

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

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Summary

1. Recent observations indicate that climatic change is altering biodiversity, and models suggest that the consequences of climate change will differ across latitude. However, long-term experimental field manipulations that directly test the predictions about organisms' responses to climate change across latitude are lacking. Such experiments could provide a more mechanistic understanding of the consequences of climate change on ecological communities and subsequent changes in ecosystem processes, facilitating better predictions of the effects of future climate change.

2. This field experiment uses octagonal, 5-m-diameter (*c.* 22 m³) open-top chambers to simulate warming at northern (Harvard Forest, Massachusetts) and southern (Duke Forest, North Carolina) hardwood forest sites to determine the effects of warming on ant and other arthropod populations and communities near the edges of their ranges. Each site has 12 plots containing open-top chambers that manipulate air temperature incrementally from ambient to 6 °C above ambient. Because the focus of this study is on mobile, litter- and soil-dwelling arthropods, standard methods for warming chambers (e.g. soil-warming cables or infrared heaters applied to relatively small areas) were inappropriate and new technological approaches using hydronic heating and forced air movement were developed.

3. We monitor population dynamics, species composition, phenology and behaviour of ants and other arthropods occupying these experimental chambers. Microclimatic measurements in each chamber include the following: air temperature (three), soil temperatures (two each in organic and mineral soil), photosynthetically active radiation (PAR), relative humidity and soil moisture (one each). In two chambers, we are also measuring soil heat flux, associated soil temperatures at 2 and 6 cm and volumetric water content. To assess the composition, phenology and abundance of arthropod communities within the experiment, we use monthly pitfall trapping and annual Winkler sampling. We also census artificial and natural ant nests to monitor changes in ant colony size and productivity across the temperature treatments.

4. This experiment is a long-term ecological study that provides opportunities for collaborations across a broad spectrum of ecologists, including those studying biogeochemical, microbial and plant responses to warming. Future studies also may include implementation of multifactorial climate manipulations, examination of interactions across trophic levels and quantification of changes in ecosystem processes.

Key-words: arthropod, climate change, Formicidae, long-term ecological research, open-top chamber, warming experiment

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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 effects of warming on populations and communities at multiple locales, facilitating better predictions for future climate change effects 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 effects 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, & Armbrrecht 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 offers 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 m³) open-top chambers to simulate warming at northern (Harvard Forest, Massachusetts) and southern (Duke Forest, North Carolina) hardwood forest sites to determine the effects 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 effects 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 originating from observed responses (Parmesan & Yohe 2003), including: 1. Projected atmospheric warming will lead to declines in arthropod abundances at the warmer, southern extent of their ranges. Conversely, projected atmospheric warming will lead to increases in abundance or range extensions of arthropods at the cooler, northern extent of their ranges. 2. Warming will change the relative abundance and composition of arthropod communities. 3. Warming will potentially alter ecosystem processes and services provided by arthropods, particularly with respect to the dispersal of seeds and other services to mutualistic partners.

Materials and methods

STUDY SITES

The ongoing, long-term experiment is being conducted simultaneously at two sites, Harvard Forest and Duke Forest (Fig. 1).

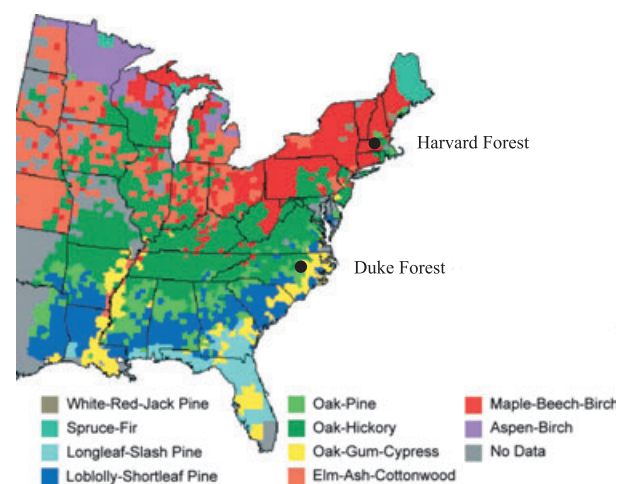


Fig. 1. Map of Eastern US forest types (from National Assessment Synthesis Team, 2000) with locations of Duke Forest and Harvard Forest.

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 difference, 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 different 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 m³ 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-efficiency 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 Insulplex 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-efficiency 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 off. Once heated, air is delivered to the chambers by blowers (FKD12XL blower; Fantech, Lenexa, KS, USA) through 15-cm-diameter plastic plena (Figs 2 and 3b). The plena, which hang 45 cm above the ground, run in two concentric

Table 1. Occurrences of ant species at Duke Forest and Harvard Forest

Species	Duke Forest	Harvard Forest
<i>Amblyopone pallipes</i>	X	X
<i>Aphaenogaster fulva</i>	X	
<i>Aphaenogaster lamellidens</i>	X	
<i>Aphaenogaster picea</i>	X	X
<i>Aphaenogaster rudis</i> complex	X	X
<i>Aphaenogaster tennesseensis</i>	X	
<i>Aphaenogaster texana</i>	X	
<i>Aphaenogaster treatae</i>	X	
<i>Brachymyrmex depilis</i>	X	X
<i>Camponotus americanus</i>	X	
<i>Camponotus caryae</i>	X	
<i>Camponotus castaneus</i>	X	
<i>Camponotus chromaiodes</i>	X	
<i>Camponotus decipiens</i>	X	
<i>Camponotus herculeanus</i>		X
<i>Camponotus mississippiensis</i>	X	
<i>Camponotus nearcticus</i>		X
<i>Camponotus novaeboracensis</i>		X
<i>Camponotus pennsylvanicus</i>	X	X
<i>Camponotus subbarbatus</i>	X	
<i>Crematogaster ashmeadi</i>	X	
<i>Crematogaster cerasi</i>	X	X
<i>Crematogaster lineolata</i>	X	X
<i>Crematogaster minutissima</i>	X	
<i>Crematogaster pilosa</i>	X	
<i>Discothyrea testacea</i>	X	
<i>Dolichoderus mariae</i>	X	
<i>Dolichoderus plagiatus</i>	X	X
<i>Dolichoderus pustulatus</i>	X	X
<i>Dolichoderus taschenbergi</i>	X	
<i>Forelius pruinosus</i>	X	
<i>Formica aserva</i>	X	X
<i>Formica difficilis</i>	X	
<i>Formica dolosa</i>		X
<i>Formica exsectoides</i>	X	
<i>Formica incerta</i>		X
<i>Formica lasioides</i>		X
<i>Formica neogagates</i>	X	X
<i>Formica obscuriventris</i>	X	
<i>Formica pallidefulva</i>	X	
<i>Formica subaenescens</i>	X	X
<i>Formica subintegra</i>	X	X
<i>Formica subsericea</i>	X	X
<i>Hypoponera opacior</i>	X	
<i>Lasius alienus</i>	X	X
<i>Lasius claviger</i>	X	X
<i>Lasius flavus</i>	X	X
<i>Lasius interjectus</i>	X	
<i>Lasius latipes</i>	X	
<i>Lasius nearcticus</i>	X	X
<i>Lasius neoniger</i>	X	X
<i>Lasius pallitarsis</i>		X
<i>Lasius speculiventris</i>	X	X
<i>Lasius subglaber</i>	X	
<i>Lasius umbratus</i>	X	X
<i>Linepithema humile</i>	X	
<i>Monomorium minimum</i>	X	
<i>Monomorium pharaonis</i>	X	
<i>Myrmecina americana</i>	X	X
<i>Myrmica americana</i>	X	X
<i>Myrmica detritinodis</i>		X
<i>Myrmica fracticornis</i>		X

Table 1. (Continued)

Species	Duke Forest	Harvard Forest
<i>Myrmica incompleta</i>		X
<i>Myrmica nearctica</i>		X
<i>Myrmica pinetorum</i>	X	
<i>Myrmica punctiventris</i>	X	X
<i>Myrmica</i> sp. 1 (= 'AF-scu')		X
<i>Myrmica</i> sp. 2 (= 'AF-smi')	X	X
<i>Neivamyrmex opacithorax</i>	X	
<i>Neivamyrmex texanus</i>	X	
<i>Pachycondyla chinensis</i>	X	
<i>Nylanderia arenivaga</i>	X	
<i>Nylanderia faisonensis</i>	X	
<i>Nylanderia parvula</i>	X	
<i>Pheidole bicarinata</i>	X	
<i>Pheidole dentata</i>	X	
<i>Pheidole morrisi</i>	X	
<i>Pheidole pilifera</i>	X	
<i>Pheidole tysoni</i>	X	
<i>Polyergus lucidus</i>	X	
<i>Ponera pennsylvanica</i>	X	X
<i>Prenolepis imparis</i>	X	
<i>Proceratium silaceum</i>	X	
<i>Protomognathus americanus</i>	X	X
<i>Pyramica clypeata</i>	X	
<i>Pyramica creightoni</i>	X	
<i>Pyramica laevinasis</i>	X	
<i>Pyramica membranifera</i>	X	
<i>Pyramica missouriensis</i>	X	
<i>Pyramica ohioensis</i>	X	
<i>Pyramica ornata</i>	X	
<i>Pyramica pergandei</i>	X	
<i>Pyramica pilinasis</i>	X	
<i>Pyramica pulchella</i>	X	
<i>Pyramica rostrata</i>	X	
<i>Pyramica talpa</i>	X	
<i>Solenopsis molesta</i>	X	X
<i>Stenamma brevicorne</i>		X
<i>Stenamma diecki</i>		X
<i>Stenamma impar</i>		X
<i>Stenamma schmitti</i>	X	X
<i>Tapinoma melanocephalum</i>	X	
<i>Tapinoma sessile</i>	X	X
<i>Temnothorax curvispinosus</i>	X	X
<i>Temnothorax longispinosus</i>	X	X
<i>Temnothorax pergandei</i>	X	
<i>Temnothorax schaumii</i>	X	
<i>Temnothorax texanus</i>	X	
<i>Tetramorium caespitum</i>	X	X
<i>Trachymyrmex septentrionalis</i>	X	

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 m³ (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 m², is 260 metric tons of CO₂ equivalent (MTCDE).

The 15 chambers are arranged spatially in three blocks, each with one chamberless control, one control chamber and three heated

chambers. We used a regression design in chamber heating to reveal potential nonlinearities and threshold effects in the relationship between temperature, arthropod community structure and associated ecosystem function. In addition, the use of a regression design recognizes that the temperature changes we achieve vary modestly and that precise ANOVA design treatment levels (e.g. +2, +4, etc.) are unrealistic. Our targets for heating each chamber range from 1.5 to 5.5 °C above ambient ('delta') (Table 2; Fig. 4). We assigned each chamber a target delta in 0.5 °C increments between 1.5 and 5.5 °C (i.e. 1.5, 2.0, 2.5, ..., 5.5 °C deltas; Fig. 3), again with the recognition that our control of target deltas is imperfect, but that such 'imperfection' is still useful within a regression framework. Within each block, we randomly assigned each of the three heated chambers to a low (1.5, 2.0, 2.5 °C), medium (1.5, 2.0, 2.5 °C) or high (4.5, 5.0, 5.5 °C) target delta. Heat delivery to chambers began in January 2010, and chambers are heated year-round at both sites.

In each chamber, we continuously record three measurements of air temperatures, two measurements each of soil temperatures in organic and mineral soil and one measurement each of photosynthetically active radiation (PAR) (model SQ110; Apogee Instruments Inc., Logan, UT, USA), relative humidity (HS-2000V capacitive polymer sensors; Precon, Memphis, TN, USA) and soil moisture (Model CS616 TDR probes, Campbell Scientific Inc., Logan, UT, USA). In two chambers, we are also continuously measuring soil heat flux (Model HFP01SC; Campbell Scientific Inc.), associated soil temperatures at two and six cm and volumetric water content (Model CS616; Campbell Scientific Inc.). At each block of chambers, we have one measurement of soil, air, humidity and soil moisture in an area adjacent to the chambers ('reference station'). The average of these three reference stations is used as the baseline for our temperature treatments (i.e. deltas). Microclimatic data are collected using automated dataloggers (CR1000; Campbell Scientific Inc.). All measurements are recorded as hourly means, minima and maxima of measurements taken every minute. These dataloggers also send control signals to the Belimo heat control valves via Campbell Scientific SDM CV04 output peripherals.

ARTHROPOD SAMPLING

We use monthly pitfall trapping and annual Winkler sampling to assess the composition, phenology and abundance of arthropod communities within the experiment; each plot has four pitfall traps (5 cm diameter) that are located c. 1 m inside of the chamber walls or edges of the chamberless control plots. Each month, pitfall traps are filled with 60–80 mL of 95% EtOH and left uncovered for 48 h during precipitation-free conditions. Once during the summer (July–August), we also collect organic matter and loose surface soil in two 0.25-m × 0.25-m quadrats on opposite sides of the plots. Litter is placed into Winkler extractors (Fisher, 1998); all arthropods captured are sorted, identified, counted and stored in 95% EtOH. Arthropod specimens are catalogued and stored at the Harvard Museum of Comparative Zoology (MCZ), Harvard Forest, or North Carolina State University.

We census artificial and natural ant nests to determine whether there are differences in ant colony size and productivity across the different treatments. To facilitate ant colonization, we have placed three varieties of artificial ant nests in all plots. Each plot has three cement pavers (23 cm × 15 cm), 10 bamboo fragments (1 cm diameter, 5 cm length) and 3 plastic-covered pine nest boxes (15 cm × 15 cm) (Lubertazzi & Adams 2010). These different artificial nests are designed to attract a variety of ants. Once each year, ants occupying plastic-covered nest boxes are identified and counted with minimal

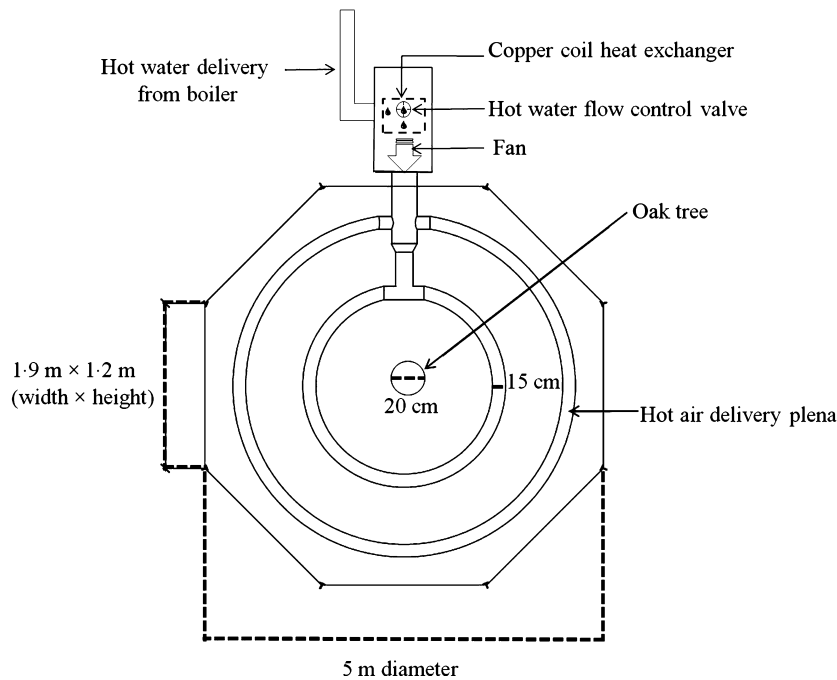


Fig. 2. Heated Chamber Diagram. Nine chambers are heated from *c.* 1.5 to *c.* 5.5 degrees Celsius above ambient air temperatures at each site. Control chambers are similar but lack hot water delivery, water flow rate control valves and copper heat exchangers.

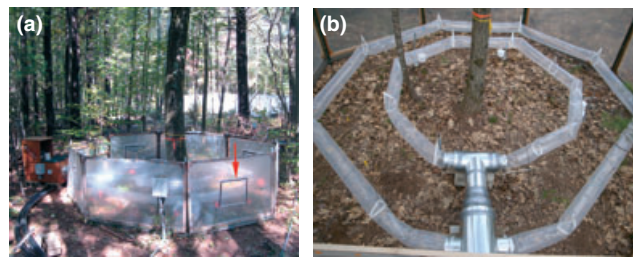


Fig. 3. Heated Chamber Photographs. The red arrow indicates sampling portal (a). Heated air is delivered to chambers through concentric rings of plastic plenum (b). These photographs were taken at Harvard Forest. Photograph credit: S. Pelini.

Table 2. Chamber air and soil temperature deltas (means and standard errors). Data are individual chamber air temperature ($^{\circ}\text{C}$) deltas (different 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

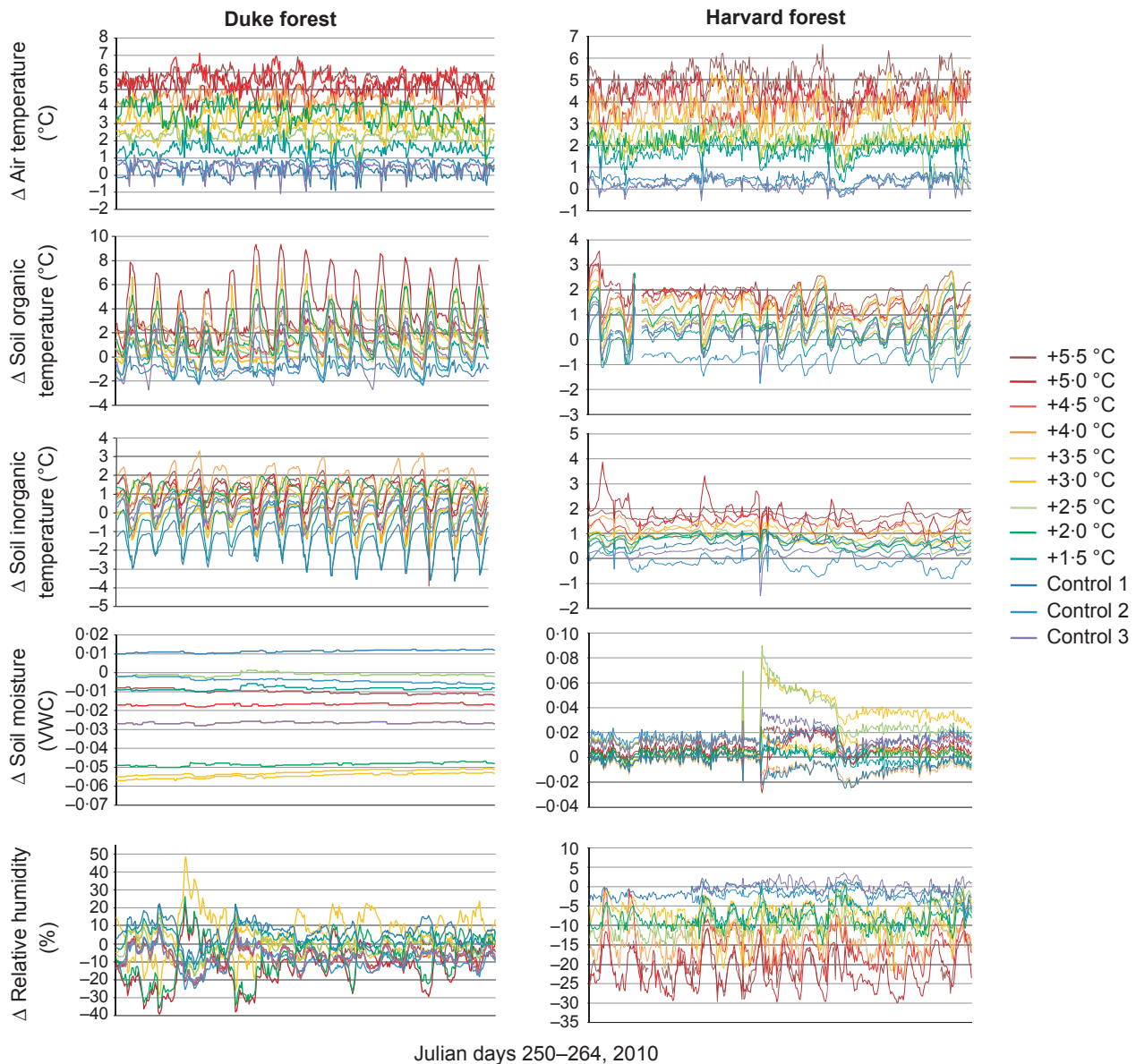


Fig. 4. Chamber Microclimate Data. Data are individual chamber microclimate (air temperature, soil temperature in organic layer, mineral soil temperature, soil moisture, relative humidity) deltas (different from ambient conditions) for Duke Forest and Harvard Forest chambers during 7–21 September 2010. Deltas are calculated relative to three reference stations at each site. Note y-axis scales often differ at the two sites.

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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References

- Adler, L.S., De Valpine, P., Harte, J. & Call, J. (2007) Effects of long-term experimental warming on aphid density in the field. *Journal of the Kansas Entomological Society*, **80**, 156–168.
- Anderson, K.E. & Munger, J.C. (2003) Effect of temperature on brood relocation in *Pogonomyrmex salinus* (Hymenoptera : Formicidae). *West North American Naturalist*, **63**, 122–128.
- Arnan, X., Rodrigo, A. & Retana, J. (2007) Uncoupling the effects of shade and food resources of vegetation on Mediterranean ants: an experimental approach at the community level. *Ecography*, **30**, 161–172.
- Barton, B.T., Beckerman, A.P. & Schmitz, O.J. (2009) Climate warming strengthens indirect interactions in an old-field food web. *Ecology*, **90**, 2346–2351.

- Beaugrand, G. & Reid, P.C. (2003) Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, **9**, 801–817.
- Cottingham, K.L., Lennon, J.T. & Brown, B.L. (2005) Regression versus ANOVA – response. *Frontiers in Ecology and the Environment*, **3**, 358.
- Cremer, S. & Heinze, J. (2003) Stress grows wings: environmental induction of winged dispersal males in Cardiocondyla ants. *Current Biology*, **13**, 219–223.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6668–6672.
- Dollery, R., Hodkinson, I.D. & Jonsdottir, I.S. (2006) Impact of warming and timing of snow melt on soil microarthropod assemblages associated with Dryas-dominated plant communities on Svalbard. *Ecography*, **29**, 111–119.
- Dunn, R.R., Parker, C.R. & Sanders, N.J. (2007b) Temporal patterns of diversity: assessing the biotic and abiotic controls on ant assemblages. *Biological Journal of the Linnean Society*, **91**, 191–201.
- Dunn, R.R., Parker, C.R., Geraghty, M. & Sanders, N.J. (2007a) Reproductive phenologies in a diverse temperate ant fauna. *Ecological Entomology*, **32**, 135–142.
- Elmes, G.W., Wardlaw, J.C., Nielsen, M.G., Kipyatkov, V.E., Lopatina, E.B., Radchenko, A.G. & Barr, B. (1999) Site latitude influences on respiration rate, fat content and the ability of worker ants to rear larvae: a comparison of *Myrmica rubra* (Hymenoptera: Formicidae) populations over their European range. *European Journal of Entomology*, **96**, 117–124.
- Fisher, B.L. (1998) Ant diversity patterns along an elevational gradient in the Réserve Spéciale d'Anjanaharibe-Sud and on the western Masoala Peninsula, Madagascar. *Fieldiana Zoology*, **90**, 39–67.
- Folgarait, P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, **7**, 1221–1244.
- Foster, D.R. & Aber, J.D. (eds) (2004) *Forests in Time. The Environmental Consequences of 1,000 Years of Change in New England*. Yale University Press, New Haven, Connecticut.
- German, A.V.O., Rivera, L.F. & Ambrecht, I. (2006) Effect of the physiological stress in two species of ants (Formicidae) that inhabit coffee plantations with and without shade. *Revista Colombiana de Entomología*, **32**, 61–66.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology & Evolution*, **25**, 325–331.
- Gotelli, N.J. & Ellison, A.M. (2004) *A Primer of Ecological Statistics*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Harmon, J.P., Moran, N.A. & Ives, A.R. (2009) Species response to environmental change: impacts of food web interactions and evolution. *Science*, **323**, 1347–1350.
- Hartley, S. & Lester, P.J. (2003) Temperature-dependent development of the argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae): a degree-day model with implications for range limits in New Zealand. *The New Zealand Entomologist*, **26**, 91–100.
- Hölldobler, B. & Wilson, E.O. (1990) *The Ants*. Belknap Press, Cambridge, Massachusetts.
- Kipyatkov, V.E., Lopatina, E.B., Imamgaliev, A.A. & Shirokova, L.A. (2004) Effect of temperature on rearing of the first brood by the founder females of the ant *Lasius niger* (Hymenoptera, Formicidae): latitude-dependent variability of the response norm. *Journal of Evolutionary Biochemistry and Physiology*, **40**, 165–175.
- Klapwijk, M.J., Grobler, B.C., Ward, K., Wheeler, D. & Lewis, O.T. (2010) Influence of experimental warming and shading on host-parasitoid synchrony. *Global Change Biology*, **16**, 102–112.
- Lessard, J.P., Sackett, T.E., Reynolds, W.N., Fowler, D.A. & Sanders, N.J. (2010) Determinants of the detrital arthropod community structure: the effects of temperature and resources along an environmental gradient. *Oikos*, **120**, 333–343.
- Lubertazzi, D. & Adams, E.S. (2010) Bayesian analysis of split sex ratios: methods and application to the ant *Aphaenogaster rudis*. *Evolutionary Ecology Research*, **12**, 169–188.
- Lynch, I.P. (2006) *The Duke Forest at 75: A Resource for All Seasons*. Office of the Duke Forest, Durham, North Carolina.
- Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H., Levesque, E., Molau, U., Molgaard, P., Parsons, A.N., Svoboda, J. & Virginia, R.A. (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, **3**, 20–32.
- Menendez, R., Megias, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B. & Thomas, C.D. (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society of London. Series B, Biological sciences*, **273**, 1465–1470.
- National Assessment Synthesis Team, U. G. C. R. P. (2000) The potential consequences of climate variability and change. Overview: Forests.
- Norby, R.J., Edwards, N.T., Riggs, J.S., Abner, C.H., Wulschleger, S.D. & Gunderson, C.A. (1997) Temperature-controlled open-top chambers for global change research. *Global Change Biology*, **3**, 259–267.
- O'Donnell, S. & Kumar, A. (2006) Microclimatic factors associated with elevational changes in army ant density in tropical montane forest. *Ecological Entomology*, **31**, 491–498.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pelini, S.L., Dzurisin, J.D.K., Prior, K.M., Williams, C.M., Marsico, T.D., Sinclair, B.J. & Hellmann, J.J. (2009a) Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. *Proceedings of the National Academy of Sciences*, **106**, 11160–11165.
- Pelini, S. L., Prior, K. M., Parker, D. J., Dzurisin, J. D. K., Lindroth, R. L. & Hellmann, J. J. (2009b) Climate change and temporal and spatial mismatches in insect communities. *Climate Change: Observed Impacts on Planet Earth* (ed. T. Letcher), pp. 215–231. Elsevier, Inc, Amsterdam.
- Pounds, J.A., Fogden, M.P.L. & Campbell, J.H. (1999) Biological response to climate change on a tropical mountain. *Nature*, **398**, 611–615.
- Ruano, F., Tinaut, A. & Soler, J.J. (2000) High surface temperatures select for individual foraging in ants. *Behavioral Ecology*, **11**, 396–404.
- Suttle, K.B., Thomsen, M.A. & Power, M.E. (2007) Species interactions reverse grassland responses to changing climate. *Science*, **315**, 640–642.
- Thomas, J.A. (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Proceedings of the Royal Society of London. Series B, Biological sciences*, **360**, 339–357.
- Villalpando, S.N., Williams, R.S. & Norby, R.J. (2009) Elevated air temperature alters an old-field insect community in a multifactor climate change experiment. *Global Change Biology*, **15**, 930–942.
- Vogt, J.T., Wallet, B. & Coy, S. (2008) Dynamic thermal structure of imported fire ant mounds. *Journal of Insect Science*, **8**, 1–12.
- Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- Wittman, S.E., Sanders, N.J., Ellison, A.M., Jules, E.S., Ratchford, J.S. & Gotelli, N.J. (2010) Species interactions and thermal constraints on ant community structure. *Oikos*, **119**, 551–559.

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