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How extreme is an extreme climatic event to a subarctic peatland springtail community?

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ABSTRACT

Extreme climate events are increasing in frequency and duration and may directly impact belowground foodwebs and the activities of component soil organisms. The soil invertebrate community, which includes keystone decomposers, might respond to these newly induced soil microclimate conditions by shifts in density, species composition, spatial patterning and/or functional traits.

To test if and how short-term extreme climatic conditions alter the structure, the vertical stratification and the community weighted trait means of the springtail (Collembola) community in sub-arctic peatbogs, we experimentally subjected *Sphagnum* peat cores in a field setting to factorial treatments of elevated temperature and episodically increased moisture content.

The large precipitation peaks did not affect the springtail community, but an average soil temperature increase of 4 °C halved its density in the shallower peat layers, mainly caused by the reduced dominance of *Folsomia quadrioculata*. A hypothesized net downward shift of the surface-dwelling springtail community, however, was not observed. We observed species-specific responses to warming but the overall community composition in subsequent organic layers was not significantly altered. Although the effects of an extreme warming event on density, species composition and vertical stratification pattern seemed subtle, functional trait analysis revealed directional community responses, i.e. an overall increase of soil-dwelling species due to warming, even though warming did not alter layer-specific community weighted trait means.

We suggest that subtle changes in moisture conditions, due to increased evapotranspiration, have decreased typically surface-dwelling species relative to soil-dwelling species. The extent to which this directional change in the community is maintained after an extreme event, and its costs for the community's resilience to multiple sequential extreme events will consequently determine its longer-term effects on the community and on ecosystem functioning.

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1. Introduction

One of the major concerns with respect to global climate change is an expected increase in frequency and duration of extreme climate events (Hansen et al., 2012). Relatively short periods of extreme temperatures, drought or high precipitation can lead to changes in species' physiological performance, relative abundances or even local-to-regional extinctions and altered distribution patterns (Easterling et al., 2000; Smith, 2011). Arctic regions are known to be particularly sensitive to climate change and extreme climatic events (Marchand et al., 2005; Post et al., 2009) which may impact on ecosystem processes such as soil organic matter breakdown through their effects on the decomposer community. For example, experimentally applying a short episode of extreme winter warming in sub-arctic tundra caused strong shifts in its soil invertebrate community structure (Bokhorst et al., 2012).

Microbivorous springtails and mites are a keystone group of soil invertebrates in arctic ecosystems (Woodin and Marquis, 1997). Although they only modestly contribute to carbon (C) turnover, their control over the biomass and activity of microbial decomposers (Lavelle, 1997; Hättenschwiler et al., 2005) can have a large impact on nitrogen (N) and C dynamics (Osler and Sommerkorn, 2007). The net effects of their activity on these dynamics are mainly dependent on: 1) their abundance; because low grazing pressure on fungi can stimulate microbial activity (Lussenhop, 1992) while high grazing pressure slows down microbial activity (Bardgett et al., 1993), 2) their identity; different species assemblages might be functionally different (Faber and

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Verhoef, 1991) and 3) the quality of the substrate; breakdown of more N-rich litter results in net N mobilization while litter with a high (easily degradable) C content leads to immobilization of N (Berg, 2000). However, these factors vary considerably throughout most soils.

In Arctic soils, strong short-scale vertical gradients of microclimate (temperature and humidity) and quality (in terms of C/N or lignin/N ratios) of decomposing litter and soil invertebrate abundance exist. Temperatures generally decline strongly down the soil profile, whereas deeper layers tend to be more humid. Shallow organic layers contain relatively easily degradable sugars, while in deeper organic layers lignin/N ratios tend to get higher and litter quality declines (Berg, 2000). These short-scale gradients in microclimate and substrate quality are generally considered to be the main responsible for soil invertebrate vertical distribution (Ponge, 2000; Berg and Bengtsson, 2007; Krab et al., 2010) as soil invertebrate abundances decline deeper down the soil profile (Ponge, 2000) and organic layers host typical species assemblages (Berg et al., 1998; Faber and Joosse, 1993; Krab et al., 2010).

Global warming will increase summer air and soil temperature and also short periods of heavy rain in arctic regions (ACIA, 2005), which can soak peatland soils. Extreme events will alter the short-scale gradient in soil temperature and moisture across soil depth. These new microclimatic conditions potentially affect the activity and vertical distribution of soil invertebrates, which are known to be sensitive to changes in moisture and temperature (Lindberg et al., 2005; Huhta and Hanninen, 2001; Krab et al., 2010; Makkonen et al., 2011). The responses of soil invertebrates to these changes seem to be species-specific and dependent on their functional traits. For example soil-dwelling, euedaphic species and surface-dwelling, epigeic species, seem to respond stronger to alterations in microclimatic conditions than intermediate located hemiedaphic species or vertically broad-ranging species (Krab et al., 2010; Makkonen et al., 2011; Bokhorst et al., 2012). This implies that changes in soil microclimate due to climate change might lead to new soil invertebrate community structures, where both overall abundances and layer-specific species composition could change.

Changes in community structure are in turn expected to impact processes to which soil invertebrates contribute, since functional roles of different soil invertebrates in C and N cycling vary vertically between decomposing layers (Faber, 1991; Kandeler et al., 1999), and between species (Heemsbergen et al., 2004; Chahartaghi et al., 2005). Climate warming has been shown to have potentially large effects on soil processes protruding down into the soil (Dorrepaal et al., 2009), and these observed effects have been shown to be strongly linked to increased activity of soil invertebrates deeper down the soil profile (Briones et al., 2007). However, to our knowledge, it has never been explicitly tested whether vertical distribution shifts of the soil invertebrate community occur due to changes in precipitation, temperature, or to both in combination, and whether such distribution shifts are community-wide or species-specific.

Due to the interaction between warming and soil moisture content, peatland soil invertebrate community responses to temperature changes or alterations in moisture content could not be tested explicitly in previous studies (Shaver et al., 2006; Strack et al., 2009; Makkonen et al., 2011). Here, we present the first explicit test of such interactions through a unique factorial experiment in which we subjected *Sphagnum* peat cores to elevated temperatures and episodically increased moisture content *in situ* in a sub-arctic peatland and investigated springtail community response to changes in soil microclimate. We hypothesize that the warming treatment will cause a net downward shift of springtails (due to increased evaporation causing drought), while moisture addition will cause a net upward shift (due to more beneficial moisture conditions in the top layers for soil-dwelling springtails). Further, we expect these shifts to differ between species, and to lead to altered layer-specific species assemblages. Finally, we will assess if species-specific traits that relate to microclimate, i.e. moisture preference, vertical stratification preference and body size, can be used to reveal mechanisms behind community responses.

2. Methods

2.1. Study site

The experiment was conducted on a blanket bog on a slope near lake Torneträsk, in Abisko, Sweden (68°21′N, 18°49′E), at an elevation of 340–370 m above sea level. The average summer temperature is 11 °C and there is an average annual precipitation of 300 mm (Abisko Scientific Research Station, Meteorological Station). This blanket bog is dominated by the moss *Sphagnum fuscum* (Schimp.) H. Klinggr., which grows intermingled with vascular plants (with a cover of about 25%) that mainly consists of *Empetrum hermaphroditum* Hagerup., *Betula nana* L., and *Calamagrostis lapponica* (Wahlenb.) Hartm. (Aerts et al., 2009). The experiment ran for 17 days, from the 28th of July until the 14th of August 2011, which is in the middle of the growing season.

2.2. Experimental setup

The experiment followed a full factorial randomized block design with five blocks, each consisting of four treatments: a control, a water addition treatment, a warming treatment and a combined warming and water addition treatment. The treatments were executed in plots of 70 × 70 cm that each contained two transparent Perspex cylinders (Ø 12 cm, 20 cm long) that were inserted into the peat profile (the top flush with the surface) in the centre of the plot one day before the start of the experiment. The cylinders were placed at least 10 cm apart. Pilot studies had shown that these Perspex cylinders were necessary to prevent horizontal efflux of water in the precipitation treatments to the untreated surroundings, which acted as a sink for additional water. One of each pair of Perspex cylinders was used for sampling springtails while the other was used for logging temperature and moisture content, limiting disturbance to the soil fauna.

Warming was obtained using Perspex tents. The tents were octagonal (Ø 53 cm, surface area ~ 2780 cm^2) 22 cm high Perspex walls covered with a transparent plastic sheet, with 2 small openings (5 cm^2) between the walls and the sheet for ventilation. The tents were placed in the centre of the 70 × 70 cm plots covering the two Perspex cylinders that were centred in the plots.

The water addition treatment consisted of simulating a total additional daily precipitation of 22.5 mm (382.5 mm over the entire experiment), by steadily watering each plot with 3.7 l water three times a day using a watering can (intervals of approximately 6 h). We used water from lake Torneträsk to mimic extreme precipitation events (Makkonen et al. 2012). This amount of precipitation reflected realistic values for a very rainy day or three heavy rain showers in the area (Abisko Scientific Research Station, Meteorological Station). Since the tents were blocked off from precipitation, the amount of ambient rainfall was compensated for in these plots.

2.3. Microclimate measurements

In four of the five blocks, plots had one soil moisture sensor (EC-5 Soil Moisture Smart Sensor – S-SMC-M005) and one temperature sensor (12-Bit Temp Smart Sensor – S-TMB-M006) inserted vertically in the *Sphagnum* core contained by the Perspex cylinder; both

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