This is a repository copy of *Earthworm distribution and abundance predicted by a process-based model*.

Earthworm distribution and abundance predicted by a process-based model

A.S.A. Johnston [a,*], M. Holmstrup [b], M.E. Hodson [c], P. Thorbek [d], T. Alvarez [e], R.M. Sibly [a]

[a] School of Biological Sciences, University of Reading, UK
[b] Department of Bioscience, Aarhus University, Denmark
[c] Environment Department, University of York, UK
[d] Environmental Safety, Syngenta Ltd., Bracknell, UK
[e] EcoRisk Solutions Ltd., Norwich, UK

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.

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).

* Corresponding author at: Room 405, Philip Lyle Building, School of Biological Sciences, University of Reading, Reading, Berkshire RG6 6AS, UK.
Tel.: +44 0 118 3785049.
E-mail address: a.s.a.johnston@pgr.reading.ac.uk (A.S.A. Johnston).

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 ($g/0.01 \, m^2$) 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).
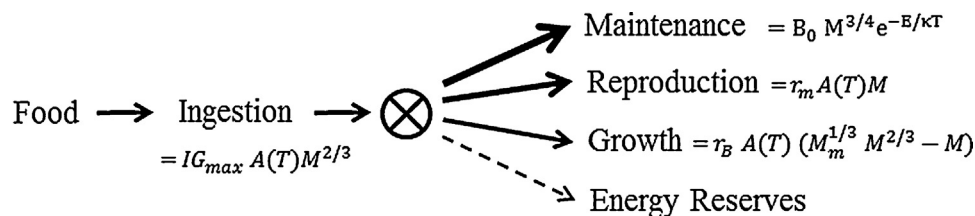
Fig. 1. Structure of the energy budget model for adult earthworms, with the thickness of solid arrows indicating priorities for allocation of energy obtained from food. Reproduction has priority over growth in sexually mature individuals. Energy remaining after allocation enters the energy reserves. 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 ($8.62 \times 10^{-5} \, eV \, K^{-1}$).

Table 1
Default parameter values of the earthworm (*Aporrectodea caliginosa*) energy budget model with sources. Further details of the parameter estimates are available in Appendix B of the Supplementary material.

Symbol	Definition	Value	Unit	Reference	Notes
A_e	Assimilation efficiency	0.19	–	Lavelle and Spain (2001)	p. 470
B_o	Taxon-specific normalization constant	968	kJ/g/day	Meehan (2006)	Calculated from Table 2, p. 881 and Eq. (4)
E	Activation energy	0.25	eV	Meehan (2006)	p. 880
E_c	Energy content of tissue	7	kJ/g	Peters (1983)	p. 235
E_s	Energy cost of synthesis	3.6	kJ/g	Sibly and Calow (1986)	Calculated from p. 54–55
E_x	Energy content of food	0.56–21.2	kJ/g	Range depends on diet. See section 2.3 and 2.4.2 for details.	
IG_{max}	Maximum ingestion rate	0.805	g/day/$g^{2/3}$	Taylor and Taylor (2014)	Table 1, p. 181
M_b	Mass at birth	0.005–0.026	g	Pedersen and Bjerre (1991)	Calculated via linear regression with mass of cocoon. See Appendix B
M_c	Mass of cocoon	0.008–0.035	g	Boström and Lofs-Holmin (1986); Boström (1987)	Calculated via linear regression with adult mass (g). See Appendix B
M_p	Mass at sexual maturity	0.50	g	Lofs-Holmin (1983)	Fig. 6, p. 35
M_m	Maximum asymptotic mass	2.00	g	Lofs-Holmin (1983)	Fig. 1, p. 32
r_B	Growth constant	0.049	/day	Lofs-Holmin (1983)	Fig. 6, p. 35
r_m	Maximum rate of energy allocation to reproduction	0.054	kJ/g/day	Spurgeon et al. (2000)	Table 2, p. 1803
T_0	Incubation period	62	days	Holmstrup et al. (1991)	Table 1, p. 181
T_{ref}	Reference temperature	288.15	kelvin	Eriksen-Hamel and Whalen (2006)	Fig. 1, p. 211
μ	Background mortality rate	0.14	%/day		p. 210

Metabolic processes have associated energetic costs: the energy cost of producing one cocoon is calculated as: $M_c(E_c + E_s)$ (Table 1), where M_c is mass of the cocoon, calculated together with M_b by regression as described in Appendix B. Cocoon mass is linearly related to the mass of the reproducing adult whilst mass at birth depends on the mass of the cocoon (minimum to maximum ranges are presented in Table 1). Energy costs of movement are assumed to be included as part of "maintenance". Some of the studies used to parameterise the energy budget model are of *A. turberculata*, previously considered a sub-species of *A. caliginosa* (e.g. Perez-Losada et al., 2009). Here we do not distinguish between these two species as they are closely related.

If any assimilated energy remains after expenditure to relevant life cycle processes it is stored in an individual's energy reserves, which may be utilised as an energy source when food is not available to pay the energy costs of maintenance and reproduction. Maximum energy reserves are proportional to an individuals mass and are taken to be $(M/2)E_c$. Below a critical energy reserve threshold $((M/4)E_c)$, individual's catabolise tissue for energy, resulting in weight loss proportional to an individual's
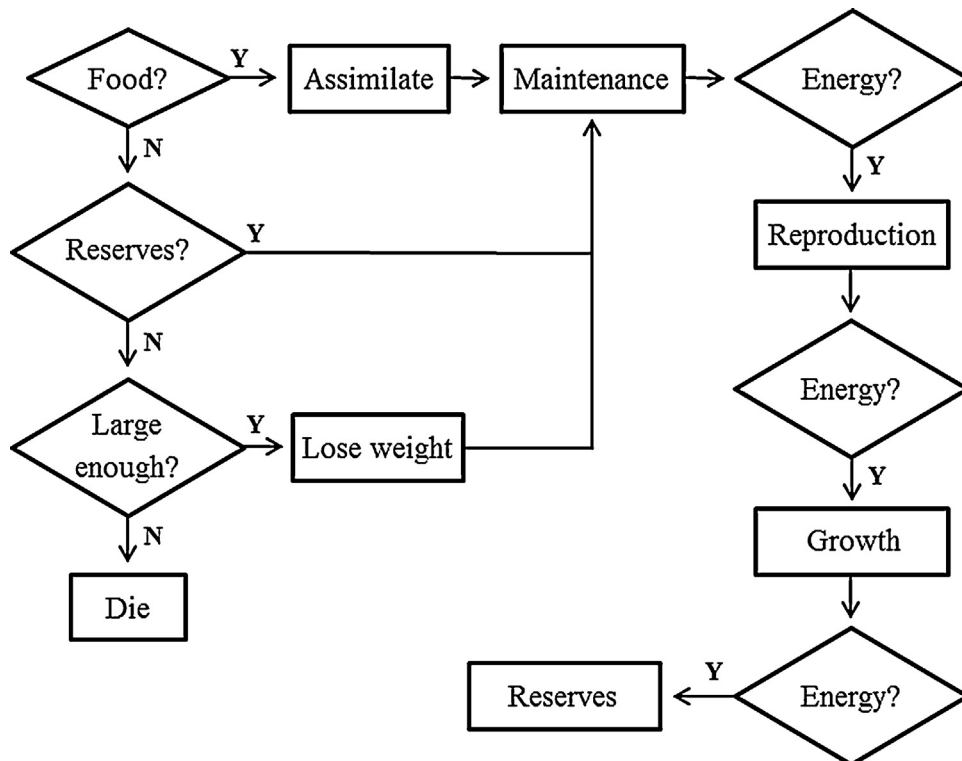
Fig. 2. Partial energy flow diagram of earthworm (*Aporrectodea caliginosa*) adults, showing the processes (rectangles) each individual goes through per time step, with diamonds indicating decision points. Energy reserves are used to pay maintenance costs when food is unavailable and individuals die if weight loss under starvation continues.

maintenance costs. An individual dies of starvation if its energy reserves are depleted (Fig. 2).

2.2. Individual based model

The IBM comprises *A. caliginosa* individuals and a model soil profile consisting of two-dimensional 0.01 m^2 patches of soil. In simulations of laboratory experiments, patches represent the horizontal soil surface, whilst in the field they represent a vertical cross-section of the soil profile. Individuals are characterized by life cycle stage (cocoon, juvenile or adult), mass and energy reserves, and patches by food availability, food quality, soil temperature, soil water content and soil texture. The model proceeds in discrete daily time-steps, at the end of which individual and patch variables are updated. Juvenile and adult movement between patches depends on food availability and soil water conditions in the soil profile, outlined in the "*Movement*" section below. Variation in food availability between patches arises from the movement and feeding of individuals in the soil profile. Soil water potential constrains individual ingestion rates and determines the onset of a resting phase (aestivation), outlined in the "*Soil water potential*" and "*Aestivation*" sections below.

2.2.1. Soil water potential

Holmstrup (2001) found decreasing soil water potentials to have a negative effect on individual *A. caliginosa* life cycle traits, as shown in Fig. 3. Here we suppose soil water potential (ψ) reduces the ingestion rate parameter (IG_{max}) as:

$$IG_{max}(\psi) = (IG_{max})e^{k\psi} \qquad (1)$$

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). Fig. 3 presents model results when the model was set up as in Holmstrup (2001). Full details and results of the model simulations are available in Appendix C.

2.2.2. Aestivation

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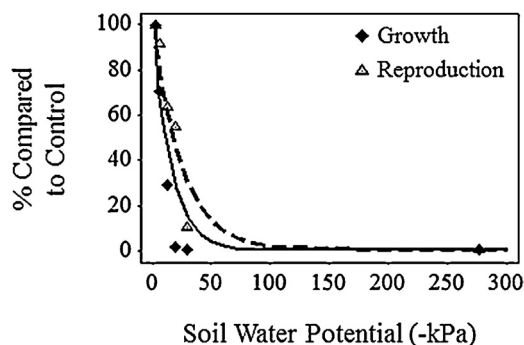
Fig. 4. Modelled decline in maintenance rates of the earthworm *Aporrectodea caliginosa* with time aestivating (line and left-hand axis) compared to oxygen consumption and carbon dioxide release data from Bayley et al. (2010) (points and right-hand axis).

aestivation, individuals utilize energy reserves to pay the energetic costs of maintenance according to the relationship between oxygen consumption and carbon dioxide release of *A. caliginosa* at different stages of aestivation recorded by Bayley et al. (2010) (Fig. 4)

2.2.3. Movement

Major factors determining the local movement of *A. caliginosa* in natural soil environments are soil water content and food quality (Lee, 1985). As *A. caliginosa* is sensitive to decreasing soil water potentials, the movement of individuals through the soil profile is primarily driven by soil water gradients when surface conditions are dry (Gerard, 1967). We assume that below a sub-optimal soil water potential of −10 kPa (e.g. growth and reproduction are not affected at −10 kPa in Holmstrup (2001)), individual movement is driven by the availability of higher soil water potentials in neighbouring patches in the model soil profile (Fig. 5). Burrowing activity of *A. caliginosa* in the top 10 cm of the soil profile is believed to reflect the presence of a higher SOM content (Jégou et al., 1998). Thus, if soil water conditions are non-limiting (greater than −10 kPa) individuals preferentially move to patches of greater food quality, represented by the parameter E_x (Fig. 5). Neighbouring patches occur both vertically and horizontally and if they do not provide better or worse conditions individuals move randomly.

Fig. 3. The effects of soil water potential (less than −2 kPa) on growth and reproduction of the earthworm *Aporrectodea caliginosa*, with data (points) from Holmstrup (2001) together with model simulation outputs (lines) for reproduction (dashed) and growth (solid).
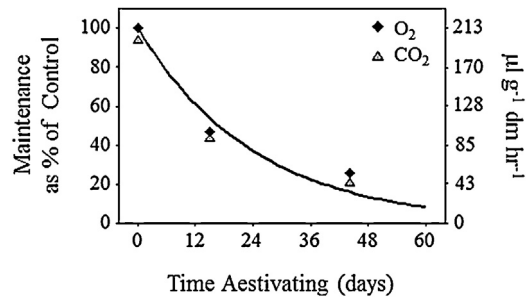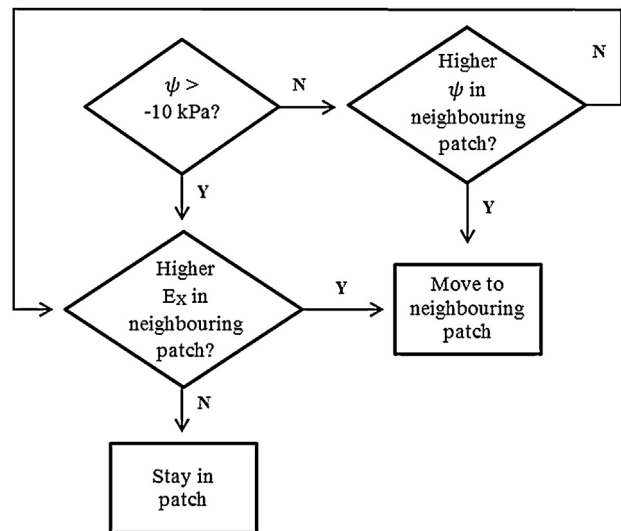
Fig. 5. Conceptual model of earthworm (*Aporrectodea caliginosa*) movement in the individual based model, where ψ represents soil water potential and E_x the energy content of food. Diamonds indicate decision points and rectangles are processes per daily time-step.

Table 2
Estimates for the energy content (E_x) of meadow fescue, barley and lucerne using values from [a]Boström and Lofs-Holmin (1986); [b]Forbes and Watson (1992) and [c]Boström (1987). CP is crude protein, EE is ether extract (mainly lipids), CF is crude fibre and NFE is nitrogen-free extract (mg/g dry matter).

	Analysis of dry matter (mg/g DM)				Digestible portion (%)	E_x (kJ/g)
	CP	EE	CF	NFE		
Meadow fescue	140[a]	26[b]	280[a]	493[b]	56.4[c]	10.42
Barley	180[a]	16[b]	230[a]	392[b]	30.4[c]	4.93
Lucerne	150[a]	22[b]	340[a]	402[b]	43.8[c]	7.91

Table 3
Experimental conditions used in model simulations for comparison with growth and reproduction data for the earthworm *Aporrectodea caliginosa*, where SOM is soil organic matters and E_x is energy content of food.

Study	Number of individuals	Food resource	SOM (%)	E_x (kJ/g)	Food quantity (g) (day provided)	Temp (°C)
Boström and Lofs-Holmin (1986)	10	Barley	7	1.33	252 (0)	15
Boström (1987)	1	Meadow fescue	5	1.018	252 (0)	15
Springett and Gray (1992)	1	Standard mix	10	1.86	40 (0)	12
Lofs-Holmin (1983)	5	Manure	10	5.76	20 (0) 40 (30) 80 (60)	15
Boström (1988)	5	Meadow fescue	5.4	1.70	260 (0)	15
Boström (1988)	5	Lucerne	5.4	1.64	260 (0)	15
Boström (1988)	5	Barley	5.4	1.56	260 (0)	15

2.3. Laboratory experiment simulations

The model was set up to mimic the conditions of published laboratory experiments, for comparisons between modelled *A. caliginosa* growth and reproduction ($N = 10$) and data. Estimates of the energy content of food (E_x) were needed for meadow fescue, barley and lucerne and these were based on the formula:

$$E_x = \frac{(2.3CP + 4.1EE + 1.9CF + 1.8NFE)}{100} \quad (2)$$

where CP is crude protein, EE is ether extract (mainly lipids), CF is crude fibre and NFE is nitrogen-free extract, measured in mg/g dry matter (Forbes and Watson, 1992). Parameter values for Eq. (2) were derived from Boström and Lofs-Holmin (1986) and Forbes and Watson (1992) (Table 2). Boström (1987) recorded the relative mass of particle fractions for each plant material. Here, we took particle lengths < 0.5 mm to be digestible, following observations by Lowe and Butt (2003).

Well-composted cattle manure was provided as food in some experiments. Following Gunadi et al. (2002)'s observations that pre-composting for 5 weeks led to a 45% decline in reproduction rates of *E. fetida*, we assumed that the energy content of well-composted cattle manure was one third that of fresh manure. Wang et al. (2011) recorded the energy content of fresh manure to be approximately 21.2 kJ/g, giving an E_x value of 7 kJ/g for well-composted manure. The energy content of the soils in the experiments was calculated assuming that soil organic matter (SOM) has an energy content of 18.62 kJ/g (Loustau, 1984). Table 3 outlines the conditions used in the experiments simulated here.

2.4. Field trial simulations

To investigate the model's ability to predict earthworm population responses to land management, we simulated *A. caliginosa* population dynamics in a field experiment by Gerard (1967) at Rothamsted, UK and Knight et al. (1992) at North Wykes Farm, UK. Gerard (1967) measured the vertical distribution and population structure (adult, juvenile and cocoon density) of *A. caliginosa* in the top 45 cm of soil under pasture. Knight et al. (1992) placed artificial cow pats on permanent grazed pasture and measured the earthworm biomass response, where *A. caliginosa* were the dominant earthworm species. The model soil profile
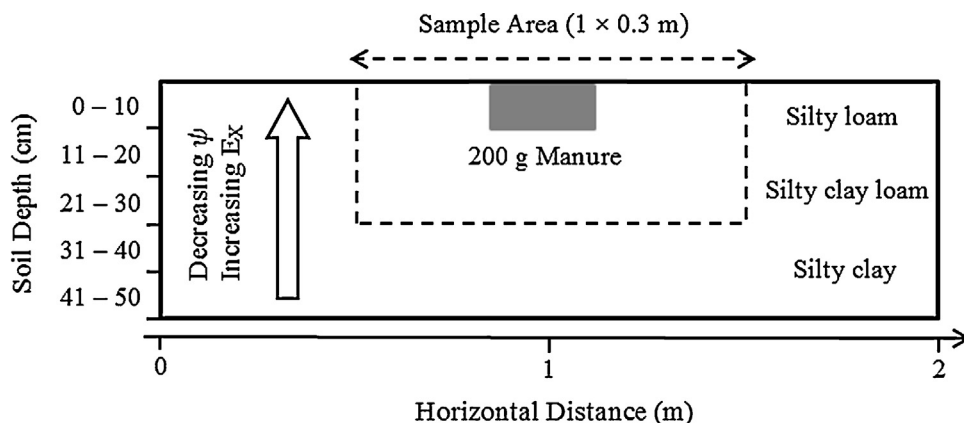
Fig. 6. Diagram of the model landscape used to simulate the field experiments for the earthworm *Aporrectodea caliginosa*, where ψ is soil water potential ($-$kPa), estimated from soil water content (cm³/cm³) and soil texture. E_x is energy content of food, predicted from soil organic matter content (%). The dashed line represents the boundary of the sampled area (1 × 0.3 m) and the shaded area represents the modelled application of manure mixed in to the top 10 cm of soil for simulation of the experiment by Knight et al. (1992).

Table 4
Parameter values for estimating the soil water potential of different soil textures. θ_r is the residual water content, θ_s is the saturated water content and α and n are curve fitting parameters. Values of θ_r, θ_s and n are taken from Leij et al. (1996) and α from Ghanbarian-Alavijeh et al. (2010).

Depth (cm)	Soil texture	θ_r	θ_s	α	N
0–20	Silt loam	0.061	0.43	0.565	1.39
21–30	Silt clay loam	0.098	0.55	0.500	1.41
31–50	Silt clay	0.163	0.47	0.600	1.39

spanned 2×0.5 m whilst the area sampled in the model was 1×0.45 m for Gerard (1967) and 1×0.3 m for Knight et al. (1992) (Fig. 6).

At the start of Knight et al.'s (1992) experiment, fresh cow manure ($E_x = 21.2$ kJ/g; Wang et al., 2011) was applied at a rate of 200 g/m^2 and assumed to be mixed into the top 10 cm of the soil profile (Fig. 6). The timing of manure application is not stated in the study but a sensitivity analysis (Appendix D) showed that the model was only sensitive to the timing of application during unfavourable soil water conditions (June–September) when aestivation is common. Here, we assume a manure application date of 1st April 1990.

Model simulations were initialized with 100 individuals of each life cycle stage (adults, juveniles and cocoons) and run for 50 years to allow the population to stabilise before making observations in the sample area. Major considerations for modelling populations under undisturbed field conditions are seasonal variations in soil temperature and soil water potential and the availability and quality of food resources, outlined in the next sections.

2.4.1. Soil temperature and soil water potential in the field

Mean monthly values and standard deviations for soil temperature under grass at 10, 20 and 30 cm and soil water content estimates were obtained from Rothamsted Experimental Station for both field trials simulated. The soil texture was reported as a silty loam with an underlying clay sub-soil, and we have assumed a transition in texture from silty loam to silt clay loam to silty clay, outlined in Fig. 6. We estimate soil water potential (ψ) from water content measurements θ (cm^3/cm^3) using the parametric van Genuchten (1980) model in the form:

$$\psi = \frac{1}{\alpha}\left(\left(\frac{\theta_s - \theta_r}{\theta - \theta_r}\right)^{\frac{n}{n-1}} - 1\right) \quad (3)$$

where ψ is in units $-$kPa, θ_r and θ_s are the residual and saturated water contents respectively, and α and n are parameters directly dependent on soil texture. The values of θ_r, θ_s, α and n were obtained from the literature for the soil textures in the field trial simulated (Table 4).

Seasonal variations in soil water potential and temperature for the soil depths sampled by Gerard (1967) for 1959 are presented in Fig. 7.

2.4.2. Soil organic matter in the field

Soil organic matter represents a key food source for endogeic earthworms like A. caliginosa (e.g. Edwards and Lofty, 1977). In the model, we use soil bulk density as a proxy for food availability and SOM represents the energy content of the food. Although this is a simplification of the diversity of resources available to earthworms, particularly epigeic and anecic species which feed at the soil surface, here we assume these details are sufficient for modelling the feeding behaviour of endogeic species in the soil profile of undisturbed pastures. Knight et al. (1992) recorded soil bulk densities of 0.75 and 1.06 g/cm^3 in the top 10 cm and deeper layers of the soil profile respectively and we assumed a bulk density of 1.10 g/cm^3 for the soil in Gerard (1967). The feeding dynamics of A. caliginosa in pasture were modelled by estimating variations in SOM with season and depth. SOM content generally declines with depth in the soil profile (Lavelle and Spain, 2001).
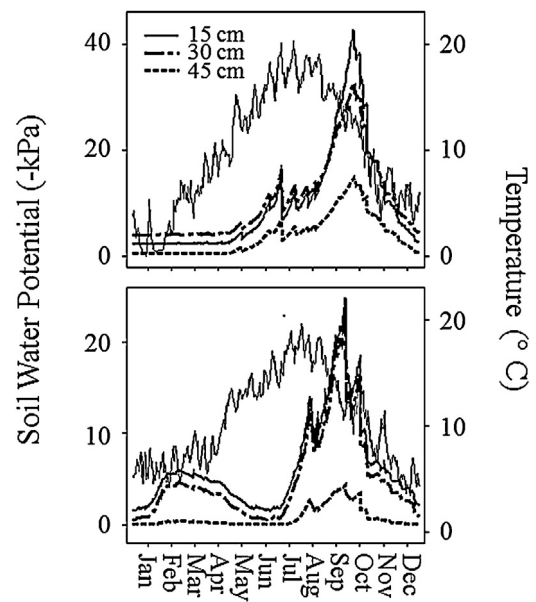

Fig. 7. Seasonal variations in soil water potential (bold lines and left-hand axis: solid, dashed and dotted lines represent mean values at 15, 30 and 45 cm soil depths respectively) with depth and mean soil temperature at 10 cm (faint solid line and right-hand axis) for (top) Gerard's (1967) and (bottom) Knight et al. (1992). Variations in soil water potential with soil depth result from differences in soil water content (cm^3/cm^3) and changes in soil texture.

Celik (2005) measured the SOM content of a pasture soil to range from 44.6 g/kg in the top 10 cm to 37.9 g/kg at a depth of 10–20 cm. The soil carbon stock of a silty loam soil was measured by Balesdent et al. (2000) as 1.53, 1.34 and 1.09 kg/m^2 at depths of 10, 20 and 30 cm respectively, which is in line with observations made by Jenkinson (1969) at Rothamsted. From these values and considering carbon to account for 58% of SOM (Guo and Gifford, 2002), we assumed a maximum SOM content of 6% for the top 30 cm of the soil profile. Our estimate is in agreement with observations from Rothamsted in the range 5–7.1% SOM (Coleman et al., 1997; Harrod and Hogan, 2008).

Although no clear seasonal variations in SOM content have been identified, some general patterns are evident in the literature for field soils (e.g. not sieved of macro-organic material). For example, McNaughton et al. (1998) found root biomass in undisturbed grasslands to peak in summer and decline in winter with a difference of around 300 g/m^2, whilst levels are similar during spring and autumn. Bardgett et al. (1997) recorded similar patterns for microbial biomass in grassland, with differences between summer and winter of 200 g/cm^2. We used these general observations to model seasonal variations in SOM as shown in Fig. 8. Daily variations in SOM, from plant, root and microbial growth and death were modelled by assigning each patch daily energy contents (kJ/g), taken at random from normal distributions as in Fig. 8. This also produced spatial heterogeneity in soil profiles.

2.5. Goodness of fit of model outputs to recorded data

We used the coefficient of determination (R^2) to evaluate how well the model's outputs fit the observed data. R^2 is defined as 1 – ((residual sum of squares)/(total sum of squares)), with values closer to 1 representing better agreement between observed and predicted values. Note the value of R^2 can be negative if the fit is poor. Conventional statistical methods of assessing the R^2 values are not applicable here because the parameter values are not

Soil Organic Matter (%)
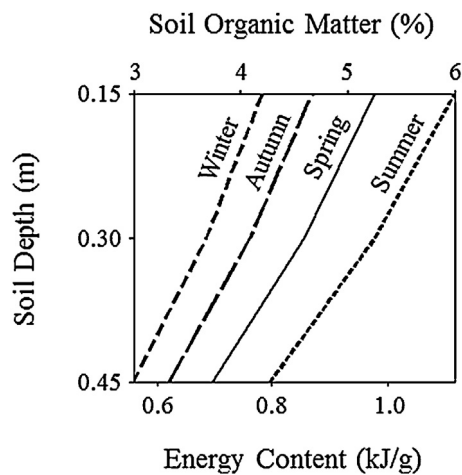
Fig. 8. Estimates of soil organic matter (%) and equivalent energy contents (kJ/g soil) in relation to depth and season for a pasture soil used to simulate the field conditions of Gerard (1967) and Knight et al. (1992). Lines represent the mean and SD is taken as 10%.

estimated from the data. However, we suggest that values of $R^2 > 0.5$ can generally be taken to indicate a good fit.

3. Results

Mechanistic models for potential use in practical applications should be evaluated to ensure that they provide an adequate representation of the real system. Here, we evaluate our model's prediction against multiple independent records of *A. caliginosa* life cycle processes in the laboratory and population dynamics in the field.

3.1. Individual life cycle processes

Life cycle data for *A. caliginosa* from experimental studies are presented together with outputs of model simulations run under the same conditions (Table 3). Fig. 9(a) and (b) show individual changes in body mass under food conditions relevant to field populations when the earthworms are fed with plant material. Fig. 9(c) and (d) show increased growth rates when individuals were fed more energy rich resources such as manure, underlining the direct link between energy assimilation and expenditure to life cycle processes. The model outputs fit the data well as shown by the R^2 values in Fig. 9.

Boström (1988) recorded growth and cocoon production of five adult *A. caliginosa* maintained for 28 days on meadow fescue, lucerne or barley (Fig. 10). Model outputs again fit well with the recorded data.

Cumulative cocoon production of *A. caliginosa* provided with manure and meadow fescue as food was recorded by Lofs-Holmin (1983) and Boström and Lofs-Holmin (1996); respectively. There is good model agreement with the data for variation of cocoon production with temperature (Fig. 11b: $R^2 = 0.92$) and the data for cocoon production do not differ significantly from the model outputs (t test, $p > 0.05$).

3.2. Field populations

The vertical distribution of an *A. caliginosa* population reported by Gerard (1967) is compared to model simulation results in Fig. 12. In September, Gerard (1967) did not find any individuals but suggested that the whole population was present below the soil depth sampled in the experiment (45 cm). In the model, those individuals not aestivating were present below 31 cm. Model outputs fit well with the recorded data at both soil depths.
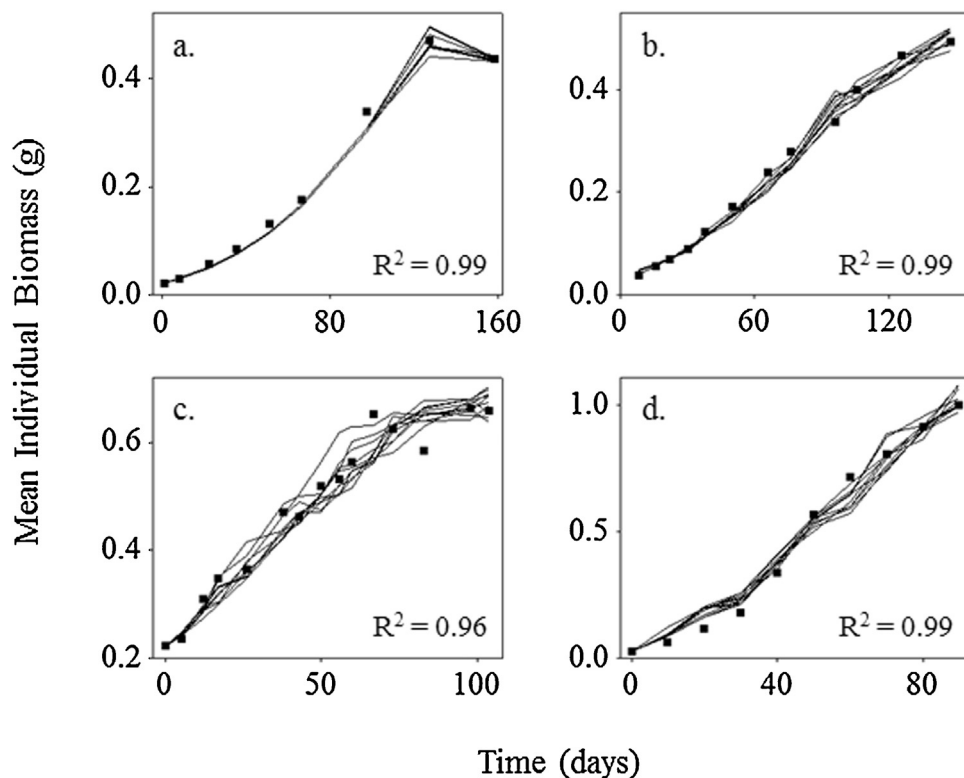
Fig. 9. Comparison between ten model simulation outputs (lines) and data (points) recording changes in individual earthworm (*Aporrectodea caliginosa*) biomass over time provided with (a) barley (from Boström and Lofs-Holmin, 1986), (b) meadow fescue (Boström, 1987), (c) a highly organic mix (Springett and Gray, 1992) and (d) cattle manure (Lofs-Holmin, 1983) for food. Average R^2 values are shown in the bottom right of each panel.
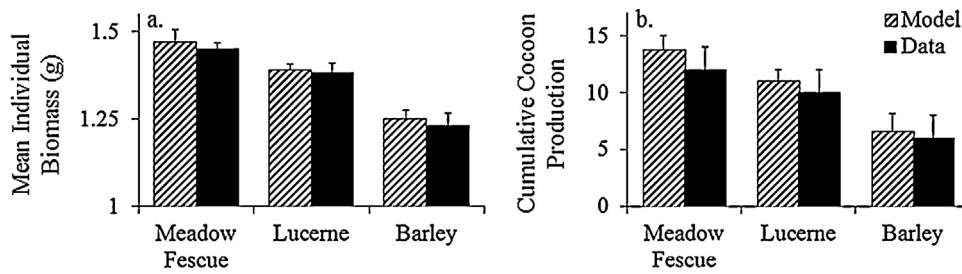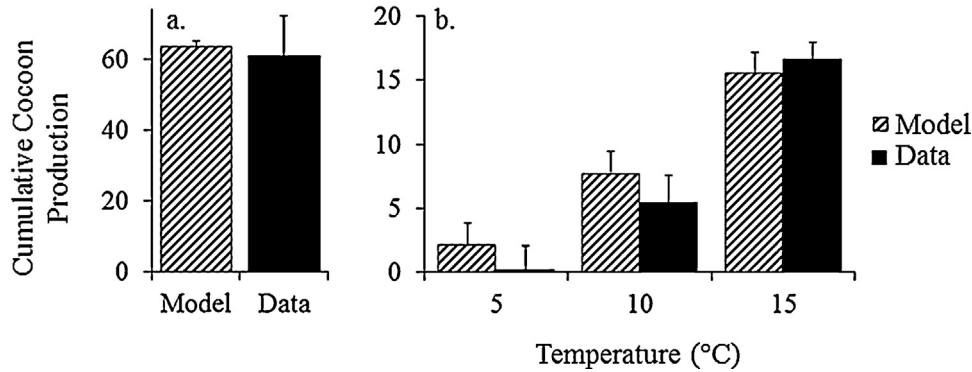
Fig. 10. Comparison between model outputs (hatched bars, mean + SE from 10 simulations) and recorded data from Boström (1988) (solid bars) for (a) individual biomass and (b) cocoon production of groups of five adult earthworms (*Aporrectodea caliginosa*) maintained on the indicated plant foods. Average R^2 values are (a) 0.96 and (b) 0.75.

The population densities of adults, juveniles and cocoons were recorded each month for the sampled year in Gerard (1967). Data from Gerard (1967) are presented alongside model outputs in Fig. 13. Although the model predicts seasonal patterns of juvenile density reasonably well (Fig. 13(b), $R^2 = 0.70$), the fits for adult densities and cocoons are poor (Figs. 13(a) and (c), $R^2 = 0.06$ and -0.08 respectively). However, the pattern of modelled adult densities replicates that of the data, with a maximum in spring, and a minimum in September (Fig. 13(a)) due to dry soil conditions

driving the population to soil depths below the sampled area (see above). The observed cocoon densities from January to June ($453 \pm 216/m^2$) are higher than predicted ($131 \pm 57/m^2$) during half of the year (Fig. 13(c)). However, the observed densities are much higher than those recorded by Boström and Lofs-Holmin (1996) in a meadow fescue lay, with a measured maximum density of 176 cocoons/m² in June.

Earthworm population biomasses reported by Knight et al. (1992) under field conditions are compared with model simulation

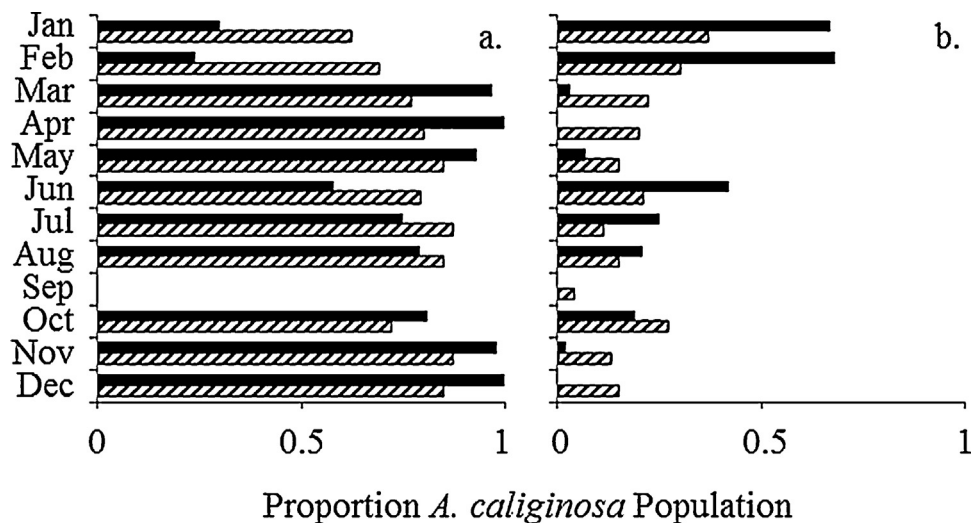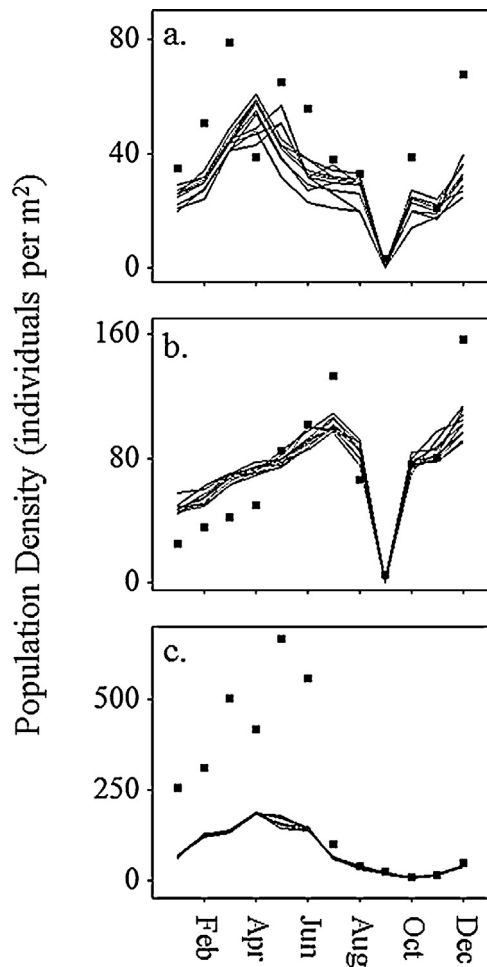**Fig. 12.** Comparison between data from Gerard (1967) (solid bars) for the vertical distribution of an earthworm (*Aporrectodea caliginosa*) population in pasture with model simulation outputs (hatched bars, mean from 10 simulations) showing monthly changes in the proportion of the population present at (a) 0–15 cm and (b) 16–30 cm of the soil profile. Average R^2 values are (a) 0.87 and (b) 0.80.

Fig. 13. Comparison of earthworm (*Aporrectodea caliginosa*) population density data from Gerard (1967) (symbols) and model outputs (lines, mean from 10 simulations) for (a) adults, (b) juveniles and (c) cocoons for the year 1959 in pasture at Rothamsted, UK. Average R^2 values are (a) 0.06, (b) 0.70 and (c) −0.08.

results for *A. caliginosa* in Fig. 14. Under control conditions (Fig. 14(a)) there is no consistent variation with time, but under experimental conditions, population biomass increases for 9 weeks after deposition of an artificial cow pat (Fig. 14(b)). The field data are higher than the model output under both conditions. However, *A. caliginosa* only comprised on average 44.5% of the total population, and when this is taken into account agreement is better (Fig. 14(c) and (d)).

Knight et al. (1992) recorded an earthworm density of 354 ± 73 individuals/m^2 in pasture. Considering *A. caliginosa* to comprise 44.5% gives a population density and biomass of 158 ± 33 individuals/m^2 and 20.6 g/m^2. Model simulations recorded a mean population density and biomass of 147 ± 23 individuals/m^2 and 20.9 ± 4.1 g/m^2 ($\pm$SE, $N = 4$), closely matching the observations of Knight et al. (1992).

3.2.1. Sensitivity analysis

The implications for modelling movement as a trade-off between soil water potential and food quality, as in Fig. 5, were evaluated by comparing model outputs when the movement is assumed to be random for the Knight et al. (1992) manure experiment. Fig. 15 shows how important capturing directional movement is for predicting the dynamics of earthworm populations following land management scenarios.

Model outputs are sensitive to the SOM content of the soil as shown in Fig. 16. Earthworm density and biomass change linearly by 14% for each 10% change in SOM content in the modelled Knight et al. (1992) pasture trial.

4. Discussion

Our model fits well the records of individual cocoon production and growth of body mass in *A. caliginosa* for all the experimental studies we know of. It is the first published model to consider temperature, soil moisture and resources, which are fundamental ecological drivers for understanding earthworm populations (Schneider and Schröder, 2012). Simulated laboratory studies varied in the foods provided (Figs. 9–11) and were carried out at several different temperatures (Fig. 11(b)). The ability of the model
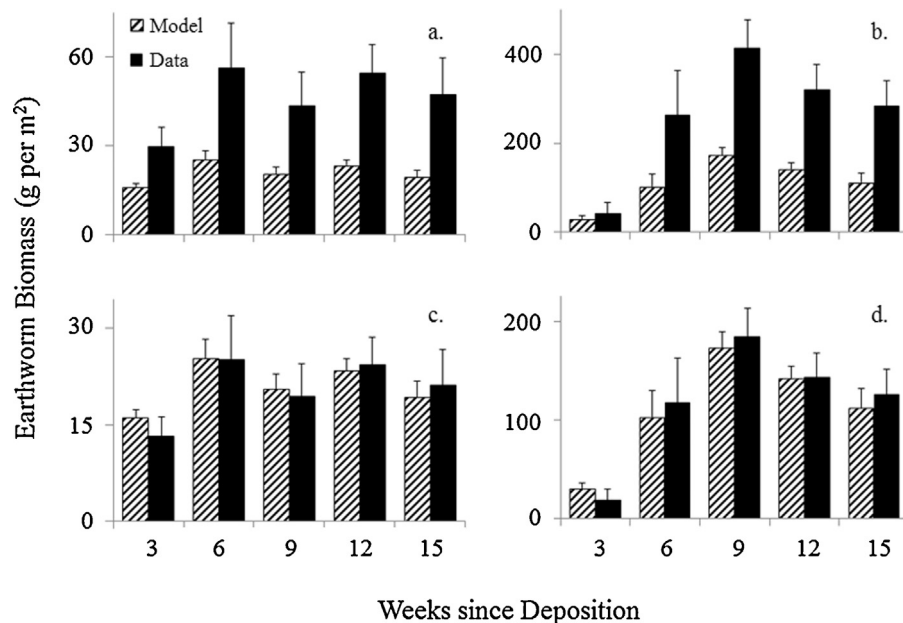
Fig. 14. Comparison between model simulation results (hatched bars, mean + SE from 10 simulations) and earthworm population biomass data (solid bars) recorded by Knight et al. (1992) for (a) a control plot under grazed pasture and (b) a cow manure deposition experiment and (c) and (d) taking 44.5% of the total recorded earthworm biomass to represent *Aporrectodea* caliginosa. Average R^2 values are (a) −6.47, (b) −0.91, (c) 0.85 and (d) 0.96.
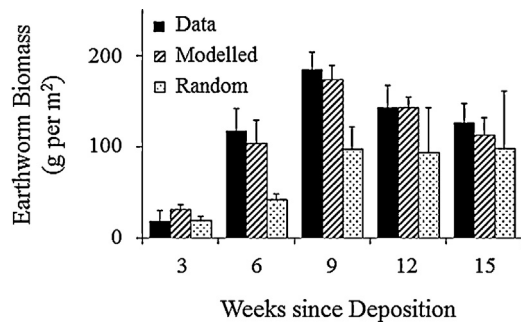
Fig. 15. Comparison between data from Knight et al. (1992); representing only *Aporrectodea* caliginosa (44.5% of the total population), for a cow manure deposition experiment (solid bars) and model simulation results when individual movement depends on soil water and food quality conditions (hatched bars: $R^2 = 0.96$) and when movement is random (dotted bars: $R^2 = -0.11$).

to adequately reproduce individual life history traits over a range of controlled conditions in the laboratory, supports our representation of individual physiology through energy budgets. In field trials, the model predicts the spatiotemporal distribution of *A. caliginosa* populations in the soil profile (Fig. 12), alongside seasonal patterns in the population stage-structure (Fig. 13). The model's ability to reproduce the patterns observed in Knight et al. (1992) (Fig. 14) illustrates how energy budget IBMs can be used to make reliable predictions of population-level exposure and responses to changing soil conditions, and thereby support informed land management decisions.

Variations in soil physio-chemical properties are known to alter the distribution and abundance of earthworms through the soil profile (Jiménez and Decaëns, 2000). Here, synthesis of knowledge on the effects of food availability and soil water potential on individual *A. caliginosa* movement account, to a large extent, for the vertical distribution of field populations in pasture (Fig. 12). In Gerard's (1967) field trial the effects of soil water potential on *A. caliginosa* movement are predominant in September (Figs. 7 and 12), when individuals move to deeper soil layers to avoid dry soil conditions. The models ability to replicate these patterns support its application to predict how environmental conditions at the soil surface affect the population's structure. However, modelling involves a trade-off between structural realism and complexity, and so when factors not captured here (e.g. pH, chemical applications, and compaction) are important in understanding
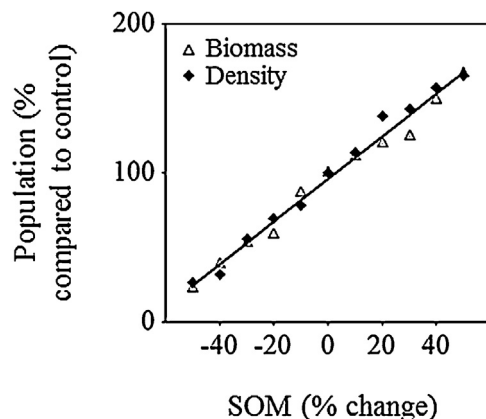
earthworm population dynamics, subsequent model development will be required.

The abundance of earthworms in pasture is closely related to organic matter inputs (e.g. Edwards and Bohlen, 1996; El-Duweini and Ghabbour, 1965). Hence, predicting realistic earthworm population dynamics in the field is dependent on accurate estimates of SOM (Fig. 16). Fraser et al. (1996) found earthworm populations to decline with time under arable cultivation and increase with time under pasture production in New Zealand, due to changes in the SOM content. A maximum population density and biomass of 950 individuals/m^2 and 185.7 g/m^2 were reported in plots used as pasture for 6–9 years. A relatively low SOM content of 3%, in comparison to the average 6% assumed for the Knight et al. (1992) field trial, was recorded. The high earthworm population abundances reported are likely due to a higher soil bulk density of 1.4 g/cm^3, which determines the amount of soil available as food. When our model is set up as in the simulation of Knight et al. (1992) but with a soil density of 1.4 g/cm^3 and SOM content of 3%, rather than 0.75–1.06 g/cm^3 and 6%, an average *A. caliginosa* population density and biomass of 636 ± 60 individuals/m^2 and 130 ± 13 g/m^2 were recorded respectively, which closely agrees with Fraser et al. (1996)'s observations. This suggests that the use of soil bulk density and SOM are useful proxies for food availability and quality for predicting earthworm population dynamics.

Many authors have reported the beneficial effects of animal waste applications to field populations of earthworms. Satchell (1955) reported a three-fold increase in earthworm population density when manure was applied to grassland, whilst Edwards and Lofty (1977) found manure applications to arable land resulted in earthworm abundances 14 times those of unmanipulated plots. At the individual level Barley (1959) found the provision of sheep manure at the soil surface increased *A. caliginosa* body weight by 111% after 40 days. The effects of providing individual *A. caliginosa* with high quality foods, such as manure, on their life cycle processes can be seen in our simulations of the laboratory experiments of Lofs-Holmin (1983) in Fig. 9(d) and Fig. 11(a). Comparing these growth and reproduction rates to those recorded when individuals were provided with plant material and soil mixtures (e.g. Fig. 9(a) and (b) and Fig. 10), highlights the direct link between the energy content of food and individual physiology.

Field population results in Fig. 14(b) and (d) clearly show how the quality of food resources affects population dynamics. The assumptions made about individual behaviour in the field, particularly movement, were essential to achieving good model fits to population data. Comparisons between model outputs for the cow manure experiment when movement was explicitly modelled as in Fig. 5, and when movement was assumed to be random in Fig. 15 suggest that the model adequately captures the factors driving the spatial distribution of earthworms. Furthermore, sensitivity analysis of SOM effects on the abundance of earthworm populations (Fig. 16) is in close agreement with observations by Hendrix et al. (1992); who found soil organic carbon (%) to describe earthworm abundance in conventional and no-tillage agroecosystems alongside grass meadows.

Earthworms are important soil engineers and so the ability to predict their abundance has wide application in ecology, conservation and land management. Our mechanistic model is able to predict the abundance and distribution of the dominant earthworm species in agro-ecosystems, *A. caliginosa*, in spatially heterogeneous soil profiles of undisturbed habitats. We hope the model will find many applications because of the vital role earthworms play in agricultural habitats (Hendrix and Edwards, 2004). For instance, earthworms are focal organisms for environmental risk assessment of pesticides in Europe (under Regulation (EC) No 1107/2009; see SANCO, 2002), and our model can help assess the population consequences of pesticides application

Fig. 16. Modelled responses of earthworm (*Aporrectodea caliginosa*) population biomass and density to 10% increments in SOM content of the pasture plot sampled by Knight et al. (1992) at 15 weeks, presented as a percentage change compared to the control population.

following inclusion of a toxicological submodel (e.g. Johnston et al., 2014). The spatial distribution of individuals in field populations is predicted by the model and so, if the fate of applied chemicals is known, then the exposure of individuals to pesticides can be calculated. For application to anecic earthworm species such as *Lumbricus terrestris*, additional model development may be required to capture more spatially explicit movement and feeding behaviour. Furthermore the model could be used to investigate population level effects of multiple stressors (e.g. tillage and pesticide applications), or variation of pesticide application timings, or climatic conditions. Considerations for modelling tillage in agroecosystems include mortality, redistribution of soil organic matter and the effects of compaction on the energy budgets and movement of individuals in the soil profile (e.g. Kretzschmar, 1990). For more widespread application, the model should also be tested in a variety of climatic conditions. The authors are currently working on applying the presented model to investigate the interactions between variable chemical, mechanical and environmental conditions. Also important is the ability to predict the local food supplies of animals that eat earthworms, including species of potential conservation concern such as wading birds (e.g. the lapwing *Vanellus vanellus*), and species sometimes regarded as pests such as flatworms (*Bipalium adventitium*) and foxes (*Vulpes vulpes*).

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2014.06.001.

References

Balesdent, J., Chenu, C., Balabane, M., 2000. Relationship of soil organic matter dynamics to physical protection and tillage. Soil Till. Res. 53, 215–230.

Bardgett, R.D., Leemans, D.K., Cook, R., Hobbs, P.J., 1997. Seasonality of the soil biota of grazed and ungrazed hill grasslands. Soil Biol. Biochem. 29, 1285–1294.

Barley, K.P., 1959. The influence of earthworms on soil fertility. II. Consuption of soil and organic matter by the earthworm *Allolobophora caliginosa* (Savigny). Aust. J. Agric. Res 10, 179–185.

Bayley, M., Overgaard, J., Høj, A.S., Malmendal, A., Nielsen, N.C., Holmstrup, M., Wang, T., 2010. Metabolic changes during estivation in the common earthworm *Aporrectodea caliginosa*. Physiol. Biochem. Zool. 83, 541–550.

Blakemore, R., 2002. Cosmopolitan Earthworms: An Eco-taxonomic Guide to the Peregrine Species of the World. VermEcology, Australia.

Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.-J., 2013. A review of earthworm impact on soil function and ecosystem services. Eur. J. Soil Sci. 64, 161–182.

Boström, U., 1987. Growth of earthworms (*Allolobophora caliginosa*) in soil mixed with either barley, lucerne or meadow fescue at various stages of decomposition. Pedobiologia 30, 311–321.

Boström, U., 1988. Growth and cocoon production by the earthworm *Aporrectodea caliginosa* in soil mixed with various plant materials. Pedobiologia 32, 77–80.

Boström, U., Lofs-Holmin, A., 1986. Growth of earthworms (*Allolobophora caliginosa*) fed shoots and roots of barley, meadow fescue and lucerne: studies in relation to particle size, protein, crude fiber content and toxicity. Pedobiologia 29, 1–12.

Boström, U., Lofs-Holmin, A., 1996. Annual population dynamics of earthworms and cocoon production by *Aporrectodea caliginosa* in a meadow fescue ley. Pedobiologia 40, 32–42.

Butenschoen, O., Marhan, S., Langel, R., Scheu, S., 2009. Carbon and nitrogen mobilisation by earthworms of different functional groups as affected by soil sand content. Pedobiologia 52, 263–272.

Celik, I., 2005. Land-use effects on organic matter and physical properties of soil in a southern Mediterranean highland of Turkey. Soil Till. Res. 83, 270–277.

Curry, J.P., 2004. Factors affecting the abundance of earthworms in soils. In: Edwards, C.A. (Ed.), Earthworm Ecology. CRC press, LLC, Boca Raton, FL, pp. 91–114.

DeAngelis, D.L., Mooij, W.M., 2005. Individual-based modelling of ecological and evolutionary processes. Annu. Rev. Ecol. Evol. Syst. 36, 147–168.

Doube, B., Styan, C., 1996. The response of *Aporrectodea rosea* and *Aporrectodea trapezoides* (Oligochaeta: Lumbricidae) to moisture gradients in three soil types in the laboratory. Biol. Fert. Soils 23, 166–172.

Edwards, C.A., Bohlen, P.J., 1996. Biology and Ecology of Earthworms, third ed. Chapman and Hall, London.

Edwards, C.A., Lofty, R., 1977. The Biology of Earthworms, second ed. Chapman and Hall, London.

El-Duweini, A.K., Ghabbour, S.I., 1965. Population density and biomass of earthworms in different types of Egyptian soils. J. Appl. Ecol. 2, 271–287.

Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C.M., Merz, M., O'Malley, M.A., Orzack, S.H., Weisberg, M., Wilkinson, D.J., Wolkenhauer, O., Benton, T.G., 2013. Do simple models lead to generality in ecology? Trends Ecol. Evol. 28, 578–583.

Eriksen-Hamel, N.S., Whalen, J.K., 2006. Growth rates of *Aporrectodea caliginosa* (Oligochaetae: Lumbricidae) as influenced by soil temperature and moisture in disturbed and undisturbed soil columns. Pedobiologia 50, 207–215.

Feller, C., Brown, G.C., Blanchart, E., Deleporte, P., Chernyanskii, S.S., 2003. Charles Darwin, earthworms and the natural sciences: various lessons from past to future. Agr. Ecosyst. Environ. 99, 29–49.

Forbes, J.C., Watson, R.D., 1992. Plants in Agriculture. Cambridge University Press, Cambridge, pp. 303.

Fraser, P.M., Williams, P.H., Haynes, R.J., 1996. Earthworm species, population size and biomass under different cropping systems across the Canterbury Plains, New Zealand. Appl. Soil Ecol. 3, 49–57.

Gerard, B.M., 1967. Factors affecting earthworms in pastures. J. Anim. Ecol. 36, 235–252.

Ghanbarian-Alavijeh, B., Liaghat, A., Guan-Hua, H., Van Genuchten, M. Th., 2010. Estimation of the van Genuchten soil water retention properties from soil textural data. Pedosphere 20, 456–465.

Granval, P., Aliaga, R., 1988. Analyse critique des connaissances sur le predateurs de lombriciens. Gibier Faune Sauvage 5, 71–94.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310, 987–991.

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. Ecol. Model. 221, 2760–2768.

Grimm, V., Railsback, S.F., 2012. Agent-Based and Individual-Based Modeling: A Practical Introduction. Princeton University Press, Princeton, NJ.

Gunadi, B., Blount, C., Edwards, C.A., 2002. The growth and fecundity of *Eisenia fetida* (Savigny) in cattle solids pre-composted for different periods. Pedobiologia 46, 15–23.

Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. Global Change Biol. 8, 345–360.

Harrod T.R., Hogan D.V., 2008. The soils of North Wyke and Rowden. Revised edition of Harrod T.R. (1981) Soils in Devon IV: Sheet SS61 (Chulmleigh). Soil Survey Rec No 70. http://www.rothamsted.ac.uk/sites/default/files/SoilsNWRowden.pdf

Hendrix, P.F., Mueller, B.R., Bruce, R.R., Langdale, G.W., Parmelee, R.W., 1992. Abundance and distribution of earthworms in relation to landscape factors in Georgia Piedmont, U.S.A. Soil Biol. Biochem. 24, 1357–1361.

Hendrix, P.F., Edwards, C.A., 2004. Earthworms in agroecosystems: research approaches, In: Edwards, C.A. (Ed.), Earthworm Ecology. second ed. St. Lucie Press, Boca Raton, pp. 287–295.

Hobbelen, P.H.F., van Gestel, C.A.M., 2007. Using dynamic energy budget modeling to predict the influence of temperature and food density on the effect of Cu on earthworm mediated litter consumption. Ecol. Model. 202, 373–384.

Holmstrup, M., Østergaard, I.K., Nielsen, A., Hansen, B., 1991. The relationship between temperature and cocoon incubation time for some Lumbricid earthworm species. Pedobiologia 35, 179–184.

Holmstrup, M., 2001. Sensitivity of life history parameters in the earthworm *Aporrectodea caliginosa* to small changes in soil water potential. Soil. Biol. Biochem. 33, 1217–1223.

Jager, T., Reinecke, S.A., Reinecke, A.J., 2006. Using process-based modelling to analyse earthworm life cycles. Soil. Biol. Biochem. 38, 1–6.

Jégou, D., Cluzeau, D., Wolf, H.J., Gandon, Y., Tréhen, P., 1998. Assessment of the burrow systems of *Lumbricus terrestris*, *Aporrectodea giardia*, and *Aporrectodea caliginosa* using X-ray computed tomography. Biol. Fert. Soils 26, 116–121.

Jenkinson D.S., 1969. Radiocarbon dating of soil organic matter. Rep. Rothamsted Exp. Stn. For 1968. Pt. 2:103-109.

Jiménez, J.J., Decaëns, T., 2000. Vertical distribution of earthworms in grassland soils of the Colombian Llanos. Biol. Fert. Soils 32, 463–473.

Johnston, A.S.A., Hodson, M.E., Thorbek, P., Alvarez, T., Sibly, R.M., 2014. An energy budget agent-based model of earthworm populations and its application to study the effect of pesticides. Ecol. Model. 280, 5–17.

Keith, A.M., Robinson, D.A., 2012. Earthworms as natural capital: ecosystem service providers in agricultural soils. Economology J. 11, 91–99.

Knight, D., Ellio, W., Anderson, J.M., Scholefield, D., 1992. The role of earthworms in managed permenant pastures in Devon, England. Soil Biol. Biochem. 24, 1511–1517.

Kretzschmar, A., 1990. Burrowing ability of the earthworm *Aporrectodea longa* limited by soil compaction and water potential. Biol. Fert. Soils 11, 48–51.

Lavelle, P., Spain, A.V., 2001. Soil Ecology. Kulwer Academic Publishers, The Netherlands.

Le Bayon, R.C., Moreau, S., Gascuel-Odoux, C., Binet, F., 2002. Annual variations in earthworm surface-casting activity and soil transport by water runoff under a temperate maize agroecosytem. Geoderma 106, 121–135.

Leij, F.J., Alves, W.J., van Genuchten, M.Th., Williams, R., 1996. The UNSODA unsaturated hydraulic database. EPA/600/R-96095. U.S. Environmental Protection Agency, Cincinnati, OH.

Lee, K.E., 1985. Earthworms: Their Ecology and Relationship with Soils and Land Use. Academic Press, Sydney.

Lofs-Holmin, A., 1983. Reproduction and growth of common arable land and pasture species of earthworms (Lumbricidae) in laboratory cultures. Swedish J. Agr Res. 13, 31–37.

Loustau D., 1984. Morphologie et fonctionnement biodynamique de quelques humus hydromophes de l'est de la France, Thèse de 3ᵉ Cycle, Université Nancy I. (In: Lavelle, P., Spain, A.V. (Eds.), Soil Ecology, 2001, Kulwer Academic Publishers, The Netherlands) Table 1.8, p. 37.

Lowe, C.N., Butt, K.R., 2003. Influence of food particle size on inter- and intra-specific interactions of *Allolobophora chlorotica* (Savigny) and *Lumbricus terrestris.* Pedobiologia 47, 574–577.

McNaughton, S.J., Banyikwa, F.F., McNaughton, M.M., 1998. Root biomass and productivity in a grazing ecosystem: the Serengeti. Ecology 79, 587–592.

Meehan, T.D., 2006. Mass and temperature dependence of metabolic rate in litter and soil invertebrates. Physiol. Biochem. Zool. 79, 878–884.

Paoletti, M.G., 1999. The role of earthworms for assessments of sustainability and as bioindicators. Agr. Ecosyst. Environ. 74, 137–155.

Pedersen, M.B., Bjerre, A., 1991. The relationship between mass of newly hatched individuals and cocoon mass in lumbricid earthworms. Pedobiologia 35, 35–39.

Perez-Losada, M., Ricoy, M., Marshall, J.C., Dominguez, J., 2009. Phylogenetic assessment of the earthworm *Aporrectodea caliginosa* species complex (Oligochaeta: Lumbricidae) based on mitochondrial and nuclear DNA sequences. Mol. Phylogenet. Evol. 52, 293–302.

Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Riley, H., Pommeresche, R., Eltun, R., Hansen, S., Korsaeth, A., 2008. Soil structure, organic matter and earthworm activity in a comparison of cropping systems with contrasting tillage, rotations, fertilizer levels and manure use. Agr. Ecosyst. Environ. 124, 275–284.

SANCO. 2002. Guidance Document on Terrestrial Ecotoxicology under Council Directive 91/414/EEC. Santé des Consommateurs. European Commission, Health and Consumer Protection Directorate-General, SANCO/10329/2002 rev 2 (final). Brussels, Belgium. Available at: http://ec.europa.eu/food/plant/protection/evaluation/guidance/wrkdoc09_en.pdf.

Satchell, J.E., 1955. Some aspects of earthworm ecology. In: Kevan, D.M. (Ed.), Soil Zoology. Butterworths, London, pp. 180–203.

Schneider, A.-K., Schröder, B., 2012. Perspectives in modelling earthworm dynamics and their feedbacks with abiotic soil properties. Appl. Soil Ecol. 58, 29–36.

Sibly, R.M., Calow, P., 1986. Physiological Ecology of Animals. Blackwell Scientific Publications, Oxford.

Sibly, R.M., Grimm, V., Martin, B.T., Johnston, A.S.A., Kułakowska, K., Topping, C.J., Calow, P., Nabe-Nielsen, J., Thorbek, P., DeAngelis, D.L., 2013. Representing the acquisition and use of energy by individuals in agent-based models of animal populations. Methods Ecol. Evol. 4, 151–161.

Sinclair, A.R.E., 1989. Population regulation in animals. In: Cherrett, J.M. (Ed.), Ecological Concepts. Blackwell Scientific Publications, Oxford, pp. 197–241.

Springett, J.A., Gray, R.A.J., 1992. Effect of repeated low doses of biocides on the earthworm *Aporrectodea caliginosa* in laboratory culture. Soil. Biol. Biochem. 24, 1739–1744.

Spurgeon, D.J., Svendsen, C., Rimmer, V.R., Hopkin, S.P., Weeks, J.M., 2000. Relative sensitivity of life-cycle and biomarker responses in four earthworm species exposed to zinc. Environ. Toxicol. Chem. 19, 1800–1808.

Solomon, M.E., 1949. The natural control of animal populations. J. Anim. Ecol. 18, 1–35.

Taylor, A.R., Taylor, A.F.S., 2014. Assessing daily egestion rates in earthworms: using fungal spores as a natural soil marker to estimate gut transit time. Biol. Fert. Soils 50, 179–183.

van Genuchten, M.Th., 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. Soil Sci. Soc. Am. J. 44, 892–898.

Wang, L., Shahbazi, A., Hanna, M.A., 2011. Characterisation of corn stover, distiller grains and cattle manure for thermochemical conversion. Biomass Bioenerg 35, 171–178.

Wilensky, U., 1999. NetLogo. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston, IL. http://ccl.northwestern.edu/netlogo/.