

## How do climate change experiments alter plot-scale climate?

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**Data Accessibility** The MC3E database will be available at KNB (Ettinger & Wolkovich, 2018), along with all R code from the analyses included in this paper. (Currently, metadata are published there; the full database and R code are available to reviewers on github.)

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## <sup>1</sup> Abstract

<sup>2</sup> To understand and forecast biological responses to climate change, scientists frequently use field experiments  
<sup>3</sup> that alter temperature and precipitation. Climate manipulations can manifest in complex ways, however,  
<sup>4</sup> challenging interpretations of biological responses. We reviewed publications from active-warming experi-  
<sup>5</sup> ments to compile a database of daily plot-scale climate data from 15 experiments that use forced air, infrared  
<sup>6</sup> heaters, or soil cables to warm plots. We find that the common practices of analyzing primarily mean  
<sup>7</sup> changes among treatments and analyzing treatments as categorical variables (e.g., warmed verses unwarmed)  
<sup>8</sup> masks important variation in treatment effects over space and time. Our synthesis showed that measured  
<sup>9</sup> mean warming, in plots with the same target warming, differed by 1.6°C, on average, with high variation—  
<sup>10</sup> maximum differences ranged from 0.03 - 4.87°C across studies, which varied in warming design and myriad  
<sup>11</sup> ecosystem attributes. Warming treatments produce non-temperature effects as well, such as soil drying. The  
<sup>12</sup> combination of these direct and indirect effects is complex and can have important biological consequences.  
<sup>13</sup> With a case study of plant phenology, we show how accounting for drier soils with warming triples the es-  
<sup>14</sup> timated sensitivity of budburst to temperature. Our synthesis yields recommendations for future analyses,  
<sup>15</sup> experimental design, and data sharing to improve our mechanistic understanding of what drives variation  
<sup>16</sup> across studies, and thus improve the utility of climate change experiments to accurately identify and forecast  
<sup>17</sup> species' responses.

## <sup>18</sup> Introduction

<sup>19</sup> Climate change is dramatically altering earth's biota, shifting the physiology, distribution, and abundance  
<sup>20</sup> of organisms, with cascading community, ecosystem, and climate effects (Shukla & Mintz, 1982; Cox *et al.*,  
<sup>21</sup> 2000; Thomas *et al.*, 2004; Parmesan, 2006; Field *et al.*, 2007; Sheldon *et al.*, 2011; Urban *et al.*, 2012). Much  
<sup>22</sup> uncertainty exists about how particular individuals, populations, species, communities, and ecosystems will  
<sup>23</sup> respond as warming becomes more extreme (Thuiller, 2004; Friedlingstein *et al.*, 2014). Predicting biolog-  
<sup>24</sup> ical responses to current and future climate change—and their feedbacks to earth's climate and ecosystem  
<sup>25</sup> services—is one of the most significant challenges facing ecologists today.  
  
<sup>26</sup> Two common approaches for understanding biological effects of climate change are observational studies,  
<sup>27</sup> which correlate recorded biological patterns with measured climate, and process-based modeling; yet these

28 approaches are insufficient for several reasons. Observational studies and correlative models cannot disen-  
29 tangle the causal effects of warming (one aspect of climate) from other factors that have also changed over  
30 time, such as successional stage or land use. In addition, models based on correlative data may fail to make  
31 useful predictions for future conditions that fall outside the range of historical variability (e.g., Pearson &  
32 Dawson, 2004; Hampe, 2004; Ibanez *et al.*, 2006; Swab *et al.*, 2012; Chuine *et al.*, 2016). Climate change will  
33 yield warmer temperatures than the previous 150 years, and possibly warmer than at any time in the last  
34 2000 years (Ohlemüller *et al.*, 2006; Williams & Jackson, 2007; Williams *et al.*, 2007; Stocker *et al.*, 2013).  
35 Process-based models overcome some of these challenges through inclusion of explicit mechanistic relation-  
36 ships between climate and biological outcomes. However, they are limited by the processes they include (i.e.,  
37 our understanding of mechanism), as well as by the data available to parameterize those processes (Moorcroft,  
38 2006; Kearney & Porter, 2009).

39 Experimental data from field-based climate change experiments are crucial to fill these knowledge gaps and  
40 determine mechanistic links between climate change and biological responses. Experiments can quantify  
41 biological responses to different levels of climate change, and can create the “no-analog” climate scenarios  
42 forecasted for the future, particularly when they employ active-warming methods, such as forced air heaters,  
43 soil warming cables, or infrared heaters (Shaver *et al.*, 2000; Williams *et al.*, 2007; Aronson & McNulty,  
44 2009). In addition, active-warming can be combined with precipitation manipulations (e.g., snow removal,  
45 water additions or reductions), offering the ability to assess individual and interactive effects of temperature  
46 and precipitation, separate from other environmental changes (e.g., Price & Waser, 1998; Cleland *et al.*,  
47 2006; Sherry *et al.*, 2007; Rollinson & Kaye, 2012). Compared with indoor growth-chamber experiments,  
48 field-based experiments offer the possibility of preserving important but unknown or unquantified feedbacks  
49 among biotic and abiotic components of the studied systems.

50 With climate change experiments, ecologists often aim to test hypotheses about how projected warming  
51 will affect species’ growth, survival, and future distributions (Dukes & Mooney, 1999; Hobbie *et al.*, 1999;  
52 Morin *et al.*, 2010; Pelini *et al.*, 2011; Chuine *et al.*, 2012; Reich *et al.*, 2015; Gruner *et al.*, 2017). Recent  
53 research suggests, however, that climate manipulations may not always alter plot-scale climate (hereafter,  
54 microclimate) in ways that are consistent with observed changes over time (Wolkovich *et al.*, 2012; Menke  
55 *et al.*, 2014; Polgar *et al.*, 2014; Andresen *et al.*, 2016). For extrapolation of experimental findings to the real  
56 world, we need detailed assessments of how active-warming experiments alter the microclimate conditions  
57 experienced by organisms, and the extent to which these conditions are similar to current field conditions or

58 anticipated climate change.

59 Here, we investigate the complex ways that active-warming treatments alter microclimate, both directly and  
60 indirectly, across multiple studies. The qualitative challenges and opportunities of climate change experiments  
61 have been summarized previously (e.g., De Boeck *et al.*, 2015) and effects of these manipulations on some  
62 aspects of microclimate have been published for individual sites (e.g., Harte *et al.*, 1995; McDaniel *et al.*,  
63 2014b; Pelini *et al.*, 2011). However, our quantitative meta-analysis allows us to examine trends across sites  
64 and warming designs (Box 1, Table 1), and make recommendations based on this information. Using plot-  
65 level daily microclimate data from 15 active-warming experiments (yielding 59 experiment years and 14,913  
66 experiment days; Table S1), we show the direct and indirect ways that experimental manipulations alter  
67 microclimate. We use a case study of spring plant phenology to demonstrate how analyses that assume a  
68 constant warming effect and do not include non-temperature effects of warming treatments on biological  
69 responses lead to inaccurate quantification of plant sensitivity to temperature shifts. Finally, we synthesize  
70 our findings to make recommendations for future analysis and design of climate change experiments (Box 2).

## 71 MicroClimate from Climate Change Experiments (MC3E) database

72 To investigate how climate change experiments alter microclimate, we first identified published, active-  
73 warming field experiments, many of which included precipitation manipulations. We focused on *in situ*  
74 active-warming manipulations because recent analyses indicate that active-warming methods are the most  
75 controlled and consistent methods available for experimental warming (Kimball, 2005; Kimball *et al.*, 2008;  
76 Aronson & McNulty, 2009; Wolkovich *et al.*, 2012). We do not include passive-warming experiments because  
77 they have been analyzed extensively already and are known to have distinct issues, including reduction in  
78 wind, overheating, and great variation in the amount of warming depending on irradiance and snow depth  
79 (Marion *et al.*, 1997; Shaver *et al.*, 2000; Wolkovich *et al.*, 2012; Bokhorst *et al.*, 2013, see also Table S2).

80 We carried out a full literature review to identify potential active-warming field experiments to include in  
81 the database. We followed the methods and search terms of Wolkovich *et al.* (2012) for their Synthesis of  
82 Timings Observed in iNcrease Experiments (STONE) database (Wolkovich *et al.*, 2012), but restricted our  
83 focus to active-warming experiments. Further, because our goal was to tease out variation in microclimate  
84 (including temperature and soil moisture), we focused on warming studies that included both/either multiple

85 levels of warming and/or precipitation treatments. These additional restrictions constrained the list to 11  
86 new studies published after the STONE database, as well as six of the 37 studies in the STONE database.  
87 We contacted authors to obtain daily microclimate and phenological data for these 17 studies and received  
88 data (or obtained publicly available data) for 10 of them, as well as datasets from five additional sites offered  
89 or suggested to us over the course of our literature review and data analysis. The daily temperature and  
90 soil moisture data from these 15 experiments comprise the MicroClimate from Climate Change Experiments  
91 (MC3E) database (Figures 1 and S1, Table S1), which is available at KNB (Ettinger & Wolkovich, 2018). We  
92 examined how these experiments altered microclimate, using mixed-effects models that allowed for inherent  
93 differences among studies (through a random effect of study on the intercept), while also estimating various  
94 across-study effects, such as degree of warming or warming type.

## 95 **Complexities in interpreting experimental climate change**

96 Climate change experiments often include detailed monitoring of climate variables at the plot-level, yielding  
97 large amounts of data, such as daily or hourly temperature and other climate variables, over the course of  
98 an experiment. Ecologists, however, are generally interested in the ecological responses (e.g., community  
99 dynamics, species' growth, abundance, or phenology), which are collected on much coarser timescales (e.g.,  
100 seasonally or annually). Not surprisingly then, when analyzing ecological responses, authors typically provide  
101 detailed information on the observed biological responses, and report only the mean change in climate over  
102 the course of the experiment and whether it matched their target level of change (e.g., Price & Waser, 1998;  
103 Rollinson & Kaye, 2012; Clark *et al.*, 2014a,b). Several studies have conducted detailed, independent analyses  
104 of microclimate data from warming experiments (e.g., Harte *et al.*, 1995; Kimball, 2005; Kimball *et al.*, 2008;  
105 McDaniel *et al.*, 2014b; Pelini *et al.*, 2011). While these detailed analyses provide valuable case studies of  
106 experimental effects on microclimate data alone, they have generally not been incorporated into analyses of  
107 ecological responses.

108 In interpreting ecological responses to climate change manipulations, the focus has been primarily on mean  
109 shifts in microclimate, but the imposed manipulations result in much more complex shifts. The magnitude  
110 of change in these manipulations varies in time and space, and the presence of experimental equipment  
111 alone (with no heat added) often alters environmental conditions. These factors, discussed below, challenge  
112 our interpretation of how experimental warming studies forecast effects of climate change on organisms and

113 ecosystems. When possible, we compare and contrast these factors across different study methodologies, such  
114 as infrared warming versus forced air chambers and constant wattage versus feedback control, because effects  
115 on microclimate may vary across these different methodologies (Box 1).

## 116 Effects on microclimate vary over time and space

117 Reporting only the mean temperature difference across the duration of a warming study masks potentially  
118 important temporal variation in temperature among treatments (compare Figure 2 to Figure S2). Using  
119 the MC3E database, we found that active-warming reduces the range of above-ground daily temperature  
120 by  $0.37^{\circ}\text{C}$  per  $^{\circ}\text{C}$  of target warming (Table S3, see also Table S1, which details the different methods used  
121 to measure and warm temperatures). Active-warming decreased above-ground daily temperature range by  
122 differentially affecting maximum and minimum temperatures: warming increased daily minima by  $0.81^{\circ}\text{C}$   
123 per  $^{\circ}\text{C}$  of target warming, but only increased daily maxima by  $0.48^{\circ}\text{C}$  per  $^{\circ}\text{C}$  of target warming (Table S3).  
124 These effects varied by site (Table S3), but we found no clear patterns by warming type (e.g., infrared versus  
125 forced air) or warming control (feedback versus constant). Soil daily temperature range was not affected by  
126 experimental warming, as warming altered minimum and maximum daily temperatures similarly (Table S4).

127 We observed strong seasonal and annual variations in the effects of experimental warming (Figures 1, 2, Table  
128 S5). Warming generally appears close to targets in winter and early spring, and farthest below targets in  
129 summer (day of year 150-200, when evapotranspiration within a robust plant canopy can dissipate energy  
130 and act to cool vegetation surfaces), though patterns differ among sites (Figure 1). The variation in warming  
131 effectiveness may be driven by interactions between warming treatments and daily, seasonal, and annual  
132 weather patterns, since the magnitude of warming can vary as weather conditions change. Both infrared  
133 heaters and soil cables fail to achieve target temperature increases during rainstorms (Peterjohn *et al.*, 1993;  
134 Hoeppner & Dukes, 2012) and with windy conditions (Kimball, 2005; Kimball *et al.*, 2008). Differences  
135 between target and actual warming are likely to be particularly great for studies employing constant wattage,  
136 rather than feedback control (Box 1, Figure 2). In addition, treatments are often applied inconsistently within  
137 or across years. Heat applications are frequently shut off during winter months, and some heating methods,  
138 even if left on throughout the year, do not warm consistently (e.g., Clark *et al.*, 2014a,b; Hagedorn *et al.*,  
139 2010).

140 Treatment effects also vary spatially, further complicating interpretation of climate change experiments. The

141 MC3E database contains six studies that used blocked designs, allowing us to examine spatial variation in the  
142 amount of warming (i.e., the difference between treatment and control plots within a block). These studies  
143 include two infrared with feedback control, three infrared with constant wattage, and one soil warming cable  
144 with feedback control experiments. We found that the amount of observed warming frequently varied by  
145 more than 1°C (mean= 1.6°C, maximum = 4.9°C) among blocks (Figure 2, Table S6). This variation in  
146 warming is substantial, as it is equivalent to the target warming treatment for many studies, and appears  
147 to vary substantially among sites, which differ in warming methodologies and environmental characteristics,  
148 though low sample sizes make disentangling the effect of warming method difficult (Box 1). The differences in  
149 warming among blocks may be caused by fine-scale variation in vegetation, slope, aspect, soil type, or other  
150 factors that can alter wind or soil moisture, which in turn affect warming (Peterjohn *et al.*, 1993; Kimball,  
151 2005; Kimball *et al.*, 2008; Hoeppner & Dukes, 2012; Rollinson & Kaye, 2015).

152 Of course, identical experimental treatments across space and time are neither necessary, nor realistic, for  
153 robust analysis of experimental results and forecasting. Indeed, the spatial and temporal variation we re-  
154 port could improve and refine models, and—at least in some regions—may be consistent with contemporary  
155 patterns of climate change (Stocker *et al.*, 2013). Taking advantage of this variation, though, requires under-  
156 standing and reporting it (e.g., Milcu *et al.*, 2016). However, because fine-scale and temporal variations in  
157 warming treatments are rarely analyzed explicitly with ecological data, the implications for interpretation of  
158 experimental findings are unclear.

## 159 Experimental infrastructure alters microclimate

160 Experimental structures themselves can alter temperature and other important biotic and abiotic variables in  
161 ways that are not generally examined in experimental climate change studies. The importance of controls that  
162 mimic a treatment procedure without actually applying the treatment is widely acknowledged in biology (e.g.,  
163 Dayton, 1971; Spector, 2001; Johnson & Besselsen, 2002; Quinn & Keough, 2002). Though some experimental  
164 climate change studies include treatments with non-functional warming equipment as well as ambient controls,  
165 the magnitude and effects of experimental infrastructure alone on climate are rarely interpreted or analyzed.  
166 To investigate the magnitude of infrastructure effects, we compared temperature and soil moisture data  
167 from five active-warming studies at two sites: Duke Forest and Harvard Forest (Farnsworth *et al.*, 1995;  
168 Clark *et al.*, 2014b; Marchin *et al.*, 2015; Pelini *et al.*, 2011)(see Supplemental Materials for model details).

169 These were the only studies in the MC3E database that monitored climate in two types of control plots:  
170 structural controls (i.e., ‘shams’ or ‘disturbance controls,’ which contained the warming infrastructure: soil  
171 cables (n=1), forced air chambers (n=2), or both (n=2), but with no heat applied) and ambient controls with  
172 no infrastructure added. Other studies monitored environmental conditions in only structural controls (n=4)  
173 or ambient controls (n=5). We were unable to compare ambient and structural controls for experiments  
174 using infrared heating, because no studies in our database included both control types. A separate analysis  
175 suggested that there may be infrastructure effects on microclimate for infrared studies in our database (see  
176 Supplemental Materials, especially Table S7), and infrastructure effects have been documented in other  
177 studies (e.g., shading, Table 1 Kimball *et al.*, 2008).

178 We found that experimental structures altered above-ground and soil temperatures in opposing ways: above-  
179 ground temperatures were higher in the structural controls than in ambient controls, whereas soil tempera-  
180 tures were lower in structural controls compared with ambient controls (Figure 3a-d). This general pattern  
181 was consistent across different temperature models (mean, minimum, and maximum temperatures), although  
182 the magnitude varied among seasons, studies, and years (Figure 3a-d, Tables S8-S11). We also found that  
183 experimental infrastructure decreased soil moisture relative to ambient conditions across all seasons, studies,  
184 and years (Figure 3e, Tables S12, S13).

185 There are several possible reasons for the observed climatic differences between ambient and structural con-  
186 trols. Infrastructure materials may shade the plots, reduce airflow, reduce albedo relative to surroundings,  
187 or otherwise change the energy balance, particularly in chamber warming (i.e., 4 of the 5 studies included in  
188 the above analysis). Specifically, soil temperatures may be cooler in structural controls for forced air studies  
189 because the experimental structures block sunlight from hitting the ground surface, causing less radiative  
190 heating of the ground in structural controls compared to ambient controls. In addition, above-ground tem-  
191 peratures may be warmer in structural controls because the structures radiatively warm the air around them  
192 and block wind, inhibiting mixing with air outside of the plot. Structures may also interfere with precipi-  
193 tation hitting the ground, thereby reducing local soil moisture and snowpack, with its insulative properties.  
194 These effects may be most dramatic in studies that employ chambers, rather than open-air designs, such as  
195 infrared heating (Aronson & McNulty, 2009). Finally, for some warming types (e.g., soil cables), structural  
196 controls experience increased soil disturbance compared with ambient controls; this may alter water flow and  
197 percolation, and introduce conductive material via the cables or posts.

198 To the extent that differences between ambient and structural controls have been reported in previous studies,  
199 our findings appear to be consistent. Clark *et al.* (2014b), who used forced air and soil cables with feedback  
200 control for warming, state that “control of the air temperature was less precise, in part due to air scooping on  
201 windy days.” Marchin *et al.* (2015), who used forced air warming with feedback control, note that structural  
202 controls had mean spring air temperatures about 0.5°C or more above ambient temperatures. Peterjohn *et*  
203 *al.* (1994), who warmed soil with heating cables and feedback control, reported cooler soil temperatures  
204 in structural controls than in ambient controls at shallow soil depths. Similarly, we found the greatest  
205 difference in soil temperature between structural and ambient controls in shallow soils (e.g., exp10, in which  
206 soil temperature was measured at a depth of 2cm). If addressed, the focus to date has been largely on these  
207 abiotic impacts of experimental structures, but structures may also alter herbivory and other biotic conditions  
208 (Kennedy, 1995; Moise & Henry, 2010; Wolkovich *et al.*, 2012; Hoeppner & Dukes, 2012).

209 Our analyses suggest that warming experiments that calculate focal response variables relative to ambient  
210 controls (e.g., Price & Waser, 1998; Dunne *et al.*, 2003; Cleland *et al.*, 2006; Morin *et al.*, 2010; Marchin *et al.*,  
211 2015) may not adequately account for the ways in which infrastructure affects microclimate. Results from  
212 studies reporting only structural controls (e.g., Sherry *et al.*, 2007; Hoeppner & Dukes, 2012; Rollinson &  
213 Kaye, 2012), should be cautiously applied outside of an experimental context, as—without ambient controls—  
214 their inference is technically limited to the environment of the structural controls. Our results suggest that  
215 studies aiming to predict or forecast the effects of climate change on organisms and ecosystems would benefit  
216 from employing both structural and ambient controls so that they may separate artifacts due to infrastructure  
217 from the effects of experimental warming. Increased use of both structural and ambient controls together  
218 would also help answer important questions of how infrastructure effects vary across ecosystem types, and  
219 warming designs (Box 1).

## 220 Indirect and feedback effects of climate change manipulations

221 Climate change experiments often seek to manipulate temperature or precipitation separately as well as  
222 interactively. Manipulating either of these variables in isolation is notoriously difficult. Treatments involving  
223 precipitation additions typically reduce temperatures in climate change manipulations (Sherry *et al.*, 2007;  
224 Rollinson & Kaye, 2012; McDaniel *et al.*, 2014b). For example, Sherry *et al.* (2007) observed that a doubling  
225 of precipitation reduced mean air temperatures by 0.44°C, on average, during their one-year observation

226 period.

227 In the MC3E database, there are four experiments that manipulated both temperature and precipitation,  
228 and provided daily above-ground temperature data (three of these also measured soil temperature). Across  
229 these studies, all of which used infrared heating (two with feedback control and one with constant warming),  
230 we found that increasing the amount of added precipitation reduced daily minimum and maximum above-  
231 ground temperatures, at rates of 0.01 and 0.02°C, respectively, and soil temperatures, at a rate of 0.01°C for  
232 both minimum and maximum temperature, per percent increase in added precipitation (Table S14). Thus,  
233 a 50% increase in precipitation would be expected to decrease temperature by 0.5°C. This is likely because  
234 increasing soil moisture (an effect of precipitation additions) typically shifts the surface energy balance to  
235 favor latent (i.e., evapotranspiration) over sensible energy fluxes, reducing heating of the air overlying the  
236 soils. Maintaining target warming levels is a challenge even for independent feedback systems, which vary  
237 energy inputs using ongoing temperature measurements, particularly during seasons or years with wetter  
238 soils and higher evapotranspiration (Rich *et al.*, 2015).

239 In addition to its effects on temperature, experimental warming often increases vapor pressure deficit and  
240 reduces soil water content (e.g., Harte *et al.*, 1995; Sherry *et al.*, 2007; Morin *et al.*, 2010; Pelini *et al.*, 2014;  
241 Templer *et al.*, 2016). Of the 15 experiments in the MC3E database, we examined the 12 that continuously  
242 measured and reported soil moisture. We included target warming, warming type, and their interaction  
243 as predictors (excluding data from plots with precipitation treatments) and accounted for other differences  
244 among studies by including a random effect of study (see Supplemental Materials for details). We found  
245 that experimental warming reduced soil moisture across all warming types, with substantial variation among  
246 experiments (Figure 5, Table S15). The drying effect varied by warming type (-0.80% for infrared versus -  
247 0.33% for forced air, per °C of target warming, Table S16). Soil moisture can be difficult to measure, with high  
248 spatial and temporal variation (Famiglietti *et al.*, 1999; Teuling & Troch, 2005), but these results highlight  
249 that changes in soil moisture often accompany temperature changes in active-warming experiments.

250 Warming and precipitation treatments, and their indirect effects on soil moisture and other abiotic factors,  
251 can also alter the biotic environment, which may produce cascading effects. Many studies have found shifts  
252 from herbaceous to woody plant communities over time with experimental warming (e.g., Rollinson & Kaye,  
253 2012; McDaniel *et al.*, 2014b,a; Harte *et al.*, 2015). These community shifts may affect resource levels, such  
254 as moisture, carbon, and nutrient levels in the soil (McDaniel *et al.*, 2014b,a; Harte *et al.*, 2015) and feed

255 back to affect microclimate (Harte *et al.*, 2015).

256 The presence of these feedback effects is both a strength of and a challenge for climate change experiments.  
257 They may represent important and ecologically realistic effects that became apparent only with the *in situ* field  
258 experiment. Alternatively, they may represent artifacts that are unlikely to occur outside of an experimental  
259 context. Quantifying, interpreting, and reporting these non-temperature effects in experiments is critical  
260 to distinguish these possibilities and to understand mechanisms underlying observed biological responses to  
261 climate change.

262 The widespread presence of indirect effects of climate manipulations highlights the importance of measuring  
263 environmental conditions at the plot-level, and using these measurements in analysis and interpretation of  
264 results. Many papers published on climate change experiments—including 10 of the 15 references listed  
265 in Table S1—analyze warming and/or precipitation treatments as simple categorical predictors (e.g., as in  
266 a two-way ANOVA). Our findings, however, demonstrate a need for alternative modelling approaches to  
267 fully understand the experimental results and to make mechanistic links between changes in climate and  
268 ecological responses. One straightforward alternative is to include the continuous climate data (e.g., plot-  
269 level temperatures) as predictors of the focal response variable, such as phenological state or species density  
270 (e.g., Marchin *et al.*, 2015; Pelini *et al.*, 2014).

## 271 Ecological implications

272 We have highlighted a suite of factors that complicate interpretation of climate change experiments. These  
273 indirect effects are likely to have biological implications for many of the responses studied in warming exper-  
274 iments (e.g., Figure 5). Interpretation of experimental climate change effects on biological responses may be  
275 misleading because the intended climate treatments (i.e., categorical comparisons or target warming levels)  
276 are often used as explanatory variables in analyses (Table S1). The interpretation is likely to be altered by  
277 using fine-scale, measured climate as explanatory variables. For example, biological responses may be muted  
278 (Figure 5b) or exaggerated (Figure 5c) when direct and indirect effects of climate manipulations interact.

279 To investigate the ecological implications of non-target abiotic responses to climate warming, we used a  
280 simple case study of plant phenology. We used the MC3E database to test if estimates of the temperature  
281 sensitivity of phenology vary when calculated using target warming versus plot-level climate variables. We

282 fit two separate mixed-effects models, which differed in their explanatory variables: one used target warming  
283 and one used measured climate. Both models had budburst day of year as the response variable, and both  
284 included random effects of study (which modeled other differences between studies that may have affected  
285 phenology), year (nested within study, which modeled differences due to weather variability among years that  
286 may have altered phenology), and species (which often vary in their phenology). All random effects were  
287 modeled on the intercept only; see Supplemental Materials for details.

288 We found that phenological sensitivities to temperature estimated from the two modeling approaches varied  
289 three-fold. The target warming model estimated temperature sensitivity of budburst to be -1.91 days/°C  
290 (95% CI -2.17, -1.86; Table S17, solid black line in Figure 6), whereas the measured climate model estimated  
291 temperature sensitivity of budburst to be -6.00 days/°C (95% CI: -6.74, -5.26; Table S17). Further, all  
292 measured climate models with both temperature and moisture had improved model fit compared to the target  
293 warming model (Table S18). The best-fit model included mean daily minimum above-ground temperature,  
294 mean winter soil moisture, and their interaction as explanatory variables, suggesting that these variables are  
295 important drivers of budburst timing (Tables S17, S18). In addition, the measured climate model estimated  
296 a significant effect of soil moisture on budburst of -1.51 days/% VWC (95% CI: -1.76, -1.26; Table S17,  
297 Figure 6). This negative effect is expected, if reducing moisture delays budburst (Table S17, Figure 6), and  
298 is consistent with previous work showing that budburst requires water uptake (Essiamah & Eschrich, 1986).

299 The increase in estimated temperature sensitivity with measured (rather than target) temperature has two  
300 major causes. First, plot-level warming often does not reach target levels (Figure 2), producing a muted effect  
301 of temperature in models using target warming. Second, experimental warming's dual effects of decreasing  
302 soil moisture and increasing temperature impact budburst in contrasting ways. Decreasing soil moisture  
303 has a delaying effect on budburst phenology, opposing the advancing effect of rising temperatures (Figure  
304 5b); thus the effect of temperature is underestimated when moisture is not included in the model. This  
305 example shows how the common method of using target warming alone, or even measured temperature  
306 alone as done in previous analyses of the particular experiments included here (exp01, exp03, exp04, exp10,  
307 Clark *et al.*, 2014a,b; Polgar *et al.*, 2014; Marchin *et al.*, 2015), to understand biological responses may yield  
308 inaccurate estimates of temperature sensitivity in warming experiments. In this case, the underestimation  
309 may be substantial enough to account for previously described discrepancies between phenological responses  
310 to warming in observational versus experimental studies (Wolkovich *et al.*, 2012; Polgar *et al.*, 2014), though  
311 further investigation is required.

312 Accounting for both direct and indirect effects of warming is critical for accurate interpretation of the conse-  
313 quences of climate change (Kharouba *et al.*, 2015). Of particular importance is the extent to which abiotic  
314 and biotic effects are realistic forecasts of future shifts that are likely to occur with climate change, or due to  
315 artifacts that are unlikely to occur outside of experimental systems (Hurlbert, 1984; Moise & Henry, 2010;  
316 Diamond *et al.*, 2013). For many important climatic and ecological metrics, experimental findings of abiotic  
317 and biotic effects appear to be consistent with observations. Altered above-ground daily temperature range  
318 (i.e., temperature minima changing more than maxima, Table S3) with experimental warming is consistent  
319 with observed changes in many places. Global minimum temperatures increased more rapidly than max-  
320 imum temperatures from 1950-1980, reducing above-ground daily temperature range (Thorne *et al.*, 2016;  
321 Vose *et al.*, 2005). In addition, the acclimation response of leaf respiration to temperature (Aspinwall *et al.*,  
322 2016; Reich *et al.*, 2016), responses of soil respiration to warming (Carey *et al.*, 2016), and declines in soil  
323 carbon at one site (Harte *et al.*, 2015), also appear to be consistent across experiments and observations.  
324 These cases suggest that many responses observed in climate change experiments, including indirect effects of  
325 treatments, may be accurate harbingers of future biological responses to climate change.

326 In contrast, some responses documented in climate change experiments may not be in line with future  
327 climate change—or may be too uncertain for robust prediction, and thus need explicit analyses and cautious  
328 interpretation. Although surface warming inevitably increases soil water evaporation, it does not necessarily  
329 translate to a decrease in soil water content. Precipitation forecasts with climate change are more uncertain  
330 than temperature forecasts, as are, consequently, future changes in soil moisture (Cook *et al.*, 2018). For  
331 example, soil drying is forecasted in some regions, such as the southwestern United States, mainly because of  
332 reductions in precipitation and increased evaporative demand associated with warmer air (Dai, 2013; Seager  
333 *et al.*, 2013). The northeastern United States, on the other hand, has been trending wetter over time (Shuman  
334 & Burrell, 2017), even though temperatures have warmed. Shifts in soil moisture are likely to vary by region,  
335 season, vegetation type, and soil depth (Seager *et al.*, 2014; Berg *et al.*, 2017; Cook *et al.*, 2018). The  
336 uncertainty associated with forecasting changes to soil moisture makes replicating future water availability  
337 regimes in climate change experiments especially challenging; one way to meet this challenge and make  
338 predictions—even given high uncertainty—is to quantify soil moisture effects in climate change experiments.  
339 The altered light, wind, and herbivory patterns documented under experimental infrastructure (Kennedy,  
340 1995; Moise & Henry, 2010; Wolkovich *et al.*, 2012; Hoeppner & Dukes, 2012; Clark *et al.*, 2014b) represent  
341 other non-temperature effects that may be potential experimental artifacts and are worth quantifying in

342 future analyses to provide improved estimates of temperature sensitivity.

343 An additional challenge in relating experiments to observations is that experimental findings may not scale  
344 up in space and time. Short-term responses to climate change frequently differ from long-term responses  
345 (Woodward, 1992; Elmendorf *et al.*, 2012; Andresen *et al.*, 2016; Reich *et al.*, 2018). Differences may be, in  
346 part, because many experiments typically impose some mean shift in climate, but patterns of climate change  
347 are likely to be more variable. Many climate models project complex shifts in precipitation: more intense  
348 extreme precipitation events (e.g., heavy downpours), more dry days (i.e., less total precipitation events),  
349 or both (Polade *et al.*, 2014). In addition, the small spatial scale of experiments may result in responses  
350 that are unlikely to be observed at larger scales (Woodward, 1992; Menke *et al.*, 2014). Experimental plots  
351 range in area from 1.5 to 36 square meters (Table S1), which may be too small to encapsulate, for example,  
352 the rooting zones of perennial plants (Canadell *et al.*, 1996), or foraging ranges for animals (Menke *et al.*,  
353 2014). One approach to overcome these challenges is to conduct larger, longer experiments (Woodward,  
354 1992), though this frequently is not logistically possible and does not easily address how to capture potential  
355 shifts in climate variability.

## 356 Conclusions

357 As climate change continues across the globe, ecologists are challenged to not only document impacts, but  
358 also make quantitative, robust predictions. Our ability to meet this challenge requires a nuanced mechanistic  
359 understanding of how climate directly and indirectly alters biological processes. Climate change experiments,  
360 which have been underway for nearly four decades (e.g., Tamaki *et al.*, 1981; Carlson & Bazzaz, 1982; Melillo  
361 *et al.*, 2017), provide invaluable information about biological responses to climate change. Yet the full range  
362 of changes in environmental conditions imposed by these experiments is rarely presented, and we need a fuller  
363 understanding of the variable effects across different warming methodologies. We have compiled a database  
364 of microclimate data from multiple warming experiments and shown how time, space, experimental artifacts,  
365 and indirect effects of treatments may complicate interpretations of these experimental results. The relative  
366 importance of each of these factors is likely to vary across warming designs (Box 1), as well as myriad other  
367 attributes of sites, making more studies that measure climate similarly and include full infrastructure controls  
368 important for progress. We hope this work provides a foundation for gaining the most knowledge and utility  
369 from existing experiments via robust analyses, for designing new experiments (see Box 2), and for improved

<sup>370</sup> understanding of biological responses to a changing world.

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Table 1: **Summary of measured warming and documented non-temperature effects, by warming technique**, for studies included in the MC3E database. Summaries of the target warming treatments ( $^{\circ}\text{C}$ ) and measured warming for above-ground temperature, and soil temperature are given. Measured warming is standardized per degree of target warming, and is shown here for warming treatments only (precipitation treatments are excluded). Thus, measured warming is the difference between mean annual temperature (MAT) of control plots and MAT of each treatment level within year (and block, if applicable) of a study. Mean difference (with standard error) and the range of differences in warming are shown, across all years (and blocks, if applicable). n is the number of studies of each warming technique and control type combination in the MC3E database. ‘Soil drying’ indicates figures showing an effect of warming on soil water content and references of previous studies reporting such effect. ‘Other non-temperature effects’ indicates other effects that have been studied in individual previous studies for each type of warming. See Table S1 for additional details of studies included in the MC3E database.

| warming type           | warming control | study          | target (min-max) | aboveground mean (se) | aboveground range | soil mean (se) | soil range | n | soil drying  | other nontemperature effects  |
|------------------------|-----------------|----------------|------------------|-----------------------|-------------------|----------------|------------|---|--|---|
| infrared               | constant        | exp05,06,11-14 | 2.2 (1.2-4)      | 0.52 (0.03)           | -5.22-2.16        | 0.68 (0.02)    | -0.07-1.56 | 6 | Fig. 4, Tab. S15-16, Kimball et al. 2005                       | +shading (Kimball et al. 2005)  |
| infrared               | feedback        | exp01,02,09    | 2.5 (1-4)        | 0.84 (0.05)           | -0.19-1.86        | 0.96 (0.05)    | -0.03-1.85 | 3 | Fig.4, Tables S15-S16, Kimball et al. 2005, Sherry et al. 2007 | +freeze-thaw cycles (McDaniel et al. 2013)<br>+shading (Kimball et al. 2005)<br>VPD (Morin et al. 2010) |
| forced air             | feedback        | exp07,10,15    | 3.5 (1.5-5.5)    | 0.95 (0.02)           | 0.43-1.73         | 0.36 (0.02)    | -0.42-1.06 | 3 | Fig.3-4<br>Norby et al. 1997                                   | +VPD (Norby et al. 1997)<br>air flow (Norby et al. 1997)  |
| soil cables            | feedback        | exp08          | 5                |                       |                   | 1.01 (0.02)    | 0.9-1.08   | 1 | Fig.3-4, Peterjohn et al. 1993                                 | +CO <sub>2</sub> flux (Peterjohn et al. 1993)<br>+N mineralization (Peterjohn et al. 1993)              |
| force air, soil cables | feedback        | exp03,04       | 4 (3-5)          | 0.49 (0.06)           | -0.02-0.94        | 0.75 (0.07)    | 0.01-1.05  | 2 | Fig.3-4  | air flow (Clark et al. 2013)  |

621 **Figures**

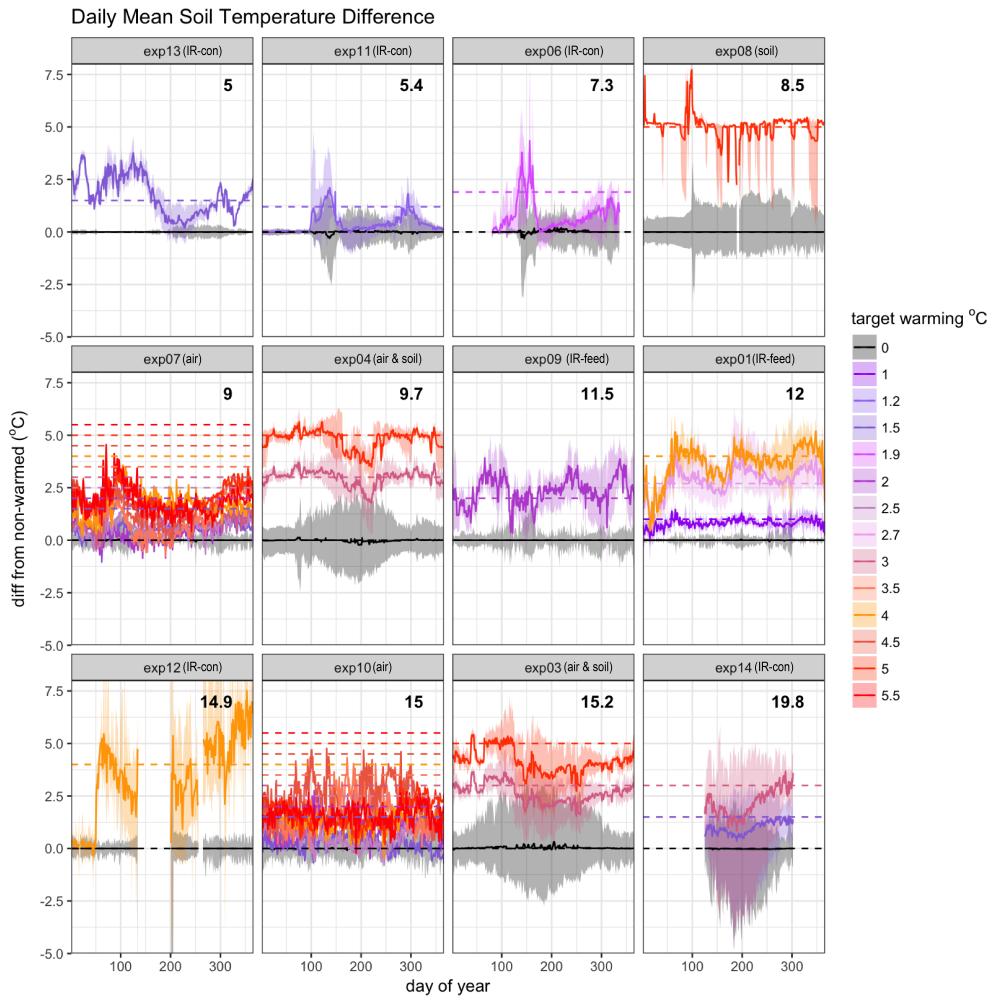
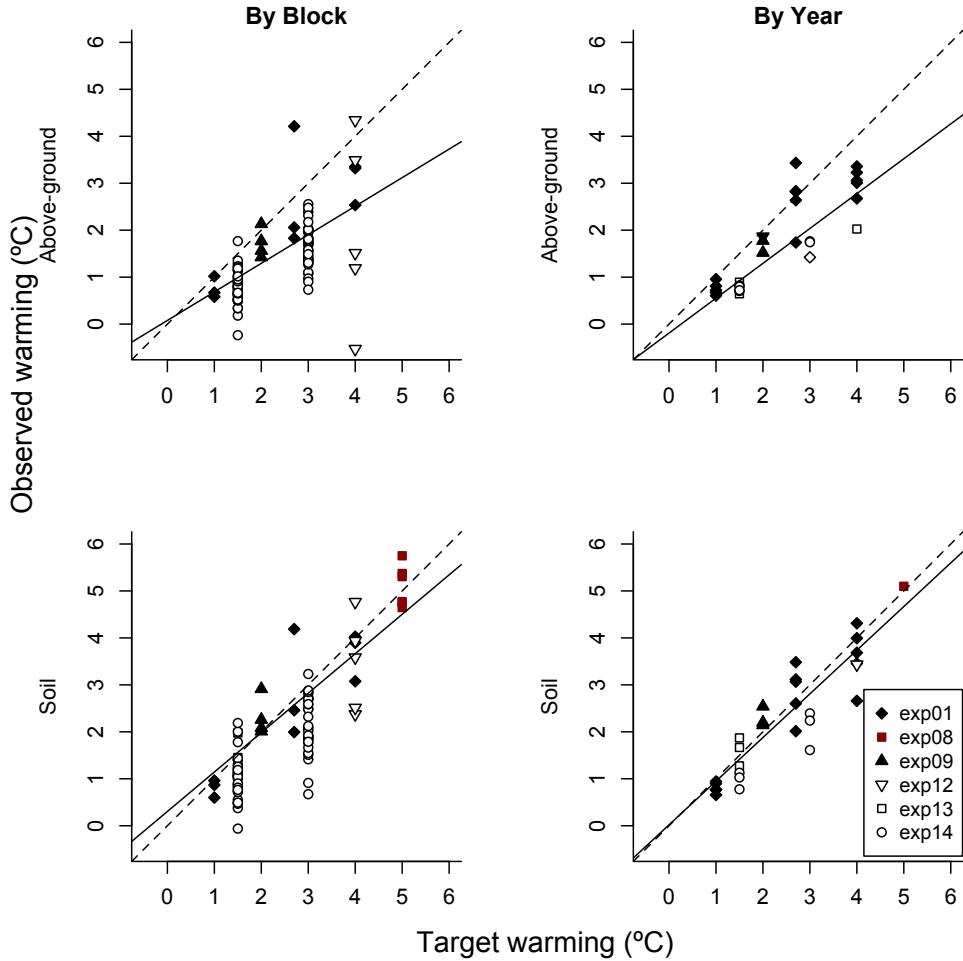
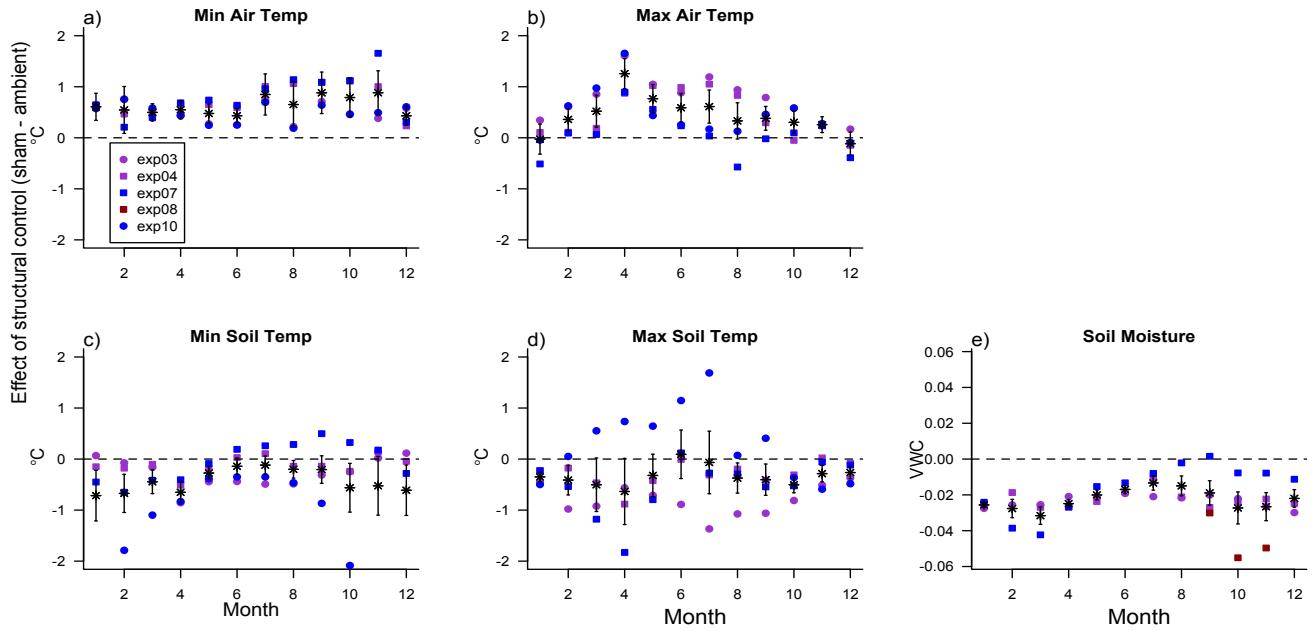


Figure 1: **Deviations in daily observed warming from mean control soil temperature for 12 study sites**, excluding data from plots that manipulated precipitation. We show soil, rather than above-ground, temperature, as this was the most frequently recorded temperature variable in the MC3E database. 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. (Note that the following sites had no explicit target temperature: exp06, exp11, exp12; in exp01, only the highest warming treatment had a target temperature; for these studies and treatments, we used their reported level of warming.) Two sites not shown here did not monitor soil temperature. Sites are ordered by low to high mean annual soil temperature (shown in the upper right corner of each panel). The heating type is listed in parentheses next to the site number (IR= infrared, soil= soil cables, air= forced air; con= constant wattage warming control).



**Figure 2: Observed warming over space and time, for above-ground and soil temperatures,** excluding data from plots that manipulated precipitation. Above-ground temperature includes air, canopy, and surface temperature. Points represent the difference between treatment and control plots by block (i.e., one data point per block) and by year (i.e., one data point per year). 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). Black symbols represent studies using infrared; red represents soil warming cables (only exp08); no studies with forced air heating used a blocked design. Open symbols represent constant wattage control and filled symbols represent feedback control. Note that the following studies had no explicit target temperature: exp06, exp11, exp12; for these studies, we used their reported level of warming. For exp01, only the treatment with the greatest warming had a target temperature. See Supplemental Materials (especially Tables S5 and S6) for details.



**Figure 3: 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 (which include includes air, canopy, and surface temperatures) were higher (a,b), whereas soil temperature (c,d) and soil moisture (e) 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 squares (for the three studies conducted at Harvard Forest in Massachusetts, USA) and circles (the two studies conducted at Duke Forest in North Carolina, USA). Colors vary by heating type: red represents soil warming cables, blue represents forced air; purple represents combined soil warming cables and forced air heating (no studies with infrared heating included both control types). All studies included used feedback warming control. See Supplemental Materials for details (Tables S8-S13).

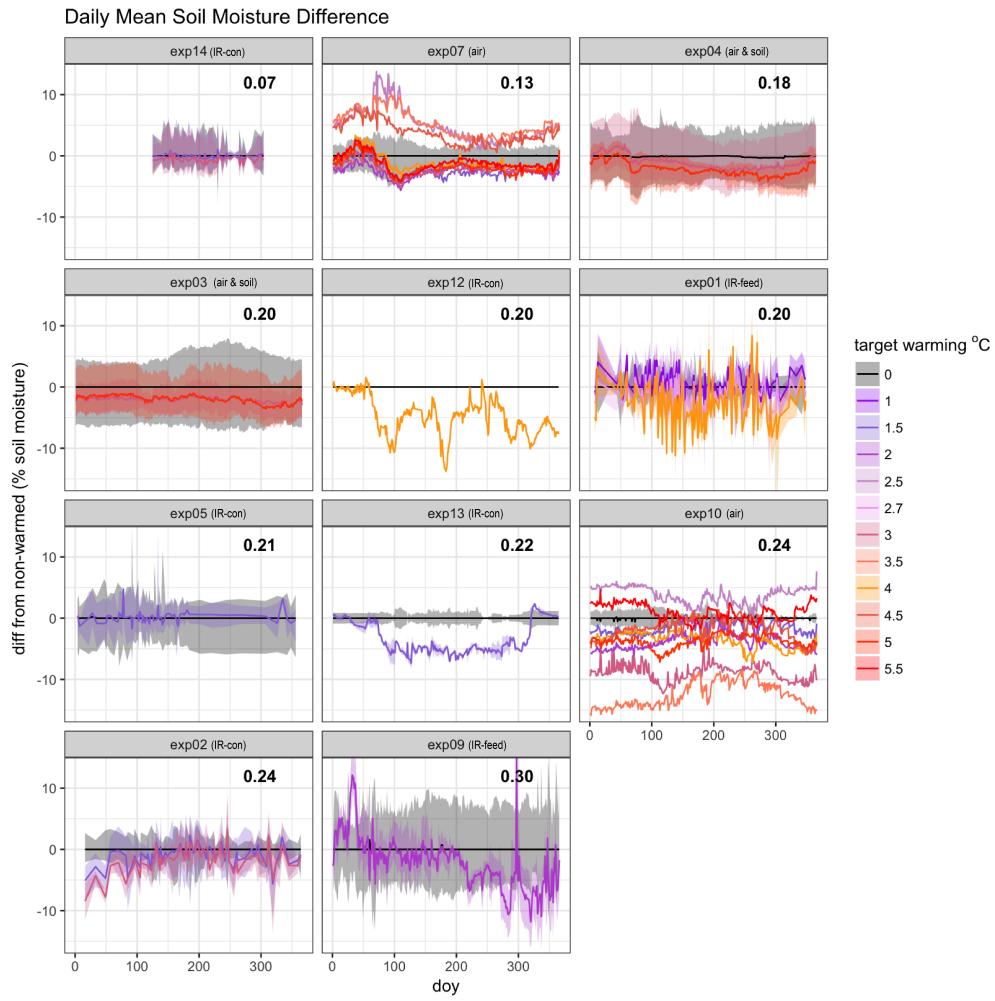
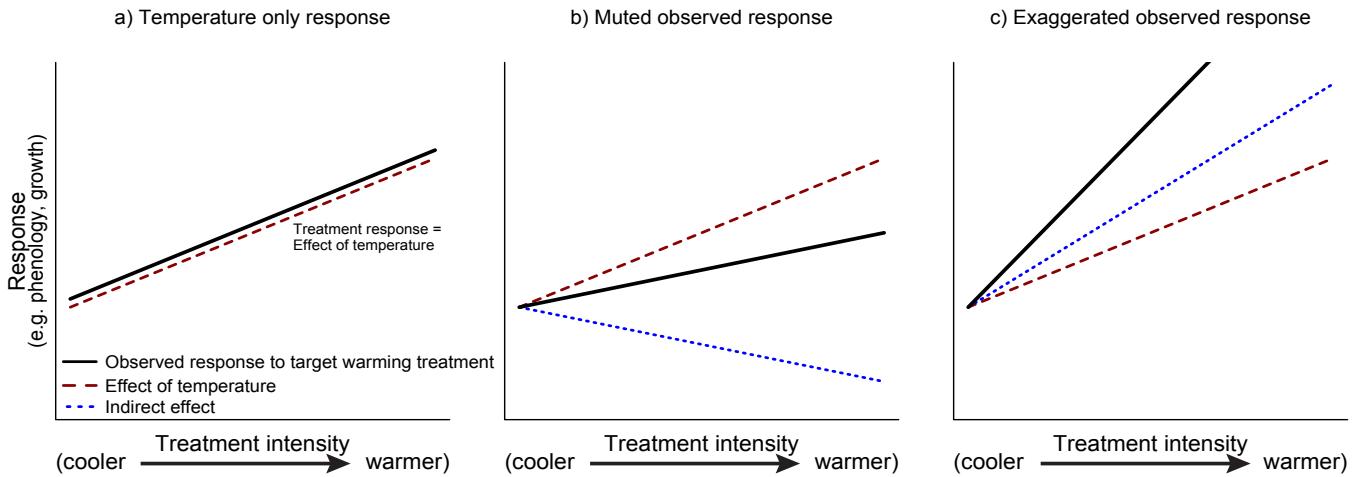


Figure 4: **Deviations in daily observed soil moisture**, shown for the 11 study sites that continuously monitored soil moisture, excluding data from plots that manipulated precipitation. Black lines represent control plots, and colored lines represent warming treatments with various target warming levels (or reported warming, if there was no explicit target temperature). The number of temperature treatment levels vary from one (e.g., exp08, exp11) to nine (exp07 and exp10, which used an unreplicated regression design). Sites are ordered by low to high mean annual soil moisture (shown in the upper right corner of each plot). All experiments measured soil moisture in volumetric water content, as a percentage of the soil volume in the sample, scaled from 0 to 100; the absolute difference between treatment and control plots is shown. Heating type is listed in parentheses next to the site number: IR-con= infrared with constant wattage, IR-f= infrared with feedback control), soil= soil cables, air= forced air.



**Figure 5: Theoretical biological responses to experimental warming and their interpretation.** Direct responses to temperature alone (a) can be easily understood. Complications arise when biological responses are a mix of the direct temperature and indirect non-temperature effects of experimental warming. Then experimental warming may cause biological responses to be muted (b) or exaggerated (c). Quantifying, interpreting, and reporting these non-temperature effects in experiments is critical, and their presence is both a strength and a challenge of climate change experiments. They may represent ecologically realistic effects that might not have been predicted without the *in situ* field experiment. Alternatively, they may represent artifacts that are unlikely to occur outside of an experimental context. The relationship between these effects could be more complex (e.g., nonlinear; antagonistic, multiplicative, or otherwise interactive).

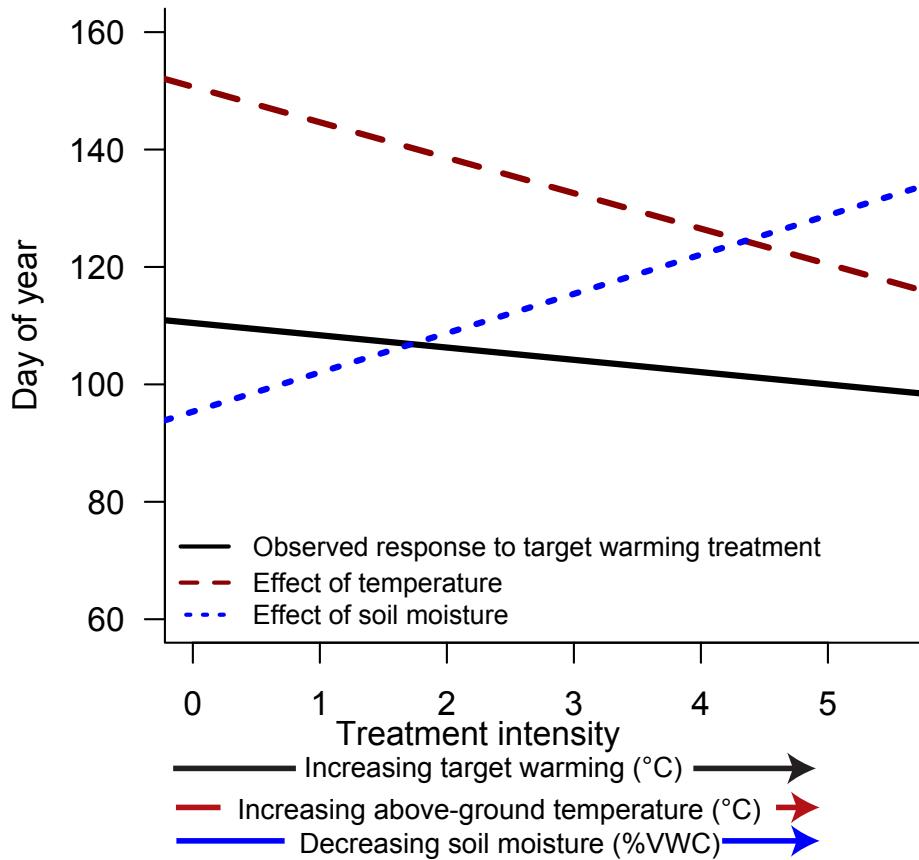


Figure 6: **Observed response of budburst day of year to experimental climate change** is an example of a muted response: the observed response to increasing treatment intensity (i.e., the coefficient of a model fit with only target [or reported, if there was no explicit target] temperature as the explanatory variable, black line; units for x-axis are  $^{\circ}\text{C}$  of target warming) 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, for which x-axis units are  $^{\circ}\text{C}$  of measured temperature) and soil moisture (dotted blue line, for which x-axis units are % VWC, decreasing from left to right in conjunction with warming intensity), as well as their interaction. Analysis includes all studies that monitored budburst and measured soil moisture and above-ground temperature (exp01, exp03, exp04, exp07, exp10); structural control data were used for this analysis (ambient controls were excluded from those studies that contained both). See Supplemental Materials, especially Tables S17 & S18, for additional details.

**622 Box 1: Different methods for achieving warming.**

623 Active-warming experiments may differ both in the way that they achieve warming (“warming type” in Table  
624 S1), and the way that warming is controlled (“warming control” in Table S1). There are three warming types  
625 used by studies in the MC3E database. These are infrared (n=9), an open-air method in which infrared  
626 heaters are mounted above the ground; forced air (n=3), in which air is heated and then pumped through an  
627 airflow system into a chamber; and soil warming (n=1), a chamber-less method in which soil is heated with  
628 buried electric resistance cable. Two additional studies in the database used combined forced air in chambers  
629 and soil warming. Warming is controlled by either constant wattage, in which an unvarying energy output  
630 is used, or by feedback control, in which energy outputs are linked to a thermometer and varied depending  
631 on the measured temperature in plots, in order to maintain consistent warming levels.

632 In this paper, we describe complications and non-temperature effects associated with active warming exper-  
633 iments, across these divergent warming methodologies. Some of the non-temperature effects described may  
634 be more likely to occur with particular methods than others. Alterations to airflow, for example, may be  
635 most dramatic with methods employing chambers. Plot shading and precipitation interference are likely to  
636 occur in chamber and infrared techniques, which both involve above-ground infrastructure, and less likely  
637 in methods that only warm from the soil. The biological impacts of such effects may be further enhanced  
638 or muted based on site characteristics (e.g., if a site is already heavily shaded, impacts from infrastructure  
639 shading may be lower).

640 Table 1 highlights that there may be differences in non-temperature effects across these different warming  
641 methodologies. In the MC3E database, sample sizes within each warming and control type were quite low, so  
642 we were unable to statistically distinguish differences in non-temperature effects across the different methods  
643 in all analyses. For example, the constant wattage control studies have greater average variation (2.2 °C  
644 variation on average for constant versus 1.1 °C variation for feedback), but this difference is not significant  
645 ( $p=0.21$ ). We note that the studies showing both the greatest and least variation employed constant wattage  
646 (greatest: plots in exp12, with target warming of 4.0 °C, varied by as much as 4.87 °C on average; least:  
647 plots in exp13 with 1.5 °C of target warming, varied by 0.03 °C per °C of target warming). These results are  
648 not conclusive, because our sample size is quite low (n=3 studies for constant and n=2 studies for feedback  
649 studies with blocked designs).

We expect that the list of non-temperature effects in Table 1 is not exhaustive, but represents what we can document here or has been documented previously. We recommend additional detailed studies of these, and other, effects across warming designs. This will allow future researchers to more fully evaluate the challenges and opportunities of each method, and select an experimental approach well-suited to their particularly research focus.



Soil cable warming experiment at Harvard Forest, Petersham, Massachusetts, USA (Melillo et al. 2017). Photograph credit: A. Barker-Plotkin.



Forced air chamber warming experiment at Duke Forest, Hillsborough, North Carolina, USA (exp10, Pelini et al., 2011). Photo credit: A. Ellison.



Infrared warming experiment in Pennsylvania, USA (exp09, Rollinson et al., 2012). Photo credit: C. Rollinson.



Infrared warming experiment in Montpellier, France (exp02, Morin et al., 2010). Photo credit: I. Chuine.

## 655 Box 2: Recommendations for future climate change experiments

- 656 1. *Collect and analyze plot-level climate data.* This includes analyzing and interpreting minimum and  
657 maximum values, as well as variance and critical thresholds (e.g., the number and duration of freeze-thaw  
658 events and accumulated chilling hours, McDaniel *et al.*, 2014b; Vasseur *et al.*, 2014). We suggest saving  
659 the raw data from data loggers (often collected at hourly or higher resolution) to allow quantification  
660 of variance (and other summaries) at different temporal resolutions. In assessing which frequency of  
661 measurements is most appropriate for analyses (e.g., hourly, twice daily), it is critical to consider the  
662 chronobiology of the event and organisms of interest. For ants, this might mean that temperatures be  
663 monitored every minute (Helm & Shavit, 2017); for bacteria, even more frequently.
- 664 2. *Analyze measured climate variables rather than targets.* There can be substantial variation in the effects  
665 of warming and precipitation treatments among plots and across time (Figure 2). Analyzing measured  
666 climate will allow much more in-depth understanding of the drivers and biological effects of variation  
667 in temperature and moisture.
- 668 3. *Publish high quality, usable data and metadata.* Given that climate manipulations are logistically  
669 challenging and expensive (Aronson & McNulty, 2009), and that they often produce a large volume of  
670 fine-scale climate data, good curation and data sharing will ensure wider use and deeper understanding  
671 of these valuable data. When studying biological implications of a global challenge as large as climate  
672 change, progress will come from designing and reporting experiments in ways that facilitate an eventual  
673 global data set. Researchers should also be explicit in their warming design (e.g., infrared heating with  
674 feedback control or forced air heating with constant wattage) to aid future analyses of the performance  
675 of different designs, across sites and over time (Box 1, Table 1).
- 676 4. *Include both structural and ambient controls* and collect, use, and report microclimate and biological  
677 data within them. Fewer than half of the studies in our MC3E database reported microclimate data  
678 from these two control types (6 out of 15 studies); however, all experiments that did include both  
679 control types showed significant effects of infrastructure (Figure 3).
- 680 5. *Design relevant manipulations* by consulting observational records and forecasts, including seasonal  
681 and annual variation in projected warming. When it is not possible or desirable to match anticipated  
682 changes in climate, studies should report how imposed treatments compare to projected changes and

683 past observations (e.g., Hoover *et al.*, 2014; Zhu *et al.*, 2016). In addition, if continuous treatments are  
684 not applied throughout the study, we recommend reporting the seasonality and timing of treatments  
685 and monitoring the climate throughout the year.

- 686 6. *Maximize the duration of climate change experiments* by running some experiments for as long as  
687 possible, since the magnitude of climate change treatments can vary considerably among years (Figure  
688 2). In addition, long-term responses of individuals and populations can differ from transient responses  
689 (Saleska *et al.*, 2002; Franklin, 1989; Giasson *et al.*, 2013; Harte *et al.*, 2015). We were able to acquire  
690 data extending for  $\geq 5$  years for only one study in the MC3E database (exp01), restricting our ability  
691 to investigate the effect of study length on experimental climate change.
- 692 7. *Conduct syntheses across studies.* As more detailed data are published from experimental climate  
693 change studies in divergent ecosystems and warming types, meta-analyses will advance our under-  
694 standing of the ways that warming affects microclimate and biotic interactions. For example, it would  
695 be useful to compare microclimate data among studies using infrared warming applied with constant  
696 wattage versus infrared warming that varies energy inputs based on measured temperatures (Box 1).