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State of knowledge of enchytraeid communities in German soils as a basis for biological soil quality assessment

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Abstract

Within a project aiming to improve the preconditions for the protection of the habitat function of soils in Germany, the database 'Bo-Info' was established. In this database soil biological data from permanent soil monitoring sites of several German states as well as from the literature were compiled. Soil biological data on the abundance and dominance of Enchytraeidae (potworms) were analysed with respect to their distribution, site characteristics (habitat type, land use) and soil properties (pH, texture, organic matter). Reliable data for potworms were available from 133 of 208 sites. In total, 96 species of the 122 species known to occur in Germany were present in the database, 24 of which were very common. Ecological preferences regarding land use, pH, soil organic matter (SOM) and soil texture were derived for these 24 plus another 16 species typical for specific habitat types. The occurrence of enchytraeids at the species and ecological-group level was most strongly determined by land use and pH value and less by soil texture. A distinction between litter and soil dwelling species was found regarding SOM. Enchytraeid communities of habitat types representing the four major land use types (grassland, arable land, deciduous and coniferous forests) clearly differed. Using three examples from different land use forms, typical species could be identified at the second level of detail of habitat types, given a sufficient number of data. As a result, qualitative expectation (= reference) values for species richness and composition are proposed for the most important habitat types (e.g. different types of arable land, grassland and coniferous forests). The data basis regarding taxonomy, biogeography and ecology of German enchytraeids clearly needs to be enlarged. Due to their ecological relevance, the use of enchytraeids for soil biological site classification and assessment is recommended.

Keywords Biogeography | habitat function | Enchytraeidae | permanent soil monitoring sites | reference system | Oligochaeta | Clitellata

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1. Introduction

1.1. Background

Soils are an essential component of terrestrial ecosystems. They host highly diverse organism communities organized in complex food webs that strongly contribute to natural soil functions (de Ruiter et al. 1993, Ekschmitt & Griffiths 1998, Bardgett et al. 2005, Brussaard et al. 2007, Turbé et al. 2010, Mulder et al. 2011). Despite this high ecological significance, the structural and functional diversity of soil organisms – and thus the biological quality of soils – is presently insufficiently protected (van Camp et al. 2004). In Germany, according to § 2 of the German Federal Soil Protection Act (BBodSchG 1998), the habitat function of soils must be protected, but specifications on how to fulfil this obligation are missing in the follow-up Federal Soil Protection Ordinance (BBodSchV 1999). In some German federal states, abiotic (in particular pedological) parameters are used to assess the biological soil quality (Blossey & Lehle 1998). However, this indirect approach is not sufficient because soil biodiversity itself as well as biological soil quality can only be effectively assessed using biological parameters (Ekschmitt et al. 2003, Beylich et al. 2005). Hence, since the late 1990s several research projects have been conducted in Germany, at both the state and the federal level, to create a basis for a soil biological classification and assessment system (e.g., Römbke et al. 2000, 2002a), thus following-up a long tradition of biological soil assessment (e.g. Volz 1962, Dunger 1968, Graefe 1995). In parallel, similar concepts have also been developed in other countries, often taking limnological assessment approaches as an example (in particular the British RIVPACS; Wright 2000). In recent years essential contributions on biological soil assessment were made in the Netherlands, e.g., on the use of microbial parameters (Bloem et al. 2006) or on the definition of reference sites (Rutgers et al. 2008). These authors mostly suggest a 'battery-approach' using several invertebrate groups as well as microbial parameters for the assessment of soil quality (see Gröngröft et al. 2001, Römbke & Breure 2005a,b). There is also a general agreement that an assessment should best be performed using pre-defined reference values. Similar conceptual approaches to the definition of reference states for soil organism communities (especially for arthropods) are also presented in Lennartz (2003), Roß-Nickoll et al. (2004), Toschki (2008) and within a guideline for the monitoring of effects of genetically modified organisms (GMO) on soil organisms by the Association of German Engineers (VDI; Ruf et al. 2013).

Under the responsibility of the German Federal states, about 800 permanent soil monitoring sites (Bodendauerbeobachtungsflächen, BDF) have been installed mainly in agricultural, grassland and forest sites. The primary purpose of these is the characterization of soil conditions and their changes due to external impacts (Werner 2002). Since 1990 a standard guideline (ISO 2004) addresses the selection of BDF (e.g., their representativeness for land use, landscape and European climatic regions). Proposals for which biological parameters are to be investigated in BDF also exist (Barth et al. 2000), but so far no generally accepted approach has been implemented. Usually only isolated parameters (in particular microbial respiration and diversity of lumbricid earthworms) are recorded, but not by all federal states and only at irregular intervals (UBA 2007). For further details regarding the use of BDF for biological soil quality assessments see Römbke et al. (2012).

1.2. Present state of knowledge of European Enchytraeidae

Potworms belong to the soil mesofauna (body diameter 0.1–2 mm). Globally, about 700 species belong to the family Enchytraeidae (Schmelz & Collado 2012). In Europe the species number is estimated at 230-300 (Fauna Europaea Web Service 2007), including 122 from Germany (Schmelz, pers. comm.). Enchytraeids are sapro-microphytophagous, i.e. they feed on dead soil organic matter (SOM), including fungi and bacteria attached to this material (Didden 1993, Briones & Ineson 2002). Thus, they affect the decomposition of organic matter by regulating the microbial community mainly responsible for this activity (Brussaard et al. 2012). In addition, like earthworms (but at smaller spatial scales) they can influence processes such as soil formation by their burrowing activity (Didden 1990, Topoliantz et al. 2000). For example, in the Dutch BISQ project, in the 170 sites studied enchytraeids (besides earthworms) were found to highly influence the 16 ecosystem services studied (Mulder et al. 2011).

The basis of enchytraeid taxonomy is the monograph of Nielsen & Christensen (1959, 1961, 1963). This key is considered to be a milestone in enchytraeid taxonomy but it is now outdated; partly because many new species have been described, and partly because new morphological characters have been identified in the meantime. Following the detailed revision of the species-rich genus *Fridericia* by Schmelz (2003), Schmelz & Collado (2010) published a key for the terrestrial potworms of Europe. In addition, first studies on the molecular phylogeny of this family have been published (Christensen & Glenner 2010, Erseus et al. 2010), which supports the division of the family in two subfamilies: the Achaetinae (primarily species of the genus *Achaeta* and some tropical genera; Černosvitov 1937) and all other potworms. In addition, it is becoming clear that a high cryptic diversity exists in the family Enchytraeidae (Collado et al. 2012): for example, under the current species name *Enchytronia parva* various, partly even morphologically different taxa are known (R. Bloch and R. Schmelz, pers. comm.).

Information on the ecological preferences of individual species (mainly on their reaction to soil pH and soil moisture) has been compiled by Graefe & Schmelz (1999). Synecological data are growing in number (e.g. Didden 2003), but are still far from being exhaustive. However, it is possible to divide enchytraeids into three ecological groups, using criteria such as their distribution in the soil profile (EFSA 2010): litter dwellers, mineral soil dwellers and intermediates.

Due to their sensitivity towards anthropogenic stress (in particular chemicals), enchytraeids are used in ecotoxicological laboratory tests, semi-field and field studies (Römbke 2003). In order to survey enchytraeids in the field, soil samples are taken with a corer (diameter usually between 5 and 7.5 cm). These samples are separately placed onto sieves hanging in plastic bowls filled with water, and the enchytraeids are driven via wet-extraction from the soil. This procedure has been internationally standardized (ISO 2006). Species identification is only possible with living specimens, which limits the number of samples that can be handled in parallel.

The highest abundance but often lowest species richness of enchytraeids are usually found in acidic soils (e.g. moorland, or coniferous forests) (e.g. Standen 1984). Density and diversity are low at crop sites due to intensive soil management, e.g. ploughing or the application of fertilizers or pesticides, and are intermediate or high in grassland. Abiotic factors (in particular soil moisture and soil properties, e.g. pH) dominate enchytraeid abundance and diversity (Maraldo & Holmstrup 2010, Graefe & Schmelz 1999). In forests, biotic factors, especially the quality of litter material and the amount of microbial biomass also play an important role (Scheu et al. 2003). First proposals for reference values (diversity, species number and abundance) of enchytraeids at different sites have been given for the Netherlands and Northern Germany (Rutgers et al. 2008, Beylich & Graefe 2009). So far, potworms have been recommended for use in various monitoring programmes or assessment schemes (e.g. Schouten et al. 1999, Jänsch et al. 2005, Barth et al. 2000, Bispo et al. 2009).

1.3. Aims of the project and of this contribution

In 2009, the authors of this contribution began a research project within the scope of the German ‘National Strategy for Biological Diversity’ and supported by the German Federal Environmental Agency. This German national strategy intends to improve the protection of the habitat function of soils, e. g. by broadening soil biological monitoring at existing permanent soil monitoring sites (BDF). The aim of this project was the improvement of the preconditions for the protection of soils’ habitat function as described in § 2 of the German Federal Soil Protection Act (1998), in particular by, first, identifiying suitable biological indicators (i.e. organism groups) for the assessment of soil quality and, second, establishing reference values useful for selected habitat types to be used for evaluating whether a soil fulfils the habitat function or not. The main activity of this project was the establishment of a database, called Bo-Info, in which the existing information on certain soil invertebrates were compiled (Römbke et al. 2012). In the meantime, this data has been transferred to the expert-driven information system ‘Edaphobase’, developed and hosted by the Senckenberg Museum of Natural History Görlitz (www.edaphobase.org; Burkhardt et al. 2013), which also delivers the data to the Global Biodiversity Information Facility (GBIF; www.gbif.org).

This contribution focusses on enchytraeids. In detail, the aims of this paper are:

- Description of the actual status of enchytraeid biodiversity in Germany;
- Compilation of ecological profiles of the most common 37 enchytraeid species;
- Preparation of recommendations for the use of enchytraeid worms for the evaluation of the habitat function of soils.

2. Material and Methods

2.1. Data basis and evaluation strategy

Data on the occurrence of enchytraeids in Germany were collected in the above-mentioned Bo-Info database. 208 sites (including 60 BDF) were covered, yielding about 8,000 datasets, 2,000 of which are from BDF. The latter were contributed by the federal states of Brandenburg, Hamburg, North Rhine-Westphalia, Schleswig-Holstein and Thuringia. The geographical distribution of the sites with available enchytraeid data is depicted in Fig. 1. As already mentioned, data from BDF are restricted to five

German federal states, which becomes most obvious with the distribution of arable land sites, i.e. the different habitat types were not evenly sampled throughout Germany. Many sampling sites in Berlin and Baden-Württemberg originate from research projects performed in these regions.

After data compilation a reliability check was performed. In analogy to the classification system of Klimisch et al. (1997), data were classified as either I. Reliable, II. Reliable with restrictions, III. Not reliable, or IV. Not assignable. The following criteria were used: Is the site geographically identifiable? Is the documentation comprehensive? Which sampling method was used? Is the taxonomic determination trustworthy? In detail, these criteria are not quantifiable, meaning that the classification was performed via expert knowledge on a case-by-case basis. Finally, data from 133 sites were classified as being suitable for further assessment (i.e. belong to Class I or II).

2.2. Establishment of a reference system

In order to facilitate the use of biocoenotical data at the landscape level, a standard frame of reference is needed that allows comparable statements on biodiversity and factors influencing the biocoenosis, specified for habitat types. In order to operationalize the assessment of biodiversity, a site-specific reference system was developed. It can be described as comprising reference values for the biocoenosis at certain habitat types by evaluating biocoenosis-site-relationships and will ultimately lead to the identification of threshold values with which a significant change of the biocoenosis can be indicated (Fig. 2).

Thus, a reference system for the site-specific diversity of soil organisms consists of:

- Reference values: lists of species expected to occur at a certain site with its specific conditions (e.g., climate, soil factors, region etc.);
- A quantification of deviations from these reference values that indicate impacted habitat function.

In order to develop reference values that link soil and site parameters with the occurrence of soil organisms, the landscape had to be classified into a limited number of 'site categories'. For this purpose we used the habitat classification concept compiled in the German Red Data Book on endangered habitats (Riecken et al. 2006, 2009). It comprises 44 basic types (first level) with approximately 1,000 hierarchically organised sub-types (second level). This concept is already accepted by German authorities, since it has been used in the areas of FFH (Flora - Fauna - Habitat) legislation, nature conservation management, GMO (Genetically Modified Organisms) authorization and prospectively also pesticide registration. From this habitat type list, 21 basic types were identified as being relevant for the classification of soil organisms including enchytraeids (Römbke et al. 2012). Most sites containing data on enchytraeids could be allocated to only four of these 21 basic habitat types, representing the four major land use types (Table 1).

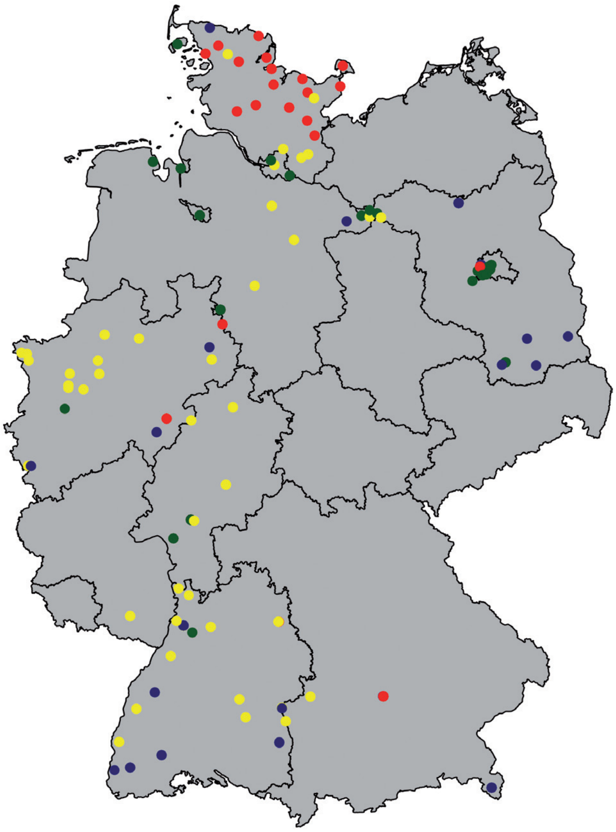

Figure 1. Enchytraeid sampling sites in Germany, differentiated by the main land use types. **Red** – crop sites, **green** – grasslands, **yellow** – deciduous forests, **blue** – coniferous forests.

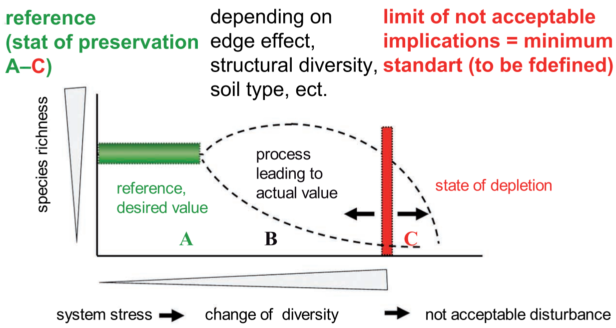

Figure 2. Principle of threshold values in regard to a system of reference values: A, B and C correspond to different states of preservation related to increasing system stress (e.g., FFH legislation, EU 1992).

2.3. Evaluation strategy

2.3.1. Ecological profiles of single species

Four site and soil properties (major land use type, pH-value, texture and OM content) that potentially influence the distribution of enchytraeids were each classified into four to five categories (Römbke et al. 2000). Based on this data, ecological profiles were created for 40 species (the 24 most common species, i.e. occurring at more than 25 sites, plus 16 species typical for at least one habitat type). The relative frequency of occurrence (%) for a given species in regard to the classified site factors was evaluated. Thus, the preferences or tolerances for these factors of each species as well as their overall frequency within the factor categories could be assessed without introducing skewed results due to observational bias. Differences in occurrence between different factor classes were analyzed using the Chi²-test with Bonferroni correction, which thus indicated whether a given factor

Table 1. Habitat types, derived from the German Red Data Book on endangered habitats (Riecken et al. 2006, 2009), used in this study for the establishment of a reference system to evaluate the biological state of the soil. **Bold** – types at first hierarchical level. **Normal** – types at second hierarchical level.

Habitat type number	Description
33	**Arable and fallow land (in the following abbreviated 'arable land')**
33.01	Farmed and fallow land on shallow skeletic calcareous soil
33.02	Farmed and fallow land on shallow skeletic silicaceous residual soil
33.03	Farmed and fallow land on sandy soil
33.04	Farmed and fallow land on loess, loam or clay soil
33.05	Farmed and fallow land on peaty or half-bog soil
34	**Natural dry grasslands and grasslands of dry to humid sites (in the following abbreviated 'grassland')**
34.01	Xeric grassland
34.02	Semi-dry grassland
34.03	Steppic grassland (subcontinental, on deep soil)
34.04	Dry sandy grassland
34.05	Heavy-metal grassland
34.06	Mat-grass swards
34.07	Species-rich grassland on moist sites
34.08	Species-poor intensive grassland on moist sites
34.09	Trampled grass and park lawns
43	**Deciduous and mixed woodlands and forest plantations (deciduous share >50 %) (in the following abbreviated 'deciduous forest')**
43.01	Birch bog woodland
43.02	Carr woodland
43.03	Swamp forest (on minerogenic soil)
43.04	Alluvial forest
43.05	Tidal alluvial forest
43.06	Ravine, boulder-field and scree forests
43.07	Deciduous and mixed forest on damp to moist sites
43.08	Deciduous (mixed) forest on dry or warm dry sites
43.09	Deciduous (mixed) plantations with native tree species
43.10	Deciduous (mixed) plantations with introduced tree species (including subspontaneous colonisations)
44	**Coniferous (mixed) woodlands and forest plantations (in the following abbreviated 'coniferous forest')**
44.01	Bog woodland (coniferous)
44.02	Natural and near-natural dry to intermittently damp pine forest
44.03	Spruce/fir (mixed) forest and spruce (mixed) forest
44.04	Coniferous (mixed) plantations with native tree species
44.05	Coniferous (mixed) plantations with introduced tree species (including subspontaneous colonisations)

had a statistically significant influence on the distribution of a species. Thus, a total of 160 analyses were performed (4 factors for 40 species). Due to the high number of figures it is not possible to present the ecological profiles of all 40 species here in detail. Two examplary species are presented in section 3.2.; the ecological profiles for 38 other species are included as supplementary data (available online at www.soil-organisms.org).

In order to compare the preferences or tolerances of the 24 most common species evaluated, these were depicted together in one diagram per ecological factor. The data basis was the previously determined relative frequency of each species within each factor class. These were stacked and normalized to 100%, thus representing the theoretical overall distribution of a species while assuming an even number of sampled sites for each factor class (Formula 1). From the proportion of each factor class, the preference or tolerance of each species regarding the factors can be estimated and allows a comparison between the ecological profiles of different species. Thus, ecologically similar species can be grouped. However, it must be kept in mind that hereby the information on the absolute frequency of occurrence for a species is lost.

Formula 1: $$Z_i = \frac{x_i/y_i}{\sum_{i=1}^{n} x_i/y_i} * 100$$

With: Z_i = Relative proportion of species records from sites belonging to factor class i
x_i = Absolute number of species, records in sites belonging to factor class i
y_i = Absolute number of sampled sites belonging to factor class i

2.3.2. Derivation of reference values

Using the relative frequency of individual species (based on presence/absence data), those species (and thus ultimately communities) were identified that can be expected in sites belonging to specific habitat types and being unaffected by contamination or other forms of anthropogenic stress other than the land use itself (see also Chapter 2.2.). As a criterion for being a typical species for a specific habitat type, an occurrence in more than 50% of all sites belonging to that habitat type was applied. This was first performed for the basic habitat types representing the four major land use types. In a second step, this exercise was repeated for the second hierarchical level of habitat types given a sufficient availability of data. No statistical analysis was conducted for the second level of habitat types as the number of available sites was usually too small (n < 10).

3. Results and Discussion

3.1. Species number and their distribution in regard to soil and site properties

A total of 96 enchytraeid species were recorded from the soil sites included in our analysis. A complete list of all 122 species found in Germany so far is given in Appendix 1. In the following, 24 species with sufficient data availability are presented further (Table 2). Missing from the data base is *Enchytraeus albidus*, which occurs often in Germany but, with few exceptions (e.g. a marsh meadow close to the coast of the North Sea), has only been recorded from decaying organic material in the marine littoral or in compost heaps. The genus *Fridericia* is the most species-rich and common (seven species), followed by the genus *Enchytraeus* (four species) and the genus *Achaeta* (three species). The last ten species belong to seven different genera, among them *Marionina*, which is not well-defined (Rota et al. 2008). Seven species are classified as litter dwellers, ten as mineral soil dwellers and seven species as intermediates (Table 2). Species belonging to the same genus are not always in the same ecological group.

The habitat type was known for all 133 sites with reliable data on enchytraeids; 114 sites belong to one of the four major land use types. Data on pH, SOM and texture were available for 118, 85 and 96 sites, respectively (Fig. 3). The number of sites is more or less evenly distributed between the four habitat types (arable land, grassland, deciduous and coniferous forests). The same is also generally true for pH value and SOM content, while for texture the number of sites with silty and clayey soils is underrepresented (Fig. 3).

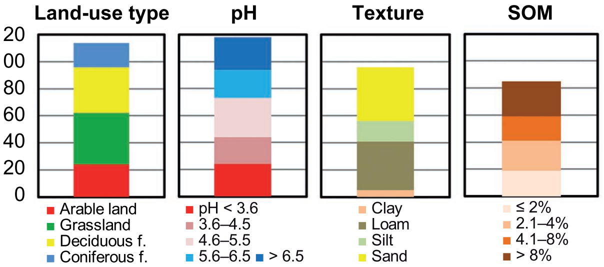

Figure 3. Number of sites with enchytraeid data (y-axis) and data for those factors most frequently present in the database: habitat types, pH-value, texture and soil organic matter (SOM) content.

3.2. Occurrence and ecological profiles of selected enchytraeid species

A complete overview of the ecological profiles of the 24 selected enchytraeid species is given in the electronic supplement to this publication (www.soil-organisms.org).

Here we present, as an example, the ecological profiles of the closely related species *Cognettia sphagnetorum* and *C. glandulosa*. Besides being morphologically very similar they also have in common the possibility of asexual reproduction via fragmentation; very often this is the only mode of reproduction. *C. sphagnetorum* is currently the only enchytraeid species considered to be an 'ecosystem-engineer' (Lavelle et al. 1997, Brussaard et al. 2012).

Table 2. Enchytraeid species considered here, including the number of sites (out of 133 sites included) in which the species has been found and the ecological group to which they belong. For author & year of species names see Appendix 1.

Litter dwellers	Number of sites
Achaeta aberrans	33
Achaeta affinis	32
Achaeta camerani	29
Buchholzia appendiculata	52
Cognettia sphagnetorum	62
Marionina communis	27
Mesenchytraeus glandulosus	29
Intermediates	Number of sites
Enchytraeus buchholzi	73
Enchytraeus christenseni	78
Enchytraeus lacteus	26
Henlea perpusilla	57
Henlea ventriculosa	51
Marionina clavata	44
Oconnorella cambrensis	39
Mineral soil dwellers	Number of sites
Enchytraeus norvegicus	52
Enchytronia minor	34
Enchytronia parva	48
Fridericia bisetosa	39
Fridricia bulboides	74
Fridericia christeri	36
Fridericia galba	55
Fridericia paroniana	33
Fridericia ratzeli	39
Fridericia sylvatica	26

3.2.1. *Cognettia sphagnetorum* (Vejdovský, 1878) (litter dweller)

C. sphagnetorum is widely distributed in the Palaearctic (Römbke 1992). This species was recorded at 62 sites (i.e. 47% of all sites), evenly distributed in Germany (Fig. 4). The occurrence of *C. sphagnetorum* depended significantly on pH and soil organic matter (SOM) content of the soil, but not on soil texture (Fig. 5A–C). It occured in almost all sites with a pH ≤ 4.5 and a C_{org} content > 8%. The species was found significantly more often in both forest types (> 90%) than in arable or grassland sites (Fig. 5).

These findings are consistent with the classification of *C. sphagnetorum* as a typical litter dweller (Standen & Latter 1977, Haimi & Siira-Pietikäinen 2003). In Czech forest sites, *C. sphagnetorum* has been found in high densities in all soil texture classes, slightly preferring sandy soils, but also occurring in more than 50% of all clayey soils under study (Schlaghamerský 1998). Our findings differ slightly from this assessment, but confirm the general impression that the occurrence of this species is not strongly determined by soil texture. Regarding pH-value, a strong compliance of our data with the literature exists: in both cases *C. sphagnetorum* is considered to be strongly acidophil (i.e. very abundant at pH < 4.5–5.0), and it is only rarely found in soils with a pH > 6.5 (Healy 1980, Graefe & Beylich 2003). Concerning SOM content, a similarly highly significant preference for soils with an SOM content > 4% exists both in our evaluation and in the literature (Schlaghamerský 1998). According to the Bo-Info data *C. sphagnetorum* is a typical forest species only rarely found in arable land. In German and Scandinavian coniferous (and partly deciduous) forests, it occurs with a dominance of almost always 100% (e.g. Abrahamsen 1972, Römbke 1989, Jänsch 2001). In addition, very high densities are recorded from moorlands (Peachey 1963, Springett 1970). The latter observation is in line with the

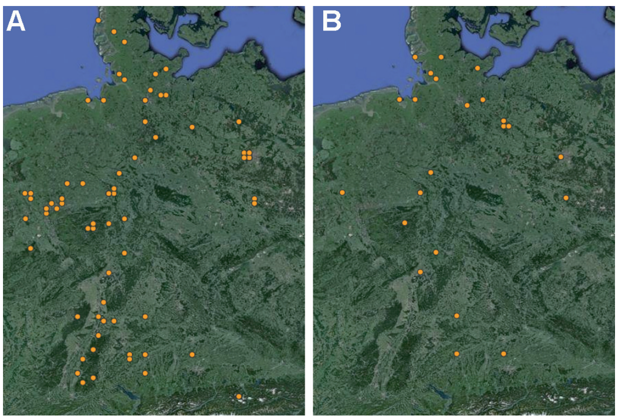

Figure 4. Records of *Cognettia sphagnetorum* (Vejodvský, 1878) (**A**) and *C. glandulosa* (Michaelsen, 1888) (**B**) from the sites in Germany analysed in this study.

fact that this species prefers moist sites but can tolerate dry sites (Healy 1980). However, drought-tolerant populations show differences at the morphological and molecular level and may belong to a species of their own (Schmelz & Collado 2010, Schmelz pers. com.).

3.2.2. *Cognettia glandulosa* (Michaelsen, 1888) (litter dweller)

The distribution range of this species is not known, but it is assumed to commonly occur in the Palaearctic (Schmelz & Collado 2010), often in wet soils (Healy 1980) and probably also the Nearctic (Nurminen 1973, Schlaghamerský this volume). *C. glandulosa* was recorded from only 12 sites (i.e. 9% of all sites) (Fig. 4). With the exception of a cluster of sites in the Middle Elbe region, its occurrence does not show any biogeographical peculiarities (this is probably a sampling bias since the Elbe floodplain was intensively studied in one research project (Beylich & Graefe 2007b). It was found significantly more often in clayey soils compared to other soil types (Fig. 6A). Regarding soil pH, *C. glandulosa* preferred slightly acidic soils (pH 4.6–5.5), but has been found in low frequencies almost throughout the entire range (Fig. 6B). This species was recorded significantly more often in soils with a medium SOM content (4.1–8%), but never at sites with a SOM content less than 2% (Fig. 6C). *C. glandulosa* significantly preferred grasslands and deciduous forests over arable sites and coniferous forests (Fig. 6D). In grasslands, *C. glandulosa* was found throughout Germany. However, the low absolute number of sites at which this species was found must be taken into consideration when assessing these data.

According to the literature but also based on a relatively small number of available data, *C. glandulosa* has a tendency for higher occurrence in sandy soils (Jänsch 2001). This impression is not backed by the more extensive data in Bo-Info, which indicates a preference for clayey soils. Regarding soil pH, good agreement exists between our evaluation and literature data, which both indicate a preference for slightly acidic (>4.5–5.5 (Schmelz & Collado 2010) or even basic (up to 7) soils (Healy 1980). No detailed information could be found on SOM content preferences by the species. Our data indicate that, despite a preference for relatively high SOM content (4–8%), this species is surely not a typical litter-dweller, since *C. glandulosa* has only been rarely found at sites with a very high SOM content (>8%). Actually, it would fit better in the intermediate group. According to the literature, *C. glandulosa* prefers moist to wet sites (Healy 1980, Schmelz & Collado 2010), occurs rarely in forests (Jans & Funke 1989, but see the contrary for North-American deciduous forests in Nurminen 1973) and may occur at grassland sites with high densities (Heck et al. 1999). This profile is confirmed by the Bo-Info data. Differences, especially concerning occurrence in different soil-texture classes, may be caused by the overall low number of literature data; furthermore the typical habitat of this species may have been poorly covered by the sites selected for this study. The additional information gathered here nonetheless improves the knowledge on the ecological requirements of this species.

3.2.3. Comparison of both species

C. sphagnetorum and *C. glandulosa* prefer different soil texture classes (silt versus clay) and also different land-use forms (forests versus grassland). Both species are classified as litter dwellers, but while both showed a preference for soils with a high SOM content (4.1–8%), only *C. sphagnetorum* was also found at sites with very high SOM contents (i.e. >8%). Even more pronounced are the differences between both species regarding pH: *C. glandulosa* preferred slightly acidic soils (4.6–5.5), while *C. sphagnetorum* is classified as strongly acidophilous (i.e. pH-values ≤ 4.5–5.0).

Summarising the findings regarding the ecological profiles of these two closely related species, ecologically they seem to differ strongly, especially concerning their preferences for soil pH, SOM content and land-use form:

- *C. sphagnetorum* is a widely distributed, often highly dominant species at sites with very acidic soils and a well-developed litter layer and is well adapted to stress [e.g. recovers quickly after clear cutting in Swedish forests (Lundkvist 1983)].
- *C. glandulosa* is a less abundant species regularly found in moist to wet and slightly acidic soils with a medium SOM content. So far no mass occurrence of this species has been reported in Europe

This example shows that any evaluation of biological soil quality should be based on species-level data (not genus-level), because they provide the most detailed information on the relationship between environmental factors and the occurrence of organisms.

3.3. Autecological requirements at the group level

3.3.1. Occurrence in relation to soil texture

Regarding soil texture the 24 enchytraeid species were classified into two groups (Fig. 7), separated by occurrence vs. absence in soils with ≥70% sand/silt content:

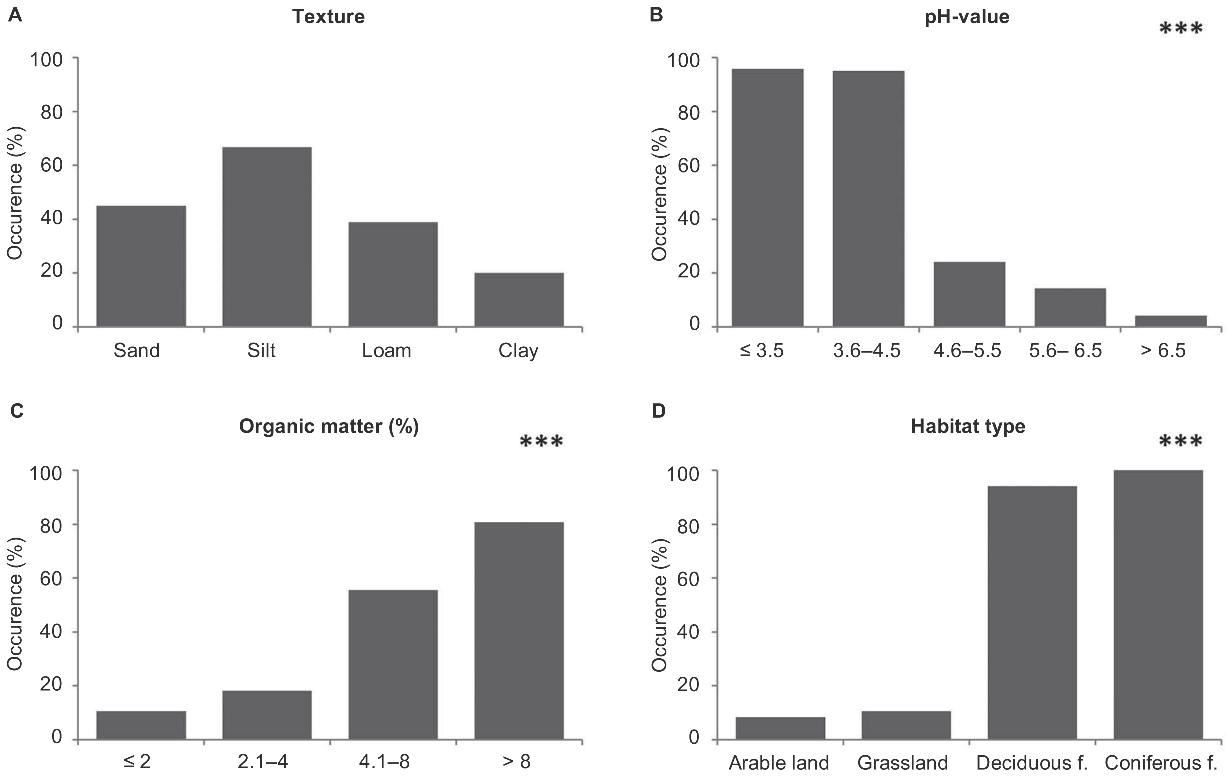

Figure 5. Relative frequency of *C. sphagnetorum* in sites with different soil properties. Data basis: number of sites at which this species was found (Table 2). Stars indicate statistically significant differences (Chi^2-Test); *** $p \leq 0.001$.

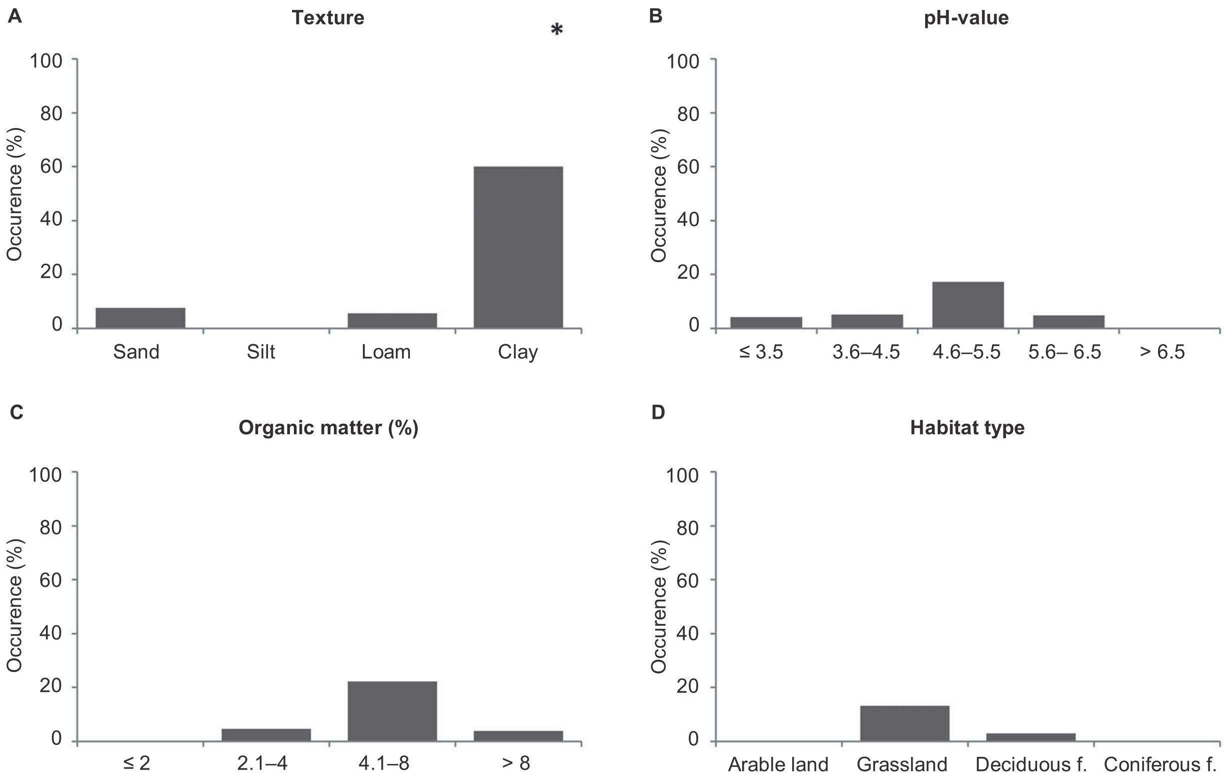

Figure 6. Relative frequency of *C. glandulosa* depending on the soil properties (a) texture, b) pH-value, c) organic matter content and land use forms (d). Data basis: number of sites at which this species was found (n = 12). Stars indicate statistically significant differences (Chi^2-Test): * $p \leq 0.05$.

- Seven species avoid clayey soils but do not show any preference concerning the other three texture classes. This group contains species from five genera and all three ecological groups (four litter dwellers, two intermediate species and one mineral dweller); i.e. a tendency towards litter dwellers avoiding clayey soils.
- All other species (17) can occur in all four texture classes. However, depending on the individual species, the occurrence in one specific class can differ between 10 to 40 % (clayey soils), 20 to 40 % (sandy soils) or 20 to 30 % (two other classes). These species belong to seven genera and three ecological groups (three litter dwellers, five intermediate species and nine mineral dwellers). One special case is *E. norvegicus*, which occurred at a proportion of less than 70 % in sandy/silty soils but was never found in clayey soils. This result is possibly influenced by the fact that in total only five clayey soils were included in this survey.
- This result differs clearly from the previous study mentioned above (Jänsch & Römbke 2003), which listed 26 out of 32 species having a preference for (mostly) one specific texture class. Some of the species were even classified as preferring sandy or silty soils (e.g. *B. ehlersi*, *C. glandulosa*, *C. sphagnetorum*). Such preferences could not be confirmed here. However, the difference might be a data artefact, since these species are litter dwellers, i.e. they are only indirectly affected by the texture of the mineral layer. No other evaluation of the distribution of enchytraeid species depending on soil texture is known.

3.3.2. Occurrence in relation to soil pH

The distribution of the 24 enchytraeid species was strongly influenced by the pH value of the soil (Fig. 8). Interestingly, almost all species were found at sites with very different pH-values, covering more or less the entire spectrum. However, when regarding their preferences, three groups (with some notable exceptions) can be distinguished, which means that all species show broad ranges of tolerance but different optima:

- Neutrophilous species (14), i.e. those species occurring only rarely at sites with a pH-value <4.5 (<20 % of all sites). In this group species of five genera are represented. These are mineral dwellers (seven *Fridericia*- and one *Enchytronia*-species) and intermediate species (three *Enchytraeus*- and two *Henlea*-species). Only one litter dweller (*M. communis*) is classified as neutrophilous. This species – plus three mineral dwellers – were never found in soils with a pH <4.5.
- Species without a pH-preference (3) occurring in sites belonging to all five pH classes in more or less similar frequencies. One litter dweller (*B. appendiculata*) and two mineral dwellers (*E. norvegicus, E. parva*) belong to this group.
- Acidophilous species (7) are those occurring in more than 70 % of all sites with a pH <4.5. This group, consisting of species from five genera, consists mainly of litter dwellers (5) and intermediate species (2); no acidophilous mineral dwellers were identified. Two species (*A. camerani*, *O. cambrensis*) were almost never found in soils with a pH >4.5.

Half of these species were already classified according to their pH preference by Jänsch & Römbke (2003), who, using data from 213 European (not only German) sites, found the same species preferences as listed here. Graefe & Beylich (2003) published the pH preference of nine enchytraeid species, based on samples from BDF-sites in Northern Germany (i.e. a subset of the data used here). Again, no differences exist in their classification and ours. In contrast to the results found for earthworms (Römbke et al. 2013), there is no simple correlation between ecological classification and pH-preference: neutrophilous enchytraeid species mainly live in the mineral soil but acidophilous species are either litter dwellers (as in the case of earthworms) or also mineral dwellers.

3.3.3. Occurrence in relation to SOM content

When assessing the relationship between SOM content and the occurrence of the 24 enchytraeid species three groups could be distinguished (Fig. 9):

- Nine species from four genera were mainly (i.e. in more than 75 % of all sites) found in soils that contain less than 4 % organic matter. These are mainly mineral dwellers of the genera *Fridericia* (5 species) and *Enchytronia* (1 species). In addition, two intermediate species (*Henlea* sp.) and one litter dweller (*M. communis*) belong to this group.
- Eight species showed a similar preference for soils with a low SOM content (<4 %) and soils with a high SOM content (>4 %). Again, a broad taxonomic and ecological range is represented here: Four mineral dwellers (two *Fridericia*-, one *Enchytronia*- and one *Enchytraeus*-species), three intermediate species (all belonging to the genus *Enchytraeus*) and one litter dweller (*B. appendiculata*) were found.

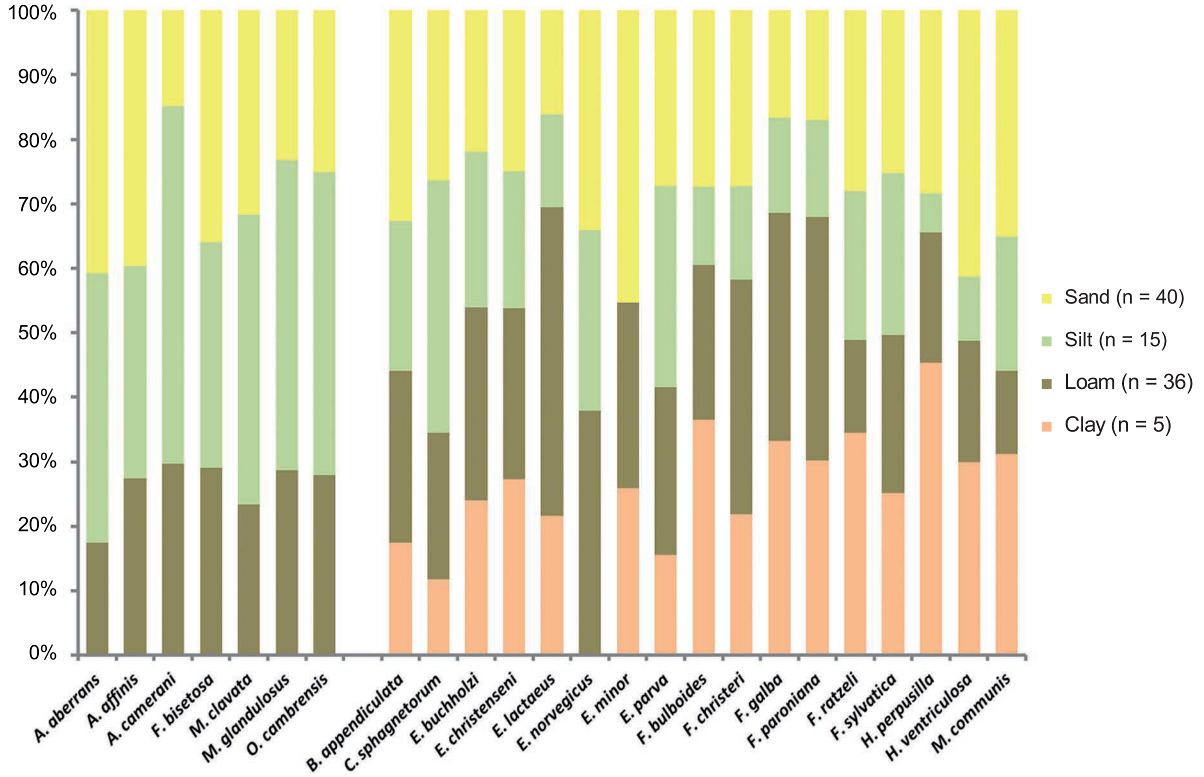

Figure 7. Occurrence of 24 enchytraeid species in regard to the four classes of soil texture; for details see Chapter 3.3.

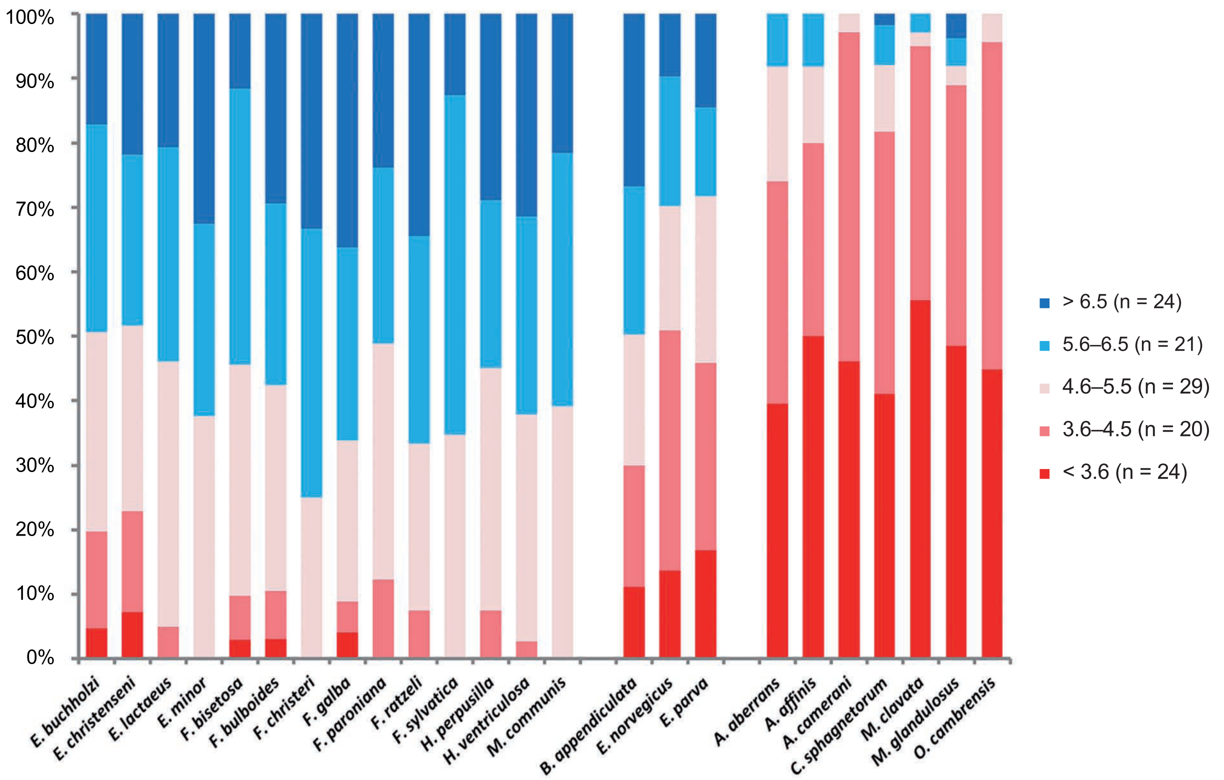

Figure 8. Occurrence of 24 enchytraeid species in regard to the five pH classes; for details see Chapter 3.3.

- Seven species were identified with a clear preference (i.e. in more than 75 % of all sites) for soils with a high SOM content (OM > 4 %). Almost all of these species (5) belonging to this group are litter dwellers (three *Achaeta*-, one *Cognettia*- and one *Mesenchytraeus*-species). The other two are intermediate species (*M. clavata*, *O. cambrensis*).

No results concerning the SOM preferences of enchytraeid species could be found in the literature. Graefe & Schmelz (1999) presented a list of 'H'-type species, which characterise individual species according to their preference for different humus forms and humus layers. However, a distinction between soil dwelling and litter-inhabiting species is not possible since the deepest layer considered there is the Ah-layer, i.e. the border zone between litter and mineral soil. In some case the same tendencies between the data presented here and the 'H'-list were found [e.g. in the case of *Fridericia* species, usually living in the deepest layer analysed (i.e. the Ah)], but in detail preferences for humus forms/layers and SOM content in the soil are not the same.

3.3.4. Occurrence in relation to habitat type

The distribution of enchytraeid species differed in the four main land use forms (Fig. 10). Three groups could be distinguished:

- Species (13) with a high preference for arable and grassland sites (together more than 70 % and up to 100 % of all sites). Most of them (7 species) are mineral dwellers from the genus *Fridericia*, but four intermediate species of the genera *Henlea* (two species), *Enchytronia* (one species) and *Marionina* (one species) also belong to this group.
- Species (4) without a clear preference: two species of the genus *Enchytraeus* and one species each of the genera *Buchholzia* and *Enchytronia*.
- Species (11) with a high preference for forest sites (> 80 % of all records): This group includes five litter dwellers (three *Achaeta*-species, *C. sphagnetorum* and *M. glandulosus*) as well as two intermediate species (one each from *Marionina* and *Oconnorella*, respectively). The surprising finding of the acidophilous species *C. sphagnetorum* at a crop site might be explained by the fact that this specific site had a soil pH lower than average crop sites: 4.3 compared to 5–6 (Graefe & Beylich 2003).

To our knowledge, such a classification regarding the four main land use forms has not been made for enchytraeids so far. However, Graefe & Beylich (2003) presented the land-use preference for nine species (again from a subset of the current data set), but differentiated only three land use forms: crop sites, grasslands and forests. Since there is overlap in the data assessed, it is not surprising that no differences are obvious when comparing the preferences for these nine species.

3.4. Reference values

In the following, the identification of reference values for the enchytraeid communities at sites belonging to the habitat level 1 (= four major land use forms) is described. In the second subchapter, this exercise is repeated for the second hierarchical level of habitat types. However, this could only be performed for three examples due to lack of data.

3.4.1. Characterization of habitat types at level 1 (= major land use forms)

In Table 3, 25 species are listed which occurred at least at > 50 % of all sites belonging to one of the four major land use forms. For 22 of these species, it could be confirmed that differences in occurrence between the four land use forms were statistically significant. Crop and grassland sites can be clearly distinguished from forest sites by their enchytraeid community composition (see also Fig. 10): the former are characterized by species of the genera *Fridericia, Enchytraeus* and *Henlea*: out of 17 species occurring with a frequency of > 50 %, 15 belong to these three genera. The forests are dominated by more genera (*Achaeta*, *Cognettia*, *Marionina, Mesenchytraeus* and *Oconnorella*): of 19 species occurring with a frequency of > 50 %, 17 belong to these five genera. In general there is almost no overlap in enchytraeid species occurrence between arable and grassland sites on the one hand and forest sites on the other hand. Actually, only one species (*Enchytraeus buchholzi*) occurred at more than 50 % of all sites belonging either to the crop/grassland sites or to the forest sites.

The mean quantitative data do not considerably distinguish the four land use forms. Concerning mean abundance two groups can be identified: in crop and grassland sites 14,000–20,000 ind/m^2 are expected, while the respective number for forest sites is about 50,000 ind/m^2. In the literature, usually focusing on Central and Northern Europe in general and not only Germany, ranges have been published which are in the same order of magnitude as the numbers given here (Petersen & Luxton 1982, Didden 2002, Römbke et al. 2002a, Beylich & Graefe 2009): 10,000–40,000 ind/m^2

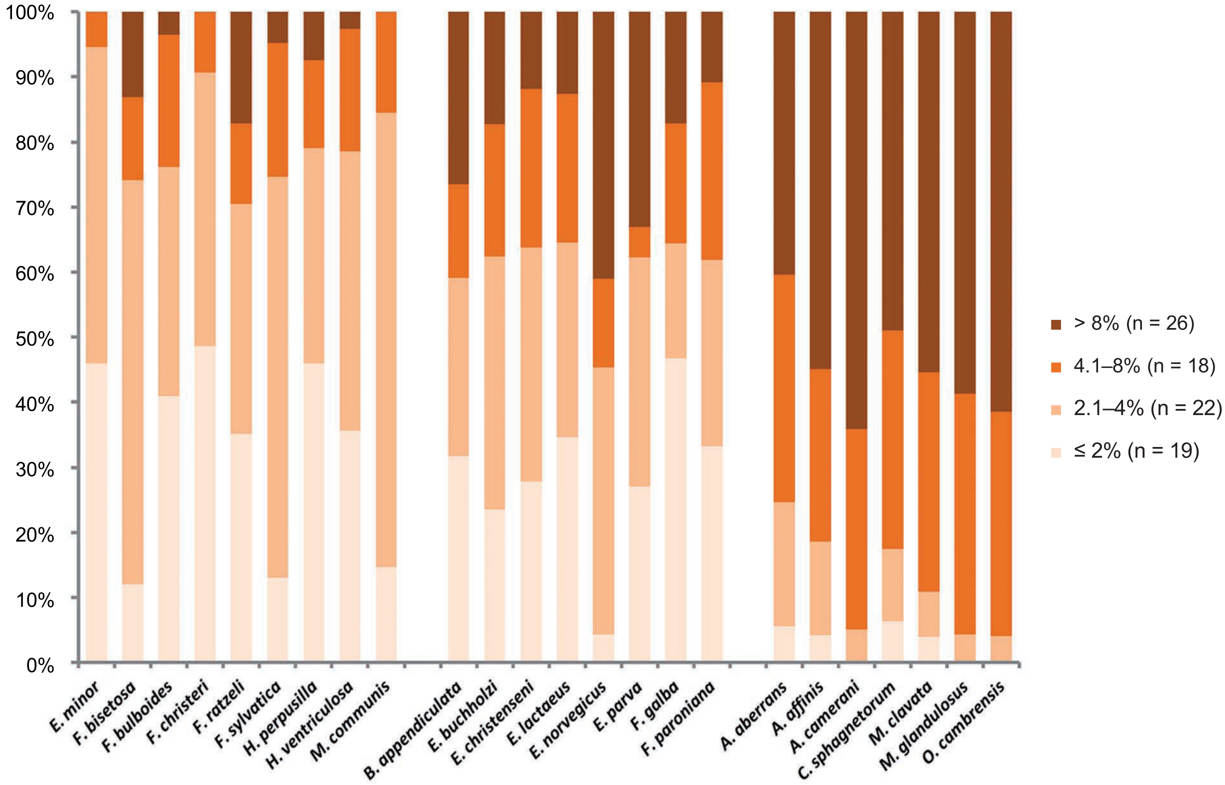

Figure 9. Occurrence of 24 enchytraeid species in regard to the four SOM classes; for details see Chapter 3.3.

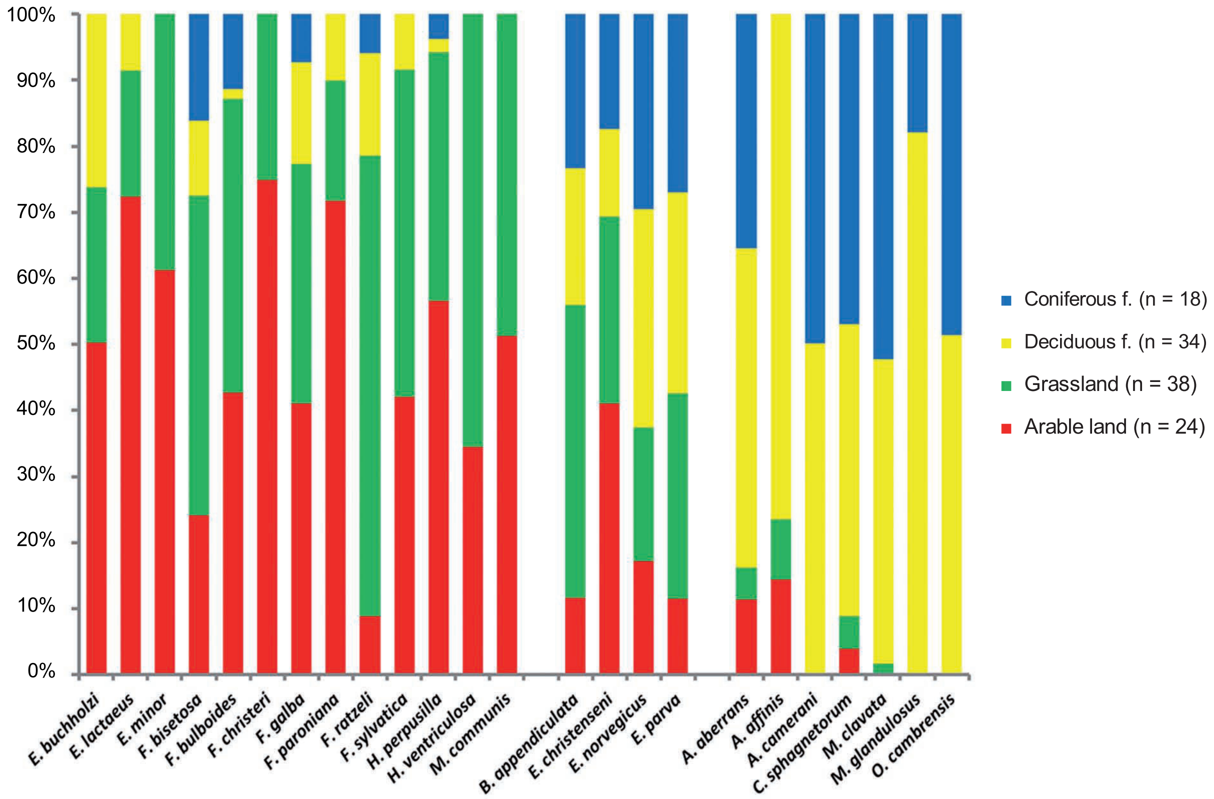

Figure 10. Frequency of 24 enchytraeid species in regard to the four biotype classes of the 1st hierarchical level (major land use forms); for details see Chapter 3.3.

in crop and grassland sites; 17,000–54,000 ind/m² in forests. This comparison is biased, since the data from Germany are partly the same [Beylich & Graefe (2003) based their numbers of BDF data from Northern Germany]. In general, however, this similarity can be seen as an indication that enchytraeid numbers in atlantic and continental regions of Europe (almost no data are available for alpine, arctic or mediterranean regions) are determined by the same environmental factors. The fact that the mean abundance is higher in crop sites than in grasslands should not be over-interpreted, i.e. there is no statistically significant difference between them as indicated by the overlap in the standard deviations. Van Cappele et al. (2012), comparing published data on tillage effects on enchytraeid abundance in German agroecosystems, found the highest abundances at sites with reduced tillage compared to sites with conventional tillage and no tillage, respectively, and concluded that a slight amount of tillage is favourable for enchytraeids. In coniferous forests on average nine species were found, while 12–14 species per site in the other three main land use forms. The high mean species number per crop site might appear surprising, considering the strong anthropogenic stress at these sites. However, the average species number does not differ between all four land use forms, again as indicated by the overlap in the standard deviations. In an older compilation based on numbers from throughout Northern and Central Europe

Table 3. Species number and species composition as well as the mean total abundance, separated according to the four land-use forms/habitat types at the 1st hierarchal level, using the information from the Bo-Info data base (juveniles not included). **Cro** – Crop sites, **Gra** – Grassland sites, **Dec** – Deciduous forest sites, **Con** – Coniferous forest sites. Typical species (= those with a frequency of more than 50% of all sites) given in bold. Asterisks indicate a statistically significant influence of habitat type on species distribution at $p < 0.05$ (*), 0.01 (**) and 0.001 (***).

Species	Cro (33) (n = 24)	Gra (34) (n = 38)	Dec (43) (n = 34)	Con (44) (n = 18)	Chi²-Test Bonf.-corr.
Achaeta aberrans	12.5	5.3	**52.9**	38.9	**
Achaeta abulba	8.3	5.3	23.5	**66.7**	***
Achaeta affinis	8.3	5.3	**64.7**	27.8	***
Achaeta bohemica	4.2	7.9	17.6	**55.6**	**
Achaeta camerani	0.0	0.0	**55.9**	**55.6**	***
Buchholzia appendiculata	16.7	**63.2**	29.4	33.3	-
Cognettia sphagnetorum	8.3	10.5	**94.1**	**100.0**	***
Enchytraeus buchholzi	95.8	44.7	**50.0**	0.0	***
Enchytraeus christenseni	**91.7**	**63.2**	29.4	38.9	**
Enchytraeus lacteus	**50.0**	13.2	5.9	0.0	**
Enchytraeus norvegicus	29.2	34.2	**55.9**	**50.0**	-
Enchytronia minor	**50.0**	31.6	0.0	0.0	***
Fridericia bisetosa	25.0	**50.0**	11.8	16.7	-
Fridericia bulboides	**83.3**	**86.8**	2.9	22.2	***
Fridericia christeri	**70.8**	23.7	0.0	0.0	***
Fridericia galba	**62.5**	**55.3**	23.5	11.1	*
Fridericia paroniana	**62.5**	15.8	8.8	0.0	***
Fridericia ratzeli	8.3	**65.8**	14.7	5.6	***
Fridericia striata	0.0	0.0	**55.9**	16.7	***
Henlea perpusilla	**83.3**	**55.3**	2.9	5.6	***
Henlea ventriculosa	37.5	**71.1**	0.0	0.0	***
Marionina clavata	0.0	2.6	**73.5**	**83.3**	***
Mesenchytraeus glandulosus	0.0	0.0	**76.5**	**16.7**	***
Mesenchytraeus pelicensis	0.0	0.0	26.5	**55.6**	***
Oconnorella cambrensis	0.0	0.0	**76.5**	**72.2**	***
Mean Ind./m² ± SD	20,165 ± 14,561	13,834 ± 11,312	51,241 ± 30,677	52,087 ± 43,837	
Mean species no./site ± SD	13.7 ± 4.3	12.2 ± 5.2	12.4 ± 5.5	9.2 ± 3.9	

(Römbke et al. 1997), slightly lower mean numbers are given: in crop sites nine species, in grassland 10 species, in deciduous forests 16 to 26 species and in coniferous forests 4 to 10 species (note that the lower and higher numbers in the forests refer to sites with acidic and basic soils, respectively). As a general tendency in forests, species number is lower at sites with lower pH values (Beylich & Graefe 2009).

Only *E. buchholzi* occurred at more than 50 % of both open land and forest sites. However, this species in fact consists of a group of closely related species that are difficult to distinguish morphologically (Schmelz & Collado 2010). In almost all grassland and crop sites, small to medium-sized individuals belonging to the '*E. buchholzi*' group occurred (e.g. *E. coronatus*, *E. christenseni*, *E. luxuriosus*; Schmelz & Collado 2010). They are usually subdivided according to their appearance under the light microscope into *Enchytraeus* 'gran' (= with granulated coelomocytes) and *Enchytraeus* 'pale' (with pale, agranulate coelomocytes).

3.4.2. Characterization of selected habitat types at the second hierarchical level

In the following whether second-level habitat types (Table 1) can be characterized by reference values for species composition is assessed. However, for only three of the four main land-use forms (arable land, grassland and coniferous forests) were enough data available for this purpose.

Crop sites (Table 4). For the habitat type arable land (nr. 33), data for two subtypes are available (nr. 33.03; 5 sites: 'farmed and fallow land on sandy soil' and nr. 33.04; 13 sites: 'farmed and fallow land on loess, loam or clay soil arable land on sandy soils'). Both subtypes cannot be distinguished quantitatively: the mean abundance differs only by a factor of 1.5 and the mean species number is almost identical (14.2 vs. 14.4). Qualitatively there is also some overlap, since six species occur at both habitat types with > 50 % of all sites (*E. buchholzi, E. christenseni, E. minor, F. bulboides, F. christeri, H. perpusilla*). However, there are also clear differences

Table 4. Species number and species composition as well as mean abundance, separated according to two level-2 arable land habitat types, using the information from the Bo-Info data base (juveniles not included). Typical species (i.e. those with a frequency of more than 50 % of all sites) given in bold.

Species	Occurence	
	33.03 (n = 5)	33.04 (n = 13)
Achaeta aberrans	**60.0 %**	0.0 %
Achaeta bibulba	**60.0 %**	7.7 %
Enchytraeus buchholzi	80.0 %	100.0 %
Enchytraeus bulbosus	20.0 %	**69.2 %**
Enchytraeus christenseni	100.0 %	100.0 %
Enchytraeus lacteus	20.0 %	**69.2 %**
Enchytraeus norvegicus	**60.0 %**	7.7 %
Enchytronia annulata	**60.0 %**	0.0 %
Enchytronia minor	80.0 %	53.8 %
Enchytronia parva	**60.0 %**	7.7 %
Fridericia bulboides	80.0 %	92.3 %
Fridericia christeri	60.0 %	84.6 %
Fridericia deformis	0.0 %	**53.8 %**
Fridericia galba	0.0 %	**84.6 %**
Fridericia granosa	**60.0 %**	7.7 %
Fridericia isseli	0.0 %	**76.9 %**
Fridericia paroniana	0.0 %	**92.3 %**
Henlea perpusilla	100.0 %	84.6 %
Henlea ventriculosa	80.0 %	15.4 %
Marionina brendae	0.0 %	**76.9 %**
Mean ind./m² ± SD	28,924 ± 23,698	19,686 ± 11,242
Mean species no./site ± SD	14.2 ± 4.0	14.4 ± 4.5

Table 5. Species number and species composition as well as the mean abundance, separated according to two grassland habitat level-2 types, using the information from the Bo-Info data base (juveniles not included). Typical species (= those with a frequency of more than 50% of all sites) given in bold.

Species	Occurrence	
	34.08 (n = 6)	34.09 (n = 7)
Achaeta pannonica	0.0%	**85.7%**
Buchholzia appendiculata	83.3%	85.7%
Enchytraeus buchholzi	33.3%	**57.1%**
Enchytraeus christenseni	16.7%	**100.0%**
Enchytraeus norvegicus	16.7%	**57.1%**
Enchytronia minor	0.0%	**71.4%**
Enchytronia parva	**83.3%**	28.6%
Fridericia benti	**83.3%**	28.6%
Fridericia bisetosa	16.7%	**71.4%**
Fridericia bulboides	83.3%	**85.7%**
Fridericia christeri	0.0%	**57.1%**
Fridericia galba	**66.7%**	42.9%
Fridericia lenta *	0.0%	**57.1%**
Fridericia ratzeli	100.0%	71.4%
Henlea perpusilla	83.3%	14.3%
Henlea ventriculosa	66.7%	71.4%
Mean ind./m² ± SD	12,480 ± 8,476	13,168 ± 11,347
Mean species no./site ± SD	9.5 ± 4.3	15.0 ± 4,0

* as *F. leydigi* in the Bo-Info database. According to Schmelz (2003) *F. lenta* is largely identical with *F. leydigi* sensu Nielsen & Christensen (1959), the identification guide used by most of the identifiers, whereas the identity of *F. leydigi* as originally described (Vejdovský 1878, 1879) is uncertain.

Table 6. Species number and species composition as well as the mean abundance, separated according to two coniferous forest habitat level-2 types, using the information from the Bo-Info data base (juveniles not included). Typical species (= those with a frequency of more than 50% of all sites) given in bold.

Species	Occurrence	
	44.02 (n = 12)	44.04 (n = 5)
Achaeta abulba	75.0%	60.0%
Achaeta bohemica	**75.0%**	20.0%
Achaeta brevivasa	8.3%	**80.0%**
Achaeta camerani	58.3%	60.0%
Cognettia sphagnetorum	100.0%	100.0%
Enchytraeus christenseni	50.0%	20.0%
Enchytraeus norvegicus	**66.7%**	20.0%
Enchytronia parva	**50.0%**	20.0%
Marionina clavata	83.3%	100.0%
Mesenchytraeus pelicensis	41.7%	**80.0%**
Oconorella cambrensis	**91.7%**	20.0%
Mean ind./m² ± SD	32,480 ± 24,681	105,543 ± 38,868
Mean species no./site ± SD	9.8 ± 4.0	8.2 ± 4.1

in species composition (> 50 % occurrence in one habitat type, less than 20 % in the other one):

- only in 33.03: *A. aberrans, A. bibulba, E. norvegicus, E. annulata, E. parva, F. granosa* and *H. ventriculosa*;
- frequently only in 33.04: *E. lacteus*, *E. minor* and *M. brendae*, plus several species of the genus *Fridericia*: *F. deformis, F. galba, F. isseli* and *F. paroniana*.

Keeping in mind that the number of sites (especially for habitat type 33.03) is very small, it would be premature to speculate which factors might be responsible for these differences.

Grassland sites (Table 5). For habitat level-1 type nr. 34 (Table 1), enchytraeid data are available for two subtypes: 'species-poor intensive grassland on moist sites' (nr. 34.08; 6 sites) and 'trampled grass and park lawns' (nr. 34.09; 7 sites). Clear quantitative differences in terms of species number were found (15 species in sites of nr. 34.08 vs. 9 species in sites of nr. 34.09), but not regarding the mean total abundance: in both cases on average about 13,000 ind./m^2 were found. Only four species are frequently sampled at both grassland subtypes (i.e. at > 50 % of all sites): *B. appendiculata, F. bulboides, F. ratzeli, H. ventriculosa*. Typical for grassland sites belonging to nr. 34.08 are *E. parva, F. benti, F. galba* and *H. perpusilla*, while in grasslands belonging to 34.09 *A. pannonica, E. buchholzi, E. christenseni, E. minor, F. bisetosa, F. christeri* and *F. lenta* commonly occur (Table 5). The species of the latter group were only rarely found (i.e. in less than 20 %) in the sites belonging to nr. 34.08. This is not true vice versa: three of the four species (i.e. not *H. perpusilla*) typical for the sites belonging to nr. 34.08 sites were also found at more than 20 % at sites belonging to 34.09. In some cases, the difference between the two subtypes already becomes evident at the generic level: in sites belonging to nr. 34.08 species of the genus *Achaeta* were never found. This result is very interesting, since the species of this genus are not suitable for reference values for the four main land use forms, but very well between subtypes of grassland (Table 5) and also arable sites (Table 4). However, since the number of studied sites belonging to each subtype is still quite small (5–7), it is clear that these findings are just a first indication for differences between these two habitat level-2 types. Clearly, more research is needed here.

Coniferous forest sites (Table 6). Among coniferous woodlands (habitat type 44) enough data are available for 'natural and near-natural dry to intermittently damp pine forests' (nr. 44.02; 12 sites) as well as 'coniferous (mixed) plantations with native tree species' (nr. 44.04; 5 sites) A clear quantitative difference can be seen between the two subtypes regarding the abundance of enchytraeids: on average three times more potworms were found in sites belonging to nr. 44.04 than in those belonging to 44.02. However, there was only a small difference in mean species number: eight in the former and ten in the latter group.

Despite the small number of data available, a clear difference in species composition existed between the two subtypes. In both, *C. sphagnetorum* and *M. clavata* were found in almost all sites. In addition, two species of the genus *Achaeta* occurred in about 60–80 % of all sites belonging to these two habitat subtypes (*A. abulba*, *A. camerani*).

- Both subtypes are differentiated by the regular occurrence (i.e. in 50–90 % of all sites of this habitat type) of five species occurring in the sites belonging to nr. 44.02: *A. bohemica, E. christenseni, E. norvegicus, E. parva* and in particular *O. cambrensis*.
- On the other hand, *A. brevivasa* and *M. pelicensis* are typical for sites belonging to nr. 44.04.
- Both subtypes are characterized by the lack of neutrophilous species, in particular species of the genera *Fridericia* and *Henlea*.

In summary, near natural coniferous forests can be well differentiated from coniferous plantations by their enchytraeid communities. This is an important result because enchytraeids are highly abundant in such acidic forest soils. Especially the species *C. sphagnetorum*, often occurring in very high densities, can be considered to be an 'ecosystem engineer' due to its role as a regulator of microbial activity, thus influencing organic matter breakdown as well as nitrogen cycling (Laakso & Setälä 1999, Lavelle et al. 2006, Brussaard et al. 2012).

3.5. Discussion

We used the information compiled in the Bo-Info database to investigate whether potworm communities can indicate the soil function of habitat for soil invertebrates. For this it must be possible to derive reference values for specific site types. We choose the habitat-type classification (Riecken et al. 2006), because it was developed for use in environmental conservation and therefore is adapted to the main driving environmental factors. It is moreover a hierarchical system and allows the use of several levels of characterization (e.g. first level with a very broad definition for less well described sites, second level for sites where more information is available). The endpoints abundance and species richness are not enough to differentiate habitat types of the first and second level. However, species composition is the most differentiated and least variable parameter for distinguishing habitat types.

Thus, we propose here draft 'reference values' (= list of typical species; here preliminarily defined as those occurring at more than 50 % of all sites belonging to a specific habitat type) for the characterization of the four main land use forms (i.e. level 1 habitat habitat types). A further differentiation (e.g. for level-2 habitat types) should be possible in the future, but failed due to a lack of data (< 10 sites could be assigned to level-2 types). Thus, it must be highlighted that these proposals for reference values are considered to be preliminary (i.e. their robustness is limited). We expect that the new database and information system Edaphobase will enhance the data basis for further assessment and thus will improve the assessment of the habitat function of soils considerably (Burkhardt et al. 2013).

We also propose new samplings of potworms in the east and south of Germany because of lack of data in these regions. To render data comparable, standardized methods for sampling and processing enchytraeids are crucial and should be applied. About one third of the data from sites in Germany could not be used for this study since they did not fulfil basic requirements in terms of data quality (e.g., inadequate sampling methods or lack of documentation).

Our approach is in agreement with similar studies or literature reviews (e.g. Schouten et al. 1999, Barth et al. 2000, Jänsch et al. 2005, Bispo et al. 2009, EFSA 2010, Turbé et al. 2010), which, independently from the regions studied or methods used, recommend including enchytraeids in monitoring programs for the evaluation of soil quality. Unfortunately, it is difficult to compare our reference values with those values (diversity, species number and abundance) for enchytraeids as proposed in the Netherlands and Northern Germany (Rutgers et al. 2008, Beylich & Graefe 2009), since their classification of sites and the statistical tools used are quite different. However, there is agreement that for the derivation and use of reference values qualitative information, preferably species composition, should be used. The evaluation shown here confirms that neither species number nor abundance values are well suited for the derivation of reference values. Both quantitative endpoints are too variable, both in time (differencs within and between years) and space (differences within and between sites). In addition, they are more sensitive to the influence of the sampling methodology.

4. Summary and conclusions

The main results of this investigation may be summarized as follows:

- The diversity of German enchytraeids was largely captured in the Bo-Info database: of the 122 species known so far from Germany: 96 species were included (= 76 %), 24 species were abundant/common enough to be evaluated.
- The available data for enchytraeids are heterogeneously distributed over the biogeographical regions in Germany.
- Ecological profiles regarding habitat type, pH-value, SOM content and soil texture were determined for the 38 most common species, increasing considerably the ecological knowledge of these potworm species.
- The occurrence of enchytraeid species is clearly determined by land use, inter-correlated with pH-value and less by soil texture. Regarding the preference for certain levels of soil organic matter content, the species can be divided into three groups: litter dwellers, mineral soil dwellers, and intermediate species.
- Thus, a classification of enchytraeids in ecological groups (in analogy to earthworms) is possible, but experience is still limited.
- A characterization of habitat types through the structure of the enchytraeid community is possible at the first hierarchical level of habitat types (corresponding to major land-use types) and also at a second habitat-type level, provided that sufficient data is available (e.g. on the habitat and on species composition).
- Despite long-term knowledge of the correlation between the occurrence of single species or whole communities with site and soil parameters, the derivation of quantitative reference values remains difficult. However, first proposals of species lists for habitat levels 1 and 2 (some selected examples) could be made.
- Filling data gaps (abiotic and biological) is still necessary: with the exception of a few federal states, regional monitoring, in particular in arable sites, is needed to prepare more robust reference values.
- The use of enchytraeids for the monitoring of biological soil quality assessment, i.e. the function of soil as a habitat for soil organisms, is recommended.
- Reaching this goal seems to be possible since an EU-wide key for terrestrial enchytraeids is now available (Schmelz & Collado 2010). In addition,

barcoding of enchytraeids is considered to be a promising tool for monitoring activities (e.g. Christensen & Glenner 2010).

- In addition, experience gained when using other organism groups for the evaluation of soil quality should be taken into consideration, for example the use of modelling (e.g. with earthworms: Palm et al. 2013).

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Supplementary data is provided for this paper at www.soil-organisms.org.

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Appendix 1. List of German enchytraeid species (124) without exclusively marine species (13), compiled by R. M. Schmelz (ECT Oekotoxikologie GmbH).

Achaeta aberrans Nielsen & Christensen, 1961
Achaeta abulba Graefe, 1989
Achaeta affinis Nielsen & Christensen, 1959
Achaeta bibulba Graefe, 1989
Achaeta bifollicula Chalpuský, 1992
Achaeta bohemica (Vejdovský, 1879)
Achaeta bohemica (Vejdovský, 1879) sensu Nielsen & Christensen (1959)
Achaeta brevivasa Graefe, 1980
Achaeta bulbosa Nielsen & Christensen, 1961
Achaeta camerani (Cognetti, 1899)
Achaeta danica Nielsen & Christensen, 1959
Achaeta diddeni Graefe, 2007
Achaeta eiseni Vejdovský, 1878 ('1877')
Achaeta hallensis Möller, 1976
Achaeta pannonica Graefe, 1989
Achaeta unibulba Graefe, Christensen & Dózsa-Farkas, 2005
Achaeta urbana Heck & Römbke, 1991
Bryodrilus ehlersi Ude, 1892
Bryodrilus librus (Nielsen & Christensen, 1959)
Buchholzia appendiculata (Buchholz, 1862)
Buchholzia fallax Michaelsen, 1887
Buchholzia simplex Nielsen & Christensen, 1963
Cernosvitoviella aggtelekiensis Dózsa-Farkas, 1970
Cernosvitoviella atrata (Bretscher, 1903)
Cernosvitoviella carpatica Nielsen & Christensen, 1959
Cernosvitoviella minor Dózsa-Farkas, 1990
Cernosvitoviella palustris Healy, 1979
Cognettia clarae Bauer, 1993
Cognettia cognettii (Issel, 1905)
Cognettia glandulosa (Michaelsen, 1888)
Cognettia sphagnetorum (Vejdovský, 1878 ('1877'))
Enchytraeus albidus Henle, 1837
Enchytraeus bigeminus Nielsen & Christensen, 1963
Enchytraeus buchholzi Vejdovský, 1879
Enchytraeus bulbosus Nielsen & Christensen, 1963
Enchytraeus capitatus von Bülow, 1957
Enchytraeus christenseni Dózsa-Farkas, 1992
Enchytraeus coronatus Nielsen & Christensen, 1959
Enchytraeus dichaetus Schmelz & Collado, 2010
Enchytraeus lacteus Nielsen & Christensen, 1961
Enchytraeus luxuriosus Schmelz & Collado, 1999
Enchytraeus norvegicus Abrahamsen, 1969
Enchytraeus variatus Bougenec & Giani, 1987
Enchytronia annulata Nielsen & Christensen, 1959
Enchytronia parva Nielsen & Christensen, 1959
Fridericia alata Nielsen & Christensen, 1959
Fridericia argillae Schmelz, 2003
Fridericia benti Schmelz, 2002
Fridericia bisetosa (Levinsen, 1884)
Fridericia brunensis Schlaghamerský, 2007
Fridericia bulboides Nielsen & Christensen, 1959
Fridericia christeri Rota & Healy, 1999
Fridericia connata Bretscher, 1902
Fridericia cusanica Schmelz, 2003
Fridericia cylindrica Springett, 1971
Fridericia deformis Möller, 1971
Fridericia discifera Healy, 1975
Fridericia dozsae Schmelz, 2003
Fridericia dura (Eisen, 1879)
Fridericia galba (Hoffmeister, 1843)
Fridericia glandifera Friend, 1913
Fridericia granosa Schmelz, 2003
Fridericia hegemon (Vejdovský, 1878 ('1877'))
Fridericia isseli Rota, 1994
Fridericia lenta Schmelz, 2003
Fridericia maculata Issel, 1905
Fridericia maculatiformis Dózsa-Farkas, 1972
Fridericia magna Friend, 1899
Fridericia minor Friend, 1913
Fridericia monochaeta Rota, 1995
Fridericia nemoralis Nurminen, 1970
Fridericia nielseni Möller, 1971
Fridericia nix Rota, 1995
Fridericia parathalassia Schmelz, 2002
Fridericia paroniana Issel, 1904
Fridericia perrieri (Vejdovský, 1878)
Fridericia ratzeli (Eisen, 1872)
Fridericia reducata Dózsa-Farkas, 1974
Fridericia regularis Nielsen & Christensen, 1959
Fridericia semisetosa Dózsa-Farkas, 1970
Fridericia singula Nielsen & Christensen, 1961
Fridericia striata (Levinsen, 1884)
Fridericia sylvatica Healy, 1979
Fridericia tubulosa Dózsa-Farkas, 1972
Fridericia ulrikae Rota & Healy, 1999
Fridericia waldenstroemi Rota & Healy, 1999
Globulidrilus riparius (Bretscher, 1899)
Hemifridericia parva Nielsen & Christensen, 1959
Henlea heleotropha Stephenson, 1922
Henlea jutlandica Nielsen & Christensen, 1959
Henlea nasuta (Eisen, 1878)
Henlea perpusilla Friend, 1911 augm. Černosvitov, 1937
Henlea similis Nielsen & Christensen, 1959
Henlea ventriculosa (d'Udekem, 1854)
Lumbricillus arenarius (Michaelsen, 1889)
Lumbricillus buelowi Nielsen & Christensen, 1959
Lumbricillus fennicus Nurminen, 1964
Lumbricillus kaloensis Nielsen & Christensen, 1959
Lumbricillus lineatus (Müller, 1774)
Lumbricillus pagenstecheri (Ratzel, 1868)
Lumbricillus rivalis Levinsen, 1884

Marionina argentea (Michaelsen, 1889)
Marionina brendae Rota, 1995
Marionina clavata Nielsen & Christensen, 1961
Marionina communis Nielsen & Christensen, 1959
Marionina filiformis Nielsen & Christensen, 1959
Marionina hoffbaueri Möller, 1971
Marionina minutissima Healy, 1975
Marionina simillima Nielsen & Christensen, 1959
Marionina southerni Černosvitov, 1937
Marionina subterranea (Knöllner, 1935b)
Mesenchytraeus armatus (Levinsen, 1884)
Mesenchytraeus beumeri (Michaelsen, 1886)
Mesenchytraeus flavidus Michaelsen, 1887
Mesenchytraeus flavus (Levinsen, 1884)
Mesenchytraeus gaudens Cognetti, 1903
Mesenchytraeus glandulosus (Levinsen, 1884)
Mesenchytraeus pelicensis Issel, 1905
Mesenchytraeus sanguineus Nielsen & Christensen, 1959
Oconnorella cambrensis (O'Connor, 1963)
Oconnorella tubifera (Nielsen & Christensen, 1959)
Stercutus niveus Michaelsen, 1888