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Making Waves: Modeling bioturbation in soils – are we burrowing in the right direction?

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Highlights:

- Soil bioturbation model hypotheses have not been tested with adequate observations
- Experimental and modeling advances in aquatic bioturbation should be adapted to soils
- Cooperation between modelers, soil and sediment ecologists will help fill these gaps

Abstract

The burrowing, feeding and foraging activities of terrestrial and benthic organisms induce displacements of soil and sediment materials, leading to a profound mixing of these media. Such particle movements, called “sediment reworking” in aquatic environments and “bioturbation” in soils, have been thoroughly studied and modeled in sediments, where they affect organic matter mineralization and contaminant fluxes. In comparison, studies characterizing the translocation, by soil burrowers, of mineral particles, organic matter and adsorbed contaminants are paradoxically fewer. Nevertheless, models borrowed from aquatic ecology are used to predict the impact of bioturbation on organic matter turnover and contaminant transport in the soil. However, these models are based on hypotheses that have not been tested with adequate observations in soils, and may not necessarily reflect the actual impact of soil burrowers on particle translocation. This paper aims to (*i*) highlight the possible shortcomings linked to the current use of sediment reworking models for soils, (*ii*) identify how recent progresses in aquatic ecology could help to circumvent these limitations, and (*iii*) propose key steps to ensure that soil bioturbation models are built on solid foundations: more accurate models of organic matter turnover, soil evolution and contaminant transport in the soil are at stake.

Keywords:

Bioturbation; sediment reworking; particle tracking; biodiffusive model; random walks; fractional Brownian motion

1. Bioturbation: definition and significance

The earliest study reporting on bioturbation – the transport of soil particles carried out by the soil fauna, essentially invertebrates, including earthworms, enchytraeids, ants, termites, and millipedes – dates back to 1837. That year, in an address to the Royal Geological Society, Charles Darwin highlighted the role of earthworms on topsoil formation, and concluded his lecture stating that “every particle of [the topsoil] has passed through the intestines of worms” (Darwin, 1840). Since that time, bioturbation has received a considerable attention, both experimentally and by modeling, mostly in aquatic sediments, where the word "bioturbation" refers to both the translocation of sediment particles by living organisms (termed sediment reworking or bio-mixing), and to bio-irrigation, the transport of solute induced by these organisms (Kristensen et al., 2012; Van de Velde and Meysman, 2016). In these media, bioturbation affects organic matter mineralization and contaminant fluxes (Maire et al., 2008).

Bioturbation also affects the vertical transfer of contaminants in the soil. Compared to aquatic environments, the transport processes of organic or mineral soil particles – as well as adsorbed contaminants – during the burrowing, foraging or feeding activities of soil organisms have received much less attention. A search on the Clarivate Web of Science indicates that soils have never accounted for more than twenty percent of the total number of studies published annually on bioturbation. However, particle translocation models borrowed from aquatic ecology have been used for more than 25 years to analyze the vertical transfer in soils of radionuclides and persistent contaminants, organic matter turnover and soil evolution (Elzein and Balesdent 1995; Cousins et al., 1999; Jagercikova et al., 2017).

In 2006, Meysman et al. noted that aquatic and terrestrial bioturbations “are studied by separate scientific communities which communicate their results in targeted disciplinary journals [resulting] in a rather slow transfer of ideas between the different research fields”. With the objective to foster this transfer, the present perspective highlights salient features of bio-mixing modeling in aquatic sediments. Next, it discusses the shortcomings of applying these models in terrestrial environments, before identifying critical steps to implement soil bioturbation models on firm foundations.

2. Bio-mixing in aquatic environments

Aquatic ecologists have developed tracing and visualization techniques, often involving radioisotopes or particulate fluorescent tracers, to characterize sediment reworking by recording 1D profiles or 2D distributions of tracer concentrations over time (Maire et al., 2008). They permitted to characterize the mixing behavior of different aquatic organisms and to propose a typology of bio-mixing (Kristensen et al., 2012). Models, generally one-dimensional, have been developed to relate bio-mixing types to their impact at the macroscopic (decimeter) scale and at the sediment particle scale.

2.1. Biodiffusion and other related models

Some aquatic animals have been classified as biodiffusors because their behavior leads to a local mixing of sediment particles that can be well described by a diffusive process, characterized by a unique parameter, the biodiffusion coefficient D_b (m^2 $year^{-1}$) (Goldberg and Koide, 1962). The rationale is that after many translocation events, at the microscopic scale, the apparent movement of individual sediment particles appears to be random, while at the macroscopic scale particle fluxes satisfy Fick's law (Meysman et al., 2008; Metzler and Klafter, 2000). When organisms move the sediment particles in a non-isotropic way, an advection term characterized by a constant velocity w_B (m s^{-1}) has been added to the diffusion equation to account for the resulting downward or upward movement of the particles. It leads to the advection-dispersion equation

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial z}\left(D_{\mathrm{b}}(z)\frac{\partial C}{\partial z} - w_{\mathrm{b}}(z)\,C\right) \qquad \text{Eq.(1)}$$

where $C(t,z)$ represents the concentration of a transported substance or tracer, t and z represent the time and depth respectively. D_{b} and w_{b} are allowed to vary with depth. The sediment porosity is assumed to be constant.

Other organisms, classified as upward conveyors, behave in a different way: they ingest particles at depth and release them as casts at the sediment-water interface, resulting in the slow burial of the sediment profile. Particle ingestion is accounted for by a sink term in the advection-diffusion equation and particle egestion at the sediment-water interface is included in the upper boundary condition. A downward advection velocity w_{B} that depends on the particle ingestion rate in the feeding zone completes the particle mass balance of this "conveyor-belt" model (Robbins et al., 1986; Delmotte et al., 2007).

2.2. The stochastic approach in sediment reworking.

At the sediment particle scale, the seemingly random movements of the particles have been mimicked by random walks that accumulate independent jumps separated by periods of immobility (Meysman et al., 2008, 2010). In the framework of continuous-time random walks (CTRWs), the length of each jump and the duration of each immobility period are stochastic variables. They are drawn from independent jump-length and waiting-time distributions characterized by their variance σ^2 and mean τ respectively. If σ and τ are finite, it can be shown that a large number of translocation events achieves the continuous limit of the CTRW that coincides with the diffusive model (Brownian motion). The ratio $\sigma^2/(2\tau)$ is the biodiffusion coefficient. If moreover the mean μ of the jump-length distribution is non-zero, $w_B=\mu/\tau$ (Metzler and Klafter, 2000).

Meysman et al. (2010) called the jump-length and waiting-time distributions the 'bioturbation fingerprint' of the aquatic infauna. Bernard et al. (2012) made a first step to determine this fingerprint experimentally by following the individual trajectories of fluorescent 35 μm tracer particles resulting from the activity of a bivalve in 2D aquaria. For this, the authors used high-resolution cameras and an advanced particle-tracking algorithm.

Maire et al. (2007) compared the capacity of the CTRW and of the (advective-)diffusive model to describe tracer concentration profiles resulting from the activity of another bivalve. They showed that when the experimental duration was short compared to τ, a CTRW provided a better description of their data than – and should be preferred over – the (advective-)diffusive model. As expected from theory, at longer time both the diffusive and stochastic models coincided. This coincidence occurs provided a set of conditions are met, including: (*i*) finite values of σ^2 and τ, and (*ii*) independence of successive translocation events (Meysman et al, 2010). These authors proposed to classify the bio-mixing types and associated models in two categories according to their asymptotic limit: 'normal mixing' for organism behaviors that lead to a diffusive mixing, and 'anomalous mixing' for behaviors that deviate from the asymptotic diffusive model.

2.3. Anomalous mixing

Anomalous mixing can be accounted for by at least three conceptually different classes of models that generalize the biodiffusive normal mixing model.

The first class assumes that the jump-length distribution of the sediment particles may have an infinite variance σ^2. Such distributions may result from infauna moving ingested particles over extremely long distances, instead of just pushing them aside during foraging activities. Lévy flights with infinite variance are the paradigm of random walks making rare but very large displacements. This formalism was used once to model the distribution of polycyclic aromatic hydrocarbons in sediments, although the experimental data did not permit a compelling test of the validity of this approach (Reible and Mohanty, 2002).

The second class is composed of CTRWs combining jumps of finite variance with waiting-time distributions having an infinite mean. In this case, a displacement observed between times t_1 and t_2 depends not only on t_2-t_1 but also on t_1: displacements are not stationary. This leads to slower mixing dynamics than the biodiffusive model (Metzler and Klafter, 2000). Such waiting-time distributions may stem from particles immobile for long times, such as particles in casts lining the walls of worm burrows that are likely to remain immobile for the lifespan of the tubes. This possibility, proposed by Meysman et al. (2008), has not been used in a model although the data reported by Bernard et al. (2012) strongly suggest considering it.

Finally, fractional Brownian motions (FBMs, Mandelbrot, 1982) are characterized by stationary particle displacements and strong correlations between displacements and between particle positions. For these reasons they differ fundamentally from the abovementioned CTRWs. FBMs can induce subdiffusive behavior, as CTRWs do. But they also include superdiffusion (superlinearly evolving mean squared displacement). To date, FBMs have never been considered in sediment reworking studies. However, their success in describing mass transport in a variety of natural environments (Ganti et al., 2009; Barkai et al., 2012) suggests considering them at least to challenge existing models.

Most of these stochastic processes have probability density functions evolved by equations that have the same structure as Eq. (1) with w_b=0, but present significant changes in the right hand side: the diffusion coefficient may include a non-local in time operator, or a factor $t^{\pm a}$ or the second order derivative may be replaced by a derivative of non-integer order.

Examples of sample paths for three of the stochastic processes mentioned above are shown Fig. 1b, left panel.

3. Bioturbation in soils

3.1. Observations

Two particular forms of bioturbation have been extensively studied both under field and laboratory conditions: (*i*) the formation of burrows by the soil macrofauna, and their impact on water and soluble contaminant fluxes, and (*ii*) the characterization of earthworm casts on the soil surface. The repartition of casts inside the soil has received comparatively less attention (e.g., Capowiez et al., 2014). The translocation of soil particles (mineral or organic) and of particulate or adsorbed contaminants during the digging activities of the soil burrowers, or by ingestion, transport, and release have been even much less documented. Early field-scale studies have documented the role of the soil macrofauna on the transport of radionuclides from nuclear fallouts (McCabe et al., 1990; Müller-Lemans and van Dorp, 1996; Tyler et al., 2001). In controlled conditions, at the mesocosm scale, the few published studies highlighted considerable downward movements of micro- and macro-plastics (Huerta Lwanga et al., 2017; Zhang et al., 2018), nanoparticles (Baccaro et al., 2019), wood ash and fluorescent tracer particles (McTavish et al., 2020); upward or downward movements of arsenic (Covey et al., 2010) and upward movements of mercury from a lower contaminated soil layer (Ferber et al., 2019).

Bioturbation by organisms of the soil mesofauna such as enchytraeids has been overlooked, in spite of their large abundance and activity in the topsoil. The few studies that addressed enchytraeids bioturbation concluded that they may influence porosity and aggregation and be the main organisms responsible for cesium redistribution in the topsoil (Didden 1990; Van Vliet et al., 1993; Tyler et al., 2001).

3.2. Bioturbation : an essential process in models of soil functioning.

The transport of particles by soil burrowers cannot be ignored in models of soil functioning such as carbon, nutrients and water cycling. Accordingly, models of organic matter turnover, phosphorous cycle, soil formation and transport of strongly adsorbing and persistent contaminants usually include a bioturbation process (Elzein and Balesdent, 1995; Cousins et al., 1999; Finke and Hutson, 2008; Li et al., 2019; Gray et al., 2020). In these models, bioturbation is essentially described at the macroscopic scale on the basis of the (advective-)diffusive model directly borrowed from aquatic sediments ecology without further justification of its relevance.

There are two exceptions: radionuclide transport was modeled (*i*) at the microscopic particle scale with a continuous space random walk model (Bunzl, 2002), and (*ii*) at the macroscopic scale, using the conveyor-belt model in the same form as in aquatic sediments (Matisoff et al., 2011), or adapted to account for anecic earthworms that release a fraction of the ingested soil particles in the soil profile and the remaining on the soil surface (Jarvis et al., 2010).

3.3. Shortcomings in terrestrial bioturbation modeling.

In a few instances, models of soil functioning were confronted with extensive datasets, allowing the comparison of several models differing in the processes they incorporated. For example, Jarvis et al. (2010) and Matisoff et al., (2011) showed that radionuclide transport in the upper soil could not be described by a solute transport model that did not include bioturbation. Jarvis et al. (2010) further showed that a simple biodiffusion model was inadequate to model these data, and that among the three tested models, the conveyor belt model was the best candidate.

But in most cases, the models of soil functioning (*i*) accounted for several other mechanisms beside bioturbation (e.g. water and solute transfer, geochemistry, tillage, soil volume changes), (*ii*) their outputs have been compared to data collected in experimental situations that were not specifically designed to study bioturbation mechanisms and often lacked a characterization of the species, abundance, biomass and habits of soil burrowers, (*iii*) the parameters D_b and w_B of the (advective-)diffusive model have mainly been determined by adjusting them to fit the – often sparse – experimental data. Overall, this probably (*i*) limited the capacity of these studies to test the adequacy of the bioturbation model hypotheses and (*ii*) yielded values of D_b and w_B that cannot be used to predict bioturbation in different experimental situations. Indeed, in general, different structures of complex models and/or different sets of parameters often reproduce equally well observed experimental data (Beven and Freer, 2001).

A spatially uniform value of D_b was often found insufficient to describe experimental data. An exponential decrease in D_b with depth – presumably supported by a decrease of the number of soil burrowers with depth – allowed a better fit of the model (Covey et al. 2010, Keyvanshokouhi et al. 2019). Furthermore, to represent the bioturbation pattern arising from epigeic and endogeic earthworms that are active close to the soil surface and in the first 20 cm of soil respectively, Tonneijck et al. (2016) used a biodiffusion coefficient that varied with depth according to the sum of two Gaussians. This multiplicity of strategies to reproduce experimental data suggests that the (advective-)diffusive model borrowed from aquatic sediments – although it is conceptually simple and easy to implement, which probably explains its success – may not be the most appropriate concept to model bioturbation in soils.

To parameterize the more elaborate models proposed by Jarvis et al. (2010) or Matisoff et al. (2011), it is necessary to know *a priori* the distributions with depth of particle ingestion and egestion rates, data that are not available in the literature so far. In the absence of such data, both authors hypothesized uniform ingestion rates with depth. Their models were able to fit reasonably well the profiles of radionuclide concentrations. However, the model by Matisoff et al., (2011) overestimated radionuclide concentration next to the surface. The model by Jarvis et al., (2010) led to fitted ingestion rate and fraction of egestion at the soil surface that were respectively six-fold higher and twice smaller than estimated a priori from biological observations. These mixed results suggest that detailed observations of soil invertebrate behavior are required to parameterize these models and to test their underlying assumptions.

Finally, to be valid, the (advective-)diffusive model requires finite values for σ and τ. However, just as in aquatic sediments, it is not unlikely that soil particles released as casts lining the walls of earthworm burrows will remain immobile for long periods of time, typically the lifespan of the galleries (up to seven years, Potvin and Lilleskov, 2017). This suggests considering CTRW models with possibly infinite average waiting-times. Moreover, models based on Lévy flights should not be disregarded since Lévy flights were found to optimize the success of random food searches for a number of living organisms (Viswanathan et al., 1999). Whether this occurs during the foraging activities of soil invertebrates and affects particle translocation remains an open question. Lastly, the independence of successive bioturbation events, a prerequisite for normal biodiffusion, has never been examined in soils. Because the possibilities of particle immobilization, long-distance movement and correlations of bioturbation events have not been ruled out in soils, the current use of the biodiffusive model does not rest on solid foundations.

4. Toward bioturbation models based on solid ground

4.1. Characterize bioturbation and soil invertebrate behavior

There is a considerable dearth of experimental studies characterizing and quantifying the transport of soil particles by the soil fauna at the macroscopic scale. Soil ecologists should address this issue by adapting experimental situations used to characterize bio-mixing in aquatic sediments. These may include recording fluorescent tracer profiles resulting from bioturbation by various soil burrowers, alone and combined, using 2D or 3D terraria as recently proposed by McTavish et al. (2020) and illustrated Fig. 1a, right panel. In three dimensions, X-ray tomography, a technique used to characterize invertebrate burrows could also help to quantify bioturbation nondestructively at several time-points during the particle translocation process. This may be achieved by using particulate contrast agents and *ad hoc* image processing methods as proposed by Schlüter and Vogel (2016) and Grayling et al. (2018). Similar efforts should also target small organisms such as enchytraeids, taking advantage on the increasingly easier access to laboratory micro-tomography setups. These techniques would provide richer (space- and time-resolved) data, compared to the sparse profiles of tracer concentration collected by destructive methods, and would help to discriminate among different models based on different process descriptions or structures during comparative model testing exercises. These experiments should be contemplated over sufficiently long time-scales if they aim at testing the capability of the diffusive model to describe the data.

It is also critical to quantify – across different soil classes and climates – specific organism behaviors that are needed to parameterize and test further existing models. These include: particle ingestion and egestion rates as a function of depth, ingestion selectivity for a contaminant, the impact of food abundance, type and location on bioturbation.

4.2. Test the validity of the diffusive bioturbation model

At the particle scale, the current limit to test the validity of the (advective-)diffusive bioturbation model in soils, and more generally to choose which model could be used successfully, is the absence of data quantifying the individual trajectories of tracer particles. In a first step, the pioneering experimental situation proposed by Bernard et al. (2012) should be adapted to determine these trajectories in 2D terraria (Fig. 1a, left panel). Tracking tracer particles in large 3D soil cores remains a challenge. Particle tracking by positron emission tomography may be a suitable tool to address this, once adapted to cope with the long monitoring periods required in bioturbation studies (Parker et al, 1997).

The next step will be to determine the most suitable class of models to describe these trajectories, even before attempting to determine hypothetical jump-length and waiting-time distributions that are only meaningful if the trajectories actually correspond to CTRWs. This task will be facilitated by recent theoretical efforts that led to powerful diagnostic tools to analyze experimental trajectories of individual particles (Barkai et al, 2012).

One of them, the p-variation, is an easily computed functional of the individual particle trajectories. It is highly sensitive to whether these trajectories correspond to CTRWs (including the advective-diffusive model) or to fractional Brownian motions (Magdziarz et al. 2009, 2010). If the particle trajectories correspond to CTRWs, the p-variation will contain information on the waiting-time distribution. It will also indicate whether Lévy flights-based models are worth being considered. Finally, it is insensitive to confinement constraints, a situation that is likely to occur in the finite terraria or soil cores used to determine the experimental particle trajectories. In view of these properties, this tool represents an appealing opportunity to test previously proposed bioturbation models, both in terrestrial and aquatic environment. Being able to determine the most appropriate model would represent a significant progress, as the stochastic transport models mentioned above have significantly different distributions for various quantities. One example is the first passage time, which could help to assess the risk of a contaminant reaching a specific depth before being degraded.

Finally, other functionals of particle trajectories (Metzler et al. 2014, Krapf et al. 2019), and the large deviation approach (Thapa et al. 2021), will help to estimate the parameters of the models highlighted by the p-variation.

Conclusions

Bio-mixing models borrowed from the aquatic sediment community – and the biodiffusive model in particular – are used to represent bioturbation in soils despite a substantial lack of biological observations to test the relevance of their hypotheses in this substrate and to determine parameter values for soil organisms. To tackle this issue, soil ecologists must address the long-overlooked topic of soil particle transport by the soil fauna.

- Advances in aquatic ecology will contribute to this goal. First, experimental situations successfully used in sediments should help characterizing bioturbation by different soil burrowers at the decimeter and particle scales. As for sediments, this will allow the development of a typology of bioturbation – and associated models – in soils. Second, in sediments, a recent body of literature has discussed the limitations of the biodiffusive model and suggested alternative models to simulate bio-mixing. The conclusions of these publications are generic and are worth considering when modeling soil bioturbation.

- Choosing the best model for a particular dataset, parameterizing this model, and comparing its outputs with comprehensive data are concerns shared by the soil and sediment scientific communities. Accordingly, the advances in mathematics and non-destructive imaging highlighted in this perspective are relevant in both aquatic and terrestrial environments.

- Meeting these experimental and modeling objectives will require a strong cooperation between soil and sediment ecologists, modelers, mathematicians and statisticians: more accurate bioturbation models – and hence more accurate models of soil and sediment evolution, organic matter turnover, and transport of persistent and strongly adsorbing pollutants – are at stake.

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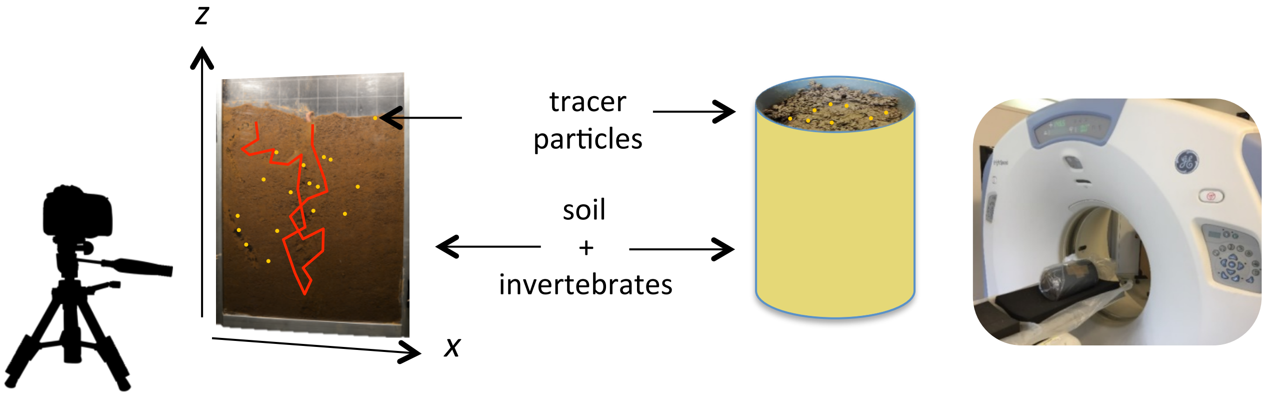
Figure caption

Fig. 1. (*a*) Experimental situations proposed to record *individual trajectories* of tracer particles in 2D terraria (left) and tracer *concentration profiles* in soil mesocosms (right) after incubation with soil invertebrates. X-ray tomography and appropriate tracers should permit to record concentrations profiles at several time-points during incubation (right). (*b)* Particle trajectories will be used to determine the most suitable models to represent bio-mixing. Left panel: 1D examples of sample paths for three of these models classes: Brownian motion (1, black), Continuous Time Random Walk with waiting-time distribution having an infinite mean (2, red), stable Lévy motion (3, green). Model 2 exhibits immobile stages. Model 3 performs sudden (but rare) large motions; right panel. Right panel: appropriate model equations and parameters will be determined by comparing experimental (dots) and modeled (line) tracer concentration profiles (fictitious data for illustrative purposes).

Individual trajectories **Concentration profiles**

of tracer particles

(a)



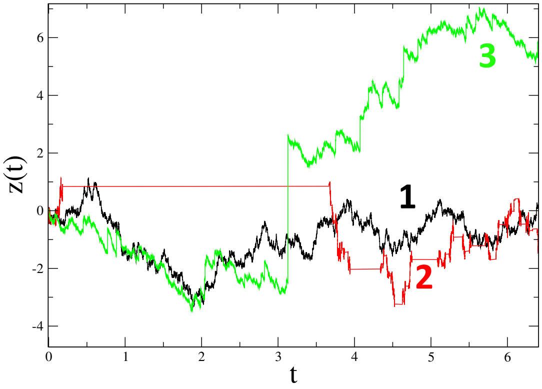
tracer particles

soil + invertebrates

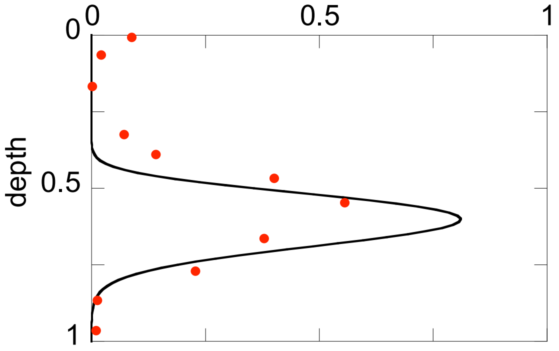
(b)

Stochastic models for trajectories and profiles

sample path of 3 models



tracer concentration



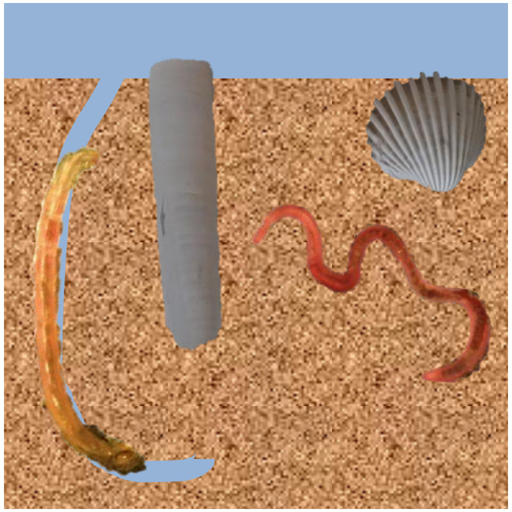
Determine the most appropriate models to represent bioturbation → appropriate equations and parameters

Typology of bioturbation and associated models in soils

Fig. 1. (*a*) Experimental situations proposed to record *individual trajectories* of tracer particles in 2D terraria (left) and tracer *concentration profiles* in soil mesocosms (right) after incubation with soil invertebrates. X-ray tomography and appropriate tracers should permit to record concentrations profiles at several time-points during incubation (right). (*b)* Particle trajectories will be used to determine the most suitable models to represent bio-mixing. Left panel: 1D examples of sample paths for three of these models classes: Brownian motion (1, black), Continuous Time Random Walk with waiting-time distribution having an infinite mean (2, red), stable Lévy motion (3, green). Model 2 exhibits immobile stages. Model 3 performs sudden (but rare) large motions; right panel. Right panel: appropriate model equations and parameters will be determined by comparing experimental (dots) and modeled (line) tracer concentration profiles (fictitious data for illustrative purposes).

Modeling bioturbation

in SEDIMENTS



observations

↓

typology of bioturbation

↓

models:

biodiffusion
conveyor-belt
random walks

biodiffusion → ? biodiffusion

in SOILS

Build-up cooperation between sediment and soil ecologists