



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

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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 CO₂ 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 CO₂ 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 CO₂ efflux
81 from soils. However, it is poorly understood how altered temperature and soil moisture
82 availability will affect soil CO₂ 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 O₂ 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 CO₂ 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⁻² y⁻¹, which are also similar to the
563 values between 890 and 963 g C m⁻² y⁻¹ 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⁻² y⁻¹ (*Domínguez et al., 2015*), which is also consistent with our results suggesting
568 annual SR between 323 and 345 g C m⁻² y⁻¹.

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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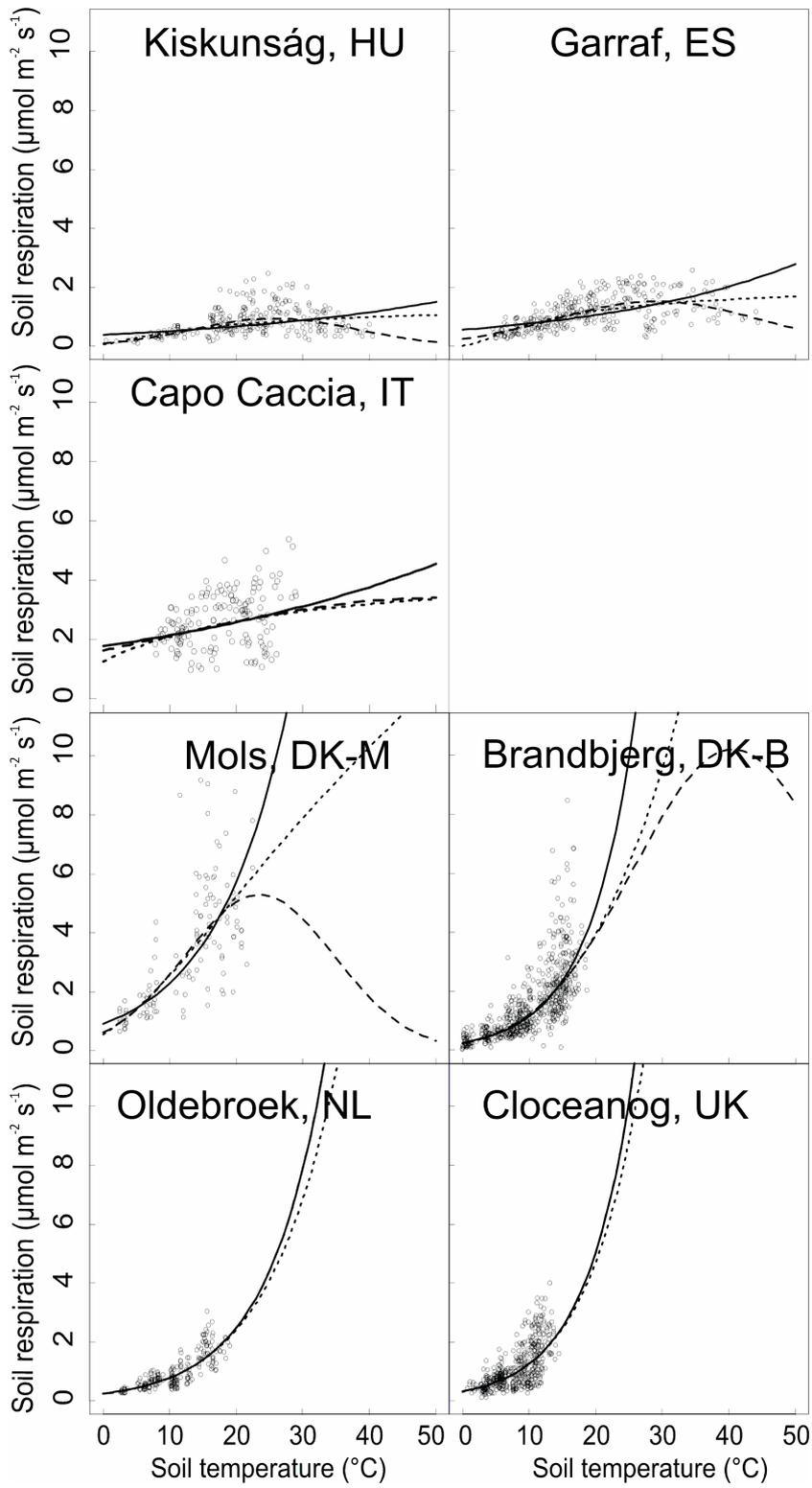
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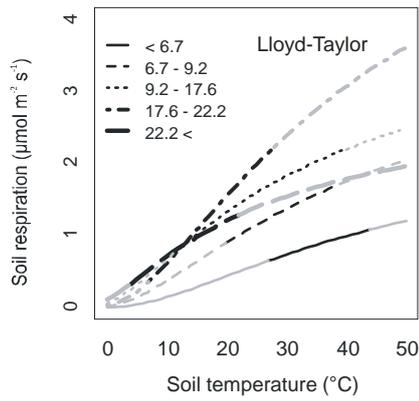
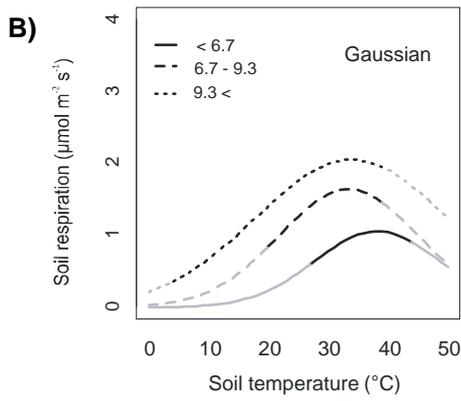
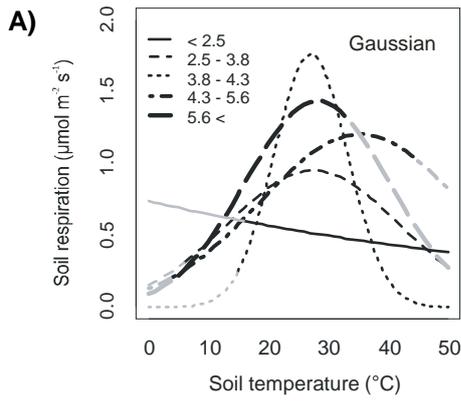
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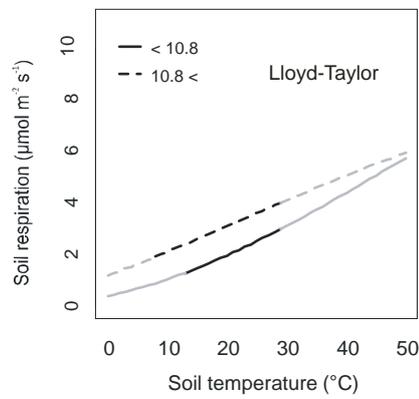
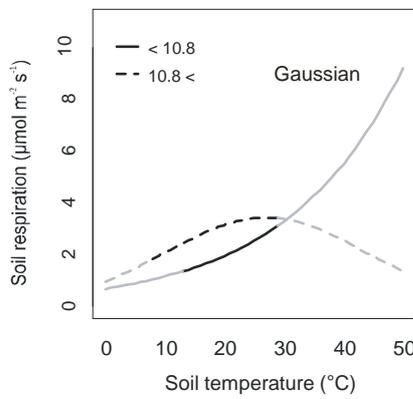
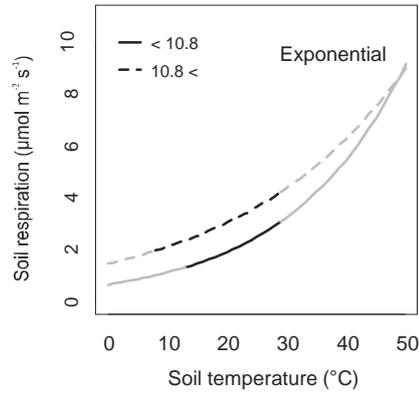
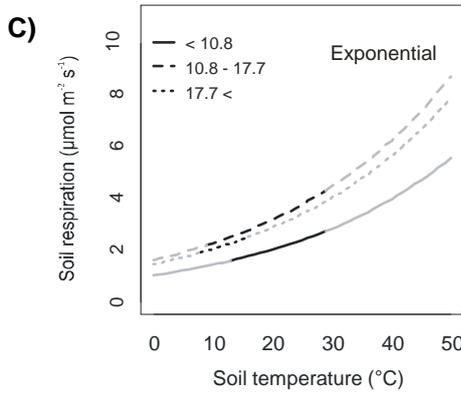
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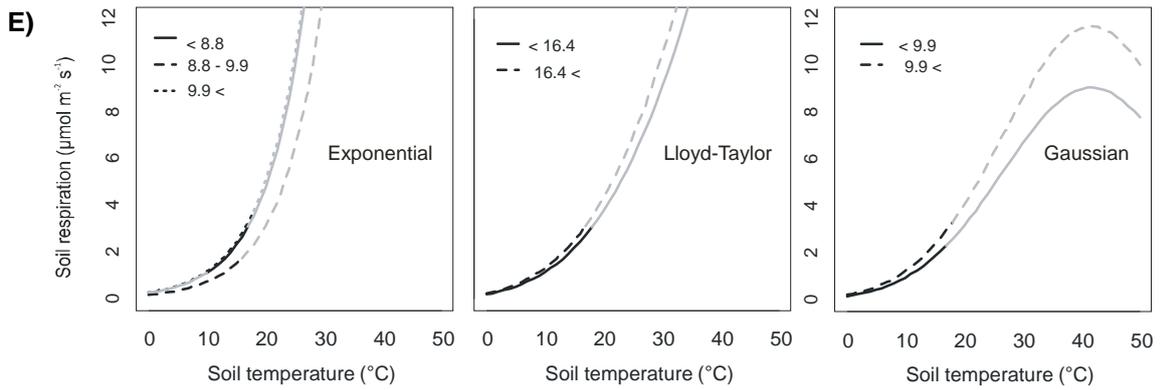
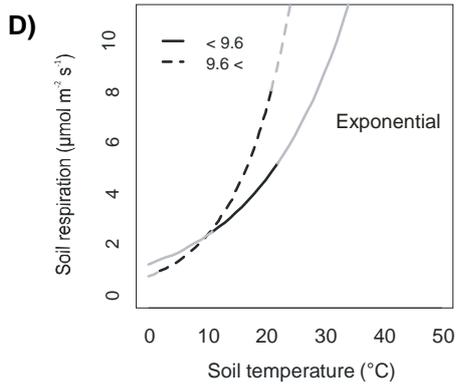




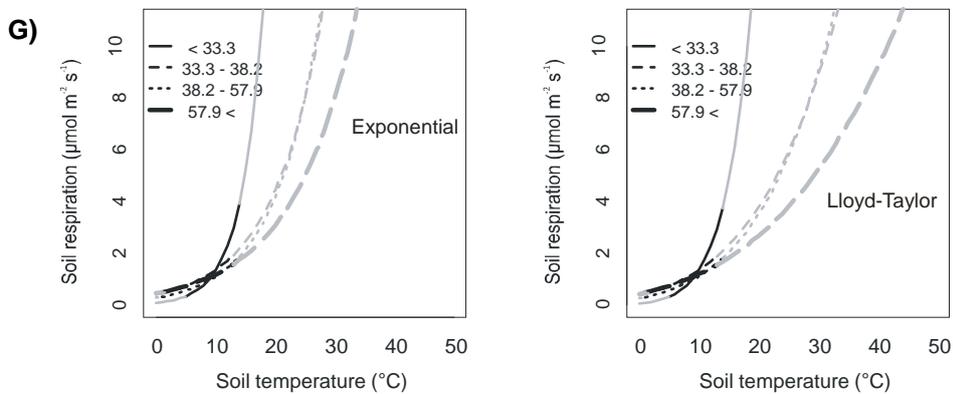
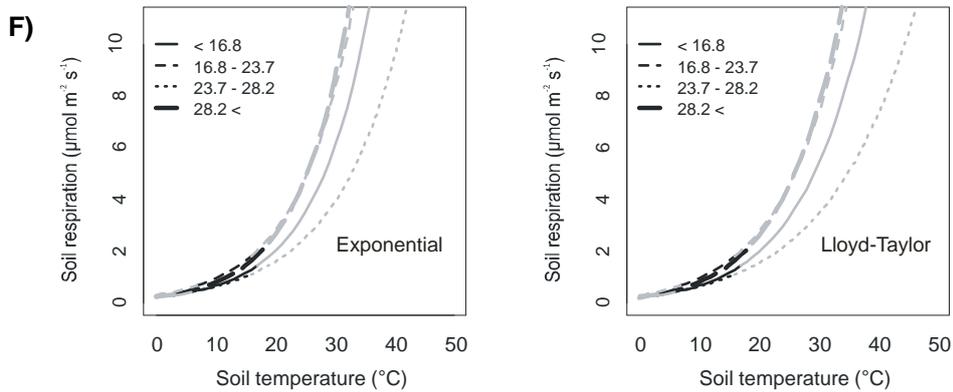
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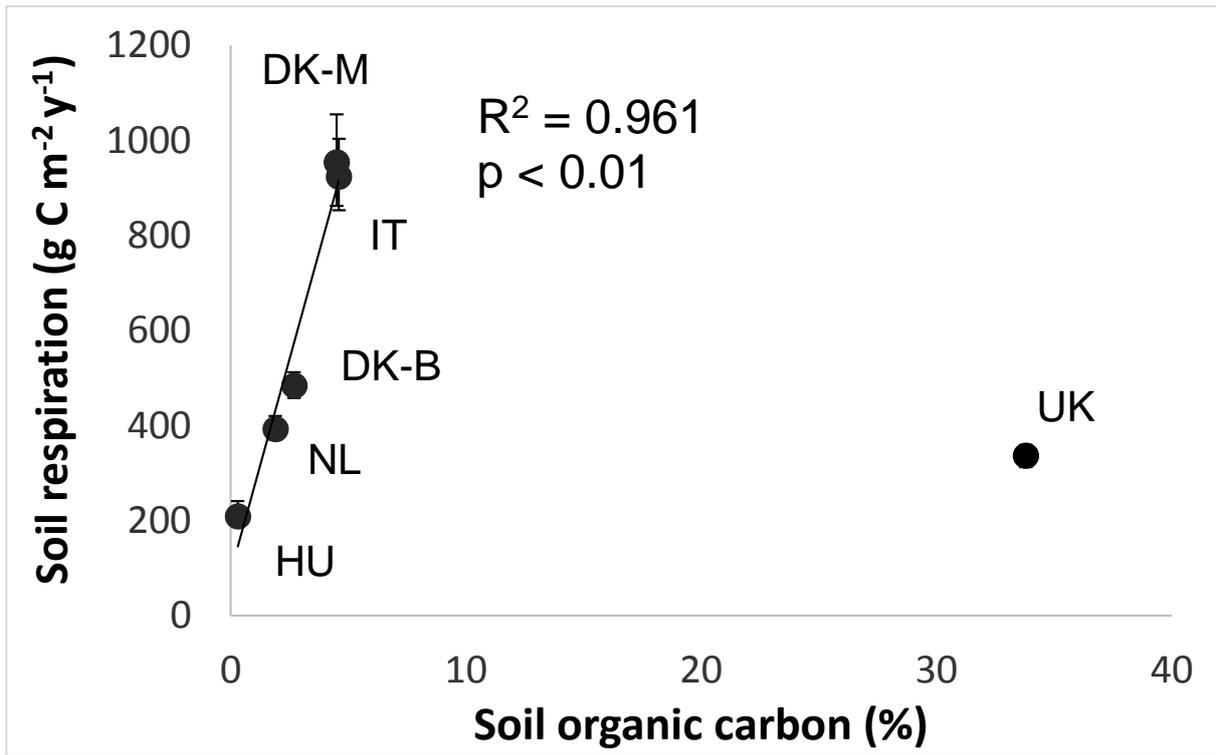


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836 *Figure 2.*

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840

841 *Figure 3.*

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843

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.*

868

869

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

Country	Site	Location	Altitude	MAT (Jan.;July)	MAP	Gausse-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

871

872

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

875

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 (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)

878

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881

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	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

884

885 b)

Akaike-weights			
Site, Country	Soil moisture is not considered		
	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

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	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

888

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890

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	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

892

893

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	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)

899

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 H₂O; 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