Relationships between microannelid and earthworm activity

Anneke Beylich*, Ulfert Graefe

IFAB Institut für Angewandte Bodenbiologie GmbH, Sodenkamp 59, 22337 Hamburg, Germany
* Correspondence: e-mail: anneke.beylich@ifab-hamburg.de; phone: +49 40 50064963; fax: +49 40 50016823

Abstract

Principal abiotic factors controlling the activity of enchytraeids and earthworms are generally known. Far less information is available on the influence of interactions between both groups. Data from soil monitoring sites in North-Western Germany provide information on earthworm and microannelid activity. Changes in the relation of both groups require interpretation with respect to soil condition changes. The data were analysed with respect to possible patterns in the relationship of earthworm and microannelid activity and influencing factors concerning antagonistic or similar development of both groups. The total abundance of both groups is not significantly correlated for the land-use types forest, grassland and cropland. Stronger correlations are found on the genus or species level. We selected a number of site examples with repeated sampling for opposing trends of both annelid groups as well as similar trends and specify for each case possible determining environmental factors. When abundances of earthworms and microannelids show antagonistic behaviour, this is mostly due to the rise or fall of only one or two species in each group. Probably competition in case of restricted resources plays also a role. Information on land management (fertilization, tillage etc.) and environmental factors (soil properties, climate) are crucial for the interpretation of the results. However, species-specific information on food preferences and behavioural responses on environmental changes are too limited to assess the role of competition between species from the analysed field data.

Keywords: Enchytraeidae; Lumbricidae; abundance; competition; *Dendrobaena attemsi*; land use

1. Introduction

Soil biological investigations at soil monitoring sites aim at detecting long-term changes in the biological soil condition. In three German federal states earthworms as well as microannelids (mainly enchytraeids) are investigated at soil monitoring sites as faunistic indicators of the biological soil condition. This offers the opportunity to assess interrelations between both groups, and thus to add new aspects to the interpretation of activity patterns with respect to soil condition changes. Main soil properties influencing the occurrence of earthworms as well as of enchytraeids are soil moisture, pH and texture (Beylich & Graefe 2009, Krück et al. 2006). In cultivated land also management practices play a decisive role. Some factors affect both groups in a similar way. For example, intensive tillage or drought are known to have negative consequences for the abundance of earthworms and enchytraeids (Langmaack et al. 1996, Plum & Filser 2005), while reduced tillage and organic fertilizer application can have positive effects (Langmaack et al.1996, Pfiffner 1993, Sauerlandt & Marzusch-Trappmann 1959). On the other hand, we find situations where earthworms and microannelids show opposed reactions to environmental changes. Studies on forest soil liming often proved that earthworms profit from increasing pH while enchytraeid abundances decrease (Hartmann et al. 1989, Graefe 1990). In this case, as in most experimental field studies aiming at examining the effect of a certain factor, there is mostly one sampling before the impact and one or more samplings afterwards, documenting the development of the relation between earthworms and enchytraeids as reaction to the environmental changes.

On the other hand, we find field investigations with only one sampling occasion providing us with information on the relationship of both groups as a response to the actual environmental conditions. Also for this latter approach researchers find either antagonistic behaviour (Górny 1984) or both groups showing relatively high abundance, e.g. at some grassland sites (Bauer 2003, Rutgers et al.

2008). The influencing factors are sometimes less obvious in these cases than in experimental setups with defined manipulation of one or a few factors. Thus, data on soil properties and management practices are inevitable for the interpretation of the results.

To assess influencing factors as moisture or liming, but also species composition, laboratory experiments have been conducted. Results are inconsistent. The presence of earthworms can reduce enchytraeid density in mesocosm studies (Räty & Huhta 2003, Räty 2004), but enchytraeids may also increase earthworm mortality in the experiments (Haukka 1987), depending on the experimental setup. The selection of species investigated seems to be essential due to species-specific size differences, habitat requirements and food preferences.

The formulation of reference ranges for the abundance of enchytraeids and earthworms, based on soil monitoring data, showed us general patterns for the relation of both groups, but also deviating behaviour in many cases (Beylich & Graefe 2009). The aim of the current data analysis was to (a) find patterns in the relationship of earthworm and microannelid activity (=abundance) for different land use types, (b) to identify influencing factors concerning antagonistic or similar development of the activity of enchytraeids and earthworms in time series, (c) to detect species-specific effects and (d) to find possible clues for competition for similar resources.

2. Material and methods

The data analysed in this work originate from investigations of 55 soil monitoring sites (Boden-Dauerbeobachtungsflächen, BDF) situated in Germany in the federal states of Schleswig-Holstein, North Rhine–Westphalia and Hamburg. The land-use types were forest (22 sites), grassland (17 sites) and cropland (16 sites). At all monitoring sites earthworms and microannelids were studied. Microannelids in this work comprise mainly enchytraeids, but sometimes also tubificids and polychaetes. For convenience, the terms “enchytraeids” and “microannelids” are used synonymously here. The parameters studied were abundance of earthworms and microannelids, earthworm biomass, vertical distribution of microannelids and species composition of both groups. Ten samples were taken at each monitoring site. Samplings are generally repeated after 5-10 years, so that most sites have undergone two or three samplings so far. Several site-examples with repeated samplings were chosen to demonstrate antagonistic or similar trends in earthworm and microannelid activity.

Earthworm sampling was carried out by a combination of formalin extraction (0.25 m²; ISO 2006), hand-sorting and Kempson extraction. For hand-sorting the samples were taken with a soil corer (250 cm², 20 cm depth cropland, 10 cm depth grassland and forest). The hand-sorted samples were afterwards extracted with a Kempson extractor (heat extraction) to obtain very small specimens that had been overlooked during hand-sorting. Assuming that individuals of similar size might be more likely to compete, the mean individual weight was calculated by dividing mean biomass by mean abundance for some species. For earthworm biomass determination the worms, fixed in formalin, were weighed with a scale-reading precision of 0.01 g (fresh weight with gut contents).

Soil samples for enchytraeids were taken according to ISO (2007) with a split soil corer (diameter 3.8 cm (cropland) or 5 cm (forest, grassland)). Sampling depth was 24 cm at cropland sites and 10 cm at forest and grassland sites. The different sampling depths take into account that the vertical activity reaches farther down in cropland sites due to tillage. Samples were divided vertically into 4 sub-samples of equal height. Soil samples were extracted over 48 h by a wet-funnel technique without heating (following Graefe 1984, as cited in Dunger & Fiedler 1989, p. 301; DIN ISO 2007). The extracted animals were counted and identified alive.

For the interpretation of abundance data, reference ranges according to Beylich & Graefe (2009) were consulted for comparison. For the correlation of the abundances of both annelid groups, of dominant genera or species, significance of correlation was checked with Spearman’s rho correlation of SPSS 15.0. In addition to correlation analysis for land-use types, several sites are presented in detail to exemplify certain patterns. The site

Tab. 1. Site characteristics for the forest sites presented in section 3.1. BDF = soil monitoring site; OH = organic horizon. (Data from Haag et al. 2009, Metzger et al. 2005).

Forest site	Soil Type	Humus form	Vegetation	Texture	pH OH ($CaCl_2$)	Remarks
BDF-NW 1.5 Elberndorf	Gleyic Cambisol	Mor	*Picea abies*	silt loam	2.8	-
BDF-NW 1.12 Castrop-Rauxel	Planosol	Mor / moder	deciduous forest, mainly *F. sylvatica*	sandy loam	3.6	clay in subsoil; liming 2001
BDF-NW 1.9 Duisburg Wald	Dystric Cambisol	Mor	*Fagus sylvatica*	sandy loam	4.1	liming 1990; 2001?
BDF-NW 2.1 Mattlerbusch	Gleyic Cambisol	Mor / moder	*Quercus robur*	silt loam, sandy loam	3.6	cropland up to 100 years ago

Tab. 2. Site characteristics for the grassland and cropland sites presented in section 3.2 and 3.3, respectively. BDF = soil monitoring site, GW = groundwater, n.d. = no data (Data from LLUR 2007, Haag et al. 2009, Metzger et al. 2005).

Site	Soil Type	Land use	Texture	pH ($CaCl_2$)	GW influence topsoil	Remarks
BDF-SH 13 Kleihof	Gleysol (marsh)	meadow/pasture	clay loam	5.4	+	
BDF-SH 25 Kudensee	Histosol	meadow/pasture	- (peat)	4.7	+	summer sampling 1995
BDF-NW 3.2 Lütkenberg	Cambisol	meadow	silt loam	5.3		
BDF-HH Amsinckpark	n.d.	park meadow	n.d.	4.3		
BDF-SH 04 Stadum	Gleyic Podzol	maize field	sand	4.7		• dung up to first sampling • no dung 1998-2007, no liming until 2008 • dung again since 2007, liming 2008 • reduced tillage since 2007

Tab. 3. Correlations between the abundance of earthworms and enchytraeids or single taxa of these groups for different land-use types. rs: Spearman's rho rank-correlation coefficient.

Land use	Taxa correlated	significance	r_s
All land uses	earthworms vs. enchytraeids	** p = 0.01	- 0.412
Forest	earthworms vs. enchytraeids	n.s.	- 0.100
	Dendrobaena attemsi vs. enchytraeids	** p = 0.01	- 0.752
	Dendrobaena attemsi vs. Achaeta sp.(affinoides)	n.s.	- 0.528
Wet grassland	earthworms vs. enchytraeids	n.s.	0.169
	epigeic earthworms vs. *Enchytronia* species	n.s.	0.055
	epigeic earthworms vs. *Fridericia* species	n.s.	- 0.130
	Eiseniella tetraedra vs. *Fridericia* species	* p = 0.05	- 0.612
	Aporrectodea caliginosa vs. enchytraeids	n.s.	0.405
	Aporrectodea caliginosa vs. *Fridericia* species	n.s.	0.297
Grassland	earthworms vs. enchytraeids	n.s.	- 0.044
	earthworms vs. *Enchytronia* species	* p = 0.05	- 0.468
	earthworms vs. *Enchytraeus* species	* p = 0.05	0.480
	anecic earthworms vs. *Enchytraeus* species	** p = 0.01	0.651
	earthworms vs. *Fridericia* species	** p = 0.01	0.489
	A. caliginosa vs. *Fridericia*, *Enchytraeus* and *Enchytronia* species	n.s.	< 0.310
Cropland	earthworms vs. enchytraeids	n.s.	- 0.022
	earthworms vs. *Enchytronia* species	n.s.	- 0.254
	earthworms vs. *Enchytraeus* species	n.s.	0.153
	earthworms vs. *Fridericia* species	** p = 0.01	0.505

characteristics for these examples are given in Tabs. 1 and 2. Soil texture was translated from German into English according to Schrey (2009), soil types were translated according to BGR (2008).

3. Results

The correlation analysis between microannelid abundance and earthworm activity showed a significant trend for enchytraeid abundance to be higher at low earthworm activity (Fig. 1, Tab. 3). However, low to medium microannelid abundance could be found with high as well as with low earthworm activity. To extract possible patterns concerning microannelid and earthworm activity, data were analysed separately for the land-use types forest, grassland and cropland.

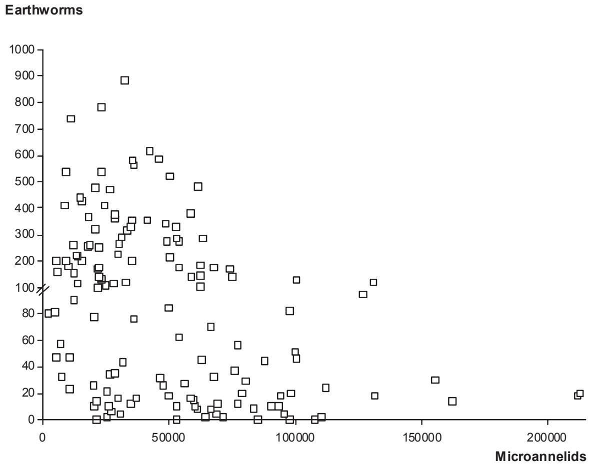

Fig. 1. Correlation of abundances (Ind. m^{-2}) between earthworms and microannelids at 55 German soil monitoring sites (forest, grassland, cropland). N=141 samplings.

3.1. Acid forest soils

All forest soil monitoring sites investigated were characterised by acid soil conditions with pH ($CaCl_2$) < 4.0 in the mineral topsoil (22 sites with 61 samplings). Earthworm abundance ranged from 0 to 520 Ind. m^{-2}, while enchytraeids abundance laid between 21,543 and 212,784 Ind. m^{-2}. There was no significant correlation between both parameters (Tab. 3). In Fig. 2 four examples for acid forest sites are compiled, showing different relations between earthworm and enchytraeid activity. Principal site characteristics are given in Tab. 1. The most acid site (Elberndorf) showed lowest earthworm abundance at all three sampling dates in comparison with the other three examples. In contrast, enchytraeid densities at this site were comparatively high. The sites Castrop-Rauxel and Duisburg Wald had in common (a) abundance of earthworms > 140 Ind. m^{-2}, (b) dominance of the epigeic earthworm species *Dendrobaena attemsi* between 63 and 98%, (c) enchytraeid abundance < 60,000 Ind. m^{-2} and (d) pH ($CaCl_2$) > 3.4. The fourth example, site Mattlerbusch, showed at the first two sampling dates similarities with the most acid site, that is: high enchytraeid abundance, low earthworm abundance and absence or low dominance of *Dendrobaena attemsi*. However, at the third sampling the picture resembled rather that of the other two sites, with a dominance of *D. attemsi* of 85%. The enchytraeid abundance at Mattlerbusch in 2007 amounted to only about one third of the abundance in 2002, which was mainly due to dropping numbers of *Achaeta* sp. (*affinoides*).

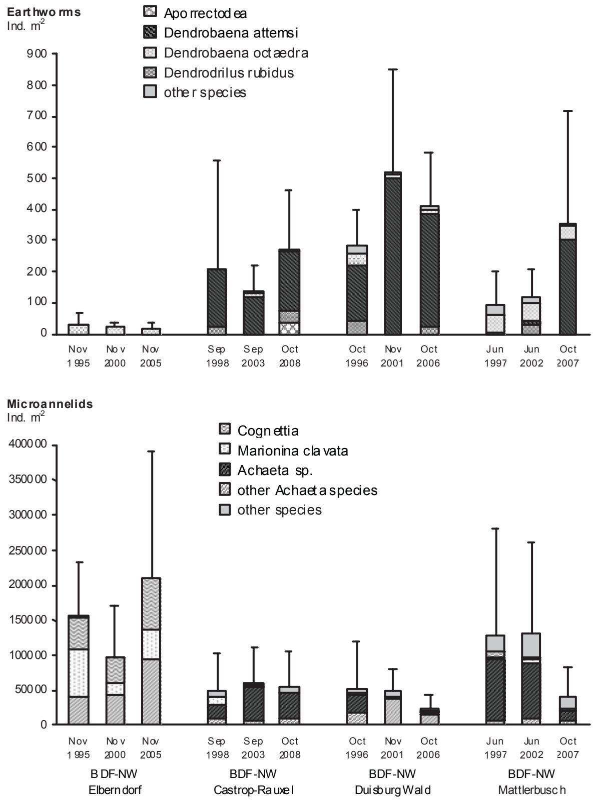

Fig. 2. Abundance of earthworms (above) and microannelids (below) at four acid forest sites. Three sampling dates for each site. Error bars: standard deviation.

The species numbers of Elberndorf were 8-9 for enchytraeids and 1-2 for earthworms respectively. The species numbers for the other three forest sites amounted to 11-20 for enchytraeids and 3-4 for earthworms respectively. If we considered all samplings with *Dendrobaena attemsi* present, we found a significantly negative correlation between the abundance of this earthworm species and the total enchytraeid abundance (Tab. 3). *Dendrobaena attemsi* occurred always in combination with *Achaeta* sp. (*affinoides*). The correlation between both species was also negative but not significant.

3.2. Grassland

Among the grassland sites there were five with groundwater influence in the topsoil at least part of the year. These sites will be termed “wet grassland” in the following, separating them from the rest that will be termed “grassland”.

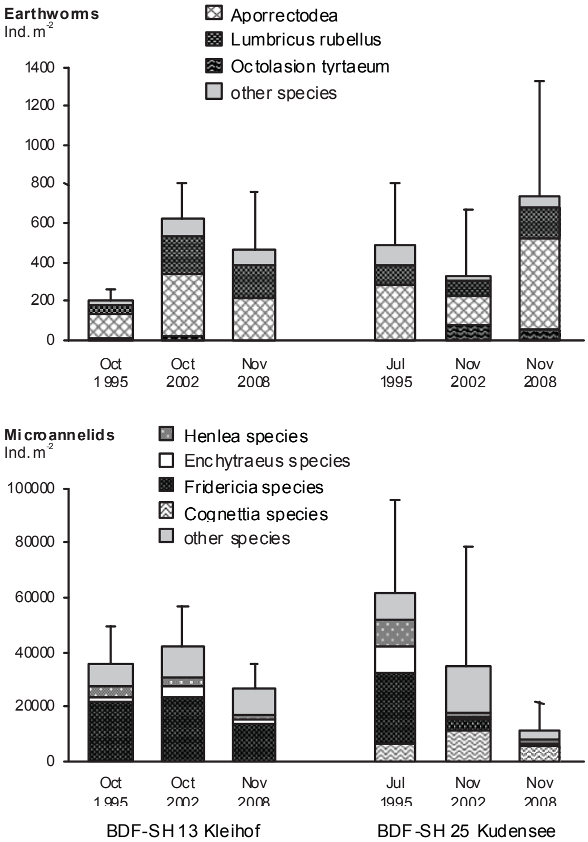

Fig. 3. Abundance of earthworms (above) and microannelids (below) at two wet grassland sites. Three sampling dates for each site. Error bars: standard deviation.

Two examples of wet grassland with different relationships between earthworms and microannelids have been chosen for Fig. 3. Site characteristics are given in Tab. 2. At the site SH 13, abundances of both groups showed parallel fluctuations. A threefold increase of earthworm numbers between 1995 and 2002 did not result in decreased microannelid numbers at the sampling date in 2002. At BDF SH 25, by contrast, the highest earthworm abundance of the three sampling dates coincided with the lowest enchytraeid abundance. Due to high groundwater levels, the microannelids at BDF-SH 13 were concentrating at the topmost 2.5 centimeters at all three sampling dates (Fig. 4). At BDF-SH 25 the vertical distribution of microannelids was much more balanced at the first sampling, which, as an exception, had taken place in summer. As the habitable space reached down to at least 10 cm, total abundance of enchytraeids was higher than at the other sampling dates. The species numbers for earthworms were 4 (BDF-SH 13) and 5-8 (BDF-SH 25) and for microannelids 18-21 (BDF-SH 13) and 18-23 (BDF-SH 25) respectively. Anecic earthworm species were absent.

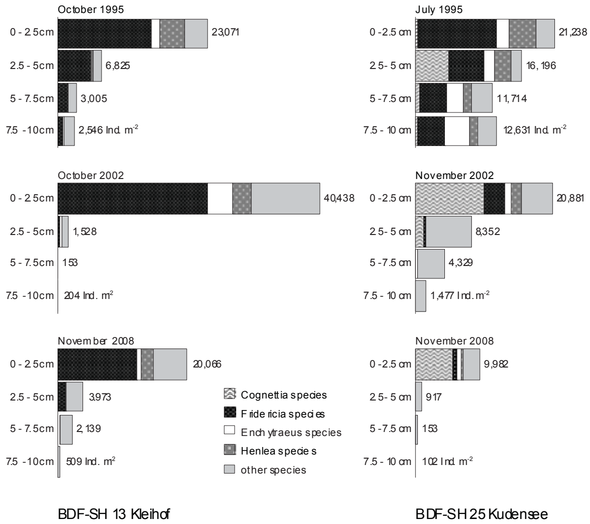

Fig. 4. Vertical distribution of microannelids for two wet grassland sites (same samplings as in Fig. 3).

Earthworm abundance of all five investigated wet grassland sites ranged from 200 to 739 Ind. m^{-2}, while microannelid abundance lay between 8,913 and 63,458 Ind. m^{-2} (14 samplings). Both parameters were not correlated (Tab. 3). Correlations between epigeic earthworms and *Fridericia* or *Enchytronia* species showed no significant relationships, while the abundance of the epigeic species *Eiseniella tetradedra* was significantly negatively correlated with the abundance of the genus *Fridericia*. In contrast, the endogeic species *Aporrectodea caliginosa* showed positive correlation coefficients when correlated with enchytraeids as a whole and with the genus *Fridericia*, but these results were not significant.

While *Eiseniella tetraedra* is a small species (mean individual biomass 0.04 g Ind^{-1}, 4 samplings), *Aporrectodea caliginosa* is of medium size (mean individual biomass 0.17 g Ind^{-1}, 12 samplings). However, individual biomass is naturally variable. At some samplings, high numbers of small (juvenile) individuals of *A. caliginosa* were recorded. This was striking at the third sampling at BDF-SH 25 (Fig. 3), where high numbers of earthworms with individual biomass below average coincided with low numbers of enchytraeids.

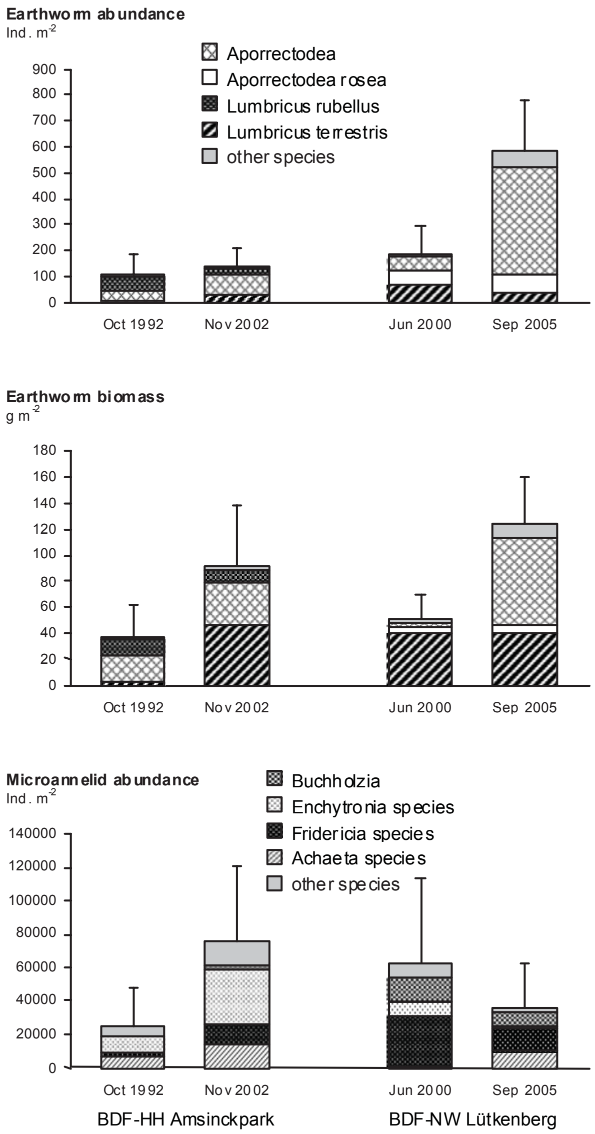

Fig. 5. Abundance of earthworms (above) and microannelids (below) and earthworm biomass (middle) at two grassland sites. Two sampling dates for each site. Error bars: standard deviation.

This situation could also be found on grassland sites not influenced by groundwater (soil characteristics Tab. 2). Fig. 5 shows that an increase of earthworms by a factor of three, mainly caused by *A. caliginosa*, was accompanied by a decrease of microannelids (BDF-NW Lütkenberg). Mean individual biomass of *A. caliginosa* is 0.27 g on grassland sites (27 samplings). At site Lütkenberg mean individual weight of this species was well below average (0.17 g), indicating high numbers of small juveniles. The decline of enchytraeids here was mainly due to falling numbers of the genera *Fridericia* and *Enchytronia*. At the same time, species number of microannelids rose from 20 to 26. However, increased earthworm activity can also coincide with increased microannelid abundance. At an urban park meadow (BDF-HH Amsinckpark), the abundance of earthworms was about 30% higher at the second sampling compared to the first sampling (Fig. 5). This was partly caused by an increase of the big anecic species *Lumbricus terrestris*, so the rise was even more pronounced regarding the earthworm biomass (145 % increase). Microannelid abundance also rose by a factor of three in the same period, *Enchytraeus* species being the most dominant.

Earthworm abundance of all 12 investigated grassland sites ranged from 91 to 886 Ind. m^{-2}, while microannelid abundance lay between 9,218 and 75,274 Ind. m^{-2} (27 samplings). Abundances of microannelids and earthworms were not correlated (Tab. 3). However, at genus level significant correlations were found. The genus *Enchytronia* was negatively correlated with earthworms while the genera *Enchytraeus* and *Fridericia* were positively correlated with earthworm occurrence. The correlation of the genus *Enchytraeus* was even more pronounced with the occurrence of anecic species (*Lumbricus terrestris* and *Aporrectodea longa*). The common species *A. caliginosa* showed no significant correlation with total enchytraeid abundance nor with the abundance of the genera *Enchytraeus*, *Fridericia* and *Enchytronia*.

3.3. Cropland

We chose one example for cropland sites only to show the difficulties in generalizing the relationships between earthworm and microannelid abundance for this land-use type (Fig. 6). At site BDF-SH 04 maize had been grown since the start of our investigations without crop rotation (Tab. 2). Earthworms did not show much variation between the first two samplings, being represented by one single species (*Aporrectodea caliginosa*). At the same time the microannelid community changed completely: while the genus *Enchytraeus* had dominated strongly at the first sampling, it has nearly vanished seven years later. At that time, indicators of moderate acidity belonging to the genus *Achaeta* were dominating the scene. At the third sampling, again the picture has changed completely. In addition to the still dominating *Achaeta* species we found *Enchytraeus* species again, but also representatives of the genera *Fridericia* and *Henlea*. Species number of the enchytraeids rose from five (1996) to twelve (2009). Further, three additional epigeic earthworm species were found in 2009. Total abundance for both annelid groups was highest in 2009.

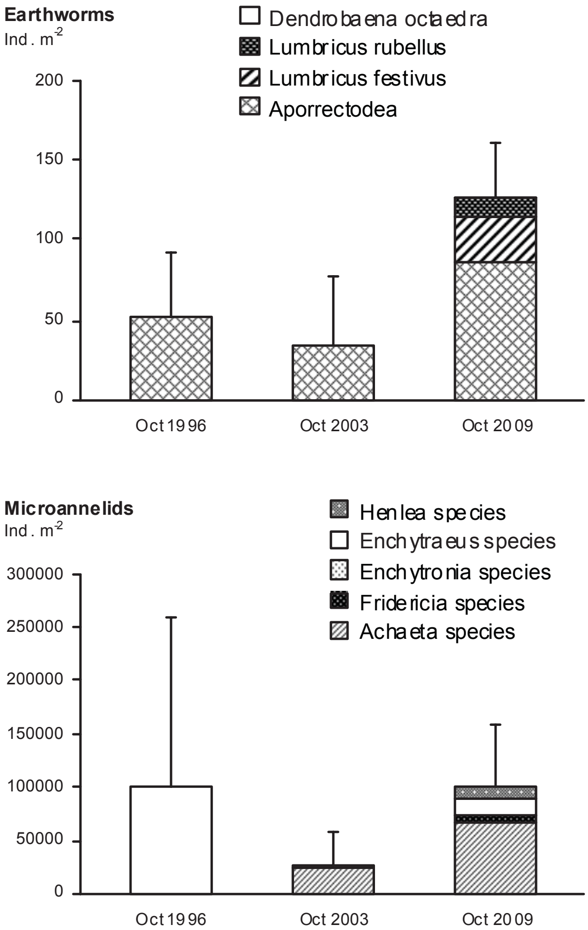

Fig. 6. Abundance of earthworms (above) and microannelids (below) at a maize field in Schleswig-Holstein (BDF-SH Stadum). Three sampling dates. Error bars: standard deviation.

Earthworm abundance of all 17 investigated cropland sites ranged from 0 to 782.8 Ind. m^{-2}, while enchytraeid abundance lay between 2,037 and 100,607 Ind. m^{-2} (38 samplings). The abundance of earthworms was not correlated with microannelids in general and not with the genera *Enchytreaus* and *Enchytronia*, either (Tab. 3). A significant correlation was found between earthworms and the genus *Fridericia*.

4. Discussion

Earthworms shape the topsoil habitat, e.g. by their burrowing activity, by depositing casts and by influencing microbial activity. These activities can affect enchytraeids, which on the other hand might compete for food resources with earthworms. In addition, both groups are influenced by abiotic and biotic factors independent of their reciprocal interaction. Obviously, we cannot expect a simple relationship between both groups, but rather a network of relations, mostly at species level, influencing the total abundance of both groups in various ways.

4.1. Acid forest soils

The BDF-NW Elberndorf showed a situation as found occasionally in strongly acid forest soils throughout northern and western Europe (Nielsen 1955, Abrahamsen 1972 a, b, Haag et al. 2009). Very few earthworm species are able to exist under these adverse conditions, *Dendrobaena octaedra* often being the only species present in low numbers. Among enchytraeids several species do not only tolerate strongly acid conditions but also reach high population densities. In any case, enchytraeid abundance of > 100,000 Ind. m^{-2} does not seem to be the rule at forest soils with a moder or mor humus layer, and the prerequisites for such very high numbers are not clear. Enchytraeid densities between 50,000 and 100,000 Ind. m^{-2} are most common in combination with earthworm abundance well below 100 Ind. m^{-2} (Fig. 2; Abrahamsen 1972a,b). Whether the low numbers of *D. octaedra* at Elberndorf were mainly due to very low pH or to less successful competition with the numerous enchytraeids for food resources or to other factors, cannot be deduced from the data presented. The pH can have a considerable effect on the competitive performance of species (Hyvönen et al. 1994). Although *Dendrobaena octaedra* is acid tolerant, it reaches higher densities at pH ($CaCl_2$) above 4.0. In laboratory studies Huhta & Viberg (1999) found numbers of *Cognettia sphagnetorum* suppressed in presence of *D. octaedra* at higher pH values (pH 5.5). Liming experiments have shown that the total abundance of autochthonous enchytraeid communities of acid forest soils with mor humus layers, consisting of a few acid tolerant species, is affected negatively by liming while lumbricid activity rises (Bååth et al. 1980, Abrahamsen 1983, Schauermann 1985, Makeschin & Rodenkirchen 1994). This is generally supported by the results of the forest sites NW Castrop-Rauxel and Duisburg Wald, which had been limed in 2001. However, experiments of Pokarzhevskii & Persson (1995) suggest that *C. sphagnetorum*, generally the most numerous enchytraeid species in acid forest soils, is not directly affected by high pH but rather by increased competition of other species. Further, a changed microbial community composition after liming, e.g. concerning the ratio fungi / bacteria, could be an decisive factor.

While the higher pH at the forest sites Castrop-Rauxel, Duisburg Wald and Mattlerbusch could be seen as one principal factor causing low numbers of *Cognettia sphagnetorum* and probably other indicators of extreme acidity among the enchytraeids at these sites, we would expect higher numbers of *Dendrobaena octaedra*. According to Huhta (1979) also *Dendrodrilus rubidus* benefits from pH increase. However, the epigeic earthworm *Dendrobaena attemsi* seems to profit more successful from liming than the other epigeic earthworm species at the sites investigated here. The reason for the increase of *D. attemsi* at site Mattlerbusch is not known. The site was not limed, but had been cropland until roughly 100 years ago. *D. attemsi* here seems to have a competitive advantage compared to the other earthworm species as well as the enchytraeids. Experimental studies to assess interspecific interactions of *D. attemsi* have not been published. In Germany *Dendrobaena attemsi* is not very common and has mainly been found near settlements, often after liming (Beylich 1995, Römbke et al. 2000, Haag et al. 2009). It occupies the humus layer as well as *Dendrobaena octaedra* and the enchytraeid species typical for mor humus layers, as *Cognettia sphagnetorum*. Thus, competition for food resources seems possible.

4.2. Grassland

For the wet grassland sites two examples are presented with similar and antagonistic relationships of microannelids and earthworms respectively. Based on the results of BDF-SH Kleihof we conclude that under generally favourable conditions (pH, food resources) very high numbers of earthworms are compatible with more than average enchytraeid abundance according to the reference range (Beylich & Graefe 2009), even if habitable space is limited to the upper few centimeters due to anoxic conditions in deeper soil layers. In contrast to Kleihof the site Kudensee had peaty soil with lower pH values. Whether the low number of enchytraeids at this site at the third sampling was only caused by severe lack of oxygen or due to further adverse conditions or direct competition with earthworms, is unclear. Adult earthworms, kept in water saturated soil, have been reported to leave their hind end at the soil surface, while the front end remains in deeper layers (feeding?) (Roots 1956). In case also juveniles of *Aporrectodea caliginosa* were capable of this behaviour, this could explain their ability to exist in high numbers in water saturated soil in contrast to microannelids at BDF SH 25. Also our results of other BDF show, that enchytraeids show more often negative short-term reactions to water-logged soil than earthworms. Further, the comparatively low pH might have played a role at the site SH Kudensee. Species number rose from first to third sampling due to an increase of acidity indicators suggesting increasing soil acidity, but not all enchytraeid species occurring at this site, that are tolerating low pH, are simultaneously tolerating wetness. It should be noted that in soils influenced by groundwater the activity may change to a great degree with varying water levels within several months (Beylich & Graefe 2007, Plum & Filser 2005). For the description of the biological soil condition the abundance data are thus of limited informative value and should always be complemented by species composition data.

The fact that single species contribute very differently to changes in total abundance of the whole group explains why we find correlations rather at species or genus level than at family level. A negative correlation between *Eiseniella tetraedra* and *Fridericia* species at wet grasslands suggests direct competition. This small epigeic earthworm species occupies the upper few centimeters, where enchytraeids concentrate as well in times of oxygen deficiency in soil. However, *Eiseniella tetraedra* occurred on two of the wet grassland sites only, so the basis for establishing this relationship is weak.

In contrast to the wet grassland sites, the genus *Enchytraeus* was significantly positively correlated with earthworm abundance at the other grassland sites, which was probably mainly due to a strong relation with the abundance of anecic earthworms, which were not found at the wet grassland sites. Some studies have shown that enchytraeids settle on earthworm casts and consume them, apparently making use of material more easily digestible than the surrounding soil (Dawod & FitzPatrick 1993, Topoliantz et al. 2000, Räty 2004). Also earthworm burrows proved to be more attractive for enchytraeids than the adjacent soil in a woodland study (Dózsa-Farkas 1978). Possibly the opportunistic *Enchytraeus* species profit more from microhabitats created by the deep-burrowing earthworms (casts, burrow coatings), than some other enchytraeid species. Further, both groups prefer slightly acid to neutral soils. Räty (2004) found that earthworms (*Lumbricus terrestris, Aporrectodea caliginosa*) decreased topsoil acidity in a laboratory study. Also the middens of *L. terrestris* showed higher pH than the untreated soil and were preferentially inhabited by an *Enchytraeus* species.

The genus *Enchytronia* showed a quite opposed behavior at the grassland sites, providing an example of antagonistic behavior of earthworms and enchytraeids. This genus was predominantly represented by *Enchytronia parva* at most sites, which is an indicator of moderately acid soils (according to Graefe & Schmelz 1999, Graefe & Beylich 2003), thus indicating conditions not at optimum for anecic and endogeic earthworms. In addition, the study of Dózsa-Farkas (1978) on colonization of earthworm burrows by enchytraeids showed, that the preference of *E. parva* for earthworm burrows is less pronounced than in other enchytraeid species.

The abundance relationship between *Aporrectodea caliginosa* and enchytraeids or enchytraeid genera is difficult to interpret. Sometimes we found examples for antagonistic behavior, especially when small juvenile individuals of *A. caliginosa* occurred in great quantities (BDF-SH Kudensee and BDF-NW Lütkenberg). A meta-analysis conducted by Eisenhauer (2010) on the impact of earthworms on soil microarthropods showed negative effects of endogeic earthworm species on microarthropods, especially at high earthworm densities. The reasons suggested by the author are a) modification of soil structure by burrowing and thereby disturbing microarthropods and their eggs b) higher competitive strength of earthworms concerning competition for food resources. Similar effects on enchytraeids, belonging to the same size range and partly exploiting the same food sources as microarthropods, are imaginable.

4.3. Cropland

In contrast to grassland sites, we found no correlation between the genus *Enchytraeus* and anecic earthworms at cropland sites. One reason might be the fact that anecic species were almost or completely absent at some cropland sites. Especially on sandy cropland sites lumbricid earthworms are often limited to one or few endogeic species (Graefe 1999, Beylich & Graefe 2009). Tillage induced disturbances affect enchytraeids as well as earthworms, reducing the abundance of both groups (Langmaack et al. 1996), but there is also evidence that both groups react differently to tillage measures (Topoliantz et al. 2000). Food supply on cropland sites is variable in amount, frequency and type (organic / inorganic fertilizer), favouring the occurrence of colonizer species. Among earthworms, mainly the epigeic species, normally inhabiting the litter layer, can be considered as colonizers. As epigeic earthworms are mostly missing at cropland sites, earthworms are often not represented with colonizer species here at all. Among enchytraeids colonizers belong mainly to the genus *Enchytraeus*, which is regularly found at cropland sites. Due to their high reproductive ability *Enchytraeus* species can exploit sporadic food supplies more successful than other species. Furthermore, their populations recover easier after management impacts. Consequently, their abundance is not correlated with that of the other genera, which require more time for population stabilization after a collapse (K-strategists). The latter comprise e.g. the genera *Fridericia* and *Henlea* as well as endogeic earthworms, which also share habitat requirements, inhabiting the upper mineral soil, preferring slightly acid to neutral soil. This would explain a positive correlation between endogeic earthworms and *Fridericia* species, at least in case of sufficient food resources.

The fundamental changes in community structure at BDF-SH Stadum illustrate management effects. Dung application in the years before the first sampling brought forward *Enchytraeus* species (first sampling). As liming was neglected, acid tolerant *Achaeta* species dominated at the second sampling. In the years preceding the third sampling the site was limed, dung application was restarted and tillage was reduced. As a consequence, we found colonizers (*Enchytraeus* species), acid tolerant species (*Achaeta* species), but also indicators of neutral to slightly acid conditions (genera *Fridericia* and *Henlea*). In addition, epigeic earthworm species occurred, profiting from crop residues and weeds not being ploughed in. Management measures here improved conditions for many species with some profiting even more (opportunists) than others. Hence, abundance of both annelid groups exceeded the reference range for sandy field soils at the third sampling (Beylich & Graefe 2009).

No site example has been presented for low abundance of both annelid groups. The reference ranges derived from soil-monitoring data (Beylich & Graefe 2009) show that low densities of earthworms and enchytraeids occur more frequently in cropland than in grassland. At cropland sites earthworms and enchytraeids are often exposed to multiple stressors such as tillage, compaction and pesticides (Langmaack et al. 1996). Additional disadvantageous factors, e.g. adverse weather conditions, then might cause populations of both groups to collapse.

4.4. General conclusions

The abundance of earthworms and microannelids in soil is influenced by a complex of abiotic and biotic parameters causing short-term fluctuations and long-term changes. The detection of relationship patterns of the abundance of both animal groups by analysis of the presented field data is difficult due to the heterogeneity of soil properties, land use and management. It was demonstrated that

- correlations between total microannelid and earthworm abundance in general are often missing,
- correlations and especially antagonistic behaviour are species specific,
- small earthworm species or juveniles of medium-sized species (endogeic, epigeic) tend more to show antagonistic relationships with enchytraeids than large, anecic species,
- abundances of species with similar habitat requirements can be positively related if there is no resource limitation,
- conditions favouring both groups can result in increasing activity of both groups (e.g. favourable management measures on cropland).

The field data hardly allow to detect the influence of competition, as abiotic factors are overlaying and influencing possible competition effects. Other biotic factors such as the composition of the microbial community (Huhta 1984) or excretions / secretions (Górny 1984, Haukka 1987) might also play a role. In addition, competition can occur not only between earthworms and microannelids but also between species within these groups (Uvarov 2009) and between microannelids and microarthropods (Huhta et al. 1998). Information at species level on food preferences or strategies to cope with e.g. adverse moisture conditions are missing, but would help to estimate competition effects.

We often find decreasing enchytraeid abundance accompanied by increasing species numbers, e.g. after liming (Graefe 1990) or during acidification of forest or grassland sites respectively. This supports the conclusion that the development of the biological soil condition cannot be interpreted by abundance data alone, as these fluctuate considerably. Interpretations with respect to soil condition evaluation should always refer not only to abundance of both groups but also to species composition, which might show opposed trends.

So far, few publications discussing relationships between earthworm and enchytraeid abundance in the field were primarily designed to investigate interactions. Better understanding of interactions would render insight in changes of soil fauna communities triggered by environmental alterations and their effects on ecosystem services. Soil monitoring data are needed to underpin decision-making and to develop adaption strategies and measures in the fields of e.g. climate and land-use change, invasion/introduction of new species, deliberate release of GMO (genetically modified organisms) or multiple contaminations. However, most soil monitoring sites are not designed for the study of processes and interactions. Thus it would be helpful, to 1) identify information that is needed to interpret monitoring data thoroughly but is missing so far and 2) to target research projects especially to these topics. At present, university research and soil monitoring seem rather detached from each other, although in our opinion both could profit from cooperation.

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