M and DK-B, high silt content at ES and UK, and relatively high clay content at the Mediterranean ES and IT sites. Soil pH was alkaline at HU, ES and IT, while it was acidic at the Atlantic UK, NL, DK-M and DK-B sites. Soil organic carbon content, the main substrate for SR, was highly variable among sites (Table 2).

Soil temperature, moisture and SR all differed markedly among the different sites and over the studied period (Table 3). Soil temperature at 5 cm depth showed the largest range in HU between 0.4°C in early spring and 40.5°C in summer, while the lowest range was recorded in the UK between 0.6°C in winter and 14.3°C in summer. Volumetric soil moisture content was always higher than the wilting point at the UK, DK-B, DK-M, and the NL sites, but could approach the wilting point at the ES, IT and HU sites (Table 5). The lower soil moisture content in ES and IT than the wilting point is due to the offset caused by the stone fraction (>2 mm) of these soils, which is not included in the determination of the wilting point and field capacity.

SR varied among sites during the measurement periods (Table 3). Overall mean of observed SR rates ranged from 0.84 μmol CO_2 m^{-2} s^{-1} at the HU site to 3.71 μmol CO_2 m^{-2} s^{-1} at the DK-M site.

Temperature control on SR

The best model fit based on Akaike's Information Criteria (AICc) value, varied among sites (Table 4a, Fig. 1). Refer to Table S2 for parameter estimates of the models.

At four of the seven study sites the exponential soil temperature-respiration model was not supported by the empirical data (i.e. Akaike weights were lower than 0.1). At the Mediterranean ES site, and the Continental HU site, with relatively wide soil temperature ranges (Table 3), we found the Gaussian temperature dependence function to be unequivocally the best model (Table 4b), while at the Atlantic heathland of the DK-M site the Lloyd-Taylor and the Gaussian temperature dependence functions also achieved a low AICc value, i.e. high Akaike weight. At the Atlantic heathland of DK-B the Lloyd-Taylor model showed the lowest AICc value and was accepted with approximately a level of support in the data similar to that of the Gaussian model (see Akaike weights in Table 4b).

At the other three sites, including the Capo Caccia (IT) with Mediterranean climate, and the Atlantic heathlands of Oldebroek (NL) and Clocaenog (UK), the exponential model showed the lowest AICc value, while the other two models were also supported by the data (Table 4a,b). However, at the NL and UK sites the Gaussian model had a c parameter of 0, which corresponds to the exponential model (see Table S2).

Additive and interactive soil temperature and soil moisture control on SR

Inclusion of soil moisture improved model performance in all cases. Table 5 shows the effects of soil moisture characteristics identified by conditional inference trees for the three temperature response functions of SR. We identified separate soil moisture intervals for every study site. Number of intervals ranges from 1 (DK-B, DK-M, NL) to 5 (HU, ES) (Table S2), suggesting the existence of thresholds in the soil moisture effect on SR. Thresholds identified at individual sites were very consistent across the three different models (Table S2). In additive models, functions fit for different soil moisture intervals differed in parameter a, which increased with increasing soil moisture, thus at the same temperature higher moisture resulted in higher SR.

Assuming interactions between soil moisture content and temperature, we found several soil moisture intervals that were homogeneous in the parameters of temperature dependence (Table S2). At most sites we could not find any trend in the parameter values of temperature dependence functions fit with changes in soil moisture intervals, resulting in crossing curves in the plotted functions (Fig. 2), suggesting that optimal soil temperature for SR depended also on moisture.

We found that in most cases (except the IT and the DK-B sites) only the models with an interactive soil moisture effect were supported by the empirical data. At the Mediterranean IT site the exponential temperature model with both additive and interactive moisture models were supported, as well as the Gaussian and the Lloyd-Taylor temperature functions with an interactive moisture effect (Table 4). (The Gaussian model with additive soil moisture model had a c parameter of 0, which corresponds to the exponential model (see Table S2)). The other exception was the Atlantic DK-B site where models with an additive soil moisture effect performed better, and the three temperature models were almost equally supported (Table 4a,c). At the Atlantic DK-M site the exponential function had unequivocally the best fit, whilst at the Atlantic NL and UK sites the exponential and the Lloyd-Taylor temperature functions, each with interactive moisture effect, were supported by the data (all these models had an Akaike weight above 0.1). At the Mediterranean ES and the Continental HU sites the Gaussian temperature model had the highest Akaike weight; at the HU site this model could be found being unequivocally better than any others, while at the ES site also the Lloyd-Taylor temperature model proved to be supported, all with interactive soil moisture integration (Table 4a,c).

Thresholds in soil moisture influencing soil temperature dependence of SR

The applied method revealed significant soil moisture thresholds in the temperature dependence functions showing how the temperature sensitivity was altered at different soil moisture levels. Some thresholds identified by the best model fits were close to the field capacity or wilting points of the studied ecosystems (Table 5), others may reflect characteristic temperature and moisture relations of a given season, see below.

The Continental HU and the Mediterranean ES sites had the most thresholds: these were at the zone of limited water availability approaching the wilting point, and near field capacity (Table 5, Fig. 2A,B). At the ES site the curve that represented the highest soil moisture threshold (at 22.2 Vol%, only found with the Lloyd-Taylor model) showed a decrease in SR under the highest soil moisture conditions, indicating lower microbial response to soil moisture during the colder days between November and March, when these higher soil moisture values occurred (Fig. 2B). At the other Mediterranean site in IT, one threshold point was also found above the wilting point, and a second threshold (only found with the additive moisture model) between the wet (winter and spring) and the dry (summer and early autumn) periods (Table 5, Fig. 2C). Similar to the curve of the Lloyd-Taylor model at the ES site, at the IT site the curve above this second threshold of the additive exponential model represents the wet season (highest soil moisture above 17.7 Vol% and lowest soil temperature below 15°C) (Fig. 2C). At the mesic DK-M, the only threshold for SR was found above the wilting point, but far below the field capacity value (Table 5, Fig. 2D). The similar DK-B site also presented this threshold (Table 5, Fig. 2E). At the mesic Atlantic NL site, the first threshold was found between wilting point and field capacity, while the next threshold was found near the field capacity, close to the third threshold. At the NL site, the lowest SR rates were measured at soil moisture contents between 23.7 and 28.2 Vol%, coinciding with the winter inactive period between October and March, while higher soil moisture occurred often in July and August. At soil moisture contents below 23.7 and above 28.2 Vol%, the SR rates increased with increasing soil moisture (Table 5, Fig. 2F). At the hydric Atlantic UK site two thresholds for SR were found near field capacity and also far above field capacity. In this wet ecosystem SR rates decreased with higher soil moisture content (Table 5, Fig. 2G), because of anaerobic soil conditions.

Annual SR

To compare the performances of the SR models, we calculated annual SR using the parameterized models (see model parameters in Table S2) and the daily meteorological data from the sites. The results for the six sites, HU, IT, DK-M, DK-B, NL and UK (Table 6) demonstrate that the annual SR estimated by the significant exponential models are in most cases higher than those estimated by the significant (DK-B) and non-significant (DK-M, NL) Gaussian models, however, the differences are mostly under 3%. Only at NL were the differences 7 to 25%. Also, for HU the non-significant exponential model overestimated SR relative to the significant Gaussian model. Only at the IT and UK sites did the exponential models not predict higher annual SR than the other models. At the IT site, the models produced similar estimates. At the UK site, depending on year, the estimates were either not significantly different or the Gaussian model predicted 20% higher annual SR than the exponential and Lloyd-Taylor models. Relative to models without moisture effects, models that included soil moisture resulted in 8, 2, and 14% higher estimates of annual SR for the mesic sites DK-M, DK-B and NL, respectively. For the semiarid HU and the arid IT sites, models without moisture effects underestimated annual SR when it was humid in 2010, but overestimated annual SR in drier years. For the hydric UK site this tendency was reversed, annual SR was overestimated by the models without moisture effects in the more humid years but underestimated annual SR in 2010 when precipitation was lowest (see Table 6). Soil organic matter content, used as a proxy for soil microbial activity, varied highly among the study sites (Table 2). Apart from the UK site, a significant relationship between annual SR and the soil organic matter content was found (Fig. 3 ; $r^2 = 0.961$). However, at the UK site with considerably higher soil organic matter content, estimated annual SR was near the mean rate at the other sites (Fig. 3), which is likely the result of anaerobic limitation of decomposition and the associated accumulation of organic matter at this site (Table 2).

Discussion

Temperature control on SR

To accurately predict SR from ecosystems in future climates it has become necessary to parameterise models with a wider range of temperatures than currently used. In this study we examined the temperature response functions of SR at seven European shrubland sites of different climatic conditions from Atlantic heathlands through Mediterranean macchias to Continental poplar shrubland, thus extending the temperature and moisture range of our previous SR investigations (*Lellei-Kovács et al., 2011*). In most previous field studies, the temperature-SR function used was fit to a relatively narrow range of soil temperatures, usually below 30°C. Typically, the exponential temperature function fits respiration data well in a relatively narrow temperature range below 30°C, whereas the relationship is weaker at higher temperatures. Thus our approach increases the predictive power when forecasting the response to a warming future climate, if temperatures are expected to be higher than 30°C (*Mielnick & Dugas, 2000*). When SR is studied under a wider range of temperatures, it is possible that the interaction of additional soil processes, such as substrate and water availability could alter respiration rates, resulting in lower respiration at higher soil temperatures (*Ågren et al., 1991; Tuomi et al., 2008; Reichstein & Beer, 2008; Lellei-Kovács et al., 2011; González-Ubierna et al., 2014*).

In the present study, at the Atlantic sites, we couldn't find a model that unequivocally explained one of the temperature-SR relationships, i.e. the exponential function fit was as good as the Gaussian and Lloyd-Taylor functions (Table 4b, Fig. 1). This was probably due to the narrow temperature range, always under the optimum temperature, making it impossible to detect differences in the shape of the three models. Despite our efforts to obtain data that spanned a large temperature range by including climate change treatments (Table S1), the measurements taken at the Atlantic sites biased the data to a narrower range than anticipated, with the soil temperature rarely exceeding 20°C. At the Mediterranean IT site, where the exponential SR models performed the best, soil temperature remained within the bounds of 7°C to 29°C. In this case, the relatively high winter soil temperature range was probably due to the strong moderating effect from the Mediterranean Sea that causes mild winter temperatures, in most cases above 10°C. It is therefore likely that at this site we were not able to detect either the lower or the upper temperature limitation on SR (Table 4b, Fig. 1).

At the ES and HU sites, the Gaussian function was found to be the best performing temperature-SR function. The Gaussian function assumes that there is an optimal temperature for SR, which can be detected only when field measurements are performed in a sufficiently broad range of temperatures (*Ågren et al., 1991; Lellei-Kovács et al., 2011; González-Ubierna et al., 2014*). The wide range of soil temperatures at the HU and ES sites (~40ºC) may explain why the Gaussian function proved to be the best.

The influence of soil moisture on the temperature sensitivity of SR

Our modelling approach integrated both soil moisture and temperature to examine the SR relationship. We revealed clear soil moisture thresholds in the temperature dependence of SR. This indicated that low soil moisture content was an important limiting factor of SR at both the seasonally dry Mediterranean and semiarid Continental sites, and also at the mesic Atlantic sites, whilst high soil moisture content imposing anaerobic conditions proved to limit SR at the hydric Atlantic site in the UK. In some cases, soil moisture thresholds could be connected to the wilting point or the field capacity (Table 5), but other thresholds might be related to more complex physiochemical or biological conditions (*Robinson et al., 2016*), such as the effect of soil moisture content on the availability of various soluble substrates or the effect of specific microbial enzymes with characteristic kinetic properties (*Davidson et al.,* *2006*). *Kopittke et al.* (*2014*) reported that integration of soil moisture at the mesic Atlantic NL site did not improve the model fit of the temperature dependence of SR for control treatments while it significantly improved the model fit for drought treatments. The lack of a moisture effect in control plots but appearance of an effect in the drought plots found by *Kopittke et al.* (*2014*) support our analytical approach of using all treatment data together in order to cover a wider environmental range within the same model. Under Mediterranean climate at the IT site *de Dato et al.* (*2010*) showed a significant difference between temperature sensitivity of the wet vegetative season and the dry non-vegetative season between 2002 and 2004. At this site we also found that the best fit of the exponential temperature function to the dataset between 2010 and 2011 was separated by soil moisture thresholds (Fig. 2C). These two approaches gave similar results in ecosystems where vegetation periods are determined by water availability.

Similar to our results, soil moisture content has been shown to enhance the response of SR to temperature in a continental arid desert (*Zhang et al., 2010*), in a semiarid steppe of Inner Mongolia (*Chen et al., 2009*) and in an old-field climate change experiment (*Suseela et al., 2012*). In the latter study, *Suseela et al.* (*2012*) observed that both an upper and a lower soil moisture threshold related to SR activity existed, and that changes in soil structural properties during drought resulted in a hysteresis effect. Soil moisture thresholds were also found to change SR responses to temperature in other studies. *Rey et al.* (*2002*) and *Guidolotti et al.* (*2013*) found a soil moisture threshold in Mediterranean forests, below which there was no correlation between SR and soil temperature. In a study of temperate forest ecosystems, *Wang et al.* (*2006*) found that increased temperature sensitivity (Q_{10}) was related to increasing soil moisture content, but that Q_{10} declined after reaching a soil moisture threshold. *Vicca et al.* (*2014*) also emphasized the importance of integrating soil moisture in the predictive models of SR, especially considering an altered moisture regime in the future. However, in the modelling approach of *Vicca et al.* (*2014*) soil temperature is integrated as a simple exponential function, which may weaken the extensibility of the models. For comparison, for the dataset of the ES site the exponential temperature and Gaussian moisture dependence (model 4 of *Vicca et al., 2014*) achieved an AIC of 271.63. If both temperature and moisture dependence were modelled with the Gaussian function and their effect was additive, then an AIC of 201.75 was achieved. However, for the same dataset, our model with a Gaussian temperature function and interactive moisture thresholds achieved an AIC of 152.99, indicating a better performance of the model.

Our results showed that the SR relationship with soil moisture, the latter depending mostly on precipitation, is non-monotonic, which is congruent with the findings of *Vicca et al.* (*2014*). In addition, at the plot scale this relationship can also be described as non-linear, with soil moisture thresholds being observed. We expect that the mechanisms that may explain our results are mediated by changes in the belowground community structure that are dependent on temperature and moisture (*Ågren & Wetterstedt, 2007*).

Soil moisture impacts SR directly by changing soil microbial activity and altering soil structure and porosity, and also indirectly by affecting substrate availability (*Davidson et al., 2006*). Under semiarid and arid conditions there is a strong edaphic water limitation coupled with strong pulse dynamics of resources linked to changes in microclimate (*Collins et al., 2008; Maestre et al., 2013*). The close connection between substrate availability and soil processes is also demonstrated by the relationship between annual SR and soil organic carbon content at the studied sites (Fig. 3). Similarly, *Fernandez et al.* (*2006*) demonstrated the impact of soil organic carbon and nitrogen on SR through soil texture and soil moisture availability in a cold desert ecosystem. They found that when soil moisture and temperature are both favourable, soil organic carbon and nitrogen cannot be used to predict SR. A limitation of soil substrate availability for microbes may explain why the Gaussian type soil temperature-SR model proved to be the best at the HU and ES sites (Table 5), where not only the temperature ranges were the largest (Table 3), but the soil organic matter content was also the lowest (Table 2).

Annual scale impacts on SR

The upscaled annual rates of SR showed profound differences among both years and models. As previously demonstrated at the HU site, annual SR rates calculated by the exponential function were systematically higher than those based on the Lloyd-Taylor and Gaussian functions (*Lellei-Kovács et al., 2011*). In this modelling experiment we also demonstrated that when excluding soil moisture from the models, modelled soil carbon fluxes may be overestimated especially for warm and dry years, which may be more frequent in the future. In the present study, annual SR values were also calculated from modelled data at six study sites (HU, IT, NL, DK-B, DK-M, UK), see Table 6. We found that the rate of annual SR in NL was very similar to the amount calculated by a different methodology by *Koppitke et al.* (2013, 2014) for the same period, which may validate these methods. Annual SR was also calculated in the work of *de Dato et al.* (*2010*) for three study years between 2002 and 2004, the values calculated were between 927 and 1145 g C m^{-2} y^{-1}, which are also similar to the values between 890 and 963 g C m^{-2} y^{-1} calculated by the method demonstrated here, for data between 2010 and 2011. At the UK site, annual SR decreased since 2000 because of a natural drought period that triggered an irreversible reduction in soil moisture and erosion of organic matter (*Robinson et al., 2016*). In the period between 2010 and 2012 annual SR was around 400 g C m^{-2} y^{-1} (*Domínguez et al., 2015*), which is also consistent with our results suggesting annual SR between 323 and 345 g C m^{-2} y^{-1}.

At every site, the models that included soil moisture, always improved the model fit compared to those that excluded soil moisture. Furthermore, at three of the four Atlantic sites, including soil moisture resulted in higher estimated annual SR, independently of the applied temperature dependence function. At the IT and the HU sites the direction of the alteration was dependent on the year: including soil moisture effect decreased the calculated annual SR in a drier year, and increased in a more humid year. The results are congruent with our previously published work, where excluding soil moisture resulted in an overestimation of rates of annual SR during a dry and hot year, but an underestimation of annual SR in a wet and cold year (*Lellei-Kovács et al., 2011*). In the present study, which considered the period 2010 to 2012, variation in soil moisture resulted in a difference of 1 to 25% in the outputs from the nine different models we considered. This variation in output warrants further investigation into the uncertainty of model estimations and highlights the importance of appropriate model choice in the prediction of the future impacts of climate change on SR of different ecosystems.

Conclusions

In this study of European shrubland ecosystems under Atlantic, Mediterranean or Continental climate we demonstrated that the temperature dependence function that best explains SR depended strongly on the temperature range where the study was conducted. We also showed that in these ecosystems when soil temperature range was above 30°C, the Gaussian function with optimum temperature provided a better fit to the data, than the exponential temperature function. Furthermore, we found that soil moisture strongly affected SR, not only in arid and semiarid, but also in mesic and hydric ecosystems, and the parameters of the temperature dependence functions changed significantly at distinctive soil moisture thresholds. These moisture thresholds may be connected to soil and ecosystem specific variables, such as wilting point of the plants or field capacity of the soil. In years with high precipitation and in mesic and hydric ecosystems the models that integrate moisture may estimate a higher level of annually respired carbon. These results highlight the importance of the choice from among the temperature dependence functions and the inclusion of soil moisture data when modelling SR, especially when predicting SR responses in a wide range of climatic conditions or in a changing climate.

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Figures

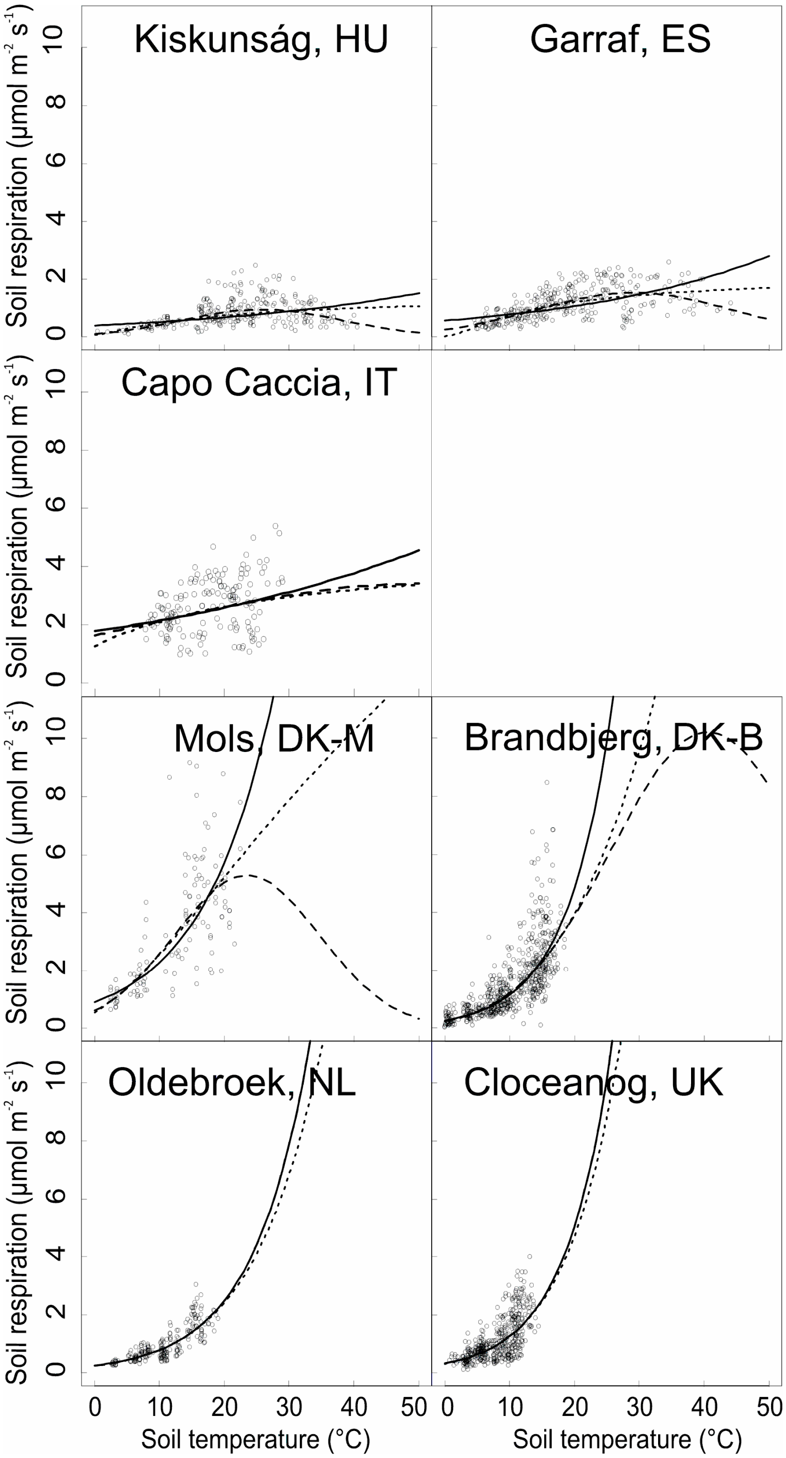
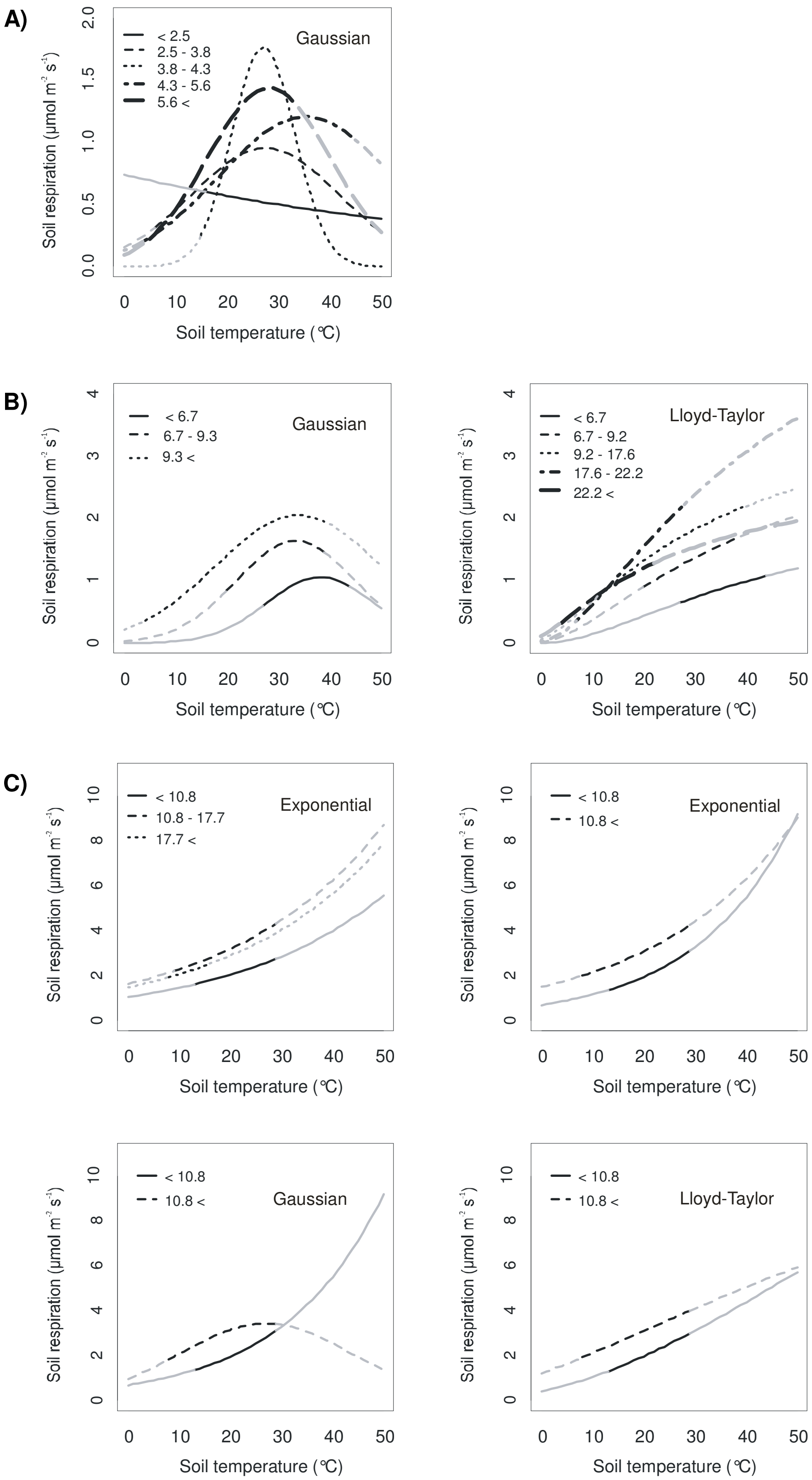


Figure 1.


A)
Gaussian
< 2.5
2.5 - 3.8
3.8 - 4.3
4.3 - 5.6
5.6 <
Soil respiration (μmol m⁻² s⁻¹)
0.0
0.5
1.0
1.5
2.0
Soil temperature (℃)
0
10
20
30
40
50
B)
Gaussian
< 6.7
6.7 - 9.3
9.3 <
Lloyd-Taylor
< 6.7
6.7 - 9.2
9.2 - 17.6
17.6 - 22.2
22.2 <
Soil respiration (μmol m⁻² s⁻¹)
0
1
2
3
4
Soil temperature (℃)
C)
Exponential
< 10.8
10.8 - 17.7
17.7 <
Exponential
< 10.8
10.8 <
Gaussian
< 10.8
10.8 <
Lloyd-Taylor
< 10.8
10.8 <
Soil respiration (μmol m⁻² s⁻¹)
0
2
4
6
8
10
Soil temperature (℃)

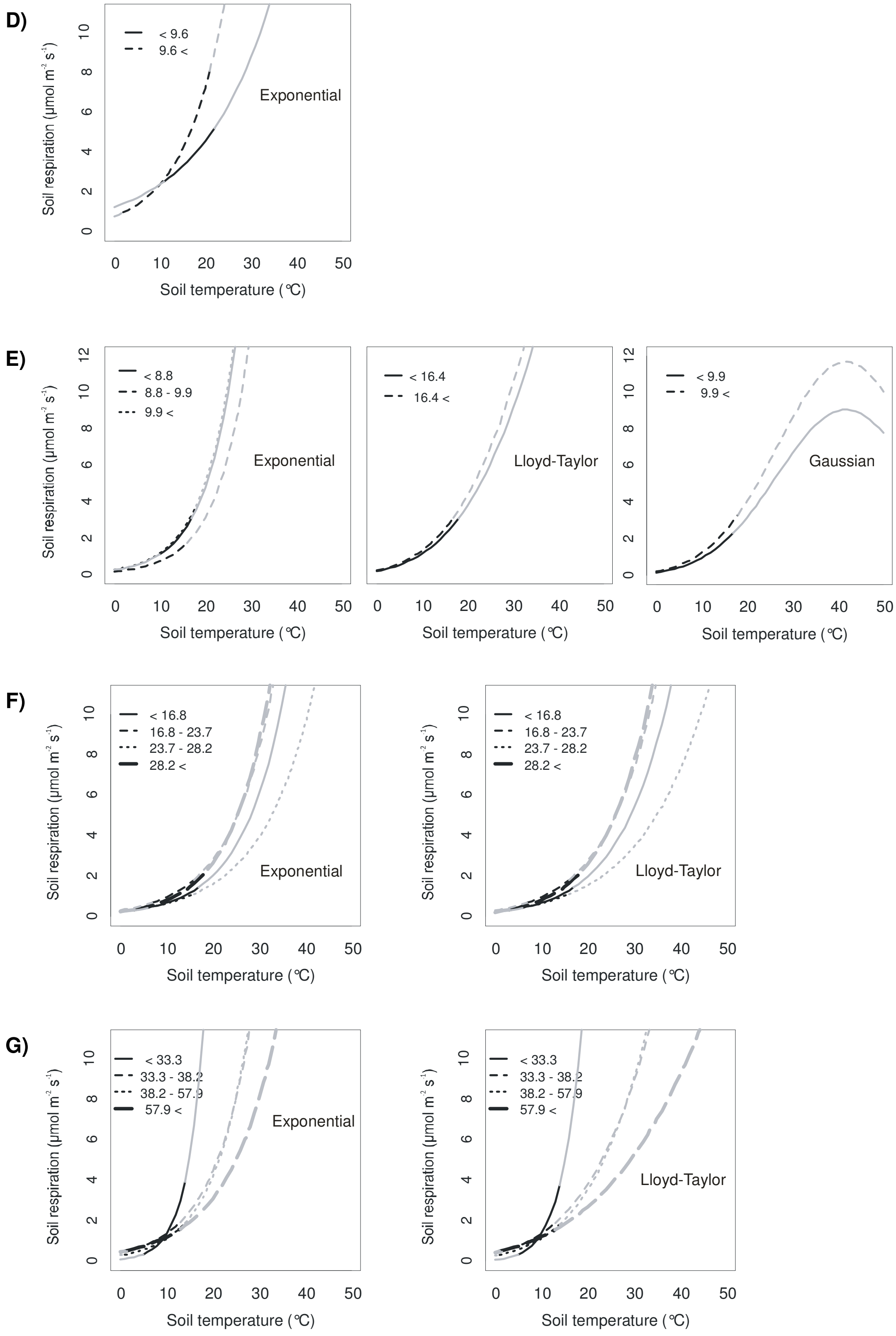

D)
< 9.6
9.6 <
Exponential
E)
< 8.8
8.8 - 9.9
9.9 <
Exponential
< 16.4
16.4 <
Lloyd-Taylor
< 9.9
9.9 <
Gaussian
F)
< 16.8
16.8 - 23.7
23.7 - 28.2
28.2 <
Exponential
Lloyd-Taylor
G)
< 33.3
33.3 - 38.2
38.2 - 57.9
57.9 <
Exponential
Lloyd-Taylor
Soil respiration (µmol m⁻² s⁻¹)
Soil temperature (℃)
0
2
4
6
8
10
12
0
10
20
30
40
50

Figure 2.

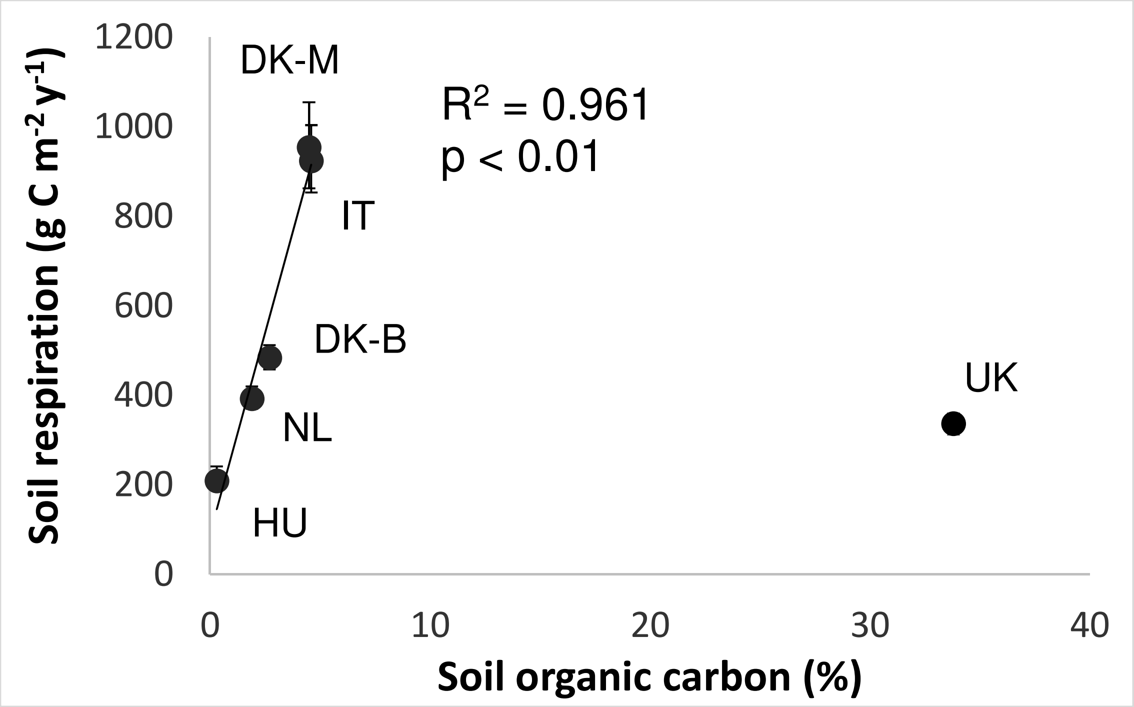

1200
1000
800
600
400
200
0
Soil respiration (g C m-2 y-1)
0
10
20
30
40
Soil organic carbon (%)
DK-M
IT
DK-B
NL
HU
UK
R² = 0.961
p < 0.01

Figure 3.

Figure legends

Figure 1. Empirical temperature dependence functions of soil respiration (Exponential as solid line, Lloyd-Taylor as dotted line and Gaussian as dashed line) fit to the data of the experimental sites with different climatic conditions. See Table S2 for parameter estimates of the functions.

Figure 2. Empirical temperature dependence models with moisture integration best fit to the site data; every box represents one of the nine models in one site, while each curve within a box is an individual soil moisture category of the models (see also Table 5); A) Kiskunság, HU; B) Garraf, ES; C) Capo Caccia, IT; D) Mols, DK-M; E) Brandbjerg, DK-B; F) Oldebroek, NL; G) Clocaenog, UK. Lines are black during the temperature intervals within which defined intervals of volumetric soil moisture contents occured in the field. Grey line segments mean extrapolated fittings outside the measured temperature range.

Figure 3. Relationship between the average annual soil respiration values (g C m^{-2} $year^{-1}$) calculated by the significant models and the soil organic carbon contents of six study sites: Kiskunság, Hungary (HU); Oldebroek, the Netherlands (NL); Brandbjerg, Denmark (DK-B); Mols, Denmark (DK-M); Capo Caccia, Italy (IT); Clocaenog, United Kingdom (UK). The ranges between the lowest and the highest annual soil respiration values calculated by all the presented models are shown to demonstrate the low interannual variability and the low variability of the model estimations compared to the high intersite variability. Apart from the UK site, a significant relationship between annual SR and the soil organic matter content is demonstrated.

Table 1. Characterization of the study sites.

Country	**Site**	**Location**	**Altitude**	**MAT (Jan.;July)**	**MAP**	**Gaussen-index (MAP / 2MAT)**
			m	°C	mm	
HU	Kiskunság	46°52'N, 19°25'E	108	10.9 (-0.1;22.0)	569	26.1
ES	Garraf	41°18'N 01°49'E	210	15.9 (8.6;24.2)	568	17.9
IT	Capo Caccia	40°36'N 08°09'E	35	16.4 (9.5;23.6)	549	16.7
DK	Mols	56°23'N 10°57'E	58	8.7 (1.1;17.9)	644	37.0
DK	Brandbjerg	55°53'N 11°58'E	2	8.0 (1.6;19.4)	613	38.3
NL	Oldebroek	52°24'N 05°55'E	25	10.5 (3.8;18.2)	1004	47.8
UK	Clocaenog	53°03'N 03°28'W	490	8.2 (3.2;13.7)	1345	82.0

Table 2. Soil characteristics of the study sites.

Country	Site	Soil type	Soil depth	Sand	Silt	Clay	pH	SOC
			cm	Soil texture %				%
HU	Kiskunság	Calcaric Arenosol	0 – 20	97.5	1.8	0.7	8.0	0.3
ES	Garraf	Petric Calcisol	0 – 12	42.9	38.7	18.4	8.1	1.3
IT	Capo Caccia	Chromic Luvisols	0 – 20	75.4	11.2	13.4	7.7	4.6
DK	Mols	Haplic Podzol	0 – 20 (*3*)	91.4	2.9	5.7	3.8	4.5
DK	Brandbjerg	Haplic Podzol	0 – 32 (*2*)	91.7	5.9	2.4	3.9	2.7
NL	Oldebroek	Haplic Podzol	0 – 16 (*4*)	93.5	6.0	0.5	3.8	1.9
UK	Clocaenog	Humo-ferric Podzol	0 – 17 (*6*)	40.2	50.0	9.8	3.8	33.8

Table 3. Measurement periods and ranges of soil temperature, moisture, and respiration.

Country	**Site**	**Measurement periods**	**Soil temperature**	**Soil moisture**	**Soil respiration**
		yyyy.mm	℃	*Vol%*	*µmol m $^{-2}$ s $^{-1}$*
HU	Kiskunság	2010.04 - 2012.11	0.40 - 40.50 (**21.97**)	2.0 - 8.1 (**4.1**)	0.11 - 2.48 (**0.84**)
ES	Garraf	2002.04 - 2003.12	4.35 - 44.25 (**19.04**)	5.6 - 31.6 (**19.0**)	0.27 - 2.60 (**1.16**)
IT	Capo Caccia	2010.02 - 2011.11	7.73 - 28.85 (**17.59**)	3.2 - 27.6 (**14.8**)	0.98 - 5.38 (**2.65**)
DK	Mols	2011.05 - 2012.09	2.32 - 22.30 (**12.82**)	5.8 - 18.3 (**12.3**)	0.65 - 17.66 (**3.71**)
DK	Brandbjerg	2011.03 - 2012.12	-0.25 - 18.48 (**9.93**)	5,4 - 30.2 (**16.3**)	0.02 - 8.48 (**1.59**)
NL	Oldebroek	2010.07 - 2012.06	2.49 - 18.89 (**10.46**)	7.4 - 39.9 (**24.7**)	0.26 - 3.05 (**0.98**)
UK	Clocaenog	2010.01 - 2012.12	0.60 - 14.29 (**7.91**)	8.7 - 71.4 (**41.7**)	0.13 - 4.00 (**1.15**)

Table 4. Results of the model intercomparisons: AICc values and Akaike weights.

a)

	Soil moisture is not considered			Additive effect between temperature and moisture			Interaction between temperature and moisture		
Site, Country	**Exponential**	**Lloyd-Taylor**	**Gaussian**	**Exponential**	**Lloyd-Taylor**	**Gaussian**	**Exponential**	**Lloyd-Taylor**	**Gaussian**
Kiskunság, HU	413.34	371.27	**326.48**	356.75	296.00	**263.50**	282.98	304.67	**246.62**
Garraf, ES	364.00	297.03	**285.46**	191.32	**185.53**	186.78	169.95	154.55	**153.58**
Capo Caccia, IT	**125.22**	127.01	127.14	**85.96**	106.56	87.96	**86.13**	87.92	88.26
Mols, DK	142.24	136.66	**135.13**	142.24	136.66	**135.13**	**131.24**	136.66	135.13
Brandjberg, DK	879.75	**874.19**	874.82	**864.36**	864.66	866.01	879.75	**874.19**	874.82
Oldebroek, NL	**107.07**	109.72	109.13	**107.07**	109.72	109.13	**67.36**	69.83	91.94
Clocaenog, UK	**610.37**	613.28	612.39	**595.29**	598.32	597.33	**565.46**	567.32	573.72

b)

Akaike-weights			
	Soil moisture is not considered		
Site, Country	**Exponential**	**Lloyd-Taylor**	**Gaussian**
Kiskunság, HU	<0.01	<0.01	**1.0000**
Garraf, ES	<0.01	<0.01	**0.9969**
Capo Caccia, IT	***0.5679***	***0.2231***	***0.2090***
Mols, DK	0.0191	***0.3115***	***0.6694***
Brandjberg, DK	0.0346	***0.5581***	***0.4073***
Oldebroek, NL	***0.6156***	***0.1641***	***0.2203***
Clocaenog, UK	***0.6266***	***0.1458***	***0.2276***

c)

Akaike-weights									
	Soil moisture is not considered			Additive effect between temperature and moisture			Interaction between temperature and moisture		
Site, Country	**Exponential**	**Lloyd-Taylor**	**Gaussian**	**Exponential**	**Lloyd-Taylor**	**Gaussian**	**Exponential**	**Lloyd-Taylor**	**Gaussian**
Kiskunság, HU	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	**0.9998**
Garraf, ES	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	***0.3809***	***0.6190***
Capo Caccia, IT	<0.01	<0.01	<0.01	***0.3437***	<0.01	***0.1182***	***0.3157***	***0.1206***	***0.1018***
Mols, DK	<0.01	0.0406	0.0873	<0.01	0.0406	0.0873	**0.6114**	0.0406	0.0873
Brandjberg, DK	<0.01	<0.01	<0.01	***0.4301***	***0.3701***	***0.1885***	<0.01	<0.01	<0.01
Oldebroek, NL	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	***0.7747***	***0.2253***	<0.01
Clocaenog, UK	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	***0.7087***	***0.2799***	0.0114

Table 5. The best fit soil temperature-soil respiration models.

Country	**Site**	**Wilting point (Vol%)**	**Field capacity (Vol%)**	**The BEST temp. models with moist. integration**	**Threshold moisture values (Vol%) of the BEST models (p<0.05).**
HU	Kiskunság	1.0	8.0	Gaussian	**2.5** ; **3.8** ; 4.3 ; **5.6**
ES	Garraf	8.0	26.0	Lloyd-Taylor, Gaussian	**6.7** ; **9.2**^{L} ; **9.3**^{G} ; 17.6^{L} ; **22.2**^{L}
IT	Capo Caccia	7.8	28.0	Exponential, Lloyd-Taylor, Gaussian	**10.8** ; **17.7**^{Additive}
DK	Mols	4.0	18.0	Exponential	9.6
DK	Brandbjerg	2.5	38.0	Exponential, Lloyd-Taylor, Gaussian	8.8^{E} ; 9.9^{E,G} ; 16.4^{L}
NL	Oldebroek	4.5	34.5	Exponential, Lloyd-Taylor	16.8 ; **23.7** ; 28.2
UK	Clocaenog	7.0	39.0	Exponential, Lloyd-Taylor	**33.3** ; 38.2 ; 57.9

Table 6. Annual soil respiration values (g C m^{-2} year^{-1}) from six study sites.

a)

Country	Year	No soil moisture effect		
		Exponential	Lloyd-Taylor	Gaussian
HU	**2010**	216.7 (201.9 , 232.3)	188.4	198.9 (189.2 , 209.1)
	2011	220.2 (205.9 , 236.2)	192.8	206.3 (196.5 , 216.7)
	2012	225.0 (211.2 , 240.5)	198.1	208.7 (199.1 , 219.2)
IT	**2010**	931.2 (889.2 , 976.7)	928.9	930.5 (887.7 , 975.5)
	2011	939.1 (895.9 , 984.6)	935.5	938.1 (894.1 , 983.9)
DK-M	**2011**	914.5 (858.0 , 974.4)	944.3	959.3 (896.1 , 1027.1)
	2012	866.2 (809.8 , 924.5)	899.3	914.9 (853.2 , 980.1)
DK-B	**2011**	499.8 (481.9 , 518.2)	492.2	492.7 (474.7 , 511.4)
	2012	456.6 (441.3 , 472.1)	455.0	455.4 (440.3 , 471.4)
NL	**2011**	350.4 (337.7 , 363.8)	348.8	350.4 (337.7 , 363.8)
	2012	340.9 (328.6 , 353.3)	339.5	340.9 (328.6 , 353.3)
UK	**2010**	338.5 (326.7 , 350.8)	337.4	338.5 (326.7 , 350.8)
	2011	362.7 (349.9 , 375.9)	362.4	362.7 (349.9 , 375.9)
	2012	346.3 (334.3 , 358.7)	345.7	346.3 (334.3 , 358.7)

b)

Country	Year	Additive soil moisture effect			Interactive soil moisture effect		
		Exponential	Lloyd-Taylor	Gaussian	Exponential	Lloyd-Taylor	Gaussian
HU	**2010**	217.0 (204.4 , 230.5)	212.0	218.2 (206.6 , 230.7)	232.4 (219.1 , 247.2)	194.4	**225.3** (210.8 , 241.3)
	2011	224.6 (211.8 , 238.2)	199.9	209.0 (200.0 , 218.6)	207.3 (196.4 , 218.6)	180.3	**201.9** (192.0 , 212.6)
	2012	222.9 (210.4 , 235.9	201.4	208.4 (199.7 , 217.5)	206.2 (195.6 , 217.4)	197.5	**199.7** (190.2 , 210.0)
IT	**2010**	**939.0** (897.7 , 982.2)	910.3	**939.0** (897.7 , 982.2)	**957.8** (917.1 , 1000.6)	**957.9**	**963.3** (926.1 , 1002.4)
	2011	**889.3** (852.6 , 927.9)	880.5	**889.3** (852.6 , 927.9)	**903.1** (864.3 , 943.4)	**901.2**	**901.6** (873.8 , 931.3)
DK-M	**2011**	914.5 (858.0 , 974.4)	944.3	959.3 (896.1 , 1027.1)	**985.2** (919.6 , 1055.2)	944.3	959.3 (896.1 , 1027.1)
	2012	866.2 (809.8 , 924.5)	899.3	914.9 (853.2 , 980.1)	**923.6** (862.2 , 987.2)	899.3	914.9 (853.2 , 980.1)
DK-B	**2011**	**511.9** (492.9 , 531.5)	**512.3**	**504.6** (494.3 , 515.6)	499.8 (481.9 , 518.2)	492.2	492.7 (474.7 , 511.4)
	2012	**461.0** (445.8 , 477.0)	**456.0**	**458.3** (453.7 , 463.3)	456.6 (441.3 , 472.1)	455.0	455.4 (440.3 , 471.4)
NL	**2011**	350.4 (337.7 , 363.8)	348.8	350.4 (337.7 , 363.8)	**393.1** (369.7 , 418.0)	**391.4**	364.2 (298.0 , 451.2)
	2012	340.9 (328.6 , 353.3)	339.5	340.9 (328.6 , 353.3)	**393.5** (369.5 , 420.1)	**392.8**	296.4 (266.2 ,327.0)
UK	**2010**	335.5 (323.8 , 347.4)	335.9	335.5 (323.8 , 347.4)	**342.9** (330.0 , 356.3)	**340.9**	340.0 (328.8 , 351.0)
	2011	354.8 (342.3 , 367.8)	356.2	354.8 (342.3 , 367.8)	**345.1** (331.1 , 359.9)	**345.2**	348.8 (336.5 , 361.7)
	2012	329.7 (317.1 , 343.3)	330.8	329.7 (317.1 , 343.3)	**323.4** (310.6 , 336.6)	**322.8**	388.9 (384.0 , 395.5)

Table legends

Table 1. Characterization of the study sites.

MAT (mean annual temperature) and MAP (mean annual precipitation) between 2001 and 2012, except for ES between 2002 and 2003 and DK-B between 2006 and 2012. Gaussen-index of aridity, as modified by Peñuelas et al. (2007) related to annual climatic data of the study sites, highlighting the climatic differences between them.

Table 2. Soil characteristics of the study sites.

Soil depth stands for the sampling depth for soil moisture and other measurements, representing the most active soil layers. Parenthetical numbers represents the thickness of the organic soil layers; pH was measured in H_2O; SOC stands for the soil organic carbon content.

Table 3. Measurement periods and ranges of soil temperature at 5 cm soil depth, soil moisture measured in the soil depths presented in Table 2., and soil respiration during the measurements. Overall average values are in bold within brackets.

Table 4. Results of the model intercomparisons: a) Corrected Akaike Information Criterion (AICc) values of all temperature dependence models (Eq. 1-3); best AICc values by moisture considerations are in bold; b) Akaike weights of the models without considering soil moisture; c) Akaike weights of all models compared. Values of supported models (>0.1) are in bold and italic. In case of only one supported model, Akaike weight is highlighted in bold.

Table 5. The best fit soil temperature-soil respiration models according to the AIC, and the thresholds in soil moisture of the best models ($p<0.05$), ranked by the splitting up points of the decision trees; thresholds in moisture at $p<0.01$ significance level are highlighted. When a threshold is not supported by all the significant models, it is marked with the abbreviation of the concerned models. The field capacity at pF=2.1 (-0.02 MPa) and wilting point at pF=4.2 (-1.58 MPa) for every site are also included to help the comparison of the thresholds.

Table 6. Annual soil respiration values (g C m^{-2} $year^{-1}$) from six study sites, median and, for the exponential and the Gaussian models only, the boundaries of the 90% confidence interval in brackets. Calculations by the 9 models were based on the site meteorological data in the control plots of each site. (Confidence intervals would be extremely wide for the Lloyd-Taylor model because of the collinearity between its parameters.) Annual values by the overall best fit models are highlighted.

Supplemental Material

Table S1. Measurement periods and ranges of soil temperature, soil moisture, and soil respiration of the seven sites in the control, drought and warming treatments during the measurements.

Table S2. Model parameters of the nine temperature dependence models of the seven sites.