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# Self-organization in a simple consumer–resource system, the example of earthworms

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**Abstract**

Classical predator–prey or host–parasitoid models often lead to spatial self-organization due to local interactions and limited dispersal ability of the resource (prey or host) and consumers (predator or parasitoid). We hypothesized that self-organization may also arise in soil organisms when the resource is passive and has a constant renewal rate. Earthworm density is correlated with soil properties, but soil heterogeneity only explains a small proportion of spatial variations in earthworm densities. We hypothesized that this could be partially due to self-organization. These two hypotheses were tested with an original model parameterized for a savannah earthworm population. The model simulates an earthworm population divided in 1 $m^2$ cells. It is based on the assumption that fine soil aggregates constitute the only limiting resource influencing mortality, fecundity and dispersal and that this resource is renewed according to a constant rate independent of earthworm dynamics. Simulations lead to aggregated spatial distributions when the sensitivity of mortality or fecundity to the availability of the limiting resource is high, and when earthworm mobility is low. Such parameters values are consistent with what is known about earthworm biology. Applicability to different ecological systems and resulting population dynamical properties are discussed.


*Keywords:* Earthworm; Self-organization; Spatial distribution; Soil structure; Spatial demography

## 1. Introduction

Earthworms are ecosystem engineers (Jones et al., 1997) that ingest soil and feed on soil organic matter and litter (Edwards, 2004). Since, they process huge amounts of soil, they greatly influence soil structure and soil chemical properties (Lavelle and Spain, 2001). Earthworm distributions, at the scale of a hectare, are never homogeneous and often present larges patches with higher densities of individuals (Poier and Richter, 1992; Decaëns and Rossi, 2001; Rossi, 2003; Whalen and Costa, 2003). A first hypothesis to explain such patterns is that there are more earthworms where soil is intrinsically more favorable. Hence, either because individuals move to the best soil patches or because mortality is higher in unfavorable patches this would lead to spatial variations in earthworm densities. However, earthworm densities are only weakly correlated, if at all, with pre-existing spatial variations in soil properties (Phillipson et al., 1976; Poier and Richter, 1992; Rossi et al., 1997). This suggests that other factors than pre-existing soil heterogeneity influence earthworm distributions. A second hypothesis is that earthworm populations are locally self-regulated. They would decrease the availability of a limiting resource in such a way that when earthworm density increases their survival or fecundity decrease. In interaction with dispersal this could create heterogeneous spatial distributions. The first hypothesis involves soil characteristics that can hardly be changed by earthworms or only very slowly (soil texture, soil humidity due to microtopography or total content in organic matter). The second hypothesis is related to soil characteristics than can be easily changed by earthworms (soil distribution into aggregates size classes, content in the fraction of the total organic matter pool that can be assimilated by earthworms). This second hypothesis

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corresponds to the assumption that aggregative spatial distribution can appear in earthworms due to self-organization (Rohani et al., 1997).

Self-organization in animal populations has been pointed out by many models. The idea is that simple mechanisms at the individual scale may lead to complex non-random patterns at the population scale. It has been particularly shown that non-random spatial patterns can appear solely due to internal demographic mechanisms without any external constraint that would impose a non-random spatial pattern. Two main kinds of system have been considered: predator–prey systems (de Roos et al., 1991; Cuddington and Yodzis, 2000) and host–parasitoid systems (Hassel and Comins, 1991). Both spatially explicit host–parasitoid and predator–prey systems involve the local consumption of a resource (prey or host) and its renewal due to biological sensible mechanisms: migration and reproduction (de Roos et al., 1991; Hassel and Comins, 1991). In these cases, the renewal of the resource in a local patch depends on the local density of preys (or hosts): the number of immigrating individuals depends on the number of preys (hosts) in the neighboring cells, and the number of new born depends on the number of parents, i.e. the number of surviving preys (hosts) in the focal patch. In other words the resource is not passive.

We test here through a simulation model that self-organization and non-random spatial distributions may also arise, in the case of earthworms, when the resource has a very simple dynamics, i.e. when its renewal only depends on a fixed rate independent of the local resource availability. Taken together, our simulation model was used to test whether: (1) self-organization can arise in consumer–resource systems when the resource has a constant renewal rate, (2) such a principle can be applied to earthworms, (3) biologically sensible parameters for earthworm (mobility and sensitivity of life-history parameters to soil quality) lead to patchy distributions through self-organization processes. Due to point 1, our model has a theoretical value in its own right. Points 2 and 3 aimed at testing whether it is possible to apply the model to real systems. To do so our spatially explicit simulation model (SoFaDy for Soil Fauna Dynamics) was parameterized for the species *Millsonia anomala* in the humid savannah of Lamto (Côte d'Ivoire).

## 2. Material and methods

### 2.1. Model description

SoFaDy is a coupled lattice model. Space is divided in 1-m wide cells and the density of earthworms, considered as an integer, is tracked in each square of a $50\,\mathrm{m} \times 50\,\mathrm{m}$ plot. The density of earthworms taken into account is considered to be the density during the rainy season during which all earthworm activities (and especially reproduction) take place and is modified at each time step, i.e. each year. There is a priori no general rule to predict which factors limit locally the density of earthworms. On the long term and at a large spatial scale, earthworm populations are obviously controlled by vegetation types and climatic conditions (Curry, 2004). At smaller temporal and spatial scales, earthworm densities might be regulated by soil types, local soil conditions (humidity, texture) and the availability of food (organic matter of suitable quality) (Curry, 2004). Here, one source of soil heterogeneity has been taken into account: the percentage of soil in two size classes of aggregate: coarse ($\varnothing \geqslant 5\,\mathrm{mm}$) and fine ($5\,\mathrm{mm} > \varnothing$). During simulations percentages of the soil mass in these two size classes, $\mathrm{sp}_1$ (fine aggregates) and $\mathrm{sp}_2$ (coarse aggregates, compacted soil) are tracked in each cell. *M. anomala* is considered to be the only compacting factor: it feeds on fine aggregates and produces coarse aggregates that it cannot reingest, probably because of the morphology of their mouth (Blanchart et al., 1997). Decompacting factors are multiple: other species of earthworms such as species of the Eudrilidae family, other soil macroorganisms such as termites and roots, and finally climate (Blanchart et al., 1997). These factors transform coarse aggregates into fine aggregates and are independent from *M. anomala* population. The following coefficients were used to compute the percentages of the mass of soil that switch aggregate class: compacting factors, $C$ (% individual$^{-1}$ year$^{-1}$); decompacting factors, $D$ (% year$^{-1}$, all parameters are described in Table 1). $D$ must be evaluated for average soil conditions. Fine aggregates are not truly *M. anomala* resource. The limiting factor is the organic matter contained in these aggregates, but since *M. anomala* cannot access to the organic matter contained in big aggregates, small aggregates can be considered as a proxy for resource availability. $n_\mathrm{T}$ being the local number of earthworms, this leads to the following formula for the dynamics of fine aggregates:

$$\mathrm{sp}_1(t+1) = \mathrm{sp}_1(t) + D - Cn_\mathrm{T}.$$

Table 1
Name and definition of the model parameters

| Parameter | Description | Values |
|---|---|---|
| $\delta_{\min}$ | Minimum mortality obtained when environmental conditions are optimal | 0.6 |
| $\sigma$ | Coefficient of the Gaussian distribution used to simulate dispersal | [0.2, 3.0] |
| $\beta$ | Fecundity | 2 or 4 |
| $e_\delta$ | Exponent defining the sensitivity of mortality to soil quality | [0.02, 2.4] |
| $e_\sigma$ | Exponent defining the sensitivity of dispersal to soil quality | [−3, 3] |
| $e_\beta$ | Exponent defining the sensitivity of fecundity to soil quality | [0.02, 2.4] |
| $C$ | Quantity of fine aggregates transformed by one *M. anomala* into coarse aggregates (expressed as a percentage of soil mass) | 0.301 |
| $D$ | Quantity of coarse aggregates transformed into fine ones by decompacting factors (expressed as a percentage of soil mass) | 5.658 |

All fluxes and rates are defined for a 1-year time step.

Since $sp_1$ and $sp_2$ are percentages the simulation program also include tests to maintain their values between 0 and 100 and we always have $sp_2 = 100 - sp_1$.

$C$ is assumed to correspond to the optimal quantity of soil ingested annually by a *M. anomala* and is therefore used to compute environment-dependant mortality, dispersal, and fecundity (see below for the formula). When the quantity of available fine aggregates is limiting (see below), $C$ is no longer multiplied by the local number of earthworms to compute the quantity of fine aggregates transformed into coarse ones: all fine aggregates are considered to be consumed. No between years environmental variation is considered so that parameters are deemed constant.

*M. anomala* life-cycle is modelled using a reproduction rate ($\beta$, number of newborn offspring produced each year by each earthworm) and a minimum mortality rate ($\delta_{min}$) corresponding to the survival rate of individuals in optimal environmental conditions, i.e. appropriate humidity, low percentage of compacted soil, high content of soil organic matter. Fine aggregates are assumed to be the limiting resource. The number of worms that can feed optimally, i.e. without suffering extra mortality, on available fine aggregates is calculated. When there are actually fewer worms than this number the minimum mortality rate is applied ($\delta_{min}$). Otherwise, $n_T$ being the number of worms in the considered cell (and $sp_1$ being the percentage of soil in the finer aggregate class, see above), the theoretical percentage of "starving" worms is calculated

$$\frac{n_T - sp_1/C}{n_T}$$

and is used to calculate the environment-dependant ($rate_{envt}$) mortality rate. Taken together we have

$$\delta_{envt} = \max\left[\left(\frac{n_T - sp_1/C}{n_T}\right)^{1/e_\delta}, \delta_{min}\right],$$

$1/e_\delta$ is the exponent determining how likely "starving" worms are to die, i.e. the sensitivity of mortality to the percentage of fine aggregates. (i) If $1/e_\delta = 1$ all "starving" worms die; (ii) if $1/e_\delta > 1$ less worms die; (iii) if $0 \leqslant 1/e_\delta < 1$ more worms die. $C$ corresponds to the amount of fine aggregates an earthworm must ingest for its mortality to be minimum. Thus, if worms share the soil resource ($0 < e_\delta < 1$), worms that ingest sub-optimal amounts of soil tend not to die (case ii). Conversely, if some individuals monopolize the greatest share of the resource ($1 < e_\delta$), other worms tend to die (case iii). When $e_\delta$ increases the strength of the influence of the availability of fine aggregates on mortality increases. Therefore, $e_\delta$ is hereafter referred to as the sensitivity of mortality to the percentage of fine aggregates (or for short to soil aggregation).

Worms can emigrate from their 1-m wide cells and their dispersal distances along the $x$ and $y$ axes of the grid were considered to follow a centered Gaussian law with variance $\sigma^2$ which corresponds to the hypothesis of a random walk: the mean dispersal distance is always 0 but the more mobile earthworms are, the more likely they are to end up far from their initial position after their random walk and the larger $\sigma$ should be. New positions of worms were calculated assuming that worms are located originally in the middle of their cells. At each time step the processes described above are applied in the following order: reproduction, mortality, dispersion, compaction of the soil, decompaction of the soil. In some simulations, dispersal was applied before mortality.

In some cases, the availability of fine aggregates was also considered to influence either dispersal or the production of juveniles. This was implemented as for mortality, calculating environment-dependent dispersal ability ($\sigma_{envt}$) and fecundity ($\beta_{envt}$) as follows:

$$\sigma_{envt} = \sigma\left(1 + \frac{n_T - sp_1/C}{n_T}\right)^{e_\sigma},$$

and

$$\beta_{envt} = \min\left[2\beta\left(1 - \left(\frac{n_T - sp_1/C}{n_T}\right)^{1/e_\beta}\right), \beta\right].$$

$e_\sigma$ and $e_\beta$ are, respectively, the sensitivity of mobility and fecundity to the percentage of fine aggregates. If $e_\sigma > 0$, the mobility of earthworms increases when the number of starving individuals increases, i.e. when environment quality decreases. This would occur if earthworms have evolved a strategy to avoid low-quality patches of soil. Conversely, if $e_\sigma < 0$, the mobility of earthworms decreases when the percentage of coarse aggregates increases, i.e. when environmental quality decreases. This could be the case if it is more difficult for *M. anomala* to move in a compacted soil, coarse aggregates playing the role of obstacles. When the number of "starving individuals" increases, above a threshold, fecundity decreases and the higher $e_\beta$ is the quicker this decrease is (necessarily $0 \leqslant e_\beta$). When all worms are starving fecundity is null.

SoFaDy is not truly individual-based since only the density of worms in each cell is tracked and since all worms are considered identical. However, the integer number of surviving earthworms among the $n_T$ worms of a cell was determined stochastically: for each individual a random number is drawn between 0 and 1, and if this number is lower than $\delta_{envt}$, the individual dies. Similarly, the dispersal distance of each individual was determined stochastically according to a bivariate Gaussian law $N(0, \sigma^2)$(see above). Finally, the total number of newborn earthworms in a cell was determined multiplying $n_T$ by the fecundity of the cell, $\beta$. Developing a truly individual-based model was not an option due to the high number of worms to be monitored (more than 60 000 for a mean density of 25 individuals $m^{-2}$) and the necessity to run many simulations (1020 for Fig. 2). However, monitoring integer numbers of individuals in each cell and conditioning their fate (survival, dispersal distance) to probability laws is realistic and allows for demographic stochasticity.

Parameters were estimated, when possible, using empirical data gathered in Lamto shrub savannas. To estimate the parameters of soil compaction/decompaction we used Blanchart et al. (1997)'s experiment, but their results were rescaled to fit in our 1 $m^2$-1-year time step frame work. The compaction parameter ($C$) was recalculated on a basis of one earthworm by square meter, so that this parameter was multiplied by the density of worms during simulations to determine the quantity of fine aggregates theoretically ingested for no earthworm to be starving ($C = 0.301$). It must be kept in mind that we can only estimate an average parameter of decompaction ($D$) based on average soil conditions, and an average density of Eudrilidae (we corrected our parameters to take into account the high Eudrilidae densities used in Blanchart et al.'s experiment, $D = 5.658$).

Life cycles parameters were estimated using Lavelle's PhD thesis (Lavelle, 1971). Fecundity and survival were estimated using field sampling, breeding in laboratory and breeding in the field. An annual mortality rate of 0.8 was found in the field and 0.2 in the laboratory. The laboratory conditions were optimal regarding aggregate availability, which is what we need, but optimal climatic conditions were probably leading to an overestimation of survival. In the field, aggregate availability was not optimal. Consequently $\delta_{\min}$ value was chosen to be 0.6. An annual production of 2–4 newborn worms per adult appears to be a good estimation. Lavelle found that sexual maturity was reached roughly at the age of 1 year which justifies the 1-year time step used in our model, although there are yearly two periods of reproduction.

Boundaries of the grid were wrapped-around to avoid boundary effects, i.e. to avoid that boundary cells have less neighboring cells than the others. For each simulation the model was run for 100 time steps (years) starting from a situation where the density of earthworms and the percentage of fine aggregates are randomly chosen, respectively, in the intervals [0, 25] and [20, 40]. Preliminary simulations showed that after 100 time steps (1) the total number of earthworms, over the whole simulated plot, always reaches equilibrium or makes very small oscillations around a plateau, (2) initial conditions have virtually no influence on the outcome of the model as soon as initial earthworm densities are not too low for the population not to go extinct due to demographic stochasticity. Thus, running all simulations for 100 years allowed comparing simulations that stabilize after different numbers of years (typically low values of mobility lead to longer times of stabilization). We analyzed the effect of the two parameters, which were not assessed using empirical data (see Figs. 1 and 2): the sensitivity of mortality to the percentage of fine aggregates ($e_\delta$) and mobility ($\sigma$). $17 \times 15$ combinations of these two parameters ($e_\delta \in [0.4, 50]$ and $\sigma \in [0.2, 3.0]$) were tested for each set of simulation conditions. In certain cases, the sensitivity of fecundity ($e_\beta \in [0.4, 50]$) or mobility ($e_\sigma \in [-3, 3]$) to soil aggregation was varied instead of the sensitivity of mortality. In all cases 5 repetitions were achieved for each parameter combination and the means of the studied variables over these 5 repetitions are displayed (Figs. 1 and 2).

### 2.2. Comparison of model outputs to empirical data

The mean and the variance of *M. anomala* density have already been assessed in Lamto shrub savannas using a suitable data set (Lavelle, 1978): densities were assessed along the year through an exhaustive search in many independent 1 $m^2$ wide blocks. Due to the size of the sampling unit the assessed densities can be directly compared to our simulation results. The mean density calculated monthly over 12 blocks ranged between 12 and 30 individuals $m^{-2}$ (mean over 19 months 20 individuals $m^{-2}$), while the standard deviation ranged between 5 and 16 individuals $m^{-2}$ (mean over 19 months 8 individuals $m^{-2}$).

Spatial distributions of *M. anomala* have been studied in Lamto in $50 \times 50$ m plots, earthworm densities being measured in one $0.25 \times 0.25$ m wide blocks every 5 m (Rossi, 2003). Due to this sampling and especially to the small size of sampling units, which is likely to modify drastically the estimations of the variance of the density (Levin, 1992; Rossi and Nuutinen, 2004), it is difficult to compare directly these data set to our simulation results. Yet, the empirical data sets were analyzed using geostatistics and variograms (Rossi, 2003). Spherical models were fitted to the semivariance estimations (Goovaerts, 1997) according to the following:

$$\text{if} \quad h < a, \quad \gamma(h) = C_0 + C_s\left[\frac{3}{2}\frac{h}{a} - \frac{1}{2}\left(\frac{h}{a}\right)^3\right]$$

$$\text{if} \quad h \geqslant a, \quad \gamma(h) = C_0 + C_s.$$

The model is characterized by three parameters (cf. Fig. 3C and D): $C_0$, the nugget variance; $C_s$ the spatial variance; $a$, the range. The semivariance is assessed on all pairs of sampled points lying within a certain distance class from each other. The semivariance increases from $C_0$ at the origin (distance = 0) to a plateau (the semivariance is then $C_0 + C_s$) which is reached when distance = $a$. For our purpose, the range is of particular interest because it is the distance at which the semivariance reaches its maximum values (the sill) and remains constant. In the case of an aggregative distribution, it is thus an indication of the scale at which autocorrelation is expressed as shown by empirical studies for *M. anomala*. In the field, patches of soil with high *M. anomala* densities can be as large as 20 m wide, and lead to high range values as estimated through spherical models (Rossi, 2003). Our simulation results where analyzed using the same method and range values higher than 10 m were considered as a good qualitative fit between the model and empirical data.

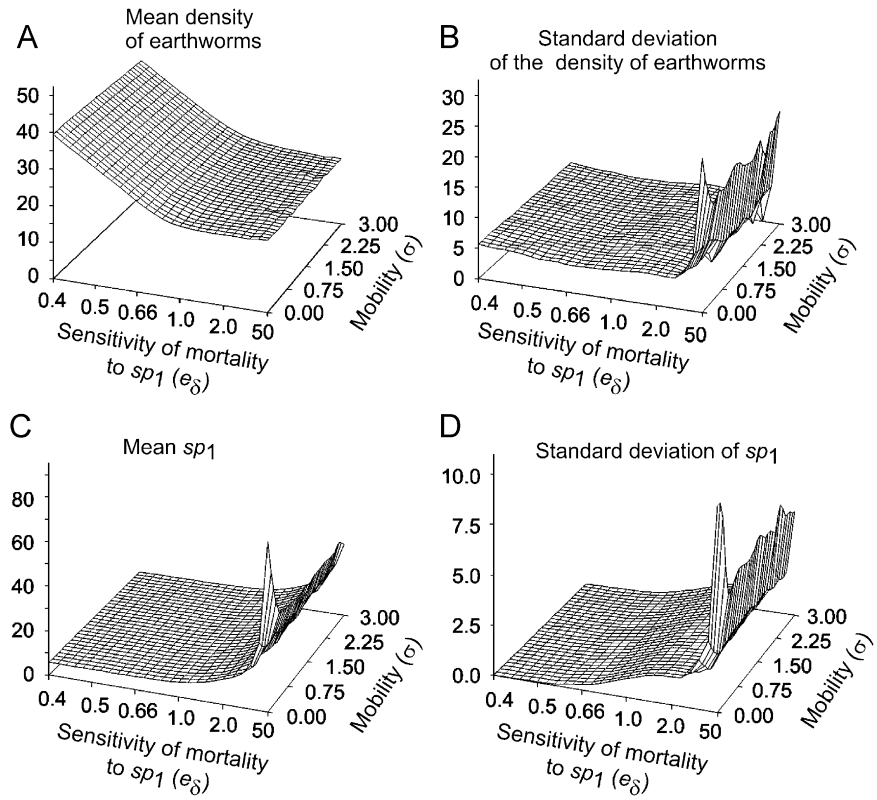


Fig. 1. Basic simulation results. For each 3D graph, the $x$ and $z$ axes correspond, respectively, to the sensitivity of mortality ($e$) to the availability of fine aggregates ($sp_1$), and to the mobility ($\sigma$). Each graph displays on the $y$-axis a different variable that has been calculated for the $50 \times 50$ cells of a simulation run: the mean and the standard deviation of *M. anomala* density and the percentage of fine aggregates in each 1 $m^2$ cell. $\beta = 4$, dispersal is applied before mortality, only mortality depends on soil aggregation. Its must be noted that the $x$-axis is no linearly graduated.

## 3. Results

### 3.1. General behavior of the model

The mean density of earthworms increases when the sensitivity of mortality to soil aggregation ($e_\delta$) decreases (Fig. 1A). The mean density does not depend on mobility ($\sigma$). The standard deviation of earthworm density is low (about 5) when sensitivity of mortality to soil aggregation is lower than 2 (Fig. 1B). The standard deviation of the density increases non-linearly when the sensitivity of mortality increases. Thus, the standard deviation and the mean are negatively correlated.

Since *M. anomala* consumes fine aggregates, the mean percentage of fine aggregates ($sp_1$) increases when the density of *M. anomala* decreases (Fig. 1C), i.e. for high sensitivities of mortality to soil aggregation. The variability in the percentage of fine aggregates (the resource) logically also increases (Fig. 1D) when the variability in earthworm (the consumer) density increases (Fig. 1B), i.e. again for high sensitivities of mortality to soil aggregation. The key point is that for high values of the sensitivity of mortality to soil aggregation the mean and the standard deviation of the percentage of fine aggregates increase steeply (and much more neatly than the standard deviation of the earthworm density) for low mobility values ($\sigma < 0.5$). This is the first effect of dispersion and space pointed out by our model. As other measures of local variability (standard deviations of the earthworm density and the percentage of fine aggregates), the nugget and spatial variances estimated for the variograms of earthworm distribution increase abruptly when the sensitivity of mortality to environmental quality is high ($5 < e_\delta$, graphs not displayed).

### 3.2. Spatial distribution

The patterns described so far are common to all simulations and do not depend on fecundity (either 2 or 4) or the order in which mortality and dispersal are applied. They are encountered either when fecundity, mortality or dispersal depend on soil aggregation. However, these factors determine whether a heterogeneous spatial structure appears, with low and high earthworm density patches. In most cases, there is no long-range spatial structure (see Fig. 2A), i.e. the range estimated for the variogram of the earthworm density is very low (see Fig. 3D). In other cases the range becomes higher than 10 m for some combinations of the mobility and the sensitivity of mortality or fecundity to soil aggregation (Fig. 2B–D). Typically this happens either for low values of

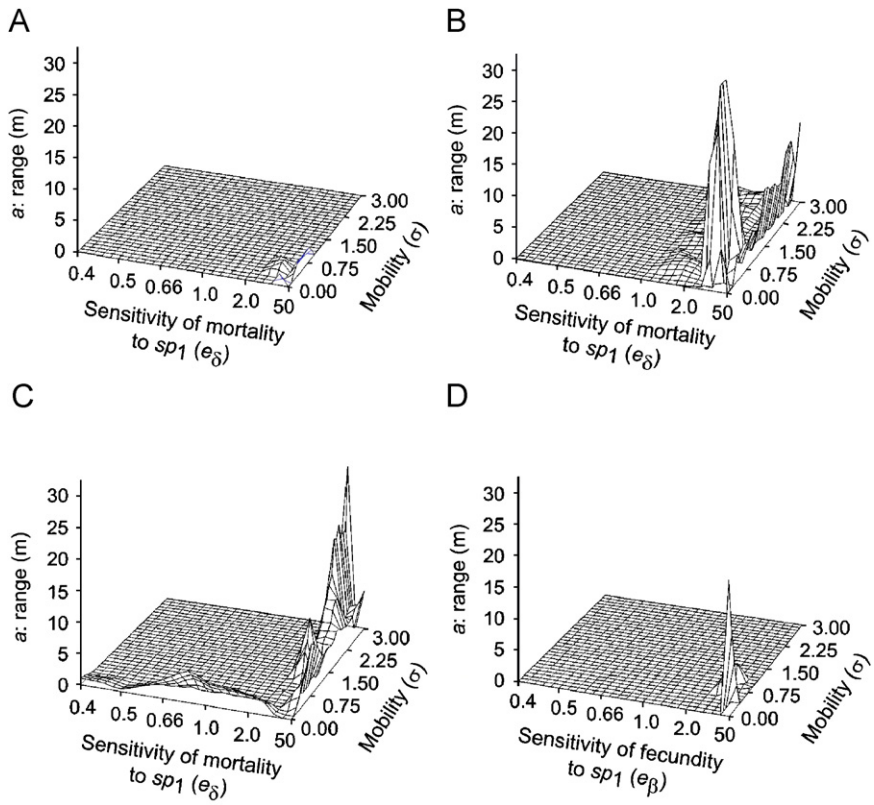


Fig. 2. Analysis of earthworm spatial distribution. Variogram range, as defined by a spherical model, is displayed as a function of earthworm mobility and the sensitivity of their mortality (or fecundity) to the percentage of fine aggregates ($sp_1$). Earthworm densities were log-transformed to compute the variogram. (A) $\beta = 2$, dispersal then mortality, only mortality depends on soil aggregation; (B) $\beta = 4$, dispersal then mortality, only mortality depends on soil aggregation; (C) $\beta = 4$, dispersal then mortality, mortality and dispersal depend on soil aggregation ($e_\sigma = -2$ so that mobility decreases when the percentage of coarse aggregates increases); (D) $\beta = 4$, mortality then dispersal, only fecundity depends on soil aggregation.

mobility ($\sigma < 0.5$) and high sensitivities to soil aggregation ($2 < e_\delta$ or $e_\beta < 0.5$, see Fig. 2D), or for high sensitivities to soil aggregation, the range increasing when mobility increases (Fig. 2C). Both features can appear in the same set of simulations (Fig. 2B).

Fig. 3 gives two examples of simulated spatial distributions. In the first case (panel A), an aggregative spatial structure appears with large patches (>10 m in diameter) with higher earthworms densities and large gaps with low earthworm densities. In the second case (panel B), the spatial variability in earthworm density is lower and the spatial structure remains homogeneous. These differences in structures are made clear by the variograms (Fig. 3C and D). Variograms are flat when spatial structure is homogeneous and the range is then null (Fig. 3D). For non-random spatial distributions, the semi-variance increases with distance before reaching a plateau, which leads to non-null range values (Fig. 3C). Generally speaking, spatial aggregation and large range values only appear when variability in both earthworm density and percentage of fine aggregates is high (Fig. 1), i.e. when the sensitivity of mortality to soil aggregation is high.

We investigated systematically the effect of fecundity (2 or 4), the order in which mortality and dispersal are applied, and the demographic parameters depending on soil aggregation (fecundity, mortality, or dispersal). In Table 2 are displayed the results for which only one parameter depends on soil aggregation. In Table 3 are displayed the results for which two parameters depend on soil aggregation. Dependence of dispersal, as opposed to mortality and fecundity, on soil aggregation never results, alone, in large-scale spatial structures. Spatial aggregation tends to appear when fecundity is high ($\beta = 4$) and when dispersal occurs before mortality. There are exceptions to this general pattern. For example, when both dispersal and fecundity depend on soil aggregation, aggregative spatial structure only appears when mortality is applied before dispersal (bottom of Table 3).

### 3.3. Comparison with empirical data

High sensitivities of mortality (see Fig. 1) or fecundity to soil aggregation (graph not displayed) lead to values for the mean and standard deviation of *M. anomala* density, and for the percentage of fine aggregates, that are compatible with empirical data. Hence, the simulated mean and standard deviation are respectively around 20

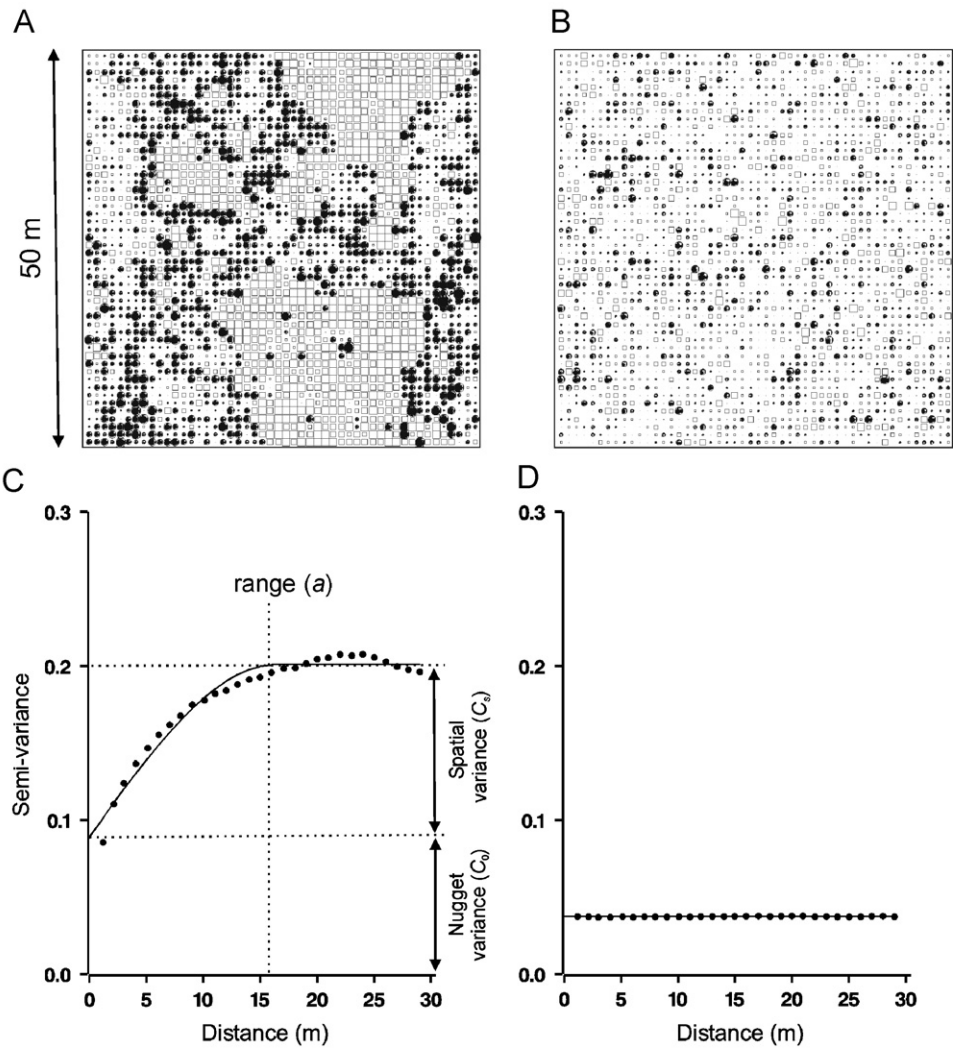


Fig. 3. Example of model outputs corresponding to the simulation conditions of Fig. 2B. Earthworm density maps are displayed with the corresponding variograms for which spherical models were fitted according to a spherical model (Goovaerts, 1997). For the variograms, the logarithm of densities was used. The spherical model is defined by three parameters: $C_0$, the nugget variance; $C_s$ the spatial variance; $a$, the range (see text for details). Maps display the density of earthworms in each 1 $m^2$ cell. Squares are used for densities above the mean, dots for densities below the mean. The size of the symbol is proportional to the difference to the mean. $\beta = 4$, mortality then dispersal, only mortality depends on soil aggregation. Panel A, $\sigma = 1.0$, $e_\delta = 12.5$, large-scale spatial structures; panel B, $\sigma = 2.0$, $e_\delta = 1.0$, homogeneous spatial structure.

individuals $m^{-2}$ and between 10 and 20 individuals $m^{-2}$ while empirical data show that they belong respectively to the intervals [12, 30] and [5, 16]. Percentages of fine aggregates found with the same simulations, between 30% and 60%, are also compatible with observed values (Blanchart et al., 1997). Alone, dependence of dispersal on soil aggregation does not permit the auto-regulation of the population and leads to density values much too high to be realistic.

It was possible to find aggregative earthworm distributions with large-size patches (long ranges as estimated using variograms, Fig. 2). Such patterns arise when sensitivity of mortality or fecundity to soil aggregation is high and either when mobility is low or high. Such patterns are compatible with those described empirically (Rossi, 2003) as far as the spatial scale is concerned (the range).

## 4. Discussion

### 4.1. The mechanism of spatial aggregation

The first pattern to be explained is the increase in the variability in earthworm density for high values of the sensitivity of mortality to soil aggregation. For low values of this sensitivity fecundity is always large enough to make up for mortality so that the remaining variability (constant standard deviation around 5) must be due to demographic stochasticity (this was checked suppressing stochasticity in the simulation program). For large values of the sensitivity of mortality, fecundity is no longer able to make up for mortality in one reproductive event (1 year). Consequently there are square meters with low earthworm densities. These densities increase progressively during several years and, when they exceed the optimal density (that allows all

Table 2
Results of simulations

| Dispersal/mortality | $e_\delta$ | $e_\sigma$ | $e_\beta$ | Fecundity (# new-born year$^{-1}$ adult$^{-1}$) | Large-scale spatial structure |
|---|---|---|---|---|---|
| *Only mortality depends on soil aggregation* | | | | | |
| MD | var | — | — | 2 | No |
| DM | var | — | — | 2 | No |
| MD | var | — | — | 4 | No |
| DM | var | — | — | 4 | Yes |
| *Only dispersal depends on soil aggregation* | | | | | |
| MD | — | var | — | 2 | No |
| DM | — | var | — | 2 | No |
| MD | — | var | — | 4 | No |
| DM | — | var | — | 4 | No |
| *Only fecundity depends on soil aggregation* | | | | | |
| MD | — | — | var | 2 | No |
| DM | — | — | var | 2 | No |
| MD | — | — | var | 4 | Yes |
| DM | — | — | var | 4 | Yes |

Simulation conditions are defined by a fecundity value and the order in which mortality and dispersal are applied (MD when mortality is applied before dispersal, DM otherwise). For each set of simulations $15 \times 17$ combinations of the mobility and the sensitivity of one demographic parameter to soil aggregation were tested. This variable demographic parameter is denoted by the term "var", in the corresponding column (respectively, $e_\delta$, $e_\sigma$ and $e_\beta$ for mortality, mobility, and fecundity). The symbol "—" was written to indicate the parameters that were not variable for a given set of simulations. The last column of the table indicates whether some of these simulations lead to aggregated spatial patterns as defined by range values higher than 10 m (cf. Fig. 3C).

Table 3
Results of simulations

| Dispersal/mortality | $e_\delta$ | $e_\sigma$ | $e_\beta$ | Fecundity (# new-born year$^{-1}$ adult$^{-1}$) | Large-scale spatial structure |
|---|---|---|---|---|---|
| *Both mortality and dispersal depend on soil aggregation* | | | | | |
| DM | var | 2 | — | 2 | No |
| DM | var | 2 | — | 2 | No |
| MD | var | 2 | — | 4 | No |
| DM | var | 2 | — | 4 | Yes |
| MD | var | −2 | — | 2 | No |
| DM | var | −2 | — | 2 | No |
| MD | var | −2 | — | 4 | No |
| DM | var | −2 | — | 4 | Yes |
| *Both mortality and fecundity depend on soil aggregation* | | | | | |
| MD | var | — | 10 | 2 | No |
| DM | var | — | 10 | 2 | No |
| MD | var | — | 10 | 4 | No |
| DM | var | — | 10 | 4 | Yes |
| MD | var | — | 0.5 | 2 | No |
| DM | var | — | 0.5 | 2 | No |
| MD | var | — | 0.5 | 4 | No |
| DM | var | — | 0.5 | 4 | Yes |
| *Both dispersal and fecundity depend on soil aggregation* | | | | | |
| DM | — | 2 | var | 2 | No |
| DM | — | 2 | var | 2 | No |
| MD | — | 2 | var | 4 | Yes |
| DM | — | 2 | var | 4 | No |
| MD | — | −2 | var | 2 | Yes |
| DM | — | −2 | var | 2 | No |
| MD | — | −2 | var | 4 | Yes |
| DM | — | −2 | var | 4 | No |

Same caption as for Table 2. Here two demographic parameters depend on soil aggregation for each set of simulations. These parameters (respectively, eδ, eσ and eβ for the sensitivity of mortality, mobility and fecundity to soil aggregation) are marked either by the term "var" when 17 values of this parameter were tested or by the fixed value used for this parameter. For each set of simulations (each line of the table) 15 values of mobility were tested in combination with the 17 values of sensitivity. The last column of the table indicates whether some of these simulations lead to aggregated spatial patterns as defined by range values higher than 10 m.

earthworms to access to fine aggregates), mortality becomes very high due to the high sensitivity of mortality to aggregation. This automatically increases the variability (in space and time) in earthworm density.

The second pattern to be explained is the apparition of aggregative spatial distributions when the sensitivity of mortality to soil aggregation is high and when mobility is low. A necessary condition to get an aggregative spatial pattern is to have an important variability in earthworm density which requires large values for the sensitivity of mortality to soil aggregation (as explained above). To get an aggregative spatial structure, spatial auto-correlation is also required and depends on mobility. Dispersal must be efficient enough to synchronize neighboring cells, i.e. to allow neighboring cells to host similar earthworm densities during several years, but when dispersal becomes too efficient earthworm density tends to be homogeneous. This analysis is supported by models published on spatial predator–prey systems (de Roos et al., 1998; Hosseini, 2003). Here, fecundity, the order in which the simulation program applies reproduction and mortality, and dependence of mobility on soil aggregation influence in a non intuitive way the level of mobility necessary to get aggregative distributions for earthworms (see Fig. 2).

### 4.2. Earthworm spatial distribution

Our model has a theoretical value on its own right, as an original type of consumer–resource model. Before dealing with this point, we discuss our results in the context of earthworm dynamics. We have shown using a simple model that local interactions and self-organization are good candidates to explain, at least partially, earthworm patchy distributions and the weak correlations between earthworm distribution and pre-existing soil heterogeneity (Phillipson et al., 1976; Poier and Richter, 1992; Rossi et al., 1997). Although two critical parameters of the model have not been assessed and have probably never been assessed for any earthworm, three elements support this conclusion: (1) Patchy distributions, with large patches comparable to the ones observed in the savannah (large ranges as estimated using variograms), appear with parameter values (fecundity, minimum mortality, compaction and decompaction) assessed using field data. (2) This occurs when the mobility of earthworms is low and when the sensitivity of earthworm demographic parameters to soil aggregation is high, which is compatible with what is know about their biology (see below). (3) In these cases the simulated means and standard deviations of earthworm density and percentages of fine aggregates in the soil are compatible with empirical observations.

Preliminary simulations showed that initial spatial distributions of earthworms and percentages of fine aggregates have virtually no influence on spatial distribution of earthworms at equilibrium and on the location of high and low earthworm density patches. Yet, in Lamto savannahs as well as in other ecosystems (Phillipson et al., 1976; Poier and Richter, 1992; Rossi et al., 1997), pre-existing sources of spatial heterogeneity are likely to influence the earthworm aggregative distribution independently of self-organization processes. First, other resources such as soil organic matter could influence earthworm distribution, especially because plant distribution is likely to cause a permanent heterogeneous distribution of soil organic matter. For example, in Lamto, as in most savannahs, trees grouped in clumps are likely to supply earthworms with organic matter of better quality than grasses. Second, soil texture, which is not homogeneous, can hardly be modified by earthworms (unless they mix different soil layers having different textures) and probably causes spatial variations in the stability of coarse aggregates (clay being a stabilizing factor). Clay also leads to a better storage of soil organic matter, the endogeic earthworm food resource. These factors could be incorporated in the model, which will allow analyzing how self-organization factors and external constraint interplay to determine spatial distributions of earthworm populations.

### 4.3. Limitations of the model

The main simplifying assumption of SoFaDy is that demographic parameters are constant in time while it is well known that earthworms are sensitive to climatic variability (Lavelle and Spain, 2001). In the tropics earthworms are particularly sensitive to variations in the length and intensity of the dry season during which mortality is often high in spite of migration to deeper soil layers and quiescence. In climatically unfavorable years density-independent mortality increases, densities decrease, and local self-regulation processes, i.e. increase in mortality due to the shortage of a resource, are likely to be less efficient. The reverse happens in climatically favorable years. Density-dependence being due to the availability of fine aggregates, a drastic decrease in the mean earthworm density during 1 year is not likely to suppress all spatial variations in survival because several years with low earthworm densities are necessary to regenerate the fine aggregates. For these reasons temporal variations in demographic parameters are not likely to impede heterogeneous spatial structures to appear through self-organization.

Density-dependence in earthworms has already been documented in some earthworm species, but underlying mechanisms are often unknown (Butt et al., 1994; Kammenga et al., 2003). A key assumption of the model is that density-dependence in *M. anomala* is due to a main limiting resource, i.e. soil fine aggregates. It is indeed known that the availability of food, i.e. soil organic matter, is often limiting (Lavelle and Spain, 2001) and that the quality of soil organic matter is also influential, especially for *M. anomala* (Lavelle et al., 1989). Besides, predator could locally reduce earthworm density, probably more in the case of anecic species than for endogeic species such as *M. Anomala* (Judas, 1989; Klok et al., 1997). This could in

turn participate in creating a patchy distribution in earthworms. Taking into account such factors would benefit the model.

Spatial structures with large patches arise in two cases: for very low values of mobility and for much higher ones (Fig. 2) that seem less realistic. Endogeic earthworm horizontal mobility has been assessed very rarely (Marinissen and van den Bosch, 1992) but their mobility is likely to be low. Although they move quasi constantly to feed it seems realistic that they move horizontally in random directions and that there straight dispersal distance in 1 year is at most 1 or 2 m. Such a low mobility leads to heterogeneous spatial structures in earthworm density but experiments are needed to assess precisely earthworm mobility, one difficulty being that a marking technique has first to be developed. It could be argued that earthworms move randomly only when soil properties are homogeneous and favorable. As soon as soil is heterogeneous, evolution should favour strategies that enable earthworms to move along gradients in soil properties, and thus to chose their habitats. Indeed, our simulations show that such strategies influence earthworm distribution and may be involved in self-organization, but empirical results pointing at such strategies are very scarce (Mather and Christensen, 1992). More generally, although our model is based on several PhD theses which have resulted in the publication of about twenty empirically based papers on *M. anomala*, our modelling efforts should foster new field and experimental studies to assess the mobility of earthworms and the sensitivity of their life-history parameters to soil quality.

### 4.4. Self-organisation in simple consumer–resource systems

Our model is conceptually very simple and general. It describes the demography of a population regulated by density-dependent processes mediated by the local depletion in a resource as other spatial model of host–parasitoid (Hassel and Comins, 1991) or predator–prey system (de Roos et al., 1991). As in classical spatial resource–consumer models (de Roos et al., 1991; Hassel and Comins, 1991) spatial organization results from local resource depletion. Together with limited dispersal this decreases the mean consumption rate but increases the variability of this consumption rate (Hosseini, 2003) which increases spatial and temporal variations in the consumer demographic parameters and density. Limited dispersal ability avoids a constant homogenization of the consumer density but allows for a certain level of synchronization between neighboring sites which leads to large patches with higher consumer densities.

As hypothesized, self-organization arises in our model although resource renewal is passive and does not depend on the local availability of the resource, as it is the case with preys and hosts. This is an important result that could be applied to a wide range of ecological systems. (A) We can think about all soil organisms which, as earthworms, feed on a certain type of litter or a certain fraction of soil organic matter (Lavelle and Spain, 2001). Such a resource is likely to be renewed at a fixed rate depending on primary production and plant biomass turnover. On the long term the action of these organisms could interact with primary production since they are involved in nutrient cycling. However, on shorter time scales the resource dynamics is unlikely to depend on these organisms. In the same vein, (B) predators or (C) herbivores with low mobility could locally exhaust their resource that could be renewed integrally independently of the level of exhaustion. This should arise if the prey (the plant) has a very high dispersal ability leading to global dispersal or if the prey population has a very high growth rate and can quickly recover from a few individuals (or a low biomass) because it is locally only limited by predation (herbivory) and not by any limiting resource. Finally, our model is related to spatially explicit models of plants taking explicitly into account plant effect on local nutrient availability (D) through nutrient absorption, local recycling of organic matter (Colasanti and Grime, 1993) and nitrogen fixation (Jenerette and Wu, 2004). In this type of model, as in ours, resource (mineral nutrients) renewal/depletion only depends on the consumer density and not on the availability of the resource. Such models usually also result in self-organization (Rietkerk et al., 2004).

Our model leads to the same properties of the consumer population as models involving more complex resource dynamics (de Roos et al., 1991; Durrett and Levin, 2000). At a large scale, consumer (i.e. earthworm) density always reaches an equilibrium value hiding temporal and spatial variations in local densities. Asynchronic variations in the local densities of consumer would lead to a stabilization of the whole population density (de Roos et al., 1991) (but see Hosseini (2003)). Spatial patterns are not fixed in time in the sense that local neighboring patches (cells of our lattice model) are synchronized for a certain period and then get asynchronised. In other words, the shape of high and low density areas changes continuously leading to a 'spatial chaos' as in some host–parasitoid systems (Hassel and Comins, 1991; Comins et al., 1992).

## 5. Conclusion

Finally, why should we go on bothering with earthworm spatial patterns? First, models attempting to parameterize a spatial resource–consumer model for an animal population and to compare the model outputs with empirical patterns are relatively scarce (Wilson et al., 1999). Second, earthworms are ecosystem engineers (Jones et al., 1997) and very few models have been published on the dynamics of an ecosystem engineer and the way it modifies ecosystems (Cuddington and Hastings, 2004; Wright et al., 2004). Finally, earthworms influence plant growth in different ways (Scheu, 2003; Brown et al., 2004; Blouin et al., 2006): through their ecosystem engineering activities that have rarely been modelled and through their effect on

organic matter mineralization. Taking soil organic matter content and mineralization into account would thus be an important development of SoFaDy to predict the effect of earthworms on plant dynamics.

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