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Annelids of beech forests on basaltic bedrock: findings from two forest reserves in Germany

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Abstract. The annelid communities (microannelids and earthworms) of woodruff beech forest in two Strict Forest Reserves on moderately base-rich soil (basaltic bedrock) were studied. For the Weiherskopf (Hesse) Strict Forest Reserve, a reference site that was under forest management was included in the investigation. While the investigations at Weiherskopf took place in 2014, the Nonnenstromberg (North Rhine-Westphalia) Strict Forest Reserve was studied already 1991/1993. Site conditions at Weiherskopf and Nonnenstromberg were similar in many respects, apart from the fact that at both Weiherskopf sites several heavy storms had caused extensive windthrow in 1990, resulting in different amounts of deadwood at the sites. Despite this, the species composition was similar at the studied sites (Sørensen Similarity Index between 0.73 and 0.83). At all three sites a species-rich annelid community was present, the majority of species indicating either slightly or moderately acid soil conditions. Among the microannelid species with the highest frequency were *Hrabeiella periglandulata, Enchytronia parva* and *Buchholzia appendiculata*. At all sites, the same humus form (F-mull) was developed, being closely linked to the presence of endogeic and anecic earthworms. Possible distinguishing features between annelid communities on basalt and calcareous bedrock respectively are discussed.

Keywords. Enchytraeidae; earthworms; deciduous forest; humus form; *Dendrobaena pygmaea; Hrabeiella periglandulata.*

INTRODUCTION

Beech forests are an important component of the natural vegetation of Central Europe and currently constitute approximately 15 % of the forested area in Germany (BMEL 2016). According to trophic soil conditions two main groups of beech forests can be distinguished: *1.* forests on oligo- to mesotrophic soils, being poor in bases, with moder humus forms, and *2.* forests on base-rich meso- to eutrophic soils with mull humus forms (Bohn & Gollub 2007). Since the 1980s, investigations on earthworms and microannelids in beech forest soils have focused on oligotrophic, acid forest soils, triggered by concerns about increasing anthropogenic acidification (Beck 1987, Römbke 1989). Some studies include base-rich sites for comparison (Graefe 1990, Schaefer & Schauermann 1990, Schoch-Bösken & Greven 1987), but investigations dealing chiefly with microannelid communities in beech forests on base-rich soils are rather limited (Mellin 1988, Schlaghamerský 2010). Among base-rich soils, those on basaltic bedrock (siliceous) often differ in soil properties like pH from those on limestone and other calcareous parent materials due to the different mineral composition of the parent material. Thus, we distinguish moderately base-rich soils (on basalt) from base-rich soils (on calcareous bedrock) in this study.

Old growth beech forests can display high biodiversity (Assmann *et al.* 2007). Strict forest reserves are, besides core zones of national parks and biosphere reserves, the only areas in Germany, where natural forest development can proceed undisturbed by management and resource use (Wolf & Striepen 2007). More than 700 strict forest reserves have been established in Germany since 1970 to study forest development at minimized human impact.

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We investigated microannelids and earthworms of woodruff beech forests in two strict forest reserves with moderately base-rich soils on basaltic bedrock. The Nonnenstromberg (North Rhine-Westphalia) Strict Forest Reserve was investigated already in 1991/1993 with a focus on the impact of soil acidification. At the Weiherskopf (Hesse) Forest Reserve the occurrence of several heavy storms in 1990 caused extensive windthrow. In 2014 the investigation of microannelids and earthworms was undertaken as part of a study to assess the possible impact of deadwood management on the ecosystem. However, this aspect is not within the main focus of the present publication.

The present contribution aims at characterizing the annelid community of beech forests on basaltic parent material concerning *a*) species diversity and typical species composition, and *b*) indicators of soil acidity, life-form types and strategy-types of species. The results enable a comparison with communities of other types of beech forests, *e.g.* on calcareous bedrock.

MATERIAL AND METHODS

Study sites

The Weiherskopf Strict Forest Reserve is situated in the Vogelsberg region in the Federal State of Hesse in Germany. In this area, two sites were investigated that had been affected by severe windthrow 24 years before the investigation. In the strict forest reserve, the deadwood had not been removed (site WK-DW), while deadwood had partly been taken out at the reference site (WK-RF), which is situated about 600 m south of WK-DW outside the strict forest reserve. The forest community is woodruff beech forest (*Galio odorati-Fagenion*); often a variant with wood-barley is dominating (NW-FVA 2015). At both sites, the forest at present forms an irregular pattern of patches with the original beech population (age ≥ 100 years) and patches with young-growth forest, that developed since the windthrow (< 25 years) and consisting apart from beech mainly of Norway maple and ash.

The Nonnenstromberg (NB) Strict Forest Reserve belongs to the Siebengebirge region in the Federal State of North Rhine-Westphalia in Germany. The trees in the old growth beech forest had an age of about 110 years in the year of investigation. The forest community is woodruff beech forest (*Galio odorati-Fagenion*), with woodruff and wood melick dominating.

Information on principal site conditions and soil properties is given in Table 1. The humus form was specified according to the German soil classification (Ad-hoc-AG Boden 2005). An OH horizon, which would be an identifier for moder and mor humus forms, was lacking at most sample points, while an OF horizon was mostly well developed. The humus form was thus classified as F-mull, being an intermediate humus form between L-Mull (OL-layer only) and Moder (OL-, OF- and OH-layers). Information on the soil type was transferred from the German classification to categories of the world reference base for soil resources (IUSS Working Group WRB 2015). As both systems show fundamental differences, translation of soil types is not always consistent. Thus, in Table 1 the soil type is given according to both classification systems.

Sampling

At the WK Strict Forest Reserve 10 sample points for each of the two sites, WK-DW and WK-RF, were selected on the nodes of a regular grid of 100 × 100 m. At the NB Strict Forest Reserve, 8 sample points were selected along a transect of about 200 m at the north-facing slope and 6 sample points each along two transects of about 150 m at the south-facing slope of the central hill (total of 20 sample points). All three transects were running roughly in north-south direction.

The soil faunistic analyses included earthworms and microannelids. Soil samples for microannelids were taken with a split soil corer (diameter 5 cm) to a total sampling depth of 10 cm. The core samples were divided into 4 subsamples of 2.5 cm thickness to assess the vertical

Table 1. Characterization of the study sites Weiherskopf (WK) and Nonnenstromberg (NB) (Data sources: Bundesanstalt für Landwirtschaft und Ernährung 2007, Landesbetrieb Wald und Holz Nordrhein-Westfalen 2018). Soil types of the German classification transferred according to IUSS Working Group WRB (2015).

	WK	**NB**
Coordinates	N 50°22’16“ E 9°26’34“ WK-DW N 50°21’34“ E 9°27‘05“ WK-RF	N 50°41‘8“ E 7°13‘12“
Parent material	basalt with loess cover of variable thickness	basalt with loess cover of variable thickness
Height [m.a.s.l.]	310–410 m	240–335 m
Annual precipitation [mm]	969 mm	844 mm
Mean annual temperature [°C]	7.7°C	9.4°C
Vegetation	old-growth forest: *Fagus sylvatica* with few *Quercus petraea;* young-growth forest: mainly *Acer platanoides, Fraxinus excelsior*	old-growth forest: mainly *Fagus sylvatica* with few *Quercus petraea; Tilia cordata* and *Fraxinus excelsior* at steep slopes
Forest community	Woodruff-Beechwood	Woodruff-Beechwood
Strict forest reserve since	1989	1989 (nature protection area since 1965)
pH (KCl)	5.5–5.6 (humus layer) 4.2–4.4 (mineral topsoil)	4.1–4.7 (mineral soil)
pH (H_2O)	6.0–6.1 (humus layer) 5.3–5.6 (mineral topsoil)	5.3–6.3 (mineral soil)
Texture	silt loam	silty clay loam
Soil type (WRB)	Luvisol, Stagnic Luvisol	Cambisol
Soil type (German classification)	Pseudogley-Parabraunerde	Braunerde, partly Pseudogley-Braunerde
Humus form	mainly F-Mull, partly transition to moder	mainly F-Mull, partly transition to moder

distribution of microannelids. The sub-samples were extracted over 48 h by a wet-funnel technique without heating, changing the water once after 12−24 h. The extracted animals were counted and identified in vivo, following the keys of Nielsen & Christensen (1959), Schmelz (2003) and Schmelz & Collado (2010). Microannelid samples were vertically divided at fixed depth levels and not at humus horizon boundaries, as this enables the calculation and comparison of mean abundance per m^2 for these depth levels at all three sites independently from the varying thickness of humus horizons. To link the occurrence of species to specific horizons and to compare humus layer thickness, at the WK sites, for each microannelid core sample the organic horizons, their thickness and their distribution over the above mentioned vertical sub-samples were recorded. For the NB site only the thickness of the humus layer in total was measured.

The earthworms were sampled by formalin extraction in combination with hand-sorting and Kempson extraction (ISO 23611-1, 2006). Fomalin extraction was performed on a soil surface area of 0.25 m^2. For hand-sorting two samples were taken at each sample point using a corer of 250 cm^2 to a depth of 10 cm. The samples were hand-sorted in the laboratory and subsequently underwent a Kempson extraction to be sure that all individuals were found. Earthworms were fixed in NOTOXhisto^{TM} and determined according to Sims & Gerard (1985). Earthworm biomass was determined for fixed animals with gut content. The earthworm results comprise abundance, biomass, species composition and dominance of life form types (epigeic, endogeic, anecic).

Sampling took place in the Weiherskopf (WK) Forest Reserve at the end of April 2014. The Nonnenstromberg (NB) Forest Reserve was investigated in October 1991 (microannelids and earthworms) and April 1993 (earthworms only). At NB the first earthworm sampling was performed without formalin extraction as anecic earthworms had not been expected due to the relatively low pH (NB1991). The results, *i.e.* the occurrence of endogeic earthworms and the presence of mull humus forms, indicated the possible presence of anecic earthworms. Thus a second sampling including also formalin extraction was performed at 10 out of the original 20 sampling points in 1993 (NB1993), as hand-sorting and Kempson extraction are less effective for deep-burrowing species. These 10 sampling points covered the north-facing slope (4 samples) as well as the south-facing slope (6 samples).

Samples were taken irrespective of the deadwood present to varying degrees at the sample points, *i.e.* we did not sample decaying deadwood or soil below it or in its immediate surroundings at any of the sites.

Data analysis

The results were analyzed with respect to species composition, total abundance and vertical distribution of the community as well as dominance and frequency of species. Functional traits of individual species, as strategy type and acidity indicator group, were assigned according to Graefe & Schmelz (1999). The originally nine-step scale of acidity indicator values presented in Graefe & Schmelz (1999) was here condensed to three acidity indicator groups: indicators of strong acidity (acidity indicator values 1−3), indicators of moderate acidity (acidity indicator values 4−6) and indicators of slight acidity (acidity indicator value 7). In terms of strategy types, indicators of strong and moderate acidity together are termed as A-strategists, while all k-strategists, *i.e.* persistent species with a low reproduction rate, are indicators of slight acidity. R-strategists are opportunistic species with a high reproduction rate (sexual or by fragmentation) and also belong to the indicators of slight acidity (Graefe & Schmelz 1999).

Statistical analyses were performed with SYSTAT 13. Data were checked for normality with the Shapiro-Wilk Test. Data were not normally distributed in some cases. This was partly due to the occurrence of several sample points with no earthworm findings. Square root transformation did not improve the situation. Thus, differences in abundance and earthworm biomass between sites were checked for significance with the non-parametric Kruskal-Wallis Test, followed by Conover-Inman Test for all pairwise comparisons.

Similarity of species composition was assessed with the Sørensen Similarity Index (Mühlenberg 1989), calculated according to: QS= 2*C / (A+B), where A and B are the numbers of species in sites A and B, respectively, and C is the number of species shared by the two sites. QS ranges between 0 and 1, where 1 represents an identical species composition of two communities. As the index uses just presence / absence data, the species lists for earthworms for NB1991 and NB1993 were pooled.

RESULTS

Species composition and quantitative parameters

At the two sites of the Weiherskopf Strict Forest Reserve the same 9 earthworm species were found. All three life-form types were represented (Table 2). The only anecic species *Lumbricus terrestris* was found with low abundance and frequency. Total earthworm abundance was very similar at both sites. The total earthworm biomass did not differ significantly either ($p < 0.005$).

The two samplings at the Nonnenstromberg Strict Forest Reserve yielded significantly lower abundance data for earthworms ($p < 0.005$). The earthworm biomass was on a similar level as at the Weiherskopf sites when, at the second sampling at the Nonnenstromberg site (NB1993), formalin extraction was applied and the anecic species *Lumbricus terrestris* was found. The species found at NB were generally the same ones as at WK, except from *Octolasion tyrtaeum* which was missing at NB.

The species number of microannelids ranged between 27 (NB) and 34 (WK-DW). The majority of species belonged to the family Enchytraeidae, whereas two species, *Hrabeiella periglandulata* and *Parergodrilus heideri* are Polychaeta. The latter only occurred at WK-DW, while *Hrabeiella periglandulata* was present at all three sites with high frequency and abundance (Table 3). Among the enchytraeid species occurring most frequently and at all three sites were *Buchholzia appendiculata, Stercutus niveus, Enchytronia parva, Enchytraeus christenseni* and *Enchytraeus buchholzi*. Among the frequent species are two that have not been formally described so far, but are known to the authors from investigations on soil monitoring sites in Germany. These are given as *Enchytronia* sp. (sept) and *Achaeta* sp. (dzwi) in Table 3. *Achaeta* sp. (affi) belongs also into this category. This species occurs only in a few samples, but in very high numbers (WK-DW and NB).

The total enchytraeid abundance was similar at WK-RF and NB, but more than twice as high at WK-DW ($p < 0.05$), although variability at WK-DW was comparatively high due to the agglomerated occurrence of *Achaeta* sp. (affi).

Table 2. Species composition of earthworms at the studied sites. F: frequency, A: abundance, B: biomass. $^{a, b}$: abundance or biomass data with different exponents differ significantly.WK-DW: Weiherskopf with deadwood, WK-RF: Weiherskopf reference site, NB1991: Nonnenstromberg, sampling 1991 without formalin extraction, NB1993: Nonnenstromberg, sampling 1993 with formalin extraction

Site	**WK-DW**			**WK-RF**			**NB1991**			**NB1993**		
	F	A ind. m^{-2}	B g m^{-2}	F	A ind. m^{-2}	B g m^{-2}	F	A ind. m^{-2}	B g m^{-2}	F	A ind. m^{-2}	B g m^{-2}
epigeic species												
Dendrobaena octaedra (Savigny, 1826)	80%	30.0	2.2	70%	30.0	2.2				20%	4.0	0.4
Dendrobaena pygmaea (Savigny, 1826)	70%	23.6	0.4	60%	15.6	0.3	15%	5.0	0.1			
Dendrodrilus rubidus (Savigny, 1826)	20%	4.0	0.4	20%	2.4	0.3	20%	7.0	0.3	10%	2.0	0.3
Lumbricus rubellus Hoffmeister, 1843	10%	4.0	0.1	10%	2.0	5.5				30%	5.2	3.3
endogeic species												
Aporrectodea caliginosa (Savigny, 1826)	70%	16.8	7.6	90%	42.0	15.4	30%	8.0	1.6	50%	14.4	7.4
Aporrectodea limicola (Michaelsen, 1890)	40%	4.8	0.9	80%	26.8	2.1				30%	2.8	0.3
Aporrectodea rosea (Savigny, 1826)	80%	20.0	2.1	40%	6.0	0.8	10%	3.0	0.1	20%	2.4	0.3
Octolasion tyrtaeum (Savigny, 1826)	100 %	36.4	5.4	80%	16.0	2.6						
anecic species												
Lumbricus terrestris Linnaeus, 1758	20%	2.0	4.0	10%	0.4	0.9				40%	3.2	5.6
Total arithmetic mean		**141.6**^{a}	**23.1**^{a}		**141.2**^{a}	**30.1**^{a}		**23.0**^{b}	**2.1**^{b}		**34.0**^{b}	**17.7**^{a}
standard deviation		58.7	20.5		77.9	33.2		36.9	3.6		26.1	20.5
Species number	**9**			**9**			**4**			**7**		

Table 3. Species composition of microannelids at the studied sites. F: frequency, AB: abundance. WK-DW: Weiherskopf with deadwood, WK-RF: Weiherskopf reference site, NB: Nonnenstromberg. AcInd: Acidity indicator group, str: indicator of strong acidity, m: indicator of moderate acidity, sli: indicator of slight acidity. Informal species name with acronym in brackets: Species not formally described, but known to the authors. $^{a, b}$: abundance data with different exponents differ significantly

Site	**WK-DW**		**WK-RF**		**NB**		**Ac Ind**
	F	AB	F	AB	F	AB	
Enchytraeidae							
Cernosvitoviella atrata (Bretscher, 1903)	20%	7		-	40%	16	x
Cognettia sphagnetorum (Vejdovský, 1878)	40%	13	30%	9	35%	18	str
Achaeta camerani (Cognetti, 1899)	10%	6	10%	48		-	str
Mesenchytraeus pelicensis Issel, 1905		-	10%	1		-	str
Achaeta sp. (affi)	20%	726		-	25%	334	m
Cognettia cognettii (Issel, 1905)	10%	4		-		-	m
Oconnorella cambrensis (O'Connor, 1963)	20%	112		-	25%	118	m
Achaeta sp. (glin)	40%	79	50%	50		-	m
Enchytraeus norvegicus Abrahamsen, 1969	20%	9	30%	12	30%	17	m
Marionina simillima Nielsen & Christensen, 1959	10%	1		-		-	m
Mesenchytraeus glandulosus (Levinsen, 1884)	30%	5	30%	6	20%	10	m
Enchytronia parva Nielsen & Christensen, 1959	70%	100	90%	77	95%	193	m
Enchytronia sp. (sept)	80%	18	50%	18	65%	42	m
Fridericia striata (Levinsen, 1884)	20%	6		-	60%	24	m
Oconnorella tubifera Nielsen & Christensen, 1959	40%	42	30%	46	15%	115	m
Achaeta bohemica (Vejdovský, 1879)	50%	21	30%	8	75%	92	sli
Achaeta unibulba Graefe, Dózsa-Farkas & Christensen, 2005	10%	1		-	5%	1	sli
Achaeta sp. (dzwi)	70%	107	60%	51	90%	345	sli
Buchholzia appendiculata (Buchholz, 1862)	80%	82	100%	168	60%	151	sli
Enchytraeus buchholzi Vejdovský, 1879	40%	21	60%	18	55%	20	sli
Enchytraeus christenseni Dózsa-Farkas, 1992	100%	72	80%	65	60%	59	sli
Enchytraeus lacteus Nielsen & Christensen, 1961		-		-	5%	1	sli
Enchytronia sp. (holo)	40%	49	10%	1		-	sli
Fridericia benti Schmelz, 2002	40%	8	30%	3		-	sli
Fridericia bisetosa (Levinsen, 1884)	60%	16	60%	25	45%	14	sli
Fridericia connata Bretscher, 1902	40%	12	90%	44	15%	6	sli
Fridericia galba (Hoffmeister, 1843)	30%	11	40%	5	5%	1	sli
Fridericia isseli Rota, 1994		-	20%	7		-	sli
Fridericia maculata Issel, 1905	20%	11	10%	1		-	sli
Fridericia miraflores Sesma & Dózsa-Farkas, 1993	50%	114	50%	14	10%	2	sli
Fridericia cf. nielseni Möller, 1971		-		-	5%	1	sli
Fridericia paroniana Issel, 1904		-	10%	1	15%	4	sli
Fridericia waldenstroemi Rota & Healy, 1999		-	10%	2		-	sli
Fridericia sp. juv.	70%	124	100%	125	90%	63	sli
Henlea nasuta (Eisen, 1878)	10%	5		-		-	sli
Marionina argentea (Michaelsen, 1889)	30%	8	30%	26	5%	1	sli
Mesenchytraeus armatus (Levinsen, 1884)	10%	1		-		-	sli
Stercutus niveus Michaelsen, 1888	80%	51	60%	70	45%	14	sli
Polychaeta							
Hrabeiella periglandulata Pizl & Chalupský, 1984	100%	239	90%	137	90%	175	m
Parergodrilus heideri Reisinger 1925	10%	7		-		-	sli
Total		2088		1038		1837	
Total ind. m^{-2} arithmetic mean		106,341^{a}		52,865^{b}		46,779^{b}	
standard deviation		104,979		30,162		23,341	
Species number		**34**		**28**		**27**	

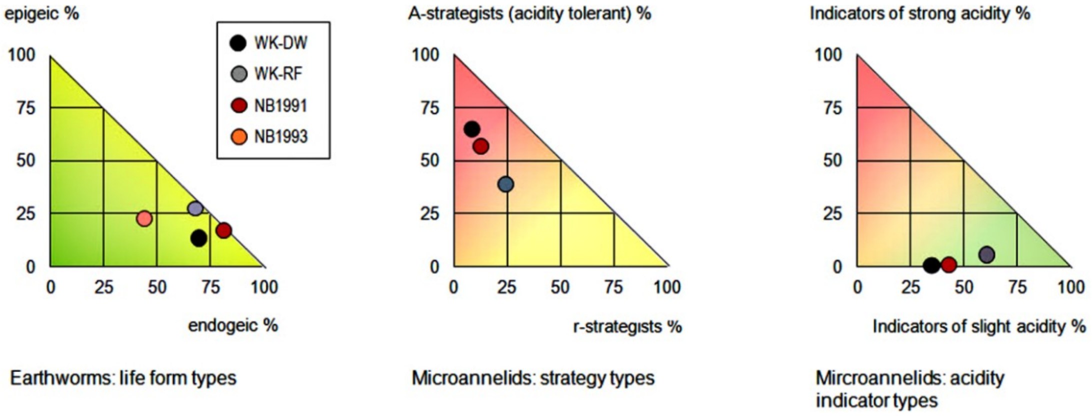
Acidity indicator groups, strategy types and life-form types

The biomass proportion of the three life-form types of earthworms is illustrated in Figure 1 (left). The percentage of epigeic species was below 30 % at all sites. The proportion of endogeic species was equal at the two WK sites.

For the microannelids, we differentiate between the strategy types r-, A- and k-strategists (Figure 1, centre). In the category r-strategists, species with a potentially high reproduction rate are pooled, *i.e.* most *Enchytraeus* species and *Buchholzia appendiculata*. This group showed a comparatively high percentage at WK-RF, due to a high dominance of *Buchholzia appendiculata* at this site (16%). However, the microannelid community was generally dominated by A-strategist species at all three sites. At WK-DW and NB they represented more than 50% of the species, to which *Achaeta* sp. (affi) contributed the greatest part. At WK-RF k-strategist species reached almost the percentage of A-strategists. To the category A-strategist belong indicators of moderate as well as of strong acidity. Figure 1 (right) differentiates according to the three groups of acidity indicators given in Table 3. It becomes evident that the A-strategists include mainly indicators of moderate acidity here, while indicators of strong acidity had by far the smallest proportion of the three indicator groups at all investigated sites.

Humus profiles and vertical distribution of microannelids

The humus layer of the soil profile was restricted to the uppermost microannelid subsample (0–2.5 cm) at all three sites (Figure 2, data not shown for NB). The microannelid activity showed generally a decline in the deeper subsamples (figure 3). At site WK-RF the border between humus layer and mineral soil was located within the uppermost sub-sample, where the highest microannelid density was found. At WK-DW and NB the microannelid density was highest in the second depth layer. At these both sites, also the border between humus layer and mineral soil was located slightly deeper than at WK-DW and often coincided with the border between first and second sub-sample. The high abundance in the 2.5–5 cm layer at WK-DW and NB was partly produced by the mass occurrence of *Achaeta* sp. (affi) in this layer in single samples. Some species concentrated in specific horizons: *Buchholzia appendiculata* occurred most numerously in the uppermost layer, which consisted mainly of the organic layer. In contrast, other species, as *Hrabeiella periglandulata* and *Stercutus niveus* occurred predominantly in the mineral topsoil (A-horizon).



Earthworms: life form types

Microannelids: strategy types

Mircroannelids: acidity indicator types

Figure 1. Life-form types (left), strategy types (centre) and acidity indicator types (right). Percentage of biomass (earthworms) or abundance (microannelids). In the diagrams, the parameter complementing the shown values to 100% is: anecic biomass (left), k-strategists (centre) and indicators of moderate acidity (right). Strategy types according to Graefe & Schmelz (1999). WK-DW: Weiherskopf with deadwood, WK-RF: Weiherskopf reference site, NB1991: Nonnenstromberg, sampling 1991 without formalin extraction of earthworms, NB1993: Nonnenstromberg, sampling 1993 with formalin extraction of earthworms

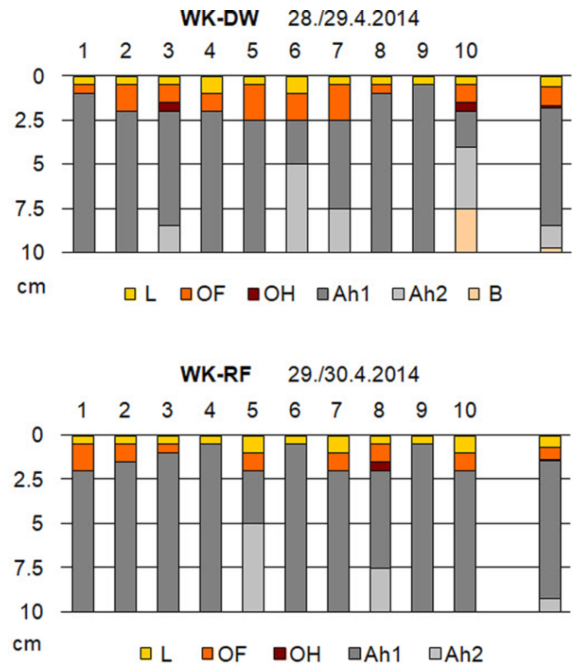


Figure 2. Humus profiles of the two Weiherskopf study sites at the 10 sample points and arithmetic means of horizon thickness (right column). L: undecayed litter, OF: fragmented litter, OH: humified litter, Ah: mineral topsoil, B: subsurface horizon. WK-DW: Weiherskopf with deadwood, WK-RF: Weiherskopf reference site.

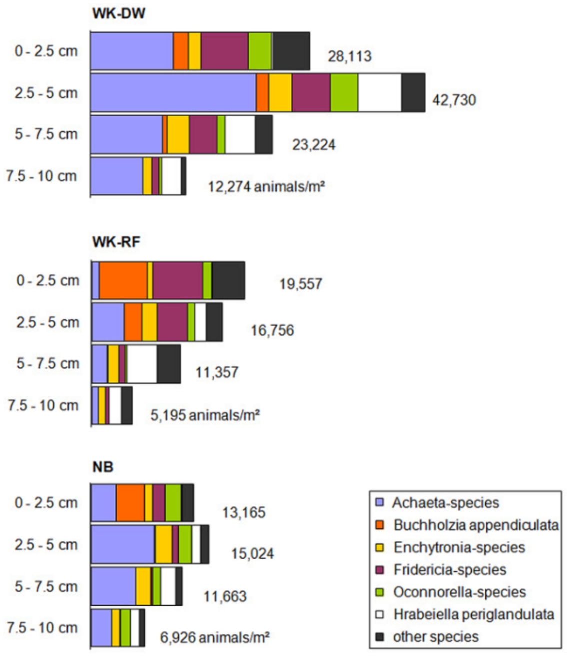


Figure 3. Vertical distribution of microannelids at the study sites. WK-DW: Weiherskopf with deadwood, WK-RF: Weiherskopf reference site, NB: Nonnenstromberg.

Sørensen Similarity Index

The Sørensen Similarity Index was computed for the whole annelid community as well as for microannelids only. Taking into account all annelid species it took values between 0.83 and 0.78, while the exclusion of earthworms from the index yielded slightly lower values (Table 4). While the species spectra of WK-DW / WK-RF and WK-DW / NB overlap almost to the same degree, the similarity between WK-RF and NB was slightly lower.

Table 4. Sørensen Similarity Index of the investigated sites. WK-DW: Weiherskopf with deadwood, WK-RF: Weiherskopf reference site, NB: Nonnenstromberg.

Earthworms and microannelids:	**Sørensen Index**
WK-DW *vs* WK-RF	0.83
WK-DW *vs* NB	0.82
WK-RF *vs* NB	0.78
Microannelids only:	
WK-DW *vs* WK-RF	0.77
WK-DW *vs* NB	0.79
WK-RF *vs* NB	0.73

DISCUSSION

While the site WK-DW had been strict forest reserve for 25 years at the time of investigation, the Nonnenstromberg strict forest reserve was only established two years before the first investigation at the site NB. However, this site had been part of a nature protection area for several decades before, which also implies reduced human impact. We thus consider the sites WK-DW and NB similar concerning their protection status for ≥ 25 years. Site WK-RF is still under forest management, which includes deadwood removal to some extent. Amounts of deadwood varied strongly horizontally at all sites. At the Weiherskopf sites, windthrow had been patchy, WK-DW being more affected by it than WK-RF. In our opinion, a correlation of deadwood presence with the zoological data would have required the assessment of deadwood stocks and distribution at each of the sample points, but this was not part of our research contract. Thus, the possible influence of windthrow and deadwood management on species composition, abundance and biomass data of earthworms and microannelids was not explored in detail. As we took soil-samples and did not sample specifically under or in the vicinity of decaying deadwood, we assume that the soil properties were principal determining factors for community composition.

Species composition of earthworms was very similar at the three investigated sites. The much lower earthworm abundance at the Nonnenstromberg site indicates that the habitat conditions might not have been optimal at the sampling occasions in 1991 and 1993. Also comparison with other studies shows that the abundance data for the Nonnenstromberg site were rather low (Bonkowski 1991). Whether soil properties or other factors, as *e.g.* unfavourable weather conditions (drought) have been the reason, is hardly possible to detect more than 20 years after the investigation. When we encounter a very low abundance, this can relate to lower species numbers. Species we would expect might then be seemingly absent, because they were not covered by the sampling, *e.g.* due to sparseness or inactivity. This might have been the case for *Octolasion tyrtaeum* at site NB.

For microannelids the significantly higher abundance at WK-DW is mainly due to high numbers of *Achaeta* sp. (affi) at one sample point. This mass occurrence, which contributed more than one third to the total abundance of this site, was probably caused by the slightly lower pH at this point, as *Achaeta* sp. (affi) is an indicator of moderate acidity. A mass development of this species occurs to a lesser extend also at NB and has been encountered elsewhere as well (Graefe 2004).

With respect to community characterization we consider quantitative parameters, like abundance, that can show high short-term variability, less relevant than parameters linked to the species composition, as proportion of indicator groups or occurrence of functional key species. In this respect, the communities at the three investigated sites shared characteristics that indicate similar soil habitat conditions. As has been repeatedly demonstrated, the characteristics of soil fauna communities are closely linked to humus form development (Jabiol *et al.* 1995, Graefe & Beylich, 2006). At the investigated sites, all three life form types of earthworms were present. Anecic and endogeic earthworm species are considered main actors in the formation of mull humus forms. In addition to these, *Stercutus niveus* among the microannelids is characteristic for the decomposer community type typical for forest soils with mull humus forms according to Graefe (1993). At the studied sites we found a variant of this community type, including a high dominance of endogeic earthworms, along with a reduced presence of anecic earthworms. Further the generally quite rare species *Dendrobaena pygmaea* occurred regularly. Among microannelids a high dominance of *Hrabeiella periglandulata* and the occurrence of several species that are indicators of moderate acidity characterized the community type variant at the studied sites. Given pH values below 5 in the mineral topsoil, indicators of slight acidity, as anecic earthworms and most *Fridericia* species, are near the lower limits of their $pH_{(CaCl2)}$ tolerance range (Graefe & Beylich 2003), even when we consider that measurement in $CaCl_2$-solution would produce slightly higher values than measurement in KCl-solution as used in the present study.

Due to the low frequency of anecic earthworms, the incorporation of organic matter into the soil was limited at the studied sites, resulting in the formation of an OF-layer of partly fragmented organic material. Thus, the main humus form was an F-Mull (Ad-hoc-AG Boden 2005). Although there were patches with a thin OH-horizon, suggesting a transition to moder humus forms, we always found numerous microannelids to a depth of 10 cm, indicating a biologically active A-horizon, being an integral part of mull humus forms (Jabiol *et al.* 1995). A closer look at the vertical distribution of microannelids in relation to the border between the humus layer and the mineral soil suggests a high decomposition activety just in this border zone. The high dominance of the r-strategist *Buchholzia appendiculata* in the uppermost layer is related to this. The preference of this species for the litter layer (OL- and OF-layer) is well established (Dózsa-Farkas 1992, Graefe & Schmelz 1999). The fact that *Fridericia* species, all of which are considered indicators of only slight acidity, showed the highest dominance in the uppermost layer, could relate to the fact that the organic layer had higher pH-values than the mineral topsoil.

The high species diversity associated with a considerable proportion of species tolerating at least moderate acidification distinguishes the community on basalt from that of limy soils on calcareous bedrock. Along a gradient from basalt to limestone, Schlaghamerský (1998) found a higher species number on basalt than on limestone, with *Cognettia sphagnetorum* and *Enchytronia parva* (indicators of strong and moderate acidity respectively according to Graefe & Schmelz 1999) showing significantly lower densities in the calcareous soil. At the same sites, Bonkowski's (1991) investigations on earthworms yielded a high diversity. The species *Dendrobaena pygmaea* showed a lower biomass on limestone than on basalt. Whether differences in species dominance were due to the lime content or rather differences in other factors could not be ascertained. The fact that soils on calcareous bedrock are frequently shallow and running dry readily may cause problems in relating community characteristics directly to the presence of lime. Our own investigations in the "Hünstollen" Strict Forest Reserve in Lower Saxony on calcareous soil on limestone showed a similarly high annelid diversity as in the current study (26 species), but hardly indicators of moderate acidity (Beylich *et al.* 1995). Notably, the most common species at our current study sites on basalt indicating moderate acidification, *i.e. Enchytronia parva* and *Hrabeiella periglandulata*, did not occur at the "Hünstollen" site. However, Mellin (1988) found in his investigations in beech forests on limestone a microannelid community extremely rich in species, including also *Enchytronia parva* and other indicators of moderate acidity, although the pH (KCl) was mostly between 5 and 6 and thus slightly higher than at our study sites on basalt. Anyhow, also soils on limestone can show advanced acidification favouring a broad species spectrum comprising species with varying pH preferences. Schoch-Bösken & Greven (1987) found 24–26 species in a beech forest on limestone in the Egge Mountains (Germany), ranging from indicators of strong to slight acidity (mean pH ($CaCl_2$) 4.1–4.3). Apparently, it is difficult to draw a clear line between the annelid community of moderately base-rich soils on basaltic bedrock and the community of base-rich soils on calcareous bedrock. There rather seems to be a smooth transition between both, depending on the degree of acidification of the soil.

For faunistic studies on other animal groups in strict forest reserves, Sørensen values of > 60% are considered as "high" (Dorow 2014). The similarity of the three investigated sites on basalt according to the Sørensen Index is thus quite striking, supporting the conclusion that comparable site conditions led to the development of similar annelid communities. The high similarity also shows that, at least within the given sampling design, differences concerning community composition between the two Weiherskopf sites due to different deadwood management are not traceable. Although the inclusion of the above mentioned studies on basalt or limestone by other researchers into the calculation of Sørensen Indices would have been interesting, it was not undertaken, as the revision of species and description of new species during the last decades makes direct comparison of species lists in particular cases difficult (*e.g.* Schmelz 2003).

Corresponding to the delineated variant of decomposer community, also botanists distinguish within beech forests with mull humus forms (Galio-odorati Fagenion) between communities on moderately base-rich soils as opposed to those on calcareous soils (Ellenberg 1986). Both, the decomposer community as well as the plant community typical for moderately base-rich soils free of calcium carbonate apparently do not comprise distinct character species, but are characterized by the co-occurrence of indicators of slight and moderate acidity. On the other hand, the decomposer community of forest sites with moder humus forms is characterized by indicator species for strong acidity among the microannelids and the lack of endogeic and anecic earthworms, as outlined by Graefe *et al.* (2002). While reference ranges concerning abundance, biomass and species number for earthworms and microannelids have been published for these acid forest sites with moder humus forms in Beylich & Graefe (2009), no such values were proposed for moderately base-rich and limy sites so far due to the comparatively low number of relevant studies.

According to the Red List of Earthworms Germany (BfN 2016), the species *Dendrobaena pygmaea* is considered very rare, though unthreatened. An enquiry at the public database Edaphobase (Burkhardt *et al.* 2014) rendered only about twenty entries for this species in Germany, mostly in mixed deciduous forests, never in grassland or agricultural sites. We consider this species as one of the few species occurring predominantly in moderately base-rich to base-rich forest soils. The species *Aporrectodea limicola* is classified as rare in the Red List, and endangered to unknown degree, a more precise categorization being impeded by insufficient data.

We conclude that beech forests on basalt with F-mull are associated with a specific type of decomposer community, including also some rare species. Comparison with communities on calcareous bedrock shows considerable overlap in species composition. Characterization of both types could be strengthened by comparative studies.

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