

How do climate change experiments actually change climate?

A.K. Ettinger, I. Chuine, B. Cook, J. Dukes, A.M. Ellison, M.R. Johnston, A.M. Panetta,
C. Rollinson, Y. Vitasse, E. Wolkovich

January 10, 2017

Introduction

Ongoing climatic changes are causing dramatic alterations to Earth’s biota, increasingly altering the physiology, distribution, and abundance of organisms, and resulting in cascading community and ecosystem effects (Shukla & Mintz, 1982; Cox *et al.*, 2000; Thomas *et al.*, 2004; Parmesan, 2006; Field *et al.*, 2007; Sheldon *et al.*, 2011; Urban *et al.*, 2012). Much uncertainty remains, however, about how particular individuals, populations, species, communities, and ecosystems will respond as shifts in temperature and precipitation regimes become more extreme. Predicting these biological responses to current and future climate change, as well as they will feedback to affect earth’s climate and ecosystem services, are among the most significant challenges facing biologists today.

Researchers have sought to understand and forecast biological responses through a variety of strategies, including observational studies, model-based approaches, and experiments. Much work is on temperature because increased greenhouse gas emissions has a relatively straightforward effect on this climatic variable, at least as compared to precipitation (Stocker *et al.*, 2013). Observational studies typically correlate observed biological patterns with trends in climate; however, it is challenging to disentangle the causal effect of warming from other factors that have also changed, such as successional stage or land use. In addition, future climate change is expected to result in conditions that are outside those that have been observed historically (Ohlemüller *et al.*, 2006; Williams & Jackson, 2007; Williams *et al.*, 2007; Stocker *et al.*, 2013). Modelling techniques can be useful in this regard, but these methods often rely on untested assumptions, for example, that climate limits performance (Pearson & Dawson, 2004; Ibanez *et al.*, 2006; Swab *et al.*, 2012). Experiments are therefore a critical component of the biologist’s toolkit for understanding climate change impacts, and are often considered the “gold standard” of knowledge (e.g. Box *et al.*, 1978; Gelman, 2014). In situ climate warming experiments allow effects of temperature and precipitation to be isolated from other environmental changes that can confound conclusions drawn from observational data sets. In addition, a range of warming and precipitation treatments can be applied, such that potential non-linear responses may be evaluated. Compared with controlled growth-chamber experiments, field-based experiments offer the possibility of preserving important, but unknown or unquantified, in situ biotic and abiotic drivers and interactions. Climate change experiments in the field may therefore be able to elucidate many biological responses to future climate change.

Experimental climate manipulations take a variety of forms, manipulating temperature, precipitation, atmospheric CO₂, and other variables using a wide range of techniques (Shaver *et al.*, 2000; Aronson & McNulty, 2009). In the field, temperature increases can be simulated using “passive” warming infrastructure, such as open-top chambers, that trap energy already available in the environment or “active” warming methods, which heat ecosystems using external energy inputs (e.g., gas-powered forced air heaters, electrical-powered soil warming cables or infrared heaters (Shaver *et al.*, 2000). Many field experiments have explored biological responses to interacting environmental changes: active warming methods have been combined with precip-

itation manipulations, (e.g. snow removal, water additions and reductions), in an effort to create climatic conditions such as those forecasted under future climate change scenarios (Price & Waser, 1998; Cleland *et al.*, 2006; Sherry *et al.*, 2007; Rollinson & Kaye, 2012).

Seeking to prepare for future, altered biological conditions, scientists and others often attempt to extrapolate the results of in situ climate change experiments to forecast how organisms and ecosystems will respond to particular climate change scenarios. Even in cases where extrapolation is not the explicit goal of climate change experiments, these studies are often used to draw conclusions about how anthropogenic warming will affect species' performance (e.g. growth and survival) and distributions (Dukes & Mooney, 1999; Hobbie *et al.*, 1999; ?; Gruner *et al.*, 2016). Despite these applications, a detailed assessment of how different types of experimental warming alter the environmental conditions experienced by organisms, and the extent to which these conditions accurately simulate current field conditions and anticipated climate change, is lacking. In addition comparing experimental results with observations and forecasts, there is a need to reconcile experimental results across the diverse methods, locations, and species to date.

To realize the forecasting potential of climate change experiments, a nuanced understanding of how climate change experiments actually alter climate is critical. Here, we use plot-level daily microclimate data from 12 climate change experiments that manipulate temperature and precipitation to demonstrate the direct and indirect ways in which environmental conditions are altered by active warming technologies. We then highlight the challenges associated with quantifying and interpreting biological responses to these climate manipulations, and using these interpretations to forecast more widespread responses to contemporary climate change. Finally, we use findings from our synthesis to make recommendations for future climate change experiments. We focus on in situ active warming manipulations, because recent analyses indicate that active warming methods are the most controlled, consistent, and “true to climate change predictions” (Kimball, 2005; Kimball *et al.*, 2008; Aronson & McNulty, 2009; Wolkovich *et al.*, 2012). The data we use were collected between 1991 and 2014 from North American and European climate change experiments and have been merged into a new, publicly available Climate from Climate Change Experiments (C3E) database (see Supplemental Materials for details).

Complications in extrapolating experimental climate change

Climate change experiments often include detailed monitoring of climate variables at the plot level, yielding large amounts of data, such as daily or hourly temperature and other climate variables, over the course of the experiment. However, biologists are generally interested primarily in the biological responses associated with each treatment (e.g. growth, abundance, or phenology of a species). Not surprisingly, then, authors typically provide detailed information on the observed biological responses, and report only the mean change in climate over the course of the experiment and whether or not that mean change matched their target level of change (Price & Waser, 1998; Clark *et al.*, 2014a,b; Rollinson & Kaye, 2012).

Though the published focus is often on shifts in the mean, the imposed climate manipulations result in much more complex shifts of climate, for several reasons that we discuss in more detail below. First, in addition to shifting mean temperatures, experimental warming treatments may alter temperature variance as well. Second, the magnitude of change in these manipulations is likely to vary in time and space. Third, the equipment required to conduct these manipulations can also alter climate at the plot level. All of these complications challenge our interpretation of how experimental warming studies can be applied to forecast effects of climate change, and we discuss them in more detail below.

Treatments alter the variance, as well as the mean

ADD THIS SECTION AND A FIGURE!

Treatments vary over time

The common practice of reporting only the mean temperature difference, across the duration of the study, may hide variations in daily, seasonal, and annual temperatures among treatments. For example, as described above, warming treatments can cause decrease in the diurnal temperature range within experimental plots, compared with ambient conditions (Hoeppepner & Dukes, 2012). This may be similar to what is projected for parts of world; however, this will likely vary spatially, as some regions have experienced higher daytime warming than nighttime warming, whereas others have experienced the opposite (Stocker *et al.*, 2013).

In addition to daily fluctuations, there are frequently strong seasonal variations in experimental warming effects (Figure 1). This may occur because treatments are not applied consistently over the year, either because heat applications are frequently shut off during some seasons such as when snow cover is present or because some heating methods, even if left on throughout the year, are not capable of applying consistent warming year-round (e.g. Clark *et al.*, 2014a,b; Hagedorn *et al.*, 2010). For example, seasonal precipitation patterns can alter the effectiveness of warming treatments, since both infrared heaters and soil cables may fail to achieve the target temperatures during rainstorms (Peterjohn *et al.*, 1993; Hoeppepner & Dukes, 2012). Wind has also been shown to alter thermal efficiency of infrared heaters, so if heater capacity is limited, target warming levels may not be reached during windy conditions (Kimball (2005); Kimball *et al.* (2008)).

Experimental warming effects can also vary across years (Figure 2). This can be due to interactive effects of warming treatments and precipitation, wind, or other aspects of weather that may vary annually, as well as seasonally, as discussed above. Of course, there is bound to be variation in the amount of warming at daily, seasonal, and annual scales as anthropogenic warming progresses, as well. We do not wish to suggest that experimental treatments must be consistent one hundred percent of the time, in order to be relevant. Rather, we wish to call attention to the fact that variations in warming treatments at daily, seasonal, and annual time scales are rarely analyzed explicitly. It is unknown how divergent these annual, seasonal, and daily variations may be from real (i.e. non-experimental) climate patterns. To better understand this potential divergence, we need a detailed comparison of the variation present in climate change experiments to observations in non-experimental settings, as well as to projected future changes given expected greenhouse gas emissions.

Treatments vary in space

In addition to temporal variation, there can be spatial variation in experimental warming effects, such that extrapolation of experimental warming to forecast climate change impacts may not be a straightforward space-for-time substitution (Johnson & Miyanishi, 2008; Jochner *et al.*, 2013). For example, the C3E database contains three studies that used blocked designs, allowing us to examine spatial variation in the amount of warming (i.e. the difference between treatment and control plots within a block). We found that the amount of warming may vary by more than one degree among blocks (Figure 2, Table 1), resulting in lower warming treatments that varied almost 100% of their target temperature and higher warming treatments varying 20% (EMW: I am eye-balling, give exact values).

Potential causes of these differences:

Presumably, there will be spatial variation in future climate change effects, given that warming to date has varied spatially (Stocker *et al.*, 2013). Accurate extrapolation of climate change experiments may therefore depend on the extent to which experiments encompass a representative amount of existing natural variation (e.g. gradients in slope and aspect) present at the scale at which the extrapolation is being made. More detailed comparisons of experimental and observational studies are necessary to better understand how this spatial variation in warming affects our interpretation of responses to warming.

Experimental infrastructure alters climate

The experimental structures themselves alter temperature and other important biotic and abiotic variables, in ways that are not generally examined or reported in experimental warming studies. The possible existence of these effects are widely acknowledged, and some studies include ‘shams’ or ‘disturbance controls’ to account for them. However, the magnitude and implications of structural effects on climate are rarely discussed or interpreted in climate change studies.

To investigate the magnitude of these effects, we compared temperature and soil moisture data from five active warming studies at two sites: Duke Forest and Harvard Forest (Farnsworth *et al.*, 1995; Clark *et al.*, 2014a; Marchin *et al.*, 2015; Pelini *et al.*, 2011). These were the only studies in our database that included two types of control plots: structural controls (i.e. ‘shams’ or ‘disturbance controls,’ which contained all the warming infrastructure, such as soil cables or infrared heating units but with no heat applied) and ambient controls with no infrastructure added (see Supplemental Materials for details). Other studies include only the structural controls (n=3) or only the ambient controls (n=4).

We found that experimental structures altered air and soil temperatures in opposing ways: air temperatures were higher in the structural controls, compared with the ambient air with no structures installed, whereas soil temperatures were lower in the structural controls compared with ambient soil (Figure 3). This was consistent across the different temperature models we fit (mean, minimum, and maximum), and the sign of the effects was consistent across study-sites and months, although the magnitude varied among sites (Table 3) and across seasons (Figure 3). Soil moisture was lower in structural controls compared with ambient conditions (Figure 1S).

Possible mechanisms for these observed differences

In addition to these documented effects, experimental structures may alter conditions by creating shade, intercepting precipitation, and altering herbivory and other biotic interactions. Further documentation and analysis of the effects of these experimental structures on abiotic and biotic factors, as well as in depth interpretation of how these effects may alter focal variables, is an important next step for climate change experimentation, particularly if we wish to apply results to forecasting.

Secondary effects of climate change manipulations

Climate change experiments often seek to manipulate one or two climate variables, such as temperature and precipitation. However, there are likely to be non-target abiotic and biotic factors that are also affected by these manipulations. For example, precipitation treatments typically reduce temperatures in climate change manipulations (Sherry *et al.*, 2007; Rollinson & Kaye, 2012; ?). McDaniel *et al.* (2014) observed that a twenty percent increase in precipitation reduced mean hourly temperatures by 0.3 degrees Celsius over the course of their two-year experiment. The magnitude of this effect can vary in space and time, however (Figure 2).

In addition, experimental warming typically reduces vapor pressure deficit and soil water content (e.g. Figure 3S Sherry *et al.*, 2007; Morin *et al.*, 2010; Templer *et al.*, 2016). Of the twelve experiments in the C3E database, ten measured and reported soil moisture, and five measured air and soil temperature in addition to soil moisture. We applied linear mixed effects models to analyze the effects of temperature treatment on soil moisture in those five experiments. We used year and site as random effects to account for variation in yearly climate and warming protocols, infrastructure, and depth of soil moisture measurement among sites. Candidate fixed effects were air and soil temperature minima, maxima, and means, though we constrained models to use only one soil and one air temperature variable to minimize predictor collinearity. Season and day of year were included in all models to account for temporal variation in the data, and models were distinguished by AIC scores. The most parsimonious model had mean air temperature and maximum soil temperature as explanatory variables; both significantly affected soil moisture. Soil temperature, predictably,

was inversely related to soil moisture: a one degree ($^{\circ}\text{C}$) increase in maximum soil temperature yielded a modeled decline in soil volumetric water content of 0.0028 (1.7 percent of the median soil moisture across all sites and treatments). Surprisingly, however, air temperature was slightly positively related to soil moisture: a one degree increase in mean air temperature was associated with an increase in soil volumetric water content of 0.00071. Potentially, this result could be explained by the closing of plant stomata in response higher air temperatures (and therefore a higher vapor pressure deficit); this would decrease the gradient between soil and leaf water concentration, resulting in comparatively less water being pulled from the soil (?).

Warming and precipitation treatments, and their indirect effects on abiotic factors such as soil moisture, can also alter the biotic environment, which in turn can produce additional secondary effects that alter climate. For example, Rollinson et al (2010) reported that tree composition shifted after three years of warming and modified precipitation treatments (Rollinson & Kaye, 2012). These shifts in composition may change competitive dynamics and, in turn, affect resource levels, such as moisture in the soil. In addition, given that warming reduces soil water content, it is likely to affect soil microbial communities, and therefore available nutrients as well. The magnitude of all of these effects are also likely to vary in space and time; some may be transient whereas others may be more permanent.

It can be difficult to tease apart the specific abiotic and biotic drivers climatic conditions in climate change experiments, but understanding the effects of an experimental treatment on these interrelated variables is critical when trying to determine mechanistic explanations for observed responses to warming. Even when experimental artifacts are introduced (such as artificial drying of soils or altered plant composition, due to experimental structures), if these secondary effects are quantified, they can be helpful in understanding how abiotic and biotic factors interact to affect physiological responses. For example, we can learn about the controls on stomatal conductance when the normal covariance between temperature, humidity, and soil moisture is altered.

Biological implications

We have highlighted a suite of factors that complicate interpretations of warming experiments. We argue that these largely unintended alterations are important for scientists to fully understand and report in their research (Figure 4). This is especially important because unintended climate alterations are likely to have biological implications, including for many of the major responses studied in warming experiments.

Shifted plant phenology is one response often reported in warming experiments. Yet understanding exactly what drives shifted phenology may be more complicated than simply comparing shifts to the direct warming effects of the experiment. This is because phenology is likely to be altered in opposing ways by the increased air temperatures—which generally advance phenology ()—and decreased soil moisture—which may delay phenology (need refs!)—characterized by warming treatments. Indeed, these opposing drivers may be responsible for the observed discrepancy between observational and experimental phenology responses to warming (Wolkovich *et al.*, 2012). In addition, plant phenology responds to minimum temperatures, as well as mean and maximums (Shen *et al.*, 2016; Fu *et al.*, 2016; Piao *et al.*, 2015). This may also play a role in the discrepancy between observational and experimental studies, since diurnal versus night temperatures are affected differently by warming treatments (Shen *et al.*, 2016; Matthews & Mazer, 2016).

Plant growth is also likely to be altered in opposing ways by the increased air temperatures and decreased soil moisture levels in experimentally warmed plots. For example, with warming and decreased vapor pressure deficit, stomata closure may reduce sapflow and growth (Templer *et al.*, 2016). Even small shifts in temperature may have a big effect, since the photosynthetic response to temperature is nonlinear (Berry & Bjorkman, 1980). Climate change experiments offer the opportunity to get these (and other) physiological measurements from a wide range of temperature conditions, which is essential for improving accuracy of ecosystem models and their forecasts.

Direct and indirect effects of climate change experiments are also likely to affect soil respiration in ways that may alter net mineralization and therefore have other cascading effects. Yann: please add a few sentences and citations here! (Jamieson *et al.*, 2015; Kharouba *et al.*, 2015) A meta-analysis based on studies using different techniques of warming has shown that soil warming significantly increased soil respiration rate, net nitrogen mineralization rate and plant productivity, especially in temperate forest ecosystems (Rustad *et al.* 2001). .

Stoichiometry laws suggest that, in forest ecosystems, the redistribution of a relatively small amount of this newly available nitrogen from the soil to the trees could result in a substantial increase in carbon storage in woody tissues (Fatichi *et al.* 2014). However, this principle holds only if plants are in an active stage when the microbial activity reaches a high level in early spring with warmer temperatures. Soil warming experiments may increase net mineralization in early spring or even in winter while phenology of plants is not expected to advance as much as it would if air warming would be additionally applied. -> so just to say that soil warming will affect soil biotic communities but likely not much phenology (that rely more on air temperature) making a mismatch that is not expected to occur under natural warming...I guess there are also interactions plant-insects, especially with moths overwintering in the soil... (I mean when using soil heating cables only).

Other biotic interactions are also likely to be affected by direct and indirect affects of climate change treatments. For example, Hoeppner and Dukes (2012) found that rodent disturbance varied by warming treatment (as well as year) in their climate change experiment. Anne-Marie, Yann, and/or Jeff- please add other examples (with citations) if you can think of some good ones? The HF/DF experiment was explicitly aimed at effects on physiology, genetic make up, and community dynamics of ants (the Clarke/Mellilo exp was aimed at plants). Here are a bunch of examples

heat shock proteins change in response to warming (Stanton-Geddes *et al.*, 2016) Decomposition and soil carbon dynamics shift with IR heating and soil warming(Del Toro *et al.*, 2015).

Diversity and community structure change in response to active warming, but differently at different parts of their geographic range. (Pelini *et al.*, 2014; Diamond *et al.*, 2016)

A critical question is the extent to which these shifts in biotic interactions (and their effects on focal responses) are accurate forecasts of future shifts that are likely to occur with climate change, or due to side-effects that are unlikely to occur outside of experimental systems. (Diamond *et al.*, 2013) Yann: that must be also true for fungi pathogens (like the oak powdery mildew). F with infrared lamps drying air so that it avoid the infection in contrast to control plots.

Recommendations for future climate change experiments

Climate change experiments provide invaluable information about biological responses to climate change, yet our results highlight that we do not fully explore the ways in which these climate change experiments are actually altering climate. These complications should not suggest that experimental climate change studies are not worthwhile. Instead we believe these complications and the relating climate data provide the foundation to designing better experiments, and gaining the most knowledge and utility from existing experiments. Below we describe recommendations to improve implementation, interpretation, and communication of future climate change experiments.

No more ANOVAs! Treat the treatments as continuous rather than discrete, since they are continuous (i.e. they're variable in space and time). This seems like it would be comparatively easy to implement and could make a huge difference. Figure 1 is really great (target versus actual change). A good recommendation would be for this to be a standard plot in any paper reporting a climate change experiment. .

Design realistic manipulations by consulting climate change projections for the study region, and selecting

warming and precipitation treatment methods that most accurately mimic anticipated changes. When it is not possible to match anticipated changes in climate, studies should report how imposed treatments compared to projected changes. In addition, the timing of these treatments should be carefully considered and ideally should match forecasts. If it is not possible to apply continuous treatments throughout the study, the seasonality and timing of treatments should be explicitly reported. We found that only 4/12 studies used shams, yet all of them showed effects of shams. Recommendations for future climate change experiments

Include both structural and ambient controls and collect, use, and report data collected within them. This will facilitate separating mechanisms due to experimental design from mechanisms due to actual shifts in climate.

Maximize the length of climate change experiments by running them for as long as possible. This will allow study of how inter-annual variations interact with climate change treatments, especially when looking at non-linear and multiyear processes such as phenology. It will also allow us to understand how long-term responses may differ from transient ones. Citations, anyone? Yann: for the soil for example there is 'acclimation' to warmer temperatures after several years of warming... (new community of bacteria more adapted to warmer temperatures: citations: all the previously cited ant work, 3-5years. Mellilo experiments on soil warming are > 20 years now.

Collect fine-scale climate data, at least twice daily, and ideally hourly, to allow for minimum and maximum values to be analyzed and interpreted, in addition to mean values. more importantly, the frequency of measurements should be tied to the chronobiology of the organisms of interest. For ants, this might be by minute or more. For bacteria, even faster, for trees maybe slower, but should think on the organisms time scale not on people's time scale.

Publish high quality, usable data and metadata such that data can easily be shared and used by others. In the metadata, report the number and cause of missing data points for climate, especially those collected in warming treatments. (For example, are data missing because the heaters went out, or because rodents at the sensors?) Report the timing of applied warming treatments (i.e. exact start and end dates, within and across years), as well as variations in daytime and nighttime and seasonal variations in climate variables. This is very important as now we know that there are some carry over effect of warming on one year to the other

Consider implementing and following community standards for reporting climate data Do we have community standards for climate data? Ben- do you have any ideas of resources for this? also to report how temperature is measured is essential: 2m air temperature or 50cm is quite different, unprotected air temperature is great to catch minimum temperatures as close as plant tissues experiment but is not appropriate for the maximum temperatures... When studying biological implications of a global challenge as large as climate change, it facilitate progress if we can design, run, and report experiments in such a way that we can eventually create global dataset. This recommendation stems from our work gathering and analyzing data from many climate change experiments. We found that studies report a diverse range of climate variables, collected in different ways (i.e. soil temperature collected at different depths; soil moisture using different units and methods). It has been difficult to synthesize these data in a comprehensive way that can fully address important questions.

Documenting biological impacts of climate change has over a 20 year history in ecology today. Over this time situ field experiments have been critical in making the mechanistic link between warming and a number of major biological impacts—changes in productivity, soil respiration, the phenology of plant and animals and shifted community and ecosystem dynamics. Yet as climate change across the globe continues with projected warming of XX C over the next 80 years, ecologists are challenged to not only document impacts but make quantitative robust predictions. Our ability to meet this challenge requires building on the data from current and past experiments to best understand how altered climate changes ecological processes and build better experiments. As a first step, we have compiled the first database of fine-scale climate data from warming experiments and shown how time, space and artifacts may hinder simple interpretations of climate change experiments. The next steps require the ecological community to build on these data and their findings to develop and use new approaches in the experiments to provide more accurate estimates of altered climate in

theses experiments and in turn, more accurate estimates of critical biological changes.

References

- Shukla, J. & Mintz, Y. Influence of land-surface evapotranspiration on the earth's climate. *Science* **215**, 1498–1501 (1982).
- Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187 (2000).
- Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* **427**, 145–148 (2004). PT: J.
- Parmesan, C. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* **37**, 637–669 (2006). PT: J.
- Field, C. B., Lobell, D. B., Peters, H. A. & Chiariello, N. R. Feedbacks of terrestrial ecosystems to climate change*. *Annu. Rev. Environ. Resour.* **32**, 1–29 (2007).
- Sheldon, K. S., Yang, S. & Tewksbury, J. J. Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecology Letters* **14**, 1191–1200 (2011).
- Urban, M. C., Tewksbury, J. J. & Sheldon, K. S. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society B-Biological Sciences* **279**, 2072–2080 (2012). PT: J; NR: 38; TC: 1; J9: P ROY SOC B-BIOL SCI; PG: 9; GA: 925RT; UT: WOS:000302779600025.
- Stocker, T. *et al.* IPCC, 2013: climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change (2013).
- Ohlemüller, R., Gritti, E. S., Sykes, M. T. & Thomas, C. D. Towards European climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931–2100. *Global ecology and biogeography* **15**, 395–405 (2006).
- Williams, J. W. & Jackson, S. T. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* **5**, 475–482 (2007). PT: J.
- Williams, J. W., Jackson, S. T. & Kutzbach, J. E. Projected distributions of novel and disappearing climates by 2100 AD. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 5738–5742 (2007). PT: J.
- Pearson, R. G. & Dawson, T. P. Bioclimate envelope models: what they detect and what they hide - response to Hampe (2004). *Global Ecology and Biogeography* **13**, 471–473 (2004). PT: J.
- Ibanez, I. *et al.* Predicting biodiversity change: Outside the climate envelope, beyond the species-area curve. *Ecology* **87**, 1896–1906 (2006). PT: J.
- Swab, R. M., Regan, H. M., Keith, D. A., Regan, T. J. & Ooi, M. K. J. Niche models tell half the story: spatial context and life-history traits influence species responses to global change. *Journal of Biogeography* **39**, 1266–1277 (2012). PT: J; NR: 63; TC: 0; J9: J BIOGEOGR; PG: 12; GA: 961GP; UT: WOS:000305452500006.
- Box, G. E., Hunter, W. G., Hunter, J. S. *et al.* Statistics for experimenters (1978).
- Gelman, A. *Experimental reasoning in social science experiments*, chap. 7, 185–195 (New Haven, CT: Yale University Press, 2014).

- Shaver, G. R. *et al.* Global Warming and Terrestrial Ecosystems: A Conceptual Framework for Analysis
Ecosystem responses to global warming will be complex and varied. Ecosystem warming experiments hold great potential for providing insights on ways terrestrial ecosystems will respond to upcoming decades of climate change. Documentation of initial conditions provides the context for understanding and predicting ecosystem responses. *BioScience* **50**, 871–882 (2000).
- Aronson, E. L. & McNulty, S. G. Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology* **149**, 1791–1799 (2009).
- Price, M. V. & Waser, N. M. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* **79**, 1261–1271 (1998).
- Cleland, E. E., Chiariello, N. R., Loarie, S. R., Mooney, H. A. & Field, C. B. Diverse responses of phenology to global changes in a grassland ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 13740–13744 (2006). LR: 20140908; JID: 7505876; 0 (Soil); 142M471B3J (Carbon Dioxide); N762921K75 (Nitrogen); OID: NLM: PMC1560087; 2006/09/05 [aheadofprint]; ppublish.
- Sherry, R. A. *et al.* Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 198–202 (2007). LR: 20140907; JID: 7505876; OID: NLM: PMC1713188; 2006/12/20 [aheadofprint]; ppublish.
- Rollinson, C. R. & Kaye, M. W. Experimental warming alters spring phenology of certain plant functional groups in an early successional forest community. *Global Change Biology* **18**, 1108–1116 (2012).
- Dukes, J. S. & Mooney, H. A. Does global change increase the success of biological invaders? *Trends in Ecology Evolution* **14**, 135–139 (1999). PT: J.
- Hobbie, S. E., Shevtsova, A. & Chapin III, F. S. Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos* 417–434 (1999).
- Gruner, D. S. *et al.* Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. *Oikos* (2016).
- Kimball, B. Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology* **11**, 2041–2056 (2005).
- Kimball, B. A. *et al.* Infrared heater arrays for warming ecosystem field plots. *Global Change Biology* **14**, 309–320 (2008).
- Wolkovich, E. M. *et al.* Warming experiments underpredict plant phenological responses to climate change. *Nature* **485**, 494–497 (2012). PT: J; UT: WOS:000304344500041.
- Clark, J. S., Salk, C., Melillo, J. & Mohan, J. Tree phenology responses to winter chilling, spring warming, at north and south range limits. *Functional Ecology* **28**, 1344–1355 (2014a).
- Clark, J. S., Melillo, J., Mohan, J. & Salk, C. The seasonal timing of warming that controls onset of the growing season. *Global Change Biology* **20**, 1136–1145 (2014b).
- Hoeppner, S. S. & Dukes, J. S. Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology* **18**, 1754–1768 (2012).
- Hagedorn, F. *et al.* Short-term responses of ecosystem carbon fluxes to experimental soil warming at the Swiss alpine treeline. *Biogeochemistry* **97**, 7–19 (2010).
- Peterjohn, W. T., Melillo, J. M., Bowles, F. P. & Steudler, P. A. Soil warming and trace gas fluxes: experimental design and preliminary flux results. *Oecologia* **93**, 18–24 (1993).

- Johnson, E. A. & Miyanishi, K. Testing the assumptions of chronosequences in succession. *Ecology Letters* **11**, 419–431 (2008).
- Jochner, S., Caffarra, A. & Menzel, A. Can spatial data substitute temporal data in phenological modelling? A survey using birch flowering. *Tree physiology* **33**, 1256–1268 (2013).
- Farnsworth, E., Nunez-Farfan, J., Careaga, S. & Bazzaz, F. Phenology and growth of three temperate forest life forms in response to artificial soil warming. *Journal of Ecology* 967–977 (1995).
- Marchin, R. M., Salk, C. F., Hoffmann, W. A. & Dunn, R. R. Temperature alone does not explain phenological variation of diverse temperate plants under experimental warming. *Global change biology* **21**, 3138–3151 (2015).
- Pelini, S. L. *et al.* Heating up the forest: open-top chamber warming manipulation of arthropod communities at Harvard and Duke Forests. *Methods in Ecology and Evolution* **2**, 534–540 (2011).
- Morin, X., Roy, J., Sonié, L. & Chuine, I. Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist* **186**, 900–910 (2010).
- Templer, P. H., Phillips, N. G., Ellison, A. M. & Pelini, S. L. Ecosystem warming increases sap flow rates of northern red oak trees. *Ecosphere* **7** (2016).
- Shen, M. *et al.* Strong impacts of daily minimum temperature on the green-up date and summer greenness of the Tibetan Plateau. *Global change biology* (2016).
- Fu, Y. H. *et al.* Three times greater weight of daytime than of night-time temperature on leaf unfolding phenology in temperate trees. *New Phytologist* (2016).
- Piao, S. *et al.* Leaf onset in the northern hemisphere triggered by daytime temperature. *Nature communications* **6** (2015).
- Matthews, E. R. & Mazer, S. J. Historical changes in flowering phenology are governed by temperature \times precipitation interactions in a widespread perennial herb in western North America. *New Phytologist* **210**, 157–167 (2016).
- Berry, J. & Bjorkman, O. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31**, 491–543 (1980).
- Jamieson, M. A., Schwartzberg, E. G., Raffa, K. F., Reich, P. B. & Lindroth, R. L. Experimental climate warming alters aspen and birch phytochemistry and performance traits for an outbreak insect herbivore. *Global change biology* **21**, 2698–2710 (2015).
- Kharouba, H. M., Vellend, M., Sarfraz, R. M. & Myers, J. H. The effects of experimental warming on the timing of a plant–insect herbivore interaction. *Journal of Animal Ecology* **84**, 785–796 (2015).
- Stanton-Geddes, J. *et al.* Thermal reactionomes reveal divergent responses to thermal extremes in warm and cool-climate ant species. *BMC genomics* **17**, 1 (2016).
- Del Toro, I., Ribbons, R. R. & Ellison, A. M. Ant-mediated ecosystem functions on a warmer planet: effects on soil movement, decomposition and nutrient cycling. *Journal of Animal Ecology* **84**, 1233–1241 (2015).
- Pelini, S. *et al.* Geographic differences in effects of experimental warming on ant species diversity and community composition. *Ecosphere* **5**, 1–12 (2014).
- Diamond, S. E. *et al.* Climate warming destabilizes forest ant communities. *Science Advances* **In press** (2016).
- Diamond, S. E. *et al.* Using physiology to predict the responses of ants to climatic warming. *Integrative and comparative biology* **53**, 965–974 (2013).

Tables

	Chisq	Df	Pr(>Chisq)
(Intercept)	139.127	1.000	0.000
temptreat	466.811	3.000	0.000
block	2.907	2.000	0.234
temptreat:block	40.704	6.000	0.000

Table 1: Effects of warming vary by block, as summarized by a linear mixed effects model of mean soil temperatures, with year and site as nested random effects

	Chisq	Df	Pr(>Chisq)
(Intercept)	1455.294	1.000	0.000
temptreat	126.093	3.000	0.000
year	16.676	1.000	0.000
temptreat:year	61.646	3.000	0.000

Table 2: Effects of warming vary by year, as summarized by a linear mixed effects model of mean soil temperatures, with year and site as nested random effect

The below are all tables related to the sham and ambient comparisons. i want to include more information in the tables, probably (random effects- intercepts, and variance), and most will be in the supplemental (perhaps just the mean soil and air in the main text?) .

	Estimate	Std. Error	t value
(Intercept)	12.691	1.648	7.699
controltypeambient	-0.311	0.092	-3.380

Table 3: Summary of linear mixed effects model testing difference in mean air temperatures of structural controls compared with ambient controls (i.e.with no control chambers or warming infrastructure in place). The model included a fixed effect of control type and an intercept-only random effect of studysite to account for study and measurement, as well as environmental, differences.

	Estimate	Std. Error	t value
(Intercept)	11.315	1.373	8.243
controltypeambient	0.450	0.067	6.682

Table 4: Summary of linear mixed effects model testing difference in mean soil temperature (at the shallowest depth measured) of structural controls compared with ambient controls. The model included a fixed effect of control type and an intercept-only random effect of studysite to account for study and measurement, as well as environmental, differences.

	Estimate	Std. Error	t value
(Intercept)	7.178	1.397	5.138
controltypeambient	-0.343	0.092	-3.744

Table 5: Summary of linear mixed effects model testing difference in minimum air temperatures of structural controls compared with ambient controls (i.e.with no control chambers or warming infrastructure in place). The model included a fixed effect of control type and an intercept-only random effect of studysite to account for study and measurement, as well as environmental, differences.

	Estimate	Std. Error	t value
(Intercept)	10.503	1.343	7.823
controltypeambient	0.386	0.068	5.693

Table 6: Summary of linear mixed effects model testing difference in minimum soil temperature (at the shallowest depth measured) of structural controls compared with ambient controls. The model included a fixed effect of control type and an intercept-only random effect of studysite to account for study and measurement, as well as environmental, differences.

	Estimate	Std. Error	t value
(Intercept)	18.204	1.915	9.504
controltypeambient	-0.278	0.097	-2.851

Table 7: Summary of linear mixed effects model testing difference in maximum air temperatures of structural controls compared with ambient controls (i.e.with no control chambers or warming infrastructure in place). The model included a fixed effect of control type and an intercept-only random effect of studysite to account for study and measurement, as well as environmental, differences.

	Estimate	Std. Error	t value
(Intercept)	13.602	1.674	8.125
controltypeambient	0.588	0.076	7.770

Table 8: Summary of linear mixed effects model testing difference in maximum soil temperature (at the shallowest depth measured) of structural controls compared with ambient controls. The model included a fixed effect of control type and an intercept-only random effect of studysite to account for study and measurement, as well as environmental, differences.

Figures

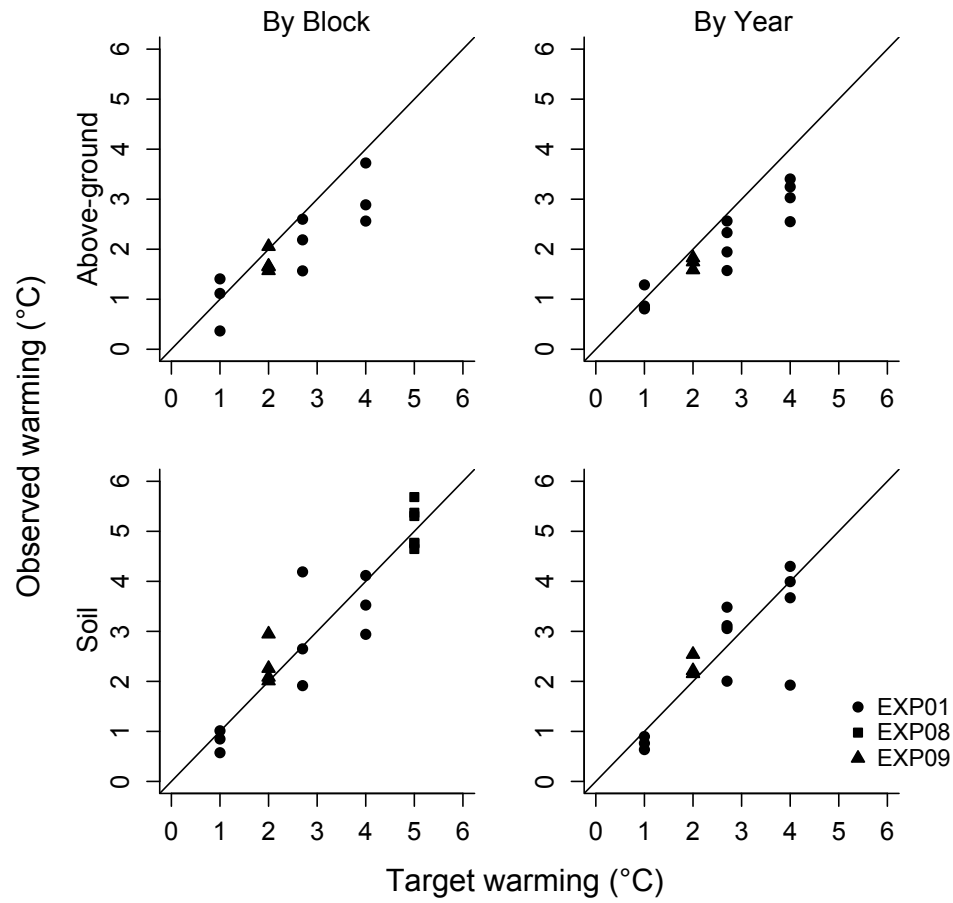


Figure 1: The amount of warming (i.e. the difference between treatment and control plots, within each block) varies among blocks (left panels), as well as among years (right panels). See Tables 1 and 2 for statistical differences.

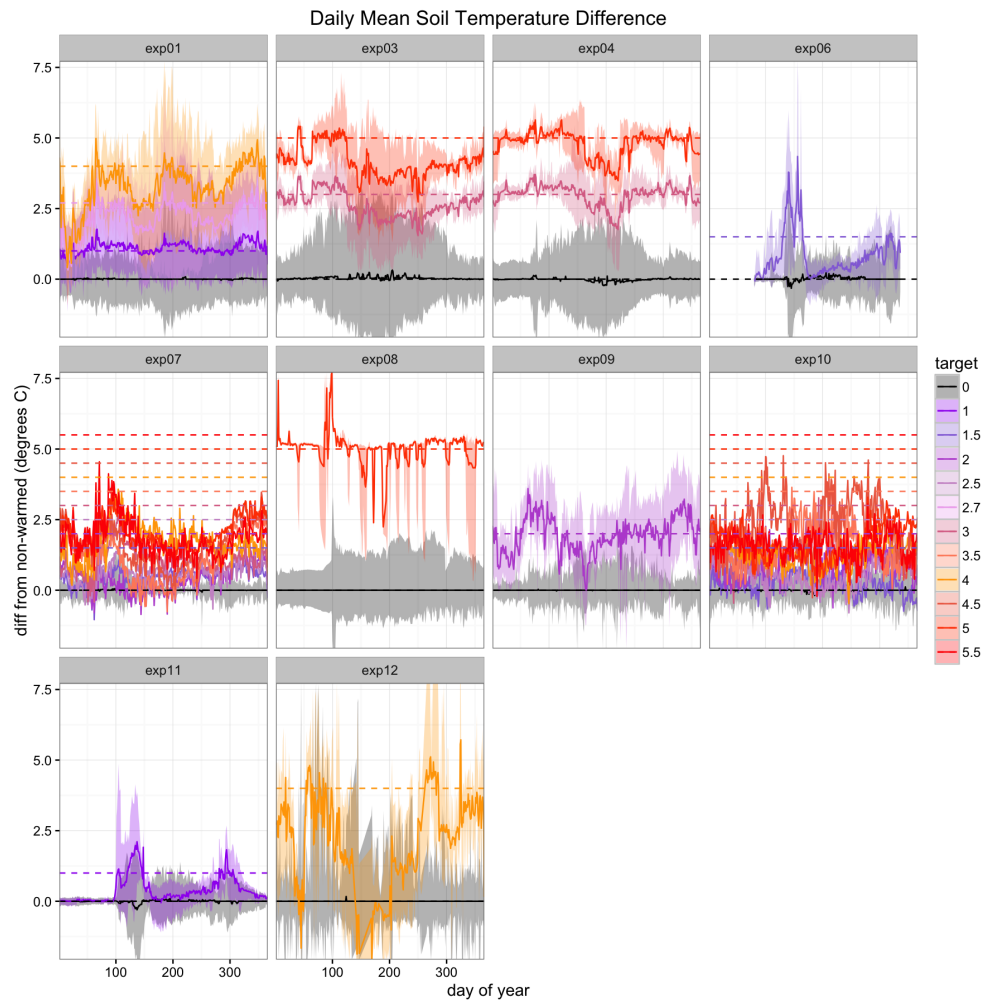


Figure 2: Time series of deviations from mean soil temperature over one year, in control (black line) and warming treatments with various target warming levels at 10 study sites.

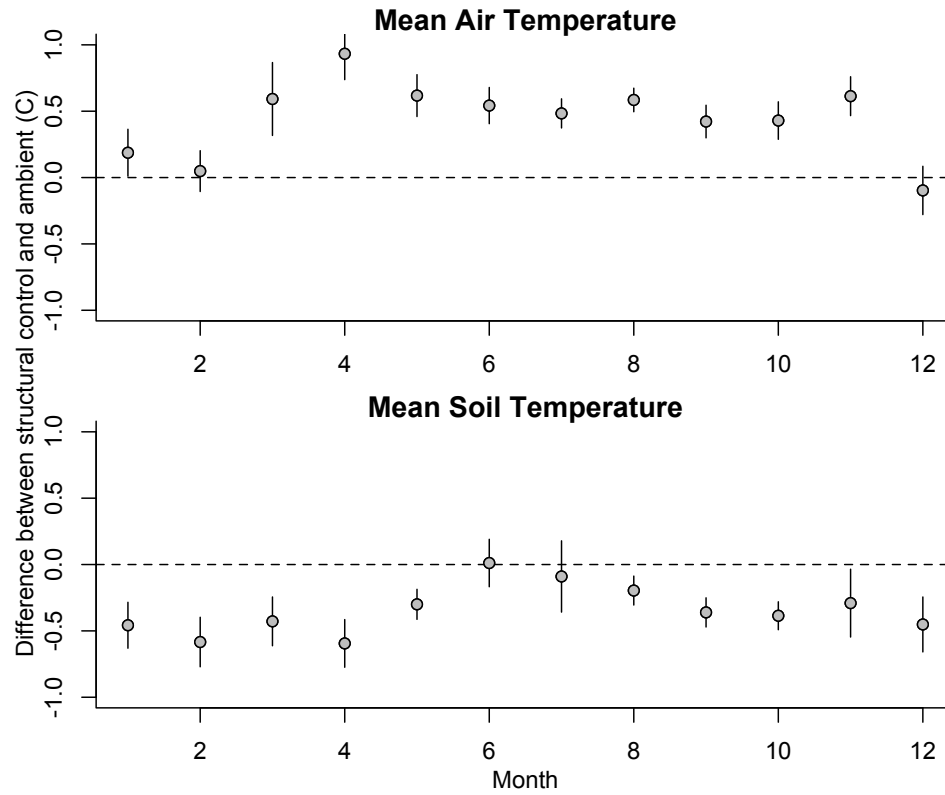


Figure 3: Difference between mean air and soil temperatures in structural controls compared with ambient controls, with no control chambers or warming infrastructure in place. Air temperatures were higher, whereas soil temperatures were lower in the structural controls compared with ambient conditions. We show fixed effects from a mixed effects model that accounts for differences in experimental design and other factors among sites by including site as an intercept-only random effect (see Supplemental Materials for details).

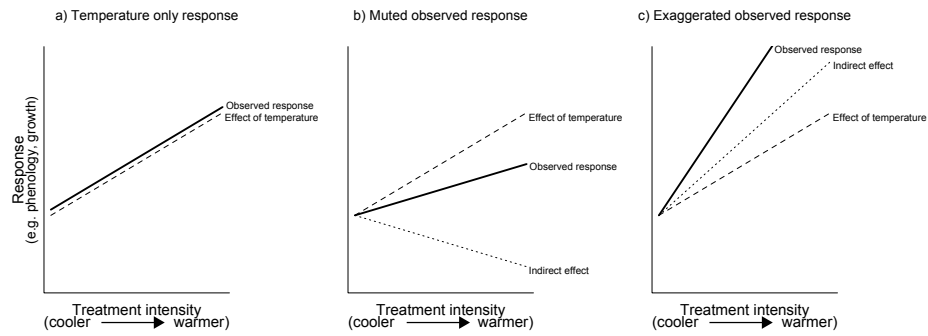


Figure 4: Experimental warming may cause biological responses to be muted or exaggerated, compared to direct responses to temperature alone, when indirect effects of experimental warming are also drivers of focal responses. For example, phenology may appear to be less sensitive to warming in experiments versus observational studies (Wolkovich *et al.*, 2012) because experimental warming reduces soil moisture, perhaps more than natural warming.

Supplemental Materials

Description of database

Search terms used and criteria for selecting the 12 studies that we ended up with. Climate variables included, and where database and metadata are housed.

Supplemental Methods

Statistical methods

Need description of block and year analyses (see Tables 1 and 2) To account for differences in the type of warming and other unmeasured site/study differences (e.g. forced air for Ellison and Marchin; heating cables for Farnsworth and ??), we fit linear mixed effects models with random effect of study-site. Response variables were daily soil or air temperature (models with daily mean, minimum, and maximum were all fit) and , and the explanatory variable was control type (infrastructure or ambient). We used a random intercepts structure, so that the mean temperature was allowed to vary across study-sites. We fit models across the entire year, as well as separate models for each month to examine if effects varied seasonally.