TRACE document

This is a TRACE document ("TRAnsparent and Comprehensive model Evaludation") which provides supporting evidence that our model presented in:

> **Meli, M., Auclerc, A., Palmqvist, A., Forbes, V.E. and Grimm, V., 2013. Population-level consequences of spatially heterogeneous exposure to heavy metals in soil: an individual-based model of springtails. Ecological Modelling 250, 338-351**

was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

> Schmolke A, Thorbek P, DeAngelis DL, Grimm V. 2010. Ecological modelling supporting environmental decision making: a strategy for the future. *Trends in Ecology and Evolution* 25: 479-486.

and uses the updated standard terminology and document structure in:

> Grimm V, Augusiak J, Focks A, Frank B, Gabsi F, Johnston ASA, Kułakowska K, Liu C, Martin BT, Meli M, Radchuk V, Schmolke A, Thorbek P, Railsback SF. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling*

and

> Augusiak J, Van den Brink PJ, Grimm V. 2014. Merging validation and evaluation of ecological models to 'evaludation': a review of terminology and a practical approach. *Ecological Modelling*.

If this document include **hyperlinks**, navigation forth and back along previously chose links works via "ALT" + "←" or "ALT" + "→".

Note: The original publication, Meli et al. (2014), provides, in the Supplementary Material, a previous version of the TRACE document, which followed the original TRACE format and terminology suggested by Schmolke et al. (2010).

Content

1 Problem formulation

This TRACE element provides supporting information on: The decision-making context in which the model will be used; the types of model clients or stakeholders addressed; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

Summary:

Suitable habitat for soil organisms may be scarce, thus leading to locally high population densities, because soil, being more static than water or air, is heterogeneous: physical conditions often vary widely on a scale of a few centimetres. Moreover, toxic chemicals are likely to be unevenly distributed in the soil as well. The spatially explicit individual-based model presented in Meli et al. (2014) is developed to explore the consequences of these heterogeneities for the population dynamics of soil invertebrates, in particular the collembolan *Folsomia candida*. *F. candida* is a common arthropod that occurs in soils worldwide and is used as a standard test organism for estimating the effects of pesticides on non-target soil arthropods.

The model is designed to estimate the effects of toxicants on collembolans at the population level, and will be used for hypothesis-testing and for evaluating and improving standard ecotoxicological tests based on the modelled species, *Folsomia candida* (Willem 1902).

The purpose of the model is to investigate the effects of spatial heterogeneity in soil contamination on the population dynamics of *Folsomia candida*. *F. candida* has been used extensively as a model arthropod in many ecological and evolutionary studies. Moreover, it is

used as a standard test organism for toxicity tests: a 28-day reproduction test (ISO 11267, 1999; OECD, 2009) is included in the refinement options for ecological risk assessment of plant protection products to soil organisms. However, one of the limitations of virtually all standard toxicity tests with soil organisms is that soil contamination is assumed to be homogeneous, whereas the heterogeneous nature of soil is well known. Spatial heterogeneity in soils occurs at widely different scales, from continental and regional to micro aggregates within specific soil horizons. Moreover, contamination of soils is heterogeneous as well because the distribution of chemicals in soil depends on the source of contamination (i.e., point vs. non-point source) and on specific soil properties that result in different interactions between chemicals and soil particles. The ability of *F. candida* to sense and avoid contamination in soil is known and currently being used to develop a guideline to establish a standardized avoidance test (Boiteau et al., 2011). Our model is designed to simulate the avoidance behavior of *F. candida* and the effect of heterogeneously contaminated soil on population dynamics. To obtain a more comprehensive understanding of how behavioral responses such as avoidance affect population dynamics, population structure, and distribution of individuals in soils with heterogeneous contamination, population models can help to overcome the logistical constraints of short-term laboratory experiments.

The model is built using data related to the effects of **copper sulfate**, and therefore model predictions can be considered valid to gain insight into the population dynamics of springtails only for heavy metals. To extend its **validity** to other classes of compounds with different environmental behavior, it would be necessary to implement degradation processes, and make the individuals' exposure dependent on the varying toxic concentration.

2 Model description

This TRACE element provides supporting information on: The model. Provide a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex submodels it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

Summary:

Here we present the complete model description following the ODD format.

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm et al., 2006; Grimm et al., 2010). The model was implemented in NetLogo 5.0 (Wilensky, 1999), a free software platform for implementing individual-based models. The NetLogo code has been made available in the Supplementary Material of Meli et al. (2014).

2.1 Purpose

The purpose of the model is to simulate *Folsomia candida* population dynamics and to investigate how they are affected by spatial distribution of toxic contamination in soil, with a special focus on interactions with food availability and local population density.

2.2 Entities, state variables and scales

The model includes three kinds of entities: eggs, female springtails (juveniles and adults), and grid cells they live on. Eggs are immobile and are characterized by age (in days) and position (continuous coordinates). Springtails are represented as mobile individuals with state variables for their age (in days), position (continuous coordinates), direction for movement, energetic status (days-to-death), cumulative distance (in cm) walked in each hourly time-step

(which affects the energy used for movement), and time (h) spent on contaminated grid cells. Grid cells are characterized by their food level and concentration of toxicant (mg kg^{-1} soil). The model world is two-dimensional. Each cell of a 100x100 cells square grid represents a square patch of soil of 1 cm^2.

The global environment is characterized by six "seasons" (spring and fall are divided into "early" and "late"), which determine the temperature-dependent life-cycle parameters of the springtails: data from literature allowed the implementation of four different parameter sets, reflecting the temperature ranges 0-5°C (winter), 12-15°C (early spring and late fall), 19-21°C (late spring and early fall) and 24-26°C (summer).

2.3 Process overview and scheduling

Each of the following processes are run, in the given order and by the category of entities given in parentheses, once per day, except for the foraging procedure, which is executed at hourly time-steps (Figure 1). If no executing category of entities is given in the list of processes, the process is run by the program, or "observer" (Wilensky, 1999). The order in which the model entities are processed is randomized at each time step, and state variables are updated immediately. The submodels representing the processes are described in detail in Section 2.2.7.

Seasons: At the beginning of a new season, individuals get a new set of life-cycle parameters, whose values reflect the change in the temperature range.

Foraging (springtails): Individuals move to look for food, but also to avoid contaminated patches of soil.

Re-growth of food (grid cells): When the amount of resource on a food cell is depleted, it is restored at the beginning of the next day.

Aging/growth (springtails): Age is increased by one day. Based on the age, the hatching time and the maturation time, springtails are divided into three stages: eggs, juveniles and adults. When an egg hatches, its age is set to 0.

Reproduction (springtails): Springtails may reproduce when they reach maturity, and afterwards reproduce according to the values of the parameters "time between broods" and "number of broods".

Hatching (eggs): Eggs hatch according to their viability when they reach an age equal to the hatching time. Hatching success depends also on the concentration of toxicant of the grid cell on which the eggs are laid.

Density-dependence and starvation effects (springtails): Fecundity of springtails is reduced when they experience high population density on their grid cell, due to jostling effects. If they do not feed, their energetic status decreases, with consequences for fecundity and survival. Because reproduction requires energy, and *F. candida* do not lay eggs while they are feeding, this procedure is scheduled so that they first look for food and afterwards check for local population density.

Mortality (springtails): Two different rules, based on survival parameters, are implemented for juveniles and adults. In addition to a background rate of mortality, survival depends on the concentration of toxicant and the amount of time the organism spends on contaminated patches.

Update output: The last action executed at daily intervals is an update of model outputs, i.e. plots are updated as well as summary statistics.

2.4 Design concepts

Emergence. Population dynamics and the spatial arrangement of individuals emerge from the behaviour of single organisms, their interactions with each other and their habitat: population dynamics are regulated by the number of reproducing individuals, which themselves depend on population density and the amount of food resources. Life cycle, reproduction, and survival rates are partly imposed via empirical rules and parameters; partly emerge from the movement path taken by an individual, which will differ among individuals and in terms of contamination, density and resource availability experienced.

Stochasticity. Values of almost all parameters are drawn from uniform or normal probability distributions, in order to reflect heterogeneity among individuals (Table 1). Stochasticity is also used for initializing springtails' starting positions, as well as causing individual behaviours (movement, reproduction, hatching, mortality) to occur with specified frequencies, which depend on the values of said parameters.

Sensing. Individuals sense the amount of food and the presence of other individuals within a defined distance. They also sense whether or not the grid cell they are currently on, and the grid cell which is ahead in their direction of movement, is contaminated.

Adaptation. Individuals implicitly try to optimise their fitness by preferentially selecting cells with high food resources and by avoiding both cells occupied by too many other individuals and too high contamination levels.

Interaction. Individuals compete for food and space; competition is assumed to be of the scramble type.

Observation. Size and structure of the population as well as spatial distribution of the individuals for different concentrations of toxicant, food resource amounts and distributions are compared.

2.5 Initialization

A simulation starts the first day of the year, and therefore in the winter season. Usually, 5% of the grid cells, which are randomly chosen, are made to be "food cells", with maximal food levels as determined in Section 3.2. Simulations start with 10 randomly distributed juvenile springtails; values for their state variables are drawn from the distributions reported in Table 1. Four different scenarios for the extent and spatial distribution of contaminated areas are used (see Section 2.5, "Simulation experiments", below).

2.6 Input data

This model has no time-series inputs or external environmental drivers.

2.7 Submodels

All parameters, their meaning, range of possible values, and source for parameterization are listed in Table 1.

Seasons: Individual variability is represented by independently drawing, for each individual, at the beginning of a new season, parameter values from a certain interval corresponding to a different temperature range (Table 1). When the temperature is too low, springtails are inactive. (Joosse and Testerink, 1977) observed that below 10°C the percentage of *Orchesella cincta* individuals in a fed state decreases dramatically, while Takeda (1984) reported that in a population of *Folsomia octoculata* overwintering adults were in an immature state, and they became mature with the stimulation of increasing temperature. Verhoef (1996) noted that during the winter period nearly all the adults of the collembolan *Anurida maritima* died, and it

appeared that this was due to starvation caused by low locomotor activity in situations of low temperature. Therefore during the time interval corresponding to winter, individuals in the model do not execute any actions except for aging and mortality: all adults die during winter, while 50 % of the eggs survive, as it is typical of many insects that embryos tolerate cold better than the other life stages.

Foraging: This submodel is comprised of two parts: first, organisms check whether they are on a contaminated grid cell. If one of the neighbouring cells has a lower concentration, the springtail moves onto it with a chance equal to its avoidance probability, which is proportional to the toxicant's concentration (Table 2). The second part of the submodel contains rules for feeding. Movement is triggered by the reduction of the collembolan's energy level. This process is executed with a frequency determined by a probability of movement, which includes two components: a baseline probability and a multiplier (up to two) proportional to the olfactory stimulus representing the amount of food present within the range of perception. This multiplier has been introduced to represent the characteristic periods of activity/inactivity shown by several collembolan species (de With and Joosse, 1971). From experimental observations reported in the literature, it is known that collembolans go through periods of inactivity (i.e. they do not move and do not feed), for instance during the moulting process (Joosse and Testerink, 1977; Marshall and Kevan, 1962). Therefore, in order to account for these periods of inactivity, individuals in the model do not move at each time-step, but according to a given probability (*probab_mov*), which is proportional to the amount of food sensed by the individual (i.e. to the strength of the attractive olfactory stimulus).The minimum value for *probab_mov* occurs when the organism does not sense any food; the maximum value for *probab_mov* is twice the minimum. The value for minimum *probab_mov* was determined via sensitivity analysis and pattern-oriented parameterization (details in Sections 2.3 and 2.4), but has initially been set to 0.1. While springtails forage, they decrease the stock on the food cell on which they are feeding by one food item per time step. The probability of movement is calculated as:

$$probab\_mov = 0.1 \times \left(1 + \frac{\text{mean amount of food on food cells within sensing range}}{\text{maximum amount of food initialized on a food cell}}\right)$$

The foraging submodel is described below using pseudo-code. The rationale for each part of the code and the values of parameters involved and the equations used are explained in more detail in the Supplementary Material. A visualisation of the resulting movement patterns is shown in Fig. 2.

Pseudo-code:

```
for all springtails
        if current cell is contaminated and one of the neighbouring cells is not
                move towards it according to p_avoid
        if current energy reserve is below energy_max – 24*en_reduce_hour
                if any food patches in a 2.5 cm radius and if total food in a 2.5 cm radius is
                more than 1 food item
                        Set movement probability dependent on average food in 2.5 cm radius.
                else
                        Set movement probability to minimum movement probability
                While no food found and energy spent for foraging (nr steps moved *
                en_reduce_step) is below threshold (tradeoff_mov)
                        if food on current patch is at least 1
                                Eat
                        if no food on current patch and food on one of the grid cells in the
                        semicircle of radius 2.5 cm the individual is facing to contains more
                        food than 1
                                Turn towards one of these grid-cells
                        else
```

```
                        Turn randomly by 0-359°
                    if cell ahead 1 cm is contaminated
                        Move towards it according to p_avoid
                        Update exposure counter
                    else
                        Move towards one of the uncontaminated neighbour cells
                    Calculate energy loss due to movement
        Update energy reserves: old value plus food intake minus energy loss
Update grid cell variable “local_density” for all grid cells.
```

Reproduction, density dependence and starvation effects: Individuals, after they reach maturity, have a certain probability to reproduce at every reproductive instar (Table 1), which is drawn from a specified distribution for every season. They lay a predetermined number of eggs, which depends not only on the season but also on the local density (i.e., number of organisms on the same patch) and the energy level of the organism. As shown by Green (1964a), fecundity of springtails is reduced when they experience high population density, due to jostling effects: the effect of crowding upon fecundity has been calculated as an exponential function (Table 2) that interpolates data from Green (1964a). The same type of mathematical relationship has been assumed to exist between energetic status of the organism and number of eggs laid (Table 2). In addition to the effect on fecundity, the energetic status affects the survival of an organism: if energy level is below the minimum (energy_min), the individual dies.

The number of eggs laid also depends on the contamination experienced by the organism, in terms of concentration and time spent on a contaminated patch. From literature data (Sandifer and Hopkin, 1996), a log-linear regression (Table 2) between concentration and reduction of fecundity has been calculated. Dose-response curves for reproduction or survival are usually modelled as logistic functions, but have been implemented as log-linear regression because published data did not allow further analysis and, in order to keep the model as simple and easy to re-implement as possible, only data already available have been used. The performance of the model with these data has been tested and [1]discussed later.
To account for the fact that the toxicity data used for this regression are the result of 28 days of exposure to homogeneous contamination, it has been corrected by the ratio of the toxicity counter (number of hours spent on contaminated patches) and the number of hours in 28 days, i.e. 672 hours. When the toxicity counter of an individual is greater than 672, this coefficient is set to one.

F. candida can sense the presence of conspecifics (Leonard and Bradbury, 1984) and therefore they move to look for a less crowded area if on the current cell other individuals are present. In the model it is assumed that the range within which the olfactory stimulus of other individuals is perceived is the same as for food. This process is described using pseudo-code below; the underlying assumptions are explained in more detail in the Supplementary Material.

```
for springtails with energy above tradeoff_repr and age above matur_time
        if local_density on any cell in a radius of 2.5 cm is lower than local_density of
        current cell
                While local_density on any cell in the semicircle of radius 2.5 cm the
                individual is facing is lower than local_density of current cell, and energy
                spent for moving (nr steps moved * en_reduce_step) is below tradeoff_dens
                        Turn towards one of these grid-cells
                        if cell ahead 1 cm is contaminated
                                Move towards it according to p_avoid
```

[1] Insert „will be“?

```
                    Update exposure counter
                else
                    Move towards one of the uncontaminated neighbour cells
                Calculate energy loss due to movement
        Update energy reserves: old value minus energy loss
Update grid cell variable "local_density" for all grid cells.
```

Hatching (eggs): Hatching success of eggs, besides the natural viability, depends on the concentration of toxicant of the grid cell on which the eggs are laid. From the data reported in Xu et al. (2009), the concentration-effect relationship for the reduction of egg viability caused by copper has been derived (Table 2). When an egg hatches, it changes its status to "springtail"; age is set to 0, and energy level is set to maximum.

Mortality: Juvenile survival is implemented as the probability to survive each day until maturation:

$$Probability\ to\ survive = (juvenile\ survival)^{1/(maturation\ time)}$$

Adult survival is implemented via the age of death: every organism, when it hatches and again when the season changes, draws a value for this parameter from a normal distribution, which is different for every season of the year, and every day it checks if its own age is still below this value, otherwise it dies.

Survival is reduced by exposure to the toxicant. From literature data (Sandifer and Hopkin, 1996), a linear regression between the logarithm of the concentration and reduction in survival (where 0 equals no reduction, 1 equals no surviving organisms) has been calculated (Table 2) and applied to both juveniles and adults. The same coefficient used for the regression between concentration of toxicant and reduction of fecundity, which takes into account the amount of time spent on a contaminated patch, was applied.

Table 1. Parameters and values used in the *Folsomia candida* model. For parameters that were directly determined, the source of the data is indicated in the "References" column. Parameters indirectly or inversely determined via calibration are identified. Direct parameterization is documented in detail in the TRACE element 'Data evaluation' and inverse parameterization is documented in the element 'Model output verification'.

Parameter	Units	Temperature (°C)	Distribution	Value	References
maturation time: time to reach adulthood (matur_time)	Days	12-15	Uniform	30-40	Milne, 1960
		19-21		13-29	Snider, 1973
		24-26		11-30	Marshall and Kevan, 1962
Hatching time: time needed for the eggs to develop and hatch to juveniles (hatch_time)	Days	5	Uniform	90	Milne, 1960
		12-15		13-19	Milne, 1960; Fountain and Hopkin, 2005
		19-21		7-15	Marshall and Kevan, 1962
		24-26		7-9	Milne, 1960
Number of eggs per brood, general value for the season (nr_eggs_season)	Number	12-15	Uniform	19-98	Milne, 1960; Snider, 1973; Grimnes and Snider, 1981
		19-21		30-50	Fountain and Hopkin, 2005
		24-26		26-68	Snider, 1973; Green, 1964b
Nr of broods per female: max number	Number	12-15	Uniform	9-16	Milne, 1960; Snider, 1973; Grimnes and Snider, 1981

of reproductive events (max_num_repr)		19-21		3-20	Snider, 1973
		24-26		4-6	Snider, 1973; Green, 1964b
Time between broods (repr_interv)	Days	12-15	Uniform	13-15	Snider and Butcher, 1973
		19-21		6-16	Marshall and Kevan, 1962
		24-26		11-13	Marshall and Kevan, 1962
Egg viability: percentage of eggs that successfully hatch (egg_viab)	Number	12-15	Normal	Mean 94.50% S.D5%	Snider and Butcher, 1973
		19-21		Mean 92% SD 5%	Snider and Butcher, 1973
		24-26		Mean 81% SD 9%	Snider and Butcher, 1973
Juvenile survival., expressed as probability to survive until age at maturity (j_surv)	Number	12-15	Normal	Mean 98% SD 2%	No reference for this temperature; value has been derived from other temperatures
		19-21		Mean 95% SD 2%	Marshall and Kevan, 1962
		24-26		Mean 83.30% SD 2%	Snider, 1973
Adult survival., expressed as the age of death of the individual (a_surv)	Days	12-15	Normal	Mean 241 SD 50	Snider and Butcher, 1973
		19-21		Mean 140 SD 25	Snider and Butcher, 1973
		24-26		Mean 73 SD 26	Snider and Butcher, 1973
Probability to reproduce at every reproductive instar (repr_probab)	Number	12-15	Uniform	96 - 100%	Milne, 1960; Snider, 1973; Grimnes and Snider, 1981
		19-21		95 - 99%	Milne, 1960; Snider, 1973; Grimnes and Snider, 1981
		24-26		94 - 98 %	No reference for this temperature; value has been derived from other temperatures

Distance within which food and conspecifics are sensed	Cm	Independent from temperature	Constant	2.5	Auclerc et al., 2010
Energy level (energy)	Days-to-death	Independent from temperature	Constant	Initial values Max: 30 Min: 0	Final values determined via sensitivity analysis and parameterization
Energy reduction per time-step (en_reduce_hour)	Days-to-death	Independent from temperature	Constant	Initial value 0.042	Final value determined via sensitivity analysis and parameterization)
Energy gained by food intake (food)	Days-to-death	Independent from temperature	Constant	Initial value 0.5	Final value determined via sensitivity analysis and parameterization)
Energy reduction per step moved (en_reduce_mov)	Days-to-death	Independent from temperature	Constant	Initial value 0.01	Final value determined via sensitivity analysis and parameterization)
Probability to move at each time-step (probab_mov)	Number	Independent from temperature	Constant	Initial value 0.1	Final value determined via sensitivity analysis and parameterization)
Maximum energy spent for foraging at each time-step (tradeoff_mov)	Days-to-death	Independent from temperature	Constant	Initial value 0.2	Final value determined via sensitivity analysis and parameterization)
Tradeoff between energy and reproduction (tradeoff_repr)	Days-to-death	Independent from temperature	Constant	Initial value 20	Final value determined via sensitivity analysis and parameterization)
Maximum energy spent for avoiding high density at each time-step (tradeoff_dens)	Days-to-death	Independent from temperature	Constant	Initial value 0.1	Final value determined via sensitivity analysis and parameterization)

3 Data evaluation

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

Summary:

All life-cycle parameters of *Folsomia candida* used in the model, with the exceptions of those related to the energy expenditures, have been directly derived from empirical data published in the literature, as well as individual-level toxicity data for copper. Qualitative observed patterns were also used to design the overall model structure.

As reported in Table 1, values for all the life-cycle parameters with the exceptions of those related to the energy expenditures have been determined from the literature. However, expert judgment was also involved in the choice of the chosen probability distributions. The criterion

used for this choice was: whenever the only information available was the range of observed values for a specific parameter, a uniform probability distribution was chosen. When the available information was a mean and standard deviation of the observed values, a normal distribution was assumed.

As published empirical evidence suggests, the number of eggs laid by *Folsomia candida* depends not only on the temperature but also on the local density (i.e. number of organisms on the same patch) and the energy level of the organism. As shown by Green (1964a), fecundity of springtails is reduced when they experience high population density, due to jostling effects: the effect of crowding upon fecundity has been calculated as an exponential function (Table 2) that interpolates Green (1964a) data. The same type of mathematical relationship has been assumed to exist between energetic status of the organism and number of eggs laid (Table 2).

The number of eggs laid also depends on the contamination experienced by the organism, in terms of concentration and time spent on a polluted patch: from literature data (Sandifer and Hopkin, 1996), a linear regression (Table 2) between concentration and reduction of fecundity has been calculated, and then a coefficient that takes into account the amount of time spent on a contaminated patch was applied.

Hatching success depends also on the concentration of toxicant of the grid cell on which the eggs are laid. From the data reported in Xu et al (2009), the concentration-effect relationship for the reduction of egg viability caused by copper has been derived (Table 2).

Survival is also reduced by exposure the toxicant: from literature data (Sandifer and Hopkin, 1996), a linear regression between the logarithm of the concentration and reduction of survival (where 0 equals no reduction, 1 equals no surviving organisms) has been calculated (Table 2) and applied to both juveniles and adults. To account for the fact that the toxicity data used for this regression are the result of 28 days exposure to homogeneous contamination, it has been corrected by the ratio of the toxicity counter (number of hours spent on contaminated patches) and the number of hours in 28 days, i.e. 672 hours. When the toxicity counter of an individual is greater than 672, this coefficient is set to one.

According to Boiteau et al. (2011), *F. candida* can sense and avoid copper-contaminated patches of soil. Therefore, organisms in the model check whether they are on a contaminated grid cell. If one of the neighbouring cell's concentration is lower, than they move on it with a chance equal to their avoidance probability, which is proportional to the toxicant's concentration (Table 2)

For more information on the calculations behind the toxicity effects, see Appendix 1.

Table 2. Equations for the linear regressions used in the model.

Independent variable	Dependent variable	Regression	R^2	Reference
ln concentration	Reduction of survival	$y = 0.0824x - 0.1366$	0.847	Sandifer and Hopkin, 1996
ln concentration	Reduction of fecundity	$y = 0.2189x - 0.8743$	0.919	Sandifer and Hopkin, 1996
ln concentration	Nr of hatched eggs (Normalized to the control)	$y = -0.2243x + 1.8893$	0.932	Xu et al., 2009
ln concentration	Percentage of avoidance	$y = 5.7475x - 1.4235$	0.926	Boiteau et al., 2011
Local density	Normalized nr of eggs	$y = 1.0637e^{-0.305x}$	0.942	Green, 1964a

Energy	Normalized nr of eggs	$y = 0.01e^{4.6052x}$	1	Assumed

To model specific behaviours of the species of interest, qualitative patterns that have been observed for the species or closely related ones have been used, as more quantitative data were not available. These patterns are listed below, with references to the published observations and a description of how they have been translated into the model:

- *F. candida* can sense the presence of conspecifics (Leonard and Bradbury, 1984) and therefore they move to look for a less crowded area: in the model it is assumed that the range within which the olfactory stimulus of other organisms is perceived is the same as for food.
- When the temperature is too low, springtails are inactive. Joosse and Testerink (1977) observe that below 10°C the percentage of *Orchesella cincta* individuals in a fed state is significantly lower, while Takeda (1984) report that in a population of *Folsomia octoculata* overwintering adults are in an immature state, and they become mature with the stimulation of increasing temperature. Verhoef (1996) notes that during the winter period nearly all the adults of the collembolan *Anurida maritima* die, and it appears that this is due to starvation caused by low locomotor activity in situations of low temperature. Therefore during the time interval corresponding to winter, individuals in the model do not execute any actions except for aging and mortality.
- From experimental observations reported in the literature, it is known that collembolans go through periods of inactivity (i.e. they do not move and do not feed), for instance during the moulting process (Joosse and Testerink, 1977; Marshall and Kevan, 1962). Therefore, in order to account for these periods of inactivity, individuals in the model do not move at each time-step, but accordingly to a given probability (*probab_mov*), which is proportional to the amount of food sensed by the individual (i.e. to the strength of the attractive olfactory stimulus), with a minimum value when the organism does not sense any food; the maximum value for *probab_mov* is twice the minimum. The value for minimum *probab_mov* was determined via sensitivity analysis and pattern-oriented parameterization, but has initially been set to 0.1. While springtails forage, they decrease the stock on the food cell on which they are feeding by one food item. The probability of movement is calculated as:

$$prob\_mov = 0.1 * (1 + \frac{mean\ amount\ of\ food\ on\ food\ cells\ within\ sensing\ range}{maximum\ amount\ of\ food\ initialized\ on\ a\ food\ cell})$$

The foraging submodel is described below using pseudo-code. The rationale for each part of the code, the values of parameters involved, and the equations used are explained below (see numbered references in square brackets).

Pseudo-code:

```
for all springtails
       if current cell is contaminated and one of the neighboring cells is not
              move towards it according to p_avoid
       if current energy reserve is below energy_max – 24*en_reduce_hour
              if any food patches in a 2.5 cm radius and if total food in a 2.5 cm radius is
              more than1 food item
                     Set movement probability dependent on average food in 2.5 cm radius. [1]
              else
                     Set movement probability to minimm movement probability
```

```
        While no food found and energy spent for foraging (nr steps moved *
        en_reduce_step)is below threshold (tradeoff_mov) [2]
                if food on current patch is at least 1
                        Eat
                if no food on current patch and food on one of the grid cells in
                thesemicircleofradius 2.5 cmthe individual isfacing to contains more
                food than 1
                        Turn towards one of these grid-cells [3]
                else
                        Turn randomly by 0-356°
                if cell ahead 1 cm is contaminated
                        Move towards it according to p_avoid [4]
                        Update exposure counter
                else
                        Move towards one of the uncontaminated neighbor cells
                Calcuate energy loss due to movement

        Update energy reserves: old value plus food intake minus energy loss

Update grid cell variable “local_density” for all gridcells.
```

[1] The energetic level of every individual after hatching is maximum, and at every tick this value is reduced, to take into account the energy expenditure for all the vital functions. Values for the parameters related to the energetic status of the individuals have been indirectly estimated from the literature, and are expressed in terms of number of days an individual could survive without feeding. These parameters have then been refined via sensitivity analysis and pattern-oriented parameterization.

Tully and Ferriere (2008) observe that survival of *F. candida* offspring is affected by dietary and crowding conditions: the mortality rate is multiplied by 12 under high density and starvation, and that during periods with low food conditions the reproductive investment is low. Booth and Anderson (1979) observe that after 10 weeks of starvation, about 50 % of the organisms in the cultures are still alive. They however also note that the culture dishes could not be kept perfectly sterile, and small fungal growths were occasionally observed which could be grazed. Furthermore, Smit et al. (1998) report that although a natural soil was used during their experiment, in the treatments where no food was added, food naturally present in soil (fungi and nematodes) was insufficient for *F. candida* to reach maturity. Therefore the initial values of energy levels and living costs have been chosen so that organisms could theoretically survive 30 days without food, which it has been assumed to be a good estimation of real conditions.

Besides survival, the energetic status influences also the fecundity of an individual. It is known from the literature that if the organisms are starved the size of egg clutches is reduced (Usher et al., 1971; Booth and Anderson, 1979). In the model the initial assumption is that they stop reproducing if they do not feed for 10 days, and the number of eggs laid decreases exponentially with the energy level.

[2] Individuals keep repeating these actions until the two conditions are met: when they find food or the energy spent for moving during the current time-step passes the threshold, they exit the foraging procedure. Initial values of the parameters involved in this process are: 0.5 for the energy gained by food intake (*en_gain_food*), 0.2 for the maximum energy an individual can spend during one time-step to look for food (*tradeoff_mov*), while for every step moved, the cost in terms of energy has initially been set to 0.01 (*en_reduce_step*).

[3] If organisms sense food they move towards it, otherwise they move randomly; according to Auclerc et al, 2010, the average maximum distance at which *F. candida* can detect food is

2.5 cm. Organisms move 1 cm at a time; movement costs energy, and they keep moving until they find food or as long as their energy balance allows it. This balance, for the hourly time-step *t*, is calculated as:

$$energy_t = energy_{t-1} + food - energy\ loss,$$

Where *energy loss* is proportional to the distance the organism has moved.

[4] While the organism is looking for food, before it moves, it also checks if the patch towards which it is directed is contaminated: in this case, according to its probability of avoidance (p_avoid), it can turn in another direction or walk on the contaminated patch. The probability to avoid different copper concentrations has been calculated from Boiteau et al. (2011) data (Table 2). If the organism walks on a contaminated grid cell, a toxicity counter is increased; it is assumed that the whole time step (1 hour) is spent on the polluted patch.

In the version object of this document, the model is built using data related to the effects of copper sulfate, and therefore model predictions can be considered valid to gain insight into the population dynamics of springtails only for heavy metals. To extend its validity to other classes of compounds with different environmental behavior, it would be necessary to implement degradation processes, and make the individuals' exposure dependent on the varying toxic concentration.

4 Conceptual model evaluation

This TRACE element provides supporting information on: The simplifying assumptions underlying a model's design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

Summary:

The conceptual model is represented in Figure 1. The design concepts underlying model design are presented in section 2, Model description. Further information regarding simplifying assumptions is presented in section 3, Data evaluation.

5 Implementation verification

This TRACE element provides supporting information on: (1) whether the computer code implementing the model has been thoroughly tested for programming errors, (2) whether the implemented model performs as indicated by the model description, and (3) how the software has been designed and documented to provide necessary usability tools (interfaces, automation of experiments, etc.) and to facilitate future installation, modification, and maintenance.

Summary:

In order to ensure that the computer code implementing the model works according to its specification in the ODD model description, a series of tests has been performed. These tests included syntax checking of the code, visual testing through NetLogo interface, print statements, spot tests with agent monitors, stress tests with extreme parameters values, test procedures and test programs, and code reviews.

The tests executed to verify the implementation of the model ranged from very simple

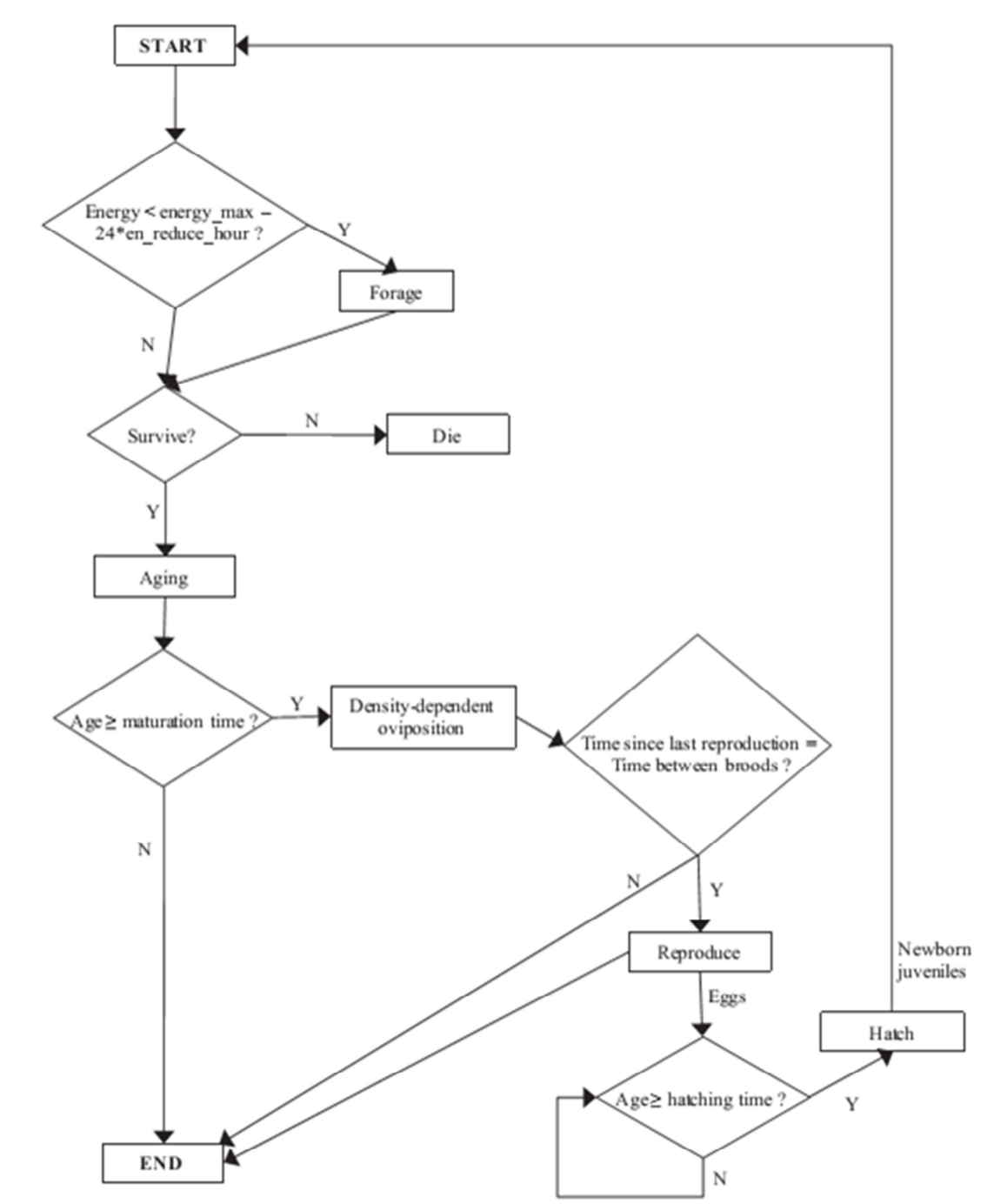


Figure 1. Conceptual model, presented as a flow chart describing the model's schedule.

checks using the tools provided by the software platform NetLogo, to more in-depth analyses. Tests included:

- Syntax checking of the code.
- Visual testing through NetLogo interface.

- Print statements, i.e. inserting statements that write information out to the display or to a file so it is possible to see what is going on. Common use of print statements is to output the value of key variables at different times to help diagnose when and why a model behaves unexpectedly (Railsback and Grimm, 2012).
- Spot tests with "agent monitors", i.e. opening a few NetLogo "agent monitors" and manually recording the value of the variables, calculating by hand how they should change, and then stepping the model through one iteration of its schedule and seeing if the change reported by the agent monitor matches the expectation (Railsback and Grimm, 2011).
- Stress tests with extreme parameters values to expose errors that may be hidden under normal conditions.
- Test procedures, i.e. adding new procedures to the code just to produce intermediate output, used only for testing.
- Test programs, i.e. writing a separate short program that serves only to test a particular algorithm or procedure. This test has been executed on most of the submodels: for instance, to test the procedure for background mortality and toxicity-dependent survival, a test program has been written, where individuals do not do anything else but grow old and die. This makes it easy to record the proportion of individuals surviving during the simulation, and confront it with the theoretical survival curves. In the full model this would not be possible, as the organisms are reproducing and the number of entities in the model depends on both births and deaths.
- Code reviews. The program has been checked by a reviewer to check for logical errors and other mistakes, and compare it to the model formulation.

Software

The model has been implemented in NetLogo (Wilensky 1999), a free software platform. The program is available in the Supplementary Material of Meli et al. (2014). After installing NetLogo 5.0, which is available for all major operating systems, users can run our model and use the graphical user interface and an integrated tool to perform simulation experiments ("BehaviorSpace", Wilensky and Shargel, 2002). The developers of NetLogo always provide transition guides to new version of NetLogo, and keep old versions for download. Modifications of the program require knowledge of NetLogo.

6 Model output verification

This TRACE element provides supporting information on: (1) how well model output matches observations and (2) how much calibration and effects of environmental drivers were involved in obtaining good fits of model output and data.

Summary:

In this section it is described how many and which parameters were inversely determined via calibration. To inversely determine the values of these parameters we made the model reproduce several patterns observed in laboratory populations at different scales and levels of biological organization ("pattern-oriented modelling" (Grimm et al., 2005)).

Comparisons of model output and data and empirical observations are included in the main document, Meli et a. (2014).

Parameterisation: As shown in Table 1, for some parameters it was not possible to find values in the literature. These are all related to the energy level of individuals and their movement. Initial values have been indirectly estimated from observations reported in the literature. A sensitivity analysis was used to identify those parameters having the strongest effect on model output, and these were selected for calibration.

According to Wiegand et al. (2003), we used different patterns to determine unknown parameters using an inverse modelling approach. The central idea of pattern-oriented parameterization is to make the model produce multiple patterns simultaneously, so that the structural realism of the model is increased, i.e., the internal organization of the modelled system is more likely to be captured sufficiently for the intended purpose of the model.

The following patterns have been used for model design and parameterization:

Pattern 1: Food-dependence (Usher et al., 1971). Three different observations describe this pattern: population growth with excess food, with marginally limiting food and with limiting food supply. Usher et al (1971) observed that when food is not a limiting factor or is only marginally limiting, being supplied in proportion to population density, the establishment of an equilibrium population size is achieved, but the speed of establishment is proportional to the rate at which food is supplied, and population densities approach those reached with excess food. When the food supply is independent of density and limiting, equilibrium population size is reduced.

Pattern 2: Population growth rate and density dependent population size (Seifert et al., 1979). Microcosm experiments on *F. candida* run by Seifert et al (1979) showed that population growth rates had decreased in all cultures before the termination of the experiments after 43 days, which indicated density-dependent effects. Estimates of exponential rates of increase were based on population increases from the 7^{th} through the 31^{st} day from the beginning of experiment.

The three observations that comprise the first pattern were used as filters to progressively exclude combinations of parameter values: 10 replicate simulations with every combination of the relevant parameters within a range of ±20% around the initial value were run and then compared to the first observation (population growth with excess food) using chi-square statistics. The 20 best combinations were chosen, and the same procedure repeated for the other two observations (population growth with limiting and slightly limiting food). Sets of values that met all of the three observations were then used to simulate pattern 2. Simulated ranges of final population size and exponential growth rate were compared to the observation from Seifert et al. (1979), and the parameter set which gave the best fit, in terms of overlapping ranges, was chosen. The resulting final parameter set was used in all subsequent simulations.

The final parameter set, after using patterns 1 and 2 as filters, was: energy_max = 30, energy_min = 4, en_reduce_hour = 0.0462, tradeoff_mov = 0.18 and probab_mov = 0.12. The outputs of simulations run with the best parameter set are compared to the data sets that comprise Pattern 1 and 2 in Tables 3 and 4 respectively.

Table 3 Pattern-oriented parameterization results: outputs of simulations with the best parameter set (average and 95% confidence limits: 10 replicates) are compared to the three observations in Pattern 1 (data from Usher et al., 1971)

Time (days)	Excess food				Slightly limiting food				Limiting food			
	Observed	Simulated			Observed	Simulated			Observed	Simulated		
		Mean	95% LCL	95% UCL		Mean	95% LCL	95% UCL		Mean	95% LCL	95% UCL
0	6	6	6	6	6	6	6	6	6	6	6	6
5	6	6	6	6	6	6	6	6	6	6	6	6
10	6	6	6	6	6	6	6	6	6	6	6	7
15	13	6	6	7	8	8	6	10	8	11	6	15
20	45	13	10	17	26	26	13	39	18	33	18	48
25	75	27	18	37	50	35	17	53	40	56	31	81
30	130	49	33	65	85	35	17	52	70	67	39	94
35	220	83	62	104	120	36	19	54	120	69	40	97
40	310	142	111	173	140	43	26	59	125	73	43	103
45	410	236	189	282	155	64	38	90	127	81	48	114
50	550	400	313	487	166	106	47	164	128	93	56	129
55	690	644	513	775	175	150	69	232	122	115	69	161
60	870	929	768	1090	185	177	80	275	140	135	77	192
65	1090	1211	1054	1367	195	185	93	277	170	156	91	221
70	1380	1430	1288	1572	210	203	115	292	200	186	112	260
75	1450	1552	1446	1657	230	264	171	357	230	217	143	290
80	1485	1579	1494	1665	260	337	236	438	260	235	167	304
85	1490	1579	1502	1657	290	383	292	475	285	256	193	319
90	1500	1577	1499	1654	340	423	355	492	305	268	212	325
95	1500	1577	1499	1654	400	445	388	502	325	270	210	329
100	1500	1577	1499	1654	430	453	394	513	340	275	208	342
105	1500	1577	1499	1654	440	456	394	518	365	279	207	351
110					460	461	402	520	390	293	216	370
115					500	466	408	523	420	299	222	376
120					550	466	409	523	455	296	227	366
125					610	468	409	523	500	289	228	350

Table 4. Pattern-oriented parameterization results: outputs of simulations with the best parameter set are compared to the observations in Pattern 2 (data from Seifert et al., 1979). The area of the simulation arena is the same as the vessels used in the microcosm experiment by Seifert et al. (1979).

	Final population density (individuals/culture)		Population growth rate (r)	
	Mean	Range	Mean	Range
Observed	463,21	207,62 – 774,67	0,178	0,166 – 0,199
Simulated	548,6	442 – 670	0,163	0,158 – 0,175

7 Model analysis

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

Summary:

A sensitivity analysis was performed to explore the behavior of the model in response to variations in the values of parameters that were not directly determined from the literature. Two different model outputs, final population size and average weekly population growth rate, have been used in this sensitivity analysis. Results are shown in Table 5.

A sensitivity analysis was used to identify those parameters having the strongest effect on model output, and these were selected for inclusion in the pattern-oriented parameterization described in the previous section of the present document.

The initial values assigned to these parameters were used as a central condition. Subsequently, analysis was carried out by running multiple replicates of input parameter sets varied around this central condition. Parameters were adjusted independently to ±10, ±20, ±30, ±40, ±50 % of their central values. Linear and second order polynomial regressions were calculated between the relative changes in each parameter value and the two model outputs, final population size and average weekly population growth rate. For this analysis, 40 replicate simulations of 120 days were run for each parameter value, and, in order to simplify interpretation of the results, all simulations were run at a constant temperature interval of 19-21°C. All statistical analyses were performed using Systat ver. 13.0.

Among the parameters included in the sensitivity analysis, only those for which the regressions were statistically significant ($p < 0.01$) for both dependent variables were selected for calibration, i.e., energy maximum and minimum, metabolic rate, maximum energy spent to forage at each time-step and probability to move at each time-step (see Table 5).

Table 5. Results of sensitivity analysis.

Parameter	Final population size				Growth rate			
	Adjusted R^2	First order coefficient	Second order coefficient	Regression p-value	Adjusted R^2	First order coefficient	Second order coefficient	Regression p-value
Energy_max	0.787	-534.836	-1,825.769	0.000	0.788	-0.015	-0.044	0.000
Energy_min	0.545	410.150	864.528	0.000	0.026	-0.006	-0.007	0.000
En_reduce_hour	0.816	-1,803.183	-1,778.808	0.000	0.772	-0.069	-0.150	0.000
Tradeoff_repr	0.045	85.709	-104.307	0.000	0.000	0.002	0.004	0.510
En_reduce_step	0.013	-25.216	-7.567	0.022	0.006	-0.001	0.001	0.109
Tradeoff_mov	0.494	-205.477	-230.536	0.000	0.387	-0.006	-0.007	0.000
Tradeoof_dens	0.273	-115.350	222.016	0.000	0.012	-0.001	-0.003	0.025
Food	0.000	-11.811	-14.892	0.227	0.000	0.000	0.002	0.293
Probab_mov	0.621	-282.907	-227.11	0.000	0.420	-0.008	-0.008	0.000

8 Model output corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

Summary:

Three patterns have been identified from the literature, which have been numbered 3-5 to distinguish them from the patterns used for calibration (1-2).

For model output verification we identified and used three observed patterns. In fact, the more patterns a model reproduces simultaneously, the lower the risk that the model is completely unrealistic. These observations are:

Pattern 3: Number of generations per year (Marshall and Kevan, 1962). The authors observed that in a greenhouse (constant temperature 22° C) *F. candida* can have as many as 12 generations per year.

Pattern 4: Seasonal variation in population size in the soil of a temperate forest (Klironomos and Kendrick, 1995). In this study, a 100 m^2 plot was set up in a sugar maple forest in Canada. The soil profile was divided into layers (i.e. litter (forest floor), 0-10 cm, 10-20 cm and 20-30 cm) and sampling was carried out four times throughout the year (May 1991, July 1991, October 1991 and February 1992) to account for seasonal variation. For comparison with the model, data for the litter layer were considered. Results of this survey showed that the highest population density was reached in October, with a relatively high peak also in May, while in July and February population abundance was very low.

Pattern 5: Instantaneous rate of population increase (r_i) under copper contamination (Herbert et al., 2004). Soil concentrations of copper up to 12,800 µg g^{-1} were tested. Calculated r_i values ranged from -0.086 (extinction) to 0.077 (in one replicate at 200 µg g^{-1}). The mean control r_i was calculated as 0.041, although the authors noted that adult survival and juvenile production in the controls were lower than specified in the ISO guidelines. Copper significantly affected r_i with significant differences found between the control and treatment at concentrations of 3,200 µg g^{-1} and higher.

For pattern 3, the mean number of generations produced during model simulations lasting one year at constant temperature range (19-21°C) was compared to the number of generations obtained in a greenhouse (Marshall and Kevan, 1962), also at constant temperature (22°C). The model output ranged from 11 to 13 generations per year, with an average of 11.6 compared to the 12 generations found by Marshall and Kevan (1962).

A comparison of the population abundance (individuals/m^2) predicted by the model with the data reported by Klironomos and Kendrick (1995) (Pattern 4, Fig. 2), shows a good fit for the data for spring, summer and winter, whereas the fall peak predicted by the model was lower. The highest peak in the simulated population abundance occurred in June, but since there were no data points for this month in Klironomos and Kendrick (1995), it is not possible to compare this model prediction with a field observation.

Finally, we tested the performance of the IBM in predicting population-level effects of copper on *F. candida* (Pattern 5). Toxic effects were implemented using only individual-level data (Table 2), with endpoints on fecundity, survival, hatching success and avoidance; therefore we compared model output to the data presented in Herbert et al. (2004), where the authors measured the instantaneous rate of population increase (r_i) after exposure to different copper

concentrations. Results are shown in Fig. 3. There was a higher simulated growth rate for the control and the two lowest concentrations, however for higher toxicant levels the model output and data matched well.

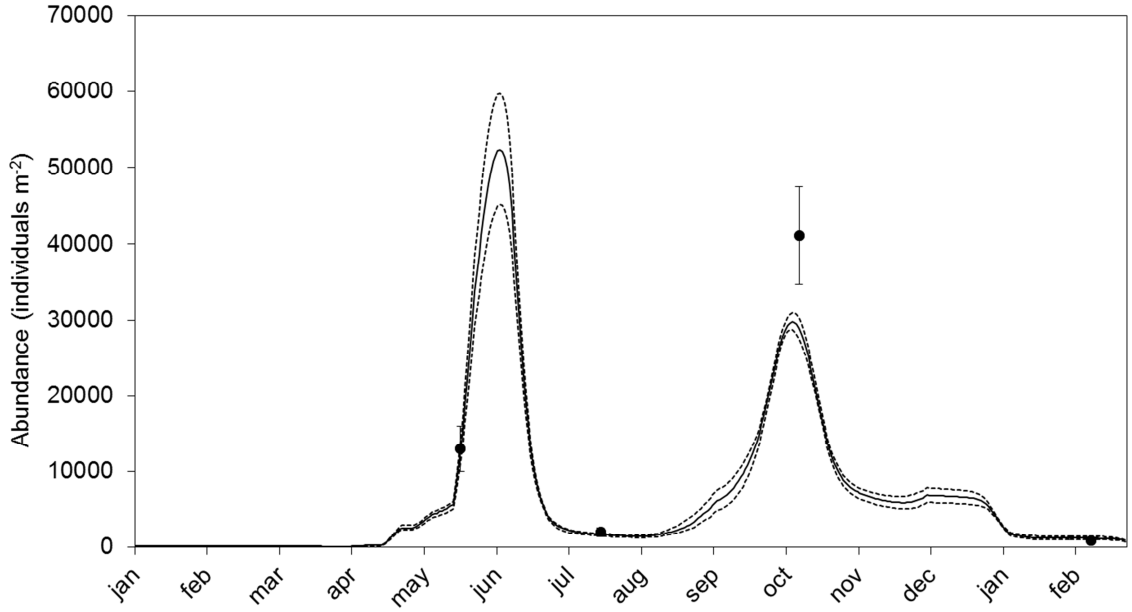
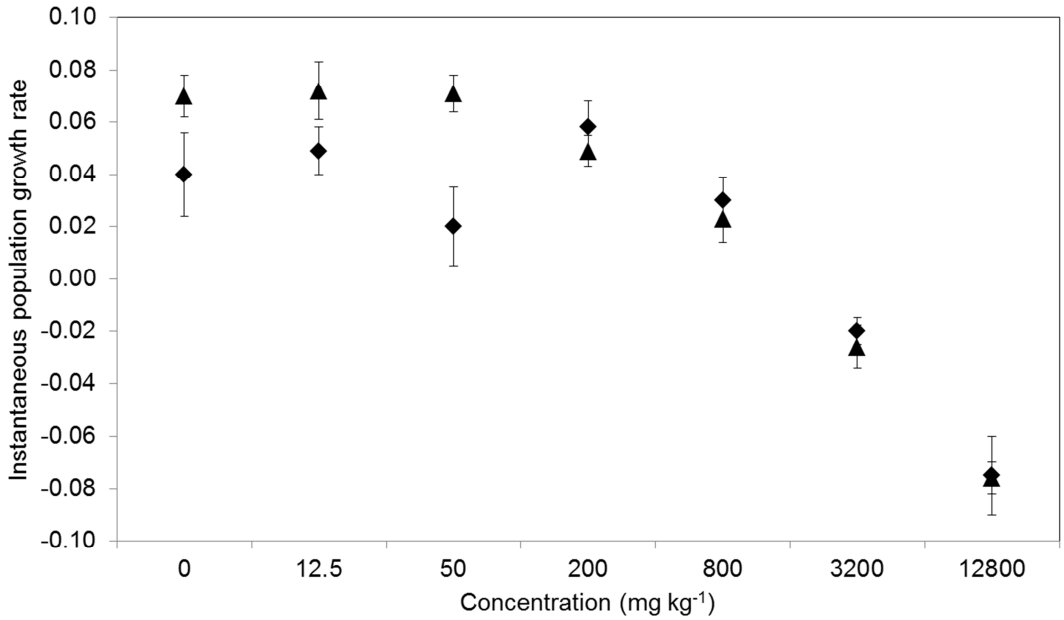


Figure 3. Pattern 5: mean (±SEM, four replicates) instantaneous rate of population increase of *F. candida* exposed to different copper concentrations. Herbert et al., (2004) data represented with (▲), simulation results with (♦).



9 APPENDIX 1

Calculation of toxicity parameters

For calculation of the percentage effect per concentration of the tested substance or per soil dilution (in case of contaminated natural soil), the number of springtails in the test soil is compared with the number of springtails in the control soil in accordance with

$$x = \left(\frac{n_c - n_t}{N} \right) \times 100$$

where

- *X* is avoidance, expressed as a percentage;
- *n*c is the number of springtails in the control soil (either per vessel or in the control soil of all replicates);
- *nt* is the number of springtails in the test soil (either per vessel or in the test soil of all replicates);
- *N* is the total number of springtails (either per vessel or in the control soil of all replicates).

Table A1. Avoidance data for Folsomia candida and copper sulfate (Boiteau et al., 2011)

Concentration (mg Cu kg^{-1})	% animals in control soil	Nr animals in control soil (60 animals per concentration in total)	Nr animals in test soil (60 animals per concentration in total)	% avoidance (according to ISO method)
0	51	31	29	2
150	60	36	24	20
200	63	38	22	26
800	70	42	18	40
1600	70	42	18	40
3200	75	45	15	50

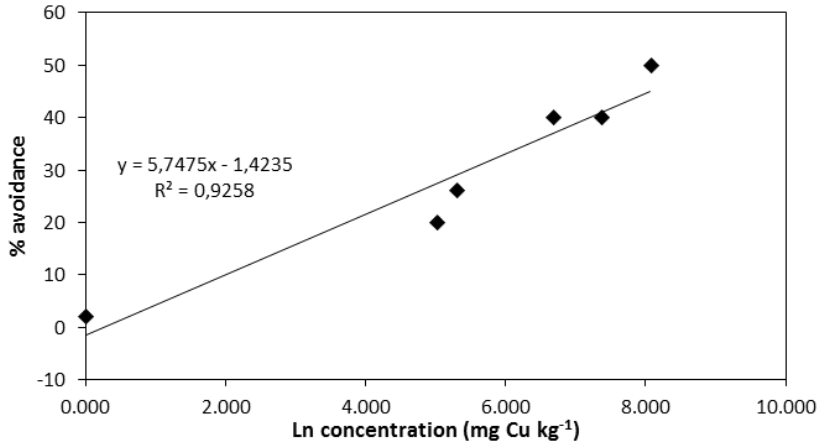


Figure A1. Regression line for the percentage of avoidance versus logarithm of the concentration.

Table A2. Experimental data for the effects of copper sulfate on reproduction and survival of Folsomia candida. From Sandifer and Hopkin (1996) (pH=6, temperature=20°C).

Concentration (mg Cu kg^{-1})	Survival			Reproduction		
	mean	std error	std dev	mean	std error	stdev
0	6,5	1,2	2,4	797	95,18	190,36
10	8,8	0,6	1,2	1032	169	338
40	7,5	1,2	2,4	801	46	92
200	6	0,6	1,2	774	27	54
1000	5	0,8	1,6	291	46	92
3000	3	1,5	3	0	0	0

Table A3. Experimental data for the effects of copper on hatching of 20 *Folsomia candida* eggs exposed to different concentrations of toxicant. From (Xu et al., 2009).

Concentration (mg Cu kg^{-1})	**Eggs hatched (mean)**	**S.E. of mean**	**Eggs hatched (normalized to the control)**
0	19	0,71	1
100	17,5	0,65	0,921
200	13,8	1,31	0,726
400	7,5	1,71	0,395
800	7,75	1,65	0,408
1600	4,25	1,8	0,224
3200	2,5	1,04	0,132

The number of eggs hatched at 100 mg/kg is not significantly different than the control; therefore for concentrations below 100 mg/kg in the model is assumed that eggs hatch with the normal viability.

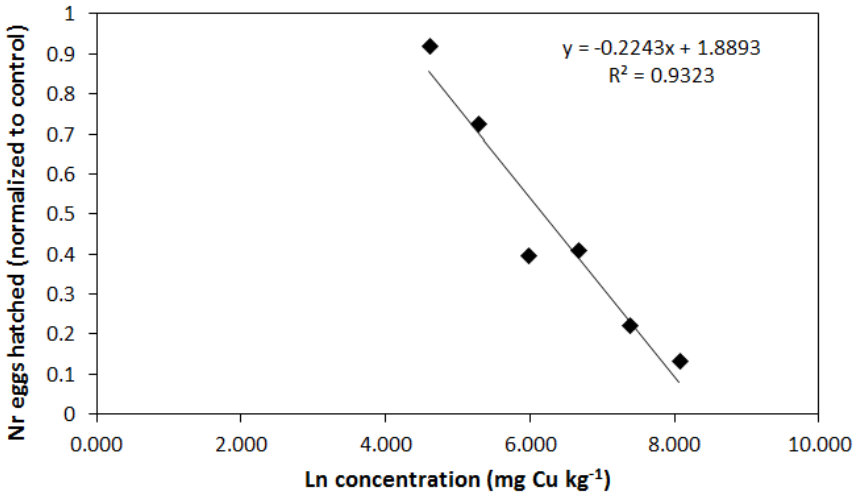


Figure A2. Regression line for the normalized hatching success versus logarithm of the concentration.

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