

S4: ODD of modified models

¹Useful models are often modified to represent new knowledge or serve new purposes. In such cases, it makes sense to take the original ODD and highlight the new elements. Here we provide an example, which was compiled for this supplement. Following the recommendations from the main article, and from Supplement S5, all three versions would have included a license agreement that explicitly allows, under the stated conditions, the re-use of the earlier ODD. When using earlier ODDs, or writing your own, please make sure to include a license agreement.

The ODD protocol below includes changes in model descriptions across three EEEworm (Energy – Environment – Earthworm) models. The original earthworm model (M1 and black text throughout) was developed for the epigeic (=living in the topsoil) earthworm species *Eisenia fetida* to investigate different pesticide effects (Johnston et al., 2014a). The second model (M2 and blue text throughout) was developed for the endogeic (=moving in the soil parallel to the surface) earthworm species *Aporrectodea caliginosa* to translate management (pesticide and tillage) effects on individuals to field populations (Johnston et al., 2014b; Johnston et al., 2015). The third model (M3 and red text throughout) was developed for the anecic (=making permanent vertical burrows in the soil) earthworm species *Lumbricus terrestris* to forecast the effects of tillage intensity and soil warming on their populations in the field (Johnston et al., 2018).

Please note that here often later versions, M2 and M3, replace earlier versions, for example for ODD element 1, “Purpose and Patterns”, while in other cases, as in some submodels, M3 is a mixture of old and new versions. Leaving replaced ODD elements in the current ODD is useful as it might still explain how certain parts of the model were designed, but it has to be made clear, for example using a footnote, that the latest version overrides all earlier versions in the current ODD.

²1 Purpose and patterns

³M1: The purpose of the model is to simulate *Eisenia fetida* population dynamics under varying environmental conditions representative of those encountered in the field and investigate how energy budgets can be used to investigate how pesticides achieve their physiological effects. The patterns used to assess the models ability to realistically capture these processes included changes in body mass and reproductive outputs over time and in response to varying temperatures, food availabilities and pesticide active ingredients and concentrations. Population dynamics in the field were assessed with limited data on seasonal *E. fetida* population abundance, biomass and stage (adult, juvenile and cocoon) structure in a manure heap.

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² The three ODDs merged here were written before the new guidance in Supplement S1 existed.

³ This ODD describes M3, so that „Purpose and patterns“ for M1 and M2 are obsolete. They are still kept in the ODD to better understand how the design of the model developed.

M2: The purpose of the model is to simulate *Aporrectodea caliginosa* population dynamics in agricultural fields. We investigate how food quality and soil water conditions alter individual life cycle processes and movement in the soil profile, key to predicting the exposure of populations to pesticide applications and tillage events at the soil surface. Finally, we investigate the effects of different management practices (pesticide and herbicide applications and tillage intensity) in different environmental scenarios. Individual- and population-level patterns were evaluated to ensure individual physiology, behaviour and interactions with one another and their environment were realistically captured by the model. At the individual level, changes in body mass and cocoon production were observed in various temperature, food availability and quality, soil water potential and population density conditions. At the population level, population dynamics were observed from multiple field experiments measuring population abundance, biomass and stage structure in control conditions and in response to organic amendments and pesticide applications. The vertical distribution of the population in the soil profile was also important in identifying whether the model realistically captured individual movement behaviours in response to environmental variables.

M3: The purpose of the model is to simulate *Lumbricus terrestris* population dynamics in field conditions. We investigate how tillage intensity leads to varying declines in *L. terrestris* populations by testing the effects of food availability and quality, soil water and temperature conditions on individual movement, and the effects of tillage on direct earthworm mortality, burrow destruction and litter removal. Finally, we forecast the interactive effects of tillage intensity and soil warming. As in M1 and M2, patterns of individual growth and reproduction in response to varying temperatures, soil water potentials and food availability and quality were assessed. At the population level, the vertical distribution of the population across seasons and population abundance and biomass in response to varying field conditions were evaluated with independent data.

2 Entities, state variables and scales

M1: The IBM comprises a number of individual *E. fetida* individuals and a model landscape consisting of two dimensional 0.01 m^2 patches of soil. Individuals are characterized by life cycle stage (cocoon, juvenile or adult), mass and energy reserves, and landscape patches by pesticide concentration, food density, soil temperature and soil moisture. The model proceeds in discrete daily time-steps. Metabolic calculations are in units of energy per unit time (kJ day^{-1}).

M2 & M3: EEEworm represents individual earthworms with their own energy budgets and behavioural decisions, interacting with each other and their environment in a spatially explicit IBM. The model environment represents a vertical cross-section of a soil profile, comprising $10 \times 10\text{ cm}$ or $1 \times 1\text{ cm}$. Field scenarios were set up with model soil profiles spanning 2 m (horizontal) $\times 0.5\text{ m}$ (vertical), or $3\text{ m} \times 1\text{ m}$, and soil patches were characterized by temperature, water content, texture, bulk density, soil organic matter (SOM) content and plant litter quantity and quality inputs (Figure 1). EEEworm proceeds in daily or hourly time-steps here with a 12:12 hour day:night cycle. Daily and seasonal fluctuations in soil conditions (e.g.

soil temperature, SOM, plant litter) are modelled according to observed seasonal and vertical relationships.

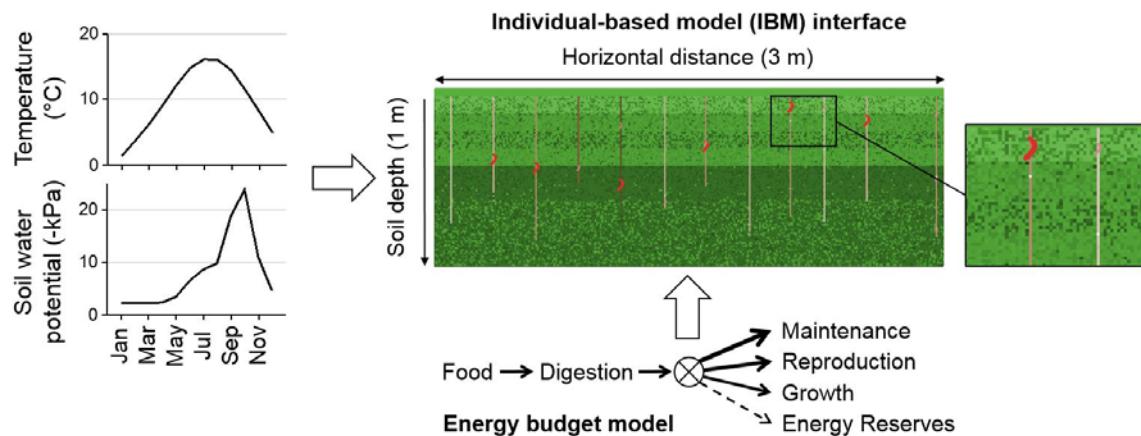


Figure 1. Overview of the EEEworm model. Unique individual earthworms inhabit vertical burrows. The model environment replicates weather and management conditions, and population dynamics emerge from model simulations. The IBM interface presented here is for *Lumbricus terrestris* with weather data from Gerard (1967).

3 Process overview and scheduling

M1 – M3: The model proceeds in discrete daily or hourly time-steps, at the end of which individual and landscape state variables are updated. Juveniles and adults move randomly, in response to trade-offs between food quality and soil water conditions or food quality, soil water and temperature conditions in the landscape (*Movement*), assimilating a fixed proportion of energy from ingested food (*Ingestion and Energy Uptake*) that fuels life cycle processes (*Maintenance*, *Burrowing*, *Growth & Reproduction*) (Figure 2). Feeding by individuals depletes landscape patches and the food density changes accordingly. Cocoons cannot feed or move but pay maintenance costs from energy reserves until they are fully developed at the end of the temperature-dependent incubation period, when they hatch as juveniles (Sousa et al., 2010). Juveniles transform to adults once they reach a body mass threshold for sexual maturity (Ma, 1984; Springett and Gray, 1992). Food was provided in the same amounts as in the experiment being simulated, and food densities in landscape patches depleted as individuals ingested food. When food was not available, energy reserves were used to cover maintenance costs. Once the energy reserves are depleted to a critical level, individuals catabolise energy from tissue to meet maintenance demands (*Energy Reserves and Starvation*). Individual survival is determined by the availability of energy resources to maintain life cycle processes, together with background mortality rates which are either environment- or density-dependent (*Survival*). In the field soil water and soil texture variations are used to calculate soil water potentials (-kPa), which constrain individual growth and reproduction (*Soil water potential*). If the soil water potential drops to a critical level under dry conditions, juveniles and adults enter a resting phase of aestivation in which their metabolic rate is reduced (*Aestivation*). Land management practices, including pesticide applications and tillage events, affect survival and/or life cycle processes. Pesticides were

applied in the IBM at the concentrations and times specified in the experiment being simulated. Individuals experiencing these concentrations were affected as indicated by potential ‘toxicity submodels’ (*Pesticide Effects*). Tillage events were simulated to different soil depths, and affect earthworm populations through direct earthworm mortality in the tilled soil layers, changes in soil physical conditions (soil water content, SOC, bulk density and litter layer) and the destruction of burrows (*Tillage Effects*).

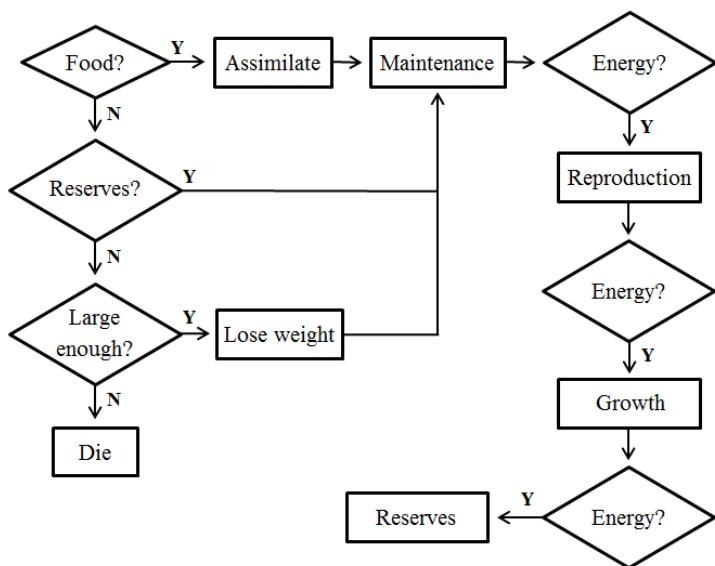


Figure 2. Partial energy flow diagram of earthworm *Aporrectodea caliginosa* adults, showing the processes (rectangles) each individual goes through per time step, with diamonds indicating decision points. Energy reserves are used to pay maintenance costs when food is unavailable, and individuals die if weight loss under starvation continues.

Individual behaviour is modelled according to individual life stage, size, energy status, and environmental and population density conditions. Inevitably, some of the complex behaviours exhibited by *L. terrestris* are simplified in the EEEworm model. A conceptual model of the behavioural decisions made by individuals in hourly time-steps are outlined in Figure 3 and described in further detail in ‘Submodels’.

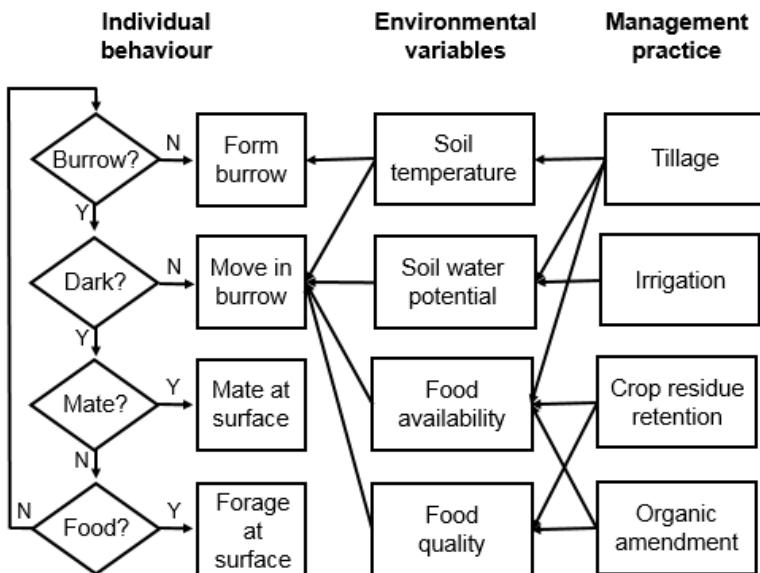


Figure 3. Conceptual model of *L. terrestris* individual behaviour per hourly time-step in EEEworm. Behavioural rules in the diamond and square boxes are described fully in the text. If individuals do not already inhabit a burrow, they will prioritise burrow formation above all other behaviours. During dark hours individuals mate and forage at the soil surface. Adults prioritise searching for a mate (if required: every three months for sperm transfer) in neighbouring burrows before foraging on plant litter. During light hours individuals are largely inactive in their burrows but can move to optimise their position in the burrow according to prevailing environmental conditions. Different management practices affect different environmental variables in the soil profile, which also affect individual energy budgets.

4 Design Concepts

Basic Principles. – Key processes in the model determine how energy consumption and expenditure direct life cycle processes in response to environmental conditions. Individual energy budgets follow fundamental principles of physiological ecology and scale with body mass and temperature according to known allometric relationships (Sibly et al., 2013). Individual movement decisions are made according to trade-offs in the environmental conditions of neighbouring patches, whereby individuals optimise their position in the soil profile.

Emergence. – Variation in food availability between patches arise from the movement and feeding of individuals across the landscape. Population dynamics emerge from differential energy allocation amongst individuals which is affected by pesticide concentration, soil temperature and food availability. Individuals move through the soil profile in response to food quality and soil water content in neighbouring soil patches. In general, soil water increases and food quality (SOM) decreases with depth, causing the vertical distribution of the population to change in response to daily environmental fluctuations. Aestivation (a period of inactivity) is triggered when soil conditions become too dry: individuals then use their energy reserves to pay the energetic costs of maintenance. Individuals forage on plant litter at the soil surface, typically within a 50 cm radius of the burrow mouth (Nuutinen and

Butt, 2005). If food is limited, individuals can forage to greater distances from their burrows and return to a closer unoccupied burrow if available at day light. During daylight periods *L. terrestris* individuals stay within their burrows to avoid high predation risk. While in their burrow, individuals optimise their position according to non-linear trade-offs between food quality, soil temperature and soil water conditions. Individuals sense patch quality within their burrow and preferentially move towards vertical patches of higher favourability. If a neighbouring soil patch is more favourable than an individual's existing burrow patch, it will extend its burrow to include this patch if the associated energy requirements of burrowing can be met. Individuals may ingest soil if energy requirements cannot be met during daylight hours, or if there is insufficient availability of litter (e.g. Marhan and Scheu (2005)).

Adaption. – Individuals move according to a trade-off between soil water and feeding conditions, so that when soil water conditions are favourable individuals exploit more energy rich food resources at the soil surface. Conversely, when soil moisture is limiting individuals move to deeper soil layers to avoid dry conditions.

Interaction. – Individuals need a mate (any other adult as earthworms are hermaphrodite (Dominguez et al., 2003)) present in the same patch to reproduce. Adults and juveniles interact indirectly by competing for food within patches, and both affect patches by depleting food. Adult *L. terrestris* require copulation with other adults every 3 months to transfer sperm and produce cocoons (Butt and Nuutinen, 1998). In EEWorm, when an individual requires a mate it will sense the presence of another adult within a 20 cm radius of itself at the soil surface during dark hours. If another adult is available within this area, the individual will move towards the other adult until they mate. Adults can then produce cocoons for 3 months after copulation, before needing to mate again. If the population is space-limited, co-habitation of a single burrow can occur between a maximum of two adults, whilst cohabitation of a burrow between a parent and its juvenile offspring can occur at any time (Lowe and Butt, 2002; Grigoropoulou et al., 2008).

Stochasticity. – Movement and background mortality are random amongst juveniles and adults, with specified probability density functions.

Observation. – Population density and biomass, stage class structure (cocoon, juvenile, adult), individual reproduction and growth rates were analysed.

5 Initialization

Simulations were initialised with individuals randomly distributed in the landscape. Simulated laboratory experiments replicated the microcosm size, soil temperature and moisture, food density, earthworm numbers, life cycle stages and body masses recorded for each experiment. Field population simulations were initialised with 50 individuals from each life stage (cocoon, juvenile and adult), or 10 juveniles and 10 adults, and the population was allowed to stabilise over a 50 year, or 25 year, period with field trial specific environmental inputs before observations were made.

6 Input data

M2: The model was set up to mimic the conditions of independent field trials used to validate the model. Environmental and weather inputs from each field trial (SOM, bulk density, soil temperature, soil water content and soil texture), together with management practices (pesticide applications, irrigation, weed management).

M3: Environmental and weather inputs from different independent field trials, together with management practices (tillage depth), were used to validate the model's ability to capture earthworm population responses to different tillage intensities. Long-term weather data from Rothamsted, UK, was used to model the effects of 'baseline' weather projections over the following 50 years. Projections were constructed as an extrapolation of observed increases and variations in soil temperature and water potentials over the previous 50 years.

Submodels

Energy budgets

Species-specific energy budget parameters were derived from the literature for the different earthworm species as shown in Table 1. Details of parameter calculations are available in the Supporting Information of the respective modelling papers. The following sections describe the energy budget model (Figure 1) in terms of metabolic organisation at the individual level.

Table 1. Default parameter values of the EEEworm energy budges, for earthworm species *Eisenia fetida* (M1), *Aporrectodea caliginosa* (M2) and *Lumbricus terrestris* (M3).

Symbol	Definition	M1	M2	M3	Unit
A_e	Assimilation efficiency	0.50	0.19	0.55	---
B_o	Taxon-specific normalization constant	967		360	kJ/day kJ/hour
E	Activation energy	0.25		0.32	eV
E_c	Energy content of tissue	7			kJ/g
E_s	Energy cost of synthesis	3.6			kJ/g
E_x	Energy content of food	21.2	0.56 – 21.2		kJ/g
IG_{max}	Maximum ingestion rate	0.70	0.805	0.37	g/day/g ^{2/3} g/hour/g ^{2/3}
h	Half saturation coefficient	3.5			
M_b	Mass at birth	0.011	0.005 0.026	– 0.053	g
M_c	Mass of cocoon	0.015	0.008 0.035	– 0.061	g
M_p	Mass at sexual maturity	0.25	0.50	4.2	g
M_m	Maximum asymptotic mass	0.50	2.00	8.5	g
r_B	Growth constant	0.177	0.049	0.0023	/day /hour
r_m	Maximum rate of energy allocation to reproduction	0.182	0.054	2.10 × 10 ⁻⁴	kJ/g/day kJ/g/hour
T_0	Incubation period	23	62	90	days
T_{ref}	Reference temperature	298.15	288.15	288.15	K
μ	Background mortality rate		0.14	0.18	%/day
B_c	Energy cost of burrowing			0.0103	kJ/cm/hour
B_s	Burrowing speed			0.97	cm/hour
C_s	Crawling speed			18.81	cm/hour

Maintenance

The basal metabolic rate (B) is the level of metabolism below which an organism cannot survive (Fry, 1971; Sibly and Calow, 1986), and is used here as a measure of maintenance costs. Costs of movement, small in earthworms, are here included in maintenance. B is known to scale with body mass (M) as a power law and temperature (T), measured in grams and kelvins respectively, according to the equation:

$$B = B_0 M^{3/4} e^{-E/kT} \quad \text{Eq. S1}$$

where B_o is a taxon-specific normalization constant, $M^{3/4}$ is the scaling with body mass, $e^{-E/kT}$ is the exponential Arrhenius function, E is the activation energy, κ is the Boltzmann's constant (8.62×10^{-5} eV K⁻¹) and T_{ref} is a reference temperature (Table 1) (Peters, 1983; Brown et al., 2004). The effect of temperature on metabolic rate, $e^{\frac{-E}{\kappa} \left(\frac{1}{T} - \frac{1}{T_{ref}} \right)}$, is referred to as the Arrhenius function.

Ingestion and Energy Uptake

Variation in food density affects the rate of ingestion of food up to an asymptote according to a type II functional response (Holling, 1959; Ricklefs and Miller, 2000), so that:

$$\text{Ingestion rate} \propto \frac{X}{(h+X)}$$

where X is food density and h is a constant that shows how quickly the response curve reaches its maximum as food density increases. Functional response relationships were excluded from M2 and M3 because density dependence emerges from competition between individuals within patches. If the sum of individual ingestion rates in a patch exceeds food availability, resources are shared according to individual mass, so that larger individuals have a larger share than smaller individuals.

The ingestion rate is proportional to the surface area ($M^{2/3}$) of an individual as the search rate depends on the food gathering apparatus (Pilarska, 1977; Kooijman and Metz, 1984) and also on the effects of body mass and temperature, giving:

$$\text{Ingestion rate} = IG_{\max} e^{\frac{-E}{\kappa} \left(\frac{1}{T} - \frac{1}{T_{ref}} \right)} \frac{X}{(h+X)} M^{2/3} \quad \text{Eq. S2}$$

where IG_{\max} is the maximum ingestion rate recorded for *E. fetida* under optimal feeding conditions (g/(day/g)). After ingestion, food is processed by the digestive system and a proportion, governed by the energy content of food and assimilation efficiency, becomes available for allocation to the various functions shown in Figure 1. The value of the assimilation efficiency (A_e) (Table A1) depends on diet but not body mass (Hendriks, 1999).

Burrowing

Burrowing costs in *L. terrestris* scale to the 2/5 power of body mass (M), according to: $B_c M^{2/5}$, where B_c is the energy cost of burrowing parameter with a value of 0.0103 kJ/cm/hr ((Quillin, 2000), Table 1). Burrowing speed (B_s , cm/hr) also scales with body mass according to: $B_s = 0.97M^{0.06}$, which is used in EEEworm as a maximum burrowing speed to calculate hourly energy costs of burrowing. Energy costs associated with moving along the soil surface (crawling) during foraging and mating activities are met by 'Maintenance' costs. The maximum crawling speed (C_s , cm/hr) was found to not differ as a function of body mass according to: $C_s = 18.81M^{0.0006}$, which is implemented in EEEworm (Table 1).

Growth

After expenditure to maintenance and, in the adult stage, to reproduction, individuals allocate remaining energy to somatic growth. The maximum growth rate of an individual under optimal conditions is assumed to follow the Von Bertalanffy (1957) growth equation:

$$M = M_m \left(1 - \left(\frac{M_b}{M_m}\right)^{1/3}\right) e^{-r_B t/3} \quad \text{Eq. S3a}$$

where M_b and M_m denote mass at birth and maximum mass respectively and r_B is the Bertalanffy growth constant, obtained by fitting Eq. S3a to data recording the increase in individual biomass over time under optimal conditions. The maximum growth rate per time-step is obtained from:

$$\Delta M = r_B e^{\frac{-E}{\kappa} \left(\frac{1}{T} - \frac{1}{T_{ref}} \right)} (M_m^{1/3} M^{2/3} - M) \quad \text{Eq. S3b}$$

(Sibly et al., 2013). The energy costs of growth are determined from the new mass calculated from Eq. 3b and the energy costs of production ($E_c + E_s$) (Table A1). Eq. S3b shows how the maximum rate at which resources can be allocated to growth changes as an individual's mass increases. If insufficient energy is available to support maximal growth, growth rate is reduced accordingly.

Reproduction

Reproduction is assumed to take priority over growth in adults, because in the absence of a sexual partner, indeterminate growers grow larger than normal. Energy allocated to reproduction by adults goes directly to the production of an egg until oviposition inside a cocoon. The maximum rate of energy allocation to reproduction per day increases linearly with adult mass (Mulder et al., 2007):

$$\Delta R = r_m e^{\frac{-E}{\kappa} \left(\frac{1}{T} - \frac{1}{T_{ref}} \right)} M \quad \text{Eq. S4}$$

where r_m is the maximum rate of energy allocation to reproduction per unit of adult mass (kJ/g/day). The energy cost of producing a hatchling depends on the mass of cocoon (M_c): $M_c (E_c + E_s)$ and the hatchling's energy reserve content is initially $M_c E_c$, which is utilized for maintenance during the incubation period.

Energy Reserves and Starvation

If any assimilated energy remains after expenditure on relevant life processes (Fig. A.1) it is stored in an individual's energy reserves. Energy is stored as glycogen (Byzova, 1977), costing $E_s = 3.6$ kJ to store 1g with an energy content of $E_c = 7$ kJ (Peters, 1983; Sibly and Calow, 1986). When energy is not available from ingested material, maintenance costs are taken from energy reserves, allowing individuals to survive for some time under starvation (Sousa et al., 2010). Furthermore, as evidence supports the assumption that reproduction continues even when food is limiting (Reinecke and Viljoen, 1990), the energy reserves are assumed to be utilized for reproduction above a threshold of 50% of an individual's maximum energy reserves, taken as $M/2$ (E_c) (e.g. Peters (1983)). If food limitation continues and the energy reserves decline below 50% of an individual's maximum energy reserves, individuals are considered to be in a state of starvation. Under these conditions tissue is catabolised to cover maintenance costs, resulting in net weight loss (Gunadi and Edwards, 2003); individuals die if their mass falls to that at birth (M_b) following Reinecke and Viljoen (1990).

Survival

M1: The survival of individuals living in field populations is determined by the availability of energy resources to maintain life cycle processes alongside temperature and soil moisture

specific mortality rates. Individuals die of starvation if their energy resources are depleted, and additional mortality rates were imposed using the regression equation derived from Presley et al. (1996):

$$\text{Mortality Rate (\%)} = 12.7 - 0.0010 SM - 0.0861 T + 0.000009 SM^2 + 0.000147 T^2 \quad \text{Eq. S5}$$

where SM is soil moisture (%) and T is soil temperature (K). Individual adults and juveniles die according to Bernoulli processes with daily mortality rates given by Eq. S5. In M2 & M3 daily background mortality rates as in Table 1 are random amongst juveniles and adults, with specified probability density functions.

Soil water potential

M2 & M3: Soil moisture is a major driver of earthworm population dynamics and distribution in the field (Lee, 1985). Holmstrup (2001) found decreasing soil water potentials to have a negative effect on individual *A. caliginosa* life cycle traits. Here we suppose soil water potential (ψ) reduces the ingestion rate parameter (IG_{max}) as:

$$IG_{max}(\psi) = (IG_{max}) e^{k\psi} \quad \text{Eq. S6}$$

where IG_{max} is the parameter value at a soil water potential of -2 kPa (Table 1) and k takes the value 0.040. This results in less energy being available for allocation to growth or reproduction, than under optimal conditions of soil water potential (-2 kPa).

Aestivation

M2: Holmstrup (2001) reported aestivation in *A. caliginosa* to be induced at soil water potentials in the range -19 to -29 kPa at a constant temperature of 15 °C, whilst Doube and Styan (1996) found the closely related species *A. trapezoides* to avoid soil water potentials below -25 kPa. Here, we assumed a soil water potential of -25 kPa triggers aestivation, independent of temperature (e.g. Laverack (1963); Edwards and Bohlen (1996)). As facultative diapause is a condition that may terminate as soon as soil conditions become favourable (Lee, 1985), we assumed a soil water potential of -20 kPa prompts the re-emergence of individuals from aestivation and that growth and reproduction then resume. During the aestivation phase individuals utilize energy reserves to pay the energetic costs of maintenance. Bayley et al. (2010) found oxygen consumption and carbon dioxide release of *A. caliginosa* to vary at different stages of aestivation. Here, we assume a proportional exponential decline in the maintenance parameter B_0 during aestivation, for a maximum duration of 60 days, as in Figure 4.

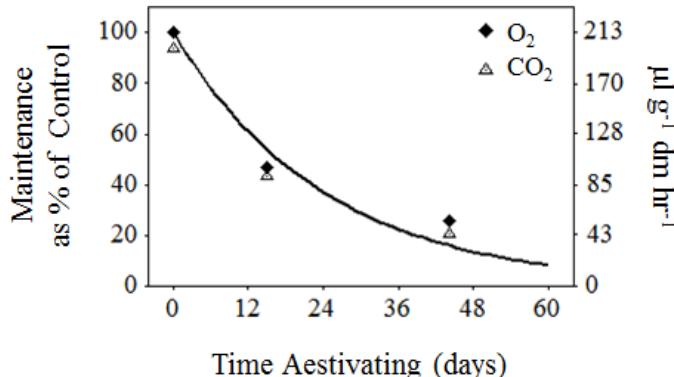


Figure 4. Modelled decline in maintenance rates of the earthworm *Aporrectodea caliginosa* with time aestivating (line and left-hand axis) compared to oxygen consumption and carbon dioxide release data from Bayley et al. (2010) (points and right-hand axis).

Movement

M1: On the basis that Kobetičová et al. (2010) found movement in *E. fetida* individuals to be random, we modelled individual movements as random in direction from a uniform distribution between -90° and 90° and distance travelled as 0.5 patches per time-step.

M2: Major factors determining the movement of *A. caliginosa* in natural soil environments are soil water content and food quality. Understanding how these factors interact is essential in modelling representative field populations. As *A. caliginosa* is sensitive to decreasing soil water potentials, the movement of individuals along the soil profile is primarily driven by soil water gradients when surface conditions are dry (Gerard, 1967). Thus, we assume that under a sub-optimal soil water potential of -10 kPa individual movement is driven by the availability of higher soil water potentials in neighbouring patches in the model landscape (Figure 5). Burrowing activity of *A. caliginosa* in the top 10 cm of the soil profile is believed to reflect the presence of a higher organic matter content (McKenzie and Dexter, 1993; Jégou et al., 1997). The closely related species *A. tuberculata* has also been observed to exhibit random movement until food is encountered, thereafter burrowing in the area of the food source (Cook and Linden, 1996). Thus, if soil water conditions are non-limiting (> -10 kPa) individuals preferentially move to patches of greater food quality, represented by the parameter E_X (Figure 5).

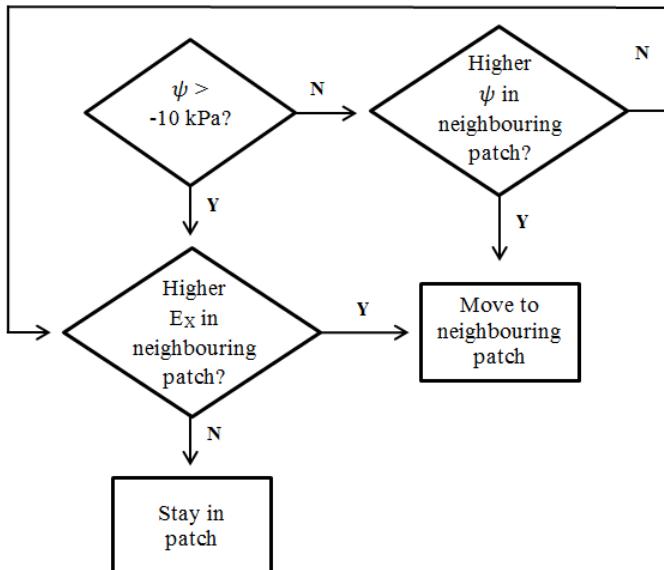


Figure 5. Conceptual model of earthworm (*Aporrectodea caliginosa*) movement in the individual based model, where ψ represents soil water potential and E_x the energy content of food. Diamonds indicate decision points and rectangles are processes per daily time-step.

Movement decisions are based on non-linear trade-offs between food quality, soil temperature and water potential conditions. For instance, *L. terrestris* has been shown to avoid cold ($< 5^{\circ}\text{C}$) and dry soil conditions ($<-15 \text{ kPa}$) (Daniel, 1991; Perreault and Whalen, 2006), with typical positions between 20 and 30 cm in the soil profile suggesting trade-offs with higher quality food resources in shallower soil layers (Grigoropoulou et al., 2008). In EEEworm the favourability of different soil and burrow patches are represented by an index of patch quality (Q_p), which accounts for the favourability of a patches energy content of food (E_x), soil temperature (T) and soil water potential (SWP), according to:

$$Q_p = Q_{Ex} + Q_T + Q_{SWP} \quad \text{Eq. S7}$$

The quality of patches according to specific environmental variables follow linear regression equations which change above or below specific thresholds of favourability as follows:

$$\begin{aligned} \text{If } E_x < 2.5 \text{ kJ/g: } Q_{Ex} &= 0.80E_x \\ \text{If } E_x \geq 2.5 \text{ kJ/g: } Q_{Ex} &= 1.8 + (0.12E_x) \end{aligned}$$

$$\begin{aligned} \text{If } T < 15^{\circ}\text{C: } Q_T &= 0.065T \\ \text{If } T \geq 15^{\circ}\text{C: } Q_T &= 1.75 - (0.05T) \end{aligned}$$

$$\begin{aligned} \text{If } SWP < 5 \text{ kPa: } Q_{SWP} &= 0.80SWP \\ \text{If } SWP \geq 5 \text{ kPa: } Q_{SWP} &= 5 - (0.20SWP) \end{aligned}$$

Individuals sense patch quality within their burrow and preferentially move towards vertical patches with a higher Q_p value. If a neighbouring soil patch is more favourable than an

individual's existing burrow patch, it will extend its burrow to include this patch if the associated energy requirements of burrowing can be met. Figure 6 shows the non-linear trade-off between the three environmental variables. Individuals may also ingest soil if energy requirements cannot be met during daylight hours, or if there is insufficient availability of litter (e.g. Marhan and Scheu, 2005).

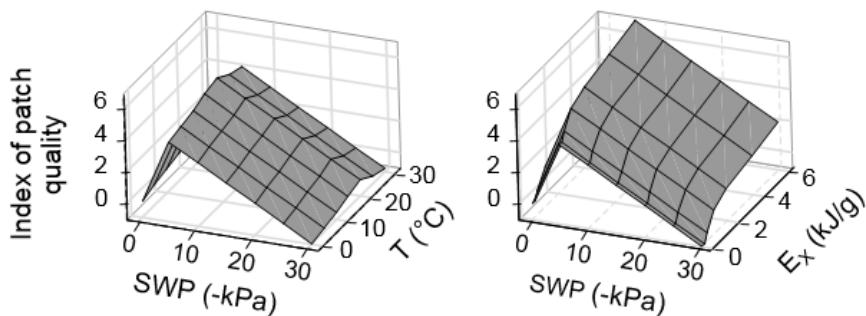


Figure 6. Representation of index of patch quality in EEEworm. Higher patch values represent higher quality soil patches. Generally, soil water potential has a greater influence during light hours, and energy content of food (E_x) during dark hours.

Pesticide Effects

The model is designed to simulate laboratory based toxicology experiments from the literature, typical of lower tier risk assessment. Pesticide applications are simulated by applying a chemical concentration to each patch at the specified concentration and time/s. Individuals experience the patch concentration on contact and the effect of this concentration persists unchanged for the duration of the experiment. The physiological effects of a pesticide were identified using toxicity submodels (Table 2), which were evaluated using data from the experiment being simulated. We converted individual biomass and cocoon production values during different treatment concentrations in each case study to percentages of the control value, to identify the reduction in sublethal endpoint due to chemical exposure. The data was then generally well fitted by exponentially declining curves, of the form:

$$R(C) = e^{(kC)} \quad \text{Eq. S8}$$

where $R(C)$ is the effect at a specific concentration (C) recorded as % compared to control, k is a chemical-specific coefficient calculated by regressing $\log(\% \text{ trait compared to control}/100)$ against chemical concentration (C) in mg/kg. Eq. S8 represents the dose-response relationship between chemical concentration and a life cycle trait (growth or reproduction). However, the toxicity data does not specify which physiological parameter was affected by exposure to result in the observed response in that life cycle trait. To find the most likely physiological parameter affected in each case study we investigated the various possibilities, here called toxicity submodels. Inspection of the energy budget indicates that chemicals can affect ingestion, assimilation, maintenance, growth or reproduction, the rates of which are governed by physiological parameters IG_{max}, A_e, B_0, r_B or r_m respectively (Table 1). Here, we investigate four potential toxicity submodels, describing how altering specific

physiological parameters modifies individual growth and reproduction rates (Table 2). The four submodels tested here were selected on the basis that modifying the specific parameters has effects on growth and reproduction simultaneously, rather than one metabolic rate alone. This was done by supposing that the chemical-specific toxicity coefficient (k) obtained by fitting Eq. S8 to the dose-response data determines the relationship of the chemical concentrations with a physiological parameter, rather than with the life cycle trait, calculated as:

$$P_c = \frac{P_0}{100} e^{(kC)} \quad \text{Eq. S9}$$

where P_c is the parameter value at concentration (C), P_0 is the parameter value under control conditions as indicated in Table 1 and k is the toxicity coefficient determining the dose-response relationship. Effects on the sublethal endpoints growth and reproduction then emerge from model simulations. For example, a decline in the value of the parameter IG_{max} with increasing chemical concentration would reduce individual ingestion, thus reducing the amount of energy available for allocation to metabolic processes. Following the preferential allocation principles for earthworms this would lead to reduced growth but have little impact on reproduction as adults allocate energy preferentially to reproduction before growth. Toxicity submodel T4 requires an increase in the value of the maintenance parameter B_0 to eliminate/detoxify the toxin or repair damage (rather than a decline as in toxicity submodels T1-T3). Here we assumed that above a concentration of 100 mg/kg there is a linear relationship between B_0 and C so that: $B_0 = B_0 \text{control}$, if $C \leq 100$; $B_0 = B_0 \text{control} \times 0.01 C$, if $C > 100$.

Table 2. Tested toxicity submodels used to identify the physiological pathways disrupted by pesticides. In each case the specified physiological parameters were affected according to dose-response curves parameterised with laboratory data. IG_{max} is maximum ingestion rate, r_m is maximum rate of energy allocation to reproduction, r_B is the von Bertalanffy growth constant and B_0 is a taxon-specific normalization constant used for calculating maintenance rates.

Toxicity Submodel	Parameter	Predicted Observations in Adult Life Cycle Traits
T1	IG_{max}	Growth more reduced than reproduction
T2	IG_{max} & r_m	Growth and reproduction similarly reduced
T3	r_m & r_B	Reproduction more reduced than growth
T4	B_0	Growth more reduced than reproduction or accelerated weight loss under resource limitation

M2: The value of k in Eq. S8 was estimated for the toxic standard carbendazim by least sum of squares fit to the data of Lofs-Holmin (1982), recorded as a proportion of the control (symbols in Figure 7a). We also modelled the effects of a hypothetical herbicide using fictitious data (symbols in Figure 7b). The response curves specify how r_B and r_m are affected by the pesticide relative to values in control conditions given in Table 1. Estimated values of the toxicity coefficient (k) for growth, reproduction and survival are -2.66,-1.28 and -1.05 for carbendazim (Figure 7a) and -0.06,-0.04 and -0.006 for the hypothetical herbicide (Figure 7b), respectively. We also assumed that carbendazim leads to an increase in maintenance costs,

either to eliminate the toxin or repair toxic damage (e.g. Givaudan et al. (2014), assuming a linear relationship between the maintenance parameter B_0 and C following: $B_0(C) = B_0(4.5 \times C)$.

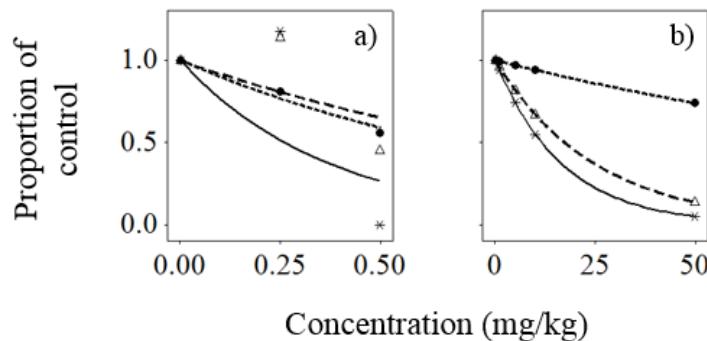


Figure 7. Modelled dose-response relationships specifying the effects of pesticide concentrations on life cycle traits for: a) carbendazim derived from the laboratory data of (Lofsd-Holmin, 1982) and b) a hypothetical herbicide. Growth (solid line), reproduction (dashed line) and survival (dotted line) are represented as a proportion of the life cycle trait in control conditions. Symbols represent laboratory data for growth (asterisks), reproduction (triangles) and survival (circles).

Tillage Effects

We simulated the effects of zero (our control treatment), reduced and conventional tillage (to a soil depth of 0, 10 and 20 cm respectively (Kassam et al., 2009) on both direct earthworm mortality and soil physical conditions (soil water content, SOC and bulk density). SOC has been observed to be 0.7 – 1.8 kg C/m² less under conventional tillage than in zero tillage systems in the top 15 cm of soils (Kern and Johnson, 1993). Soil bulk density follows a similar pattern (as reviewed by Balesdent et al. (1990)); declining by around 0.13 g/cm³ in the top 30 cm of soils under conventional tillage (Balesdent et al., 1990). Moreover, these soil properties decline or increase exponentially with time during the use of tillage practices and after the cessation of tillage, respectively (Francis and Knight, 1993). Based on these studies, SOM and bulk density, which in the model together represent food availability and quality, were modelled as outlined in Figure 8. We also assumed a soil temperature increase of 0.70 °C and soil water content decrease of 0.04 cm/cm³ following tillage, as in Pelosi et al. (2008). Direct earthworm mortality during tillage is assumed to be 50 % in the tilled soil layer for adults and juveniles (Marinissen, 1992).

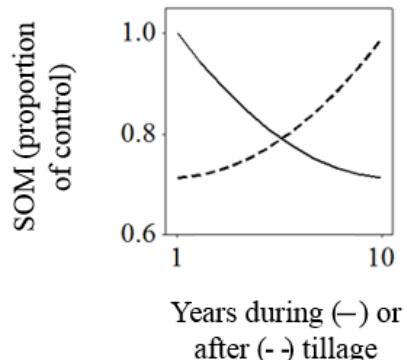


Figure 8. Modelled effects of tillage on SOM and bulk density over time relative to zero tillage control conditions.

Direct mortality. We take a direct earthworm mortality rate of 50% during tillage, as was used for endogeic earthworms (Johnston et al., 2015). There is little evidence to support a higher or lower direct mortality rate for anecic earthworms. For instance, Crittenden et al. (2014) found earthworm populations to decline by 70% five days after moldboard ploughing in conventional arable fields. Longer-term data suggests higher mortality rates but this is presumably a combination of direct and indirect effects on soil conditions (e.g. (Wyss and Glasstetter, 1992). In EEEworm, the 50% mortality rate is applied to the population present in the tilled soil layers, which depends on tillage practice.

Litter removal. The amount of plant litter at the soil surface is reduced following tillage events, and retained litter is redistributed within the tilled soil layers. The amount of plant residue that is retained varies between the surface tilled/direct drilled and chisel/deep ploughed scenarios. Yang and Wander (1999) reported litter retention of 78 % and 0.08 % in disk tilled and moldboard ploughed fields respectively, compared to no-till control plots. These values were used to model reductions in the quantity of litter available following tillage events, presented in (Figure 9).

Burrow destruction. Burrow structures are destroyed by converting 100 % of the burrow patches in the tilled/ploughed soil layers to soil patches.

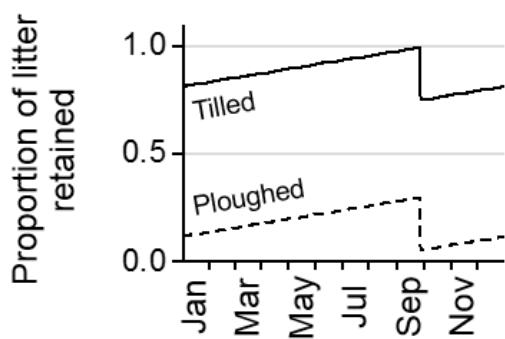


Figure 9. Modelled reductions in plant litter retained at the soil surface in tilled (to 5 or 10 cm) and ploughed (to 12.5, 20 or 30 cm) field experiments, based on observations from Yang and Wander (1999). The plot is based on tillage (solid line) and ploughing (broken line) on 1st October.

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