

Soil Biota and Global Change

Soil biota and global change at the ecosystem level: describing soil biota in mathematical models

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Abstract

All current mathematical models of the soil system are underpinned by a wealth of research into soil biology and new research continues to improve the description of the real world by mathematical models. In this review we examine the various approaches for describing soil biology in mathematical models and discuss the use of each type of model in global change research. The approaches represented among models participating in the Global Change and Terrestrial Ecosystems (GCTE) Soil Organic Matter Network (SOMNET) are described. We examine the relative advantages and constraints of each modelling approach and, using these, suggest appropriate uses of each. We show that for predictive purposes at ecosystem scale and higher, process-orientated models (which have only an implicit description of soil organisms) are most commonly used. As a research tool at the ecosystem level, both process-orientated and organism-orientated models (in which functional or taxonomic groups of soil organisms are explicitly described) are commonly used. Because of uncertainties introduced in internal model parameter estimation and system feedbacks, the predictive use of organism-orientated models at the ecosystem scale and larger is currently less feasible than is the use of process-orientated models. In some specific circumstances, however, an explicit description of some functional groups of soil organisms within models may be required to adequately describe the effects of global change. No existing models can adequately predict the feedback between global change, a change in soil community function, and the response of the changed system to future global change. To find out if these feedbacks exist and to what extent they affect future global change, more research is urgently required into the response of soil community function to global change and its potential ecosystem-level effects.

Keywords: ecosystem, global environmental change, mathematical models, soil biota, soil organic matter network (SOMNET), soil organic matter

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Introduction

An ecosystem is to some extent shaped by its soil biota. The soil biota are the main agents in mediation of the rate of nutrient release, which in turn influences the

growth and community structure of plants, and thereby the functioning of the whole ecosystem. The vast wealth of soil biological research, even if it not apparent from the model structure, underpins all current mathematical models of the soil system. New soil biological research continues to improve the description of the real world

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by mathematical models. In this review we examine the various approaches for incorporating soil biology into mathematical models and discuss the use of each type of model in global change research.

A number of recent reviews have dealt in some way with the role of soil biota in ecosystem models and soil organic matter (SOM) models, e.g. Paustian (1994), McGill (1996), Molina & Smith (1997), and Brussaard (1997). These reviews are collectively quite comprehensive and we will not attempt to cover the same ground here — instead we will give an overview of the types of models available for simulating and predicting the ecosystem-level effects on soil of global environmental change. We present the approaches reflected in models participating in the Global Change and Terrestrial Ecosystems (GCTE) Soil Organic Matter Network (SOMNET; Smith *et al.* 1996a,b; Powlson *et al.* 1998). We also suggest situations in which each type of model is most appropriately used to study global change considering the main advantages and constraints of each approach.

McGill (1996) presents a scheme for classifying and comparing SOM models in which he examined nine SOM models used in a model evaluation and comparison exercise (Powlson *et al.* 1996; Smith *et al.* 1997a). One aspect he examined was the biotic component of models; indeed one of his three main conclusions was that a more mechanistic treatment of soil organisms was required. He also emphasized (a) the importance of cross-scale (temporal and spatial) comparisons, links to geographical information system (GIS), and of determining an appropriate level of detail needed as a function of scale; and (b) the importance of physical fractionations of soil to relate soil structure through organism-substrate accessibility to turnover rates.

Paustian (1994) provides a review closely focused on the description of soil organisms in simulation models. He reviewed nine groups of models and emphasized the distinction between 'process-oriented' and 'organism-oriented' models. These terms are used throughout this paper and are described in greater detail below. In common with McGill (1996), Paustian emphasized the importance of relating soil structure to soil organic matter and nutrient dynamics and on reconciling measurable organic matter pools with the theoretical pools used in models. These arguments, further developed by Elliott *et al.* (1996) and Christensen (1996), have yet to be resolved. The other main area he identified for future development was a greater examination of the links between soil community structure and soil processes. He further identified a need for comprehensive model validation across a range of soil climate and management conditions and recognized experimental site networks, GIS, and adoption of modular programming methods as factors that would facilitate these developments.

Brussaard (1997) divides models into food web models (analogous to Paustian's organism-orientated models) and organic matter models (analogous to Paustian's process-orientated models). In organic matter models, he noted that apart from inclusion of the microbial biomass, soil biota were ignored. In food web models, he noted that although the soil biota were divided into functional groups, soil organic matter and litter were not specified beyond roots and detritus. He also presents examples of comparisons between process- and organism-orientated approaches and provides a thoughtful discussion of the relative advantages and limitations of food web models when used in global change research.

Two approaches — process-orientated models and organism-orientated models

Both process-orientated and organism-orientated models use information derived from soil biological research, but each uses the information in a different way. Paustian (1994) describes process-orientated models as those which focus on the processes mediating the movement and transformations of matter or energy; soil organisms are mainly implicit in the model formulations and organism components, if present, tend to represent a generic soil biomass, i.e. an undifferentiated mass of organisms in the soil. In many models, the soil microbial biomass is treated as an active (and often measurable) pool of soil organic matter (e.g. Molina *et al.* 1983; Parton *et al.* 1988; Jenkinson 1990; Arah 1996; Mueller *et al.* 1996). As McGill (1996) emphasizes, there is some justification for this approach but he suggests that this simple treatment of biomass precludes the possibility of simulating changes that occur because of changes in the activity or characteristics of the soil organisms. Process-orientated models describe fluxes of soil carbon with varying levels of complexity. Some use one-compartment (e.g. Jenny 1941), some two (e.g. Jenkinson 1977), some are noncompartmental, describing decomposition as a continuum (e.g. Bosatta & Ågren 1985), but most have more than two compartments, i.e. they are multicompartment (see McGill 1996). Models differ in detail but an example of the structure of a multicompartment process-orientated model, in this case DAISY, is shown in Fig. 1.

Organism-orientated models (called food web models by Brussaard 1997) are more diverse in nature than are process-based models but fewer have been developed (see below). All model the flows of matter or energy through different groups of soil organisms, which are described either by functional or taxonomic groups. Examples of organism-orientated models include a fungal growth model developed by Paustian (1985), a model of decomposition in grasslands which includes functional groups of microbial biomass but does not divide the

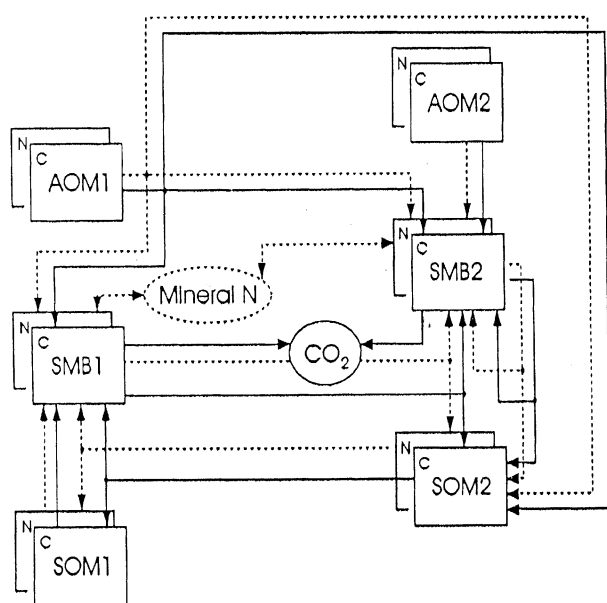


Fig. 1 Example of the structure of a multicompartimental, process-orientated model, in this case DAISY (from Mueller *et al.* 1996). AOM = Added organic matter; SMB, Soil microbial biomass; SOM, Soil organic matter.

biomass by taxonomic group (Hunt 1977), and other models of Hunt and coworkers which describe the detrital food web by taxonomic group (e.g. Hunt *et al.* 1987; see also Wardle *et al.* (1998, this volume) for further discussion of food webs). Other researchers have also used organism-orientated models extensively, notably those among the group at AB-DLO, Haren, The Netherlands. This group has used such models to explore N mineralization in arable soils (e.g. de Ruiter *et al.* 1993a), and C and N mineralization in grassland soils (e.g. Hassink *et al.* 1994). Many uses are described in a number of other studies (de Ruiter *et al.* 1993b, 1994, 1995). An example of the structure of an organism-orientated model, in this case the detrital food-web model of de Ruiter *et al.* (1993a), is shown in Fig. 2.

A few models have incorporated aspects of both process-orientated and organism-orientated approaches. Paustian *et al.* (1990), for example, use this approach in their description of C and N flows through various groups of soil organisms in agroecosystems. McGill *et al.* (1981) developed a predominantly process-orientated model but bacteria and fungi were assumed to directly control decomposition. In the model of van Veen & Frissel (1981) the rate constant for decomposition was assumed to be controlled by microbial biomass. There is no intrinsic reason why ecosystem models should not include aspects of both process- and organism-orientated approaches if required, especially if they are programmed in a modular way. The possibility of further combined approaches is discussed later.

Models represented within the GCTE Soil Organic Matter Network (SOMNET)

The models described in this section participate in the GCTE SOMNET [full details of all models can be found on the GCTE SOMNET World-Wide-Web page at URL: <http://yacorba.res.bbsrc.ac.uk/cgi-bin/somnet>; a summary of all model (and experimental) metadata can be found in Smith *et al.* (1996b)]. Models participating in SOMNET (with notes and key references) are shown in Table 1 and are categorized as either process- or organism-orientated, according to the classification of Paustian (1994). None, however, fall into the organism-orientated category which may partly reflect the way in which the network was established; it initially focused on models that could describe soil organic matter dynamics in long-term field experiments (Powlson *et al.* 1996) as historically, process-orientated models have always been deemed more appropriate for simulating SOM dynamics over long periods. The fact that no organism-orientated models are represented in SOMNET may also reflect the fact that far fewer organism-orientated models have been developed.

Many of the process-orientated models shown in Table 1 do contain some description of organisms but this is confined to generic biomass as described earlier. There are subtle differences in the way in which biomass is included in the models but elaboration of these differences would require unwarranted space in a review of this kind. Molina & Smith (1997) provide a more detailed description.

Some of the models specify microbial biomass (i.e. excluding meso- and macro-fauna; Pankhurst & Lynch 1994) but only one model, SOMM, describes larger organisms (earthworms and microarthropods) specifically. In SOMM, which was originally developed for forest soils, there are some distinctions of humus forms based on different abundances and roles of microarthropods and earthworms. These differences in turn affect the way the model treats organic matter turnover (Chertov & Komarov 1996). Despite this distinction, the model is predominantly process-orientated.

Different uses of each type of model in global change research

Models may be used for a range of purposes (Pielou 1981) and there are many possible applications of models in global change research. Among other things, models can be used as research tools to test hypotheses about the soil system, for example to examine contrasting hypotheses of nitrogen mineralization and immobilization. They can also be used predictively, for example to estimate fluxes of CO₂ and trace gases after changes in

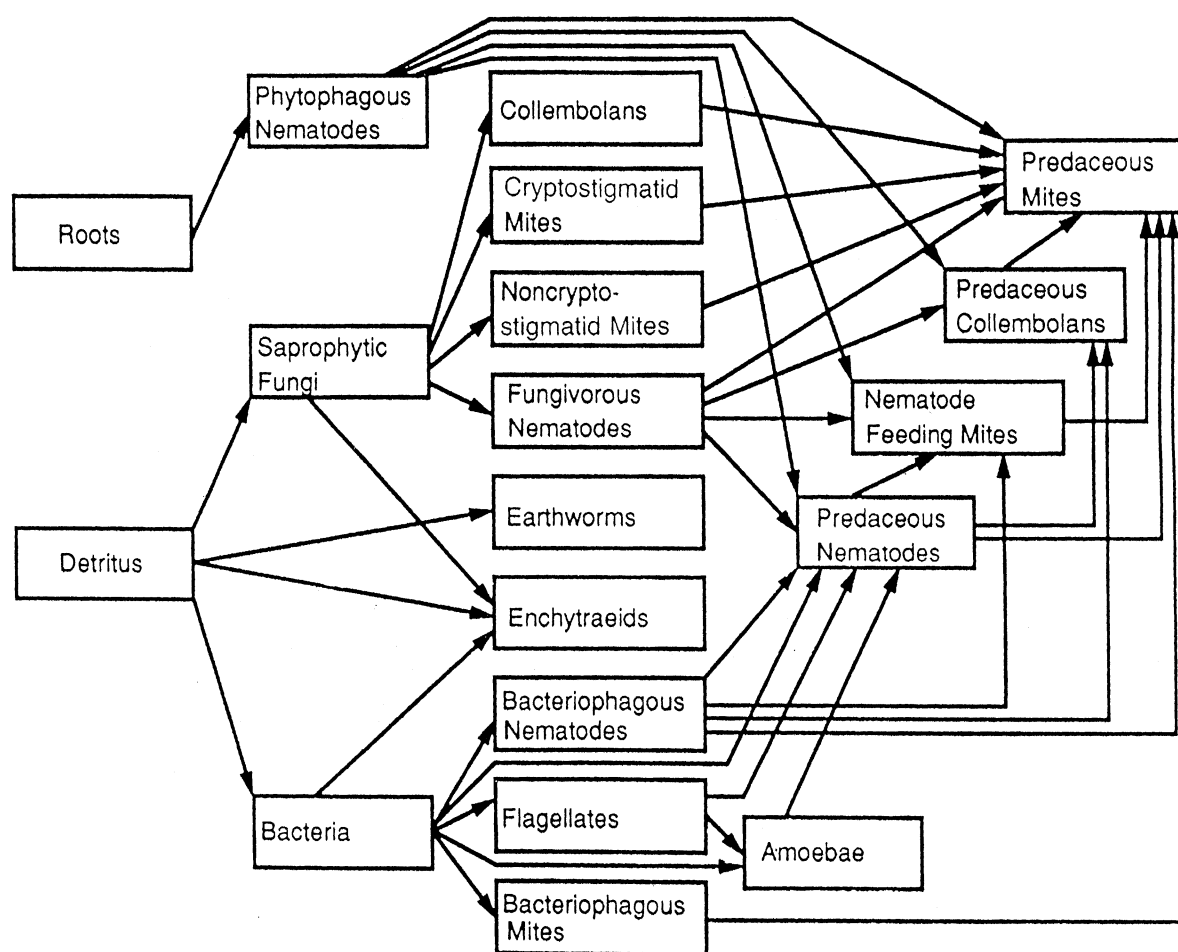


Fig. 2 Example of the structure of an organism-orientated model, in this case the detrital food-web model of de Ruiter *et al.* (1993a). The figure shows the food web at Lovinkhoeve experimental farm, Marknesse, Noordoostpolder, The Netherlands.

land-use or during climate change. As well as being used to answer different types of question, models are also used at vastly different scales. Some models are intended to be used at the microsite scale over periods of hours or days whilst others are used at the ecosystem, regional and global scales for periods of years or decades. When assessing the suitability of each type of model in global change research it is important to clearly identify the question being asked and at what scale the question is best answered. In this paper we consider both purpose and scale; in terms of scale (in line with the objectives of this volume) we consider the use of models only at the ecosystem scale and greater, whilst in terms of purpose, we consider the use of models both as research tools and predictive tools.

Use of soil ecosystem models as research tools

Both process-orientated and organism-orientated models are used as research tools. All of the process-orientated

models in Table 1 and the models given as examples of organism-orientated models above have been used to test our understanding of the soil system and its response to various environmental perturbations. Often, the different approaches have been applied to the same problem; for example the processes of nitrogen mineralization and immobilization have benefited from the application of both process-orientated models (e.g. Molina *et al.* 1983) and organism-orientated models (e.g. Hunt *et al.* 1987).

Organism-orientated models have already provided insights into the details of C and N flows through food webs (Hunt *et al.* 1984, 1987; Paustian *et al.* 1990), and particularly the role of soil biota in C and N mobilization (Paustian 1994). They have also proved to be useful tools in environmental risk assessment and in assessing the environmental effects of soil contaminants (P.C. de Ruiter, personal communication); in guiding monitoring programs and as a link to above ground food webs (O.W. Heal, personal communication); and as a tool to look at spatial variability at different scales (M. Van Noordwijk,

Table 1 Broad categorizations of the models participating in SOMNET

Model	Model type	Notes	Reference
ANIMO	Process	Biomass included	Rijtema & Kroes (1991)
Candy	Process		Franko <i>et al.</i> (1995), Franko (1996)
CENTURY	Process	Biomass included	Parton <i>et al.</i> (1988)
DAISY	Process	Biomass included	Svendsen <i>et al.</i> (1995), Mueller <i>et al.</i> (1996)
DNDC	Process	Biomass included	Li <i>et al.</i> (1994)
DSSAT	Process		Hoogenboom <i>et al.</i> (1994)
D3R	Process		Douglas & Rickman (1992)
ecosys	Process	Biomass included	Grant <i>et al.</i> (1993a,b), Grant (1995)
EPIC	Process	Biomass included	Williams (1990)
FERT	Process	Biomass included	Kan & Kan (1991)
GENDEC	Process	Biomass included	Moorhead & Reynolds (1991)
Hurley Pasture ITE(Edinburgh) Forestry Model	Process	Biomass included	Thornley & Verberne (1989) Thornley & Cannell (1992)
KLIMAT-SOIL-YIELD	Process	Biomass included	Sirotenko (1991)
McCaskill & Blair			
CNSP Pasture Model	Process		McCaskill & Blair (1990a,b)
Model of Humus Balance	Statistical *	Static model based on statistical relationships *	Schevtsova & Mikhailov (1992)
MOTOR	Process	Biomass included user-defined inputs and outputs	Whitmore (1995)
NAM SOM	Process	Two differential equations	Ryzhova (1993)
NCSOIL	Process	Biomass included	Molina <i>et al.</i> (1983)
O'Leary Model	Process	Fallow-Wheat only	O'Leary (1994)
Q-Soil	Process	Non-compartmental model	Ågren & Bosatta (1987)
RothC	Process	Biomass included	Jenkinson & Rayner (1977)
SOCRATES	Process	Biomass included	Grace & Ladd (1995)
SOMM	Process	Some distinctions of humus forms based on different roles of soil fauna (microarthropods and earthworms)	Chertov & Komarov (1996)
Sundial	Process	Biomass included	Smith <i>et al.</i> (1996), Bradbury <i>et al.</i> (1993)
Verberne	Process	Biomass included	Verberne <i>et al.</i> (1990)
VOYONS	Process	Composite model using many submodels	André <i>et al.</i> (1994)
Wave	Process	Biomass included	Vanclooster <i>et al.</i> (1995)

* All other models are dynamic process-orientated models. Note that none are organism-orientated

pers. comm.). Brussaard (1997) makes a convincing case for using organism-orientated (food web) models for integrating current knowledge and for guiding research in a very complex system. Food web models are, of course, also of critical importance when assessing the stability of the below-ground food webs under global change (De Ruiter *et al.* 1995; Brussaard 1997).

The main advantage of organism-orientated models for use in global change studies at the ecosystem level is the inclusion of an explicit description of soil biota which potentially allows the simulation of changes in soil C, N, SOM or energy that occur due to changes in the activity or characteristics of those organisms. McGill (1996) also noted that without the explicit inclusion of soil organisms, process-orientated models could not include such feedback mechanisms. A note of caution is required here:

there is evidence that organism abundances rarely limit process rates at the ecosystem level (see Paustian 1994). Reasonable arguments have been made which claim that the soil organisms are there and they do their job — which is why first-order kinetics work so well in the simple models (e.g. Andrén *et al.* 1994). The ecosystem can also be viewed as a hierarchy, with processes at a high level, fairly isolated from the organisms and their interactions well below (O'Neill *et al.* 1986). This view has been modified, or to some extent challenged (Beare *et al.* 1994), but the 'importance' of species numbers, population dynamics, etc. for ecosystem processes remains an open question.

Despite the need for caution outlined above, there are probably qualitative and quantitative changes in soil community structure which occur as a result of environ-

mental perturbation that will affect ecosystem level process rates, and such feedbacks may be best simulated by an explicit description of soil organisms. Large and immediate environmental changes, for example a change in land-use from grassland or forest to arable agriculture, may be relatively easy to define in terms of changes in the soil community. Ecosystems and possible functional groups of soil organisms where this may be necessary are detailed elsewhere in this volume (e.g. Swift *et al.* 1998, this volume).

It should be noted, however, that although organism-orientated models (with some process-based components) have been used to study the effects of climate change (Hunt *et al.* 1991), much research is still required into the effects of global change on soil community function so that models can be parameterized to simulate and predict system feedbacks. The problem of defining the feedback between global change, its effects on soil community function, and the subsequent response of the system to further global change is discussed further in the last section in this paper.

Use of soil ecosystem models as predictive tools

Most mathematical models of the soil were developed as research tools; as encapsulations of a number of hypotheses of how the soil functions. However, policy-makers (and others) increasingly demand that models be used to predict how the soil system will respond to various changes in the future. For this reason we need to consider which type of model is most appropriate for use as a predictive tool at spatial scales as large as the ecosystem and larger, and at temporal scales of many years or decades. Although organism-orientated models have been used to assess the impact of global change at the ecosystem level (e.g. Hunt *et al.* 1991), process-orientated models are currently far more commonly used (e.g. Post *et al.* 1982; Jenkinson *et al.* 1991; Donigan *et al.* 1994; Schimel *et al.* 1994; Parton *et al.* 1995).

There are a number of reasons for the greater use of process-orientated models for predictive purposes compared with organism-orientated models: first, their internal parameters (such as rate constants or rate modifiers) are easier to estimate. These are often derived from field experiments (e.g. Jenkinson & Rayner 1977), and less commonly from laboratory incubations (e.g. Molina *et al.* 1983). Consequently, it is simpler to calibrate process-orientated models for a specific purpose. Site specific calibration of organism-orientated models involves more complex and labour-intensive measurements. For example, the model described by Hunt *et al.* (1987) requires that for each group of organisms, the following parameters be measured or estimated: feeding preferences, nitrogen contents, life spans, assimilation efficien-

ies, production:assimilation ratios, decomposabilities and population sizes. Since there are inevitably many functional or taxonomic groups of organisms present in the soil community, the estimation of these parameters is difficult and introduces a large degree of uncertainty into the process of model parameterization. Some authors have questioned if the organism-orientated approach can ever give insights into real systems when all possible errors are taken into account, particularly since organism populations and their preferences and activities fluctuate at varying rates (see, e.g., Andr  n *et al.* 1990). The topic of uncertainty in organism-orientated models was dealt with in some depth by de Ruiter *et al.* (1993a, 1994) and Paustian (1994).

Second, and related to the problem of parameter estimation, is the problem of ecosystem specificity. Many of the most widely used process-orientated models have been applied successfully to a range of ecosystems (e.g. arable rotations, permanent grass, grass-arable rotations, forestry, natural woodland regeneration) without adjusting internal model parameters (e.g. CENTURY – Kelly *et al.* 1997; Rothamsted Carbon Model – Coleman *et al.* 1997; NCSOIL – Molina *et al.* 1997) though not all simulate plant dynamics in addition to the soil ecosystem. One factor that makes this possible is that process-orientated models are less sensitive to soil community structure. They can therefore be more easily applied to a range of soils and environments regardless of large differences in soil community structure between ecosystems. The downside of the lack of specific soil community description, is that any special features of a given ecosystem that result from its particular soil community will not be adequately simulated by process-orientated models. At least for temperate agroecosystems and forestry, however, many process-orientated models appear to work adequately (see Smith *et al.* 1997b).

Third, Brussaard (1997) considers that the main limitations of using current food web models for predictive purposes are, (a) the quality of organic matter consumed at each trophic interaction is poorly known, (b) despite seemingly working well, a number of functional groups are not included, (c) different spatially restricted habitats of the four guilds of soil animals (root herbivores, litter degraders, litter transformers and ecosystem engineers) are not acknowledged, and (d) many biological interactions in the soil are nontrophic in nature.

Finally, process-orientated models are used more frequently for predictive purposes for technical reasons which are not insurmountable. Compared to organism-orientated models, process-orientated models have a relatively simple structure and (often) a larger integration time-step (e.g. months). This means that the computer processing time is likely to be shorter than for more complex organism-orientated models making them more

suitable (from a technical point of view) for running simulations over longer periods (years, decades). Organism-orientated models are more commonly used for periods of days rather than years, decades or centuries (e.g. Hunt *et al.* 1984). The same technical reasons also make process-orientated models more suitable for use at larger scales (landscape, regional, global) since multiple runs are frequently required. Many process-orientated models have been linked to GIS systems. CANDY, for example has GIS capability (Franko 1996), CENTURY (e.g. Donigan *et al.* 1994) and RothC (e.g. Parshotam *et al.* 1995) have also been linked to GIS for regional scale calculations, and some models have been used for global calculations (e.g. with RothC – Post *et al.* 1982; Jenkinson *et al.* 1991; and with CENTURY – Schimel *et al.* 1994).

Despite their more common use for predictive purposes, process-orientated models suffer from the same problem as organism-orientated models for global change studies: they will not be able to predict adequately the effects of a global change if the change affects the way in which the soil system responds to future global change. This problem is discussed further in the final section of this paper.

Combined process- and organism-orientated models

Combined approaches using both process- and organism-orientated components within the same model (e.g. Hunt *et al.* 1991), show some promise. de Ruiter & Van Faassen (1994) used both approaches and concluded that although the food web components of models may at present play an explanatory, rather than a predictive role, there was potential for a predictive model incorporating aspects of both modelling approach. There may be some limitations in our understanding that could hinder progress towards predictive combined models (Brussaard 1997). From a logistical point of view also, combined models may be constrained by the data requirements of the organism-orientated components. A modular approach to programming (as emphasized by Paustian 1994) would facilitate the development of combined models. Some progress has been made since Paustian's review toward modular programming systems in which modellers can swap modules with each other to build custom models for a specific purpose. However, it is fair to say that modular programming remains the holy grail of ecosystem modelling.

Most combined approaches have focused on the trophic role of the soil biota in nutrient turnover; few have examined the role of soil biota as 'ecosystem engineers'. One example of combining a process-orientated approach with an explicit description of the action of soil biota as ecosystem engineers was provided by Lavelle *et al.* (1997). In this study, an attempt was made to simulate the effect

of earthworm activities on the three kinetically defined organic pools of the CENTURY model (Parton *et al.* 1988). Earthworm activity was simulated by calibrating CENTURY pool decomposition rates to those observed in worm casts. The study suggested that slow decomposition soil C may be influenced significantly by earthworm activities and it was concluded that earthworms may play an important role in stabilizing SOM, and hence maintaining the SOM stock and soil structure in the long term.

Earthworms also enhance the decomposition and turnover of soil organic matter by facilitating the transfer of surface litter to the mineral soil and its comminution; their burrowing action also speeds up the flow of water, gases and nutrients in the soil profile. O'Brien (1984) used a simple two-compartment process-orientated model to quantify the enhancement of soil C turnover rate by earthworm activity in a comparative experiment at two sites in a paddock where earthworms were present or absent. A much larger C input rate to the soil was observed where worms were present. The worm-rich soil exhibited a much shorter decomposition time of 52 years against 148 years for the wormless pasture, indicating the presence of more labile C and higher microbial activity where worms were present. The efficient transport of C down the profile was also indicated in the presence of worms, this soil having a diffusivity parameter more than twice that of wormless pasture.

These studies provide examples of how a more explicit description of the effects of soil biota can be achieved within a process-orientated model without explicitly including population descriptions and interactions of soil organisms. Some apparent conflicts between the process- and organism-orientated approach may be resolved by adjusting process-orientated models as described above, or by using even simpler approaches, e.g. Andrén & Kätterer (in press).

Problems in modelling the soil biota-mediated effects of global change

The most comprehensive evaluation and comparison of SOM models to date has now been completed (Smith *et al.* 1997a). This exercise, focusing entirely on process-orientated models, reveals that many models can adequately simulate SOM dynamics in a range of ecosystems but that most still require significant site-specific calibration. Advances in modelling techniques to allow these models to be used truly predictively are still required (Smith *et al.* 1997b). Given that the relatively simple process-orientated models cannot yet be used predictively with full confidence suggests that the predictive use of organism-orientated models may still be some way off.

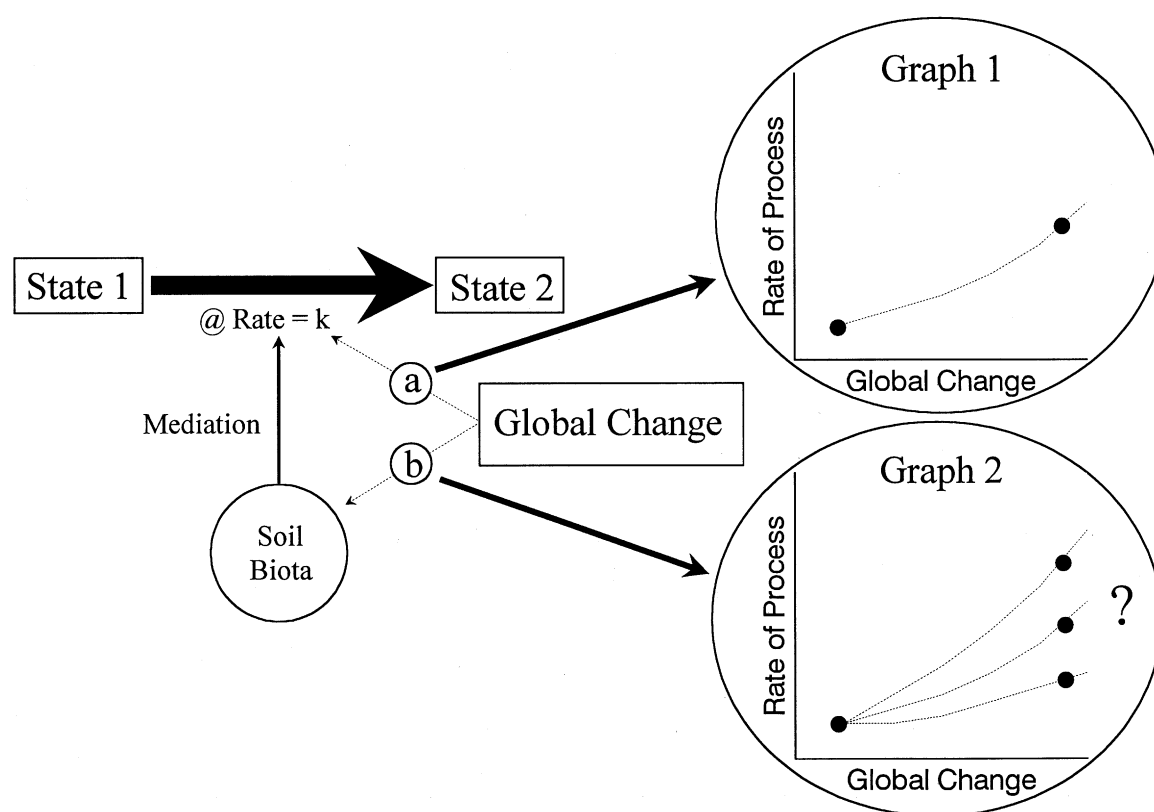


Fig. 3 Schematic diagram of a soil process converting a component from state 1 to state 2 at rate k . It is assumed that the process rate is mediated by the soil biota present. It is postulated that global change may affect the process rate directly (route 'a') or through an effect on soil community function (route 'b'). If global change acts only through route 'a', the future process rate should be predictable as long as the change is within limits of model calibration. If global change also acts through route 'b', and the mediating effect of the soil biota on the process rate is altered, the future process rate may not be predictable. For full explanation, see text.

Figure 3 presents a schematic diagram of how global change may affect a given process in the soil. Graphs 1 and 2 in the figure are developed from ideas presented by Schimel & Gullledge (this volume).

As a global change occurs, for example through a change in temperature, the process rate may simply be adjusted according to a simple relationship ('a' in Fig. 3). This may occur through a purely physico-biochemical response (e.g. a Q10 response) or may implicitly involve the soil biota (e.g. through increasing or decreasing the size of the microbial biomass). In either case, there is an assumption that the response of the system will remain predictable within calibrated limits, i.e. that the response surface remains the same (Fig. 3, Graph 1; see also Schimel & Gullledge 1998, this volume). All current models, whether process- or organism-orientated, assume a change in process rate according to Graph 1 in Fig. 3, i.e. a shift along a single response surface.

Alternatively, global change may also adjust the process rate indirectly by affecting the way in which the system responds to global change in the future ('b' in Fig. 3). As described above, route 'a' may include an implicit

description of soil biota in which the system responds predictably within the calibrated limits of the model. Route 'b' differs, however, in that the global change may affect the soil biota in such a way that the system no longer responds to future change in the predicted way, i.e. there may be a change from one response surface to another (Graph 2 in Fig. 3). Global change via route 'b' suggests that the future rate of a process may, in certain circumstances, be radically different from that predicted if only route 'a' were considered. No current models, whether process- or organism-orientated, take account of process rate adjustments via route 'b'.

Should the effects of global change on process rates mediated by changes in the soil community (route 'b') prove to affect significantly a given process in a given environment, only models that can explicitly account for this will be able to predict accurately the effects of global change. The inclusion of route 'b' is possible for either process- or for organism-orientated models. In a process-orientated model, route 'b' would take the form either of a rate-modifying factor to approximate the change, or of an internal switch in the model to move the process

response from one surface to another. In an organism-orientated model, changes in the populations of the key functional groups involved in a process would respond to global change in the model and this would subsequently change the response of the soil community to future global change.

Route 'b' is not included in any model because soil ecosystems are only part of systems of a higher order. More is known about what to expect from global change at the atmospheric level than down the chain to the soil biota — at this level the driving forces remain unknown. So although there is a considerable body of research into the effects of global change on soil biodiversity, the reason that route 'b' is not included in any model is that not enough is known about: (i) the impacts of global change on functional groups of soil organisms and how widespread these are; (ii) the significance of these impacts for function; and (iii) the likely change in response of the soil system to future global change as a result of these impacts on functional groups.

The ecosystem-level significance of route 'b' in specific circumstances remains unknown as does the extent of its occurrence for specific global changes in particular ecosystems. Some of the other papers in this volume (e.g. Swift *et al.* 1998 this volume; Schimel & Gullledge 1998, this volume) point to possible examples of where route 'b' may be critical. A further example might be land-use change leading to an increase in earthworms. This may lead to a significant quantity of the soil organic matter being sequestered within worm casts thus making SOM accessible only to anaerobic methanogens. In this case rates of methanogenesis might be radically altered. Another possible example is a switch from predominantly nitrate-N to predominantly ammonium-N in the soil following soil acidification. This may occur since nitrifiers, which convert ammonium to nitrate, are particularly sensitive to pH. Any global change resulting in a decrease in soil pH could lead to this biota-mediated change.

Only through further research into the gaps in knowledge identified above will we be able to ascertain the importance of explicitly including route 'b' in our mathematical models. Even though much of the research outlined elsewhere in this volume addresses issues (i) and (ii) above, much work is yet required to answer (iii). Route 'b' cannot be modelled until we have a mechanistic understanding of how process-response surfaces will change in the future, i.e. which line on Graph 2 of Fig. 3 will be followed. To predict with confidence the effects of global change at the ecosystem level using mathematical models, further research is urgently required to address the gaps identified here.

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