



# Warming favours small-bodied organisms through enhanced reproduction and compositional shifts in belowground systems



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## ABSTRACT

The increased prevalence of smaller-bodied species under warmer conditions (community downsizing) is hypothesized as an ecologically critical consequence of climate change, leading to changes in trophic transfer efficiency, and rates of nutrient and energy flux within ecosystems. This study used 100 intact peat-soil mesocosms to measure changes in belowground biodiversity under three manipulated climate variables: elevated temperature, elevated CO<sub>2</sub>, and altered water table. Changes in species richness, abundance, community composition and body size spectra were used to determine whether climate change factors led to community downsizing, and elucidate any underlying mechanisms. Warming was the primary driver of compositional shifts in belowground fauna communities with the strongest effect among the smaller-bodied, non-sexually reproducing species. Increases in abundance driven by enhanced reproduction in small-bodied species rather than an increased extinction-rate among large-bodied predators was the basis of the observed downsizing. The overall consequences of warming-induced changes in belowground systems on ecosystem function are still unclear. However, as body size is intricately linked to metabolism, observed community downsizing suggests reductions in food web trophic transfer efficiency with consequences for nutrient and energy dynamics in belowground systems.

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## 1. Introduction

Belowground (soil) biodiversity is central to ecosystem-level function, multifunctionality (Bradford et al., 2014; Wagg et al., 2014) and ecosystem services (Barrios, 2007). As primary and secondary decomposers, the abundance and activity of soil fauna is particularly important for soil carbon (C) and nitrogen (N) dynamics. How changes in soil biodiversity will be affected by global climate change (changes in atmospheric temperature, carbon dioxide concentration, and precipitation) is an active topic given that current rates of climate change are unparalleled in recent geologic time, leading to shifts in many ecological communities. Previous studies have shown that warming tends to have an overall negative effect on species richness and soil fauna abundance (Haimi et al., 2005; Bokhorst et al., 2008; Briones et al., 2009; Kardol et al., 2011) associated with reduced soil moisture under higher temperatures (Blankinship et al., 2011; Wu et al., 2014). Drought conditions impact and alter soil microarthropod community

composition (Blankinship et al., 2011; Lindo et al., 2012), but under moisture saturated conditions, drying can enhance pore space, benefitting some species (Turnbull and Lindo, 2015). The effects of elevated CO<sub>2</sub> on soil communities are less well studied, but generally demonstrate weak or neutral effects of CO<sub>2</sub> enrichment (Niklaus et al., 2003; Haimi et al., 2005; Kardol et al., 2011). Understanding how belowground biodiversity will change is an important first step in predicting how ecosystem-level processes, like C and N dynamics, will change under future climate scenarios. However, understanding and generalizing patterns of soil biodiversity and linking to ecosystem function or soil processes will require the development, application, and advancement of general principles and theories in soil ecology (Lavelle, 2009).

The majority of literature reporting effects of experimental warming on soil microarthropods is negative with respect to abundance and richness (Haimi et al., 2005; Bokhorst et al., 2008; Briones et al., 2009; Kardol et al., 2011). However, warming-induced changes are often functional group or taxon-specific, leading to changes in community structure concomitant with changes in food resource availability (Bokhorst et al., 2008; Briones et al., 2009; Wu et al., 2014). For instance, non-random loss of top predators in soil communities has been shown under habitat loss

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and fragmentation (Gonzalez et al., 1998), as well as drought conditions and warming (Lindo et al., 2012), leading to corresponding trophic cascade prey release (Staddon et al., 2010), and alterations in C and N dynamics (Mulder and Elser, 2009; Staddon et al., 2010). It is well established that non-random species loss under environmental change is correlated with a suite of species-specific traits, including large body size, low population abundance, high trophic position and low fecundity; traits that tend to co-occur in top predators (Cardillo, 2003). At the same time, Brose et al. (2012) have suggested that increased temperature will impact below-ground communities by accelerating metabolic rates including growth, reproduction, respiration and mortality of small-bodied, fast reproducing species, with indirect warming effects manifesting as 'thermal cascades' altering predator: prey ratios. Expanding on this, climate warming and elevated CO<sub>2</sub> is purported to increase resource addition to soil communities via enhanced root exudates and litter decomposability associated with changes in aboveground plant communities (Wardle, 2006; Dieleman et al., 2015), contributing to these bottom-up effects.

Both these top-down (non-random species loss) and bottom-up (metabolic and resource addition) scenarios predict reductions in the average body size of organisms in the community under warming, a phenomenon called 'community downsizing' (Sheridan and Bickford, 2011). The negative relationship between population abundance and body size is well established (the body size spectra) (Sheldon et al., 1972), and has recently been suggested as a community metric for soil ecology (Turnbull et al., 2014). Community downsizing can be observed through an increase in the intercept and/or a steepening of the slope of the body size spectra. Changes in the linearized slope and intercept of this relationship have been observed for soil fauna under various environmental change scenarios (e.g. nutrient addition, drought) (Mulder and Elser, 2009; Lindo et al., 2012; Turnbull and Lindo, 2015), but community downsizing under climate warming has not been empirically shown in an experimental soil context, nor has the underlying mechanisms of community downsizing been explored.

Here I use an experimental mesocosm study of northern peatland soil to observe changes in belowground soil biodiversity under three manipulated climate variables: elevated temperature, elevated atmospheric CO<sub>2</sub> and lowered water table. Specifically I examined changes in species richness, abundance, community composition and body size spectra (slope and intercept) for peatland microarthropods under these future climate scenarios. To explain changes in the body size spectra, I look for non-random predator loss and a corresponding top-down trophic cascade using predator: prey ratios. I also examine whether changes in the body size spectra are due to increased developmental rates as measured by juvenile: adult ratios.

## 2. Materials and methods

### 2.1. Experimental design

One hundred 25 kg intact peat soil monoliths (30.5 cm diameter × 30 cm) were collected from a nutrient-poor forested fen (48°21'N, 85°21'W) blanketed by *Sphagnum* moss in August 2012. The poor fen area is approximately 4.5 ha, dominated by *Sphagnum magellanicum* Brid. (other species < 20% include: *S. angustifolium*, *S. fallax*, *S. cuspidatum* and *S. fuscum*), with low densities of black spruce (*Picea mariana* (Mill.) B.S.P.) and tamarack (*Larix laricina* (Du Roi) K. Koch). Other vegetation included low densities of leatherleaf (*Chamaedaphne calyculata* (L.) Moench) and Labrador tea (*Ledum groenlandicum* Oeder), small cranberry (*Vaccinium oxycoccos* L.) and Canadian blueberry (*Vaccinium myrtilloides* Michx.), *Carex magellanica* Lam. and *Carex disperma* Dewey. Soils, derived from

Precambrian bedrock, are compacted fine sandy sediment and coarse sandy deposits which occur 1.5–3 m below the peat surface and were not sampled as part of the mesocosms. The study area has been previously described in detail in McLaughlin and Webster (2010).

Monoliths were transported in 18.93 L plastic pails to the University of Western Ontario's Biotron Environmental Climate Change Research Centre and installed with a 2 cm ABS barbed fitting port attached to a 16 mm PVC pipe French drain to manipulate and maintain water table treatments. The mesocosms were housed at 11.5 °C (average Boreal forest growing season temperature) for ten weeks recovery time. Four mesocosms did not sufficiently recover and were eliminated from the study. Twelve mesocosms were initially destructively sampled in December 2012 (T<sub>0</sub>) to quantify above- and belowground diversity, soil nutrient status and several water quality variables. The remaining 84 mesocosms were randomly divided into replicates of a lowered (–20 cm) or a saturated (–5 cm) water table treatment and randomly placed in six environmentally controlled state-of-the-art greenhouses at three temperature (ambient, ambient +4 °C, ambient +8 °C) and two atmospheric CO<sub>2</sub> conditions (430 ppm, 750 ppm) (2 water tables × 3 temperatures × 2 CO<sub>2</sub> levels × 7 replicates = 84 mesocosms). Mesocosms were maintained with simulated rain events biweekly (1.375 L/week) using a dilute Rudolph's solution adjusted to pH 5.8.

The experimental chambers used in this study are custom-designed environmentally controlled enhanced Level 2 greenhouses (state-of-the-art facilities) located on the roof of an isolated five-story building, flanked on either side by non-experimental chambers to control for edge effects. All chambers face south for maximum natural light and are constantly monitored for abiotic variables such as UV radiation and light intensity, and humidity; all factors, which in addition to temperature and CO<sub>2</sub> levels, are fully controlled by an automated system. Chambers were set at 60% relative humidity and ambient light. Practical considerations prevented replication at the chamber level, however, to control for any potential chamber effects, all mesocosms and associated chamber-level treatment conditions were moved to a new chamber every six months.

Two chambers of each of three temperature treatments were run isothermally from December 2012/13 to April 2013/14 under the following temperatures: 11.5 °C, 15.5 °C and 19.5 °C to correspond with the average Boreal peatland growing season temperature (ambient 11.5 °C), ambient +4 °C and ambient +8 °C. Increases of +8 °C have been forecasted for high boreal and subarctic regions of Canada which are peatland dominated (IPCC, 2007). From April 2013 until November 2013 temperature treatments followed the 5-year running average daily maximum and minimum temperatures (ambient, ambient +4 °C and ambient +8 °C). The daily temperatures ramped between highs and lows continuously with the maxima and minima occurring at the actual times in the instrumental record for any given day. The average temperature over this period was 16.9 °C in the ambient biomes. The maximum summer temperature reached under ambient conditions was 28.1 °C on August 1st (see Supplementary Information Fig. S1).

### 2.2. Sampling and calculations

Fauna samples from the 12 initial (T<sub>0</sub>) destructively sampled mesocosms were extracted from ~5 g wet weight *Sphagnum* substrate collected from the top 5 cm of the peat profile. Fauna were extracted over 72 h using Tullgren funnels with 25 watt light bulbs into 75% EtOH. Additional *Sphagnum* litter collected from the destructively sampled T<sub>0</sub> mesocosms were used to create 252 (defaunated) litterbags (10 cm × 7 cm with 1 mm mesh), which

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