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Long-term multifactorial climate change impacts on mesofaunal biomass and nitrogen content

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ABSTRACT

Rising atmospheric CO_2 concentration accompanied by temperature increases and altered precipitation patterns calls for assessment of long-term effects of these climatic changes on soil organisms that are essential for ecosystem functioning.

In a long-term, full-factorial climate change field experiment, with factors elevated atmospheric CO_2 concentration, warming and prolonged summer drought, we assessed the responses of Collembola, oribatid and mesostigmatic mites and enchytraeid worms after 8 years of treatment. Both the biomasses and N content of oribatid and mesostigmatic mites increased at elevated CO_2, or tended do so. In contrast, enchytraeid N content decreased at elevated CO_2. Soil microbial biomass N pool and litter C:N ratio also increased with elevated CO_2, which suggests that mite biomasses are more coupled to microbial biomass, whereas enchytraeid biomass to a larger extent is governed by litter nitrogen concentration, i.e. litter quality. Structural equation modelling confirmed the positive coupling between soil microbial N content and oribatid biomass and further between oribatid and mesostigmatic biomass. The SEM also revealed a negative relationship between microbial N content and enchytraeid biomass.

The biomass of all mesofaunal groups was reduced by spring drought, especially when combined with warming. Enchytraeid and especially collembolan biomass suffered greater drought declines than mite biomasses.

We conclude that under long-term elevated CO_2 exposure, energy and elements will to a larger extent pass through decomposer organisms such as oribatid mites, which are based on food sources with relatively high nitrogen content.

After eight years of repeated spring drought events, soil mesofauna did not show signs of adaptation to acute stress effects imposed by drought. However, Collembola and enchytraeids were more drought-sensitive than mites, and although the soil temperature increase in warmed treatments was very modest, warming exacerbated the drying of soil and thus also the negative drought impact on soil mesofauna.

1. Introduction

The globally rising atmospheric CO_2 concentration since the beginning of industrialization is accompanied by climatic changes, the magnitude, pace and direction of which varies at regional scales. In Northern Europe we expect an annual mean temperature increase between 0.1 and 0.4 °C per decade and more extreme precipitation patterns, for instance prolonged summer droughts (IPCC, 2013).

During recent years, global change has prompted substantial research into the potential effects of increased atmospheric CO_2, elevated temperature and drought events on ecosystem functioning (e.g. Phillips et al., 2011; Reinsch et al., 2013) and organisms (e.g. Maraldo et al., 2010; Kardol et al., 2011; Blankinship et al., 2011). Given that we already see, or expect to see, these factors changing rapidly during the coming decades it is relevant to study the effects elicited by such changes. CO_2 level, temperature and drought may interact in ways that are not easily extrapolated from single-factor effects. For instance, when applied as a single factor, elevated CO_2 increased net primary production of a temperate grassland, but the positive effect of warming and increased precipitation on net primary production decreased when warming

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and increased precipitation were combined with elevated CO_2 (Shaw et al., 2002). Hence, the predictive power of studies that only consider a single or two factors may be limited.

Soil mesofauna is central for the functioning of terrestrial ecosystems, especially microbial decomposition and nutrient turnover, both of which are usually stimulated by microarthropods and oligochaetes (Laakso and Setälä, 1999; Kampichler and Bruckner, 2009). Detritivores, e.g. oribatid mites and enchytraeids, physically comminute dead organic matter, and soil and detritus are mixed upon passage through the enchytraeid gut (Abrahamsen, 1990; Didden, 1990; Marinissen and Didden, 1997), both of which facilitate microbial decomposition. Further, faunal excretion of ammonium may stimulate microbial degradation processes. Predatory mesofauna, e.g. mesostigmatic mites, also impact ecosystem functioning via top-down effects on herbivore nematodes and detritivore and microbivore nematodes and microarthropods (Koehler, 1999).

Elevated CO_2, warming and prolonged summer droughts as well as the combination of these factors potentially influence the mesofauna both directly and indirectly. Enchytraeids, not least *Cognettia sphagnetorum*, the dominant species in many heathlands, including the one studied here, are very vulnerable to low soil moisture (Maraldo et al., 2008, 2009), but populations may recover within months depending on the drought intensity (Maraldo and Holmstrup, 2009; Holmstrup et al., 2012). Although Collembola and certainly mites are less vulnerable to low soil moisture, drought also reduced their numbers in some (Lindberg et al., 2002; Petersen, 2011), but not all (Kardol et al., 2011) studies. Indirectly, drought-induced decline in microbial activity or changes in microbial community composition and litter quantity and quality may impact decomposer organisms.

Elevated atmospheric CO_2 probably have negligible direct effects on soil-dwelling mesofauna, as they are adapted to high CO_2 concentrations in the soil environment (van Veen et al., 1991). However, increased primary production followed by increasing litter and root turnover at elevated atmospheric CO_2 levels, which has been documented at our heathland site (Arndal et al., 2013, 2014) and in other ecosystems (Lipson et al., 2005; Adair et al., 2009; Dijkstra et al., 2010) can have cascading effects on decomposer organisms. Further, litter quality changes in response to elevated CO_2, e.g. C:N ratio increases (Andresen et al., 2009; Larsen et al., 2011; Dray et al., 2014) and altered root exudation quantity and quality (Hodge et al., 1998; Phillips et al., 2011) may also change dynamics in the decomposer food web (Dray et al., 2014).

In temperate Northern Europe the predicted temperature increase will probably only have modest direct effects on mesofauna. However, even modest warming may enhance evaporation and exacerbate drought effects. On the other hand, elevated CO_2 may reduce stomatal evapotranspiration and hence counteract negative effects of drought on soil moisture (Ainsworth and Rogers, 2007). This clearly illustrates that anticipated climate change effects on decomposer fauna cannot be thoroughly evaluated unless combined effects of single climate factors are evaluated.

Further, the individual and combined effects of elevated CO_2, warming and drought events on ecosystems and organisms must be considered on a long-term scale. Vegetation responses may build up over several growth seasons, and the potential indirect effects of altered primary production, root exudation, litter quality, vegetation composition, microbial abundance and community composition may take several years to manifest at the higher trophic levels of the decomposer food web.

Recently, there has been a remarkable advance in the empirical modelling of ecological processes using structural equation modelling (SEM) that allows parameterizing complex models with many parameters and latent variables. It has been demonstrated how the use of these modelling techniques provides unprecedented possibilities for detecting causal ecological relationships, testing compound ecological hypotheses, and making ecological predictions with quantitative estimates of the uncertainty that is associated with ecological predictions (e.g. Grace et al., 2010, 2011; Damgaard et al., 2014). More specifically, the effect of global change on soil food webs and biodiversity has been investigated by Eisenhauer et al. (2012), where SEM revealed cascading effects of elevated CO_2 on constituents of the soil food web at the Cedar Creek BioCON experiment in Minnesota, USA. Here we apply SEM to investigate complex relationships between climate change factors, litter quality, soil microbial N and decomposer mesofauna.

The CLIMAITE experiment gives us the opportunity to study the long-term (eight years) effects of elevated CO_2, warming and repeated spring drought applied both as single treatments and in all possible treatment combinations. We hypothesize: 1. with increased primary production at elevated CO_2 more plant litter and microbial production is available for detritivores and microbivores; hence through cascading effects, elevated CO_2 will increase mesofaunal biomass; 2. with decreased plant and litter nitrogen concentration at elevated CO_2 detritivores become nitrogen limited; 3. drought will decrease decomposer fauna biomass, and 4. we expect that Collembola and enchytraeids are more drought-sensitive than mites; 5. we expect that warming will exacerbate the negative effect of drought on decomposer fauna, whereas 6. elevated CO_2 will indirectly reduce the negative effect of drought via reduced stomatal evapotranspiration, which counteracts soil moisture loss. We do not expect warming alone or combined with elevated CO_2 to impact mesofaunal biomass.

2. Materials and methods

2.1. Experimental set-up

The CLIMAITE field site is a dry heathland/grassland ecosystem situated in North Zealand, Denmark (55°53′N, 11°58′E). The soil is a nutrient-poor sandy deposit, and *Deschampsia flexuosa* and *Calluna vulgaris* dominate the vegetation. Mean annual temperature is 8.0 °C, and mean annual precipitation is 613 mm.

The experiment was initiated in October 2005 with the following treatments: elevated atmospheric CO_2 concentration (CO_2), increased temperature (T), prolonged drought in late spring or summer (D) and ambient control treatments (A). We applied all treatments singly and in all possible combinations (A, T, D, TD, CO_2, TCO_2, DCO_2, $TDCO_2$). All treatments were replicated six times in a split plot design with six octagons exposed to ambient CO_2 concentrations and six octagons fumigated with additional CO_2. Each octagon was 6.8 m in diameter, and each of the four treatment plots within individual octagons was 9.1 m^2. To prevent CO_2 contamination of ambient CO_2 octagons from neighbouring CO_2 fumigated octagons the minimum distance between octagons was at least 17 m.

In CO_2-fumigated octagons we applied CO_2 by a Free Air Carbon Enrichment (FACE) system from 30 min after sunrise to 30 min before sunset all year round, except during periods with full snow cover of the vegetation. The target CO_2 concentration in fumigated octagons was 510 ppm. The daytime CO_2 concentrations in non-fumigated (ambient CO_2) and CO_2-fumigated octagons recorded during 2011 and 2012 are shown in Fig. 1. We raised the temperature in T plots by passive night-time warming, where a curtain in 0.5 m height that reflects the outgoing infrared radiation covered the vegetation from sunset to sunrise. In case of rain or heavy winds (>7 m s^{-1}) during the night the curtains were automatically retracted to avoid hydrological disturbance or damage to the curtains. Once a year precipitation was excluded from drought plots for approximately one month during late spring