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SYNTHESIS AND EMERGING IDEAS

An Absorbing Markov Chain approach to understanding the microbial role in soil carbon stabilization

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Abstract The number of studies focused on the transformation and sequestration of soil organic carbon (C) has dramatically increased in recent years due to growing interest in understanding the global C cycle. While it is readily accepted that terrestrial C dynamics are heavily influenced by the catabolic and anabolic activities of microorganisms, the incorporation of microbial biomass components into stable soil C pools (via microbial living cells and necromass) has received less attention. Nevertheless, microbial-derived C inputs to soils are now increasingly recognized as playing a far greater role in stabilization of soil organic matter than previously believed. Our understanding, however, is limited by the difficulties associated with studying microbial turnover in soils. Here, we describe the use of an Absorbing Markov Chain (AMC) to model the dynamics of soil C transformations among three microbial states: living microbial biomass, microbial necromass, and C removed from living and dead microbial sources. We find that AMC provides a powerful quantitative approach that allows prediction of how C will be distributed among these three states, and how long it will take for the entire amount of initial C to pass through the biomass and necromass pools and be moved into atmosphere. Further, assuming constant C inputs to the model, we can predict how C is eventually distributed, along with how much C sequestrated in soil is microbial-derived. Our work represents a first step in attempting to quantify the flow of C through microbial pathways, and has the potential to increase our understanding of the microbial role in soil C dynamics.

Keywords Markov Chain · Microbial biomass · Microbial necromass · Carbon stabilization

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Carbon (C) stabilization in soil (in the past often called "humification") is a critical process in terrestrial organic C dynamics. Yet, despite the large body of literature related to humification, most studies have been focused on chemical characterization and abiotic factors rather than on microbial involvement in formation of stable C (Balser 2005). Microbial contributions to soil C sequestration have historically been regarded as low or even negligible because

active microbial biomass makes up less than 5% of soil organic matter (Dalal 1998; Wardle 1992), and total microbial biomass C is often less than 4% of soil organic C (Anderson and Joergensen 1997; Sparling 1992). However, this may be misleading as living biomass size alone does not indicate potential long-term microbial contribution to soil C pools. In recent years, newer analytical techniques and research reports increasingly indicate a far greater role for the incorporation of microbial biomass and necromass into soil stable C pools than previously believed (Grandy and Neff 2008; Kiem and Kogel-Knabner 2003; Kindler et al. 2006, 2009; Kramer et al. 2003; Liang and Balser 2008; Miltner et al. 2009; Simpson et al. 2007; von Lützow et al. 2006; Yao and Shi 2010; Zech et al. 1997). These studies show that the importance of microorganisms includes their ability to "leave behind" senesced biomass, and to produce recalcitrant compounds that accumulate in soils. Driven by their relatively rapid turnover time, microorganisms add to soil C in the continuously iterative process of cell generation, population growth and death. Potthoff et al. (2008) recently revealed that net changes in microbial biomass strongly underestimate the incorporation of substrate-C into a stable fraction, indicating the standing biomass of microbes does not necessarily reflect microbial function to soil C storage. Microbial cellular components may also be selectively preserved because of their characteristic chemical structure and organo-mineral complexes (Baldock and Skjemstad 2000; Sollins et al. 1996; von Lützow et al. 2006). Thus, despite the relatively small absolute amount of living microbial biomass in a given soil, it is essential to evaluate the importance of microbial biomass-C stabilization processes. However, a reliable approach to differentiate between the C bound in microbial residues (living or dead biomass) and background soil organic C is elusive and technically difficult. Alternatively, modeling conceptual C pools can help us understand different compartments of soil C (Allison et al. 2010; Falloon and Smith 2000; Feng 2009a, b). Here we describe the use of Markov Chain analysis to increase our understanding of the microbial contribution to stable soil C.

The Markov Chain is a powerful mathematical modeling tool developed to describe certain stochastic processes evolving in time, and has been widely applied in economics, the health services, and engineering among others (Ching and Ng 2005). At each step in a Markov Chain, the system of interest may either change state from its current state to another, or may remain in the same state according to a certain probability distribution. The changes of state are called transitions, and the probabilities associated with various state-changes are called transition probabilities. We propose that a Markov model might be used for describing C dynamics among the states of living microbial biomass, microbial necromass and atmosphere (CO_2 in air) in aerobic terrestrial environments.

To elucidate the microbial contribution to stable soil C, it is necessary to tease apart the living and dead microbial biomass-C and distinguish it from background soil C. By defining C transformation as a function of three microbial states: living biomass (L), necromass (D), and air (A, removed from the microbial processing regime) (Fig. 1), the Markov Chain provides a quantitative approach to making such distinctions. In particular, the model proposed

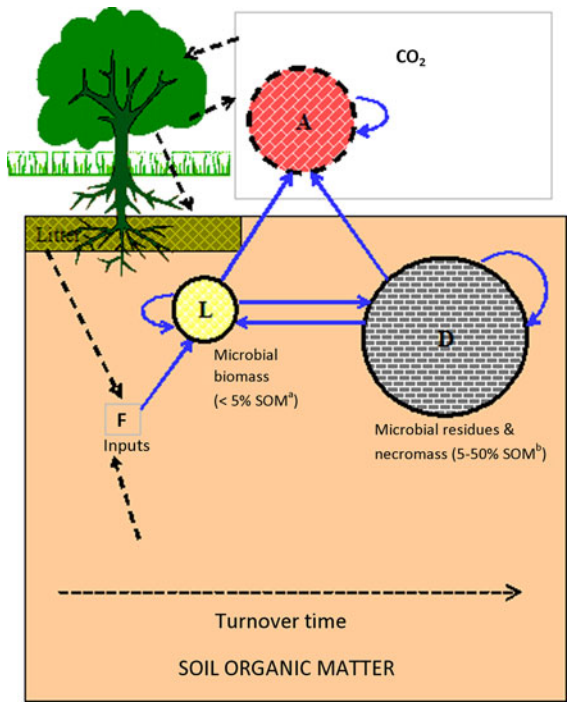

Fig. 1 Characterization of the microbial states and their relationship to soil C dynamics in an aerobic terrestrial system. The *total box* represents soil C. Pools are not sized to accurate scale. *L*, *D* and *A* represent the three states of living microbial biomass, microbial necromass and C removed from microbial sources to the air, respectively. *Solid arrows* represent transition events. F represents input to the model from litter and soil C sources. *Dotted arrow lines* indicate transitions not included in the model structure. [a] Dalal 1998; [b] Simpson et al. 2007

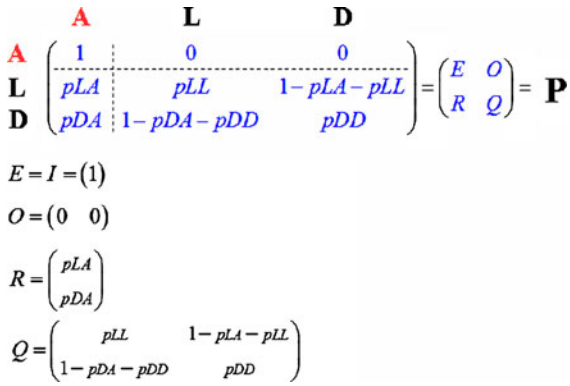

Fig. 2 Transition matrix P for absorbing Markov model. *L*, *D* and *A* represent the three states of living microbial biomass, microbial necromass and C removed from microbial sources to the air, respectively. p_{ij} is the *transition probability* from state i to state j ($p_{AA} = 1$), $p_{AL} = 0$, $p_{AD} = 0$, p_{LD} and p_{DL} are calculated by Eq. 1; transition probability distribution is represented by the *transition matrix* with the ij covering all states, i.e. P = [p_{ij}]; E and O are identity matrix and zero matrix. *E*, *O*, *R* and *Q* are defined in the figure as well

here is an "Absorbing Markov Chain" (AMC) because it has an "absorbing state": carbon released as CO_2 to the air is "absorbed" into that state indefinitely and is not returned to the soil. This is based on the assumption that atmospheric CO_2 is not directly accessed and utilized by soil microbial communities. The overwhelming majority of C entering a microbial state is derived from plant fixed and soil extant C.

Transitions among states in a Markov Chain are determined by the use of a matrix (here labeled **P** (Fig. 2)) to quantify transition probabilities. In order to achieve the goal of quantifying the size and rate of sequestrated C in soils as determined by microbial inputs, the following quantities are necessary as inputs to the model: (i) living microbial biomass at present; (ii) microbial necromass (senesced biomass) over time; (iii) a transformation rate among the three states (living (L), dead (D), and air (A)).

The transition matrix in Fig. 2 can be expressed in canonical form by four block matrices *E*, *O*, *R* and *Q*, where, in our matter, they are respectively

$$E = I = (1); \quad O = (0 \quad 0); \quad R = \begin{pmatrix} pLA \\ pDA \end{pmatrix};$$
$$Q = \begin{pmatrix} pLL & 1 - pLA - pLL \\ 1 - pDA - pDD & pDD \end{pmatrix}$$

$$\text{where } \sum_{j=1}^{n} p_{ij} = 1(\text{i} = 1, 2, \ldots, \text{n}) \tag{1}$$

If we allow $X^{(t)}$ to denote the distribution of C among the three states after t-step transitions from the initial state $X^{(0)}$, then based on the Markov Chain, we know that $X^{(t)} = X^{(0)}\mathbf{P}^t$ and the transition matrix **P** can be calculated by

$$\mathbf{P}^t = \begin{pmatrix} E & O \\ Rt & Q^t \end{pmatrix} \tag{2}$$

where $Rt = (I + Q + Q^2 + \ldots + Q^{t-1})R$.
$X^{(t)}$ can thus be computed as

$$X^{(t)} = X^{(0)} \begin{pmatrix} 1 & O \\ Rt & Q^t \end{pmatrix} \tag{3}$$

where Q^t will degenerate to zero as $t \to \infty$ since there exists an absorbing state in this Markov Chain model.

This provides us with an estimate of the fate of microbial C as it flows into different pools over time. However, we are also interested in how long an initial amount of microbial C might remain stabilized in soil. An AMC model can help with this as well. The "C residence time" in a soil system depends on the number of all transitions among states before the C enters into the air (absorbing state). We can calculate the number of transitions from the state i to j using the below expectation

$$M\left[\sum_{S=0}^{\infty} C(S)\right] = \sum_{S=0}^{\infty} p_{ij}^{(S)} = \mathbf{n}ij \tag{4}$$

where C(S) is the number of transitions from state i to j, and M(S) is mathematical expectation of the random variable C(S) (Note that C(S) is random in this case).

The element n_{ij} in the above is actually the (*i*, *j*)-th element of the "fundamental matrix", **N**, which can be determined for any AMC. **N** is defined for our model in (5) and (6).

$$\text{I}-\mathbf{Q} = \begin{pmatrix} 1 - pLL & pLA + pLL - 1 \\ pDA + pDD - 1 & 1 - pDD \end{pmatrix} \tag{5}$$

$$\mathbf{N} = (\text{I} - \text{Q})^{-1} = I + Q + Q2 + Q3 + \ldots = \begin{pmatrix} Lx & Ly \\ Dx & Dy \end{pmatrix} \tag{6}$$

where **N** is a 2-by-2 square matrix, and

$$Lx = \frac{1 - pDD}{pLA + pDA - pDApLA - pDDpLA - pDApLL}$$

$$Ly = \frac{1 - pLA - pLL}{pLA + pDA - pDApLA - pDDpLA - pDApLL}$$

$$Dx = \frac{1 - pDA - pDD}{pLA + pDA - pDApLA - pDDpLA - pDApLL}$$

$$Dy = \frac{1 - pLL}{pLA + pDA - pDApLA - pDDpLA - pDApLL}$$

Based on the derivations (provided in Appendix), we can approximate the time that C can exist in the microbial system by

$$T = [m/(m+n)](Lx + Ly - 2) + [n/(m+n)](Dx + Dy - 2) \quad (7)$$

where *m/n* is the initial ratio of L/D.

From Eq. 7, the sum of Lx and Ly will tell us how long the C may remain in living microbial biomass (L) before entering the air (absorbing state A); likewise, the sum of Dx and Dy will tell us how long the C may stay in microbial necromass (D). Furthermore, if we know the initial C distribution ratio *m/n* between living microbial biomass (L) and microbial necromass (D), we can approximate how long the initial C might persist in the microbial system by Eq. 7.

Note that Q^t will degenerate to zero as $t \to \infty$ in this AMC Model (Eq. 3). Thus, without continuous C inputs, all C in the system will eventually enter the air (be removed through microbial processing). In reality, vegetation and soil organic matter supplies C continuously to the soil microbial community. When we let a constant F = [f; 0] represent the continuous input vector to our AMC system, where f corresponds to the input of L, we can obtain the stable status (by the derivations in the Appendix) of the states of L and D, given the above inputs:

$$X_{t\to\infty}^{(t)} = F \cdot N = (f \cdot Lx \quad f \cdot Ly) \quad (8)$$

where $L_{(stable)} = f \cdot Lx$; $D_{(stable)} = f \cdot Ly$.

One consequence of Eq. 8 is that an AMC with constant inputs will stabilize to a stable state, which is irrelevant to initial distribution but depends on the input vector F. Therefore, with constant C inputs in our proposed model, we can predict that C will be stabilized in the living microbial biomass and microbial necromass in the future at $f \cdot Lx$ and $f \cdot Ly$, respectively. This may indicate a microbial analog to the concept of "ecosystem carrying capacity", which technically refers to the equilibrium maximum of the population of a species that a given ecosystem can support (del Monte-Luna et al. 2004). The AMC analysis thus predicts a soil "microbial carrying capacity" that represents the amount of C that microorganisms can sustain. Depending on ecosystem properties, the microbial C-carrying capacity may vary for different soils, or may change over time when limiting factors get changed. Eq. 8 is also significant in that it presents the first quantitative estimation ($f \cdot Lx + f \cdot Ly$) of the total size of microbial-derived C persisting in soil.

Given the difficulty of validating the model with existing data, and the technical challenges involved in directly quantifying these pools and transitions, we present a sample of model output using rough and theoretical data that is not intended to accurately represent any particular system. The intention is to demonstrate model output and behavior for a sample set of parameters (Fig. 3). With constant inputs to AMC, one of the model's strengths is its ability to output steady-state pool information after sufficient transitions in soils (Eq. 8). The model output reveals that, given this rough set of transition probabilities, the stable state of the necromass pool ($D_{stable} = 444.26$) is almost 40 times that of the living biomass pool ($L_{stable} = 11.17$).

As a whole, using the proposed transition matrix in an AMC system, we can predict several quantities that improve our understanding of C cycling in soils. The Markov model is uniquely useful in its assumption that the soil system changes involve a random component (stochastic) and that absolute predictions of a future state are impossible. The Markov model allows us to consider statistical probabilities and conditional distributions of the system's future. In particular, the AMC model is able to predict the future's "state" after a fixed number of steps and also calculate expected number of steps necessary to complete absorption. Consequently, this provides an estimate of how an initial amount of C will be distributed among the three states (L, D and A) over time, and also how long it will take for the entire amount of initial C to move out of the microbial processing regime into air. Furthermore, adding constant plant C and soil extant C inputs (F) allows

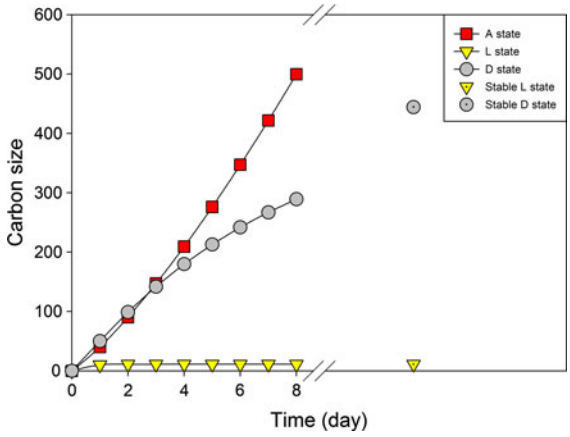

Fig. 3 Absorbing Markov Chain model output for a sample set of parameters. *L*, *D* and *A* are the model pools of C in the living microbial biomass, microbial necromass and air, respectively. Stable states for *L* and *D* are calculated as shown in Eq. 8. Carbon units are arbitrary; time units as parameterized are in days but are also arbitrary. Note: Model parameterization for this demonstration is as follows. The pools are all initially set to 0 for this model run. The daily constant input F is set to 100. The probability values for pool transfers are using a daily timestep. C in the air remains in the air, thus pAA = 1 (absorbing pool). C is transferred from living microbial biomass to CO_2 with a probability of 1-CUE (the carbon use efficiency, e.g. Allison et al. 2010). Here we use pLA = 0.4, setting CUE to 0.6 (Feng 2009a, b). A death probability of pLD = 0.5 (Feng 2009a, Table 1 and references therein) allows a derivation of the probability of C remaining in living microbial biomass (1 − pLD − pLA), pLL = 0.1. The probability of microbial necromass C having been transferred into the living pool, pDL = 0.000114, was parameterized by converting the inverse of the mean residence time of soil microbial residues (24 years per Feng 2009b, Table 1) to a daily timestep. The probability that C will have been transferred from necromass to CO_2, possibly by passing through the living biomass, by the next timestep is pDA. An estimate for the reuptake rate (25%, based on the results of Kindler et al. 2006) is multiplied by an estimate of the probability that such reuptake would have been mineralized to CO_2 by the next timestep (50%, based on the results of Kindler et al. 2006), giving a parameter value of 0.125. The probability of C remaining in microbial necromass (1 – pDL − pDA), pDD = 0.874886

us to predict the stable distribution of C in each state after sufficient transitions in different soils.

Further work is needed to create datasets and parameterizations that would allow for formal model testing to monitor and predict microbial-derived C flow in soils. We are currently unable to satisfactorily validate this model using published values because we lack accurate experimentally obtained transformation rates among the three states. However, we see promise in using isotopically labeled substrate C incubated in aerobic microcosms as a way to provide an indirect estimation of the necessary parameters. Samples collected in a time-series and analyzed for living microbial biomass, microbial necromass and CO_2 evolution, using microbial biomarker PLFA and amino sugar analysis in combination (see Liang et al. 2008), with isotopic tracers, may allow quantification of the C present in the three model microbial states at the different sampling times. These measurements would allow us to estimate the transition matrix under the assumption that AMC is stationary. Specifically, the transition matrix at each step can be solved from a system of equations (Eq. 3), and the estimated transition matrix can be calculated as the weighted average of the transition matrices estimated for each transition. The weights are calculated as the values which minimize the error between the predicted values and actual values. In addition, the model can be further enhanced by disjoining general microbial identity into fungi and bacteria, in order to obtain a more complete picture of microbial C dynamics. We are currently completing a laboratory study to access these model parameters in this way.

In summary, our AMC model is a quantitative approach that allows quantification of C stabilization in soils through microbial inputs and actions. We acknowledge that this is a somewhat limited application; nevertheless we hope it provokes discussion of the possible importance of microbial necromass. In addition, its elucidation of microbial C processing can help clarify and quantify the percentage of total C in soil that is microbially derived. This could then be incorporated into more conventionally accepted models. Our work represents a first step in quantifying the flow of C through microbial pathways, and has the potential to increase our understanding of the full microbial role (both catabolic and anabolic) in soil C dynamics.

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Appendix

Prove why $T = [m/(m + n)](Lx + Ly - 2) + [n/(m + n)](Dx + Dy - 2)$ holds:

Step 1: we first show that the expected number of transitions from state L to state D is the (1; 2)-th element of the fundamental matrix **N** minus one, i.e. Ly − 1.

Let C(s) = 1 if the C starts from L and enters D in the s-th step, C(s) = 0 otherwise. In order to calculate the expectation of C(s), we need to know the probability of the event that C starts from L and enters D in the S-th step, denoted by $p_{LD}^{(S)}$. In other words, the expectation is

$$M[C(S)] = \sum_{S=1}^{\infty} p_{LD}^{(S)}$$

By the Markov Chain rule, we know $p_{LD}^{(S)}$ equals to the (2, 3)-th element of P^S. Furthermore, we know it also equals to the (1, 2)-th element of Q^S by the canonical form of P^t. Hence, we have

$$M[C(S)] = \sum_{S=1}^{\infty} p_{LD}^{(S)} = \sum_{S=1}^{\infty} Q_{12}^{(S)} = Ly - 1$$

The last equality follows from Eq. 6

$$\mathbf{N} = (\mathrm{I} - \mathrm{Q})^{-1} = \mathrm{I} + \mathrm{Q} + \mathrm{Q}^2 + \mathrm{Q}^3 + \ldots$$

Step 2: We next calculate the expected number of transitions that the C transit from the state L or D to the air state. We consider two cases: (i) C starts from L; (ii) C starts from D.

For the case (i), the expected number of transitions from *L* to *L* (*D*) is *Lx* − 1 and *Ly* − 1, respectively, based on the results in step 1. For the case (ii), the expected number of transitions from *D* to *L* (*D*) is *Dx* − 1 and *Dy* − 1, respectively, based on the results in step 1. Then, the expected number of total transitions equal to

P(C starts from L) × (*Lx* + *Ly* − 2) + *P*(C starts from D) × (*Dx* + *Dy* − 2) =

$$[m/(m+n)](Lx + Ly - 2) + [n/(m+n)](Dx + Dy - 2)$$

This completes the whole proof.

Prove why L(stable) = f · Lx and D(stable) = f · Ly holds:

We first have the following relations:

$$\mathrm{Z}^{(0)} = \left[\mathrm{L}^{(0)}; \mathrm{D}^{(0)}\right]$$
$$\mathrm{Z}^{(1)} = \mathrm{Z}^{(0)}\mathrm{P} + [\mathrm{f}; 0]$$
$$\mathrm{Z}^{(2)} = \mathrm{Z}^{(1)}\mathrm{P} + [\mathrm{f}; 0]$$
$$\ldots$$

where $(L^{(0)}; D^{(0)})$ are the initial distribution of (L; D), respectively. Based on the above relation, we can prove that

$$\left[\mathrm{L}^{(\mathrm{k})}; \mathrm{D}^{(\mathrm{k})}\right] = \left[\mathrm{L}^{(0)}; \mathrm{D}^{(0)}\right]\mathrm{Q}^k + [f; 0]\left(I + \sum_{i=1}^{k-1} Q^i\right)$$

through mathematical inductions. Since our model is the AMC, $Q^k \to \infty$ as $k \to \infty$. Then we have

$$\left[\mathrm{L}^{(\mathrm{k})};\ \mathrm{D}^{(\mathrm{k})}\right] \to [f; 0]\left(I + \sum_{i=1}^{k-1} Q^i\right) \to [f; 0]N$$

by the equation that $N = (I - Q)^{-1} = I + Q + Q^2 + \ldots$

Hence we have L(stable) = f · Lx and D(stable) = f · Ly as k approaches infinity.

This completes the whole proof.

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