

Earthworm distribution and abundance predicted by a process-based model



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ABSTRACT

Earthworms are significant ecosystem engineers and are an important component of the diet of many vertebrates and invertebrates, so the ability to predict their distribution and abundance would have wide application in ecology, conservation and land management. Earthworm viability is known to be affected by the availability and quality of food resources, soil water conditions and temperature, but has not yet been modelled mechanistically to link effects on individuals to field population responses. Here we present a novel model capable of predicting the effects of land management and environmental conditions on the distribution and abundance of *Aporrectodea caliginosa*, the dominant earthworm species in agroecosystems. Our process-based approach uses individual based modelling (IBM), in which each individual has its own energy budget. Individual earthworm energy budgets follow established principles of physiological ecology and are parameterised for *A. caliginosa* from experimental measurements under optimal conditions. Under suboptimal conditions (e.g. food limitation, low soil temperatures and water contents) reproduction is prioritised over growth. Good model agreement to independent laboratory data on individual cocoon production and growth of body mass, under variable feeding and temperature conditions support our representation of *A. caliginosa* physiology through energy budgets. Our mechanistic model is able to accurately predict *A. caliginosa* distribution and abundance in spatially heterogeneous soil profiles representative of field study conditions. Essential here is the explicit modelling of earthworm behaviour in the soil profile. Local earthworm movement responds to a trade-off between food availability and soil water conditions, and this determines the spatiotemporal distribution of the population in the soil profile. Importantly, multiple environmental variables can be manipulated simultaneously in the model to explore earthworm population exposure and effects to combinations of stressors. Potential applications include prediction of the population-level effects of pesticides and changes in soil management e.g. conservation tillage and climate change.

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1. Introduction

Earthworms are major contributors to soil biodiversity, are significant ecosystem engineers in terrestrial soils, and represent a large component of the stock of natural soil capital from which a range of ecosystem services flow (Keith and Robinson, 2012; Blouin et al., 2013). Earthworms can bring c. 40 t/ha/year of soil to the surface by casting and potentially change erosion rates by

increasing surface roughness (Feller et al., 2003). Below ground, earthworms create soil aggregates which maintain soil structure, aid plant growth and promote carbon sequestration (e.g. Le Bayon et al., 2002; Butenschoen et al., 2009). Earthworms are also an important component of the diet of many European animal species, both vertebrate and invertebrate (Granval and Aliaga, 1988), and so are significant in ecosystem food chains. Thus, an ability to predict the spatiotemporal abundance of earthworm populations has important applications in forecasting how changing environmental conditions alter the provision of soil ecosystem services. However, previous models have neglected the major ecological drivers affecting earthworm populations in natural environments (e.g. movement in the soil, soil temperature, soil moisture and resources) (Schneider and Schröder, 2012).

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To predict how populations respond to environmental changes, understanding is needed of how the underlying life cycle processes of individuals are altered by ecological factors present in field conditions. Food supply is well recognised as a major factor limiting animal populations (Solomon, 1949; Sinclair, 1989) and is instrumental in structuring earthworm communities (Curry, 2004). Both the quantity and the quality of the food supply are important (Lee, 1985). For example, earthworm population abundance in the field has been found to vary in response to changes in soil organic matter (SOM) content, associated with habitat quality and land management practices (e.g. Edwards and Bohlen, 1996; El-Duweini and Ghabbour, 1965; Hendrix et al., 1992). Soil moisture is also a key factor in determining the abundance and distribution of earthworm populations (Lee, 1985). Clear relationships between soil water potential and earthworm physiology (*A. caliginosa* activity, growth and reproduction rates) were identified by Holmstrup (2001). In the field, Gerard (1967) demonstrated how soil water potential governed the vertical movement of earthworm populations in the soil profile.

Understanding the links between environmental factors and population dynamics is not possible using classical population models (e.g. matrix models) as these consider populations as collective entities and landscapes as homogeneous (DeAngelis and Mooij, 2005). However, aiming to capture biological realism often results in models which are complex, require extensive parameterisation, are hard to evaluate and become species- and site-specific (Grimm et al., 2005). Instead, key drivers of the system should be integrated with generic frameworks explaining biological responses. This requires a process-based approach (Evans et al., 2013).

A process-based approach ideally begins by modelling how individual physiological processes relate to external environmental drivers through energy budgets. Individual based models (IBMs) can then be used to simulate the interactions between individuals and their environments, from which population dynamics emerge (Grimm and Railsback, 2012). Combining these approaches is necessary to mechanistically extrapolate from individual life history to population dynamics in realistic environments (e.g. Sibly et al., 2013). The resulting models can then be used to analyse population responses to a variety of environmental conditions and land management practices through manipulation of landscape variables.

A process based model of earthworm populations would be particularly beneficial to agro-ecosystems, where the functions provided by earthworm activity are replaced by chemical and mechanical practices (Chan, 2001). Previous earthworm models have largely concentrated on easily reared species of importance in toxicity testing, vermiculture and waste management (e.g. Jager et al., 2006; Hobbelen and van Gestel, 2007; Johnston et al., 2014). However, the earthworm species considered are not commonly found in agricultural landscapes (Paoletti, 1999). Earthworm species inhabiting agricultural habitats are normally adapted to low quality food resources and regular periods of food

limitation. The endogeic earthworm *A. caliginosa* is the dominant earthworm in arable soils (Riley et al., 2008) and its global distribution is wider than that of other species (Blakemore, 2002). Here we construct an energy-budget IBM for *A. caliginosa* and investigate the potential of this process-based approach to predict life histories and population dynamics under variable soil temperature, soil moisture and resource conditions in the laboratory and field. Although agricultural land management scenarios are not simulated here, we aim to capture the mechanisms governing the spatiotemporal distribution and abundance of *A. caliginosa* populations in field conditions, so that future exploration of agricultural management effects can be better understood. For example, the effects of pesticides on earthworm populations are routinely tested in pasture (SANCO, 2002), and so it is important to understand these systems for applications to ecological risk assessment.

2. Methods

The purpose of the model is to simulate *A. caliginosa* population dynamics under varying environmental conditions, representative of those encountered in the field, particularly food availability and quality, soil water conditions and soil temperature. Population dynamics emerge from environmental conditions constraining energy allocation amongst individuals; the way this happens is represented by an individual based model (IBM) in which each individual has its own energy budget. Here we give an outline summary of the model. A full description, following the ODD protocol for describing IBMs (Grimm et al., 2010) is presented in Appendix A in Supplementary material and Johnston et al. (2014) for *Eisenia fetida*. The model is implemented in Netlogo 5.0.4 (Wilensky, 1999), a platform for building IBMs.

2.1. Energy budget model

Individuals assimilate energy from ingested food and expend available energy on maintenance, growth and reproduction in the order of priority outlined in Fig. 1.

The energy budget model was parameterised for *A. caliginosa* with data relating to species-specific growth and reproduction rates under optimal environmental conditions as shown in Table 1. Sub-optimal feeding, temperature and soil water conditions then reduce metabolic rates. If food is limiting, the amount of food available in a patch ($\text{g}/0.01 \text{ m}^2$) is divided between the individuals living there. A proportion of ingested energy, determined by the energy content of food (E_x) and assimilation efficiency (A_e), becomes available for allocation to the various processes outlined in Fig. 1. E_x (kJ/g) varies depending on the diet of the individuals whilst A_e is assumed to be constant. If less energy is available than is required for maximum reproduction or growth then priorities operate as in Fig. 1 and reproduction and/or growth are reduced accordingly. Temperature alters individual metabolic rates according to the Arrhenius function (Fig. 1).

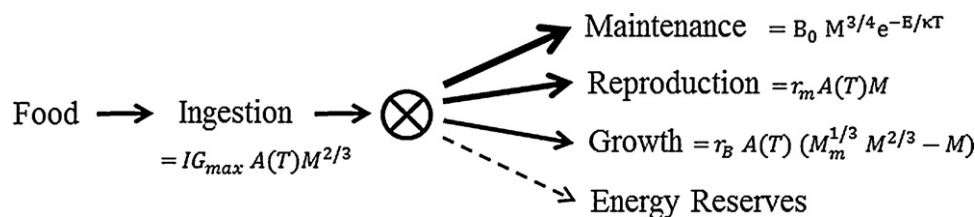


Fig. 1. Structure of the energy budget model for adult earthworms, with the thickness of solid arrows indicating priorities for allocation of energy obtained from food. Reproduction has priority over growth in sexually mature individuals. Energy remaining after allocation enters the energy reserves. Equations are used to calculate maximum daily metabolic rates which depend on mass, M in grams; temperature, T in kelvin and parameters as defined in Table 1 for *Aporrectodea caliginosa*. $A(T)$ is the Arrhenius function of temperature, $A(T) = e^{-E/\kappa(1/T-1/T_{ref})}$, where κ is the Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$).

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