

Coordinated responses of soil communities to elevation in three subarctic vegetation types

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Global warming has begun to have a major impact on the species composition and functioning of plant and soil communities. However, long-term community and ecosystem responses to increased temperature are still poorly understood. In this study, we used a well-established elevational gradient in northern Sweden to elucidate how plant, microbial and nematode communities shift with elevation and associated changes in temperature in three highly contrasting vegetation types (i.e. heath, meadow and *Salix* vegetation). We found that responses of both the abundance and composition of microbial and nematode communities to elevation differed greatly among the vegetation types. Within vegetation types, changes with elevation of plant, microbial and nematode communities were mostly linked at fine levels of taxonomic resolution, but this pattern disappeared when coarser functional group levels were considered. Further, nematode communities shifted towards more conservative nutrient cycling strategies with increasing elevation in heath and meadow vegetation. Conversely, in *Salix* vegetation microbial communities with conservative strategies were most pronounced at the mid-elevation. These results provide limited support for increasing conservative nutrient cycling strategies at higher elevation (i.e. with a harsher climate). Our findings indicate that climate-induced changes in plant community composition may greatly modify or counteract the impact of climate change on soil communities. Therefore, to better understand and predict ecosystem responses to climate change, it will be crucial to consider vegetation type and its specific interactions with soil communities.

Global warming has begun to have a major impact on the species composition and functioning of plant communities (Walther 2004), as well as on many groups of soil organisms (Kardol et al. 2010, Blankinship et al. 2011, Classen et al. 2015, Jarvis et al. 2015). In arctic and alpine ecosystems, this has resulted in a wide-spread increase in the abundance of shrubs (Sturm et al. 2001, Tape et al. 2006, Walker et al. 2006, Chen et al. 2011) and these vegetation shifts can be associated with shifts in soil community composition (Eskelinen et al. 2009). However, the rate at which plants and soil organisms respond to climate warming differs depending on their genotypic adaptation (Jump and Peñuelas 2005), phenotypic plasticity (Kardol et al. 2014), and rates of dispersal and colonization (Walther et al. 2002, Berg et al. 2010, Blankinship et al. 2011, van der Putten 2012). For example, plant species may expand their ranges faster in response to warming than soil organisms (Engelkes et al. 2008, Morrien et al. 2010). As a result of this, plant–soil interactions are likely to be altered in response to warming (Bardgett et al. 2013, Classen et al. 2015, van der Putten

et al. 2016). Moreover, warming-induced shifts in soil community composition may have important consequences for the functioning of soil communities and hence may impact on key ecosystem processes such as carbon sequestration and nutrient mineralization (Classen et al. 2015, van der Putten et al. 2016). However, there are difficulties in predicting long-term community and ecosystem responses to increased temperature from short-term warming experiments (Wolkovich et al. 2012, Sundqvist et al. 2013). Therefore, we have limited knowledge of the long-term impact of climate warming on plant and soil community reordering (Bardgett et al. 2013).

Elevational gradients are powerful tools for studying long-term ecosystem responses to temperature when other environmental factors are held constant (Fukami and Wardle 2005, Sundqvist et al. 2013, Mayor et al. 2017). With increasing elevation there are usually large changes in vegetation both among and within species. As such, at higher elevations, and thus lower temperatures, plants with slower growth rates and adaptations to stressful conditions increase

in abundance (Körner 2003). Such plants generally exhibit nutrient-conservation strategies that involve the production of litter with more recalcitrant organic compounds and lower nutrient concentrations (Sundqvist et al. 2011b, De Long et al. 2016). It has been shown that changes in the plant community may shape how different components of the soil community respond to elevation (Richardson et al. 2005, Bahram et al. 2012), largely because plant species and plant communities are often associated with highly specific microbial and nematode communities (De Deyn et al. 2004, Bezemer et al. 2010, Berendsen et al. 2012). Further, warming may impact directly on the composition and functioning of soil communities by stimulating microbial activity and hence key ecosystem processes such as nutrient cycling (Frey et al. 2008, Classen et al. 2015, van der Putten et al. 2016). Like plant communities, these soil communities can show more conservative nutrient strategies under harsher environmental conditions which can have important functional consequences. For example, as fungi are often better adapted for decomposing recalcitrant litter but less adapted for breaking down high quality litter relative to bacteria (van der Wal et al. 2013), an increase in the relative abundance of fungi (versus bacteria) has often been shown to be associated with more conservative and slower nutrient cycling (Bardgett et al. 1996, de Vries et al. 2012). However, it is little understood as to what extent whole soil food webs change in response to elevation and how different groups within the food web are related to one another as elevation changes.

To elucidate how the composition of plant, microbial and nematode communities shifts with increasing elevation and thus declining temperature in three highly contrasting vegetation types, i.e. heath, meadow and *Salix*-vegetation, we used a well-established elevational gradient in northern Sweden, which ranges from 440 m to 900 m (Sundqvist et al. 2011a, Kardol et al. 2014, De Long et al. 2015a, Veen et al. 2015). The temperature difference between the highest and lowest elevation during the growing season across this gradient is approximately 3°C, which is on par with the magnitude of projected temperature increases expected by the end of the current century (IPCC 2013). The three vegetation types are the most common vegetation types in the subarctic (Björk et al. 2007) and all occur at each elevation across the elevational gradient. To test vegetation type-specific responses of soil communities to elevation, we quantified the abundance and community composition of different taxonomic and (functional) groups of soil organisms in each vegetation type. We then used two complementary approaches (i.e. multivariate statistics focusing on taxonomic responses and a network approach focusing on functional group responses) to show how shifts in plant and soil community composition are coordinated within each of the vegetation types across the elevational gradient. Finally, we considered how the changes in soil community composition may drive potential changes in the functioning of soil communities such as their role in nutrient cycling.

Our hypotheses were that: 1) vegetation type will moderate the response of microbial and nematode communities to elevation, in that for less fertile vegetation (i.e. heath), soil communities will show a weaker response to elevation (i.e. smaller shifts in species abundances and community composition) relative to more fertile vegetation (i.e. meadow).

This reflects what we know to occur for the plant community, where species composition in meadow communities is more responsive to elevation than in heath (Sundqvist et al. 2011a). Further, we predict that *Salix* vegetation will show an intermediate response, based on previous measurements of phosphorous and nitrogen availability in the soil (Veen et al. 2015); 2) responses of microbial, nematode and plant communities to elevation will be coordinated, because the soil food web is often strongly controlled by shifts in plant community composition (De Deyn et al. 2004, Bezemer et al. 2010, Prober et al. 2015, Thakur and Eisenhauer 2015). We use our findings to consider the potential consequences of warming-induced changes in soil community composition for soil nutrient cycling, by exploring shifts in the ratio of fungi to bacteria and of fungal-feeding to bacterial-feeding nematodes, both of which are known to be associated with shifts in nutrient cycling strategies (Wardle et al. 2004, de Vries et al. 2012, Kergunteuil et al. 2016). Our study provides new insights regarding vegetation-type specific responses in soil communities to changes in elevation and for understanding whether or not plant and soil communities change in concert with elevational shifts in temperature. Addressing these issues will help us to better predict how advancing climate change will alter species ranges, community composition and ecosystem functioning in subarctic tundra.

Methods

Study site

The study was conducted along an elevational gradient on the northeast facing slope of Mt Suoroaivi (1193 m), approximately 20 km southeast of Abisko, northern Sweden (68°21'N, 18°49'E) (Sundqvist et al. 2011a). The climate in the study region is subarctic. For the elevations studied, the mean air temperature during the summer of 2012 (6 July until 31 August) was 10.2°C at 440 m, 9.2°C at 690 m, and 7.6°C at 900 m (measured in meadow vegetation using a temperature logger inside a solar radiation shield at 15 cm above the soil surface). This range across elevations is in line with the projected increase in temperature in this region by the end of this century (IPCC 2013). The mean annual precipitation in Abisko is 310 mm (1913–2000; Abisko Scientific Research Station), with most of the precipitation falling in July (51 mm) and the least in April (12 mm) (Kohler et al. 2006). Along this gradient summer precipitation ranges from 230 to 290 mm between June and October, and the amount of precipitation does not differ among elevations (Karlsson et al. 2005, Sundqvist 2011). The bedrock consists of salic igneous rocks and quartic and phyllitic hard schists (Sundqvist et al. 2011a).

Three dominant vegetation types co-occur in a mosaic at all elevations above and below the treeline across the gradient: heath, meadow and *Salix*-dominated vegetation. Heath vegetation is dominated by ericaceous dwarf-shrubs (Sundqvist et al. 2011a, Veen et al. 2015) and is usually found in drier microhabitats. Meadow vegetation and *Salix*-dominated vegetation are found in shallow depressions, with *Salix*-dominated vegetation commonly found

in more wet locations (Veen et al. 2015). Meadow vegetation is dominated by herbaceous species (Sundqvist et al. 2011a). The *Salix* vegetation is dominated by 50–100 cm tall *Salix* shrubs (which consist of a mixture of several species including *Salix glauca*, *Salix lanata* and their hybrids), with an understory of herbaceous species (Veen et al. 2015). The treeline is formed by *Betula pubescens* spp. *czerepanovii* and is situated at an elevation of approximately 500–600 m at the study site (Sundqvist et al. 2011a).

Experimental design

In June 2012 we established five 1 × 1 m replicate plots in heath, meadow and *Salix* vegetation at each of three elevations, i.e. 440 m (range 423–452 m), 690 m (range 679–707 m) and 900 m (range 890–907 m), resulting in 45 plots in total. These plots were grouped into five blocks, with each block consisting of nine plots, i.e. one plot of all possible combinations of elevation and vegetation type. Plots were assigned to blocks based on their elevation within each of the three main elevations in the manner designated by Veen et al. (2015), i.e. block 1 consisted of the plots that had the highest elevation within each vegetation type within each of the main elevations; block 2 consisted of the plots with the second highest elevation, etc. Within vegetation types within elevations the median distance between plots was ca 40 m and between vegetation types the median plot distance was ca 100 m, with a maximum distance of 270 m. Because of the high small-scale spatial heterogeneity in these communities (Björk et al. 2007), this distance is sufficient to ensure adequate independence among plots. All plots were east or northeast facing, and the mean slope of the plots was 4° (measured with an electronic clinometer).

Soil abiotic properties

On 2 July 2012, during the early stages of the growing season, we collected three to six soil samples from the top 10 cm (including soil from the O and A horizon), i.e. the most active layer for biological activity and the zone in which most plant roots are located, in each plot with a PVC soil corer (ø 4.5 cm) to yield a minimum of 0.2 l of soil, for measurements of soil abiotic and microbial properties (Supplementary material Appendix 1 Table A1). Soil samples were processed and used to measure soil moisture, soil organic matter content (SOM), pH, soil nutrient availability and total soil carbon, nitrogen and phosphorous content. In addition, we measured soil temperature year round, from 15 September 2012 until 15 September 2013 in each plot at a depth of 3 cm using I-buttons. More details on soil sample processing and measurements of abiotic soil properties can be found in Supplementary material Appendix 1.

Plant, microbial and nematode communities

Between 10 and 18 July 2012 we recorded the identity of each plant species present in each plot. Cover of plant species was assessed using point quadrat analysis (Goodall 1952) by recording the total number of times each species was intercepted from a total of 100 downward projecting points in each plot (Wardle et al. 2003). Species that were observed

in the plot, but that were not intercepted by a pin were assigned a 0.5 hit. Plant species were assigned to one of several functional groups, i.e. dwarf shrubs, ferns, forbs, grasses, *Salix*, sedges, horsetails, feather mosses, or other mosses. In addition, we have also recorded the number of times a pin intercepted lichen.

A subsample of soil from each plot was freeze-dried and ground, and used for assessing the microbial community using phospholipid fatty acid (PLFA) analysis (Bligh and Dyer 1959). Different groups of the microbial community have unique PLFA patterns, making PLFA markers useful for answering questions about the response of the microbial community to changes in environmental conditions (Frostegård et al. 2011). The PLFA extractions were done according to Frostegård et al. (1991), and the abundance of PLFAs is expressed in nmol g⁻¹ organic matter (Sundqvist et al. 2011a). We used i14:0, 14:0, i15:0, a15:0, 15:0, i16:0, 16:1ω9, 16:1ω7c, 16:1ω7t, i17:0, a17:0, 17:1ω8, cy17:0, 17:0, 18:1ω7, cy19:0 as indicators for bacteria (Frostegård and Bååth 1996), 10:Me16, 10:Me17 and 10:Me18 for actinomycetes (Kroppenstedt 1985), 16:1ω5 for arbuscular mycorrhizal fungi (AMF) (Olsson et al. 1999) and 18:2ω6 for fungi (Frostegård and Bååth 1996). Note that there are no PLFAs that are specific to ecto- or ericoid mycorrhizal fungi. We used the PLFA data to calculate the biomass for bacteria, actinomycetes, AMF and fungi, and the ratio of fungal to bacterial biomass (F:B ratio) to enable assessment of the relative importance of fungal and bacterial energy channels.

At the same time that soils were collected for abiotic and microbial properties, approximately 15 additional cores were collected from each plot to a depth of 10 cm using a 1.7 cm diameter corer, and these were bulked in order to obtain a sample representative of the whole plot (i.e. sufficiently capture the spatial heterogeneity) (Bokhorst et al. 2015). These composite samples were used for nematode extraction. Nematodes were extracted from an unsieved, homogenized 250 ml subsample of this soil following a modified sugar floatation method (Jenkins 1964), and heat-killed and fixed using a 4% formaldehyde solution. A minimum of 150 nematodes per plot were identified to family level and placed into one of five functional feeding groups, following Yeates et al. (1993), i.e., bacterial feeders, fungal feeders, plant feeders, omnivores and carnivores. Nematode abundances were expressed per gram dry soil. We used the nematode abundance values to calculate the ratio of fungal-feeding nematodes to bacterial-feeding nematodes (FF:BF ratio) to enable assessment of the relative importance of fungal- and bacterial-based energy channels.

We used the vascular plant cover and nematode abundance data to determine the total number of plant species per m² (species richness) and the total number of nematode taxa per g dry weight soil, respectively.

Data analysis

We used two-way ANOVAs to test the effect of vegetation type and elevation on plant, microbial and nematode groups; block was used as a random variable. Whenever ANOVAs revealed significant main effects, we used post hoc tests (Tukey HSD) to further explore differences among means. To test the influence of vegetation type and elevation on the

composition of plant, microbial and nematode communities, we used multivariate analyses. We used detrended correspondence analyses to find the length of the gradients for each of our three communities (ter Braak and Smilauer 2012). Plant community data had a gradient of > 4 SD, indicative of a unimodal response and were analyzed using canonical correspondence analysis (CCA) (ter Braak and Smilauer 2012). Nematode and microbial community data had a gradient of ≤ 1.5 SD, indicative of a linear response, and were therefore analyzed using redundancy analysis (RDA) (ter Braak and Smilauer 2012). Abundance data were log-transformed and used as response variables; vegetation type, elevation and their interaction were used as predictor variables; and block was used as a covariate. The significance of effects of vegetation type, elevation and their interaction were tested using Monte Carlo permutation tests with 999 permutations, where permutations were restricted by blocks.

For each of the three vegetation types we applied co-correspondence analyses (CoCA) using the entire community-level data set to test for the strength of relationships in community composition between plants and microbes, plants and nematodes, and microbes and nematodes (ter Braak and Schaffers 2004). The CoCA approach finds ordination axes that maximize the co-variance between two community-level data sets. Table weights were averaged, so that both communities played a mutually symmetric role in the analyses. We computed four CoCA axes and report the cross-correlation between the first two CoCA axes, the total

variation (inertia) in the two communities and the variation explained by the CoCA analyses. Further, we used a network approach to visualize relationships between plant and nematode functional groups and bacteria, fungi, actinomycetes, AMF and soil abiotic properties (see Scherber et al. 2010 for an approach), as well as the responses of each of the (functional) groups to elevation. To do this, we used Spearman correlations to determine correlations between (functional) groups and soil properties for each of the vegetation types separately, with each of the 15 plots for that vegetation type treated as an independent data point.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.d11rv>> (Veen et al. 2017).

Results

Plant community responses

The cover of the majority of plant functional groups was affected by an interaction between vegetation type and elevation, indicating that plant community responses to elevation differed between vegetation types (Table 1, Fig. 1). For example, for meadow vegetation forb cover was lower at 900 m compared to 440 and 690 m, while grass cover was

Table 1. ANOVA results testing the effect of vegetation type, elevation and their interaction on the abundance of functional groups of plants (cover percentage), microbial groups (nmol PLFA g organic matter⁻¹) and nematode feeding groups (number g dry soil⁻¹) and community-level measures. Values represent F-values (p-values). Values in boldface represent $p < 0.05$. Numerator degrees of freedom were 2 for vegetation type, 2 for elevation and 4 for the interaction, denominator degrees of freedom were 32. PLFA = phospholipid fatty acids.

	Vegetation type (V)	Elevation (E)	V × E
Plants			
Dwarf shrubs	659.02 (<0.001)	31.30 (<0.001)	14.76 (<0.001)
Forbs	87.90 (<0.001)	3.37 (0.047)	8.82 (<0.001)
Grasses	23.38 (<0.001)	6.85 (0.003)	6.25 (0.001)
<i>Salix</i> sp.	116.86 (<0.001)	11.14 (<0.001)	6.56 (<0.001)
Sedges ¹	32.89 (<0.001)	32.12 (<0.001)	7.43 (<0.001)
Ferns	6.32 (0.005)	12.58 (<0.001)	6.32 (<0.001)
Horse tail	6.67 (0.004)	1.52 (0.233)	3.89 (0.011)
Feather mosses	64.63 (<0.001)	28.02 (<0.001)	29.47 (<0.001)
Other mosses	1.54 (0.231)	18.62 (<0.001)	2.67 (0.050)
Lichen	8.79 (<0.001)	7.92 (<0.001)	1.36 (0.268)
Microbes			
Bacteria	10.91 (<0.001)	2.02 (0.150)	6.49 (<0.001)
Fungi	24.43 (<0.001)	19.02 (<0.001)	1.79 (<0.001)
AMF ²	14.89 (<0.001)	0.20 (0.821)	4.81 (0.004)
Actinomycetes	18.63 (<0.001)	2.06 (0.144)	9.12 (<0.001)
Nematodes			
Plant feeders ¹	0.66 (0.525)	4.17 (0.025)	0.57 (0.683)
Bacterial feeders	5.67 (0.008)	9.52 (<0.001)	0.64 (0.639)
Fungal feeders ¹	13.89 (<0.001)	6.80 (0.004)	0.64 (0.639)
Omnivores	2.50 (0.098)	5.12 (0.012)	4.67 (0.004)
Carnivores	8.13 (0.001)	0.67 (0.517)	0.16 (0.959)
Community-level measures			
F:B ratio ³	63.56 (<0.001)	21.31 (<0.001)	1.02 (0.413)
FF:BF ratio ⁴	2.52 (0.097)	8.07 (0.002)	1.67 (0.181)

¹Data were $\ln(x + 1)$ -transformed to obtain normality and homogeneity of variances

²AMF = arbuscular mycorrhizal fungi

³F:B = fungal:bacterial ratio

⁴FF:BF = ratio of fungal:bacterial feeding nematodes

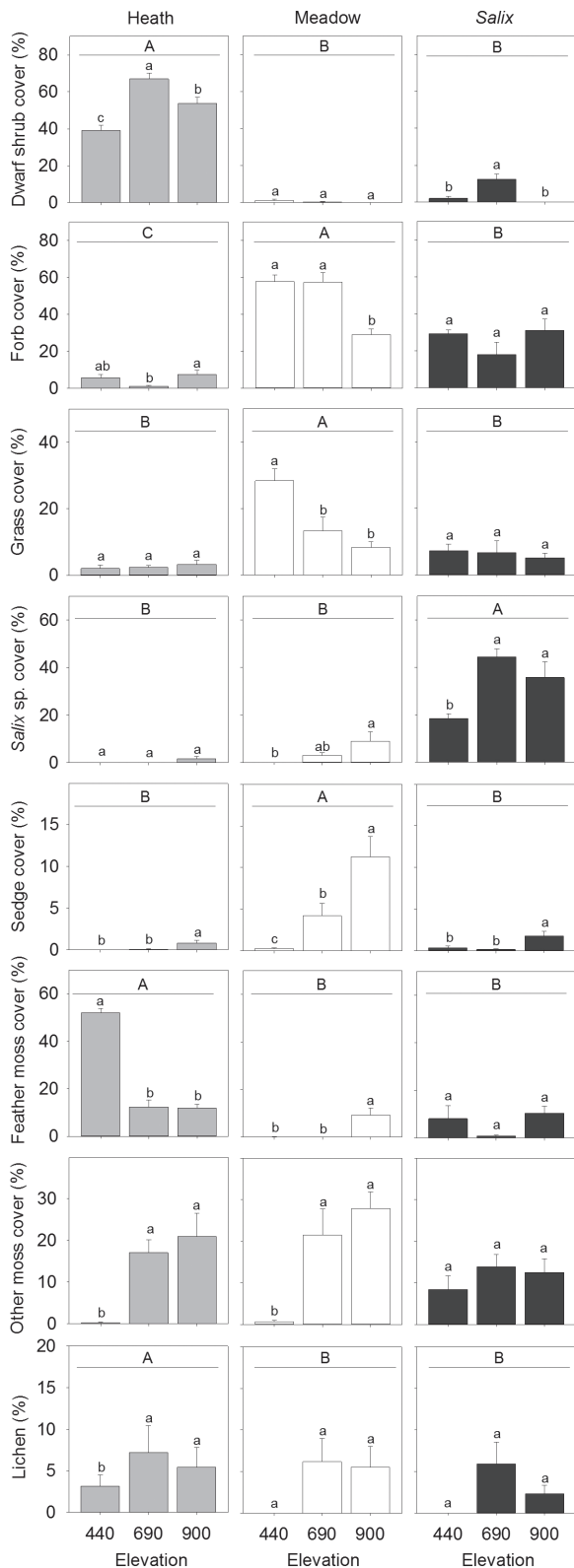


Figure 1. Mean cover (%) per plant functional group (\pm SE) for each vegetation type at each elevation ($n = 5$). For each functional group panels topped by different capital letters indicate that vegetation types were significantly different at $p < 0.05$ (Tukey's HSD test). Within each vegetation type, bars topped by different lower case letters were significantly different at $p < 0.05$ (Tukey's HSD test). ANOVA results are presented in Table 1.

ca 2 to 3 times higher at 440 m than at 690 and 900 m. Forb and grass cover did not differ among elevations for heath and *Salix* vegetation. The cover of feather mosses was ca 4 times higher at 440 m than at 900 m in heath vegetation, while it was ca 100 times lower at 440 than 900 m in meadow vegetation and not different between elevations in *Salix* vegetation.

The community composition of plants was significantly affected by vegetation type, elevation, and their interaction (Fig. 2a, Table 2), with different plant species being characteristic for each of the vegetation types at each of the elevations (Fig. 2a). Although, for each vegetation type we observed shifts in plant community composition along the elevational gradient, these shifts were less pronounced for the heath vegetation than for the meadow and the *Salix* vegetation.

Microbial community responses

The biomass of the different microbial groups was influenced by interactions between vegetation type and elevation, indicating that microbial responses to elevation differed between vegetation types (Table 1, Fig. 3). For example, in meadow vegetation bacterial biomass was lowest at 900 m, while in *Salix* vegetation it was highest at 900 m. Meanwhile, abundance of arbuscular mycorrhizal fungi (AMF) was lower at 900 m than at 440 m in meadow and higher at 900 m than at 440 m in *Salix*.

The fungal:bacterial ratio was affected by vegetation type and elevation, but not their interaction (Fig. 4a, Table 1); the ratio was overall highest in heath vegetation and greatest at 690 m (i.e. the mid elevation).

Microbial community composition was affected by vegetation type and its interaction with elevation, and tended to be affected by the main effect of elevation (Fig. 2b, Table 2). Most bacterial and actinomycete PLFAs were negatively associated with heath vegetation, while the fungal PLFA was positively associated with heath vegetation, particularly at the lower two elevations. Meadow vegetation was positively associated with the majority of bacterial and actinomycete PLFAs. High-elevation meadows differed from low- and mid-elevation meadows in microbial community composition because some PLFA markers were strongly associated with low- and mid-elevation meadows. For *Salix* vegetation, most PLFAs increased with elevation, except the fungal PLFA.

Nematode community responses

The abundance of different nematode feeding groups was generally not influenced by interactive effects of vegetation type and elevation (Fig. 5, Table 1) but rather by their main effects. For example, the abundance of bacterial feeders was highest overall in the heath and lowest in meadow, and was higher at 440 m than at 900 m across all vegetation types. However, we did find interactive effects of vegetation type and elevation for omnivorous nematodes, with the highest abundance at 690 m for meadow, and at 440 m for *Salix*.

The ratio of fungal-feeding nematodes to bacterial-feeding nematodes did not differ between the vegetation types and

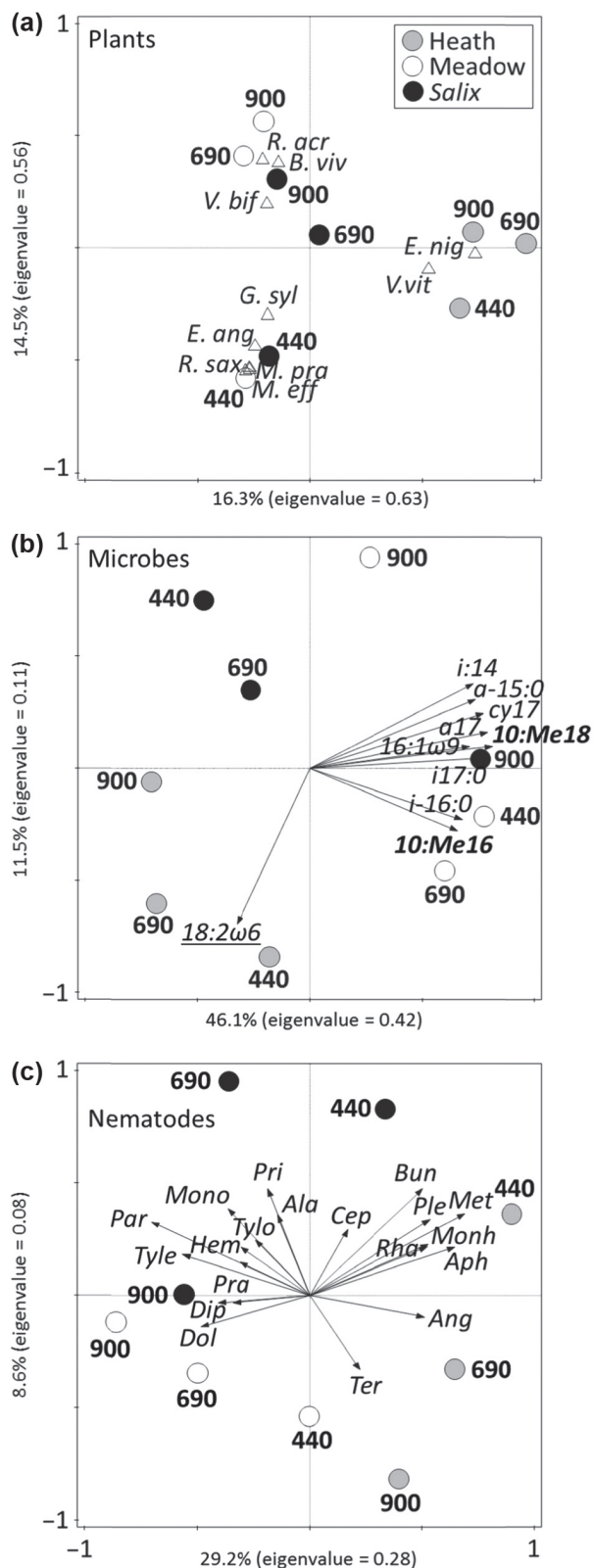


Figure 2. (a) Biplot of CCA of plant community composition. *B. viv* = *Bistorta vivipara*; *E. ang* = *Epilobium angustifolium*; *E. nig* = *Empetrum nigrum*; *G. syl* = *Geranium sylvaticum*; *M. eff* = *Milium effusum*; *M. pra* = *Melampyrum pratense*; *R. acr* = *Ranunculus acris*; *R. sax* = *Rubus saxatilis*; *V. bif* = *Viola biflora*; *V. vit* = *Vaccinium vitis-idaea*. (b) Biplot of RDA of microbial community composition with bacterial PLFAs are represented in italics, fungal PLFAs underlined and actinomycetes PLFAs bold, (c) Biplot of RDA

Table 2. Results of Monte Carlo permutations testing the effects of vegetation type, elevation and their interaction on plant, microbial and nematode community composition. Values represent pseudo F-values (p-values). Values in boldface represent significant effects at $p < 0.05$. For plant communities, effects were tested by canonical correspondence analysis, while for microbial and nematode communities effects were tested using Redundancy analysis (see Methods for details).

	Vegetation type (V)	Elevation (E)	V \times E
Plants	6.3 (<0.001)	5.3 (<0.001)	2.9 (<0.001)
Microbes	9.9 (<0.001)	2.3 (0.062)	6.1 (<0.001)
Nematodes	9.3 (<0.001)	6.0 (<0.001)	1.4 (0.043)

was lowest at 440 m for both heath and meadow vegetation (Fig. 4b, Table 1). Nematode community composition was affected by vegetation type, elevation and their interaction (Fig. 2c, Table 2), with different nematode taxa generally being characteristic for each of the vegetation types at each of the elevations (Fig. 2c). High-elevation meadow communities were negatively associated with nematode families characteristic of low-elevation heath communities. Moreover, low-elevation *Salix* communities were associated with the same families as low-elevation heath communities, while high-elevation *Salix* communities were more similar to high-elevation meadow communities.

Linking composition of plant, microbial and nematode communities

Co-correspondence analyses (CoCA) showed that all communities, except for microbial and nematode communities in the heath, were significantly correlated with each other (Table 3), indicating that the plant and soil communities changed in concert. However, for most communities the amount of variation (i.e. total inertia in Table 3) in the communities was much larger than the variation captured by CoCA (i.e. explained variation in Table 3). This means that the cross-correlations between the communities explained only a relatively small part of the variation in community composition.

The network analyses showed that correlations between (functional) groups of plants, microbes and nematodes and abiotic soil properties differed between vegetation types (Fig. 6). Moreover, the number of coordinated responses across subsets of the ecological community varied among vegetation types (i.e. there were few for heath, more for meadow,

of nematode community composition. *Ala* = *Alaimidae*; *Ang* = *Anguinidae*; *Aph* = *Aphelenchoididae*; *Bun* = *Bunonematidae*; *Cep* = *Cephalobidae*; *Dip* = *Diptherophoridae*; *Dol* = *Dolichodoridae*; *Hem* = *Hemicyclophoridae*; *Met* = *Metateratocephalidae*; *Monh* = *Monhysteridae*; *Mono* = *Mononchidae*; *Par* = *Paratylenchidae*; *Ple* = *Plectidae*; *Pra* = *Pratylenchidae*; *Pri* = *Prismatolaimidae*; *Rha* = *Rhabditidae*; *Ter* = *Teratocephalidae*; *Tyle* = *Tylencholaimidae*; *Tylo* = *Tyloitylenchidae*. In the biplot of the CCA analysis (a) species are represented by centroids; in the biplots of the RDA analyses (b, c) species are represented as arrows. We show the 10 best fitting species for (a), the 10 best fitting PLFAs (phospholipid fatty acids) for (b), and the 20 best fitting taxa for (c), where fit was determined as the percentage of variation explained by the plotted ordination axes. Percentage values presented on each axis indicates the proportion of total variation explained by that axis, with the eigenvalue of that axis presented in parentheses.

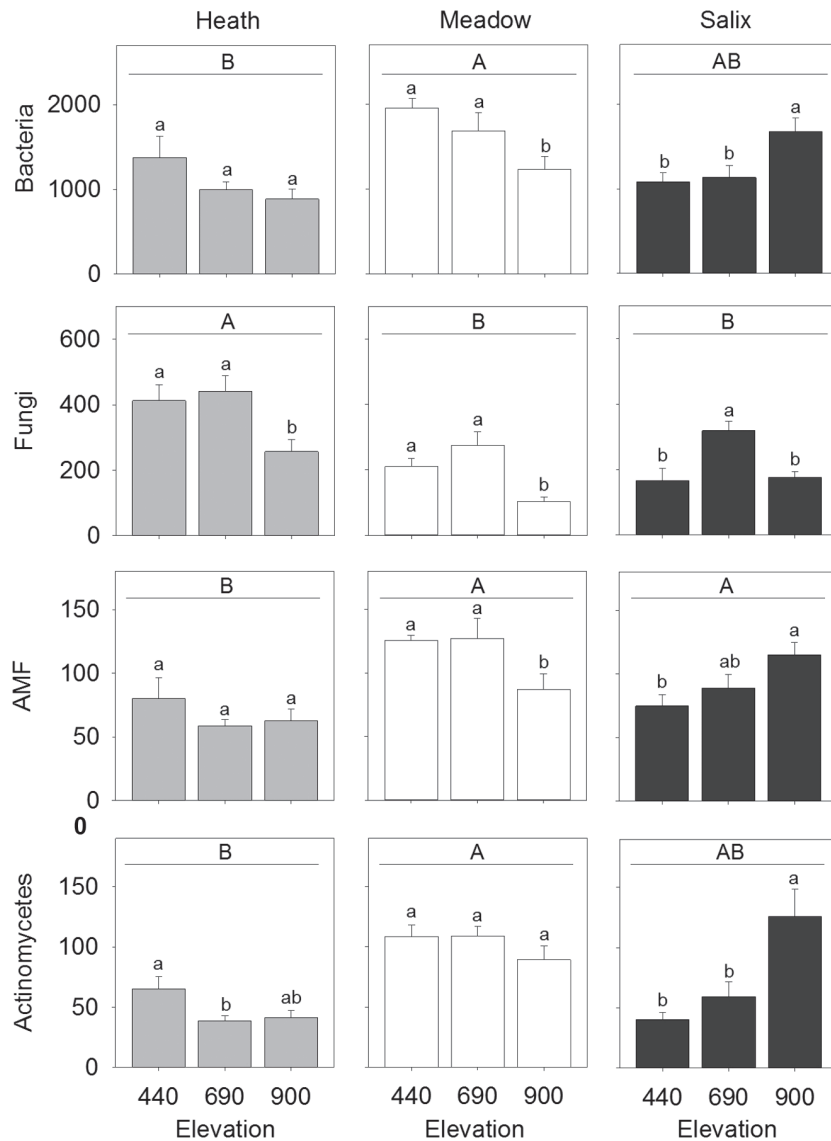


Figure 3. Mean abundance (nmol PLFA g organic matter⁻¹) of microbial functional groups for each vegetation type at each elevation (n = 5). For each functional group, panels topped by different capital letters indicate that vegetation types were significantly different at $p < 0.05$ (Tukey's HSD test). Within each vegetation type, bars topped by different lower case letters were significantly different at $p < 0.05$ (Tukey's HSD test). ANOVA results are presented in Table 1. All values are expressed as nmol PLFA per g soil organic matter. PLFA = phospholipid fatty acids; AMF = arbuscular mycorrhizal fungi.

and most for *Salix* vegetation). Within the plant, microbial and nematode communities, groups that were positively correlated often showed a similar response to elevation. For example, in meadow plant communities, sedges, and mosses were positively correlated with *Salix* and all increased with increasing elevation, whereas grass abundance was negatively correlated to *Salix* and mosses and decreased with increasing elevation. Similarly, in *Salix* vegetation bacterial, actinomycetes and AMF PLFAs were positively correlated with one another and these all increased with increasing elevation, while bacterial-feeding, fungal-feeding and omnivorous nematodes were positively correlated with each other and all decreased with increasing elevation. For all vegetation types there were fewer correlations between plant, microbial and

nematode communities than within each of the communities, but several relationships still occurred. For example, there was a negative correlation between the cover of sedges and the abundance of bacterial-feeding nematodes in heath vegetation, which is in line with their opposing response to elevation. Also, in meadow vegetation there was a negative correlation between *Salix* cover (which increased with elevation) and bacterial-feeding nematodes (which decreased with elevation), while grass cover (which decreased with elevation) was positively related to bacterial-feeding nematodes. The number of correlations in our networks was higher than would be expected by chance for all vegetation types (heath 3.4 times higher, meadow 4.8 times higher and *Salix* 4.6 times; 1000 permutations; $p < 0.001$).

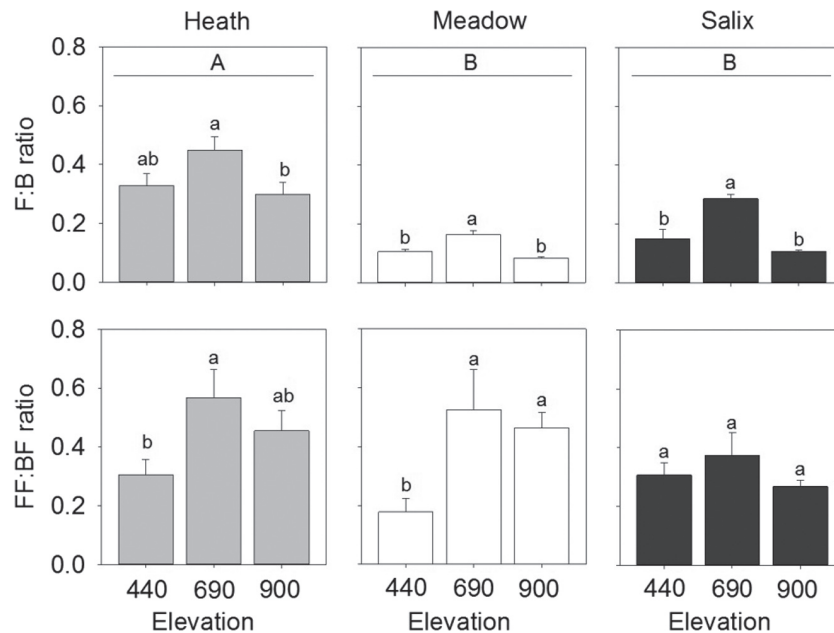


Figure 4. Fungal versus bacterial energy channel ratios for each vegetation type at each elevation ($n = 5$). For each ratio, panels topped by different capital letters indicate that vegetation types were significantly different at $p < 0.05$ (Tukey's HSD test). Within each vegetation type, bars topped by different lower case letters were significantly different at $p < 0.05$ (Tukey's HSD test). ANOVA results are presented in Table 1. F:B ratio = the ratio of fungal to bacterial PLFAs (phospholipid fatty acids); FF:BF ratio = the ratio of fungal feeding nematodes to bacterial feeding nematodes.

Moreover, in all vegetation types the abundances of many (functional) groups were linked to changes in soil abiotic conditions (Fig. 6). For example, SOM was negatively correlated to most microbial PLFAs in heath and *Salix*, while in meadow pH was negatively correlated to changes in fungal and bacterial PLFAs. Notably, for heath and *Salix* vegetation none of the (functional) groups were correlated with shifts in soil temperature, and in meadow only *Salix* and moss cover were negatively, while grass cover was positively, correlated to temperature. In summary, the network analyses revealed that there were some coordinated responses to elevation between (functional) groups, but that these mostly occurred within plant, microbial or nematode communities.

Discussion

We tested how three contrasting vegetation types modulated ecological responses to elevation throughout levels of the soil food web. The abundance and community composition of both microbes and nematodes responded to increasing elevation and these responses varied according to vegetation type. Further, within vegetation types, changes in plant, microbial and nematode community composition co-varied, indicating that community shifts in response to environmental factors across our elevational gradient is likely to be coordinated. Finally, nematode communities shifted towards those known to be associated with more conservative nutrient cycling strategies with increasing elevation in heath and meadow, while for microbial communities, conservative strategies were most pronounced at the mid-elevation. Below we discuss how interactions between plant, microbe and nematode communities respond to increasing

elevation and discuss the implications of these findings for understanding how communities may respond to increases in global temperatures.

Soil communities across vegetation types

In contrast to our first hypothesis, we did not find consistent evidence that soil community responses to elevation were stronger for the meadow, intermediate for the *Salix* vegetation and weakest for the heath. This is because interactive effects of vegetation type and elevation on shifts in the abundance and composition of the soil community did not indicate differences in the magnitude of responses, but rather in their direction (Table 1, Fig. 1–3, 5). However, the direction of both microbial and nematode community responses to elevation was often specific to vegetation type. Different soil food webs from contrasting vegetation types resulted in unique, and sometimes opposite, responses to elevation for each of the three vegetation types. For example, the amounts of bacterial, AMF and actinomycete PLFAs generally decreased with elevation in both heath and meadow vegetation, but often increased in *Salix* vegetation (Fig. 2). Further, the taxonomic composition of nematode communities shifted with elevation, and these shifts were specific to the type of vegetation (Fig. 5c). Such vegetation-specific shifts in soil food web responses to elevation (and thus temperature) may result in contrasting impacts of increasing temperature on key soil ecosystem functions such as plant productivity or nutrient cycling. In contrast, nematode abundances responded in a similar way for all vegetation types, with the abundances for all nematode functional groups generally being lower at higher elevations, likely because of harsher climatic conditions (Dam et al. 2012). Finally, plant-feeding

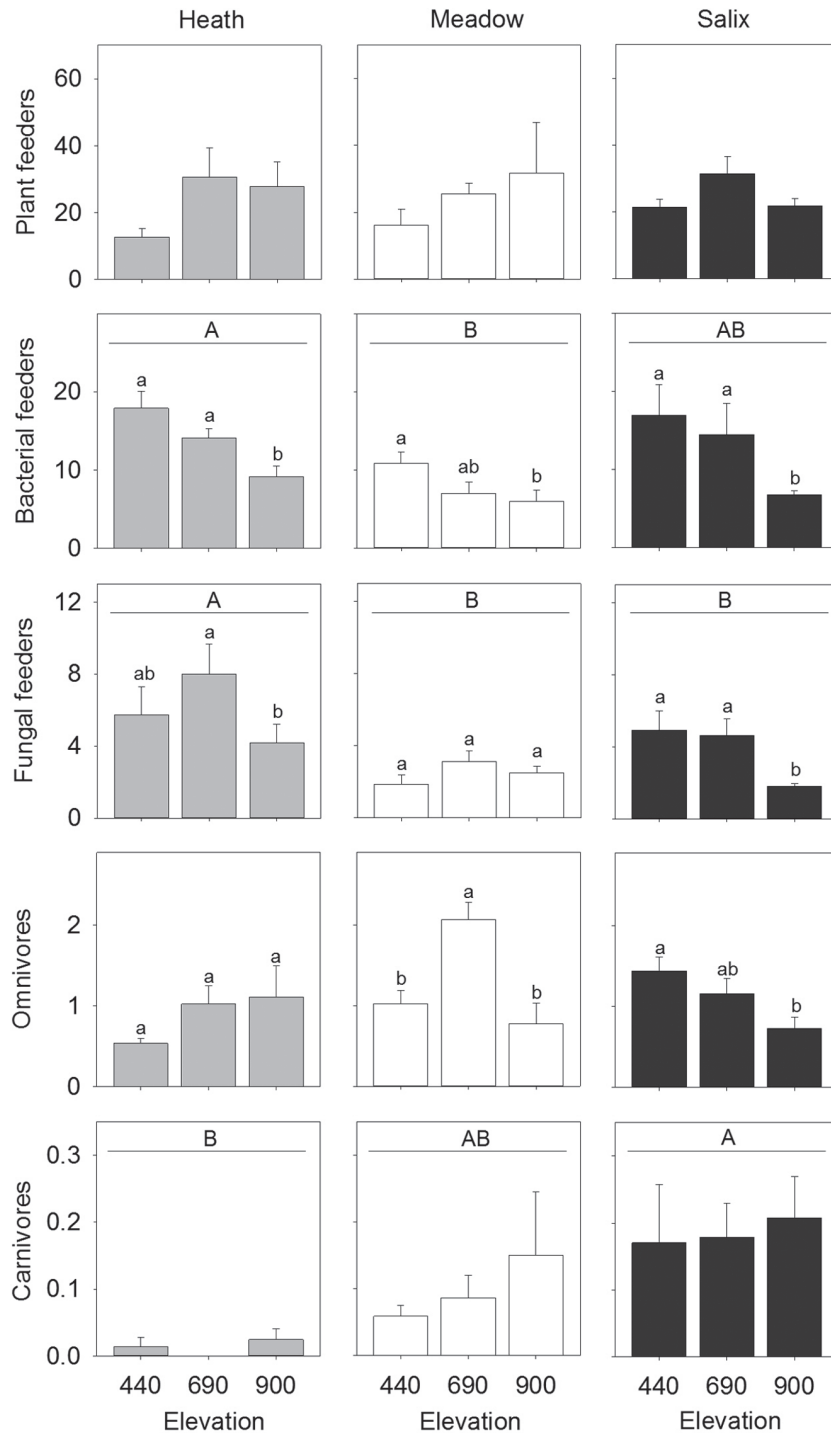


Figure 5. Mean abundance (number g dry soil⁻¹) of nematode feeding groups for each vegetation type at each elevation (n = 5). For each functional group, panels topped by different capital letters indicate that vegetation types were significantly different at $p < 0.05$ (Tukey's HSD test). Within each vegetation type, bars topped by different lower case letters were significantly different at $p < 0.05$ (Tukey's HSD test). ANOVA results are presented in Table 1. All values are expressed as number per g dry soil.

nematodes did not shift in abundance with elevation, suggesting that there is a limited scope for plant-parasitic nematodes to affect plant productivity via levels of herbivory as a result of warming or, conversely, that higher plant productivity with warming does not necessarily increase levels of root herbivory by nematodes (but see Bakonyi and Nagy 2000).

Furthermore, shifts in the abundance and composition of soil organisms with elevation may not only be mediated by vegetation-specific responses of soil organisms to elevation. For example, higher temperatures at lower elevations may directly increase enhance microbial activity, thereby stimulating key ecosystem functions such as nutrient cycling or plant productivity (Frey et al. 2008, Classen et al. 2015).

Table 3. Results of co-correspondence analyses (Co-CA) testing multivariate correlations between plant, microbial, and nematode community composition for each vegetation type across three elevations. Corr. Axes 1 and 2 represent the cross-correlation between the first and second Co-CA axes, respectively; total inertia represents the amount of variation in each community; explained variation represents the amount of variation explained by all Co-CA axes; 1st axis lambda (p)-value represents the test statistic and p-value for testing the cross-correlation between the two communities in the first axis. Significant cross-correlations for the first axes at $p < 0.05$ are represented in boldface.

Community 1	Community 2	Corr. axes 1	Corr. axes 2	Total inertia comm. 1	Total inertia comm. 2	Explained variation (all axes)	1st axis lambda (p)-value
Heath							
Plants	Microbes	0.843	0.912	1.463	0.033	0.007	0.004 (0.043)
Plants	Nematodes	0.936	0.941	1.456	0.257	0.041	0.024 (0.002)
Microbes	Nematodes	0.937	0.892	0.032	0.260	<0.001	0.001 (0.366)
Meadow							
Plants	Microbes	0.930	0.910	2.577	0.031	0.011	0.006 (0.013)
Plants	Nematodes	0.862	0.902	2.593	0.517	0.134	0.064 (0.022)
Microbes	Nematodes	0.841	0.861	0.032	0.507	0.002	0.001 (0.006)
Salix							
Plants	Microbes	0.910	0.933	2.176	0.053	0.015	0.010 (0.020)
Plants	Nematodes	0.967	0.964	2.251	0.356	0.084	0.041 (<0.001)
Microbes	Nematodes	0.845	0.927	0.055	0.354	0.002	0.002 (0.031)

Changes in temperature and other environmental conditions along elevation gradients can also have a strong impact on soil moisture conditions (Supplementary material appendix 1 Table A1) by altering evapotranspiration patterns. As moisture is a key factor driving the composition and functioning of soil communities (Bakonyi and Nagy 2000, Fierer et al. 2003, Brockett et al. 2012), part of the response of soil organisms to changes in elevation may be driven by altered moisture conditions.

Shifts in the relative abundance of fungi and bacteria may be indicative of shifts in nutrient cycling strategies, with an increase in the relative abundance of fungi often being associated with more conservative strategies (Bardgett et al. 1996, de Vries et al. 2012). In our study, the relative abundance of fungi and bacteria (i.e. the fungal:bacterial ratio) did not change unidirectionally with elevation, providing limited support for warming-induced changes in nutrient cycling strategies (Cregger

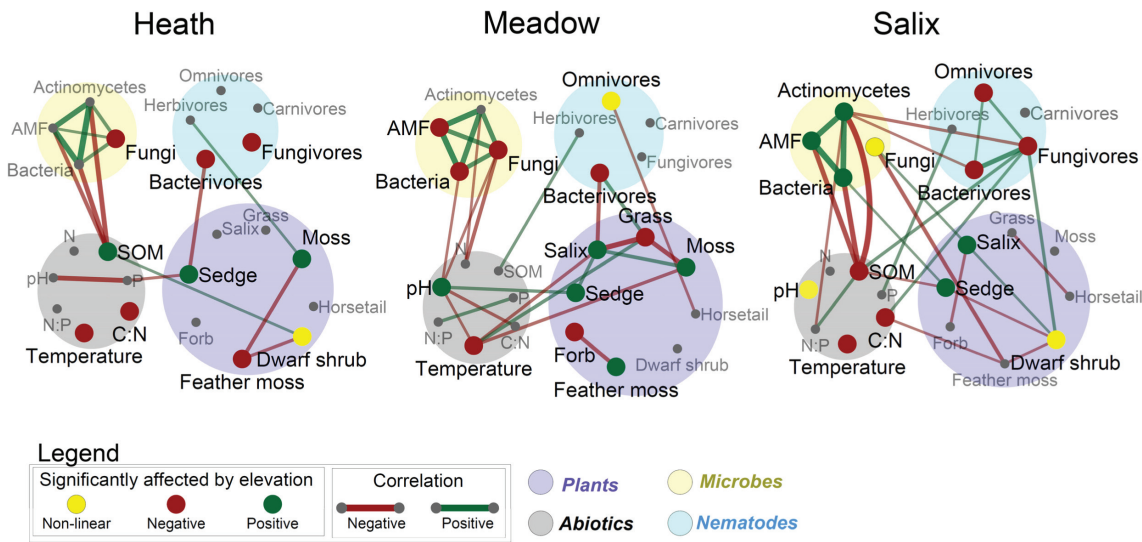


Figure 6. Networks showing Spearman correlations between functional groups and soil abiotic properties for each of three vegetation types, in which the 15 plots for each type represent independent data points. Nodes represent functional groups or abiotic properties. Large nodes represent functional groups or abiotic properties that responded significantly to elevation (ANOVA; $p < 0.05$), and the colour of the large nodes represents the direction of the response to elevation (red = decline with elevation, green = increase with elevation, yellow = unimodal response). Lines between pairs of nodes represent significant correlations with a Spearman correlation coefficient between -1 and -0.6 or between 0.6 and 1 . The width corresponds to the strength of the correlation, as indicated by Spearman's correlation coefficient and the colour with the direction (red = negative; green = positive). By comparing the correlations between each pair of connecting nodes (represented by the connecting lines) we can assess the relationships between them. In total this diagram therefore shows the nature of relationships of functional groups and abiotic properties with elevation and whether they correlate with each other. Abbreviations for soil abiotic properties: N = soil ammonium concentration ($\mu\text{g g}^{-1}$), P = soil phosphate concentration ($\mu\text{g g}^{-1}$), SOM = soil organic matter content (g g^{-1}), C:N = total soil carbon (%) to total soil nitrogen (%) ratio; and Temperature = mean year soil temperature ($^{\circ}\text{C}$; measured between September 2012 and September 2013).

et al. 2014, De Long et al. 2015b, van der Putten et al. 2016). However, in both the heath and meadow vegetation the relative abundance of fungal-feeding to bacterial-feeding nematodes increased towards higher elevations (Fig. 4), indicative of nutrient cycling strategies becoming more conservative with elevation. This is consistent with previous work in this study system (Sundqvist et al. 2011a, Vincent et al. 2014, De Long et al. 2016) and supports findings from other elevational gradients (Pérez and Frangi 2000, Wagai et al. 2011, Wagg et al. 2011, Looby et al. 2016) and warming studies (Cregger et al. 2014, De Long et al. 2015b, van der Putten et al. 2016). The strong response of the nematode community could be due to a greater contribution of nematodes to nutrient cycling at higher elevations, because at these elevations nematodes may replace the role of macrofauna (Kergunteuil et al. 2016). However, in *Salix* vegetation we did not find shifts in the ratio of fungal to bacterial feeders. This may be because there was little change in the relative abundance of dominant plant functional groups in *Salix* vegetation (Fig. 1) and, hence, a relatively constant input of resources across the gradient to the soil food web. Differential responses of microbial and nematode communities in terms of nutrient conservation strategies, as we observed in heath and meadow vegetation types, have also been shown in previous studies (Chen et al. 2015, Wardle et al. 2015). This could be explained by top-down and bottom-up processes having contrasting effects on bacteria and fungi (Rousk et al. 2009) and the nematodes that feed upon them (Wardle and Yeates 1993). Alternatively, fungal and bacterial biomass measures (as provided by PLFA) may not necessarily reflect the growth and activity of these groups, and food webs can therefore be more or less fungal-based in terms of their function than is indicated by biomass alone (Rousk et al. 2009, Strickland and Rousk 2010).

Our study focused on soil community responses to elevation for contrasting vegetation types. However, it is well known that warming will not only induce shifts in plant and soil communities within vegetation types, but will also strongly affect the relative abundance of the different vegetation types themselves (Myers-Smith et al. 2015). As a result, shifts in soil food webs and soil ecosystem functioning within vegetation types could be modified or counteracted by landscape-scale vegetation changes (Bragazza et al. 2015). Generally, it is predicted that warming will enhance shrub dominance in subarctic ecosystems (Sturm et al. 2001, Tape et al. 2006, Walker et al. 2006), which may lead to an increase in soil communities associated with these vegetation types at the landscape level (Eskelinen et al. 2009, de Vries et al. 2012). These landscape-level shifts in dominant vegetation types may be opposite to the within-vegetation type shifts that we found. For example, while warming may favor microbial activity and bacterial-based energy channels within shrub-dominated vegetation types (Fig. 4), landscape-level shrubification (Sturm et al. 2001, Tape et al. 2006, Walker et al. 2006) might result in a shift towards a fungal-based food web (Fig. 2). As a result, landscape-level responses to warming could overrule local-scale responses within vegetation types (Kardol et al. 2010).

Coordinated responses

In partial support of our second hypothesis, the co-correspondence analyses (CoCA) showed that microbial, nematode and plant taxonomic composition often changed in concert (Table 3). Therefore, at the level of plant species, microbial PLFAs and nematode families, there are linkages across groups, indicating that shifts in community composition in response to environmental conditions across our study site may be coordinated. This supports previous work showing that plant community composition exerts a major control on the composition of both microbial and nematode communities (De Deyn et al. 2004, Eskelinen et al. 2009, Veen et al. 2010, Prober et al. 2015), and that soil communities can be important drivers of plant community composition (van der Putten et al. 1993). Our findings indicate that links between plants, microbes and nematodes can be highly species- or taxon-specific (Bezemer et al. 2010).

However, in contrast to our second hypothesis, our network analysis revealed that plant, microbial and nematode community responses showed no or weak coordination at the functional group level in heath and meadow vegetation (Fig. 6). This was apparent through the low density of links in the network within these vegetation types (Fig. 6) and is consistent with the different nutrient cycling strategies found between the microbial and nematode communities (Fig. 4). However, network links between functional groups were more numerous for the *Salix* vegetation than for heath vegetation, and were intermediate for meadow vegetation. This highlights that the degree of coordination between components of the soil communities in their responses to elevation can differ between different types of vegetation. In the more fertile *Salix* and meadow vegetation types, nutrient cycling may have shifted towards less conservative strategies (as indicated by a lower fungal:bacterial ratio; Fig. 4), which may be linked to tighter connections between soil organisms (De Long et al. 2015a). However, abiotic soil conditions such as pH may also directly shape microbial community composition (Fierer and Jackson 2006, Peay et al. 2015). Notably, in nutrient poor systems such as heath vegetation, abiotic drivers may be of greater relative importance (Wardle and Zackrisson 2005), resulting in weaker connections between organisms. Furthermore, strict classification of what constitutes an abiotic versus biotic soil property is often subjective, due to complex relationships between living and non-living compartments of the soil (Bardgett and Wardle 2010). As a result of this interplay between biotic and abiotic soil properties, specific links between species or functional groups may be obscured by responses of plant, microbial and nematode communities to climate-induced changes in soil abiotic conditions (De Long et al. 2015a).

The differences in the degree of coordination between different functional groups observed in the three vegetation types suggest that the response seen within one vegetation type is not necessarily predictive for the responses of other vegetation types (Kardol et al. 2005). This may result in vegetation-specific community responses to climate warming. It has been shown that different subsets of communities (e.g. plants and soil organisms) respond at different rates to changes in climate (Berg et al. 2010, Morrien et al. 2010), and this can lead to decoupling of plant-soil interactions

(Bardgett et al. 2013, van der Putten et al. 2016, Mayor et al. 2017). Notably, vegetation types that show strongly coordinated responses, such as *Salix*, may be vulnerable to decoupled plant and soil responses, creating novel interactions between species and altered community dynamics (Gilman et al. 2010).

Conclusion

Our findings show that soil microbial and nematode communities often responded to elevation in contrasting ways for different vegetation types. This indicates that climate-induced changes in plant community composition may modify or counteract the impact of climate change on soil communities. Within vegetation types, we showed that coordination of plant and soil community responses to elevation can extend across trophic levels in the soil web. Finally, our findings provide some support for an increase in conservative nutrient cycling strategies at higher elevations (i.e. under a harsher climate); however, this was not observed for all vegetation types. Collectively, our results highlight the need to consider vegetation type in aiming to determine how climate change may impact on plant, microbial and nematode communities (Kardol et al. 2010), and in improving the predictive power of models aiming to assess future ecological responses to climate change. Finally, our results indicate that advancing climate change may lead to altered community composition and potential novel interactions between and within trophic groups (Gilman et al. 2010, Bardgett et al. 2013), with likely implications for ecosystem functioning both above- and belowground.

Acknowledgements – We thank Ebba Okfors and Hanna Vestman for their help in the field. We thank Reiner Giesler, the Climate Impact Research Center (Umeå University), and the Abisko Scientific Research Station, Abisko, Sweden for access to their laboratory facilities. Iris Chardon, Rebecca Pas, Margareta Söderström and Debbie Weddle analyzed plant, litter and soil chemical properties.

Funding – GFV was supported by a Rubicon Fellowship from the Netherlands Organisation for Scientific Research (NWO) to GFV. GFV, JRDL, MKS and DAW were supported by a Wallenberg Scholar Award to DAW.

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Supplementary material (available online as Appendix oik-04158 at <www.oikosjournal.org/appendix/oik-04158>). Appendix 1.