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Contrasting responses of springtails and mites to elevation and vegetation type in the sub-Arctic

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ABSTRACT

Climate change is affecting the species composition and functioning of Arctic and sub-Arctic plant and soil communities. Here we studied patterns in soil microarthropod (springtails and mites) communities across a gradient of increasing elevation that spanned 450 m, across which mean temperature declined by approximately 2.5 °C, in sub-Arctic Sweden. Across this gradient we characterized microarthropod communities in each of two types of vegetation, i.e., heath and meadow, to determine whether their responses to declining temperature differed with vegetation type. Mite abundance declined with increasing elevation, while springtail abundance showed the opposite response. Springtail communities were dominated by larger species at higher elevation. Mite abundance was unaffected by vegetation type, while springtail abundance was 53% higher in the heath than meadow vegetation across the gradient. Springtails but not mites responded differently to elevation in heath and meadow vegetation; hemi-edaphic species dominated in the heath at higher elevation while epi-edaphic species dominated in the meadow. Our results suggest that sub-Arctic mite and springtail communities will likely respond in contrasting ways to changes in vegetation and soil properties resulting from climate warming.

1. Introduction

Arctic regions are subject to some of the greatest warming rates on earth, resulting in potentially large changes in vegetation composition, soil communities and soil process rates (AMAP, 2011; Elmendorf et al., 2012; Hartley et al., 2012), all of which could feed back to climate change (Macias-Fauria et al., 2012; Pearson et al., 2013). Understanding the response of each ecosystem component to warming is therefore crucial for understanding future global climate change. Microarthropods, such as springtails (Collembola) and mites (Acari), are major soil biotic drivers of soil nutrient and carbon cycling (Filser, 2002; Seastedt and Crossley, 1980) and changes in their abundance and community composition can greatly affect decomposition rates (Wall et al., 2008). Several experimental climate manipulations aimed at quantifying microarthropod responses to climate warming scenarios have been performed, but these are often relatively short-term (Bokhorst et al., 2008; Convey et al., 2002; Hodkinson et al., 1998; Kardol et al., 2011; Makkonen et al., 2011) and the methodologies can have drawbacks in terms of realism (such as altering the frequency of temperature extremes) or affect multiple microclimate conditions (e.g., moisture deficits, wind speed and shade). This can make it difficult to determine the nature of causality behind response variables (Bokhorst et al., 2013b). Elevational gradients are an alternative approach to quantify climate change effects as they encompass temperature gradients and allow assessment of ecological responses over much larger temporal and spatial scales than is possible through experimental manipulations (Sundqvist et al., 2013). Although many studies have explored the responses of aboveground organisms to elevation (see reviews of Hodkinson, 2005; Sundqvist et al., 2013), fewer have studied whether belowground organisms show similar responses (e.g., Jarvis et al., 2015; Nash et al., 2013; Veen et al., 2017).

Studies that have considered how springtail and mite communities

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Table 1
Soil temperature variables (mean with SE in brackets) in response to elevation (E: 450 m, 700 m and 900 m) and vegetation type (V: heath and meadow) and ANOVA results (*F*-values). Values are mean of five replicate measurements. Numbers within columns followed by different letters are significantly different (Tukey HSD): * < 0.05, ** < 0.01, *** < 0.001. Data was recorded during September 2012 to September 2013 and is derived from Veen et al. (2017).

	Mean annual T (°C)	Degree day sums	Minimum T (°C)	Maximum T (°C)	Temperature range	Freeze-thaw cycles
Heath vegetation						
450 m	2.2 (0.1)^{a}	982 (49)^{a}	−2.1 (0.5)^{a}	12.9 (0.6)	15.0 (1.1)^{a}	10 (4)
700 m	0.2 (0.2)^{b}	808 (38)^{b}	−9.0 (0.9)^{b}	13.6 (1.1)	22.6 (1.7)^{bc}	3 (1)
900 m	0.3 (0.1)^{b}	818 (46)^{b}	−7.3 (0.3)^{b}	13.0 (0.9)	20.3 (1.2)^{abc}	3 (1)
Meadow vegetation						
450 m	3.0 (0.1)^{a}	1266 (63)^{a}	-2.0 (0.6)^{a}	14.9 (0.8)	16.9 (1.3)^{a}	7 (2)
700 m	2.3 (0.5)^{a}	1064 (71)^{b}	-2.7 (0.8)^{a}	14.5 (0.5)	17.2 (0.9)^{ab}	5 (4)
900 m	0.2 (0.5)^{b}	909 (37)^{b}	-9.3 (1.3)^{b}	17.4 (1.2)	26.6 (2.5)^{c}	8 (2)
ANOVA (*F*-values)						
$V_{(1,17)}$	35.4 ***	32.3 ***	6.0 *	9.9 **	0.5	1.2
$E_{(2,17)}$	52.8 ***	13.5 ***	30.7 ***	0.8	12.2 ***	1.9
$V \times E_{(2,17)}$	8.9 **	2.1	14.0 ***	1.7	7.7 **	1.6

respond to elevational gradients show great variability in the response of abundance and richness to elevation (e.g., Hasegawa et al., 2006; Illig et al., 2010; Lamoncha and Crossley, 1998; Nash et al., 2013; Sadaka and Ponge, 2003). These contrasting responses may be due to variation among different elevational gradients in such factors such as vegetation or soil type, precipitation, snowfall, elevational range, and temperature range and extremes, all of which affect microarthropod traits and distribution patterns (Hodkinson, 2005). Vegetation characteristics determine soil properties and food supply for soil microarthropods, thereby affecting their growth and reproduction (Maunsell et al., 2013; Wardle et al., 2004). Vegetation can also promote a spatially heterogeneous environment that selects for a community dominated with sexually reproductive (versus asexually reproductive) taxa (Becks and Agrawal, 2010), which could allow for stronger evolutionary adaptability to environmental changes. Vegetation also greatly affects soil insulation and therefore the soil thermal regime for ectothermic organisms such as microarthropods (Bråten et al., 2012; Kennedy, 1999). As such, vegetation cover mediates temperature extremes at the soil surface (Graae et al., 2012; Shreve, 1924; Walton, 1982); greater temperature extremes may select for microarthropods with life history characteristics such as larger body size and thermal acclimation abilities (Leinaas, 1983; Sømme, 1989; van Dooremalen et al., 2013; Zettel, 2000). In particular, snow is an important insulator against winter freezing and a sufficiently thick snowpack (ca. 20 cm) can greatly insulate the soil against very low ambient temperatures (Bokhorst et al., 2016; Sturm et al., 1997). Therefore, a reduction in snow thickness can strongly affect microarthropod communities due to increased freezing intensity (Bokhorst et al., 2012, 2013a; Coulson et al., 2000; Slatyer et al., 2017). Microarthropod community patterns along elevational gradients are therefore mediated by a complex interplay between vegetation composition and temperature regime, and these may not necessarily change consistently with elevation.

In the present study, we explored how springtails and mites responded to elevation for each of two highly contrasting types of vegetation, i.e., heath and meadow, along an elevational gradient ranging from 450 m to 900 m in sub-Arctic Sweden. Mean summer soil temperature differs by about 2.5 °C between the lowest and highest elevations of this gradient for both vegetation types (Veen et al., 2017). The heath vegetation is dominated by typical tundra dwarf shrub species such as *Vaccinium vitis-idaea*, *V. uliginosum, Empetrum hermaphroditum* and *Betula nana* and the soil has a high organic matter content, with a low pH (4.5) and a high ratio of soil fungi to bacteria (Veen et al., 2017). In contrast, the meadow vegetation is dominated by graminoids and herbs and the soil contains less organic material, has a higher pH (5.5) and supports a lower ratio of fungi to bacteria (Veen et al., 2017). As soil organic matter content and fungal biomass are important resources for most soil microarthropods (Filser, 2002; Illig et al., 2010), we expected higher soil microarthropod abundance in heath vegetation than in meadow vegetation. By comparing the soil microarthropod responses between two contrasting vegetation types we aimed to better understand which factors play a dominant role as potential drivers of soil community composition along elevational gradients.

We tested three hypotheses. First, we hypothesized that microarthropod abundance and richness would decline with increasing elevation due to lower temperatures and increasing soil temperature variability in our study system. Second, we hypothesized that the microarthropod community would become dominated by larger and surface-dwelling species with sexual reproduction at higher elevations. This is because larger surface-dwelling microarthropod species tend to have better thermal acclimation capabilities that enable them to cope with the colder conditions encountered at higher elevations (van Dooremalen et al., 2013; Zettel, 2000). Third, we hypothesized that the heath vegetation would support higher microarthropod abundance due to the thicker soil organic layer (Filser, 2002; Wall et al., 2008), and that this difference between vegetation types persists with increasing elevation. Together, addressing these hypotheses will increase our understanding of how changing temperatures influence soil microarthropod communities in sub-Arctic landscapes and how this effect is mediated by vegetation type.

2. Materials and methods

The study was conducted along an elevational gradient ranging from 450 m to 900 m elevation on the north-east facing slope of Mt Suorooaívi (1193 m a.s.l.), approximately 20 km south-east of Abisko in sub-Arctic Sweden (68°21′N, 18°49′E). For this gradient, mean annual temperature declines with elevation from about 2.5 °C at 450 m to close to 0 °C at 900 m (Table 1). The gradient starts in open birch forest (*Betula pubescens* ssp. *czerepanovii*) at 450 m while the sites at 700 m and 900 m are in open tundra. These vegetation changes integrate the ecosystem and soil characteristics that result from climate differences along the elevational gradient. Along this gradient there are two distinct vegetation types that occur at all elevations, i.e., heath vegetation and meadow vegetation. Based on previous findings from this study system, we know that changes in soil nutrient concentrations, notably phosphorus (Vincent et al., 2014), and organic matter content (Veen et al., 2017) increased consistently with elevation in the heath but not in the meadow (Table S1).

Soil sampling for the present study was done at each of three elevations (450 m, 700 m and 900 m) for each of the two vegetation types. The sampling sites at 450 m were within open birch forest (*Betula pubescens* ssp. *czerepanovii*), while the sites at 700 m and 900 m were above the tree line. The sampling points were within 50 cm of the study plots of previous work done on vegetation and soil characteristics along