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Spatial analysis of riparian forest soil macrofauna and its relation to abiotic soil properties

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ABSTRACT

Soil macrofauna play major roles in ecosystem functioning; however the ecological effects of macrofauna are influenced by their spatial distribution. Close relationships to soil properties are one major factor for determining spatial pattern of macrofauna. Information about macrofauna distribution pattern is scarce especially at regional scales. The limited numbers of studies available suggest a considerable influence of soil properties on macrofauna distribution. Therefore, this study was conducted in riparian forest to elucidate spatial patterns of soil macrofauna and their relationship to abiotic soil properties at regional scale. Soil macrofauna abundance, diversity, richness and evenness were analyzed at 200 sampling points along parallel transects which ran perpendicular to a river. The hierarchical sampling design comprised maximum distances of 0.5 km and minimum distances of 1 m between samples. Soil macrofauna was extracted from 50 cm × 50 cm × 25 cm soil monoliths by hand-sorting. At each transect point additional soil samples were taken for analysis of soil texture, standard soil properties and electrolytic conductivity. Data were analyzed using geostatistics (variograms and cross-variograms) in order to describe and quantify the spatial continuity of macrofauna characteristics and their relation to soil properties. The variograms revealed the presence of spatial autocorrelation in the majority of parameters. Also, relationships between macrofauna and soil properties such as soil texture and electrolytic conductivity, could be detected. To get more information about macrofauna distribution patterns and macrofauna–soil-relationships, subsets of the complete dataset were analyzed by means of applied time series analysis. The basic pattern of diversity value along the spatial series could be estimated by an autoregressive model. In addition, state-space analysis revealed that soil texture (silt) was important for estimating soil macrofauna diversity along transects. The study shows that geostatistical analyses as well as applied time series are suitable methods for analyzing macrofauna characteristics and for detecting relationships to soil properties. In contrast to geostatistics, state-space analysis yields additional information about the relative importance of different parameters for estimating macrofauna characteristics.

1. Introduction

Invertebrate soil macrofauna play major roles in ecosystem functioning. Soil macrofauna such as millipedes (Blower, 1985) or insect larvae (Gonglanski et al., 2005) and earthworms affect the physical structure and function of soils and modulate the habitat for other species (Graff and Hartge, 1974; Lawton and Jones, 1995). Since macrofauna can be assessed by means of relatively simple methodological approaches, such as handsorting, soil macrofauna represents a good model for analysis of basic functional aspects of biodiversity in soil. Knowledge about invertebrate macrofauna may thus considerably improve the understanding of ecosystem functioning (Barrios, 2007).

The ecosystem effect of the soil macrofauna like any other component of soil biodiversity is dependent on the spatial distribution of the population (Lawton and Jones, 1995).

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Prerequisite of any estimation of functional effects of macrofauna is therefore an assessment of their distribution patterns. At the field scales, the spatial variability of macrofauna has been the subject of several publications (Guild, 1952; Poier and Richter, 1992; Rossi et al., 1997; Cannavacciuolo et al., 1998; Nuutinen et al., 1998; Decaens and Rossi, 2001; Jimenez et al., 2006; Joschko et al., 2006). Given the ample literature about spatial patterns at the field scale, spatial structures of earthworm populations at the regional scale appeared to be likely (Poier and Richter, 1992; Rossi et al., 1997; Nuutinen et al., 1998).

However, the analysis of biodiversity patterns and their relation to environmental factors at the regional scale is still a challenge for soil biodiversity research. For the regional scale, information about the variability of macrofauna is scarce (Joschko et al., 2006). It is however needed for better understanding the ecology of macrofauna, for predicting macrofauna activity and for designing appropriate management schemes at this scale. One main reason responsible for the absence of information about macrofaunal diversity at the regional scale is the lack of adequate methods for sampling and analyzing data at this dimension.

A key feature of soil information is that each observation relates to a particular location in space. Knowledge of an attribute value is thus of little interest unless location of measurement is known and accounted for in the analysis (Goovaerts, 1999). Including the sample locations in the analysis allows us to observe a spatial process within the sample domain. However, important information may be lost if locations of the observations are not considered (Nielson and Wendroth, 2003). The procedures which do not consider the spatial coordinates of the attributes, can lead to errors in the interpretation of the results (Nielsen and Alemi, 1989) for example the spatial process or the spatial continuity of the observations could not be captured (Nielson and Wendroth, 2003). Geostatistics provides descriptive tools such as variograms to characterize the spatial pattern of continuous and categorical soil attributes (Goovaerts, 1999; Gringarten and Deutsch, 2001). Also, applied time series analysis offers techniques to investigate spatial pattern of soil properties (Nielson and Wendroth, 2003; Timmer, 1998). The potential of applied time series techniques for improving soil biological studies has only started to be exploited (Joschko et al., 2006).

Species distributional patterns are likely to be controlled by many factors acting at different scales (Jimenez et al., 2001). Factors that determine spatial patterning of soil macro-organisms can be divided into two categories: abiotic factors such as climate, soil physical and chemical properties or resource availability, and biotic factors such as inter- and intra-specific competition or dispersal abilities (Aubert et al., 2003; Sereda et al., 2012). Little is known about the factors that control or influence the observed spatial pattern of soil macro-fauna at different scales; presumably, abiotic factors are responsible at least partly, for the spatial pattern of soil macro-invertebrates (Jimenez et al., 2001). In agricultural soils, close relationships between earthworm species and abiotic soil properties have been detected by spatial methods (Joschko et al., 2006).

As factors shaping the spatial pattern of macrofauna, soil properties such as soil texture (Joschko et al., 2006, 2009) have been ascertained. The underlying mechanism of the relationship between macrofauna and abiotic soil properties such as soil texture is their moisture requirement (Graff and Hartge, 1974). Spatial analysis of the relationships between macrofauna and soil properties may be a first step for better understanding macro-ecological principles in different landscapes.

In the last 15–20 years, riparian forests have become recognized as important components of landscapes and serve as a vital link between the aquatic environment and upland ecosystems (Giese et al., 2000). Riparian ecosystems are aquatic-terrestrial ecotones with unique biotic, biophysical and landscape characteristics (Lyon et al., 1998). They are an essential ecotone, since they contribute to restoring and maintaining regional diversity, besides controlling surface water quality by regulating the nutrient inputs (Fernandez-Alaez et al., 2005). Accordingly, sustainability and maintenance of riparian vegetation or restoring of degraded sites is critical to sustain inherent ecosystem function and values (Giese et al., 2000).

The first objective of this study is to analyze spatial relationships between macrofauna (abundance, evenness, richness and diversity) and abiotic soil properties (soil clay and silt content, ECe and organic matter) at the regional scale in an Iranian riparian forest. The basic hypothesis for this study was that spatial analysis may considerably improve the estimation of macrofauna community properties from soil properties compared to classical correlation analysis. The estimation of macrofauna community properties from soil properties would possibly enable prediction of macrofauna distribution from relevant soil maps and could serve as an important tool for regional scale biodiversity studies. The second objective of this study is to evaluate different statistical approaches for modelling spatial relationships between macrofauna and abiotic soil properties. Close links between soil macrofauna and soil properties such as soil texture and soil organic matter are to be expected due to their habitat and feeding requirements. Since soil properties are usually spatially structured in most soils (Goovaerts, 1999), classical correlation analysis is insufficient to detect these relationships (Taylor and Bates, 2013). Two different approaches to spatial analysis were taken: geostatistical analysis and time series analysis. Within the time series analysis approach, the autoregressive and the state-space methods were applied.

A third objective arises from the sampling design. Since the sampling design of the study was optimized for geostatistical analyses with hierarchically organized data sets, the question has to be addressed how time series analysis can be adapted to analyze geostatistically optimized data sets.

2. Materials and methods

2.1. Location and experimental design

The study was carried out in Wildlife Refuge of Karkhe in the riparian forest of the south-western Iran (31°57′–32°05′N and 48°13′–48°16′E). The climate of the study area is semi-arid; average yearly rainfall is about 325.8 mm with a mean temperature of 24 °C. Plant cover mainly comprises *Populus euphratica* and *Tamarix* sp. The sampling was done in March 2009 within a period of 15 days. At this time moisture and temperature are suitable and soil macrofauna reach their highest abundance.

Spatial sampling has to regard the extent, the sampling interval, and the support (area or volume of an individual sample) (Legendre and Legendre, 2012). These parameters must be chosen based on the scientific question as well as physical and practical limitations. According to Mathieu et al. (2004); soil biodiversity is shaped by the co-action of numerous factors. Because these factors act at different spatial scales, and may interact, ecological processes are scale dependent and hierarchically structured. Thus, the study tries to consider spatial variation of soil macrofauna from the local (quasi-homogeneous units of some square meters) to the regional scale (several square kilometres). To address the regional scale, the extent of the study has to stretch over several hundred meters. However, to reveal spatial variation starting at the topic dimension, sampling intervals must include distances of less than 10 m. Due to limited resources (time, workforce) only a certain number of samples could be analysed. Also, the sample support has to be small enough to resolve spatial variation within a few meters, but being large enough suppress micro-variability (within the submeter scale). Consequently, for the description of spatial interaction of macrofauna and soil properties, a hierarchical sampling procedure was chosen. The sampling design consisted of 200 sampling points along parallel transects (perpendicular to the river) (Fig. 1). The distance between transects was 0.5 km. We considered maximum distances between samples of 0.5 km forming the basic grid. Around certain grid points, samples were taken at 250 m, 100 m, 50 m, 20 m, 15 m, 10 m, 5 m, 2 m and 1 m intervals (Fig. 1 and Table 1). These grid points with associated samples on distances <0.5 km are called nests. We considered the gradient of vegetation density to locate the nests. It means that the nests were located in the areas with different gradient of vegetation density; low to high density and vice versa. Hierarchical (or nested) sampling is particularly useful to reveal the scales of spatial processes.

2.2. Soil macrofauna

Soil macrofauna was defined according to Warren and Zou (2002) as invertebrates visible at the naked eye (macroscopic organisms). In this study, geobionts (large soil invertebrates that permanently inhabit the soil), also geophiles (organisms that live in the soil only for some phase of their life) (Maggenti et al., 2005) were assessed.

The macrofauna was extracted from 50 cm × 50 cm × 25 cm soil monoliths by hand-sorting the samples in the field. After detection, the organisms were placed in plastic bags and transported to the lab for species (group) determination and biomass assessment. The number of individuals for each sample was determined on the day of collection.

2.3. Soil analyses

At each transect point, in approximately 1 m distance from the macrofauna sample location, three bulk soil samples (1 kg each) were taken from the upper soil horizon (0–25 cm) for physical and chemical analyses at each sampling campaign. Soil texture was determined by the Bouyoucos hydrometer method (Bouyoucos, 1962). The electrolytic conductivity (ECe) of the mineral soil was determined on a soil: water suspension (1 w:1 v) (Burt, 2004). Soil organic matter was determined using the Walkley–Black method (Bremner, 1960).

2.4. Data preparation

Number of animals (abundance), evenness (Sheldon index), richness (Menhinick index) and diversity (Shannon *H*' index) that are useful to quantify spatial patterns (Gonglanski et al., 2005, 2008) by using PAST version 1.39 (Palaentological Statistics Software Package 2006) were determined in each sample.

The distribution of variables was analyzed with *Q*–*Q* plots (Timmer, 1998). Soil properties and macrofauna abundance were log normally distributed; therefore a log-transformation (log $(x+1)$) was carried out before further analysis.

2.5. Non-spatial statistics

For the initial analysis of the relationship between earthworm parameters and abiotic soil properties, we calculated the correlation among soil properties and macrofauna using the rank correlation coefficient (r_s) (STATISTICA 7.0).

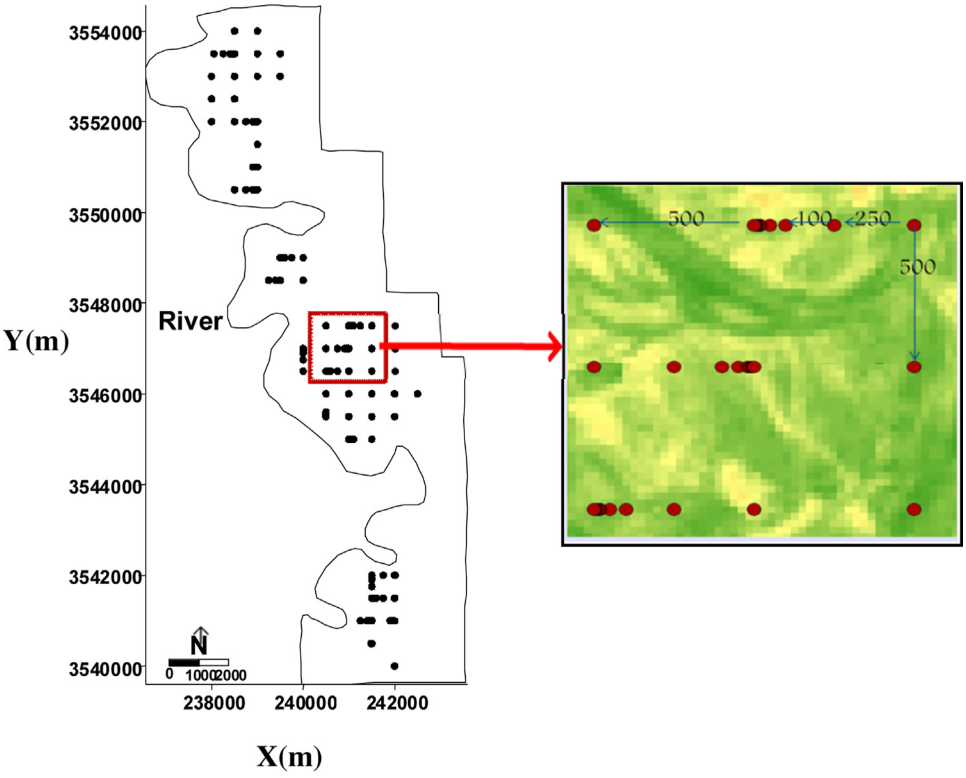

Fig. 1. Experimental design of the study. 200 sampling points arranged along parallel transects. The distance between transects was 0.5 km. Maximum distances between samples was 0.5 km, but samples were also taken at 250 m, 100 m, 50 m, 20 m, 15 m, 10 m, 5 m, 2 m and 1 m at different locations. The coloured subset shows the arrangement of sampling points in more detail. Information was extracted from Indian Remote Sensing Satellite (IRS P_6), Linear imaging self scanner (LISS III).

Table 1
Number of samples which are characterized by the resp. Distance.

Distance (m)	500	250	100	50	30	25	20	15	10	5	2	1	Total number
Number of samples	57	13	16	15	1	1	16	15	16	16	17	17	200

2.6. Geostatistics

The basic tool of geostatistics is the (semi) variogram. The semivariance ($\gamma(h)$) quantifies the dissimilarity of pairs of observations of one variable depending on their spatial separation distance h (Eq. (1)):

$$\gamma(h) = \frac{1}{2N(h)}\sum_{i=1}^{N(h)}[Z(X_i) - Z(X_i + h)]^2 \tag{1}$$

where z is the measured variable (soil macrofauna abundance, evenness, richness and diversity and soil clay content, soil silt content, ECe and organic matter), x_i is the coordinate of one sample, $x_i + h$ is the coordinate of another sample at distance (lag) h and $N(h)$ is the number of pairs of samples $z(x_i)$ and $z(x_i + h)$. The semivariance essentially expresses the average variance of pairs of points at a given distance.

Empirical variograms are plots of the semivariances, averaged over distance classes (called lags), against the lag distance. To describe spatial autocorrelation of a variable quantitatively, a (theoretical) variogram model can be fitted to the empirical variogram in order to obtain the model parameters nugget, sill and range. The nugget effect is the variogram's values at lag distance zero (positive intercept on the ordinate). It summarizes the micro-variability, which cannot be captured due to sampling design, and the measurement error. The sill of the variogram is the variance at which the variogram model reaches (asymptotically) a maximum. In many cases the empirical variogram levels out at a certain distance. These cases are described by so called bounded variogram models like the spherical or exponential model (Webster and Oliver, 2009). The lag distance at which the bounded variogram reaches the sill is called the range. At distances smaller than the range we can observe spatial autocorrelation while observations with distances larger than the range are regarded as spatially independent (Gringarten and Deutsch, 2001; Webster and Oliver, 2009). An indicator of the strength of the spatial autocorrelation is the nugget to sill ratio. A variable is considered to have a strong spatial dependence if the ratio is less than 25%, and has a moderate spatial dependence if the ratio is between 25% and 75%; otherwise, the variable has a weak spatial dependence (Sun et al., 2003).

In order to get good estimates of the empirical (and theoretical) variogram, it is advisable to have more than 100 pairs per lag interval. To obtain sufficient number of pairs over small distances for variogram modelling sampling design can be optimized by so called nested sampling (Webster and Oliver, 2009). In nested sampling the points are not arranged on a regular grid. Instead sampling distances are varied from small to large, often chosen in a geometric progression. This kind of geostatistical sampling design provides a higher proportion of sample pairs over small distance as compared with sampling on regular grids. Eventually this leads to better model of the variogram at its origin and a better estimate of the nugget.

In order to gather information about the spatial connection between any two variables, and to compare the similarity of their spatial structure patterns, cross-variograms can be constructed. Empirical cross-variograms are plots of the cross-semivariance against the lag distance. The cross-semivariance for two variables is calculated as follows (Eq. (2)):

$$\gamma(h) = \frac{1}{2N(h)}\sum_{i=1}^{N(h)}[Z_u(X_i) - Z_u(X_i + h)] \times [Z_v(X_i) - Z_v(X_i + h)] \tag{2}$$

where z_u is the primary variable, (soil macrofauna abundance, evenness, richness and diversity), z_v is the covariate (soil clay content, soil silt content, ECe and organic matter), x_i is the coordinate of the sample, $N(h)$ is the number of pairs of samples $z(x_i)$ and $z(x_i + h)$, separated by the separation distance (lag) h (Webster and Oliver, 2009). Geostatistical analysis was performed using the software GS+ version 5.1.1 (Gamma Design Software, 1995).

2.7. Time series analysis and state-space analysis

Time series analysis was developed for data that have been observed at different points in time; these data series are often characterized by correlation introduced by the sampling of adjacent points (Shumway and Stoffer, 2000). Time series analysis techniques may also be applied to spatial data, for instance, from soil or agricultural sciences (Nielsen and Alemi, 1989; Nielson and Wendroth, 2003; Legendre and Legendre, 2012). For the analysis, data have to be sampled in a certain order and in a close enough distance for showing autocorrelation between data points. Usually, the adequate sampling design is found in transect studies with evenly spaced sampling locations (Nielson and Wendroth, 2003).

However, time series techniques may be applied to non-transect data, if data are re-organized or reoriented for analysis. E.g. Stevenson et al. (2001) successfully analyzed data, obtained in a block design experiment, with time-series analysis, after reorganization of data. In the same sense, Joschko et al. (2009) analyzed earthworm abundances and soil properties assessed along four transects in a farmer's field. For spatial analysis, values for each earthworm parameter and soil properties along the four transects were combined to one single data row and plotted as a continuous sequence beginning with the first plot of the left transect and ending with the first plot of the right transect The sequence of plots at the endpoints of the transects was chosen so that distances between plots were minimized.

The nested sampling design in our study, which was optimized for geostatistical analysis, necessitates a reorganization of the data for time series analysis. First, a sequence was created by using data with distances from 1 to 500 m, starting with sample point 1 in the left hand corner; the sampling locations (200) were connected by moving from one sampling location to the next from one row to the other while minimizing distances between locations.

The distance between sampling points deserves special attention. The ideal experimental design is the use of regular, equal distances (Nielson and Wendroth, 2003). If distances are irregular they should at least belong to one distance class, if time series analysis is to be applied (Nielsen, pers. comm.).

Distances from 1 to 500 m or even 10–500 m are unsuited for assembling them in one distance class (Nielsen, pers. comm.) Therefore, two data sets, characterized by different distances between data points, were prepared. One group (Series I) comprised main distances from 10 to 100 m which were the distances within the sampling nests. Eighteen sampling nests (data point) were connected with the aim of minimizing distances between them. Consequently, distances between the sampling nests were variable and in most cases exceeded 100 m.

The second group of data (Series II) comprised distances between 50 and 500 m, spaced evenly over the study area. With these three data sets (all data, Series I, Series II), the following calculations were carried out. First, the distribution of data was analyzed with *Q*–*Q* plots (Timmer, 1998). Subsequently, the data series were tested for first and second order stationary (Shumway and Stoffer, 2000).

Subsequently, autocorrelation functions, partial autocorrelation functions and cross correlation functions were calculated. For this purpose, the open source program ASTSA (Stoffer, 2010) was used. When autocorrelation in data series is detected, this information can be used in autoregressive modelling.

2.7.1. ARMA models

In autocorrelated data series, the ARMA modeling allows to quantify the autocorrelation by introducing an autoregressive (AR) term and a moving average (MA) term (Shumway and Stoffe, 2000; Nielson and Wendroth, 2003). The variable of interest Z_i (soil macrofauna abundance, evenness, richness and diversity) is estimated by relating the observation at location i to the observation at location $i-1$ (or to locations $i-1$, $i-2$, $i-3$, $i-n$, depending on the order p of the AR model). In addition, for estimating the variable of interest, the moving average of order q is used, according to Eq. (1) (Nielsen and Alemi, 1989).

$$Z = \sum_{n=1}^{p} Z_{i-n} - \sum_{n=1}^{q} \omega_{i-n} + \omega_i \tag{3}$$

ω_i is a white noise (independent and identically distributed normal variable). While the autocorrelation function (number of lags of autocorrelation) determines the order of the MA-term, the partial autocorrelation function is used as indicative of the order of the AR term (Shumway and Stoffer, 2000). For evaluating the model, the autocorrelation function of the residuals of the autoregressive model was calculated. All calculations were carried out with ASTSA (Stoffer, 2010). For these section, the following parameters were used: p (autoregressive order) = 1, d (distance order) = 0, q (moving average) = 1.

2.7.2. State space models

With state-space analysis, the system's state, characterized by a state variable or a set of variables, is analyzed on its way through space or time (Nielson and Wendroth, 2003). The state Z_i at a given location i is related to the state at the previous location $i-1$ described by the state equation $Z_i = \Phi Z_{i-1} + \omega_i$, where Φ is a matrix of transition coefficients and ω_i is an error term (Nielsen and Alemi, 1989; Wendroth et al., 1992, 1997; Shumway and Stoffer, 2000; Nielson and Wendroth, 2003). The state variables are related to observed variables Y_i (soil macrofauna abundance, evenness, richness and diversity) through $Y_i = M_i Z_i + \omega_i$, where M_i is a matrix of observation coefficients characterizing the relationship between underlying state and observation, Z_i (soil clay content, soil silt content, ECe and organic matter) is the true state vector and ω_i is an error term quantifying the measurement uncertainty or noise (Nielsen and Alemi, 1989; Wendroth et al., 1992, 1997; Nielson and Wendroth, 2003; Timm et al., 2003). A Kalman filter with an EM (Expectation–Maximization) algorithm helps to separate between noise and reliable data (Nielsen and Alemi, 1989; Nielson and Wendroth, 2003).

The challenge is to select appropriate variables which characterize the system's state under consideration. For state-space modelling, variables showing autocorrelation and cross-correlations were selected for the state vector (Nielson and Wendroth, 2003). Subsequently, state-space analysis was carried out according to Nielson and Wendroth (2003). First, the data were normalized (Nielson and Wendroth, 2003). For analysis the program STATE (Applied Statistical Time Series Analysis 2010, R. Shumway, provided by courtesy of Ole Wendroth) was used.

3. Results

3.1. Rank correlation analysis between macrofauna and abiotic soil properties

The soil macrofauna comprised the systematic groups of beetles (Coleoptera, 27% of individuals), millipedes (24%), snails (21%), earthworms (*Lumbricidae*) (9%), Diptera (15%) and others, for example spiders (4%), ants (about 0.5%), reaching an abundance of 43.1 individuals/m^2. Thus, not only geobionts, but also geophiles were assessed.

Rank correlation analysis of soil macrofauna diversity indices and soil properties indicated only weak relationships between macrofauna indices and soil properties (Table 2). Significant relationships were found between macrofauna diversity indices (abundance, evenness, richness, diversity) and silt content (positive), macrofauna diversity indices (abundance, evenness, richness, diversity) and clay content (negative), macrofauna diversity indices (except abundance) and ECe (negative) and, with respect to some macrofauna indices, weak positive relationships to soil organic matter content (Table 2).

3.2. Geostatistical analysis of macrofauna and soil properties

Macrofauna diversity indices were spatially structured: the variograms revealed the presence of spatial autocorrelation. For all these indices, bounded semivariograms were found. The variograms of macrofauna diversity indices were characterized by relatively large nugget values, which can be explained by sampling error and short range variability.

The parameters characterizing soil properties were spatially structured as well. The parameters of the theoretical models fitted to the experimental variograms are given in Table 3. The variogram of clay content was spherical; silt content and ECe were exponential. The variograms of macrofauna diversity indices (evenness, richness and diversity) were exponential. But, macrofauna abundance showed a spherical model. All variograms showed positive nugget.

Spatial similarity between variables, indicating potential relationships between macrofauna and soil properties, was evaluated by cross-variograms for pairs of macrofauna indices and measured soil properties (clay, silt, ECe). Model parameters (nugget, sill, range) are presented in Table 4. According to the cross-variogram, soil texture (clay and silt) was spatially closely related to macrofauna indices (Table 4)

Table 2
Rank correlation coefficients (r_s) between macrofauna and soil properties.

	Silt (%)	Clay (%)	ECe (dS/m)	OM (%)
Abundance	0.201	−0.195	0.009	0.071
Evenness	0.120	−0.214	−0.070	−0.019
Richness	0.200	−0.238	−0.082	0.188
Diversity	0.199	−0.219	−0.101	0.150

ECe: electrolytic conductivity; OM: soil organic matter content; abundance: number of animals; evenness (Sheldon index); richness (Menhinick index) and diversity (Shannon H' index).

Table 3
Parameters of the theoretical models fitted to the experimental variograms (macrofauna and soil properties).

Variable	Model	Nugget (C_0)	Sill ($C_0 + C$)	Nugget to sill ratio	Range (m)	R^2	R^2 of cross-validation
Abundance	Spherical	0.61	1.49	0.41	500	0.81	0.30
Evenness	exponential	0.08	0.28	0.29	2937	0.65	0.29
Richness	exponential	0.20	0.48	0.42	2295	0.50	0.29
Diversity	exponential	0.15	0.31	0.48	952	0.59	0.29
Clay	Spherical	0.07	0.14	0.50	365	0.59	0.47
Silt	exponential	0.05	0.16	0.31	2515	0.48	0.49
OM	Spherical	0.54	1.08	0.50	269	0.68	0.20
ECe	exponential	0.49	1.46	0.33	500	0.81	0.54

Co: nugget variance: the variogram values at lag distance zero. Sill: the variance at which the variogram model reaches a maximum; C: structural variance; range: the lag distance at which the bounded variogram reaches the sill; nugget to sill ratio: the indicator of the strength of the spatial autocorrelation, the variable is considered to have a strong spatial dependence if the ratio is less than 25%, and has a moderate spatial dependence if the ratio is between 25% and 75%; otherwise, the variable has a weak spatial dependence. R^2: goodness of fit of theorical model fitted to the experimental variogram; R^2 of cross-validation: regression coefficient. ECe: electrolytic conductivity; OM: soil organic matter content; abundance: number of animals; evenness: Sheldon index; richness: Menhinick index; diversity: Shannon H' index.

Table 4
Parameters of cross-semivariograms for pairs of measured macrofauna and soil properties.

Pair of properties	Model	Nugget (C_0)	Sill ($C_0 + C$)	Nugget to sill ratio	Range (m)	R^2	R^2 of cross-validation
Abund.-silt	Exponential	0.10	0.27	0.37	568	0.70	0.23
Abund.-ECe	Spherical	1.46	9.88	0.15	136	0.85	0.31
Abund.-clay	Exponential	0.12	0.36	0.33	800	0.80	0.23
Abund.-OM	Spherical	0.36	0.84	0.43	253	0.80	0.29
Evenness-silt	Exponential	0.03	0.07	0.43	434	0.75	0.21
Evenness-ECe	Spherical	0.43	3.28	0.13	109	0.68	0.22
Evenness-clay	Exponential	0.03	0.10	0.30	798	0.87	0.21
Evenness-OM	Spherical	0.09	0.22	0.41	259	0.91	0.21
Richness-silt	Exponential	0.04	0.09	0.44	420	0.62	0.23
Richness-Ece	Exponential	0.99	6.68	0.15	990	0.92	0.22
Richness-clay	Spherical	0.06	0.28	0.21	5037	0.84	0.23
Richness-OM	Exponential	0.22	0.44	0.50	540	0.81	0.21
Diversity-silt	Exponential	0.03	0.17	0.18	2843	0.61	0.24
Diversity-Ece	Exponential	0.78	5.01	0.16	846	0.91	0.25
Diversity-clay	Exponential	0.04	0.15	0.27	1207	0.90	0.24
Diversity-OM	Spherical	0.17	0.33	0.52	359	0.83	0.24

Co: nugget variance; C: structural variance; R^2: goodness of fittness of theorical model fitted to the experimental variogram; R^2 of cross-validation: regression coefficient. ECe: electrolytic conductivity, OM: soil organic matter content, Abund. = abundance: Number of animals, Evenness (Sheldon index), Richness (Menhinick index) and Diversity (Shannon H' index).

3.3. Time series analysis: autocorrelation functions of macrofauna and abiotic soil properties

In contrast to geostatistical analysis, time series analysis required a data transformation prior to analysis to derive a one-dimensional arrangement. Based on the data selection of series I and II, the following results in macrofauna and soil texture variables were found (Table 5). Except ECe in data series II all variables showed autocorrelation; the number of lags however was mostly between 1 and 2. Only in case of soil texture the autocorrelation stretched over more, maximally 4 lags.

Table 5
Autocorrelation function of data series I (10–100 m) and series II (50–500 m).

ACF	10–100	Lags	50–500	Lags
Abundance	Yes	2	Yes	1
Eveness	Yes	2	Yes	1
Richness	Yes	2	Yes	1
Diversity	Yes	1	Yes	1
ECe	Yes	2	No	0
Clay	Yes	4	Yes	2
Silt	Yes	4	Yes	3

ACF: autocorrelation function, ECe: electrolytic conductivity, abundance: number of animals, evenness (Sheldon index), richness (Menhinick index) and diversity (Shannon H' index).

3.4. Autoregressive models of macrofauna indices

The presence of autocorrelation could be used in modelling the data series by means of an autoregressive (AR) model. In the following, the procedure of AR modelling is shown with the variable Shannon index (50–500 m). First, the autocorrelation function is shown, which indicates autocorrelation over one lag, because its autocorrelogram value exceeds coefficient interval in one lag (Fig. 2a). This made it eligible to be incorporated in first order autoregressive state-space model. The order of the moving average (MA) model part is thus one. Second, the partial autocorrelation function is shown (Fig. 2b) which indicated autocorrelation also in the first lag that justifies an AR model with the order one. The respective AR model (1,1) estimates the basic pattern of diversity value change along the spatial series (Fig. 3). The residuals however, despite a lack of autocorrelation, were still very large. Also, most of the fluctuations were not grasped by the model. Similar results were found in the variables macrofauna abundance, evenness and richness.

3.5. Cross-correlation functions of macrofauna and soil properties

In order to improve the modelling, cross-correlation functions between macrofauna indices and soil properties were calculated (Table 6). In the 10–100 m spatial series, three pairs yielded cross-correlations (Table 6). The relationship between evenness and clay was negative but the relationship between Menhinick or Shannon

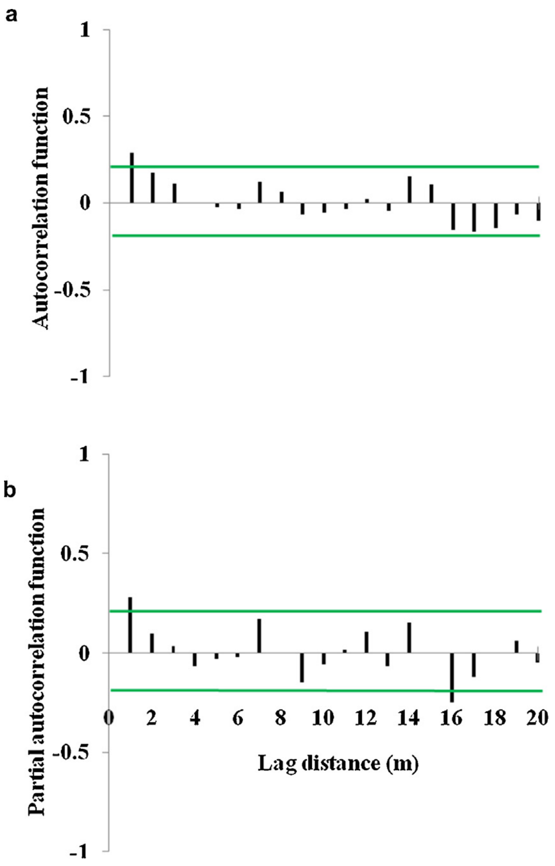

Fig. 2. Autocorrelogram for Shannon *H′* (50–500 m spatial series); a: autocorrelation function of Shannon *H′* (50–500 m spatial series) and b: partial autocorrelation function of Shannon *H′* (50–500 m spatial series). Shannon *H′*: diversity; upper and lower lines: 95% confidence interval is ±0.197.

index and silt was positive. In Fig. 4, the positive relationship between Shannon index and silt is shown. In the 50–500 m spatial series, the only cross-correlation function was found in the variables of Shannon and silt; the results indicated again a positive relationship between the two series (Fig. 5).

3.6. Autoregressive state-space model of macrofauna

On the basis of these findings, autoregressive state-space analysis was carried out to estimate macrofauna diversity at each location with soil properties. With the data series I (10–100 m), however, based on the three variable pairs showing cross-correlations between macrofauna indices and soil properties, no reasonable state-space model could be found.

In contrast, in the data series II (50–500 m), a state-space model could be found for estimating a macrofauna index based on soil property. With state-space analysis, the Shannon index could be estimated with soil texture (silt) (Fig. 6). The coefficient of determination was $R^2 = 0.82$. About 38% of variability of the Shannon index could be explained with silt content; however, the contribution of preceding values of the Shannon index (SH_{i-1}) to the estimation was considerably higher (62%) (Fig. 6).

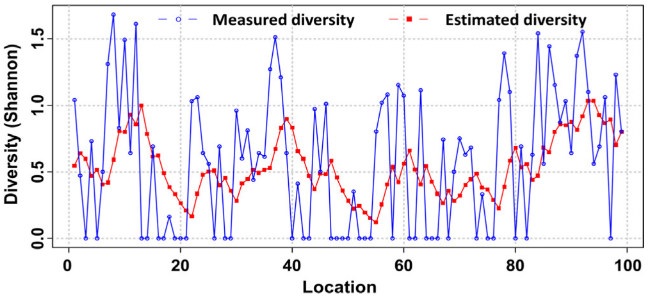

Fig. 3. ARMA model of the spatial series of Shannon (50–500 m spatial series).

Table 6
Results of cross-correlation function analysis.

CCF, 10–100 m	ECe	Clay	Silt
Abundance	No	No	No
Evenness	No	Yes	No
Richness	No	No	Yes
Diversity	No	No	Yes
CCF, 50–500 m	ECe	Clay	Silt
Abundance	No	No	No
Evenness	No	No	No
Richness	No	No	No
Diversity	No	No	Yes

CCF: cross-correlation function; ECe: electrolytic conductivity, abundance: number of individuals, evenness (Sheldon index), richness (Menhinick index) and diversity (Shannon *H′* index).

A comparison of the different statistical methods used in this study and their corresponding results that were obtained are given in Table 7.

4. Discussion

This study addresses macrofauna abundance, diversity, evenness and richness along transects in the riparian forest of the south-western Iran. Emphasis was laid upon the relationship between macrofauna and soil properties such as soil texture. However, biotic interactions as well can contribute to the formation of spatial patterns in soil fauna (Birkhofer et al., 2010). Sereda et al. (2012) pointed out the importance of considering biotic and abiotic processes when studying the distribution of macrofauna.

As expected, all macrofauna indices studied were spatially structured, with ranges of several hundred meters and more. It may be because of large scale heterogeneity, reflecting gradients of soil texture and vegetation system (Ettema and Wardle, 2002). Spatial relationship between soil macrofauna diversity and vegetation density have been found by Gholami et al. (2014) in this area, that may confirm the effect of vegetation beside soil properies, on spatial variability of soil macrofauna diversity at large ranges. Small-scale variability was not captured well, which is indicated by the large nugget variance (Joschko et al., 2009). It can be explained by sampling error, short range, random and inherent variability.

Due to the spatial structure of macrofauna community properties, the possibility for the application of classical statistics for analysis of the macrofauna–soil properties relationship was limited (Joschko et al., 2009; Taylor and Bates, 2013). So predictably, rank correlation analysis with data that shows spatial dependencies, revealed, that relationships between macrofauna and soil properties were not strong.

Since soil properties also showed spatial dependencies, cross semivariograms were calculated. With this approach, relationships were detected between macrofauna indices and soil properties, especially soil texture, i.e. silt and clay content. However, with the geostatistical approach, no further details of the relationship between macrofauna and soil properties could be identified.

Therefore, the time series approach was chosen in order to get more information about the nature of this relationship. Comparable to the geostatistical results, the time series analyses showed spatial autocorrelation in almost every parameter studied, with autocorrelation over 1–2 lags, corresponding to distances of

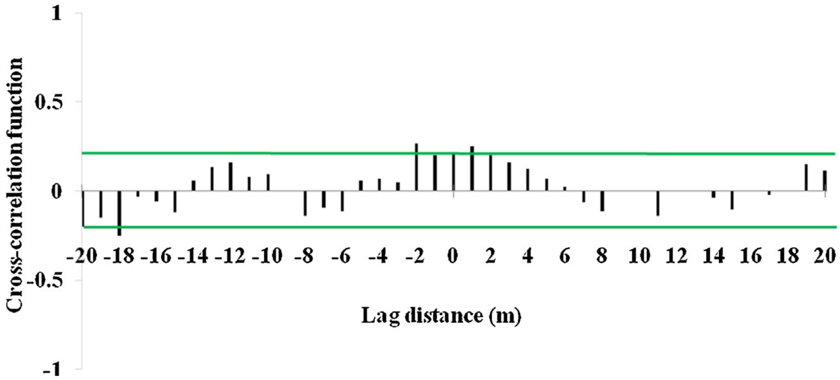

Fig. 4. Cross-correlation function between Shannon index and silt (10–100 m spatial series). Upper and lower lines: 95% confidence interval is ±0.197.

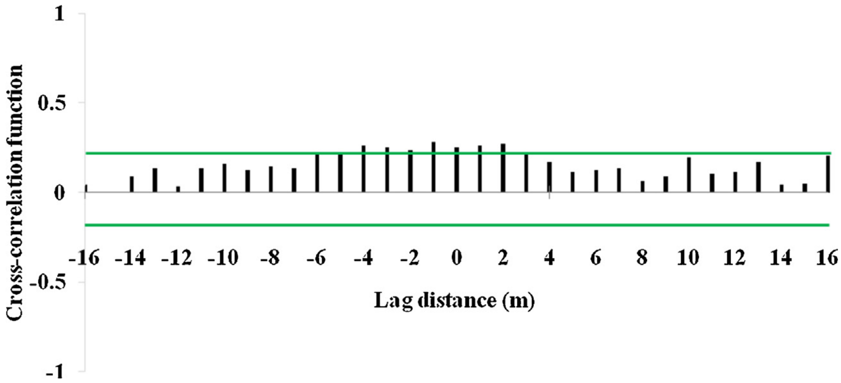

Fig. 5. Cross-correlation function between Shannon and silt (50–500 m spatial series). Upper and lower lines: 95% confidence interval is ±0.197.

maximally 200 m (10–100 m series) or 1000 m (50–500 m). The autocorrelation function provides information about the separation distance with which a measured value is related to its neighbours and, it is a manifestation of the fact that at or beyond the lag distance, observations will vary at random (Nielson and Wendroth, 2003).

Classical, ordinary least squares linear regression analysis was unsuitable because observations were not independent from each other (Joschko, 2009; Aquino et al., 2015). Therefore, quantification of the macrofauna community properties–soil relationships across transects was carried out by autoregressive state-space analysis (Nielson and Wendroth, 2003). In fact, autoregressive (AR) models were tested positively for estimating macrofauna indices along transects. However, there were still considerable large residuals which necessitate further efforts to better describe the spatial distribution of macrofauna indices.

The AR model was used for the 50–500 m space data points. The question arises, how biodiversity indices could be autocorrelated at this spacing. The likely reason is close relationships of biota to spatially structured soil properties, as already suggested by Ettema and Wardle (2002). Therefore, as a next step, cross-correlation functions were calculated. The numbers of cross-correlations were considerably lower than the number of valid cross-variograms. This fact is probably due to the amount of data available for the geostatical analysis (200 data points) compared to the less than 100 data for the CCF analysis. With this approach, positive

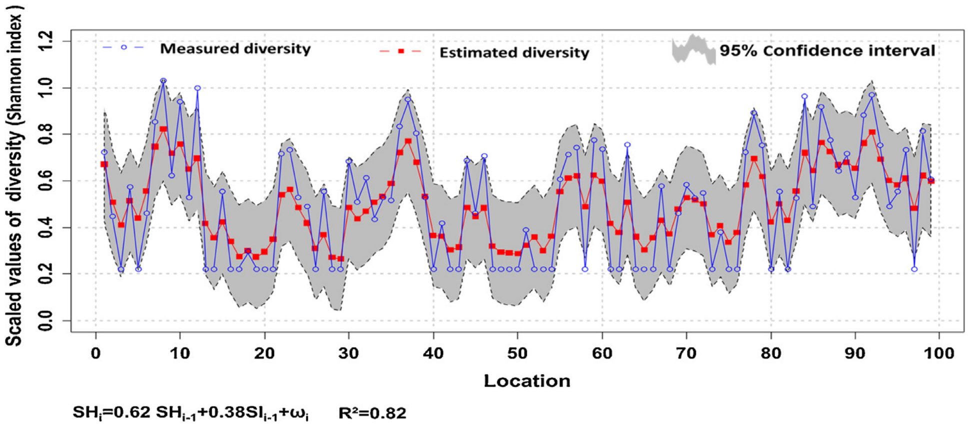

Fig. 6. Estimating the Shannon Index (diversity) of soil macrofauna with silt; state-space analysis, data series II (50–500 m). SH: Shannon index; SI: silt.

Table 7
Comparison of the statistical methods applied in this work.

	Rank correlation co-efficient	Geostatistics (variogram)	Autoregressive moving average (ARMA)	State—space model
Approach	Aspatial global approach	Spatial global approach	Serial/spatial global approach	Serial/spatial local approach
Results	Rank correlation analysis of soil macrofauna diversity indices and soil properties indicated only weak relationships between macrofauna indices and soil properties	The variograms revealed the presence of spatial autocorrelation. According to the cross-variograms, soil texture (clay and silt) was spatially closely related to macrofauna indices	Time series analysis yields more information about the relationship between fauna and soil than geostatistics alone. The ARMA model shows reasonable estimation of diversity values along the spatial series	State-space analyses described macrofauna diversity as a function of soil texture. It was found, that for estimating macrofauna diversity (Shannon Index), the silt content contributed with about 38%
Hierarchical sampling design	Applicable	Applicable	In contrast to geostatistical analysis, time series analysis required a data transformation prior to analysis to derive a one-dimensional arrangement	In contrast to geostatistical analysis the sampling design has to be optimized and adapted with ideally an equidistant sampling design
Advantage	rank correlation analyses helped to select the most important soil properties being related to macrofauna properties	Variography analyze the spatial autocorrelation of the variables	The ARMA model shows estimation of diversity values along the spatial series	State-space analysis has a great potential for analyzing relationships between different spatial series of data such as soil biodiversity and environmental variables at regional scales
Weakness	Due to the spatial structure of macrofauna and soil properties, the possibility for the application of classical statistics such as Pearson's or Spearman's correlation is limited for two reasons: 1) technically, spatial autocorrelation violates the underlying assumption of "independent observations" in the classical statistical methods; 2) from the ecological standpoint, classical methods do not suffice since they cannot discriminate between "external" and "internal" drivers of the macrofauna's spatial distribution	Variography is less suitable to assess the interactions between two more variables. Multivariate variography, based on cross-variograms, can be become very complex and difficult to interpret. And it is not well suited to sort out the contribution of "external" and "internal" effects on spatial distribution	ARMA, is not fully compatible with the spatial data set used here. Data transformation was necessary before ARMA was applicable	State-space analysis, is not fully compatible with the spatial data set used here. Data transformation was necessary before state-space was applicable

relationships between macrofauna and silt content, negative relationships to clay content were detected. Interestingly, these general relations correspond to the rank correlation analysis, which however must not always be the case.

State-space models or dynamic linear models have been used to characterize macrofauna diversity at each location with soil properties (Shumway and Stoffer, 2000). This approach has been widely and successfully applied in agronomy, mainly when compared to classical models of multiple regressions (Aquino et al., 2015). Interestingly, the first data set yielded no valid state-space models. Obviously, the design with large distances between sampling nests was not adequate for the state-space approach which necessitates ideally equidistance between data points. Only the second data set, consisting of widely distributed samples 50–500 m apart dispersed over the whole study area, yielded a reasonable state-space model, with an R^2 of 0.82 between observed and estimated values. Also in this case, confidence limits were still very large, and the coefficient of determination relatively low (Nielson and Wendroth, 2003), but the results indicate that this approach was an important step in the right direction.

With this state-space approach, the relative importance of the soil to estimating the variable of interest could be ascertained. State-space analyses enabled to describe macrofauna diversity along transects as a function of soil texture. It was found, that for estimating macrofauna diversity (Shannon Index), the silt content contributed with about 38% to the estimation.

Soil properties are important for soil biota and often determine their distribution by texture (Joschko et al., 2010) that characterizes the physical environment for macrofauna. The silt content indicates the water availability in soils. Soil moisture is one of the most important environmental variables for soil biota. Recently, soil texture, especially clay and fine silt, has been used for classifying earthworm populations in sandy agricultural soils in Germany (Joschko et al., 2009). Our observations thus partly support the findings of Joschko et al. (2009) that showed soil texture is important for estimating earthworm parameters along transects using state-space analysis.

Contributing to these results might be the fact, that the macrofauna studied was a heterogeneous systematic group, and comprised besides geobionts, geophiles such as diptera larvae where the relationship to soil properties might be less close. The relationship can be expected to be considerably closer, if only one systematic group, e.g. earthworms, is addressed. The biodiversity as well as the soil parameters could be improved and optimized in future studies. The relationship between biodiversity characteristics and environmental variables was recently introduced as indicator of sustainability (Vellend et al., 2007). This concept might also be applicable to soil ecological parameters and should be studied more closely.

5. Conclusion

Spatial studies considerably improve the analysis of macrofauna distribution and the analysis of macrofauna–soil relationships at the regional scale. Time series analysis yields more information about the relationship between fauna and soil than geostatistics alone. As revealed by state-space analysis, soil silt content is a strong predictor for macrofauna diversity. State-space analysis may help to better explore and understand relationships between soil biodiversity and environmental variables at regional scales. However, for the application of AR modelling and state-space analysis, the sampling design has to be optimized and adapted with ideally an equidistant sampling design. It was known in this study that the application of modern statistical techniques helps to identify links between biodiversity and its environment and may thereby advance future biodiversity researches.

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