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An energy budget agent-based model of earthworm populations and its application to study the effects of pesticides

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ABSTRACT

Earthworms are important organisms in soil communities and so are used as model organisms in environmental risk assessments of chemicals. However current risk assessments of soil invertebrates are based on short-term laboratory studies, of limited ecological relevance, supplemented if necessary by site-specific field trials, which sometimes are challenging to apply across the whole agricultural landscape. Here, we investigate whether population responses to environmental stressors and pesticide exposure can be accurately predicted by combining energy budget and agent-based models (ABMs), based on knowledge of how individuals respond to their local circumstances. A simple energy budget model was implemented within each earthworm *Eisenia fetida* in the ABM, based on a priori parameter estimates. From broadly accepted physiological principles, simple algorithms specify how energy acquisition and expenditure drive life cycle processes. Each individual allocates energy between maintenance, growth and/or reproduction under varying conditions of food density, soil temperature and soil moisture. When simulating published experiments, good model fits were obtained to experimental data on individual growth, reproduction and starvation. Using the energy budget model as a platform we developed methods to identify which of the physiological parameters in the energy budget model (rates of ingestion, maintenance, growth or reproduction) are primarily affected by pesticide applications, producing four hypotheses about how toxicity acts. We tested these hypotheses by comparing model outputs with published toxicity data on the effects of copper oxychloride and chlorpyrifos on *E. fetida*. Both growth and reproduction were directly affected in experiments in which sufficient food was provided, whilst maintenance was targeted under food limitation. Although we only incorporate toxic effects at the individual level we show how ABMs can readily extrapolate to larger scales by providing good model fits to field population data. The ability of the presented model to fit the available field and laboratory data for *E. fetida* demonstrates the promise of the agent-based approach in ecology, by showing how biological knowledge can be used to make ecological inferences. Further work is required to extend the approach to populations of more ecologically relevant species studied at the field scale. Such a model could help extrapolate from laboratory to field conditions and from one set of field conditions to another or from species to species.

1. Introduction

Earthworms are significant contributors to the ecosystem services provided by arable soils (Daily et al., 1997; Keith and Robinson, 2012; Blouin et al., 2013) and they respond rapidly to alterations in soil quality (Fraser et al., 1996), tillage (Chan, 2001) and exposure to chemical toxicants (Vorphal et al., 2009). Consequently, they are focal organisms for environmental risk assessments of agricultural chemicals in Europe (OECD, 1984). However, current regulatory guidance for risk assessment is limited to short-term laboratory studies supplemented if necessary by site-specific field trials to investigate population-level effects (SANCO, 2002). Laboratory studies have limited ecological relevance since they are carried out in standardised conditions, whilst field trials are expensive, time-consuming and challenging to interpret for a wide range of agricultural landscapes (Jänsch et al., 2006). Here, we investigate a mechanistic approach to modelling organism

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responses to environmental and chemical exposure. This approach has the potential to act as a refinement option for chemical risk assessments if it can accurately predict population-level responses to the agricultural uses of plant protection products (PPPs) under a range of different conditions (Thorbek et al., 2010).

As individual physiologies direct the life cycle processes (e.g. growth and reproduction) which give rise to a population's dynamics, modelling at the individual level is crucial in mechanistic effects modelling for chemical risk assessment (Grimm et al., 2005; DeAngelis and Mooij, 2005). Individual physiology can be described by energy budgets and modelled using well-established principles of energy and mass conservation (Sousa et al., 2010; Sibly et al., 2013). Organisms uptake resources (in the form of food) from their environment and expend assimilated energy on maintenance, growth and reproduction (Karasov and Martinez del Rio, 2007; Sibly and Calow, 1986), but the allocation of energy to metabolic processes depends on a combination of environment- and organism-specific conditions (e.g., Nisbet et al., 2000). Dynamic energy budget (DEB) theory (Kooijman, 2010) provides a method for modelling individual physiology and DEB models have been previously developed for earthworm species by Baveco and de Roos (1996) and Klok et al. (2007). We do not follow DEB theory here because DEB models implement a 'kappa rule' which assumes that a fixed proportion of assimilated resources are allocated to maintenance and growth and the remainder to reproduction throughout life. It is important to realise that the kappa rule is (1) not in accord with the principles of physiological ecology as outlined in e.g. Karasov and Martinez del Rio (2007) and Sibly and Calow (1986); (2) denies the possibility of allocation trade-offs between growth and reproduction which are widely believed to occur (see e.g. Stearns, 1992); (3) has been shown not to apply to *Daphnia magna*, the species for which DEB was initially devised, by Glazier and Calow (1992) and Nisbet et al. (2004), who showed the proportion allocated to growth reduces from 1 early in life to <0.05 later; (4) is contradicted by the finding that in the absence of a sexual partner, earthworms grow larger, indicating that reproduction has priority over growth in adults (Neuhauser et al., 1980) and; (5) is contradicted by observations of continued reproduction during weight loss by earthworms under limiting feeding conditions (Reinecke and Viljoen, 1990). Baveco and de Roos (1996) and Klok et al. (2007) offer no evidence that the kappa rule applies to earthworms. We therefore felt it necessary to develop a more accurate mechanistic energy budget model based on accepted principles of physiological ecology and have followed the approach of Sibly et al. (2013).

The purpose of this study is to develop and evaluate a mechanistic model of earthworm responses to local conditions, describing physiological responses to biotic and abiotic factors at the individual level, and seeing how this translates to the population level. We construct an energy-budget-driven ABM for the earthworm species *Eisenia fetida*, and compare model outputs to experimental data from the literature on both individual life cycle processes and population dynamics. In the experiments we simulated, individuals were kept for periods of time with depleting food supplies. To simulate these experiments mechanistically, model landscapes incorporating spatially and temporally varying food availability are required, so that the necessary interactions between individuals, stress exposure and lack of food can occur. Following its success in simulating published data from non-toxic environments, we develop and evaluate methods for considering how individual physiological processes are altered by toxic stress. Adopting the methodology of Jager and Zimmer (2012) we assume that pesticides impose stress on specific physiological parameters, which have predictable effects on growth, reproduction and/or starvation following energy allocation principles. Although not common in the field, *E. fetida* is used as a model species due to the ample quantity

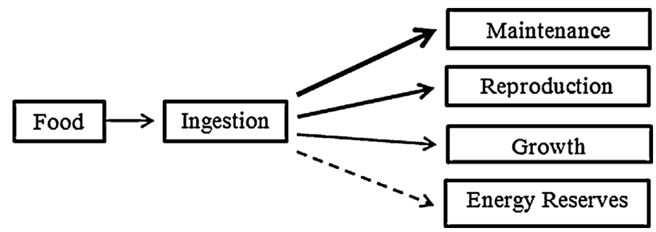

Fig. 1. Structure of the energy budget model for adult *E. fetida*, with the thickness of arrows indicating priorities for energy allocation from food. Cocoons and juveniles are also in the model though cocoons do not grow and juveniles do not reproduce. Energy remaining after allocation enters the energy reserves which may be used for other functions when food is limited.

of literature data available for model development and evaluation at the individual level. However, we anticipate that our model can be developed for application to other species and environmental conditions.

2. Methods

Here we provide a full model description and give an outline summary of model evaluation methods. Full details following guidelines for transparent and comprehensive ecological modelling documentation (TRACE) (Schmolke et al., 2010) are presented in the supplementary material.

2.1. Model description

The model description follows the ODD (Overview, Design concepts, and Details) protocol for describing ABMs (Grimm et al., 2010). The model is implemented in Netlogo 5.0.2 (Wilensky, 1999), a platform for building ABMs. The Netlogo code is available in supplementary material.

2.1.1. Purpose

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.

2.1.2. Entities, state variables and scales

This ABM 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 characterised by life cycle stage (cocoon, juvenile or adult), mass and energy reserves, and landscape patches by food density, soil temperature, soil moisture and pesticide concentration. The model proceeds in discrete daily time-steps. Metabolic calculations are in units of energy per unit time (kJ/day).

2.1.3. Process overview and scheduling

Each individual in the ABM has its own energy budget. The energy budget model includes algorithms for how energy uptake and expenditure direct life cycle processes based on fundamental principles of physiological ecology, and generally follows the methodology of Sibly et al. (2013). Individuals assimilate energy from ingested food (*Ingestion and Energy Uptake*) and expend available energy on maintenance (*Maintenance*), growth (*Growth*) and reproduction (*Reproduction*) in the order of priority outlined in Fig. 1. Total available energy is limited by the amount of food an organism can ingest, whilst mass and temperature have scaling effects on individual metabolic rates (Brown et al., 2004).