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Abstract

Worldwide human activities threaten soil quality in terms of the soil's ability to deliver ecosystem services. This ongoing process of land degradation asks for effective strategies of soil protection. In this context, it is important to understand processes that build up and regenerate soil.

The present study investigated how the soil ecosystem, including soil organisms, vegetation and soil ecological processes, develops during the process of soil formation in a chronosequence in a glacier forefield in Iceland. We hypothesised that along successional age we see increases in nutrient content, vegetation cover, and plant species richness linked to increases in soil food webs biomass and complexity.

In line with our expectations all measured pools of carbon and nitrogen, and vegetation cover increased with age in the glacial forefield, but plant species richness levelled off after 30 years. Soil organisms generally increased in biomass with successional age, although some of the groups of soil organisms peaked at an intermediate successional stage. In contrast to our expectations, some of the calculated food web complexity metrics such as the number of trophic groups and trophic chain length did not increase linearly, but showed an intermediate peak or even decreased with successional age. However, plant cover and pools of carbon and nitrogen still increased after 120 years. From these results we conclude that soil ecosystem development takes more than a century under Icelandic climatic conditions to fully develop in terms of vegetation succession, food web structure and biogeochemical cycling.

Keywords

Glacial succession, soil food web structure, vegetation development, ecosystem functioning, Iceland

Introduction

Soil is an essential natural resource for life on Earth, and provides important ecosystem services, such as food and fibre production, carbon sequestration and nutrient cycling (Schulte et al., 2015). Given the current threats for soil quality due to human activities it is important that we protect soil, and that we improve our understanding of natural processes that build up and regenerate soil. Studying natural soil ecosystem development is the first step in understanding these processes, and at the same time fundamental for developing ecological theory (Walker et al., 2010). The formation of soil is well-studied from a chemical and physical perspective (Matthews, 1992), but much less from a biological perspective, although it is well-known that soil organisms can play an important role in soil formation (Brown and Jumpponen, 2014).

In the present study we analysed soil development from an ecosystem perspective looking at food web development, vegetation succession and soil ecological processes during soil formation along a retreating glacier. Glaciers are retreating due to the temperature rise of the last decades and provide natural chronosequences in soil formation and weathering (Egli et al., 2001; Milner et al., 2009; Schmalenberger and Noll, 2010; Stevens and Walker, 1970; Vilmundardóttir et al., 2014). Chronosequences are considered to be sequences of soils, developed on similar parent materials and relief under the influence of constant, or ineffectively varying, climate and biotic factors. Differences between these soils can thus potentially be ascribed to the continuous processes during the laps of time since the initiation of soil formation (Huggett, 1998). This reasoning makes glacier forefields good model systems for studying soil formation and the concomitant colonization and succession of above- and belowground organisms (Hämmerli et al., 2007; Ingimarsdóttir et al., 2012; Noll and Wellinger, 2008; Walker et al., 2010). Glacier forefields on islands at high latitude form a special case, as vegetation succession is limited by geographic isolation, low temperatures and low nutrient availability (Hodkinson et al., 2003; Mori et al., 2017).

Plant succession in glacial forefields has been extensively studied (Chapin et al., 1994), but studies linking this to belowground community development are scarce (Hodkinson et al., 2003; Kaufmann, 2001). Even less is known about how soil food webs, i.e. the communities of soil organisms, assemble and develop during soil formation. Soil food web assembly has been studied in chronosequences of primary non-glacial succession in sand dunes and in a

layer of sawdust in an arable field (Neutel et al., 2007; Wardle et al., 1995) and secondary succession in abandoned agricultural fields (Holtkamp et al., 2008; Korthals et al., 2001), but these studies either did not relate soil food webs with the aboveground vegetation or were hampered by a legacy from the previous agricultural land use, thereby focusing on different systems. Of the studies that have been performed on belowground organisms in glacial forefields, most studies focused on microbes, showing that microbial populations increase in biomass and metabolic efficiency with soil age (Hämmerli et al., 2007; Insam and Haselwandter, 1989; Lazzaro et al., 2009; Ohtonen et al., 1999; Rime et al., 2015; Sigler and Zeyer, 2002). Studies that have looked at other organisms than microbes in glacier forefields focused mostly on single clades of organisms, especially (aboveground) microarthropods (Hågvar et al., 2009; Hodkinson et al., 2003; Kaufmann, 2001). Despite these previous studies in glacier forefield chronosequences, we lack an ecosystem perspective of soil formation, in terms of nutrient cycling, vegetation succession and soil food web development.

Understanding soil food web development during the process of soil formation is fundamental for both soil conservation and ecological theory (Neutel et al., 2007). Following the hypotheses initially posed by Odum (1969) (energy efficiency, production, standing biomass, species diversity, organism size, nutrient build-up and conservation, as well as food chain length are hypothesized to increase with succession), the observations on soil food webs done in primary chronosequences in sand dunes by Neutel et al. (2007), and on microbial organisms in glacial forefields by Ohtonen et al. (1999), we expect soil food webs to increase in number of trophic groups and biomass, linked to increases in soil nutrient contents, vegetation cover and plant species richness in the course of time after glacial retreat. Additionally, we expect a succession from bacterial-dominated to fungal-dominated soil communities with age, because bacteria have been shown to faster colonize recently glaciated sites (Rime et al., 2015), whereas older successional stages under presumed low nutrient availability require higher microbial metabolic efficiency, suggesting a fungal dominated community (Ohtonen et al., 1999). To test these hypotheses, we investigated soil food webs in terms of the presence and abundance of microbes (bacteria, fungi) and soil fauna (protozoa and nematodes), representing dominant taxonomic groups and trophic levels in soil communities. From these measurements, various food web metrics were calculated, i.e. mean and maximum trophic level and trophic chain length. To place soil food web assembly in the context of soil ecosystem development and functioning, soils were characterized in terms of

soil pH, carbon (C) and nitrogen (N) pools, mineralisation rates. In addition, plant species cover and composition were measured. The study was carried out in the forefield of the glacier Skaftafellsjökull in Iceland.

Methods

Site description

The proglacial area of Skaftafellsjökull (S, Iceland) is an outlet glacier extending from the Vatnajökull ice cap down south to the lowlands, with an elevation of 90-120 m asl. The climate is cold-temperate oceanic with average annual temperature of 5°C, and a yearly precipitation of 1800 mm (Vilmundardóttir et al., 2014). The outlet glaciers south of Vatnajökull have retreated since 1890 up to 5 km, exposing poorly sorted sediments, while leaving behind moraines resulting from short glacier advances in 1890 (S4), 1945 (S3), 1980 (S2) and 2010 (S1, on the edge of the glacier) (Figure 1; Hannesdóttir et al., 2015; Vilmundardóttir et al., 2014). Samples were taken on top of these moraines, to prevent influences of erosion and sedimentation fluxes by glacial creeks, and for certainty of the age of the soil material. In addition, we sampled a reference site further from the glacier (beyond the furthest reach of the glacial tongue) hosting a natural vegetation (S5). The shrub dominated vegetation in this site is considered fully developed after at least 500 years under the local climatic conditions (temperature, precipitation, wind). The glacial retreat has escalated rapidly over the past decade (averaging about 100 m yr^{-1}). Parent material consists of moraines (gravel), whereas tephra and other volcanic ejecta are also a substantial component of the soils. Rock formations in the area consist mainly of basaltic lava and hyaloclastite (Vilmundardóttir et al., 2014). Texture of the soil was loamy sand to silt. The depth of the organic horizon increased from absent at the glacial edge, to an A horizon of about 15 cm in the reference site (Vilmundardóttir et al., 2014). The proglacial area has been traditionally grazed by sheep before the establishment of Skaftafell National Park in 1967.

Soil and vegetation sampling

Samples from the topsoil (0-5 cm) were taken in June 2011. At each site (successional age) three randomly placed plots separated by 30-40 m were established on the moraines. We took composite soil samples (ca. 1 kg) by use of a shovel for microbial (bacteria, fungi), faunal

(protozoa, nematodes), soil chemical and physical measurements. Soil was shipped to the lab in plastic boxes in large cooling boxes, and kept at 4°C prior to analysis. Vegetation cover and composition were measured in 0.50 x 0.50 m quadrants at all plots using the Braun-Blanquet scale. Based on the vegetation data alpha diversity (absolute number of plant species) and Bray-Curtis dissimilarity between replicates within chronosequence stages (one minus the number of shared species divided by the sum of species) were calculated.

Soil biochemical parameters

Soil pH was measured electrochemically (Microprocessor pH Meter pH196 WTW, Weilheim, Germany) in H_2O at a soil:solution ratio of 1:2.5 (Burt, 1992). Total organic carbon (TOC) and nitrogen (TN) contents were quantified by dry combustion using an elemental analyser (Carlo Erba NA 1500 analyser). Hot-water-extractable carbon (HWC) was measured as the C present in solution (4 g soil in 30 ml water) after 16h at 80°C. Potentially mineralisable nitrogen (PMN) was measured as the increase in NH_4 during 1 week of anoxic incubation in slurry at 40°C (Canali and Benedetti, 2006). Potential carbon and nitrogen mineralisation were measured weekly by incubation of 200 g of homogenised and sieved soil for 6 weeks at 20°C (Bloem et al., 1994). Results of the first week (disturbance) were not used. N mineralisation was calculated from the increase in mineral N (nitrate and ammonium) between week 1 and week 6. Total concentrations of O_2 and CO_2 were measured weekly using a gas chromatograph (Carlo Erba GC 6000) equipped with a hotwire detector (HWD 430) and helium as carrier gas, and weekly rates were calculated from that. Only bottles in which O_2 concentration dropped below 15% within the 6-week period, were flushed and reset to environmental concentrations to prevent O_2 limitation. For the statistical analyses, we took the average of weekly rates of CO_2 mineralisation over the 5-week period after the first week.

Soil food web characteristics

Soil biological measurements included the presence and abundance of the major taxonomic groups of soil organisms: microbes (bacteria, fungi) and soil microfauna (protozoa and nematodes). Within these taxonomic groups we defined ‘trophic groups’ based on diet and life-history traits (Yeates et al.,1993). Abundances were transformed into estimates of biomass based on body-size information, and expressed in units of micrograms of carbon per gram dry soil. Untransformed data is available in a supplementary table (Appendix A).

Bacterial biomass, fungal biomass, leucine incorporation, and protozoan abundance were measured after a pre-incubation period of 2 weeks at 20°C. Bacterial numbers and cell volumes, and fungal hyphal lengths were measured in microscopic slides (Bloem and Vos, 2004). Bacterial cell numbers and volumes were determined using confocal laser scanning microscopy combined with an image analysis system. The data were transformed into bacterial biomass, taking a specific carbon content of 3.20 x 10^{-13} g C μm^{-3} (Bloem et al., 1995). For the transformation of fungal hyphal lengths to fungal biomass we described fungal volume as a cylinder with spherical ends ($V = (\pi/4)\ W^2\ (L - W/3)$, where V = volume in μm^3, L = length in µm, and W= diameter in µm), with a mean hyphal diameter of 2.5 µm and a specific carbon content of 1.30 x 10^{-13} g C μm^{-3} (Bakken and Olsen, 1983). Bacterial growth activity was estimated by measuring incorporation rates of [^{14}C]leucine (Bloem et al., 2006).

Two trophic groups of protozoa (flagellates and amoebae) were measured using the most-probable-number method (Bloem et al., 1994). Numbers were converted to biomass assuming a spherical shape with diameters of 4.6 µm and 9.1 µm for flagellates and amoebae, respectively, and a volume to C conversion factor of 1 x 10^{-13} C μm^{-3} (Bloem et al., 1994).

Soil nematodes were counted in 9 mL soil solution extracted by Oostenbrink elutriators from 100 g of soil. Numbers per trophic group (bacterivore, fungivore, herbivore, omnivore, predaceous) were derived from species composition in the samples (Bongers, 1988). Nematode biomasses were calculated using fresh weight data from Didden et al. (1994), and taking a moisture content of 75% and a carbon content of 40% (Didden et al., 1994).

To describe the structure of the soil food webs, we calculated a number of commonly used food web metrics: mean and maximum trophic level, and maximum chain length. Trophic level (mean and max) of the groups in the food web was calculated (slightly adjusted) following Holtkamp et al. (2008) as $TL = 1 + \sum_j^n (TL_i \cdot \frac{F_{ij}}{\sum_1^k F_{ij}})$ in which TL_i represents trophic level of the prey, F_{ij} represents the feeding rate of predator *j* on prey *i* calculated according to de Ruiter et al. (1995), *k* is the total number of trophic groups consumed by predator *j*, and *n* the total the number of trophic groups in the food web. Base trophic levels of labile detritus, recalcitrant detritus and roots were set to 1. Maximum chain length was determined as the maximum number of trophic groups in a single chain from detritus to the highest trophic level present.

Statistics

We analysed the data using a Kruskal-Wallis non-parametric analysis of variance with successional stage as factor, because due to the low number of replicates normality was rarely met. The advantage of using a Kruskal-Wallis test is that due to its robustness, significant differences found here are also significant when other statistical techniques are used. Vegetation cover, vegetation diversity and Bray-Curtis as function of the independent variable successional age were analysed using maximum likelihood methods for non-linear regression (Bolker, 2008). Best fits were based on Akaike's Information Criterion and ecological context (Arnold, 2010).

To examine food web assembly and vegetation community composition, Nonmetric Multi-Dimensional Scaling (NMDS) multivariate analysis was performed using the Bray-Curtis dissimilarity matrix based on trophic group biomasses and plant species abundances (Minchin, 1987). Stability of ordination convergence was checked by running ordinations 10 and 20 times for each of the matrices (to check the effects of randomized starting values), and comparing configurations using Procrustes errors. To formally quantify the relationship between soil food web data and vegetation data a co-correspondence analysis was performed. Statistical analyses were carried out using R (3.4.2; R Core Team (2015)) and Canoco 5.0 (for the multivariate analyses) (Ter Braak & Šmilauer, 2012).

Results and discussion

Vegetation development

The first stage on the edge of the glacier (one year old) was still bare. From the second stage (30 yr) on, vegetation cover increased significantly from a small pioneer vegetation with a cover of 7% to a fully covering dwarf shrub vegetation at the reference site (Figure 2A). The relatively low vegetation cover at the intermediate stages (65, 120 yr) might have been due to extensive grazing by sheep (until 1967), the relatively geographic isolation at high latitude (Gunnlaugsdóttir, 1985), and the cold climatic conditions including frequent freeze/thaw cycles and low summer temperatures (lower radiation intensity), but could also be the result of N limitation. Averaged Ellenberg values for nutrient availability (Hill et al., 1999) did not differ between stages, and with a value of around 2.5 indicated a low nutrient availability even at the reference stage (Appendix B). Nitrogen fixing plant species can speed up the soil

ecosystem development (Bormann and Sidle, 1990). The fast colonization of the area surrounding the glacial forefield by the introduced *Lupinus nootkatensis* shows that N-fixation can be an advantageous plant trait under these local conditions (Arnalds and Runolfsson, 2004). However, N fixing vascular plant species (*Lathyrus japonicus* ssp. *maritimus* and *Dryas octopetala*) were only present with a very low cover (<5%) in all stages older than 30 years. We have no clear explanation for the absence of N-fixing vascular plant species. The dominant moss species in stages 2-4, *Rhacomitrium ericoides*, has been described as N-fixer via symbiosis with endophytic cyanobacteria (Henriksson et al., 1987), but this moss species was absent at the reference stage where the strongest increase in N-content took place. In terms of important mechanisms in soil ecosystem development at this glacial forefield, plant-based N-fixing is therefore less likely. Also atmospheric N deposition is estimated to be low in Iceland, whereas N fixation by cyanobacteria in the soil is supposed to be high and thereby presumed to be the dominant N supply in the soil (Vilmundardóttir et al., 2015).

Alpha diversity of the vegetation stabilized from around stage 4 (120 yr) onwards (Figure 2B). Bernasconi et al. (2011) found in the forefield of the Damma Glacier in Switzerland a slightly faster stabilization of vegetation diversity, showing an initial increase in plant species richness that levelled off after 60-80 years of development. Bray-Curtis dissimilarity between replicates within successional stages decreased with age (Figure 2C), indicating an increasing homogeneity within the stages. This can be explained through the colonization of single pioneer species at the earliest stages, showing a high variation between replicates, whereas the later successional species are dominating all replicates within the later stages, leading to a decrease in dissimilarity.

Soil biochemical parameters

Soil pH, as a plant and weathering related factor, is an important driver for soil community development, especially determining shifts in bacterial and fungal communities (Knelman et al., 2012). In the present study we saw that soil pH in the Skaftafell forefield showed a decrease in pH from a very high value of 8.9 at the youngest stage to 5.7 in the reference site (Table 1), comparable to an earlier study in Skaftafell that showed a decrease from 7.4 after 9 years to 5.7 after 120 years of deglaciation (Vilmundardóttir et al., 2014).

All measured carbon (TOC, HWC) and nitrogen (TN, PMN) pools showed an increase with age (Table 1). This increase has been found in many other studies on other primary

chronosequences (Chapin et al., 1994; Egli et al., 2010; Egli et al., 2001; He and Tang, 2008; Insam and Haselwandter, 1989; Stevens and Walker, 1970). The maximum values of 2.5% of TOC and 0.1 % N at the fully vegetated reference site fall within the range of values earlier found in Skaftafell (Vilmundardóttir et al., 2015). These values indicate that nutrient availability at the glacier forefield remained very low. The C:N ratio (indicative for organic matter quality) was high in the youngest stage (1 yr), low in the second stage (30 yr), and showed an increase from the second stage towards the reference sites. The increase in the ratio of C:N could be linked to the increase in the occurrence of woody plant species with age, decreasing the degradability of the litter. In comparison with the total N content in other, much older soils in Iceland (N-content 0.4-1.2%; Lehtinen et al., 2015), total N content in the reference site was still low, which indicates that even our reference site in Skaftafell could still be in a developing phase.

Potential N mineralisation, reflecting net mineralisation, showed a statistically significant decrease with age. The increase in mineralisable N with age on one hand and the decrease in potential N mineralisation by microbes on the other, imply a strong immobilisation of N by microbes in the soil, hence a strongly N limited system with a low N availability for plants. This was also clearly shown by the plant species composition at the glacier forefield, representing species often growing in sites with a low nutrient availability, indicated by the averaged Ellenberg values (Appendix B).

Soil food web characteristics

Based on the biomass measurements of trophic groups of organisms, we constructed soil food web diagrams for all stages, showing an increasing food web complexity with successional age (Figure 3). Total soil food web biomass increased with age (Table 2). Similarly, biomasses at the 1st and 2nd trophic level increased with age, whereas biomass at the 3rd trophic level decreased again after 65 years. The number of trophic groups in the soil food web increased from 5 at the initial stages to 11 after 65 years (Table 2). Similarly, mean and maximum trophic level and maximum trophic chain length peaked (at maximum 6 groups: the longest possible chain contains trophic groups 1-3-4-5-9-10) after 120 years. These results suggest that, in the Icelandic climate, soil food web structure took more than a century to fully develop in terms of trophic groups and complexity. In terms of trophic group biomass, food web development still continued after a century, as shown by the increase in fungal biomass.

Whether bacterial and fungal communities also show changes in composition during successional development as found in other glacial forefields (Ohtonen et al., 1999; Rime et al., 2015), remains to be determined in our glacial forefield in Iceland.

At the youngest stage (1 yr) fungi were not yet found, while fungal biomass increased towards 96 µg C/g at the reference site (Table 1). Also bacterial biomass increased with age, although not statistically significant. Due to the steeper increase in fungal biomass, the fungal to bacterial biomass ratio increased with age (Table 1) following our expectations and shown before in other studies (Ohtonen et al., 1999; Rime et al., 2015; Sigler and Zeyer, 2002).

Regarding food web activity, C mineralisation rate was high in the youngest stage (1 yr), low in the second stage and from there showed an increase towards the values in the reference sites. Microbial efficiency, calculated as the reciprocal of relative microbial respiration (qCO_2, calculated as g CO_2–C per g microbial C), showed a statistically significant increase with age. This could be related to the increase in the fungal to bacterial biomass ratio with age (Pearson correlation, $r=-0.70$, $p<0.005$), a higher efficiency of fungi compared to bacteria (Six et al., 2006) and an adaptation to the less degradable litter from woody shrub species such as *Calluna vulgaris* and *Empetrum nigrum*, dominating the later stages. This vegetation type has been shown to be dominated by fungal decomposition in other areas (Holtkamp et al., 2008).

At the youngest two successional stages (1, 30 yr) nematode presence was below the detection limit, subsequently peaked at intermediate stages (65 yr) especially for herbivorous and omnivorous nematodes, and decreased again at the oldest stages (120 yr, reference), whereas fungivore nematodes increased with age (Table 1), following the increase in fungal biomass (Pearson correlation, $r = 0.614$, $p<0.05$). The intermediate peak and subsequent decrease in nematode biomass was unexpected, because soil organic carbon and nitrogen pools, as well as vegetation cover showed an increase towards the oldest stages. They are also in contrast to earlier studies on the glacier forefield in Damma (Brankatschk et al., 2011), and observations on nematode biomass in the Franz Josef glacial forefield in New Zealand showing an increase until an age of 5000 years (Doblas-Miranda et al., 2008). The absence of nematodes in the first two successional stages could indicate potentially undersampling of soil nematodes in our sites. The used morphological method for nematode analysis has a higher detection threshold in comparison to molecular and DNA-based methods, but is potentially less biased

towards plant-parasitic nematodes. However, a potential undersampling had no differential effect between the successional stages, as the same method was used for all samples.

Linking above- and belowground

Ordination analysis using NMDS based on the vegetation data shows separation of all successional stages (Figure 4B), although stages three (65 yr) and four (120 yr) are in close proximity, indicating a strong similarity in plant community. When the same analysis is done based on belowground trophic group biomasses, a similar pattern was found, with a clear distinction between stages 1, 2, and 5, whereas the belowground communities in stages 3 and 4 were strongly similar, as depicted by the close proximity in ordination space (Figure 4A). The soil food web shows little development in the first 30 years of development in the chronosequence we studied. This pattern can also be directly seen in the food web diagrams (Figure 3), in which stages one (1 yr) and two (30 yr) show similar food webs. Combining the two NMDS analyses indicates that plant community development from the second (30 yr) to the third (65 yr) successional stage did have a strong effect on soil food web development. Also in the co-correspondence analysis the ordination axes of food web and vegetation data were highly correlated (cross-correlation values of 0.94 and 0.92 for the first two axes, Figure 5). However, these results have to be interpreted with caution, as the inertia of the two tables (0.23 for the soil food web, and 2.21 for the vegetation data were much larger than the explained variation (0.081) captured by the co-correspondence analysis. Effects of individual plant species on the soil food web have previously been found in experimental studies (Wardle et al., 2003) and on microbial community structure in a glacier forefield in Alaska (Bardgett and Walker, 2004). In our chronosequence, the soil food web complexity (number of trophic groups) increased when plant cover, especially the cover of dominating *Racomitrium ericoides* mosses, increased. This could be the effect of capturing windblown organic matter by the mosses subsidizing the soil food web. However, clear evidence for a strong effect of any of the other individual plant species on soil food web development could not be extracted.

A paradigm in literature dictates that a successional increase in plant cover leads to an increase in the input of C and N in the soil, which is the resource for a growing soil microbial and faunal community, hence plants are the drivers of ecosystem development (facilitation-model) (Chapin et al., 1994; Knelman et al., 2012; Ohtonen et al., 1999). However, as shown

previously for aboveground arthropod communities (Hodkinson et al., 2001; Ingimarsdóttir et al., 2013; Kaufmann, 2001), also the arrival of heterotrophic soil organisms can precede establishment of plants, hence do not depend on plant derived organic matter inputs and instead may subsidize the primary nutrients for plant uptake through mineralisation of exogenous compounds. In our study of soil ecosystem development, we indeed found paralleled below- and above-ground development, in line with the findings of Hedlund et al. (2003), without indications for vegetation driven facilitation effects in the early successional stages. However, from the third stage (65 yr) vegetation reached a substantial cover and may have subsidized higher trophic levels in the soil food web, as from this point onwards the soil food web switched from a simple microbial system to a fully developed soil food web.

In conclusion, our results show that soil ecosystem development takes about a century under Icelandic climatic conditions to fully develop in terms of vegetation succession and soil food web structure and even longer to reach the full soil organism community and biogeochemical cycling. This information can be helpful in restoring agricultural soils losing their productivity. Glacier forefields display extreme conditions, and are therefore less representative for agricultural production in the form of arable field, but can provide information on productivity of pastures, in terms of recovery time or as reference from a natural context. However, our study provides only a first overview of complete soil ecosystem development combining above- and below-ground succession and should therefore encourage further investigations. Topics that require future investigation are identifying the underlying mechanisms of the intermediate peaks in the nematode succession pattern, as well as explaining the surprising lack of colonization by N-fixing plant species in the forefield.

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Tables

Table 1 Soil physicochemical and biological properties and biologically mediated processes at different stages in the chronosequence in Skaftafell (Iceland). All values represent mean and standard deviation (between brackets), measured in the topsoil (0-5 cm); [-]: not sampled/tested; nd: not detected. Adjusted test statistics (*H*) and *p*-values from a Kruskal-Wallis non-parametric analysis of variance with successional age as factor are presented in the last two columns. Superscript letters denote statistically significant differences between successional ages assessed with a pairwise comparison with Dunn correction.

Stage	1	2	3	4	5	*H* (df=4)	*p*-value
Age	1 yr	30 yr	65 yr	120 yr	ref		
pH (H_2O)[1]	8.93	8.06	6.78	6.46	5.71	[-]	[-]
HWC[2] (mg C g^{-1})	-0.043^{a} (0.015)	-0.001^{a} (0.012)	0.081^{a} (0.038)	0.18^{a} (0.017)	0.59^{b} (0.18)	16.11	0.009
TOC[3] (mg C g^{-1})	2.57^{a} (0.18)	1.63^{a} (0.12)	3.43^{a} (0.66)	5.96^{a}(0.72)	25.5^{b} (3.86)	15.92	0.010
PMN[4] (µg N g^{-1})	-0.21^{a} (0.072)	0.47^{a} (0.25)	5.05^{a} (2.50)	6.26^{a} (0.60)	17.8^{b} (4.98)	15.64	0.012
Total N (mg N g^{-1})	0.11^{a} (0.006)	0.11^{a} (0.000)	0.17^{a} (0.023)	0.26^{a} (0.015)	0.91^{b} (0.12)	16.03	0.009
C:N (g C g^{-1} N)	24.1^{bc} (2.08)	14.8^{a} (1.12)	20.4^{b} (1.25)	23.2^{b} (1.50)	28.1^{c} (1.47)	14.57	0.012
Bacteria (µg C g^{-1})	8.71 (1.20)	7.43 (2.72)	11.6 (3.48)	10.9 (2.72)	21.5 (3.92)	13.21	0.053
Fungi (µg C g^{-1})	nd^{a}	2.35^{a} (2.09)	29.7^{b} (12.1)	14.9^{ab} (2.64)	96.1^{c} (6.50)	15.98	0.010
Fungal:bacterial biomass ratio	0^{a} (0)	0.28^{ab} (0.16)	2.90^{bc} (1.91)	1.40^{ab} (0.14)	4.56^{c} (0.81)	15.05	0.015
Microbial biomass (µg C g^{-1})	8.71^{a} (1.20)	9.78^{a} (4.81)	41.3^{b} (11.0)	25.8^{ab} (5.33)	117^{c} (7.45)	15.45	0.014
Amoebae (µg C g^{-1})	0.002^{a} (0.002)	0.019^{ab} (0.009)	0.023^{ab} (0.012)	0.132^{ab} (0.104)	0.102^{b} (0.046)	14.33	0.015
Flagellates (µg C g^{-1})	0.005 (0.007)	0.002 (0.002)	0.037 (0.018)	0.385 (0.291)	0.285 (0.101)	14.24	0.016*
Bacterivore nematodes (µg C g^{-1})	nd^{a}	nd^{a}	0.034^{ab} (0.020)	0.022^{ab} (0.013)	0.049^{b} (0.007)	12.33	0.015
Fungivore nematodes (µg C g^{-1})	nd^{a}	nd^{a}	0.007^{ab} (0.006)	0.012^{b} (0.001)	0.012^{b} (0.004)	11.26	0.024
Herbivore nematodes (µg C g^{-1})	nd^{a}	nd^{a}	0.034^{c} (0.010)	0.026^{bc} (0.007)	0.016^{ab} (0.005)	12.33	0.012
Omnivore nematodes (µg C g^{-1})	nd^{a}	nd^{a}	0.18^{b} (0.046)	0.084^{a} (0.043)	0.016^{a} (0.017)	14.78	0.011
Predaceous nematodes (µg C g^{-1})	nd	nd	nd	0.004 (0.007)	0.004 (0.007)	2.84	0.519
Total nematode biomass (µg C g^{-1})	nd^{a}	nd^{a}	0.25^{c} (0.062)	0.15^{bc} (0.053)	0.097^{ab} (0.007)	15.64	0.010
N min[5] (µg N g^{-1} yr^{-1})	6.59^{ab} (2.62)	17.3^{b} (10.3)	5.89^{ab} (4.20)	1.04^{a} (0)	1.04^{a} (1.04)	14.46	0.018
C min[6] (mg C g^{-1} yr^{-1})	0.43^{ab} 0.010)	0.21^{a} (0.038)	0.26^{a} (0.081)	0.36^{ab} (0.031)	0.63^{b} (0.18)	14.33	0.017

Leu[7] (pmol g^{-1} h^{-1})	54.8 (70.7)	147 (14.1)	113 (16.4)	52.8 (20.8)	105 (16.4)	8.39	0.077
qCO_2 (g C g^{-1} yr^{-1})	49.7^{b} (8.30)	26.1^{a} (13.3)	6.45^{a} (1.23)	9.40^{a} (5.79)	5.32^{a} (1.32)	14.90	0.014

[1] Samples not replicated, hence differences not statistically tested; [2]Hot water extractable Carbon (negative values occur due to lab value corrections with the control, should be considered to be zero); [3] Total Soil Organic Carbon; [4] Potential mineralisable Nitrogen (a negative value occurred due to correction with control in the lab, should be considered zero); [5] Nitrogen mineralisation rate; [6] Carbon mineralisation rate; [7] bacterial activity: Leucine incorporation rate; *Significant in Kruskal-Wallis, but no differences found in pairwise comparisons with Dunn correction.

Table 2 Soil food web characteristics at the chronosequence in Skaftafell (Iceland): number of trophic groups, total biomass (µg C g^{-1}), biomasses of the separate trophic levels (µg C g^{-1}), mean and maximum trophic level and maximum chain length. All values represent mean and standard deviation (between brackets), measured in the topsoil (0-5 cm). Adjusted test statistics (*H*) and *p*-values from a Kruskal-Wallis non-parametric analysis of variance with successional age as factor are presented in the last two rows. Superscript letters denote statistically significant differences between successional ages assessed with a pairwise comparison with Dunn correction.

Age	Trophic groups	Total biomass	Biomass			Mean trophic level	Max trophic level	Max chain length
			Level 1	Level 2	Level 3			
1 yr	4.33^{a} (0.58)	8.72^{a} (1.20)	8.71^{a} (1.20)	0.005^{a} (0.007)	0.002^{a} (0.002)	1.39^{a} (0.10)	2.00^{a} (0.001)	3.33^{a} (0.58)
30 yr	6.67^{b} (0.58)	9.80^{a} (4.82)	9.78^{a} (4.81)	0.002^{a} (0.002)	0.02^{a} (0.009)	1.56^{a} (0.10)	2.33^{ab} (0.58)	3.67^{ab} (0.58)
65 yr	11.00^{b} (0.00)	41.6^{b} (11.1)	41.3^{b} (11.0)	0.08^{ab} (0.03)	0.20^{b} (0.05)	2.22^{b} (0.02)	3.46^{bc} (0.18)	5.00^{bc} (0.58)
120 yr	11.33^{b} (0.58)	26.4^{ab} (5.29)	25.8^{ab} (5.32)	0.42^{b} (0.28)	0.22^{b} (0.12)	2.29^{b} (0.10)	3.73^{c} (0.45)	5.33^{c} (0.58)
reference	11.00^{b} (1.00)	118^{c} (7.57)	118^{c} (7.45)	0.35^{ab} (0.10)	0.12^{ab} (0.06)	2.24^{b} (0.14)	3.54^{bc} (0.48)	5.00^{abc} (1.00)
H (df=4)	14.61	15.45	15.45	14.58	13.58	12.83	12.36	12.64
p-value	0.012	0.014	0.014	0.013	0.012	0.022	0.025	0.016

Figures

Figure 1 Sampled sites in the glacial forefield of Skaftafell (Iceland). Photos are taken from successional stages S1 1 yr (a), S2 30 yr (b), S3 65 yr (c), S4 120 yr (d) and reference stage (e).

Figure 2 Vegetation development in the glacial forefield of Skaftafell (Iceland). Presented are total vegetation cover (Braun-Blanquet scores represented as class averages) (A), alpha diversity (absolute number of plant species present, (B) and Bray-Curtis dissimilarity (one minus the number of shared species divided by the sum of species, (C) of the vegetation communities along successional ages. Point size increases when data points overlap. Stage 1 is excluded from B and C due to absence of vegetation. Best fitting regression curves: $\exp(-2.2978+0.0093\,x)/(1+\exp(-2.2978+0.0093\,x))$ with Normal errors for A, $13.292(1-\exp(-0.0414\,x))$ with Poisson errors for B, and $0.5036\exp(-0.0012\,x)$ with Normal errors for C.

Figure 3 Food web assembly in the glacial forefield of Skaftafell (Iceland) of the successional stages. The numbers refer to the observed trophic groups: 1, labile detritus; 2, recalcitrant detritus; 3, bacteria; 4, flagellates; 5, amoebae; 6, fungi; 7, bacterivorous nematodes; 8, fungivorous nematodes; 9, omnivorous nematodes; 10, predatory nematodes; 11, plant roots; 12, herbivorous nematodes. Years refer to soil age. Colours represent energy source (brown: detritus, red: bacteria, blue: fungi, green: plant roots, black: omnivorous). Note that figures represent maximum number of trophic groups per successional stage, a dashed box around a number indicates that the group was missing in one or two individual replicates.

Figure 4 Nonmetric Multi-Dimensional Scaling (NMDS) ordination graphs based on soil food web data (A) and vegetation data (B) in the glacial forefield of Skaftafell (Iceland).

614 Points represent individual data points of the successional stages: 1 yr (S1a,b,c), 30 yr
615 (S2a,b,c), 65 yr (S3a,b,c), 120 yr (S4a,b,c) and reference stage (S5a,b,c). For abbreviations
616 see Appendix A (belowground groups) or Appendix B (vegetation).

617 **Figure 5** Co-correspondence graph showing ordination based on a soil food web data (A) and
618 vegetation data (B) in the glacial forefield of Skaftafell (Iceland). Ordination is based on
619 averaged case weights from both tables, and soil properties are projected as arrows in the left
620 panel (Nmin: nitrogen mineralisation rate, Cmin: carbon mineralisation rate.TN: total
621 nitrogen, HWC: hot water extractable carbon, TOC: total organic carbon, PMN: potentially
622 mineralisable nitrogen). Red circles indicate location of successional stages in multivariate
623 space. For abbreviations see Appendix A (belowground groups) or Appendix B (vegetation).

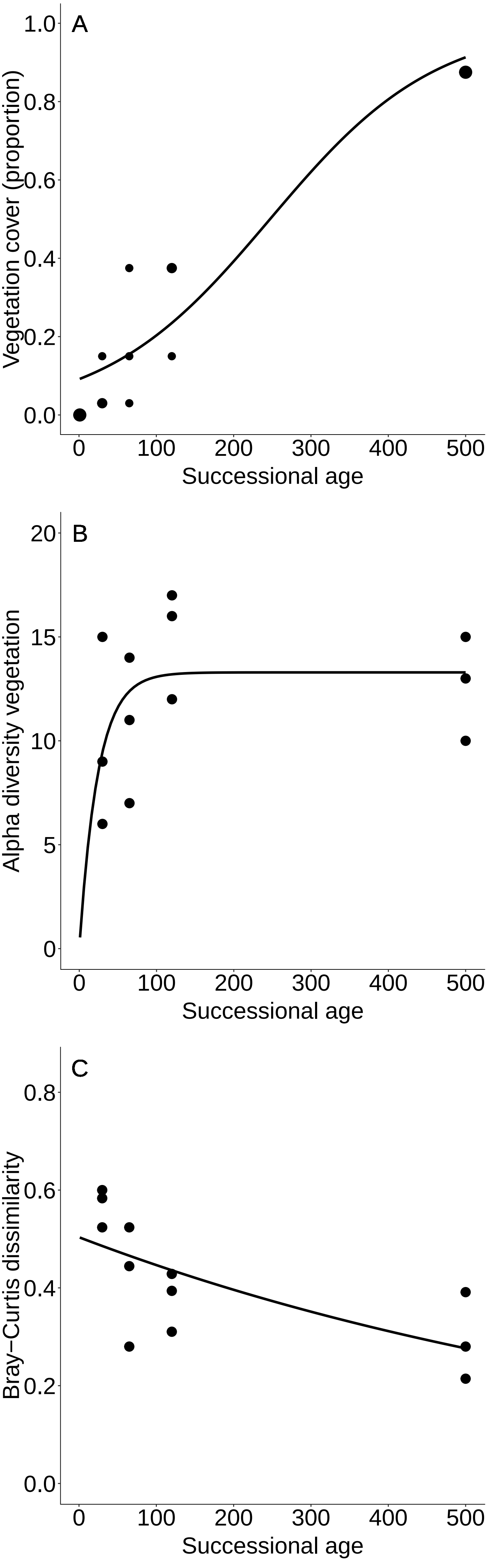

a)

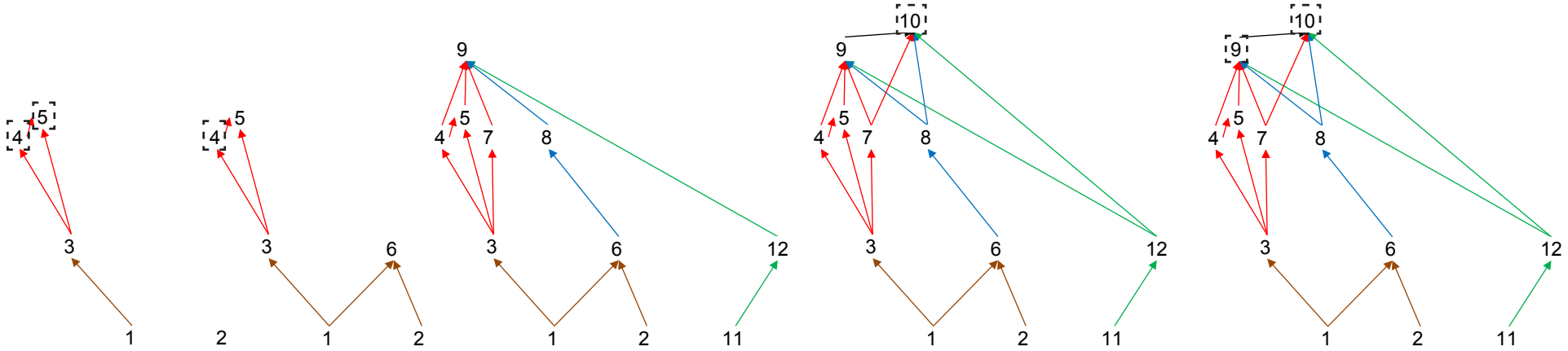

b)


c)


d)


e)


A
1.0
0.8
0.6
0.4
0.2
0.0
Vegetation cover (proportion)
0
100
200
300
400
500
Successional age
B
20
15
10
5
0
Alpha diversity vegetation
0
100
200
300
400
500
Successional age
C
0.8
0.6
0.4
0.2
0.0
Bray–Curtis dissimilarity
0
100
200
300
400
500
Successional age



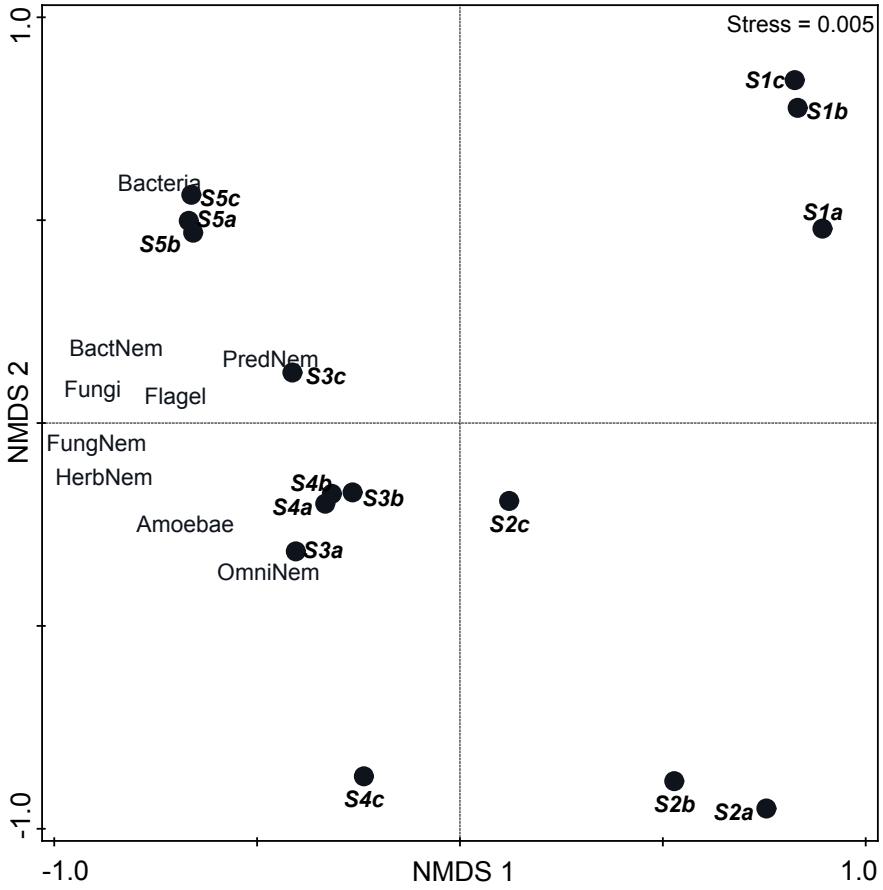
1 yr
Stage 1

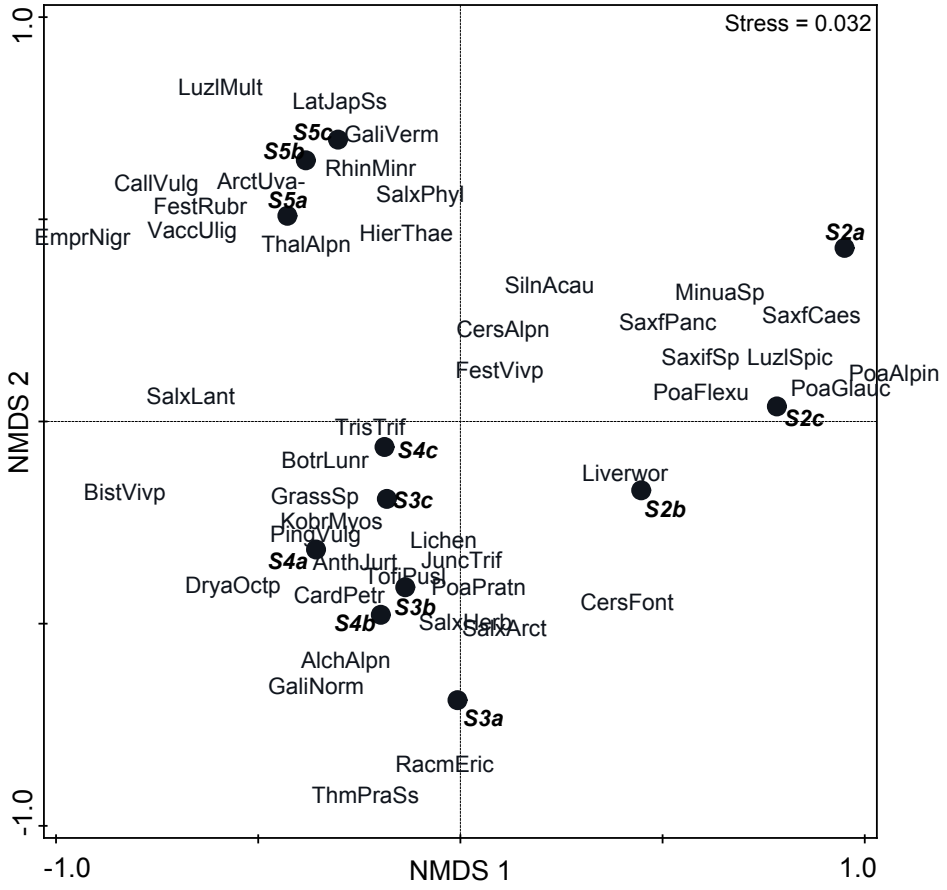
30 yr
Stage 2

65 yr
Stage 3

120 yr
Stage 4

Reference
Stage 5


Stress = 0.005
S1c
S1b
S1a
Bacteria
S5c
S5a
S5b
BactNem
PredNem
S3c
Fungi
Flagel
FungNem
HerbNem
S4b
S4a
S3b
Amoebae
S2c
S3a
OmniNem
S4c
S2b
S2a
1.0
-1.0
NMDS 2
-1.0
NMDS 1
1.0


Stress = 0.032
LuzlMult
LatJapSs
S5c
GaliVerm
S5b
RhinMinr
CallVulg
ArctUva-
SalxPhyl
FestRubr
S5a
EmprNigr
VaccUlig
ThalAlpn
HierThae
S2a
SilnAcau
MinuaSp
SaxfPanc
SaxfCaes
CersAlpn
SaxifSp
LuzlSpic
PoaAlpin
FestVivp
PoaFlexu
PoaGlauc
SalxLant
S2c
TrisTrif
S4c
BotrLunr
Liverwor
BistVivp
GrassSp
S3c
S2b
KobrMyos
PingVulg
Lichen
S4a
AnthJurt
JuncTrif
TofiPusl
DryaOctp
CardPetr
PoaPratn
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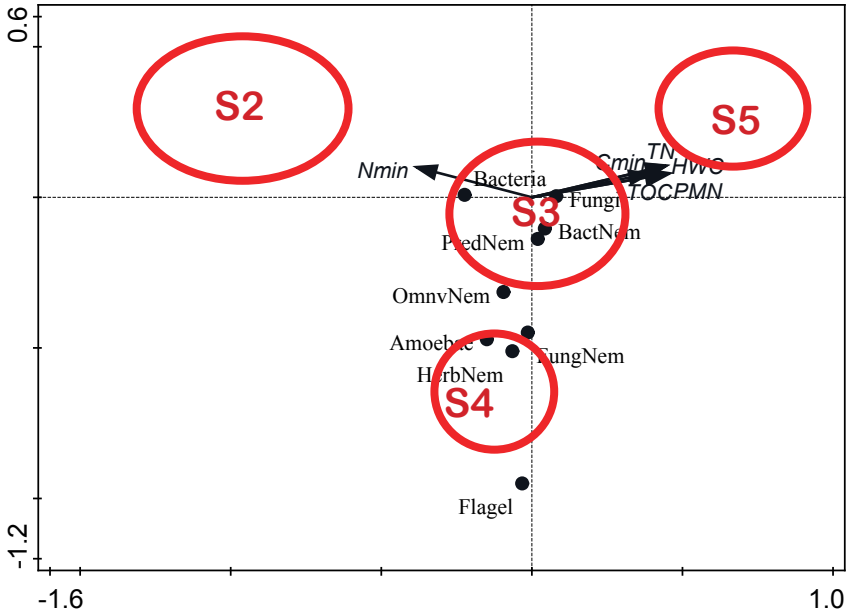
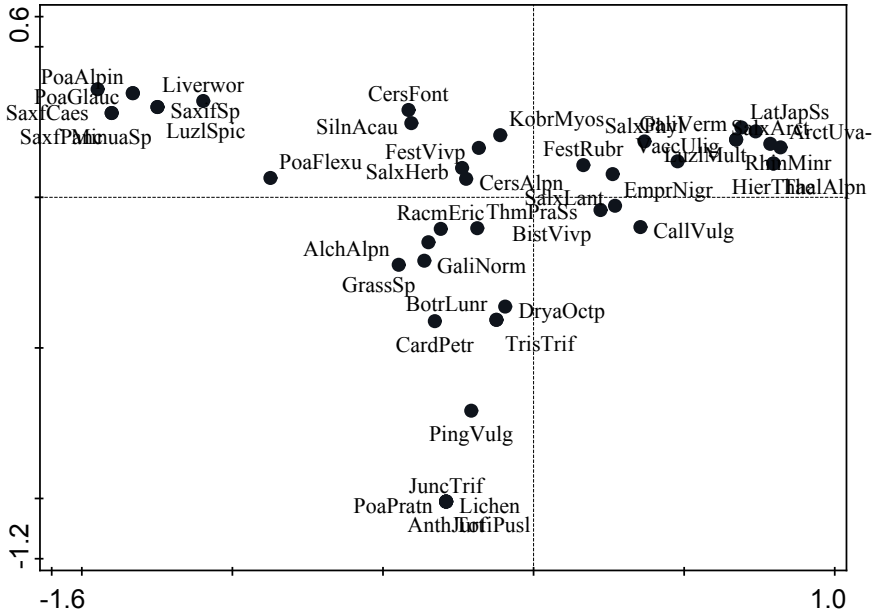
AlchAlpn
GaliNorm
S3a
RacmEric
ThmPraSs
1.0
-1.0
NMDS 2
-1.0
NMDS 1
1.0


0.6
-1.2
-1.6
1.0
S2
S5
S3
S4
Nmin
TN
HWC
TOCPMN
Bacteria
BactNem
OmnvNem
FungNem
HerbNem
Flagel


0.6
-1.2
-1.6
1.0
PoaAlpin
PoaGlauc
SaxfCaes
Liverwor
SaxfSp
LuzlSpic
CersFont
SilnAcau
KobrMyos
FestVivp
PoaFlexu
SalxHerb
FestRubr
CersAlpn
EmprNigr
SalxLant
RacmEric
ThmPraSs
BistVivp
CallVulg
AlchAlpn
GaliNorm
GrassSp
BotrLunr
DryaOctp
CardPetr
TrisTrif
PingVulg
JuncTrif
PoaPratn
Lichen
LatJapSs
RhodMinr