



# Soil carbon and nitrogen mineralization: Theory and models across scales

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## ABSTRACT

In the last 80 years, a number of mathematical models of different level of complexity have been developed to describe biogeochemical processes in soils, spanning spatial scales from few  $\mu\text{m}$  to thousands of km and temporal scales from hours to centuries. Most of these models are based on kinetic and stoichiometric laws that constrain elemental cycling within the soil and the nutrient and carbon exchange with vegetation and the atmosphere. While biogeochemical model performance has been previously assessed in other reviews, less attention has been devoted to the mathematical features of the models, and how these are related to spatial and temporal scales. In this review, we consider  $\sim 250$  biogeochemical models, highlighting similarities in their theoretical frameworks and illustrating how their mathematical structure and formulation are related to the spatial and temporal scales of the model applications. Our analysis shows that similar kinetic and stoichiometric laws, formulated to mechanistically represent the complex underlying biochemical constraints, are common to most models, providing a basis for their classification. Moreover, a historic analysis reveals that the complexity and degree and number of nonlinearities generally increased with date, while they decreased with increasing spatial and temporal scale of interest. We also found that mathematical formulations specifically developed for certain scales (e.g., first order decay rates assumed in yearly time scale decomposition models) often tend to be used also at other spatial and temporal scales different from the original ones, possibly resulting in inconsistencies between theoretical formulations and model application. It is thus critical that future modeling efforts carefully account for the scale-dependence of their mathematical formulations, especially when applied to a wide range of scales.

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## 1. Introduction

About three-fourth of the organic carbon contained in terrestrial ecosystems and the majority of organic nitrogen are found in plant residues and soil organic matter (Schlesinger, 1997; Lal, 2008). Both organic carbon and macro-nutrients are mineralized to simple inorganic forms by a highly dynamic community of microbial and faunal decomposers (Brady and Weil, 2002; Berg and McClaugherty, 2003; Paul, 2007). Although this process of mineralization occurs at the decomposer cell scale and is affected by the soil physical and biological interactions (e.g., climate and vegetation), it involves globally a gross release of carbon dioxide to the atmosphere in amounts one order of magnitude larger than the anthropogenic emissions (Schlesinger, 1997; Lal, 2008) and provides most of the inorganic nutrients necessary for plant growth

in natural ecosystems (Waksman et al., 1928; Brady and Weil, 2002).

Since the 1930s, several mathematical models at different levels of detail have been developed to quantitatively describe these processes (e.g., Tanji, 1982; Dewilligen, 1991; McGill, 1996; Molina and Smith, 1998; Benbi and Richter, 2002; Shibu et al., 2006). The number and variety of these models mirror a relentless effort to describe and quantify the complex nature of soils and the elemental cycling within them. Soils are spatially heterogeneous at molecular to continental scales (Ettema and Wardle, 2002; Young and Crawford, 2004), and their temporal dynamics span a wide range of scales going from the hourly responses to environmental fluctuations (Austin et al., 2004; Schwinning and Sala, 2004) and changes in resource supply (Zelenev et al., 2000), to the decadal time scales of ecosystem and climatic changes and the even longer time scales characteristic of soil development (Richter and Markewitz, 2001). The extreme variety of biogeochemical processes is further complicated by climatic and anthropogenic external forcing factors.

The development of a mathematical model generally follows three subsequent steps (Ulanowicz, 1979): i) definition of the state

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variables for the scale of interest; ii) identification of inputs, outputs, and possible interactions; iii) model verification. Most of the previous reviews on biogeochemical modeling primarily address the verification step (e.g., Dewilligen and Neeteson, 1985; Andr n and Paustian, 1987; Melillo et al., 1995; Powlson et al., 1996; Jans-Hammermeister and McGill, 1997; Smith et al., 1997; Moorhead et al., 1999; Zhang et al., 2008). Fewer works focus on the first two critical steps: describing the effects of different choices of the state variables (e.g., Bolker et al., 1998; Bruun et al., 2004; Pansu et al., 2004; Fontaine and Barot, 2005) and comparing different formulations of the interactions among them (Molina and Smith, 1998; Ma and Shaffer, 2001; McGechan and Wu, 2001; Plante and Parton, 2005; Manzoni and Porporato, 2007; Wutzler and Reichstein, 2008).

The goal of this review is not to test modeling hypotheses or assess model performances, but to provide an extensive comparison of mathematical approaches to soil carbon (C) and nitrogen (N) cycling and discuss a model classification based on kinetic laws and stoichiometry. The difficulty of classifying soil biogeochemical models according to their mathematical formulation arises because of the large number of possible combinations of different model structures (e.g., number of variables and mass flow architecture) and reaction terms (e.g., linear vs. nonlinear kinetic laws). However, all these models deal with processes controlled by similar biogeochemical constraints, and basically describe the transfer of matter from organic to inorganic compounds. This mineralization process can be regarded as a complex, biologically mediated series of reactions, where organic substrates are converted into living biomass and mineral residues (Swift et al., 1979). It is typically modeled by kinetic laws describing organic matter degradation, where microbial stoichiometric relationships are employed to regulate the associated C–N balances. In what follows we will compare the mathematical formulations used to describe these two fundamental aspects of C and N cycling, with the hope to highlight possible limitations of current approaches and help future cross-disciplinary theoretical developments.

A simplified mathematical representation of the substrate–microbial biomass interactions will be presented and guide our model classification, where indices of model structure and complexity are included, along with a characterization of key biogeochemical processes (Table A2). About 250 mathematical models developed during nearly eight decades are reviewed, considering both highly cited sources and less known theoretical analyses describing the various aspects of soil dynamics, as well as soil organic matter submodels embedded in hydrologic or ecosystem models. Since model structure and formulations are expected to change with the scale and level of resolution needed for the particular applications (Manzoni and Porporato, 2007; Manzoni et al., 2008b), we also analyze the relationships between model formulations and the temporal and spatial scale of application.

The review is organized as follows:

- Section 2 describes the general structure of soil biogeochemical models, with an emphasis on stochastic components, mathematical formalisms, and level of complexity (e.g., the dimension of the phase-space), and relates these features to the scales of interest.
- Section 3 presents an overview of the mathematical formulations used to characterize two key processes in C and N cycling in soils, i.e., decomposition of organic matter and nitrogen mineralization and immobilization. Both processes are analyzed under the common framework of substrate–decomposer stoichiometry, thus stressing the role of the microbial biomass as both an SOM degrading agent and as a controlling factor of N cycling. This approach allows us to

compare mathematical models coming from different fields, ranging from microbiology to ecosystem ecology.

- Section 4 analyzes the relationships between model formulation and scale, discussing how the different formulations are used across or at individual scales.
- Section 5 puts the previous analyses into perspective with respect to the dominant trends in soil biogeochemical modeling and discusses the main limitations of the current approaches. Based on these conclusions, we provide some guidelines for future research.
- Finally, Appendix A reports the list of the reviewed models and their most important mathematical features with respect to this synthesis.

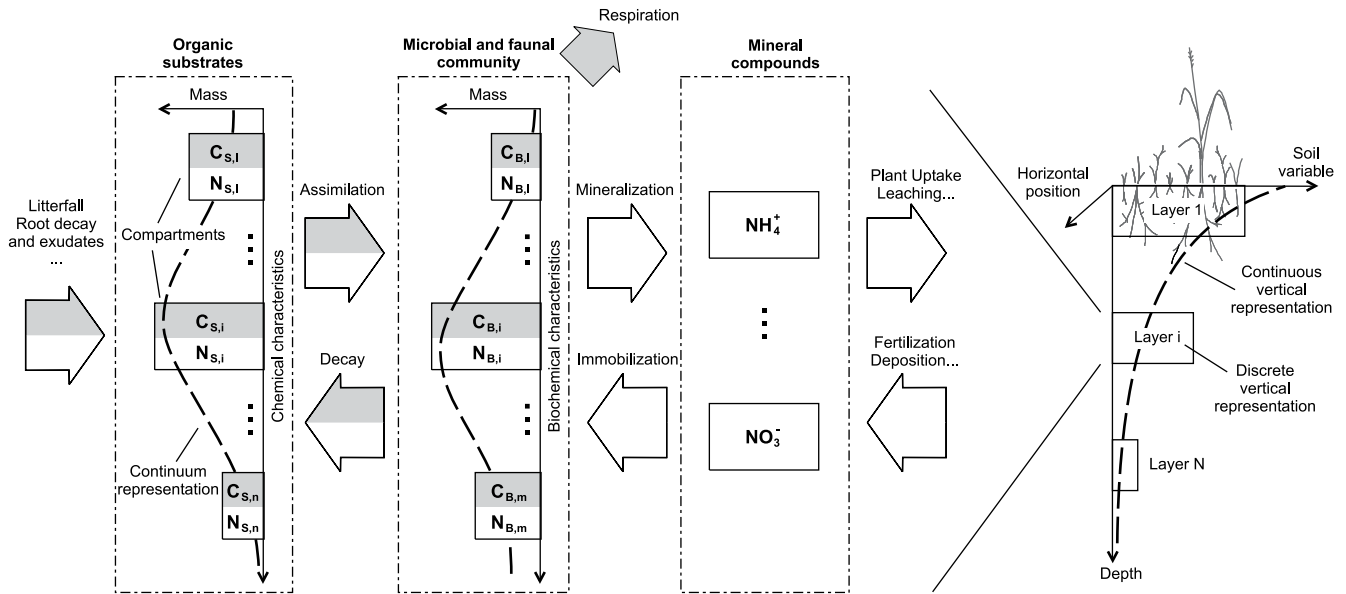
## 2. Historic appraisal of mathematical structure and complexity in soil biogeochemical models

Soil biogeochemical models describe a system including SOM constituents (both passive substrates and active biological decomposers), interacting with inorganic compounds, environmental variables, and subject to external inputs and outputs (Fig. 1). Here we review how the mathematical description of such a complex system is framed. We discuss the general model structure and spatial resolution (Sections 2.1–2.3), the number of variables used at different scales (Sections 2.4 and 2.5), and the presence of stochastic elements (Section 2.6).

### 2.1. From compartment to continuum-quality models

Although SOM is an extremely heterogeneous mixture of compounds (Swift et al., 1979), early mathematical models described the processes of decomposition and mineralization using simple chemically and spatially lumped models (Table A2; Fig. 2a). Nikiforoff (1936) was probably the first to suggest that the formation of humus may be described by multiple coupled equations each characterizing a pool with different turnover times. Later, Minderman (1968) developed similar ideas to describe the macroscopic patterns of organic matter degradation resulting from the compound effects of different substrates. This idea resulted in a number of compartmental models. As noted by Halfon, “Compartmental analysis is a phenomenological and macroscopic approach for modeling a physicochemical process. A compartment (or state variable [...]) is a basic unit of functional interest” (Halfon, 1979, p. 2). Recent models employ a number of such chemically homogeneous compartments, which interact among them and possibly with the microbial biomass (Fig. 1). Most soil food web models are also compartment models, where particular attention is given to the trophic interactions among microbial and faunal groups (Hunt et al., 1987; Deruiter et al., 1993; Zheng et al., 1999; Zelenov et al., 2006).

In compartment models, all the organic matter molecules with similar chemical characteristics or degradability are included in the same pool and the information regarding the age or residence time of biogeochemical compounds within each compartment (or in general since the introduction of organic matter into the soil system) is not explicitly tracked. Nevertheless, the distribution of the ages of SOM compounds can be reconstructed knowing the model structure and how the fluxes among the pools are defined (Bruun et al., 2004; Manzoni et al., in preparation). In contrast to typical compartment models, some biogeochemical models explicitly track the evolution of any organic matter “cohorts” (i.e., “sets of items of the same age”, Gignoux et al., 2001) from their incorporation into the litter or humus and until their complete degradation (Furniss et al., 1982; Pastor and Post, 1986;  gren and



**Fig. 1.** Conceptual scheme of the main interactions between soil substrates and organisms, as represented by spatially lumped and spatially continuous representations. Gray and blank boxes respectively represent carbon and nitrogen compartments and fluxes. The dashed lines in the SOM boxes (left) qualitatively illustrate how the substrate and decomposer variables are treated as a continuum in the Q-model (Ågren and Bosatta, 1996).

Bosatta, 1996; Gignoux et al., 2001). This approach provides one way to interpret tracer studies and other paleoecological dating techniques (Bruun et al., 2004; Bruun et al., 2005).

In contrast to the discrete representation of soil organic matter, continuum-quality models (Carpenter, 1981; Bosatta and Ågren, 1985; Forney and Rothman, 2007) based on a distribution of C and

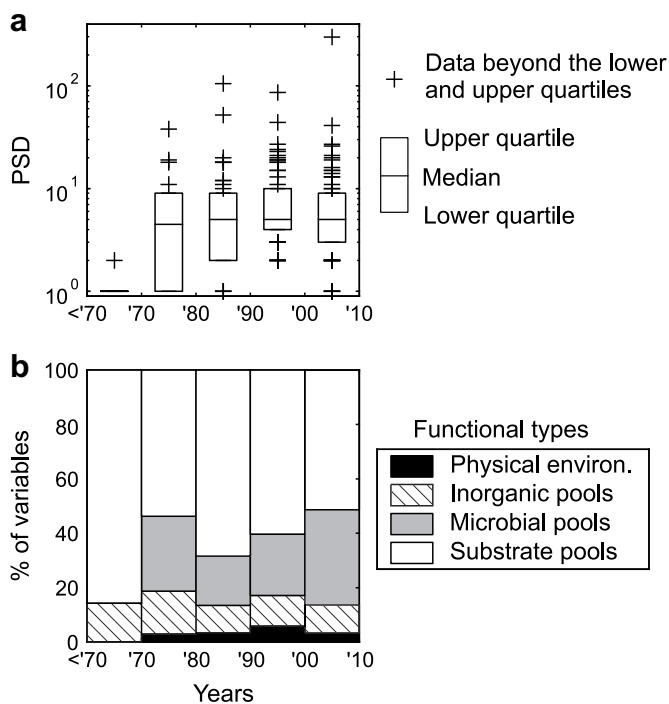
N substrates along a quality axis (Fig. 1, dashed lines) analytically describe both single and multiple cohort dynamics as well as different substrate–microbe networks through a specific function controlling the quality evolution during microbial assimilation and turnover (Ågren and Bosatta, 1996).

## 2.2. Modeling spatial variability

Soils are highly spatially heterogeneous, with variability of chemical and physical properties along the vertical profile (Brady and Weil, 2002), around small-scale biologically active patches and individual plants, and at the landscape scale (Ettema and Wardle, 2002; Young and Crawford, 2004). Compartment models have been in part extended to account for spatial variability (Fig. 1). While the biogeochemical processes along vertical soil profiles are addressed by a number of models, only few attempt an explicit description of spatial heterogeneities from the soil aggregate to the landscape scales.

Some early biogeochemical models already employed either a discrete representation of soil layers with different chemical and physical features (Beek and Frissel, 1973; van Veen and Paul, 1981) or a continuous description of SOM and nutrient dynamics along the soil profile (O'Brien and Stout, 1978). Today, most soil and ecosystem models consider different soil layers, often connected through the water flow, which drives the advection of organic and inorganic dissolved compounds along the profile (Hansen et al., 1991; Li et al., 1992; Parton et al., 1993; Folking et al., 2001; Garnier et al., 2001; Grant, 2001; Kirschbaum and Paul, 2002; Liu et al., 2005; Maggi and Porporato, 2007; Wu et al., 2007; Jenkinson and Coleman, 2008). Some models provide a continuous description of the soil profile (Bosatta and Ågren, 1996), possibly also considering diffusive transport due to slow mixing processes (O'Brien and Stout, 1978; Elzein and Balesdent, 1995; Bruun et al., 2007).

There are fewer models explicitly describing the spatial dynamics of water, organic matter, or nutrients at the bacterial cell- or colony-scale (Allison, 2005; Ginovart et al., 2005; Masse et al., 2007), in the pore space (Long and Or, 2005), within soil aggregates (Lefelaar, 1993; Arah and Smith, 1989), or around a root (Darrah, 1991; Toal et al., 2000; Kravchenko et al., 2004; Raynaud et al., 2006). Horizontal spatial variability at the individual plant scale is



**Fig. 2.** Historic trends of model complexity and variable functional type. (a) Box plots of the number of variables in the litter and one soil layer (phase-space dimension, PSD); (b) percentage of total PSD in each functional class of variables: physical environment, inorganic, microbial, and organic substrate pools. Continuous quality models, with infinite-dimensional phase-space, are not considered; all models published before 1970 are grouped together (most of them have one variable only, so that the mean and the quartiles in (a) coincide).

generally neglected in soil biogeochemical models, while some describe landscape level heterogeneity in SOM and litter inputs (Walter et al., 2003) or soil hydraulic properties (Acutis et al., 2000), the effects of erosion and SOM redistribution (Rosenbloom et al., 2001), or horizontal transport of nutrients (Tonitto and Powell, 2006). Overall, there is a lack of spatially explicit models properly describing soil carbon and nutrient dynamics at different spatial scales.

### 2.3. Mathematical formalism and model solution

Some earlier biogeochemical models employed difference equations or geometric series to compute organic matter and litter accumulation at the yearly time scale (Salter and Green, 1933; Nikiforoff, 1936; Jenny et al., 1949; Minderman, 1968; Jenkinson and Rayner, 1977). However, the ordinary differential equation (ODE) formalism, introduced in soil biogeochemistry by Henin and Dupuis (1945), allows the description of SOM dynamics in continuous time and has been predominantly used since then. Almost all compartment models can be recast into systems of first order ODEs, each describing the mass balance of a compartment (possibly within a cohort) or a soil layer. The number of equations in these systems of ODEs varies from model to model (Section 2.4) as does their degree of nonlinearity (Section 3.2). Linear systems of ODEs with constant coefficients can be solved analytically, regardless of their compartmental organization (e.g., Olson, 1963; Bolker et al., 1998; Kätterer and Andrén, 2001; Nicolardot et al., 2001; Baisden and Amundson, 2003; Saffih-Hdadi and Mary, 2008; Manzoni et al., in preparation), while in general nonlinear models need to be solved numerically. Despite the presence of nonlinearities, a number of models can at least be solved analytically at steady state (by setting the time derivatives of the ODEs to zero), thus providing useful information on the asymptotic behavior of the system (e.g., Loreau, 1998; Daufresne and Loreau, 2001; Manzoni et al., 2004; Fontaine and Barot, 2005; Manzoni and Porporato, 2007; Wutzler and Reichstein, 2008).

In contrast to compartment models, those based on the continuum quality concept, involving both time and organic matter quality as independent variables, are in the form of systems of partial (and sometimes integro-) differential equations (PDEs) (Carpenter, 1981; Ågren and Bosatta, 1996). Such equations are amenable to analytical solution only for suitable choices of the decomposer growth and decay functions (Ågren and Bosatta, 1996; Bosatta and Ågren, 2003), in which case leading to relatively compact representations of the complex soil dynamics. To our knowledge, only one model uses delayed differential equations (DDEs) and describes nitrogen mineralization as a piston flow, i.e., mineralization at time  $t$  is assumed equal to the N flux entering the soil at the time  $t - \Delta t$  (Thornley et al., 1995). DDEs can be interpreted as a special form of PDEs, and like them can be seen as equivalent to infinite-dimensional systems of ODEs.

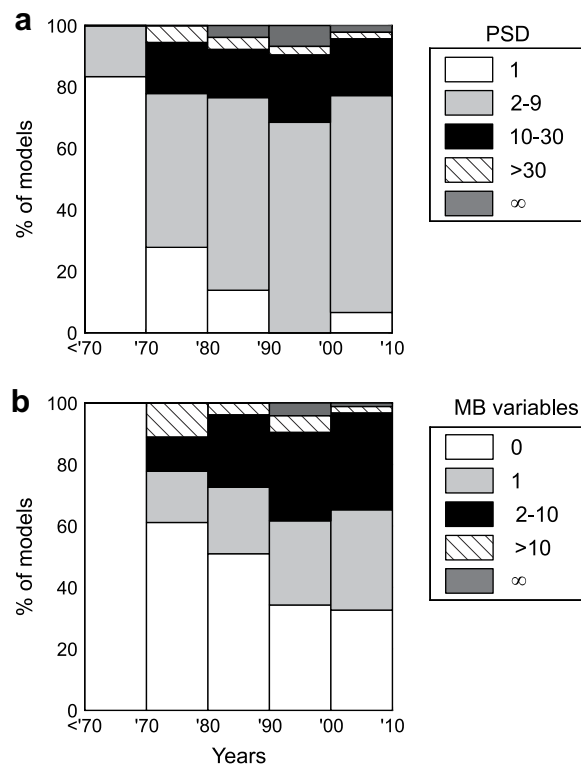
### 2.4. Historic evolution of model complexity

A first measure of model complexity (not to be confused with the measures of dynamic complexity) is analyzed in this section by considering the number of first order differential equations necessary to represent the dynamics of litter and an individual soil layer. Section 3 will analyze model complexity in terms of internal nonlinearities and feedbacks.

The systems of equations describing soil biogeochemical models can be interpreted as dynamical systems (Argyris et al., 1994; Strogatz, 2000; Manzoni et al., 2004) and the number of first order ODEs defines the so-called phase-space dimension of the dynamical system (PSD). When counting the number of ODEs in this

comparison we only consider one soil layer in vertically discrete models to allow the comparison between models with different vertical resolution, and group the relevant variables according to their functional role. We distinguish four groups of variables based on their specific function, variables used to describe i) microbial biomass, ii) soil organic matter substrates, iii) mineralization products (e.g., ammonium and nitrate), and iv) the physical environment (e.g., soil moisture and temperature).

The summary of the analysis of these characteristics from the ~250 models classified in Table A2 is reported in Fig. 2, where the ten-year block averages of the number of variables per soil layer (Fig. 2a) and the relative importance of each functional type of variables are shown (Fig. 2b). Clearly, the increase in computational power in the 1970s was paralleled by an increase in model detail (Shaffer et al., 2001). Since then, the median number of variables stabilized around five, while the variance decreased. This indicates that in the 1970s few models had a very large phase-space dimension (e.g., Patten, 1972; Hunt, 1977; Smith, 1979), while many models were still extremely simple; since the 1980s fewer minimalist models have been proposed, leading to relatively smaller variance in PSD (Fig. 2a). In the last decade, however, some extremely detailed models that include multiple element dynamics and complex biogeochemical interactions have been presented (e.g., Grant, 2001). Today, about 70% of the models have 2–10 variables, and more than 90% have less than 30 variables, including all functional types (Fig. 3a). This suggests that in most cases a relatively small number of variables may be sufficient to describe soil C and N dynamics (in agreement with analyses by Bolker et al., 1998), while a high number of variables may be needed to detail specific processes (e.g., methanogenesis and denitrification in addition to C and N mineralization).



**Fig. 3.** Percentages of models with given number of variables (phase-space dimension, PSD) (a), and with given number of decomposer variables (b). Models based on partial and delay differential equations are indicated by  $\infty$ .



Regarding specifically the number of state variables devoted to microbial biomass, Fig. 2b shows that it has remained proportional to the other functional types (e.g., substrate pools), suggesting that modelers tend to favor a balance between the level of detail in the passive and the biologically active compartments. Nevertheless, the histogram of biomass variables has changed through time (Fig. 3b). In the 1970s, only about 40% of the models explicitly accounted for the decomposers, but 15% had very detailed microbial models (above 10 variables). In contrast, more recently, fewer models do not include any dynamic compartment for the microbial biomass: about 70% have at least one, the majority of which have at most ten, with very few models employing a large number of variables (Fig. 3b). Also, earlier models did not include variables for the physical environment, while today many models consider soil moisture and temperature as dynamic components (Fig. 2b), often by coupling soil water and heat balance equations to the biogeochemical model.

## 2.5. Model complexity across spatial and temporal scales

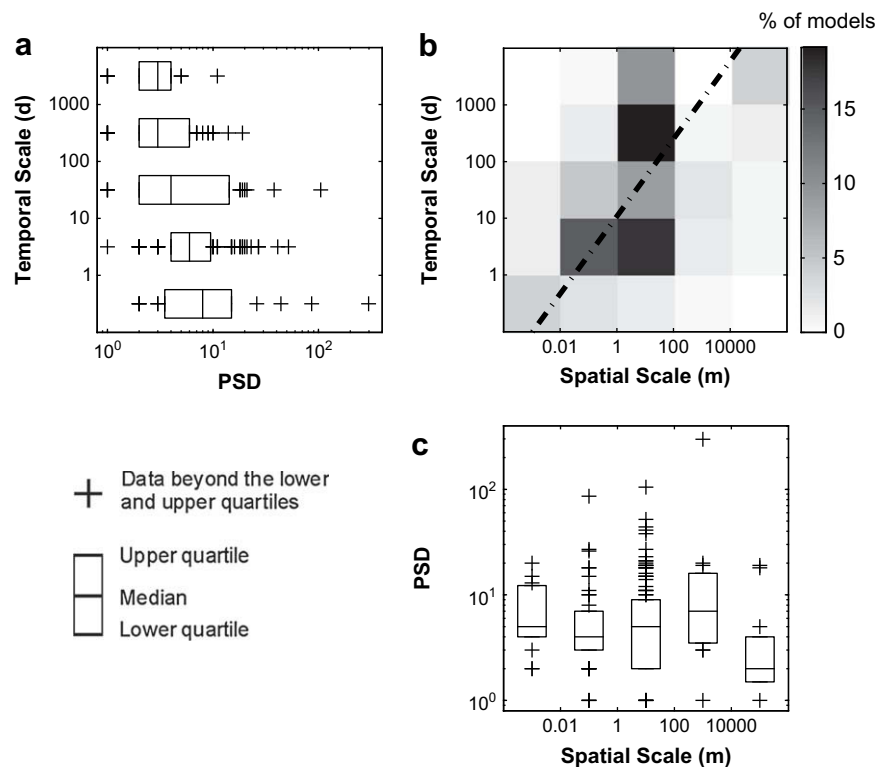
We analyzed the spatial and temporal scales at which each model is interpreted in their typical applications (see Appendix 1 and Table A1 for details), and compared them to the model phase-space dimension (PSD). Fig. 4a shows a clear inverse relationship between the average PSD and the temporal scale of the model, which mirrors the necessity to describe in detail (i.e., with large enough number of variables) highly dynamic small-scale processes. Similarly, Fig. 4c seems to indicate a trend towards lower model complexity (in terms of PSD) for medium-to-large spatial scales, possibly reflecting the use of few highly aggregated variables at those scales. In this regard, McGill (1996) hypothesized that a correlation between spatial and temporal scales of each model

should exist, on the ground that “short time intervals are most appropriate for fine levels of spatial resolution, and that longer time intervals may be valid over coarser spatial scales” (McGill, 1996, p. 119). Despite the large scatter, our results confirm this view (Fig. 4b), showing a highly significant positive correlation between spatial and temporal scales.

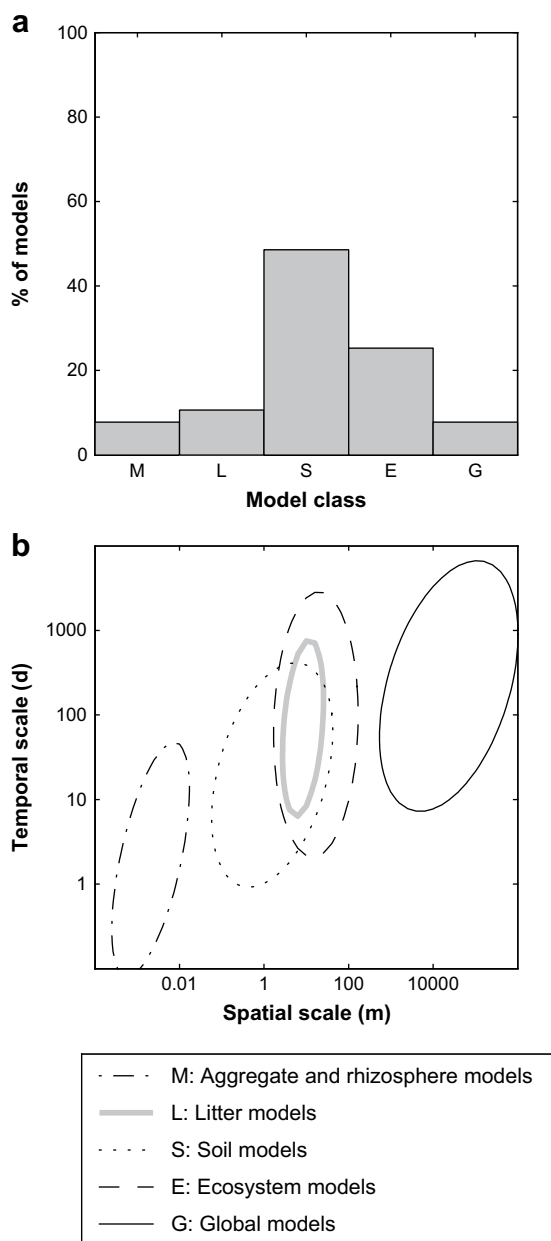
As it will be shown in the next sections, a number of mathematical features tend to be linked more to the field of application than to the spatial and temporal scales at which the models are applied. We denoted these application fields as “classes”, and distinguished among models describing small-scale processes (microbiology, rhizosphere, and aggregate models, indicated by M), plant residue decomposition (L), SOM dynamics (S), coupled soil–plant dynamics (E), and models developed for global-scale applications (G). As shown in Fig. 5a, most models are in class S, and fewer are in classes R, L, and G. These application fields often cover a wide range of spatial or temporal scales (Fig. 5b). Rhizosphere and aggregate models are applied at fine spatial and temporal scales, while litter decomposition and ecosystem models are generally applied at the field scale and at monthly-to-yearly time scales. Models used for global simulations and climate change projections are frequently designed for daily or monthly time scales, and mainly applied on regional domains. This indicates that the temporal resolution is perceived to be more important than the level of spatial detail in such models. Finally, SOM models (S) tend to be used at relatively small spatial scales (up to the field scale), and at daily-to-yearly time scales.

## 2.6. Deterministic vs. stochastic models

Due to the existence of a large number of internal processes, highly intermittent external forcing (e.g., hydroclimatic



**Fig. 4.** Scales and model complexity. (a) Box plots of the phase-space dimension (PSD) as a function of temporal scale in days; (b) percentage of models with given spatial and temporal scales, along with the type II regression line between them (dot-dashed line;  $R = 0.45$ ,  $P < 0.0001$ ); (c) box plots of PSD as a function of spatial scale. Detailed data for each model are reported in Table A2.



**Fig. 5.** (a) Percentage of biogeochemical models in different model classes (see also Table A1 for code explanation); (b) typical spatial and temporal scales of the model classes. Each line marks the ranges of temporal and spatial scales within which 50% of the models in each class lie (assuming that the joint pdf of spatial and temporal scales is lognormal).

fluctuations, disturbance events, etc.), uncertainty in structure and coupling of state variables, and spatial heterogeneity, a detailed description of the soil system would in principle require the use of an extremely high number of variables. However, given the impossibility of achieving such a detailed modeling, it is highly desirable to shift from high-dimensional models (i.e., large PSD and highly fluctuating variables in space and time) to a suitable combination of deterministic variables and random functions or stochastic processes (Katul et al., 2007), thereby providing a more parsimonious and balanced representation of the soil system. At the same time a stochastic representation makes it possible to go beyond a specific simulation and obtain results that are representative of a whole range of environmental conditions or structural features, each leading to a different trajectory for the system. In this

manner, it becomes possible to characterize the model results in term of means, distributions around them, and frequency of extremes in a statistically meaningful way. Hence such models may help assess the role of climatic variability and quantify uncertainties in model projections (D'Odorico et al., 2004). In this section we discuss the use of stochastic terms to account for internal (i.e., structural), spatial, and temporal uncertainties, while we do not consider sensitivity analyses based on Monte Carlo simulations.

Despite the clear need of a stochastic approach, only few biogeochemical models employ stochastic components. Among the few available examples of internal randomness, the Q-model employs a statistical description of the substrate quality to overcome limitations in the uncertainty in model structure (Carpenter, 1981; Bosatta and Ågren, 1985). The quality of the degraded substrate is considered as an internal random variable described by a probability density function (PDF) evolving in time according to dynamic interactions of the substrate with biotic and abiotic factors (Ågren and Bosatta, 1996), and in space along the soil profile according to convective and dispersive mechanisms (Bosatta and Ågren, 1996). As noted before, the use of a PDF to describe the quality evolution in time substitutes with a flexible framework the common compartmental deterministic structure (Fig. 1). Moreover, the continuum decomposability concept has recently been given a theoretical interpretation based on the physical limitations to substrate diffusion in a random porous medium (Forney and Rothman, 2007; Rothman and Forney, 2007). Regarding the use of internal stochastic components to control soil fluxes, the only other example that we found is the individual-based model by Ginovart et al. (2005), where the maximum number of particles that can be assimilated per unit time and unit cell area is a random variable extracted from a normal distribution. All the other models we reviewed compute the fluxes according to deterministic kinetic equations.

There are numerous examples in the literature of randomly distributed parameters to account for spatial variability. In the aggregate-scale model of denitrification developed by Arah and Smith (1989), both aggregate radius and oxygen demand are assumed to be random variables lognormally distributed. Other models based on distributed parameters (Huwe and Totsche, 1995; Whitehead et al., 1998; Acutis et al., 2000; Walter et al., 2003; Botter et al., 2006) account for soil heterogeneity at the field to the landscape scale. We note that also the spatially explicit models that employ advection diffusion equations can be interpreted as macroscopic representations of biased random walk processes at the particle scale and according to this interpretation would belong to the category of stochastic models (O'Brien and Stout, 1978; Darrah, 1991; Elzein and Balesdent, 1995; Bosatta and Ågren, 1996; Bruun et al., 2007; Jenkinson and Coleman, 2008). The model by Walter et al. (2003) accounts for the random spatial variability of SOM content and land use, which in turn drives the litter input into the soil. Also, the temporal change from one land use to another is controlled by a Markov chain in this model.

A few models address the stochastic nature of the climatic forcing (van Veen et al., 1984; Pastor and Post, 1986; Porporato et al., 2003; Botter et al., 2008; Daly et al., 2008; Wang et al., 2009), which affects through soil moisture and temperature the rates of soil biogeochemical fluxes. In the last four papers, for example, rainfall was treated as a marked Poisson process in time. This allows one to assess how the SOM and mineral compartments respond to intermittent wetting events at different time scales and to quantify the propagation of hydrodynamic fluctuations through the system components (D'Odorico et al., 2003). The same stochastic rainfall model has been also recently used to drive a simple basin-scale nitrate transport model (Botter et al., 2006). The statistics of denitrification resulting from stochastic rainfall patterns were

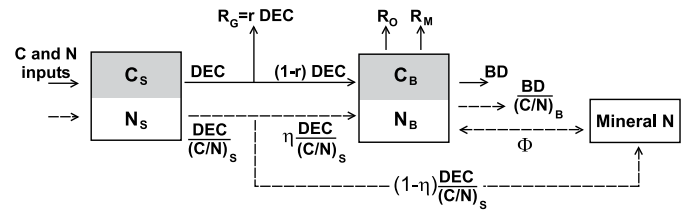
computed by [Ridolfi et al. \(2003\)](#) starting from empirical relationships between denitrification fluxes and soil moisture, but with no dynamic component.

### 3. Modeling decomposition and N mineralization

Most models of soil substrate–decomposer interactions can be cast in a common form in terms of balance equations (Section 3.1), allowing us to track the historic evolution of the mathematical structure of biogeochemical models from the 1930s to the present day. To this purpose we introduce a simplified theoretical framework for the substrate–decomposer dynamics to explain the differences and similarities in the formulations of decomposition (Section 3.2) and nutrient mineralization (Sections 3.3, 3.4; symbols are explained in [Table 1](#), other codes in [Table A1](#)). Using this general framework we review the various models in terms of how they logically and historically collocate themselves with respect to it. We emphasize the laws regulating microbial stoichiometry, which deal with the combination of the structural and nutritional elements allowing the growth of decomposer communities. We further focus on the interplay between carbon, which is the typical energy source for heterotrophs, and nitrogen, often considered to be the most limiting nutrient for soil and litter decomposers. A similar mathematical framework may be used to describe the role of other limiting nutrients, such as phosphorus, potassium, and sulfur ([Smith, 1979](#); [Hunt et al., 1983](#); [Parton et al., 1988](#); [Bosatta and Ågren, 1991](#); [Sinsabaugh and Moorhead, 1994](#); [Cherif and Loreau, 2009](#); [Manzoni et al., under review](#)).

#### 3.1. General microbial biomass balance equations

Because microbial biomass is the driver of most soil carbon and nitrogen cycling, we begin by writing a general form of the microbial C and N balance equations. We consider a simplified soil system where a single compartment of substrate, including both carbon ( $C_s$ ) and nitrogen ( $N_s$ ), is decomposed by the microbial biomass ( $C_B$  and  $N_B$  are microbial carbon and nitrogen concentrations). With reference to [Fig. 6](#), and focusing only on the equations relevant for the microbial dynamics, we can write for the microbial carbon balance



**Fig. 6.** Carbon and nitrogen pools and fluxes in the simplified model of microbial biomass–substrate interactions (Eqs. (1) and (2)). Continuous and dashed lines represent C and N fluxes; gray and blank compartments are the C and N pools, respectively. The microbial biomass compartment and related fluxes are detailed in [Fig. 9](#). The scheme is used to define the specific processes discussed in the text, and is not meant to be the most general model structure for soil C and N models (for example, it does not consider multiple substrates and decomposer populations).

$$\frac{dC_B(t)}{dt} = \text{DEC} - R_G - R_M - R_O - \text{BD}, \quad (1)$$

where DEC is the decomposition flux (discussed in Section 3.2), BD is the microbial decay term;  $R_G$  and  $R_M$  are respectively the growth and maintenance respiration fluxes, while  $R_O$  represents C overflow associated with N-limitation. Growth respiration is generally assumed to be proportional to DEC (i.e.,  $R_G = r \text{ DEC}$ ) and represents the only respiration flux considered in most models (denoted by GRW in [Table A2](#)). Maintenance respiration (MNT) depends on metabolic activities not related to growth and is generally modeled as a linear function of microbial biomass (e.g., [Daufresne and Loreau, 2001](#); [Pansu et al., 2004](#); [Moorhead and Sinsabaugh, 2006](#)). Some models, indicated by G&M in [Table A2](#), consider both growth and maintenance respiration in their microbial biomass balance equations. In contrast to maintenance respiration, the C overflow flux ( $\text{CO}$ ) is defined to accommodate decomposer stoichiometric requirements in conditions of nutrient limitation (sensu [Schimel and Weintraub, 2003](#)), as discussed in Section 3.4.1. Other metabolic processes leading to C overflow (e.g., [Russell and Cook, 1995](#)) are seldom accounted for in soil models and will not be dealt with here. It is important to stress that Eq. (1) illustrates in a simplified way the pathways of C exchange with the decomposer biomass, where each respiration term plays a distinct functional role. This idealization of the metabolic processes occurring at the cell scale allows us to classify the different model formulations that have been proposed.

The flux DEC not only controls C, but also determines the organic N decomposition. In fact, N is generally assumed to follow the C fluxes, as both elements are bound into the organic compounds. As a result, the amounts of C and N made available through decomposition are proportional to the substrate. While C can only be assimilated and recycled through the microbial biomass, or respired (Eq. (1); [Figs. 1 and 6](#)), N dynamics are more complex. N can be directly assimilated in organic forms, mineralized to ammonium and eventually nitrate, or immobilized by the microbes from these mineral pools. Accounting for all these pathways, the microbial N balance can be written as

$$\frac{dN_B(t)}{dt} = \eta \frac{\text{DEC}}{(C/N)_s} - \Phi - \frac{\text{BD}}{(C/N)_B}, \quad (2)$$

where the first term is the organic N assimilation, which depends on the organic N assimilation efficiency  $\eta$  (i.e., the fraction of organic N directly assimilated by the microbes, see Section 3.3). The second term,  $\Phi$ , is the net N flux exchanged between the microbial biomass and the mineral N compartment (Section 3.4), while the last term represents the N losses due to microbial decay.

The overflow respiration and mineralization fluxes are generally defined to ensure a given composition of the microbial biomass,

**Table 1**

Explanation of symbols (see also [Figs. 6 and 9](#)).

Symbol	Description
BD	Microbial biomass decay
$C_B(N_B)$	Microbial carbon (nitrogen) concentration
$C_s(N_s)$	Substrate carbon (nitrogen) concentration
$(C/N)_B$	Microbial C/N ratio
$(C/N)_{CR}$	Critical C/N ratio, defined as $(C/N)_B/(1-r)$
$(C/N)_{IMM}$	Net immobilization threshold, defined as $\eta(C/N)_B/(1-r)$
$(C/N)_{LIM}$	Mineral N-limitation threshold
DEC	Carbon decomposition flux (Eqs. (3)–(5))
$IMM_{gross}$	Gross immobilization (Eq. (8))
$IMM_{max}$	Maximum immobilization
$k_{S,LIN}, k_{S,MULT}, k_{S,MM}$	Decomposition rates for linear, multiplicative, and Michaelis–Menten formulations (Eqs. (4), (5), and (3), respectively)
$K_{MM}$	Michaelis–Menten constant (Eq. (3))
N	Mineral N concentration
$r$	Fraction of DEC that is respired
$R_G$	Growth respiration
$R_M$	Maintenance respiration
$R_O$	C overflow losses (Eq. (10))
$\eta$	Organic N assimilation efficiency
$\phi^{MN}(\phi^{ON})$	Mineral (organic) N inhibition factor (Eqs. (9) and (11), respectively)
$\Phi$	Microbial stoichiometric imbalance (Eq. (7))

which in soils tends to vary within a relatively narrow range of values both across substrate qualities (Cleveland and Liptzin, 2007) and in time (Garcia and Rice, 1994; Jensen et al., 1997). The next sections describe the different formulations used to model each term in Eqs. (1) and (2), and how the different models balance the C and N fluxes according to microbial stoichiometry.

### 3.2. The decomposition function

The definition of the decomposition flux, DEC, is one of the most critical issues in soil C and N models, for it embeds most biotic and abiotic controls on the organic C and N flow towards more stable forms or mineral pools (Manzoni and Porporato, 2007; Wutzler and Reichstein, 2008). Here we follow the more common practice of basing the stoichiometric equations on organic carbon,  $C_S$ , although in some models they are defined as a function of  $N_S$  (Daufresne and Loreau, 2001; Raynaud et al., 2006), or both elements (Smith, 1979; Neill and Gignoux, 2006). Here we focus on the degree of nonlinearity in the decomposition equation, and restrict our attention to decomposition under optimal nutrient conditions, while corrections to DEC due to N-limitation are considered in Section 3.4.1.

Decomposition can be regarded as an enzyme catalyzed reaction, where the C flux from the organic substrate degradation depends on both the substrate and the available enzyme concentration (Schimel and Weintraub, 2003; Fang et al., 2005; Sinsabaugh et al., 2008). These enzymes are produced by the decomposer community, and hence may be assumed to be proportional to the amount of microbial biomass. Accordingly, the Michaelis–Menten equation (MM), often used to describe enzyme catalyzed reaction, is a realistic but parsimonious choice (Panikov and Sizova, 1996; Blagodatsky and Richter, 1998),

$$DEC = k_{S,MM} C_B(t) \frac{C_S(t)}{K_{MM} + C_S(t)}, \quad (3)$$

where  $K_{MM}$  is the Michaelis constant and  $k_{S,MM}$  accounts for the chemical composition of the substrate and the effects of climatic conditions during decomposition.

On the one hand, more complex nonlinear models (NL) have also been adopted, including negative feedbacks due to microbial density (Garnier et al., 2001), or both microbial density and co-metabolism effects (McGill et al., 1981; Hunt et al., 1991). In these cases, however, more parameters are needed and model calibration becomes more difficult. On the other hand, simplified versions of Eq. (3) have been often used as well. In its more drastic simplification it is assumed that either the microbial pool is constant or the substrate concentration is much larger or, in contrast, negligible with respect to  $K_{MM}$ . Thus if  $C_B$  is assumed to change slowly with respect to the substrate, and  $C_S \ll K_{MM}$ , Eq. (3) can be approximated by simple first order rate kinetics (LIN),

$$DEC = k_{S,LIN} C_S(t), \quad (4)$$

where  $k_{S,LIN}$  is the first order decay rate. Eq. (4) has been used since the earliest models describing organic C and N decrease in agricultural systems (Jenny, 1941), or litter and humus accretion in grasslands and forested ecosystems (Nikiforoff, 1936; Olson, 1963). These pioneering works established the paradigm of linear, donor controlled decomposition rate (Table A2), which today still characterizes most biogeochemical models, as shown in Fig. 7 (Dewilgen, 1991; McGill, 1996; Molina and Smith, 1998). The linear model accounts for the substrate chemistry and “provides an excellent first approximation, especially during early stages of decay” (Berg and McLaugherty, 2003, p. 2); however, it completely neglects the role of microbial biomass and its enzymatic products in the decomposition process. In these donor-controlled models the

microbial biomass is thus regarded as “a substrate of decomposition, rather than as a decomposer” (Fang et al., 2005). According to other interpretations, Eq. (4) implicitly assumes that microbial activity changes so quickly that microbial biomass itself is never a limiting factor (Paustian, 1994; Smith et al., 1998), or that physical processes independent of microbial biomass and activity limit decomposition (Rothman and Forney, 2007; Kemmitt et al., 2008).

When microbial responses to environmental stresses or priming effects are involved, Eq. (4) is too simple, and the biotic component of decomposition cannot be neglected (Schimel, 2001; Neill and Gignoux, 2006). In these cases, Eq. (3) can be simplified by only assuming  $C_S \ll K_{MM}$ , while still considering the variability of the microbial biomass. We thus obtain the multiplicative model (MULT),

$$DEC = k_{S,MULT} C_S(t) C_B(t), \quad (5)$$

which includes the basic coupling of both reaction participants (i.e., decomposers and substrate), while being simpler than Eq. (3) (Harte and Kinzig, 1993; Whitmore, 1996b; Porporato et al., 2003; Schimel and Weintraub, 2003; Moore et al., 2005). In Eq. (5) the substrate–decomposer coupling is analogous to a Lotka–Volterra predator–prey interaction, and it may similarly give rise to damped oscillatory dynamics, as sometimes observed in soil variables (Manzoni and Porporato, 2007).

Finally, and differently from the previous simplifications, some models assume that  $C_S \gg K_{MM}$ , thus leading to a model linear with respect to the variable  $C_B$  (LINB). This assumption can be made when the actual limiting factors for decomposition are the microbial enzymes, and not the substrates, as in case of recalcitrant SOM (Fontaine and Barot, 2005). This decomposition formulation is also implicit in steady state models where linear microbial or faunal death rates are used, and implies a top-down control in the detritus food chain (Hunt et al., 1987; Deruiter et al., 1993).

Given the variety of model types employed in the past, it is important to emphasize that the choice of the decomposition model affects the model ability to describe complex dynamics. Linear models, although employing multiple pools, behave like pure decay functions and cannot produce fluctuating dynamics under constant environmental conditions (Bolker et al., 1998; Baisden and Amundson, 2003). Manzoni and Porporato (2007) showed that nonlinear models can describe complex dynamics

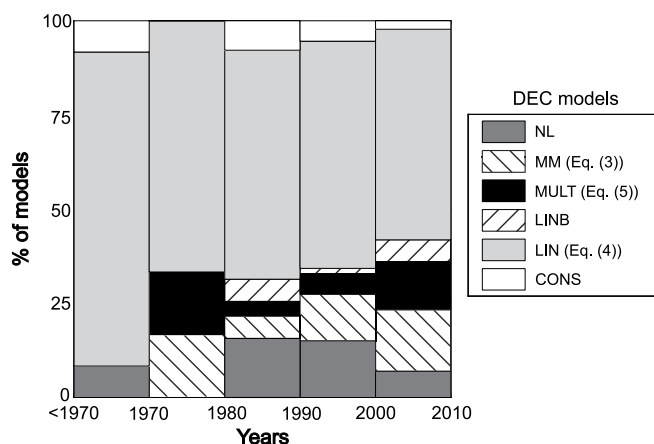


Fig. 7. Historic trends of the percentages of models using different decomposition functions (DEC). CONS, constant decay rate; LIN and LINB, first order rate with respect to the substrate or the microbial biomass, respectively; MULT and MM, multiplicative and Michaelis–Menten formulations, respectively; NL, other nonlinear decomposition equations (see also Table A1; details on the individual models are reported in Table A2).



(e.g., fluctuations) occurring at short time scales when the coupling between substrates and decomposers is particularly strong, as in the rhizosphere (Zelenev et al., 2000).

Historically, linear models have been predominant, although the more recent biogeochemical models often adopt nonlinear or mixed decomposition formulations (Fig. 7). While this tendency mirrors the criticism against the linear decomposition paradigm (Schimel and Weintraub, 2003; Fang et al., 2005; Neill and Gignoux, 2006; Kuzyakov et al., 2009), some recent theoretical considerations and experimental evidence also support the concept of linear, substrate-controlled decomposition (Forney and Rothman, 2007; Rothman and Forney, 2007; Kemmitt et al., 2008). In any case, notwithstanding the trend towards more nonlinear formulations, more than 50% of models developed in the last decade are based on first order decomposition kinetics. Notably, there is also an increase in the use of linear kinetics with respect to the microbial biomass (LINB), which allow analytical tractability (contrary to the nonlinear formulations) while accounting for the role of microbial activity. How decomposition should be modeled remains currently an unresolved issue, and it is likely that the answer is scale-dependent, as discussed in Section 4, and related to the specific purpose of the model.

### 3.3. Mineralization–immobilization pathways

In order to model the mineralization and immobilization fluxes (i.e., the terms  $\eta \text{ DEC}(\text{C/N})_S^{-1}$  and  $\Phi$  in Eq. (2); see also Fig. 6), two alternative schemes have been originally proposed. The first scheme is based on the Mineralization–Immobilization Turnover (MIT) hypothesis, which was developed after early  $^{15}\text{N}$  tracer studies demonstrated the existence of a strong N cycling between organic and the mineral fractions (Kirkham and Bartholomew, 1954, 1955; Jansson, 1958). This scheme assumes that the organic N is transferred to the mineral pool before assimilation by microbes. From a modeling point of view this implies that  $\eta = 0$  and therefore that the only N assimilation pathway available is from the mineral pool through  $\Phi$ . Although at the micro-scale the MIT pathway is not physiologically realistic, because the deamination reactions resulting in ammonium formation are endogenous (Swift et al., 1979), such a recycling may be reasonable at the soil-core scale ( $\approx 10^{-1}$  m), where the heterogeneous distribution of N-rich and N-poor substrates (the former mineralizing N, the latter immobilizing it) may drive strong N recycling (Schimel and Bennett, 2004).

The second alternative scheme more realistically assumes the existence of some direct assimilation of organic N in low weight compounds, namely amino-acids, the N surplus of which is released in mineral form. Accordingly, in Eq. (2),  $\eta = 1$  and all available organic N is directly assimilated prior to mineralization (Direct hypothesis, DIR; Molina et al., 1983). For its simplicity and realism, the DIR scheme became prevalent in biogeochemical models during the 1970s (Fig. 8; Table A2), gradually replacing the MIT scheme.

In real cases, however, a combination of the DIR and MIT pathways is typically observed at the macroscopic level, justifying the adoption of models that employ either one or the other pathway depending on the decomposer group (denoted by MIX), and of the more flexible Parallel scheme (PAR, e.g., Barraclough, 1997; Garnier et al., 2001). In particular, the PAR scheme bridges DIR and MIT by using an organic nitrogen assimilation efficiency  $\eta$  that may take any value between zero (MIT) and one (DIR). Thus, while a fraction  $\eta$  is directly assimilated, the fraction  $(1 - \eta)$  is mineralized without assimilation (Eq. (2); Fig. 6). A derivation of the link between  $\eta$  and soil chemical heterogeneity has been proposed by Manzoni et al. (2008b), who showed that N cycling

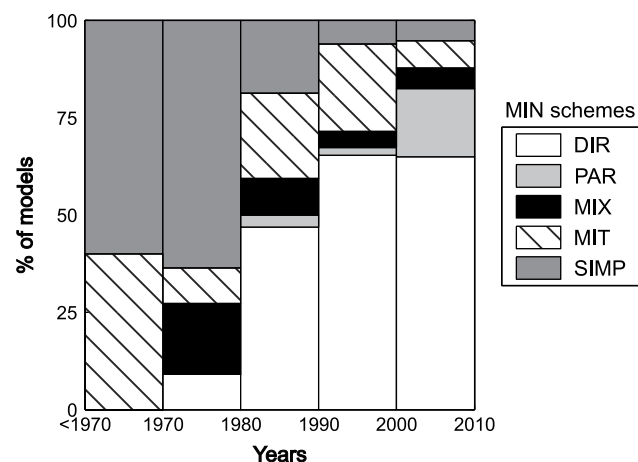


Fig. 8. Historic trends of the percentages of models using different mineralization pathways (MIN). DIR, MIT and PAR: direct, mineralization–immobilization turnover, and parallel schemes, respectively; MIX, other schemes with simultaneous mineralization and immobilization; SIMP, simplified mineralization formulations (see also Table A1; details on the individual models are reported in Table A2).

tends to behave according to the DIR hypothesis in relatively homogeneous soils, while the macroscopic-scale behavior of more heterogeneous soils is better represented by the PAR scheme. The value of  $\eta$  can thus be interpreted as an effect of soil chemical heterogeneity, and the estimated values span the whole range between zero and one (Manzoni and Porporato, 2007; Manzoni et al., 2008b). As it will become clear in the next sections, this value, and thus the structure of N cycling, plays a major role in the microbial C and N balances when inorganic N availability is assumed limited. As shown in Fig. 8, the PAR scheme is becoming increasingly more used.

### 3.4. Modeling microbial stoichiometry

In this section we first describe the basic equations that are commonly employed in biogeochemical models to define the C and N demand of the microbial biomass when  $(\text{C/N})_B$  is assumed to be constant and how they are interpreted to account for a possible imbalance between organic C and N availabilities, with the possible limiting effect of inorganic N (Sections 3.4.1 and 3.4.2). Finally we discuss the effects of flexible microbial elemental composition, i.e.,  $(\text{C/N})_B \neq \text{constant}$  and review the models that adopt this generalization (Section 3.4.3).

#### 3.4.1. Stoichiometry of homeostatic decomposers

Traditionally, in biogeochemical models the microbial biomass has been considered to be strictly homeostatic (i.e., with composition independent of the substrate characteristics; see Sterner and Elser (2002), Cleveland and Liptzin (2007)). In our theoretical framework (Section 3.1) this translates into a constant  $(\text{C/N})_B$ , and hence  $d(\text{C/N})_B/dt = 0$ . Using Eqs. (1) and (2), this implies that the total C input in the microbial pool must be equal to the total N input multiplied by  $(\text{C/N})_B$  (see also Fig. 6), that is

$$(1 - r)\text{DEC} - R_O - R_M = (\text{C/N})_B \left[ \eta \frac{\text{DEC}}{(\text{C/N})_S} - \Phi \right]. \quad (6)$$

Eq. (6) is extremely general and, as it will be shown in the following, can be used to derive specific equations for microbial C and N balances when either organic C or organic N controls microbial growth. Assuming that the decomposition model (DEC) and the

mineralization scheme ( $\eta$ ) have been chosen, and that the microbial parameters  $(C/N)_B$  and  $r$  are known, there are different possible ways (and thus modeling schemes) to ensure constant microbial biomass composition while the substrate N concentration changes. For the sake of simplicity, we will now neglect the maintenance respiration term  $R_M$ , in agreement with some observations (McGill et al., 1981) and as typically done in biogeochemical models (Table A2), and consider only the C overflow fluxes involved in maintaining the decomposer stoichiometric balance. These simplifications allow deriving from Eq. (6) a number of expressions often used in soil models to describe C and N fluxes. We start by discussing the case of relatively high concentration of organic N in the substrate, and then move to progressively lower N availability (i.e., increasing  $(C/N)_S$ , as schematically depicted from top to bottom of Fig. 9).

When  $(C/N)_S$  is relatively low (organic N in excess; top of Fig. 9), carbon limits decomposition, so that no C overflow is necessary ( $R_O = 0$ ). On the contrary, N is in excess, and net N mineralization is needed to keep  $(C/N)_B$  constant and let the microbes grow at a rate controlled by the C decomposition, i.e.,  $(1-r)DEC$ . The N demand for the microbes is thus given by  $(1-r)DEC(C/N)_B^{-1}$ , which is smaller than the amount of organic N assimilated,  $\eta DEC(C/N)_S^{-1}$ . As a result,  $\Phi$  is positive and is computed from Eq. (6) to compensate the excess N, that is,

$$\Phi = DEC \left[ \frac{\eta}{(C/N)_S} - \frac{1}{(C/N)_{CR}} \right], \quad (7)$$

where  $(C/N)_{CR} = (C/N)_B / (1-r)$  is the critical C-to-N ratio of the substrate (Bosatta and Staaf, 1982; Manzoni and Porporato, 2007).

Fig. 10a plots the function  $\Phi/DEC$  from Eq. (7). Clearly, when the N content of the substrate decreases, the excess mineralization is progressively reduced until the threshold  $(C/N)_{IMM} = \eta(C/N)_{CR}$  is reached, corresponding to  $\Phi = 0$ . When the substrate C/N is further increased beyond that threshold (central part of Fig. 9),

$\Phi$  becomes negative and immobilization of mineral N is needed to compensate for the relative scarcity of organic N from the substrate (hatched areas in Fig. 10). Lower organic N assimilation efficiencies  $\eta$  favor immobilization, as more mineral N is needed. When  $\eta = 0$  (MIT) the N demand becomes independent of the substrate, because all N needed for growth is immobilized from the mineral pool (dotted lines in Fig. 10a). The combinations of organic N assimilation efficiency  $\eta$  and substrate C/N leading to net mineralization or immobilization are also illustrated in Fig. 10b. Higher  $\eta$  allows net mineralization at high  $(C/N)_S$ , while mineral N availability controls the onset of mineral N-limitation, as discussed below.

When organic N availability further decreases,  $\Phi$  becomes increasingly negative, and larger amounts of mineral N are extracted from the soil. The mineral N pool, however, is not always able to supply enough N, in which case mineral N-limitation may occur (lower part of Fig. 9; shaded areas in Fig. 10). The threshold of substrate C/N at which N-limitation occurs is defined as  $(C/N)_{LIM}$  (Fig. 10b). Biogeochemical models account for such a limitation in various ways. Commonly, a factor is defined to reduce potential immobilization and decomposition, as a function of the available mineral N (Fig. 11a). Alternatively, a C overflow to eliminate excess C is employed (Fig. 11b). These two modeling approaches are described next.

- *N inhibition hypothesis (INH)*. According to this scheme, immobilization is limited by mineral N availability, and decomposition is reduced to the point that ensures the correct C/N in the flux feeding the biomass pool. To model this mathematically, we follow Manzoni and Porporato (2007) and first define the actual gross immobilization as the product of the potential N demand  $\Phi$  (Eq. (7)) and a reduction coefficient ( $\phi^{MN}$ ) that accounts for mineral N availability (Eq. (9)),

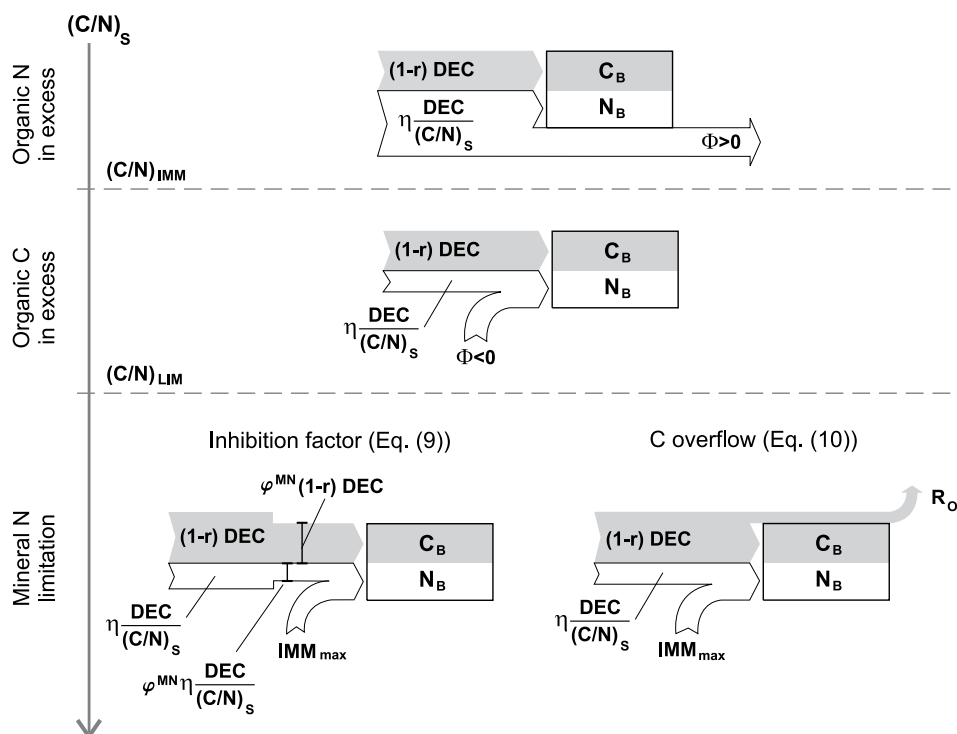
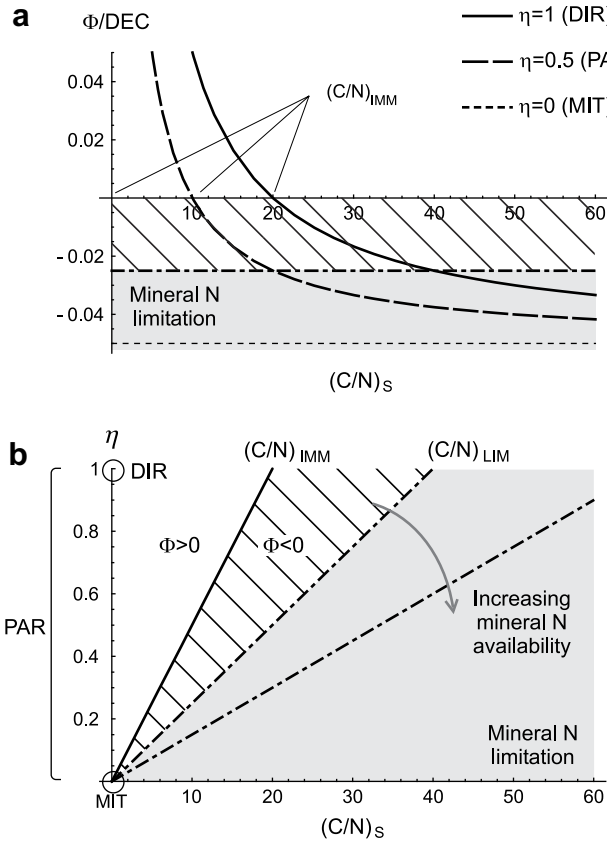


Fig. 9. Conceptual view of the effects of increasing substrate C/N on decomposer stoichiometric models (see also Figs. 10 and 11). Shaded arrows represent the C fluxes, blank arrows the N fluxes; the width of the arrows illustrates the relative importance of C and N fluxes in relation to the decomposer requirement  $(C/N)_B$ .



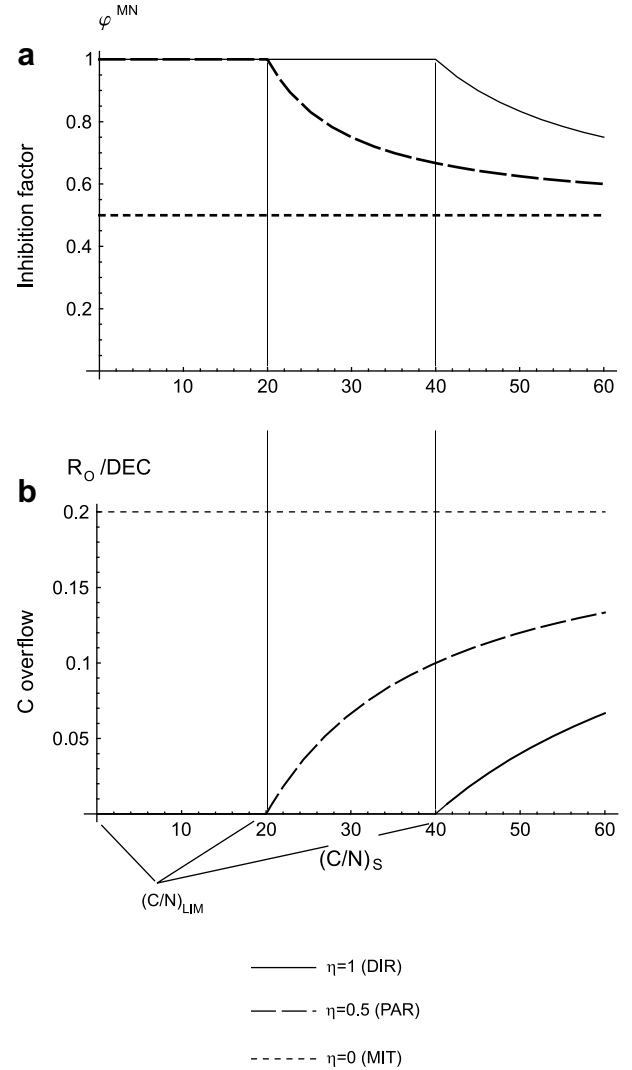
**Fig. 10.** (a) Normalized N imbalance  $\Phi/DEC$  (Eq. (7)) as a function of  $(C/N)_S$  and establishment of mineral N demand ( $-\text{IMM}_{\max} < \Phi < 0$ , hatched area) or limitation ( $\text{IMM}_{\max} < |\Phi|$ , shaded area) for different values of organic N assimilation efficiency  $\eta$ . In (b) the combinations of  $(C/N)_S$  and  $\eta$  that lead to N surplus (when  $\Phi \geq 0$  and  $(C/N)_S \leq (C/N)_{\text{IMM}}$ ), mineral N demand ( $\Phi < 0$  and  $(C/N)_{\text{IMM}} < (C/N)_S \leq (C/N)_{\text{LIM}}$ ), or mineral N-limitation ( $(C/N)_S > (C/N)_{\text{LIM}}$ ) are shown.

$$\text{IMM}_{\text{gross}} = \begin{cases} 0, & \Phi \geq 0 \\ \varphi^{\text{MN}} |\Phi|, & \Phi < 0 \end{cases} \quad (8)$$

Different formulations of gross immobilization can be obtained from the general Eq. (8), depending on the choice of  $\varphi^{\text{MN}}$ . If no control of mineral N on immobilization is considered (i.e.,  $\varphi^{\text{MN}} = 1$ ), immobilization only depends on the potential demand, and microbes are implicitly assumed to always satisfy their N requirements. Certain models assume that immobilization is unrestricted below a maximum gross immobilization threshold,  $\text{IMM}_{\max}$ , while it is N-limited above it.  $\text{IMM}_{\max}$  can be described by linear (Kirkham and Bartholomew, 1955; Hunt, 1977; Parton et al., 1993) or nonlinear kinetic laws, possibly involving also the microbial biomass (McGill et al., 1981; Rastetter et al., 1991; Grant, 2001; Porporato et al., 2003; Tonitto and Powell, 2006). The N content of the organic substrate triggers the switch from one regime to the other, as it controls the N demand in Eq. (7). Hence, following Eq. (8), a general formulation for  $\varphi^{\text{MN}}$  can be given as (Porporato et al., 2003; Manzoni and Porporato, 2007; Fig. 11a)

$$\varphi^{\text{MN}} = \begin{cases} 1, & |\Phi| \leq \text{IMM}_{\max} \\ \frac{\text{IMM}_{\max}}{|\Phi|}, & |\Phi| > \text{IMM}_{\max} \end{cases} \quad (9)$$

The function  $\varphi^{\text{MN}}$  is used as a reduction factor for the decomposition flux DEC. By reducing DEC,  $\varphi^{\text{MN}}$  also decreases the mineral N demand of the microbes (Eq. (7)), thus allowing



**Fig. 11.** (a) Mineral N inhibition factor (Eq. (9)) and (b) C overflow (Eq. (10)), as a function of  $(C/N)_S$  and organic N assimilation efficiency  $\eta$ .

a balanced (although inhibited) C and N assimilation. In these conditions, mineral N becomes the most limiting factor to microbial growth.

A limiting case is represented by models that do not consider the switch mechanism and always assume  $\text{IMM}_{\text{gross}} = \text{IMM}_{\max}$ , regardless of the potential demand  $\Phi$  (Hadas et al., 1987; Thornley and Verberne, 1989; Rastetter et al., 1991; Harte and Kinzig, 1993). In this case, immobilization only depends on the availability of mineral N through  $\text{IMM}_{\max}$ .

- **C overflow hypothesis (CO).** An alternative scheme to model the effects of N-limitation involves C-overflow mechanisms (Fig. 11b). According to this scheme, when immobilization is controlled by the mineral N availability, decomposition is not reduced as in the case of N inhibition, but the excess C assimilated by the microbes is eliminated (Kersebaum and Richter, 1994; Hadas et al., 1998; Schimel and Weintraub, 2003; Raynaud et al., 2006). From a metabolic point of view, such mechanisms involve catabolic  $\text{CO}_2$  production (Russell and Cook, 1995) or polysaccharide excretion (Blagodatsky et al., 1993; Hadas et al., 1998; Neill and Gignoux, 2006), leading to increased losses of C from the microbial cells under

N limiting conditions. The C overflow flux,  $R_O$ , can be easily computed from Eq. (6) as the difference between the assimilated C,  $(1-r)DEC$ , and the C fixed in new biomass thanks to the total incoming N (from both organic and mineral sources, Fig. 11b),

$$R_O = \begin{cases} 0, & |\Phi| \leq IMM_{\max} \\ DEC(1-r) - (C/N)_B \left[ \eta \frac{DEC}{(C/N)_S} + IMM_{\max} \right], & |\Phi| > IMM_{\max} \end{cases} \quad (10)$$

A limiting case is represented by models where  $IMM_{\max} = 0$ , so that the C overflow perfectly balances any demand for mineral N, and immobilization is not necessary (Baisden and Amundson, 2003; Schimel and Weintraub, 2003). Interestingly, in this case, Eq. (10) can be rewritten as  $R_O = (C/N)_B |\Phi|$ , which shows that C overflow and N mineralization fluxes (Eqs. (10) and (7), respectively) are perfectly symmetric representations of similar overflow mechanisms. Mineralization in this context is thus interpreted as N overflow conceptually similar to  $R_O$  (Hunt et al., 1983; Raynaud et al., 2006).

### 3.4.2. Stoichiometry of homeostatic decomposers with preferential assimilation of organic N

The previous section described models where the decomposition fluxes are limited by organic C availability, except for very low organic N concentrations, when mineral N becomes a limiting factor. In this section we discuss a few alternative models that are instead based on the assumption that organic N limits decomposer activity when  $(C/N)_S > (C/N)_{IMM}$  (Parnas, 1976; Bosatta and Berendse, 1984), possibly in co-limitation with mineral N (Parnas, 1975; Berendse et al., 1987). For simplicity, here we neglect mineral N immobilization, and focus on the effect of organic N availability only.

From a mathematical point of view, we compute the C demand depending on the available organic N as  $\eta DEC (C/N)_B (C/N)_S^{-1}$ , and compare it with the larger flux  $(1-r)DEC$  that would be potentially used for biomass growth. The difference between the two is C in stoichiometric excess, which cannot be assimilated if  $(C/N)_B$  is to remain constant. For  $(C/N)_B$  to be constant, a decoupling of C and N decomposition is necessary, where organic N is preferentially decomposed and assimilated, while C decomposition is slowed (Parnas, 1975; Sinsabaugh and Moorhead, 1994). Similar to the inhibition mechanisms discussed in Section 3.4.1, a factor  $\varphi^{ON}$  is thus defined to decrease the potential C decomposition to  $\eta DEC (C/N)_B (C/N)_S^{-1}$ ,

$$\varphi^{ON} = \begin{cases} 1, & \Phi \geq 0 \\ \frac{\eta (C/N)_B}{(1-r)(C/N)_S}, & \Phi < 0 \end{cases} \quad (11)$$

Fig. 12 shows how  $\varphi^{ON}$  changes with substrate N content and organic N assimilation efficiency. The decrease of  $\varphi^{ON}$  is triggered by lower  $(C/N)_S$ , in contrast to  $\varphi^{MN}$  (Eq. (9); Fig. 12), so that DEC is reduced earlier along the  $(C/N)_S$  gradient. Also, the lower  $\eta$  the stronger the inhibition effect, because more N is routed towards the mineral pool. Using the MIT scheme the organic N assimilation efficiency is zero, so that  $\varphi^{ON} = 0$  and microbial activity is completely (and obviously unrealistically) halted. The few models that employ  $\varphi^{ON}$  either assume  $\eta = 1$  (Bosatta and Berendse, 1984), or allow some mineral N immobilization (dashed arrow in Fig. 12; Parnas, 1975; Berendse et al., 1987). This N-limitation scheme has been seldom used in biogeochemical models, despite the fact that it does not need additional parameters and that its performance could be easily tested against the classical models that only consider the effects of mineral N (Section 3.4.1).

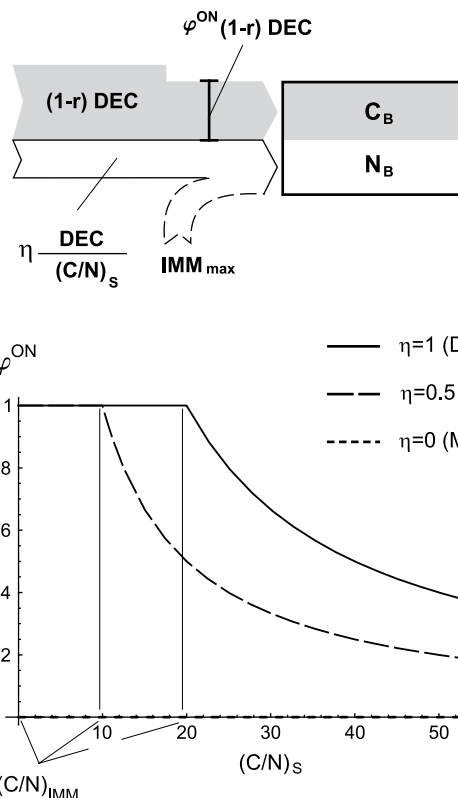


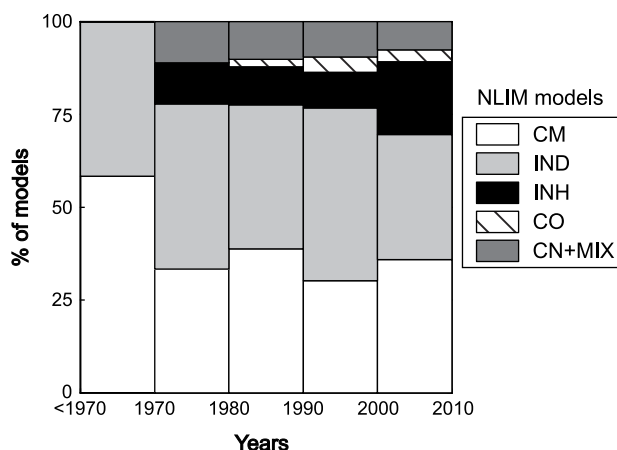
Fig. 12. Top, schematic representation of the effect of the inhibition factor  $\varphi^{ON}$  (Eq. (11)) on DEC. Bottom,  $\varphi^{ON}$  as a function of  $(C/N)_S$  and organic N assimilation efficiency  $\eta$ . The dashed arrow indicates possible mineral N immobilization, in co-limitation with organic N availability.

Alternatively, one might assume that C overflow occurs in response to limited organic N. The C overflow flux in this case is computed following Eq. (10) with  $IMM_{\max} = 0$ , as discussed in Section 3.4.1, or by changing the C use efficiency  $(1-r)$ . Recently, Manzoni et al. (2008a) showed how the C use efficiency of plant detritus decomposers decreases with decreasing litter initial N content in different ecosystems. This suggests that increased C losses, possibly related to C-overflow mechanisms, might be a widespread decomposer response to low-N substrates.

### 3.4.3. Stoichiometry of decomposers with variable $(C/N)_B$

Some models assume that the decomposer biomass is not strictly homeostatic and hence  $(C/N)_B$  may change in time, in response to nutrient availability or following microbial succession during decomposition. Accordingly, they assume that  $(C/N)_B$  can vary in response to imbalanced C and N sources (Fig. 13, indicated by CN; see details in Table A2). Two alternative schemes have been implemented. The first is based on the idea that as soon as the C and N decomposition fluxes are not suitably balanced, the elemental composition of microbial biomass changes, resulting in turn in altered mineralization and immobilization fluxes (Smith, 1979; McGill et al., 1981; Knapp et al., 1983; Hunt et al., 1991; Korsaeht et al., 2001). In the alternative scheme, mineral N controls  $(C/N)_B$  according to a negative feedback scheme. In this case, the altered  $(C/N)_B$  compensates the elemental imbalance by decreasing the demand for the more limiting element (van Veen et al., 1984; Grant et al., 1993; Parton et al., 1993; Del Grosso et al., 2001; McMurtrie et al., 2001). Finally, some models combine flexible  $(C/N)_B$  and inhibition factors, leading to more complicated formulations (Hunt et al., 1983; Paustian and Schnurer, 1987).





**Fig. 13.** Historic trends of the percentages of models using the different N-limitation schemes (NLIM), including C-only models (CM). IND, no N-limitation; INH, inhibition factor; CO, carbon losses in response to N-limitation; CN, variable microbial or substrate C/N; MIX, multiple formulations are simultaneously used (see also Table A1; details on the individual models are reported in Table A2).

It should be noted that in general  $(C/N)_B$  is only allowed to fluctuate within a relatively restricted range of values (realistically between about 5 and 15), so that the relatively small decomposer biomass has only limited capacity to compensate for large fluctuations in substrate C/N. For this reason, in most applications it is reasonable to assume constant  $(C/N)_B$ .

#### 3.4.4. Historical evolution of N-limitation models

Fig. 13 summarizes the historic evolution of the different N-limitation schemes (see also Table A2). The figure shows that the number of models that neglect N dynamics (CM) has been decreasing in time, while different formulations of N-limitation are more frequently used. However, not all the N models include the effects of mineral N-limitation, so that microbial activity and decomposition are often independent of mineral N availability (indicated by IND). Among the models considering N-limitation effects, most use inhibition factors similar to  $\phi^{MN}$  and  $\phi^{ON}$  (INH), others assume that nitrogen shortage increases the C/N ratios of microbes or substrate (CN; see Section 3.4.3), while only fewer recent approaches include C-overflow mechanisms (CO). The choice of the microbial stoichiometry model, however, has important consequences. If a model neglects the overflow mechanisms, it may underestimate the heterotrophic respiration rate, while it might overestimate microbial activity and decomposition rates, when neglecting the inhibition mechanisms. To our knowledge, no model accounts for both N inhibition and C-overflow mechanisms, although it seems likely that they both occur in reality.

### 4. Nonlinearities and mineralization pathways in relation to scale

In this section we discuss the relationships between decomposition, mineralization and mineral N-limitation formulations in relation to the spatial and temporal scales at which the reviewed models are applied (Fig. 14) and in relation to the model class (Fig. 15).

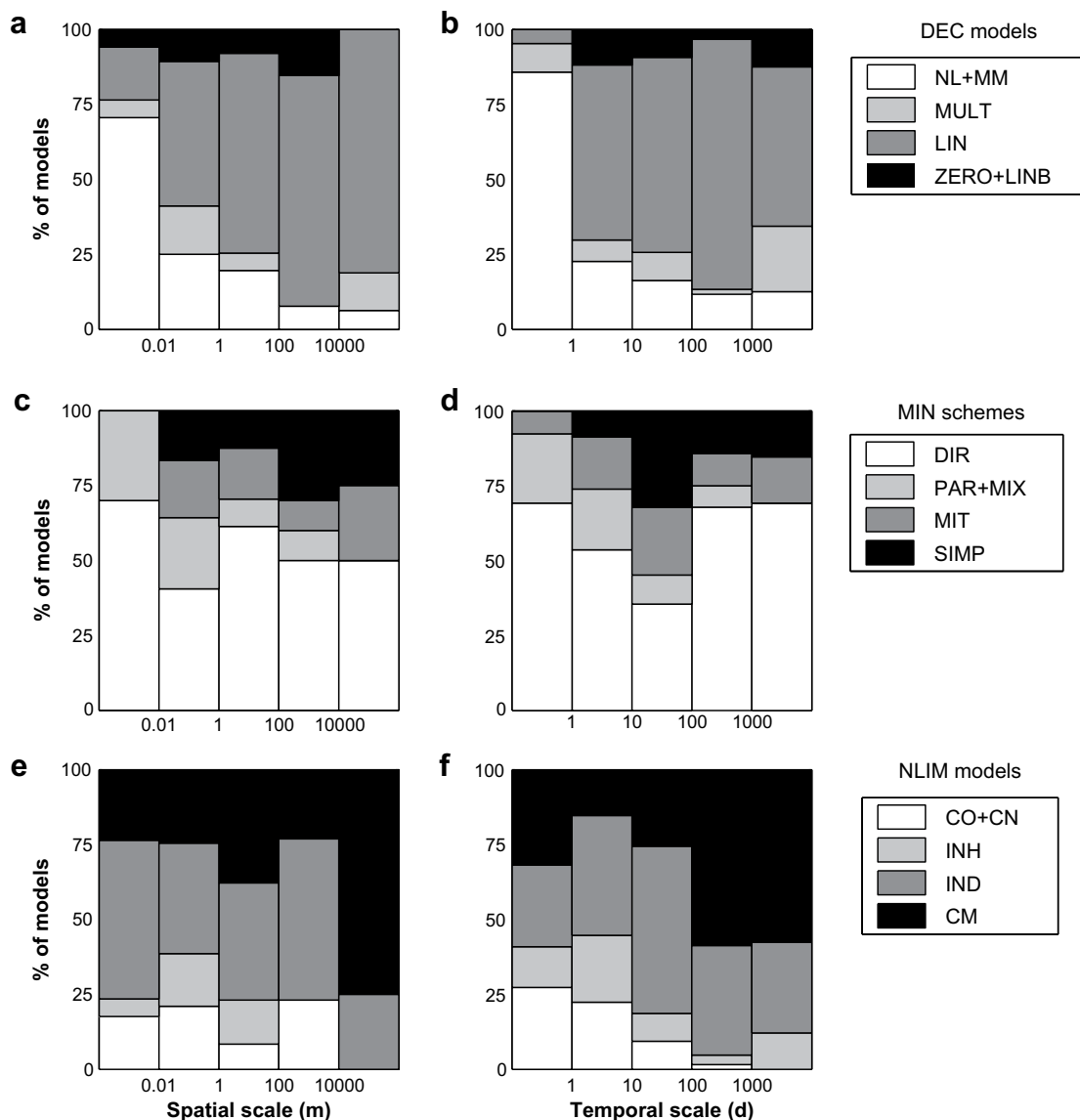
Given the complexity and hierarchical structure of the soil system, it is natural that several scale-specific processes regulate SOM dynamics (McGill, 1996). For example, decomposer–substrate interactions result in fluctuations of microbial biomass under constant environmental conditions only at fine scales, e.g., in the

highly active rhizosphere environment and at hourly-to-daily time scales, as shown by Zelenev et al. (2000, 2006). On the contrary, oscillations are not generally observed during long-term incubations of larger soil samples, where organic matter and microbial biomass are homogeneously distributed (e.g., Whitmore, 1996b; Petersen et al., 2005b). As these oscillating dynamics are better described by nonlinear models (Manzoni and Porporato, 2007), it seems important to choose the model formulation according to the scale of interest. This has often not been the case in the literature, as biogeochemical models with similar structure and formulations have been used across scales with no or very little modification.

Paustian (1994) pointed out that the question of whether decomposition should be explicitly coupled with microbial biomass dynamics may be dependent on the scale of interest. He suggested that at yearly or longer time scales climatic factors predominate, a fact that would justify neglecting the microbial dynamics at such long time scales. Accordingly, simple linear decomposition functions and fewer variables describing microbial biomass may be suitable at long time scales, while nonlinear models and explicit description of the biologic components may become necessary at short scales (Schimel, 2001; Manzoni and Porporato, 2007). Simple models for long-term analyses could be derived from more complex short-term models by successive approximations. Similar considerations may be drawn regarding spatial scales, that is, the smaller the scale, the more detailed the microbial components and the description of their nonlinear relationships with the substrates. We can thus hypothesize that decomposition formulations could be ordered according to their suitability to increasingly large (or long) scales starting from the more nonlinear (NL, MM) to the linear and zero order ones (LIN, CONS). As shown in Figs. 14a, b, and 15a, models developed for fine-scale analyses (predominantly M class) preferentially employ highly nonlinear decomposition formulations. On the contrary, most biogeochemical models at landscape or larger spatial scales, including global scale models (G), are linear. Most litter (L) and ecosystem (E) models, typically interpreted at the daily-to-annual time scale (Fig. 5), are also linear. These trends are in agreement with the above hypothesis, suggesting a general consensus regarding the effects of scale on the decomposition function.

Recently, Manzoni et al. (2008b) suggested that the N mineralization parameterization also is scale-dependent. The DIR hypothesis seems more suitable to describe dynamics at the microscopic scale, while PAR and mixed (MIX) model schemes and the limit case, the MIT pathway, capture the macroscopic N cycling patterns (Manzoni et al., 2008b). In principle, we might also expect that more sophisticated methods to compute N-limitation feedbacks may be needed at fine scales, where nutrient availability may vary strongly in space and time. Accordingly, carbon overflow (CO, Eq. (10)) or N-limitation effects on microbial or substrate stoichiometry (CN, see Section 3.4.3) would be suitable at small scales, while the somewhat simpler inhibition factors (INH, Eq. (9)) would suffice at larger scales. In long-term studies, N-limitation for the microbial biomass might even be neglected (IND), or C-only models (CM) could be used, because at such scales positive net mineralization is predominant.

Despite these logical hypotheses, Fig. 14c and d respectively shows the lack of correlation between mineralization pathways and spatial and temporal scales, due to the widespread use of the DIR scheme across scales. Similarly, Fig. 14e and f highlights a weak correlation between the mineral N limitation scheme and scale, with the exception of the complex CO and CN formulations, predominantly used at fine scales (as hypothesized above). Most of the global scale models are based on the DIR hypothesis (Fig. 15b) and they typically do not model either N dynamics or N-limitation effects (Fig. 15c). Litter decomposition models are often used at scales comparable to the ecosystem models (Fig. 5) and both



**Fig. 14.** Percentages of models using different decomposition (DEC; upper panels), mineralization (MIN, central panels), and mineral N-limitation formulations (NLM, bottom panels; see code descriptions in Table A1), at different spatial and temporal scales (left and right panels, respectively). DEC, MIN, and NLM are represented in darker tones according to their hypothesized suitability to increasingly larger scales (see text for details).

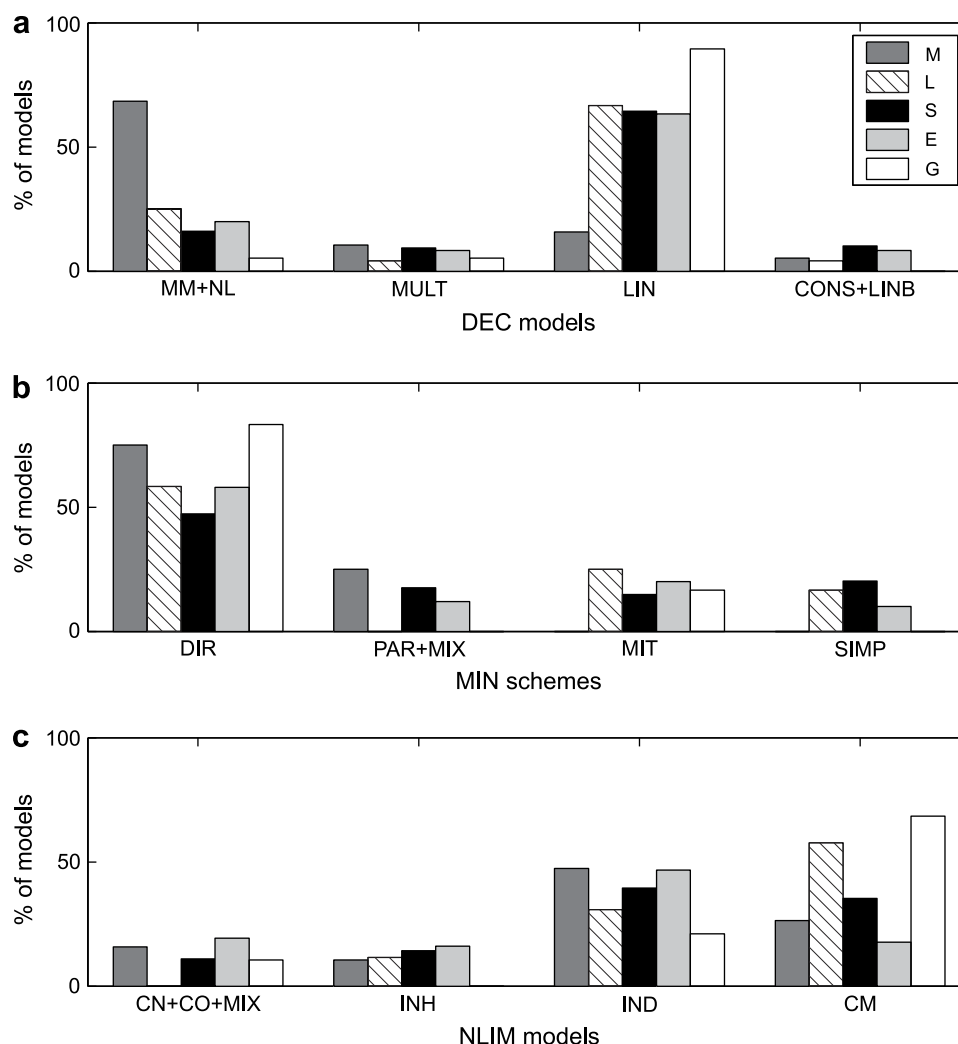
generally employ the DIR scheme as well. Less than 40% of models in each class consider N-limitation effects (Fig. 15c), suggesting that in most cases inorganic nutrients are only considered a product of the decomposition process. Hence, it seems that no consensus regarding the modeling of soil N cycling across scales and model classes has been reached. The DIR scheme has been particularly successful, although it may underestimate N immobilization in lumped models at the soil-core (or larger) scale (Manzoni et al., 2008b). Thus, when the DIR scheme is applied at these higher levels of aggregation it needs to be complemented by more detailed chemical characterization of the soil substrates and the corresponding decomposers (multi-compartment approach) in order to capture the N recycling between compartments of contrasting nutrient concentration.

## 5. Future directions and conclusions

According to our database (Table A2), the number of soil C and N models is increasing at a 6% annual rate (Fig. 16). Most new models

are improvements over earlier ones, leading to many similar model structures and formulations. These mathematical features have changed slowly in time (see Figs. 3, 7, 8, and 13). While this has generally produced more robust and effective models (as shown by model inter-comparisons and validation studies), on the other hand, it may have hindered significant theoretical advances and shifted attention from some important questions that have therefore remained unexplored. We thus conclude our review by discussing some of these theoretical gaps and suggesting how they could be addressed by future modeling efforts.

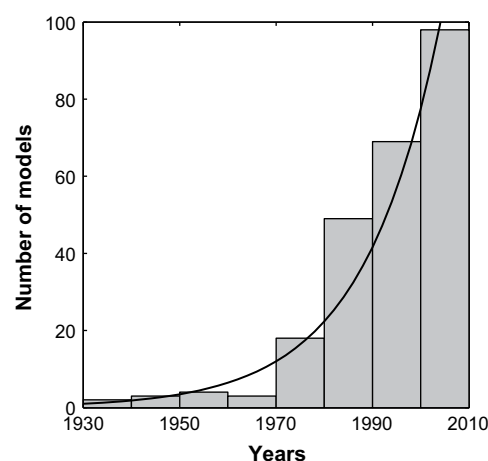
A more mechanistic and scale-dependent description of microbial biomass and activity had been advocated by Paustian (1994) and McGill (1996). Since then, models have been using increasingly detailed formulations of decomposer biomass and its relationships with organic substrates and inorganic nutrients (Figs. 7 and 13), but further efforts in this direction are certainly necessary. For example, characterizing of the level of microbial activity through dedicated state variables, and not only the amount of microbial biomass, is fundamental to describe transient flushes in



**Fig. 15.** Percentages of models in each model class (Fig. 5; Table 1A) using different decomposition (a), mineralization (b), and N-limitation formulations (c). DEC, MIN, and NLIM formulations are shown from left to right in order of suitability to increasingly larger scales.

response to environmental fluctuations (Bar et al., 2002; Schwinning and Sala, 2004) or substrate supply (Blagodatsky and Richter, 1998). Similarly, explicitly including stoichiometric theory into soil models at all scales is important to better link decomposer activity and metabolism, nutrient availability, vegetation growth, and climate dynamics (Sterner and Elser, 2002; Cherif and Loreau, 2007; Cleveland and Liptzin, 2007; Manzoni et al., 2008a; Sinsabaugh et al., 2008). Neglecting C overflow and respiratory pathways that become important under N limiting conditions (Section 3.4) may lead to underestimate the soil C efflux to the atmosphere, with potential implications in estimating global-scale climate change scenarios (Manzoni et al., 2008a). Within the context of properly representing the biological degradation drivers, a shift is needed in the way soil fauna is considered. Its role is “generally believed to be one mainly of assisting in mechanical disintegration” (Smith, 1979, p. 585), and such a viewpoint remains somehow paradigmatic (Paustian, 1994; Smith et al., 1998), despite evidence that all the elements of such food webs should be considered in their specificity (Beare et al., 1995; Osler and Sommerkorn, 2007). Very few works have attempted a description of the whole soil food web dynamics (Hunt et al., 1987; Hunt et al., 1991; Deruiter et al., 1993), also because modeling a complete soil food web easily leads to extremely complicated models, which tend to be site-specific and difficult to calibrate. As a result, modelers have often fallen back on

the use of aggregated variables for soil biota and microbial biomass: it is important however that the potential errors during these aggregation exercises are quantified, to understand which



**Fig. 16.** Temporal trend in the number of soil C and N models; the solid line is the exponential least square regression of the data, indicating a 6% increase per year.

functional characteristics of the biotic component need to be explicitly maintained.

A second major gap is the lack of mechanistic representations of small-scale processes. Most models describe soil biogeochemistry at core-to-field spatial scales and daily-to-monthly time scales (Fig. 4). Their mathematical formulations are mainly empirical and not rigorously derived from biochemical and physical constraints at the pore-scale, where the processes driving SOM degradation, mineralization, and stabilization occur (Blanco-Canqui and Lal, 2004; Six et al., 2004). Similarly, accounting for spatial heterogeneity at the landscape-to-regional-scale is necessary to make models suitable for global-scale applications (McGill, 1996).

Semi-empirical relationships are used to complement theoretical equations and develop predictive models at the desired scale (Del Grosso et al., 2001). While such an approach may effectively account for the small-scale processes in specific cases, it cannot remain purely empirical, if it is meant to provide the generality needed for long-term projections under different conditions. One way to proceed is by using individual-based models (Allison, 2005; Ginovart et al., 2005; Masse et al., 2007), from which macroscopic patterns may be inferred. Another way (frequently employed in hydrology and fluid dynamics) is by developing coupled transport and biological reaction equations accounting for physical heterogeneity, and biological, stoichiometric, and thermodynamic constraints (e.g., Westerhoff et al., 1982). While stoichiometric theory is already embedded in many soil biogeochemical models, only sporadic attempts have been made to explicitly describe biological reactions in the physically and chemically heterogeneous soil micro-environment, and derive kinetic equations valid at the soil-core scale from  $\mu\text{m}$ -to- $\text{mm}$  scale processes. The extremely large number of complex biogeochemical and physical processes is daunting (Young and Crawford, 2004; Ahuja et al., 2006) and has so far discouraged more systematic endeavors at modeling biogeochemical cycles based on first principles. For example, the existing models of aggregate turnover that are based on first-order mass transfer among aggregate classes do not attempt to mechanistically describe such dynamics and the SOM-microbial-mineral soil coupling (Plante et al., 2002; De Gryze et al., 2006). On the other hand, more physically sound biogeochemical models at the pore-scale are often based on aggregate functional units which do not evolve in time, but only provide a particular micro-environment for microbial processes (Arah and Smith, 1989; Leffelaar, 1993). Similarly, models describing biologically and chemically active interfaces consider such physical discontinuities static in time (e.g., soil pore, rhizosphere, and detritusphere interfaces; Toal et al. (2000), Kuka et al. (2007), and Ingwersen et al. (2008)). As a result, physical processes recognized to affect soil structural properties (e.g., tillage, wetting-drying cycles, and aggregate turnover) are not included in biogeochemical models although they likely affect C stabilization, microbial function, and substrate, nutrient, and water redistribution (Sollins et al., 1996; Six et al., 2004; von Luetzow et al., 2008).

This tendency to neglect small-scale physical processes has somewhat changed recently. Starting from probabilistic considerations on enzyme-substrate interactions in heterogeneous environments, Rothman and Forney (2007) derived a core-scale decomposition equation for marine sediments, which has been successfully applied to litter and SOM degradation (Forney and Rothman, 2007). They found that when substrate diffusion is limiting and microbial biomass can be assumed stationary, a continuum of first order decomposition rates well captures the long-term decomposition patterns, in agreement with earlier studies (Carpenter, 1981; Bosatta and Ågren, 1985). Similar approaches where both transport and biological reaction are accounted for (e.g., Liu, 2007) would help understand under which conditions and at which scales the decomposition equations should

be linear or nonlinear (discussed in Section 3.2), thus reconciling these two different viewpoints.

As discussed throughout this review, the tendency of more recent models towards more sophisticated (and generally more mathematically complex) approaches is not always paralleled by improved model performance or ability to interpret observed patterns. Simple models based on physically and biologically based variables and parameterizations often provide equal or better insights in soil and litter dynamics than complex ones. Perhaps a little bit paradoxically, we hope that by advocating a more mechanistic representation of complex physical and biological processes from first principles, we will end up with simpler and more general, highly aggregated formulations, possibly leading to analytically tractable models, as opposed to a large number (Fig. 16) of specific and complicated models (Ågren and Bosatta, 1990).

To conclude, “further inquiry into the scale-dependence and cross-scale adaptability of models is warranted” (McGill, 1996, p. 120). Scaling up pore-scale coupled biogeochemical and physical dynamics to the scale typical of observations is the way to spur novel modeling approaches and provide new insights into plant residue and soil organic matter dynamics.

**Table A1**

Description of codes in Table A2. NA indicates processes that are not included in the model or not clearly defined in the literature source.

Codes	Description
<b>CL</b>	<b>Model class</b>
M	Soil microbiology, soil aggregate, and rhizosphere models
L	Litter decomposition model
S	Soil model with no dynamic vegetation components
E	Coupled soil-plant dynamic model
G	Coupled soil-plant-atmosphere model for global applications
<b>SS</b>	<b>Spatial scale</b>
1	$< 10^{-2}$ m
2	$10^{-2} - 10^0$ m
3	$10^0 - 10^2$ m
4	$10^2 - 10^4$ m
5	$> 10^4$ m
<b>TS</b>	<b>Temporal scale</b>
1	$< 10^0$ days
2	$10^0 - 10^1$ days
3	$10^1 - 10^2$ days
4	$10^2 - 10^3$ days
5	$> 10^3$ days
<b>PSD</b>	<b>Phase-space dimension</b> (Section 2)
<b>MB</b>	<b>Number of variables for decomposers</b> (Section 2)
<b>RESP</b>	<b>Respiration model</b> (Sections 3.1 and 3.4)
GRW	Growth respiration
MNT	Maintenance respiration
G&M	Both growth and maintenance respiration
CO	Respiration defined to compensate stoichiometric imbalances
<b>DEC</b>	<b>Decomposition model</b> (Section 3.2)
CONS	Constant rate
LIN	Linear model with respect to $C_s$ (Eq. (4))
LINB	Linear model with respect to $C_B$
MULT	Multiplicative model (Eq. (5))
MM	Michaelis-Menten model (Eq. (3))
NL	Other nonlinear or mixed formulations
<b>MIN</b>	<b>Mineralization scheme</b> (Section 3.3)
DIR	Direct hypothesis
MIT	Mineralization-Immobilization Turnover
PAR	Parallel hypothesis
MIX	Other schemes with simultaneous mineralization and immobilization
SIMP	Simplified model or regression equation (no microbial stoichiometry)
<b>NLIM</b>	<b>N-limitation model</b> (Section 3.4)
CM	C-only (or dry weight-only) models neglecting N dynamics
IND	No N-limitation
INH	Inhibition factors (Eq. (9) and (11))
CO	Carbon overflow (Eq. (10))
CN	N-limitation effects on microbial or substrate C/N (Section 3.4.3)
MIX	Multiple N-limitation effects are considered



**Table A2**

Main features of the reviewed models (see Table A1 for code descriptions). When different model versions are described in the same source, the characteristics of each one are given.

Model	Reference	CL	SS	TS	PSD	MB	RESP	DEC	MIN	NLIM	Notes
–	Salter and Green (1933)	S	3	4	1	0	NA	LIN	SIMP	CM-IND	Simple C or N loss equations
–	Nikiforoff (1936)	S	3	4	1	0	NA	LIN	NA	CM	
–	Jenny (1941)	S	3	4	1	0	NA	LIN	SIMP	IND	
–	Henin and Dupuis (1945)	S	3	3	1	0	NA	LIN	NA	CM	<sup>15</sup> N model
–	Jenny et al. (1949)	L	3	4	1	0	NA	LIN	NA	CM	
–	Kirkham and Bartholomew (1954)	S	2	2	2	0	NA	CONS	MIT	IND	
–	Kirkham and Bartholomew (1955)	S	2	2	2	0	NA	LIN	MIT	IND	<sup>15</sup> N model
–	Eriksson and Welander (1956)	G	5	5	1	0	NA	NL	NA	CM	C isotope model
–	Craig (1957)	G	5	5	1	0	NA	LIN	NA	CM	
–	Olson (1963)	L	3	4	1	0	NA	LIN	NA	CM	
–	Russell (1964)	S	3	3	1	0	NA	LIN	SIMP	IND	N-only model
–	Minderman (1968)	L	3	4	1	0	NA	LIN	NA	CM	
–	Stanford and Smith (1972)	S	2	3	1	0	NA	LIN-MULT	SIMP	IND	
PWNEE	Patten (1972)	E	3	3	19	16	NA	LIN	SIMP	IND	Soil food web model
–	Beek and Frissel (1973)	S	3	2	11	2	GRW	LIN	MIT	INH	
ABISKO	Bunnell and Dowding (1974)	E	3	2	6	0	NA	LIN	NA	CM	Soil food web model
–	Mehran and Tanji (1974)	S	2	2	5	0	NA	LIN	SIMP	IND	
ABISKO II	Bunnell and Scoullar (1975)	E	3	2	9	0	NA	LIN	NA	CM	Soil food web model
–	Harte and Levy (1975)	E-G	5	5	2–3	1	GRW	MULT	SIMP	IND	
–	Parnas (1975)	S	2	2	4	0	GRW	MM	MIX	CN	Mineral and organic N co-limitation
–	Russell (1975)	E	3	3	1	0	NA	LIN	SIMP	IND	
–	Parnas (1976)	M	1	1	2	0	NA	MM	NA	IND	Organic N control (Eq. (11))
ELM	Hunt (1977), Reuss and Innis (1977)	E	3	2	18	2	G&M	LIN	DIR	INH	
RothC	Jenkinson and Rayner (1977)	S	3	4	5	1	GRW	LIN	NA	CM	Continuous soil profile model Includes P and K dynamics <sup>13</sup> C model N-only model Continuum-quality model
–	Aber et al. (1978)	L	3	4	7	0	NA	LIN	SIMP	IND	
–	Holland (1978)	G	5	4	1	0	NA	LIN	NA	CM	
–	O'Brien and Stout (1978)	S	3	4	1	0	GRW	LIN	NA	CM	
–	Smith (1979)	E	3	3	38	12	G&M	MM	MIX	CN	
–	Bolin (1981)	G	5	4	2	0	NA	LIN	NA	CM	
–	Bosatta (1981)	S	3	3	3	1	NA	LIN	PAR	IND	
–	Carpenter (1981)	S	2	3	∞	0	NA	LIN	NA	CM	
–	Emanuel et al. (1981)	G	5	4	2	0	NA	LIN	NA	CM	
PHOENIX	McGill et al. (1981)	E	3	2	18	4	G&M	NL	DIR	CN	
PAPRAN	Seligman and Van Keulen (1981)	E	3	2	42	0	GRW	NL	MIT	MIX	Litter cohort model Includes P and S N fixation balances N-limitation Mineralization functions based on Seligman and Van Keulen (1981), stochastic climatic forcing Organic N control (Eq. (11))
–	Svirezhev and Tarko (1981)	G	5	5	4	0	NA	LIN	NA	CM	
–	van Veen and Paul (1981)	L-S	2	2–4	5–12	1	GRW	LIN	NA	CM	
–	Bosatta and Staaf (1982)	L	3	4	3	1	GRW	LIN	DIR	IND	
–	Furniss et al., (1982)	L	3	3	105	0	GRW	LIN	NA	CM	
–	Hunt et al. (1983)	S	3	2	52	22	G&M	NL	DIR	CN	
–	Knapp et al. (1983)	S	2	1	7	4	G&M	MULT	MIT	CN	
NCSOIL	Molina et al. (1983)	S	2	2	7	2	GRW	LIN	DIR	INH	
EPIC	Williams et al. (1984), Jones et al. (1984)	E	3	2	72	0	GRW	NL	MIT	MIX	
–	Bosatta and Berendse (1984)	S	2	3	2	0	GRW	MULT	DIR	CO	
–	Janssen (1984)	L	3	4	1	0	NA	LIN	NA	CM	N-only model
–	Juma et al. (1984)	S	2	3	1	0	NA	CONS-NL	SIMP	IND	
–	Van veen et al. (1984)	S	2	2	18	2	GRW	LIN	MIT	CN	
Q-model	Bosatta and Ågren (1985)	S	3	4	∞	0	GRW	LIN	DIR	IND	Continuous quality model; C <sub>B</sub> is assumed proportional to C <sub>S</sub>
–	Chapman and Gray (1986)	M	2	3	3	1	G&M	LINB	NA	CM	N-only model
–	Deans et al. (1986)	S	2	3	1–2	0	NA	LIN	SIMP	IND	
JABOWA	Pastor and Post (1986)	E	4	4	7	0	NA	LIN	MIX	IND	
–	Smith et al. (1986)	S	2	2	3	1	G&M	LINB	MIT	IND	N-only model
–	Addiscott and Whitmore (1987)	S	3	2	3	0	NA	CONS	SIMP	IND	
–	Andrén and Paustian (1987)	L	3	2	1–2	0	NA	CONS-LIN	NA-SIMP	CM-IND	
–	Balesdent (1987)	S	3	4	5–7	0	NA	LIN	NA	CM	<sup>14</sup> C model
–	Berendse et al. (1987)	L	3	4	5	1	GRW	NL	MIT	IND	
NCSOIL	Hadas et al. (1987)	S	2	2	7	2	GRW	LIN	DIR-MIT	INH	
–	Hunt et al. (1987)	S	3	3	18	15	GRW	LINB	DIR	IND	Soil food web model
SOILN	Johnsson et al. (1987)	E	3	2	9	0	GRW	LIN	DIR	INH	
CENTURY	Parton et al. (1987)	E	4	3	7	1	GRW	LIN	DIR	IND	
–	Paustian and Schnurer (1987)	M	1	1	7	4	G&M	MM	MIX	MIX	Fungal growth model
–	Leffelaar (1988)	M	1	1	5	2	G&M	MM	DIR	IND	Explicit soil aggregate dynamics

(continued on next page)

Table A2 (continued)

Model	Reference	CL	SS	TS	PSD	MB	RESP	DEC	MIN	NLIM	Notes
–	Leffelaar and Wessel (1988)	S	2	1	11	2	G&M	MM	DIR	IND	
CENTURY	Parton et al. (1988)	E	3	3	20	3	GRW	LIN	DIR	IND	P and S included; based on Parton et al. (1987)
–	Harvey (1989)	G	5	5	1–3	0	NA	LIN	NA	CM	
–	Robinson et al. (1989)	M	1	3	4	2	GRW	LIN	DIR	IND	
Hurley	Thornley and Verberne (1989)	E	3	3	12	1	GRW	NL	MIX	INH	
Rothamsted	Jenkinson (1990)	S	3	3	4	1	GRW	LIN	NA	CM	Based on Jenkinson and Rayner (1977)
Verberne	Verberne et al. (1990)	S	3	2	9	2	GRW	LIN	DIR	IND	Soil physical protection of OM
VEGIE	Aber et al. (1991)	E	3	4	10	0	GRW	LIN	DIR	IND	
Q-model	Bosatta and Ågren (1991)	S	3	4	∞	0	GRW	LIN	DIR	IND	Continuous quality, cohort model; P and S included; $C_B \propto C_S$
–	Darrah (1991)	M	1	1	4	1	G&M	MM	NA	CM	
DAISY	Hansen et al. (1991)	E	3	2	11	2	G&M	LIN	DIR	IND	
GEM	Hunt et al. (1991)	E	3	2	25	12	G&M	NL	MIX	CN	Based on McGill et al. (1981), detailed soil food web
GENDEC	Moorhead and Reynolds (1991)	L	3	2	6	1	GRW	LIN	DIR	INH	
TEM	Raich et al. (1991)	G	5	3	4	0	NA	LIN	MIT	IND	
MBL-GEM	Rastetter et al. (1991)	E	3	4	5	0	GRW	LIN	MIT	INH	
ANIMO	Rijtema and Kroes (1991)	S	3	2	7	0	NA	LIN	DIR	IND	
FOREST-BGC	Running and Gower (1991)	G	3	4	5	0	NA	LIN	DIR	IND	
NLEAP	Shaffer et al. (1991)	E	3	2	5	0	NA	LIN	DIR	CO	
CERES	Godwin and Jones (1992)	E	3	2	10	0	GRW	NL	MIT	INH	
–	Griffiths and Robinson (1992)	M	1	3	4–5	2–3	GRW	LIN	DIR	IND	
DNDC	Li et al. (1992)	S	3	1	15	2	GRW (G&M)	LIN (MM)	DIR (NA)	INH (IND)	Decomposition (denitrification) submodels
SUNDIAL	Bradbury et al. (1993)	S	3	3	7	1	GRW	LIN	DIR	INH	Based on Jenkinson and Rayner (1977)
G'DAY	Comins and McMurtrie (1993)	E	3	4	8	1	GRW	LIN	DIR	IND	Based on Parton et al. (1987)
–	DeRuiter et al., (1993)	S	3	4	19	17	GRW	LINB	DIR	IND	Soil food web model
Ecosys	Grant et al. (1993)	S	2	1	86	20	G&M	MM	DIR	IND	$(C/N)_B$ is controlled by organic C and N availability
–	Harte and Kinzig (1993)	E	3	5	3–4	1	NA-CO	NL	MIT	IND	
FBM	Kindermann et al. (1993)	G	5	2	2	0	NA	LIN	NA	CM	
CENTURY	Parton et al. (1993)	E	4	3	20	4	GRW	LIN	DIR	CN	Based on Parton et al. (1987)
CASA	Potter et al. (1993)	G	5	3	18	2	GRW	LIN	DIR	IND	Based on Parton et al. (1987)
–	Ryzhova (1993)	E	3	4	2	0	GRW	LIN	NA	CM	
–	Trumbore (1993)	S	3	4	4	0	NA	LIN	NA	CM	$^{14}C$ model
Q-model	Bosatta and Ågren (1994)	S	3	4	∞	∞	GRW	LIN	NA	CM	Continuum quality, cohort model
–	Kersebaum and Richter (1994)	S	2	2	7	2	G&M	MM	DIR	CO	
MEAD	Sinsabaugh and Moorhead (1994)	L	3	3	4	1	GRW	NL	NA	IND	Mass loss rate model based on enzyme activity; P included
Q-model	Bosatta and Ågren (1995)	S	3	3	∞	∞	GRW	LIN	MIT	CN	Continuum quality
–	Elzein and Balesdent (1995)	S	3	4	3	0–1	NA-GRW	LIN	NA	CM	Vertically explicit
DEMETER	Foley (1995)	G	5	5	5	0	GRW	LIN	NA	CM	
WHNSIM	Huwe and Totsche (1995)	E	3	2	6	0	NA	LIN	MIT	IND	Distributed soil and climatic parameters
–	Thornley et al. (1995)	E	3	4	1	0	NA	LIN	NA	IND	N-only model; mineralization as a delayed N transfer
NICCCE	van Dam and van Breemen (1995)	E	3	2	24	2	G&M	NL	PAR	CN	Vertically explicit
–	Ågren and Bosatta (1996)	E	3	5	2	0	GRW	LIN	DIR	IND	
Q-model	Bosatta and Ågren (1996)	S	3	4	∞	∞	GRW	LIN	DIR	IND	Vertically explicit; P, S included
SCM	Panikov and Sizova (1996)	S	2	1	3	2	G&M	MM	NA	CM	
–	Saggar et al. (1996)	S	3	4	3	1	MNT	LIN	NA	CM	$^{14}C$ model
8SV	Schwinning and Parsons (1996)	E	3	4	2	0	NA	LIN	SIMP	IND	Based on Thornley et al. (1995)
–	Whitmore (1996b)	S	2	3	1	1	GRW	MULT	NA	CM	$C_B \propto C_S$
–	Whitmore (1996a)	S	2	3	2	1	NA	LIN	NA	CM	
ICBM	Andrén and Kätterer (1997)	S	3	4	2	0	GRW	LIN	NA	CM	
SOMM	Chertov and Komarov (1997)	S	2	3	18	0	MNT	LIN	DIR	IND	P, K, Mg, Ca included
DocMod	Currie and Aber (1997)	S	4	3	13	1	GRW	LIN	MIT	IND	
Hybrid	Friend et al. (1997)	G	3	2	23	6	GRW	LIN	DIR	CN	Based on Parton et al. (1993)
–	Hassink and Whitmore (1997)	S	2	4	3–4	1	GRW	LIN	NA	CM	Based on van Veen et al. (1984) and Jenkinson (1990); nonlinear SOM adsorption kinetics
–	Tateno and Chapin (1997)	E	3	4	2	0	NA	LIN	DIR	IND	
–	Van Wensem et al. (1997)	S	2	2	7	3	G&M	NL	NA	IND	
–	Zheng et al. (1997)	S	3	5	4	3	GRW	LIN-MULT	NA	CM	Soil food web model
NICA	Blagodatsky and Richter (1998)	S	2	1	7	3	GRW	MM	DIR	MIX	
NCSOIL	Hadas et al. (1998)	S	2	2	6	3	GRW	MM	MIT	CO	$R_0$ by polysaccharide production
–	Loreau (1998)	E	3	5	3	1	NA	MULT	DIR	IND	N-only model
FLUAZ	Mary et al. (1998)	S	2	2	4–5	1	NA	CONS	MIT-MIX	IND	$^{15}N$ model

Table A2 (continued)

Model	Reference	CL	SS	TS	PSD	MB	RESP	DEC	MIN	NLIM	Notes
INCA	Whitehead et al. (1998)	S	4	2	3	0	NA	CONS	SIMP	IND	Distributed catchment scale model
TRACE	Currie et al. (1999)	E	3	3	21	0	GRW	LIN	MIT	IND	Also <sup>15</sup> N model; based on Currie and Aber (1997)
RISK-N	Gusman and Marino (1999)	S	4	3	6	0	NA	LIN	SIMP	IND	
–	Henriksen and Breland (1999)	S	2	2	15	6	GRW	LIN	DIR	MIX	
TCS	Luo and Reynolds (1999)	E	3	4	19	4	GRW	LIN	DIR	IND	Based on Parton et al. (1987)
–	Zheng et al. (1999)	E	3	4	4	2	GRW	CONS-MULT	DIR	IND	Soil food web model
LEACHN	Acutis et al. (2000)	E	4	2	9	0	GRW	LIN	DIR	IND	Distributed soil hydraulic parameters; stochastic rainfall
NITS-SHETRAN	Birkinshaw and Ewen (2000)	S	3	2	9	0	GRW	LIN	DIR	IND	
IBIS	Kucharik et al. (2000)	G	5	2	19	2	GRW	LIN	DIR	IND	Based on Verberne et al. (1990)
DNDC	Li et al. (2000)	E	3	1	44	12	G&M	NL	DIR	INH	Based on Li et al. (1992)
–	Toal et al. (2000)	M	1	1	3	1	G&M	MM	NA	CM	
BACWAVE	Zelenev et al. (2000)	M	1	1	2	1	GRW	MM	NA	CM	
–	Brenner et al. (2001)	E	3	5	2	0	NA	LIN	SIMP	IND	
–	Daufresne and Loreau (2001)	E	3	5	2	1	MNT	LIN	DIR	INH	
DAYCENT	Del Grosso et al. (2001)	E	3	2	41	8	GRW	LIN	DIR	CN	Based on Parton et al. (1987)
PDM	Frolking et al. (2001)	S	3	5	1	0	NA	NL	NA	CM	Cohort model
CANTIS	Garnier et al. (2001)	S	3	2	15	3	GRW	MM	PAR	INH	
SOMKO	Gignoux et al. (2001)	S	3	2	9	2	G&M	NL	DIR	INH	Cohort model
ecosys	Grant (2001)	E	4	1	298	180	G&M	MM	DIR	CN	P included
ICBM	Kätterer and Andrén (2001)	S	2–3	2–4	2–4	0–1	GRW	LIN	DIR	IND	
SOILN-NO	Korsaeth et al. (2001)	E	2	2	10	2	GRW	LIN	DIR	CN	Based on Johnsson et al. (1987)
–	Loreau (2001)	E	3	5	11	5	NA	LIN-MULT	DIR	IND	
G'DAY	McMurtrie et al. (2001)	E	3	4	14	1	GRW	LIN	MIT	CN	Based on Parton et al. (1993)
TerraFlux	Neff and Asner (2001)	E	3	2	8	2	GRW	LIN	NA	CM	Based on Parton et al. (1987)
–	Nicolardot et al. (2001)	S	2	2	3	1	G&M	LIN	DIR	IND	
CREEP	Rosenbloom et al. (2001)	E	4	5	1	0	NA	LIN	NA	CM	
–	Thornley and Cannell (2001)	S	3	4–5	2–4	0	GRW	LIN	NA	CM	
–	Bar et al. (2002)	M	2	2	3	2	NA	NA	NA	CM	Biologic crust model, water limitation only
CenW	Kirschbaum and Paul (2002)	E	3	2	16	1	GRW	LIN	DIR	IND	Based on Parton et al. (1993)
–	Baisden and Amundson (2003)	E	3	5	3	0	CO	LIN	DIR	IND	
TRACE	Currie (2003)	E	3	3	21	0	GRW	LIN	MIT	IND	Also <sup>15</sup> N model; energy content and fluxes included; based on Currie et al. (1999)
DyDOC	Michalzik et al. (2003)	S	3	2	31	0	GRW	LIN	NA	CM	
TAO	Pansu and Thuries (2003)	S	2	2	5	1	NA	LIN	PAR	IND	
–	Porporato et al. (2003)	S	3	2	7	1	GRW	MULT	DIR	INH	Stochastic rainfall
–	Sanderman et al. (2003)	S	3	4	1	0	NA	LIN	NA	CM	
–	Schimel and Weintraub (2003)	S	2	2	6	2	G&M	MULT-MM	DIR	CO	
LPJ	Sitch et al. (2003)	G	4	3	4	0	GRW	LIN	NA	CM	
–	Walter et al. (2003)	S	4	4	1	0	NA	LIN	NA	CM	Stochastic landscape features
–	Bruun et al. (2004)	S	3	5	1–3	0	GRW	LIN	NA	CM	Age distribution computation
–	Foereid and Yearsley (2004)	M	1–2	2	4–5	1–2	GRW	MM	DIR	IND	
–	Kravchenko et al. (2004)	M	1	1	4	2	GRW	MM	NA	INH	
–	Moore et al. (2004)	E	3	5	4	2	GRW	MULT	NA	CM	Litter food web model
MOMOS	Pansu et al. (2004)	S	2	2	5–6	1	GRW-MNT-G&M	LIN	DIR	IND	One model version based on Jenkinson and Rayner (1977)
EnzModel	Allison (2005)	M	1	1	13	7	MNT	MM	DIR	IND	Individual-based bacterial model
–	Fontaine and Barot (2005)	E	3	5	2–5	1–2	MNT	LINB	NA-DIR	CM-INH	
INDISIM-S	Ginovart et al. (2005)	M	1	1	13	4	G&M	NL	MIX	IND	Individual-based bacterial model
–	Kuijper et al. (2005)	L	3	4	9	5	GRW	MM	DIR	IND	Litter food web model
Yasso	Liski et al. (2005)	S	3	4	7	0	NA	LIN	NA	CM	
IBIS	Liu et al. (2005)	G	4	2	19	2	GRW	LIN	DIR	CN	Based on Verberne et al. (1990)
–	Long and Or (2005)	M	1	1	4	2	GRW	MM	NA	CM	Individual-based bacterial model
–	Moore et al. (2005)	L	3	4	6	5	GRW	NL	NA	CM	Litter food web model
CN-SIM	Petersen et al. (2005a,b)	S	2–3	2–3	6–8	2	G&M	LIN	NA-DIR	CM-INH	Based on Hansen et al. (1991)
–	Botter et al. (2006)	S	4	2	3	0	GRW	CONS	SIMP	IND	Based on Porporato et al. (2003)
GDM	Moorhead and Sinsabaugh (2006)	L	3	3	6–3	1–3	MNT-G&M	MM	MIT	INH	
–	Neill and Gignoux (2006)	S	2	2	2	1	G&M	NL	PAR	IND	
–	Raynaud et al. (2006)	M	1	2	20	6	G&M	MULT	MIX	CO	
–	Tonitto and Powell (2006)	E	3	4	2	1	NA	NA	NA	INH	Spatially explicit; N-only model
BACWAVE-WEB	Zelenev et al. (2006)	S	2	1	26	11	GRW	MULT	MIX	CN	Food web model

(continued on next page)

Table A2 (continued)

Model	Reference	CL	SS	TS	PSD	MB	RESP	DEC	MIN	NLIM	Notes
–	Cherif and Loreau (2007)	M	2	5	3	1	GRW	MULT	DIR	INH	
–	Forney and Rothman (2007)	L-S	3	4	∞	0	NA	LIN	NA	CM	$k_{S,LIN}$ is a random variable from a log-uniform distribution
CIPS	Kuka et al. (2007)	S	2	2	5	1	GRW	LIN	NA	CM	
–	Maggi and Porporato (2007)	S	3	1	2	1	NA	NA	NA	NA	Water limitation only
MIOR	Masse et al. (2007)	S	1	2	10	2	MNT	LINB	NA	IND	Individual-based bacterial model
–	Manzoni and Porporato (2007)	S	2	2	4	1	GRW	LIN-MULT-MM	PAR	INH	
MOMOS-6	Pansu et al. (2007)	S	2	2	6	1	MNT	LIN	DIR	IND	Texture-dependent respiration
–	Stewart et al. (2007)	S	3	4	1–2	0	NA	LIN-NL	NA	CM	SOM adsorption kinetics
–	Wang et al. (2007)	E	3	4	9	0	GRW	LIN	PAR	INH	Coupled C, N, P model
SPACSYS	Wu et al. (2007)	E	3	2	15	1	G&M	LIN	DIR	IND	
FLDM	Zhang et al. (2007)	L	3	4	6	0	NA	LIN	DIR	IND	
–	Botter et al. (2008)	S	3	2	2	0	GRW	CONS	SIMP	IND	Stochastic rainfall and distributed nitrate transport parameters
CEM	d'Annunzio et al. (2008)	L	3	4	∞	∞	GRW	LIN	DIR	IND	Based on Ågren and Bosatta (1996)
NICA	Ingwersen et al. (2008)	M	1	1	15	6	GRW	MM	DIR	MIX	Based on Blagodatsky and Richter (1998)
Roth PC-1	Jenkinson and Coleman (2008)	S	3	3	5	1	GRW	LIN	NA	CM	Based on Jenkinson (1990)
–	Kumada et al. (2008)	L	3	4	5	0	NA	LIN	NA	CM	
TOUGHREACT-N	Maggi et al. (2008)	S	2	2	27	5	GRW	MM	NA	IND	
–	Manzoni et al. (2008a)	L	3	4	2	0	GRW	NA	DIR	NA	
–	Manzoni et al. (2008b)	S	2	2	3	0	GRW	LIN-MULT	PAR	INH	$C_B \propto C_S$
MOMOS-6	Pansu et al. (2008)	E	3	2	6	1	MNT	LIN	NA	CM	
–	Roy et al. (2008)	L	3	3	4	2	GRW	MULT	NA	CM	
AMG	Saffih-Hdadi and Mary (2008)	S	3	4	2	0	GRW	LIN	NA	CM	
–	Cherif and Loreau (2009)	E	3	5	3	1	GRW	NA	NA	IND	Food web model
–	Manzoni et al. (under review)	L	3	4	3	0	GRW	NA	DIR	NA	Based on Manzoni et al. (2008a); P included
–	Wang et al. (2009)	S	3	2	7	1	GRW	MULT	PAR	INH	Based on Porporato et al. (2003)

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## Appendix A

We selected biogeochemical models according to different criteria, ranging from the number of citations to the originality of their approaches to describe soil processes. Models have been searched by keywords in web databases (mainly the ISI Web of Knowledge), or in referenced publications, so that not only journal articles, but also book chapters, model user guides, and meeting or workshop proceedings have been used. We selected publications where a new model was proposed, or where an existing one was applied at different scales or in markedly different conditions with respect to the original work (e.g., one-compartment linear models applied to SOM or litter, at core or field scales). Different versions of the same model have been reviewed individually when significant modifications to the original version had been proposed. Table A1 explains the codes used in Table A2 to characterize the models.

We determined the model scales as the spatial and temporal dimensions at which the model is interpreted and applied. These dimensions, if not explicitly reported, have been inferred from the typical resolution of the data in input (e.g., climatic variables), the temporal frequency and level of aggregation of calibration and validation datasets (e.g., laboratory soil incubations, SS = 2; average mass loss from litterbags left in different locations at a given site, SS = 3), and the scales reported in the figures.

The total number of variables in each model has been computed as the sum of the variables describing the litter layer

and the ones describing an individual mineral soil layer. Similarly the spatial dimension in continuous-in-space models (Toal et al., 2000; Tonitto and Powell, 2006; Maggi and Porporato, 2007) has not been considered. In this way, we only accounted for the actual interacting biogeochemical variables independently of the spatial discretization scheme. This allowed us to compare lumped and spatially explicit models (Fig. 2). Since partial and delay differential equations can be considered infinite-order ordinary differential equations, they also have an infinite-dimensional phase-space, as reported in Table A2 for the continuum-quality models (Ågren and Bosatta, 1996) and few other cases. In cohort models, we only accounted for variables in an individual age class, again allowing the comparison with standard compartment models. Moreover, quantities that are proportional to other variables (e.g., N content when the C/N ratio of that compartment is assumed constant) are not counted as state variables because no differential equations are needed to describe their dynamics and therefore they do not contribute to the system phase space.

Microbial respiration (RESP) and mineralization (MIN) are defined when microbial biomass metabolism and stoichiometry are at least implicitly considered in the model. In other cases, these fields have been classified as NA.

All the data reported in Table A2 have been gathered with the highest possible accuracy and objectivity. Nonetheless, many data could only be inferred by interpreting the equations, the model descriptions, and the figures reported in the original publications, thus necessarily introducing a subjective component in the dataset.

## References

- Aber, J.D., Botkin, D.B., Melillo, J.M., 1978. Predicting effects of different harvesting regimes on forest floor dynamics in northern hardwoods. Canadian Journal of Forest Research. (Revue Canadienne De Recherche Forestiere) 8, 306–315.



- Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., Pastor, J., Boone, R.D., 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. *Ecological Applications* 1, 303–315.
- Acutis, M., Ducco, G., Grignani, C., 2000. Stochastic use of the LEACHN model to forecast nitrate leaching in different maize cropping systems. *European Journal of Agronomy* 13, 191–206.
- Addiscott, T.M., Whitmore, A.P., 1987. Computer-simulation of changes in soil mineral nitrogen and crop nitrogen during autumn, winter and spring. *Journal of Agricultural Science* 109, 141–157.
- Ågren, G.I., Bosatta, E., 1990. Theory and model or art and technology in ecology. *Ecological Modelling* 50, 213–220.
- Ågren, G.I., Bosatta, E., 1996. *Theoretical Ecosystem Ecology. Understanding Element Cycles*. Cambridge University Press, Cambridge, United Kingdom.
- Ahuja, L.R., Ma, L.W., Timlin, D.J., 2006. Trans-disciplinary soil physics research critical to synthesis and modeling of agricultural systems. *Soil Science Society of America Journal* 70, 311–326.
- Allison, S.D., 2005. Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. *Ecology Letters* 8, 626–635.
- Andrén, O., Kätterer, T., 1997. ICBM: the introductory carbon balance model for exploration of soil carbon balances. *Ecological Applications* 7, 1226–1236.
- Andrén, O., Paustian, K., 1987. Barley straw decomposition in the field – a comparison of models. *Ecology* 68, 1190–1200.
- d'Annunzio, R., Zeller, B., Nicolas, M., Dhote, J.F., Saint-André, L., 2008. Decomposition of European beech (*Fagus sylvatica*) litter: combining quality theory and N-15 labelling experiments. *Soil Biology & Biochemistry* 40, 322–333.
- Arah, J.R.M., Smith, K.A., 1989. Steady-state denitrification in aggregated soils – a mathematical model. *Journal of Soil Science* 40, 139–149.
- Argyris, J., Faust, G., Haase, M., 1994. *An Exploration of Chaos*. North Holland.
- Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141, 221–235.
- Baisden, W.T., Amundson, R., 2003. An analytical approach to ecosystem biogeochemistry modeling. *Ecological Applications* 13, 649–663.
- Balesdent, J., 1987. The turnover of soil organic fractions estimated by radiocarbon dating. *Science of the Total Environment* 62, 405–408.
- Bar, M., von Hardenberg, J., Meron, E., Provenzale, A., 2002. Modelling the survival of bacteria in drylands: the advantage of being dormant. *Proceedings of the Royal Society of London Series B – Biological Sciences* 269, 937–942.
- Barracough, D., 1997. The direct or MIT route for nitrogen immobilization: a N-15 mirror image study with leucine and glycine. *Soil Biology & Biochemistry* 29, 101–108.
- Beare, M.H., Coleman, D.C., Crossley, D.A., Hendrix, P.F., Odum, E.P., 1995. A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. *Plant and Soil* 170, 5–22.
- Beek, J., Frissel, M.J., 1973. *Simulation of Nitrogen Behavior in Soils*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Benbi, D.K., Richter, J., 2002. A critical review of some approaches to modelling nitrogen mineralization. *Biology and Fertility of Soils* 35, 168–183.
- Berendse, F., Berg, B., Bosatta, E., 1987. The effect of lignin and nitrogen on the decomposition of litter in nutrient-poor ecosystems – a theoretical approach. *Canadian Journal of Botany (Revue Canadienne De Botanique)* 65, 1116–1120.
- Berg, B., McLaugherty, C.A., 2003. *Plant Litter. Decomposition, Humus Formation, Carbon Sequestration*. Springer, 286 pp.
- Birkinshaw, S.J., Ewen, J., 2000. Nitrogen transformation component for SHETRAN catchment nitrate transport modelling. *Journal of Hydrology* 230, 1–17.
- Blagodatsky, S.A., Larinova, A.A., Yevdokimov, I.V., 1993. Effect of mineral nitrogen on respiration rate and growth efficiency of soil microorganisms. *Eurasian Soil Science* 25, 85–95.
- Blagodatsky, S.A., Richter, O., 1998. Microbial growth in soil and nitrogen turnover: a theoretical model considering the activity state of microorganisms. *Soil Biology & Biochemistry* 30, 1743–1755.
- Blanco-Canqui, H., Lal, R., 2004. Mechanisms of carbon sequestration in soil aggregates. *Critical Reviews in Plant Sciences* 23, 481–504.
- Bolin, B., 1981. Steady state and response characteristics of a simple model of the carbon cycle. In: Bolin, B. (Ed.), *Carbon Cycle Modelling*. John Wiley & Sons, pp. 315–331.
- Bolker, B.M., Pacala, S.W., Parton, W.J., 1998. Linear analysis of soil decomposition: insights from the century model. *Ecological Applications* 8, 425–439.
- Bosatta, E., 1981. A qualitative-analysis of the stability of the root-microorganism soil system. 1. Carbon-nitrogen status and nitrogen mineralization. *Ecological Modelling* 13, 223–236.
- Bosatta, E., Ågren, G.I., 1985. Theoretical-analysis of decomposition of heterogeneous substrates. *Soil Biology & Biochemistry* 17, 601–610.
- Bosatta, E., Ågren, G.I., 1991. Theoretical-analysis of carbon and nutrient interactions in soils under energy-limited conditions. *Soil Science Society of America Journal* 55, 728–733.
- Bosatta, E., Ågren, G.I., 1994. Theoretical-analysis of microbial biomass dynamics in soils. *Soil Biology & Biochemistry* 26, 143–148.
- Bosatta, E., Ågren, G.I., 1995. Theoretical analyses of interactions between inorganic nitrogen and soil organic-matter. *European Journal of Soil Science* 46, 109–114.
- Bosatta, E., Ågren, G.I., 1996. Theoretical analyses of carbon and nutrient dynamics in soil profiles. *Soil Biology & Biochemistry* 28, 1523–1531.
- Bosatta, E., Ågren, G.I., 2003. Exact solutions to the continuous-quality equation for soil organic matter turnover. *Journal of Theoretical Biology* 224, 97–105.
- Bosatta, E., Berendse, F., 1984. Energy or nutrient regulation of decomposition – implications for the mineralization immobilization response to perturbations. *Soil Biology & Biochemistry* 16, 63–67.
- Bosatta, E., Staaf, H., 1982. The control of nitrogen turn-over in forest litter. *Oikos* 39, 143–151.
- Botter, G., Daly, E., Porporato, A., Rodriguez-Iturbe, I., Rinaldo, A., 2008. Probabilistic dynamics of soil nitrate: coupling of ecohydrological and biogeochemical processes. *Water Resources Research* 44.
- Botter, G., Settin, T., Marani, M., Rinaldo, A., 2006. A stochastic model of nitrate transport and cycling at basin scale. *Water Resources Research* 42.
- Bradbury, N.J., Whitmore, A.P., Hart, P.B.S., Jenkinson, D.S., 1993. Modeling the fate of nitrogen in crop and soil in the years following application of N-15-labeled fertilizer to winter-wheat. *Journal of Agricultural Science* 121, 363–379.
- Brady, N.C., Weil, R.R., 2002. *The Nature and Properties of Soils*, 13th ed. Prentice Hall, Upper Saddle River, New Jersey.
- Brenner, D.L., Amundson, R., Baisden, W.T., Kendall, C., Harden, J., 2001. Soil N and N-15 variation with time in a California annual grassland ecosystem. *Geochimica et Cosmochimica Acta* 65, 4171–4186.
- Bruun, S., Christensen, B.T., Thomsen, I.K., Jensen, E.S., Jensen, L.S., 2007. Modeling vertical movement of organic matter in a soil incubated for 41 years with C-14 labeled straw. *Soil Biology & Biochemistry* 39, 368–371.
- Bruun, S., Six, J., Jensen, L.S., 2004. Estimating vital statistics and age distributions of measurable soil organic carbon fractions based on their pathway of formation and radiocarbon content. *Journal of Theoretical Biology* 230, 241–250.
- Bruun, S., Six, J., Jensen, L.S., Paustian, K., 2005. Estimating turnover of soil organic carbon fractions based on radiocarbon measurements. *Radiocarbon* 47, 99–113.
- Bunnell, F.L., Dowding, P., 1974. ABISKO – a generalized decomposition model for comparisons between tundra sites. In: Holding, A.J., Heal, O.W., MacLean, D.A., Flanagan, L.B. (Eds.), *Soil Organisms and Decomposition in Tundra*. Tundra Biome Steering Committee, Stockholm, Sweden, pp. 227–247.
- Bunnell, F.L., Scoullar, K.A., 1975. ABISKO II. A computer simulation model of carbon flux in tundra ecosystems. In: Rosswall, T., Heal, O.W. (Eds.), *Structure and Function of Tundra Ecosystems*, p. 448. Stockholm.
- Carpenter, S.R., 1981. Decay of heterogeneous detritus – a general-model. *Journal of Theoretical Biology* 89, 539–547.
- Chapman, S.J., Gray, T.R.G., 1986. Importance of cryptic growth, yield factors and maintenance energy in models of microbial-growth in soil. *Soil Biology & Biochemistry* 18, 1–4.
- Cherif, M., Loreau, M., 2007. Stoichiometric constraints on resource use, competitive interactions, and elemental cycling in microbial decomposers. *American Naturalist* 169, 709–724.
- Cherif, M., Loreau, M., 2009. When microbes and consumers determine the limiting nutrient of autotrophs: a theoretical analysis. *Proceedings of the Royal Society B – Biological Sciences* 276, 487–497.
- Chertov, O.G., Komarov, A.S., 1997. SOMM: a model of soil organic matter dynamics. *Ecological Modelling* 94, 177–189.
- Cleveland, C.C., Liptzin, D., 2007. C:N:P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass? *Biogeochemistry* 85, 235–252.
- Comins, H.N., McMurtrie, R.E., 1993. Long-term response of nutrient-limited forests to CO<sub>2</sub> enrichment – equilibrium behavior of plant–soil models. *Ecological Applications* 3, 666–681.
- Craig, H., 1957. The natural distribution of radiocarbon and the exchange time of carbon dioxide between atmosphere and sea. *Tellus* 9, 1–17.
- Currie, W.S., 2003. Relationships between carbon turnover and bioavailable energy fluxes in two temperate forest soils. *Global Change Biology* 9, 919–929.
- Currie, W.S., Aber, J.D., 1997. Modeling leaching as a decomposition process in humid montane forests. *Ecology* 78, 1844–1860.
- Currie, W.S., Nadelhoffer, K.J., Aber, J.D., 1999. Soil detrital processes controlling the movement of N-15 tracers to forest vegetation. *Ecological Applications* 9, 87–102.
- D'Odorico, P., Laio, F., Porporato, A., Rodriguez-Iturbe, I., 2003. Hydrologic controls on soil carbon and nitrogen cycles. II. A case study. *Advances in Water Resources* 26, 59–70.
- D'Odorico, P., Porporato, A., Laio, F., Ridolfi, L., Rodriguez-Iturbe, I., 2004. Probabilistic modeling of nitrogen and carbon dynamics in water-limited ecosystems. *Ecological Modelling* 179, 205–219.
- Daly, E., Oishi, A.C., Porporato, A., Katul, G.G., 2008. A stochastic model for daily subsurface CO<sub>2</sub> concentration and related soil respiration. *Advances in Water Resources* 31, 987–994.
- Darrah, P.R., 1991. Models of the rhizosphere. 1. Microbial-population dynamics around a root releasing soluble and insoluble carbon. *Plant and Soil* 133, 187–199.
- Daufresne, T., Loreau, M., 2001. Ecological stoichiometry, primary producer–decomposer interactions, and ecosystem persistence. *Ecology* 82, 3069–3082.
- De Gryze, S., Six, J., Merckx, R., 2006. Quantifying water-stable soil aggregate turnover and its implication for soil organic matter dynamics in a model study. *European Journal of Soil Science* 57, 693–707.
- Deans, J.R., Molina, J.A.E., Clapp, C.E., 1986. Models for predicting potentially mineralizable nitrogen and decomposition rate constants. *Soil Science Society of America Journal* 50, 323–326.
- Del Grosso, S.J., Parton, W.J., Mosier, A.R., Hartman, M.D., Brenner, J., Ojima, D.S., Schimel, D.S., 2001. Simulated interaction of carbon dynamics and nitrogen trace gas fluxes using the DAYCENT model. In: Shaffer, M.J., Ma, L., Hansen, S. (Eds.), *Modeling Carbon and Nitrogen Dynamics for Soil Management*. Lewis Publishers, pp. 303–332.

- Deruiter, P.C., Moore, J.C., Zwart, K.B., Bouwman, L.A., Hassink, J., Bloem, J., Devos, J.A., Marinissen, J.C.Y., Didden, W.A.M., Lebbink, G., Brussaard, L., 1993. Simulation of nitrogen mineralization in the belowground food webs of two winter-wheat fields. *Journal of Applied Ecology* 30, 95–106.
- Dewilligen, P., 1991. Nitrogen turnover in the soil–crop system – comparison of 14 simulation-models. *Fertilizer Research* 27, 141–149.
- Dewilligen, P., Neeteson, J.J., 1985. Comparison of six simulation-models for the nitrogen-cycle in the soil. *Fertilizer Research* 8, 157–171.
- Elzein, A., Balesdent, J., 1995. Mechanistic simulation of vertical-distribution of carbon concentrations and residence times in soils. *Soil Science Society of America Journal* 59, 1328–1335.
- Emanuel, W.R., Killough, G.E.G., Olson, J.S., 1981. Modelling the circulation of carbon in the world's terrestrial ecosystems. In: Bolin, B. (Ed.), *Carbon Cycle Modelling*. John Wiley & Sons, pp. 335–353.
- Eriksson, E., Welanders, P., 1956. On a mathematical model of the carbon cycle in nature. *Tellus* 8, 155–175.
- Ettema, C.H., Wardle, D.A., 2002. Spatial soil ecology. *Trends in Ecology & Evolution* 17, 177–183.
- Fang, C., Smith, P., Smith, J.U., Moncrieff, J.B., 2005. Incorporating microorganisms as decomposers into models to simulate soil organic matter decomposition. *Geoderma* 129, 139–146.
- Foereld, B., Yearsley, J.M., 2004. Modelling the impact of microbial grazers on soluble rhizodeposit turnover. *Plant and Soil* 267, 329–342.
- Foley, J.A., 1995. An equilibrium-model of the terrestrial carbon budget. *Tellus Series B – Chemical and Physical Meteorology* 47, 310–319.
- Fontaine, S., Barot, S., 2005. Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation. *Ecology Letters* 8, 1075–1087.
- Forney, D.C., Rothman, D.H., 2007. Decomposition of soil organic matter from physically derived decay rates. In: *American Geophysical Union Fall Meeting*, San Francisco, CA.
- Friend, A.D., Stevens, A.K., Knox, R.G., Cannell, M.G.R., 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecological Modelling* 95, 249–287.
- Frolking, S., Roulet, N.T., Moore, T.R., Richard, P.J.H., Lavoie, M., Muller, S.D., 2001. Modeling northern peatland decomposition and peat accumulation. *Ecosystems* 4, 479–498.
- Furniss, P.R., Ferrar, P., Morris, J.W., Bezuidenhout, J.J., 1982. A model of savanna litter decomposition. *Ecological Modelling* 17, 33–51.
- Garcia, F.O., Rice, C.W., 1994. Microbial biomass dynamics in tallgrass prairie. *Soil Science Society of America Journal* 58, 816–823.
- Garnier, P., Neel, C., Mary, B., Laforie, F., 2001. Evaluation of a nitrogen transport and transformation model in a bare soil. *European Journal of Soil Science* 52, 253–268.
- Gignoux, J., House, J., Hall, D., Masse, D., Nacro, H.B., Abbadie, L., 2001. Design and test of a generic cohort model of soil organic matter decomposition: the SOMKO model. *Global Ecology and Biogeography* 10, 639–660.
- Ginovart, M., Lopez, D., Gras, A., 2005. Individual-based modelling of microbial activity to study mineralization of C and N and nitrification process in soil. *Nonlinear Analysis – Real World Applications* 6, 773–795.
- Godwin, D.C., Jones, C.A., 1992. Nitrogen dynamics in soil–plant systems. In: *Modeling Plants and Soil Systems*. ASA-CSSA-SSSA, pp. 287–321.
- Grant, R.F., 2001. Modeling transformations of soil organic carbon and nitrogen at different scales of complexity. In: Shaffer, M.J., Ma, L., Hansen, S. (Eds.), *Modeling Carbon and Nitrogen Dynamics for Soil Management*. Lewis Publishers, pp. 597–630.
- Grant, R.F., Juma, N.G., McGill, W.B., 1993. Simulation of carbon and nitrogen transformations in soil – mineralization. *Soil Biology & Biochemistry* 25, 1317–1329.
- Griffiths, B., Robinson, D., 1992. Root-induced nitrogen mineralization – a nitrogen-balance model. *Plant and Soil* 139, 253–263.
- Gusman, A.J., Marino, M.A., 1999. Analytical modeling of nitrogen dynamics in soils and ground water. *Journal of Irrigation and Drainage Engineering – ASCE* 125, 330–337.
- Hadas, A., Molina, J.A.E., Feigenbaum, S., Clapp, C.E., 1987. Simulation of N-15 immobilization by the model Ncsoil. *Soil Science Society of America Journal* 51, 102–106.
- Hadas, A., Parkin, T.B., Stahl, P.D., 1998. Reduced CO<sub>2</sub> release from decomposing wheat straw under N-limiting conditions: simulation of carbon turnover. *European Journal of Soil Science* 49, 487–494.
- Halfon, E., 1979. Preview: theory in ecosystem analysis. In: Halfon, E. (Ed.), *Theoretical Systems Ecology*. Advances and Case Studies. Academic Press, pp. 1–13.
- Hansen, S., Jensen, H.E., Nielsen, N.E., Svendsen, H., 1991. Simulation of nitrogen dynamics and biomass production in winter-wheat using the Danish simulation-model Daisy. *Fertilizer Research* 27, 245–259.
- Harte, J., Levy, D., 1975. On the vulnerability of ecosystems disturbed by man. In: van Dobben, W.H., Lowe-McConnell, R.H. (Eds.), *Unifying Concepts in Ecology*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, p. 302.
- Harte, J., Kinzig, A.P., 1993. Mutualism and competition between plants and decomposers – implications for nutrient allocation in ecosystems. *American Naturalist* 141, 829–846.
- Harvey, L.D.D., 1989. Effect of model structure on the response of terrestrial biosphere models to CO<sub>2</sub> and temperature increases. *Global Biogeochemical Cycles* 3, 137–153.
- Hassink, J., Whitmore, A.P., 1997. A model of the physical protection of organic matter in soils. *Soil Science Society of America Journal* 61, 131–139.
- Henin, S., Dupuis, M., 1945. Essai de bilan de la matière organique du sol. *Annales Agronomiques* 3, 17–29.
- Henriksen, T.M., Breland, T.A., 1999. Nitrogen availability effects on carbon mineralization, fungal and bacterial growth, and enzyme activities during decomposition of wheat straw in soil. *Soil Biology & Biochemistry* 31, 1121–1134.
- Holland, H.D., 1978. *The Chemistry of the Atmosphere and Oceans*. Wiley-Interscience, 351 pp.
- Hunt, H.W., 1977. A simulation model for decomposition in grasslands. *Ecology* 58, 469–484.
- Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C., Rose, S.L., Reid, C.P.P., Morley, C.R., 1987. The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils* 3, 57–68.
- Hunt, H.W., Stewart, J.W.B., Cole, C.V., 1983. A conceptual model for interactions among carbon, nitrogen, sulphur, and phosphorus in grasslands. In: Bolin, B., Cook, R.B. (Eds.), *The Major Biogeochemical Cycles and their Interactions*. John Wiley & Sons, pp. 303–325.
- Hunt, H.W., Trlica, M.J., Redente, E.F., Moore, J.C., Detling, J.K., Kittel, T.G.F., Walter, D.E., Fowler, M.C., Klein, D.A., Elliott, E.T., 1991. Simulation-model for the effects of climate change on temperate grassland ecosystems. *Ecological Modelling* 53, 205–246.
- Huwe, B., Totsche, K.U., 1995. Deterministic and stochastic modelling of water, heat and nitrogen dynamics on different scales with WHNSIM. *Journal of Contaminant Hydrology* 20, 265–284.
- Ingwersen, J., Poll, C., Streck, T., Kandeler, E., 2008. Micro-scale modelling of carbon turnover driven by microbial succession at a biogeochemical interface. *Soil Biology & Biochemistry* 40, 864–878.
- Jans-Hammermeister, D.C., McGill, W.B., 1997. Evaluation of three simulation models used to describe plant residue decomposition in soil. *Ecological Modelling* 104, 1–13.
- Janssen, B.H., 1984. A simple method for calculating decomposition and accumulation of young soil organic-matter. *Plant and Soil* 76, 297–304.
- Jansson, S.L., 1958. Tracer studies on nitrogen transformations in soils with special attention to mineralization–immobilization relationships. *Annals of the Royal Agricultural College of Sweden* 24, 101–361.
- Jenkinson, D.S., 1990. The turnover of organic-carbon and nitrogen in soil. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences* 329, 361–368.
- Jenkinson, D.S., Coleman, K., 2008. The turnover of organic carbon in subsoils. Part 2. Modelling carbon turnover. *European Journal of Soil Science* 59, 400–413.
- Jenkinson, D.S., Rayner, J.H., 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science* 123, 298–305.
- Jenny, H., 1941. *Factors of Soil Formation. A System of Quantitative Pedology*. McGraw-Hill, New York, 281 pp.
- Jenny, H., Gessel, S.P., Bingham, F.T., 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. *Soil Science* 68, 419–432.
- Jensen, L.S., Mueller, T., Magid, J., Nielsen, N.E., 1997. Temporal variation of C and N mineralization, microbial biomass and extractable organic pools in soil after oilseed rape straw incorporation in the field. *Soil Biology & Biochemistry* 29, 1043–1055.
- Johnsson, H., Bergström, L., Jansson, P.E., Paustian, K., 1987. Simulated nitrogen dynamics and losses in a layered agricultural soil. *Agriculture Ecosystems & Environment* 18, 333–356.
- Jones, C.A., Cole, C.V., Sharp, A.N., Williams, J.R., 1984. A simplified soil and plant phosphorus model. 1. Documentation. *Soil Science Society of America Journal* 48, 800–805.
- Juma, N.G., Paul, E.A., Mary, B., 1984. Kinetic-analysis of net nitrogen mineralization in soil. *Soil Science Society of America Journal* 48, 753–757.
- Kätterer, T., Andrén, O., 2001. The ICBM family of analytically solved models of soil carbon, nitrogen and microbial biomass dynamics descriptions and application examples. *Ecological Modelling* 136, 191–207.
- Katul, G., Porporato, A., Oren, R., 2007. Stochastic dynamics of plant–water interactions. *Annual Review of Ecology and Systematics* 38, 767–791.
- Kemmitt, S.J., Lanyon, C.V., Waite, I.S., Wen, Q., Addiscott, T.M., Bird, N.R.A., O'Donnell, A.G., Brookes, P.C., 2008. Mineralization of native soil organic matter is not regulated by the size, activity or composition of the soil microbial biomass – a new perspective. *Soil Biology & Biochemistry* 40, 61–73.
- Kersebaum, K.C., Richter, O., 1994. A model approach to simulate C and N transformations through microbial biomass. *European Journal of Agronomy* 3, 355–360.
- Kindermann, J., Ludeke, M.K.B., Badeck, F.W., Otto, R.D., Kludius, A., Hager, C., Wurth, G., Lang, T., Donges, S., Habermehl, S., Kohlmaier, G.H., 1993. Structure of a global and seasonal carbon exchange model for the terrestrial biosphere – the Frankfurt biosphere model (Fbm). *Water, Air and Soil Pollution* 70, 675–684.
- Kirkham, D., Bartholomew, W.V., 1954. Equations for following nutrient transformations in soil, utilizing tracer data. *Soil Science Society of America Proceedings* 18, 33–34.
- Kirkham, D., Bartholomew, W.V., 1955. Equations for following nutrient transformations in soil, utilizing tracer data: II. *Soil Science Society of America Proceedings* 19, 189–192.
- Kirschbaum, M.U.F., Paul, K.I., 2002. Modelling C and N dynamics in forest soils with a modified version of the CENTURY model. *Soil Biology & Biochemistry* 34, 341–354.

- Knapp, E.B., Elliott, L.F., Campbell, G.S., 1983. Carbon, nitrogen and microbial biomass interrelationships during the decomposition of wheat straw – a mechanistic simulation-model. *Soil Biology & Biochemistry* 15, 455–461.
- Korsaeth, A., Molstad, L., Bakken, L.R., 2001. Modelling the competition for nitrogen between plants and microflora as a function of soil heterogeneity. *Soil Biology & Biochemistry* 33, 215–226.
- Kravchenko, L.V., Strigul, N.S., Shvityov, I.A., 2004. Mathematical simulation of the dynamics of interacting populations of rhizosphere microorganisms. *Microbiology* 73, 189–195.
- Kucharik, C.J., Foley, J.A., Delire, C., Fisher, V.A., Coe, M.T., Lenters, J.D., Young-Molling, C., Ramankutty, N., Norman, J.M., Gower, S.T., 2000. Testing the performance of a dynamic global ecosystem model: water balance, carbon balance, and vegetation structure. *Global Biogeochemical Cycles* 14, 795–825.
- Kuijper, L.D.J., Berg, M.P., Morrien, E., Kooi, B.W., Verhoef, H.A., 2005. Global change effects on a mechanistic decomposer food web model. *Global Change Biology* 11, 249–265.
- Kuka, K., Franko, U., Ruhlmann, J., 2007. Modelling the impact of pore space distribution on carbon turnover. *Ecological Modelling* 208, 295–306.
- Kumada, S., Kawanishi, T., Hayashi, Y., Ogomori, K., Kobayashi, Y., Takahashi, N., Saito, M., Hamano, H., Kojima, T., Yamada, K., 2008. Litter carbon dynamics analysis in forests in an arid ecosystem with a model incorporating the physical removal of litter. *Ecological Modelling*. doi:10.1016/j.ecolmodel.2008.02.022.
- Kuzyakov, Y., Blagodatskaya, E., Blagodatsky, S.A., 2009. Comments on the paper by Kemmitt et al. (2009) 'Mineralization of native soil organic matter is not regulated by the size, activity or composition of the soil microbial biomass – a new perspective' [*Soil Biology & Biochemistry* 40, 61–73]. The biology of the regulatory gate. *Soil Biology & Biochemistry* 41 (2), 435–439.
- Lal, R., 2008. Carbon sequestration. *Philosophical Transactions of the Royal Society B – Biological Sciences* 363, 815–830.
- Leffelaar, P.A., 1988. Dynamics of partial anaerobiosis, denitrification, and water in a soil aggregate – simulation. *Soil Science* 146, 427–444.
- Leffelaar, P.A., 1993. Water-movement, oxygen-supply and biological processes on the aggregate scale. *Geoderma* 57, 143–165.
- Leffelaar, P.A., Wessel, W.W., 1988. Denitrification in a homogeneous, closed system – experiment and simulation. *Soil Science* 146, 335–349.
- Li, C.S., Aber, J., Stange, F., Butterbach-Bahl, K., Papen, H., 2000. A process-oriented model of N<sub>2</sub>O and NO emissions from forest soils: 1. Model development. *Journal of Geophysical Research – Atmospheres* 105, 4369–4384.
- Li, C.S., Frolking, S., Frolking, T.A., 1992. A model of nitrous-oxide evolution from soil driven by rainfall events. 1. Model structure and sensitivity. *Journal of Geophysical Research – Atmospheres* 97, 9759–9776.
- Liski, J., Palosuo, T., Peltoniemi, M., Sievänen, R., 2005. Carbon and decomposition model Yasso for forest soils. *Ecological Modelling* 189, 168–182.
- Liu, J.X., Price, D.T., Chen, J.A., 2005. Nitrogen controls on ecosystem carbon sequestration: a model implementation and application to Saskatchewan, Canada. *Ecological Modelling* 186, 178–195.
- Liu, Y., 2007. Overview of some theoretical approaches for derivation of the Monod equation. *Applied Microbiology and Biotechnology* 73, 1241–1250.
- Long, T., Or, D., 2005. Aquatic habitats and diffusion constraints affecting microbial coexistence in unsaturated porous media. *Water Resources Research* 41.
- Loreau, M., 1998. Ecosystem development explained by competition within and between material cycles. *Proceedings of the Royal Society of London Series B – Biological Sciences* 265, 33–38.
- Loreau, M., 2001. Microbial diversity, producer–decomposer interactions and ecosystem processes: a theoretical model. *Proceedings of the Royal Society of London Series B – Biological Sciences* 268, 303–309.
- Luo, Y.Q., Reynolds, J.F., 1999. Validity of extrapolating field CO<sub>2</sub> experiments to predict carbon sequestration in natural ecosystems. *Ecology* 80, 1568–1583.
- Ma, L., Shaffer, M.J., 2001. A review of carbon and nitrogen processes in nine U.S. soil nitrogen dynamics models. In: Shaffer, M.J., Ma, L., Hansen, S. (Eds.), *Modeling Carbon and Nitrogen Dynamics for Soil Management*. Lewis Publishers, pp. 55–102.
- Maggi, F., Gu, C., Riley, W.J., Hornberger, G.M., Venterea, R.T., Xu, T., Spycher, N., Steefel, C., Miller, N.L., Oldenburg, C.M., 2008. A mechanistic treatment of the dominant soil nitrogen cycling processes: model development, testing, and application. *Water Resources Research* 113 (G2).
- Maggi, F., Porporato, A., 2007. Coupled moisture and microbial dynamics in unsaturated soils. *Water Resources Research* 43 (7).
- Manzoni, S., Jackson, R.B., Trofymow, J.A., Porporato, A., 2008a. The global stoichiometry of litter nitrogen mineralization. *Science* 321, 684–686.
- Manzoni, S., Porporato, A., Schimel, J.P., 2008b. Soil heterogeneity in lumped mineralization–immobilization models. *Soil Biology & Biochemistry* 40, 1137–1148.
- Manzoni, S., Porporato, A., 2007. Theoretical analysis of nonlinearities and feedbacks in soil carbon and nitrogen cycles. *Soil Biology & Biochemistry* 39, 1542–1556.
- Manzoni, S., Porporato, A., D'Odorico, P., Laio, F., Rodriguez-Iturbe, I., 2004. Soil nutrient cycles as a nonlinear dynamical system. *Nonlinear Processes in Geophysics* 11, 589–598.
- Manzoni, S., Trofymow, J.A., Jackson, R.B., Porporato, A. Stoichiometric controls on the dynamics of carbon, nitrogen, and phosphorus in decomposing litter. *Ecological Monographs*, under review.
- Manzoni, S., Katul, G., Porporato, A. Linear theory of soil biogeochemistry: an analysis of soil carbon residence times, in preparation.
- Mary, B., Recous, S., Robin, D., 1998. A model for calculating nitrogen fluxes in soil using N-15 tracing. *Soil Biology & Biochemistry* 30, 1963–1979.
- Masse, D., Cambier, C., Brauman, A., Sall, S., Assigbetse, K., Chotte, J.L., 2007. MIOR: an individual-based model for simulating the spatial patterns of soil organic matter microbial decomposition. *European Journal of Soil Science* 58, 1127–1135.
- McGeachan, M.B., Wu, L., 2001. A review of carbon and nitrogen processes in European soil nitrogen dynamics models. In: Shaffer, M.J., Ma, L., Hansen, S. (Eds.), *Modeling Carbon and Nitrogen Dynamics for Soil Management*. Lewis Publishers, pp. 103–172.
- McGill, W.B., 1996. Review and classification of ten soil organic matter (SOM) models. In: Powlson, D.S., Smith, P., Smith, J.U. (Eds.), *Evaluation of Soil Organic Matter Models. Using Existing Long-Term Datasets*. Springer, pp. 111–132.
- McGill, W.B., Hunt, H.W., Woodmansee, R.G., Reuss, J.O., 1981. Phoenix, a model of the dynamics of carbon and nitrogen in grassland soils. In: Clark, F.E., Ross, T. (Eds.), *Terrestrial Nitrogen Cycles. Processes, Ecosystem Strategies and Management Impacts*. Ecological Bulletins, 49–115. Stockholm.
- McMurtrie, R.E., Medlyn, B.E., Dewar, R.C., 2001. Increased understanding of nutrient immobilization in soil organic matter is critical for predicting the carbon sink strength of forest ecosystems over the next 100 years. *Tree Physiology* 21, 831–839.
- Mehran, M., Tanji, K.K., 1974. Computer modeling of nitrogen transformations in soils. *Journal of Environmental Quality* 3, 391–396.
- Melillo, J.M., Borchers, J., Chaney, J., Fisher, H., Fox, S., Haxeltine, A., Janetos, A., Kicklighter, D.W., Kittel, T.G.F., McGuire, A.D., McKeown, R., Neilson, R., Nemani, R., Ojima, D.S., Painter, T., Pan, Y., Parton, W.J., Pierce, L., Pielke, R., Prentice, C., Rizzo, B., Rosenbloom, N.A., Running, S., Schimel, D.S., Sitch, S., Smith, T., Woodward, I., 1995. Vegetation ecosystem modeling and analysis project – comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate-change and CO<sub>2</sub> doubling. *Global Biogeochemical Cycles* 9, 407–437.
- Michalzik, B., Tipping, E., Mulder, J., Lancho, J.F.G., Matzner, E., Bryant, C.L., Clarke, N., Lof, S., Esteban, M.A.V., 2003. Modelling the production and transport of dissolved organic carbon in forest soils. *Biogeochemistry* 66, 241–264.
- Minderman, G., 1968. Addition, decomposition and accumulation of organic matter in forests. *Journal of Ecology* 56, 355–362.
- Molina, J.A.E., Clapp, C.E., Shaffer, M.J., Chichester, F.W., Larson, W.E., 1983. Ncsoil, a model of nitrogen and carbon transformations in soil – description, calibration, and behavior. *Soil Science Society of America Journal* 47, 85–91.
- Molina, J.A.E., Smith, P., 1998. Modeling carbon and nitrogen processes in soils. In: *Advances in Agronomy*, vol. 62, pp. 253–298.
- Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J., Wall, D.H., 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters* 7, 584–600.
- Moore, J.C., McCann, K., de Ruiter, P.C., 2005. Modeling trophic pathways, nutrient cycling, and dynamic stability in soils. *Pedobiologia* 49, 499–510.
- Moorhead, D.L., Currie, W.S., Rastetter, E.B., Parton, W.J., Harmon, M.E., 1999. Climate and litter quality controls on decomposition: an analysis of modeling approaches. *Global Biogeochemical Cycles* 13, 575–589.
- Moorhead, D.L., Reynolds, J.F., 1991. A general-model of litter decomposition in the northern Chihuahuan desert. *Ecological Modelling* 56, 197–219.
- Moorhead, D.L., Sinsabaugh, R.L., 2006. A theoretical model of litter decay and microbial interaction. *Ecological Monographs* 76, 151–174.
- Neff, J.C., Asner, G.P., 2001. Dissolved organic carbon in terrestrial ecosystems: synthesis and a model. *Ecosystems* 4, 29–48.
- Neill, C., Gignoux, J., 2006. Soil organic matter decomposition driven by microbial growth: a simple model for a complex network of interactions. *Soil Biology & Biochemistry* 38, 803–811.
- Nicolardot, B., Recous, S., Mary, B., 2001. Simulation of C and N mineralisation during crop residue decomposition: a simple dynamic model based on the C:N ratio of the residues. *Plant and Soil* 228, 83–103.
- Nikiforoff, C.C., 1936. Some general aspects of the chernozem formation. *Soil Science Society of America Proceedings* 1, 333–342.
- O'Brien, B.J., Stout, J.D., 1978. Movement and turnover of soil organic-matter as indicated by carbon isotope measurements. *Soil Biology & Biochemistry* 10, 309–317.
- Olson, J.S., 1963. Energy storage and the balance of producer and decomposers in ecological systems. *Ecology* 44, 322–331.
- Osler, G.H.R., Sommerkorn, M., 2007. Toward a complete soil C and N cycle: incorporating the soil fauna. *Ecology* 88, 1611–1621.
- Panikov, N.S., Sizova, M.V., 1996. A kinetic method for estimating the biomass of microbial functional groups in soil. *Journal of Microbiological Methods* 24, 219–230.
- Pansu, M., Bottner, P., Sarmiento, L., Metselaar, K., 2004. Comparison of five soil organic matter decomposition models using data from a C-14 and N-15 labeling field experiment. *Global Biogeochemical Cycles* 18.
- Pansu, M., Martineau, Y., Saugier, B., 2008. A modeling method to quantify in situ the input of carbon from roots and the resulting C turnover in soil. *Plant and Soil*. doi:10.1007/s11104-008-9791-1.
- Pansu, M., Sarmiento, L., Metselaar, K., Herve, D., Bottner, P., 2007. Modelling the transformations and sequestration of soil organic matter in two contrasting ecosystems of the Andes. *European Journal of Soil Science* 58, 775–785.
- Pansu, M., Thuries, L., 2003. Kinetics of C and N mineralization, N immobilization and N volatilization of organic inputs in soil. *Soil Biology & Biochemistry* 35, 37–48.

- Parnas, H., 1975. Model for decomposition of organic material by microorganisms. *Soil Biology & Biochemistry* 7, 161–169.
- Parnas, H., 1976. A theoretical explanation of the priming effect based on microbial growth with two limiting substrates. *Soil Biology & Biochemistry* 8, 139–144.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic-matter levels in Great-Plains grasslands. *Soil Science Society of America Journal* 51, 1173–1179.
- Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.C., Seastedt, T., Moya, E.G., Kamnalrut, A., Kinyamario, J.L., 1993. Observations and modeling of biomass and soil organic-matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* 7, 785–809.
- Parton, W.J., Stewart, J.W.B., Cole, C.V., 1988. Dynamics of C, N, P and S in grassland soils – a model. *Biogeochemistry* 5, 109–131.
- Pastor, J., Post, W.M., 1986. Influence of climate, soil-moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2, 3–27.
- Patten, B.C., 1972. Simulation of shortgrass prairie ecosystem. *Simulation* 19, 177–186.
- Paul, E.A. (Ed.), 2007. *Soil Microbiology, Ecology and Biochemistry*. Elsevier, New York, p. 532.
- Paustian, K., 1994. Modelling soil biology and biochemical processes for sustainable agriculture research. In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R., Grace, P.R. (Eds.), *Soil Biota. Management in Sustainable Farming Systems*. CSIRO, p. 262.
- Paustian, K., Schnurer, J., 1987. Fungal growth-response to carbon and nitrogen limitation – a theoretical-model. *Soil Biology & Biochemistry* 19, 613–620.
- Petersen, B.M., Berntsen, J., Hansen, S., Jensen, L.S., 2005a. CN-SIM – a model for the turnover of soil organic matter. I. Long-term carbon and radiocarbon development. *Soil Biology & Biochemistry* 37, 359–374.
- Petersen, B.M., Jensen, L.S., Pedersen, A., Henriksen, T.M., Sorensen, P., Trinsoutrot-Gattin, I., Berntsen, J., 2005b. CN-SIM: a model for the turnover of soil organic matter. II. Short-term carbon and nitrogen development. *Soil Biology & Biochemistry* 37, 375–393.
- Plante, A.F., Feng, Y., McGill, W.B., 2002. A modeling approach to quantifying soil macroaggregate dynamics. *Canadian Journal of Soil Science* 82, 181–190.
- Plante, A.F., Parton, W., 2005. The dynamics of soil organic matter and nutrient cycling. In: Paul, E.A. (Ed.), *Soil Microbiology, Ecology and Biochemistry*. Elsevier, New York, NY, pp. 433–470.
- Porporato, A., D'Odorico, P., Laio, F., Rodriguez-Iturbe, I., 2003. Hydrologic controls on soil carbon and nitrogen cycles. I. Modeling scheme. *Advances in Water Resources* 26, 45–58.
- Potter, C.S., Randerson, J.T., Field, C.B., Matson, P.A., Vitousek, P.M., Mooney, H.A., Klooster, S.A., 1993. Terrestrial ecosystem production – a process model based on global satellite and surface data. *Global Biogeochemical Cycles* 7, 811–841.
- Powlson, D.S., Smith, P., Smith, J.U. (Eds.), 1996. *Evaluation of Soil Organic Matter Models. Using Existing Long-term Datasets*. Springer, p. 429.
- Raich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Steudler, P.A., Peterson, B.J., Grace, A.L., Moore, B., Vorosmart, C.J., 1991. Potential net primary productivity in South-America – application of a global-model. *Ecological Applications* 1, 399–429.
- Rastetter, E.B., Ryan, M.G., Shaver, G.R., Melillo, J.M., Nadelhoffer, K.J., Hobbie, J.E., Aber, J.D., 1991. A general biogeochemical model describing the responses of the C-cycle and N-cycle in terrestrial ecosystems to changes in CO<sub>2</sub>, climate, and N-deposition. *Tree Physiology* 9, 101–126.
- Raynaud, X., Lata, J.C., Leadley, P.W., 2006. Soil microbial loop and nutrient uptake by plants: a test using a coupled C:N model of plant-microbial interactions. *Plant and Soil* 287, 95–116.
- Reuss, J.O., Innis, G.S., 1977. A grassland nitrogen flow simulation model. *Ecology* 58, 379–388.
- Richter, D.D., Markewitz, D., 2001. *Understanding Soil Change*. Cambridge University Press, Cambridge, UK.
- Ridolfi, L., D'Odorico, P., Porporato, A., Rodriguez-Iturbe, I., 2003. The influence of stochastic soil moisture dynamics on gaseous emissions of NO, N<sub>2</sub>O, and N<sub>2</sub>. *Hydrological Sciences Journal. (Journal Des Sciences Hydrologiques)* 48, 781–798.
- Rijtema, P.E., Kroes, J.G., 1991. Some results of nitrogen simulations with the model Animo. *Fertilizer Research* 27, 189–198.
- Robinson, D., Griffiths, B., Ritz, K., Wheatley, R., 1989. Root-induced nitrogen mineralization – a theoretical-analysis. *Plant and Soil* 117, 185–193.
- Rosenbloom, N.A., Doney, S.C., Schimel, D.S., 2001. Geomorphic evolution of soil texture and organic matter in eroding landscapes. *Global Biogeochemical Cycles* 15, 365–381.
- Rothman, D.H., Forney, D.C., 2007. Physical model for the decay and preservation of marine organic carbon. *Science* 316, 1325–1328.
- Roy, M., Mandal, S., Ray, S., 2008. Detrital ontogenic model including decomposer diversity. *Ecological Modelling*, doi:10.1016/j.ecolmodel.2008.02.020.
- Running, S.W., Gower, S.T., 1991. FOREST-BGC, a general-model of forest ecosystem processes for regional applications. 2. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology* 9, 147–160.
- Russell, J.B., Cook, G.M., 1995. Energetics of bacterial-growth – balance of anabolic and catabolic reactions. *Microbiological Reviews* 59, 48–62.
- Russell, J.S., 1964. Mathematical expression of seasonal changes in soil organic matter. *Nature* 204, 161–162.
- Russell, J.S., 1975. Mathematical treatment of effect of cropping system on soil organic nitrogen in two long-term sequential experiments. *Soil Science* 120, 37–44.
- Ryzhova, I.M., 1993. The analysis of stability and bifurcation of carbon turnover in soil-vegetation systems on the basis of the nonlinear model. *Systems Analysis Modelling Simulation* 12, 139–145.
- Saffih-Hdadi, K., Mary, B., 2008. Modeling consequences of straw residues export on soil organic carbon. *Soil Biology & Biochemistry* 40, 594–607.
- Saggar, S., Parshotam, A., Sparling, G.P., Feltham, C.W., Hart, P.B.S., 1996. C-14-labelled ryegrass turnover and residence times in soils varying in clay content and mineralogy. *Soil Biology & Biochemistry* 28, 1677–1686.
- Salter, R.M., Green, T.C., 1933. Factors affecting the accumulation and loss of nitrogen and organic carbon in cropped soils. *Journal of the American Society of Agronomy* 25, 622–630.
- Sanderman, J., Amundson, R.G., Baldocchi, D.D., 2003. Application of eddy covariance measurements to the temperature dependence of soil organic matter mean residence time. *Global Biogeochemical Cycles* 17.
- Schimel, J.P., 2001. Biogeochemical models: implicit versus explicit microbiology. In: Schulze, E.D., Heimann, M., Harrison, S., Holland, E., Lloyd, J., Prentice, I.C., Schimel, D.S. (Eds.), *Global Biogeochemical Cycles in the Climate System*. Academic Press, p. 350.
- Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85, 591–602.
- Schimel, J.P., Weintraub, M.N., 2003. The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biology & Biochemistry* 35, 549–563.
- Schlesinger, W.H., 1997. *Biogeochemistry. An Analysis of Global Change*. Academic Press, 588 pp.
- Schwinning, S., Parsons, A.J., 1996. Analysis of the coexistence mechanisms for grasses and legumes in grazing systems. *Journal of Ecology* 84, 799–813.
- Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in and semi-arid ecosystems. *Oecologia* 141, 211–220.
- Selgman, N.G., Van Keulen, H., 1981. PAPRAN: a simulation model of annual pasture production limited by rainfall and nitrogen. In: Frissel, M.J., van Veen, J.A. (Eds.), *Simulation of Nitrogen Behavior in Soil-Plant Systems*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, p. 283.
- Shaffer, M.J., Halvorson, A.D., Pierce, F.J., 1991. Nitrate leaching and economic analysis package (NLEAP): model description and application. In: Follett, R.F., Keeney, D.R., Cruse, R.M. (Eds.), *Managing Nitrogen for Groundwater Quality and Farm Profitability*. SSSA, Madison, Wisconsin, pp. 285–322.
- Shaffer, M.J., Ma, L., Hansen, S., 2001. Introduction to simulation of carbon and nitrogen dynamics in soils. In: Shaffer, M.J., Ma, L., Hansen, S. (Eds.), *Modeling Carbon and Nitrogen Dynamics for Soil Management*. Lewis Publishers, pp. 1–10.
- Shibu, M.E., Lefelaar, P.A., Van Keulen, H., Aggarwal, P.K., 2006. Quantitative description of soil organic matter dynamics – a review of approaches with reference to rice-based cropping systems. *Geoderma* 137, 1–18.
- Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C., Contosta, A.R., Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K., Keeler, B.L., Powers, J.S., Stursova, M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein, M.D., Zak, D.R., Zeglin, L.H., 2008. Stoichiometry of soil enzyme activity at global scale. *Ecology Letters* 11, 1252–1264.
- Sinsabaugh, R.L., Moorhead, D.L., 1994. Resource-allocation to extracellular enzyme-production – a model for nitrogen and phosphorus control of litter decomposition. *Soil Biology & Biochemistry* 26, 1305–1311.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9, 161–185.
- Six, J., Bossuyt, H., Degryze, S., Denef, K., 2004. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. *Soil & Tillage Research* 79, 7–31.
- Smith, J.L., McNeal, B.L., Cheng, H.H., Campbell, G.S., 1986. Calculation of microbial maintenance rates and net nitrogen mineralization in soil at steady-state. *Soil Science Society of America Journal* 50, 332–338.
- Smith, O.L., 1979. Analytical model of the decomposition of soil organic-matter. *Soil Biology & Biochemistry* 11, 585–606.
- Smith, P., Andr n, O., Brussaard, L., Dangerfield, M., Ekschmitt, K., Lavelle, P., Tate, K., 1998. Soil biota and global change at the ecosystem level: describing soil biota in mathematical models. *Global Change Biology* 4, 773–784.
- Smith, P., Smith, J.U., Powlson, D.S., McGill, W.B., Arah, J.R.M., Chertov, O.G., Coleman, K., Franko, U., Frolking, S., Jenkinson, D.S., Jensen, L.S., Kelly, R.H., Klein-Gunnewiek, H., Komarov, A.S., Li, C., Molina, J.A.E., Mueller, T., Parton, W.J., Thornley, J.H.M., Whitmore, A.P., 1997. A comparison of the performance of nine soil organic matter models using datasets from seven long-term experiments. *Geoderma* 81, 153–225.
- Sollins, P., Homann, P., Caldwell, B.A., 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma* 74, 65–105.
- Stanford, G., Smith, S.J., 1972. Nitrogen mineralization potential of soils. *Soil Science Society of America Journal Proceedings* 36, 465–472.
- Sterner, R.W., Elser, J.J., 2002. *Ecological Stoichiometry. The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton and Oxford.
- Stewart, C.E., Paustian, K., Conant, R.T., Plante, A.F., Six, J., 2007. Soil carbon saturation: concept, evidence and evaluation. *Biogeochemistry* 86, 19–31.
- Strogatz, S.H., 2000. *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering*. Da Capo Press, 512 pp.
- Svirezhev, Y.M., Tarko, A.M., 1981. The global role of the biosphere in the stabilization of atmospheric CO<sub>2</sub> and temperature. In: Bolin, B. (Ed.), *Carbon Cycle Modelling*. John Wiley & Sons, pp. 355–364.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*. University of California Press, Berkeley and Los Angeles, 372 pp.



- Tanji, K.K., 1982. Modeling of the soil nitrogen cycle. In: Stevenson, F.J. (Ed.), *Nitrogen in Agricultural Soils*. ASA-CSSA-SSSA, Madison, WI, pp. 721–772.
- Tateno, M., Chapin, F.S., 1997. The logic of carbon and nitrogen interactions in terrestrial ecosystems. *American Naturalist* 149, 723–744.
- Thornley, J.H.M., Bergelson, J., Parsons, A.J., 1995. Complex dynamics in a carbon-nitrogen model of a grass legume pasture. *Annals of Botany* 75, 79–94.
- Thornley, J.H.M., Cannell, M.G.R., 2001. Soil carbon storage response to temperature: an hypothesis. *Annals of Botany* 87, 591–598.
- Thornley, J.H.M., Verberne, E.L.J., 1989. A model of nitrogen flows in grassland. *Plant Cell and Environment* 12, 863–886.
- Toal, M.E., Yeomans, C., Killham, K., Meharg, A.A., 2000. A review of rhizosphere carbon flow modelling. *Plant and Soil* 222, 263–281.
- Tonitto, C., Powell, T.M., 2006. Development of a spatial terrestrial nitrogen model for application to Douglas-fir forest ecosystems. *Ecological Modelling* 193, 340–362.
- Trumbore, S.E., 1993. Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. *Global Biogeochemical Cycles* 7, 275–290.
- Ulanowicz, R.E., 1979. Prediction, chaos, and ecological perspective. In: Halfon, E. (Ed.), *Theoretical Systems Ecology. Advances and Case Studies*. Academic Press, pp. 107–117.
- van Dam, D., van Breemen, N., 1995. Nicce – a model for cycling of nitrogen and carbon isotopes in coniferous forest ecosystems. *Ecological Modelling* 79, 255–275.
- van Veen, J.A., Ladd, J.N., Frissel, M.J., 1984. Modeling C and N turnover through the microbial biomass in soil. *Plant and Soil* 76, 257–274.
- van Veen, J.A., Paul, E.A., 1981. Organic carbon dynamics in grassland soils. 1. Background information and computer simulation. *Canadian Journal of Soil Science* 61, 185–201.
- Van Wensem, J., Van Straalen, N.M., Koopman, S., 1997. Carbon and nitrogen fluxes in decomposing leaf litter with microbial–detritivore interactions: model simulations compared to microcosm ecotoxicity tests. *Ecological Modelling* 96, 175–189.
- Verberne, E.L.J., Hassink, J., Dewilligen, P., Groot, J.J.R., van Veen, J.A., 1990. Modeling organic-matter dynamics in different soils. *Netherlands Journal of Agricultural Science* 38, 221–238.
- von Luetzow, M., Kogel-Knabner, I., Ludwig, B., Matzner, E., Flessa, H., Ekschmitt, K., Guggenberger, G., Marschner, B., Kalbitz, K., 2008. Stabilization mechanisms of organic matter in four temperate soils: development and application of a conceptual model. *Journal of Plant Nutrition and Soil Science. (Zeitschrift Fur Pflanzenernahrung Und Bodenkunde)* 171, 111–124.
- Waksman, S.A., Tenney, F.G., Stevens, K.R., 1928. The role of microorganisms in the transformation of organic matter in forest soils. *Ecology* 9, 126–144.
- Walter, C., Rossel, R.A.V., McBratney, A.B., 2003. Spatio-temporal simulation of the field-scale evolution of organic carbon over the landscape. *Soil Science Society of America Journal* 67, 1477–1486.
- Wang, L., D'Odorico, P., Manzoni, S., Porporato, A., Macko, S.A., 2009. Carbon and nitrogen dynamics in southern African savannas: the effect of vegetation-induced patch-scale heterogeneities and large scale rainfall gradients. *Climatic Change*, doi:10.1007/s10584-009-9548-8.
- Wang, Y.P., Houlton, B.Z., Field, C.B., 2007. A model of biogeochemical cycles of carbon, nitrogen, and phosphorus including symbiotic nitrogen fixation and phosphatase production. *Global Biogeochemical Cycles* 21.
- Westerhoff, H.V., Lolkema, J.S., Otto, R., Hellingwerf, K.J., 1982. Thermodynamics of growth – non-equilibrium thermodynamics of bacterial-growth – the phenomenological and the mosaic approach. *Biochimica et Biophysica Acta* 683, 181–220.
- Whitehead, P.G., Wilson, E.J., Butterfield, D., 1998. A semi-distributed integrated nitrogen model for multiple source assessment in catchments (INCA): part I – model structure and process equations. *Science of the Total Environment* 210, 547–558.
- Whitmore, A.P., 1996a. Alternative kinetic laws to describe the turnover of the microbial biomass. *Plant and Soil* 181, 169–173.
- Whitmore, A.P., 1996b. Describing the mineralization of carbon added to soil in crop residues using second-order kinetics. *Soil Biology & Biochemistry* 28, 1435–1442.
- Williams, J.R., Jones, C.A., Dyke, P.T., 1984. A modeling approach to determining the relationship between erosion and soil productivity. *Transactions of the ASAE* 27, 129–144.
- Wu, L., McGechan, M.B., McRoberts, N., Baddeley, J.A., Watson, C.A., 2007. SPACSYS: integration of a 3D root architecture component to carbon, nitrogen and water cycling-model description. *Ecological Modelling* 200, 343–359.
- Wutzler, T., Reichstein, M., 2008. Colimitation of decomposition by substrate and decomposers – a comparison of model formulations. *Biogeosciences* 5, 749–759.
- Young, I.M., Crawford, J.W., 2004. Interactions and self-organization in the soil-microbe complex. *Science* 304, 1634–1637.
- Zelenev, V.V., van Bruggen, A.H.C., Leffelaar, P.A., Bloem, J., Semenov, A.M., 2006. Oscillating dynamics of bacterial populations and their predators in response to fresh organic matter added to soil: the simulation model 'BACWAVE-WEB'. *Soil Biology & Biochemistry* 38, 1690–1711.
- Zelenev, V.V., van Bruggen, A.H.C., Semenov, A.M., 2000. "BACWAVE", a spatial-temporal model for traveling waves of bacterial populations in response to a moving carbon source in soil. *Microbial Ecology* 40, 260–272.
- Zhang, C.F., Meng, F.R., Bhatti, J.S., Trofymow, J.A., Arp, P.A., 2008. Modeling forest leaf-litter decomposition and N mineralization in litterbags, placed across Canada: a 5-model comparison. *Ecological Modelling* 219, 342–360.
- Zhang, C.F., Meng, F.R., Trofymow, J.A., Arp, P.A., 2007. Modeling mass and nitrogen remaining in litterbags for Canadian forest and climate conditions. *Canadian Journal of Soil Science* 87, 413–432.
- Zheng, D.W., Ågren, G.I., Bengtsson, J., 1999. How do soil organisms affect total organic nitrogen storage and substrate nitrogen to carbon ratio in soils? A theoretical analysis. *Oikos* 86, 430–442.
- Zheng, D.W., Bengtsson, J., Ågren, G.I., 1997. Soil food webs and ecosystem processes: decomposition in donor-control and Lotka–Volterra systems. *American Naturalist* 149, 125–148.