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SWORM: an agent-based model to simulate the effect of earthworms on soil structure

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Summary

Soil structure can be defined as the spatial organization of solid mineral and organic particles, and pore space. It is of great importance for soil functioning as it drives ecosystem functions (carbon sequestration, emission of greenhouse gases, nutrient cycling, primary productivity, etc.). Soil structure results from biotic and abiotic factors. Among biotic factors, numerous studies have shown the importance of organic matter, microorganisms, roots and invertebrates. Earthworms are known to play a key role in soil structure formation and maintenance through a continuous production of biogenic structures (casts and burrows). As far as we know, no models describe or quantify the effect of soil invertebrates on soil aggregation and porosity. It is a challenge to describe the physical soil environment for purposes of modelling because a soil is a multi-scale heterogeneous, three-dimensional and dynamic environment. An approach based on fractal theory (often used in soil sciences) was chosen to model such a real complex environment; it was integrated into a multi-agent system (MAS), which allows us to simulate agents (e.g. earthworms) situated in a virtual world (e.g. soil). It is a bottom-up approach that allows us to describe a system at a micro level (e.g. earthworms and their local soil environment) in order to observe, during simulations, macroscopic changes (e.g. soil structure evolution, organic matter dynamics, and microbial functions). In this paper we describe the SWORM (for 'Simulated Worms') model and the simulator, and present the results of the simulation applied to a case study. The effect of compacting and decompacting earthworm species on the structure of humid savanna soil at Lamto in Côte d'Ivoire has been widely studied. Quantitative and graphical outputs (e.g. thin sections of the virtual soil) indicate that the simulator was able to reproduce the effects of both compacting and decompacting species. Different ways to improve the model are discussed.

Introduction

Soil structure can be defined as the spatial organization of solid mineral and organic particles, and pore space (Marshall & Holmes, 1988), or as the spatial heterogeneity of different components or soil properties (Dexter, 1988). Soil structure is of great importance for soil functioning as it influences water regime, infiltration, aeration, nutrient retention and repartition, and soil microbial activity. It is thus a major soil property driving ecosystem functions (carbon sequestration, emission of greenhouse gases, nutrient cycling, etc.) (Hassan *et al*., 2005).

Soil structure results from biotic and abiotic factors. Among biotic factors, numerous studies have shown the importance of organic matter (polysaccharides, plant debris), microorganisms (bacteria, fungi) and soil invertebrates in soil aggregation (e.g. Oades, 1993; Young *et al*., 1998), and of large invertebrates and roots in the development of burrows and channels (Angers & Caron, 1998; Bastardie *et al*., 2005).

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Several models have been proposed to study soil structure (Young *et al*., 2001). They are based on various theoretical approaches adapted to ecology, biology, computer science, etc. Different methods and models used in soil (or sediment) science can be distinguished: (i) Boolean models (Kamphorst *et al*., 2005), (ii) neural networks (Baker & Ellison, 2008), (iii) fractals (Vidales & Miranda, 1996; Bird & Perrier, 2003; Pachepsky *et al*., 2006), (iv) network models (Monga, 2007), (v) other mathematical models (Braudeau *et al*., 2004), (vi) cellular automata (Choi *et al*., 2002; Prosperini & Perugini, 2007), and (vii) multi-agents systems (Masse *et al*., 2007).

According to the approach used, models provide (by calculations or simulations) different types of results (water flows can be described from fractal models while modification of soil structure can be assessed from cellular automata). The choice of a model thus depends on the kind of results expected. The study of the effects of soil engineers (such as earthworms) on soil structure (both at micro- and macro- levels) should be satisfactorily modelled with individual-based models (IBM) (often used in ecology, e.g. Grimm *et al.*, 2005) such as cellular automata or multi-agent systems (MAS). The commonest approach is to create an IBM to model the space studied (e.g. the soil or the sediment) as a 2D or a 3D regular grid and to locate moving particles or agents (e.g. animals) within it (Choi *et al.*, 2002). With this approach, it is easy to observe particle movements and modifications of soil structure. The main difference between cellular automata and MAS is that modelling by cellular automata is based on a grid of cells, each of them characterized by a finite number of states and common rules for updating the state of neighbouring cells (Turing, 1952). Conversely, MAS are composed of an environment (in general a grid of cells) in which autonomous entities (agents) are situated and are able to move, to modify cell states and to interact (Ferber, 1999). Actions made by the agents (movement, modification of the environment) result from the execution of their behaviour rules. These rules can be determined at the individual agent or at the group (of agents) level. However, in this latter approach, modelling the environment as a grid of regular cells does not account satisfactorily for the complexity of a real environment. We thus developed a hybrid model based on both fractal theory and MAS. Fractal theory allows us to create a multi-scale virtual environment. Agent theory allows us to describe different endogeic earthworm species, each with specific behaviour rules. These agents are located in, and act on, the multi-scale virtual environment.

In the present paper, we present the SWORM model (for 'Simulated Worms') and the simulator. Then, the results of the simulation on a case study are provided, showing how the model reproduced the effects of compacting (earthworms whose activity increases bulk density) and decompacting (earthworms whose activity decreases bulk density) endogeic earthworms in the soil of humid savannas at Lamto in Côte d'Ivoire (Blanchart *et al.*, 1997).

Model and simulator

The model

The soil was modelled as a dynamic and multi-scale MAS environment based on the agent pore solid fractal (APSF) approach (for more details, see Marilleau *et al.*, 2008). APSF is an improvement of the pore solid fractal (PSF) approach developed by Perrier *et al.* (1999) originating from the work of Neimark (1989), where it was applied to the characterization of soil aggregation and fragmentation processes (Perrier & Bird, 2002) and to the modelling of soil water retention and water flows (Bird & Perrier, 2003). PSF describes a soil as a fractal milieu. APSF distorts PSF fractal property in order to model heterogeneous environments such as soils characterized by different concentrations and sizes of particles.

APSF models a real space as a multi-scale MAS environment. This virtual soil is composed of an organized, discrete set of cells, which belong to three categories: (i) pore cells representing soil cavities; (ii) solid cells representing compact particles without any cavities, such as sand particles or organic debris; and (iii) decomposable cells representing a sub-space that can be decomposed into smaller pores, solid or decomposable cells when the resolution needed increases (Figure 1).

Different patterns called 'canvases' can be defined in an APSF model (Marilleau *et al.*, 2008). Each canvas characterizes a spatial organization of cells. All canvases are associated together, by a tree, to define a heterogeneous space whose structure evolves according to the location in space and to the scale. A canvas is defined at the root of the tree. It models the structure of the space at the highest level (level 1). For each decomposable cell of this first canvas, a new canvas is defined which models a local architecture of a sub-space (at level 2). The same approach is used for each level of the environment. Note that tree leaves are recursive, in order to permit a theoretically unlimited fractal decomposition.

Agents (one or different earthworm species in the present case) are characterized by specific behaviours and limited abilities to interact with the virtual soil. Agent movements result from behaviour rules, which take into account the filling rate of their guts and the quality of cells around them (pores, organic or mineral matter). Two main behaviours drive their movements: (i) movement and ingestion behaviour; when moving, agents eat organic debris and bulk soil, and create pores (in response to their perception, agents move to the neighbouring cell containing the highest level of organic matter that is an organic or decomposable cell); and (ii) movement and egestion behaviour; when their gut is filled, agents perceive the size of the neighbouring pores and move to the largest one, where they excrete soil as casts until their gut becomes empty.

The simulator

The model was implemented in a simulator that describes soil functioning in a $20 \times 20 \times 20$ cm^3 monolith. We created a canvas tree, which recursively divides a cubic fractal cell into 1000 sub-cells (each side of a cell is divided by 10). Therefore, the side of a cell was 20 mm at level 0, 2.0 mm at the first level, 0.2 mm at the second level, etc. (Table 1).

The simulation requires different types of inputs, and produces various results as output. Soil properties needed to run a simulation are: organic matter content (OM), soil texture (clay 0–2 μm, fine silt 2–20 μm, coarse silt + fine sand 20–200 μm and coarse sand 200–2000 μm), bulk density and particle density. These data are used to construct the canvas that defines the initial virtual soil structure. Information specific to earthworm casts is also needed to create the virtual cast structure; that is, the number of species and, for each species, its average size (the

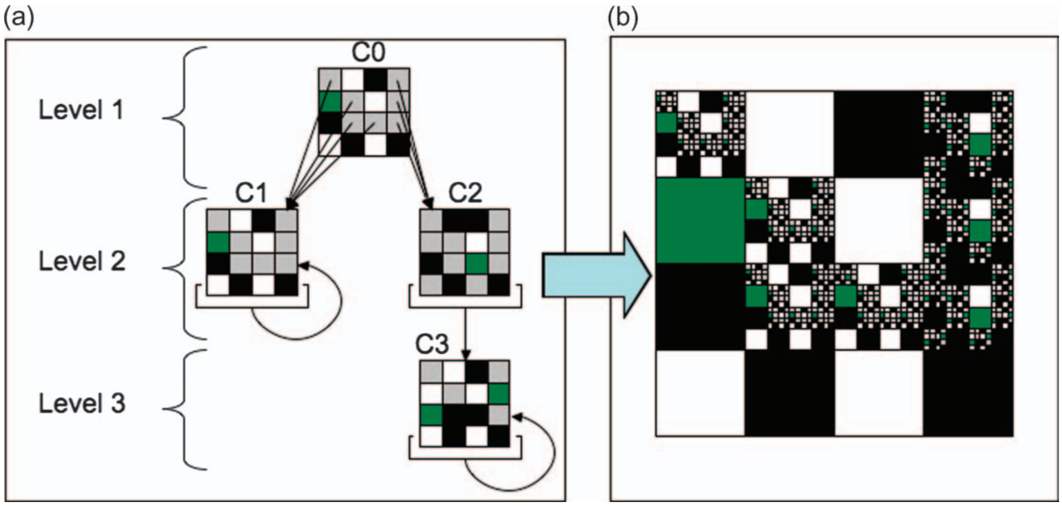

Figure 1 Representation of the virtual soil in the APSF model. It is composed of different types of cells: (i) pore cells (white), (ii) organic solid cells (green), (iii) mineral solid cells (black), and (iv) decomposable cells (grey). (a) Examples of canvases associated together, by a tree. Decomposable cells at level 1 follow either the pattern C1 or the pattern C2. All decomposable cells of C1 follow the pattern C1. All decomposable cells of C2 follow the pattern C3. (b) Resulting heterogeneous space.

diameter of individuals), abundance (number of individuals) in the simulation, soil consumption (g/day/individual), assimilation rate and particle selection. With regard to particle selection, it is well known (Barois *et al*., 1999) that earthworms selectively ingest soil particles, avoiding coarse sands and gravels. In a given soil, large earthworms can ingest all soil particles without selection (the value of particle selection is then 100%) while small earthworms avoid sand particles (the value of particle selection is then lower than 100% and can reach 0% if none of the sand particles are ingested).

A simulation generates various outputs at micro- and macroscopic levels. 3D spatial data are produced that allow scientists to observe earthworm movements and soil structure changes by means of animations, VRML (virtual reality markup language), 3D views and virtual soil sections. In addition, the model provides the evolution of global soil data (e.g. organic matter content, mineral matter content, amounts of ingested soil, etc.). All these data can be directly analysed by scientists or can be processed after the simulation in order to obtain results about earthworm effects.

Case study

Soils of Lamto's savannas (Côte d'Ivoire) are ferruginous sandy soils (Ferralsols, FAO) with 100 g kg^{-1} clay, 90 g kg^{-1} silt, 260 g kg^{-1} fine sand, and 550 g kg^{-1} coarse sand; they do not contain any particles larger than 2 mm. Organic carbon (OC) content is *c*. 10 g kg^{-1} in the upper 5 cm of soil. Bulk density is *c*. 1.2–1.3 Mg m^{-3} in the upper 10 cm of soil (with mineral particle density equal to 2.62 Mg m^{-3} and organic matter density equal to 0.8 Mg m^{-3}). As a consequence, a given volume of soil is composed of 63.1% mineral particles, 0.8% organic matter and 28.1% pores. Such soils have a macroaggregated structure in the upper 20 cm (Blanchart, 1992). The main earthworm species are *Millsonia anomala* (Omodeo & Vaillaud, 1967) (Megascolecidae), and species belonging to the family Eudrilidae (*Chuniodrilus zielae*, Omodeo, 1958, *C. palustris*, Omodeo & Vaillaud, 1967, and *Stuhlmannia porifera*, Omodeo & Vaillaud, 1967) (Lavelle, 1978). *M. anomala* is a mesohumic (ingesting soil from the upper 0–20 cm layer), endogeic species of medium size (17 cm length, 6 g at the adult stage). Eudrilid earthworms are polyhumic (ingesting surface soil rich in organic matter) endogeic species of small size (7 cm length, 200 mg at the adult stage). These species occur in all savanna facies; their population density is *c*. 20 individuals m^{-2} (5–19% of the whole earthworm community), and 200–300 individuals m^{-2} (72–91%), respectively, for *M. anomala* and eudrilid worms (Lavelle, 1983). Adults of *M. anomala* and eudrilid worms daily ingest *c*. four times their own weight of soil (i.e. 10–25 g g^{-1} d^{-1} dry soil and 0.28–0.35 g g^{-1} d^{-1} dry soil, respectively, for *M. anomala* and eudrilid worms). Assimilation rate of organic matter is *c*. 9% for *M. anomala*. No data are available for eudrilid species (Lavelle, 1978; Martin *et al*., 1991), but

Table 1 Proportion (%) of mineral, organic, pore and decomposable cells at each level of canvas tree

Level	Cell size /mm	Mineral particles	Organic particles	Pores	Decomposable cells
0	20	0	0	0	100
1	2	13	0.085	20	66.915
2	0.2	29	0.54	20	50.46
3	0.02	22	1.8	20	56.2
4	0.002	29	4.9	59	7.1

they can assimilate all sizes of organic matter from large debris to clay-sized organic particles (Martin, 1991). The gut transit rate is 2–3 hours. During soil ingestion, eudrilid worms, and *M. anomala* to a lesser extent, select soil particles and avoid coarse particles. As a consequence, the coarse sand (0.2–2 mm) content is 500–550 g kg^{-1}, 320 g kg^{-1} and 460 g kg^{-1}, respectively, in soil, eudrilid casts and *M. anomala* casts. The effect of these earthworms on soil structure formation and conservation has been studied in a number of experiments (Blanchart *et al*., 1989, 1990; Blanchart, 1992; Blanchart *et al*., 1997). Eudrilid worms produce piles of small (1–2 mm diameter) pellets while *M. anomala* excrete large (0.5–2 cm) rounded casts that they cannot re-ingest. *M. anomala* casts are very compact; their bulk density ranges from 1.8 to 2.0 Mg m^{-3}. Experimental studies showed that *M. anomala* and eudrilid worms had a complementary action on soil structure (Blanchart *et al*., 1997). *M. anomala*, through the production of large and compact casts, increased both macroaggregate soil content and bulk density while eudrilid worms, through the production of small casts, decreased both variables. *M. anomala* and eudrilid worms were therefore called compacting and decompacting species, respectively (Blanchart *et al*., 1997).

Simulation

Environment (virtual soil) properties

The simulator reproduces soil bioturbation in a $20 \times 20 \times 20\ cm^3$ monolith. The virtual soil is composed of cells sized according to a regular distribution (factor 10). This distribution allowed us to model coarse sand (0.2–2 mm), coarse silt + fine sand (0.02–0.2 mm), fine silt (0.002–0.02 mm) and clay (<0.002 mm). The quantities of these elements were chosen according to Lamto soil characteristics (Table 2) and they determined the simulated soil characteristics.

From the soil characteristics presented in Table 2, an APSF canvas tree was established. It was composed of five levels (Table 1). Because the soil of Lamto does not contain any particles larger than 2 mm, level 0 consisted only of decomposable cells.

Agent (virtual earthworms) characteristics

In this simulation, two earthworm species were simulated (*M. anomala* and eudrilid worms). Each group was characterized by specific properties and behaviours (Table 3). During the simulation, we used the relative abundance of each species (1 *M. anomala* individual for 10 eudrilid individuals in the field). All earthworms ingest four times their own weight of soil and have the same assimilation rate. When ingesting soil, *M. anomala* can ingest almost all (90%) coarse mineral particles whereas eudrilid worms select particles and ingest only 60% of these coarse particles.

A simulated day was divided into 20 periods (i.e. 10 ingestion periods alternating with 10 egestion periods). Ingestion behaviour rules and egestion behaviour rules were executed during ingestion and egestion periods, respectively. Both species were characterized by the same ingestion behaviour (i.e. they cannot re-ingest their own casts but can ingest casts from other species). In the present simulation, earthworm behaviours were synchronized (i.e. all earthworms ingested soil at the same time). Earthworm velocity was constant and equal to one cell (at level 2, i.e. 2 mm side) per time step (one step being 5 s).

The main difference between the behaviour of earthworms appears during the egestion: *M. anomala* agents generate one or two large casts (depending on the cavity size) composed of several cast cells whilst eudrilid agents generate several small casts, each composed of one cell (2mm side).

The present simulation was performed over a period of 700 000 steps (i.e. 40 days).

Table 2 Soil parameters used for the simulation

OM content /g kg^{-1}	Clay /g kg^{-1}	Fine silt /g kg^{-1}	Coarse silt + fine sand /g kg^{-1}	Coarse sand /g kg^{-1}	Bulk density /Mg M^{-3}	Mineral particle density /Mg M^{-3}	Organic particle density /Mg M^{-3}
14	98	44	276	582	1.2	2.62	0.8

Results of the simulation

At the end of the simulation, different output results are available. Curves of the evolution of organic and mineral matters in soil during the simulation provide two types of information. Over the short term (24 hours), these curves enabled us to observe regular rhythms of soil ingestion and egestion by earthworms (Figure 2). With regard to the mineral matter, a descending part of the curve corresponds to the ingestion of soil by earthworms (Figure 2a). After a short period of movement, earthworms excrete their casts and all mineral matter was returned back to the soil. The simulation of soil organic matter was slightly different because earthworms assimilate a part of it before cast egestion; as a consequence, the curve decreased with time (Figure 2b). These short-scale patterns were similar for *M. anomala* and eudrilid worms. Over the longer term (40 days) differences in the behaviour of earthworms can be distinguished (Figure 3). The mineral and organic matter curves for *M. anomala* show that soil consumption decreased after 22 days (Figure 3a,b). *M. anomala* experience more and more difficulties in finding coarse organic debris (the main food resource) because coarse debris are included in casts that earthworms can not re-ingest. This shortage of food explains the strong decrease in soil consumption. The curves for Eudrilidae did not have the same pattern (Figure 3c,d) because after 40 days, coarse organic debris were still available.

Sections of virtual soil (20 × 20 cm) allow the visualization of the soil structure at all steps of the simulation. At the beginning

Table 3 Earthworm parameters used for the simulation

	Individual size (diameter) /mm	Individual weight /g	No. of individuals per block	Consumption /g g^{-1} day^{-1}	Assimilation rate /%	Ingestion of coarse particles /%
M. anomala	2	5	20	20	9	90
Eudrilidae	1	0.125	200	0.5	9	60

of the simulation, the decomposable structure of the virtual soil leads to soil profiles with soil structures differing with respect to the concentration and distribution of solid, pore and decomposable cells. As examples, Figure 4a and d represent two sections of the initial virtual soil. The proportion of solid, pore and decomposable cells was 12%, 16% and 72% in the first soil section (Figure 4a), and 8%, 31% and 61% in the second (Figure 4d). It also appears that the diameter of macro-pores was smaller in the first than in the second soil section. Note that, because of the chosen canvas tree structure (the zero level canvas was composed only of decomposable cells), the first level canvas was reproduced 1000 times.

Soil structure, at the end of the simulation, was influenced by the initial structure of the soil and the earthworm species. As seen above, results indicate that at the end of the simulation, *M. anomala* was lacking food and almost all the soil was

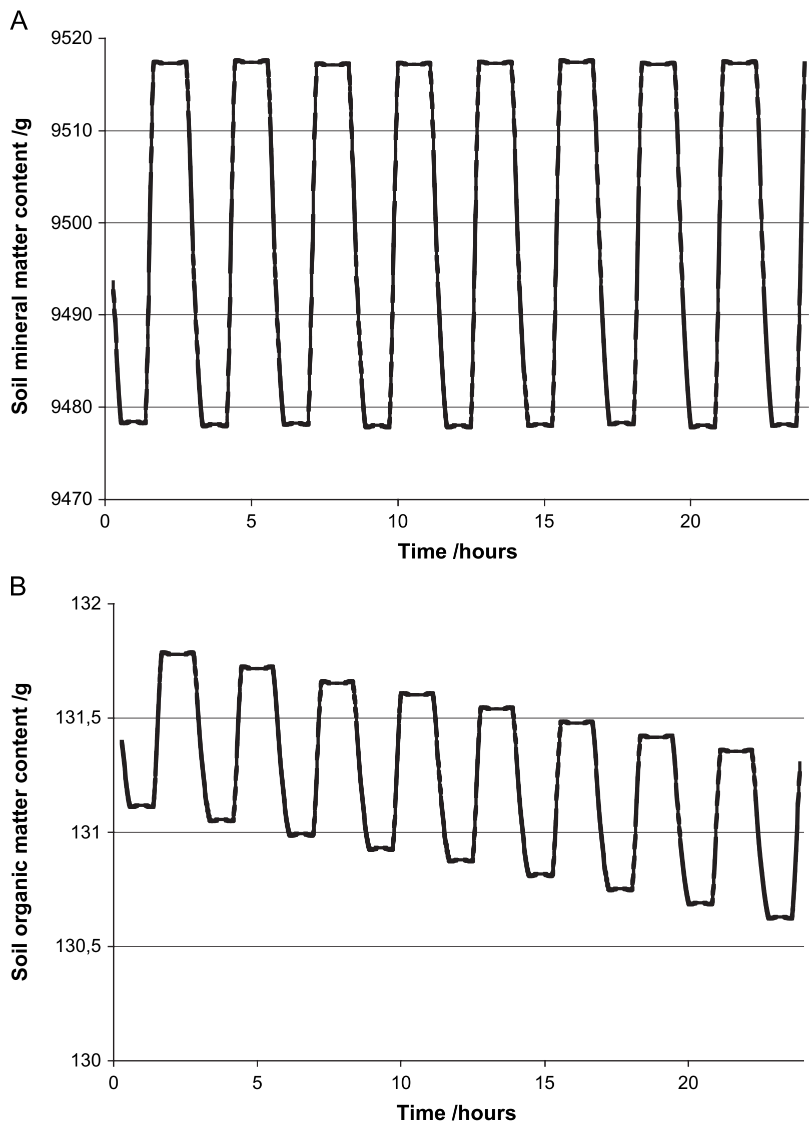

Figure 2 Changes in presence of solid particles over the short term (24 hours) in a soil block (20 × 20 × 20 cm^3). (a) Changes in presence of mineral particles. (b) Changes in presence of organic particles.

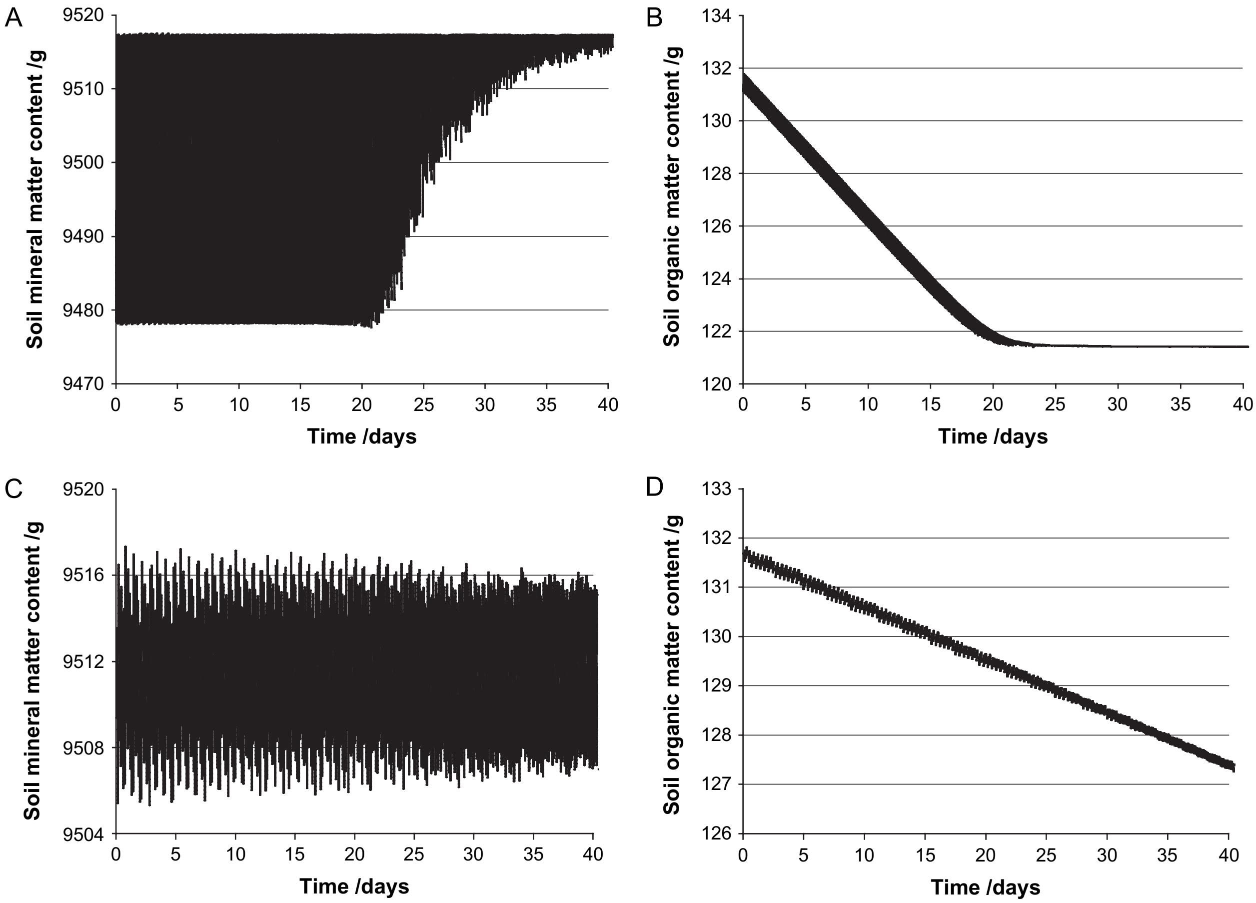

Figure 3 Changes in presence of solid particles over the long term (40 days) in a soil block (20 × 20 × 20 cm^3). (a) Changes in presence of mineral particles in soil with *M. anomala*. (b) Changes in presence of organic particles in soil with *M. anomala*. (c) Changes in presence of mineral particles in soil with eudrilid worms. (d) Changes in presence of organic particles in soil with eudrilid worms.

consumed by earthworms. This can also be seen from soil sections (Figure 4b,e) in which only a few uningested decomposable cells were still present. The proportion of cells varied according to the initial soil structure. From the first initial soil section (Figure 4a), final soil sections had 46.3% pore cells, 1.1% solid cells, 0.002% uningested decomposable cells and 52.6% cast cells (Figure 4b). From the second initial soil section (Figure 4d), the respective proportions were 43.8%, 0.9%, 0.004% and 55.2% (Figure 4e). Because gravity was not considered in our simulation, the overall bulk density did not change during the simulation. Nevertheless, the action of *M. anomala* led to the formation of a macro-aggregated structure, comparable to that measured in field conditions (Blanchart, 1992; Blanchart *et al.*, 1997). The simulation of the effects of eudrilid species led to different results. Because these worms did not ingest all soil, the proportions of pore, solid, uningested decomposable cells and cast cells were 23.6%, 12.0%, 48.4% and 16.0%, respectively, in the soil modified from the first initial soil section (Figure 4c), and 48.2%, 7.9%, 27.5% and 16.4%, respectively, in the soil from the second initial soil section (Figure 4f).

These results are in accordance with results obtained from the field. Soils with experimentally inoculated *M. anomala* have a dominance of large-size aggregates (> 2.0 mm) while soils with Eudrilidae are characterized by the dominance of medium-size aggregates (0.5–2 mm) (Blanchart *et al.*, 1997).

Conclusions

The SWORM model aims to describe the effect of endogeic earthworms on soil structure. The first simulations of this model indicated that it is possible to reproduce the effect of compacting and decompacting endogeic, geophagous species. As a consequence this model could be useful to improve understanding of soil functioning. It has often been demonstrated that biogenic structures (casts and burrow walls) have specific physical, chemical and biological properties that are different from the initial material (Blanchart *et al.*, 1999; Amador & Görres, 2007; Jouquet *et al.*, 2008). Biogenic structures are thus often characterized as hot-spots of microbial activity and influence organic matter decomposition and nutrient release (Martin & Marinissen,

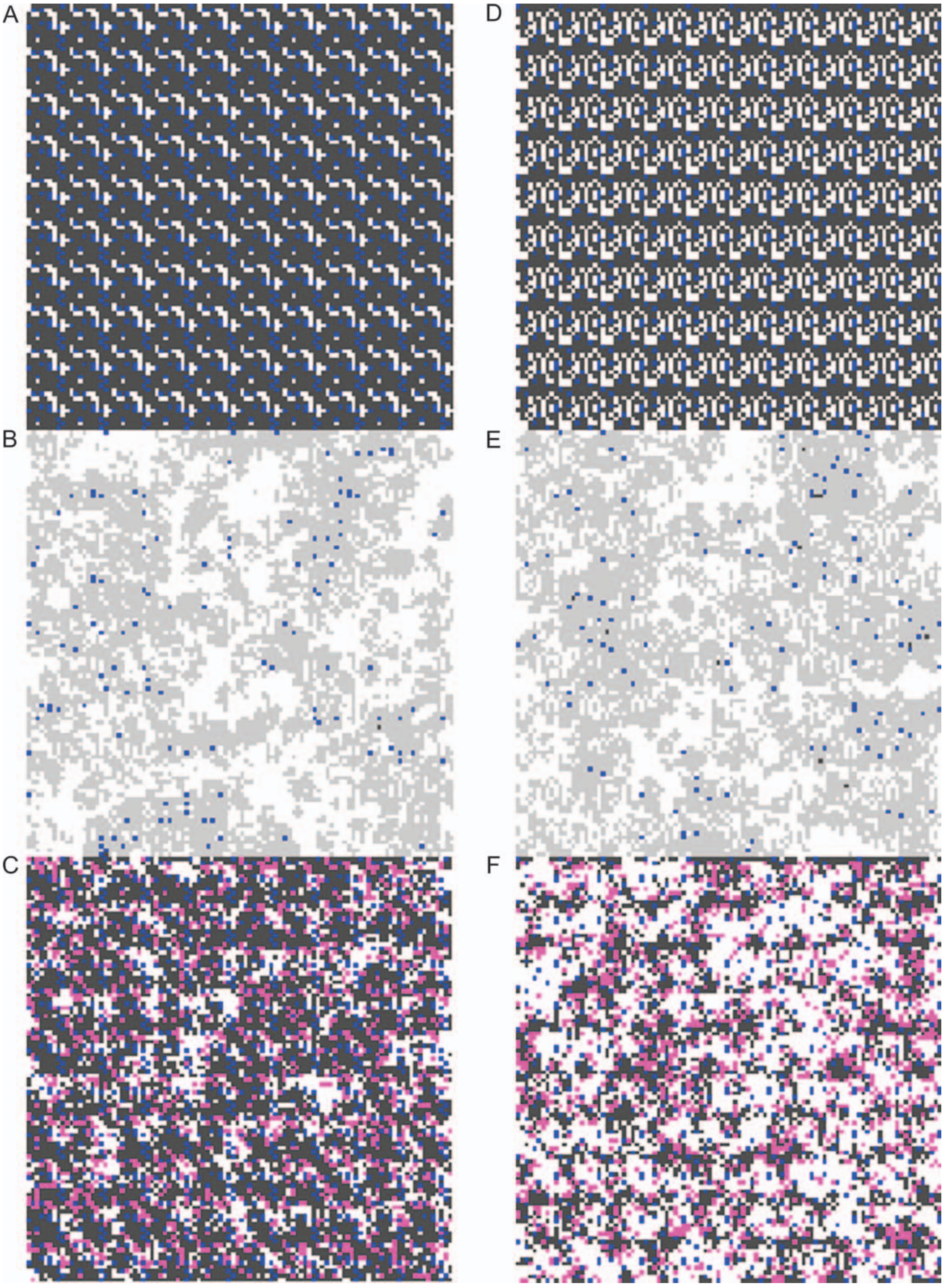

Figure 4 Sections of the virtual soil (20 × 20 cm). (a) and (d): Two different soil sections at the beginning of the simulation (initial soil structure) showing pore (white), solid (blue) and decomposable (black) cells. (b) and (e): Soil sections at the end of the simulation (40 days) with *M. anomala* showing pore (white), organic (blue), uningested decomposable (black), and cast (grey) cells. (c) and (f): Soil sections at the end of the simulation (40 days) with eudrilid worms showing pore (white), organic (blue), uningested decomposable (black) and cast (pink) cells.

1993; Amador & Görres, 2007; Marhan *et al*., 2007). The specific properties of these structures abundant in soil are never taken into account in models of organic matter dynamics or nutrient release. The SWORM model could thus be used in order to link physical and biological processes in models of soil functioning.

Nevertheless, the current model could be improved in different ways. Adding processes linked to gravity could highly improve the model. In our model, soils before and after earthworm activity have the same bulk density, while in a real situation bulk density changes according to earthworm activity. In a real situation, cavities resulting from *M. anomala* activity collapse and bulk density increases through gravitational effects. A space layer should appear above the soil surface in future development of the SWORM model. In addition, this natural soil structural change may have an impact on earthworm behaviour and their actions on the soil, which is not considered in the present model.

At present, the soil in the model is defined as a mesocosm without any exchange with the exterior. For example, neither organic matter inputs nor water infiltration/retention are taken into account in the present SWORM model and these phenomena have major impacts on soil functioning and earthworm life cycle.

The final objective of the SWORM model is to describe, understand and predict soil functioning (microbial activity and diversity, gas and nutrient fluxes, etc.). One way to reach this goal could be to link the SWORM model with other existing and validated mathematical models and then use this to consider the interactions (in terms of physical, chemical and biological properties) existing between biogenic and physicogenic structures. Such an approach was adopted by Bastardie *et al*. (2002), who linked an MAS describing anecic earthworm behaviours and burrow construction to a capillary model of water infiltration.

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