Decomposition of heterogeneous organic matter and its long-term stabilization in soils

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Abstract. Soil organic matter is a complex mixture of material with heterogeneous biological, physical, and chemical properties. Decomposition models represent this heterogeneity either as a set of discrete pools with different residence times or as a continuum of qualities. It is unclear though, whether these two different approaches yield comparable predictions of organic matter dynamics. Here, we compare predictions from these two different approaches and propose an intermediate approach to study organic matter decomposition based on concepts from continuous models implemented numerically. We found that the disagreement between discrete and continuous approaches can be considerable depending on the degree of nonlinearity of the model and simulation time. The two approaches can diverge substantially for predicting long-term processes in soils. Based on our alternative approach, which is a modification of the continuous quality theory, we explored the temporal patterns that emerge by treating substrate heterogeneity explicitly. The analysis suggests that the pattern of carbon mineralization over time is highly dependent on the degree and form of nonlinearity in the model, mostly expressed as differences in microbial growth and efficiency for different substrates. Moreover, short-term stabilization and destabilization mechanisms operating simultaneously result in long-term accumulation of carbon characterized by low decomposition rates, independent of the characteristics of the incoming litter. We show that representation of heterogeneity in the decomposition process can lead to substantial improvements in our understanding of carbon mineralization and its long-term stability in soils.

Key words: continuous quality theory; coupled carbon and nitrogen cycling; ecological heterogeneity; organic matter decomposition; representation error; substrate decomposability.

Introduction

Organic matter in soils is a highly heterogeneous mix of detritus from plants, as well as a mix of macro- and microorganisms with the products of their metabolic activity (Swift et al. 1979). Modeling this heterogeneity has always been an important topic in decomposition studies. Early attempts to represent the process of decomposition (Jenny et al. 1949, Olson 1963) described organic matter in soils as a single pool that decomposes at a constant rate. Later models have approach heterogeneity of organic matter by partitioning the total amount of soil carbon into pools of different residence times. Some of the most popular decomposition models, such as RothC, CENTURY, Biome-BGC, or CASA, contain between three and six different pools that represent the heterogeneous nature of organic matter in soils (Parton et al. 1987, Jenkinson et al. 1990, Potter et al. 1993, Burke et al. 2003, Luo and Zhou 2006). However, the paradigm of a single rate constant that

describes the entire process is still embedded in more recent analyses that focus on the process of soil respiration (e.g., Lloyd and Taylor 1994, Mahecha et al. 2010). In contrast to single or multiple pools, continuous distributions of organic matter quality have been proposed to address more explicitly the heterogeneity of organic matter decomposition in soils (Carpenter 1981, Ågren and Bosatta 1996).

Although significant progress in the understanding of terrestrial biogeochemical cycling has been achieved by the use of these different modeling approaches in the past decades (Manzoni and Porporato 2009), it is still unclear whether these different approaches yield coherent predictions of carbon dynamics over time. Further, it is not clear what type of system behaviors emerge by the use of explicit (and more complex) representations of organic matter decomposition in comparison to those emerging from simpler models assuming homogeneous substrates.

There are several reasons to believe that explicit representations of substrate heterogeneity in models are important for predicting carbon and nutrient release from soils. One is that a heterogeneous substrate is composed of material with different chemical and

physical characteristics and different levels of accessibility to decomposers. The total amount of substrate that can be consumed by decomposers therefore depends on the relative proportions of substrate at different qualities and levels of accessibility. This combination between quality and accessibility determine the rate at which a substrate decomposes. If the proportion of slowly decomposing substrate at a given time is high, less carbon can be consumed than if this proportion is low or if the substrate is homogeneously distributed in all levels of quality and accessibility. In this way, the overall rates at which carbon and other elements can be mineralized in a soil would therefore depend on the distribution of substrates in different qualities and levels of accessibility. Moreover, substrates with different properties will respond differently to environmental drivers such as temperature and moisture, so the total response of the system to a change in the environment will depend on the relative proportions of material with different characteristics. Additionally, processes within the soil may constantly change the quality of the substrate or the degree of physical or chemical protection leading to complex behaviors over time.

In this manuscript we explore the consequences of treating substrate heterogeneity explicitly in a decomposition model. Our working hypothesis is that substrate heterogeneity produces a set of system behaviors that cannot be observed by assuming a single homogenous pool. To address this hypothesis we asked a set of specific questions. First, do discrete and continuous models yield similar predictions of carbon mineralization over time? Second, under what conditions can a heterogeneous substrate be adequately modeled as a homogeneous one? Third, what behaviors are introduced by representing continuous transformations in litter characteristics over time? We focused on the mineralization of carbon and how it is distributed among different classes of decomposability. For this purpose, we made extensive use of the continuous quality theory developed by Ågren and Bosatta (1996), implemented in a numerical framework. The code, implemented in the R environment for computing, is given in the Supplement for examination, modification, and public use.

In the section *Discrete vs. continuous representations* we present an analysis of the consequences of introducing heterogeneity in a cohort of organic matter subject to decomposition without transformations of quality. This section focuses on answering questions one and two above. Then, in the section *Quality transformations during decomposition*, we extend the analysis to multiple cohorts with heterogeneous inputs and continuous transformations of quality to address question three above.

A note on terminology

In this manuscript we present a slight deviation in terminology from the original continuous quality terminology in Ågren and Bosatta (1996). Instead of *quality*, we use the term *decomposability*. There has been much debate in the literature about the role of intrinsic substrate quality vs. external factors that protect substrates from microbial consumption (e.g., Kleber 2010, von Lützow and Kögel-Knabner 2010), whereby litter of inherently high quality may nevertheless display low decomposability due to physical or chemical protection in the soil matrix. Thus, quality by itself is not the only factor that determines the rate of organic matter decomposition. Although in the original continuous quality model other factors in addition to quality are incorporated, the term quality by itself does not necessarily capture this additional complexity. For this reason we use the term decomposability, defined as an attribute of the organic matter constituents that determines the instantaneous rates of microbial consumption and therefore the rates of element mineralization. Decomposability is determined by many different factors, but primarily by the quality of the substrate and the degree of physical and chemical protection from microbial consumption. It is a measure used only to rank the heterogeneous mixture of organic matter into homogenous components ordered according to the rate at which they decompose. We use the Greek letter psi (ψ) to refer to the decomposability rank in our model formulation, instead of q, which is used in the original continuous quality model. Values of ψ range between 0 to 1, indicating the lowest and maximum possible decomposition rates, respectively.

DISCRETE VS. CONTINUOUS REPRESENTATIONS

Discrete compartment models are special cases of the more general continuous models (Manzoni et al. 2009). In compartment models, the total amount of carbon is partitioned among different pools with different decomposition rate constants, while in the continuous approach, a density function is used to assign the proportion of the total amount of carbon to an index of quality or decomposability. This index is also related to a decomposition rate by a continuous function. In essence, the amount of carbon in different pools is an approximation to a density function, and the assignment of decomposition rates to compartments is an approximation of a continuous function between decomposition rate and quality or decomposability. If they both are representations of the same properties, there is potential for a quantitative discrepancy between these two approaches.

Quantitative discrepancy

If the continuous and discrete approaches for modeling soil organic matter are conceptual representations of the same soil properties, there is potential for a quantitative discrepancy between these two types of models. This discrepancy is conceptually similar to the error obtained with numerical approximations to a definite integral by a Riemann sum (Fig. 1a). The
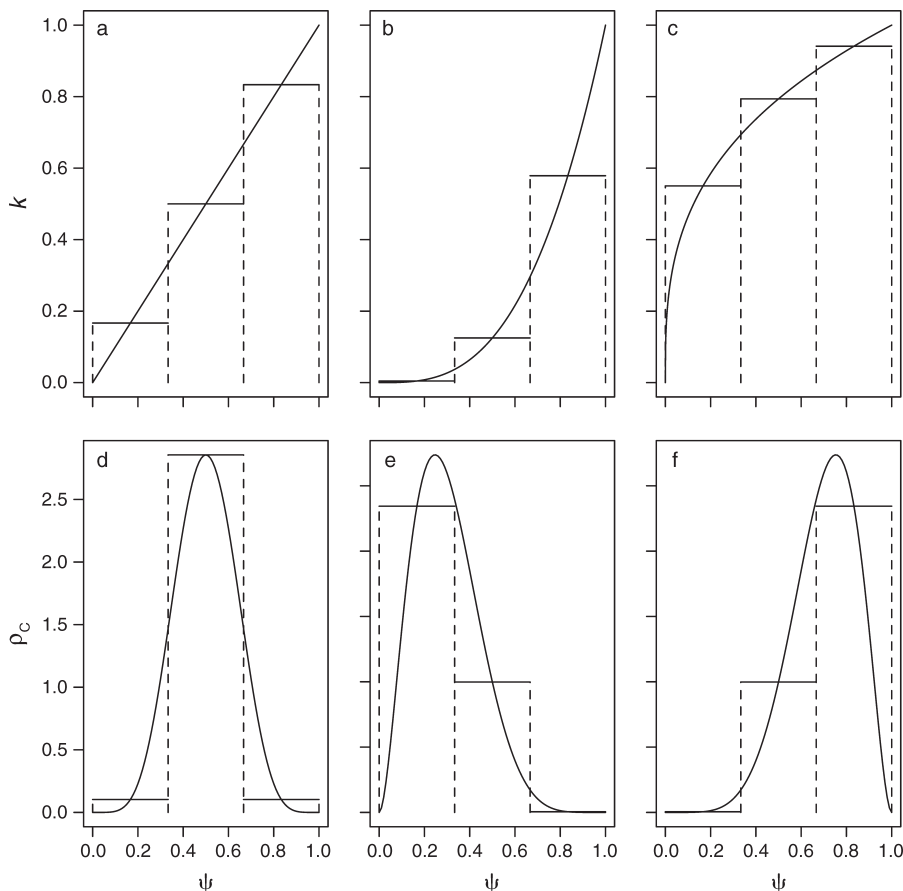
Fig. 1. Discrepancy between a discrete (three pool) and a continuous approach in the representation of decomposition rates, k (upper row), and amount of carbon, ρ_C, in different decomposability classes (lower row). Hypothetical relationships between decomposability ψ (unitless) and k (shown in relative units) are presented as (a) linear $[k = \psi, f''(\psi) = 0]$, (b) convex $[k = \psi^3, f''(\psi) > 0]$, and (c) concave $[k = \psi^{1/3}, f''(\psi) < 0]$. Hypothetical relationships between ψ and ρ_C are presented as (d) symmetric centered on an average value, (e) asymmetric skewed toward low decomposability, and (f) asymmetric skewed toward high decomposability. The amount of carbon (ρ_C) is shown in units of mass of carbon per mass of soil; the actual numbers on the y-axes are arbitrary.

decomposition rate for each pool generally describes the average decomposition rate within the pool, which geometrically is similar to the midpoint approximation of the Reimann method. The absolute error for approximating the area under a curve using the midpoint method is

$$E = \frac{(b - a)}{24} h^2 f''(\xi)$$

where a and b are the lower and upper limits of integration, $h = (b - a)/m$ is the width of the compartments, m is the total number of compartments or pools, and f is a function that describes the relationship between the decomposition rate constant and its decomposability rank. This error also depends on the second derivative of a point ξ within each compartment. As the number of compartments m increases, h decreases as well as the absolute error ($E = O(h)$ as $h \to 0$).

The choice of discrete pools with constant decomposition rates necessarily implies lumping specific amounts

of organic matter within these categories. This discretization introduces another discrepancy in relation to the continuous approach, which is again conceptually similar to an approximation error in a geometrical context (Fig. 1b). Similarly, this error depends on the number of pools and is equal to

$$E = \frac{(b - a)}{24} h^2 g''(\xi)$$

where g is a function that describes the distribution of carbon in the decomposability continuum.

In its simplest representation, the decomposition of organic matter follows an exponential mass loss over time (Olson 1963). When the total amount of carbon is partitioned in m number of pools with specific decomposition rates k for each pool i, the decomposition process can be represented as

$$C_{t,i} = C_{t=0,i} \exp(-k_i t) \tag{1}$$

where $C_{t,i}$ is the amount of carbon in the pool i at time t.

The total amount of carbon at any given time is then

$$C_t = \sum_{i=1}^{m} C_{t,i}. \tag{2}$$

Both terms in Eq. 1 depend on the number of pools in which total carbon is partitioned; therefore, the representation error imbedded in both propagates to the total amount of carbon at each time step proportionally to

$$E_{C_{t,i}}^2 \propto \left(\frac{(b-a)}{24} h^2 f''(\xi_1)\right)^2 + \left(\frac{(b-a)}{24} h^2 g''(\xi_2)\right)^2 \tag{3}$$

or

$$E_{C_{t,i}}^2 = O\left(h^2\right) \quad \text{as} \quad h \to 0. \tag{4}$$

Two important consequences can be inferred from Eq. 3. First, the two sources of error depend on the degree of convexity or concavity of the functions being approximated. As the concavity or convexity increases, measured by the second derivative of the function, the quantitative discrepancy increases. Second, when the relationship between decomposability and decomposition rate is linear, $f''(\psi) = 0$, so there is no approximation error for k, and the total error is dominated by the error incurred approximating the distribution of $C_{t=0}$. As a consequence, the quantitative discrepancy between approaches can only be zero when both functions can be described by straight lines.

The discrepancy between modeling approaches decreases as the number of pools increases; i.e., as h tends to zero (Eq. 4). This discrepancy, measured as the relative error, can be calculated for any different number of pools using Eq. 1 and different values of m. We calculated the relative approximation error for the different forms of the functions presented in Fig. (1). This error was calculated for $t = 5$, before all the remaining organic matter was completely decomposed. The results show that the approximation error is large when only a few pools are considered. For example, when only three pools are considered, the approximation error can be as large as 30–40% (Fig. 2, upper row of figures). Furthermore, the relative error increases over simulation time (Fig. 2, lower row of figures), which suggests that the discrepancy between approaches is more significant for long-term predictions of soil carbon dynamics.

Overall, this analysis suggests that, even though continuous and discrete modeling approaches are mathematical representations of the same soil properties, their predictions diverge as more complexity is added in the model. In our analysis, this complexity is expressed as the number of compartments and the degree of nonlinearities. In addition, the discrepancy between approaches tends to increase over time, posing challenges to simulate and synthesize model predictions from different approaches at long-term time scales.

An intermediate approach between continuous and discrete models

A numerical implementation of a continuous model is, by definition, a discretization of the continuous approach (Soetaert and Herman 2009); therefore, it is an intermediate approach between discrete and continuous approaches. This intermediate approach has the advantage of allowing the representation of a finite number of pools using a small set of parameters from the continuous functions. Compared to the continuous approach, it has the disadvantage that explicit mathematical solutions to the system of differential equations cannot be derived. However, the numerical implementation often provides solutions to mathematical representations where analytical solutions are not possible to obtain.

To explore different representations of substrate heterogeneity in the decomposition processes, we developed a numerical model that implements the continuous quality model of Ågren and Bosatta (1996). This model has been widely used for theoretical predictions of ecosystem behavior, mostly using analytical solutions of systems of differential equations centered on the first moment (i.e., the mean) of the distribution of qualities.

We made adjustments to the model to include the more general concept of decomposability as opposed to simply quality. One of the advantages of our numerical approach is that we can represent different shapes of the distribution of carbon in the decomposability continuum without restricting our analysis to the first (mean) or second moments (variance) of these distributions.

Model description.—The core of the model is similar to the continuous quality theory, which is well described in Bosatta and Ågren (1985, 1991), and Ågren and Bosatta (1996). Here we briefly present the main equations used to implement the continuous theory numerically. For simplicity, we focus here exclusively on carbon, but the same analysis can be performed for other nutrients. The code in the Supplement also contains nitrogen.

We begin by presenting the conceptual dynamic equation for carbon, and then we present a particular solution. Specific details about the solution presented here can be found in Ågren and Bosatta (1996). The dynamic equation for carbon is given by

$$\frac{\partial \rho_C(\psi, t)}{\partial t} = -\frac{f_C u(\psi) \rho_C(\psi, t)}{e(\psi)}$$
$$+ \int_0^\infty f_C D(\psi, \psi') u(\psi') \rho_C(\psi', t)\, d\psi' \tag{5}$$

where $\rho_C(\psi, t)$ is the density function of carbon, and $\rho_C(\psi', t)\, d\psi$ is the amount of carbon in the interval of decomposabilities $[\psi, \ \psi + d\psi]$. Additionally, f_C is the concentration of carbon in the decomposer biomass, which here is assumed to be constant or homeostatic
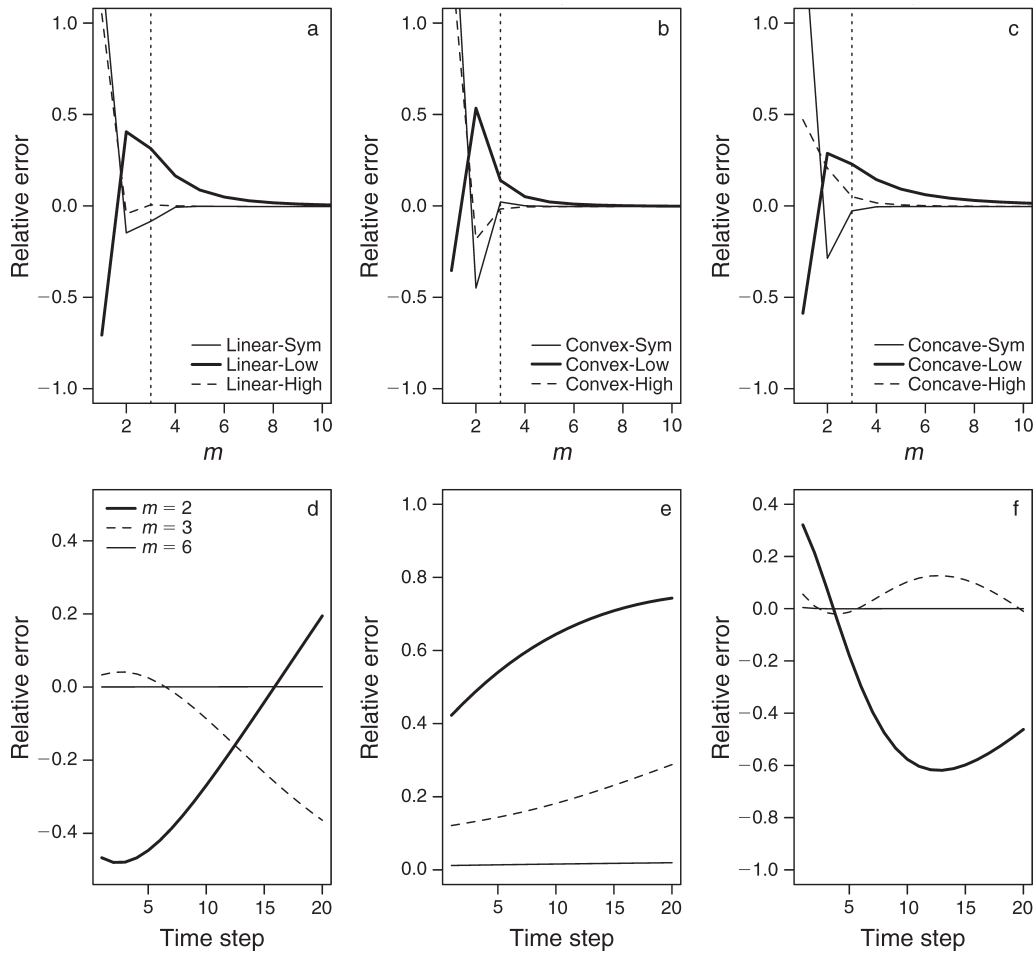
FIG. 2. Quantitative discrepancy in modeling the decomposition of organic matter by different number of pools, m (upper row), and as a function of time (lower row). The relative error was calculated proportionally to predictions with $m = 500$. (a) Combination of a linear decomposition rate and a symmetric distribution (Linear-Sym), an asymmetric distribution skewed toward low decomposability (Linear-Low), and asymmetric distribution skewed toward high decomposability (Linear-High). (b) Same combinations as in panel (a), but with a convex function between ψ and k. (c) Same combinations, but with a concave function. The dotted vertical line indicates the predicted values when decomposition is modeled with only three pools. Lower row: (d) relative error at each time step using a symmetric initial distribution of carbon, (e) initial distribution skewed toward low decomposability, and (f) initial distribution skewed toward high decomposability.

(Sterner and Elser 2002). The decomposer growth rate as a function of litter decomposability is represented by $u(\psi)$, with an efficiency $e(\psi)$ that represents the production-to-assimilation ratio of the decomposers. $D(\psi, \psi')$ is a function that represents how carbon is moved from decomposability rank ψ' to ψ. The first term in Eq. 5 represents the net amount of carbon that is taken up by the decomposers from the soil organic matter. The second term represents how carbon is transferred within the range of decomposabilities. Since changes in the ranking of decomposabilities do not imply gains or losses of substrate (conservation of mass), $\int_0^\infty D(\psi, \psi')d\psi = 1$, we can simplify Eq. 5 to obtain the time derivative of the amount of carbon

$$\frac{dC(t)}{dt} = \int_0^\infty -\frac{f_C u(\psi)\rho_C(\psi, t)}{e(\psi)} + f_C u(\psi)\rho_C(\psi, t)\, d\psi \quad (6)$$

$$= -\int_0^\infty \frac{1 - e(\psi)}{e(\psi)} f_C u(\psi)\rho_C(\psi, t)\, d\psi \quad (7)$$

$$= -\int_0^\infty k(\psi)\rho_C(\psi, t)\, d\psi \quad (8)$$

where

$$k(\psi) = f_C u(\psi)\frac{1 - e(\psi)}{e(\psi)}. \quad (9)$$

A simple solution for Eq. 8 can be obtained assuming

TABLE 1. Functional relationships considered for representing the efficiency $e(\psi)$ and growth rate $u(\psi)$ of decomposers.

Function shape	$e(\psi)$	$u(\psi)$	Comments
Constant	0.2	0.25	Efficiency and growth rate are constants.
Linear	0.2	0.5ψ	The growth rate of decomposers only depends on decomposability. No physical protection.
Convex	$0.2\psi^{2.4}$	$0.5\psi^3$	Efficiency grows faster for lower than for higher decomposability ranks (convex function). Organic matter is physically protected.
Concave	$0.2\psi^{0.5}$	$0.5\psi^3$	Efficiency grows faster for higher than lower decomposability ranks (concave function). Organic matter is physically protected.

Note: See also Fig. 3.

that decomposers do not modify the decomposability of the substrate, in which case

$$\rho_C(\psi, t) = \rho_C(\psi, 0)\exp\left[-k(\psi)t\right] \quad (10)$$

and

$$C(t) = \int_0^\infty \rho_C(\psi, t)d\psi. \quad (11)$$

Notice that Eqs. 10 and 11 are the continuous equivalents of Eqs. 1 and 2, but in this case, the decomposition rate k is expressed in terms of the growth rate and the efficiency of the decomposers (Eq. 9).

The dependency of e and u on ψ can be represented by the following equations:

$$e(\psi) = e_0 + e_1\psi^\alpha \quad (12)$$

$$u(\psi) = u_0\psi^\beta \quad (13)$$

with ψ expressed in relative terms; i.e., $\psi \in [0, 1]$. The coefficients α and β represent the rate at which e and u increase with quality. One interpretation of β is that it can represent the degree of physical and chemical protection of organic matter (Bosatta and Ågren 1985, Ågren and Bosatta 1996). As the quality increases, the material can become more physically accessible by increasing its surface area. A value of $\beta = 3$ captures this physical protection.

Numerical implementation.—Given that the set of equations in the previous section provides an analytical solution to the dynamic problem (Eq. 5), the numerical implementation of this model does not incur errors associated with finding a solution for the system of partial differential equations. However, this numerical implementation may introduce approximation error, but as shown in Fig. 2, with a large number of pools the approximation error is close to zero.

The first step for the numerical implementation of the model was defining decomposability as a vector of length m (number of pools): $\Psi = \{\psi_1 = h/2, \ldots, \psi_m = 1 - h/2\}$, where the interval width is given by $h = 1/m$. Then we can define the initial conditions for the distribution of carbon in vector form $\rho_C(\Psi, 0)$ calculating the density for each element of Ψ from a known probability density function. The total amount of carbon at each time step is calculated as

$$C(t) = \sum_{\psi=h/2}^{1-h/2} \rho_{C_\psi}. \quad (14)$$

For each decomposability rank ψ, $\rho_{C\psi}$ is calculated with Eq. 10. To assure a negligible approximation error, we ran the model for $m = 500$.

Distribution of carbon and decomposition rates in the decomposability continuum

There are two important characteristics that help to define how heterogeneous a substrate is. One is the way different amounts of carbon are distributed along the decomposability continuum, and the other is how decomposition resistance changes along this ranking. Combinations of these two characteristics produce a wide range of possibilities to represent substrate heterogeneity, which can provide interesting insights on the temporal behavior of organic matter during the decomposition process.

Different combinations of the shapes of the relationships between decomposability and decomposition rate, and decomposability and carbon density, were considered in this analysis as illustrative examples of alternative representations of substrate heterogeneity. Different combinations of the parameters in Eqs. 12 and 13 were used to define microbial characteristics in various forms (Table 1, Fig. 3). The purpose of these different definitions was to explore how different function shapes that result from particular combinations of parameter values can affect litter decomposition and the subsequent mineralization of carbon.

Since the decomposition rate k is a familiar concept to ecologists, and it encapsulates the effect of decomposers on the decomposition process (Eq. 9), we chose four different functional forms of the relationship between decomposition rate and decomposability rank to represent substrate heterogeneity. For comparison purposes, the first functional form considered was a constant decomposition rate for all ranks. This is similar to assuming a homogeneous substrate that decomposes at a single rate (Fig. 3). Biologically, this assumption is
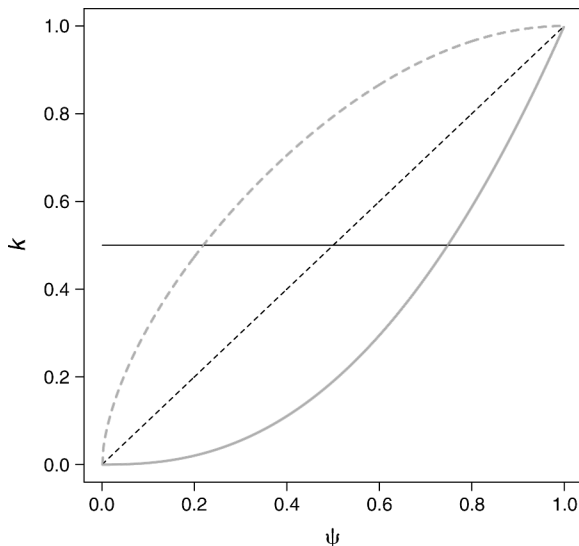
FIG. 3. Hypothetical shapes of the relationship between decomposability, ψ, and decomposition rate, k, both in relative units. A constant function is represented by the thin black line, a linear function is shown by the thin dashed black line, a convex function is shown by the thick gray line, and a concave function is shown by the thick dashed gray line. See Table 1 for details about assumptions for each functional shape.

equivalent to a process in which the efficiency and the growth rate of decomposers is always constant and independent of quality or accessibility (Table 1).

The second functional form chosen was a linear and increasing relationship between decomposition rate and decomposability (Fig. 3). This shape is obtained by assuming that decomposer efficiency is constant for all decomposability ranks and decomposer growth rates increase linearly with decomposability (Table 1). In this case, $\beta = 1$, which is equivalent to assuming that the accessibility of the substrate increases linearly (Bosatta and Ågren 1985, Ågren and Bosatta 1996). Physical protection of organic matter was represented by setting $\beta = 3$, which is the parameter chosen for the other functional forms considered.

Convex and concave relationships between decomposability and decomposition rate were also considered to contrast the rates at which decomposition resistance decreases with increases in decomposability (Fig. 3). For lower decomposability ranks the resistance to decomposition can decrease rapidly, which leads to a concave functional form. In contrast, if decomposition resistance decreases slowly as decomposability increases, the functional form is convex. These functional shapes were obtained by representing the efficiency of decomposers as either concave or convex functions of decomposability (Table 1).

These functional forms were combined with different assumptions about the initial distribution of carbon (Fig. 4). For this purpose we used different probability density functions to assign values of carbon density to all the m decomposability ranks. First, we considered the assumption that all carbon is centered around an average value of decomposability μ_1 with variance σ_1^2, which can be represented with a density function $S_1 = f(\psi) \sim \mathcal{N}(\mu_1, \sigma_1^2)$, where $\mathcal{N}$ is normal distribution. The second distribution of qualities assumed was also centered on an average value μ_1, but with larger spread, such that its variance was twice as large as the variance considered in the first distribution assumed; i.e., $\sigma_2^2 = 2\sigma_1^2$ and $S_2 = f(\psi) \sim \mathcal{N}(\mu_1, \sigma_2^2)$ (Fig. 4).

We also assumed that the initial amount of carbon in the substrate can be skewed toward either lower or higher decomposability ranks. To represent these assumptions, we used the beta probability distribution (Fig. 4). These two distributions mirror each other, so $S_3 = f(\psi) \sim B(a, b)$ and $S_4 = f(\psi) \sim B(b, a)$. Values for a and b were chosen such that $\sigma_3^2 = \sigma_4^2 = \sigma_2^2$.

In the examples presented in the section, we assumed there is no transfer of carbon among different decomposability classes. This is similar to the assumption of parallel compartments in decomposition models (Manzoni and Porporato 2009). Transfer of carbon among classes is included in subsequent sections.

The combination of these assumptions provided insights into the effects of substrate heterogeneity on the temporal dynamics of carbon during decomposition of a single cohort of organic matter (Fig. 5). We observed that an increase in variance of the distribution of decomposability did not affect the behavior of the release of C (Fig. 5a, b). However, more interesting behaviors were obtained with the different functional forms for the relationship between decomposition rate
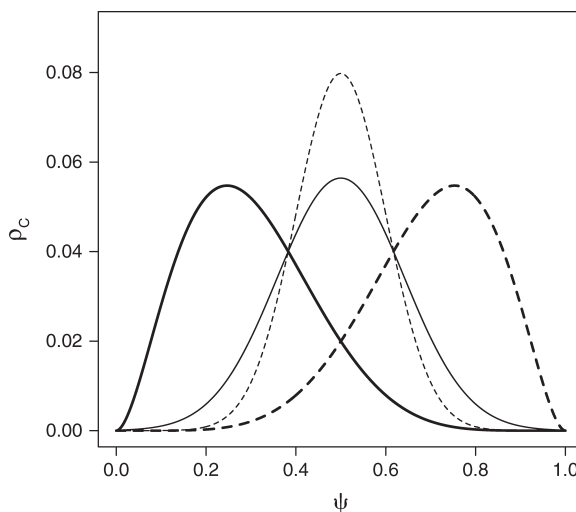

FIG. 4. Density functions representing the initial distribution of carbon $\rho_C(\psi, 0)$ in the decomposability ranks ψ. The thin dashed line represents $\mathcal{N}(\mu_1, \sigma_1^2)$, the thin continuous line shows $\mathcal{N}(\mu_1, 2\sigma_1^2)$, the thick continuous line represents $B(a, b)$, and the thick dashed line shows $B(b, a)$; μ_1 is the average value of decomposability, σ_1^2 is the variance, $\mathcal{N}$ is normal distribution, B is the beta probability function, and a and b are the lower and upper limits of integration. For all functions, $m = 500$.
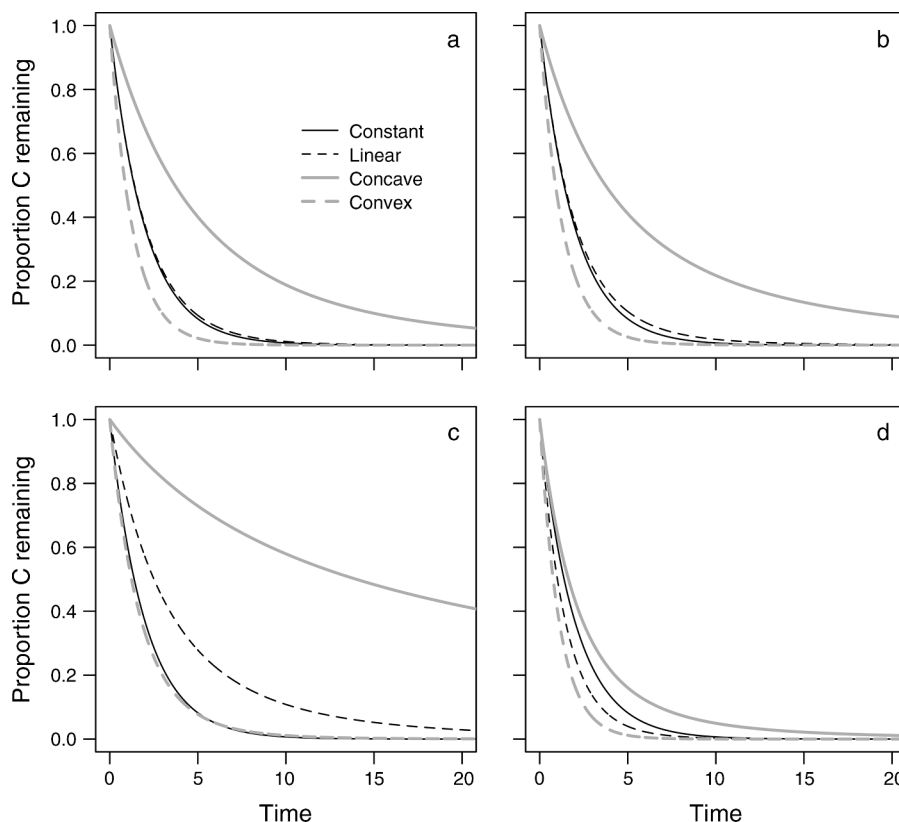
FIG. 5. Temporal dynamics of carbon for different assumptions about the initial distribution of carbon in different decomposability ranks: (a) $\mathcal{N}(\mu_1, \sigma_1^2)$, (b) $\mathcal{N}(\mu_1, 2\sigma_1^2)$, (c) asymmetric distribution skewed toward low decomposability $B(a, b)$, (d) asymmetric skewed toward high decomposability $B(b, a)$. The shape of the function between decomposability and decomposition rate is represented with different line types.

and decomposability. The assumption of constant decomposition rate for all ranks provided the same results as the assumption of a linear increase of decomposition rate with decomposability. This result suggests that the assumption of a homogeneous substrate can be valid when decomposition rate increases linearly with decomposability, provided that the distribution of the substrate in the decomposability ranks is symmetric (see next paragraph). Relative to the constant and linear assumptions, convexity or concavity of the relationship between k and ψ can lead to slow or fast carbon release, respectively (Fig. 5).

Introduction of skewness in the distribution of the initial amount of carbon provided additional insights. The results showed that, with asymmetric distributions, the constant and linear shapes produce different behaviors in the mineralization of carbon (Fig. 5c, d). This result suggests that the assumption of a homogeneous substrate does not hold when carbon is skewed to low or high decomposability values, even when decomposability and decomposition rates are linearly related. In addition, the asymmetry of the distribution of carbon determines how fast element mineralization proceeds. If the substrate is skewed toward low decomposability substrate (i.e., low decomposition rate), element miner-

alization proceeds slowly, and the opposite behavior is true for substrate skewed to high decomposability. This behavior is the result of the weighting of the decomposition rates by the distribution of carbon in different ranks.

QUALITY TRANSFORMATIONS DURING DECOMPOSITION

In the previous sections we have assumed that there is no transfer of carbon among different decomposability classes. This assumption is problematic because it is well known that decomposers transform organic matter in a myriad of different chemical compounds (Waksman et al. 1928, Swift et al. 1979, Sollins et al. 1996). It is also known that, over time, a portion of the original organic matter that enters the soil is sequentially transformed into recalcitrant compounds. Recalcitrant organic matter is highly resistant to degradation by microbes and enzymes with prolonged turnover times in soils.

In addition to microbial transformations, other physical and chemical factors interact to produce *stable* organic matter, which is the integrated effect of different biological, physical, and chemical mechanisms that protect organic matter from mineralization (Sollins et al. 1996, von Lützow et al. 2006). A substrate could be

stable but not necessarily recalcitrant if it is physically or chemically protected; nevertheless, a stable substrate is highly resistant to degradation and has long turnover times.

There are a variety of mechanisms that lead to stable organic matter as the end result. We refer here to them as short-term stabilization and destabilization mechanisms. These are physical and chemical factors that either increase or decrease the quality of the organic matter, chemical interactions with other compounds and minerals, and the degree of physical accessibility (Sollins et al. 1996). These mechanisms operate simultaneously, but in opposite directions.

The continuous quality theory presented above (see subsection *Model description*) is adequate to represent changes in quality due to microbial transformations that lead to recalcitrance, but it does not account for other processes related to stabilization. Solutions to the dynamic system (Eq. 5) have been developed using dispersion models that depend on the growth rate and efficiency of the decomposers (Ågren and Bosatta 1996, Bruun et al. 2009). Although it would be useful to introduce physical and chemical controls on these dispersion functions, the solution to the system of differential equations might be very challenging to derive analytically.

Here we take a different approach for representing transformations of organic matter during the decomposition process. Our main assumption is that the substrate is continually being transformed by the full suite of biological, chemical, and physical mechanisms. The change in decomposability is represented as a Markov process, in which decomposability is considered as a state variable with finite transition probabilities within the decomposability domain.

The Markov process

Transformations in the decomposability of organic matter at each time step are represented as a Markov process (Bharucha-Reid 1960) in which a transition matrix is used to calculate the amounts of substrate that are transferred among decomposability ranks (Baisden and Amundson 2003).

Assume that at each time step the transition from decomposability rank j to rank i is given by the transition matrix $\mathbf{P}$,

$$\mathbf{P} = \begin{pmatrix} p_{11} & p_{12} & \cdots & p_{1j} & \cdots & p_{1m} \\ p_{21} & p_{22} & \cdots & p_{2j} & \cdots & p_{2m} \\ \vdots & \vdots & \ddots & \vdots & \cdots & \vdots \\ p_{i1} & p_{i2} & \cdots & p_{ij} & \cdots & p_{im} \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ p_{m1} & p_{m2} & \cdots & p_{mj} & \cdots & p_{mm} \end{pmatrix}$$

and the distribution of carbon in all m ranks at time $t = 0$ is given by the vector $\rho_C(\mathbf{\Psi}, 0)$; i.e., the initial state of the system,

$$\rho_C(\mathbf{\Psi}, 0) = \begin{pmatrix} \rho_C(1, 0) \\ \rho_C(2, 0) \\ \vdots \\ \rho_C(m, 0) \end{pmatrix}.$$

We can set values for all transition probabilities p_{ij} according to certain assumptions about the behavior of the system, with the only requirement that $\sum_i p_{ij} = 1$. Transitions from time step n to $n + 1$ can be obtained by the product $\mathbf{P}\rho_C$, but we need to represent the dynamic behavior of the system first.

We will continue using the approach of representing decomposability in m different classes, but now, instead of using m analytical solutions, we will find m numerical approximations to the system of differential equations for each time step n, with l representing the size of each time increment. This approach will allow us to introduce the transition scheme at each time step. The state of the system at some time $n + 1$ will be represented by $\mathbf{U}^{n+1}$, which is the result of the update of the system by the transition matrix $\mathbf{P}$ and an r-order finite difference approximation $D_r f'(\mathbf{U}^n)$ to the system of differential equations for C, so

$$\mathbf{U}^{n+1} = \mathbf{P}[\mathbf{U}^n + l\, D_r f'(\mathbf{U}^n)]. \tag{15}$$

which is equivalent to

$$\mathbf{U}^{n+1} = \mathbf{P}\left[\begin{pmatrix} \rho_{C,\psi_1}(n) \\ \rho_{C,\psi_2}(n) \\ \vdots \\ \rho_{C,\psi_m}(n) \end{pmatrix} + l \begin{pmatrix} D_r f'(\rho_{C,\psi_1}) \\ D_r f'(\rho_{C,\psi_2}) \\ \vdots \\ D_r f'(\rho_{C,\psi_m}) \end{pmatrix}\right] \tag{16}$$

where for each $\psi \in \{\psi_1, \ldots, \psi_m\}$ the system of differential equations is given by

$$f'(\rho_{C,\psi}) = \frac{d\rho_{C,\psi}}{dt} = -k_\psi \rho_{C,\psi}. \tag{17}$$

The finite difference approximation chosen to find solutions for the m systems in Eq. 16 was the fourth-order Runge-Kutta method, which in general provides solutions with high accuracy; that is, $E = O(l^4)$ (LeVeque 2007).

Short-term stabilization and destabilization of organic matter

Since we already have relationships to obtain values of $u(\psi)$ and $e(\psi)$ for each decomposability class, we only need to specify $\mathbf{P}$ to solve Eq. 15. Although the Markovian structure of Eq. 15 provides opportunities for representing complex transitions in the decomposability domain, we took a very simple approach here to test two different assumptions about sequential transformations of decomposability. First, we assumed that, at each time step, a portion of the carbon is transferred to the immediately adjacent rank in the direction toward lower decomposability. There are no transitions to better decomposability ranks. This is equivalent to assuming no short-term destabilization mechanisms, or

that short-term stabilization outweighs any short-term destabilization process.

Assuming that at each time step the amount of carbon that is transferred to the adjacent decomposability rank is 50% of the current amount, then

$$\mathbf{P}_1 = \begin{pmatrix} 1 & 0.5 & 0 & \cdots & 0 \\ 0 & 0.5 & 0.5 & \cdots & 0 \\ \vdots & 0 & 0.5 & \cdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & 0.5 \\ 0 & 0 & 0 & \cdots & 0.5 \end{pmatrix}.$$

Notice that the first element implies that, once a certain amount of carbon is transferred to the lowest decomposability rank, it remains confined there indefinitely. In other words, once a certain amount of carbon is transformed to a stable compound, it cannot be transformed into a substrate of better quality or liberated from chemical or physical protection.

The second assumption considered includes short-term destabilization mechanisms for each decomposability rank. At each time step we assumed that 50% of the substrate stays in the same rank, while 25% is transferred to the adjacent higher rank and 25% gets transferred to the adjacent lower rank. For the lowest decomposability rank, we assumed that 25% of the material is destabilized at each time step, so the transition matrix for our second assumption is defined as

$$\mathbf{P}_2 = \begin{pmatrix} 0.75 & 0.25 & 0 & \cdots & 0 \\ 0.25 & 0.5 & 0.25 & \cdots & 0 \\ 0 & 0.25 & 0.5 & \cdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & 0.5 \\ 0 & 0 & 0 & \cdots & 0.5 \end{pmatrix}.$$

We incorporated this Markovian approach in the decomposition model for the two different assumptions $\mathbf{P}_1$ and $\mathbf{P}_2$, also assuming that the initial amount of carbon was normally distributed, and $m = 200$.

The model successfully represented the gradual change in the overall decomposability of the substrate over time, as well as a reduction in the total amount of carbon and nitrogen as an effect of decomposer activity (Figs. 6 and 7). Over time, for the stabilization assumption ($\mathbf{P}_1$), an increasing amount of carbon accumulates in the lowest rank because the decomposition rate there is very close to zero and the material does not transition to higher ranks (Fig. 6). However, when the decomposition rate is constant for all decomposability classes, including the lowest class, carbon is lost continually from the system (Fig. 6a). At the end of the simulation, all the carbon remaining is stored in the lowest rank, with the total amount depending on the functional relationship between k and ψ. For the assumption of simultaneous short-term stabilization and destabilization, the final amount of carbon was stored in a wider range of ranks, mainly of lower

decomposability, with the exception of the constant functional shape.

Decomposition proceeded faster when the relationship between k and ψ was represented with a concave function and slower when represented with a convex one (Fig. 8a, b). Although this was already observed in previous simulations, it can be seen in Fig. 6c and d that the convex shape leads to higher accumulation of substrate with low decomposability. Since low decomposability substrate decomposes faster in the concave functional form, decomposition proceeds faster and less material accumulates in the more stable fractions.

When both short-term stabilization and destabilization were considered in the transition matrix, very small amounts of substrate remained at the end of the simulation period (Fig. 8b). With the exception of a constant decomposition for all ranks, most of the remaining substrate was accumulated in the lower decomposability ranks, decreasing exponentially in the higher ranks. This is a more realistic distribution than when destabilization was not included in the transition matrix. The assumption of constant decomposition leads to a final material similar in decomposability to the initial distribution of the substrate.

Litter inputs and their heterogeneity

Litter from aboveground plant parts and roots is by far the dominant input of organic matter to the soil. This litter enters the soil in a variety of amounts and decomposability that depend on the dominant vegetation, its phenology, and the climate, among other factors. Litter decomposability or quality for different pools is often defined by the chemical characteristics of the material such as the contents of carbon and nutrients, as well as the relative proportions of compounds such as lignin, cellulose, polyphenols, and so on.

In this analysis we used a qualitative description of the distribution of carbon in different decomposabilities for a small set of plant parts. Leaves, fine roots, branches, wood, bark, and coarse roots were the different pools considered, and we defined hypothetical shapes of their carbon distribution in the decomposability continuum (Fig. 9).

The distribution of carbon entering the soil at each time step n is given by

$$\mathbf{L}^n = \mathbf{L}_{lv}^n + \mathbf{L}_{fr}^n + \mathbf{L}_{br}^n + \mathbf{L}_{wd}^n + \mathbf{L}_{bk}^n + \mathbf{L}_{cr}^n \qquad (18)$$

where $\mathbf{L}$ is a vector of length m that represents the distribution of carbon of incoming litter for each decomposability rank. The subscripts represent different plant parts: lv, leaves; fr, fine roots; br, branches; wd, wood; bk, bark; and cr, coarse roots. These distributions were produced using beta probability distribution functions with arbitrary parameters selected to reproduce hypothetical shapes for each pool (see Fig. 9).

The system of equations for representing organic matter decomposition can now be expressed to include
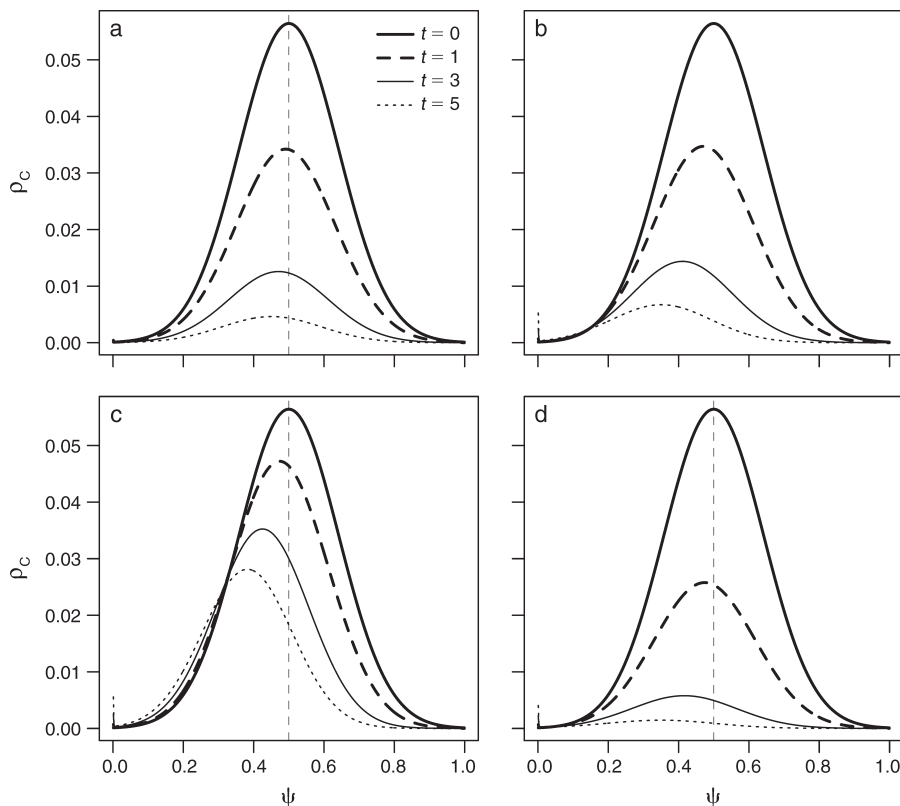
Fig. 6. Distributions of the density of carbon in the decomposability continuum at different time steps t assuming only stabilization processes ($\mathbf{P}_1$; see subsection *Short-term stabilization and destabilization of organic matter*). Each panel depicts different assumptions about the relationship between k and ψ: (a) constant, (b) linear, (c) convex, and (d) concave.

litter inputs by simply adding the $\mathbf{L}^n$ term to Eq. 15 as follows:

$$\mathbf{U}^{n+1} = \mathbf{P}[\mathbf{U}^n + l\, D_r f'(\mathbf{U}^n)] + \mathbf{L}^n \qquad (19)$$

so now the system includes both inputs and losses to and from the soil. To include variability in the inputs of litter, we selected random amounts of carbon from a normally distributed average amount of inputs for each pool.

Accumulation of carbon over time

If only short-term stabilization is included in the transition matrix, carbon accumulates linearly over time (Fig. 8c). However, when decomposition is constant for all ranks, the system quickly reaches steady state. In contrast, when short-term stabilization and destabilization are both included in the transition matrix, the total amounts of carbon accumulate asymptotically (Fig. 8d).

The final distribution of carbon tends to accumulate most of the substrate in the lower decomposability ranks, with the exception of the constant functional shape, which presents a distribution of carbon similar to the distribution of the incoming litter (Fig. 10). For the concave shape, which decomposes the substrate faster and reaches equilibrium faster than the other shapes, the amount of carbon in higher ranks is relatively high. This

reflects the relative importance of the incoming material once the system has reached equilibrium.

These results suggest that the substrate that accumulates over time tends to be of similar decomposability, with an important fraction accumulated in the lower ranks and a fraction accumulated in higher ranks representing the fresh litter. This distribution of substrate in different decomposability ranks depends on the shape of the relationship between ψ and k. The concave shape, which decomposes the substrate faster than the other shapes, tends to accumulate significantly higher proportions of carbon in high decomposability ranks.

DISCUSSION

The results obtained in this analysis provide support for our working hypothesis: The inclusion of substrate heterogeneity in modeling decomposition introduces properties and behaviors that cannot be obtained by representing homogeneous substrates. When substrates were assumed to be heterogeneous, we found behaviors leading to different amounts of carbon mineralization over time. Short-term dynamics created in the decomposition of heterogeneous substrates can potentially create behaviors associated with the long-term stability of organic matter in soils.
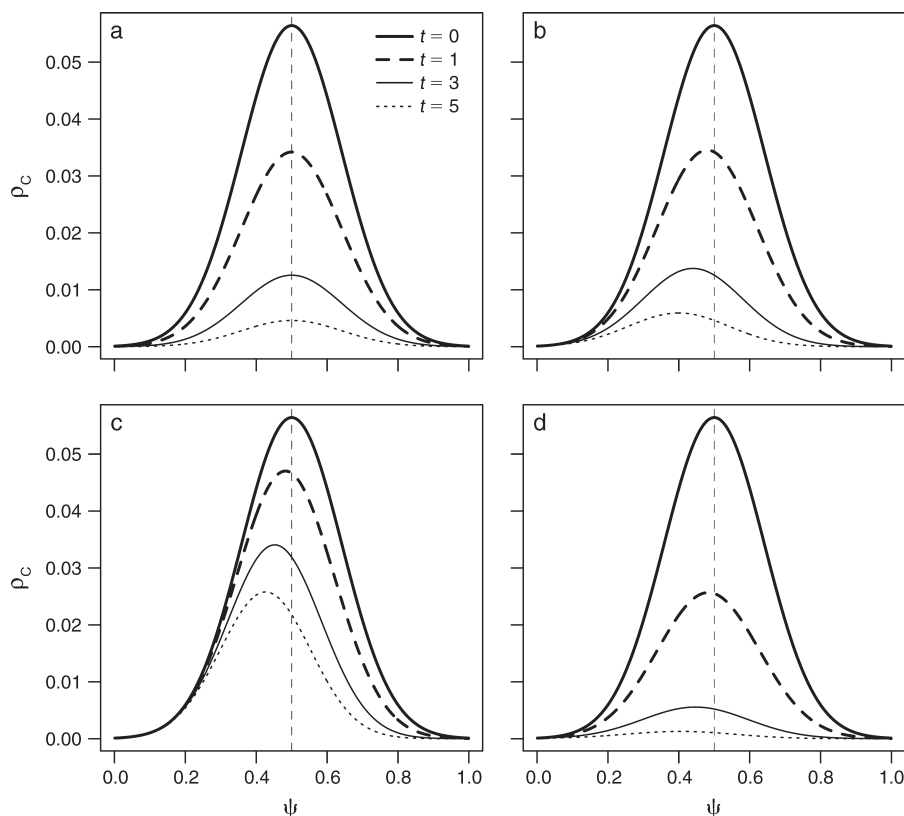
FIG. 7. Distributions of the density of carbon in the decomposability continuum at different time steps t assuming simultaneous stabilization and destabilization processes (P_2; see subsection *Short-term stabilization and destabilization of organic matter*). Each panel depicts different assumptions about the relationship between k and ψ: (a) constant, (b) linear, (c) convex, and (d) concave.

To the questions asked initially, we can answer: First, the disagreement between continuous and discrete approaches is high when the discrete model consists of a small number of pools without substrate transformations. As the number of pools increases, the discrete model better resembles continuous functions and the mismatch decreases. For models with a small number of pools (two to three), the mismatch with continuous approaches increases over simulation time. Second, we found that representing a heterogeneous substrate as a homogeneous one is only appropriate under the limited case of a linear relation between decomposability and decomposition rates, and uniform or Gaussian distribution of the substrate. Third, continuous transformations in the decomposability of organic matter over time produce accumulation of substrate in the lower decomposability ranks. This is the result of simultaneous short-term stabilization and destabilization processes that result in convergent distributions of organic matter skewed toward lower ranks.

Our results suggests that explicit treatment of substrate heterogeneity of organic matter in decomposition models is of fundamental importance to simulate processes related to long-term carbon dynamics. For this purpose it is necessary to represent this heterogeneity in models with a significant number of pools or continuous

models. Quality or decomposability as a continuous variable can be easily implemented in numerical models. One of the main advantages of this approach is that the number of parameters needed to represent decomposition rates for different pools is reduced to just one or two parameters describing a functional relationship between decomposability and decomposition rate. Complex functions describing the heterogeneity of a substrate can also be implemented without dealing with finding complex analytical solutions.

Finding parameters and functions to describe growth rate and efficiency of decomposers with decomposability may be challenging. There are a number of laboratory techniques that seem to be promising for providing representations of substrate quality in a continuous fashion. Bruun et al. (2009) reviewed a large number of methods with potential application for describing substrates in a continuum of qualities. The methods can be grouped into physical, chemical, and biological fractionations, as well as spectroscopy methods. Although there is not much research on the applications of these methods for modeling decomposition in the continuous quality framework, there are enormous research opportunities. Many laboratory methods are currently used for parameterizing compartment models, but it is still an open question if the operationally
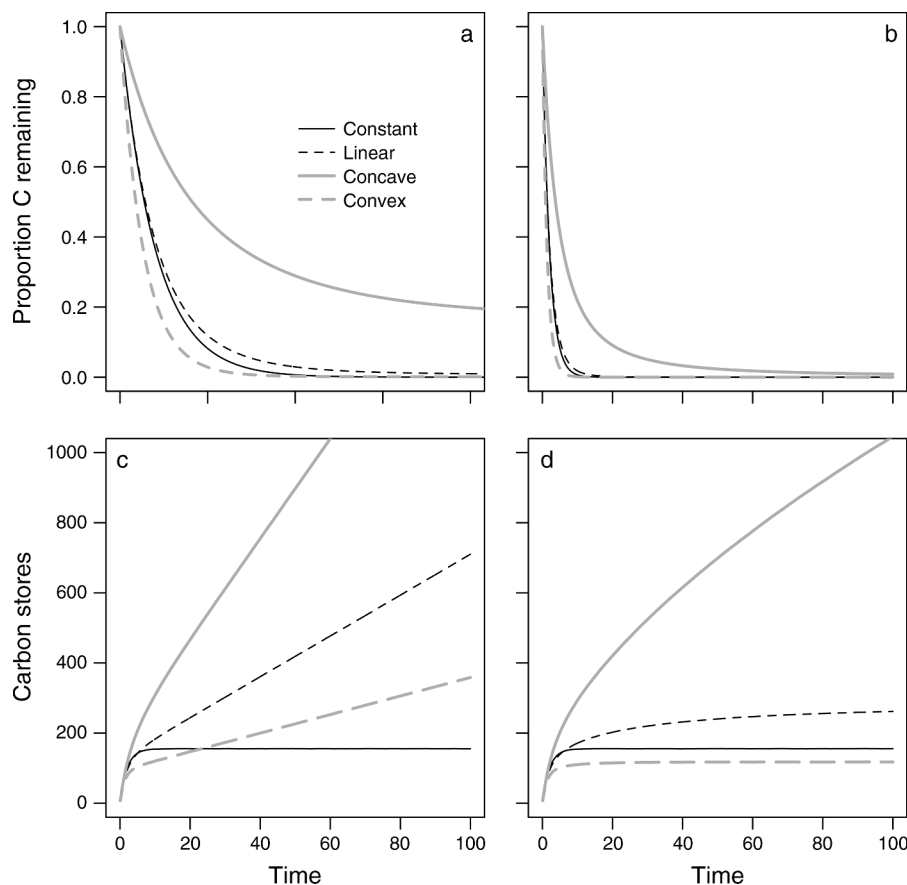
FIG. 8. Effects of the assumptions of stabilization only (P_1, left panels) and simultaneous stabilization and destabilization (P_2, right panels) on carbon dynamics over time. The upper row of panels shows results from simulations of a single litter cohort, and the lower row shows simulations with litter inputs. Lines types depict different assumptions of the relationship between k and ψ. Carbon strores are in units of mass of carbon; the actual numbers are arbitrary.

defined partitioning of chemical or physical fractions correspond to the assignment of quality compartments in models. The continuous approach in this case may actually help to solve this dilemma, since compartmentalization is not necessary when quality or decomposability are treated continuously.

Overall rate of carbon mineralization

Traditionally, it has been assumed that the overall rate of carbon mineralization can be described by a single decomposition rate (e.g., Jenny et al. 1949, Olson 1963). Although most models now deal with a number of pools to represent substrate heterogeneity, the assumption of a single process rate is still imbedded in current soil respiration studies. As the results from this analysis showed, this assumption is only valid when the substrate subject to decomposition has homogeneous properties that can be considered constant over the time period in question. The overall decomposition rate of a substrate is the result of a combination of decomposition rates for different decomposability classes weighted proportionally by the amount of carbon. If more carbon is stored in lower than in higher decomposability classes,

the overall rate of carbon release would be slower than if a higher proportion is stored in higher classes. Therefore, decomposition rates by themselves only provide part of the information needed to determine how fast decomposition proceeds for a given substrate.

The behavior of decomposers' growth and efficiency in lower decomposability ranges is also a significant factor determining the overall rates of mineralization. As the substrate becomes more recalcitrant and less accessible, decomposers might decrease their activity drastically or more moderately, which results in convex or concave shapes of their activity on the decomposability continuum, respectively. This marginal response can produce dramatic differences in the overall rates of carbon and nitrogen mineralization, in addition to the relative proportions of substrates in different classes.

Moreover, the continuous redistribution of organic matter to different decomposabilities results in a gradual accumulation of material at lower ranks. On the whole, this process tends to reduce the overall rates of mineralization. When we considered simultaneous short-term stabilization and destabilization mechanisms in our model, the proportions of material passing to low
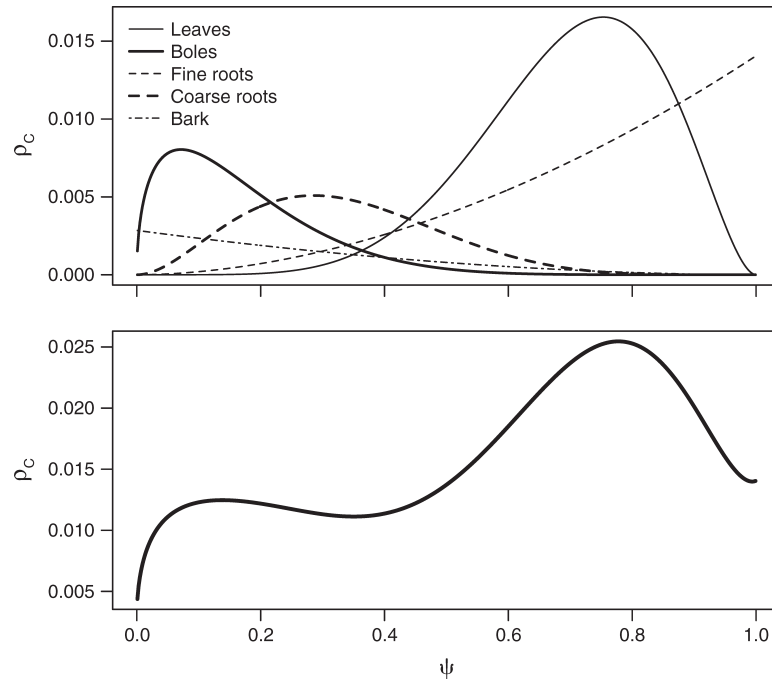
FIG. 9. Hypothetical distributions of carbon for different litter pools in the decomposability continuum. The upper panel shows the distribution of carbon for each individual pool, and the lower panel shows the total amounts.
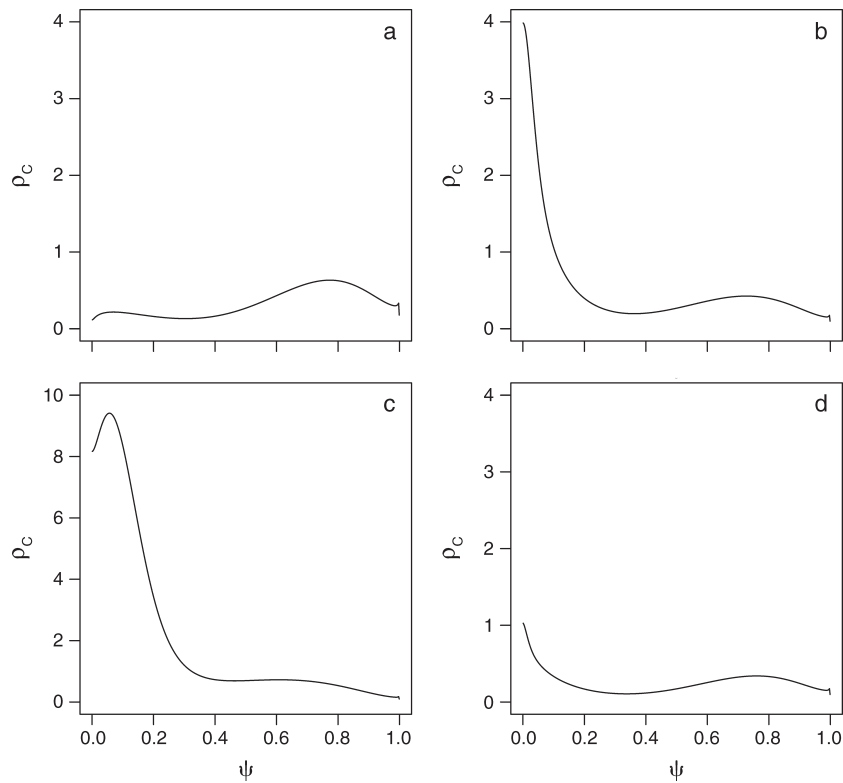

FIG. 10. Distribution of carbon at the final time step when both stabilization and destabilization are included in the transition matrix $\mathbf{P}_2$. Each panel represents different assumptions about the relationship between k and ψ: (a) constant, (b) linear, (c) convex, and (d) concave.

and high decomposability ranks were equal for most of the quality range. However, the material at lower ranks has lower decomposition rates, and more carbon accumulates in lower classes, which eventually results in a decrease of the overall mineralization rate.

Ågren and Bosatta (1996) suggest that, when changes in quality or decomposability are faster than the changes in quantity, a finite amount of substrate always remains, which causes linear accumulation of organic matter over time. In addition to this, our results also suggests that when short-term stabilization processes change quality in one single direction, organic matter linearly accumulates in the lowest quality class (see the first element of $\mathbf{P}_1$).

The continuous transformation of organic matter results in a relatively similar distribution of substrate regardless of the incoming litter. This behavior in our model is consistent with observations of ^{13}C nuclear magnetic resonance (NMR), which show that the proportions of complex molecular structures such as alkyls, O-alkyls, aromatics, and carbonyls are remarkably similar in soils worldwide independent of land use, climate, and management (Mahieu et al. 1999). Results from long-term large-scale decomposition studies suggest that litter tends to reach a phase of slow decomposition in the long-term (Melillo et al. 1989, Harmon et al. 2009), which could be explained by the accumulation of low-decomposability substrate. This accumulation of substrate in lower ranks is also consistent with the concept of *convergence* of the decomposition process (Swift et al. 1979), by which the branching of substrate degradation through different food webs converges to final products of similar characteristics. Since under certain mathematical conditions Markov chains converge to stationary distributions regardless of the initial conditions (Bharucha-Reid 1960), they appear to provide useful representations of transformations of soil organic matter characteristics. In fact, the use of transition matrix to represent the decomposition process has provided insightful results in previous studies (Baisden and Amundson 2003).

Convergence of the Markov chain to a stationary distribution is an emergent property of the system. This implies that representing long-term stability of organic matter in soils can be achieved by the convergence properties of Markov chains, i.e., by the properties of short-term dynamics of organic matter transformations.

Summary and Conclusions

This analysis suggests that including substrate heterogeneity in the decomposition of organic matter helps to elucidate complex temporal behaviors associated with the long-term stabilization of organic matter in soils. The assumption of homogenous substrates implies equal efficiencies and growth rates for all different substrates present in the soil organic matter. This assumption can only provide realistic behaviors when the relationship between decomposability and decomposition rate is linear and the substrate is symmetrically distributed around an average value. In all other cases, the assumption of homogeneous substrates produces different amounts and rates of mineralization for carbon and nitrogen.

Substrate heterogeneity can be described with multiple-pool or continuous models. They both are representations of the same soil properties, but their predictions can differ considerably. The discrepancy between the two approaches is proportional to the size of the compartments and the convexity (or concavity) of the functions that best represent substrate heterogeneity. Their predictions also differ significantly over simulation time, which imposes challenges to compare predicted long-term behaviors between the two approaches.

The temporal behaviors in the mineralization of carbon are highly dependent on the functions that describe the efficiency and growth rate of decomposers with decomposability; i.e., the convexity of the relationship between decomposition rate and decomposability rank.

The continuous transformations of organic matter in the soil tend to accumulate carbon in organic matter of low decomposability independent of the characteristics of the incoming litter. This emergent property can only be represented by short-term stabilization and destabilization mechanisms operating simultaneously. Without short-term destabilization processes, carbon will accumulate linearly in soils.

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SUPPLEMENT

R code implementing the decomposability model described in this paper. Description of parameters and some examples are provided in the source code (*Ecological Archives* M081-022-S1).