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Combined effects of abiotic factors on Collembola communities reveal precipitation may act as a disturbance

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ABSTRACT

Global increases in temperature and atmospheric CO_2, coupled with increasingly sporadic and intense precipitation regimes, may affect the biodiversity of boreal forest communities, potentially leading to shifts in functional process rates such as decomposition. However, the effects of these factors on microarthropod community composition have not been thoroughly studied in combination in controlled settings. We conducted a full factorial experiment exposing moss/soil mesocosms to three temperatures (11.5, 15.5, and 19.5 °C), two CO_2 levels (430 ppm and 750 ppm), and three moisture levels (drought, intermediate, and saturated conditions) for 18 weeks. Following treatment, we quantified effects on species diversity of a representative group of mesofaunal microarthropods, the Collembola. We also quantified the effects of these factors on the distribution of collembolan body sizes as an indicator of functional changes in the community. We found that moisture regime was a dominant factor, with increased precipitation leading to decreased collembolan abundance and richness. The mechanisms of these detrimental effects are unclear but may be due to the saturation of air-filled soil pore space or competition with moisture-tolerant species. Severe precipitation regimes caused a general loss of abundance in species of all sizes, which may have long term effects on boreal forest soil food webs.

1. Introduction

The Canadian boreal forest is predicted to be strongly affected by global environmental change with predicted temperature increases between 2 and 8 °C by 2100 and global increases in atmospheric CO_2 concentrations rising to 540–970 ppm by the end of the century (IPCC, 2013). Additionally, there is a high likelihood of a 0.1–0.4 mm increase in annual mean daily precipitation rate in this region by 2100, delivered by more sporadic and intense precipitation events compared to the historic norms (IPCC, 2013). Previous studies have shown that these changes in the intensity and frequency of precipitation events may act as a disturbance that can shape forest biodiversity through both drought (e.g. Archaux and Wolters, 2006) and flooding (e.g. Chaneton and Facelli, 1991; Bornette and Amoros, 1996).

Soil biodiversity contributes substantially to overall boreal forest biodiversity, (e.g. Chagnon et al., 2000) and plays an important role in decomposition and nutrient cycling processes. It has been suggested that soil fauna in northern boreal forests and soil mesofauna (Acari and Collembola) in particular are especially important drivers of microbial community structure and ecosystem function because of the relatively low diversity and abundance of macrofauna which stimulate microbial communities in other systems (Swift et al., 1979). Changes in soil biodiversity and community structure as a result of environmental change could change soil fauna functions, with ramifications for C cycles at regional scales (Wall et al., 2008), because boreal systems represent a major global carbon sink (Nielsen et al., 2011). Understanding how both long-term changes in prevailing conditions (such as increased temperature and atmospheric $[CO_2]$) and short-term disturbance events (such as drought or precipitation) can affect soil biodiversity (Blankinship et al., 2011; Kardol et al., 2011) can be difficult as there is strong potential for interactions between these factors; increased temperatures are expected to decrease soil moisture content through evaporation (IPCC, 2013), but increased atmospheric $[CO_2]$ may decrease evapotranspiration by plants and therefore increase soil moisture content (Dermody et al., 2007). Increased CO_2 may also alter plant growth rates where other nutrients are not limiting, leading to changes in litter and root resource quality (e.g. Ruf et al., 2006). Many previous experiments on the effects of global

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environmental change factors on soil mesofauna have examined the effects of temperature, CO_2, and precipitation regimes separately, despite the fact that they will each be changing simultaneously (e.g. Hansen et al., 2001; Tsiafouli et al., 2005; Briones et al., 2009).

One mesofaunal group of particular interest is the Collembola (Hexapoda: Entognatha) due to their ubiquity, high densities, and central position in soil food webs. Previous studies have noted drought sensitivity in Collembola, reporting decreased abundances and species richness (Pflug and Wolters, 2001; Tsiafouli et al., 2005; Kardol et al., 2011; Makkonen et al., 2011), with desiccation intolerance related to their small size, cutaneous respiration, and relatively thin exoskeleton (Tsiafouli et al., 2005; Bellinger et al., 2014). Smaller species with higher surface area to volume ratios are especially susceptible to desiccation (Krab et al., 2010; Makkonen et al., 2011) and as such, are generally euedaphic (dwelling deeper in the soil profile). The effects of changes in temperature and atmospheric CO_2 on Collembola are not as well studied as soil moisture effects (Blankinship et al., 2011). Kardol et al. (2011) who present the interactive effects of increased temperature (+3 °C), increased CO_2 (+300 ppm), and drought conditions (−3.9% moisture) found a positive correlation between moisture content and collembolan richness; however, there were no effects of increased temperature or CO_2 when the effects on soil moisture were controlled for.

The effects of environmental change on soil microarthropod communities are typically quantified in terms of abundance, species richness, and diversity using species-level taxonomic resolution (e.g. Pflug and Wolters, 2001; Krab et al., 2014; Salmon et al., 2014). Although taxonomic approaches are common, shifts in the richness and abundance of species do not necessarily equate to shifts in ecosystem function (Lavelle et al., 2006; Coleman, 2008; Lavelle, 2009). As such, several ecologists have begun to quantify the diversity of traits in biological communities to better quantify the relationship between biodiversity and ecosystem function (see McGill et al., 2006). It has been shown that traits are better able to predict responses to disturbance than species identities (Mouillot et al., 2013), and that trait diversity is a better predictor of ecosystem function than species diversity (Petchey et al., 2004; Cadotte et al., 2011; Lavorel and Grigulis, 2012). Trait-based approaches have only very recently been applied to collembolan communities, but these studies have demonstrated a strong relationship between traits and response to climate change (Makkonen et al., 2011), and community-level recovery from fire disturbance (Huebner et al., 2012).

One morphological trait that has been proposed as a “universal indicator” of an organism's ecological role is body size (Petchey and Belgrano, 2010). Body size is an easily measurable characteristic for most organisms and scales to many aspects of physiology and life history through allometry (Brown et al., 2004). Quantifying organism body size requires less expertise than taxonomic-intensive approaches and may allow approximation of trophic complexity and stability. At the community level, the average body size of an organism ($\log_{10}$-transformed masses) plotted against the abundance of that organism (also $\log_{10}$-transformed) generates a body size spectrum (BSS) (Turnbull et al., 2014), where both the intercept and slope are informative of community-wide changes. The intercept indicates overall changes in community abundance and the slope indicates changes in the distribution and evenness of body sizes (Jennings et al., 2002; Jennings and Mackinson, 2003; Barnes et al., 2010). While Turnbull et al. (2014) have recently proposed the inclusion of BSS as a standard descriptor of soil communities, few soil studies have used this approach. Those that have demonstrate the loss of larger bodied species in response to experimental warming (Brose et al., 2012) and drought (Lindo et al., 2012). In collembolan communities, because body size is species-specific but also related to the age of the individual, the community-wide body size distributions incorporate reproductive as well as trait information.

In this study we evaluate the individual and interactive effects of elevated temperature, elevated CO_2, and precipitation severity on the abundance, richness, species diversity, species composition, and body size distribution of Collembola in moss mesocosms using a full factorial experimental design. We hypothesized that increased temperature and CO_2 would increase overall abundances through increased metabolic and reproductive activity, and resource availability (e.g. microbial biomass), but that changes in precipitation events, specifically drought conditions and intense precipitation events would result in a general loss of abundance and species richness (Pflug and Wolters, 2001; Tsiafouli et al., 2005; Kardol et al., 2011). Specifically, the loss of large epigeic (i.e. surface dwelling) Collembola species as previously observed (e.g. Huebner et al., 2012; Lindo et al., 2012) would lead to a steeper BSS slope. Mechanistically this could arise through higher water or energetic demands in larger species (drought conditions), or greater difficulty utilizing moist refugia in the soil pore matrix (severe precipitation conditions). Despite having higher individual desiccation resistance (Kaersgaard et al., 2004), larger bodied species generally have smaller population sizes, which renders them more susceptible to local population extirpation or extinction, and less able to recover following disturbance (Cardillo, 2003). Increases in BSS slope are also expected under increased temperature as juveniles and faster reproducing smaller-bodied species would increase.

Interactively, we predicted that the negative effects of precipitation treatments would be more pronounced at higher temperature as increased temperature reduces soil moisture through increase evaporation (Harte et al., 1996). While increased atmospheric CO_2 has been shown to decrease plant evapotranspiration and therefore increase soil moisture (Dermody et al., 2007), it is also possible for increased plant growth caused by higher CO_2 to increase exudation of labile carbon from plant roots, which has been shown to increase C availability for microbes and higher soil trophic levels (Ruf et al., 2006). However, as these results are all indirect, we did not expect any significant effects of elevated atmospheric CO_2 conditions on abundance, richness or body size distribution during our mesocosm study (see Wall et al., 2005 for further details).

2. Methods

2.1. Sample collection

Forest floor soil and moss samples were collected from a black spruce (*Picea mariana* (Mill.)) forest east of Lac St. Jean, Quebec, Canada (48°23′N, 71° 25′W). The average temperature in this region is 2.6 °C with average total precipitation of 864.9 mm; in October, when sampling was performed, it is generally warmer with an average temperature of 5.4 °C and a monthly average of 63.5 mm precipitation (Roberval A station, data 1981–2010, Environment Canada, 2013). Four forest floor patches measuring 30 cm × 50 cm × 15 cm deep were removed and placed in individual Rubbermaid® bins. These were promptly transported to the University of Western Ontario in London, Ontario, and stored in a cold room at 4 °C. Each forest floor sample was covered by a 2–3 cm deep moss carpet dominated by the feathermosses *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Bridel) Mitten.

2.2. Mesocosm set-up and experimental design

The forest floor samples were removed and cut into 7 cm × 7 cm subsamples. Bin origin was recorded to check for between-bin