Darwin was right, in any given field, the spatial variability of earthworm communities in pastures isn't driven by measurable soil properties.

Short title: Spatial variability of earthworm communities in pastures isn't driven by measurable soil properties

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Abstract

Abundance and distribution of earthworms in agricultural fields is frequently proposed as a measure of soil quality assuming that observed patterns of abundance are in response to improved or degraded environmental conditions. However, it is not clear that earthworm abundances can be directly related to their edaphic environment, as noted in Darwin's final publication, perhaps limiting or restricting their value as indicators of ecological quality in any given field.

We present results from a spatially explicit intensive survey of pastures within United Kingdom farms, looking for the main drivers of earthworm density at a range of scales. When describing spatial variability of earthworm abundance within any given field, the best predictor was earthworm abundance itself within 20 – 30 m of the sampling point; there were no consistent environmental correlates with earthworm numbers, suggesting that biological factors (e.g. colonisation rate, competition, predation, parasitism) drive or at least significantly modify earthworm distributions at this spatial level. However, at the national scale, earthworm abundance is well predicted by soil nitrate levels, density, temperature and moisture content, albeit not in a simple linear fashion. This suggests that although land can be managed at the farm scale to promote earthworm abundance and the resulting soil processes that deliver ecosystem services, within a field, earthworm distributions will remain patchy. The divergence in the interpretative value of earthworm abundance as an ecological indicator is a function of spatial scale, corresponding to species specific biological factors as well as a response to environmental pressures. Species abundance can effectively be used as ecological indicators, even if, at first, distributions seem random. However, care must be exercised, in the sampling design for the indicator species, if its abundance is to be used as a proxy for environmental quality at a particular scale (e.g. a management scale such as field scale).

Keywords: earthworms; soil quality; indicators; ecosystem services; geostatistics; population distributions

Introduction

The study of the spatial variation in a species abundance has often resulted in significant insights into their biology and ecology, e.g. [1]. This has not been the case in pasture earthworms, where the reasons for the spatial patterns of species abundance observed within any given field still remain unclear. The apparent random distribution of earthworms at the field scale has been the object of study over many years. Charles Darwin's final publication was a detailed study of earthworms [2]. Among other insights he commented that "even on the same field worms are much more frequent in some places than in others, without any visible difference in the nature of the soil". This is important because it is widely agreed that earthworms, as ecosystem engineers, are fundamental in driving a range of soil processes that give rise to many ecosystem services, particularly in agriculture, e.g. [3], [4], [5]. Thus, understanding the distribution of earthworms may allow us to manage the services that they provide.

It is because earthworms drive soil processes that contribute to ecosystem services that it is frequently suggested that earthworms are good indicators of a healthy soil; earthworm counts feature in a number of schemes for assessing the ecological quality of the soil and farming environment, e.g. [6], [7], [8], [9], [10], [11], [12]. In field surveys and controlled laboratory experiments earthworms are known to respond to a variety of key environmental drivers such as pH, temperature, soil texture and soil density e.g. [13] and the spatial distribution of earthworms must in some way represent an integrated response to these, and potentially other, environmental variables. This raises the prospect that spatially resolved measures of earthworm diversity and abundance may provide a good approximation both to soil health / quality and also the ecosystem services delivered by them.

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78 A variety of studies investigating controls on the distributions of earthworms in fields have
79 reached similar conclusions to those of Darwin. In studies using variograms, Spatial Analysis
80 by Distance Indices (SADIE) methods and other statistical methods involving correlations
81 and comparisons of sampling sites and their physical and chemical properties, earthworm
82 distribution has been found to be spatially correlated but also patchy in both arable and
83 pasture systems with typical patches of earthworms / spatial dependence of earthworm
84 numbers on the scale of 20 – 60 m (Table S1, Supporting Information). The evidence from
85 these studies is that these patches are either unrelated to measured soil properties or
86 correlate with particular site specific soil properties with no consistency across the studies.
87 This raises concerns about the robustness of using earthworm abundance as an ecological
88 indicator of soil quality.

89

90 The above studies were carried out at the scale of thousands to tens of thousands of square
91 metres on different land uses and often in different climatic zones on different continents. At
92 these scales patchiness can be generated either by: 1) earthworms moving to patches of soil
93 of “good” quality, (which would support their use as quality indicators on the field scale); 2)
94 self-regulation with a limiting resource decreasing in response to increased earthworm
95 density leading to a decrease in survival / fecundity tied to low mobility such that earthworms
96 are unable to migrate sufficiently rapidly to resource-rich areas when limiting resources fall
97 below a critical level [14], 3) reproduction being more rapid than dispersion [15]; 4) predation
98 and 5) parasitism. All but the first of these causes would suggest that earthworms are not
99 necessarily a good indicator of soil quality. At a larger landscape scale, studies suggest that
100 earthworm numbers increase with decreasing management intensity across different land
101 uses (e.g. arable < pasture < woodland, [16]; pasture < young spruce plantation < old beech
102 coppice, [17] and that changes happen relatively rapidly, within three years [16]. Schmidt
103 and Briones’ recent meta-analysis indicates that most studies on arable fields show that a

reduction in tillage of arable fields leads to an increase in earthworm abundance [18].
However, studies on the effects of varying levels of intensification within other land uses are
still lacking.

The existing work on controls on earthworm distributions suggest to us that, although
earthworms are undoubtedly integrators of soil properties and responsible for soil processes
that give rise to ecosystem services, their use as soil quality indicators is still far from
straightforward. To address this issue, we conducted a spatially nested survey of earthworm
abundances in pasture fields managed at varying levels of intensity across Britain, at farms
located across the dominant national climatological gradients (temperature and rainfall). We
used our data to test the hypotheses that at a field scale the spatial variation of earthworm
abundance is random whilst at a national scale the variation in earthworm abundance is
driven by climate.

Methods

Site locations

We surveyed four fields at each of seven farms across Britain (Fig. 1). The locations, and the
four pasture fields (F1 to F4) sampled at each farm were chosen to represent a wide range
of soil properties, land management practices and climatic conditions (Table S2, Supporting
Information). For each farm and sample location we obtained geology and predominant soil
groups from the Soil surveys of England and Wales [19], and of Scotland, and aspect,
elevation and slope from a digital elevation map [20]. Within each farm we sampled four
fields covering a gradient of land management intensity, from unimproved rough grazing to
improved pasture; fields had been in pasture management for at least three years, and the
majority for far longer (Table S2, Supporting Information). Farmers were asked to rank the
four sampled fields in terms of management intensity from “lowest” to “low to medium” to

“medium to high” to “highest”. These classes were determined by conversation with the land owner / farmer and are relative measures within each farm but not between farms. Within each field, we characterised the spatial distribution of earthworms by an intensive spatial sampling scheme where we measured earthworm abundances and soil properties.

Fig 1. Sampling locations in the UK and their relationship to average annual rainfall and average annual temperature, illustrating the temperature and soil moisture gradient used to help determine the farms sampled. Sampling was carried out at SRUC, Craibstone Aberdeen (CBS), Torr Organic, Dumfries (TOR), Skeffling, Yorkshire (SKF), Loddington, Leicester (LOD), Manor Farm, Somerset (MAN), Elm Farm Berkshire (ELM) and Swanage, Dorset (DST).

Earthworm sampling and identification

Sampling was carried out 7th October – 15th December, 2013. We chose these dates as earthworm abundance is less likely to be detrimentally affected by seasonal weather conditions in late autumn; in the hotter, drier months earthworms either die or aestivate e.g. [21] which would hinder investigating controls on their distribution. We sampled earthworms in pits and preserved them in 80% industrial methylated spirits. Adult individuals (with a clitellum) were identified (by DTJ and VJB) to both species level following [22] and [23] and functional group. Juvenile individuals were grouped into functional group (endogeic, epigeic or anecic species) based on colour, size and external morphology [24]. An average of 18.9 ± 1.4 (std. dev, $n = 28$) pits were sampled per field with the maximum (and target) number of pits being 20 and the minimum 16. When fewer than 20 pits were sampled this was due to time constraints; typically we had three days sampling time at each farm in an attempt to ensure all the samples collected from a single farm were collected under similar environmental conditions. Within each field the pits were positioned using a random number

generator that ensured the distances separating any one pit from every other pit in the same field could vary from a few meters to > 100 m depending on the overall size of the field. The sampling sites were allocated randomly to ensure no spatial bias and to ensure that sufficient separation distance was sampled for an effective estimation of the model variogram (see below). Pits falling within 5 m of the field boundary were reassigned a new random position. The geolocation of each pit was recorded with a Garmin eTrex 10 GPS. At each site temperature at 5 cm and 10 cm depth was measured with a soil thermometer and averaged. Four moisture readings were made using a Delta-T Moisture metre (Delta-T Devices, Cambridge, England) with attached Theta probe and then averaged. Each soil pit had a surface area of 20 cm x 20 cm. The earthworms were sampled using the well-established method of hand sorting and mustard extraction, e.g. [25]. The soil monolith (pit) was dug out with a spade to a depth of 10 cm and placed on a plastic sheet. Immediately upon removing the soil 2 litres of mustard solution (12g Colman's mustard powder in 1 L of water) were poured into the soil pit. The extracted soil and plant roots were searched by hand and all earthworms collected. Any earthworms emerging from the bottom of the pit during the 15 minutes following the application of the mustard solution were collected separately. Vegetation cover was assessed for several broad functional type groups around the vicinity of the pits using the Daubenmire counting method [26].

Soil sampling and analysis

Two soil samples, approximately 50 g each, were collected from each soil pit during the earthworm sampling, one was used for bulk density and subsequent measurements on dry soil, the other was used for measurements that required field moist soil. We measured a wide range of explanatory variables from each pit. Soil temperature was measured in the field at a depth of 5 and 10 cm in each soil pit. Field moist subsamples of each soil sample were stored at 4 °C and analysed for microbial activity using fluorescein diacetate hydrolysis within one week of sampling [27]. Soil density samples were oven dried and weighed to

calculate dry bulk density and soil moisture content. The soil samples were then sieved to < 2mm and analysed for particle size distribution using a Malvern Mastersizer 2000. pH was measured in water using a 10g:25mL ratio [28]. Total carbon and total nitrogen content (%C and %N) of soil was measured by combustion using a Vario MacroElemental (CN) Analyser. Extractable nitrate (nitrate-N) and ammonia (ammonia-N) by 1M KCl and extractable phosphate (phosphate-P) by 0.5M NaHCO₃ were analysed by autoanalyser [29]. Bulk composition was determined by aqua regia digest [30] and analysis by inductively coupled plasma – optical emission spectrometry (ICP-OES). Detection limits were calculated for solution analyses by repeated measurements of procedural blanks and precision (which was generally > 95%) by repeated measurements of selected solutions (Tables S3 and S4, Supporting Information). For the aqua regia digests recoveries were $\geq$ 95% for analysis of the San Joaquin NIST SRM 2709a.

Statistical analysis

Our approach comprises an initial set of national (across all farms) models using Bayesian Belief Networks [31] to determine which are the key factors in determining the total earthworm abundance. We subsequently modelled the species responses to these key factors using generalised linear models. At the farm scale, across fields, linear models of coregionalization (LMCR) [32] were then used to describe both the spatial variation in total abundances and their possible spatial co-dependency to the measured soil properties at the field to farm scale.

Bayesian Belief Networks (BBN) are a set of probabilistic influence networks that are increasingly being used in ecological studies, as they are well-suited to complex data sets and incomplete knowledge, which are common to ecological systems, [31], [33]. The BBN modelling was conducted in Netica [34]. The influence network for the BBN included data measured at each sample pit location (soil properties, vegetation cover), field management

intensity, and landscape attributes (soil type, geology, aspect and slope) with the total earthworm abundances as the response variable. Conditional probabilities describe the relationships between the sample pit location, farm and landscape level factors and the earthworm abundances. These were obtained through processing individual cases, where each case represented a point observation of abundance and factor values found at a given location. All nodes in the BBN models were assigned five states, based on round values and distributions for predictors, and equal intervals for the abundance predictions. The conditional probabilities produced for the five levels of abundance were visualised as a heat map using R version 3.2.2 [35]. The resultant BBN structure is shown in the Supporting Information (Figure S1, Supporting Information).

For the species response models we undertook curve fitting for individual earthworm species using generalised linear modelling on the entire dataset (using CANOCO 5 [36], which has a generalised linear model curve fitting module). We fitted null, linear and quadratic models and calculated AIC for each model for each species and chose the model in each case that had the lowest AIC. A poisson error distribution was used for each species-level model with a log link function, as was appropriate for count data.

Linear Models of Coregionalisation: The sampling design at the farm level was such that spatial variation of earthworm abundance can be described using variograms, and its spatial covariation with likely drivers by cross variograms. These are models which describe spatial patterns, are used for predictions at unsampled locations (generating maps), and assess the uncertainty associated with these predictions. The variogram represents a measure of dissimilarity as a function of distance between points, and the cross variogram a measure of the joint variability between the earthworm abundances and a particular soil property. From the variogram model we can obtain a set of parameters. The nugget variance (c_0), is the point at which the model crosses the intercept and represents the variation observed in the data that is either not spatially correlated or is correlated but at a finer distance than that sampled in this study (5 m). The sill variance (c_1) is the value of semivariance at which the

variogram model levels off and represents the total observed variation in the dataset under consideration. The ratio of nugget to sill variance ($c_0/(c_0 + c_1)$) expresses the fraction of variation which can be ascribed to spatial processes. Here the larger the ratio, the more of the observed variation can be described as spatially autocorrelated. If the variable under observation approximates a spatially random process, then this ratio would approach 0. All variogram and cross variogram models were fit individually at each farm using the gstat package [37] in R version 3.2.2 [35].

Results and Discussion

Observed earthworm abundances

Our full data set is provided in the Supporting Information (Table S5, Supporting Information). Across all the sample sites, juvenile earthworms were more abundant than adults of any one species. Of the three ecotypes of earthworm, endogeics were more abundant than epigeics which were in turn more abundant than anecic species (Fig. 2a).

Fig 2. Abundances of earthworms by (a) species (total numbers). Total numbers = 13298 earthworms (endogeics = 77%, epigeics = 17%, anecics = 6%).* = continues to 6126 individuals; open bars indicates endogeic species, closed bars epigeics and checked bars anecics and (b) sampling site (mean abundance $m^{-2} \pm$ standard error, $n = 15 - 20$). F1 to F4 for each sampling site are fields 1 through 4 and for each farm are arranged in order from lowest management intensity on the left to highest intensity on the right. The intensity levels are relative and not necessarily comparable between farms.

There is a paucity of systematic distribution data for earthworm species in the UK [38]. However, our data are typical of other pasture surveys of earthworms in the UK and similar

climatic regions. As with other studies populations are dominated by juvenile and particularly juvenile endogeic earthworms e.g. [39], [40], [41], [42], [43], while among adult populations, endogeic earthworms, notably, *Allolobophora chlorotica* and *Apporectodea caliginosa* often dominate with *Lumbricus rubellus* and / or *Lumbricus castaneus* being the most abundant epigeic species; *Aporrectodea longa* and *L. terrestris* are the only two UK anecic species e.g. [40], [41], [42], [43], [44], [45]. All the farm sites apart from Manor Farm had significant differences in earthworm numbers between fields (ANOVA on Ranks for BS, SKF, LOD, MAN, ELM, DST; ANOVA for TOR; $p \leq 0.05$) but using this simple linear modelling approach, we found no consistent pattern between relative level of management intensity and earthworm numbers. The relationship between earthworm numbers, management intensity and field properties was therefore further investigated using Bayesian Belief Networks.

National and farm level drivers of earthworm distribution.

At a national scale, the Bayesian belief network developed for the entire data set, was able to describe about 57 % of the observed variation in abundances (absolute error of 19.72, and root mean square error of 26.12). Given the scale and nature of the ecological dataset, these results are not unreasonable. For this model, the overall most influential variables were found to be Field temperature, Soil bulk density, Moisture and Nitrate-N followed by Soil type and Underlying geology. The main analytically measured continuous variables were % clay, % carbon, % nitrogen, Soil bulk density, Temperature at 5 and 10 cm, Soil moisture and Particle distribution < 2 μ m fraction. The sensitivity of the BBN is presented in Fig 3, and Table 1. There are clear climatic effects in the abundance data, with field moisture and temperature as key drivers. Management intensity, as it was conditional on a particular farm, was modelled as a child node of farm, and therefore, at this level, had little influence on abundances.

287

288 Fig 3. Panels show the sensitivity of the overall Bayesian belief network to main continuous
 289 variables used to predict values of total earthworm counts across all 7 farms. Values of the
 290 continuous variables were split into 5 bins (where Bin 1 has the lowest values and 5 the
 291 highest) as defined for this dataset. For details of bin ranges see Table 1; the more intense
 292 the colour the more likely this value is for this number of earthworms. For example, at a
 293 depth of 5 cm, if temperature is in the range 12 – 16 °C then earthworm abundance is most
 294 likely to be low (0 – 13 individuals), if the observed temperature is in the range 9.1 – 10.8 °C,
 295 then the earthworm abundance will probably be in the range of 25 - 34 individuals, and at an
 296 observed temperature range 6.9 – 9.1 °C then the abundance is most likely to be high (34 –
 297 110 individuals), at a farm scale. Soil properties are shown in rank order of importance for
 298 predicting earthworm counts.

299

300 Table 1. The ranges of soil properties associated with each of the 5 bins used in the BBN. Bins 1–5 correspond to the positions of the boxes
 301 indicated in Fig 3. The net had an absolute error of 19.72, and root mean square error of 26.12.

Total number of earthworms	% clay	% carbon	NO ₃ -N	% nitrogen	Density	Temperature @ 10 cm	Temperature @ 5 cm	Soil moisture content	State
0 – 13	0 – 0.04	1.5 – 3.4	-0.3 – 0.5	0.15 – 0.3	0.23 – 0.69	4.7 – 6.9	4.6 – 6.9	17 – 41	1
13 – 19	0.04 – 0.5	3.4 – 4.6	0.5 – 1.1	0.3 – 0.45	0.69 - 0.83	6.9 – 9.2	6.9 – 9.1	41 – 47	2
19 – 25	0.5 – 0.7	4.6 – 6.3	1.1 – 2.9	0.45 – 0.56	0.83 – 0.92	9.2 – 10.9	9.1 – 10.8	47 – 54	3
25 – 34	0.7 – 1.1	6.3 – 9	2.9 – 6	0.56 – 0.8	0.92 – 1.1	10.9 – 11.9	10.8 – 12	54 – 61	4
34 - 110	1.1 – 7.7	9 - 42	6 - 105	0.8 – 2.2	1.1 – 1.7	11.9 - 20	12 - 16	61 - 96	5

When species level response curves were considered in the full dataset by simply fitting quadratic equations to soil parameters (Table S5), we found that bulk density and nitrate level in particular are significantly related to earthworm numbers across a range of species (Fig. 4). However, a majority of the plots show that a unimodal curve was the best fit response to the environmental gradients. Nitrate-N, for example has snarrow optima for *Allobophora chlorotica*, *Aporrectodea caliginosa* and *Aporrectodea longa*, showing that they are less abundant at low and high nitrate concentrations. Bulk density shows a much flatter response for most species while still typically showing optimal values. The response to soil moisture is more idiosyncratic, because of the presence of *Aporrectodea limicola*, a species often found in waterlogged soils [23] and *Aporrectodea caliginosa*, which is tolerant of flooding [46]. For bulk density, nitrate-N, pH and soil moisture content *A. chlorotica* show the narrowest peaks, suggesting that this species has more marked preferences, and possibly sensitivities, to these soil properties. Both bulk density and nitrate were highlighted in the BBN of the entire dataset as exerting important controls on earthworm numbers.

Fig 4. General linear model fits between measured soil parameters and numbers of earthworms at a species level across all sampling sites. a) bulk density, b) nitrate-N, c) pH, d) soil moisture content (SM%). Details of the models including uncertainties are given in Table S6. Only species where numbers vary with the particular soil parameter are shown. (Al-chl = *Allobophora chlorotica*, A pros = *Aporrectodea rosea*, L-rub = *Lumbricus rubellus*, L-cas = *Lumbricus castaneus*, Ap-lim = *Aporrectodea limicola*, Ap-cal = *Aporrectodea caliginosa*, Ap-lon = *Aporrectodea longa*, M-mul = *Murchieona muldall*, L-fes = *Lumbricus festivus*, L-ter = *Lumbricus terrestris*).

Field level spatial patterns of earthworm abundances

We were able to determine spatial autocorrelation, and fit authorised variogram models to 5 of the 7 farms, with DST and MAN exhibiting only pure nugget variation (Fig. 5, Table 4). Of these five farms, SKF exhibited the longest range at 114 m, with the others ranging between 19 and 30 m. This suggest that for the majority of the farms (with the exception of SKF), earthworm populations exhibited either short range spatial autocorrelation or no spatial autocorrelation at all. Where autocorrelation was observed, the variance component which was spatially autocorrelated was generally substantial (from an estimated 37% to 91% of the observed variation in earthworm abundance). These variogram results are in general agreement with other studies across a range of land uses, climates and species (Table S1), and it is therefore clear that in any given field, the spatial variability in earthworm abundances will be short range and patchy in nature, i.e. earthworm abundance will be high in patches of c. 30 – 100 m width, and those patches appear to be randomly distributed within fields.

For those farms where we observed spatial autocorrelation in earthworm abundances, we subsequently fitted LMCRs but observed no spatial covariation with the earthworm abundances in any of the soil properties (e.g. soil organic carbon, pH, density, nitrate-N) at the distance intervals for which earthworms show spatial autocorrelation. This would indicate that none of these properties were key drivers of the abundance of the earthworms at the farm scale despite our species response curves (Fig. 4) and the results of the full dataset BBNs (Fig. 3, Table 2) and the well-established literature concerning the physico-chemical factors that earthworms are sensitive to (see the many references in [13]). Since our results show that soil properties of themselves do not control the spatial variability of earthworm communities they suggest that instead biological and ecological factors, such as rates of reproduction and migration, predation and parasitism, as proposed by Satchell [15], are the driving factors for short scale variation in abundance in a way that then confounds the short range effect of edaphic factors.

Table 4. Variogram parameters for the seven sites. Range reflects the extent to which the spatial autocorrelation extends, c_i is the sill variance, and c_o is the nugget variance, $c_i/(c_i+c_o)$ represents the variance component that is spatially autocorrelated. No spatial autocorrelation was found for DST and MAN.

Site	Range (m)	c_i	c_o	$c_i/(c_i+c_o)$
LOD	27	230	22	91%
SKF	114	33..7	22	61%
DST	-	-	-	-
TOR	23	47	80	37%
CBS	19	124	20	86%
ELM	30	103	40	72%
MAN	-	-	-	-

Fig 5. Within field and farm distribution of earthworms for three representative sites, a) CBS, b) DST and c) SKF. Contoured colours represent the interpolated (predicted) values of total earthworm counts, coloured dots represent the observed counts within each sampling point. Inserts show the variograms used to generate the interpolated surfaces, with the separation distances on the x-axis, and semivariance (earthworm counts, log for DST) on the y-axis.

Conclusions

Although Darwin's insights were based on sparse quantitative data it seems that his essential intuition was correct: at the field scale, the spatial variation in earthworm abundance is controlled or at least heavily influenced by some factor other than soil properties, most likely biotic (possibly reproduction, migration rates, competition and predation), giving the appearance of a spatially random distribution of ~30 - ~100 m patches of high earthworm abundance. This suggests that the use of individual based models, that incorporate biological behaviour e.g. [47], [48], [49], [50] are likely to be a better route for understanding the distribution of earthworms in fields than measures of soil properties. For most fields, earthworms are spatially correlated at

short distances and a knowledge of their distribution does not provide spatially resolved information about factors such as soil pH, density, nitrate content and organic matter content. Thus, individual samples are unreliable indicators of earthworm populations and other soil properties. Further, the level of variability in earthworm numbers between sampling sites within a field suggests that for any monitoring scheme that requires a reliable estimate of earthworm numbers, whether earthworm numbers are of direct interest or are being used as a proxy for other specific soil properties such as organic matter content or more diffuse measures such as soil health / quality, multiple samples are required because these properties show significant within-field variation. A recent national level survey aimed at using earthworms to assess soil health of arable fields used a sampling density of 10 pits per field with a total survey time of 60 minutes per field [12]. The survey achieved high levels of participation and cost-effectiveness and supported the accepted wisdom that tillage has a negative effect on earthworm numbers. It was suggested that numbers of pits could be reduced to 5 per field with little decrease in the quality of the results. In our study, if we assume comparable threshold qualitative values as described by Stroud [12], then in order to determine the difference between good and poor quality soil in pasture fields on the basis of earthworm abundances, based on a power analysis of our data, we would recommend about 8-10 pits per field.

At a national scale, earthworm abundance appears to be related to both soil temperature and moisture reflecting natural gradients but also soil nitrate levels and soil density. In broad terms at the national level more intensely managed farms will have higher N inputs leading to higher levels of nitrate N e.g. [51], [52], [53], [54]. Similarly, increasing intensity of farm management is likely to be linked to more on-field traffic with consequent compaction and density increases. Our definition of management intensity at the farm level is qualitative and based on discussion with the resident farmers. Thus, our ranking of relative intensity is not directly comparable between farms. However, the lack of a linear relationship between earthworm numbers and intensity at each farm and the unimodal species response curves for soil density and soil nitrate-

N suggests that there is a role for management interventions to maximise earthworm populations and, if earthworm populations are an indicator of soil quality, that a certain level of management intensification can improve soil quality.

If we want to manage earthworm populations to help drive the soil processes that deliver ecosystem services our findings suggest that management and observation will have to be at the broader farm scale, rather than the narrower within-field scale.

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Supporting information captions

Table S1. Summary of selected previous studies that investigated the spatial distribution of earthworms.

Table S2. Land use history of sampling sites according to land owners. Numbers indicate minimum time that field has been used as pasture. “Never” indicates no use other than pasture.

Table S3. Detection limits for soil analyses

Table S4. Repeat ICP-OES analyses for precision

Table S5: Earthworm and soil data set – separate Excel file

Table S6: Summary of General linear model fits to species data – separate Excel file

Fig. S1. Typical BBN structure for the entire dataset.

Mean abundance of earthworms (+/- s. d.) per m²

a)

Farm CBS

Total Earthworm Counts

b)

Total Numbers of Earthworms

0 30 60 120 Meters

c)

Earthworm counts

TOTall	<2µm	Carbon%	NitrateN	Nitrogen%	Soil Bulk Density	Temp10cm	Temp5cm	Soil moisture	State
0 - 13	0 - 0.04	1.5 - 3.4	-0.3 - 0.5	0.15 - 0.3	0.23 - 0.69	4.7 - 6.9	4.6 - 6.9	17 - 41	1
13 - 19	0.04 - 0.5	3.4 - 4.6	0.5 - 1.1	0.3 - 0.45	0.69 - 0.83	6.9 - 9.2	6.9 - 9.1	41 - 47	2
19 - 25	0.5 - 0.7	4.6 - 6.3	1.1 - 2.9	0.45 - 0.56	0.83 - 0.92	9.2 - 10.9	9.1 - 10.8	47 - 54	3
25 - 34	0.7 - 1.1	6.3 - 9	2.9 - 6	0.56 - 0.8	0.92 - 1.1	10.9 - 11.9	10.8 - 12	54 - 61	4
34 - 110	1.1 - 7.7	9 - 42	6 - 105	0.8 - 2.2	1.1 - 1.7	11.9 - 20	12 - 16	61 - 96	5

Figure

Figure

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