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Clusters in earthworm spatial distribution

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Summary

The spatial distribution of two earthworm groups (*Sthulmania porifera* and *Chuniodrilus zielae* (Eudrilidae) on the one part and *Millsonia anomala* (Megascolecidae) on the other part) was analysed using the SADIE system. Earthworms were sampled in November 1995 in a grass savanna at Lamto (Côte d'Ivoire) using 100 sampling points distributed in a square grid (mesh size 5 m). The investigated plot was a 45 × 45 m square. The global index of aggregation I_a, available in the SADIE method, indicated that both groups were significantly clustered. Further analyses were conducted using the "Red-Blue" plots approach. This new method is based on a standardized and dimensionless index that makes it possible to identify patches and gaps. Results indicated the presence of significant patches for both groups. Clusters corresponded to areas of various size and shape. As an example, in *M. anomala*, patches and gaps represented respectively 22.8 % and 17.6 % of the total area under study. Size and shape of the observed clusters were very variable and contour maps of the clustering indices allowed visualizing of these structures. For the eudrilids, one patch and two gaps were reported while there were six patches and six gaps in the case of *M. anomala*. The spatial distribution of cluster centroids did not differ significantly from complete spatial randomness. In addition, no spatial association was reported between the clusters of these earthworm groups.

Key words: Earthworms, clusters, patches, gaps, SADIE system, spatial pattern

Introduction

The horizontal distribution of earthworms is complex and structured at different spatial scales (Phillipson et al. 1976; Poier & Richter 1992; Rossi et al. 1997; Nuutinen et al. 1998; Decaëns & Rossi 2001; Jiménez et al. 2001). The spatial distribution of a species may feature clusters that are defined as regions of either relatively large (i.e. a patch) or low (i.e. a gap) density (Perry et al. 1999). Therefore patches and gaps are defined as areas where local species density is either significantly higher or lower than the mean population density. Until recently there was no statistical tool available to perform cluster analysis on the basis of species count data. A corpus of methods called the SADIE system was proposed by Perry et al. (1996) to perform various spatial analyses of count data (e.g. beetle larvae: Perry et al. 1996; cyst nematodes: Perry 1998; cereal aphid: Perry et al. 1999). In this work, the SADIE analysis was used to assess the spatial distribution of the eudrilids *Sthulmania porifera* (Omodeo & Vaillaud) and *Chuniodrilus zielae* (Omodeo) and the megascolecid *Millsonia anomala*

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(Omodeo) in an African grass savanna (Lamto, Côte d'Ivoire). Beyond determining whether distributions were random or not, this survey aimed at finely describing clusters and assessing their spatial distribution. The earthworm species under study were defined as important factors in soil structure dynamics (Blanchart et al. 1997) and therefore the distribution of their populations can have important consequences for soil functioning.

Materials and Methods

Sites and species

Earthworms were sampled in November 1995 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 is 28 °C. Monthly variations in rainfall and temperature define a drought season from December to February and a rainy season from March to November, interrupted by a decrease in rainfall during August. The investigated plot was randomly located within a large area covered with *L. simplex* and sparse palm trees (*Borassus aethiopium*). The soil is sandy (sand ca. 80 %) with low organic matter content (ca. 1.5 %). Two important earthworm functional groups were sampled. The decompacting earthworm group mainly includes two small-sized species belonging to the Eudrilidae family, namely *Chuniodrilus zielae* and *Sthulmannia porifera* (Blanchart et al. 1997). They excrete small casts, destroy large aggregates and tend to decrease soil bulk density. The second group investigated here contains only one species, the megascolecid *Millsonia anomala* that is a medium-sized endogeic earthworm that dominates the earthworm community in terms of biomass. It ingests small aggregates (< 2.0 mm in diameter) and excretes casts larger than 5.0 mm. It thus belongs to the functional group of soil compacting earthworms (Blanchart et al. 1990).

Earthworms were sampled in November, at the time populations reach their highest density and biomass (Lavelle 1978). Samples were taken in a 10 × 10 grid, the points being separated by 5 m. Earthworms were hand-sorted from a 25 × 25 × 10 cm soil monolith. They were identified, counted and released back into the soil. Because adult individuals with visible external sexual organs are required to distinguish *C. zielae* and *S. porifera*, both species were recorded as a single group and hereafter referred as the "Eudrilidae" group.

Statistical analyses

Earthworm counts were analysed using the Spatial Analysis using Distance IndicE (SADIE) (Perry et al. 1996; Perry 1998; Perry et al. 1999). The approach is specifically adapted to count data and provides a global index of aggregation, I_a. For a random distribution the expected index value is 1, while it is larger for aggregated patterns (Perry et al. 1996). A local cluster index was estimated for each sampling point. The latter index may be either positive or negative indicating that the corresponding unit tends to be respectively a member of a patch or a gap (see Perry et al. 1999 for a complete description of the method). Positive and negative index values are respectively referred to as vi and vj following the original notation by Perry et al. (1999). The vi and vj values are tested for departure from randomness using a set of 1560 permutations (Perry et al. 1999). The index values were submitted to further statistical analyses in order to examine the presence of spatial autocorrelation. The spatial dependence was tested using a Moran's I correlogram, with Bonferroni correction (Oden 1984, Legendre & Fortin 1989). Variograms were also estimated and the index values were mapped after interpolation by block kriging using 1 × 1 m blocks (Webster & Oliver 1990).

Following the original proposition by Perry et al. (1999) we used heuristic thresholds of 1.5 and –1.5 for vi and vj index values, respectively: sampling units associated with index values >1.5 indicated patches, whereas sampling units associated with index values <–1.5 revealed the presence of gaps. Isolating these points made it possible to a) identify clusters and determine their type, b) compute their surface and c) derive the coordinates of their centroids.The spatial distribution of the clusters themselves was explored using mean nearest neighbour distance analysis (Clark & Evans 1954) applied to coordinates of cluster centroids. In addition, the spatial association between clusters of both earthworm groups was assessed using the new SADIE extension proposed by Winder et al. (2001).

The analyses reported here can be summarised in 4 steps: 1. SADIE analysis of count data (statistical testing) 2. Contour mapping of indices values (identification of clusters) 3. Mapping of values exceed the threshold (filtering significant values) 4. Cluster spatial pattern and shape analysis.

Results

Descriptive statistics and aggregation indices

Means of counts were respectively 7 and 1.67 individuals per sampling unit for the eudrilids and *M. anomala*, respectively. The variance of counts was high and led to a significant variance-to-mean aggregation in-

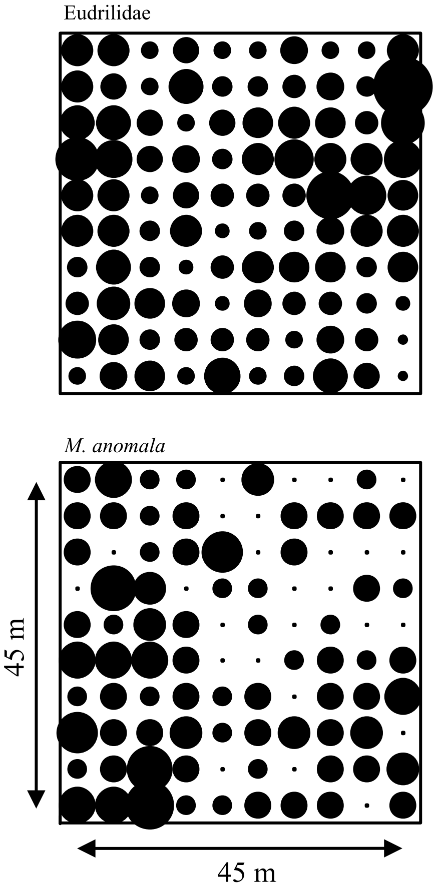


Fig. 1. Spatial distribution of counts for Eudrilidae and *M. anomala*

dex, as ascertained by a chi-square test (Southwood & Henderson 2000) (Table 1). Fig. 1 shows the spatial distribution of these counts.

The global aggregation index I_a was high (1.5 and 1.9 for eudrilids and *M. anomala* respectively) and significant (Table 1). Mean positive and negative values of this index were significant ($P < 0.05$) and thus indicated the presence of patches and gaps, respectively (Table 1).

Autocorrelation analyses and contour mapping

A Moran's *I* autocorrelogram was computed for vi and vj values of each earthworm group. It indicated the presence of a significant spatial autocorrelation for aggregation index values vi and vj ($P < 0.05$ after Bonferroni's correction). Variograms (Fig. 2) similarly expressed the autocorrelation through a typical shape fitted to spherical function (Webster & Oliver 1990). Model parameters are given in Table 1. Despite a relatively large amount of nugget variance (ca. 28 and 52 % for eudrilids and *M. anomala*, respectively), the variograms clearly picked up the structure of the autocorrelation. Ranges of variograms (Table 1) were consistent with values cited in the literature (ca. 20–30 m). Block kriging estimates were contoured to produce maps of aggregation index values (Fig. 3). These maps showed the presence of earthworm clusters either defining patches or gaps. Additional mapping of index values larger than 1.5 was carried out to better depict the shape and distribution of clusters (Fig. 4). The eudrilid distribution mainly included three clusters (one patch and two gaps). The pattern of *M. anomala* featured six patches and six gaps (Fig. 4). Table 2 presents the area of each cluster and synthetic parameters such as the average patches and gaps area and the cluster cover defined as the ratio of cluster area to the total area (i.e. 2025 m^2). Interestingly, the cluster size was highly variable, ranging from e.g. 2 to 318 m^2 for gaps and from 3 to 257 m^2 for patches (*M. anomala*). This variability was reflected in the high standard deviation of the mean cluster size (Table 2). These observations

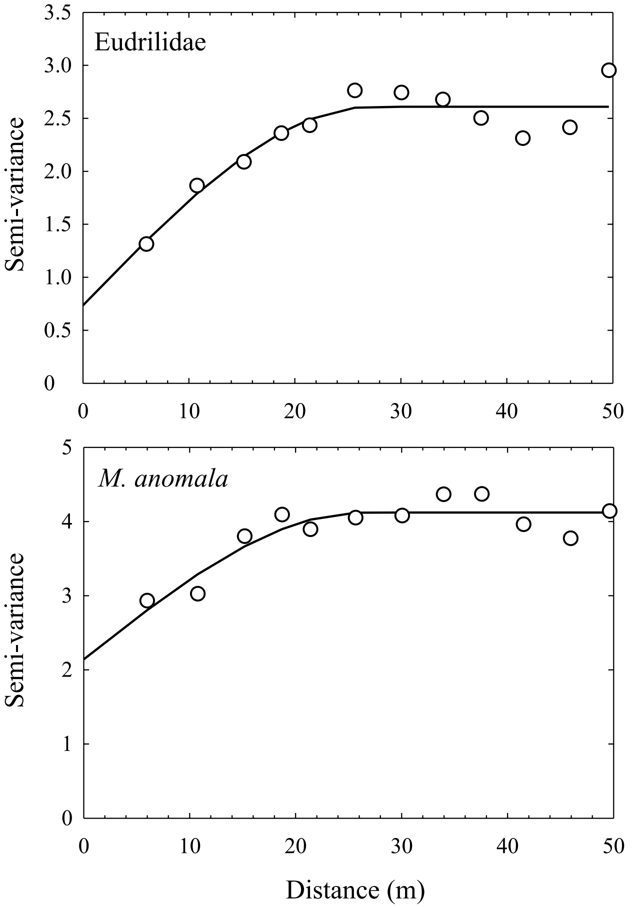
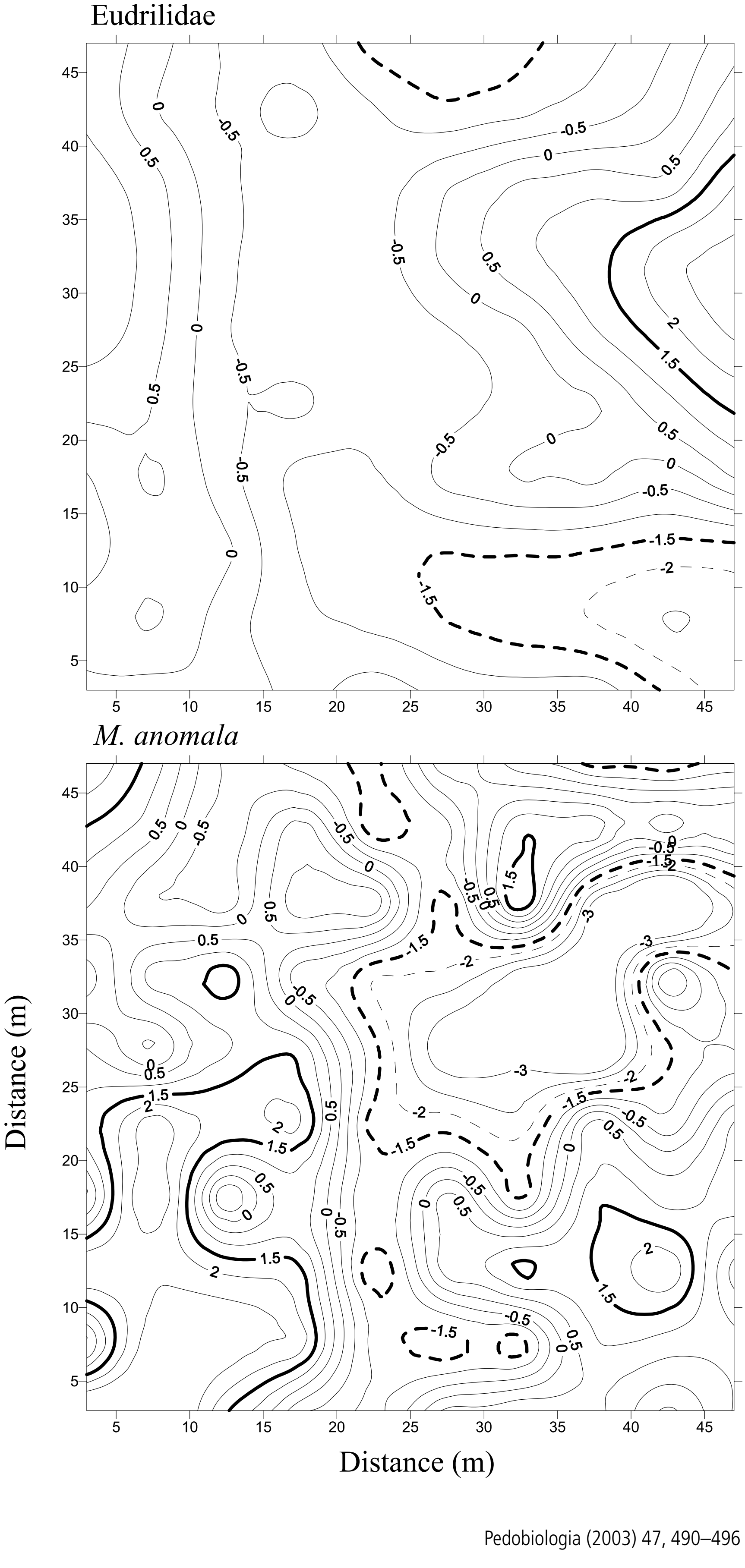
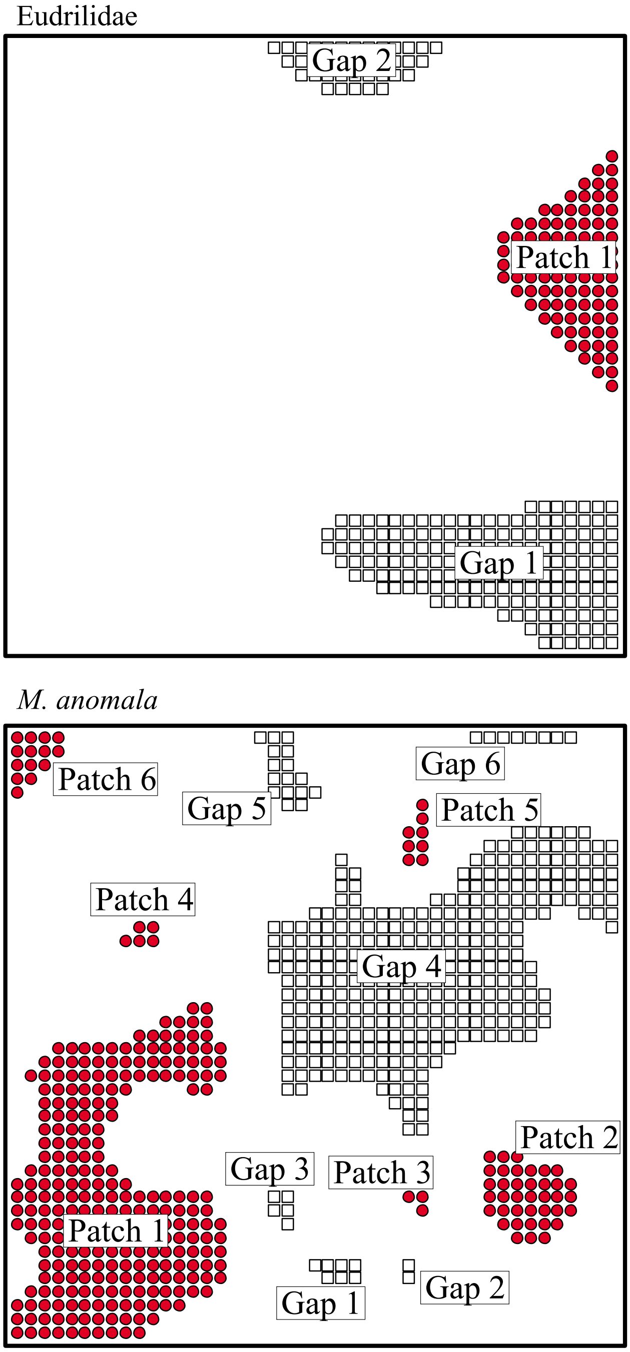


Fig. 2. Variograms of cluster index values for Eudrilidae and *M. anomala*. Fitted models are spherical (see Table 1 for function and model parameters)

Fig. 3. Contour maps of the clustering index computed from data of Figure 1 for Eudrilidae and *M. anomala*. Maps are derived from interpolated values using block kriging (1 m² blocks). Areas within contour lines with values greater than 1.5 indicate strong clustering




Eudrilidae

M. anomala

Fig. 4. Map of clusters for Eudrilidae and *M. anomala*. Points contributing to a patch or a gap are represented by circles ($vi > 1.5$) or squares ($vj < -1.5$), respectively

Table 1. General statistics, SADIE aggregation indices and variogram model parameters for Eudrilidae and *M. anomala*. I_a is a global index of aggregation. Mean vj and mean vi represent mean negative and positive index values that indicates gaps or patches, respectively. Indices were tested for departure from randomness using 1560 permutations and were all significant (associated probabilities are referred as to P_a, P(mean v_j) and P(mean v_i)). C_0 and C are respectively the nugget variance and the structural variance of the variogram models spherical function:
for $h < a$, $\gamma(h) = C_0 + C\left((1.5\,h/a) - 0.5 \cdot (h/a)^3\right)$,
for $h \geq a$, $\gamma(h) = C_0 + C$

	Eudrilidae	***Millsonia anomala***
Mean	7.05	1.67
Variance	19.04	2.26
Variance-to-mean index	2.7*	1.35*
I_a	1.451	1.889
P_a	0.0141	0.0006
Mean v_j	−1.368	−1.808
P(mean v_j)	0.0308	0.0006
Mean v_i	1.378	1.604
P(mean v_i)	0.0224	0.0019
C_0	0.74	2.14
C	1.87	1.98
Sill	2.61	4.12
Range	27.22	26.29

* $p < 0.05$ chi-square test

Table 2. Cluster type, surface (m²) and cover (% of the plot surface) for Eudrilidae and *M. anomala*

	Eudrilidae		***M. anomala***	
Cluster number	Gap surface	Patch surface	Gap surface	Patch surface
1	167	96	7	257
2	38	–	2	38
3	–	–	5	3
4	–	–	318	5
5	–	–	16	8
6	–	–	8	14
Cluster surface				
Mean	102.5	96	59.3	54.2
Standard deviation	64.5	–	51.8	40.9
Cluster cover	10.1	4.7	17.6	22.8

tend to underline the strong heterogeneity of an earthworm distribution constituted of a mosaic of small and large clusters. However, the cluster cover remained moderate for both patches and gaps, irrespective of the earthworm group. The cluster cover for *M. anomala* (40.4 %) was ca. 2.5 times higher than for eudrilids (14.8 %). The cluster position was submitted to a mean nearest neighbour distance analysis based on cluster centroids for *M. anomala* only (the number of clusters was too low in the case of eudrilids). Results showed that neither patch nor gap spatial distributions differed significantly from complete randomness. When pooled together the same result was obtained for all cluster types. The spatial association between eudrilids and *M. anomala* was not significant, the overall measure of association being X = −0.0156 (P = 0.5551).

Discussion

The results reported here show that eudrilids and *M. anomala* are undoubtedly spatially aggregated. The presence of randomly distributed clusters of very variable size suggests that factors responsible for the observed pattern are acting locally and therefore the hypothesis of an environmental control by large-scale gradients of texture or soil organic matter content is not very convincing. Yet the latter soil attributes may be quite patchy in some soils and thus the hypothesis of environmental control remains valid. The vegetation is mainly homogeneous at the plot scale. Therefore it is unlikely to influence the within-plot earthworm distribution. However, individual plant distribution as well as root architecture and activity may strongly affect earthworm patterns at small scales, e.g. metric, particularly in the case of polyhumic species, i.e. *C. zielae* and *S. porifera*. Micro-topography, or intrinsic population processes like dispersal, reproduction or competition may also influence the spatial distribution of earthworms (Ettema & Wardle 2002). Interestingly it can be seen from the experimental variograms that the ranges of autocorrelation are similar in both earthworm groups. Possibly the distribution of these species is, at least partly, driven by identical ecological factors or different factors acting at comparable scales.

The absence of a direct association between clusters of both species would at first glance suggest a complete independence between them. However, when comparing maps of eudrilids and *M. anomala* clusters (Fig. 4), it appears that clusters of one species tend to occur neither in patches nor in gaps of the other group, but rather in areas where clustering of the other group is not significant. Given that both groups have a very contrasted and complementary effect upon soil structure dynamics (Blanchart et al. 1997), the reported spatial heterogeneity suggests that earthworms affect soil structure dynamics through a mosaic of discrete units, being either dominated by one or the other functional group. However, understanding functional consequences of such a distribution would require information on its temporal dynamics (Rossi 2003). If the earthworm distribution were stable in time then one would expect a consistent spatial pattern in various soil attributes (e.g. soil aggregate size distribution, bulk density).

The SADIE approach has proven very helpful in this study by allowing a proper and meaningful way of describing clusters of earthworm counts. Accurately identifying clusters facilitates further investigation (e.g. patches or gaps shape description) of soil biota distribution on the basis of metrics developed in landscape ecology (Forman 1995).

There is no prerequisite for applying the SADIE analyses regarding the sampling design. Data collected on regular grids can be processed as well as data collected using irregular sampling schemes (e.g. random sampling). It must also be noticed that this method offers some advantages compared to more conventional approaches like geostatistics. Geostatistics have been originally developed to process continuous variables studied commonly in geology and soil science (e.g. metal grades, pollutant and trace element concentrations, see Armstrong 1998, p. 18). These variables often meet the fundamental hypotheses of stationarity. On the other hand animal and plant count data are not continuous data and are often distributed exceedingly patchily including a majority of zero values. Therefore such data might occasionally not verify the prerequisites for applying geostatistics (Perry 1998).

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