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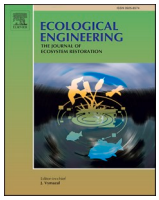

Soil fauna development during heathland restoration from arable land: Role of soil modification and material transplant

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ABSTRACT

Heathlands are threatened habitats throughout the whole Europe, which have initiated numerous restoration programmes aimed mostly at plant community reconstruction; however, little is known about soil fauna restoration. Here we have studied newly established wet and dry heathlands in the Netherlands after topsoil removal of previously agricultural land, where we manipulated the soil pH (acidification by Sulphur or liming by Ca ions as Dolokal) and introduced plant or soil material to speed up the restoration process. We sampled experimental plots and nearby mature heathlands (used as local reference habitat) over five years (2013–2017) for nematodes, mesofauna (mainly springtails and mites) and macrofauna. Although soil inoculation proved to be a substantive step in target plant community development and also helped to shift soil faunal assemblages towards the target, the latter were still far from reference heathland after five years. Only macrofaunal densities showed similar densities in 2017 as in local reference spots. The succession dynamics of all studied groups and trophic composition of macrofauna and nematodes differed in wet and dry heathlands. Soil amendments improved the initial colonisation as well as liming at the wet sites, which probably created suitable microhabitats for soil fauna development.

1. Introduction

Heathlands are one of the oligotrophic habitats characterized as a landscape covered by dwarf shrubs of the ericoid species forming a closed canopy, and by the absence or scarcity of trees (Waterbolk, 1993). Still, there have been several threats affecting heathlands throughout history or in the present day. On a large scale, high N deposition and consequent eutrophication and acidification (Bobbink and Roelofs, 1995; De Graaf et al., 1998) is the biggest threat to the last remaining heathlands, causing a vegetational shift to acidic grasslands (De Graaf et al., 2009). However, for the last 200 years the main reason for the mass losses of heathlands was a conversion to arable land or intensively used meadows, where additional nutrients were applied as fertilizers. Moreover, liming was typically applied in agricultural land to increase the pH, which again favored grasses against heather. Later on, this agricultural history can affect soil microbial communities even 50 years after abandonment (Turley et al., 2020). As heathlands have always been a characteristic part of the mosaic of landscapes in many European countries that have almost disappeared, in order to return them to the Netherlands, restoration of heathlands on ex-arable fields is inevitable.

Removal of excess nutrients and establishing a slightly acidic pH is thus a basic precondition of successful heathland restoration. A rather drastic technique that can achieve a substantial lowering of nutrients in soil is to remove the whole topsoil (Aerts et al., 1995; Rasran et al., 2007). As for another abiotic requirement, in the past such acidification was the result of centuries-long overgrazing, where not only biomass was taken away, but also the base cations that it contained. Experiments have shown that a low pH can be satisfyingly achieved by the addition of sulphurous amendments during the first stages of restoration (Owen and Marrs, 2001; Tibbett and Diaz, 2005).

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However, topsoil removal leaves behind subsoil which typically does not contain diaspores of target plant and soil biota communities (Mudrák et al., 2010). After initial manipulation of the abiotic starting conditions described above, a further succession of such de novo habitats towards functional heathlands can take place. This can be done either with human assistance, or occur spontaneously. The latter can be time-consuming and with uncertain outcomes, whereas assisted succession or reclamation, if done correctly, is much faster and has better predictable outcomes (Baasch et al., 2012; Frouz et al., 2007). In such cases, often some kind of biological inoculum is used to reach the target quickly. In previous studies the introduction of seed in the form of hay, sods or even the whole turfs containing intact soil fauna assemblages were applied (Kardol et al., 2009a; Klimkowska et al., 2010; Moradi et al., 2018).

Current restoration projects aim mostly at target plant communities (Omand et al., 2018; Wubs et al., 2018), but there is still a gap in knowledge about the processes driving the succession of soil fauna (Duddigan et al., 2020). However, at the same time there is an emerging opinion in recent papers that soil biota is as equally important as vegetation for the functioning of newly formed heathlands (Cross et al., 2019; Lane et al., 2020; Radujković et al., 2020; van der Bij et al., 2018). While knowledge for a succesful management of the aboveground community is widely available (Bakker, 1989), this is not the case for the soil community. Yet, improper development of belowground communities might lead to the loss of one or more essential soil functions and hamper initial restoration successes from developing further into fully functional heathlands.

Heathlands in the Netherlands can be divided into dry or wet heaths according to the perennial fluctuations of soil water level (Aerts and Heil, 1993). Although plant communities in dry or wet heathlands have been widely studied (Aerts et al., 1995; Allison and Ausden, 2004; Vogels et al., 2020), there are no studies comparing soil fauna communities and factors affecting their development between those two water regimes. A proper restoration of fauna in heathland soil is important also for a future conservation of this particular habitat, because similar factors that threaten the aboveground biodiversity can be observed also belowground (Vogels et al., 2017). Existing studies focusing on the faunal aspect of heathland restoration are usually limited to one taxon or a small group of soil fauna (Hacala et al., 2020; Pedley et al., 2013; Siepel et al., 2018), but papers covering a wide array of different soil organisms are scarce, if any.

The inevitable role of soil fauna for ecosystem restoration has been recognized for quite some time (De Deyn et al., 2003; Scheu et al., 2005), but rarely put into account when planning restoration projects. In the present study we conducted an experiment on former agricultural fields where topsoil was removed in an attempt to restore new heathland quickly. We investigated both the effects of manipulation of the soil pH and biotic addition on the succession of three major groups of soil fauna in a full-factorial setup. Here we have tested three hypotheses: 1) sites treated with soil amendments resemble reference sites more than sites without such treatment; 2) wet heathlands develop faster towards the reference than dry heathlands, and 3) acidified substrates will more likely develop towards the target community than non-acidified ones.

2. Materials and methods

2.1. Sites description

The location of our experiment lies in the centre of the lowland heathlands in Dwingelderveld National Park (N $52^0$48′14.3, E $6^0$24′38.6) in the Netherlands. The altitude is 7 m, the average annual temperature 8.8 °C and the average rainfall is 783 mm. This area of approximately 200 ha was converted into agricultural land in the 1930's, but restored into heathlands again in 2011–2012. Topsoil removal was applied up to a depth of 40 cm to lower high nutrient content, which created oligotrophic substrate suitable for heathlands (Van der Bij et al., 2018). Values of pH were still higher than in reference heathlands (De Graaf et al., 2009).

2.2. Experimental plots

The experimental setup was the same for the two sites – wet and dry heathlands. 27 random squares were set in November 2011 right after topsoil removal of 15 × 15 m and 22 × 22 m in dry and wet sites respectively in a 3 × 3 factorial experiment. One level of manipulation was a change of abiotic conditions: i) substrate acidification by application of elemental sulphur (150 g per m^2); ii) substrate liming by calcium carbonate (Dolokal; 200 g per m^2) and iii) control plots left without any treatment. The second level of manipulation was the introduction of biotic material: i) addition of fresh herbage harvested from nearby heathlands in ratio 1:2; ii) addition of sods (plant + soil material) in ratio 1:15 and iii) control plots left without any treatment. Liming and acidification was done in November 2011; sods were spread in December 2011 as well as plant material, but as the seed occurrence was low, the latter was reapplied in September 2012, at the first possible moment that the seeds were ready. A more detailed description of treatments, as well as vegetation and soil chemistry development in individual treatments, can be found in van der Bij et al. (2018). Three areas of dry heathland and three areas of wet heathland, located 100 to 500 m from the experimental plots, were used as a local reference. Individual sampling points were regularly distributed around the experimental sites and located north, southwest and southeast from these sites, and we compared data from the experimental plots with the average of local references from all sampled years.

2.3. Soil fauna sampling

2.3.1. Nematodes

Nematodes in experimental plots and also in adjacent developed heathlands were sampled once a year during the succession in October/November 2013, 2014, 2015, 2016 and 2017. Local reference samples in 2016 were not taken due to technical difficulties. Three cores 5 cm in diameter were taken in each plot and mixed into a composite sample. Samples were then kept in a cooling box, transported to the laboratory and kept in a refrigerator until further manipulation. Nematodes were extracted in modified Baermann's funnels according to Háněl (1995) from 20 g of fresh soil for 48 h, then killed by hot formaldehyde (3,5–4% solution) and transferred through ethanol and glycerol solutions to anhydrous glycerol. Permanent slides in paraffin were made and inspected under a light microscope (125× to 1000× magnification), identified into genus level (Bongers, 1994; Andrássy, 2005, 2007, 2009; de Goede et al., 1993) and assigned into one of six trophic groups (bacterial feeders, plant parasites, fungal feeders, omnivores, predators, and algal feeders; (Yeates et al., 1993)).

2.3.2. Mesofauna

Samples for mesofauna were taken in the same manner as those for nematodes described above but only in the years 2013 and 2017. The whole composite sample was extracted using Tullgren apparatus for a week under a heat source (25 W) and sorted and identified under a dissection microscope. The mesofaunal group consisted mainly of springtails and mites.

2.3.3. Macrofauna

Macrofauna samples were also obtained only in 2013 and 2017. Standardized sampling was done as follows: composite samples from three cores of surface 625 m^2 each were taken, transported into the laboratory and extracted in Tullgren apparatus (for a week, heat source of 100 W). Individuals were then sorted under a dissection microscope and identified into family level and sorted into four trophic groups: herbivores, detrivores, predators, and omnivores.

2.4. Data analysis

To achieve normal distribution, mesofaunal data were transformed by $\log_{10}$ and nematodes data were transformed by $\ln(x + 1)$ formula. For the latter, families and genera were assigned CP values (Bongers, 1990) according to their life traits on a scale from 1 to 5, corresponding to r-K strategists respectively. Based on these values, various nematode community indices like Maturity index (SMI), as well as their extensions such as Enrichment index (EI) or Structural index (SI), were calculated using NINJA platform (Sieriebriennikov et al., 2014) and plotted into SE squares. We chose the Sigma Maturity Index (SMI) because for the environment assessment we wanted to include all groups. Also, the number of plant parasites as well as nematodes with cp-1 (enrichment opportunists) was quite low and therefore there were not big differences between MI25/MI and SMI (Bongers and Bongers, 1998; Yeates, 1994).

The effects of treatments were tested with Analysis of Variances (ANOVA) using Statistica programme version 13.5.0.17, and individual differences were determined by Tukey, Unequal-N or Dunnett's post-hoc test. Multivariate analyses (Canonical correspondence analysis – CCA) were performed in CANOCO software version 5.12.

3. Results

In most of the groups of soil fauna the variation of restored plots overlapped with the variation of local reference; this overlap was bigger in wet than dry heathlands (see Figure 1). However, the overall densities of the faunal groups did not reach the densities of the local reference heathlands, with the exception of macrofauna in the wet heathlands, as can be seen in Figure 2.

3.1. Nematodes

In nematodes we identified in total nearly 20,000 individuals during five years, belonging to 95 genera/families. 32 genera were present in all years: *Acrobeles*, *Acrobeloides*, *Alaimus*, *Cephalobus*, *Eucephalobus*, *Heterocephalobus*, *Mesorhabditis*, *Metateratocephalus*, *Panagrolaimus*, *Plectus*, *Rhabditis s. l.*, *Rhabdolaimus*, *Teratocephalus*, *Tylocephalus*, *Wilsonema*, *Eumonhystera*, Geomonhystera, Monhystrella, *Monhystera*, *Pratylenchus*, *Helicotylenchus*, *Mesocriconema*, *Aglenchus*, *Lelenchus*, *Aphelenchoides*, *Filenchus*, *Tylencholaimus*, *Clarkus*, *Crassolabium*, *Aporcelaimellus*, *Eudorylaimus* and *Mesodorylaimus*. At the wet experimental sites, three trophic groups of nematodes (plant parasites, omnivores, and algal feeders) differed significantly between addition treatments, whereas bacterial feeders, predators and omnivores differed between years. None of the combinations of these factors was significant for any of the trophic groups. However, in the dry sites all trophic groups changed over time (for total densities and relative densities see Appendix 1), and four of these groups (bacterial feeders, predators, omnivores, and algal feeders) significantly reacted to the different pH of the soil. Apparently, additions were significant for fungal feeders, and also, the trophic group of omnivores was the only one that differed significantly in combination of year and biota addition factors (see Table 1). While analysing indices based on trophic groups, only the treatments in years 2014 and 2017 were significantly different for SMI (see Appendix 2). Structure Index (SI) and Enrichment Index (EI) for three biota manipulation treatments are graphically represented in Figure 3. Neither SI nor EI differed significantly between treatments in one year, but there was a significant difference in SI between years, although only in wet experimental sites. In wet heathlands mean SI values (mean ± SD) were lowest in 2013 (34.84 ± 18.13) and highest in 2017 (74.72 ± 15.77), whereas in dry heathlands, the lowest value of SI was in 2017 (58.87 ± 13.71) and highest in 2014 (77.20 ± 14.95). Although total densities overall were lower at the experimental sites than at the reference sites, relative abundances of trophic groups were similar to those in local references. At the dry sites, groups that differed were plant parasites in 2013, omnivores in 2014, predators in years 2013, 2014, 2015, and 2017; algal feeders differed only in the year 2016. At the wet sites the only group that differed was predators in 2016 (One-Way ANOVA). Tukey's post hoc test revealed that acidified sites with sod amendment were similar to the reference sites. There was a clear difference in the presence of omnivores at the experimental sites in 2013, where the proportion at wet sites was <10%, whereas at the dry sites it was >40%. The long-term average proportion of this feeding group in the assemblages at the local references was below 9% in both water regimes. The first algal feeders appeared in 2015.

3.2. Mesofauna

Springtails and mites were studied as representatives of soil mesofauna. In total we found 8153 individuals. All factors and their combinations at the dry experimental sites were important for the total number of mesofauna and for the group of mites, whereas springtails there responded only to the pH of soil and its combination with addition. From all groups from the wet sites, only Collembolans responded on one factor - change of soil pH (see Table 1). Mesofauna at the dry experimental sites in 2013 that have been sod treated almost reached the numbers of total densities of the references (see Figure 4). In the dry heathlands, the reference sites and the experimental sites differed as late as in 2017 (One-way ANOVA, Tukey HSD test), where all experimental sites were different from the reference sites. In general, Acari were in higher densities than Collembola, although thorough statistical analysis did not reveal significant differences due to a high variation in samples (Factorial ANOVA, *t*-test).

3.3. Macrofauna

We found 2260 individuals of macrofauna. The total densities of macrofauna in experimental plots was significantly higher in 2017 than in 2013 in both wet and dry heathlands (Factorial ANOVA, $p < 0.01$ and $p < 0.001$ respectively). In the latter there were also significant differences in the combination of pH manipulation and year. Differences between years were also significant for the two most frequently occurring families - *Tabanidae* and *Chironomidae* - on both moisture regimes of heathlands (see Table 1). Both total and relative densities of trophic groups were quite similar between the experimental sites and the local references in 2017 (see Table 2). Dunnett's post hoc test of comparison with the control group showed that only the total density of herbivores significantly differed from the local reference in almost all treatments, with the exception of limed + plant treated sites (Factorial ANOVA, $p < 0.05$). The most prevalent group was saprophages, with a mean of 53.9% at the dry experimental sites (61.5% at the corresponding reference sites) and 62.7% at the wet experimental sites (70.1% at the corresponding reference sites).

4. Discussion

Vegetation, and in particular soil amendments, speeded up colonisation by soil organisms, especially in the wet heathland, though total densities were quite similar in both sites at the end of our observation. These results support the idea presented in some other studies that soil transfer is an important restoration technique that may speed up the ecosystem development, although its outcome is site specific (Moradi et al., 2018; van der Bij et al., 2018; Benetková et al., 2020). All of the groups were able to inhabit all sites in the six years of the experiment, but only macrofauna in the wet heathlands reached levels compared to those found in the local reference heathlands, which corroborates with a metaanalysis of 71 papers covering studies of fauna rehabilitation of ex-mining land in Australia published by Cristescu et al. (2012). However, in soil and vegetation amended treatments, the development seems to be comparable or faster than in unamended restoration trial 15 years after topsoil removal reported by Frouz et al. (2009).

Not only did the succession of soil fauna differ in wet and dry

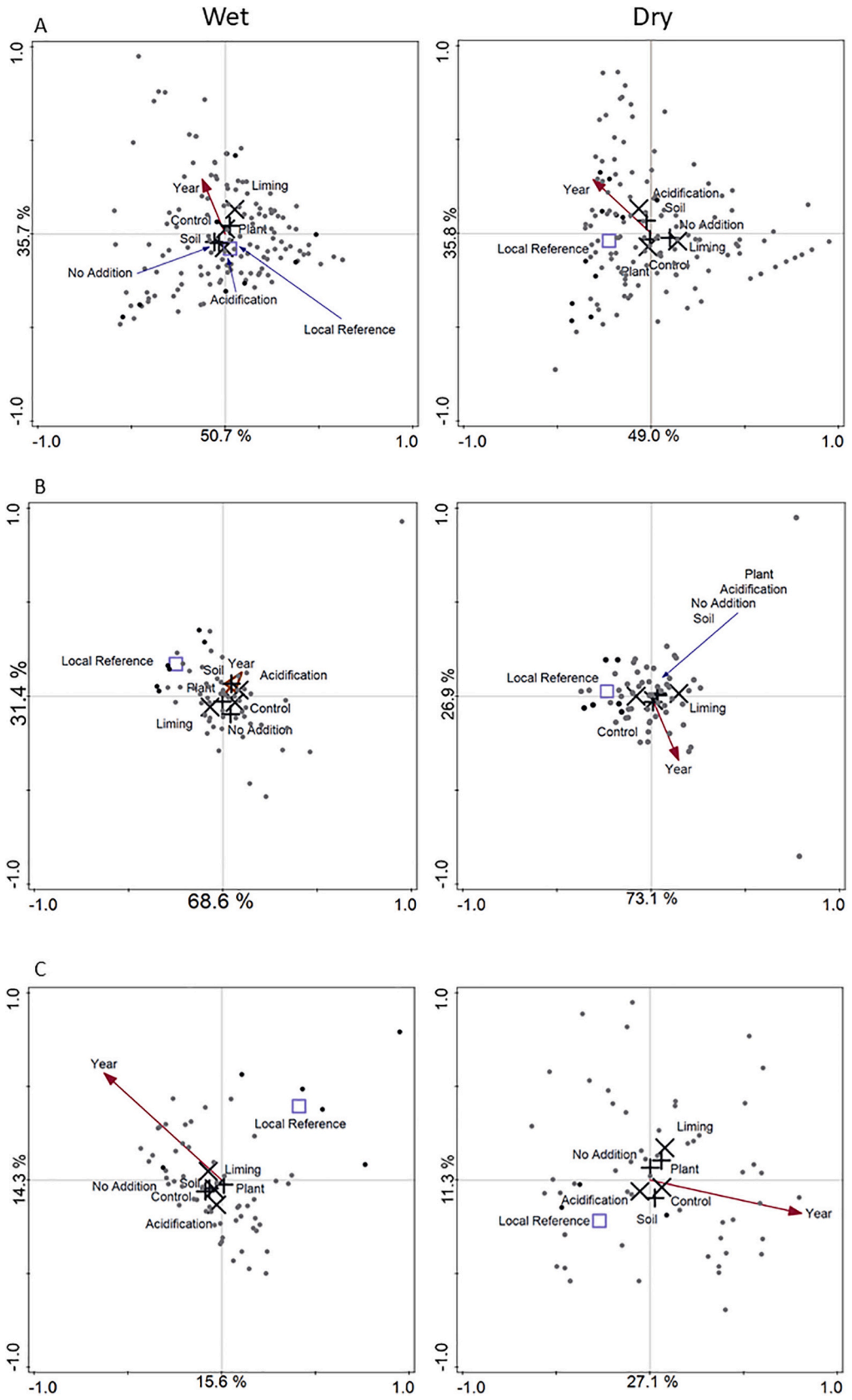

Fig. 1. Principal component analysis (PCA) ordination diagram of nematodes (A), springtails and mites (B) and macrofauna (C) on wet (left column) and dry (right column) heathlands. Nematodes are based on relative abundances of trophic groups; the rest is based on ecological guilds in ind. × m-1. Crosses stand for soil biota manipulation, X mark for pH manipulation. The grey Square is for local references. Points are representations of individual samples; black points are for local references, and grey points are for experimental sites.

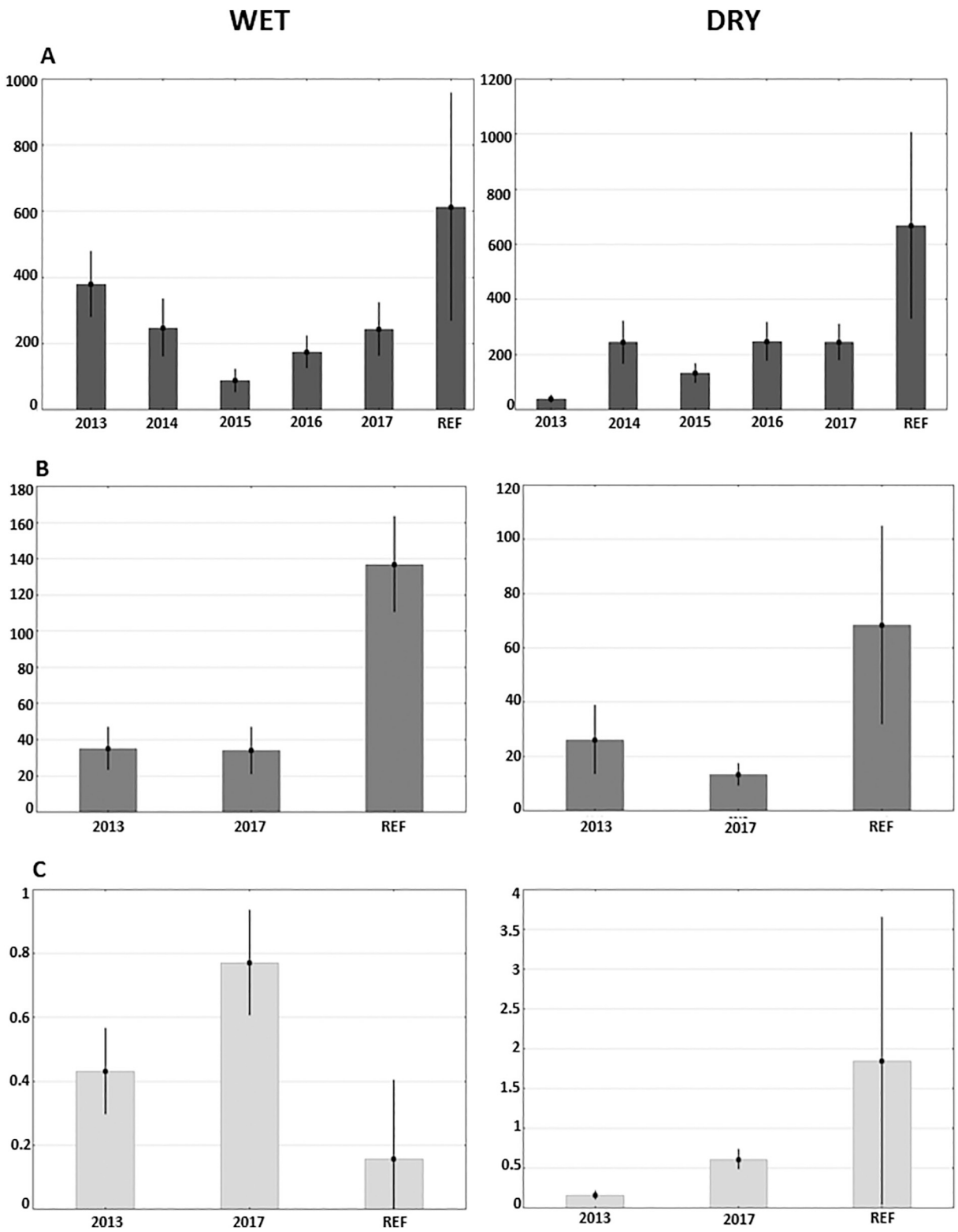

Fig. 2. Total densities of nematodes (row A), springtails and mites (row B), and macrofauna (row C) on wet (left column) and dry (right column) experimental heathlands vs local reference heathlands (REF). Numbers are thousands of individuals × m^{-2}; means ±95% confidence interval. Note different Y axes.

heathlands, the pattern of colonisation also varied between different groups of fauna with regard to their life strategy. As we had expected in our first hypothesis, nematodes showed a gradual approach to the local reference, in particular, in sites that had been acidified and supplied by soil and plant material. A similar effect of soil transplant was also found in the studies of Benetková et al. (2020) or Moradi et al. (2018).

However, as similar to Kardol et al. (2009b), we were not able to detect any significant differences between treatments and there were also no major differences in the relative proportions of trophic groups of nematodes. This close resemblance between experimental sites is probably caused by a habitat where nematodes live and feed: relatively homogenous soil pores filled with water. To achieve a recreation of these

Table 1
Significant *p*-values from ANOVA of environmental factors for all important groups of soil fauna for (A) wet heathlands and (B) dry heathlands.

A	Group	Addition	pH	Year	Addition*pH	Addition*Year	pH*Year	Addition* pH*Year
Nematoda	Total number	n.s.	n.s.	0.0001	n.s.	n.s.	n.s.	n.s.
	Bacterial feeders (%)	n.s.	n.s.	0.0041	n.s.	n.s.	n.s.	n.s.
	Fungal feeders (%)	n.s.	0.0005	n.s.	n.s.	n.s.	n.s.	n.s.
	Plant parasites (%)	0.0339	0.0038	n.s.	n.s.	n.s.	n.s.	n.s.
	Predators (%)	n.s.	n.s.	0.0004	n.s.	n.s.	n.s.	n.s.
	Omnivores (%)	0.0268	n.s.	0.0013	n.s.	n.s.	n.s.	n.s.
	Algal feeders (%)	0.0361	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Mesofauna	Total number	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Collembola	n.s.	0.0023	n.s.	n.s.	n.s.	n.s.	n.s.
	Acari	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Macrofauna	Total number	n.s.	n.s.	0.0052	n.s.	n.s.	n.s.	n.s.
	Tabanidae	n.s.	n.s.	0.0000	n.s.	n.s.	n.s.	n.s.
	Chironomidae	n.s.	0.0008	0.0002	n.s.	n.s.	n.s.	n.s.
	Aranea	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

B	Group	Addition	pH	Year	Addition*pH	Addition*Year	pH*Year	Addition* pH*Year
Nematoda	Total number	n.s.	n.s.	0.0000	n.s.	n.s.	n.s.	n.s.
	Bacterial feeders (%)	n.s.	0.0497	0.0497	n.s.	n.s.	n.s.	n.s.
	Plant parasites (%)	n.s.	n.s.	0.0200	n.s.	n.s.	n.s.	n.s.
	Fungal feeders (%)	0.0000	n.s.	0.0000	n.s.	n.s.	n.s.	n.s.
	Predators (%)	n.s.	0.0123	0.0008	n.s.	n.s.	n.s.	n.s.
	Omnivores (%)	n.s.	0.0067	0.0000	n.s.	0.0201	n.s.	n.s.
	Algal feeders (%)	n.s.	0.0340	0.0433	n.s.	n.s.	n.s.	n.s.
Mesofauna	Total number	0.0065	0.0001	0.0047	0.0221	0.0132	0.0302	0.0044
	Collembola	n.s.	0.0028	n.s.	0.0275	n.s.	n.s.	n.s.
	Acari	0.0032	0.0001	0.0003	0.0105	0.0013	0.0055	0.0012
Macrofauna	Total number	n.s.	n.s.	0.0000	n.s.	n.s.	0.0324	n.s.
	Tabanidae	n.s.	n.s.	0.0000	n.s.	n.s.	n.s.	n.s.
	Chironomidae	n.s.	n.s.	0.0000	n.s.	n.s.	n.s.	n.s.
	Aranea	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

conditions can be – at least in this case – easier than to prepare specific heterogeneous microhabitat aboveground for mostly epigeic meso- and macrofauna (Hansen and Coleman, 1998). Also, according to Schirmel and Buchholz (2011), mosaic patches are important for a high diversity of macrofauna such as spiders and beetles.

The development of upper soil layer in terms of litter accumulation and transformation suitable for maintaining soil fauna is a complex process (Frouz et al., 2009), however, the addition of fresh sods taken from mature heathlands probably speeded up the development of a primary succession of microbial communities, as can be seen in the results obtained in an initial phase of this experiment (van der Bij et al., 2018). This applied also for nematodes and springtails, in particular at the wet site, where abundances of the experimental plots reached those of local references. However, later on, this head start disappeared and abundances became more equal between treatments. This supports the finding of Moradi et al. (2018) that soil material introduced into bare substrate served as refugium for soil fauna, but was not successful further in maintaining those communities due to the harsh conditions of adjacent undeveloped soil. Sod inoculation greatly promoted the development of target plant communities even three years after the application (van der Bij et al., 2018), but an impact on soil fauna is less evident than in the work of Wubs et al. (2016), where there was an improvement in the abundance of soil fungi and nematoda after soil inoculation.

The difference between factors driving soil fauna development in different water regimes was also manifested at our experimental sites. There is a perspicuous difference between an early development of wet and dry heathland de novo. We documented a rapid increase of the smaller, soil dwelling part of fauna in wet heathlands two years after the establishment of the experiment. This can be explained by an improvement of a water regime, which is supported by the findings of Song et al. (2016), who also noted an increase of organisms after water addition in grasslands, but no changes in the trophic structure of nematode assemblages. While analysing SMI in nematodes, two contradictory trends appeared: the SMI increased with time in the wet experimental plots and decreased in the dry plots. Therefore, predictions made by Ettema and Bongers (1993) that the Maturity Index (which is fungible with the SMI used by us) will decrease together with a higher presence of opportunistic omnivores during primary succession in oligotrophic habitats can be applied in our case only on the dry heathland. However, we must mention that there could be a bias caused by really low densities of nematodes in the dry heathland (compared to the wet heathland) in the first years of sampling. Despite different densities, the numbers of omnivores were similar in both sites, whereas numbers of bacterial feeders, which are assigned with lower cp values and therefore lesser SMI/MI, were smaller in dry than in wet heathlands. We also found a higher presence of predators in experimental plots than in mature heathlands. This is in agreement with the observation of e.g. Frouz (1997) or Kaufmann (2001) that predators come to the initial successional plots early due to their better ability to move and better conditions that help them search easily for their prey. This actually supports our second hypothesis that wet heathlands will develop faster towards target soil faunal communities than dry heathlands, because predators appeared at the dry site only after the number of bacterivores (and therefore overall densities) rose in 2014, whereas they had already started appearing in samples from the wet site from 2013.

There was also a huge difference in the mesofaunal succession between wet and dry treatments. There were no significant differences between individual treatments on the level of pH manipulation, biota addition or their combination at the wet site, whereas at the dry site, all treatments led to significant differences. This has mainly to do with differences in mite density. Mites were present in much higher densities and played a much more important role in heathland mesofauna communities than springtails (Frouz et al., 2009), possibly because they have a higher tolerance to the extreme dry conditions that occur there during the summer by living mostly in the soil (Bogorodskaya et al., 2010). In

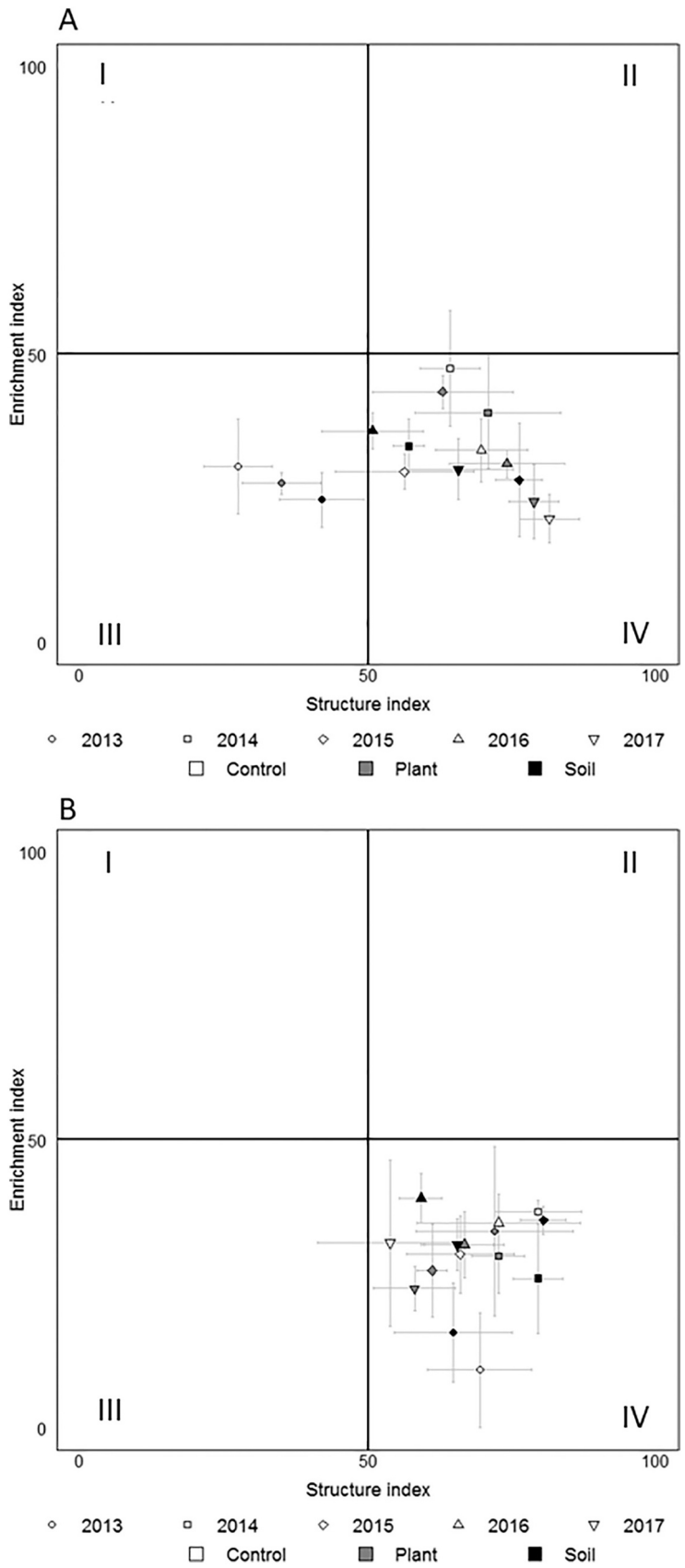

Fig. 3. Positions of the nematode faunal profiles in structural – enriched (SE) squares of sod treated, plant material treated and control sites in all years for (A) wet heathland and (B) dry heathland. Points are means; whiskers are SEMs. Quadrant I represents a stressed and nutritionally enriched environment, quadrant II represents a stable enriched environment, quadrant III is for a stressed environment depleted in nutrients and IV a stable but depleted environment.

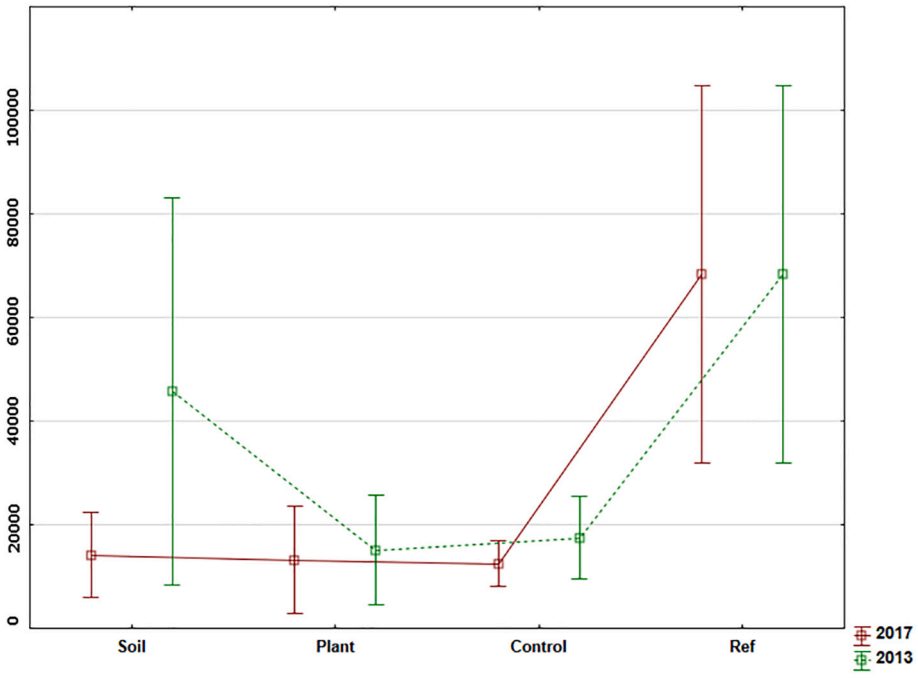

Fig. 4. Densities of mesofauna between different addition treatments in years 2013 and 2017 in the dry experimental heathlands compared to the local reference sites. Means of ind. × m^{-2} ± SEM.

Table 2
Means of relative densities of macrofaunal trophic groups in %. SD in parentheses. A – acidified; L – limed; P – plant material addition; S – sod addition; C – control (no pH manipulation and/or no additions); REF – local reference heathlands.

		Herbivores	Saprophages	Carnivores	Omnivores
DRY	AC	0.0 (0.0)	72.5 (31.9)	27.5 (31.9)	0.0 (0.0)
	AP	11.0 (13.6)	66.2 (36.1)	22.7 (22.8)	0.0 (0.0)
	AS	1.8 (3.2)	26.2 (28.3)	72.0 (28.1)	0.0 (0.0)
	CC	0.6 (1.0)	72.4 (8.3)	26.9 (8.4	0.0 (0.0)
	CP	2.5 (1.7)	39.9 (19.3)	57.6 (17.6)	0.0 (0.0)
	CS	0.0 (0.0)	55.9 (35.0)	44.1 (35.0)	0.0 (0.0)
	LC	9.8 (8.7)	40.1 (15.3)	50.1 (11.4)	0.0 (0.0)
	LP	4.8 (2.4)	46.1 (27.9)	49.0 (27.8)	0.0 (0.0)
	LS	0.9 (1.6)	66.3 (20.2)	29.2 (22.8)	3.6 (6.2)
	REF	7.5 (0.12)	61.5 (8.4)	26.0 (13.1)	5.0 (5.2)
	AC	3.6 (3.5)	74.3 (19.2)	22.1 (17.6)	0.0 (0.0)
	AP	8.1 (12.3)	57.4 (45.3)	34.5 (33.1)	0.0 (0.0)
	AS	6.5 (11.2)	22.6 (20.5)	70.9 (25.4)	0.0 (0.0)
	CC	3.7 (6.4)	82.1 (18.5)	14.2 (12.3)	0.0 (0.0)
	CP	3.9 (3.4)	74.0 (9.9)	22.1 (17.5)	0.0 (0.0)
	CS	4.0 (2.7)	63.0 (22.0)	33.0 (20.1)	0.0 (0.0)
	LC	2.2 (2.2)	77.2 (11.3)	19.3 (11.6)	1.2 (2.1)
	LP	0.6 (1.0)	57.8 (29.4)	41.6 (28.8)	0.0 (0.0)
	LS	2.3 (3.2)	55.7 (24.2)	37.5 (20.4)	4.5 (7.8)
WET	REF	5.8 (9.4)	70.9 (47.1)	23.3 (37.7)	0.0 (0.0)

the wet heathlands, the moisture content on top of and in the upper layer of soil is still buffered by the capillary rise from the nearby groundwater, but this is not the case in dry heathlands. Mesofauna has to minimize moisture losses by seeking shelter and this may be problematic during the first years after top soil removal or in highly disturbed soils, where vegetation cover is still very low and soil surrounding introduced sods is not sufficiently developed (Kardol et al., 2009b; Moradi et al., 2018).

In the macrofaunal assemblages we found higher numbers of omnivorous *Formicidae* in the wet reference sites than at the dry sites or even at the experimental sites. This may point to an earlier development of the wet heathlands, because it takes some time for ants to colonize a new space and build their nests; therefore they are usually not present in recently or continuously disturbed habitats.

We were able to prove our hypothesis in the level of abiotic-factor manipulation only in the case of dry heathlands, where all faunal groups in acidified treatments were closer to the assemblages from the reference heathlands, which supports the idea about abiotic-driven succession proposed in Cramer et al. (2008). On the other hand, in the wet experimental site, there was either no clear trend to follow or it was liming that brought the assemblages from the experimental sites closer to the local references.

Nematodes assemblages in all treatments at the wet site were very similar to the reference assemblage. We presume that the stress-driven soil forming processes keep soil constantly at some point of succession, which is easier to reach in cases of such small organisms that dwell in soil pores. On the contrary, at the dry site, acidification was forming nematode assemblages towards the target community, as was presented also by Tibbett et al. (2019).

The situation in mesofauna was similar as in nematodes. Apparently, topsoil removal accelerated the development of microbial communities, as was also found in van der Bij et al. (2017) in the very beginning of succession, which was noticeable in acidified plots even in the year 2013, especially in the dry heathlands. After that, densities of mesofauna dropped rapidly here, probably due to the unpreparedness of adjacent soil, which was also described by Rantalainen et al. (2005), or a harsh environment during dry episodes throughout the years.

After soil pH manipulation, macrofauna in wet limed treatments surprisingly, and in contrary to our hypothesis, resembled assemblages of soil fauna from reference heathlands more than in acidified treatments. The explanation may lie in temporary suitable microhabitats (e.g. greater moss stands) together with an overall higher coverage of different plants in limed plots for macrofauna to expand, as was also measured in Mudrák et al. (2010). These factors, together with high variability and overall low occurences of macrofauna in the reference heathland, can push communities in limed experimental plots towards mature heathlands more than in acidified plots. Despite the fact that smaller faunal groups did not reach reference levels, macro- and mesofauna at wet limed sites were closest to the local reference. Although the application of elemental sulphur onto bare substrate can be effective in lowering soil pH for a substantial time frame, a certain consciousness

about the pH level is in place here. A high amount of N deposition in the Netherlands may promote further acidification; thus lowering of soil animals' populations can occur (Tibbett et al., 2019).

5. Conclusions

The results of our study, which was unique not only in its length, but also in its intensity of observation of soil fauna, mostly support our hypotheses about soil fauna development during heathland restoration. The main factor affecting soil fauna development was probably water saturation of experimental plots, as the succession of soil animals differed substantially in the dry and wet heathland. The additon of soil material helped in the very first dispersal of soil communities, especially of small, soil-dwelling groups. Later on, the differences between treated and non-treated soil became less observable. Dissimilarities between treatments in the experimental plots were more pronounced in the dry heathlands, although a detailed analysis of nematodes and mesofaunal assemblages showed that communities in the wet heathlands approach target communities faster than in dry heathlands. This can be caused by water saturation causing interruption in soil communities' succession, which applies also for mature wet heathlands. There is also a stronger effect of soil pH manipulation in the dry heathand, whereas in the wet heathland communities from the limed treatments seemed to resemble target communities more. Nevertheless, there is still substantial time needed for proper development of soil fauna to support long-lasting heathland landscape and a further, maybe even deeper study of soil processes, is recommended.

Credit author statement

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Ladislav Háněl: methodology, data curation.
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Jan Frouz: supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Relative abundance (upper row) and density (lower row) of trophic groups of nematodes at the experimental sites in wet and dry heathland over the years (mean ± standard error). Letters mean homogenous groups (Tukey's post hoc test, $p < 0.05$) within each row, when differences are significant. Relative abundance is in %, density is in individuals × m^{-2}. First row in the table is total density of nematodes

Wet	2013	2014	2015	2016	2017
Total	378,837 ± 47,800 a	247,061 ± 42,381 ab	87,207 ± 16,441 c	173,816 ± 23,471 bc	242,357 ± 38,851 ab
	64.5 ± 3.9 a	47.1 ± 3.7 b	49.7 ± 5.4 ab	46.5 ± 3.3 b	46.6 ± 3.57 b
Bacterial feeders	256,617 ± 36,637 a	119,446 ± 24,244 b	46,679 ± 12,105 b	85,361 ± 12,903 b	125,617 ± 25,611 b
	0.3 ± 0.1	1.5 ± 0.5	1.3 ± 0.7	2.2 ± 0.7	1.8 ± 0.5
Plant parasites	924 ± 462	3361 ± 1154	1783 ± 976	3734 ± 1259	4771 ± 1204
	27.1 ± 4.0	27.0 ± 4.0	22.2 ± 3.7	27.1 ± 3.8	19.3 ± 3.5
Fungal feeders	100,797 ± 19,382 a	79,374 ± 23,155 ab	20,428 ± 4605 b	49,722 ± 12,801 ab	51,600 ± 11,961 ab
	1.6 ± 0.9 b	1.2 ± 0.6 b	4.3 ± 1.8 b	3.8 ± 1.5 b	13.4 ± 3.6 a
Predators	7089 ± 3482 b	2311 ± 1117 b	3980 ± 1444 b	6081 ± 2251 b	18,420 ± 3813 a
	6.4 ± 0.8 b	23.3 ± 3.7 a	21.8 ± 4.8 a	20.3 ± 3.2 a	17.3 ± 1.8 ab
Omnivores	22,193 ± 3368 ab	42,692 ± 7257 a	14,836 ± 3537 b	28,702 ± 5420 ab	38,950 ± 9082 ab
	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 0.6	0.1 ± 0.1	0.8 ± 0.4
Algal feeders	0 ± 0 b	0 ± 0 b	542 ± 397 ab	213 ± 213 ab	1442 ± 736 a

Dry	2013	2014	2015	2016	2017
Total	37,554 ± 6457 b	243,670 ± 37,752 a	131,562 ± 17,123 b	247,254 ± 33,717 a	243,650 ± 31,212 a
	44.3 ± 4.8 bc	40.3 ± 4.4 ab	43.6 ± 3.4 bc	28.6 ± 12.6 a	54.6 ± 2.8 c
Bacterial feeders	14,436 ± 2495 c	109,736 ± 23,463 ab	60,979 ± 10,995 bc	73,170 ± 12,486 ab	124,599 ± 15,253 a
	2.2 ± 1.2 b	2.3 ± 0.8 ab	7.5 ± 1.6 a	6.2 ± 2.1 ab	2.6 ± 0.6 ab
Plant parasites	1078 ± 476 b	4623 ± 1428 ab	8802 ± 1990 ab	15,027 ± 6574 a	4704 ± 946 ab
	10.4 ± 3.2 a	14.9 ± 2.3 ab	23.5 ± 3.4 bc	35.2 ± 4.9 c	23.9 ± 3.3 bc
Fungal feeders	6473 ± 2640 c	41,305 ± 12,236 cb	33,290 ± 7024 bc	109,698 ± 25,196 a	74,301 ± 17,235 ab
	1.2 ± 0.9 b	12.4 ± 2.3 a	9.6 ± 1.9 a	7.2 ± 2.2 ab	6.0 ± 1.2 ab
Predators	308 ± 213 b	31,133 ± 8423 a	12,324 ± 2596 b	12,182 ± 3214 ab	14,715 ± 3058 ab
	40.8 ± 5.6 a	30.1 ± 3.3 ab	14.7 ± 2.6 c	22.5 ± 3.7 bc	10.9 ± 1.6 c
Omnivores	14,950 ± 3119 c	56,871 ± 5855 a	15,044 ± 2274 c	37,221 ± 3020 b	21,590 ± 3020 bc
	0.0 ± 0.0 b	0.0 ± 0.0 b	1.2 ± 0.6 a	0.2 ± 0.2 ab	0.2 ± 0.1 ab
Algal feeders	0 ± 0 a	0 ± 0 a	1120 ± 591 a	462 ± 272 a	361 ± 199 a

Appendix B. ∑Maturity Index in nematodes in years 2013–2017. Mean ± SD. Letters mean significant differences (Tukey's post-hoc test) between treatments in one year. A – acidified; L – limed; P – plant material addition; S – sod addition; C – control (no pH manipulation and/or no additions)

		2013	2014	2015	2016	2017
Dry	AC	2.56 ± 0.76	2.65 ± 0.41 ab	2.42 ± 0.35	2.37 ± 0.11	1.95 ± 0.23 b
	AP	1.99 ± 1.85	2.82 ± 0.58 ab	2.53 ± 0.38	2.22 ± 0.24	2.34 ± 0.07 ab
	AS	2.86 ± 0.52	3.00 ± 0.62 ab	3.03 ± 0.39	2.39 ± 0.11	2.64 ± 0.03 ab
	CC	3.33 ± 1.15	2.86 ± 0.14 ab	2.71 ± 0.32	3.23 ± 0.07	2.52 ± 0.05 ab
	CP	2.98 ± 0.82	3.10 ± 0.32 ab	2.72 ± 0.29	3.06 ± 0.66	2.46 ± 0.09 ab
	CS	2.55 ± 0.57	2.86 ± 0.29 ab	2.69 ± 0.13	2.57 ± 0.19	2.81 ± 0.33 ab
	LC	3.67 ± 0.67	3.78 ± 0.64 a	3.06 ± 0.14	3.47 ± 0.57	2.72 ± 0.06 ab
	LP	3.97 ± 0.78	2.61 ± 0.21 ab	2.58 ± 0.44	3.05 ± 0.95	2.70 ± 0.04 ab
	LS	3.19 ± 0.57	3.19 ± 0.56 ab	3.09 ± 0.43	2.67 ± 0.72	2.42 ± 0.13 ab
Wet	AC	2.20 ± 0.06	2.61 ± 0.35 ab	2.24 ± 0.34	2.71 ± 0.67	3.12 ± 0.64 a
	AP	2.29 ± 0.17	2.37 ± 0.24 b	2.50 ± 0.71	2.87 ± 0.22	3.12 ± 0.19 a
	AS	2.28 ± 0.18	2.46 ± 0.30 ab	2.93 ± 0.57	2.24 ± 0.24	2.74 ± 0.44 ab
	CC	2.09 ± 0.06	2.67 ± 0.67 ab	2.74 ± 0.83	2.72 ± 0.29	3.18 ± 0.43 a
	CP	2.12 ± 0.06	3.36 ± 0.52 ab	2.96 ± 0.45	2.43 ± 0.09	2.93 ± 0.20 ab
	CS	2.23 ± 0.23	2.47 ± 0.16 ab	2.82 ± 0.16	2.45 ± 0.18	2.41 ± 0.18 ab
	LC	2.06 ± 0.15	2.57 ± 0.28 ab	3.04 ± 0.89	3.33 ± 0.41	2.71 ± 0.08 a
	LP	2.28 ± 0.28	2.58 ± 0.08 ab	2.61 ± 0.33	3.19 ± 0.08	2.78 ± 0.29 ab
	LS	2.47 ± 0.14	2.77 ± 0.69 ab	3.05 ± 1.08	2.53 ± 0.39	3.23 ± 0.47 ab

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