

This item is the archived peer-reviewed author-version of:

Sensitivity of decomposition rates of soil organic matter with respect to simultaneous changes in temperature and moisture

Reference:

Sierra Carlos A., Trumbore Susan E., Davidson Eric A., Vicca Sara, Janssens Ivan.- Sensitivity of decomposition rates of soil organic matter with respect to simultaneous changes in temperature and moisture
Journal of advances in modeling earth systems - ISSN 1942-2466 - (2015), p. -22
DOI: <http://dx.doi.org/doi:10.1002/2014MS000358>

1 Sensitivity of decomposition rates of soil organic
2 matter with respect to simultaneous changes in
3 temperature and moisture

Carlos A. Sierra¹, Susan E. Trumbore¹, Eric A. Davidson², Sara Vicca³, and
I. Janssens³

¹Max Planck Institute for
Biogeochemistry, Hans-Knöll-Straße 10,
Jena, Germany.

²Woods Hole Research Center, 149 Woods
Hole Road, Falmouth, MA 02540, USA.

³Research Group of Plant and Vegetation
Ecology, Department of Biology, University
of Antwerp, Universiteitsplein 1, B-2610,
Wilrijk, Belgium.

4 **Abstract.** The sensitivity of soil organic matter decomposition to global
5 environmental change is a topic of prominent relevance for the global car-
6 bon cycle. Decomposition depends on multiple factors that are being altered
7 simultaneously as a result of global environmental change; therefore, it is im-
8 portant to study the sensitivity of the rates of soil organic matter decom-
9 position with respect to multiple and interacting drivers. In this manuscript
10 we present an analysis of the potential response of decomposition rates to
11 simultaneous changes in temperature and moisture. To address this prob-
12 lem, we first present a theoretical framework to study the sensitivity of soil
13 organic matter decomposition when multiple driving factors change simul-
14 taneously. We then apply this framework to models and data at different lev-
15 els of abstraction: 1) to a mechanistic model that addresses the limitation
16 of enzyme activity by simultaneous effects of temperature and soil water con-
17 tent, the latter controlling substrate supply and oxygen concentration for mi-
18 crobial activity; 2) to different mathematical functions used to represent tem-
19 perature and moisture effects on decomposition in biogeochemical models.
20 To contrast model predictions at these two levels of organization, we com-
21 piled different datasets of observed responses in field and laboratory stud-
22 ies. Then we applied our conceptual framework to: 3) observations of het-
23 erotrophic respiration at the ecosystem level; 4) laboratory experiments look-
24 ing at the response of heterotrophic respiration to independent changes in
25 moisture and temperature; and 5) ecosystem-level experiments manipulat-
26 ing soil temperature and water content simultaneously.

1. Introduction

27 One important characteristic of current and predicted global change is that multiple
28 environmental factors change simultaneously. This contrasts with classical experimental
29 approaches in ecological and environmental sciences that mostly study the impact of single
30 factors on ecosystem properties. For example, in the past three decades a significant
31 effort has been directed to study the ecosystem effects of CO₂ fertilization [*Körner*, 2006;
32 *Körner et al.*, 2007], soil warming [*Davidson and Janssens*, 2006], nitrogen deposition
33 [*Galloway et al.*, 2008], water availability [*Nepstad et al.*, 2002; *Davidson et al.*, 2008], and
34 fire [*Balch et al.*, 2008]. Where these ecosystem manipulation experiments have included
35 the interaction with one or two additional factors, results suggest that effects are not
36 additive or predictable from individual variables alone [*Leuzinger et al.*, 2011; *Dieleman*
37 *et al.*, 2012]. However, there is a paucity of research on multi-factor ecosystem studies,
38 probably due to the difficulties of altering several global change factors simultaneously in
39 a fully replicated experiment [*Rustad et al.*, 2001; *Leuzinger et al.*, 2011; *Luo et al.*, 2011;
40 *Dieleman et al.*, 2012].

41 Soil warming studies have shown that interactions with soil moisture, nitrogen availabil-
42 ity, carbon supply, and microbial activity are fundamental to understand the response of
43 elevated temperatures on carbon release from soils [*Davidson and Janssens*, 2006; *Subke*
44 *and Bahn*, 2010; *Melillo et al.*, 2011; *Schindlbacher et al.*, 2012; *Selsted et al.*, 2012; *Poll*
45 *et al.*, 2013].

46 In soils, temperature and moisture covary at different spatial and temporal scales de-
47 scribing a trajectory in the $x y$ plane (Figure 1). These trajectories can differ at annual,

48 seasonal, and daily time-scales, often presenting hysteresis loops and dampening of oscil-
49 lations with depth [*Davidoff and Selim*, 1988; *Redding et al.*, 2003; *Liu and Luo*, 2011].
50 For example, the annual cycle of soil temperature and moisture at a deciduous temperate
51 forest shows a different trajectory for drying and warming than for cooling and wetting
52 (Figure 1a). As soil temperatures drop towards the winter months, soil moisture dras-
53 tically declines due to freezing, which removes water from the liquid phase. This effect
54 of soil ‘drying’ as temperatures drop is more important in boreal and arctic regions such
55 as the arctic tundra of Figure (1b), and less pronounced in temperate regions where it
56 occurs mostly at the surface (Figure 1a). Soil moisture can also decrease as temperatures
57 increase. In temperate and mediterranean-like climates, as soil temperature increases in
58 the spring months, soil moisture gradually decreases. On diel timescales, there may be
59 oscillations in temperature at nearly constant moisture as shown by a temperate grass-
60 land in Germany (Figure 1c). In arid regions, after a rain event, soil moisture increases
61 abruptly and decreases slowly with oscillations in diel cycles as exemplified by a Miombo
62 woodland in Zambia (Figure 1d).

63 Strong but site dependent covariation between soil temperature and moisture on a
64 range of timescales may have profound effects for predicting the effects of changes in
65 climate on the rates of soil organic matter decomposition and carbon emissions from
66 soils. Here we review and synthesize existing approaches on the sensitivity of soil organic
67 matter decomposition with respect to simultaneous changes in temperature and moisture,
68 two of the most important abiotic variables controlling the process of decomposition.
69 Our approach is theoretical and we focus our analysis on existing models and datasets.
70 This review is not exhaustive, although we cover a large variety of models, observations,

71 and experiments. Our goal is to help to 1) characterize our current ability to represent
72 environmental changes on the decomposition process, and 2) identify uncertainties and
73 potential areas for future research.

74 The manuscript is organized in four main parts. First, we present a theoretical frame-
75 work that allows us to address the sensitivity of the decomposition process for any number
76 of driving variables both in isolation and in combination. Second, we apply this framework
77 to a mechanistic model that represents reaction velocities of enzyme-substrate complexes
78 as a function of temperature, moisture, and oxygen content. Third, we apply the same
79 theoretical framework to analyze empirical functions commonly used in biogeochemical
80 models. Subsequently, we analyze empirical data to contrast model and theoretical pre-
81 dictions with observations, and in the last part of the manuscript we discuss our findings
82 and explore opportunities for future research.

2. Theoretical framework

83 To understand the sensitivity of soil organic matter decomposition and its associated
84 mineralization of carbon, it is important to improve our conceptual framework for the
85 development of experiments and models, and synthesize existing information. Mostly, it
86 is important to set clear and unambiguous definitions so confusion can be avoided. With
87 this purpose, we expand and formalize some definitions proposed earlier [*Davidson and*
88 *Janssens, 2006; Sierra, 2012*].

89 First, it is important to make a clear distinction between the *dependence* and the *sen-*
90 *sitivity* of carbon release with respect to multiple factors, terms that have often been
91 confounded in this research area. The *dependence* of a response variable Y such as het-
92 erotrophic respiration or decomposition rates, is simply defined in the context of a function

93 in which an environmental factor X_i acts as a driving variable, i.e. $Y = f(X_i, \dots)$. In con-
94 trast, the *intrinsic sensitivity* of the response variable Y with respect to an environmental
95 factor X_i , is defined as a partial derivative, that is $\partial Y / \partial X_i$. This partial derivative mea-
96 sures the absolute change in the response variable with respect to a change in the driving
97 variable (Table 1).

98 In the case of more than one driving variable the definition of *sensitivity* is more complex
99 than for the univariate case. When one studies the sensitivity of a process with respect
100 to one variable it is possible to see the effect of increasing or decreasing the value of the
101 driving variable (two directional movement on the real line). But in the case of multiple
102 variables there are infinite directions to move on n -dimensional surfaces, so one needs a
103 more complex theoretical framework to deal with more than one variable. Fortunately,
104 multivariate calculus provides a very useful analytical framework to study the sensitivity
105 of response variables with respect to multiple and simultaneous changes in the driving
106 variables.

107 Before introducing the concept of sensitivity in multiple dimensions, we define first a
108 model of soil organic matter decomposition so we can clearly point to the type of functions
109 to which we will be studying their sensitivity.

2.1. General model of organic matter decomposition

110 The predominant formalism to represent soil organic matter decomposition is by systems
111 of differential equations [Manzoni and Porporato, 2009]. These systems can be expressed
112 as vectors and matrices with dimensions equal to the number of state variables in the
113 model [Bolker et al., 1998; Pansu et al., 2004; Manzoni and Porporato, 2009; Luo and

114 *Weng, 2011; Sierra et al., 2012*]. It has been shown that most models of organic matter
 115 decomposition can be generalized by the equation [*Sierra et al., 2012*]

$$\frac{d\mathbf{C}(t)}{dt} = \mathbf{I}(t) + \xi(t) \cdot \mathbf{A} \cdot \mathbf{C}(t), \quad (1)$$

116 where the vector $\mathbf{C}(t)$ represents carbon stores in m number of pools at a given time t .
 117 $\mathbf{A} = \mathbf{T} \cdot \mathbf{K}$ is the decomposition operator, an $m \times m$ square matrix that results from
 118 the product of a diagonal matrix with constant decomposition rates \mathbf{K} and a matrix of
 119 transformation of organic matter \mathbf{T} , which contains -1 in the diagonal and coefficients
 120 $0 \leq \alpha_{i,j} \leq 1$ that represents the proportion of decomposed carbon that is transferred
 121 among pools (from pool j to pool i). $\mathbf{I}(t)$ is a time-dependent column vector describing
 122 the total amount of carbon inputs to each pool; and $\xi(t)$ is a time-dependent scalar
 123 containing the extrinsic effects on decomposition rates. For example, in the case of one
 124 single homogeneous substrate without litter inputs, equation (1) simplifies to $dC/dt =$
 125 $-\xi(t) \cdot k \cdot C$, and decomposition-derived respiration fluxes r can be obtained simply as:
 126 $r = \xi(t) \cdot k \cdot C$, where k is a decomposition rate constant. In the more general case of
 127 multiple pools, the vector of respiratory fluxes is given by

$$\mathbf{r}(t) = \xi(t) \cdot (\mathbf{R} \cdot \mathbf{K} \cdot \mathbf{C}(t)), \quad (2)$$

128 where \mathbf{R} is a diagonal matrix containing as elements respiration coefficients for each pool,
 129 where each R_j element is calculated as

$$R_j(t) = 1 - \sum_{i \neq j} \alpha_{i,j}(t), \quad (3)$$

130 with each $\alpha_{i,j}$ being an off-diagonal element of the matrix \mathbf{T} .

131 The term $\xi(t)$ is a general representation of the abiotic effects on decomposition rates.
 132 The predominant form of $\xi(t)$ is a product of different functions that depend on environ-
 133 mental variables X_i as

$$134 \quad \xi(t) = \prod_i f(X_i), \quad (4)$$

135 although polynomials or other functions such as $\min(f(X_i))$ have been proposed [*Rodrigo*
 136 *et al.*, 1997; *Bauer et al.*, 2008]. In most models however, $\xi(t)$ is a function of temperature
 137 T and moisture W of the form

$$138 \quad \xi(t) = f(T) \cdot f(W). \quad (5)$$

139 Time-dependence of the term ξ is therefore the result of the time dependence of tem-
 140 perature $T(t)$ and moisture $W(t)$. Given that T and W are projected to change over time,
 141 we will focus our analysis in studying the sensitivity of ξ with respect to simultaneous
 142 changes in T and W . Increases or decreases in ξ would result in faster or slower decompo-
 143 sition rates from soils as they affect directly all terms (decomposition rates and transfer
 144 coefficients) in \mathbf{A} .

145 The importance of the term ξ in explaining the sensitivity of decomposition can be
 146 better observed by calculating the partial derivative of the model of equation (1) with
 147 respect to an environmental variable X_i as

$$\frac{\partial \dot{\mathbf{C}}}{\partial X_i} = \frac{\partial \mathbf{I}}{\partial X_i} + \left(\frac{\partial \xi}{\partial X_i} \cdot \mathbf{A} \cdot \mathbf{C} + \xi \cdot \mathbf{A} \cdot \frac{\partial \mathbf{C}}{\partial X_i} \right), \quad (6)$$

148 where $\dot{\mathbf{C}} = d\mathbf{C}/dt$. This equation represents the intrinsic sensitivity of changes in carbon
 149 stocks with respect to a change in an arbitrary environmental variable X_i , and it is
 150 composed by the sensitivity of carbon inputs, the sensitivity of the term ξ , and the

151 sensitivity of the carbon stocks in the different pools, which is indirectly related to the
 152 sensitivity of the inputs $\left(\frac{\partial C}{\partial I} \frac{\partial I}{\partial X_i}\right)$.

153 Similarly, the sensitivity of respiration fluxes is given by the expression

$$\frac{\partial \mathbf{r}}{\partial X_i} = \frac{\partial \xi}{\partial X_i} (\mathbf{R} \cdot \mathbf{K} \cdot \mathbf{C}) + \xi \cdot \mathbf{R} \cdot \mathbf{K} \cdot \frac{\partial \mathbf{C}}{\partial X_i}, \quad (7)$$

154 which also highlights the importance of understanding the sensitivity of the term ξ for
 155 studying the sensitivity of respiration fluxes with respect to changes in the environment.

156 An analysis of the sensitivity of the soil carbon stocks \mathbf{C} , their net change $d\mathbf{C}/dt$, or
 157 even respiration fluxes is beyond the scope of this manuscript. This analysis only focuses
 158 on the sensitivity of the rates of decomposition and transfer among different pools ($\xi(t)$),
 159 which as shown in equations (6) and (7), is a fundamental component of the study of the
 160 sensitivity of soil carbon dynamics.

2.2. Definition of intrinsic and apparent sensitivity

161 Two very important concepts from multivariate calculus are used here, these are: the
 162 *gradient* and *directional derivatives*. The gradient, represented by the symbol ∇ ‘nabla’ is
 163 a vector (a collection) of partial derivatives. It quantifies the rate of change of a response
 164 variable Y with respect to independent changes of multiple explanatory variables X_i .
 165 Mathematically,

$$\nabla Y = \left[\frac{\partial Y}{\partial X_1}, \frac{\partial Y}{\partial X_2}, \dots, \frac{\partial Y}{\partial X_n} \right]. \quad (8)$$

167 Each partial derivative $\partial Y/\partial X_i$ represents the change in the response variable caused
 168 by a change in one of the driving variables when all others are held constant. Each partial
 169 derivative can be interpreted as the *intrinsic sensitivity* of the response variable with
 170 respect to one of the driving variables (Table 1).

171 The directional derivative, calculated as $\nabla Y \cdot \mathbf{u}$, measures the rate of change of Y as
 172 a consequence of simultaneous changes of all X_i in the direction \mathbf{u} , where \mathbf{u} is the unit
 173 vector with components u_1, \dots, u_n as

$$174 \quad \mathbf{u} = [u_1, \dots, u_n]^T = \left[\frac{\Delta X_1}{\sqrt{\Delta X_1^2 + \dots + \Delta X_n^2}}, \dots, \frac{\Delta X_n}{\sqrt{\Delta X_1^2 + \dots + \Delta X_n^2}} \right]^T \quad (9)$$

175 where ΔX_i is a specific change in the driving variable X_i between two times t_1 and t_2 .
 176 The directional derivative can be interpreted as the *apparent sensitivity* of the response
 177 variable when all driving variables change simultaneously in a particular direction (Table
 178 1). The terms intrinsic and apparent sensitivity as presented here are formal definitions
 179 of the same concepts introduced earlier by *Davidson and Janssens* [2006].

180 In combination, these two measures can be used to study the sensitivity of decomposition
 181 rates with respect to multiple environmental factors (X_1, X_2, \dots, X_n). In particular, the
 182 sensitivity of decomposition rates with respect to independent changes in temperature
 183 and moisture is given by the gradient

$$184 \quad \nabla \xi = \left[\frac{\partial \xi}{\partial T}, \frac{\partial \xi}{\partial W} \right]. \quad (10)$$

185 The sensitivity of decomposition rates with respect to simultaneous changes is quantified
 186 by the directional derivative in the direction \mathbf{u} , as

$$187 \quad \nabla \xi \cdot \mathbf{u} = \frac{\partial \xi}{\partial T} u_1 + \frac{\partial \xi}{\partial W} u_2. \quad (11)$$

188 For convenience, we will represent here the direction vector using a special notation.
 189 It is represented as a vector with a superscript denoting the change in temperature, and
 190 the subscript the change in moisture. For example, a direction in which temperature
 191 decreases by 2°C and moisture increases by 10% is denoted as $\mathbf{u}_{+0.1}^{-2}$.

3. Sensitivity of a mechanistic model

192 The Dual-Arrhenius Michaelis-Menten (DAMM) model [*Davidson et al.*, 2012] explains
193 mechanistically the constraints of temperature and moisture on enzyme activity. This
194 model is useful to illustrate the concepts of gradient and directional derivative. Further-
195 more, it provides a conceptual representation of the general sensitivity of the decompo-
196 sition process with respect to temperature and moisture at the level of enzyme-substrate
197 interactions. Additionally, this model explicitly addresses the theoretical limits of mi-
198 crobial activity imposed by substrate and oxygen diffusion at the enzyme reaction site
199 [Figure 2, *Skopp et al.*, 1990].

200 The foundation of the DAMM model is the Michaelis-Menten equation for the con-
201 centration of two substrates, soluble carbon $[S]$ and oxygen $[O_2]$. Including oxygen as a
202 substrate defines the scope of the model to aerobic respiration only, which is the dominant
203 form in most well-drained soils. The concentrations of both substrates are determined by
204 diffusivity functions, which are represented as functions of soil water content. Mathemat-
205 ically, the model predicts the reaction velocity R_S at the enzyme's reactive site as

$$206 \quad R_S = V_{max} \frac{[S]}{K_{Ms} + [S]} \frac{[O_2]}{K_{Mo} + [O_2]}, \quad (12)$$

207 where the maximum reaction velocity (V_{max}) and the half-saturation constants (K_{Ms} and
208 K_{Mo}) are temperature dependent, i.e. $f(T)$. V_{max} is calculated according to the Arrhenius
209 equation; therefore, it assures that, providing substrate concentrations are not limiting,
210 the respiration rate is sensitive to temperature according to Arrhenius kinetics. The
211 concentration of oxygen $[O_2]$ and the concentration of soluble organic carbon ($[S]$) are
212 moisture dependent $f(W)$. Although the DAMM model is based on first principles, it

213 relies on empirical functions for the temperature dependence of the half-saturation terms.
 214 Additional details about the model can be found in *Davidson et al.* [2012].

215 As the maximum reaction velocity follows the Arrhenius equation, $V_{max} =$
 216 $A \exp(-E/\mathcal{R}T)$, the pre-exponential factor A is modified by the unitless exponential term
 217 and the two unitless Michaelis-Menten terms in equation (12). Therefore, the reaction
 218 velocity R_S can be expressed as the product of the pre-exponential term and the mod-
 219 ifying functions for temperature and moisture, $R_S = A \cdot f(T, W)$. The dimensionless
 220 representation of R_S , obtained as $R = R_S/A$, follows the definition of ξ above (equation
 221 5); i.e. $R = f(T, W)$.

222 To simplify the presentation of this analysis, we change the notation of equation (12)
 223 to avoid long mathematical terms. Then, the DAMM model can also be expressed as

$$224 \quad R = V \frac{S}{K_S + S} \frac{O}{K_O + O}, \quad (13)$$

225 where $V = \exp(-E/\mathcal{R}T)$.

226 The gradient in this case only depends on two variables, and is given by

$$227 \quad \nabla R = \left[\frac{\partial R}{\partial T}, \frac{\partial R}{\partial W} \right], \quad (14)$$

228 OR

$$229 \quad \nabla R = \left[R \left(\frac{1}{V} \frac{\partial V}{\partial T} - \frac{1}{K_S + S} \frac{\partial K_S}{\partial T} - \frac{1}{K_O + O} \frac{\partial K_O}{\partial T} \right), \right. \\
 230 \quad \left. R \left(\frac{1}{S} \frac{\partial S}{\partial W} \frac{K_S}{K_S + S} + \frac{1}{O} \frac{\partial O}{\partial W} \frac{K_O}{K_O + O} \right) \right]. \quad (15)$$

232 Details about the derivation of this gradient with specific functions for V , S , O , K_S ,
 233 K_O are provided in the supplementary material.

234 This gradient shows that the sensitivity of the rates of an enzyme reaction with respect
 235 to temperature is a function of the temperature sensitivities of V and the half-saturation

236 constants K_S and K_O , while the sensitivity of the reaction with respect to moisture is the
237 sum of the sensitivities of substrate and oxygen concentrations.

238 Using parameters provided in *Davidson et al.* [2012] for β -glucosidase activity in organic
239 soils (Figure 2), we calculated the intrinsic sensitivity of R with respect to temperature
240 (Figure 3a) and moisture (Figure 3b). The apparent sensitivity when both variables
241 change simultaneously was assessed with the directional derivative in the directions $\mathbf{u}_{+0.2}^{+1}$
242 and $\mathbf{u}_{-0.2}^{+1}$ (Figure 3c and d).

243 This simple analysis of intrinsic and apparent sensitivities on the DAMM model (Figure
244 3) suggests that both types of sensitivity can differ significantly. The intrinsic temperature
245 sensitivity of β -glucosidase reactions shows higher sensitivities at intermediate moisture
246 levels and high temperatures. The intrinsic moisture sensitivity however, shows large
247 sensitivities at high moisture levels and high temperatures.

248 The apparent sensitivity when temperature increases by 1 K and volumetric water
249 content increases by 20% shows that β -glucosidase reaction velocities can decrease sig-
250 nificantly at high temperature and moisture levels (Figure 3c). In contrast, the same
251 temperature increase but with a decrease of 20% in volumetric water content shows larger
252 increases in reaction velocities at high temperature and moisture levels (Figure 3d).

253 More generally, this analysis confirms that high and low levels of soil moisture can
254 severely constrain rates of enzyme reactions independent of temperature. However, the
255 intrinsic sensitivities with respect to changes in temperature and moisture are very differ-
256 ent depending on the actual combinations and starting conditions; e.g. at low temperature
257 and moisture levels very small sensitivities are expected. At high temperature and mois-
258 ture, large sensitivities are expected with respect to moisture but not with respect to

259 temperature. The apparent sensitivities therefore, depend on the actual combination of
260 temperature and moisture in the system and the specific change (direction) of these two
261 variables.

4. Sensitivity in biogeochemical models

262 As mentioned before, most biogeochemical models include functions that represent the
263 effects of temperature and moisture on decomposition rates. We compiled a number of
264 those functions and included them in the SOILR package, an open source repository of
265 soil organic matter decomposition models [Table 2, *Sierra et al.*, 2012].

266 The selected temperature and moisture functions used the parameter values presented
267 in the original publications (Table 2), except for the Q_{10} function that is presented with
268 values of 2.0 and 1.4 [c.f. *Mahecha et al.*, 2010]. Furthermore, we made transformations in
269 these equations when necessary for consistency and comparability. Specifically, we trans-
270 formed all temperature functions that take as input temperatures in K and transformed
271 to degrees C. Moisture functions were normalized in such a way that the input moisture
272 values are all in a range from 0 to 1. In most cases, this transformation consisted in ex-
273 pressing the soil moisture metric (e.g. volumetric water content) relative to its maximum
274 value, which is generally dictated by soil porosity. In this way we avoid discrepancies
275 between different measures of soil moisture [c.f. *Moyano et al.*, 2012]. Interestingly, most
276 models we reviewed do exactly this in their calculation of moisture effects on decomposi-
277 tion, they take a particular metric of soil moisture and transform the variable in a range
278 between 0 to 1, and then calculate the effects on decomposition. This homogenized vari-
279 able is defined here as moisture index (W_i), only for practical reasons, and should not be
280 confounded with other definitions of this term.

281 We calculated the derivative of these functions with respect to temperature and moisture
282 numerically using the R environment for computing [Figure 4, *R Development Core Team*,
283 2012]. All code to reproduce the results presented here are provided in the supplementary
284 material.

4.1. Temperature effects on decomposition rates $f(T)$ and their intrinsic sensitivity $\partial f(T)/\partial T$

285 All the compiled functions consistently show increasing effects of temperature on decom-
286 position rates (Figure 4a). Below 0°C, almost all functions predict a consistent reduction
287 in decomposition rates. Above 0°C however, most functions diverge and predict a wide
288 range of effects of temperature on decomposition rates.

289 Despite this heterogeneity of responses, a few groups of functions can be distinguished.
290 One group of functions have a maximum value of 1 at some reference temperature, which
291 means that they only reduce decomposition rates from a maximum reference value. All
292 functions in this group have a sigmoid shape. All other functions assume a reference
293 decomposition rate in the range between 10 and 25°C, in which the functions take a value
294 of 1. The assumptions in this second group is that there is a reference temperature in
295 which decomposition rates are ‘optimal’ [*Burke et al.*, 2003].

296 Within this second group of functions it is also possible to distinguish functions that
297 grow continuously with a convex shape as in the Arrhenius equation. These functions
298 assume that the effects of temperature on decomposition rates increase proportionally
299 with the value of temperature. In contrast, other functions change their convexity in
300 the upper part of the temperature range assuming that above a threshold temperature,

301 further increases of temperature no longer stimulate decomposition rates, and often even
302 decrease them.

303 All these temperature functions produce a variety of intrinsic temperature sensitivities
304 (Figure 4b). However, most functions agree in that increases in temperature result in
305 increases in decomposition rates, except for a few functions that predict decreases in
306 decomposition rates at high temperatures ($\partial f(T)/\partial T < 0$). All derivatives are similar to
307 each other and close to their average value at low temperatures. At higher temperatures
308 however, all functions diverge considerably and none are close to the average value.

309 It is interesting to note that two of the most common functions used in biogeochemical
310 and Earth system models, the Lloyd and Taylor function and the Q_{10} function with a
311 value of 2, predict sensitivities above one standard deviation of all other functions for a
312 significant part of the temperature range (Figure 4b).

4.2. Moisture effects on decomposition rates $f(W)$ and their intrinsic sensitivity $\partial f(W)/\partial W$

313 The functions used to represent the effects of soil moisture on decomposition rates are
314 even less consistent than the temperature functions (Figure 4c). There are only two main
315 features in which these functions agree: 1) they all reduce decomposition rates from a
316 maximum ‘optimum’ value; and 2) this reduction is stronger at low values of soil moisture.
317 However, at intermediate or high values of the moisture index range the behaviors differ
318 considerably. Four functions present a maximum value of 1 in the intermediate part of the
319 W_i range and decline subsequently, representing an inhibition effect at high soil moisture
320 level. Another set of four functions exhibit an asymptotic behavior towards the maximum
321 value at high moisture levels without subsequent reductions, but the moisture level at

322 which this maximum is reached varies considerably among all functions. In the Demeter
323 model, the relationship is actually linear predicting a constant intrinsic sensitivity for the
324 entire W_i range (Figure 4c).

325 The moisture sensitivity functions differ widely, with the StandCarb function showing
326 high sensitivities at both extremes of the moisture index range, and the Gompertz function
327 with the highest sensitivity at the lower extreme. The StandCarb, Daycent, and the
328 function proposed by *Moyano et al.* [2013] show negative sensitivities at high values of
329 moisture, implying decreases in decomposition rates with increases in moisture when this
330 variable is already high. In contrast, all other functions predict increases or no change in
331 decomposition rates $\partial f(W)/\partial W \geq 0$ at high values of moisture (Figure 4d).

332 Three functions predict linear sensitivities along the W_i range, including the Demeter
333 function already mentioned. The sensitivity of the functions proposed by *Myers et al.*
334 [1982] and *Moyano et al.* [2013] are linear functions with negative slopes, representing a
335 decrease in the moisture sensitivity as W_i increases. However, Myers' function does not
336 reach negative values suggesting that increases in moisture always increase decomposition
337 rates, but at high moisture levels this sensitivity is negligible. In contrast, Moyano's
338 function predicts decreases in decomposition rates as moisture increases above an optimum
339 level. Notice that these linear sensitivities of the Myers' and Moyano's functions are
340 not associated with linear dependence functions. Instead, the dependence functions are
341 nonlinear, but their derivative results in linear functions.

342 Part of the disagreement among the functions is probably due to differences in the con-
343 ceptualization and representation of soil moisture and its effects on decomposition rates.
344 Particularly, each model was originally developed using different concepts to describe soil

345 moisture. In the Standcarb model for example, soil moisture is represented as volumetric
346 water content relative to the maximum amount of water the soil can hold [*Harmon and*
347 *Domingo, 2001*]. In Daycent, soil moisture is represented as water-filled pore space, a
348 ratio between water content per soil volume and pore space [*Kelly et al., 2000*]. Each
349 of these functions is composed of two multiplicative terms (Table 2), the first term ac-
350 counting for increases in decomposition as water increases and the second term accounting
351 for reductions. In Standcarb, these two terms explicitly account for the effects of matric
352 potential and oxygen diffusion, respectively; while in Daycent these two terms lack any
353 explicit conceptualization.

354 In the Century function, soil moisture is represented as the ratio of precipitation to po-
355 tential evapotranspiration [*Parton et al., 2001*]. This ecosystem level measure of humidity
356 is a good indicator for classifying vegetation and global soil carbon stocks according to
357 moisture constraints [*Holdridge, 1967; Post et al., 1982*], but may not be adequate to rep-
358 resent soil moisture dynamics at finer scales, as it does not take into account the capacity
359 of the soil to store water. For representing the effects of this measure of soil moisture
360 on decomposition rates, *Parton et al.* [2001] used a logistic function, but it is unclear
361 whether the choice of this function was based on explicit mechanisms. A similar approach
362 was used in the global-scale model Demeter, in which soil moisture is represented at the
363 grid level as a difference between precipitation and evapotranspiration [*Foley, 2011*]. In
364 this case, there are no mechanisms that account for reductions of decomposition rates
365 when precipitation largely exceeds evapotranspiration.

366 Another conceptual difference among the functions that consider limitations at high
367 moisture levels, is the specific mathematical form to account for this limitation. While in

368 the StandCarb and Daycent functions high moisture levels decrease decomposition rates
369 with a multiplicative term, in the functions proposed by *Myers et al.* [1982] and *Moyano*
370 *et al.* [2013] this decrease is represented by subtracting a quadratic term (Table 2). The
371 function proposed by *Skopp et al.* [1990] does not multiply or subtract the limitation term
372 because it calculates the minimum of either the limitations due to substrate or oxygen
373 diffusion. This function produces a sharp peak at its maximum value (Figure 4c), which
374 creates a discontinuity and therefore the value of the derivative can not be calculated at
375 this point.

4.3. Apparent sensitivity for specific changes in temperature and moisture

376 We calculated the apparent sensitivity of decomposition rates for all possible combi-
377 nations of the functions presented in the previous section and for different directions of
378 change in temperature and moisture. We calculated directional derivatives in the direction
379 of an increase in temperature by 1°C and a simultaneous increase of moisture index W_i by
380 20% ($\mathbf{u}_{+0.2}^+$). Similarly, in the direction of 1°C increase in temperature and a decrease by
381 20% in W_i ($\mathbf{u}_{-0.2}^+$); also, in the direction of 1°C decrease in temperature and an increase of
382 20% in W_i ($\mathbf{u}_{+0.2}^-$). Due to space limitations, we present these results as Figures (S1-S4)
383 in the supplementary material.

384 As expected from the results obtained for the intrinsic sensitivity with respect to tem-
385 perature and moisture independently, the variability of the apparent sensitivity predicted
386 by all combinations of functions was large. The range of apparent sensitivities was be-
387 tween -20 to 80% °C⁻¹ % W_i ⁻¹ (Figures S1-S4). The highest values of apparent sensitivity
388 were obtained with the temperature function Q_{10} with a value of 2, particularly at high
389 temperature values. However, other model combination predicted decreases in decomposi-

390 tion rates at high values of temperature, independent of the moisture levels. Some model
391 combinations however, presented small decreases in decomposition rates for changes in
392 temperature and moisture in this particular direction. Other models, predicted moderate
393 values of apparent sensitivity at intermediate levels of temperature.

394 Taking an average across the 80 different model combinations, it is clear that temper-
395 ature has a stronger control than moisture on the apparent sensitivity of decomposition
396 rates in the direction $\mathbf{u}_{-0.2}^{+1}$ (Figure 5a). Also, the highest apparent sensitivity across all
397 models was, on average, at the highest values of temperature and moisture, with a peak
398 around 40°C and 90% W_i .

399 These average apparent sensitivities however, are accompanied by large uncertainties as
400 measured by the standard deviation of all model combinations (Figure 5b). Uncertainties
401 increase proportionally with temperature, but are also high at the extremes of the moisture
402 range.

403 These results show that most models predict a stronger sensitivity with respect to
404 changes in temperature than to moisture, even when moisture is changed by 20% and
405 temperature only by 1°C, in contrast with the theoretical results obtained with the DAMM
406 model (Figure 3).

5. Empirical evidence

407 To some extent, most of the functions reviewed are derived from analysis of empirical
408 data [c.f. *Lloyd and Taylor, 1994; Kelly et al., 2000; Parton et al., 2001; Burke et al.,*
409 *2003*]. It is important however, to contrast independent empirical evidence against the
410 set of functions being applied in biogeochemical models to find the model or set of models
411 that most closely resemble observed data.

412 Three types of empirical studies are reviewed in this section: 1) observations of het-
413 erotrophic respiration taken from a large set of studies from around the world; 2) labora-
414 tory manipulation studies under controlled moisture and temperature levels; 3) ecosystem
415 level manipulation experiments in which both temperature and moisture are controlled
416 and monitored in situ.

5.1. Observed heterotrophic respiration in situ

417 For the past four decades, soil CO₂ fluxes have been measured using soil chambers over
418 a wide range of ecosystems. Currently, these measurements are being compiled in the Soil
419 Respiration Database [SRDB, *Bond-Lamberty and Thomson, 2010a, b*], which is publicly
420 available and we use it here to observe the patterns of heterotropic respiration across
421 ranges of mean annual temperature MAT and mean annual precipitation MAP.

422 One important issue is that heterotrophic respiration data across sites do not provide
423 enough information to accurately calculate values of ξ , and only a rough approximation
424 can be obtained. We used two methods here to obtain an approximation of ξ based
425 on values of mean annual heterotrophic respiration from the SRDB. The first method is
426 based on the assumption that the environmental effects on decomposition can be extracted
427 dividing heterotrophic respiration data by a reference value as

$$\xi_1 = \frac{r}{r_{ref}}, \quad (16)$$

428 where $r = \sum \mathbf{r}$, i.e. the sum of the respiration flux across all pools (total heterotrophic
429 respiration); and r_{ref} is a reference heterotrophic respiration, in this case the average
430 across all sites in the SRDB.

431 The second method, assumes that ξ can be obtained dividing respiration fluxes by the
 432 carbon stock at each site. The idea here is that differences in productivity across sites
 433 can be removed by normalizing the data with respect to carbon stocks. In this case,

$$\xi_2 = \frac{r}{C} \quad (17)$$

434 where $C = \sum \mathbf{C}$ is the sum of the carbon stocks in all pools at each site.

435 Obviously, both approaches are only poor approximations to ξ , which should be calcu-
 436 lated as

$$\xi = \frac{r}{\sum (\mathbf{R} \cdot \mathbf{K} \cdot \mathbf{C})}, \quad (18)$$

437 but given that we do not have any information on \mathbf{R} or \mathbf{K} from field data, we can only
 438 obtain simple approximations to ξ calculating ξ_1 and ξ_2 .

439 The results show that the values of ξ_1 and ξ_2 are generally low where MAP < 200 mm
 440 and MAT < 0°C (Figure 6). Also, they tend to increase with MAT for a wide range of
 441 MAP (above 200 mm). This dataset supports the idea that decomposition rates increase
 442 with temperature and are low at temperatures below the freeing point and under arid
 443 conditions. However, it is difficult to discern the effects of soil moisture on decomposition
 444 rates because precipitation alone is not a good indicator of the capacity of the soil to
 445 retain moisture as it is highly dependent on soil texture and structure [*Rodríguez-Iturbe*
 446 *and Porporato, 2004; Moyano et al., 2012; Vicca et al., 2012*].

447 It is important to note that it is very difficult to relate the patterns observed in this
 448 dataset with the patterns of the different functions reviewed in the previous section. Only
 449 general patters can be detected from the dataset, but they could also be influenced by the

450 effects of temperature and precipitation on productivity and therefore on carbon inputs
451 to the soil. Differences in productivity across sites obscure the effects of environmental
452 variables on decomposition, so we cannot derive a clear pattern for ξ from this dataset.

5.2. Laboratory experiments

453 Data from laboratory incubation experiments have been recently compiled by *Moyano*
454 *et al.* [2012]. One important characteristic of this dataset is that it provides different
455 measures of soil moisture such as volumetric and gravimetric water content, water sat-
456 uration, and soil water potential ψ . The majority of studies however, report volumetric
457 water content θ_v , so we use this metric here in combination with incubation temperature
458 to observe general trends on decomposition rates.

459 The incubation experiments show that decomposition rates are highly reduced at low
460 and high soil moisture levels (Figure 7). The largest values of ξ_1 were at intermediate
461 temperature and moisture levels, which suggest that interactions of these two variables at
462 their extreme values limit decomposition rates.

463 On a very broad level, this dataset suggests that the theoretical pattern predicted by the
464 DAMM model is supported by soil incubation data. However, it is important to consider
465 that the calculation of ξ_1 and ξ_2 here is only an approximation to the theoretical ξ .

466 Incubation studies also need to be considered carefully because in most cases sam-
467 ple preparation involves sieving and strong modifications of soil structure. When soil
468 structure is destroyed, substrate availability for decomposers may change dramatically.
469 Similarly, gas diffusivity and exchange are particularly affected by alterations in pore
470 size and surface-to-volume ratios, which in turn can affect the temperature and moisture
471 effects on decomposition [*Dilustro et al.*, 2005; *Plante et al.*, 2009; *Moyano et al.*, 2013].

5.3. Ecosystem-level manipulations

472 Ecosystem-level manipulation experiments in which temperature and moisture are con-
473 trolled in situ can also provide useful information on the controls of these variables on
474 soil organic matter decomposition. For this purpose, we used the Precipitation Manipula-
475 tion database [Vicca *et al.*, 2012]. This dataset includes studies in which different abiotic
476 drivers are manipulated at different ecosystem types. However, in this dataset, only a few
477 studies met the criteria of manipulating soil moisture and temperature simultaneously
478 while at the same time reporting soil respiration rates [see Fay *et al.*, 2011; Suseela *et al.*,
479 2012; Selsted *et al.*, 2012; Högy *et al.*, 2013; Poll *et al.*, 2013, and Table in supplementary
480 material].

481 From the 14 treatments that met these criteria, only 4 treatments showed significant
482 effect sizes calculated as Glass' Delta (Δ_G : (treatment mean - control mean)/control
483 standard deviation). Most of the treatments did not show significant differences in soil
484 respiration as a result of soil warming/cooling or irrigation/drought, but the treatments
485 that did show significant differences exhibited reductions in soil respiration rather than
486 increases (Figure 8a).

487 To interpret the results from these experimental manipulations, we plotted the experi-
488 mental data against the predictions of the DAMM model for the reaction velocity of the
489 β -glucosidase enzyme (Figure 8b). The experimental data, plotted as arrows indicating
490 the change from the control to the experimental treatment, show that most experiments
491 have been carried out in combinations of temperature and moisture with low reaction ve-
492 locities of β -glucosidase, so the decomposition of substrates such as cellulose likely proceed
493 slowly at these manipulation sites. Furthermore, the direction of change in temperature

494 and moisture in which most studies were implemented more likely lead to no changes
495 or decreases in reaction velocities (Figure 8b). It is therefore expected that the intrinsic
496 sensitivities with respect to temperature (Figure 8c) and moisture (Figure 8d) are at their
497 lowest levels for these manipulation experiments.

498 The results from these manipulation experiments analyzed within the framework of
499 the expected responses for enzyme reaction rates may have some important implications:
500 1) most current climate change experiments have been probably implemented in sites
501 where the combination of temperature and moisture, and their manipulation, are not
502 very relevant for the sensitivity of enzyme activity and organic matter decomposition. 2)
503 Many sites with soil temperatures between 15 and 20°C and volumetric water content
504 between 10 to 30% may show very low sensitivities to changes in climate as suggested
505 by the experimental data and the model predictions. 3) The predominant directional
506 change in soil temperature and moisture imposed in most experiments towards increases
507 in temperature by a few degrees and small decreases in soil moisture of a few % would
508 likely lead to undetectable changes or minor decreases in soil organic matter decomposition
509 and a subsequent minor decrease in respiration rates.

6. Discussion

510 After many decades of research on the abiotic controls in the process of soil organic
511 matter decomposition [*Swift et al.*, 1979; *Paul and Clark*, 1996; *Luo and Zhou*, 2006],
512 we still lack robust mathematical models and experiments to predict the consequences of
513 changes in climate on the rates of decomposition of global soil carbon stocks. Although
514 many models have been proposed and a large number of experiments and measurements
515 have been performed, it is still difficult to confront models with observations and reach

516 strong conclusions. However, from this analysis a few points of consensus have been
517 identified and some research gaps have emerged.

6.1. Consensus between models and observations/experiments

518 Although there is little consensus among the models, they all tend to agree in that
519 decomposition rates and their sensitivity are low below freezing ($< 0^{\circ}\text{C}$) and at very low
520 soil moisture contents. This is not a surprise in the context of the relatively well known
521 abiotic limitation of decomposition rates in arctic and boreal regions under permafrost
522 [Zimov *et al.*, 2006; Schuur *et al.*, 2008]. Below-freezing temperatures not only limit the
523 kinetics of soil microorganisms, but also removes water from the liquid phase making it
524 unavailable for the dissolution of substrates in the soil matrix. Psychrophilic microorgan-
525 isms can thermally adapt to below freezing temperatures by their lipid composition that
526 affects the properties of their membranes and allow them to remain in a fluid state, albeit
527 at very low levels of activity [Russell and Fukunaga, 1990; Mangelsdorf *et al.*, 2009].

528 Although this might be the only point in which all models and most observational
529 evidence agree, it is still a significant point in the sense that it helps to explain the large
530 amounts of carbon stored under permafrost soils. Less certain however, is the sensitivity
531 of decomposition as temperature increases and water content becomes more available
532 because of the change in phase of water. We will return to this point in the next section.

533 The ecosystem-level manipulation studies showed good agreement with the predictions
534 of the DAMM model even though there is a conceptual mismatch between the data and
535 the model; the empirical data reporting soil respiration and the model predicting reaction
536 velocities of the β -glucosidase enzyme. From this comparison, it seems likely that soils
537 with temperatures between 10 and 20°C and SWC between 5 and 25% would show very

538 low sensitivity to simultaneous changes in temperature and moisture; and if they do
539 show responses to climatic drivers, most likely these would manifest in reductions of
540 decomposition rates.

541 Although not an agreement among all functions, it seems that to model limitations
542 of decomposition rates at high moisture levels, it is necessary to have a function with
543 two terms; one term accounting for increases in water availability for microbial growth,
544 and a second term accounting for oxygen limitations as soil moisture reaches saturation
545 levels. This mathematical characteristic was common among the DAMM model and the
546 functions in Daycent , Standcarb and those proposed by *Skopp et al.* [1990] and *Moyano*
547 *et al.* [2012]. Furthermore, it agrees with previous observations suggesting that microbial
548 growth can be limited by both high water potential at low soil moisture levels and low
549 oxygen diffusivity at high moisture levels [*Griffin, 1963*]. What it is not clear however,
550 is the specific type of mathematical function that best describes both types of moisture
551 limitations. Multiplicative or subtracting terms have been used by these authors for the
552 dependence functions, with important consequences for the linearity or nonlinearity of the
553 sensitivity functions (Figure 4c and d).

6.2. Disagreement between models and observations/experiments

554 Unfortunately, there are still important disagreements among models as well as between
555 models and observations/experiments.

556 One of the most important points of disagreements among models is the temperature
557 dependence and sensitivity of decomposition rates at high temperatures ($> 25^{\circ}\text{C}$). Equally
558 important is the disagreement among models on the dependence and sensitivity of decom-
559 position rates across the entire soil moisture range.

560 The functions reviewed here disagree on whether there is a continuous increase, a sat-
561 uration, or a decline in decomposition rates at the upper end of the temperature range.
562 None of the datasets reviewed supports the idea included in many functions of continuous
563 increases in decomposition rates with temperature, probably because at higher temper-
564 atures soil moisture levels inevitably decrease with increases in temperature (Figure 1).
565 Most likely, this behavior would be strongly determined by the interaction with soil mois-
566 ture as temperature increases and the soil dries out. Recent studies have found support
567 for the Arrhenius equation [*Craine et al.*, 2010; *Sierra*, 2012; *Lehmeier et al.*, 2013], which
568 predicts a continuous increase in decomposition rates with temperature, but it is unclear
569 whether Arrhenius kinetics are valid for the entire temperature range.

570 This interaction between soil temperature and moisture at high temperatures is repre-
571 sented mechanistically in the DAMM model by the interaction of Arrhenius kinetics for
572 the temperature dependence, and moisture constraints on the solubility of substrates and
573 oxygen levels, expressed as Michaelis-Menten functions. In Arrhenius kinetics, enzyme ac-
574 tivities and the degradation of substrates increase continuously as temperature increases
575 without any saturation or reversing trends. However, the decline in reaction rates in this
576 model at high temperatures is caused by the interaction with the Michaelis-Menten terms
577 that significantly dampen the temperature effects.

578 In contrast, in some of the empirical models such as the widely used Q_{10} function with
579 a value of 2, and the Lloyd and Taylor function, the increases in decomposition rates as
580 temperature increase are so high that the interaction with the moisture functions cannot
581 offset the temperature effects (Figures S1-S4). In fact, it appears as these functions

582 overestimate temperature effects in comparison with other functions and the empirical
583 evidence reviewed here.

584 The larger levels of disagreement among all reviewed models was at the highest values
585 of temperature and at the extremes of the moisture range (Figure 5b). One important
586 obstacle to reduce uncertainties at these levels of temperature and moisture is that field
587 measurements and experiments are commonly developed outside these extremes, so there
588 is little empirical evidence to discern the most likely patterns. In fact, most experiments
589 are being developed at near optimum conditions of temperature and moisture and far
590 from the conditions in which the highest sensitivities are theoretically expected.

591 The empirical evidence reviewed here did not provide strong support for any particular
592 model or function. This empirical evidence can only inform about general qualitative
593 trends, which may be confounded by temperature and moisture effects on carbon inputs,
594 which in turn affect the carbon stock and its sensitivity.

595 An important point of disagreement among different models and empirical analyses is
596 also the representation of soil moisture, which can be expressed as volumetric soil water
597 content, soil water potential, or differences among precipitation and potential evapotran-
598 spiration, among others [*Seneviratne et al.*, 2010; *Moyano et al.*, 2012]. It is likely that
599 the choice of metric to represent soil moisture bias the results to either effects of suction
600 and substrate solubility or limitations for oxygen diffusion on microbial growth [*Griffin*,
601 1963; *Skopp et al.*, 1990]. If soil moisture is expressed as soil water potential or a re-
602 lated measure, it is likely that limitations due to oxygen diffusion are not accounted for.
603 However, if soil moisture is only expressed as soil water content, it is possible that the
604 energy required by a microorganism to extract water from the soil matrix is not properly

605 represented, leading to overestimations of decomposition rates at low and intermediate
606 soil moisture levels. A good representation of soil moisture therefore, would need to in-
607 corporate a mixture from these two types of metrics [*Vicca et al.*, 2012; *Moyano et al.*,
608 2013].

609 Particularly important is the uncertainty at the phase change of water at low tempera-
610 tures because these are the conditions predominant in arctic soils subjected to freeze-thaw
611 cycles. None of the models reviewed here consider explicitly the change in phase of water
612 at the freezing point. The transition from ice to liquid has not only important implications
613 in the availability of water and oxygen for microorganisms, but also modifying the physi-
614 cal structure of the soil [*Zimov et al.*, 2006; *Schuur et al.*, 2008]. Thawing therefore leads
615 to important increases in microbial activity as shown by various experimental and field
616 studies [*Clein and Schimel*, 1995; *Winston et al.*, 1997; *Dioumaeva et al.*, 2002]. However,
617 even though the change in phase of water can result in important increases in biological
618 activity, temperatures only a few degrees above the freezing point can still limit microbial
619 activity [*Pietikäinen et al.*, 2005]. This interaction between temperature and moisture
620 close to the freezing point of water is still poorly understood as evidenced here by the lack
621 of explicit representation of these processes in models and the paucity of experimental
622 research in this climate zone. It is however possible to represent the transition from ice
623 to liquid water with some of the functions currently available. In practice, freezing is
624 analogous to drying because as temperature drops liquid water is no longer available for
625 biological processes [Figure 1b, *Clein and Schimel*, 1995].

626 Also important is the uncertainty on the sensitivity of decomposition rates at the highest
627 values of temperature and moisture. At these combinations large carbon stores can be

628 found such as in tropical peatlands [*Page et al.*, 2004; *Lähteenoja et al.*, 2009]. The DAMM
629 model predicts high sensitivities with respect to changes in moisture for these conditions
630 and some empirical evidence suggests that drying tropical peatlands or changing water-
631 table depth result in very important changes in carbon release or storage [*Jauhiainen*
632 *et al.*, 2005; *Jungkunst and Fiedler*, 2007].

6.3. Research gaps and opportunities

633 This review underscored some important gaps in our understanding of the interaction
634 between temperature and moisture for modeling abiotic effects on soil organic matter
635 decomposition. These gaps open new opportunities for future research, which we now
636 outline below.

637 New experiments and observations at the extremes of temperature and moisture would
638 help to reduce uncertainties where the largest sensitivities are expected. For example, new
639 experiments could address the question of whether there is a decline or saturation effect of
640 decomposition rates as temperature increase towards larger values, provided moisture and
641 oxygen levels are not limiting for decomposers. Or whether decomposition rates decline
642 at high temperature values because of moisture limitations and not because temperature
643 effects per se [*Angilletta*, 2009].

644 New empirical work should focus not only on designing experiments looking at treat-
645 ment differences among sites or factorial designs, but also on producing mathematical
646 functions along temperature and moisture gradients. One of the main limitations we
647 found in the datasets we reviewed was their lack of consistency with the functions that
648 need to be incorporated in models. Observationally derived mathematical functions are of
649 immense value for implementation in biogeochemical models that can test the integrated

650 effects of global environmental change on the biogeochemistry of terrestrial ecosystems.
651 Mathematical functions can also be subjected to further analyses such as the calculation
652 of intrinsic and apparent sensitivities using partial and directional derivatives.

653 Given that most functions are applied to obtain temperature and moisture effects at
654 the global scale, it would be helpful to design new experimental studies with a global
655 scope. At the global level, the effects of environmental variables on productivity and
656 carbon inputs to soil need to be incorporated in the design of experiments. Standardized
657 experiments with common protocols would help to address general abiotic influences on
658 decomposition at a global scale. This concept of coordinated distributed experiments
659 [*Fraser et al.*, 2013] has been applied before to understand climatic controls on litter
660 decomposition [*Gholz et al.*, 2000; *Adair et al.*, 2008; *O'Halloran et al.*, 2013], and can be
661 further developed to test global patterns of soil organic matter dynamics.

662 However, new functions relating temperature and moisture with decomposition rates
663 are perhaps not necessary at this point. What is missing is a critical assessment and
664 formal rejection of the currently available functions so the uncertainty among different
665 models can be reduced. Such a formal analysis would require a consistent and global
666 dataset on decomposition rates directly quantifying heterotrophic consumption and not
667 just total soil respiration. By rejecting functions that cannot reproduce global patterns of
668 soil organic matter decomposition we will be able to gain confidence in our predictions.

7. Conclusions

669 Decades of research on the environmental controls of the process of soil organic matter
670 decomposition have yielded a wealth of empirical data and mathematical functions relating
671 temperature and moisture with decomposition rates. However, very few generalizations

672 can be obtained regarding the dependence of decomposition rates to temperature and
673 moisture as well as their sensitivity when both abiotic variables change simultaneously.
674 Despite large disagreements between models and data, we reached the following set of
675 conclusions:

- 676 • Formalizing the concepts of intrinsic and apparent sensitivity with partial and di-
677 rectional derivatives, respectively, can enrich analyses on the sensitivity of decomposition
678 rates when different global change factors change simultaneously. Our analysis showed
679 that sensitivities vary considerably depending on the specific combination of temperature
680 and moisture of the system, and the direction of change of these variables under a global
681 change scenario.

- 682 • Temperatures below the freezing point of water severely limit decomposition rates;
683 and the sensitivity of these rates with respect to changes in temperature is very low
684 compared to the sensitivity that can be observed at higher temperatures. Very low de-
685 composition rates, long mean residence times, and large carbon stocks can be explained
686 by this temperature limitation in arctic regions and in soils exposed to temperatures in
687 the range below 0°C. In addition to limitations due to temperature, soil moisture is highly
688 reduced at these temperatures creating a strong interaction between temperature and low
689 moisture levels.

- 690 • The largest sensitivities of decomposition rates with respect to changes in tempera-
691 ture and moisture are expected at high temperatures and the extremes of the moisture
692 range. Changes in temperature in the vicinity of the freezing point of water are associ-
693 ated with important changes in soil moisture, which synergistically can both significantly
694 increase or decrease decomposition rates depending on the direction of temperature and

695 moisture change. Similarly, large sensitivities of decomposition rates are expected at high
696 temperatures and moisture levels. Changes in water table depth, or drainage of tropical
697 peatlands for example, may produce very large changes in decomposition rates compared
698 to changes in temperature and moisture in other systems.

699 • The largest level of disagreement among models and between models and data how-
700 ever, also occur at high temperatures and the extremes of the moisture range. Ecosystems
701 under these combinations of temperature and moisture should therefore have priority in
702 the study of the sensitivity of decomposition and respiration rates with respect to simul-
703 taneous changes in temperature and moisture.

704 • Many global change experiments manipulating soil temperature and moisture are
705 currently being conducted at sites where very low sensitivities of decomposition rates
706 and enzyme activities are expected. Experiments at sites with different combinations
707 of temperature and moisture, and imposing changes of these variables in different direc-
708 tions, can potentially inform us better about the sensitivity of decomposition rates when
709 temperature and moisture change simultaneously.

710 • To decrease uncertainties about the sensitivity of the decomposition process with
711 respect to simultaneous changes in temperature and moisture it is of high priority to
712 formally reject some of the previously proposed functions. Datasets with global scope
713 can help to better define the range of possible values for the dependence functions and
714 therefore reduce the uncertainty range in model predictions.

715 **Acknowledgments.** Financial support was provided by the Max Planck Society. SV
716 is a post-doctoral research associate of the Fund for Scientific Research - Flanders. We

717 thank Markus Müller for implementation of the SoilR package and for comments on the
718 analysis. We also would like to thank many authors for their effort producing data on
719 soil respiration and making them available on public repositories. Particularly, we would
720 like to thank Ben Bond-Lamberty and Fernando Moyano for compiling these datasets.
721 Similarly, K.S. Larsen and P. Ambus provided data from the Climaite project (funded
722 by the Villum Kann Rasmussen foundation), as well as C. Poll, P.A. Fay, J. Dukes, V.
723 Suseela, and C. Picon-Cochard from their ecosystem-level manipulation experiments. O.
724 Kolle and K. Savage provided soil temperature and soil moisture data. Code and data
725 to reproduce all results presented here are provided in the supplementary information
726 material.

References

- 727 Adair, E., W. Parton, S. Del Grosso, W. Silver, M. Harmon, S. Hall, I. Burke, and
728 S. Hart (2008), Simple three-pool model accurately describes patterns of long-term
729 litter decomposition in diverse climates, *Global Change Biology*, 14(11), 2636–2660,
730 doi:10.1111/j.1365-2486.2008.01674.x.
- 731 Angilletta, M. J. (2009), *Thermal adaptation: a theoretical and empirical synthesis*, 289
732 pp., Oxford University Press.
- 733 Balch, J. K., D. C. Nepstad, P. M. Brando, L. M. Curran, O. Portela, O. d. Car-
734 valho, and J. R. P. Lefebvre (2008), Negative fire feedback in a transitional forest of
735 southeastern amazonia, *Global Change Biology*, 14(10), 2276–2287, doi:10.1111/j.1365-
736 2486.2008.01655.x.

- 737 Bauer, J., M. Herbst, J. Huisman, L. Weiermuller, and H. Vereecken (2008), Sensitiv-
738 ity of simulated soil heterotrophic respiration to temperature and moisture reduction
739 functions, *Geoderma*, *145*(1–2), 17 – 27, doi:10.1016/j.geoderma.2008.01.026.
- 740 Bolker, B. M., S. W. Pacala, and W. J. Parton (1998), Linear analysis of soil decom-
741 position: insights from the century model, *Ecological Applications*, *8*(2), 425–439, doi:
742 10.1890/1051-0761(1998)008[0425:LAOSDI]2.0.CO;2.
- 743 Bond-Lamberty, B., and A. Thomson (2010a), Temperature-associated increases in the
744 global soil respiration record, *Nature*, *464*(7288), 579–582.
- 745 Bond-Lamberty, B., and A. Thomson (2010b), A global database of soil respiration data,
746 *Biogeosciences*, *7*(6), 1915–1926, doi:10.5194/bg-7-1915-2010.
- 747 Burke, I., J. Kaye, S. Bird, S. Hall, R. McCulley, and G. Sommerville (2003), Evaluating
748 and testing models of terrestrial biogeochemistry: the role of temperature in controlling
749 decomposition, *Models in ecosystem science. Princeton University Press, Princeton,*
750 *New Jersey, USA*, pp. 225–253.
- 751 Clein, J. S., and J. P. Schimel (1995), Microbial activity of tundra and taiga soils at sub-
752 zero temperatures, *Soil Biology and Biochemistry*, *27*(9), 1231 – 1234, doi:10.1016/0038-
753 0717(95)00044-F.
- 754 Craine, J. M., N. Fierer, and K. K. McLauchlan (2010), Widespread coupling between
755 the rate and temperature sensitivity of organic matter decay, *Nature Geosci*, *3*(12),
756 854–857, 10.1038/ngeo1009.
- 757 Davidoff, B., and H. Selim (1988), Correlation between spatially variable soil moisture
758 content and soil temperature., *Soil Science*, *145*(1), 1–10.

- 759 Davidson, E. A., and I. A. Janssens (2006), Temperature sensitivity of soil carbon
760 decomposition and feedbacks to climate change, *Nature*, *440*(7081), 165–173, doi:
761 10.1038/nature04514.
- 762 Davidson, E. A., D. C. Nepstad, F. Y. Ishida, and P. M. Brando (2008), Effects of an
763 experimental drought and recovery on soil emissions of carbon dioxide, methane, nitrous
764 oxide, and nitric oxide in a moist tropical forest, *Global Change Biology*, *14*(11), 2582–
765 2590, doi:10.1111/j.1365-2486.2008.01694.x.
- 766 Davidson, E. A., S. Samanta, S. S. Caramori, and K. Savage (2012), The Dual Arrhenius
767 and Michaelis–Menten kinetics model for decomposition of soil organic matter at hourly
768 to seasonal time scales, *Global Change Biology*, *18*(1), 371–384.
- 769 Dieleman, W. I. J., S. Vicca, F. A. Dijkstra, F. Hagedorn, M. J. Hovenden, K. S. Larsen,
770 J. A. Morgan, A. Volder, C. Beier, J. S. Dukes, J. King, S. Leuzinger, S. Linder,
771 Y. Luo, R. Oren, P. De Angelis, D. Tingey, M. R. Hoosbeek, and I. A. Janssens (2012),
772 Simple additive effects are rare: a quantitative review of plant biomass and soil process
773 responses to combined manipulations of CO₂ and temperature, *Global Change Biology*,
774 *18*(9), 2681–2693, doi:10.1111/j.1365-2486.2012.02745.x.
- 775 Dilustro, J., B. Collins, L. Duncan, and C. Crawford (2005), Moisture and soil texture
776 effects on soil CO₂ efflux components in southeastern mixed pine forests, *Forest Ecology
777 and Management*, *204*, 85–95.
- 778 Dioumaeva, I., S. Trumbore, E. A. G. Schuur, M. L. Goulden, M. Litvak, and A. I. Hirsch
779 (2002), Decomposition of peat from upland boreal forest: Temperature dependence and
780 sources of respired carbon, *J. Geophys. Res.*, *107*(D3), 8222.

- 781 Fay, P. A., J. M. Blair, M. D. Smith, J. B. Nippert, J. D. Carlisle, and A. K. Knapp (2011),
782 Relative effects of precipitation variability and warming on tallgrass prairie ecosystem
783 function, *Biogeosciences*, 8(10), 3053–3068, doi:10.5194/bg-8-3053-2011.
- 784 Foley, J. (2011), An equilibrium model of the terrestrial carbon budget, *Tellus B*, 47(3).
- 785 Fraser, L. H., H. A. Henry, C. N. Carlyle, S. R. White, C. Beierkuhnlein, J. F. Cahill,
786 B. B. Casper, E. Cleland, S. L. Collins, J. S. Dukes, A. K. Knapp, E. Lind, R. Long,
787 Y. Luo, P. B. Reich, M. D. Smith, M. Sternberg, and R. Turkington (2013), Coordinated
788 distributed experiments: an emerging tool for testing global hypotheses in ecology and
789 environmental science, *Frontiers in Ecology and the Environment*, 11(3), 147–155, doi:
790 10.1890/110279.
- 791 Galloway, J. N., A. R. Townsend, J. W. Erisman, M. Bekunda, Z. Cai, J. R. Freney, L. A.
792 Martinelli, S. P. Seitzinger, and M. A. Sutton (2008), Transformation of the nitrogen
793 cycle: Recent trends, questions, and potential solutions, *Science*, 320(5878), 889–892.
- 794 Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon, and W. J. Parton (2000),
795 Long-term dynamics of pine and hardwood litter in contrasting environments: toward
796 a global model of decomposition, *Global Change Biology*, 6(7), 751–765.
- 797 Griffin, D. M. (1963), Soil moisture and the ecology of soil fungi, *Biological Reviews*,
798 38(2), 141–166, doi:10.1111/j.1469-185X.1963.tb00781.x.
- 799 Grosso, S. D., W. Parton, A. Mosier, E. Holland, E. Pendall, D. Schimel, and D. Ojima
800 (2005), Modeling soil CO₂ emissions from ecosystems, *Biogeochemistry*, 73(1), 71–91,
801 doi:10.1007/s10533-004-0898-z.
- 802 Harmon, M., and J. Domingo (2001), *A user's guide to STANDCARB version 2.0: a*
803 *model to simulate the carbon stores in forest stands*, Department of Forest Science,

- 804 Oregon State University, Corvallis, Oregon.
- 805 Högy, P., C. Poll, S. Marhan, E. Kandeler, and A. Fangmeier (2013), Impacts of temper-
806 ature increase and change in precipitation pattern on crop yield and yield quality of
807 barley, *Food Chemistry*, 136(3 - 4), 1470 – 1477, doi:10.1016/j.foodchem.2012.09.056.
- 808 Holdridge, L. (1967), *Life zone ecology*, 206 pp., Tropical Science Center.
- 809 Janssens, I., S. Dore, D. Epron, H. Lankreijer, N. Buchmann, B. Longdoz, J. Brossaud,
810 and L. Montagnani (2003), Climatic influences on seasonal and spatial differences in
811 soil CO₂ efflux, in *Fluxes of carbon, water and energy of European forests*, edited by
812 R. Valentini, pp. 233–253, Berlin.
- 813 Jauhiainen, J., H. Takahashi, J. E. P. Heikkinen, P. J. Martikainen, and H. Vasander
814 (2005), Carbon fluxes from a tropical peat swamp forest floor, *Global Change Biology*,
815 11(10), 1788–1797, doi:10.1111/j.1365-2486.2005.001031.x.
- 816 Jungkunst, H. F., and S. Fiedler (2007), Latitudinal differentiated water table control
817 of carbon dioxide, methane and nitrous oxide fluxes from hydromorphic soils: feed-
818 backs to climate change, *Global Change Biology*, 13(12), 2668–2683, doi:10.1111/j.1365-
819 2486.2007.01459.x.
- 820 Kelly, R. H., W. J. Parton, M. D. Hartman, L. K. Stretch, D. S. Ojima, and D. S. Schimel
821 (2000), Intra-annual and interannual variability of ecosystem processes in shortgrass
822 steppe, *J. Geophys. Res.*, 105(D15), 20,093–20,100, doi:10.1029/2000JD900259.
- 823 Kirschbaum, M. U. (1995), The temperature dependence of soil organic matter decom-
824 position, and the effect of global warming on soil organic C storage, *Soil Biology and*
825 *Biochemistry*, 27(6), 753 – 760, doi:10.1016/0038-0717(94)00242-S.

- 826 Körner, C. (2006), Plant CO₂ responses: an issue of definition, time and resource supply,
827 *New Phytologist*, 172(3), 393–411.
- 828 Körner, C., J. Morgan, and R. Norby (2007), CO₂ fertilization: When, where, how much?,
829 in *Terrestrial Ecosystems in a Changing World*, edited by J. G. Canadell, D. E. Pataki,
830 and L. F. Pitelka, Global Change — The IGBP Series, pp. 9–21, Springer Berlin Hei-
831 delberg.
- 832 Lähteenoja, O., K. Ruokolainen, L. Schulman, and M. Oinonen (2009), Amazonian peat-
833 lands: an ignored c sink and potential source, *Global Change Biology*, 15(9), 2311–2320,
834 doi:10.1111/j.1365-2486.2009.01920.x.
- 835 Lehmeier, C. A., K. Min, N. D. Niehues, F. B. IV, and S. A. Billings (2013), Temperature-
836 mediated changes of exoenzyme-substrate reaction rates and their consequences for the
837 carbon to nitrogen flow ratio of liberated resources, *Soil Biology and Biochemistry*,
838 57(0), 374 – 382, doi:10.1016/j.soilbio.2012.10.030.
- 839 Leuzinger, S., Y. Luo, C. Beier, W. Dieleman, S. Vicca, and C. Körner (2011), Do global
840 change experiments overestimate impacts on terrestrial ecosystems?, *Trends in Ecology*
841 *& Evolution*, 26(5), 236–241.
- 842 Liu, X., and T. Luo (2011), Spatiotemporal variability of soil temperature and mois-
843 ture across two contrasting timberline ecotones in the sergyemla mountains, southeast
844 tibet, *Arctic, Antarctic, and Alpine Research*, 43(2), 229–238, doi:10.1657/1938-4246-
845 43.2.229.
- 846 Lloyd, J., and J. A. Taylor (1994), On the temperature dependence of soil respiration,
847 *Functional Ecology*, 8(3), 315–323.

- 848 Luo, Y., and E. Weng (2011), Dynamic disequilibrium of the terrestrial carbon cycle under
849 global change, *Trends in Ecology & Evolution*, *26*(2), 96–104.
- 850 Luo, Y., and X. Zhou (2006), *Soil respiration and the environment*, 316 pp., Academic
851 Press.
- 852 Luo, Y., J. Melillo, S. Niu, C. Beier, J. S. Clark, A. T. Classen, E. Davidson, J. S. Dukes,
853 R. D. Evans, C. B. Field, C. I. Czimczik, M. Keller, B. A. Kimball, L. M. Kueppers,
854 R. J. Norby, S. L. Pelini, E. Pendall, E. Rastetter, J. Six, M. Smith, M. G. Tjoelker, and
855 M. S. Torn (2011), Coordinated approaches to quantify long-term ecosystem dynamics
856 in response to global change, *Global Change Biology*, *17*(2), 843–854.
- 857 Mahecha, M. D., M. Reichstein, N. Carvalhais, G. Lasslop, H. Lange, S. I. Seneviratne,
858 R. Vargas, C. Ammann, M. A. Arain, A. Cescatti, I. A. Janssens, M. Migliavacca,
859 L. Montagnani, and A. D. Richardson (2010), Global convergence in the tempera-
860 ture sensitivity of respiration at ecosystem level, *Science*, *329*(5993), 838–840, doi:
861 10.1126/science.1189587.
- 862 Mangelsdorf, K., E. Finsel, S. Liebner, and D. Wagner (2009), Temperature adapta-
863 tion of microbial communities in different horizons of siberian permafrost-affected
864 soils from the lena delta, *Chemie der Erde - Geochemistry*, *69*(2), 169 – 182, doi:
865 10.1016/j.chemer.2009.02.001.
- 866 Manzoni, S., and A. Porporato (2009), Soil carbon and nitrogen mineralization: Theory
867 and models across scales, *Soil Biology and Biochemistry*, *41*(7), 1355–1379, doi: DOI:
868 10.1016/j.soilbio.2009.02.031.
- 869 Melillo, J. M., S. Butler, J. Johnson, J. Mohan, P. Steudler, H. Lux, E. Burrows, F. Bowles,
870 R. Smith, L. Scott, C. Vario, T. Hill, A. Burton, Y.-M. Zhou, and J. Tang (2011), Soil

- 871 warming, carbon, and nitrogen interactions, and forest carbon budgets, *Proceedings of*
872 *the National Academy of Sciences*, 108(23), 9508–9512, doi:10.1073/pnas.1018189108.
- 873 Moyano, F. E., N. Vasilyeva, L. Bouckaert, F. Cook, J. Craine, J. Curiel Yuste, A. Don,
874 D. Epron, P. Formanek, A. Franzluebbers, U. Ilstedt, T. Kätterer, V. Orchard, M. Re-
875 ichstein, A. Rey, L. Ruamps, J. A. Subke, I. K. Thomsen, and C. Chenu (2012), The
876 moisture response of soil heterotrophic respiration: interaction with soil properties,
877 *Biogeosciences*, 9(3), 1173–1182, bG.
- 878 Moyano, F. E., S. Manzoni, and C. Chenu (2013), Responses of soil heterotrophic respira-
879 tion to moisture availability: An exploration of processes and models, *Soil Biology and*
880 *Biochemistry*, 59(0), 72 – 85, doi:10.1016/j.soilbio.2013.01.002.
- 881 Myers, R. J. K., K. L. Weier, and C. A. Campbell (1982), Quantitative relationship
882 between net nitrogen mineralization and moisture content of soils, *Canadian Journal of*
883 *Soil Science*, 62(1), 111–124, doi:10.4141/cjss82-013.
- 884 Nepstad, D., P. Moutinho, M. Dias-Filho, E. Davidson, G. Cardinot, D. Markewitz,
885 R. Figueiredo, N. Vianna, J. Chambers, D. Ray, J. Guerreiros, P. Lefebvre, L. Stern-
886 berg, M. Moreira, L. Barros, F. Ishida, I. Tohlver, E. Belk, K. Kalif, and K. Schwalbe
887 (2002), The effects of partial throughfall exclusion on canopy processes, aboveground
888 production, and biogeochemistry of an amazon forest, *Journal of Geophysical Research*,
889 *107(D20)*, 8085.
- 890 O’Halloran, L. R., E. T. Borer, E. W. Seabloom, A. S. MacDougall, E. E. Cleland, R. L.
891 McCulley, S. Hobbie, W. S. Harpole, N. M. DeCrappeo, C. Chu, J. D. Bakker, K. F.
892 Davies, G. Du, J. Firn, N. Hagenah, K. S. Hofmockel, J. M. H. Knops, W. Li, B. A.
893 Melbourne, J. W. Morgan, J. L. Orrock, S. M. Prober, and C. J. Stevens (2013),

- 894 Regional contingencies in the relationship between aboveground biomass and litter in
895 the world's grasslands, *PLoS ONE*, 8(2), e54988, doi:10.1371/journal.pone.0054988.
- 896 Page, S. E., R. A. J. Wüst, D. Weiss, J. O. Rieley, W. Shotyk, and S. H. Limin (2004), A
897 record of late pleistocene and holocene carbon accumulation and climate change from an
898 equatorial peat bog (kalimantan, indonesia): implications for past, present and future
899 carbon dynamics, *Journal of Quaternary Science*, 19(7), 625–635, doi:10.1002/jqs.884.
- 900 Pansu, M., P. Bottner, L. Sarmiento, and K. Metselaar (2004), Comparison of five soil
901 organic matter decomposition models using data from a 14c and 15n labeling field
902 experiment, *Global Biogeochemical Cycles*, 18(4), GB4022, doi:10.1029/2004GB002230.
- 903 Parton, W. J., J. A. Morgan, R. H. Kelly, and D. S. Ojima (2001), Modeling soil C
904 responses to environmental change in grassland systems, in *The potential of US graz-*
905 *ing lands to sequester carbon and mitigate the greenhouse effect*, edited by R. Follett,
906 J. Kimble, and R. Lal, pp. 371–398, CRC.
- 907 Paul, E., and F. Clark (1996), *Soil microbiology and biochemistry*, 340 pp., Academic
908 Press.
- 909 Pietikäinen, J., M. Pettersson, and E. Bååth (2005), Comparison of temperature effects
910 on soil respiration and bacterial and fungal growth rates, *FEMS Microbiology Ecology*,
911 52(1), 49–58, doi:10.1016/j.femsec.2004.10.002.
- 912 Plante, A. F., J. Six, E. A. Paul, and R. T. Conant (2009), Does physical protection of
913 soil organic matter attenuate temperature sensitivity?, *Soil Sci. Soc. Am. J.*, 73(4),
914 1168–1172.
- 915 Poll, C., S. Marhan, F. Back, P. A. Niklaus, and E. Kandeler (2013), Field-scale ma-
916 nipulation of soil temperature and precipitation change soil co2 flux in a temperate

- 917 agricultural ecosystem, *Agriculture, Ecosystems & Environment*, 165(0), 88 – 97, doi:
918 10.1016/j.agee.2012.12.012.
- 919 Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger (1982), Soil carbon
920 pools and world life zones, *Nature*, 298(5870), 156–159.
- 921 R Development Core Team (2012), *R: A Language and Environment for Statistical Com-*
922 *puting*, R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0.
- 923 Redding, T. E., G. D. Hope, M. J. Fortin, M. G. Schmidt, and W. G. Bailey (2003),
924 Spatial patterns of soil temperature and moisture across subalpine forest-clearcut edges
925 in the southern interior of British Columbia, *Canadian Journal of Soil Science*, 83(1),
926 121–130, doi:10.4141/S02-010.
- 927 Rodrigo, A., S. Recous, C. Neel, and B. Mary (1997), Modelling temperature and moisture
928 effects on C–N transformations in soils: comparison of nine models, *Ecological Modelling*,
929 102(2–3), 325 – 339, doi:10.1016/S0304-3800(97)00067-7.
- 930 Rodríguez-Iturbe, I., and A. Porporato (2004), *Ecohydrology of water-controlled ecosys-*
931 *tems: soil moisture and plant dynamics*, 442 pp., Cambridge Univ Pr.
- 932 Russell, N., and N. Fukunaga (1990), A comparison of thermal adaptation of membrane
933 lipids in psychrophilic and thermophilic bacteria, *FEMS Microbiology Letters*, 75(2-3),
934 171–182, doi:10.1111/j.1574-6968.1990.tb04093.x.
- 935 Rustad, L., J. Campbell, G. Marion, R. Norby, M. Mitchell, A. Hartley, J. Cornelissen,
936 J. Gurevitch, and GCTE-NEWS (2001), A meta-analysis of the response of soil res-
937 piration, net nitrogen mineralization, and aboveground plant growth to experimental
938 ecosystem warming, *Oecologia*, 126, 543–562.

- 939 Schindlbacher, A., S. Wunderlich, W. Borken, B. Kitzler, S. Zechmeister-Boltenstern, and
940 R. Jandl (2012), Soil respiration under climate change: prolonged summer drought off-
941 sets soil warming effects, *Global Change Biology*, *18*(7), 2270–2279, doi:10.1111/j.1365-
942 2486.2012.02696.x.
- 943 Schuur, E. A. G., J. Bockheim, J. G. Canadell, E. Euskirchen, C. B. Field, S. V. Gory-
944 achkin, S. Hagemann, P. Kuhry, P. M. Lafleur, H. Lee, G. Mazhitova, F. E. Nelson,
945 A. Rinke, V. E. Romanovsky, N. Shiklomanov, C. Tarnocai, S. Venevsky, J. G. Vogel,
946 and S. A. Zimov (2008), Vulnerability of permafrost carbon to climate change: Impli-
947 cations for the global carbon cycle, *BioScience*, *58*(8), 701–714, doi: 10.1641/B580807.
- 948 Selsted, M. B., L. van der Linden, A. Ibrom, A. Michelsen, K. S. Larsen, J. K. Pedersen,
949 T. N. Mikkelsen, K. Pilegaard, C. Beier, and P. Ambus (2012), Soil respiration is stimu-
950 lated by elevated co₂ and reduced by summer drought: three years of measurements in
951 a multifactor ecosystem manipulation experiment in a temperate heathland (climaite),
952 *Global Change Biology*, *18*(4), 1216–1230, doi:10.1111/j.1365-2486.2011.02634.x.
- 953 Seneviratne, S. I., T. Corti, E. L. Davin, M. Hirschi, E. B. Jaeger, I. Lehner, B. Orlowsky,
954 and A. J. Teuling (2010), Investigating soil moisture-climate interactions in a changing
955 climate: A review, *Earth-Science Reviews*, *99*(3-4), 125–161.
- 956 Sierra, C. A. (2012), Temperature sensitivity of organic matter decomposition in the
957 Arrhenius equation: some theoretical considerations, *Biogeochemistry*, *108*(1), 1–15.
- 958 Sierra, C. A., M. Müller, and S. E. Trumbore (2012), Models of soil organic matter
959 decomposition: the SoilR package, version 1.0, *Geoscientific Model Development*, *5*(4),
960 1045–1060, doi:10.5194/gmd-5-1045-2012.

- 961 Skopp, J., M. D. Jawson, and J. W. Doran (1990), Steady-state aerobic microbial activity
962 as a function of soil water content, *Soil Sci. Soc. Am. J.*, *54*(6), 1619–1625.
- 963 Subke, J.-A., and M. Bahn (2010), On the ‘temperature sensitivity’ of soil respiration:
964 Can we use the immeasurable to predict the unknown?, *Soil Biology and Biochemistry*,
965 *42*(9), 1653–1656.
- 966 Suseela, V., R. T. Conant, M. D. Wallenstein, and J. S. Dukes (2012), Effects of soil
967 moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in
968 an old-field climate change experiment, *Global Change Biology*, *18*(1), 336–348, doi:
969 10.1111/j.1365-2486.2011.02516.x.
- 970 Swift, M. J., O. W. Heal, and J. M. Anderson (1979), *Decomposition in terrestrial ecosys-*
971 *tems*, 372 pp., University of California Press, Berkeley.
- 972 Vicca, S., A. K. Gilgen, M. Camino Serrano, F. E. Dreesen, J. S. Dukes, M. Estiarte,
973 S. B. Gray, G. Guidolotti, S. S. Hoeppe, A. D. B. Leakey, R. Ogaya, D. R. Ort,
974 M. Z. Ostrogovic, S. Rambal, J. Sardans, M. Schmitt, M. Siebers, L. van der Linden,
975 O. van Straaten, and A. Granier (2012), Urgent need for a common metric to make
976 precipitation manipulation experiments comparable, *New Phytologist*, *195*(3), 518–522,
977 doi:10.1111/j.1469-8137.2012.04224.x.
- 978 Winston, G. C., E. T. Sundquist, B. B. Stephens, and S. E. Trumbore (1997), Win-
979 ter co₂ fluxes in a boreal forest, *J. Geophys. Res.*, *102*(D24), 28,795–28,804, doi:
980 10.1029/97JD01115.
- 981 Zimov, S., S. Davydov, G. Zimova, A. Davydova, E. Schuur, K. Dutta, and F. Chapin III
982 (2006), Permafrost carbon: Stock and decomposability of a globally significant carbon
983 pool, *Geophysical Research Letters*, *33*(20), L20,502.

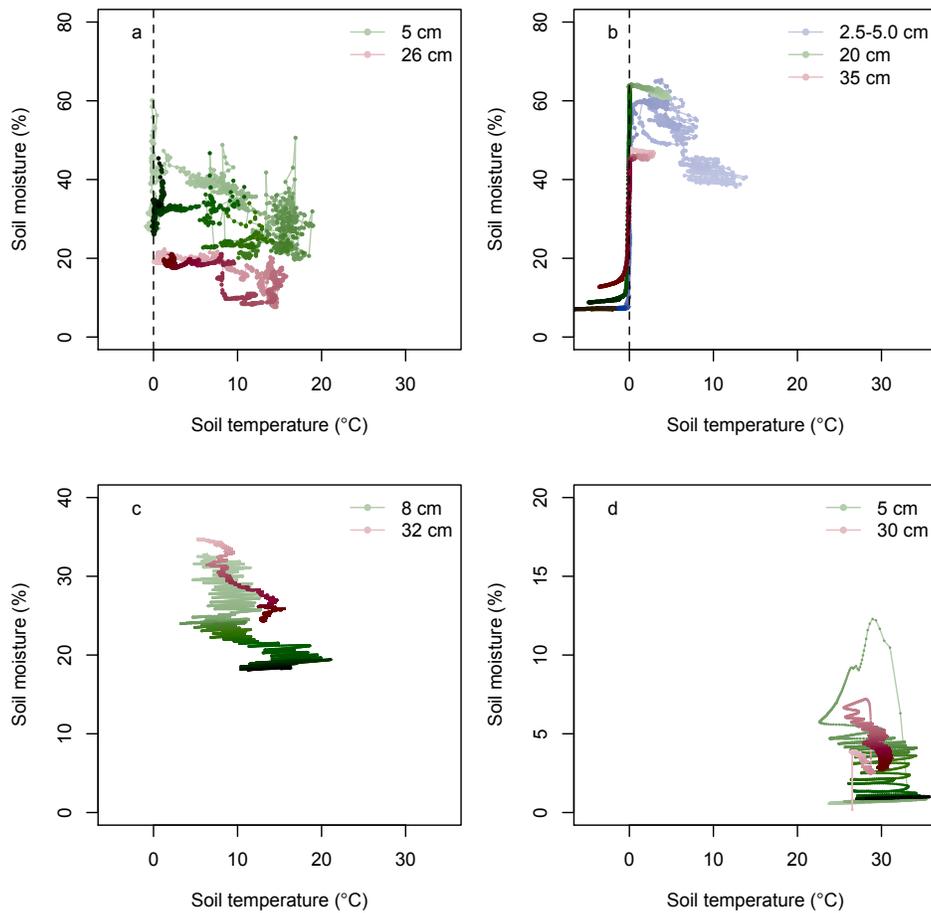


Figure 1. Trajectories of soil temperature and soil moisture (volumetric water content) for different sites at different spatial (depth) and temporal scales. Changes in color from light to dark indicate progression in time. a) Annual cycle for Harvard Forest, USA (well-drained site near flux tower), data for the period 11/03/1997 to 13/02/1998. b) Freezing season in Ivotuk, Alaska USA (ATLAS project, Met Station 1) data for the period between 7/13/1998 to 12/31/1998. c) Spring season in Jena, Germany (Wetterstation Saaleaue), data for the period 10/03/2012 to 18/05/2012. d) Wetting and drying before and after rain event in Mongu, Zambia (eddy-covariance site), for the period 20/09/2007 to 24/10/2007. Notice the differences in scale of the y -axis in the bottom panels.

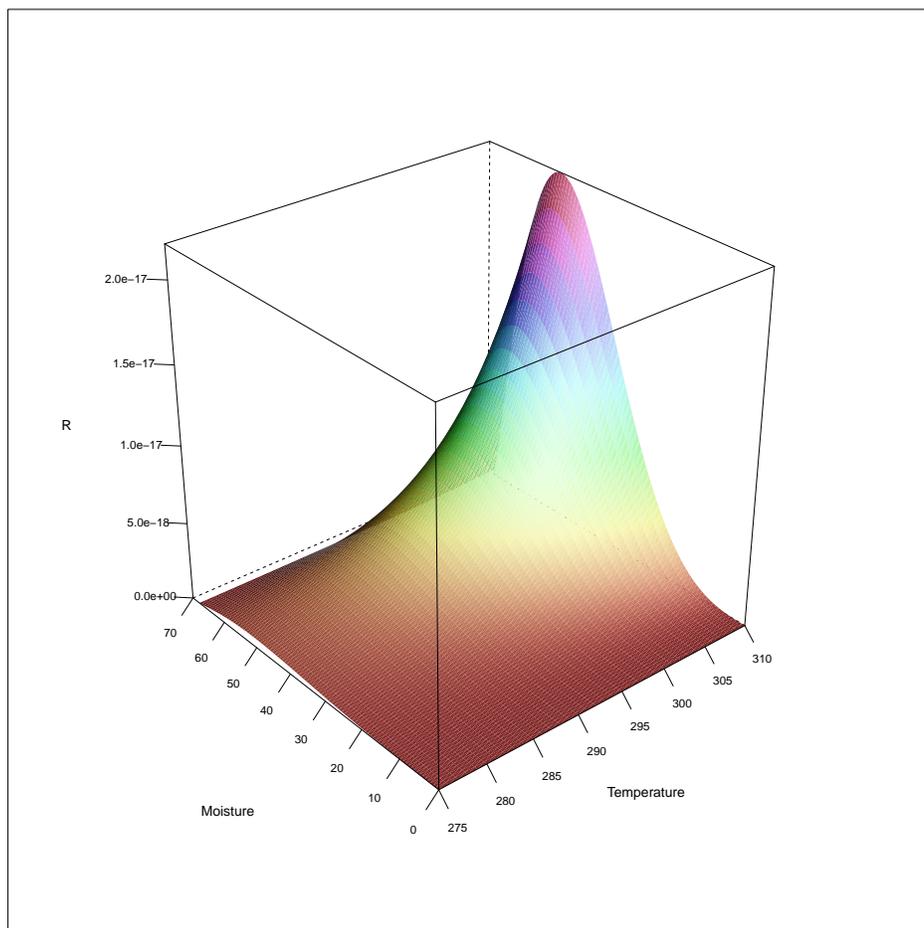


Figure 2. Reaction velocities (dimensionless) of the β -glucosidase enzyme in organic soils predicted by the DAMM model as a function of temperature (K) and moisture (volumetric soil water content %). Parameter values are based on *Davidson et al.* [2012].

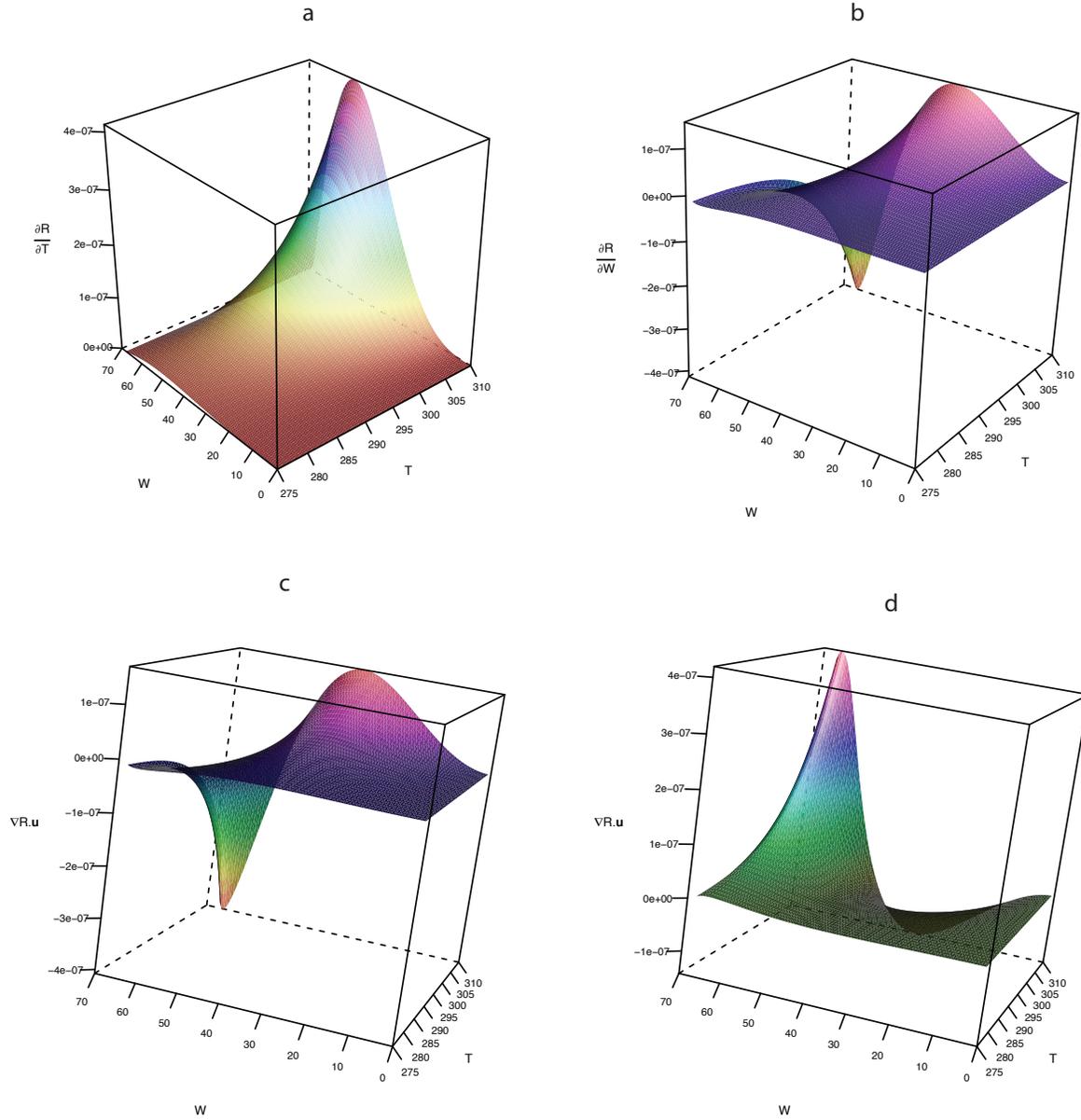


Figure 3. Intrinsic and apparent sensitivity of respiration fluxes with respect to temperature T (Kelvin) and moisture W (volumetric water content in %) in the DAMM model. a) Intrinsic sensitivity of respiration with respect to independent changes in temperature ($\partial R/\partial T$ in K^{-1}), and b) with respect to independent changes in moisture ($\partial R/\partial W$, in $\%^{-1}$). c) Apparent sensitivity with respect to simultaneous changes in temperature and moisture ($\nabla R \cdot \mathbf{u}$ in $\text{K}^{-1} \%^{-1}$) in the direction $\mathbf{u}_{+0.2}^{+1}$, and d) in the direction $\mathbf{u}_{-0.2}^{+1}$. Details about the derivation of the equations are provided in the Appendix. Parameter values are based on Davidson *et al.* [2012].

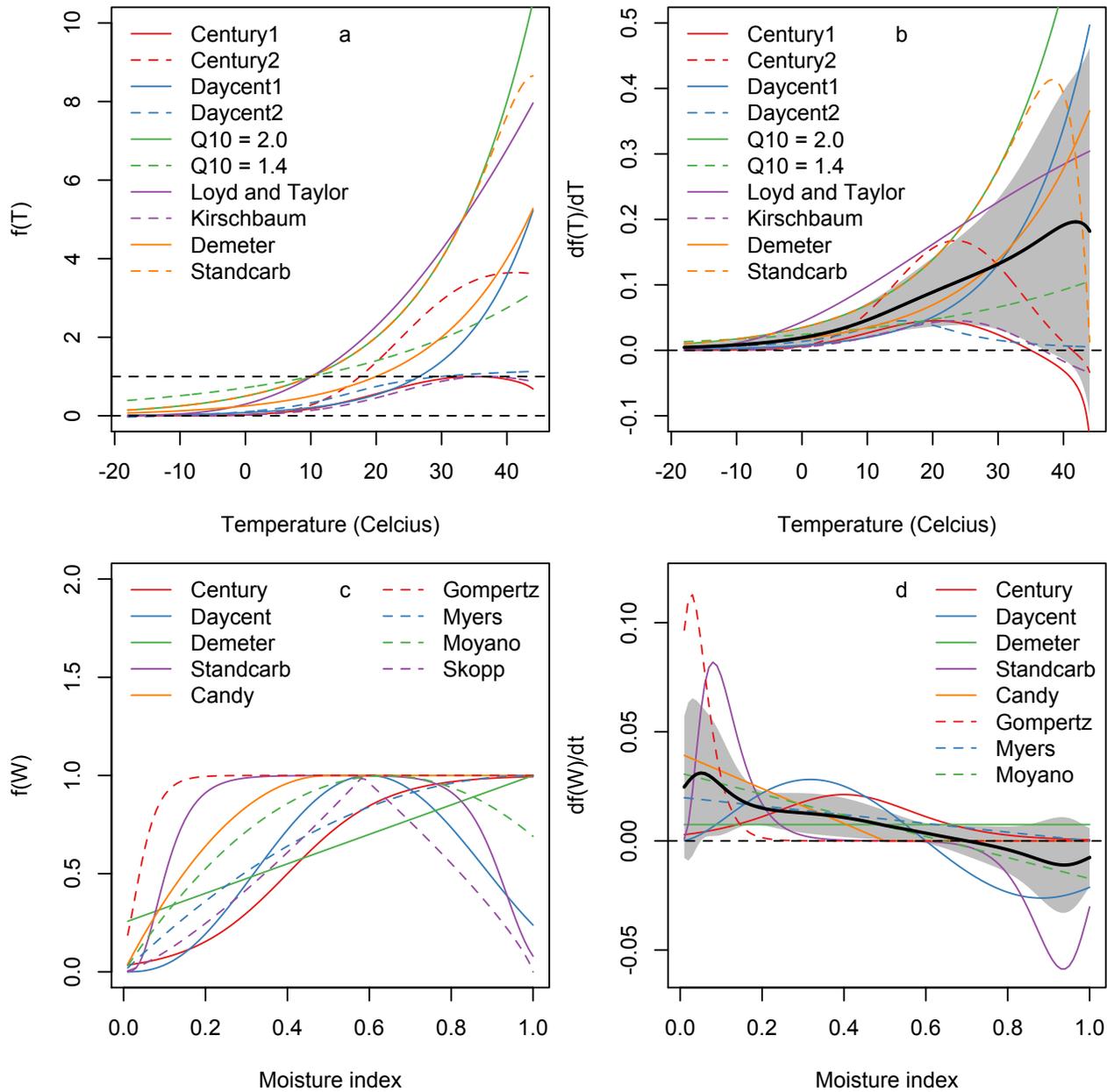


Figure 4. Functions used in different biogeochemical models to predict the effects of temperature and soil moisture on decomposition rates. a) Dependence $f(T)$ and b) sensitivities $\partial f(T)/\partial T$ with respect to temperature; and c) dependance $f(W)$ and d) sensitivity $\partial f(W)/\partial W$ with respect to moisture. The thick black line on the panels on right represents the average across models and the gray areas represent the standard deviation across models. Dashed horizontal lines are provided at values of 0 and 1 for visual reference.

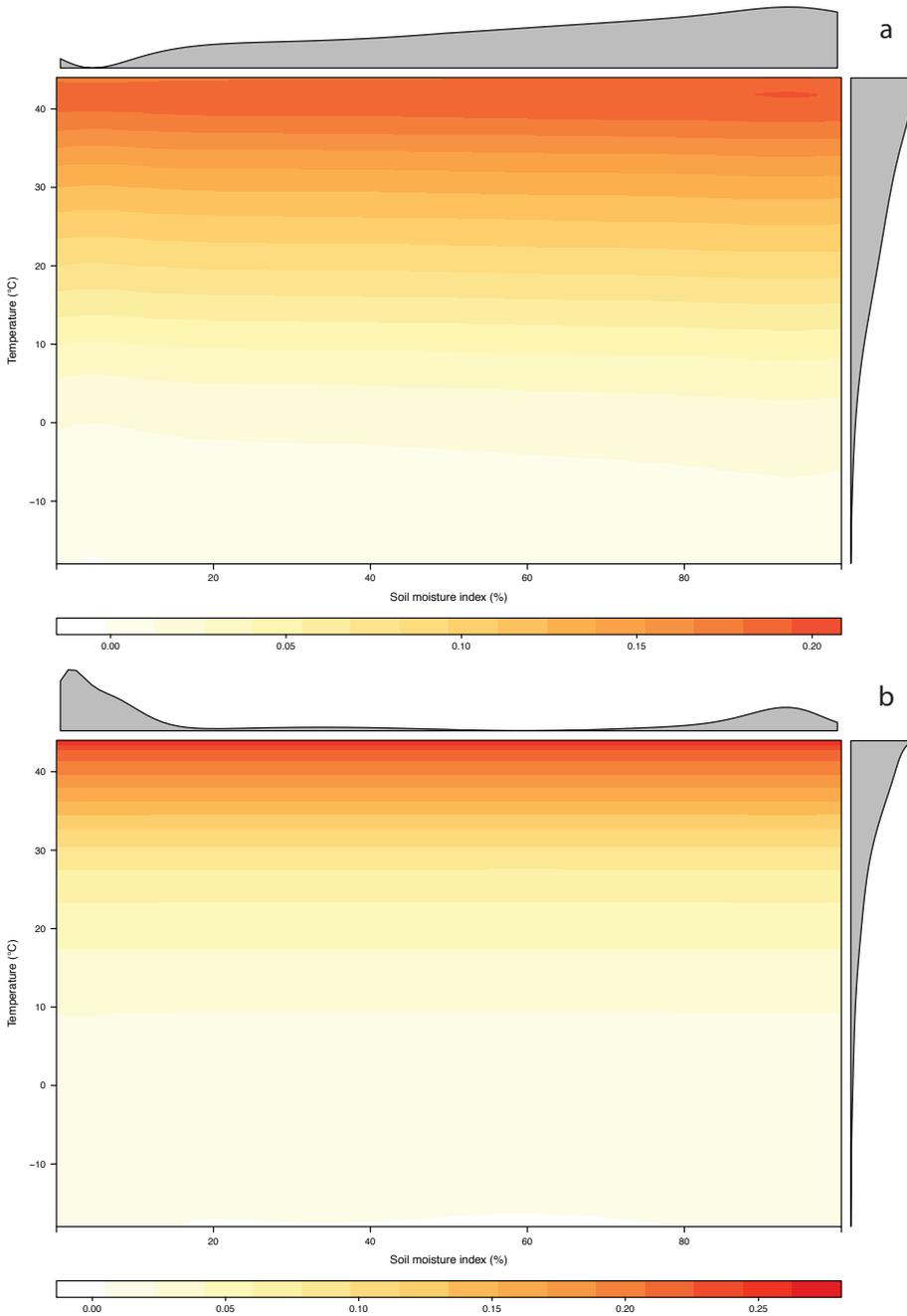


Figure 5. a) Mean ($E[\nabla\xi \cdot \mathbf{u}]$) and b) standard deviation ($\sigma[\nabla\xi \cdot \mathbf{u}]$) of apparent sensitivity in the direction $\mathbf{u}_{-0.2}^{+1}$, and calculated for all possible combinations of functions of temperature and moisture of Table 2 (80 different combinations). Curves on the margin represent averages (a) or standard deviations (b) in the vertical and horizontal directions; i.e., the top curve represents the average or standard deviation in the moisture range across temperatures, and the side curve represents the average or standard deviation in the temperature range across moisture. These curves are unscaled. Units in $^{\circ}\text{C}^{-1} \%W_i^{-1}$.

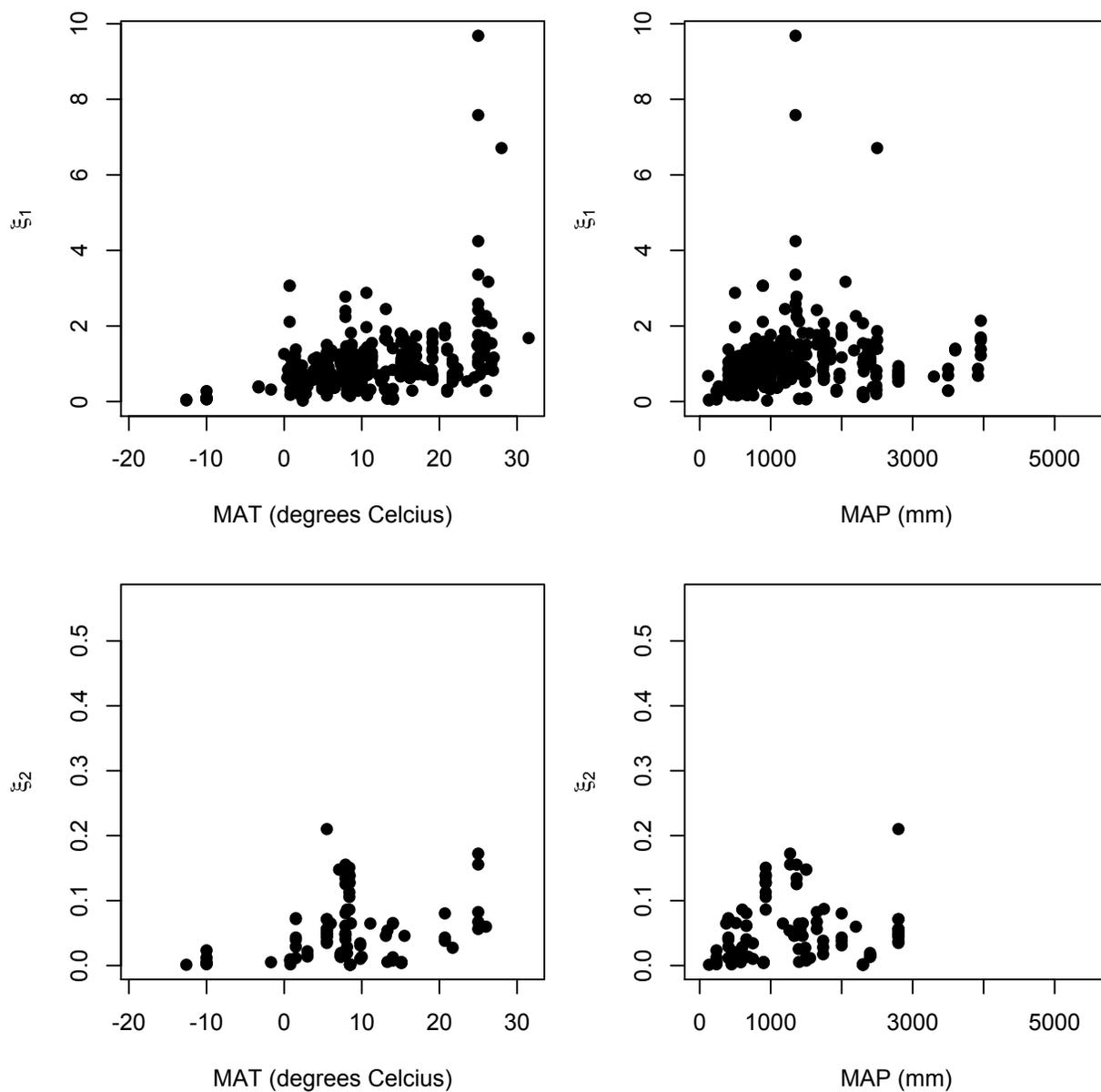


Figure 6. Effects of mean annual temperature MAT ($^{\circ}\text{C}$) and mean annual precipitation MAP (mm) on decomposition rates from the Soil Respiration Data-Base [Bond-Lamberty and Thomson, 2010b] calculated as ξ_1 (equation 16) and ξ_2 (equation 17).

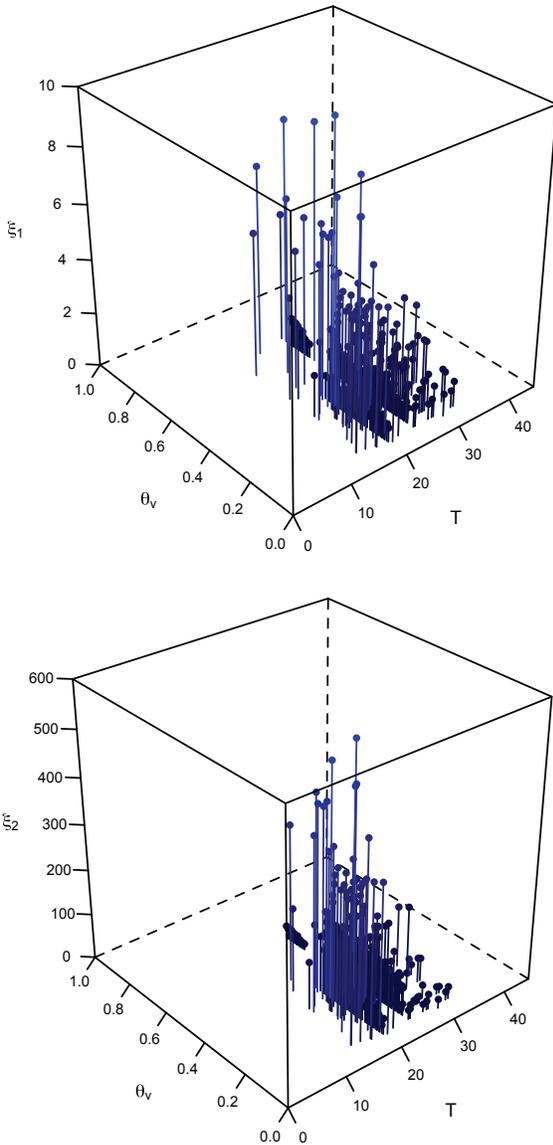


Figure 7. Effects of incubation temperature T ($^{\circ}\text{C}$) and volumetric soil water content (θ_v) on decomposition rates from the soil incubation dataset compiled by *Moyano et al.* [2012] calculated as ξ_1 (equation 16) and ξ_2 (equation 17).

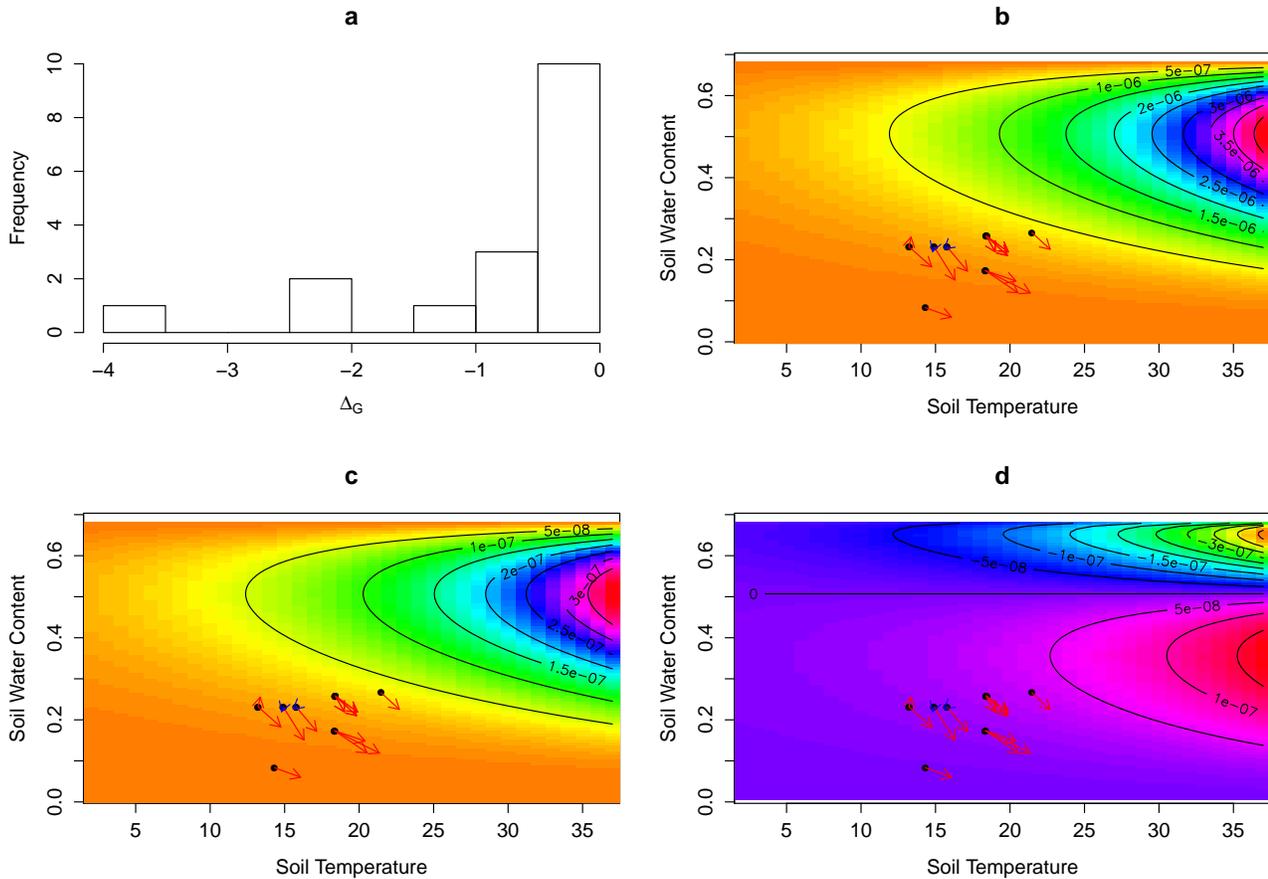


Figure 8. Results from ecosystem-level experiments compared to predictions of the DAMM model. a) Histogram of effect sizes of soil respiration from all manipulation experiments measured as Glass's delta Δ_G : the differences of means between treatment and control divided by the standard deviation of the control. b) Experimental treatments mapped over the predictions of reaction velocities of the DAMM model. Points represent the combination of soil temperature and soil water content of the control treatment, and arrows represent the direction of change imposed by the treatments. Red arrows represent soil warming while blue arrows cooling. Contours and colors in the background represent predictions of reaction velocities for the enzyme β -glucosidase in the DAMM model. c) Points and arrows same as in (b), and colors and contours represent the intrinsic temperature sensitivity $\partial R/\partial T$ of the DAMM model. d) Points and arrows same as in (b), and colors and contours represent the intrinsic moisture sensitivity $\partial R/\partial W$ of the DAMM model. Units in contours of (c) and (d) are in $^{\circ}\text{C}^{-1} \%W_i^{-1}$, while in (b) unitless.

Table 1. Formal definitions of important concepts to study the sensitivity of decomposition rates with respect to multiple variables. An example of the use of this conceptual framework applied to the Arrhenius equation is provided in *Sierra* [2012].

Term	Mathematical representation	Definition
Dependence	$Y = f(X_1, \dots, X_n)$	A dependent or response variable Y is related to one or more independent or driving variables X_i by a specific function f . This function maps the trajectory of Y in the domain of all possible combinations of X_i .
Intrinsic sensitivity	$\partial Y / \partial X_i$	The intrinsic sensitivity is expressed as a partial derivative that measures the absolute change in the response variable with respect to a change in one of the driving variables.
Apparent sensitivity	$\nabla Y \cdot \mathbf{u}$	The apparent sensitivity is the absolute change in the response variable as a consequence of a simultaneous change of all driving variables in a specific direction of a n -dimensional surface.
Direction	\mathbf{u}	It defines the specific change of the driving variables in cartesian space. Mathematically, it is defined as the normalized unit vector (see equation 9).

Table 2. Functions used in common biogeochemical models to represent the effects of temperature and moisture on decomposition rates. In all cases T is in degrees C, and W_i is unitless in a range from 0 to 1. For additional details on these functions and their implementation see *Sierra et al.* [2012].

$f(X)$	Function name	Abbr.	Source
$f(T) =$			
$\left(\frac{T_{\max}-T}{T_{\max}-T_{\text{opt}}}\right)^{0.2} \exp\left(\frac{0.2}{2.63}\left(1-\left(\frac{T_{\max}-T}{T_{\max}-T_{\text{opt}}}\right)^{2.63}\right)\right)$	Century 1	Cent1	[Burke et al., 2003]
$3.439 \exp\left(\frac{0.2}{2.63}\left(1-\left(\frac{T_{\max}-T}{T_{\max}-T_{\text{opt}}}\right)^{2.63}\right)\right)\left(\frac{T_{\max}-T}{T_{\max}-T_{\text{opt}}}\right)^{0.2}$	Century 2	Cent2	[Adair et al., 2008]
$0.8 \exp(0.095T_s)$	Daycent 1	Day1	[Kelly et al., 2000]
$0.56 + (1.46 \arctan(\pi 0.0309(T_s - 15.7)))/\pi$	Daycent 2	Day2	[Parton et al., 2001; Grosso et al., 2005]
$Q_{10}^{(T-10)/10}$	Q10	Q2, Q1.4	
$\exp\left(308.56\left(\frac{1}{56.02} - \frac{1}{(T+273)-227.13}\right)\right)$	Lloyd and Taylor	LT	[Lloyd and Taylor, 1994]
$\exp(-3.764 + 0.204T(1 - 0.5T/36.9))$	Kirschbaum	Kb	[Kirschbaum, 1995]
$\exp((\ln(Q_{10})/10)(T - 20))$	Demeter	Dem	[Foley, 2011]
$\exp(-(T/(T_{\text{opt}} + T_{\text{lag}}))^{T_{\text{shape}}})Q_{10}^{(T-10)/10}$	Standcarb	SC	[Harmon and Domingo, 2001]
$f(W) =$			
$\frac{1}{1+30 \exp(-8.5W_i)}$	Century	Cent	[Parton et al., 2001; Adair et al., 2008]
$\left(\frac{W_i-b}{a-b}\right)^{d((b-a)/(a-c))} \left(\frac{W_i-c}{a-c}\right)^d$	Daycent	Day1	[Kelly et al., 2000]
$0.25 + 0.75(W_i)$	Demeter	Dem	[Foley, 2011]
$(1 - \exp(-(3/W_{\min})(W_i + a)))^b \exp(-(W_i/(M_{\max} + c))^d)$	Standcarb	SC	[Harmon and Domingo, 2001]
$4W_i(1 - W_i)$ if $W_i \leq 0.5$; 1 if $W_i > 0.5$	Candy	Cdy	[Bauer et al., 2008]
$\exp(-\exp(a - b W_i))$	Gompertz	Gpz	[Janssens et al., 2003]
$bW_i + (1 - b)W_i^2$	Myers	Myrs	[Myers et al., 1982]
$aW_i - bW_i^2$	Moyano	Myn	[Moyano et al., 2013]
$\min[\alpha W_i^f, \beta(1 - W_i)^g]$	Skopp	Skp	[Skopp et al., 1990]