How do climate change experiments actually change climate?

A.K. Ettinger[1,2,a], I. Chuine[3,b], B.I. Cook[4,5,c], J.S. Dukes[6,d], A.M. Ellison[7,e], M.R. Johnston[8,f], A.M. Panetta[9,g], C.R. Rollinson[10,h], Y. Vitasse[11,12,i], and E.M. Wolkovich[1,8,j]

[1]Arnold Arboretum of Harvard University, Boston, Massachusetts 02131, USA

[2]Tufts University, Medford, Massachusetts 02155, USA

[3]CEFE UMR 5175, CNRS, Université de Montpellier,Université Paul-Valéry Montpellier, EPHE, Montpellier, France

[4]Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York 10964, USA

[5]NASA Goddard Institute for Space Studies, New York, New York 10025, USA

[6]Department of Forestry and Natural Resources and Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907, USA

[7]Harvard Forest, Harvard University, Petersham, Massachusetts 01366, USA

[8]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA

[9]Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309, USA

[10]The Morton Arboretum, Lisle, Illinois 60532, USA

[11]Institute of Geography, University of Neuchâtel, Neuchâtel, Switzerland

[12]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Neuchâtel, Switzerland

[a]Corresponding author; email: aettinger@fas.harvard.edu; phone: 781-296-4821; mailing address: 2204 Flagler Place NW, Washington, Distric of Columbia, 20001,USA

[b]Isabelle.CHUINE@cefe.cnrs.fr

[c]bc9z@ldeo.columbia.edu

[d]jsdukes@purdue.edu

[e]aellison@fas.harvard.edu

[f]johnston.miriam@gmail.com

[g]anpa7214@colorado.edu

[h]crollinson@mortonarb.org

[i]yann.vitasse@unine.ch

[j]wolkovich@fas.harvard.edu

November 1, 2017

Contents

Statement of authorship All authors conceived of this manuscript, which was inspired by our discussions at a Radcliffe Exploratory Seminar in 2016, and all authors contributed to manuscript revisions. A.E. and E.W. conceived of the idea for the literature review, database compilation, and related Radcliffe Exploratory Seminar. A.E. compiled the datasets; A.E. and C.R. analyzed the data and created the figures; A.E. wrote the manuscript.

Data Accessibility The C3E database will be available at KNB (Ettinger & Wolkovich, 2017), along with all R code from the analyses included in this paper. (Currently, metadata is published there; the full database and R code are available to reviewers upon request.)

Running title Experimental climate change

Key words global warming, warming experiment, microclimate, soil moisture, spring phenology, budburst

Type of article Review and Synthesis

Number of words in abstract 182

Number of words in main text 4270

Number of references 84

Number of figures 7

Number of tables 0 in main text

Number of text boxes 1

Number of words in Box 1 475

Abstract

To understand and forecast biological responses to climate change, scientists frequently use field experiments that alter temperature and precipitation in ways intended to be consistent with climate change projections. Such climate manipulations can manifest in complex and unintended ways, however, complicating interpretations of biological responses. We reviewed publications on active warming experiments to compile a new database of daily climate data from 12 active warming experiments. We find that the common practice of summarizing and analyzing only the mean changes across treatments hides potentially important variation in treatment effects over space and time.Furthermore, treatments produce unintended secondary effects, such as soil drying in conjunction with warming. The implications of these complexities are rarely explored, but have important biological consequences. We show one example of such consequences with a case study of spring plant phenology, in which accurately accounting for climate manipulation and its secondary effects triples the estimated sensitivity of budburst to warming. Based on our synthesis, we present recommendations for future analyses, as well as experimental design and data sharing, that we believe will improve the ability of climate change experiments to accurately identify and forecast species' responses.

Introduction

Climate change is dramatically altering earth's biota, shifting the physiology, distribution, and abundance of organisms, with cascading community, ecosystem, and climate 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 exists about how particular individuals, populations, species, communities, and ecosystems will respond as shifts in temperature and precipitation regimes become more extreme. Predicting biological responses to current and future climate change—and their feedbacks to earth's climate and ecosystem services—are among the most significant challenges facing scientists today.

Two common approaches for understanding biological effects of climate change are observational studies and process-based modeling; yet these approaches are insufficient for several reasons. Observational studies, which correlate recorded biological patterns with measured trends in climate, cannot disentangle the causal effects of warming from other factors that have also changed over time, such as successional stage or land use. Process-based models can overcome some of these challenges because they rely on explicit empirical relationships between observed phenomena and climate. They, however, are limited by their underlying assumptions, which may be poorly constrained, and can result in inaccurate forecasts, if the model is improperly parameterized (e.g., Pearson & Dawson, 2004; Hampe, 2004; Ibanez *et al.*, 2006; Swab *et al.*, 2012; Chuine *et al.*, 2016). In addition, neither approach is well-vetted for predicting future conditions that fall outside the range of historical variability; climate change will yield warmer temperatures than the previous 150 years, and possibly warmer than at any time in the last 2000 years (Ohlemüller *et al.*, 2006; Williams & Jackson, 2007; Williams *et al.*, 2007; Stocker *et al.*, 2013).

Field-based experiments that alter temperature address these shortcomings, and are therefore critical for determining mechanistic links between climate change and biological responses (e.g., Box *et al.*, 1978; Williams & Jackson, 2007; Gelman, 2014). Experiments can quantify biological responses to different levels of climate change, and can create the "no-analog" climate scenarios forecasted for the future, particularly when they employ active warming methods, such as forced air heaters, soil warming cables, or infrared heaters (Shaver *et al.*, 2000; Williams *et al.*, 2007; Aronson & McNulty, 2009). In addition, active warming can be combined with precipitation manipulations (e.g., snow removal, water additions, water reductions), offering the ability to isolate effects of temperature and precipitation from other environmental changes (e.g., Price & Waser, 1998; Cleland *et al.*, 2006; Sherry *et al.*, 2007; Rollinson & Kaye, 2012). Compared with indoor growth-chamber experiments, field-based experiments offer the possibility of preserving important but unknown or unquantified feedbacks among biotic and abiotic components of the studied systems.

Climate experiments allow ecologists to draw conclusions about how climate change may affect species' growth, survival, and future distributions (Dukes & Mooney, 1999; Hobbie *et al.*, 1999; Morin *et al.*, 2010; Chuine *et al.*, 2012; Reich *et al.*, 2015; Gruner *et al.*, 2017). But is it reasonable to extrapolate findings from these experiments to the real world? Do they actually alter climate in the ways intended by experimental design? Recent research suggests that climate manipulations do not alter climate in ways that are consistent with observed changes over time (Wolkovich *et al.*, 2012; Menke *et al.*, 2014). However, we lack a robust assessment of how active warming experiments alter the climate conditions experienced by organisms, and the extent to which these conditions are similar to current field conditions or anticipated climate change.

Here, we investigate if and how climate change experiments actually change climate. Though the challenges and opportunities of climate change experiments have been summarized previously (e.g., De Boeck *et al.*, 2015), an in-depth quantitative analysis is lacking. We use plot-level daily microclimate data from 12 active warming experiments (yielding 44 experiment years and 11594 experiment days) to show the direct and indirect ways that experimental manipulations alter climate. We highlight the challenges associated with quantifying and interpreting experimental shifts in climate and the resulting biological responses. We use a case study of spring plant phenology to demonstrate how the common mean-focused analysis, which ignores secondary effects of warming treatments, leads to inaccurate quantification of species' sensitivities to temperature. Finally, we use findings from our synthesis to make recommendations for future analysis and design of climate change experiments (Box 1).

Climate from Climate Change Experiments (C3E) database

To investigate how climate change experiments actually change climate, we first identified published active warming field experiments. We focus on *in situ* active warming manipulations because recent analyses indicate that active warming methods are the most controlled and consistent (Kimball, 2005; Kimball *et al.*, 2008; Aronson & McNulty, 2009; Wolkovich *et al.*, 2012). We do not include passive worming experiments because they have been analyzed extensively already and are known to have distinct issues, including overheating and great variation in the amount of warming depending on irradiance and snow-depth (Marion *et al.*, 1997; Shaver *et al.*, 2000; Wolkovich *et al.*, 2012; Bokhorst *et al.*, 2013).

We carried out a full literature review to identify potential active field warming experiments to include in the database. To find these studies, we followed the methods and search terms of Wolkovich *et al.* (2012) for their Synthesis of Timings Observed in iNcrease Experiments (STONE) database (Wolkovich *et al.*, 2012). We searched the Web of Science (ISI) for Topic=(warm* OR temperature*) AND Topic=(plant* AND phenolog*) AND Topic=(experiment* OR manip*). We restricted dates to the time period after the STONE database (i.e. January 2011 through March 2015). This yielded 277 new studies. We removed all passive warming studies from the list. In addition, a secondary goal of this database was to test hypotheses about mechanisms for the mismatch in sensitivities between observational and experimental phenological studies (Wolkovich *et al.*, 2012). Because of this secondary goal, studies included in the database had to either 1) include more than one level of warming, or 2) manipulate both temperature and precipitation. (Some studies met both of these criteria.) These additional restrictions constrained the list to 11 new studies, as well as 6 of the 37 studies in the STONE database. We contacted authors to obtain daily (or sub-daily) climate data and the most accurate phenological data for these 17 sites, as well as two additional datasets offered to us over the course of our literature review. We received data from authors of 12 of these 19 studies or 63.2%. STONE received 16.7% of data directly (Wolkovich *et al.*, 2012). (We were unable to include the following studies because authors declined to share their data or did not respond: (Schwartzberg *et al.*, 2014; Moser *et al.*, 2011; Carón *et al.*, 2015; Ellebjerg *et al.*, 2008)).

The daily temperature and soil moisture data from these 12 experiments were put together into the Climate from Climate Change Experiments (C3E) database, which is available at KNB (Ettinger & Wolkovich, 2017). This database allows us to explore the complex ways that climate is altered by active warming treatments, both directly and indirectly, across multiple studies. The database contains daily climate data collected between 1991 and 2014 from North American and European climate change experiments (Table S1, Figure 1 in the main text).

Complexities in interpreting 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 an experiment. Ecologists, however, are generally interested in the ecological responses (e.g., community dynamics, species' growth, abundance, or phenology), which are collected on much coarser timescales (e.g., weekly or annually). Not surprisingly, then, authors typically provide detailed information on the observed biological responses, but report only the mean change in climate over the course of the experiment and whether it matched their target level of change (e.g., Price & Waser, 1998; Rollinson & Kaye, 2012; Clark *et al.*, 2014a,b).

Though the published focus is often on shifts in mean climate variables, imposed climate manipulations actually result in much more complex shifts. The magnitude of change in these manipulations may vary in time and space, and the presence of experimental equipment often unintentionally alters environmental conditions. These factors, discussed below, challenge our interpretation of how experimental warming studies can be used to forecast effects of climate change.

Effects on local climate vary over time and space

Reporting only the mean temperature difference across the duration of the study hides potentially important variations in daily, seasonal, or annual temperatures among treatments (Figure S1). Using the C3E database, we found that active warming (non-significantly) reduces above-ground daily temperature range (DTR) (Table S3, see also Table S2, which details the different methods used to measure temperature). Active warming decreased above-ground DTR by differentially affecting maximum and minimum temperatures: warming increased daily minima by 0.84°C per °C of warming target, but only increased daily maxima by 0.50°C per °C of target warming (Table S3).

We observed strong seasonal and annual variations in experimental warming effects (Figures 2, 3, Table S4). These may be driven by interactions between warming treatments and daily, seasonal, and annual weather patterns, since the magnitude of warming can vary as weather conditions change. Both infrared heaters and soil cables fail to achieve the target temperatures during rainstorms (Peterjohn *et al.*, 1993; Hoeppner & Dukes, 2012) and with windy conditions (Kimball, 2005; Kimball *et al.*, 2008). In addition, treatments are often applied inconsistently within or across years. Heat applications are frequently shut off during winter months, and some heating methods, even if left on throughout the year, are not capable of applying constant warming year-round (e.g. Clark *et al.*, 2014a,b; Hagedorn *et al.*, 2010).

Treatment effects also vary spatially, adding further complication to interpreting effects of climate change experiments. The C3E database contains four 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 observed warming varied by more than 1°C among blocks (Figure 3, Table S5); this block-to-block variation in warming treatment is significant, at 60-100% of target temperatures. These differences in warming levels among blocks may be caused by fine-scale variation in vegetation, slope, aspect, soil type, or other factors that can alter wind or soil moisture, which in turn affect warming (Peterjohn *et al.*, 1993; Kimball, 2005; Kimball *et al.*, 2008; Hoeppner & Dukes, 2012; Rollinson & Kaye, 2015).

Of course, identical experimental treatments across space and time are not necessary for robust analysis of experimental results or for forecasting. Indeed, the spatial and temporal variation we report could improve and refine models, and—at least in some regions—may be consistent with contemporary patterns of climate change (Stocker *et al.*, 2013). Taking advantage of this variation, however, requires understanding and reporting it (e.g., Milcu *et al.*, 2016). In contrast, fine-scale spatial and temporal variations in warming treatments are rarely analyzed explicitly, so the implications for interpretation of experimental findings are unclear.

Experimental infrastructure alters local climate

Experimental structures themselves can alter temperature and other important biotic and abiotic variables in ways that are not generally examined nor reported in experimental climate change studies. The importance of controls that mimic a treatment procedure without actually applying the treatment is widely acknowledged in biology (e.g., Spector, 2001; Johnson & Besselsen, 2002; Quinn & Keough, 2002). Though some researchers install treatments with non-functional warming equipment in experimental climate change studies, the magnitude and implications of structural effects on climate are rarely discussed or interpreted.

To investigate the magnitude of infrastructure 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.*, 2014b; Marchin *et al.*, 2015; Pelini *et al.*, 2011). These were the only studies in the C3E database that monitored climate in 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. Other studies monitored environmental conditions in only structural controls (n=3) or only ambient controls (n=4).

We found that experimental structures altered above-ground and soil temperatures in opposing ways: above-ground temperatures were higher in the structural controls than in ambient controls, whereas soil temperatures were lower in structural controls compared with ambient controls (Figure 4a-d). This general pattern was consistent across different temperature models (mean, minimum, and maximum temperatures), although the magnitude varied among seasons, studies, and years (Figure 4a-d, Tables S6-S11). We also found that experimental infrastructure decreased soil moisture relative to ambient conditions (Figure 4e, Tables S8, S11).

There are several possible reasons for the observed climatic differences between ambient and structural controls. Infrastructure materials may shade the plots, reduce airflow, reduce albedo relative to surroundings, or otherwise change the energy balance. Specifically, soil temperatures may be cooler in structural controls because the experimental structures block sunlight from hitting the ground surface, which would therefore experience less radiative heating than ambient controls. In addition, above-ground temperatures may be warmer in structural controls because the structures radiatively warm the air around them and block wind, inhibiting mixing with air outside of the plot. Structures also interfere with precipitation hitting the ground, thereby reducing local soil moisture and snowpack, with its insulative properties. The latter likely plays a bigger role in soil temperature differences at the Harvard Forest sites (exp04, exp07, exp08), where average annual snowfall is over one meter, than at Duke Forest (exp03,exp10), where average snow accumulation each winter is 20 cm or less.

Although there is little discussion of measured temperature (or other) differences between ambient and structural control plots in published work (e.g., Farnsworth *et al.*, 1995; Pelini *et al.*, 2011; Clark *et al.*, 2014a), the few studies that do mention these differences are consistent with these findings. Clark *et al.* (2014b), whose study employed forced air and soil cables for warming, state that "control of the air temperature was less precise, in part due to air scooping on windy days." Marchin *et al.* (2015) note that structural controls had mean spring air temperatures about 0.5°C or more above ambient temperatures and Peterjohn *et al.* (1994) reported cooler soil temperatures in structural controls than in ambient controls at shallow soil depths. Similarly, we found the greatest difference in soil temperature between structural and ambient controls in shallow soils (e.g. exp10, soil depth = 2cm). Further, although the focus to date has been largely on these abiotic impacts of experimental structures, such structures may also alter herbivory and other biotic conditions (Kennedy, 1995; Moise & Henry, 2010; Wolkovich *et al.*, 2012; Hoeppner & Dukes, 2012).

Most warming experiments calculate focal response variables relative to ambient controls (e.g., Marchin *et al.*, 2015), which our analyses suggest will not properly account for infrastructure effects. Because experimental design may influence abiotic and biotic responses in warming experiments, improved documentation and analysis of infrastructure effects is an important next step in climate change experiments. Separating infrastructure artifacts from warming effects is critical if we wish to apply findings to forecasts outside of an experimental context.

Secondary and feedback effects of climate change manipulations

Climate change experiments often seek to manipulate temperature or precipitation separately as well as interactively, but manipulating either of these variables in isolation is difficult. Treatments involving precipitation additions typically reduce temperatures in climate change manipulations (Sherry *et al.*, 2007; Rollinson & Kaye, 2012; McDaniel *et al.*, 2014b): McDaniel et al. (2014) observed that a twenty percent increase in precipitation reduced mean hourly temperatures by 0.3°C over the course of their two-year experiment. This is because increased soil moisture typically shifts the surface energy balance to favor latent (i.e., evapotranspiration) over sensible energy fluxes, reducing heating of the air overlying the soils. Experimental warming typically increases vapor pressure deficit and reduces soil water content (e.g., Sherry *et al.*, 2007; Morin *et al.*, 2010; Pelini *et al.*, 2014; Templer *et al.*, 2016). Of the twelve experiments in the C3E database, we examined the ten that measured and reported soil moisture and found that experimental warming reduced soil moisture by 3.0%, on average (Figure 5, Table S13), and that this reduction occurred at a rate of 0.36% per degree of target warming (Table S12). Thus, although active warming experiments may not be explicitly designed to manipulate soil moisture, soil moisture is unavoidably affected by changing temperatures.

Warming and precipitation treatments, and their secondary effects on soil moisture and other abiotic factors, can also alter the biotic environment, which may produce cascading effects. Many studies have found shifts from herbaceous to woody plant communities over time with experimental warming (e.g., Rollinson & Kaye, 2012; McDaniel *et al.*, 2014b,a; Harte *et al.*, 2015); this, in turn, can alter microbial and herbaceous plant communities. These community shifts may change competitive dynamics and affect resource levels, such as moisture, carbon, and nutrient levels in the soil (McDaniel *et al.*, 2014b,a; Harte *et al.*, 2015), and cause positive feedbacks to local climate change (Harte *et al.*, 2015).

The widespread presence of unintended secondary effects of climate change manipulations highlights the importance of measuring environmental conditions at the plot level, and using these measurements in analysis and interpretation of results. Many climate change experiments—including seven of the 12 in the C3E database —analyze warming and/or precipitation treatments as simple categorical predictors (e.g., as in a two-way ANOVA). Our findings, however, demonstrate a clear need for alternative modelling approaches to fully understand the experimental results and to make mechanistic links between changes in climate and ecological responses. One straightforward alternative is to include the continuous climate data (e.g., plot-level temperatures) as predictors of the focal response variable, such as phenological state or species density (e.g., Marchin *et al.*, 2015; Pelini *et al.*, 2014).

Biological implications

We have highlighted a suite of factors that complicate interpretation of warming experiments. These largely unintended alterations are likely to have biological implications for many of the responses studied in warming experiments (e.g., Figure 6). Interpretation of experimental climate change effects on biological responses may be misleading because the intended climate treatments (i.e., categorical comparisons or target warming levels) are generally used as explanatory variables in analyses. The interpretation is likely to be altered by using fine-scale, measured climate as explanatory variables. Detailed examination of multiple microclimate variables (e.g., plot-level temperature and soil moisture) will allow a more complete understanding of the indirect, as well as direct, effects of treatments on abiotic and biotic drivers of focal responses.

Biological responses may be muted (Figure 6b) or exaggerated (Figure 6c) in experiments when direct and indirect effects of climate manipulations work in concert. Plant phenology provides one example of a biological response that is muted in experiments versus observational studies (Figure 6b). This is because phenology has a complex dependence on temperature and water availability (as well as other factors, Davis *et al.*, 2015) Although phenology is generally advanced by higher spring temperatures, it can also be delayed by increased winter temperature (which delays endodormancy break). In addition, reduced water availability during the spring can slow cell elongation and delay budburst (Peñuelas *et al.*, 2004; Ourcival & Rambal, 2011; Craine *et al.*, 2012; Matthews & Mazer, 2016). Effects of these different drivers may be responsible for the observed discrepancy between observational and experimental phenological responses to warming (Wolkovich *et al.*, 2012).

We demonstrate how using measured plot-level climate variables, instead of target warming, alters estimates of temperature sensitivity with data in the C3E database. Five study sites from C3E have above-ground temperature and soil moisture, as well as phenology data (day of year of budburst). We first fit a model of target warming only to these data, accounting for non-independence due to site and year with random effects (Table S14, solid black line in Figure 7). This model estimates temperature sensitivity of budburst to be -2.01 days/°C (i.e., budburst shifts earlier by two days per degree Celsius of warming). We then fit a model that included mean daily minimum above-ground temperature, mean winter (January-March) soil moisture, and their interaction as explanatory variables (with the same random effects structure, Table S14. See Supplemental Materials for details.) The slope for temperature in this temperature-soil moisture model can be directly compared to the slope for target warming in the previous model because the units are the same (change in budburst in days/°C). The temperature-soil moisture model had improved model fit compared to the target warming model (Table S15), and the slope tripled in magnitude: estimated temperature sensitivity of budburst was -6.22 days/°C (Table S14).

The increase in estimated temperature sensitivity with measured (rather than target) temperature has two major causes. First, target warming generally exceeds the measured above-ground temperature differences between treatment and control plots (Figure 3). W Second, experimental warming dries out the soil in addition to increasing temperatures, and both climate variables affect the timing of budburst. Decreasing soil moisture has a delaying effect on budburst phenology, opposing the advancing effect of rising temperatures (Figure 6b). This example shows how the common method of using target warming alone to understand biological responses is likely to yield inaccurate estimates of temperature sensitivity in warming experiments. In this case, the underestimation may be substantial enough to account for the previously observed discrepancy between observational and experimental phenological responses to warming, though further investigation is required, for example across additional phenophases (Wolkovich *et al.*, 2012).

Accounting for both direct and indirect effects of warming is critical for accurate interpretation of the consequences of climate change (Kharouba *et al.*, 2015). A critical question is the extent to which indirect abiotic and biotic effects 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 (Moise & Henry, 2010; Diamond *et al.*, 2013).Altered DTR (i.e. temperature minima changing more than maxima) with experimental warming is consistent with observed changes in many places, at least for some time periods. Minimum temperatures increased more rapidly than maximum temperatures, reducing DTR strongly and significantly from 1950-1980, but the trends have been largely insignificant from 1980 onward (Thorne *et al.*, 2016; Vose *et al.*, 2005). Soil drying in conjunction with future warming is forecasted in some regions, such as the southwestern United States, mainly because of reductions in precipitation and increased evaporative demand with warmer air.(Dai, 2013; Seager *et al.*, 2013). However, the northeastern United States has been trending wetter over time and is expected to be wetter in the future (Seager *et al.*, 2014; Shuman & Burrell, 2017). The soil moisture changes in warming experiments, and the biological changes they cause, may therefore represent an experimental artifact that is unlikely to occur with future warming. The altered light, wind, and herbivory patterns documented under experimental infrastructure (Kennedy, 1995; Moise & Henry, 2010; Wolkovich *et al.*, 2012; Hoeppner & Dukes, 2012; Clark *et al.*, 2014b) represent other potential experimental artifacts that are worth quantifying in future analyses to provide improved estimates of temperature sensitivity.

Conclusions

As climate change continues across the globe, ecologists are challenged to not only document impacts but make quantitative, robust predictions. Our ability to meet this challenge requires a nuanced mechanistic understanding of how climate directly and indirectly alters biological processes. Climate change experiments, which have been underway for nearly four decades (e.g., Tamaki *et al.*, 1981; Carlson & Bazzaz, 1982), provide invaluable information about biological responses to climate change. Yet the full range of changes in environmental conditions imposed by these experiments is rarely presented. We have compiled the first database of fine-scale climate data from multiple warming experiments and shown how time, space, and experimental artifacts may hinder simple interpretations of these climate change experiments. We hope this provides a foundation for gaining the most knowledge and utility from existing experiments via robust analyses, for designing better experiments and models in the future (see Box 1), and for improved understanding of biological responses and feedbacks in a changing world.

Acknowledgements

We are grateful to those who shared their experimental climate data with us and others in the C3E database. We thank the Radcliffe Institute for Advanced Study at Harvard University, which provided funding for an Exploratory Seminar at which the ideas in this paper were conceived. This research was also supported by the National Science Foundation (NSF DBI 14-01854 to A.E.). Any opinion, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

Box 1: Recommendations for future climate change experiments

1. *Collect and analyze fine-scale climate data.* This includes analyzing and interpreting minimum and maximum values, as well as variance and critical thresholds (e.g., the number and duration of freeze-thaw events and accumulated chilling hours, McDaniel *et al.*, 2014b; Vasseur *et al.*, 2014). We suggest saving the raw data from data loggers (often collected at hourly or higher resolution) to allow quantification of variance (and other summaries) at different temporal resolutions. In assessing which frequency of

measurements is most appropriate for analyses (e.g., hourly, twice daily), it is critical to consider the chronobiology of the event and organisms of interest. For ants, this might mean that temperatures be monitored every minute (Helm & Shavit, 2017); for bacteria, even more frequently.

2. *Analyze measured climate variables rather than targets.* There can be substantial variation in the effects of warming and precipitation treatments among plots and across time (Figure 3). Analyzing measured climate will allow much more in-depth understanding of the drivers and biological effects of variation in temperature and moisture.

3. *Publish high quality, usable data and metadata.* Given that in situ climate manipulations are logistically challenging and expensive (Aronson & McNulty, 2009), and that they often produce a large volume of fine-scale climate data, good curation and data sharing will ensure wider use and deeper understanding of these valuable data. When studying biological implications of a global challenge as large as climate change, progress will come from designing and reporting experiments in ways that facilitate an eventual global data set.

4. *Include both structural and ambient controls* and collect, use, and report climate and biological data within them. Fewer than half of the studies in our C3E database reported climate data from these two control types (5 out of 12 studies); however, all experiments that did include both control types showed significant effects of infrastructure (Figure 4).

5. *Design relevant manipulations* by consulting observational records and forecasts, including seasonal and annual variation in projected warming. When it is not possible or desirable to match anticipated changes in climate, studies should report how imposed treatments compare to projected changes and past observations (e.g., Hoover *et al.*, 2014). In addition, if continuous treatments are not applied throughout the study, the seasonality and timing of treatments should be explicitly reported and the climate should be monitored throughout.

6. *Maximize the duration of climate change experiments* by running some experiments for as long as possible. Long-term responses of individuals and populations can differ from transient responses (Saleska *et al.*, 2002; Franklin, 1989; Giasson *et al.*, 2013; Harte *et al.*, 2015). Well-designed and well-supported longer warming experiments will allow study of how inter-annual variations interact with climate change treatments, particularly when combined with observational studies and modeling (Luo *et al.*, 2011).

References

Aronson, E.L. & McNulty, S.G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, 149, 1791–1799.

Bokhorst, S., Huiskes, A., Aerts, R., Convey, P., Cooper, E.J., Dalen, L., Erschbamer, B., Gudmundsson, J., Hofgaard, A., Hollister, R.D. *et al.* (2013). Variable temperature effects of open top chambers at polar and alpine sites explained by irradiance and snow depth. *Global change biology*, 19, 64–74.

Box, G.E., Hunter, W.G., Hunter, J.S. *et al.* (1978). *Statistics for Experimenters: An Introduction to Design, Data Analysis, and Model Building*. John Wiley and Sons New York.

Carlson, R.W. & Bazzaz, F.A. (1982). Photosynthetic and growth response to fumigation with so2 at elevated co2 for c3 and c4 plants. *Oecologia*, 54, 50–54.

Carón, M., De Frenne, P., Brunet, J., Chabrerie, O., Cousins, S.A., De Backer, L., Decocq, G., Diekmann, M., Heinken, T., Kolb, A. *et al.* (2015). Interacting effects of warming and drought on regeneration and early growth of acer pseudoplatanus and a. platanoides. *Plant Biology*, 17, 52–62.

Chuine, I., Bonhomme, M., Legave, J.M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A. & Améglio, T. (2016). Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. *Global change biology*, 22, 3444–3460.

Chuine, I., Morin, X., Sonié, L., Collin, C., Fabreguettes, J., Degueldre, D., Salager, J.L. & Roy, J. (2012). Climate change might increase the invasion potential of the alien c4 grass setaria parviflora (poaceae) in the mediterranean basin. *Diversity and Distributions*, 18, 661–672.

Clark, J.S., Melillo, J., Mohan, J. & Salk, C. (2014a). The seasonal timing of warming that controls onset of the growing season. *Global Change Biology*, 20, 1136–1145.

Clark, J.S., Salk, C., Melillo, J. & Mohan, J. (2014b). Tree phenology responses to winter chilling, spring warming, at north and south range limits. *Functional Ecology*, 28, 1344–1355.

Cleland, E.E., Chiariello, N.R., Loarie, S.R., Mooney, H.A. & Field, C.B. (2006). 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.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A. & Totterdell, I.J. (2000). Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, 408, 184–187.

Craine, J.M., Wolkovich, E.M., Towne, E.G. & Kembel, S.W. (2012). Flowering phenology as a functional trait in a tallgrass prairie. *New Phytologist*, 193, 673–682.

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, 3, 52–58.

Davis, C.C., Willis, C.G., Connolly, B., Kelly, C. & Ellison, A.M. (2015). Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. *American journal of botany*, 102, 1599–1609.

De Boeck, H.J., Vicca, S., Roy, J., Nijs, I., Milcu, A., Kreyling, J., Jentsch, A., Chabbi, A., Campioli, M., Callaghan, T. *et al.* (2015). Global change experiments: challenges and opportunities. *BioScience*, 65, 922–931.

Diamond, S.E., Penick, C.A., Pelini, S.L., Ellison, A.M., Gotelli, N.J., Sanders, N.J. & Dunn, R.R. (2013). Using physiology to predict the responses of ants to climatic warming. *Integrative and comparative biology*, 53, 965–974.

Dukes, J.S. & Mooney, H.A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology and Evolution*, 14, 135–139.

Ellebjerg, S.M., Tamstorf, M.P., Illeris, L., Michelsen, A. & Hansen, B.U. (2008). Inter-annual variability and controls of plant phenology and productivity at zackenberg. *Advances in ecological research*, 40, 249–273.

Ettinger, A. & Wolkovich, E. (2017). Climate from climate change experiments (c3e).

Farnsworth, E., Nunez-Farfan, J., Careaga, S. & Bazzaz, F. (1995). Phenology and growth of three temperate forest life forms in response to artificial soil warming. *Journal of Ecology*, 83, 967–977.

Field, C.B., Lobell, D.B., Peters, H.A. & Chiariello, N.R. (2007). Feedbacks of terrestrial ecosystems to climate change. *Annu. Rev. Environ. Resour.*, 32, 1–29.

Franklin, J.F. (1989). Importance and justification of long-term studies in ecology. In: *Long-term studies in ecology*. Springer, pp. 3–19.

Gelman, A. (2014). *Experimental reasoning in social science experiments*, New Haven, CT: Yale University Press, chap. 7, pp. 185–195.

Giasson, M.A., Ellison, A.M., Bowden, R., Crill, P.M., Davidson, E., Drake, J., Frey, S., Hadley, J., Lavine, M., Melillo, J. *et al.* (2013). Soil respiration in a northeastern us temperate forest: a 22-year synthesis. *Ecosphere*, 4, 1–28.

Gruner, D.S., Bracken, M.E., Berger, S.A., Eriksson, B.K., Gamfeldt, L., Matthiessen, B., Moorthi, S., Sommer, U. & Hillebrand, H. (2017). Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. *Oikos*, 126, 8–17.

Hagedorn, F., Martin, M., Rixen, C., Rusch, S., Bebi, P., Zürcher, A., Siegwolf, R.T., Wipf, S., Escape, C., Roy, J. *et al.* (2010). Short-term responses of ecosystem carbon fluxes to experimental soil warming at the swiss alpine treeline. *Biogeochemistry*, 97, 7–19.

Hampe, A. (2004). Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography*, 13, 469–471.

Harte, J., Saleska, S.R. & Levy, C. (2015). Convergent ecosystem responses to 23-year ambient and manipulated warming link advancing snowmelt and shrub encroachment to transient and long-term climate–soil carbon feedback. *Global Change Biology*, 21, 2349–2356.

Helm, B. & Shavit, A. (2017). *Dissecting and reconstructing time and space for replicable biological research*, New Haven, CT: Yale University Press, pp. 233–249.

Hobbie, S.E., Shevtsova, A. & Chapin III, F.S. (1999). Plant responses to species removal and experimental warming in alaskan tussock tundra. *Oikos*, 84, 417–434.

Hoeppner, S.S. & Dukes, J.S. (2012). Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology*, 18, 1754–1768.

Hoover, D.L., Knapp, A.K. & Smith, M.D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, 95, 2646–2656.

Ibanez, I., Clark, J.S., Dietze, M.C., Feeley, K., Hersh, M., LaDeau, S., McBride, A., Welch, N.E. & Wolosin, M.S. (2006). Predicting biodiversity change: Outside the climate envelope, beyond the species-area curve. *Ecology*, 87, 1896–1906.

Johnson, P.D. & Besselsen, D.G. (2002). Practical aspects of experimental design in animal research. *ILAR Journal*, 43, 202–206.

Kennedy, A. (1995). Temperature effects of passive greenhouse apparatus in high-latitude climate change experiments. *Functional Ecology*, 9, 340–350.

Kharouba, H.M., Vellend, M., Sarfraz, R.M. & Myers, J.H. (2015). The effects of experimental warming on the timing of a plant–insect herbivore interaction. *Journal of Animal Ecology*, 84, 785–796.

Kimball, B. (2005). Theory and performance of an infrared heater for ecosystem warming. *Global Change Biology*, 11, 2041–2056.

Kimball, B.A., Conley, M.M., Wang, S., Lin, X., Luo, C., Morgan, J. & Smith, D. (2008). Infrared heater arrays for warming ecosystem field plots. *Global Change Biology*, 14, 309–320.

Luo, Y., Melillo, J., Niu, S., Beier, C., Clark, J.S., Classen, A.T., Davidson, E., Dukes, J.S., Evans, R., Field, C.B. *et al.* (2011). Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biology*, 17, 843–854.

Marchin, R.M., Salk, C.F., Hoffmann, W.A. & Dunn, R.R. (2015). Temperature alone does not explain phenological variation of diverse temperate plants under experimental warming. *Global change biology*, 21, 3138–3151.

Marion, G., Henry, G., Freckman, D., Johnstone, J., Jones, G., Jones, M., Levesque, E., Molau, U., Mølgaard, P., Parsons, A. *et al.* (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, 3, 20–32.

Matthews, E.R. & Mazer, S.J. (2016). Historical changes in flowering phenology are governed by temperature× precipitation interactions in a widespread perennial herb in western north america. *New Phytologist*, 210, 157–167.

McDaniel, M., Kaye, J. & Kaye, M. (2014a). Do "hot moments" become hotter under climate change? soil nitrogen dynamics from a climate manipulation experiment in a post-harvest forest. *Biogeochemistry*, 121, 339–354.

McDaniel, M., Wagner, R., Rollinson, C., Kimball, B., Kaye, M. & Kaye, J. (2014b). Microclimate and ecological threshold responses in a warming and wetting experiment following whole tree harvest. *Theoretical and applied climatology*, 116, 287–299.

Menke, S.B., Harte, J. & Dunn, R.R. (2014). Changes in ant community composition caused by 20 years of experimental warming vs. 13 years of natural climate shift. *Ecosphere*, 5, 1–17.

Milcu, A., Puga-Freitas, R., Ellison, A.M., Blouin, M., Scheu, S., Girin, T., Frechet, G., Rose, L., Scherer-Lorenzen, M., Barot, S. *et al.* (2016). Systematic variability enhances the reproducibility of an ecological study. *bioRxiv(beta)*, p. 080119.

Moise, E.R. & Henry, H.A. (2010). Like moths to a street lamp: exaggerated animal densities in plot-level global change field experiments. *Oikos*, 119, 791–795.

Morin, X., Roy, J., Sonié, L. & Chuine, I. (2010). Changes in leaf phenology of three european oak species in response to experimental climate change. *New Phytologist*, 186, 900–910.

Moser, B., Fridley, J.D., Askew, A.P. & Grime, J.P. (2011). Simulated migration in a long-term climate change experiment: invasions impeded by dispersal limitation, not biotic resistance. *Journal of Ecology*, 99, 1229–1236.

Ohlemüller, R., Gritti, E.S., Sykes, M.T. & Thomas, C.D. (2006). Towards european climate risk surfaces: the extent and distribution of analogous and non-analogous climates 1931–2100. *Global ecology and biogeography*, 15, 395–405.

Ourcival, J. & Rambal, S. (2011). Phenological responses to extreme droughts in a mediterranean forest. *Glob Change Biol*, 17, 1036–1048.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, 37, 637–669.

Pearson, R.G. & Dawson, T.P. (2004). Bioclimate envelope models: what they detect and what they hide - response to hampe (2004). *Global Ecology and Biogeography*, 13, 471–473.

Pelini, S., Diamond, S., Nichols, L., Stuble, K., Ellison, A.M., Sanders, N., Dunn, R. & Gotelli, N. (2014). Geographic differences in effects of experimental warming on ant species diversity and community composition. *Ecosphere*, 5, 1–12.

Pelini, S.L., Bowles, F.P., Ellison, A.M., Gotelli, N.J., Sanders, N.J. & Dunn, R.R. (2011). 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.

Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M. & Terradas, J. (2004). Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist*, 161, 837–846.

Peterjohn, W.T., Melillo, J.M., Bowles, F.P. & Steudler, P.A. (1993). Soil warming and trace gas fluxes: experimental design and preliminary flux results. *Oecologia*, 93, 18–24.

Price, M.V. & Waser, N.M. (1998). Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology*, 79, 1261–1271.

Quinn, G.P. & Keough, M.J. (2002). *Experimental design and data analysis for biologists*. Cambridge University Press.

Reich, P.B., Sendall, K.M., Rice, K., Rich, R.L., Stefanski, A., Hobbie, S.E. & Montgomery, R.A. (2015). Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. *Nature Clim.Change*, 5, 148–152.

Rollinson, C.R. & Kaye, M.W. (2012). Experimental warming alters spring phenology of certain plant functional groups in an early successional forest community. *Global Change Biology*, 18, 1108–1116.

Rollinson, C.R. & Kaye, M.W. (2015). Modeling monthly temperature in mountainous ecoregions: importance of spatial scale for ecological research. *Climate Research*, 64, 99–110.

Saleska, S.R., Shaw, M.R., Fischer, M.L., Dunne, J.A., Still, C.J., Holman, M.L. & Harte, J. (2002). Plant community composition mediates both large transient decline and predicted long-term recovery of soil carbon under climate warming. *Global Biogeochemical Cycles*, 16.

Schwartzberg, E.G., Jamieson, M.A., Raffa, K.F., Reich, P.B., Montgomery, R.A. & Lindroth, R.L. (2014). Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia*, 175, 1041–1049.

Seager, R., Neelin, D., Simpson, I., Liu, H., Henderson, N., Shaw, T., Kushnir, Y., Ting, M. & Cook, B.

(2014). Dynamical and thermodynamical causes of large-scale changes in the hydrological cycle over north america in response to global warming. *Journal of Climate*, 27, 7921–7948.

Seager, R., Ting, M., Li, C., Naik, N., Cook, B., Nakamura, J. & Liu, H. (2013). Projections of declining surface-water availability for the southwestern united states. *Nature Climate Change*, 3, 482.

Shaver, G.R., Canadell, J., Chapin, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L. *et al.* (2000). 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.

Sheldon, K.S., Yang, S. & Tewksbury, J.J. (2011). Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. *Ecology Letters*, 14, 1191–1200.

Sherry, R.A., Zhou, X., Gu, S., 3rd, J.A.A., Schimel, D.S., Verburg, P.S., Wallace, L.L. & Luo, Y. (2007). Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 198–202.

Shukla, J. & Mintz, Y. (1982). Influence of land-surface evapotranspiration on the earth's climate. *Science*, 215, 1498–1501.

Shuman, B.N. & Burrell, S.A. (2017). Centennial to millennial hydroclimatic fluctuations in the humid northeast united states during the holocene. *Quaternary Research*, pp. 1–11.

Spector, R. (2001). Progress in the search for ideal drugs. *Pharmacology*, 64, 1–7.

Stocker, T., Qin, D., Plattner, G., Tignor, M., Allen, S., Boschung, J., Nauels, A., Xia, Y., Bex, B. & Midgley, B. (2013). 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.

Swab, R.M., Regan, H.M., Keith, D.A., Regan, T.J. & Ooi, M.K.J. (2012). Niche models tell half the story: spatial context and life-history traits influence species responses to global change. *Journal of Biogeography*, 39, 1266–1277.

Tamaki, G., Weiss, M.A. & Long, G.E. (1981). Evaluation of plant density and temperature in predator-prey interactions in field cages. *Environmental Entomology*, 10, 716–720.

Templer, P.H., Phillips, N.G., Ellison, A.M. & Pelini, S.L. (2016). Ecosystem warming increases sap flow rates of northern red oak trees. *Ecosphere*, 7.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148.

Thorne, P., Donat, M., Dunn, R., Williams, C., Alexander, L., Caesar, J., Durre, I., Harris, I., Hausfather, Z., Jones, P. *et al.* (2016). Reassessing changes in diurnal temperature range: Intercomparison and evaluation of existing global data set estimates. *Journal of Geophysical Research: Atmospheres*, 121, 5138–5158.

Urban, M.C., Tewksbury, J.J. & Sheldon, K.S. (2012). 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.

Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D., McCann, K.S., Savage, V., Tunney, T.D. & O'Connor, M.I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society of London B: Biological Sciences*, 281, 20132612.

Vose, R.S., Easterling, D.R. & Gleason, B. (2005). Maximum and minimum temperature trends for the globe: An update through 2004. *Geophysical Research Letters*, 32, e01221.

Williams, J.W. & Jackson, S.T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, 5, 475–482.

Williams, J.W., Jackson, S.T. & Kutzbacht, J.E. (2007). 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.

Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L., Travers, S.E., Pau, S., Regetz, J., Davies, T.J., Kraft, N.J.B., Ault, T.R., Bolmgren, K., Mazer, S.J., McCabe, G.J., McGill, B.J., Parmesan, C., Salamin, N., Schwartz, M.D. & Cleland, E.E. (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature*, 485, 494–497.

Figures

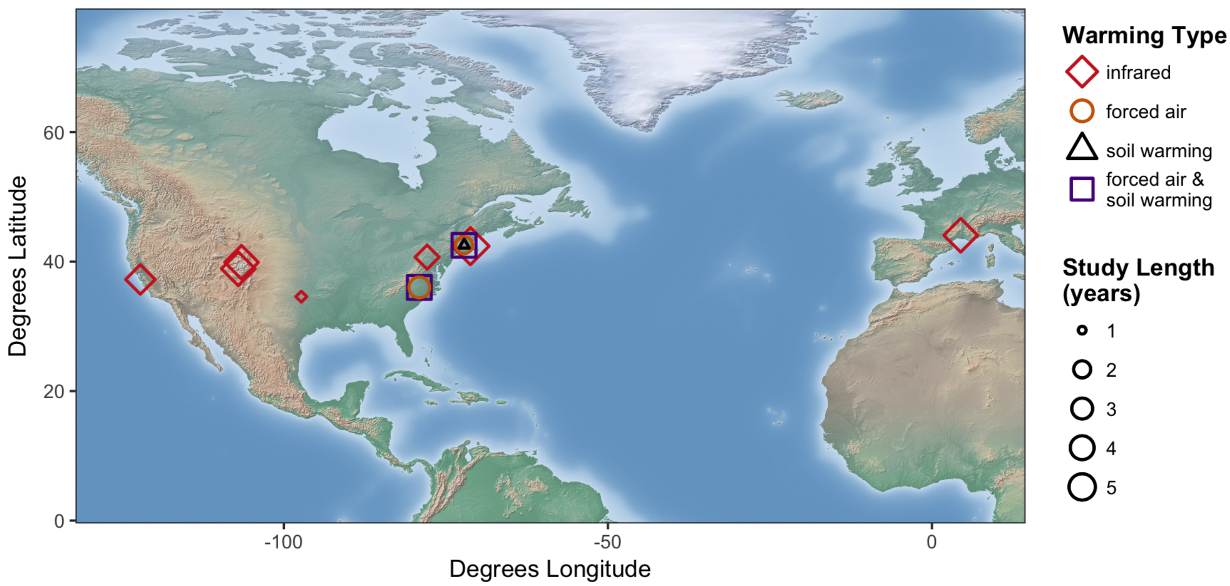

Figure 1: **Climate data from 12 climate change experiments in North America and Europe are included in the C3E database and analyzed here.** See Supplemental Materials, Tables S1 and S2 for details.

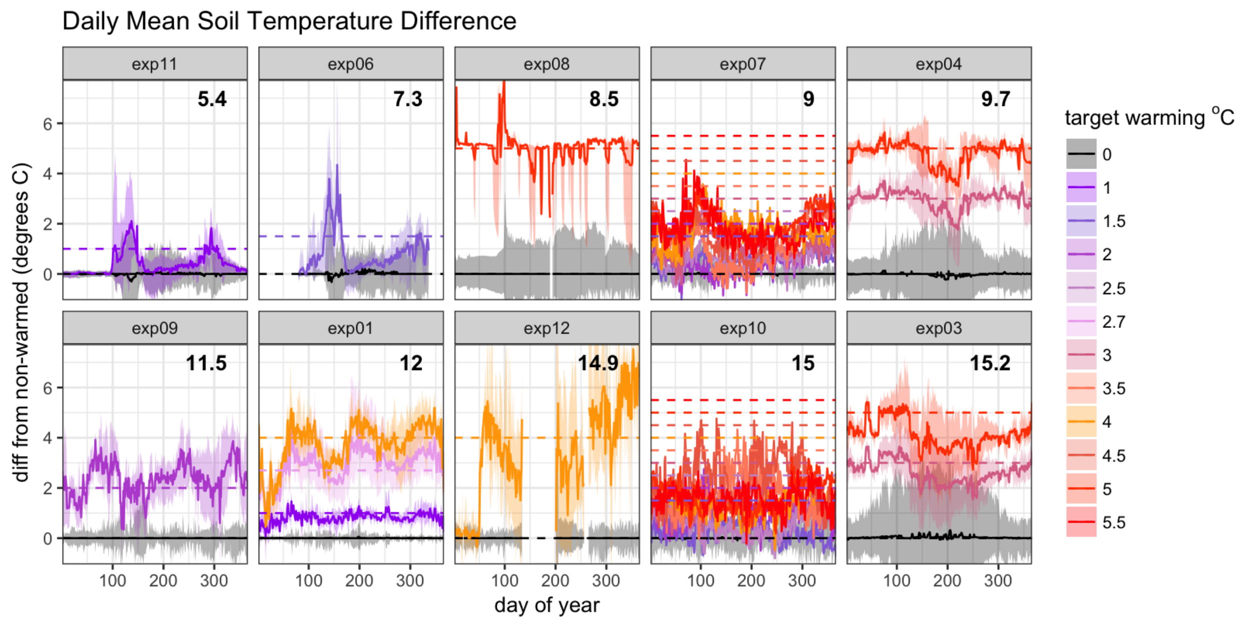

Figure 2: **Deviations in daily observed warming from mean soil temperature for 10 study sites.** We show mean soil, rather than above-ground, temperature, as this was the most frequently recorded temperature variable in the C3E database. Solid lines show observed difference between warming treatment (colors) and control (black) plots, averaged across replicates and years; shading shows 95% confidence intervals. Dashed lines represent target warming levels. Two sites not shown here did not monitor soil temperature; we also excluded data from plots that manipulated precipitation. Mean annual temperature for experimental sites are shown in the upper right corner of each panel; panels are arranged by increasing annual temperature.

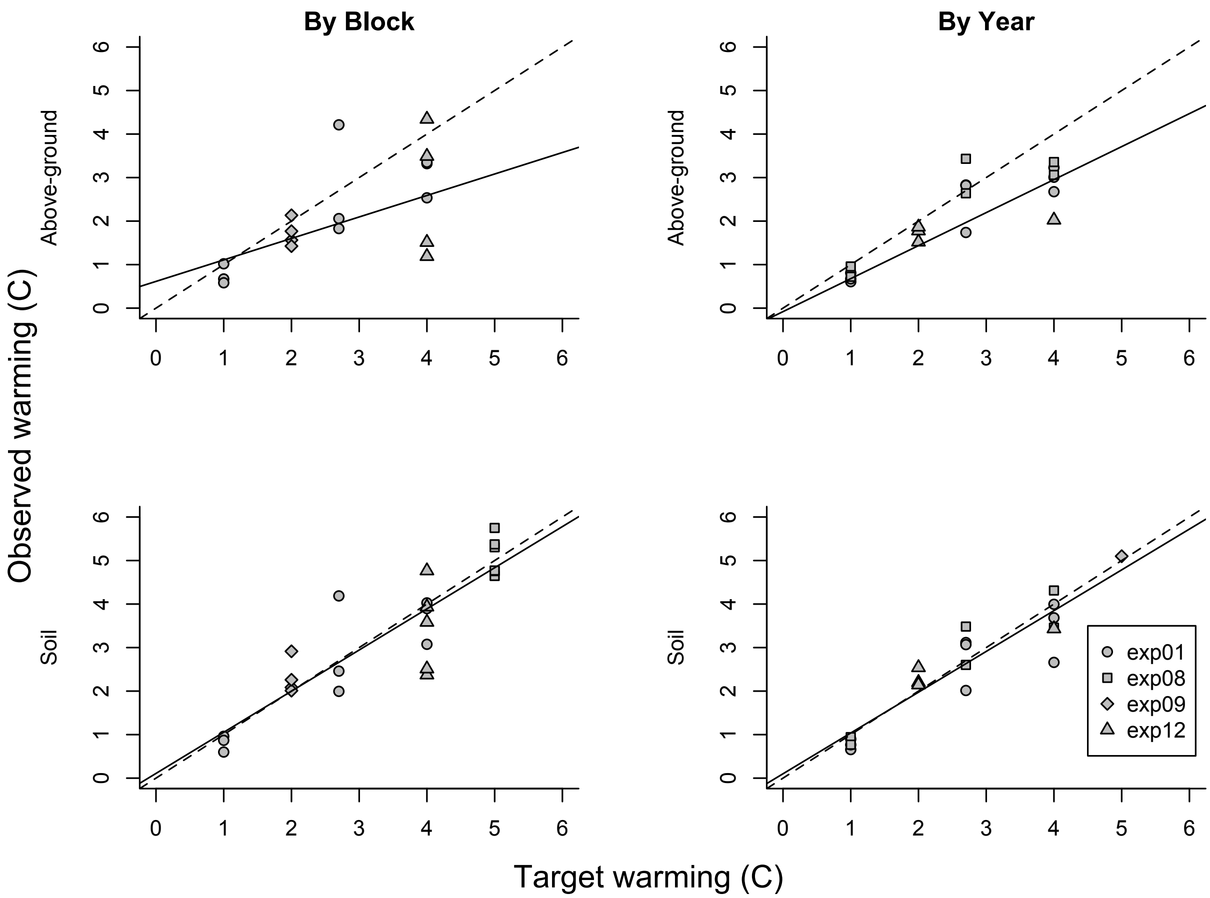

Figure 3: **Observed warming (i.e., the difference between treatment and control plots) over space and time, for above-ground and below-ground temperatures,** excluding data from plots that manipulated precipitation. The solid line is the fitted relationship between observed and target warming and the dashed line shows when observed warming is exactly equal to target warming (1:1). See Supplemental Materials (especially Tables S4 and S5) for details.

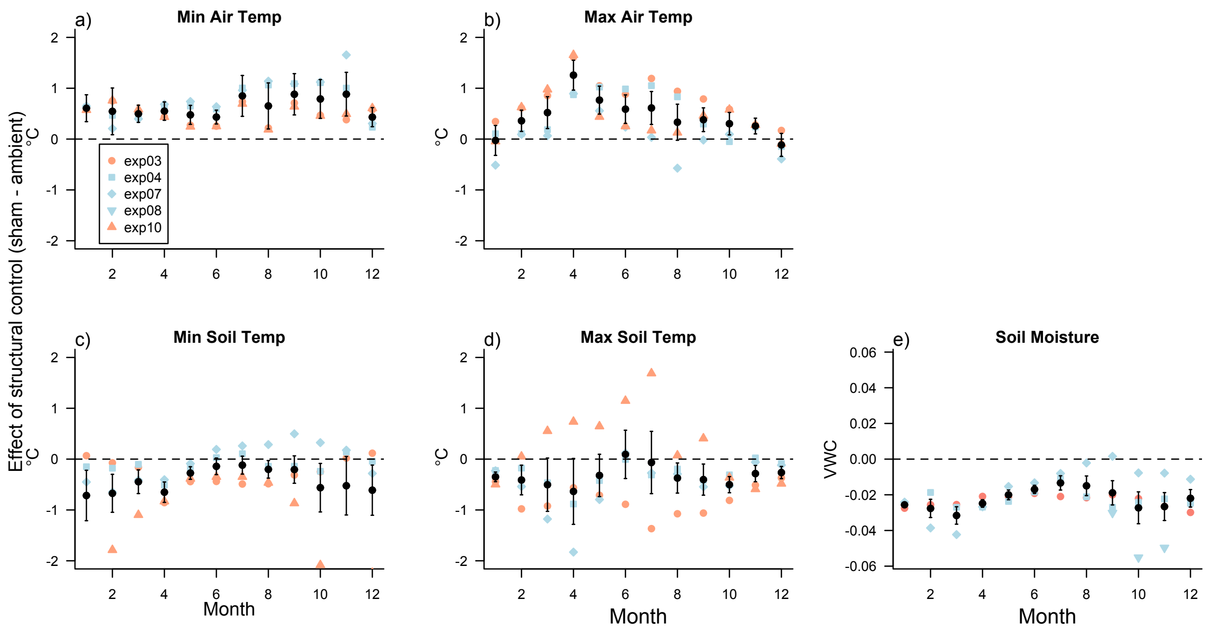

Figure 4: **Deviations in measured abiotic variables by month in structural controls compared to ambient controls** (i.e., with no control chambers or warming infrastructure in place). Above-ground temperatures were higher, whereas below-ground temperature and soil moisture were lower in structural controls compared with ambient controls. We show overall (fixed) effects in black from monthly mixed-effects models; site-level random effects are shown by symbols in blue (for the three studies conducted at Harvard Forest in Massachusetts, USA) and pink (the two studies conducted at Duke Forest in North Carolina, USA).

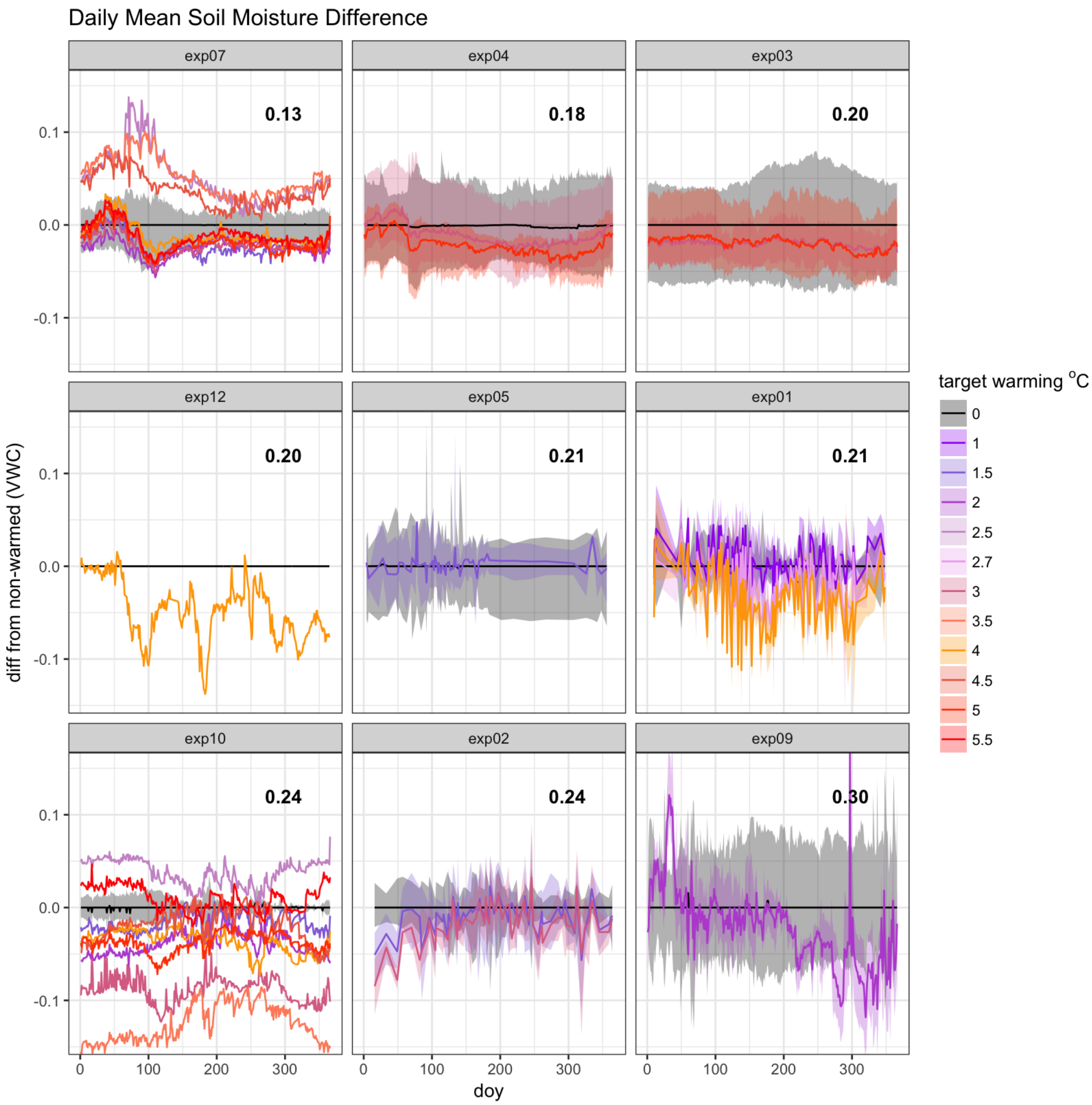

Figure 5: **Deviations in daily observed soil moisture,** shown for the nine study sites that continuously monitored soil moisture, excluding data from plots that manipulated precipitation. Black lines represent control plots, and colored lines represent warming treatments with various target warming levels. The number of temperature treatment levels vary from one (e.g. exp08, exp11) to nine (exp07 and exp10, which used an unreplicated regression design). Mean annual soil moisture for the experimental site is shown in the upper right corner of each plot, and plots are arranged by increasing mean soil moisture. All experiments measured soil moisture in volumetric water content (VWC, as a proportion of the soil volume in the sample, scaled from 0 to 1)

.

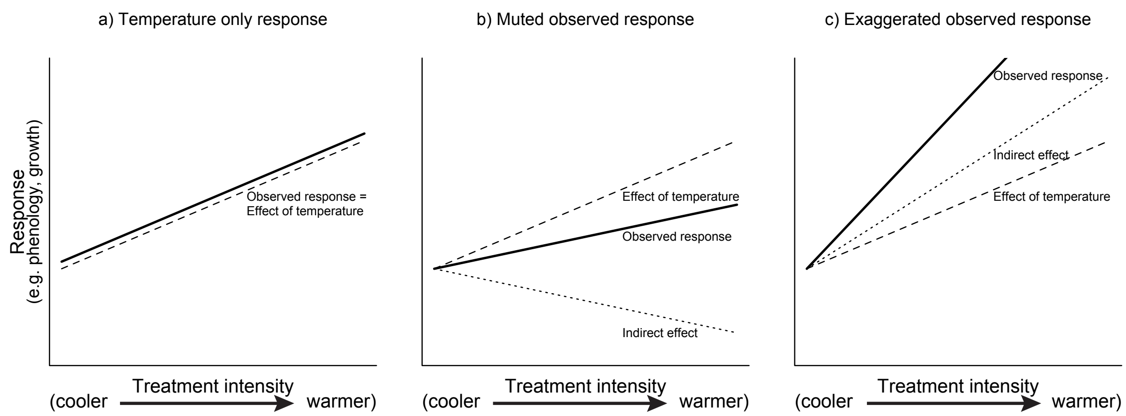

Figure 6: **Possible biological responses to experimental climate change and their interpretation**. Direct responses to temperature alone (a) can be easily understood. Complications arise when biological responses are a mix of the direct and indirect effects of experimental warming. Then experimental warming may cause biological responses to be muted (b) or exaggerated (c). Slopes of these example lines assume a linear response with additive direct and indirect effects. The relationship between these effects could be more complex (e.g., nonlinear; antagonistic, multiplicative, or otherwise interactive).

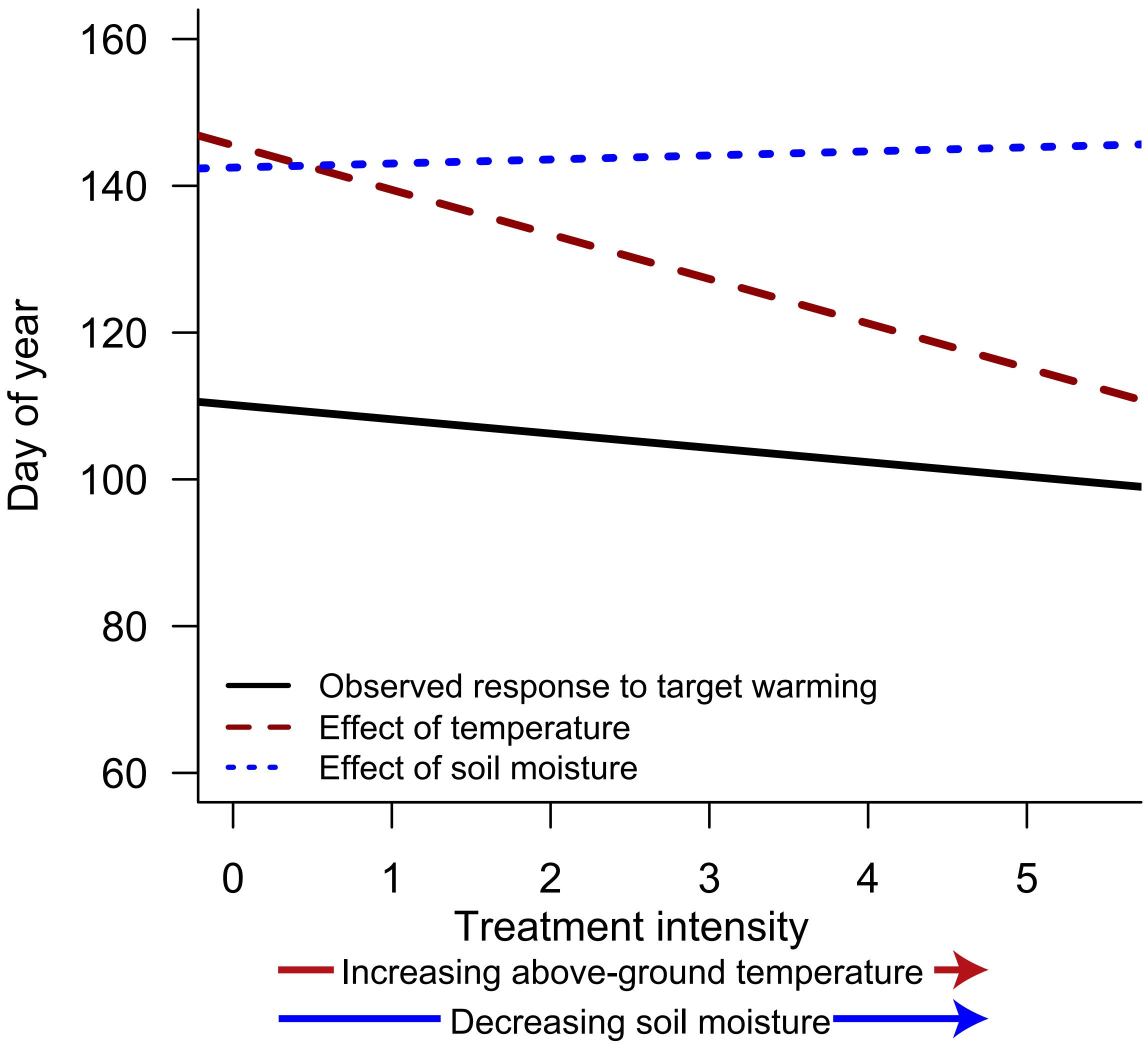

Figure 7: **Response of budburst day of year to experimental climate change** is an example of a muted response: the observed response to increaseing treatment intensity (i.e., the coefficient of a model fit with only target temperature as the explanatory variable, black line) suggests a weaker temperature sensitivity than the effect of temperature in a more biologically accurate (and better-fitting) model that includes both measured above-ground temperature (dashed red line) and soil moisture (dotted blue line), as well as their interaction. This is because experimental warming dries out the soil in addition to increasing temperatures, and both climate variables affect the timing of budburst. Whereas increasing temperatures advance budburst, decreasing soil moisture has a delaying effect. See Supplemental Materials, especially Tables S14 & S15, for model details.