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

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

3                    **Page heading: Temperature dependence of soil respiration**

4  
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44 and ELK wrote the paper.

45

46

47 *Type of Paper: Original Article*

48

49

50 **Abstract**

51 Soil respiration (SR) is a major component of the global carbon cycle and plays a  
52 fundamental role in ecosystem feedback to climate change. Empirical modelling is an  
53 essential tool for predicting ecosystem responses to environmental change, and also provides  
54 important data for calibrating and corroborating process-based models. In this study, we  
55 evaluated the performance of three empirical temperature-SR response functions  
56 (Exponential, Lloyd-Taylor and Gaussian) at seven shrublands located within three climatic  
57 regions (Atlantic, Mediterranean and Continental) across Europe. We investigated the  
58 performance of SR models by including interaction between soil moisture and soil  
59 temperature. We found that the best fit for the temperature functions depended on the site  
60 specific climatic conditions. Including soil moisture we identified thresholds in the three  
61 different response functions that improved the model fit in all cases. The direct soil moisture  
62 effect on SR, however, was weak at the annual time scale. We conclude that the exponential  
63 soil temperature function may only be a good predictor for SR in a narrow temperature range,  
64 and that extrapolating predictions for future climate based on this function should be treated  
65 with caution as modelled outputs may underestimate SR. The addition of soil moisture  
66 thresholds improved the model fit at all sites, but had a far greater ecological significance in  
67 the wet Atlantic shrubland where a fundamental change in the soil CO<sub>2</sub> efflux would likely  
68 have an impact on the whole carbon budget.

69

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

72

73 **Introduction**

74 Soil respiration (SR) is a dominant component of the terrestrial carbon cycle and has a  
75 significant influence on global radiative forcing (*IPCC 2013*). In terrestrial ecosystems  
76 atmospheric CO<sub>2</sub> is assimilated during photosynthesis, and then released either via  
77 autotrophic respiration or through heterotrophic decomposition of carbon compounds  
78 differing in recalcitrance and sensitivity to temperature (*Davidson & Janssens, 2006*). Both  
79 soil moisture availability and temperature may alter with a changing climate, and this will  
80 affect decomposition processes and root activity, potentially changing rates of CO<sub>2</sub> efflux  
81 from soils. However, it is poorly understood how altered temperature and soil moisture  
82 availability will affect soil CO<sub>2</sub> efflux across multiple ecosystems. In fact, because of the  
83 interaction of multiple environmental processes often occurring simultaneously it is hard to  
84 make predictions beyond empirical data bounds (*Vicca et al., 2014*). SR response functions  
85 derived from empirical data collected at different temporal and spatial scales could be useful  
86 for improving the predicted impact of future climate on ecosystem processes (*Kirschbaum,*  
87 *2004; Vicca et al., 2014*).

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

98 (*Lloyd & Taylor, 1994; Tuomi et al., 2008; Reichstein & Beer, 2008; Lellei-Kovács et al.,*  
99 *2011; González-Ubierna et al., 2014*).

100 Occasionally, to improve on the fit of a simple exponential model, a wider  
101 environmental range has been incorporated by fitting separate functions to subranges of  
102 temperature (*Murthy et al., 2003, Bradford et al., 2008*) and soil depth (*Pavelka et al., 2007*)  
103 or to Mediterranean wet versus dry seasons (*de Dato et al., 2010*). Other studies have used  
104 additional parameters to account for factors other than temperature like soil moisture content  
105 (*Suseela et al., 2012; Kopittke et al., 2013; Wang et al., 2014*), soil physical and chemical  
106 properties (*Wang et al., 2003; Balogh et al., 2011; Kotroczó et al., 2014*), different substrate  
107 availability (*Davidson et al., 2006*), or different SOM content and quality (*Curiel Yuste et al.,*  
108 *2010*). Other studies have also attempted to provide mechanistic explanations for the  
109 temperature dependence of SR (*Davidson et al., 2006; von Lützow & Kögel-Knabner, 2009*).  
110 In a review, *Billings & Ballantyne (2013)* examined the mechanisms that are linked to SR,  
111 and reported that temperature induced changes in microbial community structure, microbial  
112 metabolic rates and catalytic rate of exo-enzymes may lead to a decline of SR as a response to  
113 an increase in the soil temperature.

114 The relationship between soil moisture and SR has been modelled using many  
115 different functions that include linear (*Leirós et al., 1999*), exponential (*Rodrigo et al., 1997*),  
116 second-order exponential, i.e. Gaussian (*Howard & Howard, 1993; Mielnick & Dugas, 2000;*  
117 *Vicca et al., 2014*) and reverse exponential (*Zhou et al., 2007*) relationships. Limitation of SR  
118 by soil moisture has been observed when substrate diffusion is limited by low soil water  
119 availability (*Howard & Howard, 1993*), but also when the diffusion of O<sub>2</sub> is restricted by high  
120 soil water content (*Skopp et al., 1990*). Mechanistic studies of the relationship between soil  
121 moisture and SR conducted by *Davidson et al. (2006)* revealed that CO<sub>2</sub> efflux is not only  
122 influenced by moisture induced changes in soil physical properties, but also, autotrophic root

123 respiration and heterotrophic microbial decomposition are directly impacted by changes in  
124 soil moisture. Evaluation of the impact of soil moisture is more difficult than that of  
125 temperature because the efficiency of water uptake is influenced by various soil physical  
126 properties and also by physiological processes of the organisms. At any given soil moisture  
127 content water uptake may differ for numerous reasons such as soil texture (sand or clay), plant  
128 water use efficiency, stress tolerance and soil microbial composition (e.g. fungal to bacterial  
129 ratio) (*Moyano et al., 2013*).

130         The approaches to study the combined impact of temperature and moisture on SR  
131 modelling differ in two fundamental ways: 1. additive versus interactive (*Mielnick & Dugas,*  
132 *2000; Reichstein et al., 2002; Qi et al., 2002; Xu et al., 2004; Zhou et al., 2006*); 2.  
133 continuous versus threshold (*Davidson et al., 1998; Reichstein et al., 2002; Rey et al., 2002;*  
134 *Fernandez et al., 2006; Yan et al., 2011*). Moisture thresholds that alter SR activities  
135 significantly may be very important in modelling carbon fluxes, not only in arid and semiarid,  
136 but also in mesic ecosystems (*Suseela et al., 2012*).

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

148 drought reduced the rate of SR. In the Italian Mediterranean shrubland *de Dato et al. (2010)*  
149 observed a temporary decrease in SR as a short-term response to the warming and drought  
150 treatments.

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

168

169



170 **Material and methods**

171

172 *Characteristics of the studied shrubland ecosystems*

173 The study was conducted along natural temperature and precipitation gradients across Europe  
174 (*Beier et al., 2009*), in seven different shrubland ecosystems (see Table 1, 2), that included  
175 four Atlantic heathlands at two sites in Denmark (Mols, DK-M, and Brandbjerg, DK-B), one  
176 site in the Netherlands (Oldebroek, NL), and one site in the United Kingdom (Clocaenog,  
177 UK) (*Sowerby et al., 2008*), two Mediterranean garrigues, one in Spain (Garraf, ES) (*Sardans  
178 et al., 2008*) and one in Italy (Capo Caccia, IT) (*de Dato et al., 2010*), and one shrubland in  
179 the Pannonian sandy forest steppe region in Hungary (Kiskunság, HU) (*Lellei-Kovács et al.,  
180 2011*). Meteorological data between 2001 and 2012 (except ES between 2002 and 2003 and  
181 DK-B between 2006 and 2012) were recorded either directly at the sites, or at standard  
182 meteorological stations located nearby (Table 1). Mean annual temperature ranges from 8.0 at  
183 the DK-B site to 16.8 at the IT site. Mean annual precipitation varies between 549 mm in IT  
184 and 1345 mm at the UK site. The variability of climate among sites could be expressed by the  
185 modified Gausse-index (mean annual precipitation / 2 x mean annual temperature, *Peñuelas  
186 et al., 2007*) with higher aridity at its lower values (Table 1).

187

188 *Field experiments and measurements*

189 Plot-sized climate manipulation experiments were established in the seven shrubland  
190 ecosystems (see above). The experimental plots were subjected to either year-round passive  
191 night-time warming by insulating reflective curtains, extended drought periods by rain-  
192 activated transparent polyethylene roofs or an un-treated control since 1999 (ES, UK, NL,  
193 DK-M), since 2001 (HU, IT) or since 2005 (DK-B) (for detailed description of the  
194 experimental design and the effects on soil temperature and moisture, see at *Beier et al.,*

195 2004; *Lellei-Kovács et al., 2008; Mikkelsen et al., 2008; de Dato et al., 2010*). In this study,  
196 we used data from different treatments together with data from control plots, i.e. a response  
197 surface approach, where treatments are seen as a widening of the natural range of  
198 environmental variables (see also *Lellei-Kovács et al., 2011, and Table S1 for data of the*  
199 *treatment effects on soil temperature, soil moisture and SR*).

200 Two or three years of SR measurements were conducted biweekly or monthly in the  
201 experimental plots, with exception of periods with snow cover and when the soil surface was  
202 frozen. Measurements were done between 2010 and 2012, but in ES between 2002 and 2003.  
203 SR data presented are the sum of autotrophic (root respiration) and heterotrophic (microbial  
204 respiration) soil processes. SR rates were measured by infrared gas exchange systems  
205 equipped with SR chambers: LI-6400XT with LI-6400-09 chamber (LICOR Biosciences,  
206 Lincoln, NE USA) in the NL and DK sites; LI-8100 with 8100-102 chamber (LICOR  
207 Biosciences, Lincoln, NE USA) in the UK and IT sites; EGM-3 (PP Systems, Hertfordshire,  
208 UK) in manual mode to analyze air samples from a closed-type, custom-built PVC chamber  
209 in ES; ADC Leaf Chamber Analyzer 4 with PLC & 2250 Soil hood (ADC BioScientific,  
210 Hoddesdon, UK) in HU. Three permanent subplots were used within each plot to capture  
211 within-plot heterogeneity, and plot means were used in the subsequent analyses. (For further  
212 details see: *Beier et al., 2009; de Dato et al., 2010; Lellei-Kovács et al., 2011; Kopittke et al.,*  
213 *2013*.) Micrometeorological variables were recorded in every plot continuously by automated  
214 instruments (Table 3): soil temperature at 5 cm below the soil surface, and volumetric soil  
215 moisture content at the defined soil depths (Table 2).

216 Soil properties including soil texture (mechanical and Pipet Method), soil organic  
217 matter content (Tyurin method or dry combustion) and soil pH (by potentiometer with glass  
218 electrode) were measured at each site at the given soil depths (Table 2) before starting the  
219 treatments. Wilting point and field capacity were determined from the soil moisture retention

220 curve (pF curve) using soil samples from the sites (Table 5) at the defined soil depths (Table  
221 2). An exception was IT, where soil texture data were used to determine wilting point and  
222 field capacity (Saxton & Rawls, 2006).

223

#### 224 *Empirical model of the temperature and moisture sensitivity of SR*

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

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

240

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

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

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

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

246

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

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

255 Exponential:  $b \geq 0$  ;

256 Gaussian:  $c \leq 0$  ;

257 Lloyd-Taylor:  $b \leq 0, c \geq 0$  .

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

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

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

270 dependence curves of logSR.

271 In many cases, arbitrarily chosen cut-off points are used for transforming continuous  
272 variables into categories that introduces subjectivity into the modelling process. To avoid this  
273 problem, our categorizations were created by fitting decision tree models using a conditional  
274 inference framework that resulted in different soil moisture cut-off points depending on the  
275 applied temperature functions. When testing for additive effects, the residuals of the  
276 temperature functions were the dependent functions of the conditional inference trees  
277 (*Hothorn et al., 2006*) that searches for homogeneous groups of residuals (and thus parameter  
278  $a$ ) according to moisture values. We applied model-based recursive partitioning (*Zeileis et al.,*  
279 *2005*) to search for categories in soil moisture that were homogeneous in the parameters of  
280 temperature dependence. Because model-based partitioning can handle linear models only, we  
281 assumed that the parameter  $c$  of the Lloyd-Taylor function was independent of soil moisture,  
282 and equal to the value estimated in the first approach (no soil moisture effect). Based on this  
283 assumption, we fit the Lloyd-Taylor function by linear regression using  $1/(T-c)$  as  
284 independent variable.

285 To compare the performance of SR models with different number of parameters, we  
286 used corrected Akaike Information Criteria (AICc) that combines fit and complexity of  
287 models; its smaller value indicates a better model (*Johnson & Omland, 2004*). Because log-  
288 transformed SR values were used as dependent variables in all models, AICc values  
289 calculated for different models were comparable (*Burnham & Anderson, 2002*). For statistical  
290 comparison of the models we calculated the Akaike weights (*Johnson & Omland, 2004*) of  
291 the models in two ways: (i) models that considered only soil temperature; (ii) all the nine  
292 models of the three temperature functions combined with the three ways of soil moisture  
293 inclusions. Akaike weights were calculated for each site and in each of aforementioned  
294 methods separately (see in Table 4). As the sum of Akaike weights calculated in one inter-

295 comparison is 1, the model with an Akaike weight above 0.9 was considered unequivocally  
296 the best, and all the others were not interpreted. In case of more models having Akaike  
297 weights above 0.1, all these models were accepted with approximately a similar level of  
298 support in the data (*Johnson & Omland, 2004*).

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

301

### 302 *Calculations of annual SR rates by the empirical models of SR*

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

315

316 **Results**

317

318 *Variability of environmental factors and SR during the study*

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

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

333 SR varied among sites during the measurement periods (Table 3). Overall mean of  
334 observed SR rates ranged from 0.84  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at the HU site to 3.71  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$   
335 at the DK-M site.

336

337 *Temperature control on SR*

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

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

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

354

### 355 *Additive and interactive soil temperature and soil moisture control on SR*

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



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

371 We found that in most cases (except the IT and the DK-B sites) only the models with  
372 an interactive soil moisture effect were supported by the empirical data. At the Mediterranean  
373 IT site the exponential temperature model with both additive and interactive moisture models  
374 were supported, as well as the Gaussian and the Lloyd-Taylor temperature functions with an  
375 interactive moisture effect (Table 4). (The Gaussian model with additive soil moisture model  
376 had a  $c$  parameter of 0, which corresponds to the exponential model (see Table S2)). The  
377 other exception was the Atlantic DK-B site where models with an additive soil moisture effect  
378 performed better, and the three temperature models were almost equally supported (Table  
379 4a,c). At the Atlantic DK-M site the exponential function had unequivocally the best fit,  
380 whilst at the Atlantic NL and UK sites the exponential and the Lloyd-Taylor temperature  
381 functions, each with interactive moisture effect, were supported by the data (all these models  
382 had an Akaike weight above 0.1). At the Mediterranean ES and the Continental HU sites the  
383 Gaussian temperature model had the highest Akaike weight; at the HU site this model could  
384 be found being unequivocally better than any others, while at the ES site also the Lloyd-  
385 Taylor temperature model proved to be supported, all with interactive soil moisture  
386 integration (Table 4a,c).

387

388 *Thresholds in soil moisture influencing soil temperature dependence of SR*

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

394 The Continental HU and the Mediterranean ES sites had the most thresholds: these  
395 were at the zone of limited water availability approaching the wilting point, and near field  
396 capacity (Table 5, Fig. 2A,B). At the ES site the curve that represented the highest soil  
397 moisture threshold (at 22.2 Vol%, only found with the Lloyd-Taylor model) showed a  
398 decrease in SR under the highest soil moisture conditions, indicating lower microbial  
399 response to soil moisture during the colder days between November and March, when these  
400 higher soil moisture values occurred (Fig. 2B). At the other Mediterranean site in IT, one  
401 threshold point was also found above the wilting point, and a second threshold (only found  
402 with the additive moisture model) between the wet (winter and spring) and the dry (summer  
403 and early autumn) periods (Table 5, Fig. 2C). Similar to the curve of the Lloyd-Taylor model  
404 at the ES site, at the IT site the curve above this second threshold of the additive exponential  
405 model represents the wet season (highest soil moisture above 17.7 Vol% and lowest soil  
406 temperature below 15°C) (Fig. 2C). At the mesic DK-M, the only threshold for SR was found  
407 above the wilting point, but far below the field capacity value (Table 5, Fig. 2D). The similar  
408 DK-B site also presented this threshold (Table 5, Fig. 2E). At the mesic Atlantic NL site, the  
409 first threshold was found between wilting point and field capacity, while the next threshold  
410 was found near the field capacity, close to the third threshold. At the NL site, the lowest SR  
411 rates were measured at soil moisture contents between 23.7 and 28.2 Vol%, coinciding with  
412 the winter inactive period between October and March, while higher soil moisture occurred

413 often in July and August. At soil moisture contents below 23.7 and above 28.2 Vol%, the SR  
414 rates increased with increasing soil moisture (Table 5, Fig. 2F). At the hydric Atlantic UK site  
415 two thresholds for SR were found near field capacity and also far above field capacity. In this  
416 wet ecosystem SR rates decreased with higher soil moisture content (Table 5, Fig. 2G),  
417 because of anaerobic soil conditions.

418

#### 419 *Annual SR*

420 To compare the performances of the SR models, we calculated annual SR using the  
421 parameterized models (see model parameters in Table S2) and the daily meteorological data  
422 from the sites. The results for the six sites, HU, IT, DK-M, DK-B, NL and UK (Table 6)  
423 demonstrate that the annual SR estimated by the significant exponential models are in most  
424 cases higher than those estimated by the significant (DK-B) and non-significant (DK-M, NL)  
425 Gaussian models, however, the differences are mostly under 3%. Only at NL were the  
426 differences 7 to 25%. Also, for HU the non-significant exponential model overestimated SR  
427 relative to the significant Gaussian model. Only at the IT and UK sites did the exponential  
428 models not predict higher annual SR than the other models. At the IT site, the models  
429 produced similar estimates. At the UK site, depending on year, the estimates were either not  
430 significantly different or the Gaussian model predicted 20% higher annual SR than the  
431 exponential and Lloyd-Taylor models. Relative to models without moisture effects, models  
432 that included soil moisture resulted in 8, 2, and 14% higher estimates of annual SR for the  
433 mesic sites DK-M, DK-B and NL, respectively. For the semiarid HU and the arid IT sites,  
434 models without moisture effects underestimated annual SR when it was humid in 2010, but  
435 overestimated annual SR in drier years. For the hydric UK site this tendency was reversed,  
436 annual SR was overestimated by the models without moisture effects in the more humid years  
437 but underestimated annual SR in 2010 when precipitation was lowest (see Table 6). Soil

438 organic matter content, used as a proxy for soil microbial activity, varied highly among the  
439 study sites (Table 2). Apart from the UK site, a significant relationship between annual SR  
440 and the soil organic matter content was found (Fig. 3 ;  $r^2 = 0.961$ ). However, at the UK site  
441 with considerably higher soil organic matter content, estimated annual SR was near the mean  
442 rate at the other sites (Fig. 3), which is likely the result of anaerobic limitation of  
443 decomposition and the associated accumulation of organic matter at this site (Table 2).

444

445

446 **Discussion**

447

448 *Temperature control on SR*

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

465 In the present study, at the Atlantic sites, we couldn't find a model that unequivocally  
466 explained one of the temperature-SR relationships, i.e. the exponential function fit was as  
467 good as the Gaussian and Lloyd-Taylor functions (Table 4b, Fig. 1). This was probably due to  
468 the narrow temperature range, always under the optimum temperature, making it impossible  
469 to detect differences in the shape of the three models. Despite our efforts to obtain data that  
470 spanned a large temperature range by including climate change treatments (Table S1), the

471 measurements taken at the Atlantic sites biased the data to a narrower range than anticipated,  
472 with the soil temperature rarely exceeding 20°C. At the Mediterranean IT site, where the  
473 exponential SR models performed the best, soil temperature remained within the bounds of  
474 7°C to 29°C. In this case, the relatively high winter soil temperature range was probably due  
475 to the strong moderating effect from the Mediterranean Sea that causes mild winter  
476 temperatures, in most cases above 10°C. It is therefore likely that at this site we were not able  
477 to detect either the lower or the upper temperature limitation on SR (Table 4b, Fig. 1).

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

484

#### 485 *The influence of soil moisture on the temperature sensitivity of SR*

486 Our modelling approach integrated both soil moisture and temperature to examine the SR  
487 relationship. We revealed clear soil moisture thresholds in the temperature dependence of SR.  
488 This indicated that low soil moisture content was an important limiting factor of SR at both  
489 the seasonally dry Mediterranean and semiarid Continental sites, and also at the mesic  
490 Atlantic sites, whilst high soil moisture content imposing anaerobic conditions proved to limit  
491 SR at the hydric Atlantic site in the UK. In some cases, soil moisture thresholds could be  
492 connected to the wilting point or the field capacity (Table 5), but other thresholds might be  
493 related to more complex physiochemical or biological conditions (*Robinson et al., 2016*),  
494 such as the effect of soil moisture content on the availability of various soluble substrates or  
495 the effect of specific microbial enzymes with characteristic kinetic properties (*Davidson et al.,*

496 2006). *Kopittke et al. (2014)* reported that integration of soil moisture at the mesic Atlantic  
497 NL site did not improve the model fit of the temperature dependence of SR for control  
498 treatments while it significantly improved the model fit for drought treatments. The lack of a  
499 moisture effect in control plots but appearance of an effect in the drought plots found by  
500 *Kopittke et al. (2014)* support our analytical approach of using all treatment data together in  
501 order to cover a wider environmental range within the same model. Under Mediterranean  
502 climate at the IT site *de Dato et al. (2010)* showed a significant difference between  
503 temperature sensitivity of the wet vegetative season and the dry non-vegetative season  
504 between 2002 and 2004. At this site we also found that the best fit of the exponential  
505 temperature function to the dataset between 2010 and 2011 was separated by soil moisture  
506 thresholds (Fig. 2C). These two approaches gave similar results in ecosystems where  
507 vegetation periods are determined by water availability.

508         Similar to our results, soil moisture content has been shown to enhance the response of  
509 SR to temperature in a continental arid desert (*Zhang et al., 2010*), in a semiarid steppe of  
510 Inner Mongolia (*Chen et al., 2009*) and in an old-field climate change experiment (*Suseela et*  
511 *al., 2012*). In the latter study, *Suseela et al. (2012)* observed that both an upper and a lower  
512 soil moisture threshold related to SR activity existed, and that changes in soil structural  
513 properties during drought resulted in a hysteresis effect. Soil moisture thresholds were also  
514 found to change SR responses to temperature in other studies. *Rey et al. (2002)* and *Guidolotti*  
515 *et al. (2013)* found a soil moisture threshold in Mediterranean forests, below which there was  
516 no correlation between SR and soil temperature. In a study of temperate forest ecosystems,  
517 *Wang et al. (2006)* found that increased temperature sensitivity ( $Q_{10}$ ) was related to increasing  
518 soil moisture content, but that  $Q_{10}$  declined after reaching a soil moisture threshold. *Vicca et*  
519 *al. (2014)* also emphasized the importance of integrating soil moisture in the predictive  
520 models of SR, especially considering an altered moisture regime in the future. However, in

521 the modelling approach of *Vicca et al. (2014)* soil temperature is integrated as a simple  
522 exponential function, which may weaken the extensibility of the models. For comparison, for  
523 the dataset of the ES site the exponential temperature and Gaussian moisture dependence  
524 (model 4 of *Vicca et al., 2014*) achieved an AIC of 271.63. If both temperature and moisture  
525 dependence were modelled with the Gaussian function and their effect was additive, then an  
526 AIC of 201.75 was achieved. However, for the same dataset, our model with a Gaussian  
527 temperature function and interactive moisture thresholds achieved an AIC of 152.99,  
528 indicating a better performance of the model.

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

535 Soil moisture impacts SR directly by changing soil microbial activity and altering soil  
536 structure and porosity, and also indirectly by affecting substrate availability (*Davidson et al.,*  
537 *2006*). Under semiarid and arid conditions there is a strong edaphic water limitation coupled  
538 with strong pulse dynamics of resources linked to changes in microclimate (*Collins et al.,*  
539 *2008; Maestre et al., 2013*). The close connection between substrate availability and soil  
540 processes is also demonstrated by the relationship between annual SR and soil organic carbon  
541 content at the studied sites (Fig. 3). Similarly, *Fernandez et al. (2006)* demonstrated the  
542 impact of soil organic carbon and nitrogen on SR through soil texture and soil moisture  
543 availability in a cold desert ecosystem. They found that when soil moisture and temperature  
544 are both favourable, soil organic carbon and nitrogen cannot be used to predict SR. A  
545 limitation of soil substrate availability for microbes may explain why the Gaussian type soil



546 temperature-SR model proved to be the best at the HU and ES sites (Table 5), where not only  
547 the temperature ranges were the largest (Table 3), but the soil organic matter content was also  
548 the lowest (Table 2).

549

#### 550 *Annual scale impacts on SR*

551 The upscaled annual rates of SR showed profound differences among both years and models.  
552 As previously demonstrated at the HU site, annual SR rates calculated by the exponential  
553 function were systematically higher than those based on the Lloyd-Taylor and Gaussian  
554 functions (*Lellei-Kovács et al., 2011*). In this modelling experiment we also demonstrated that  
555 when excluding soil moisture from the models, modelled soil carbon fluxes may be  
556 overestimated especially for warm and dry years, which may be more frequent in the future.  
557 In the present study, annual SR values were also calculated from modelled data at six study  
558 sites (HU, IT, NL, DK-B, DK-M, UK), see Table 6. We found that the rate of annual SR in  
559 NL was very similar to the amount calculated by a different methodology by *Koppitke et al.*  
560 (2013, 2014) for the same period, which may validate these methods. Annual SR was also  
561 calculated in the work of *de Dato et al. (2010)* for three study years between 2002 and 2004,  
562 the values calculated were between 927 and 1145 g C m<sup>-2</sup> y<sup>-1</sup>, which are also similar to the  
563 values between 890 and 963 g C m<sup>-2</sup> y<sup>-1</sup> calculated by the method demonstrated here, for data  
564 between 2010 and 2011. At the UK site, annual SR decreased since 2000 because of a natural  
565 drought period that triggered an irreversible reduction in soil moisture and erosion of organic  
566 matter (*Robinson et al., 2016*). In the period between 2010 and 2012 annual SR was around  
567 400 g C m<sup>-2</sup> y<sup>-1</sup> (*Domínguez et al., 2015*), which is also consistent with our results suggesting  
568 annual SR between 323 and 345 g C m<sup>-2</sup> y<sup>-1</sup>.

569 At every site, the models that included soil moisture, always improved the model fit  
570 compared to those that excluded soil moisture. Furthermore, at three of the four Atlantic sites,

571 including soil moisture resulted in higher estimated annual SR, independently of the applied  
572 temperature dependence function. At the IT and the HU sites the direction of the alteration  
573 was dependent on the year: including soil moisture effect decreased the calculated annual SR  
574 in a drier year, and increased in a more humid year. The results are congruent with our  
575 previously published work, where excluding soil moisture resulted in an overestimation of  
576 rates of annual SR during a dry and hot year, but an underestimation of annual SR in a wet  
577 and cold year (*Lellei-Kovács et al., 2011*). In the present study, which considered the period  
578 2010 to 2012, variation in soil moisture resulted in a difference of 1 to 25% in the outputs  
579 from the nine different models we considered. This variation in output warrants further  
580 investigation into the uncertainty of model estimations and highlights the importance of  
581 appropriate model choice in the prediction of the future impacts of climate change on SR of  
582 different ecosystems.

583

#### 584 *Conclusions*

585 In this study of European shrubland ecosystems under Atlantic, Mediterranean or Continental  
586 climate we demonstrated that the temperature dependence function that best explains SR  
587 depended strongly on the temperature range where the study was conducted. We also showed  
588 that in these ecosystems when soil temperature range was above 30°C, the Gaussian function  
589 with optimum temperature provided a better fit to the data, than the exponential temperature  
590 function. Furthermore, we found that soil moisture strongly affected SR, not only in arid and  
591 semiarid, but also in mesic and hydric ecosystems, and the parameters of the temperature  
592 dependence functions changed significantly at distinctive soil moisture thresholds. These  
593 moisture thresholds may be connected to soil and ecosystem specific variables, such as  
594 wilting point of the plants or field capacity of the soil. In years with high precipitation and in  
595 mesic and hydric ecosystems the models that integrate moisture may estimate a higher level

596 of annually respired carbon. These results highlight the importance of the choice from among  
597 the temperature dependence functions and the inclusion of soil moisture data when modelling  
598 SR, especially when predicting SR responses in a wide range of climatic conditions or in a  
599 changing climate.

600

601

602

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615 **References**

616

617 Ågren GI, McMurtrie RE, Parton WJ, Pastor J, Shugart HH. 1991. State-of-the-art of models  
618 of production-decomposition linkages in conifer and grassland ecosystems. *Ecological*  
619 *Applications* 1: 118-138.

620 Ågren GI, Wetterstedt JÅM. 2007. What determines the temperature response of soil organic  
621 matter decomposition? *Soil Biology & Biochemistry* 39: 1794-1798.

622 Balogh J, Pintér K, Fóti Sz, Papp M, Cserhalmi D, Nagy Z. 2011. Dependence of soil  
623 respiration on soil moisture, clay content, soil organic matter, and CO<sub>2</sub> uptake in dry  
624 grasslands. *Soil Biology & Biochemistry* 43: 1006-1013.

625 Beier C, Emmett B, Gundersen P, Tietema A, Peñuelas J, Estiarte M, Gordon C, Gorissen A,  
626 Llorens L, Roda F, Williams D. 2004. Novel approaches to study climate change effects  
627 on terrestrial ecosystems in the field: drought and passive nighttime warming.  
628 *Ecosystems* 7: 583-597.

629 Beier C, Emmett B, Tietema A, Schmidt IK, Peñuelas J, Kovács-Láng E, Duce P, de Angelis  
630 P, Gorissen A, Estiarte M, de Dato G, Sowerby A, Kröel-Dulay G, Lellei-Kovács E,  
631 Kull O, Mand P, Petersen H, Gjelstrup P, Spano D. 2009. Carbon and nitrogen balances  
632 for six shrublands across Europe. *Global Biogeochemical Cycles* 23: GB4008.

633 Billings SA, Ballantyne IV F. 2013. How interactions between microbial resource demands,  
634 soil organic matter stoichiometry, and substrate reactivity determine the direction and  
635 magnitude of soil respiratory responses to warming. *Global Change Biology* 19: 90-  
636 102.

637 Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF,  
638 Treseder KK, Wallenstein MD. 2008. Thermal adaptation of soil microbial respiration  
639 to elevated temperature. *Ecology Letters* 11: 1316-1327.

640 Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical  
641 information-theoretic approach. 2nd Edition. Springer-Verlag New York.

642 Chen S, Lin G, Huang J, Jenerette GD. 2009. Dependence of carbon sequestration on the  
643 differential responses of ecosystem photosynthesis and respiration to rain pulses in a  
644 semiarid steppe. *Global Change Biology* 15: 2450-2461.

645 Collins SL, Sinsabaugh RL, Crenshaw C, Green L, Porras-Alfaro A, Stursova M, Zeglin LH.  
646 2008. Pulse dynamics and microbial processes in aridland ecosystems. *Journal of*  
647 *Ecology* 96: 413-420.

648 Curiel Yuste J, Ma S, Baldocchi DD. 2010. Plant-soil interactions and acclimation to  
649 temperature of microbial-mediated soil respiration may affect predictions of soil CO<sub>2</sub>  
650 efflux. *Biogeochemistry* 98: 127-138.

651 Davidson EA, Belk E, Boone RD. 1998. Soil water content and temperature as independent or  
652 confounded factors controlling soil respiration in temperate mixed hardwood forest.  
653 *Global Change Biology* 4: 217-227.

654 Davidson EA, Janssens IA, Luo Y. 2006. On the variability of respiration in terrestrial  
655 ecosystems: moving beyond Q<sub>10</sub>. *Global Change Biology* 12: 154-164.

656 Davidson EA, Janssens IA. 2006. Temperature sensitivity of soil carbon decomposition and  
657 feedbacks to climate change. *Nature* 440: 165-173.

658 de Dato GD, de Angelis P, Sirca C, Beier C. 2010. Impact of drought and increasing  
659 temperatures on soil CO<sub>2</sub> emissions in a Mediterranean shrubland (gariga). *Plant & Soil*  
660 327: 153-166.

661 Domínguez MT, Sowerby A, Smith AR, Robinson DA, Van Baarsel S, Mills RTE, Marshall  
662 MR, Koller E, Lebron I, Hall J, Emmett BA. 2015. Sustained impact of drought on wet  
663 shrublands mediated by soil physical changes. *Biogeochemistry* 122: 151-163.

664 Emmett B, Beier C, Estiarte M, Tietema A, Kristensen HL, Williams D, Peñuelas J, Schmidt  
665 I, Sowerby A. 2004. The response of soil processes to climate change: Results from  
666 manipulation studies of shrublands across an environmental gradient. *Ecosystems* 7:  
667 625-637.

668 Fernandez DP, Neff JC, Belnap J, Reynolds RL. 2006. Soil respiration in the cold desert  
669 environment of the Colorado Plateau (USA): abiotic regulators and thresholds.  
670 *Biogeochemistry* 78: 247-265.

671 González-Ubierna S, de la Cruz MT, Casermeiro MÁ. 2014. Climate factors mediate soil  
672 respiration dynamics in Mediterranean agricultural environments: an empirical  
673 approach. *Soil Research* 52: 543-553.

674 Guidolotti G, Rey A, D'Andrea E, Matteucci G, De Angelis P. 2013. Effect of environmental  
675 variables and stand structure on ecosystem respiration components in a Mediterranean  
676 beech forest. *Tree Physiology* 33: 960-972.

677 Hothorn T, Hornik K, Zeileis A. 2006. Unbiased Recursive Partitioning: A Conditional  
678 Inference Framework. *Journal of Computational and Graphical Statistics* 15: 651-674.

679 Howard DM, Howard PJA. 1993. Relationships between CO<sub>2</sub> evolution, moisture content and  
680 temperature for a range of soil types. *Soil Biology & Biochemistry* 25: 1537-1546.

681 IPCC 2013. The Physical Science Basis. *Climate Change 2013: Contribution of Working*  
682 *Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate*  
683 *Change* (eds. Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J,  
684 Nauels A, Xia Y, Bex V, Midgley PM), 1535 pp. Cambridge University Press,  
685 Cambridge, United Kingdom and New York, NY, USA.

686 Johnson JB, Omland KS. 2004. Model selection in ecology and evolution. *TRENDS in*  
687 *Ecology and Evolution* 19: 101-108.

688 Kirschbaum MUF. 2004. Soil respiration under prolonged soil warming: are rate reductions  
689 caused by acclimation or substrate loss? *Global Change Biology* 10: 1870-1877.

690 Kopittke GR, van Loon EE, Tietema A, Asscherman D. 2013. Soil respiration on an aging  
691 managed heathland: identifying an appropriate empirical model for predictive purposes.  
692 *Biogeosciences* 10: 3007-3038.

693 Kopittke GR, Tietema A, van Loon EE, Asscherman D. 2014. Fourteen Annually Repeated  
694 Droughts Suppressed Autotrophic Soil Respiration and Resulted in an Ecosystem  
695 Change. *Ecosystems* 17: 242-257.

696 Kotroczó Zs, Veres Zs, Fekete I, Krakomperger Zs, Tóth JA, Lajtha K, Tóthmérész B. 2014.  
697 Soil enzyme activity in response to long-term organic matter manipulation. *Soil Biology*  
698 *& Biochemistry* 70: 237-243.

699 Kröel-Dulay Gy, Ransijn J, Schmidt IK, Beier C, de Angelis P, de Dato G, Dukes JS, Emmett  
700 B, Estiarte M, Garadnai J, Kongstad J, Kovács-Láng E, Larsen KS, Liberati D, Ogaya  
701 R, Riis-Nielsen T, Smith AR, Sowerby A, Tietema A, Penuelas J. 2015. Increased  
702 sensitivity to climate change in disturbed ecosystems. *Nature Communications* 6:  
703 Article number: 6682.

704 Leirós MC, Trasar-Cepeda C, Seoane S, Gil-Sotres F. 1999. Dependence of mineralization of  
705 soil organic matter on temperature and moisture. *Soil Biology & Biochemistry* 31: 327-  
706 335.

707 Lellei-Kovács E, Kovács-Láng E, Kalapos T, Botta-Dukát Z, Barabás S, Beier C. 2008.  
708 Experimental warming does not enhance soil respiration in a semiarid temperate forest-  
709 steppe ecosystem. *Community Ecology* 9: 29-37.



710 Lellei-Kovács E, Kovács-Láng E, Botta-Dukát Z, Kalapos T, Emmett B, Beier C. 2011.  
711       Thresholds and interactive effects of soil moisture on the temperature response of soil  
712       respiration. *European Journal of Soil Biology* 47: 247-255.

713 Lloyd J, Taylor JA. 1994. On the temperature dependence of soil respiration. *Functional*  
714       *Ecology* 8: 315-323.

715 von Lützow M, Kögel-Knabner I. 2009. Temperature sensitivity of soil organic matter  
716       decomposition – what do we know? *Biology & Fertility of Soils* 46: 1-15.

717 Maestre FT, Escolar C, de Guevara ML, Quero JL, Lázaro R, Delgado-Baquerizo M, Ochoa  
718       V, Berdugo M, Gozalo B, Gallardo A. 2013. Changes in biocrust cover drive carbon  
719       cycle responses to climate change in drylands. *Global Change Biology* 19: 3835-3847.

720 Mielnick PC, Dugas WA. 2000. Soil CO<sub>2</sub> flux in a tallgrass prairie. *Soil Biology &*  
721       *Biochemistry* 32: 221-228.

722 Mikkelsen TN, Beier C, Jonasson S, Holmstrup M, Schmidt IK, Ambus P, Pilegaard K,  
723       Michelsen A, Albert K, Andresen LC, Arndal MF, Bruun N, Christensen S, Danbæk S,  
724       Gundersen P, Jørgensen P, Linden LG, Kongstad J, Maraldo K, Priemé A, Riis-Nielsen  
725       T, Ro-Poulsen H, Stevnbak K, Selsted MB, Sørensen P, Larsen KS, Carter MS, Ibrom  
726       A, Martinussen T, Miglietta F, Sverdrup H. 2008. Experimental design of multifactor  
727       climate change experiments with elevated CO<sub>2</sub>, warming and drought: the CLIMAITE  
728       project. *Functional Ecology* 22: 185-195.

729 Moyano FE, Manzoni S, Chenu C. 2013. Responses of soil heterotrophic respiration to  
730       moisture availability: An exploration of processes and models. *Soil Biology &*  
731       *Biochemistry* 59: 72-85.

732 Murthy R, Griffin KL, Zarnoch SJ, Dougherty PM, Watson B, Haren JV, Patterson RL,  
733       Mahato T. 2003. Carbon dioxide efflux from a 550m<sup>2</sup> soil across a range of soil  
734       temperatures. *Forest Ecology and Management* 178: 311-327.

735 Pavelka M, Acosta M, Marek MV, Kutsch W, Janous D. 2007. Dependence of the  $Q_{10}$  values  
736 on the depth of the soil temperature measuring point. *Plant & Soil* 292: 171-179.

737 Peñuelas J, Prieto P, Beier C, Cesaraccio C, de Angelis P, de Dato G, Emmett BA, Estiarte M,  
738 Garadnai J, Gorissen A, Kovács-Láng E, Kröel-Dulay G, Llorens L, Pellizzaro G, Riis-  
739 Nielsen T, Schmidt IK, Sirca C, Sowerby A, Spano D, Tietema A. 2007. Response of  
740 plant species richness and primary productivity in shrublands along a north-south  
741 gradient in Europe to seven years of experimental warming and drought: reductions in  
742 primary productivity in the heat and drought year of 2003. *Global Change Biology* 13:  
743 2563-2581.

744 Qi Y, Xu M, Wu J. 2002. Temperature sensitivity of soil respiration and its effects on  
745 ecosystem carbon budget: nonlinearity begets surprises. *Ecological Modelling* 153: 131-  
746 142.

747 R Development Core Team. 2008. R: A language and environment for statistical computing.  
748 R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL  
749 <http://www.R-project.org>.

750 Reichstein M, Tenhunen JD, Roupsard O, Ourcival JM, Rambal S, Miglietta F, Peressotti A,  
751 Pecchiari M, Tirone G, Valentini R. 2002. Severe drought effects on ecosystem  $CO_2$  and  
752  $H_2O$  fluxes at three Mediterranean evergreen sites: revision of current hypotheses?  
753 *Global Change Biology* 8: 999-1017.

754 Reichstein M, Beer C. 2008. Soil respiration across scales: The importance of a model-data  
755 integration framework for data interpretation. *Journal of Plant Nutrition and Soil*  
756 *Science* 171: 344-354.

757 Rey A, Pegoraro E, Tedeschi V, De Parri I, Jarvis PG, Valentini R. 2002. Annual variation in  
758 soil respiration and its components in a coppice oak forest in Central Italy. *Global*  
759 *Change Biology* 8: 851-866.

760 Robinson DA, Jones SB, Lebron I, Reinsch S, Domínguez MT, Smith AR, Jones DL,  
761 Marshall MR, Emmett BA. 2016. Experimental evidence for drought induced alternative  
762 stable states of soil moisture. *Scientific Reports* 6: 20018.

763 Rodrigo A, Recous S, Neel C, Mary B. 1997. Modelling temperature and moisture effects on  
764 C-N transformations in soils: comparison of nine models. *Ecological Modelling* 102:  
765 325-339.

766 Sardans J, Peñuelas J, Estiarte M, Prieto P. 2008. Warming and drought alter C and N  
767 concentration, allocation and accumulation in a Mediterranean shrubland. *Global*  
768 *Change Biology* 14: 2304-2316.

769 Saxton KE, Rawls WJ. 2006. Soil Water Characteristic Estimates by Texture and Organic  
770 Matter for Hydrologic Solutions. *Soil Science Society of America Journal* 70:1569-  
771 1578.

772 Shen Z, Shi B, Wang B, Jiang H-J. 2013. The temperature dependence of soil organic matter  
773 decomposition and CO<sub>2</sub> efflux: A review. *Shengtai Xuebao/ Acta Ecologica Sinica* 33:  
774 3011-3019. (in chinese)

775 Skopp J, Jawson MD, Doran JW. 1990. Steady-state aerobic microbial activity as a function  
776 of soil water content. *Soil Science Society of America Journal* 54: 1619-1625.

777 Sowerby A, Emmett B, Tietema A, Beier C. 2008. Contrasting effects of repeated summer  
778 drought on soil carbon efflux in hydric and mesic heathland soils, *Global Change*  
779 *Biology* 14: 2388-2404.

780 Subke J-A, Bahn M. 2010. On the temperature sensitivity of soil respiration: Can we use the  
781 immeasurable to predict the unknown? *Soil Biology & Biochemistry* 42: 1653-1656.

782 Suseela V, Conant RT, Wallenstein MD, Dukes JS. 2012. Effects of soil moisture on the  
783 temperature sensitivity of heterotrophic respiration vary seasonally in an old-field  
784 climate change experiment. *Global Change Biology* 18: 336-348.

- 785 Tuomi M, Vanhala P, Karhu K, Fritze H, Liski J. 2008. Heterotrophic soil respiration –  
786 Comparison of different models describing its temperature dependence. *Ecological*  
787 *Modelling* 211: 182-190.
- 788 Vicca S, Bahn M, Estiarte M, van Loon EE, Vargas R, Alberti G, Ambus P, Arain MA, Beier  
789 C, Bentley LP, Borken W, Buchmann N, Collins SL, de Dato G, Dukes JS, Escolar C,  
790 Fay P, Guidolotti G, Hanson PJ, Kahmen A, Kröel-Dulay G, Ladreiter-Knauss T,  
791 Larsen KS, Lellei-Kovács E, Lebrija-Trejos E, Maestre FT, Marhan S, Marshall M,  
792 Meir P, Miao Y, Muhr J, Niklaus PA, Ogaya R, Peñuelas J, Poll C, Rustad LE, Savage  
793 K, Schindlbacher A, Schmidt IK, Smith AR, Sotta ED, Suseela V, Tietema A, van  
794 Gestel N, van Straaten O, Wan S, Weber U, Janssens IA. 2014. Can current moisture  
795 responses predict soil CO<sub>2</sub> efflux under altered precipitation regimes? A synthesis of  
796 manipulation experiments. *Biogeosciences* 11: 2991-3013.
- 797 Wang B, Zha TS, Jia X, Wu B, Zhang YQ, Qin SG. 2014. Soil moisture modifies the  
798 response of soil respiration to temperature in a desert shrub ecosystem. *Biogeosciences*  
799 11: 259-268.
- 800 Wang C, Yang J, Zhang Q. 2006. Soil respiration in six temperate forests in China. *Global*  
801 *Change Biology* 12: 2103-2114.
- 802 Wang WJ, Dalal RC, Moody PW, Smith CJ. 2003. Relationships of soil respiration to  
803 microbial biomass, substrate availability and clay content. *Soil Biology & Biochemistry*  
804 35: 273-284.
- 805 Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA. 2011. Responses of terrestrial  
806 ecosystems to temperature and precipitation change: a meta-analysis of experimental  
807 manipulation. *Global Change Biology* 17: 927-942.

808 Xu L, Baldocchi DD, Tang J. 2004. How soil moisture, rain pulses, and growth alter the  
809 response of ecosystem respiration to temperature. *Global Biogeochemical Cycles* 18:  
810 GB4002.

811 Yan L, Chen S, Huang J, Lin G. 2011. Water regulated effects of photosynthetic substrate  
812 supply on soil respiration in a semiarid steppe. *Global Change Biology* 17: 1990-2001.

813 Zeileis A, Hothorn T, Hornik K. 2005. Model-Based Recursive Partitioning. *Journal of*  
814 *Computational and Graphical Statistics* 17: 492-514.

815 Zhang LH, Chen YN, Zhao RF, Li WH. 2010. Significance of temperature and soil water  
816 content on soil respiration in three desert ecosystems in Northwest China. *Journal of*  
817 *Arid Environments* 74: 1200-1211.

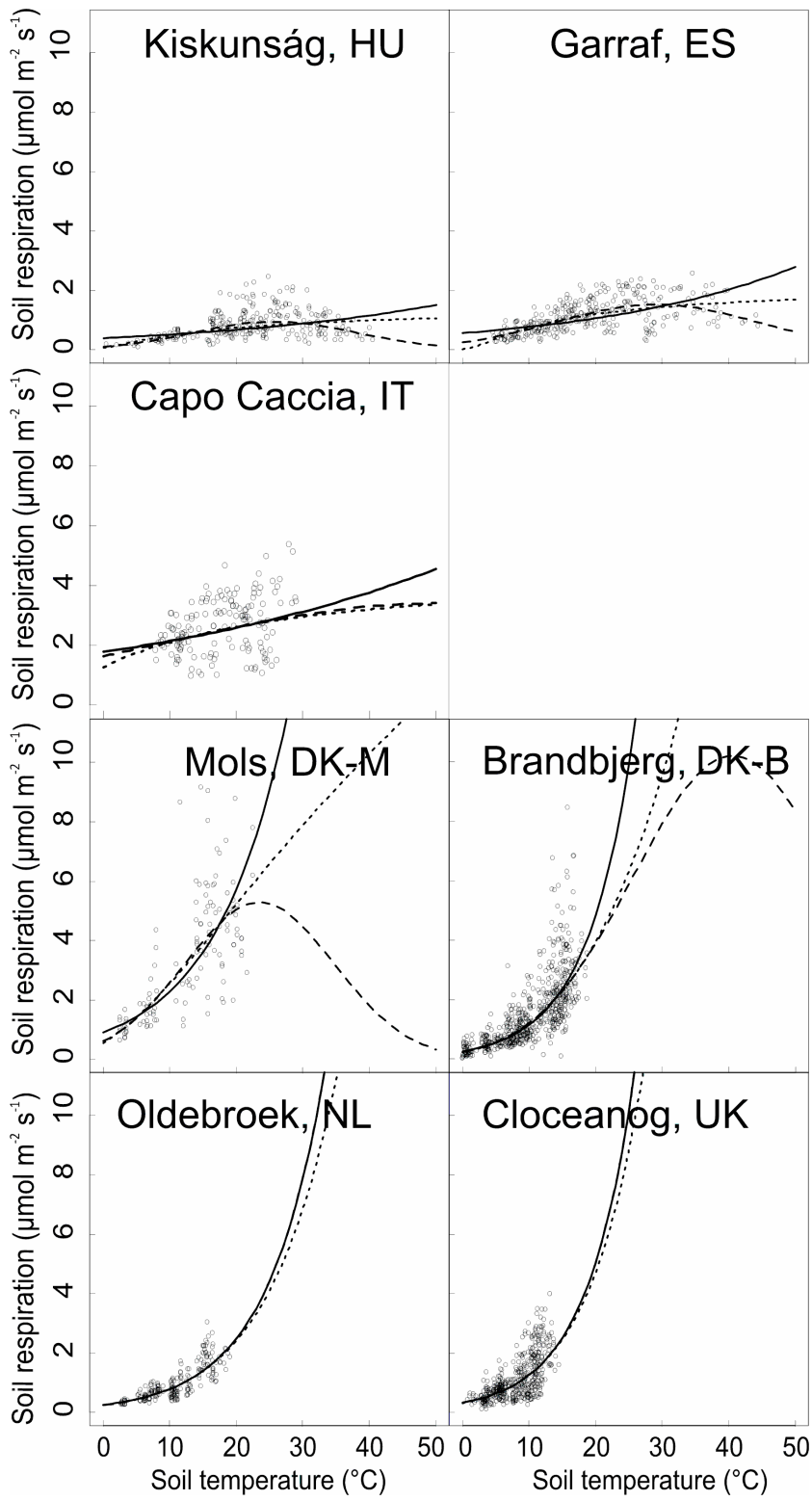
818 Zhou X, Sherry RA, An Y, Wallace LL, Luo Y. 2006. Main and interactive effects of  
819 warming, clipping, and doubled precipitation on soil CO<sub>2</sub> efflux in a grassland  
820 ecosystem. *Global Biogeochemical Cycles* 20: GB1003.

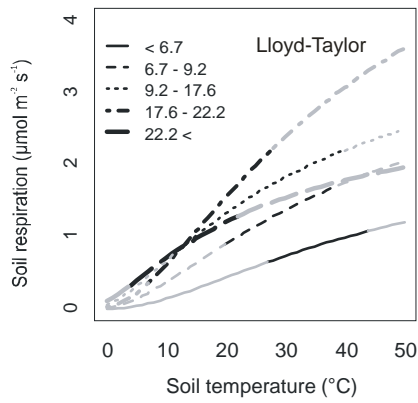
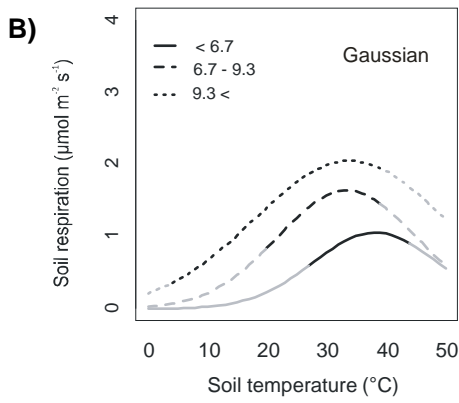
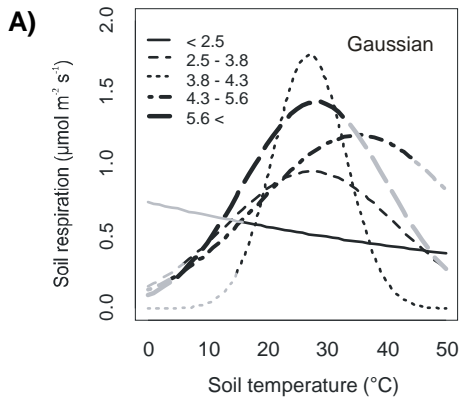
821 Zhou X, Wan SQ, Luo YQ. 2007. Source components and interannual variability of soil CO<sub>2</sub>  
822 efflux under experimental warming and clipping in a grassland ecosystem. *Global*  
823 *Change Biology* 13: 761-775.

824

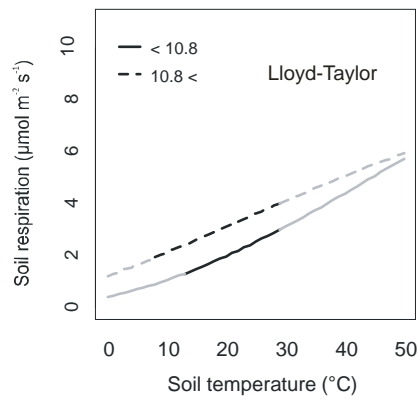
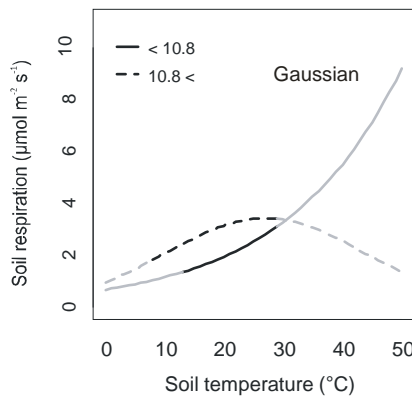
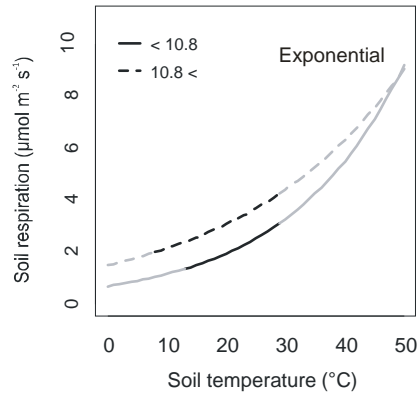
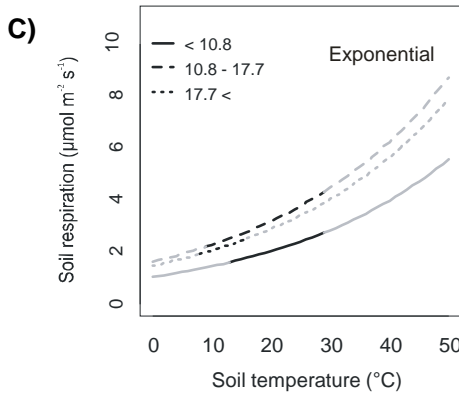
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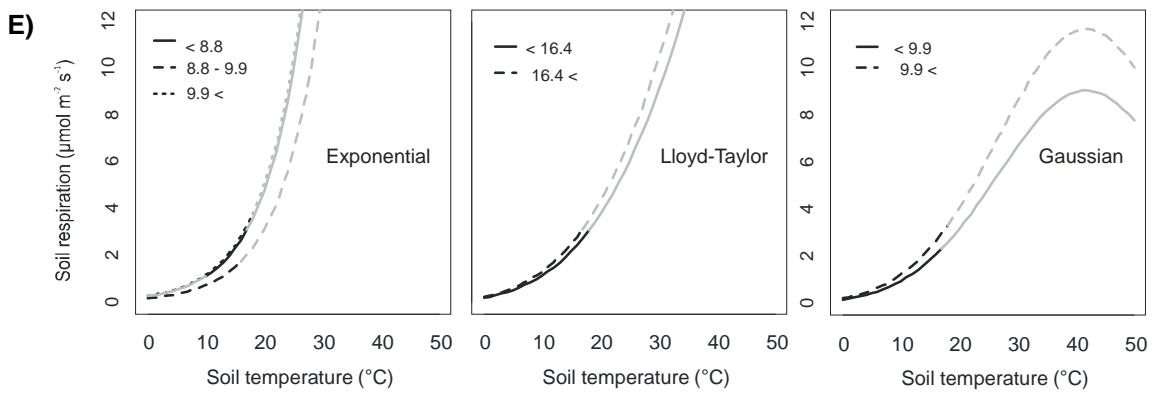
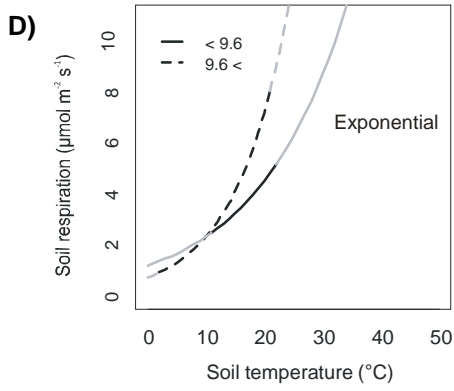




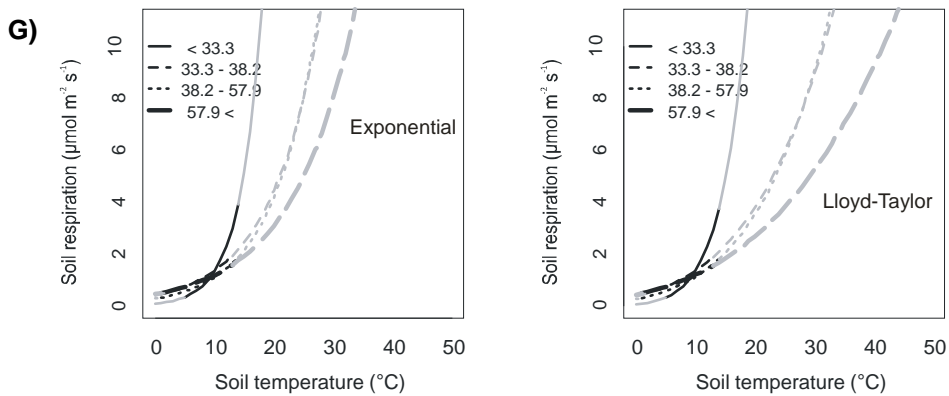
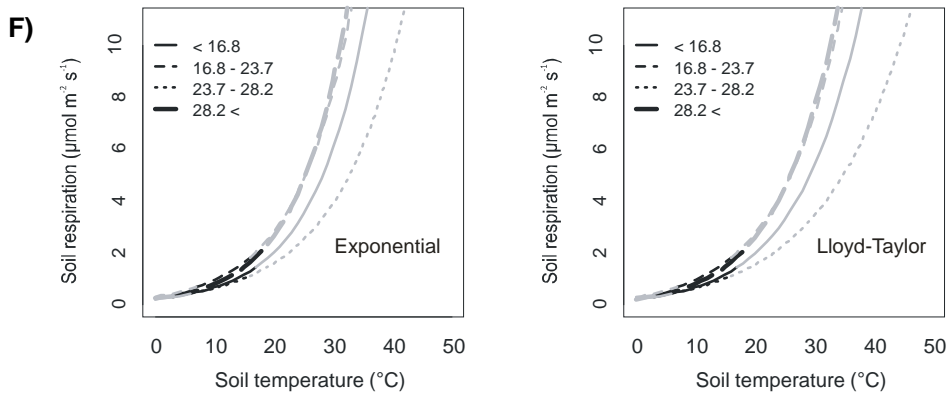
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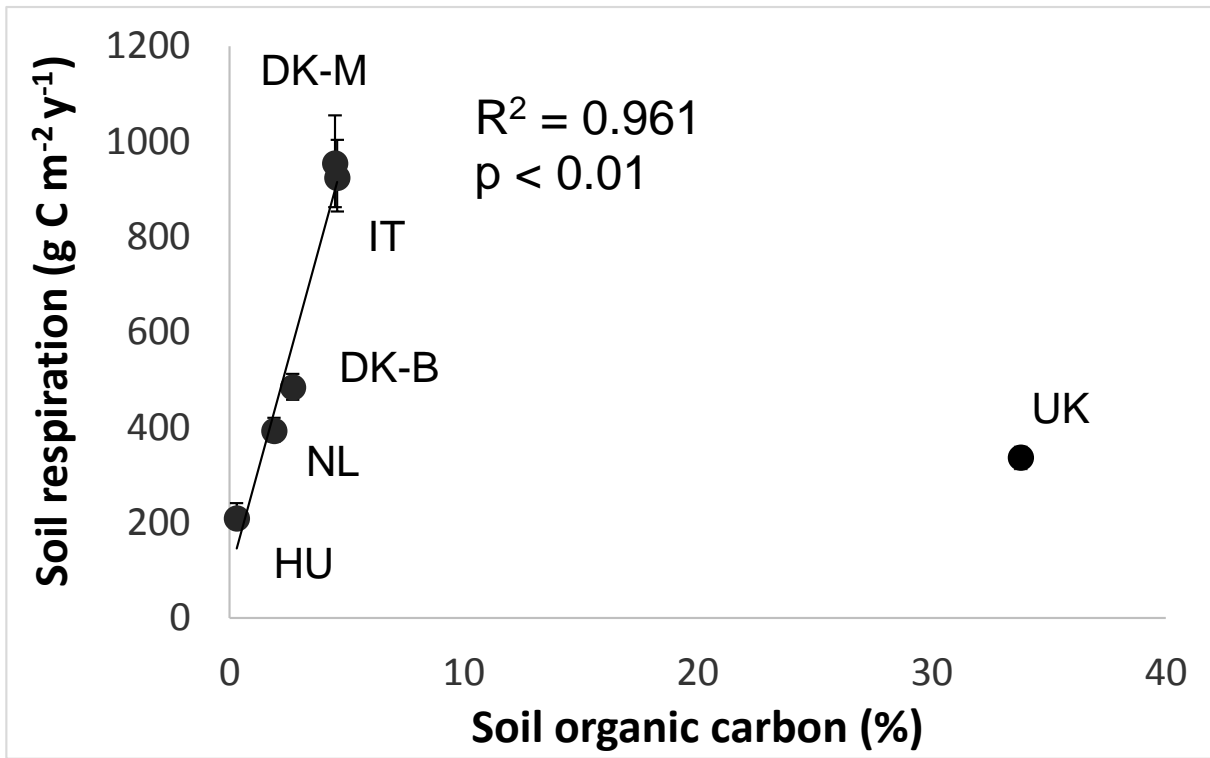
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836 *Figure 2.*

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841 *Figure 3.*

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844 **Figure legends**

845

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

850

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

858

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

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869

870 *Table 1. Characterization of the study sites.*

| Country | Site        | Location         | Altitude | MAT (Jan.;July)  | MAP  | Gausсен-index<br>(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                          |

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873

874 *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 |

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876

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

| Country | Site        | Measurement periods | Soil temperature              | Soil moisture              | Soil respiration                     |
|---------|-------------|---------------------|-------------------------------|----------------------------|--------------------------------------|
|         |             | <i>yyyy.mm</i>      | °C                            | <i>Vol%</i>                | $\mu\text{mol m}^{-2} \text{s}^{-1}$ |
| HU      | Kiskunság   | 2010.04 - 2012.11   | 0.40 - 40.50 ( <b>21.97</b> ) | 2.0 - 8.1 ( <b>4.1</b> )   | 0.11 - 2.48 ( <b>0.84</b> )          |
| ES      | Garraf      | 2002.04 - 2003.12   | 4.35 - 44.25 ( <b>19.04</b> ) | 5.6 - 31.6 ( <b>19.0</b> ) | 0.27 - 2.60 ( <b>1.16</b> )          |
| IT      | Capo Caccia | 2010.02 - 2011.11   | 7.73 - 28.85 ( <b>17.59</b> ) | 3.2 - 27.6 ( <b>14.8</b> ) | 0.98 - 5.38 ( <b>2.65</b> )          |
| DK      | Mols        | 2011.05 - 2012.09   | 2.32 - 22.30 ( <b>12.82</b> ) | 5.8 - 18.3 ( <b>12.3</b> ) | 0.65 - 17.66 ( <b>3.71</b> )         |
| DK      | Brandbjerg  | 2011.03 - 2012.12   | -0.25 - 18.48 ( <b>9.93</b> ) | 5.4 - 30.2 ( <b>16.3</b> ) | 0.02 - 8.48 ( <b>1.59</b> )          |
| NL      | Oldebroek   | 2010.07 - 2012.06   | 2.49 - 18.89 ( <b>10.46</b> ) | 7.4 - 39.9 ( <b>24.7</b> ) | 0.26 - 3.05 ( <b>0.98</b> )          |
| UK      | Clocaenog   | 2010.01 - 2012.12   | 0.60 - 14.29 ( <b>7.91</b> )  | 8.7 - 71.4 ( <b>41.7</b> ) | 0.13 - 4.00 ( <b>1.15</b> )          |

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

883 a)

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

884

885 b)

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

886

887 c)

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

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891 *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                                      | <b>2.5 ; 3.8 ; 4.3 ; 5.6</b>   |
| ES      | Garraf      | 8.0                  | 26.0                  | Lloyd-Taylor, Gaussian                        | <b>6.7 ; 9.2<sup>L</sup> ; 9.3<sup>G</sup> ; 17.6<sup>L</sup> ; 22.2<sup>L</sup></b> |
| IT      | Capo Caccia | 7.8                  | 28.0                  | Exponential, Lloyd-Taylor, Gaussian           | <b>10.8 ; 17.7<sup>Additive</sup></b>  |
| DK      | Mols        | 4.0                  | 18.0                  | Exponential                                   | 9.6  |
| DK      | Brandbjerg  | 2.5                  | 38.0                  | Exponential, Lloyd-Taylor, Gaussian           | 8.8 <sup>E</sup> ; 9.9 <sup>E,G</sup> ; 16.4 <sup>L</sup>                            |
| NL      | Oldebroek   | 4.5                  | 34.5                  | Exponential, Lloyd-Taylor                     | 16.8 ; <b>23.7</b> ; 28.2  |
| UK      | Clocaenog   | 7.0                  | 39.0                  | Exponential, Lloyd-Taylor                     | <b>33.3</b> ; 38.2 ; 57.9  |

892

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894

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

896 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)  |

897

898 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        | <b>225.3</b> (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        | <b>201.9</b> (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        | <b>199.7</b> (190.2 , 210.0)  |
| IT      | 2010 | <b>939.0</b> (897.7 , 982.2)  | 910.3        | <b>939.0</b> (897.7 , 982.2) | <b>957.8</b> (917.1 , 1000.6)    | <b>957.9</b> | <b>963.3</b> (926.1 , 1002.4) |
|         | 2011 | <b>889.3</b> (852.6 , 927.9)  | 880.5        | <b>889.3</b> (852.6 , 927.9) | <b>903.1</b> (864.3 , 943.4)     | <b>901.2</b> | <b>901.6</b> (873.8 , 931.3)  |
| DK-M    | 2011 | 914.5 (858.0 , 974.4)         | 944.3        | 959.3 (896.1 , 1027.1)       | <b>985.2</b> (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)        | <b>923.6</b> (862.2 , 987.2)     | 899.3        | 914.9 (853.2 , 980.1)         |
| DK-B    | 2011 | <b>511.9</b> (492.9 , 531.5)  | <b>512.3</b> | <b>504.6</b> (494.3 , 515.6) | 499.8 (481.9 , 518.2)            | 492.2        | 492.7 (474.7 , 511.4)         |
|         | 2012 | <b>461.0</b> (445.8 , 477.0)  | <b>456.0</b> | <b>458.3</b> (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)        | <b>393.1</b> (369.7 , 418.0)     | <b>391.4</b> | 364.2 (298.0 , 451.2)         |
|         | 2012 | 340.9 (328.6 , 353.3)         | 339.5        | 340.9 (328.6 , 353.3)        | <b>393.5</b> (369.5 , 420.1)     | <b>392.8</b> | 296.4 (266.2 , 327.0)         |
| UK      | 2010 | 335.5 (323.8 , 347.4)         | 335.9        | 335.5 (323.8 , 347.4)        | <b>342.9</b> (330.0 , 356.3)     | <b>340.9</b> | 340.0 (328.8 , 351.0)         |
|         | 2011 | 354.8 (342.3 , 367.8)         | 356.2        | 354.8 (342.3 , 367.8)        | <b>345.1</b> (331.1 , 359.9)     | <b>345.2</b> | 348.8 (336.5 , 361.7)         |
|         | 2012 | 329.7 (317.1 , 343.3)         | 330.8        | 329.7 (317.1 , 343.3)        | <b>323.4</b> (310.6 , 336.6)     | <b>322.8</b> | 388.9 (384.0 , 395.5)         |

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900

901

902



903 **Table legends**

904

905 *Table 1. Characterization of the study sites.*

906 *MAT (mean annual temperature) and MAP (mean annual precipitation) between 2001 and*  
907 *2012, except for ES between 2002 and 2003 and DK-B between 2006 and 2012. Gaussen-*  
908 *index of aridity, as modified by Peñuelas et al. (2007) related to annual climatic data of the*  
909 *study sites, highlighting the climatic differences between them.*

910

911 *Table 2. Soil characteristics of the study sites.*

912 *Soil depth stands for the sampling depth for soil moisture and other measurements,*  
913 *representing the most active soil layers. Parenthetical numbers represents the thickness of the*  
914 *organic soil layers; pH was measured in H<sub>2</sub>O; SOC stands for the soil organic carbon*  
915 *content.*

916

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

920

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

926

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

933

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

940

941

## 942 **Supplemental Material**

943

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

947

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

949