Heating up the forest: open-top chamber warming manipulation of arthropod communities at Harvard and Duke Forests

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Summary

1.

Introduction

Recent observations indicate that climatic change is altering biodiversity (Pounds, Fogden, & Campbell 1999; Beaugrand & Reid 2003; Parmesan & Yohe 2003; Menendez et al. 2006), and models suggest that the consequences of climate change will differ across latitude (Deutsch et al. 2008). However, long-term experimental field manipulations are a necessary complement to models and field observations because they directly test the e ects of warming on populations and communities at multiple locales, facilitating better predictions for future climate change e ects on biodiversity as well as ecosystem processes.

Arthropods have been highly responsive to climatic changes because many aspects of their life histories are constrained by climate and they are impacted indirectly through the e ects of climatic change on species they interact with (Suttle, Thomsen, & Power 2007; Barton, Beckerman, & Schmitz 2009; Harmon, Moran, & Ives 2009; Pelini et al. 2009b; Gilman et al. 2010). Experimental studies have shown that ant community structure is altered by temperature (Arnan, Rodrigo, & Retana 2007; Lessard et al. 2010; Wittman et al. 2010). These studies find shifts in ant composition and interactions with a decrease in temperature (owing to shading) of 2 °C or greater. Seasonal patterns of ant activity and reproduction also are strongly associated with temperature (O'Donnell & Kumar 2006; Dunn, Parker, & Sanders 2007b; Dunn et al. 2007a). Finally, laboratory studies have demonstrated that temperature strongly influences the physiology and stress of individual ants (German, Rivera, & Armbrecht 2006), foraging behaviour (Ruano, Tinaut, & Soler 2000), respiration rate (Elmes et al. 1999), initiation of development and development time (Anderson & Munger 2003; Hartley & Lester 2003; Kipyatkov et al. 2004), structure and use of ant nests (Anderson & Munger 2003; Vogt, Wallet, & Coy 2008), and even complex life-history traits, such as whether male ants grow wings to fly and disperse (Cremer & Heinze 2003). Because ants are numerically dominant and contribute to important ecosystem services such as seed dispersal and nutrient cycling (Hölldobler & Wilson 1990; Folgarait 1998), changes in ant assemblages associated with warming have the potential to ramify through ecosystems.

Previous studies of the responses of arthropods to climatic change in field conditions have used observational approaches (Warren et al. 2001; Thomas 2005; Klapwijk et al. 2010), reciprocal translocation (Pelini et al. 2009a) and small-scale warming experiments (Dollery, Hodkinson, & Jonsdottir 2006; Adler et al. 2007; Barton, Beckerman, & Schmitz 2009; Villalpando, Williams, & Norby 2009). Of these, experimental warming o ers the most potential for examining the response of entire arthropod communities to in situ warming. Previous warming studies on other taxa have used passive warming chambers, infrared heaters, soil heating cables, greenhouses, fluid-filled pipes and open-top chambers (reviewed in Marion et al. 1997). Our experiment uses open-top chambers because they minimize soil disturbance and allow for long-term, consistent warming of > 5 °C over larger spatial scales (Norby et al. 1997).

We have devised an experiment using octagonal, 5-m-diameter × 1·2-m-high (c. 22 m^3) open-top chambers to simulate warming at northern (Harvard Forest, Massachusetts) and southern (Duke Forest, North Carolina) hardwood forest sites to determine the e ects of warming on ant and other arthropod populations and communities. We monitor abundance, diversity and composition of arthropods, along with activity of focal ant species. Our response-surface experimental design with many levels of temperature, unlike more conventional ANOVA designs that examine only 2 or 3 'extreme' cases, makes our study more likely to reveal potential nonlinearities and threshold e ects in the relationship between temperature, animal community structure and associated ecosystem function (Gotelli & Ellison 2004; Cottingham, Lennon, & Brown 2005).

Hypotheses

The experiment is suitable for testing many hypotheses origi-

Harvard Forest is in central Massachusetts in the northern hardwood hemlock-white pine transition zone [42° 31′ 48″ N, 72° 11′ 24″ W, 300 m above sea level (a.s.l.)] (Foster & Aber 2004). The mean annual temperature at Harvard Forest is 7·1 °C, and the mean annual precipitation is 1066 mm. Our experimental site at Harvard Forest is in an c. 70-year-old oak-maple stand in the Prospect Hill Tract. Duke Forest is near Hillsborough, North Carolina (35° 52′ 0″ N, 79° 59′ 45″ W, 130 m a.s.l.), in the Piedmont region (Lynch 2006). The mean annual temperature at Duke Forest is 15·5 °C, and the mean annual precipitation is 1140 mm. Our experimental site at Duke Forest is in an c. 80-year-old oak-hickory stand within the Eno River Unit.

Despite their 7 °C temperature di erence, Harvard Forest and Duke Forest share more than 30 ant species (Table 1) that include a mix of both widespread species and relatively narrow endemics and species from di erent trophic levels. Furthermore, species found at both sites tend to be at or near their northern range limits in Massachusetts and at or near their southern range limits in North Carolina.

EXPERIMENTAL PLOTS

There are a total of 15 experimental plots in the forest understorey at each site. Twelve of the plots have chambers: nine are heated and three are unheated chamber controls. Each site also has three chamberless control plots that lack chambers but are equal in surface area to the chambers. The perimeters of the chamberless controls are marked with flagging tape to delineate the sampling area and to discourage trampling. Vegetation within the experimental plots was not cleared prior to chamber construction.

The octagonal chambers are 21·7 m^3 in volume: 5 m in diameter with eight walls each 1·90 m wide and 1·2 m long (Figs 2 and 3). Each chamber has a ± 20-cm-diameter oak tree (Quercus rubra at Harvard Forest and Quercus alba at Duke Forest). This tree provides a large thermal storage mass at the centre of the plot that reduces a 'cold core' in the middle of the chamber (as the chambers are essentially chimneys) and increases thermal mixing. Chamber walls are composed of wood frames attached to metal fence posts and are covered with plastic greenhouse sheeting. The bottoms of the chamber walls are elevated 2–3 cm above the ground so that movement of ants and other arthropods into and out of the chambers is not restricted. For each chamber, four of the eight chamber walls have 75-cm × 75-cm sampling portals that allow sampling and minimize trampling of the soil and vegetation inside of the chamber (Fig. 3a). These portals are covered with greenhouse sheeting that is held in place by magnetic tape when portals are not in use.

The chambers are heated by forced air blown over hydronic radiators fed by a closed-loop mixture of hot water and antifreeze (propylene glycol). Water is heated with onsite, propane-fuelled high-e ciency Prestige Solo condensing water boilers (Triangle Tube, Blackwood, NJ, USA) and is delivered to the chambers through 1- and 1¼-inch (2·54 and 3·175 cm)-diameter Insulpex piping (Rehau, Leesburg, VA, USA). For each heated chamber, heat is transferred to the air via a copper coil heat exchanger (Model HF2-17518; Smith's Environmental Products Ltd., Randolph, MA, USA), and the heat level is controlled by a Belimo valve (3-way valve set via an LR-24 actuator; Belimo America, Danbury, CT, USA). The high-e ciency boilers work best when running constantly. Thus, temperature in each chamber is controlled by adjusting fan speed and hot water flow through the Belimo valve, not by thermostats that would repeatedly cycle the boilers on and o . Once heated, air is delivered to rings, one 0·8 m and the other 1·7 m from the chamber walls. Air enters the chambers, causing minimal disturbance to surrounding vegetation, via two rows of 2-cm-diameter holes separated by 20 cm along the bottom of the plena. Air delivery in the control chambers is identical to that in heated chambers, but the former are without heated water. On average, monthly electric usage is 1500 kWh and propane usage is 8 m^3 (8000 L) for chamber operation at each site. Across the two sites, the annual carbon footprint (i.e. propane and electricity usage), for a total area of 190 m^2, is 260 metric tons of CO_2 equivalent (MTCDE).

The 15 chambers are arranged spatially in three blocks, each with

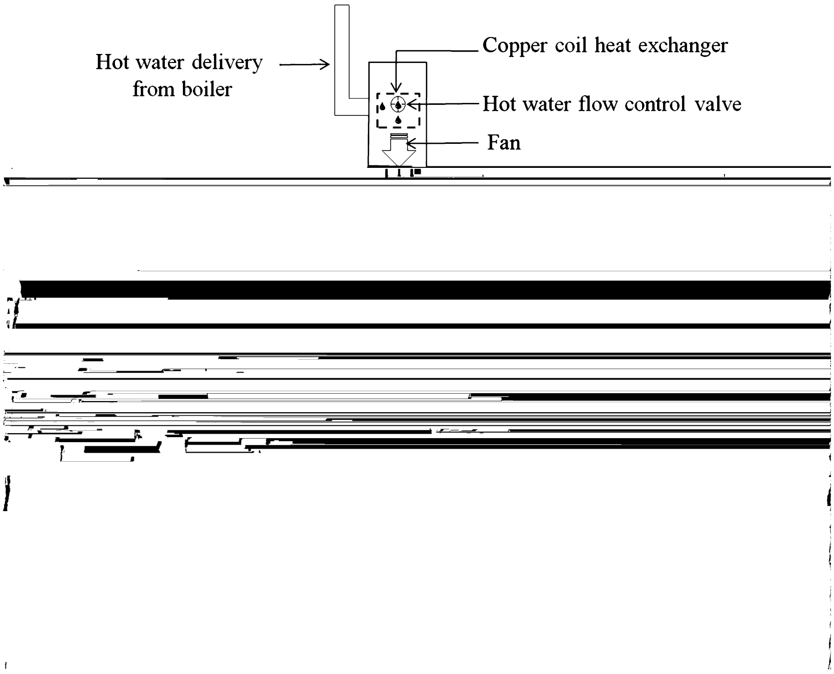

Fig. 2. Heated Chamber Diagram. Nine chambers are heated from c. 1·5 to c. 5·5 degrees Celsius above ambient air temperatures at each site. Control chambers are similar but lack hot water delivery, water flow rate control valves and copper heat exchangers.

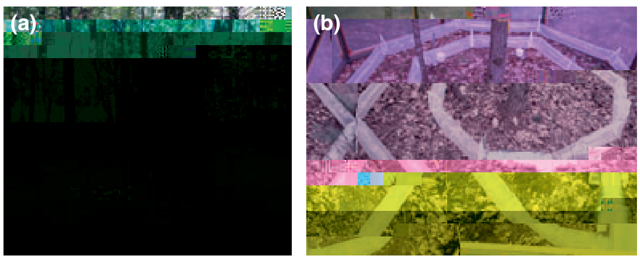

Fig. 3. Heated Chamber Photographs. The red arrow indicates sampling portal (a). Heated air is delivered to chambers through concentric rings of plastic plena (b). These photographs were taken at Harvard Forest. Photograph credit: S. Pelini.

Table 2. Chamber air and soil temperature deltas (means and standard errors). Data are individual chamber air temperature (°C) deltas (di erent from ambient temperature) for Duke Forest (February–December, 2010) and Harvard Forest (January–December, 2010) Deltas are calculated relative to three reference stations at each site

Target air temperature Δ	Air temperature Δ (SE) Duke Forest	Harvard Forest
Control 1	0·35 (0·004)	0·45 (0·01)
Control 2	0·29 (0·003)	0·35 (0·01)
Control 3	0·59 (0·004)	0·26 (0·01)
1·5	1·9 (0·01)	1·4 (0·01)
2·0	2·5 (0·02)	2·0 (0·01)
2·5	2·8 (0·01)	2·3 (0·01)
3·0	3·5 (0·01)	2·6 (0·01)
3·5	3·5 (0·01)	3·2 (0·01)
4·0	4·0 (0·02)	4·0 (0·01)
4·5	5·2 (0·01)	4·3 (0·01)
5·0	5·7 (0·01)	4·6 (0·01)
5·5	5·8 (0·01)	5·2 (0·01)

disturbance, and all artificial nests will be harvested, i.e. ants (adults and immatures) will be collected, identified and counted, at the end of the experiment.

DATA MANAGEMENT

All microclimate, energy use, arthropod and other data from both sites are archived, typically monthly, but at a maximum of 2 years after collection in the Harvard Forest data archive, data set 113 (http://harvardforest.fas.harvard.edu:8080/exist/xquery/data.xq?id = hf113). Data in the Harvard Forest archive are publicly available. Information on stored arthropod specimens (taxon, date and method of collection, sampling location and unique identifier number) are databased and held at North Carolina State University and Harvard Forest.

Future directions

This experiment is a long-term ecological study that has provided and will continue to provide opportunities for collaborations across a broad spectrum of ecologists, including those studying biogeochemical, microbial and plant responses to warming. These open-top chambers can support additional observational studies and experiments that explore other facets of the ecological consequences of climatic change on natural systems. These may include implementation of multifactorial climate manipulations, examination of interactions across trophic levels and quantification of changes in ecosystem services that result.

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