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Nematode diversity, abundance and community structure 50 years after the formation of the volcanic island of Surtsey

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Abstract

The soil nematode fauna can give important insights into soil development and other habitat changes that occur during primary succession. We investigated the generic composition, density, distribution and community structure of nematodes 50 years after the formation of a pristine volcanic island, Surtsey, Iceland. Part of the island has received additional nutrient inputs from seagulls breeding there since 1985, while the reminder has been much less affected and is at present found at a different successional sere. In total, 25 genera of nematodes were identified, of which 14 were reported on Surtsey for the first time. Nematode communities were more diverse in the more infertile area outside the gull colony, where 24 genera were found, compared to 18 inside. The trophic structure of the nematode communities showed relatively higher abundance of fungal feeders in the infertile areas, but relatively more bacterial- and plant-feeders inside the colony. Nematode abundance in surface soil was, however, significantly higher within the gull colony, with 16.7 ind. cm^{-2} compared to 3.6 ind. cm^{-2} outside. A multivariate analysis indicated that the nematode abundance and distribution on Surtsey were most strongly related to the soil C : N ratio, soil acidity, plant cover and biomass, soil temperature and soil depth.

1 Introduction

Soil invertebrates are a key group to study during the initial steps of colonization, primary succession and soil formation in an ecosystem (Walker and del Moral, 2003). One of the most important groups of soil invertebrates are the soil nematodes. They play an important role in the processes of decomposition and mineralization and, thus, they contribute notably to the nutrient turnover in the soil (Freckman, 1988; de Goede and Bongers, 1994). In general, nematode communities are highly abundant in numbers and species. They occupy different feeding habits (trophic levels) and show different responses to the soil physical- (temperature, moisture, etc.), chemical- (acidity, etc.) and vegetation-characteristics (Yeates et al., 1993; de Goede and Bongers, 1994).

Nematode communities have been studied during the primary succession of different substrate types, including sand dunes (Wasilewska, 1970, 1979; de Goede et al., 1993; Wall et al., 2002), mined lands (Dunger et al., 2004), in front of retreating glaciers (Doblas-Miranda et al., 2008; Ilieva-Makulec and Gryziak, 2009) and on pristine volcanic islands (Suatmadji et al., 1988). These studies have shown that the population density, community and trophic structure of nematodes can provide valuable insights into the changes in the soil environment and soil development during primary succession.

The island of Surtsey was formed in a volcanic eruption south of Iceland between 1963 and 1967. Since its formation, the island has been strictly protected for scientific research and for 50 years it has been visited annually by scientists interested in plant and faunal primary succession (Fridriksson, 1965, 1992; Frederiksen et al., 2001; Magnússon et al., 2014).

Studies on nematodes in Surtsey are relatively scarce despite their importance to primary succession, but still there are enough studies to coarsely follow how nematode communities have established on the island. The first report on nematodes from Surtsey dates from 1970. The first species found there was the bacterial feeder *Acrobeloides nanus*, but until 1972 the only other nematodes obtained from soil samples from Surtsey belonged to the genus *Ditylenchus* (Holmberg and Pejler, 1972; Sohlenius, 1972). The next study on the microfauna of the Surtsey soil was performed in 1976 and the only nematodes reported belonged to the genus *Monhystera* (Hedin, 1978). These results showed that the nematode colonization on Surtsey developed very slowly during the first decade of the island's formation.

The rate of primary succession of vascular plants on a confined part of Surtsey was significantly enhanced in the late 1980s as a result of seagull nesting, which started in 1985 (del Moral and Magnusson, 2014). Within the seagull colony, the level of soil nitrogen (N) increased, leading to higher vegetation cover and growth of several new vascular plant species (Fridriksson, 1992). Enhanced organic matter (OM) inputs into the soil within the colony led to enhanced soil development (Sigurdsson and Magnusson, 2010; Leblans et al., 2014) and increased the abundance of microorganisms (Frederiksen et al., 2000; Marteinsson et al., 2014), which are known to serve as food for bacterial- and fungal-feeding nematodes.

In 1995, almost 20 years after the initial studies on nematodes in Surtsey, Frederiksen et al. (2001) investigated the state of nematode succession. They reported 16 nematode taxa and compared the abundance and taxon diversity in plots with different vegetation types. They also pointed out the role of seagull colonies on Surtsey as a factor which indirectly influenced nematode communities.

The aim of our study was (i) to find out how abundant, diverse and complex nematode communities are 50 years after the formation of the island, (ii) to compare the nematode community parameters in permanent survey plots located within and outside the seagull colony; and (iii) to relate nematode community structure and abundance to environmental variables measured in the permanent study plots.

2 Materials and methods

2.1 Sampling sites and environmental conditions

The sampling of nematodes in Surtsey took place on 20–21 July 2012, adjacent to each of the 25 permanent sample plots which were distributed with respect to the substrate type and the influence of seagulls (Fig. 1). The average breeding density of seagulls within the colony was 3.7 pairs per 1000 m^2, while it was zero outside the colony (Table 1). The seagulls have had a major impact on the soil development within their colony; in 2008, the soil pH was 14 % lower and the soil carbon:nitrogen ratio (C : N ratio) was 70 % higher there than outside (Table 1; Sigurdsson and Magnusson, 2010). The average N addition rate within the seagull colony has been 47 kg N ha^{-1} y^{-1} since the seagull colonisation, while it has only been 0.7 kg N ha^{-1} y^{-1} outside the colony

(Leblans et al., 2014). This has greatly influenced the vegetation succession; the average aboveground vascular plant biomass was ten times higher within the seagull colony than in the plots outside it and vascular plant species composition has become completely different (Table 1; Magnússon et al., 2014).

2.2 Further auxiliary measurements in 2012

Measurements of the ecosystem respiration and gross photosynthetic rate (Re and GPP, μmol CO_2 m^{-2} s^{-1}), the plant surface cover (%), the soil temperature (°C) and volumetric water content (%) were performed during the sample days in 2012 as described by Sigurdsson and Magnusson (2010) and Marteinsson et al. (2014). The summer of 2012 was exceptionally dry in S-Iceland, and within the seagull colony the soil water content was 60 % lower than in the sparsely vegetated soils outside the colony (Table 1), and the Re and GPP values were lower than reported in earlier years (Sigurdsson and Magnusson, 2010; Marteinsson et al., 2014).

2.3 Nematode sampling

Samples were collected according to the generally accepted procedures for nematode sampling. Two soil cores (labeled A and B) were taken adjacent to each of the 25 permanent plots down to a depth of 20 cm. The cores were split into two layers: topsoil (0–10 cm) and subsoil (10–20 cm), where the soil depth allowed; i.e. 4 samples were processed from each permanent plot. The samples were kept in a cooler until extracted by modified Baermann method (Flegg and Hooper, 1970), at the soil lab at Möðruvellir, N-Iceland. The extracted nematodes were preserved in 4 % formaldehyde and then shipped to Poland where they were identified to genus level. In each sample, all nematodes were identified. Only in three samples, where more than 100 individuals were found, a representative subsample of 100 nematodes was identified. For the nematode identification the keys of Andrássy (1976, 1981, 1983), Bongers (1988), Goodey

(1963) and Maggenti et al. (1987) were used. Classification into trophic groups was done according to Yeates et al. (1993).

2.4 Data processing

In order to analyse the nematode communities, we chose the following parameters and indices: (i) total nematode abundance, (ii) the relative abundance of nematode trophic groups, (iii) generic richness, (iv) Shannon–Wiener index of diversity (Southwood, 1978); (v) the index of similarity according to Sørensen (Southwood et al., 2000); and (vi) Maturity index, an index based on nematode's life history parameters and ecological requirements, which can be used in assessing the stage of nematode succession (Bongers, 1990). In addition, three functional indices of nematode communities were calculated: (vii) Enrichment Index (EI), (viii) Structure Index (SI) and (ix) Channel Index (CI); (Ferris et al., 2001). EI takes into account the relative abundance of bacterial- and fungal-feeding nematodes, which have short life cycles. When food resources increase, these nematodes (especially bacterial feeders) respond quickly, reaching high population densities, albeit very often for a short period. Thus, high EI values indicate a resource-rich environment. SI takes into account nematodes with longer life cycles and more stable population dynamics, which are located on higher trophic levels (omnivores and predators). CI indicates the predominant OM decomposition pathway in the soil (Ferris et al., 2001), i.e. whether it is dominated by fungi or bacteria.

2.5 Statistical analyses

An analysis of variance (ANOVA) was applied to test the effect of plot type (inside and outside the seagull colony) and soil layer (topsoil and subsoil) on nematode abundance (total and for trophic groups). The significance ($P < 0.05$) of the differences between the mean values of the studied parameters was estimated with the non-parametric Mann–Whitney test (Sokal and Rohlf, 1981). Canonical correspondence analysis (CCA) was performed to relate the generic composition and abundance of the nematode communities to the soil physicochemical and vegetation characteristics of plots located inside and outside the gull colony (CANOCO programme (ter Braak, 1986). A Monte Carlo permutation test was applied to determine the significance of the first axis and for the overall test.

3 Results

3.1 Nematode density

The average nematode density in the 0–10 cm soil layer inside the gull colony was 16.7 ± 7.1 ind. cm^{-2} (Fig. 2). This was significantly higher ($P < 0.05$) than the abundance of nematodes outside the seagull colony, where only 3.6 ± 2.0 ind. cm^{-2} were found. Within the colony, the nematode density was 58 % lower in the subsoil than in the upper soil layer, while outside it the density of nematodes increased with depth and was 97 % higher in the subsoil (Fig. 2). In the subsoil, the density of nematodes did not differ significantly between plots inside and outside the seagull colony (Fig. 2).

3.2 Nematode generic richness

In total, 25 genera of nematodes were found in the soil on Surtsey (Table 2), 14 genera of which had not been recorded previously (Table 3). The generic richness was higher outside than inside the seagull colony; 24 and 18 genera, respectively (Tables 2, 3). The total number of genera found in plots inside the gull colony was higher in the surface layer, while in plots outside the colony more genera were recorded in the subsoil. In both habitat types a similar number of genera was found in the surface layer, while in the subsoil more genera were found outside the gull colony (Table 2). The number of nematode genera per sample was, however, highly variable within both habitats (Table 2; ranges). The lowest number of genera per sample was found in the surface

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layer in plots outside gull colonies, while the highest number was found in the subsoil layer in the same habitat.

3.3 Nematode diversity and dominance structure

Nematode generic diversity differed between the two habitats (Table 2). Shannon Diversity index H' was both the highest (subsoil) and the lowest (topsoil) outside the seagull colony, while it was intermediate for both layers inside the seagull colony (Table 2). The Sørensen's Index of similarity was lower within the seagull colony than outside, or 67 % compared to 74 %, respectively (Table 2). Moreover an index of similarity of 65 % was found between the two habitats, across both soil layers.

The frequency of occurrence was quite low for most nematode genera. Most occurred in less than 20 % of the samples (Table 3). Nematodes from the genera *Tylenchorhynchus, Cephalobus, Anaplectus*, and *Panagrolaimus* were among the most frequently recorded inside the colony (Table 3). The first two genera were also very frequent in the plots outside, where the genera *Aphelenchoides* and *Acrobeloides* also occurred with a high frequency (Table 3).

The structure of dominance of nematode genera within the seagull colony, where no subdominants were found, seemed sharper than in plots outside the colony (Table 3). Most abundant (eudominants) in the plots inside the gull colony were two bacterial feeding genera *Panagrolaimus* and *Rhabditis* and one plant feeder *Tylenchorhynchus*, while in plots outside the eudominants were the bacterial feeder *Cephalobus*, the fungal feeder *Aphelenchoides* and the plant feeder *Tylenchorhynchus* (Table 3).

3.4 Nematode trophic structure

The nematodes found on Surtsey were further classified into four trophic groups (Fig. 3). The trophic structure of nematode differed significantly between the two habitats, with a relatively higher abundance of omnivores and bacterial feeders and plant feeders within the seagull colony and a relatively higher share of fungal feeders and more omnivores outside the seagull colony (Fig. 3). The trophic structure also differed distinctly between the two soil layers in both habitats; in the topsoil of the seagull colony there were relatively more bacterial feeders and omnivorous nematodes, while in the subsoil, more plant feeders occurred. In plots outside the gull colony an extremely high percentage of fungal feeders was noted in the topsoil, while the abundance of bacterial feeders and omnivores increased relatively in the subsoil (Fig. 3; Table 3).

3.5 Nematode ecological indices

The mean values of the Maturity Index (MI) were quite low and similar for the two habitats (around 2 for both; Table 2). MI was, however, more variable in plots within the gull colony, where it ranged between 1.1 (plots 1A, 7A) and 4.1 (plot 4A). Outside the gull colony, the MI was ca. 2.0 in most plots, but the lowest MI value (1.0) for the island was found there in plot 29A and among the highest values (4.0) in plots 21A and 31B. In both soil layers the Enrichment Index (EI) was higher within the seagull colony, while the Channel Index was distinctly higher outside the seagull colony (Table 2). The Structure Index (SI) was significantly higher for the upper layer the within the seagull colony, while SI was higher in the subsoil in plots outside of the colony (Table 2).

3.6 Environmental factors and nematode abundance and distribution

Two permanent plots outside the seagull colony, 31 and 32, had to be excluded from this analysis because not all environmental parameters were available for them. The results from the Canonical Correspondence Analysis (CCA) showed that eigenvalues were 0.773 ($p = 0.01$) and 0.557 for the first and second axes, respectively, and the two first axes explained 22.9 % of the variation in genera data and 40.3 % of the total genera-environment variation (Table 4). As can be seen in Fig. 4, the CCA ordination differentiated well between the plots of the two habitats (plots 1–10 and 23 being inside the gull colony and plots 11–30 being outside the gull colony).

The position of genera which were not concentrated in the center of the diagram indicated relationships with the environmental variables (Fig. 4). The strongest relationships ($p < 0.05$) between the environmental variables and the abundance and distribution of nematode genera to the 1st CCA axis were: (i) plant surface cover ($F = 3.57$; $p = 0.01$), (ii) aboveground plant biomass ($F = 3.35$; $p = 0.01$), (iii) soil pH ($F = 2.46$, $p = 0.01$), (iv) C : N ratio ($F = 2.43$, $p = 0.01$), (v) soil depth ($F = 1.99$, $p = 0.02$) and soil temperature ($F = 1.97$, $p = 0.05$). Higher July soil temperatures and higher pH were most strongly associated with the abundance and distribution of nematode genera outside the seagull colony, while higher C : N ratios, plant cover and biomass were associated with these variables within the colony. Higher soil (or loose mineral substrate) depth was, however, associated within nematode community assemblage on plots both inside and outside the seagull colony (e.g. plots 3, 12, 17 and 20), indicating that it was an important controlling factor for nematode community structure, irrespective of vascular plant successional stage.

4 Discussion

4.1 Nematode generic diversity

The first aim of our study was to determine how abundant and diverse the nematode communities from Surtsey were 50 years after the island's formation. We found that during this period nematode communities have indeed become more numerous and more diverse in the soil of Surtsey. The number of nematode genera has steadily increased from one taxon in 1970 to 25 taxa in 2012 (Fig. 5). Such an increasing trend of nematode diversity concurs with findings in other studies of primary succession (de Goede et al., 1993; Wall et al., 2002).

The relative increase in nematode generic diversity during the initial 50 years was similar to the increase which has been observed in vascular plant species richness on Surtsey during the same period (Magnússon et al., 2014). Similar patterns in soil invertebrate communities and plant communities have been reported before, e.g. in a study on primary succession following glacial retreats (Doblas-Miranda et al., 2008).

The number of taxa and the abundance of nematodes we found on Surtsey is still low, and well below the normal lower ranges of species diversity (74 species) and density ($0.6 \times 10^6\,\mathrm{m}^{-2}$) for nematodes in grasslands (Wasilewska, 1979). No comparable studies exist from mainland Iceland, but higher generic diversity and densities have generally been found in other high-latitude ecosystems (Kuzmin, 1976; Doblas-Miranda et al., 2008). We would, however, like to draw attention to a certain similarity between nematode primary succession on Surtsey and the course of nematode colonization following climate-induced glacial retreats of Antarctic glaciers (Ilieva-Makulec and Gryziak, 2009). There, only 16 genera of nematodes were found on the oldest sites, more than 50 years after glacier retreat.

Our results showed that even if the number of nematode taxa has increased, their distribution was still patchy and their abundance highly variable within the island. There were some samples where no nematodes were found and in this respect our data was in agreement with the earlier results of Frederiksen (2001) from Surtsey. It seems, therefore, that the development of nematode communities is still in its early phase. This is in sharp contrast to the findings of e.g. Wasilewska (1970), who found that nematode generic diversity can reach stable numbers after the first decade of primary succession of sand dunes in Poland. The values of the maturity index (MI) of the nematode community in both types of habitats (with and without influence of gulls) were low and still similar to the values calculated for Surtsey by Frederiksen (2001) and also to values found in the 50 year old glacial retreat areas on Antarctica (Ilieva-Makulec and Gryziak, 2009). Such values of MI indicate a weak organisation and low maturity of nematode communities in Surtsey.

4.2 The effect of the seagulls on nematode abundance and diversity

The nematode colonization on Surtsey accelerated significantly after the gulls established their colony on the island in 1985, as shown by Frederiksen et al. (2001). The present study confirmed this finding. The nesting activity of the gulls, through enhanced seed dispersal, disturbance, and not least enhanced nutrient transport from sea to land, increased the habitat heterogeneity on the island. The seagulls increased significantly the soil fertility and organic matter contents (Leblans et al., 2014), vegetation cover and biomass (Magnússon et al., 2014), soil bacteria (Marteinsson et al., 2014) and ecosystem respiration activity (Sigurdsson and Magnusson, 2010) of the area within the seagull colony. This habitat became suitable for new nematode colonization and development. Among the dominant nematode genera found there were *Panagrolaimus* and *Rhabditis*, both of which are enrichment opportunists according to Bongers (1999), with short life cycles and large food resource requirements. They were most strongly associated with those permanent plots which had the highest densities of gull nests, as well as the highest plant biomass and soil C values. Sohlenius (1988) also found two species of *Panagrolaumus* in bird nest from Surtsey. Outside the seagull colony, nematodes from *Cephalobus* and *Acrobeloides* dominated, but they are habitat generalists with longer life cycles and lower food requirements (Bongers, 1999; Ilieva-Makulec, 2001a, b).

It is worth emphasizing that the nematode generic diversity within the seagull colony has decreased to some extent when compared to the more infertile areas outside the colony, even if the nematode abundance showed the opposite. A decrease in the taxonomic diversity of nematodes with higher successional stage has been related to a retrogressive (decline) phase due to reduced nutrient availability over time (Doblas-Miranda et al., 2008). However, the nutrient availability on Surtsey was clearly much higher inside the seagull colony than outside it (Leblans et al., 2014). Such shifts in nematode taxonomic diversity have also been related to corresponding changes in plant diversity (de Goede et al., 1993), but the plant diversity on Sutsey was also higher inside the gull colony than outside it (Magnússon et al., 2014). Therefore, it seems plausible that the more abundant nematode populations within the seagull colony have induced competitive exclusion of some genera (Ettema, 1998).

We also found a strong relationship between the abundance of nematodes and the occurrence of certain plant species. Outside the gull colony, the highest nematode density was noticed in plots where the plant species *Honckenya pebloides* dominated, while inside the colony more numerous nematodes populations were found in plots where *Poa pratenses* was present. The quality of the plant litter is likely to play an important role in the nematode plant preferences. According to the research of Ilieva-Makulec et al. (2006), nematode density and diversity are well correlated with the quality of plant litter. In their study the highest density but the lowest nematode diversity was found in litter with the lowest C : N ratio.

It appeared that Shannon Index of diversity, traditionally used to assess the community diversity, was not very helpful in the present study. This is most likely due to the fact that most nematode genera found in the soil of Surtsey were rare and in low densities (subrecedents), which led to low sensitivity of the index. We found that multivariate analysis (CANOCO) was better in relating the generic composition and abundance of the nematode communities to the soil and vegetation characteristics of plots located inside and outside the gull colony.

We also found that food-web indices based on nematode faunal analysis (Ferris et al., 2001) were a more appropriate tool than Shannon Index of diversity to assess and compare the conditions in the habitats within and outside the seagull colony. The higher values of EI within the gull colony indicated an environment rich in resources, which offered substrates of low C : N ratio where nematodes (mainly bacterial feeders from *Rhabditis* and *Panagrolaimus*) had responded with increase in their population densities. The values of CI indicated contrasting ways of organic matter decomposition in the two habitats. Across all gull-influenced plots the bacterial energy channel was predominant over the fungal, while in all plots outside the colony the fungal channel predominated over the bacterial. The results of Marteinsson et al. (2014) on bacterial counts in surface soils from inside and outside the seagull colony partly support this finding.

4.3 Comparison to Krakatau

It is interesting to compare the status of the nematode fauna on Surtsey after 50 years with the nematode diversity and trophic structure on the volcanic islands of Krakatau archipelago, Indonesia, ca. 100 years after their formation (Suatmadji et al.,1988). The higher number of nematode genera on Krakatau (77) in comparison to Surtsey (25) could partly be the result of the longer duration of nematode succession there and a larger island size (cf. MacArthur and Wilson, 1967). Direct comparison between these two locations is, however, difficult due to the differences in geographic, climatic, and edaphic factors, which are bound to impact the number of potential genera that could colonize. Nonetheless, it was noteworthy that most nematode genera found on Krakatao were microbivorous, mainly different genera of Cephalobidae, which were the pioneer colonizers there (Suatmadji et al., 1988). Similar predominance of the microbivorous *Cephalobus* and *Acrobeloides* genera was found in the infertile habitats outside the seabird colony on Surtsey. Dorylaimids (mainly omnivores) were found to be the second dominant group on Krakatao, while on Surtsey omnivores were less dominant. On Surtsey, on the other hand, we found two additional feeding groups that had a large share in the community; fungal feeders (mainly outside the colony) and plant feeders (in both habitats, but especially inside the gull colony). Hence, the foodweb structure of the nematode communities of Surtsey seemed to be more diverse than on Krakatao, even if the number of genera was lower there.

4.4 Successional trends in the nematode community

Over the course of the 50 years since the island's formation, the community trophic structure of nematodes on Surtsey has become more complex. Initially only nematodes feeding on bacteria and algae (bacterial feeders and omnivores) were recorded on the island (Sohlenius, 1972, 1974; Hedin, 1978; Frederiksen et al., 2001). In the present study a significant share of nematodes feeding on fungi (fungal feeders) and vascular plants were recorded. The absence of plant feeders in the earlier study of

Frederiksen et al. (2001), even within then recently established seagull colony, may be partly explained by the fact that they only took samples from the upper 5 cm of soil, but the plant feeders were more abundant in the subsoil in the present study. Nevertheless, there were clear trends for more complex soil food-webs had developed in the present study, even in the sparsely vegetated areas outside the seagull colony (see later).

When compared across the whole island, the changes in nematode trophic structure have followed the vegetation succession. Within the seagull colony, the increased plant diversity and biomass (Magnússon et al., 2014) has on the one hand increased the pool of potential hosts (root systems) for plant feeding nematodes (obligatory plant parasites) and on the other hand provided larger resources of dead OM for bacterial feeding nematodes. Outside the seagull colony, where less changes have occurred in aboveground plant cover and biomass (Magnússon et al., 2014), increased root exploration (Stefansdottir et al., 2014) has clearly resulted in increasing populations of soil fungi, which may serve as food for the fungal feeders there. In total, 33 soil fungal species have been recorded on Surtsey (Henriksson and Henriksson, 1974; Eyjolfsdottir, 2009), mostly based on fruitbody surveys. An interesting extension of the present work would be to further study the occurrence and growth of soil fungi on Surtsey, since it clearly plays an important role in the island's food web, especially in the more infertile areas.

We also found that the changes which had occurred at the lower trophic levels (the level of microbial feeders) were reflected at higher trophic levels. For example the two dominant nematode genera among omnivores showed different habitat preferences on Surtsey. Nematodes from the genus *Aporcelaimellus* preferred topsoil within the seagull colony, while *Eudorylaimus* preferred subsoil of plots outside the colony. The higher relative abundance of *Aporcelaimellus* could be related to a high abundance of bacterial feeders there; which may have caused diet shift in *Aporcelaimellus*, and nematodes from this genus start behaving as predators (Bongers, 1999).

It is still an open question why until now no typical predators from Mononchida have been noticed on Surtsey. The presence of mononchids has, however, often been related to the occurrence of mosses (Suatmadji et al., 1988; Ilieva-Makulec and Gryziak, 2009), but mosses are mostly confined to relatively small sheltered areas on Surtsey (Magnússon et al., 2014).

5 Conclusions

The present study showed that even if only minor changes have been observed in vegetation composition and cover during the past two decades in the infertile areas outside the gull colony, the soil nematode communities have continued to change and the number of taxa to increase, probably indicating gradual changes in the soil environment. Within the seagull colony, where vegetation succession and soil development has been greatly accelerated, the nematode communities have increased in population density and now show more complex foodwebs, but still they have become less diverse with fewer taxa than found outside. This finding was rather unexpected, partly because of the low Maturity Index values obtained in both habitats. It will therefore be interesting to follow the nematode succession further into the future; on one hand it may seem likely that the number of nematode taxa may start to decrease when the infertile *Leymus-Honckenya* plant community will gradually change into more fertile grasslands, but on the other hand more time may still be needed for nematode taxa from higher trophic levels to reach the island, which may reverse the declining diversity trend seen at present in the more fertile areas.

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Table 1. Characteristics (mean values ± s.e.) of permanent plots inside and outside the gull colony in Surtsey 2012. Data modified from different sources (see footnotes).

Characteristic	Inside	Outside
Soil depth (cm)[a]	19.8 ± 3.9	49.1 ± 7.1
Ecosystem respiration (Re; µmol m^{-2} s^{-1})[b]	0.6 ± 0.2	0.2 ± 0.04
Gross Photosynthesis (GPP; µmol m^{-2} s^{-1})[b]	−0.4 ± 0.1	−0.3 ± 0.1
Soil volumetric water content (0–5 cm; %)[b]	0.9 ± 0.2	2.3 ± 0.3
Soil temperature (0–10 cm; °C)[b]	19.2 ± 0.5	25 ± 0.5
Plant surface cover (%)[b]	88.6 ± 2.6	13.3 ± 3.1
Aboveground biomass (g m^{-2})[c]	311.6 ± 60.8	31.3 ± 10.0
Breeding density (nests 1000 m^{-2})[c]	3.7 ± 0.6	0
pH (2008)[c]	7.09 ± 0.1	8.24 ± 0.1
C : N ratio (2008)[d]	11.7 ± 0.5	6.88 ± 0.5
Dominant plant species[c] (year of first colonization in the brackets)	*Poa pratensis* (1975), *Festuca richardsonii* (1973), *Leymus arinarius* (1966), *Honkenia pebloides* (1967), *Rumex longifolius* (1996), *Puccinelia distans* (1972) *Empetrum nigrum* (1993)	*Honkenia pebloides* (1967), *Leymus arinarius* (1966), *Armeria uniflora* (1986), *Sagina procumbens* (1986)

[a] Leblans et al. (2014)
[b] cf. Marteinsson et al. (2014)
[c] Magnússon et al. (2014)
[d] Sigurdsson and Magnusson (2010)

Table 2. Diversity, similarity and functional indices (mean values ± SE) of nematode communities inside and outside of seagull colony in the permanent study plots in Surtsey in 2012.

Parameter	Inside		Outside	
	0–10 cm	10–20 cm	0–10 cm	10–20 cm
Number of genera per sample	4 (0–6)	4 (0–7)	2 (0–3)	5 (0–10)
Total number of genera	16	11	15	23
Shannon Diversity index H’	0.85 ± 0.2	0.85 ± 0.1	0.45 ± 0.1	1.44 ± 0.2
Sørensen’s Index of similarity (%)[a]	67		74	
Maturity Index (MI)[b]	2.28 ± 0.3	1.8 ± 0.4	2.11 ± 0.2	1.9 ± 0.2
Enrichment Index (%)[c]	48.3 ± 13.3	59.5 ± 22.3	33.8 ± 8.5	54.2 ± 11.6
Structure Index (%)[c]	49.8 ± 11.7	26.3 ± 17.9	10.4 ± 7.1	35.4 ± 9.6
Channel Index (%)[c]	45.7 ± 17.2	1.5 ± 1.5	60 ± 16.3	31.4 ± 14.9

[a] According to Southwood et al. (2000).

[b] According to Bongers (1990).

[c] Accoding to Ferris et al. (2001).

Table 3. Nematode generic composition adjacent to the permanent study plots in Surtsey in 2012. The frequency (% of samples in which each genus occurred), dominant status, relative occurrence in topsoil (0–10 cm), feeding habits (trophic group) and c-p value of each genus occurring in samples outside (32 samples) and inside (16 samples) the seagull colony.

Genus	Outside the colony			Inside the colony			Trophic	c-p
	Freq.	Domin.[a]	Top soil	Freq.	Domin.	Top soil	group	value[b]
Originally found before this study								
Acrobeloides	31 %	D	26 %	6 %	SR	0 %	Bacterial feeder	2
Mesorhabditis	3 %	SR	100 %	0	–	–	Bacterial feeder	1
Rhabditis	16 %	SD	31 %	19 %	ED	96 %	Bacterial feeder	1
Panagrolaimus	16 %	D	33 %	38 %	ED	90 %	Bacterial feeder	1
Prothorhabditis	13 %	D	27 %	0	–	–	Bacterial feeder	1
Plectus	13 %	SD	47 %	6 %	SR	0 %	Bacterial feeder	2
Eumonhystera	3 %	SR	0 %	6 %	SR	100 %	Bacterial feeder	1
Prismatolaimus	3 %	SR	0 %	13 %	SR	100 %	Bacterial feeder	3
Ditylenchus	3 %	SR	0 %	19 %	R	67 %	Hyphal feeder	2
Aporcelaimellus	3 %	SR	0 %	25 %	D	98 %	Omniv./Predator	5
Aphelenchoides	34 %	ED	85 %	19 %	SR	100 %	Hyphal feeder	2
New genera, both outside and inside seagull colony:								
Anaplectus	13 %	SD	17 %	56 %	D	82 %	Bacterial feeder	2
Cephalobus	47 %	ED	35 %	44 %	D	96 %	Bacterial feeder	2
Chiloplacus	13 %	R	83 %	13 %	R	75 %	Bacterial feeder	2
Seleborca	6 %	R	0 %	6 %	SR	100 %	Bacterial feeder	2
Epidorylaimus	6 %	SR	50 %	13 %	SR	100 %	Omnivorous	4
Eudorylaimus	16 %	SD	5 %	31 %	R	86 %	Omnivorous	4
Geocenamus	22 %	SD	46 %	6 %	SR	100 %	Plant feeder	3
Tylenchorhynchus	38 %	ED	30 %	50 %	ED	62 %	Plant feeder	3
New genera, found either outside or inside colony:								
Pungentus	9 %	SR	35 %	0	–	–	Omnivorous	4
Acrobeles	3 %	SR	0 %	0	–	–	Bacterial feeder	2
Cervidellus	3 %	SR	0 %	0	–	–	Bacterial feeder	2
Tylocephalus	3 %	SR	0 %	0	–	–	Bacterial feeder	2
Thonus	3 %	SR	0 %	0	–	–	Omnivorous	4
Criconematidae	0	–	–	6 %	SR	100 %	Plant feeder	3

[a] Dominance classes (Domin.): relative abundance < 1 = subrecedent (SR); 1.1–2 = recedent (R); 2.1–5 = subdominant (SD); 5.1–10 = dominant (D); > 10.1 = eudominant (ED).

[b] According to Bongers (1990).

Table 4. The results of Canonical Correspondence analysis (CCA) on nematode abundance and distribution in relation to environmental characteristics of the permanent surveyed plots on Surtsey. For more information see Table 1.

Axes	1	2	3	4
Eigenvalues	0.773	0.557	0.469	0.335
Species-environment correlations	0.980	0.951	0.915	0.925
Cumulative percentage variance:	12.8	22.9	31.4	37.5
of species data	22.6	40.3	55.4	66.3
of species–environment relation				
Sum of all unconstrained eigenvalues		5.511		
Sum of all canonical eigenvalues		3.112		
Summary of Monte Carlo test:		F ratio = 2.92, $P = 0.01$		
test of significance of first canonical axis				
overall test		F ratio = 1.3, $P = 0.01$		

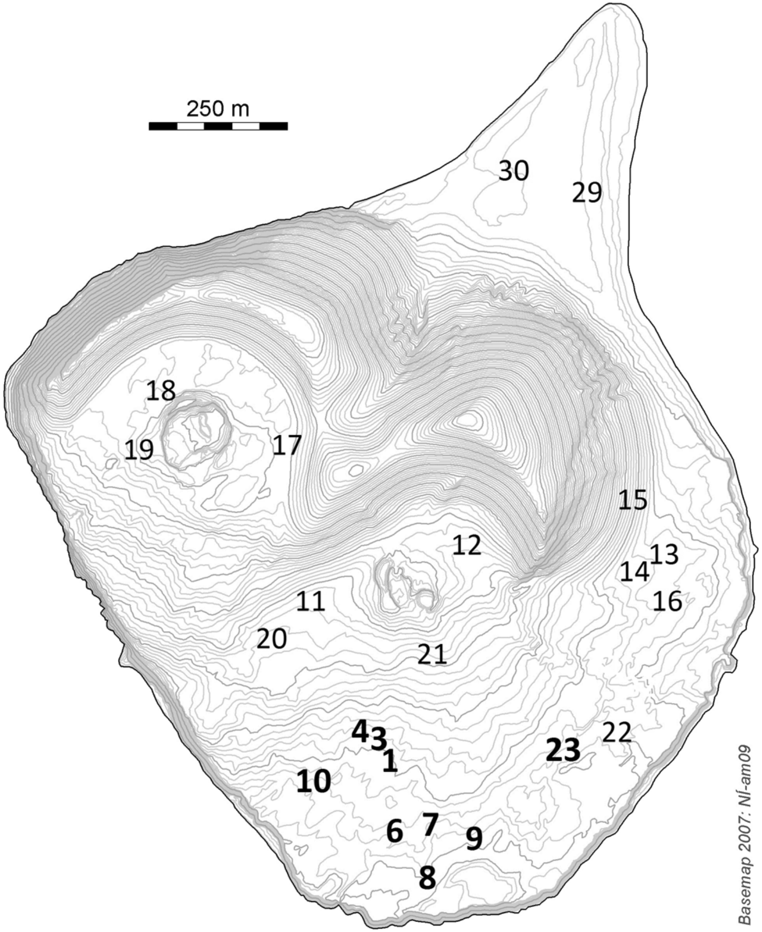

Figure 1. Location of the 25 permanent study plots on Surtsey. The plots were classified as being within a seagull colony (bold font) or outside it (normal font).

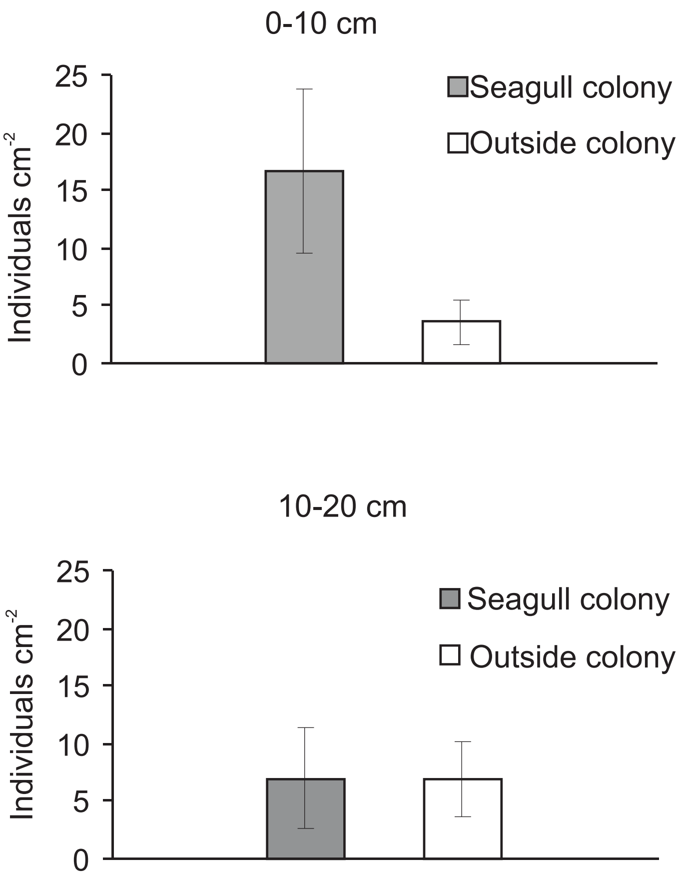

Figure 2. Nematode density in topsoil (0–10 cm) and subsoil (10–20 cm) in permanent study plots located inside and outside the seagull colony on Surtsey.

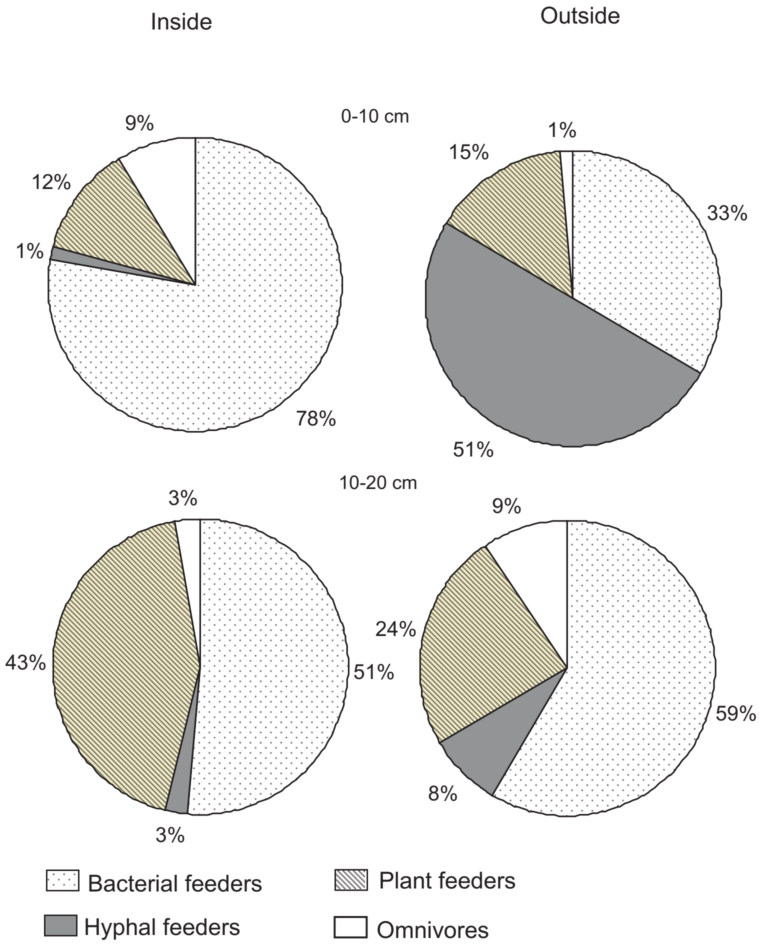

Figure 3. Trophic structure of nematode communities in topsoil (0–10 cm) and subsoil (10–20 cm) in permanent study plots located inside and outside seagull colony on Surtsey.

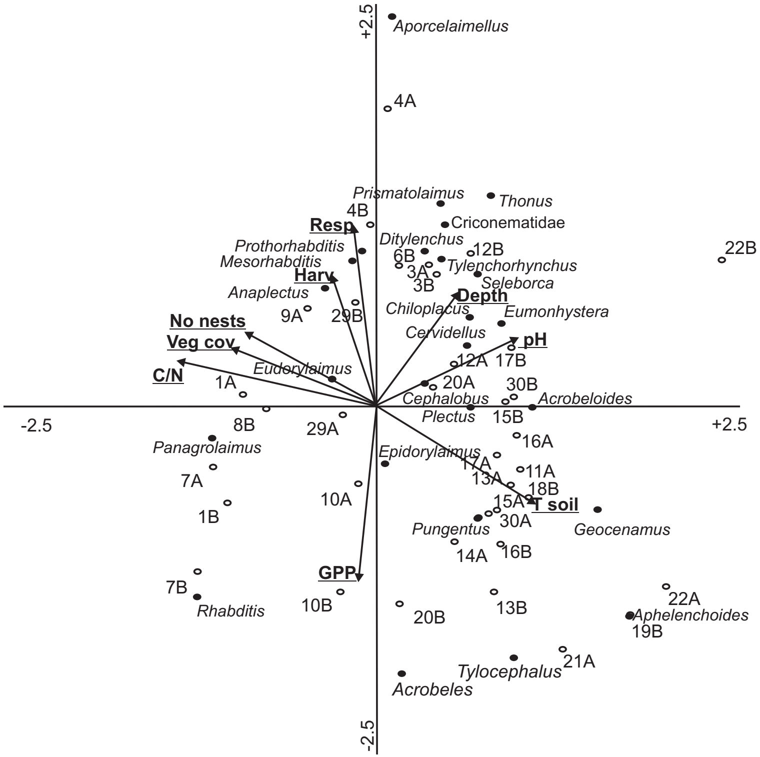

Figure 4. Plot diagram of nematode fauna on Surtsey in Canonical Correspondence (CCA) ordination. Nematode genera are indicated by black circles, permanent plots by open circles, environment variables by arrows. Plots (1–10 and 23) were located inside the seagull colony and plots (11–32) outside. From each plot two samples (A and B) were taken and total abundance in the 0–20 cm soil layer was used. For more explanation, see the text and Table 1 and Fig. 1 for plot locations.

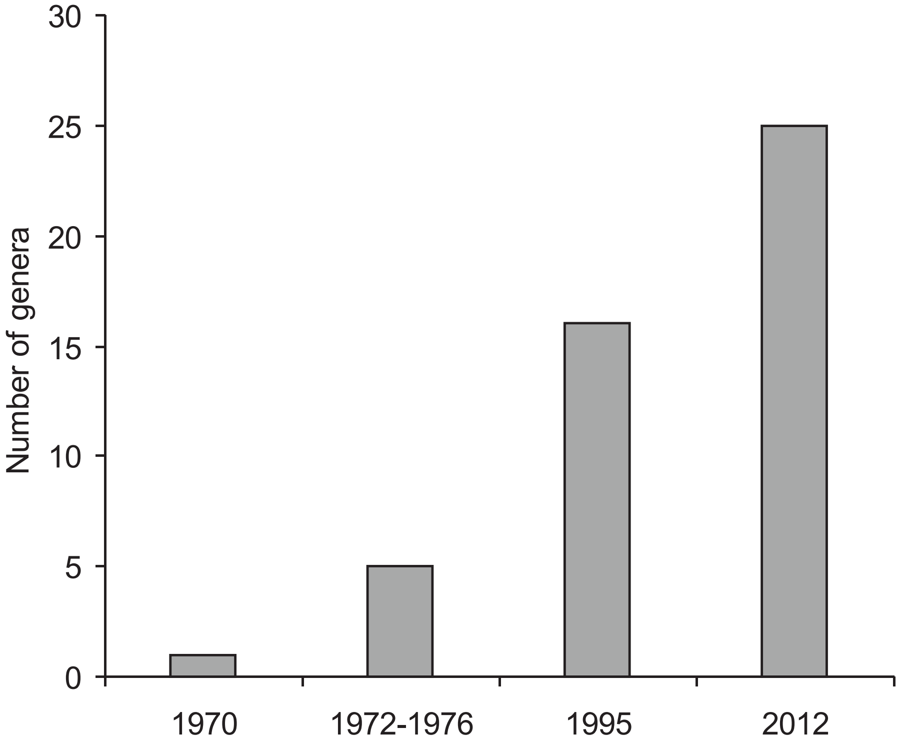

Figure 5. Number of nematode taxa found in different habitats on Surtsey during the period 1970–2012. Data from Sohlenius (1972, 1974), Hedin (1978), Frederiksen et al. (2001) and the present study.