Within-field spatial distribution of earthworm populations related to species interactions and soil apparent electrical conductivity

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ABSTRACT

Within-field spatial distribution of ecosystem engineers such as earthworms determine the spatial patterns of important ecosystem processes at the field scale. But the driving factors that shape the within-field spatial variability of earthworm populations remain largely unclear. The aim of this study was to describe the earthworm distribution patterns in a tilled arable field and to explain earthworm spatial variability as a function of biotic interactions within populations and of abiotic soil heterogeneity measured as the soil apparent electrical conductivity (EC_a).

Earthworms were sampled at 100 locations within an area of (105×75) m^2 in a harvested wheat field on a loess soil in central Belgium. The soil EC_a was measured using a mobile electromagnetic induction (EMI) sensor as a proxy for soil textural composition. Maps of earthworm density and soil EC_a were produced by variogram modeling and ordinary kriging. Two approaches were followed in the data analysis: (i) a pixel-by-pixel comparison of the spatial patterns based on categorical maps derived from a fuzzy k-means clustering, and (ii) causal modeling based on point-by-point Mantel tests.

The endogeic species Aporrectodea caliginosa and A. rosea inhabited similarly sized and overlapping patches, which were neither related to the spatial occurrence of the deep-burrowing species Lumbricus terrestris and A. longa, nor to the measured soil EC_a variability. Endogeic adults and juveniles lived closely associated in the same spatial clusters. The segregated field distributions of both deep-burrowing species were largely determined by the subsoil textural properties (as measured by EC_a) and not by competition. A. longa individuals lived in field areas with high ECav values (related to relatively higher clay content) while L. terrestris juveniles occupied regions with low ECav values. Anecic juveniles were found in larger and spatially differing clusters than adults, suggesting the dispersal of juveniles from parental clusters into neighbouring areas. L. terrestris adults were spatially organized in distinct patches of ∼15 m diameter and it is hypothesized that the particular mating behaviour of this species requires such intimate distributions.

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The rapid, easy and non-invasive geo-referenced soil characterization by means of EMI-based measurements proved to be a useful tool for determining and understanding the within-field spatial distributions of earthworms but requires further testing in a variety of (agro-)ecosystems.

1. Introduction

Ecosystem engineers such as earthworms play a major role in the regulation of ecosystem processes and, ultimately, in the services delivered by the ecosystem (Lavelle et al., 2006). The spatial variability of earthworms will likewise influence spatial patterns of important ecosystem processes such as litter decomposition and nutrient cycling (Ettema and Wardle, 2002). The patchy spatial distribution of earthworms at the field scale in a variety of ecosystems is now well accepted (e.g. Poier and Richter, 1992; Rossi et al., 1997; Cannavacciuolo et al., 1998; Nuutinen et al., 1998; Hernández et al., 2007), however the factors that determine this variability are not yet sufficiently understood. Understanding these driving factors may provide vital information about colonization rates and target earthworm densities for optimized soil ecosystem management, and for the design of adequate sampling schemes for earthworm population monitoring.

The spatial variability of earthworms at the field scale can be attributed to two types of factors: biotic and abiotic (Whalen, 2004; Aubert et al., 2005). Biotic interactions of competition, facilitation, or co-existence occur both at intra- and interspecific level, and may be responsible for the spatial structuring within and between earthworm populations. For example, it can be expected that individuals/species exhibiting similar ecological strategies may try to minimize resource competition by occurring in spatially differing locations (e.g. Jiménez et al., 2006). Abiotic conditions at the field scale are the result of the interaction between local topography, soil texture and related soil hydrology and nutrient availability. But management practices, especially tillage, also alter the spatial variability of these abiotic factors (Govers et al., 1994). Given pre-existing spatial variability in soil properties at the field scale, earthworms are expected to occur in higher densities where the soil is intrinsically more favourable. This may be either because individuals move to the best soil patches and/or reproduction is faster in favourable patches (Barot et al., 2007). Relationships between earthworm spatial distribution and soil properties have been studied before (e.g. organic carbon content and soil hydrology in Poier and Richter, 1992; Cannavacciuolo et al., 1998), but rarely were these factors able to satisfactorily explain the observed spatial variability. Earthworm activities in turn can affect soil structure and soil chemical properties, hence the importance of investigating the effect of stable soil variables such as texture on the spatial variability of earthworm populations.

Characterizing the within-field soil textural variability is time, labour and cost intensive, since it relies on extensive soil sampling and subsequent soil analyses. Recently, the use of mobile, sensor-based measurements of soil apparent electrical conductivity (EC_a) has proved to be a quick, easy and reliable method for establishing within-field spatial variability in soil texture (Cockx et al., 2005). Soil EC_a is an integrating function of soil properties such as salinity, water content, texture and cation exchange capacity and under non-saline conditions it can be used as a proxy for the soil texture (Vitharana et al., 2006).

In this study, a geostatistical analysis of the density of the most abundant anecic and endogeic earthworm species and of the soil EC_a was performed for a temperate, arable loess soil. The aims were (i) to describe the observed within-field spatial variability of earthworms and soil EC_a, and (ii) to interpret the (dis)similarities and causal relationships between these spatial patterns in terms of community (within and between ecological categories), population (juvenile vs. adult) and abiotic (EC_a) interactions.

2. Materials and methods

2.1. Study site

The study was conducted in a tilled arable field with an area of 4 ha in the loess belt of central Belgium (50°61′32″N, 4°57′14″E). The study area is characterized by a marine temperate climate. The soil is a Luvisol formed in aeolian loess that was deposited during the last glaciation. The topography is rolling with elevations between 135 and 145 m above sea level. The studied field was converted from pasture to arable land in 1966 and a rotation scheme with sugar beet and winter wheat was implemented ever since. Every year, the field is conventionally ploughed in spring to a depth of 20 cm. Every second year, before sugar beet planting, 60 t of farm yard manure per hectare is applied. In 2002, as an exception to the regular rotation scheme, chicory (*Cichorium intybus* cv. 'sativum') was grown instead of sugar beet. In November 2003, when the field sampling for this study was carried out, the wheat crop had been harvested while its stubble was still left on the field. Field sampling for this study was conducted in a representative subarea measuring 105 m × 75 m (Fig. 1). The sampled area was buffered against edge effects to the north, east and west by a strip of the same arable field of at least 100 m in width. The southern side was buffered by a narrower strip of at least 20 m. Beyond this buffer a pasture was located.

2.2. Data collection

2.2.1. Earthworm sampling

Earthworms were sampled at 100 locations within the study area between late October and mid November 2003. Temperature and moisture conditions were favourable for earthworm sampling throughout the period (RMI, 2004). 48 sampling locations were laid out on a regular grid (15 m × 15 m) while the remaining 52 sampling plots were randomly distributed over the area (Fig. 1). Earthworms were sampled by mustard
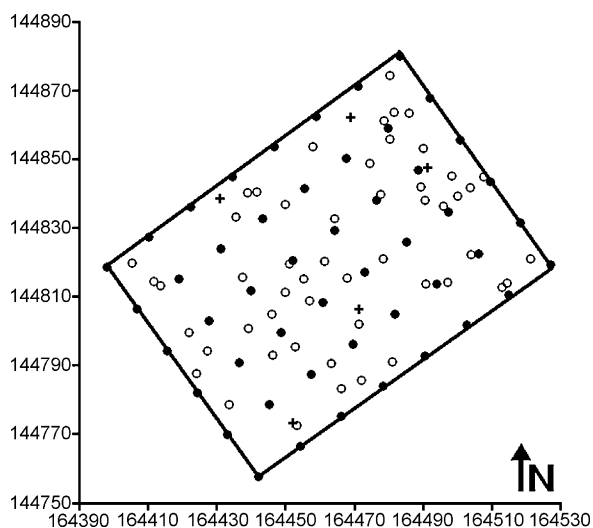
Fig. 1 – Locations of earthworm (●; 15 × 15 m grid and ○; random) samples and soil samples (+). The x **and** y **axes are expressed in meters, conforming to the Belgian Lambert 72 projection.**

extraction in 0.5 m^2 plots. A combined sampling method – mustard extraction followed by hand-sorting of a soil monolith (0.1 m^2 to a depth of 20 cm) collected in the mustard affected area – was used in 30 out of 100 randomly chosen sampling locations to determine the efficiency of mustard expulsion for different species and developmental stages. Soil monoliths were transported to the laboratory and sorted by hand under good light conditions. Collected earthworms were preserved in 5% formalin prior to identification. All individuals were identified to species level following the nomenclature of Sims and Gerard (1999) and their developmental stage ((sub)adult vs. juvenile) was recorded based on the presence of a clitellum. The key in Stöp-Bowitz (1969) was used for juvenile identification and in the minority of cases when identification to species level was not possible, specimen identified at genus or ecological group level were assigned pro rata to species level (Valckx et al., 2006). Individuals were weighed with gut contents and their biomass was expressed as g m^{-2} formalin-preserved weight. Densities per developmental stage were expressed as individuals m^{-2}.

2.2.2. EC_a measurements

In autumn 2003, when the soil moisture content was near field capacity, the soil was characterized by a mobile EC$_a$ survey. The electromagnetic induction (EMI) sensor EM38DD (Geonics Limited, Canada) was pulled by an all terrain vehicle in parallel lines 5 m apart at a steady speed of 10 km/h. EC$_a$ measurements were recorded every second and combined with GPS measurements, resulting in 720 measurements ha^{-1}. The EM38DD sensor consists of two perpendicular EM38 devices, each with its own depth response profile (McNeill, 1980). The device with a horizontally oriented dipole is most sensitive to the topsoil properties (0–0.30 m), while characteristics of deeper soil layers (0.40–0.80 m) mainly influence the signal received by the vertical dipole. The EM38DD signals penetrate to a depth of 1.5 m and actual measurements integrate the

response of the soil to an induced electrical field over this soil depth. The EM38DD thus simultaneously measures the soil bulk electrical conductivity of shallow and deeper layers. When the soil profile is heterogeneous these two measurements will show a different spatial pattern. In the case of vertically homogenous soils, the two orientations yield a similar pattern and the spatial variability can be represented by their average (ECav in the following).

2.2.3. Soil sampling

Based on the observed ECav variability, soil samples at three depth intervals (0–0.30, 0.30–0.60 and 0.60–0.90 m) were collected in the field at five locations, representing the range of ECav values (Fig. 1). These samples were used to document the variability of the soil properties. Samples were analyzed for texture, pH$_{KCl}$, gravimetric moisture and organic carbon content for each depth interval.

2.3. Data analysis

2.3.1. Geostatistical analysis

Information on the spatial variability of the earthworm species density as extracted by the mustard method (expressed in individuals m^{-2}) and the ECav (mS m^{-1}) was obtained through geostatistical analysis. The analysis was performed based on earthworm densities because it is considered that the occurrence of individuals is more important in understanding the factors controlling spatial patterns of populations than their biomass. It must be noted however that the mustard method was on average 10 and 6 times more efficient in extracting anecic adults and juveniles, respectively, than the hand-sorting method, and that the hand-sorting method was on average 2 and 5 times more efficient to retrieve endogeic adults and juveniles, respectively, than the mustard extraction. Mustard extraction consistently underestimated juvenile abundance by a factor of 3 as compared to adult abundance across all observed species (except in the case of A. rosea by a factor of 1.3). Therefore, endogeic and juvenile numbers are likely underestimated and spatial associations of endogeic species, especially when compared between adults and juveniles, should be interpreted with caution.

Omni-directional experimental variograms were computed for total populations of both anecic species (Lumbricus terrestris and A. longa) and representative endogeic species (Aporrectodea caliginosa and A. rosea), as well as for adult and juvenile individuals separately. A variogram is a plot of the average squared difference between two observations separated by a distance h as a function of this distance h. The semivariance $\gamma(\mathbf{h})$ is half of this average squared difference. All experimental variograms were best fitted with a spherical model (Goovaerts, 1997):

$$\gamma(\mathbf{h}) = \begin{cases} C_0 + C_1 \times \left[1.5\dfrac{\mathbf{h}}{a} - 0.5\left(\dfrac{\mathbf{h}}{a}\right)^3 \right], & \text{if } 0 < \mathbf{h} \le a \\ C_0 + C_1, & \text{if } \mathbf{h} > a \end{cases}$$

where h is the lag distance between observations, C_0 is the nugget effect, C_1 is the sill and a is the range. When the distance h equals the range, the semivariance reaches the sill.

The range defines the distance over which the observations are correlated with each other. The relative nugget effect (RNE) defines the contribution of the nugget effect to the total variability. It is calculated as $C_0/(C_0 + C_1)$ and used to quantify the strength of the spatial structure since it is an index of variance not attributable to spatial dependence (Isaaks and Srivastava, 1989). Strengths vary from weak (RNE > 0.75), to medium (0.25 < RNE ≤ 0.75) and strong (RNE ≤ 0.25) (Cambardella et al., 1994). The fitting of the variograms was done in VARIOWIN 2.2 and the best fit was obtained with the 'Indicator Goodness of Fit' parameter as a guide (Pannatier, 1996).

Modeled variograms of a variable Z (e.g. earthworm density) were then used to estimate the variable's value at any unsampled location x_0 through ordinary kriging (OK). OK uses a linear combination of observations within a predefined neighborhood around x_0 (Goovaerts, 1997). The OK estimator $Z^*(x_0)$ is given by:

$$Z^*_{OK}(x_0) = \sum_{\alpha=1}^{n(x_0)} \lambda_\alpha Z(x_\alpha).$$

The weights λ_α assigned to every observation $Z(x_\alpha)$ inside the neighbourhood were obtained from the variogram models. In OK the mean is assumed to be stationary within the neighborhood around x_0 and the sum of the weights must equal unity to guarantee lack of bias in the predictor.

2.3.2. Fuzzy k-means clustering

The interpolated earthworm and ECav values were used as input for a fuzzy k-means classification procedure using the FuzME sofware (Minasny and McBratney, 2002). This unsupervised classification identifies "natural clusters" in a dataset (Bezdek, 1981). Each individual is allocated a membership [0,1] to each of the k clusters through an iterative algorithm starting with a random set of cluster means. Each individual is then assigned to the closest of these means and new means are recalculated based on the distance in attribute space between the individual and the cluster mean. This is repeated until a specified convergence criterion is met. In this study the Euclidean distance is used as distance measure since only one input variable was used for each classification. The method minimizes the multivariate within-class variance, and consequently, individuals classified to the same class have similar attributes (McBratney and De Gruijter, 1992). The optimum number of clusters is determined by minimizing two indices: the fuzziness performance index, which measures the degree of membership sharing among classes, and the normalized classification entropy, which indicates the degree of disorganization in the classification (Bezdek, 1981).

2.3.3. Map comparisons

Fuzzy k-means classified maps of the spatial patterns of earthworm species and soil EC_a values were compared on a pixel-by-pixel basis. The kappa statistic (κ) (Cohen, 1960) provides a statistical measure of the degree of agreement between pixel classifications based on a 2 × 2 contingency table (k = 2). Since it accounts for chance agreement, kappa indicates how much better the results are compared with a purely random classification: the larger κ, the more accurate the classification. In spite of its wide use, several studies have criticized the kappa statistic for being inherently dependent on prevalence and claimed that this dependency introduces bias and statistical artefacts to estimates of accuracy (Byrt et al., 1993). Foody (1992) corrected κ by giving each category an equal membership probability (0.5 in the case of two categories) and called this index κ^*. κ and κ^* are members of a family of indices that follow the scale proposed by Landis and Koch (1977) to describe the degree of agreement: poor (index < 0), slight (index between 0 and 0.20), fair (index between 0.21 and 0.40), moderate (index between 0.41 and 0.60), substantial (index between 0.61 and 0.80) and almost perfect (index between 0.81 and 1.00).

However, the kappa statistics derived from a contingency table do not account for spatial relations, being similarities of spatial patterns (Power et al., 2001). Hagen (2003) introduced a new approach based on fuzzy set techniques to account for fuzziness of category and location. Fuzziness of category means that the distinction between categories is not always sharp and the vagueness among categories is set by the fuzzy category matrix. Fuzziness of location is set by a distance decay function that defines to which level neighbouring cells influence the fuzzy representation of the central cell. To account for the spatial context, fuzziness of category was not considered and fuzziness of location was set with an exponential decay function. The resulting fuzzy similarity map indicates for each cell the degree of similarity on a scale of 0–1 and allows the calculation of the average similarity (S_a). S_a ranges from 0 (fully distinct maps) to 1 (identical maps). Map comparisons were carried out by the Map Comparison Kit software (Visser and de Nijs, 2006).

2.3.4. Causal modeling

The influence of both biotic and abiotic conditions on the spatial variability of earthworm species was investigated by Mantel tests. Mantel statistics are correlations (r_M) between two dissimilarity or distance matrices. The hypothesis of a Mantel test is that the degree of dissimilarity in one dataset corresponds to the degree of dissimilarity in another independently derived dataset (Goslee and Urban, 2007). Three types of distance matrices were used (Rossi and Quénéhervé, 1998). Species distance matrices were formed by taking the unsigned differences among the values of species densities for all possible pairs of sampling locations. Analogously, a distance matrix containing the unsigned differences of ECav values between every pair of sampling locations was calculated. Finally, a geographic distance matrix was formed by calculating the Euclidean distances between every pair of sampling locations. Simple Mantel tests measure the extent to which the variation in one matrix corresponds to that in a second. The partial Mantel statistic is a partial correlation between two matrices A and B while controlling for a third matrix C. The latter approach can be used to test whether the apparent relation between two variables (e.g. earthworm density and soil EC_a) is spurious or not, i.e. whether both variables may or may not be correlated with a third common cause. In soil ecology, the spatial position of sampling points is likely to cause such spurious correlations (Rossi and Quénéhervé, 1998) but in fact any variable can be used as the controlling factor. Mantel statistics were computed and tested in the software package zt (Bonnet and Van de Peer, 2002).

One-tailed probability values were obtained by performing 10,000 permutations by jointly randomizing the rows and columns of one matrix. The Bonferroni test of global significance was used which states that for n tests, at least one p is less than α/n ($\alpha = 0.05$). If this criterion is not met, the entire set of null hypotheses cannot be rejected. If the criterion is met, then the individual tests can be evaluated (Legendre and Legendre, 1998). Both in simple and partial tests n was set to 3. The standard Mantel test only indicates that a linear relationship exists, not the direction of the relationship, which might be indicated by a positive or negative correlation in the original data (Goslee and Urban, 2007). Therefore Pearson correlations (r) were calculated from the original datasets. Since the degrees of freedom are overestimated in case of autocorrelation, no probabilities were associated with the Pearson correlation coefficients (Legendre and Legendre, 1998).

By comparing simple and partial Mantel statistics in a symmetric result matrix (see Table 4 for an example), causal models were defined (Legendre and Troussellier, 1988).

3.   Results

3.1.   Earthworm variability

In total seven earthworm species were observed of which the (epi-)anecic *L. terrestris* L. was both in terms of biomass and density the most abundant species (Table 1). It was followed by the endogeic *A. caliginosa* (SAVIGNY) and the anecic *A. longa* (UDE). The other endogeic species *Allolobophora chlorotica* (SAVIGNY), *Aporrectodea rosea* (SAVIGNY) and *Octolasion cyaneum* (SAVIGNY) were less frequently encountered. *Dendrodrilus rubidus* (SAVIGNY), the only epigeic species, was only found at two locations near the southern border of the sampled area. The same relative rankings were observed for adults and juveniles, both in terms of biomass and density. As an exception to this general pattern, adult *A. caliginosa* individuals occurred in higher densities than *L. terrestris* adults. Figures based on both

mustard and hand-sorting data (not shown) illustrate that *L. terrestris* abundance ranks second after *A. caliginosa*, mainly because of the difference in adult individuals. Anecic populations were in terms of density dominated by juvenile individuals (adult/juvenile ratio of 0.06 and 0.23, respectively, for *L. terrestris* and *A. longa*) while the adult/juvenile ratios of the endogeic species were much higher (0.42, 0.55, 0.64 and 2.52, respectively, for *O. cyaneum*, *A. caliginosa*, *A. rosea* and *A. chlorotica*).

The fitted variogram models based on earthworm densities showed medium to strong spatial structures in earthworm species with the RNE varying between 0.17 and 0.77 (Table 2; Fig. 2), meaning that between 17 and 77% of the variability consists of inexplicable or random variations. The densities of *A. rosea* and *A. longa* adults were only weakly spatially correlated (RNE = 0.77 and 0.71, respectively), while the density of *L. terrestris* adults showed a strong spatial structure (RNE = 0.17). The ranges of autocorrelation varied between 14 and 64 m. For the anecic species, the variogram range was remarkably smaller for adults than for juveniles (e.g. 14 m vs. 34 m for *L. terrestris*). As anecic population structures were dominated by juveniles (with an average adult/juvenile ratio of 0.074), the variogram ranges of total *L. terrestris* and *A. longa* populations were similar to the range of juveniles of these species (30 m vs. 34 m for *L. terrestris* and 64 m vs. 63 m for *A. longa*). In contrast, ranges of adults and juveniles were similar for endogeic populations which had a more even distribution of adults vs. juveniles (the average adult/juvenile ratio for this ecological group was 0.68): ranges of the total population were therefore comparable to the ranges of adults or juveniles separately.

In Fig. 3 it can be observed that *A. longa* densities were higher in those areas where *L. terrestris* is less abundant and the reverse. In contrast, the spatial distributions of both endogeic species were largely confined to the same area in the field and overlapped to some degree. Generally, densities of endogeic species did not show a spatial correspondence with those of anecic species.

Table 1 – Mean ($n = 100$) earthworm biomass and densities as collected by mustard extraction in a conventionally ploughed arable field. Data are given for each developmental stage per earthworm species and grouped per ecological category.

Earthworm species/ ecological category	Biomass (g fresh weight m^{-2})						Density (individuals m^{-2})					
	Adult		Juvenile		Total		Adult		Juvenile		Total	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Allolobophora chlorotica	0.922	1.329	0.119	0.326	1.042	1.452	5.2	7.50	2.0	3.35	7.2	9.26
Aporrectodea caliginosa	5.067	3.743	3.461	2.365	8.528	5.389	14.3	10.23	26.0	16.54	40.3	23.54
Aporrectodea rosea	0.315	0.431	0.215	0.266	0.531	0.556	1.9	2.46	3.0	3.51	4.9	4.89
Octolasion cyaneum	0.338	0.970	0.091	0.265	0.429	1.062	0.2	0.65	0.6	1.42	0.8	1.71
Endogeics total	6.642	4.265	3.887	2.495	10.529	6.059	21.6	13.74	31.6	18.41	53.2	28.65
Aporrectodea longa	2.730	3.759	2.076	2.071	4.806	4.624	1.6	2.12	6.9	5.88	8.5	6.63
Lumbricus terrestris	26.655	15.710	18.266	7.306	44.920	16.652	9.1	5.24	138.5	55.14	147.6	54.53
Anecics total	29.384	16.662	20.342	7.639	49.726	17.733	10.7	5.88	145.3	54.78	156.1	53.93
Dendrodrilus rubidus	0.003	0.020	0.000	0.000	0.003	0.020	0.0	0.28	0.0	0.00	0.0	0.28
Epigeics total	0.003	0.020	0.000	0.000	0.003	0.020	0.0	0.28	0.0	0.00	0.0	0.28
Total	36.030	18.328	24.228	8.227	60.258	20.635	32.4	16.23	177.0	58.89	209.3	63.25

Table 2 – Variogram model parameters for each developmental stage of the representative earthworm species (based on density). All data were best fit by spherical models. RNE: relative nugget effect. See Section 2.3.1 for further explanation.

Earthworm species	Developmental stage	Nugget C_0	Range a	Sill C_1	RNE $C_0/C_0 + C_1$
L. terrestris	–	1010	30	1960	0.34
	Adult	5	14	24	0.17
	Juvenile	1062	34	2094	0.34
A. longa	–	21	64	27	0.44
	Adult	3.1	40	1.2	0.71
	Juvenile	18.5	63	18.2	0.5
A. caliginosa	–	222	29	354	0.39
	Adult	72	33	41	0.29
	Juvenile	123	30	143	0.46
A. rosea	–	12.6	45	11	0.53
	Adult	4.6	40	1.4	0.77
	Juvenile	6.8	44	4.9	0.58

3.2. ECav variability

Since the horizontal and vertical EC_a were closely correlated ($r = 0.819$), the further analysis of EC_a variability was performed with ECav. This variable ranged between 10.4 and 22.7 mS m^{-1}, with a mean of 16.5 mS m^{-1} and a standard deviation of 2.1 mS m^{-1}.

Fig. 2c shows the ECav variogram. ECav had a strong spatial structure, indicated by a RNE of 0.229. The range of 96 m indicates the spatial extent of the ECav autocorrelation. The simple Mantel test revealed a strong and significant correlation between ECav and geographic distance ($r_M = 0.30$; $p < 0.001$). The ECav varied from low values in the southeast boundary to high values at the upper northwest boundary (Fig. 4a). Fuzzy k-means classification resulted in an optimum of 2 ECav classes (Fig. 4b). Class 1 had a centroid ECav value of 14.4 mS m^{-1}, while class 2 had a centroid value of 17.9 mS m^{-1}. The textural difference between these two classes could clearly be shown by the analyzed clay content, averaged over the soil samples per ECav class (Fig. 5). ECav class 2 was characterized by a distinctly higher clay content than ECav class 1. In both classes the clay content increased with depth, but for ECav class 2 the increase in clay content was slightly higher than for class 1 (a relative increase of the clay content from top- to subsoil of 54.8% vs. 42.5%). Similarly the moisture content was higher in class 2, but the difference between the classes was not significant. Also organic carbon and pH were not significantly different between the two ECav classes: their depth weighted mean was 0.56% and 6.84, respectively, for class 1, and 0.51% and 6.95, respectively, for class 2.

3.3. Map comparisons

3.3.1. Abiotic–biotic map comparisons

Pearson correlations between the abiotic soil conditions, represented by the ECav values, and earthworm densities were substantial for total L. terrestris ($r = -0.471$), L. terrestris juveniles ($r = -0.472$) and total A. longa ($r = 0.481$). The endogeic species did not show any correlation with ECav. Since the ECav map was optimally split into two classes ($k = 2$), and a kappa

analysis requires the same number of classes in the maps to be compared, this division was maintained for the fuzzy k-means classification of the biotic maps (Fig. 6). The results of the categorical comparison of the earthworm species and ECav confirmed the correlation analysis (Table 3). Spatial agreement between A. longa and ECav as expressed by S_a was 0.826, indicating the occurrence of A. longa in locations in the field with the highest clay content. For L. terrestris (total and juvenile densities) the spatial agreement was also high ($S_a = 0.727$), but an opposite behaviour towards soil conditions was observed (negative r).

3.3.2. Community level comparisons

Because of the negative Pearson correlation between L. terrestris and A. longa ($r = -0.151$), the categories of one variable were switched to avoid negative kappa statistics. Pixel-by-

Table 3 – Kappa indices (κ and κ^*) and average similarity (S_a) of classified maps related to biotic and abiotic interactions. Similarity measures vary between 0 (fully distinct maps) and 1 (identical maps). See Section 2.3.3 for further explanation.

|	κ	κ^*	S_a
Biotic interactions			
Species interactions			
Anecics: L. terrestris vs. A. longa	0.388	0.360	0.666
Endogeics: A. caliginosa vs. A. rosea	0.310	0.398	0.703
Interspecific interactions			
L. terrestris: juvenile vs. adult	0.027	0.020	0.521
A. longa: juvenile vs. adult	0.521	0.566	0.786
A. caliginosa: juvenile vs. adult	0.681	0.678	0.843
Abiotic interactions (ECav vs. species)			
L. terrestris	0.478	0.450	0.727
L. terrestris adult	0.110	0.124	0.442
L. terrestris juvenile	0.422	0.368	0.691
A. longa	0.646	0.698	0.826
A. caliginosa	0.193	0.328	0.668
A. caliginosa adult	0.040	0.018	0.510
A. caliginosa juvenile	0.255	0.282	0.622
A. rosea	0.098	−0.022	0.491
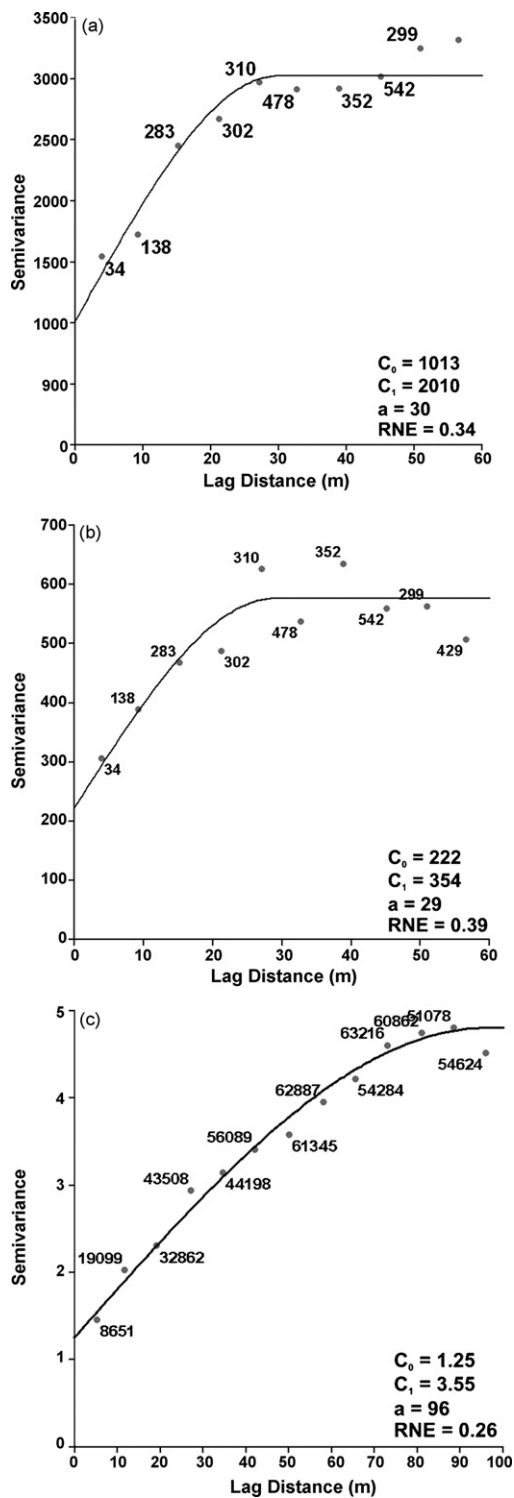
Fig. 2 – Experimental (dots) and fitted (straight line) variograms of (a) *Lumbricus terrestris* densities, (b) *Aporrectodea caliginosa* densities, and (c) soil electrical conductivity (ECav). Indicated on the graph: number of observation pairs per lag distance and the following variogram parameters: the nugget effect (C_0), the sill (C_1), the range (a) and the relative nugget effect (RNE).

Table 4 – Simple (above diagonal) and partial Mantel statistics (below diagonal) between adult *L. terrestris* density (LTad), soil electrical conductivity (ECav) and geographic distance between sampling locations (SPACE) and associated probability levels based on one-tailed tests (see also caption to Fig. 8). The partial statistic in a table cell is controlling for the variable not in the row or column headings of that particular cell.

	LTad		ECav		SPACE	
	r_M	P	r_M	P	r_M	P
LTad	–	–	0.028	0.238	−0.035	0.159
ECav	0.041	0.171	–	–	0.310	0.0001
SPACE	−0.046	0.092	0.311	0.0001	–	–

pixel comparison of the categorical maps of the anecic species resulted in a κ^* of 0.360, while S_a was 0.666 (Table 3). Thus, the poor correlation between *L. terrestris* and *A. longa* was reflected in a similar spatial variability, but based on inverted categories, indicating a considerable degree of spatial exclusion (Fig. 6a and b). For the endogeic species (Fig. 6c and d) the degree of agreement as expressed by S_a was somewhat larger (0.703), indicating a slightly stronger (and positive) spatial association. Occurrences of *A. caliginosa* and *A. rosea* were positively correlated ($r = 0.362$).

3.3.3. Population level comparisons

Occurrences of *L. terrestris* developmental stages were negatively correlated ($r = −0.163$). The degree of agreement between the categorical maps of *L. terrestris* adults (inverted categories) and juveniles was poor ($\kappa^* = 0.020$), indicating the low degree of map similarity (Fig. 7a and b; Table 3). Maps of *A. longa* adults and juveniles showed a markedly higher congruence than developmental stages of *L. terrestris* (maps not shown; $\kappa^* = 0.566$; $r = 0.197$). Developmental stages of both endogeic species were positively correlated ($r = 0.520$ for *A. caliginosa* and $r = 0.318$ for *A. rosea*). Comparison of the maps of *A. caliginosa* adults and juveniles (Fig. 7c and d) yielded a high S_a (0.843), confirming a strong spatial agreement.

3.4. Causal models

Fig. 8 depicts the causal models in relation to the simple and partial Mantel tests as introduced by Legendre and Troussellier (1988). Each model is based on a matrix as shown for adult *L. terrestris*, ECav and SPACE in Table 4. Uni-directional arrows were used because it was reasonably assumed that soil ECav or some unmeasured spatially structured variable (SPACE) could steer spatial distributions of earthworms but not the other way round. Models stating SPACE as the dependent variable were equally not considered as valid models.

3.4.1. Abiotic–biotic interactions

The spatial distribution of adult *L. terrestris* was not influenced by soil EC_a nor by some unknown factor represented by the variable SPACE (Fig. 8a). A similar lack of causal mechanisms was found for the distributions of adult endogeic individuals. Both adult and juvenile *A. longa* distributions were directed by soil EC_a but not by any other (unmeasured) variable and a similar causal relationship was found between the juvenile *L. terrestris* population and ECav,
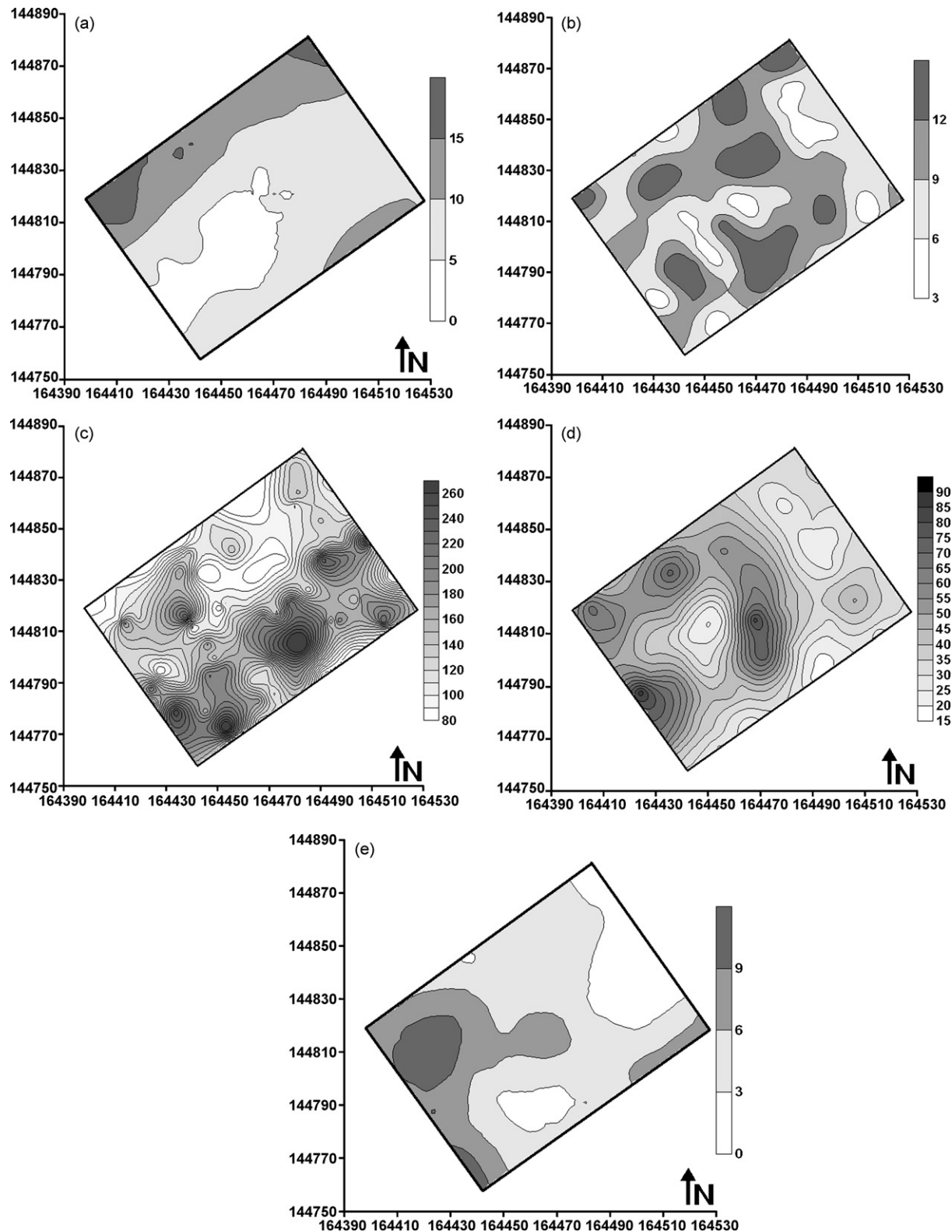
Fig. 3 – Kriged contour maps of the densities (individuals m^{-2}) of (a) *Aporrectodea longa* and (b) *Lumbricus terrestris* adults, (c) *L. terrestris* juveniles, (d) *A. caliginosa* and (e) *A. rosea*. Axes as for Fig. 1; see Section 2.3.1 for further explanation.

although only marginally significant. Juvenile occurrences of both endogeic species were not causally related to ECav but their distributions were caused by some unknown factor.

3.4.2. Biotic interactions

Causal modeling revealed that no causal relationships existed between the spatial occurrence of both deep-burrowing species *L. terrestris* and *A. longa* (Fig. 8b). On the other hand,
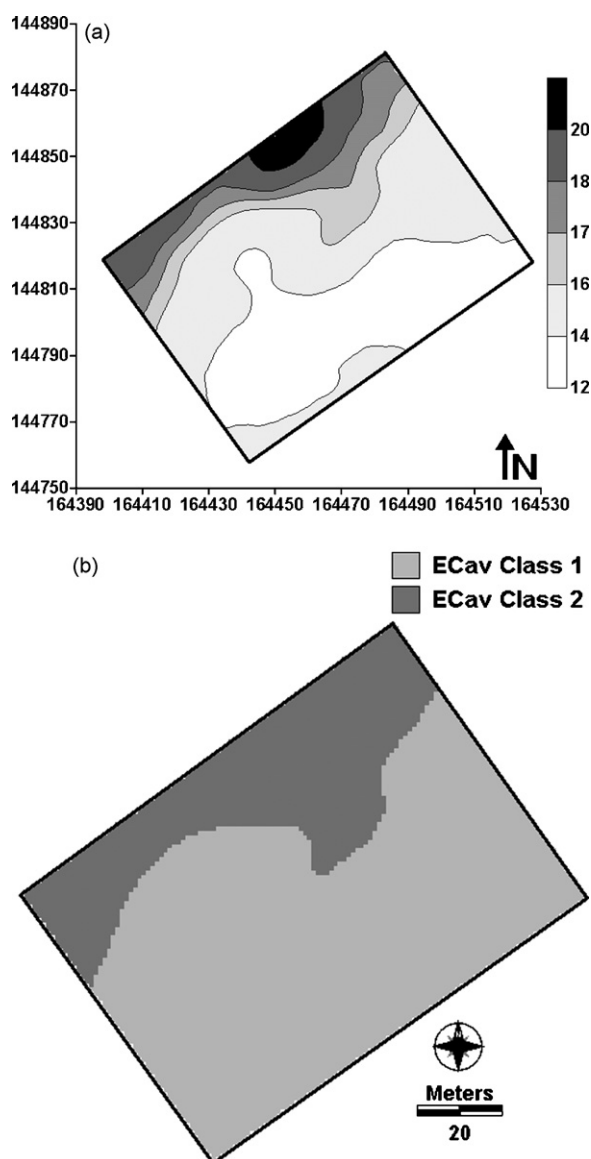
Fig. 4 – (a) Kriged contour map of soil electrical conductivity (ECav) (mS m^{-1}) and (b) fuzzy k-means classification of ECav. Axes as for Fig. 1; see Section 2.3.1 for further explanation.

Fig. 5 – Clay content (%) per depth interval in each soil electrical conductivity (ECav) class. Error bars depict standard deviations.

the distributions of endogeic species were strongly interlinked, but it could not be deducted from the results whether A. caliginosa steered the distribution of A. rosea or vice versa. Distributions of both anecic species were not causally related to endogeic distributions (causal models not shown). At population level, no causal relation between adult and juvenile stages of the anecic species could be detected. Adult and juvenile A. caliginosa individuals were strongly causally related but the model did not allow identifying the direction of the relationship.

4. Discussion

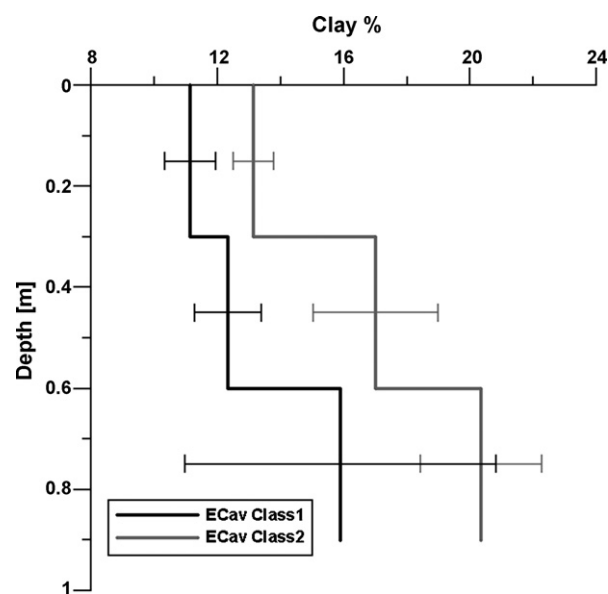This study demonstrated the spatial structure of earthworm species occurrence within a tilled agricultural field. The degree

of spatial dependence was in general medium strong with RNE varying between 0.17 and 0.58. However, the distributions of A. longa and A. rosea adults had a weak spatial structure with RNEs of 0.71 and 0.77, respectively. The methodological count resolution equal to one individual combined with the low occurrences of both species in the field (on average < 2 individuals m^{-2}) inevitably leads to a high proportion of unstructured variability.

It was found that earthworms live in spatially distinct clusters whose size was species- and life stage-specific. Map comparisons and causal modeling showed that the endogeic species A. caliginosa and A. rosea lived in close association with each other. The anecic species on the other hand had dissimilar spatial patterns as indicated by a fair agreement between the maps of L. terrestris (inverted categories) and A. longa on the scale of Landis and Koch (1977) and also causal models did not show a relationship between both species. Patches occupied by endogeic species were not spatially associated with clusters inhabited by anecic species. At the field scale, endogeic species do not seem to benefit from living in the neighborhood of deep-burrowing species, as was observed by Lowe and Butt (2002) and Sheehan et al. (2007) in their mesocosm experiments.

This study showed that the field distributions of deep-burrowing species were strongly spatially correlated with the soil conditions as measured by the EC$_a$. Occurrences of adult and juvenile A. longa were confined to zones with high ECav values while conversely L. terrestris (particularly juveniles) appeared in areas with low ECav values. Blackshaw et al. (2007) also found that juvenile abundance was spatially correlated with soil properties in an arable field, although they did not differentiate between species. The spatial segregation of the two deep-burrowing species was driven by a preference for differing soil conditions rather than by negative species interactions – such as competition for food at the soil surface
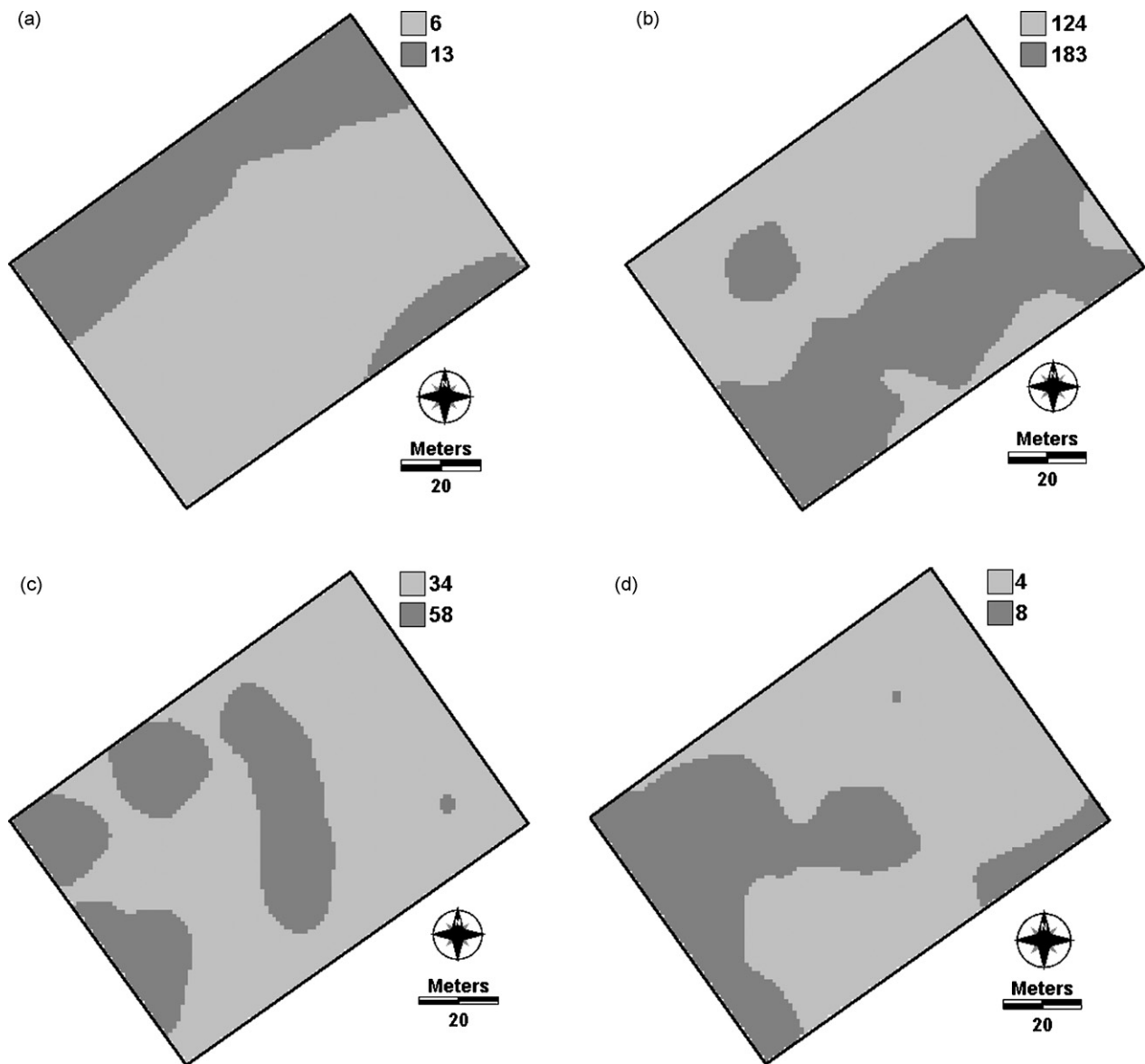
Fig. 6 – Fuzzy k-means classification of (a) *Aporrectodea longa*, (b) *Lumbricus terrestris*, (c) *A. caliginosa* and (d) *A. rosea*. Centroid values per class are given in the legend (individuals m^{-2}). See Section 2.3.2 for further explanation.

– as indicated by the causal models (Fig. 8). Although not supported by our data, Butt (1998) observed negative interactions between *L. terrestris* and *A. longa* in a laboratory context and Edwards and Lofty (1982) invoked such relations to explain the observed negative correlation between those species under field conditions. However, as was demonstrated in this study, a negative (Pearson) correlation between occurrences of two species does not necessarily mean that the species' distributions are causally related. Further research unraveling the relative importance and potential interaction of biotic and abiotic causal factors in the field is recommended.

Field distributions of the shallow dwelling species were not spatially related to soil EC$_a$ conditions. Given the homogenizing effect of the long-term applied ploughing regime on soil properties in the upper 20–30 cm of the soil profile, the EC$_a$ measurements are likely to represent the non-homogenized

subsoil properties (Cockx et al., 2008). As a consequence the EC$_{av}$ map does not represent the topsoil variability well. The practical implication of these observations is that the use of EC$_a$ measurements to predict the spatial occurrence of earthworm species is confined to earthworm activity in the deeper soil layers. Apart from their causal relationship with the spatial patterns of conspecific adults, distributions of juvenile endogeics were also related to a spatially structured variable which was not picked up by the EC$_a$ characterization as indicated by the causal relationship between geographic distance between plots and variability in endogeic earthworm density.

Within endogeic populations similar cluster sizes, high κ^* and S$_a$ values, and significant causal relationships indicate that adult and juvenile endogeics live intimately together at the field scale at the observed population densities and
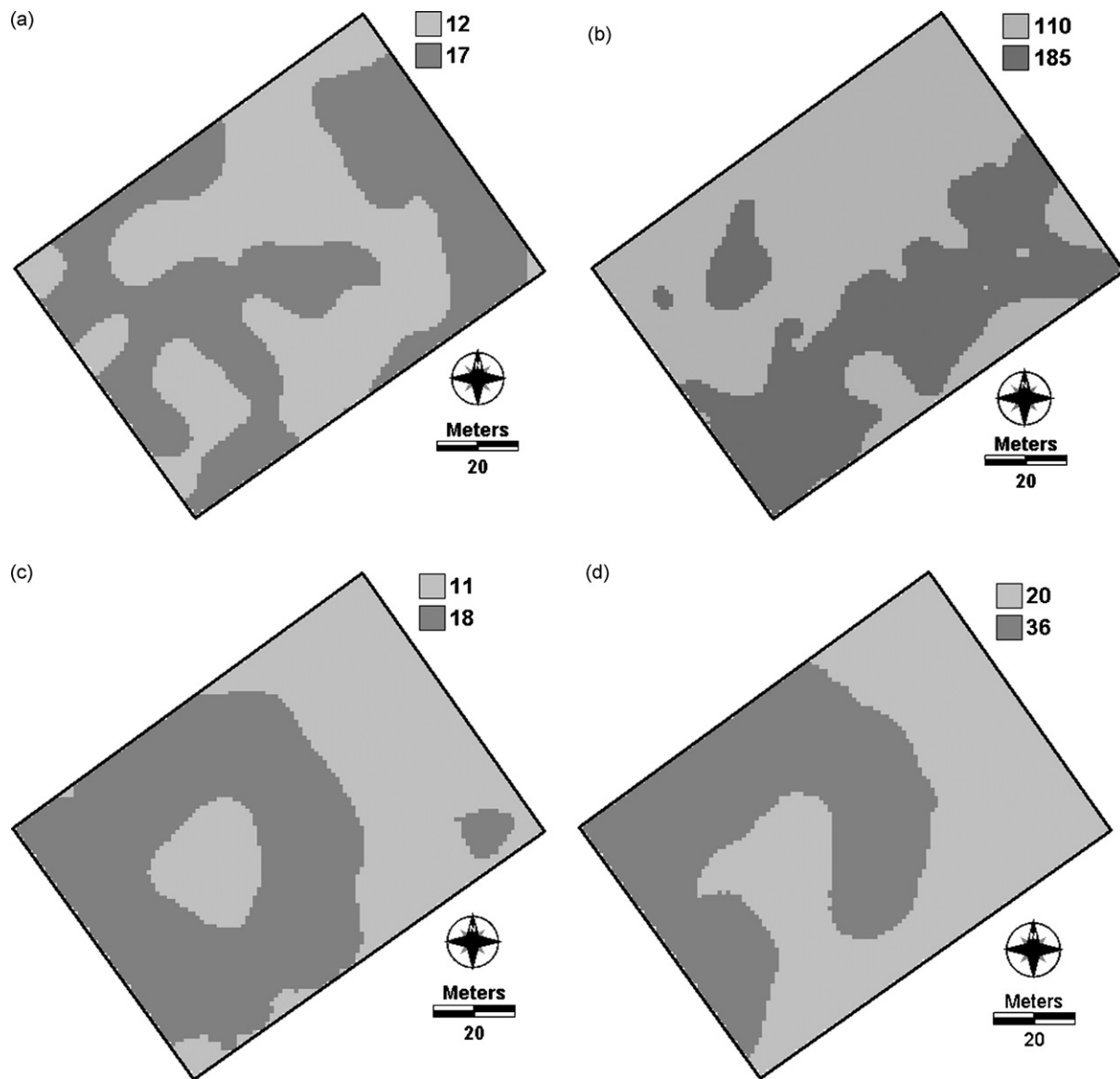
Fig. 7 – Fuzzy k-means classification of the developmental stages for one representative species per ecological category: (a) *Lumbricus terrestris* adults, (b) *L. terrestris* juveniles, (c) *Aporrectodea caliginosa* adults, and (d) *A. caliginosa* juveniles. Centroid values per class are given in the legend (individuals m^{-2}).

structures. These observations suggest that facilitation and/or co-existence help these relatively immobile species due to their assumed continuous soil inhabitance deal with the limited availability of resources. However, as the abundance of endogeic juveniles is underestimated by the mustard sampling method, a cautious interpretation of these relationships is warranted.

In contrast, no uniform conclusions could be drawn concerning the spatial (dis)association of the developmental stages of the anecic species. *L. terrestris* adults and juveniles were notably not spatially related, while the *A. longa* developmental stages had similar spatial distributions but causal modeling did not indicate a causal relationship between adults and juveniles. Nevertheless, clusters of the developmental stages of anecic species differed strongly in size with the adults inhabiting markedly smaller clusters (e.g.

14 m vs. 34 m for adult and juvenile *L. terrestris*, respectively). These results suggest that anecic juveniles tend to disperse from parental clusters into neighbouring areas and that this dispersal effect is more pronounced in the *L. terrestris* population. The much lower densities of *A. longa* as compared to *L. terrestris* might have accounted for the less explicit spatial separation of adult and juvenile *A. longa*. However, Lowe and Butt (2002) also reported stronger intra-specific competition in *L. terrestris* populations than in *A. longa* populations, particularly after juveniles were 12 weeks old and started to exhibit home range behaviour. Moreover, *L. terrestris* is known to disperse over the soil surface over significant distances at night (Mather and Christensen, 1988) while no such behaviour has been reported yet for *A. longa*. On the other hand, the distinct distribution in small clusters of *L. terrestris* adults and the absence of causal relationships between the adult *L.*
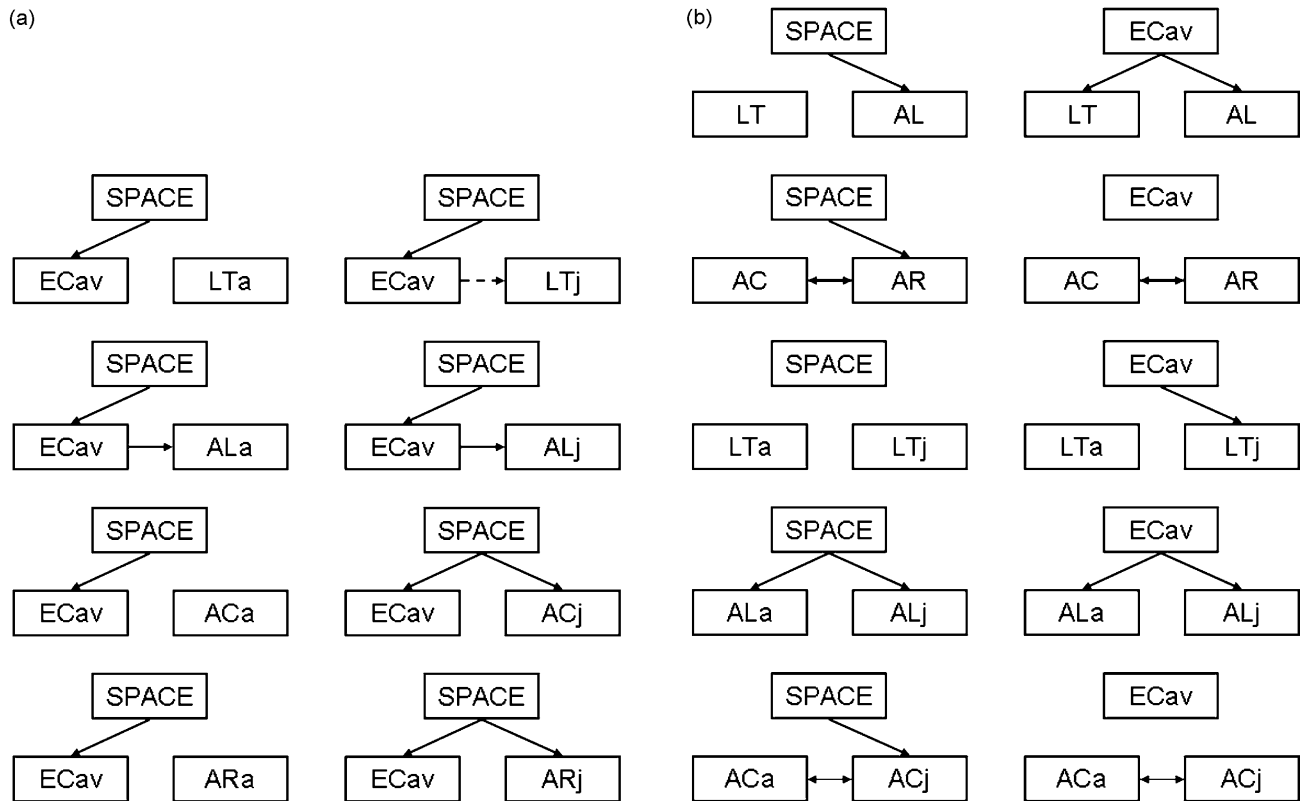
(a)

SPACE
ECav   LTa

SPACE
ECav --→ LTj

SPACE
ECav → ALa

SPACE
ECav → ALj

SPACE
ECav   ACa

SPACE
ECav   ACj

SPACE
ECav   ARa

SPACE
ECav   ARj

(b)

SPACE
LT   AL

ECav
LT   AL

SPACE
AC ↔ AR

ECav
AC ← AR

SPACE
LTa   LTj

ECav
LTa → LTj

SPACE
ALa   ALj

ECav
ALa   ALj

SPACE
ACa ↔ ACj

ECav
ACa ↔ ACj

Fig. 8 – Abiotic (a) and biotic (b) causal models indicating the causal relationships between earthworm species densities, soil EC$_a$ (ECav) and geographical distance (SPACE) based on an analysis of simple and partial Mantel statistics (Legendre and Troussellier, 1988). Solid arrows indicate relations significant at the Bonferroni-corrected probability level of 0.0167 (0.05/3) for an overall significance level of 0.05 over three simultaneous simple/partial tests. Dashed arrows similarly indicate relations marginally significant at an overall significance level of 0.1 (Bonferroni-corrected probability level of 0.033 (0.1/3)). Absence of arrows means that Mantel statistics were not significantly different from zero.
LT: *Lumbricus terrestris*; AL: *Aporrectodea longa*; AC: *A. caliginosa*; AR: *A. rosea*. Letters a and j, respectively, denote adult and juvenile populations.

terrestris distribution and ECav, unmeasured soil variables, *L. terrestris* juveniles, and other earthworm species may relate to this species' reproductive behaviour. Mating partners stay anchored in their burrows while mating at the soil surface (Nuutinen and Butt, 1997), requiring a fairly close distribution of adult conspecifics. More studies are needed to address the dynamic nature of earthworm clusters in relation to dispersal and maturation of juvenile individuals under field conditions.

The deep-burrowing *L. terrestris* was almost as abundant as the endogeic *A. caliginosa*, although Chan (2001) concluded that abundance of deep-burrowing earthworm species tends to decline under tillage. While the field had been ploughed for more than 35 years since its conversion from pasture, it is unlikely that the positive effects of the former land use have lasted until recently. Given that the field is tilled in spring, that it was exceptionally non-inversion tilled in 2002 before wheat planting, and that the food supply is ample (60 t of farm yard manure and large amounts of winter wheat residues every other year), anecic populations might recover quickly after soil disturbance and high population levels can be maintained.

Decaëns et al. (2003) found that soil type was a driving factor for the spatial distribution of earthworm community structure and diversity at the landscape scale, while at the

field scale agricultural practices had most impact. At our study site with uniform management practices we found that the spatial distributions of (juvenile) deep-burrowing earthworm species were related to the within-field spatial soil variability, measured by the ECav. As a consequence, the rapid, easy and non-destructive geo-referenced soil characterization by means of EMI-based measurements could effectively aid in the design of a field-scale stratified earthworm sampling scheme in an optimized number of locations (Corwin et al., 2006), at least for the deep-burrowing species. Care must be taken to balance sampling effort in zones with both low and high ECav, as the anecic species *L. terrestris* and *A. longa* tended to exhibit opposite behaviour towards soil EC. Since endogeic species did not explicitly co-occur with anecic species and their field distributions could not be linked to within-field soil EC variability, the optimal sampling strategy for entire earthworm communities should consist of a stratified grid sampling approach. Given the observed ranges over which species abundances are spatially related, proper grid spacing should be between 30 and 40 m, but preferably smaller (∼15 m) if the adult *L. terrestris* population is of particular interest.

Johnson et al. (2004) also demonstrated the biological relevance of soil EC$_a$ classification in a cropping system

(microbial activity, crop yield) and stated that the classification provides a point of reference through which microbial, within-field-, and field-scale data can be related. Although promising, this novel sensor-based approach to aid in determining and understanding the spatial distributions of soil organisms requires further testing in a variety of (agro-)ecosystems.

5. Conclusions

This study demonstrated that both the spatial patterns of earthworm densities and the underlying causal biotic and abiotic factors are species and life stage specific and related to the ecological category of the earthworm species concerned.

The endogeic *A. caliginosa* and *A. rosea* lived closely associated at the field scale. Their distributions could neither be linked to the spatial occurrence of anecic species nor to soil EC_a heterogeneity, although an unidentified driving factor remains to be determined in future studies.

The segregated field distributions of the deep-burrowing species *A. longa* and *L. terrestris* were largely determined by a difference in ecological niche (subsoil textural properties) rather than direct competition between these species. Anecic juveniles (particularly of *L. terrestris*) were found in areas neighbouring clusters of conspecific adults. For the first time field evidence is available to support the hypothesis that the spatial organization of adult *L. terrestris* individuals in small distinct patches is related to the particular mating behaviour of this species.

The quick and non-destructive EMI-based soil survey proved to be an easy way to characterize within-field textural variability and aided in determining the driving factors of earthworm distributions. However, more research is needed to test whether this novel approach is also valuable under different (a)biotic conditions in a variety of ecosystems.

Acknowledgements

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