Earthworm Communities in Soils of Estonian Wooded Meadows

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Abstract

Wooded meadows are traditional semi-natural meadows in the region around the Baltic Sea. They are mowed regularly once per year, and some meadows are lightly grazed by sheep or cattle in late summer after mowing. Data on soil fauna in wooded meadows are still scarce in spite of their importance to ecosystem functioning. The aim of this study was to describe the taxonomic and ecological structure of earthworm communities in relation to the chemical and microbiological characteristics of the soil and meadow restoration conditions in Estonian wooded meadows. The chemical and microbiological parameters of the soil were studied so as to characterize the habitat of the earthworms. Earthworms were collected using a mustard solution as vermifuge. In total, the earthworm communities of wooded meadows consisted of eight species. The most abundant species were the endogeic *Aporrectodea caliginosa* and *Aporrectodea rosea*. The dominant epigeic species was *Lumbricus rubellus* in meadows with higher soil moisture and *Dendrobaena octaedra* in a dry meadow. In wooded meadows, richness of plant species and diversity in earthworm communities have developed in calcareous soil conditions. Different layers of plant cover create several different microhabitats for soil invertebrates including earthworms, thus promoting diversity. The taxonomic composition of communities depends on soil conditions; mostly on soil moisture. The restored wooded meadows differ significantly from the long-term managed meadows by the ecological structure of the earthworm communities: in mowed meadows the community consists of more endogeic and fewer epigeic species compared to the restored meadows.

Key words: wooded meadows, earthworms, microbial community, diversity, restoration

Introduction

Wooded meadows are traditional semi-natural meadows in the region around the Baltic Sea belonging to Natura 2000 habitat type 6530 (Fennoscandian wooded meadows). They covered a third of Estonia's territory (total area: 850,000 ha) until the mid-20th century but have since almost disappeared (total area: 700 ha) due to fundamental changes in land management – mostly the cessation of hand- or horse-mowing. These ecosystems are characterized by: 1) their old age, i.e. regular mowing has occurred periodically over several centuries; 2) calcareous soils with a neutral pH; 3) an absence of (intensive) grazing; 4) their large size (more than tens of hectares); 5) the presence of more moist or wet patches; and 6) high tree and plant diversity (Kukk and Kull 1997). Typical deciduous trees and several shrub species are distributed in small, irregular patches with tree canopy coverage usually in the range of 0.1-0.5; this differs significantly between meadows and within single meadows. They are mowed regularly (once per year) and some are lightly grazed by sheep or cattle in late summer after mowing. In calcareous wooded meadows there are commonly over 50 plant species per square metre, which is much more than in any other community in the temperate forest zone (Kukk and Kull 1997, Kull and Zobel 1991, Luhamaa et al. 2001). The large species pool reflects the large niche diversity (in terms of light, moisture and nutrient availability) within the meadows. The number of annual species is very low and vegetative reproduction dominates (Kukk and Kull 1997).

The plant species richness and plant productivity of semi-natural meadows have been rather well studied and documented, and many authors have discovered that extensive management of meadows is the most important human factor in maintaining species richness (Myklestad and Saetersdal 2004, Niinemets and Kull 2005, Bratli et al. 2006, Van Uytvanck et al. 2008). Data on soil fauna in wooded meadows remain scarce in spite of their importance to ecosystem functioning (de Goede and Brussaard 2002). Soil microorganisms and their associated processes are responsible for many ecosystem functions, including biogeochemical cycling of most elements, mycorrhizal and rhizobia symbiosis with plants, decomposition processes and soil structure. Macrofauna affects nutrient cycling processes directly by fragmentation and transport of organic and mineral particles, and indirectly by regulating the microbial population and stimulating microbial activity (van Eekeren et al. 2007, Wakelin et al. 2009). Detritivorous invertebrates including earthworms constitute a large proportion of the invertebrate biomass in most environments and provide a key role in organic material turnover. They have been selected as indicators of landscape stress and soil degradation, as both a functional group and single taxa. The composition and structure of invertebrate fauna change rapidly in response to environmental input such as chemicals and landscape management. For this reason, invertebrates have enormous potential to be used as indicators of sustainability in agriculture and environmental change, but this potential has yet to be realized because of gaps in our knowledge about many invertebrate groups (Paoletti et al. 2007).

Earthworms are an important component of the invertebrate community in soils, in terms of their contribution to overall underground biomass and their effects on the biogeochemical cycles of soil. Particularly soil structure, but also gas dynamics, water flow, C and N turnover and stabilization as well as the activity of other organisms may be altered by the presence and structure of earthworm communities, commonly described as ‘ecosystem engineers’ (Vandenbygaart et al. 2000, Cole et al. 2006, Bartlett et al. 2009). Diverse earthworm communities are connected to the diversity of plants and the activity of the microbial community. Wardle (2002) suggests that soil organisms which create physical structure can operate as powerful determinants of plant community composition because these structures favour the establishment of certain plant species and functional types over others. Earthworms stimulate microbial activity and hence stimulate decomposition and nutrient mineralization (Lavelle 1997, Eisenhauer et al. 2009). The aim of this study was to evaluate the earthworm communities (their diversity, abundance and taxonomic and ecological structure) in relation to the chemical and microbiological characteristics of the soil and meadow restoration conditions in Estonian wooded meadows.

Material and methods

The soil communities were studied from 2006-2009 in three wooded meadows of the species-rich dry boreo-nemoral grassland site type (wooded meadow) located in western Estonia, which is a high area of wooded meadows. The studied meadows are characterised as follows:

1. Laelatu – located in Lääne County, total area of meadow: 153 ha; according to investigation data from 1997-2000, the permanently managed area was 39 ha. The meadows are dry boreo-nemoral and fresh boreo-nemoral meadows and have been partly mowed for at least 300 years. The typical soil is Rendzic Leptosols with a thin (17–22 cm) humus horizon (A) that lies directly on calcareous marine sediments and glacial moraines (C horizon). Calcaric Gambisols and Rendzic Gleisols on limestone of small or medium thickness are also common. The dominant tree species are *Quercus robur*, *Fraxinus excelsior, Populus tremula* and *Betula pendula.* The tree species common in the meadow are *Pinus silvestris, Sorbus aucuparia, Alnus incana, Acer platanoides* and *Malus domesticus.* In the shrub layer, *Corylus avellana, Swida sanguinea, Frangula alnus* and *Rhamnus cathartica* are present. Up to 76 vascular plant species per m^{-2} are found here (Kukk and Kull 1997, Luhamaa et al. 2001).

2. Nedrema – Pärnu County, the largest mown wooded meadow in Europe (the area of mown grassland was over 200 ha at the beginning of the 20^{th} century but was decreased to 2 ha in 1991). Since restoration in the 1990s the area of the meadow is app. 100 ha. The type of meadow is fresh boreo-nemoral. Calcaric Gambisols and Rendzic Leptosols are the typical soils here with a humus layer with a thickness of 20-30 cm. The dominant tree species are *Populus tremula* and *Betula pendula*, but *Quercus robur* and *Pinus silvestris* are also common. The coverage of tree canopies is 0.1-0.4. The most common shrub species is *Coryllus avellana*, with coverage of 0.1. The non-mown (abandoned) areas of the meadow are covered with *Pinus silvestris* and *Populus tremula* with a coverage of more than 0.5. The mean coverage of the grass layer is 0.68; that of mosses is 0.5. The maximum number of different vascular plant species per m^2 is 54 (Kukk and Kull 1997).

3. Viita – Lääne County, a fresh boreo-nemoral meadow with an area of 7.9 ha. The dominant soil type is Gleyic Pebble Rendzina formed on the basis of coastal sediments with a thin (16–23 cm) humus horizon (A) that lies on a gleyic pebble soil layer (C horizon). The moisture conditions of the soil vary: for a short time in spring the soils are too moist, while in summer they are too dry. The trees and bushes in the meadow grow in groups; the most common species of trees are *Betula pendula, Populus tremulus, Quercus robur* and *Fraxinus excelsior*, with coverage of trees canopies of 0.2. The shrub layer is dominated by *Corylus avellana*, while *Frangula alnus* and *Rhamnus cathartica* are also

common. Coverage is 0.05-0.12. In the grass layer, species characteristic of dry and nitrogen-poor habitats dominate, as well as species with higher moisture demands. The coverage of grasses is 0.51-0.73. The maximum number of vascular plant species per m^2 is 56 (Pork et al. 1984, Kukk and Kull 1997).

In each meadow, areas with a different duration of management following restoration were chosen for study. The main characteristics of the study areas are presented in Table 1. The samples for soil analyses were taken with a soil corer (Ø2 cm) from a soil layer of 0-20 cm at the end of October every year to describe the chemical and microbiological conditions of the soil layer most densely inhabited by earthworms (Truu et al. 2008). For each sample area the yearly composite samples from 25 random subsamples were collected. From the sieved soil samples, organic matter content (loss on ignition by Schulte 1995), moisture (gravimetric), pH_{KCl}, total nitrogen (following the method of Kjeldahl, Official Methods of Analysis 1990) and available phosphorus content (Official Methods of Analysis 1990) were determined. Microbiological analyses were performed to characterize the habitat conditions of earthworms. Substrate-induced respiration (SIR) using the Isermeyer technique was applied to measure metabolically active microbial biomass carbon according to Beck et al. (1996). The soil's microbial respiration rate (basal respiration) was measured by titration according to Öhrlinger (1996). To estimate the rate of microbial decomposition, the litter-bag method was used (Meyer 1996). 1 x 5 cm strips of α-cellulose in plastic litter bags (net Ø 1 mm) were placed on the soil's surface (23 bags in each area) in early spring 2008. These bags were collected twice per year (3-5 bags in each area), in July and November 2008 and 2009. The weight loss of α-cellulose and the nitrogen content accumulated on the strips were analysed, and all results were calculated on the basis of α-cellulose dry matter.

Table 1. Location and status of sample areas

Sample area	Location (longitude, latitude)	Soil type	Soil texture	Status of meadow	Year of restoration
Laelatu1	58°35′03″, 23°34′08″	CRL(CGL)	LS(SL)	M	
Laelatu2	58°35′12″, 23°34′08″	CGL	LS(SL)	R	1996
Laelatu3	58°35′17″, 23°34′11″	CGL	LS(SL)	R	2001
Nedrema1	58°32′57″, 24°04′50″	CC	SL	M	
Nedrema2	58°32′25″, 24°04′20″	CC	SL	R	1996
Nedrema3	58°32′15″, 24°03′56″	CCG	SL(L)	R	2001
Viita1	58°42′40″, 23°47′29″	CGL	SL(LS)	M	
Viita2	58°42′38″, 23°47′15″	CRG	L	R	1996

Status: M – managed, R - restored

Soil type: CRL – Cambi-Rendzic Leptosols, CGL – Cambi-Gleyic Leptosols, CC – Calcaric Gambisols, CCG – Cambi Calcic Gleysols, CRG – Cambi Rendzic Gleysols

Soil texture: LS – loamy sand, SL – sandy loam, L – loam

To study the earthworm communities, three randomly selected soil plots (50 x 50 cm) were examined at each site in 2006, 2008 and 2009, in September or October, when the earthworms are active in the upper soil layer. The earthworms were collected by using a 15% mustard solution as vermifuge (Gunn 1992). The collected earthworms were washed, kept in a refrigerator for 48 hours, identified and counted. The mean numbers of individuals per m^2 of soil surface (±SE) and Simpson's index of diversity (1-D) were calculated.

Classifying the earthworm species into three ecological categories is based on differences among species in burrowing and feeding activities, and vertical stratification in soil. Epigeic earthworms typically live on the soil's surface or in the upper reaches of the mineral soil, have relatively high reproductive rates and grow rapidly (represented by *Dendrobaena octaedra* (Savigny 1826)*, Lumbricus rubellus* Hoffmeister 1843 and *L. castaneus* (Savigny 1826)). Endogeic earthworms inhabit the mineral soil horizons; they consume the soil's organic matter (represented by *Aporrectodea caliginosa* (Savigny 1826)*, A. rosea* (Savigny 1826) and *Octolasion lacteum* (Orley 1885)). Anecic earthworms form permanent or semi-permanent vertical burrows in the soil and feed on dead leaves or other decaying materials on the soil's surface (represented by *Lumbricus terrestris* Linnaeus 1758 and *Aporrectodea longa* (Ude 1885)) (Bouché 1977, Edwards and Bohlen 1996).

The correlation coefficient was used to relate the soil's biological variables to its chemical parameters. ANOVA one-way variance analysis was used to assess the impact of management on the soil's biological and chemical parameters; the means were compared using the Tukey HSD test. Canonical Correspondence Analysis (CCA) was used to analyze the data of earthworm communities with regard to environmental variables using the CANOCO 4.52 programme (ter Braak 1994). The forward selection method with the Monte Carlo test (999 permutations) available in the CANOCO software was used.

Results

The soil of the wooded meadows studied was mainly calcareous, with a pH of around 7, but it differed by soil characteristic (Table 2). The Nedrema meadow differed from the other studied meadows in

Table 2. Soil characteristics (mean values ±SE) of study areas

Sample area	Soil pH	Nitrogen %	Soluble phosphorus mg/kg	Organic matter %	Soil moisture %
Laelatu1	6.98±0.35	0.577±0.436	34.32±3.67	11.18±0.96	27.5±1.52
Laelatu2	6.67±0.74	0.534±0.388	26.74±1.50	10.29±2.22	34.5±2.06
Laelatu3	6.62±0.25	0.516±0.122	29.15±2.66	9.16±0.67	37.7±1.64
Nedrema1	5.38±0.56	0.236±0.089	2.10±0.56	5.91±0.62	35,5±1.32
Nedrema2	5.46±0.44	0.271±0.121	3.83±1.01	6.58±1.23	35.8±0.90
Nedrema3	5.67±0.77	0.342±0.250	2.71±0.48	7.94±1.25	36.4±0.93
Viita1	7.01±0.45	0.344±0.278	17.20±1.89	7.69±1.65	20.5±0.56
Viita2	6.77±0.86	0.546±0.216	32.62±2.25	12.26±0.88	20.54±0.7

terms of the lower pH (5.38-5.67) ($p<0.05$) of its soil and lower OM% (5.91-7.94), N% (0.236-0.342) and P content (2.1-3.38 mg/kg). The Viita meadow differed in terms of lower soil moisture (app. 20.5%, $p<0.05$). The soil in Laelatu had the highest N% (0.516-0.577) and P content (26.74-34.32 mg/kg) values. The soils also differed in terms of the biological activity of the earthworm habitat (Table 3). The microbial biomass in Nedrema was significantly lower ($p<0.05$) than in Laelatu and respiration activity differed ($p<0.05$) in the soils from all three meadows. Microbial basal respiration correlated positively ($p<0.05$) with soil pH (R = 0.538), total nitrogen (R = 0.821) and organic matter content (R = 0.781). The rate of microbial decomposition was also measured: after two years of decomposition, the remaining į-cellulose in the litter bags was 17.6±3.9% of initial mass in Nedrema, 39.3±19.1% in Laelatu and 42.7±1.1% in Viita. There were no significant differenc-

Table 3. Characteristics of microbial communities in soils of wooded meadows

Sample area	SIR	R	Loss of α-cellulose, % of initial mass±SE	
	mg biomass C/gdw	mg CO_2/gdw h	after 1 year	after 2 years
Laelatu1	2.762	0.602	9.5±3.1	25.3±1.9
Laelatu2	2.889	0.720	29.5±8.6	80.3±6.6
Laelatu3	2.392	0.614	35.4±15.1	90.7±20.5
Nedrema1	0.629	0.235	23.8±3.3	78.1±12.9
Nedrema2	1.740	0.245	10.2±2.1	99.0±2.0
Nedrema3	1.681	0.218	11.5±1.9	81.3±5.7
Viita1	2.486	0.555	21.2±1.1	56.3±2.6
Viita2	2.326	0.569	19.1±1.2	61.6±2.1

es in mass loss between the study areas, nor between restored and managed areas, but a correlation (R = -0.85, $P<0.05$) between remaining α-cellulose and soil moisture was found. A relationship between the parameters of the microbial community (basal respiration, biomass and nitrogen content on cellulose strips accumulated in the first year) and *Octolasion lacteum* abundance was found (Figure 1).

The total abundance of earthworms was highest in the Nedrema restored meadow (154 individuals per m^2); the lowest abundance ($p<0.05$) was found in the long-term managed Viita meadow (51±17 individuals per m^2). In total, the earthworm communities of wooded meadows consisted of eight species (Table 4). The number of earthworm species in Viita (3.8±0.3) differed significantly ($p<0.05$) from that in Nedrema (6.0±0.5) and Laelatu (5.3±0.3). The Simpson diversity index had high values (0.567-0.901), and differences in species diversity on different meadows were not significant. Soil moisture correlated positively ($p<0.05$) with the number of species (R = 0.509) and the Simpson index (R = 0.49), with abundances of *Lumbricus rubellus* (R = 0.467) and *Octolasion lacteum* (R = 0.369) and the relative importance of epigeic species (R = 0.404), and negatively

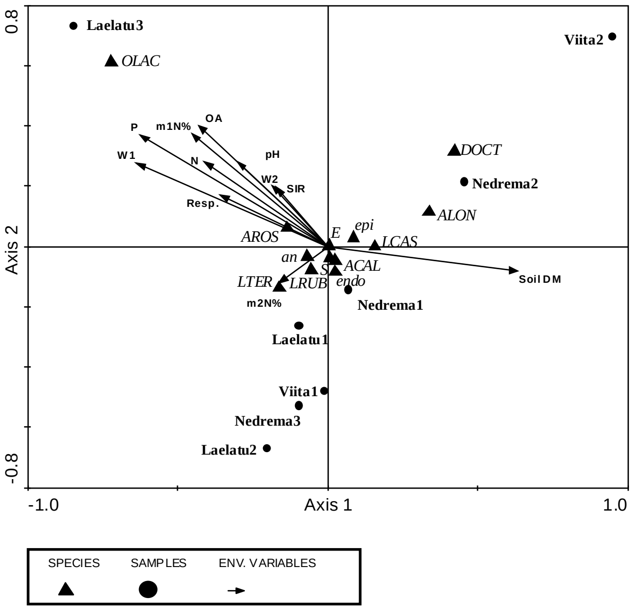

Figure 1. Ordination triplots with environmental variables based on Canonical Correspondence Analyses (CCA). Abbreviations: pH – acidity, OA – organic matter, %, Soil DM – soil dry matter, %, W1 – remaining mass of α-cellulose strips after 1 year, %, W2 – remaining mass of cellulose after 2 years, %, 1 mN% – nitrogen in α-cellulose strips after 1 year, 2 mN% – nitrogen in cellulose after 2 years, N – nitrogen % in dry soil, P – soluble phosphorus, mg per 100g dry soil, SIR – SIR biomass, Resp – respiration activity, epi – relative abundance of epigeics, endo – relative abundance of endogeics, an – relative abundance of anecics, E – number of earthworms per m^2, S – number of species in area, ACAL – *Aporrectodea caliginosa*, AROS – *Aporrectodea rosea*, ALON – *Aporrectodea longa*, LRUB – *Lumbricus rubellus*, LCAS – *Lumbricus castaneus*, OLAC – *Octolasion lacteum*, and DOCT – *Dendrobaena octaedra* (individuals per 1 m^2). The eigenvalues of the first two axes are 0.055 and 0.034; the sum of all canonical eigenvalues is 0.125.

Table 4. Characteristics of earthworm communities (mean values±SE) in wooded meadows

Sample area	E	S	EPI	ENDO	ANECIC	DIVERSITY
Laelatu1	90±15	6.0±0.1	0.15±0.01	0.81±0.01	0.09±0.02	0.625±0.028
Laelatu2	64±16	4.0±1.0	0.22±0.07	0.74±0.03	0.04±0.02	0.570±0.047
Laelatu3	127±73	6.0±1.0	0.27±0.05	0.67±0.04	0.06±0.01	0.718±0.035
Nedrema1	127±15	6.0±0.1	0.30±0.17	0.62±0.14	0.09±0.04	0.689±0.055
Nedrema2	154±29	7.0±0.5	0.26±0.11	0.70±0.08	0.04±0.03	0.901±0.017
Nedrema3	101±46	5.0±1.0	0.17±0.09	0.75±0.05	0.09±0.05	0.707±0.012
Viita1	51±17	3.5±0.5	0.11±0.05	0.84±0.01	0.06±0.06	0.678±0.146
Viita2	78±20	4.0±0.1	0.25±0.09	0.72±0.02	0.04±0.03	0.567±0.047

Abbreviations: E – number of earthworms per m^2, S – number of species, Epi – epigeic individuals, %, Endo – endogeic individuals, Anecic – anecic individuals, %, Diversity – Simpson's diversity index 1-D

($p<0.05$) with the relative importance of endogeic species (R = -0.574). There was a significant difference ($p<0.05$) in the abundance of *Lumbricus rubellus* and *L. castaneus* between Nedrema and Viita, while the abundance of *Dendrobaena octaedra* did not differ in all of the meadows. The endogeic species *Aporrectodea caliginosa* was present in all meadows. The abundance of the endogeic species *Aporrectoidea rosea* was significantly higher ($p<0.05$) in Laelatu than Viita; in Nedrema the abundance of *Aporrectodea rosea* was average. The semiaquatic species *Octolasion lacteum* was found in two meadows: Nedrema and Laelatu. Individuals of the anecic species *Lumbricus terrestris* and *Aporrectodea longa* were collected in all studied meadows; there was a significant difference ($p<0.05$) in their abundance between Laelatu and Viita.

The ecological structure of earthworm communities differed in Nedrema, where the epigeic group was more and the endogeic group less numerous compared to Laelatu and Viita; the difference was statistically insignificant. A significant ($p<0.05$) difference was found in the ecological structure of earthworm communities of long-time managed and restored meadows ($p<0.05$): there were more epigeic earthworms in restored meadows, while the relative importance of endogeics was higher in the long-term managed meadows (Figure 2). The abundance of anecic earthworms did not differ significantly between meadows with a different status of restoration.

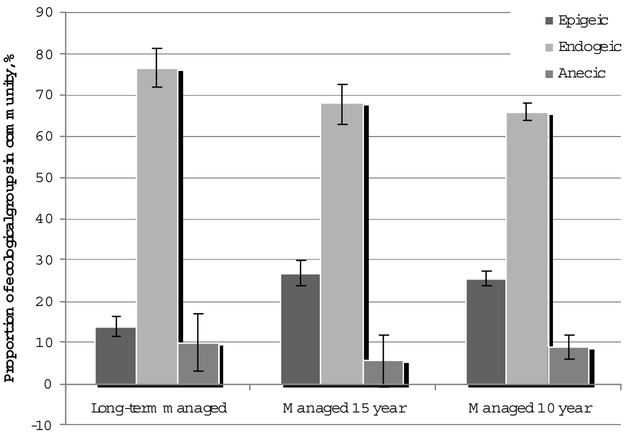

Figure 2. Ecological structure of earthworm communities (proportion of ecological group in community, % ±SE) in long-term managed and restored wooded meadows

Discussion and conclusions

The soil properties of the meadows studied are strongly influenced by the location of the area. The wooded meadows in Laelatu and Viita are located in a region of more calcareous soils, with a pH of 6.75-7.01, close to the Baltic Sea. In Nedrema the development of the soil is not influenced by coastal sediments and its soil pH is lower (5.54-5.72). The habitat conditions differed in Nedrema in terms of a lower pH and P content of soil; in Laelatu in terms of higher P and organic matter content; and in Viita in terms of a different soil type and very low soil moisture in some parts of the meadow. Soil conditions have an effect on the microbial conditions of the soil and thereby create a habitat for earthworms. The heterogeneity of local habitats in wooded meadows supports potential food items and creates suitable environments for the breeding and hibernation of animals (Kukk and Kull 1997). There is a link between the aboveground plant community and decomposer biota: the quality of plant litter plays an important role in structuring soil communities. Microfood-web structure and the interactions which occur within the web regulated by net primary productivity are clearly important determinants of decomposer communities (Wardle 2002, Porazinska et al. 2003 and Ball et al. 2009). Microbial biomass and respiration activity had high values in wooded meadows; differences between meadows in microbial characteristics correlated with soil chemical properties (pH, total N and organic matter content). The intensity of microbial decomposition (mass of decomposed α-cellulose) was positively influenced by the soil's organic matter content and negatively by its dry matter. It seems that the parameters of a microbial community are influenced more by the availability of carbon and nutrients; as such, the microbial community transforms the earthworm habitat.

The diversity of microhabitats, high activity of the microbial community and sufficient or optimal soil moisture within a wooded meadow has a positive effect on earthworm communities as concluded from our results and also earlier by Hemerik and Brussaard (2002). Earthworm diversity in the wooded meadows was high, but abundance was lower in comparison with open boreonemoral meadows (Ivask et al. 2007a). All three ecological groups of earthworms are included in communities. The dominant epigeic species was *Lumbricus rubellus* in meadows with higher soil moisture and *Dendrobaena octaedra* in the Viita meadow with low moisture. The epigeic species *Lumbricus rubellus* is very common in all types of open and wooded meadows, whereas *Lumbricus castaneus* inhabits meadows with higher soil moisture; the abundance of these two species depends on moisture being significantly higher in Nedrema and lower in the drier soil of Viita. *Dendrobaena octaedra* is an inhabitant of the forest litter layer and did not significantly depend on soil chemical parameters. The endogeic species *Aporrectodea caliginosa* and *Aporrectoidea rosea* are tolerant of variations in soil conditions (Ivask et al. 2007b) and were present in all meadows, being the most abundant species in the wooded meadows. The semi-aquatic species *Octolasion lacteum* was abundant in the wet parts of two meadows: Nedrema and

Laelatu. The studied soils were also suitable for two anecic species, *Lumbricus terrestris* and *Aporrectodea longa,* which were very abundant in the part of the Viita meadow which had wetter soil.

Regular mowing (once per year) is an important factor for wooded meadows. In the short term, defoliation by mowing can increase the abundance of soil decomposers by inducing the release of carbon-rich compounds from roots to the soil, but in the long term, defoliation and grazing often lead to reduced abundance and activity of soil decomposers (Holt 1997, Mikola et al. 2001, Sankaran and Augustine 2004). Non-managed wooded meadows became rapidly overgrown, with deciduous shrubs and trees forming a closed canopy. Recent efforts have aimed to restore overgrown wooded meadows by cutting back single shrubs and trees to open the canopy. Altered habitat conditions, as well as quantity and quality of plant litter, affect the soil food web; conversely, soil invertebrate fauna enhance grassland succession and diversity (Wardle 2002). The parameters of microbial communities did not differ significantly in the soil of either restored or long-term managed meadows. The earthworm communities of managed and restored meadows differed by ecological structure containing more endogeic individuals in long-term managed meadows, which existed as open meadows for a long period. More epigeic individuals were found in restored wooded meadow soil. This is caused by differences in litter quantity and quality – in abandoned overgrown meadows the characteristics of plant litter are more similar to forests, i.e. there are more parts of trees and shrubs, and hence typical forest epigeic species of earthworms prevail. The relative importance of endogeic earthworms in a community increases during the years following restoration. In this case the 10-15 year period of management altered the ecological structure of the earthworm communities to one more like a typical grassland community.

The aim of bioindicator-based studies is to use the living components of the environment under study (especially those with the highest diversity – the invertebrates) as the key to assessing transformations and effects and, in the case of landscape reclamation, to monitor the remediation process in different parts of the landscape over time (Paoletti 1999a). Earthworms comprise 40-90% of the soil's macrofaunal biomass in most ecosystems and are sensitive to ecosystem perturbations and rehabilitation (Decaëns and Jiménez 2002, Hole et al. 2005, Schmidt et al. 2003, Sepp et al. 2005, Tondoh et al. 2007). Many authors have concluded that earthworms are good indicators of soil conditions and climate changes (Eggleton et al. 2009, Peres et al. 2011). From these studies it was concluded that earthworms are suitable indicators of the effects of human activities because of their limited mobility and relative ease of sampling and identification (Paoletti 1999b). Based on this study we conclude that the soil parameters of the wooded meadows studied are relatively similar and that indication of the chemical and physical characteristics of the soil by earthworms is pointless. Nevertheless, the ecological structure of earthworm communities seems to have an indicative value for the management activities of meadow. The ratio between epigeic and endogeic individuals reflects the duration of human activities – the longer the meadow is mown, the greater the importance of epigeic earthworms in the community. This ratio can be used in the bioindication of the intensity and duration of management.

In conclusion, the earthworm communities of wooded meadows are diverse. Extremely high richness of plant species and high diversity of earthworm communities develop under the same specific calcareous soil conditions. Different layers of plant cover create several different microhabitats for earthworms in the soil and encourage diversity. The taxonomic composition of communities depends on the soil conditions; mostly on soil moisture. The restored wooded meadows differ significantly from the long-term managed meadows in terms of the ecological structure of earthworm communities: for 10-15 years after restoration an increase in endogeic earthworm numbers and a decrease in epigeic earthworm numbers were observed. In long-term mown meadows the community consists of more endogeic and fewer epigeic species than in restored meadows.

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СООБЩЕСТВА ДОЖДЕВЫХ ЧЕРВЕЙ В ПОЧВАХ ЛЕСНЫХ ЛУГОВ В ЭСТОНИИ

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Резюме

Лесные луга являются традиционными полуестественными лугами в регионе Балтийского моря. Они регулярно выкашиваются один раз в год, а на некоторых из них пасутся овцы или крупный рогатый скот поздним летом после сенокоса. Данные о почвенной фауне на лесных лугах все еще остаются очень незначительными, несмотря на их важное значение для функционирования экосистемы. Цель настоящего исследования состояла в описании специфической и экологической структуры сообществ дождевых червей, их разнообразия и численности в отношении к химическим и микробиологическим характеристикам почвы, а также условиям восстановленных лесных лугов в Эстонии. Химические и микробиологические параметры изучались с целью охарактеризовать местообитание дождевых червей. Сбор дождевых червей осуществлялся при помощи горчичного раствора в качестве вермицида. Сообщества дождевых червей на лесных лугах были представлены в общей сложности 8 видами. Наиболее многочисленными видами на лесных лугах были эндогейные *Aporrectodea caliginosa* и *Aporrectodea rosea*. Доминирующими эпигейными видами были *Lumbricus rubellus* на лугах с более высокой влажностью почвы и *Dendrobaena octaedra* на лугах с сухой почвой. Обилие видов растений и высокое разнообразие сообществ дождевых червей на лесных лугах развиваются в тех же специфических условиях карбонатных почв. Различные яруса растительного покрова создают несколько микроместообитаний для почвенных беспозвоночных, включая дождевых червей, и способствуют разнообразию; видовой состав сообщества зависит от условий почвы, в основном от ее влажности. Восстановленные лесные луга значительно отличаются от давно используемых лугов по экологической структуре сообществ земляных червей: на выкашиваемых лугах в сообществе дождевых червей больше эндогейных и меньше эпигейных видов по сравнению с восстановленными лугами.

Ключевые слова: лесные луга, дождевые черви, микробное сообщество, разнообразие, восстановление