

REVIEW ARTICLE

10.1002/2014MS000358

Key Points:

- Large uncertainties in the climate controls on decomposition
- Higher sensitivities in warm and moist regions
- Lower sensitivities with temperatures below the freezing point

Supporting Information:

- Readme
- Reproducible code and data
- Supplement

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Citation:

Sierra, C. A., S. E. Trumbore, E. A. Davidson, S. Vicca, and I. Janssens (2015), Sensitivity of decomposition rates of soil organic matter with respect to simultaneous changes in temperature and moisture, *J. Adv. Model. Earth Syst.*, 7, 335–356, doi:10.1002/2014MS000358.

Received 23 JUN 2014

Accepted 14 JAN 2015

Accepted article online 20 JAN 2014

Published online 11 FEB 2015

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

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Abstract The sensitivity of soil organic matter decomposition to global environmental change is a topic of prominent relevance for the global carbon cycle. Decomposition depends on multiple factors that are being altered simultaneously as a result of global environmental change; therefore, it is important to study the sensitivity of the rates of soil organic matter decomposition with respect to multiple and interacting drivers. In this manuscript, we present an analysis of the potential response of decomposition rates to simultaneous changes in temperature and moisture. To address this problem, we first present a theoretical framework to study the sensitivity of soil organic matter decomposition when multiple driving factors change simultaneously. We then apply this framework to models and data at different levels of abstraction: (1) to a mechanistic model that addresses the limitation of enzyme activity by simultaneous effects of temperature and soil water content, the latter controlling substrate supply and oxygen concentration for microbial activity; (2) to different mathematical functions used to represent temperature and moisture effects on decomposition in biogeochemical models. To contrast model predictions at these two levels of organization, we compiled different data sets of observed responses in field and laboratory studies. Then we applied our conceptual framework to: (3) observations of heterotrophic respiration at the ecosystem level; (4) laboratory experiments looking at the response of heterotrophic respiration to independent changes in moisture and temperature; and (5) ecosystem-level experiments manipulating soil temperature and water content simultaneously.

1. Introduction

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

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

In soils, temperature and moisture covary at different spatial and temporal scales describing a trajectory in the *x y* plane (Figure 1). These trajectories can differ at annual, seasonal, and daily time scales, often presenting hysteresis loops and dampening of oscillations with depth [Davidoff and Selim, 1988; Redding et al., 2003; Liu and Luo, 2011]. For example, the annual cycle of soil temperature and moisture at a deciduous temperate forest shows a different trajectory for drying and warming than for cooling and wetting (Figure 1a). As soil temperatures drop toward the winter months, soil moisture drastically declines due to freezing,

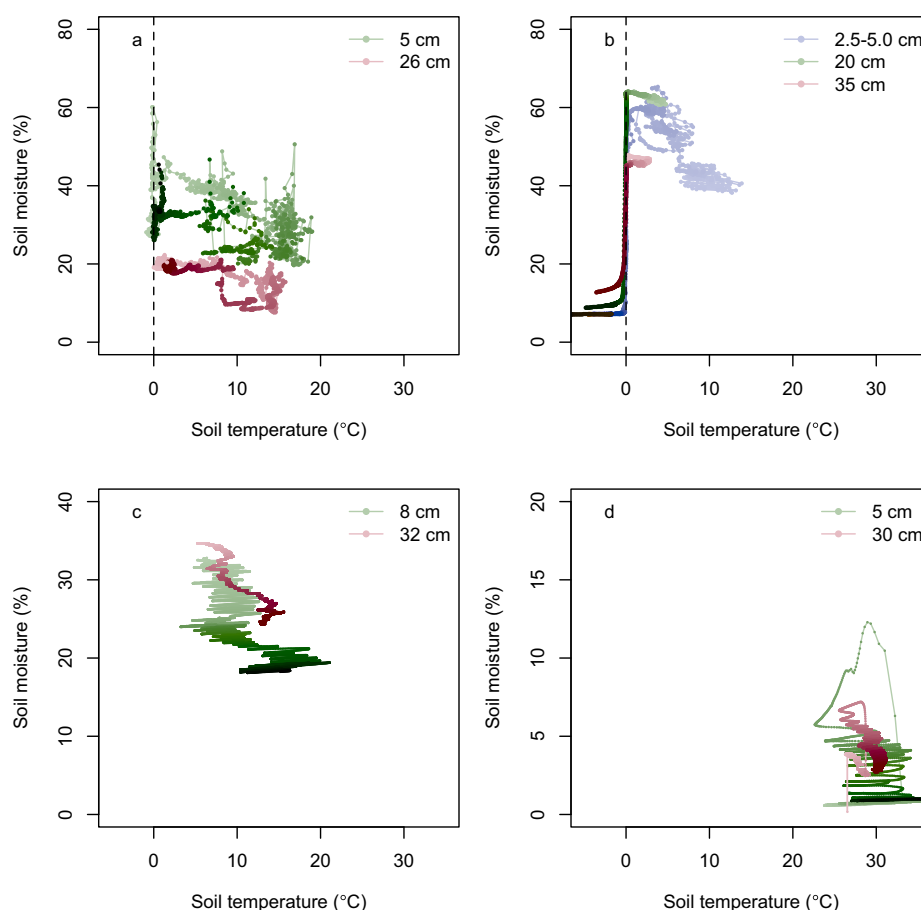


Figure 1. Trajectories of soil temperature and soil moisture (volumetric water content) for different sites at different spatial (depth) and temporal scales. Changes in color from light to dark indicate progression in time. (a) Annual cycle for Harvard Forest, USA (well-drained site near flux tower),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

which removes water from the liquid phase. This effect of soil “drying” as temperatures drop is more important in boreal and arctic regions such as the arctic tundra of Figure 1b, and less pronounced in temperate regions where it occurs mostly at the surface (Figure 1a). Soil moisture can also decrease as temperatures increase. In temperate and Mediterranean-like climates, as soil temperature increases in the spring months, soil moisture gradually decreases. On diel time scales, there may be oscillations in temperature at nearly constant moisture as shown by a temperate grassland in Germany (Figure 1c). In arid regions, after a rain event, soil moisture increases abruptly and decreases slowly with oscillations in diel cycles as exemplified by a Miombo woodland in Zambia (Figure 1d).

Strong but site-dependent covariation between soil temperature and moisture on a range of time scales may have profound effects for predicting the effects of changes in climate on the rates of soil organic matter decomposition and carbon emissions from soils. Here we review and synthesize existing approaches on the sensitivity of soil organic matter decomposition with respect to simultaneous changes in temperature and moisture, two of the most important abiotic variables controlling the process of decomposition. Our approach is theoretical and we focus our analysis on existing models and data sets. This review is not exhaustive, although we cover a large variety of models, observations, and experiments. Our goal is to help to (1) characterize our current ability to represent environmental changes on the decomposition process and (2) identify uncertainties and potential areas for future research.

The manuscript is organized in four main parts. First, we present a theoretical framework that allows us to address the sensitivity of the decomposition process for any number of driving variables both in isolation

Table 1. Formal Definitions of Important Concepts to Study the Sensitivity of Decomposition Rates With Respect to Multiple Variables^a

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)).

^aAn example of the use of this conceptual framework applied to the Arrhenius equation is provided in Sierra [2012].

and in combination. Second, we apply this framework to a mechanistic model that represents reaction velocities of enzyme-substrate complexes as a function of temperature, moisture, and oxygen content. Third, we apply the same theoretical framework to analyze empirical functions commonly used in biogeochemical models. Subsequently, we analyze empirical data to contrast model and theoretical predictions with observations, and in the last part of the manuscript we discuss our findings and explore opportunities for future research.

2. Theoretical Framework

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

First, it is important to make a clear distinction between the *dependence* and the *sensitivity* of carbon release with respect to multiple factors, terms that have often been confounded in this research area. The *dependence* of a response variable Y such as heterotrophic respiration or decomposition rates, is simply defined in the context of a function in which an environmental factor X_i acts as a driving variable, i.e., $Y = f(X_i, \dots)$. In contrast, the *intrinsic sensitivity* of the response variable Y with respect to an environmental factor, X_i , is defined as a partial derivative, that is, $\partial Y / \partial X_i$. This partial derivative measures the absolute change in the response variable with respect to a change in the driving variable (Table 1).

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

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

2.1. General Model of Organic Matter Decomposition

The predominant formalism to represent soil organic matter decomposition is by systems of differential equations [Manzoni and Porporato, 2009]. These systems can be expressed as vectors and matrices with dimensions equal to the number of state variables in the model [Bolker et al., 1998; Pansu et al., 2004; Manzoni and Porporato, 2009; Luo and Weng, 2011; Sierra et al., 2012]. It has been shown that most models of organic matter decomposition can be generalized by the equation [Sierra et al., 2012]

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

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

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

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

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

with each α_{ij} being an off-diagonal element of the matrix \mathbf{T} .

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

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

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

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

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

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

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

where $\dot{\mathbf{C}} = d\mathbf{C}/dt$. This equation represents the intrinsic sensitivity of changes in carbon stocks with respect to a change in an arbitrary environmental variable X_i , and it is composed by the sensitivity of carbon inputs, the sensitivity of the term ξ , and the sensitivity of the carbon stocks in the different pools, which is indirectly related to the sensitivity of the inputs $\left(\frac{\partial \mathbf{C}}{\partial t} \frac{\partial \mathbf{I}}{\partial X_i} \right)$.

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

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

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

An analysis of the sensitivity of the soil carbon stocks \mathbf{C} , their net change $d\mathbf{C}/dt$, or even respiration fluxes is beyond the scope of this manuscript. This analysis only focuses on the sensitivity of the rates of

decomposition and transfer among different pools ($\xi(t)$), which as shown in equations (6) and (7) is a fundamental component of the study of the sensitivity of soil carbon dynamics.

2.2. Definition of Intrinsic and Apparent Sensitivity

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

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

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

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

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

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

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

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

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

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

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

3. Sensitivity of a Mechanistic Model

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

The foundation of the DAMM model is the Michaelis-Menten equation for the concentration of two substrates, soluble carbon [S] and oxygen [O_2]. Including oxygen as a substrate defines the scope of the model to aerobic respiration only, which is the dominant form in most well-drained soils. The concentrations of both substrates are determined by diffusivity functions, which are represented as functions of soil water content. Mathematically, the model predicts the reaction velocity R_5 at the enzyme's reactive site as

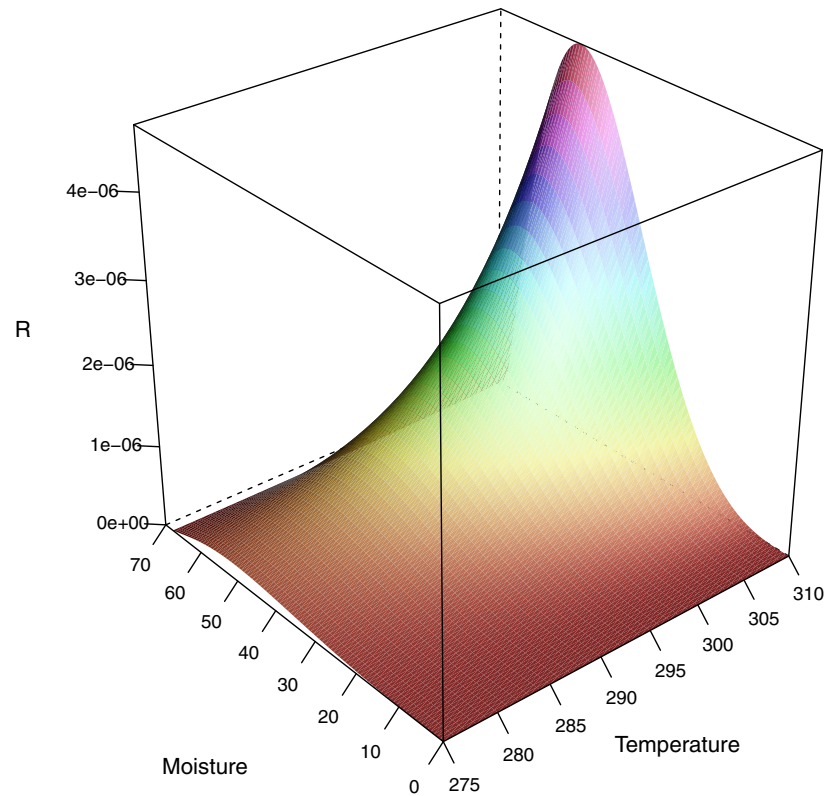


Figure 2. Reaction velocities (dimensionless) of the β -glucosidase enzyme in organic soils predicted by the DAMM model as a function of temperature (K) and moisture (volumetric soil water content %). Parameter values are based on Davidson *et al.* [2012].

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

where the maximum reaction velocity (V_{max}) and the half-saturation constants (K_{Ms} and K_{Mo}) are temperature dependent, i.e., $f(T)$. V_{max} is calculated according to the Arrhenius equation; therefore, it assures that, providing substrate concentrations are not limiting, the respiration rate is sensitive to temperature according to Arrhenius kinetics. The concentration of oxygen $[O_2]$ and the concentration of soluble organic carbon ($[S]$) are moisture-dependent $f(W)$. Although the DAMM model is based on first principles, it relies on empirical functions for the temperature dependence of the half-saturation terms. Additional details about the model can be found in Davidson *et al.* [2012].

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

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

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

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

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

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

or

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

Details about the derivation of this gradient with specific functions for V , S , O , K_S , K_O are provided in the supporting information.

This gradient shows that the sensitivity of the rates of an enzyme reaction with respect to temperature is a function of the temperature sensitivities of V and the half-saturation constants K_S and K_O , while the sensitivity of the reaction with respect to moisture is the sum of the sensitivities of substrate and oxygen concentrations.

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

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

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

More generally, this analysis confirms that high and low levels of soil moisture can severely constrain rates of enzyme reactions independent of temperature. However, the intrinsic sensitivities with respect to changes in temperature and moisture are very different depending on the actual combinations and starting conditions; e.g., at low temperature and moisture levels, very small sensitivities are expected. At high temperature and moisture, large sensitivities are expected with respect to moisture but not with respect to temperature. The apparent sensitivities, therefore, depend on the actual combination of temperature and moisture in the system and the specific change (direction) of these two variables.

4. Sensitivity in Biogeochemical Models

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

The selected temperature and moisture functions used the parameter values presented in the original publications (Table 2), except for the Q_{10} function that is presented with values of 2.0 and 1.4 [cf. Mahecha *et al.*, 2010]. Furthermore, we made transformations in these equations when necessary for consistency and comparability. Specifically, we transformed all temperature functions that take as input temperatures in K and transformed to $^{\circ}\text{C}$. Moisture functions were normalized in such a way that the input moisture values are all in a range from 0 to 1. In most cases, this transformation consisted in expressing the soil moisture metric (e.g., volumetric water content) relative to its maximum value, which is generally dictated by soil porosity. In this way, we avoid discrepancies between different measures of soil moisture [cf. Moyano *et al.*, 2012]. Interestingly, most models we reviewed do exactly this in their calculation of moisture effects on decomposition, they take a particular metric of soil moisture and transform the variable in a range between 0 and 1, and then calculate the effects on decomposition. This homogenized variable is defined here as moisture index (W_i), only for practical reasons, and should not be confounded with other definitions of this term.

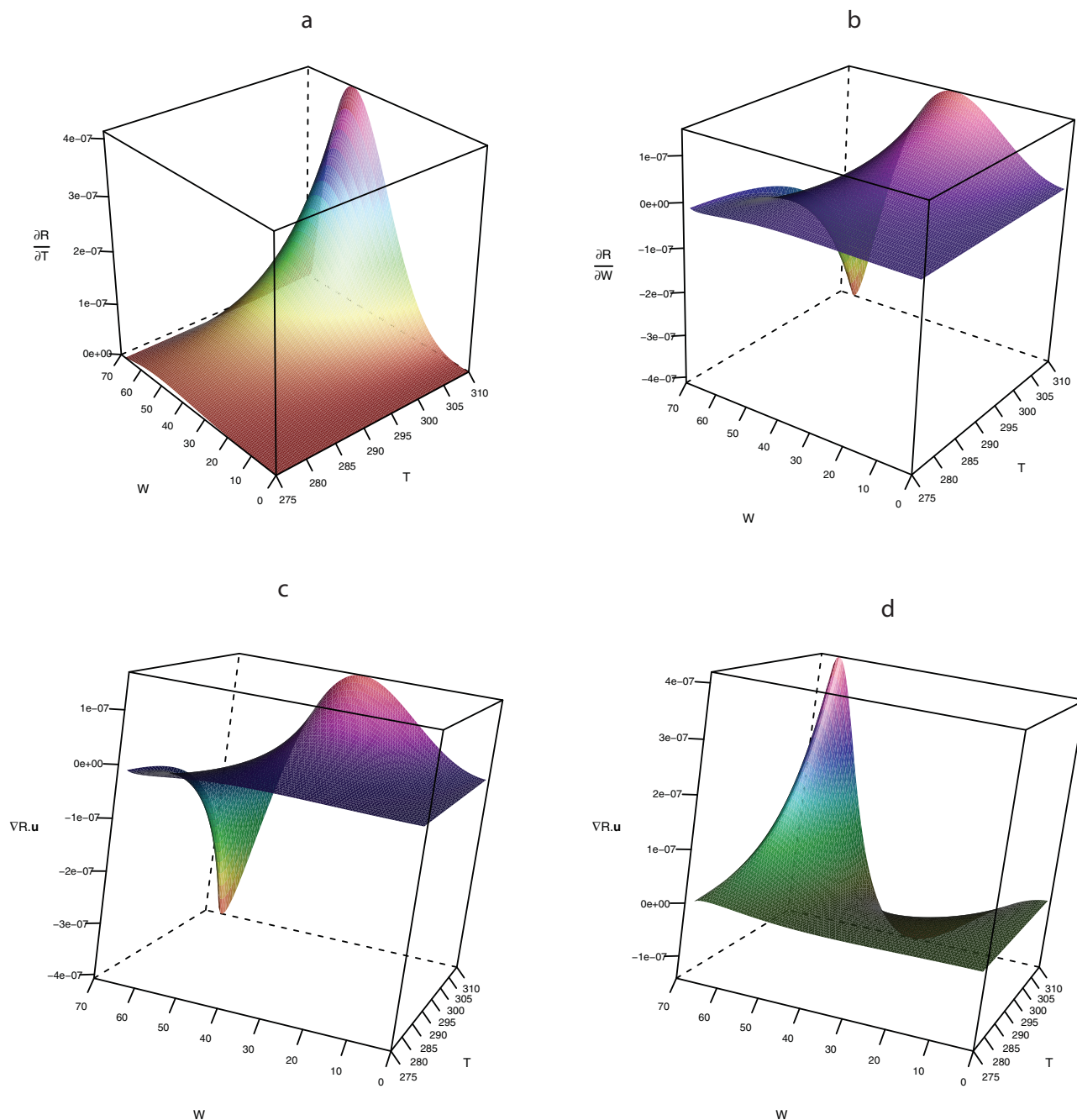


Figure 3. Intrinsic and apparent sensitivity of respiration fluxes with respect to temperature T (K) and moisture W (volumetric water content in %) in the DAMM model. Intrinsic sensitivity of respiration (a) with respect to independent changes in temperature ($\partial R/\partial T$ in K^{-1}) and (b)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

We calculated the derivative of these functions with respect to temperature and moisture numerically using the R environment for computing (Figure 4) [R Development Core Team, 2012]. All code to reproduce the results presented here are provided in the supporting information.

4.1. Temperature Effects on Decomposition Rates $f(T)$ and Their Intrinsic Sensitivity $\partial f(T)/\partial T$

All the compiled functions consistently show increasing effects of temperature on decomposition rates (Figure 4a). Below $0^\circ C$, almost all functions predict a consistent reduction in decomposition rates. Above $0^\circ C$,

Table 2. Functions Used in Common Biogeochemical Models to Represent the Effects of Temperature and Moisture on Decomposition Rates^a

$f(X)$	Function Name	Abbreviation	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]
$3.439 \exp\left(\frac{0.2}{2.63}\left(1-\left(\frac{T_{\max}-T}{T_{\max}-T_{\text{opt}}}\right)^{2.63}\right)\left(\frac{T_{\max}-T}{T_{\max}-T_{\text{opt}}}\right)^{0.2}\right)$	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] and 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]
$\exp(-3.764 + 0.204T(1 - 0.57/36.9))$	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] and 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]
$\exp(-\exp(a - bW_i))$	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]

^aIn all cases, T is in °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].

however, most functions diverge and predict a wide range of effects of temperature on decomposition rates.

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

Within this second group of functions it is also possible to distinguish functions that grow continuously with a convex shape as in the Arrhenius equation. These functions assume that the effects of temperature on decomposition rates increase proportionally with the value of temperature. In contrast, other functions change their convexity in the upper part of the temperature range assuming that above a threshold temperature, further increases of temperature no longer stimulate decomposition rates, and often even decrease them.

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

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

4.2. Moisture Effects on Decomposition Rates $f(W)$ and Their Intrinsic Sensitivity $\partial f(W)/\partial W$

The functions used to represent the effects of soil moisture on decomposition rates are even less consistent than the temperature functions (Figure 4c). There are only two main features in which these functions agree: (1) they all reduce decomposition rates from a maximum “optimum” value; and (2) this reduction is stronger at low values of soil moisture. However, at intermediate or high values of the moisture index range

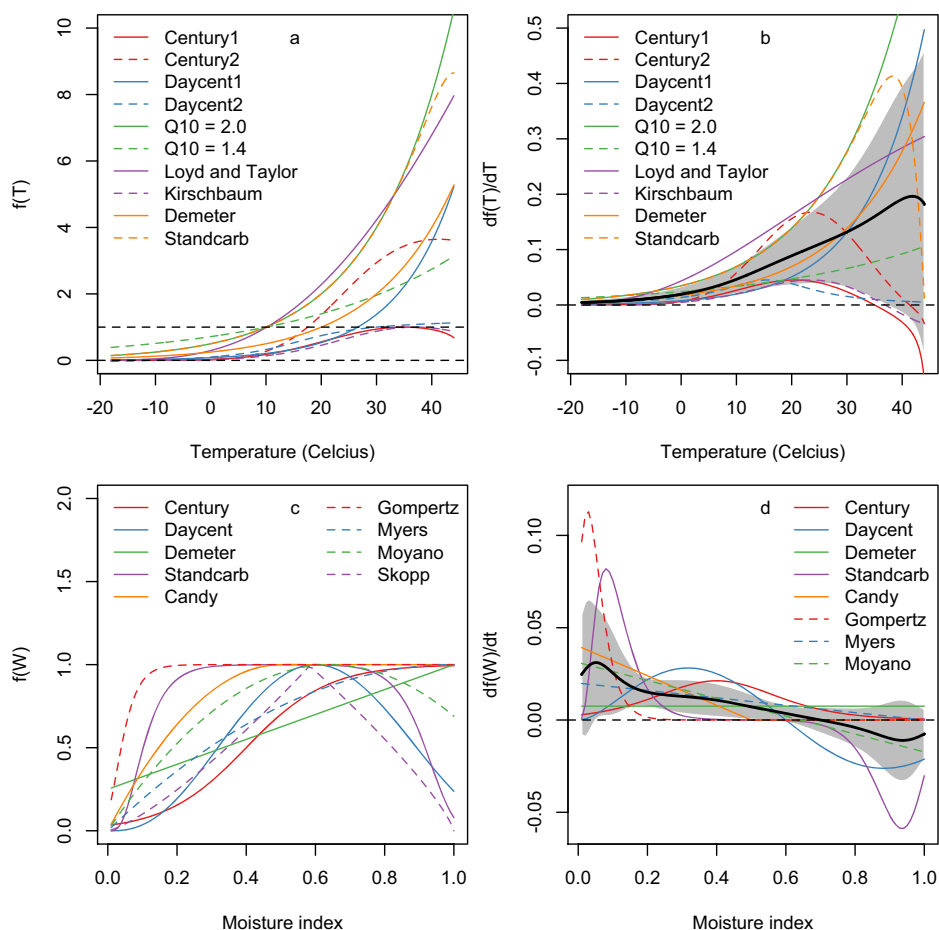


Figure 4. Functions used in different biogeochemical models to predict the effects of temperature and soil moisture on decomposition rates. (a) Dependence $f(T)$ and (b) sensitivities $\partial f(T)/\partial T$ with respect to temperature; and (c) dependence $f(W)$ and (d) sensitivity $\partial f(W)/\partial W$ with respect to moisture. The thick black line in Figures 4b and 4d 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.

the behaviors differ considerably. Four functions present a maximum value of 1 in the intermediate part of the W_i range and decline subsequently, representing an inhibition effect at high soil moisture level. Another set of four functions exhibit an asymptotic behavior toward the maximum value at high moisture levels without subsequent reductions, but the moisture level at which this maximum is reached varies considerably among all functions. In the Demeter model, the relationship is actually linear predicting a constant intrinsic sensitivity for the entire W_i range (Figure 4c).

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

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

Part of the disagreement among the functions is probably due to differences in the conceptualization and representation of soil moisture and its effects on decomposition rates. Particularly, each model was originally developed using different concepts to describe soil moisture. In the Standcarb model, for example, soil moisture is represented as volumetric water content relative to the maximum amount of water the soil can hold [Harmon and Domingo, 2001]. In Daycent, soil moisture is represented as water-filled pore space, a ratio between water content per soil volume and pore space [Kelly et al., 2000]. Each of these functions is composed of two multiplicative terms (Table 2), the first term accounting for increases in decomposition as water increases and the second term accounting for reductions. In Standcarb, these two terms explicitly account for the effects of matric potential and oxygen diffusion, respectively; while in Daycent, these two terms lack any explicit conceptualization.

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

Another conceptual difference among the functions that consider limitations at high moisture levels is the specific mathematical form to account for this limitation. While in the StandCarb and Daycent functions, high moisture levels decrease decomposition rates with a multiplicative term, in the functions proposed by Myers et al. [1982] and Moyano et al. [2013] this decrease is represented by subtracting a quadratic term (Table 2). The function proposed by Skopp et al. [1990] does not multiply or subtract the limitation term because it calculates the minimum of either the limitations due to substrate or oxygen diffusion. This function produces a sharp peak at its maximum value (Figure 4c), which creates a discontinuity and therefore the value of the derivative cannot be calculated at this point.

4.3. Apparent Sensitivity for Specific Changes in Temperature and Moisture

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

As expected from the results obtained for the intrinsic sensitivity with respect to temperature and moisture independently, the variability of the apparent sensitivity predicted by all combinations of functions was large. The range of apparent sensitivities was between -20 and $80\% \text{ } ^\circ\text{C}^{-1} \% W_i^{-1}$ (Figures S1–S4). The highest values of apparent sensitivity were obtained with the temperature function Q_{10} with a value of 2, particularly at high temperature values. However, other model combination predicted decreases in decomposition rates at high values of temperature, independent of the moisture levels. Some model combinations, however, presented small decreases in decomposition rates for changes in temperature and moisture in this particular direction. Other models predicted moderate values of apparent sensitivity at intermediate levels of temperature.

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

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

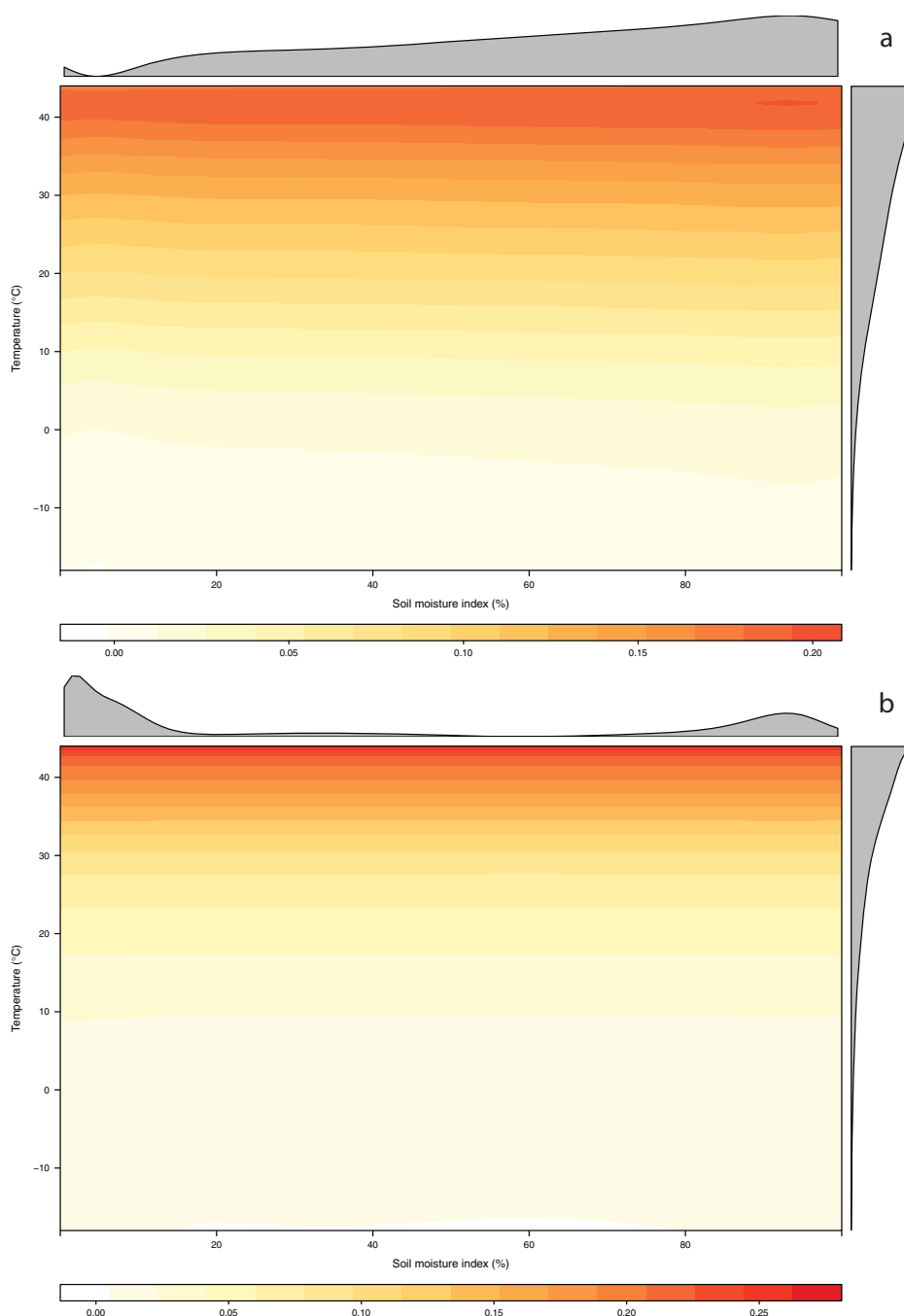


Figure 5. (a) Mean ($E[\nabla \xi \cdot \mathbf{u}]$) and (b) standard deviation ($\sigma[\nabla \xi \cdot \mathbf{u}]$) of apparent sensitivity in the direction $\mathbf{u}_{-0.2}^{+1}$, and calculated for all possible combinations of functions of temperature and moisture of Table 2 (80 different combinations). Curves on the margin represent (a) averages or (b) standard deviations 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 $^{\circ}\text{C}^{-1} \% W_f^{-1}$.

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

5. Empirical Evidence

To some extent, most of the functions reviewed are derived from analysis of empirical data [cf. Lloyd and Taylor, 1994; Kelly et al., 2000; Parton et al., 2001; Burke et al., 2003]. It is important, however, to contrast

independent empirical evidence against the set of functions being applied in biogeochemical models to find the model or set of models that most closely resemble observed data.

Three types of empirical studies are reviewed in this section: (1) observations of heterotrophic respiration taken from a large set of studies from around the world; (2) laboratory manipulation studies under controlled moisture and temperature levels; (3) ecosystem level manipulation experiments in which both temperature and moisture are controlled and monitored in situ.

5.1. Observed Heterotrophic Respiration In Situ

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

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

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

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

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

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

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

Obviously, both approaches are only poor approximations to ξ , which should be calculated as

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

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

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

It is important to note that it is very difficult to relate the patterns observed in this data set with the patterns of the different functions reviewed in the previous section. Only general patterns can be detected from the data set, but they could also be influenced by the effects of temperature and precipitation on productivity and therefore on carbon inputs to the soil. Differences in productivity across sites obscure the effects of environmental variables on decomposition, so we cannot derive a clear pattern for ξ from this data set.

5.2. Laboratory Experiments

Data from laboratory incubation experiments have been recently compiled by Moyano et al. [2012]. One important characteristic of this data set is that it provides different measures of soil moisture such as

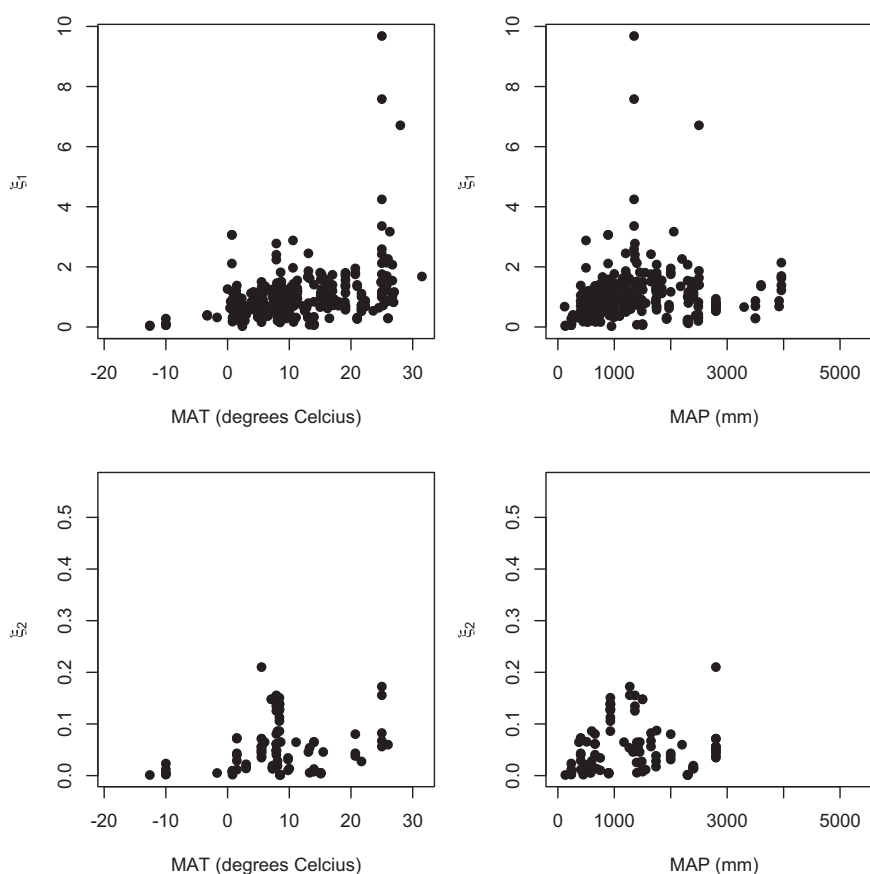


Figure 6. Effects of mean annual temperature MAT (°C) and mean annual precipitation MAP (mm) on decomposition rates from the Soil Respiration Database [Bond-Lamberty and Thomson, 2010b] calculated as ξ_1 (equation (16)) and ξ_2 (equation (17)).

volumetric and gravimetric water content, water saturation, and soil water potential ψ . The majority of studies, however, report volumetric water content θ_v , so we use this metric here in combination with incubation temperature to observe general trends on decomposition rates.

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

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

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

5.3. Ecosystem-Level Manipulations

Ecosystem-level manipulation experiments in which temperature and moisture are controlled in situ can also provide useful information on the controls of these variables on soil organic matter decomposition. For this purpose, we used the Precipitation Manipulation database [Vicca et al., 2012]. This data set includes studies in which different abiotic drivers are manipulated at different ecosystem types. However, in this data set, only a few studies met the criteria of manipulating soil moisture and temperature simultaneously while at the same time reporting soil respiration rates [see Fay et al., 2011; Suseela et al., 2012; Selsted et al., 2012; Högy et al., 2013; Poll et al., 2013] (see table in supporting information).

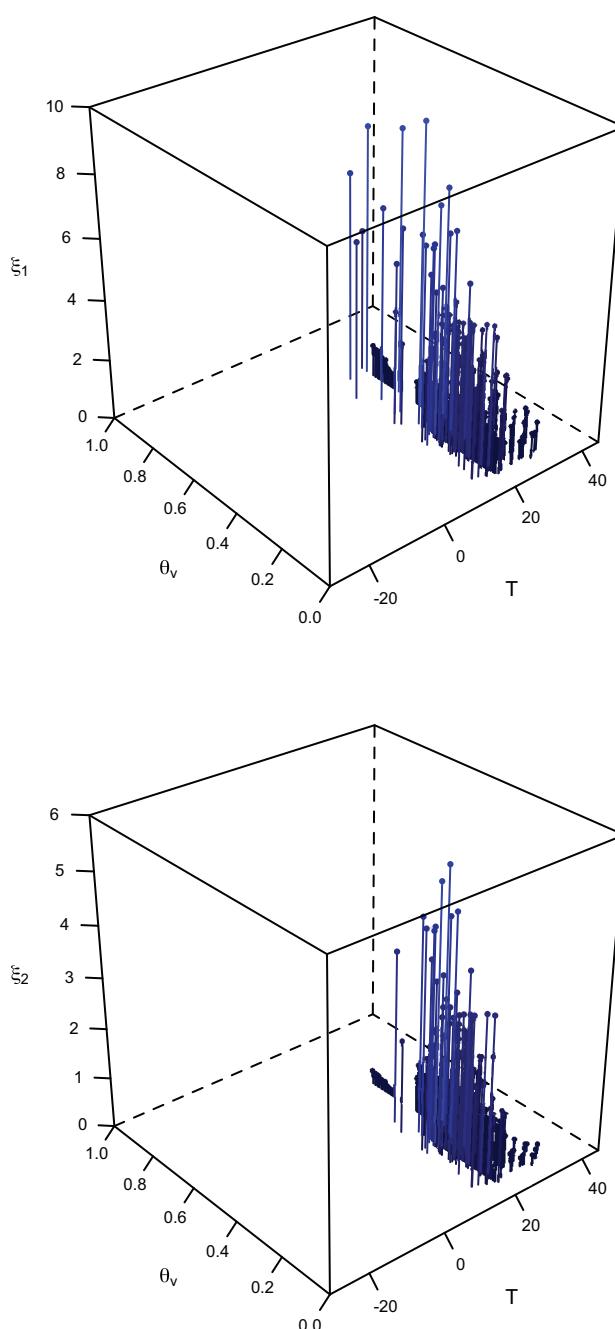


Figure 7. Effects of incubation temperature T ($^{\circ}\text{C}$) and volumetric soil water content (θ_v) on decomposition rates from the soil incubation data set compiled by Moyano *et al.* [2012] calculated as ξ_1 (equation (16)) and ξ_2 (equation (17)).

framework of the expected responses for enzyme reaction rates may have some important implications: (1) most current climate change experiments have been probably implemented in sites where the combination of temperature and moisture, and their manipulation, are not very relevant for the sensitivity of enzyme activity and organic matter decomposition. (2) Many sites with soil temperatures between 15 and 20 $^{\circ}\text{C}$ and volumetric water content between 10 and 30% may show very low sensitivities to changes in climate as suggested by the experimental data and the model predictions. (3) The predominant directional change in soil temperature and moisture imposed in most experiments toward increases in temperature by a few degrees and small decreases in soil moisture of a few % would likely

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

To interpret the results from these experimental manipulations, we plotted the experimental data against the predictions of the DAMM model for the reaction velocity of the β -glucosidase enzyme (Figure 8b). The experimental data, plotted as arrows indicating the change from the control to the experimental treatment, show that most experiments have been carried out in combinations of temperature and moisture with low reaction velocities of β -glucosidase, so the decomposition of substrates such as cellulose likely proceed slowly at these manipulation sites. Furthermore, the direction of change in temperature and moisture in which most studies were implemented more likely lead to no changes or decreases in reaction velocities (Figure 8b). It is therefore expected that the intrinsic sensitivities with respect to temperature (Figure 8c) and moisture (Figure 8d) are at their lowest levels for these manipulation experiments.

The results from these manipulation experiments analyzed within the

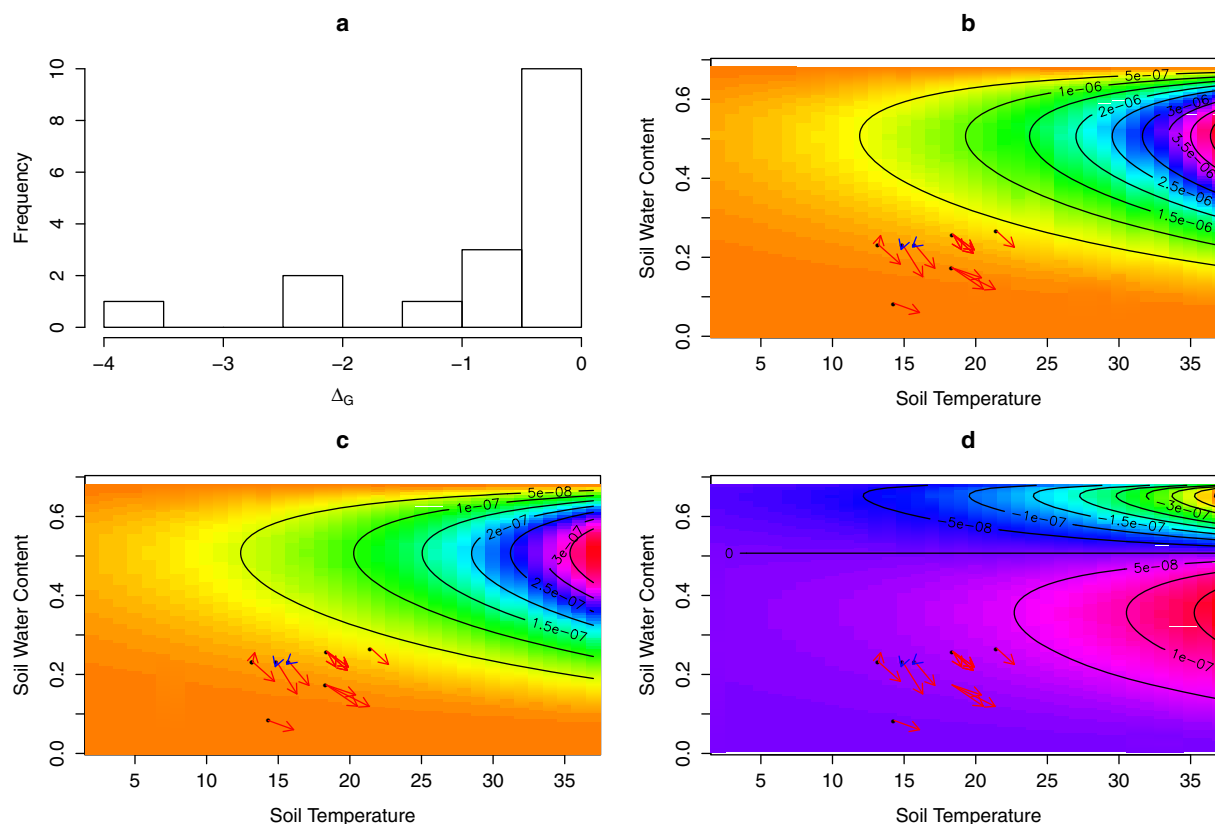


Figure 8. Results from ecosystem-level experiments compared to predictions of the DAMM model. (a) Histogram of effect sizes of soil respiration from all manipulation experiments measured as Glass's delta Δ_G : the differences of means between treatment and control divided by the standard deviation of 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 Figure 8b, and colors and contours represent the intrinsic temperature sensitivity $\partial R / \partial T$ of the DAMM model. (d) Points and arrows same as in Figure 8b, and colors and contours represent the intrinsic moisture sensitivity $\partial R / \partial W$ of the DAMM model. Units in contours of Figures 8c and 8d are in $^{\circ}\text{C}^{-1} \% W_i^{-1}$, while in Figure 8b unitless.

lead to undetectable changes or minor decreases in soil organic matter decomposition and a subsequent minor decrease in respiration rates.

6. Discussion

After many decades of research on the abiotic controls in the process of soil organic matter decomposition [Swift *et al.*, 1979; Paul and Clark, 1996; Luo and Zhou, 2006], we still lack robust mathematical models and experiments to predict the consequences of changes in climate on the rates of decomposition of global soil carbon stocks. Although many models have been proposed and a large number of experiments and measurements have been performed, it is still difficult to confront models with observations and reach strong conclusions. However, from this analysis, a few points of consensus have been identified and some research gaps have emerged.

6.1. Consensus Between Models and Observations/Experiments

Although there is little consensus among the models, they all tend to agree in that decomposition rates and their sensitivity are low below freezing ($<0^{\circ}\text{C}$) and at very low soil moisture contents. This is not a surprise in the context of the relatively well-known abiotic limitation of decomposition rates in arctic and boreal regions under permafrost [Zimov *et al.*, 2006; Schuur *et al.*, 2008]. Below-freezing temperatures not only limit the kinetics of soil microorganisms, but also remove water from the liquid phase, making it unavailable for the dissolution of substrates in the soil matrix. Psychrophilic microorganisms can thermally adapt to below-freezing temperatures by their lipid composition that affects the properties of their

membranes and allow them to remain in a fluid state, albeit at very low levels of activity [Russell and Fukunaga, 1990; Mangelsdorf et al., 2009].

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

The ecosystem-level manipulation studies showed good agreement with the predictions of the DAMM model even though there is a conceptual mismatch between the data and the model; the empirical data reporting soil respiration and the model predicting reaction velocities of the β -glucosidase enzyme. From this comparison, it seems likely that soils with temperatures between 10 and 20°C and SWC between 5 and 25% would show very low sensitivity to simultaneous changes in temperature and moisture; and if they do show responses to climatic drivers, most likely these would manifest in reductions of decomposition rates.

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

6.2. Disagreement Between Models and Observations/Experiments

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

One of the most important points of disagreements among models is the temperature dependence and sensitivity of decomposition rates at high temperatures (>25°C). Equally important is the disagreement among models on the dependence and sensitivity of decomposition rates across the entire soil moisture range.

The functions reviewed here disagree on whether there is a continuous increase, a saturation, or a decline in decomposition rates at the upper end of the temperature range. None of the data sets reviewed supports the idea included in many functions of continuous increases in decomposition rates with temperature, probably because at higher temperatures soil moisture levels inevitably decrease with increases in temperature (Figure 1). Most likely, this behavior would be strongly determined by the interaction with soil moisture as temperature increases and the soil dries out. Recent studies have found support for the Arrhenius equation [Craine et al., 2010; Sierra, 2012; Lehmeier et al., 2013], which predicts a continuous increase in decomposition rates with temperature, but it is unclear whether Arrhenius kinetics are valid for the entire temperature range.

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

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

appears as these functions overestimate temperature effects in comparison with other functions and the empirical evidence reviewed here.

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

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

An important point of disagreement among different models and empirical analyses is also the representation of soil moisture, which can be expressed as volumetric soil water content, soil water potential, or differences among precipitation and potential evapotranspiration, among others [Seneviratne *et al.*, 2010; Moyano *et al.*, 2012]. It is likely that the choice of metric to represent soil moisture bias results to either effects of suction and substrate solubility or limitations for oxygen diffusion on microbial growth [Griffin, 1963; Skopp *et al.*, 1990]. If soil moisture is expressed as soil water potential or a related measure, it is likely that limitations due to oxygen diffusion are not accounted for. However, if soil moisture is only expressed as soil water content, it is possible that the energy required by a microorganism to extract water from the soil matrix is not properly represented, leading to overestimations of decomposition rates at low and intermediate soil moisture levels. A good representation of soil moisture therefore, would need to incorporate a mixture from these two types of metrics [Vicca *et al.*, 2012; Moyano *et al.*, 2013].

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

Also important is the uncertainty on the sensitivity of decomposition rates at the highest values of temperature and moisture. At these combinations, large carbon stores can be found such as in tropical peatlands [Page *et al.*, 2004; Lähdeenoja *et al.*, 2009]. The DAMM model predicts high sensitivities with respect to changes in moisture for these conditions, and some empirical evidence suggests that drying tropical peatlands or changing water table depth result in very important changes in carbon release or storage [Jauhainen *et al.*, 2005; Jungkunst and Fiedler, 2007].

6.3. Research Gaps and Opportunities

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

New experiments and observations at the extremes of temperature and moisture would help to reduce uncertainties where the largest sensitivities are expected. For example, new experiments could address the question of whether there is a decline or saturation effect of decomposition rates as temperature increase toward larger values, provided moisture and oxygen levels are not limiting for decomposers, or whether

decomposition rates decline at high temperature values because of moisture limitations and not because temperature effects per se [Angilletta, 2009].

New empirical work should focus not only on designing experiments looking at treatment differences among sites or factorial designs, but also on producing mathematical functions along temperature and moisture gradients. One of the main limitations we found in the data sets we reviewed was their lack of consistency with the functions that need to be incorporated in models. Observationally derived mathematical functions are of immense value for implementation in biogeochemical models that can test the integrated effects of global environmental change on the biogeochemistry of terrestrial ecosystems. Mathematical functions can also be subjected to further analyses such as the calculation of intrinsic and apparent sensitivities using partial and directional derivatives.

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

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

7. Conclusions

Decades of research on the environmental controls of the process of soil organic matter decomposition have yielded a wealth of empirical data and mathematical functions relating temperature and moisture with decomposition rates. However, very few generalizations can be obtained regarding the dependence of decomposition rates to temperature and moisture as well as their sensitivity when both abiotic variables change simultaneously. Despite large disagreements between models and data, we reached the following set of conclusions:

1. Formalizing the concepts of intrinsic and apparent sensitivity with partial and directional derivatives, respectively, can enrich analyses on the sensitivity of decomposition rates when different global change factors change simultaneously. Our analysis showed that sensitivities vary considerably depending on the specific combination of temperature and moisture of the system, and the direction of change of these variables under a global change scenario.
2. Temperatures below the freezing point of water severely limit decomposition rates; and the sensitivity of these rates with respect to changes in temperature is very low compared to the sensitivity that can be observed at higher temperatures. Very low decomposition rates, long mean residence times, and large carbon stocks can be explained by this temperature limitation in arctic regions and in soils exposed to temperatures in the range below 0°C. In addition to limitations due to temperature, soil moisture is highly reduced at these temperatures creating a strong interaction between temperature and low moisture levels.
3. The largest sensitivities of decomposition rates with respect to changes in temperature and moisture are expected at high temperatures and the extremes of the moisture range. Changes in temperature in the vicinity of the freezing point of water are associated with important changes in soil moisture, which synergistically can both significantly increase or decrease decomposition rates depending on the direction of temperature and moisture change. Similarly, large sensitivities of decomposition rates are expected at high temperatures and moisture levels. Changes in water table depth, or drainage of tropical peatlands, for example, may produce very large changes in decomposition rates compared to changes in temperature and moisture in other systems.

4. The largest level of disagreement among models and between models and data, however, also occur at high temperatures and the extremes of the moisture range. Ecosystems under these combinations of temperature and moisture should therefore have priority in the study of the sensitivity of decomposition and respiration rates with respect to simultaneous changes in temperature and moisture.
5. Many global change experiments manipulating soil temperature and moisture are currently being conducted at sites where very low sensitivities of decomposition rates and enzyme activities are expected. Experiments at sites with different combinations of temperature and moisture, and imposing changes of these variables in different directions, can potentially inform us better about the sensitivity of decomposition rates when temperature and moisture change simultaneously.
6. To decrease uncertainties about the sensitivity of the decomposition process with respect to simultaneous changes in temperature and moisture, it is of high priority to formally reject some of the previously proposed functions. Data sets with global scope can help to better define the range of possible values for the dependence functions and therefore reduce the uncertainty range in model predictions.

Acknowledgments

Financial support was provided by the Max Planck Society. S.V. is a postdoctoral research associate of the Fund for Scientific Research—Flanders. We thank Markus Müller for implementation of the SoilR package and for comments on the analysis. We also would like to thank many authors for their effort producing data on soil respiration and making them available on public repositories. Particularly, we would like to thank Ben Bond-Lamberty and Fernando Moyano for compiling these data sets. Similarly, K.S. Larsen and P. Ambus provided data from the Climaite project (funded by the Villum Kann Rasmussen foundation), as well as C. Poll, P. A. Fay, J. Dukes, V. Suseela, and C. Picon-Cochard from their ecosystem-level manipulation experiments. O. Kolle and K. Savage provided soil temperature and soil moisture data. Code and data to reproduce all results presented here are provided in the supporting information.

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