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The spatiotemporal pattern of a tropical earthworm species assemblage and its relationship with soil structure

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Summary

The spatiotemporal pattern of a tropical earthworm assemblage (Lamto, Côte d'Ivoire) was assessed using a Partial Triadic Analysis (PTA). The abundance of earthworm species was estimated on five occasions covering two years within a single plot sampled with 100 sampling locations. The results showed that the earthworm community was highly structured in space and that the spatial pattern was stable through time. The Partial Triadic Analysis allowed extracting the earthworm community pattern that was common to all the dates. It was possible to identify which dates differed from the common model and which species were responsible for these discrepancies. The main pattern revealed by PTA was also submitted to spatial statistics to assess its significance. The results showed that the earthworm community is structured as a juxtaposition of patches dominated by different species. This pattern appeared to be constant during our 2-year study. When species were grouped following their impact upon soil structure dynamics the surveyed area appeared to be made of adjacent patches dominated either by compacting or decompacting earthworm species. The functional implications of this pattern are discussed and the spatial structure of the earthworm community was compared to soil bulk density distribution. The Mantel tests revealed a very strong relationship between soil bulk density and earthworm community structure.

Key words: Spatiotemporal pattern, earthworm community, soil structure, soil bulk density

Introduction

The impact of earthworms on soil properties and soil organic matter dynamics is well recognised (Giller et al. 1997; Brussaard 1999; Lavelle et al. 2001). At the population scale, the spatial distribution of individuals may also play an important role in influencing plant growth and plant community structure (Ettema & Wardle 2002). However, the majority of available studies report

information on the spatial patterning of populations on a single occasion and thus the stability of the reported distributions remains uncertain.

Blanchart et al. (1997) showed that the endogeic earthworm species inhabiting the savannas of Lamto (Côte d'Ivoire) could be categorized into two broad functional groups: the compacting and the decompact-

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ing species respectively. The activity of the compacting species tend to increase the soil bulk density whereas the decompacting species decrease it. Therefore the spatiotemporal dynamics of these functional groups is potentially an important factor of soil structure regulation.

Relating the activities of species or functional groups to ecosystem functioning (e.g. biogeochemical fluxes or soil structure dynamics) has proved awkward mainly because individual species affect processes at scales an order of magnitude below the scales at which measurements are made in the field (Anderson 1995). Most of our knowledge of mechanisms and species effect comes from microcosm experimental studies and the species effect at the ecosystem level is often derived from extrapolation i.e. a bottom-up approach.

Nevertheless, if we are to assess the actual effect of species i.e. without extrapolation, a top-down approach is required (Anderson 1995). This implies establishing both time and space scales at which species populations are effectively the primary determinant of a given process. Obviously this requires scanning various scales, implies expensive sampling strategies and necessitates adequate statistical tools.

This study was designed to assess the spatial distribution of a tropical earthworm community at different dates, to examine its constancy (Grimm & Wissel 1997) and to test for correlation between the earthworm distribution and an important soil attribute, the bulk density. The objectives were a) to extract a spatial community structure that was common to the different sampling occasions, b) to test for the presence of a consistent autocorrelation in this multispecies assemblage and c) to examine the relationship between this pattern and soil bulk density.

Materials and Methods

Sites and species

This survey was conducted in a grass savanna (*Loudetia simplex*) in the Station d'Ecologie Tropicale de Lamto (Côte d'Ivoire) (5°02'W, 6°13'N). The mean annual rainfall is ca 1200 mm and the mean temperature 28 °C. The variations in monthly rainfall define a dry season from December to February and a rainy season from March to November interrupted by a decrease in rainfall during August. The investigated plot (45 × 45 m) was randomly located within a large area covered with *L. simplex* and sparse palm trees (*Borassus aethiopium*). The soil is sandy (sand 80%) with low organic matter content (1.5%). The earthworm community was sampled on 5 occasions: May and November 1995, June and December 1996 and June 1997. Earthworms were sam-

pled during the rainy season to ensure that populations had reached their highest density and biomass in Lamto (Lavelle 1978).

Two earthworm species of the Eudrilidae family coexist, namely *Chuniodrilus zielae* (Omodeo) and *Stuhlmannia porifera* (Omodeo & Vaillaud). These endogeic species are small and belong to the functional decompacting species because they tend to decrease soil bulk density (Blanchart et al. 1989, 1997). On the other hand, the megascolecid *Millsonia anomala* (Omodeo) is a medium sized endogeic earthworm that dominates the earthworm community in terms of biomass (Lavelle 1978). This species is classified as a compacting earthworm since it increases soil bulk density (Blanchart et al. 1997). Other species are present at the site (see Lavelle 1978). *Dichogaster agilis* (Omodeo & Vaillaud) (Megascolecidae) is frequent in the grass savanna but this species is epigeic and thus weakly affects soil structure.

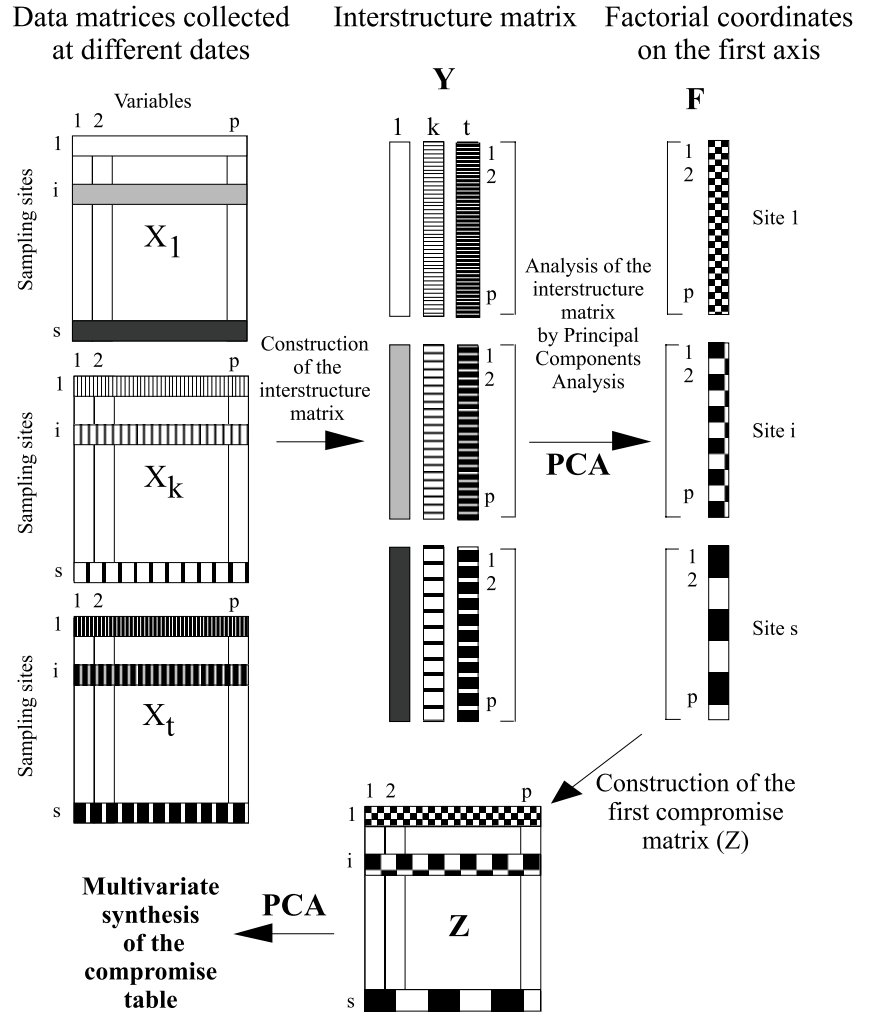
Earthworms were sampled by hand-sorting a 25 × 25 × 10 cm soil monolith, identified, counted and released in the field. Samples were taken in a 10 × 10 grid, the points being separated by 5 m. As indicated above, earthworm sampling was carried out on 5 occasions. To avoid taking two soil monoliths exactly at the same location, samples were displaced, from one date to another, along a spiral whose origin was represented by the point sampled at the first date. The difference of location was about 30 cm and was assumed to be negligible in comparison to the overall size of the investigated plots. The sample coordinates were therefore considered as identical from one date to another. Because distinguishing *C. zielae* and *S. porifera* requires adult individuals with visible external sexual organs, both species were recorded as a single group hereafter referred to as the Eudrilidae group. Earthworms (except eudrilids) were distributed among broad age class categories: adults, sub-adults and juveniles.

Soil bulk density was estimated on 2 occasions, in March and December 1996. Soil samples consisted of a soil core of 250 cm³ volume, dried for 48 h at 105 °C. Soil was sampled on an 11 by 11 points grid with a mesh size of 5 m. The grid was positioned so that each earthworm sampling point was surrounded by 4 points at which soil bulk density was measured. Bulk density was autocorrelated and led to a consistent variogram. Therefore, bulk density at the exact position of each earthworm sample was estimated by punctual kriging (Webster & Oliver 1990).

Analysis of the multivariate spatiotemporal variability: the Partial Triadic Analysis

The Partial Triadic Analysis (PTA) is a multivariate method allowing the analysis of a set of data tables

Fig. 1. General scheme of the Partial Triadic Analysis: construction of the interstructure matrix Y and extraction of the compromise table Z . The interstructure between matrices $X_1...X_t$ corresponding to the sampling dates is analysed by a simple PCA of Y . The compromise tables are derived from the coordinates of the variables at the different sites on the principal components of the PCA of Y . The figure illustrates the construction of the first compromise table from the first principal component of the simple PCA of Y . Compromise tables are then analysed by a simple PCA



(variables x sites) recorded through a series of sampling campaigns (Fig. 1). At each date, p variables are recorded at s sampling sites. The data set forms a three-dimensional data array (Fig. 1) (Thioulouse & Chessel 1987; Kroonenberg 1989). The PTA is a three-step procedure, namely the interstructure, the compromise and the infrastructure analyses. Only the first two steps were used in this work and are presented below.

The interstructure analysis provides an ordination of the sampling dates and gives a description of the sites in relation to the typology of the sampling dates for each of the variables (Thioulouse & Chessel 1987; Kroonenberg 1989).

To analyse the interstructure between t matrices $X_1...X_t$ with s rows (sampling sites) and p columns (variables i.e. species) each, it is required to compute the matrix Y by rewriting the initial matrices row by row on a single column (Fig. 1). A Principal Components Analysis (PCA) is then applied to Y (Fig. 1) and provides an inter-dates synthesis (Thioulouse & Chessel 1987; Centofanti et al. 1989).

The compromise analysis is the simple PCA of a fictive table with s rows and t columns (Fig. 1) whose values maximise the average correlations between the corresponding variables in the original tables.

The compromise matrix is a fictitious matrix constructed from a linear arrangement of initial matrices (Fig. 1). The compromise matrix is determined so as to maximise its internal inertia i.e. the correlations between the values of its variables and the corresponding values in the t original matrices. Practically the compromise matrix is obtained by taking the factorial coordinates (F) from the PCA of Y (see Fig. 1). The first compromise matrix corresponds to the first principal axis. The second factorial axis gives a second compromise matrix and so on.

The compromise analysis *sensu stricto* consists of the simple PCA of the compromise table. This operation indicates which of the variables are of importance in the structure extracted by the PCA of the interstructure table. The sampling site scores on principal axes can be used in two ways. 1) simple plots of

the sites on different axes allow identification of patterns along axes and 2) since sampling is necessarily spatially explicit, one can draw a map of the sampling site scores on a given axis (see Fig. 3). These values can also be analysed using spatial statistics in order to precisely describe the autocorrelation structure (if any).

All the computations involved in the PTA can be carried out using standard PCA software. In this study we used the module «PCA» of the software ADE-4 (Thioulouse et al. 1997).

In order to assess the relationships between soil bulk density and the first compromise of the PTA on earthworm density we applied the Mantel and partial Mantel test on a set of 3 matrices (Legendre & Fortin 1989; Rossi & Quénéhervé 1998). The size of these matrices was 100. A first matrix called “Space” was constructed. It contained the inverse of the geographic (Euclidean) distances between each pair of sampling points (Legendre & Troussellier 1988). A second matrix, hereafter referred to as “Earthworm” contained a Euclidean distance coefficient between points computed with the coordinates of sampling points upon the first factorial axis of the compromise PCA. Finally a matrix “Bulk density” was constructed with a distance coefficient derived from the symmetrical similarity coefficient of Gower (distance = 1 – similarity) (Legendre & Legendre 1998). The presence of a common structure was tested by a Mantel test between the matrices “Earthworm” and “Bulk density”. In order to ensure that the relationship was not spurious (due to a third, not explicitly measured factor) the relationship was tested by means of a partial Mantel test including the matrix “Space” (Legendre & Legendre 1998).

Results

The earthworms mainly comprised 4 frequent species, *C. zielei* and *S. porifera* (Eudrilidae), *M. anomala* and *D. agilis*. Other species like *M. lamtoiana* (Omodeo & Vaillaud) or *D. terrae-nigrae* (Omodeo & Vaillaud) were occasionally encountered. However, their density in the 0–10 cm soil layer was extremely low and these species were therefore removed from statistical analyses.

Interstructure

The decrease of the eigenvalues (Fig. 2b) was low therefore the first two factorial axes were explored. The correlation circle showed all the dates displaying

the same sign on principal axis 1 (24.05 % of the total inertia) whilst axis 2 (20.98 % of total inertia) presented an opposition between autumn sampling dates and the early summer dates (Fig. 2a). All dates with the same sign indicated a positive correlation between the corresponding set of matrices. The structure expressed through the first axis of the interstructure therefore corresponded to a community spatial pattern common to the different sampling dates.

The second interstructure factor (axis 2) was characterised by the opposition between the date 05/95 (positive correlation with axis 2) against dates 11/95 and 12/96 (negatively correlated with the axis) (Fig. 2a). Other dates had an intermediate position with a correlation particularly low between axis 2 and date 06/96. Mapping the sample coordinates upon axis 2 and comparing the resulting patterns to the raw data revealed that the second dimension of the interstructure analysis essentially accounted for the spatial structure of the Eudrilidae and *M. anomala* at a given date (05/95) that was not completely accounted for by the first axis. Therefore this second dimension was only reflecting a particular case.

Compromise

The first eigenvalue accounted for ca. 31 % of the total inertia while other factorial axes only accounted for a very limited amount of the total inertia and were not further analysed (Fig. 3b). The correlation circle (Fig. 3a) indicated a marked opposition between Eudrilidae and other earthworm groups, particularly the juveniles and the sub-adult of *M. anomala*. Maps of the sample scores along axis 1 (Fig. 3c) showed a clear spatial autocorrelation (see below). Two lateral parts of the plot were characterised by positive values (circle in Fig. 3c) which indicated that the functional group of the Eudrilidae is, on average, dominant in terms of density because that variable displayed a positive coordinate with that axis (Fig. 3a).

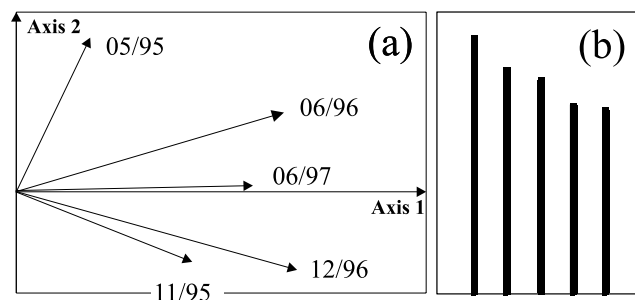


Fig. 2. Interstructure analysis. (a) Correlation circle showing the sampling dates on the factorial axes 1 and 2 of the PCA of the interstructure matrix. (b) Eigenvalues diagram

Fig. 3. Analysis of the first compromise. (a) Correlation circle featuring the 6 earthworm categories on the two first principal components. (b) Eigenvalues diagram. (c) Maps of the sampling site scores on the first principal axis. Circles and squares respectively stand for positive and negative values, the symbol surface being proportional to the corresponding unsigned score value

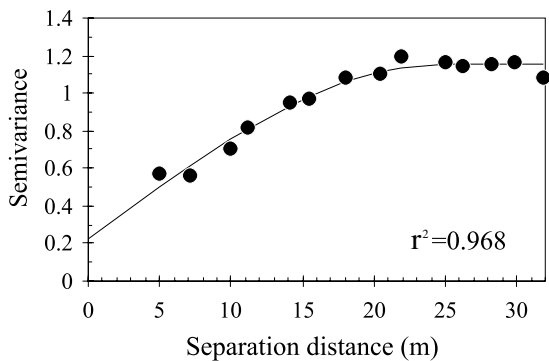
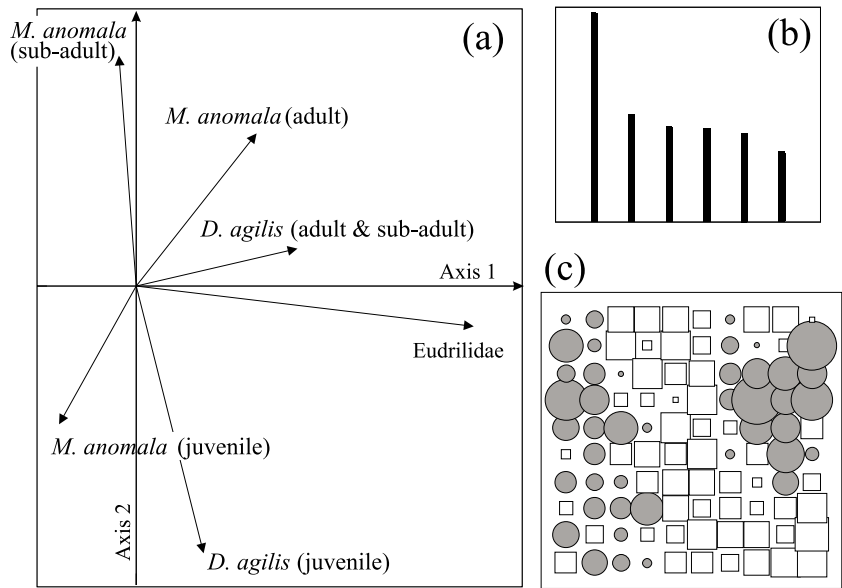


Fig. 4. Spatial analysis of the first principal component of the compromise. Variogram of the sampling site's coordinate on the first axis. The spatial structure explains ca 80% of the total variability. The fitted model is a spherical function

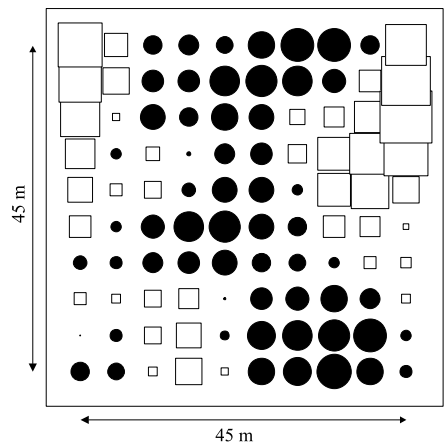


Fig. 5. Spatial pattern of soil bulk density. Graphical display of the mean values of soil bulk density as measured in March and December 1996 after data were centred. Circles and squares respectively stand for positive and negative values, the symbol surface being proportional to the corresponding absolute value

The autocorrelation of the first compromise was statistically tested by means of Moran's I autocorrelation index (Legendre & Fortin 1989). The structure was highly significant at the Bonferroni corrected level of significance (Oden 1984) ($P < 0.0001$). A geostatistical analysis of the sampling site score along the first principal component was performed. The resulting variogram was spherical (Fig. 4) with a somewhat low nugget variance ($C_0 = 0.23$), a high structural variance ($C = 0.92$) and a range of $a = 24.7$ m. These results showed that the spatial autocorrelation accounted for 80% of the total variability along axis 1 as indicated by the ratio C to $C + C_0$.

Relationships between earthworm pattern and soil bulk density

The mean soil bulk density was 1.42 and 1.45 respectively for March and December 1996. Both data sets showed consistent spatial autocorrelation and were submitted to variography. Bulk density at points where earthworms were sampled was estimated by punctual kriging. For each point, the estimated values for March and December 1996 were averaged and mapped (Fig. 5). There is a very clear spatial pattern similar to the map of the sample scores upon the first axis of the compromise PCA (Figure 3c). The small values of

bulk density (squares in Fig. 3c) corresponded to the circles in Fig. 5 (high eudrilid density). Conversely, there was an association between high soil bulk density and high *M. anomala* density.

The simple Mantel test showed the presence of a consistent correlation between the matrices "Bulk density" and "Earthworm" ($P < 10^{-4}$). The partial Mantel test between these matrices while accounting for the "Space" matrix was also significant ($P < 10^{-4}$). The latter test indicated that the relationship between soil structure and earthworm community pattern was not spurious.

Discussion

The results reported here have demonstrated the existence of a highly heterogeneous, patchy and structured assemblage in a tropical earthworm community. The reported spatial distributions are similar to what is known in the literature (Poier & Richter 1992; Rossi et al. 1995, 1997; Nuutinen et al. 1998). On the other hand, temporal stability has been poorly investigated to date (Rossi 1998; Decaëns & Rossi 2001). The persistence of a global community spatial pattern common to the different sampling dates was demonstrated by the interstructure and compromise analyses although the patterns observed at each of the sampling campaigns exhibited various departures from the general model. This structure is essentially constituted by disjunctive distributions between different species or functional groups. The scale at which these units were structured (ca. 25 m) was consistent with available data (Rossi et al. 1995, 1997; Decaëns & Rossi 2001; Jiménez et al. 2001).

Attention must be paid to the fact that the first factorial axis of the interstructure analysis accounted for 24 % of the total inertia. Since the decrease of the eigenvalues was low, the general structure accounted for by axis 1 could be of little significance. This was not the case because axis 2 only related to the discrepancy of one date (05/95) from the general pattern. Both axis 1 and 2 extracted similar structures (i.e. species assemblages with opposite patches of different functional groups). This structure did not vary consistently in time even if it was not necessarily expressed with the same strength at every sampling date. However we have no information on the long-term dynamics of this species assemblage.

The spatial distribution of soil bulk density was highly correlated with the earthworm community structure. Clumps of eudrilid species corresponded to areas of lower soil bulk density whereas patches of *M. anomala* fitted with areas of higher bulk density. *D. agilis* is an epigeic species and therefore has less effect on soil structure. However this species showed a con-

sistent spatial aggregation whose origin and consequence for soil functioning still need to be elucidated. Although endogeic earthworms are not the only regulating factors of soil structure dynamics they are very important in the savannas of Lamto (Blanchart et al. 1997). Therefore, the reported pattern suggests that the regulation of soil structure dynamics by earthworms is made through a mosaic of patches within which a given function is realised. The soil would mainly be decompacted within patches dominated by eudrilid worms while the bulk density would tend to increase in the patches of *M. anomala*.

The ecological relationships between compacting and decompacting earthworm groups are rather complex. *M. anomala* (compacting species) appears to be unable to ingest large aggregates and depends upon eudrilid worms and other factors generating small soil aggregates (Blanchart et al. 1997). Gurney & Lawton (1996) have formulated a general model for the population dynamics of ecosystem engineers. They introduced a key feature, in which the ecosystem engineer modifies its habitat, which in turn progressively decays and finally becomes unsuitable for the organism. The principle applies to *M. anomala* that progressively compacts surrounding soil and modifies mean aggregate size (Blanchart et al. 1997). If this model were correct then patches of compacting species would tend to fade away as soil is being compacted and resource availability decreases. In this 2 yr study, patches were stable but investigations over a larger time range would be necessary to fully investigate the patches' stability. Data on dispersal ability are also lacking. Distinguishing between simple patchy populations (i.e. individuals are aggregated and there is movement) and metapopulations (most individuals stay in their natal patch) is thus not possible. For earthworms, as mark-release-recapture methods are not usable, genetics seems to constitute the only approach allowing us to assess the possible isolation of patches.

The community spatial structure may be controlled by environmental heterogeneity as well as population intrinsic processes (Ettema & Wardle 2002). Soil properties like texture or soil organic matter content may be quite patchy in some soils and therefore the hypothesis of an environmental control (at least partial) remains to be tested. The vegetation cover was homogeneous within the survey plot thus soil organic matter quality is unlikely to change markedly at that scale. In addition, there is no possible soil heterogeneity due to land-use history since the study site has never been cultivated nor disturbed by humans.

The functional aspect of earthworms' distribution is to be assessed at the population scale rather than at the scale of the individuals' functional domains (i.e. the volume of soil under organism influence) simply be-

cause of complex spatial distributions. Sampling must be carried out at the ecological scale, that is the scale at which the population effects are expressed (Shachak & Jones 1995). The “top-down” view claimed by Anderson (1995) is here of utmost relevance. By explicitly integrating the spatial component of the system, we identified scales at which the emergence of species effects may be visible. Not surprisingly, this scale is local which suggests that the species effect is to be assessed at the population or population sub-units scale. At the patch scale, earthworms are potential proximate factors influencing soil processes like soil structure dynamics alongside more distal environmental factors.

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