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SUPPLEMENTARY INFORMATION

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Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures

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Supplementary Note 1

Nominal vs. actual temperature treatments and overall system performance

For the statistical analysis of phenological responses to temperature, we used the actual mean (calculated from 30-minute data) measured temperature differential (ΔT) in each plot. We calculated deviations using the mean temperature in the unheated enclosure plots as the base. Our analysis shows that the heating treatments were consistent within an enclosure, over time, and across replicates of the same nominal temperature treatment (Extended Data Table 1). The mean measured temperature differentials were generally within 0.2 °C of the target temperature differential, although in both +9.0 °C enclosures, warming treatments did not quite reach the target temperature differential during the first two years of the experiment. However, by July-December 2017, the target temperature differential was reliably achieved. The mean ΔT in the ambient environment plots (plots 21 and 07) was about -1.6 °C on average. These plots run cooler than the unheated control enclosures (plots 06 and 19) due to the enclosure wall effects on radiation and nighttime cooling (i.e., the walls act as artificial cloud cover[7]). Overall, the temperature difference between the +9.0 °C enclosures and the ambient environment plots was in excess of 10 °C.

Previous analysis has shown that belowground temperatures with the live rooting zone (0 to 40 cm below the peat hollow surfaces) were similarly uniform within an enclosure, over time and across replicate enclosures of the same nominal temperature treatment[1].

Environmental conditions relative to long-term site means for the S1 Bog

We used long-term (1960-2000) data from the S1 Bog at the Marcell Experimental Forest[2] to provide a context for the ambient environmental conditions and the warming

treatments during August 2015–December 2017 in context (Extended Data Figure 1). This analysis shows that in the unheated enclosures, daily mean temperatures were generally above the long-term daily mean, but by only about 1 SD. By comparison, daily mean temperatures in the +9.0 °C enclosures were consistently more than 1 SD above the long-term daily mean (Extended Data Figure 1a). Additionally, monthly mean temperatures in the ambient environment plots and the unheated enclosures were modestly warmer than long-term monthly mean daily mean, while monthly mean temperatures in the +4.5 °C enclosures approximately tracked the long-term monthly mean daily maxima, and monthly mean temperatures in the +9.0 °C enclosures greatly exceeded the long-term monthly mean daily maxima (Extended Data Figure 1 b). Finally, over this period, monthly precipitation in the S1 Bog was generally within 1 SD of the long-term mean, and never approached historical extremes (wettest and dryest months on record shown as “max” and “min”) (Extended Data Figure 1 c).

Supplementary Note 2

Camera-based phenological observations

This analysis focuses on spring green-up and autumn green-down dates derived from camera imagery, with separate phenological transition dates estimated for the deciduous *Larix laricina*, the evergreen *Picea mariana*, and the evergreen mixed shrub layer dominated by *Rhododendron groenlandicum* and *Chamaedaphne calyculata*. For autumn 2015 and spring 2016, we used the linear temperature model and the breakpoint temperature model. Because the elevated CO_2 treatments were turned on in June 2016, we also considered a linear model incorporating temperature (measured ΔT), CO_2 (two levels, ambient and elevated), and CO_2 x temperature interaction effects for autumn 2016, spring 2017, and autumn 2017. Results of this analysis are summarized in Extended Data Table 2.

For the linear temperature model, the T effect was in the expected direction (indicating advancement of spring green-up, and delay of autumn green-down) in 14 of 15 cases (13 of 14 significant at $P \leq 0.05$; for *Larix* in autumn 2016, the temperature sensitivity was 2.12 ± 0.95 days per 1 °C warming, $P = 0.06$). The one exception to this overall pattern was spring green-up by *Picea* in 2017, for which the T effect was unexpectedly positive (0.69 ± 1.25 days per 1 °C warming), but not significantly so ($P = 0.60$). Interestingly, however, ground observations indicated that new leaf growth in *Picea* was advanced by warming, at a rate of -3.31 ± 0.41 days per 1 °C warming. This discrepancy appears to be a legacy effect of the 2016 spring frost damage in the two +9.0 °C enclosures. For *Picea* green-up in spring 2017, green-up dates derived from PhenoCam imagery generally occurred progressively earlier with warming, from day of year ≈ 90 in the two unheated enclosures to day of year 74 in the two +6.75 °C enclosures. Across these 8 enclosures, the T effect *was* significant at $P < 0.01$ in the linear

temperature model (r =-0.87; slope ± 1 SE = -2.14 ± 0.49 days per 1 °C warming). However, in the two +9.0 °C enclosures, the estimated green-up dates were actually later, not earlier, than in any other enclosure. We believe that this difference may be partially driven by the greatly reduced leaf area carried over from previous years by the frost-damaged trees, or by stress-induced changes in the vigor of existing foliage.

For a given species and phenophase, the temperature sensitivities estimated from the linear model were generally consistent across multiple years of observations, with overlapping confidence intervals.

With the linear temperature and CO_2 model, we found only weak evidence for a CO_2 effect on phenology. In just one case (autumn green-down by *Larix* in 2017) was the CO_2 effect significant at $P < 0.05$. Notably, a comparable result was *not* observed in 2016, when the CO_2 treatments were also active. Likewise, for the 2017 ground observations of *Larix phenology* (leaves yellow, leaves dropped), neither the CO_2 effect nor the CO_2 x temperature interaction effect was significant.

With the breakpoint temperature model, we successfully identified t^* values that improved model fit in 7 of 15 cases (1 in spring; 6 in autumn). However, the estimated t^* values were generally quite high (mean ± 1 SD = 6.2 ± 1.5 °C) and poorly constrained. In all but one instance (shrub layer green-down in autumn 2017, ΔAICc = -2.0), Akaike's information criterion indicated substantially greater support (ΔAICc > 0) for the simpler linear temperature model than for the breakpoint temperature model.

Supplementary Note 3

Future climate scenarios for SPRUCE, and implications for extension of vegetation activity

To place the SPRUCE warming treatments in the context of projected future climate change, we analyzed downscaled (1/8°) climate projections from the CMIP5 model intercomparison project[3]. Specifically, we used output from the following ten earth system models:

Modeling center	Country of origin	Model name
Commonwealth Scientific and Industrial Research Organization and Bureau of Meteorology	Australia	ACCESS1.0
National Center for Atmospheric Research	USA	CCSM4
Institut Pierre-Simon Laplace	France	IPSL-CM5A-MR
Atmosphere and Ocean Research Institute; National Institute for Environmental Studies; Japan Agency for Marine-Earth Science and Technology	Japan	MIROC5
Institute for Numerical Mathematics	Russia	INM-CM4
Canadian Centre for Climate Modelling and Analysis	Canada	CanESM2
College of Global Change and Earth System Science	China	BNU-ESM
Norwegian Climate Centre	Norway	NorESM1-M
Max Planck Institute for Meteorology	Germany	MPI-ESM-MR
Community Earth System Model Contributors	USA	CESM1-BGC

Relative to the 2006-2015 mean, decadal mean temperatures generally show a consistent rising trend, although there is substantial variability among models (Extended Data Figure 2). The projected mean temperature change under the RCP 4.5 "CO_2 stabilization scenario"[4] is 1.9 ± 0.6 °C by 2055 (decadal mean ± 1 standard deviation, across n = 10 models), and 2.6 ± 0.7° C by 2095. By comparison, under the RCP 8.5 "rising CO_2 scenario"[5], the projected mean temperature change is 2.7 ± 0.5 °C by 2055, 5.9 ± 1.1 °C by 2095. For RCP 4.5, none of the models projects more than 4 °C change by the end of the century, whereas for RCP 8.5, none of the models projects more than 8 °C change by the end of the century. The two +9.0 °C warming treatments in the SPRUCE experiment are, therefore, outside the range of even the most extreme model-based climate projection for 2100.

We used the climate projections to estimate future changes in the duration of the physiologically active season for the *Larix* and *Picea* trees, as well as the mixed shrub layer. We used the derived temperature sensitivities of spring green-up and autumn green-down (Figure 2) to determine an overall temperature sensitivity of total active season length (days of active season extension per 1 °C warming), which we then multiplied by the projected mean temperature change in 2055 and 2095. We predict that the active season of the two conifer species, *Picea* and *Larix*, may be extended by ≈1 week under the modest warming projected for the RCP 4.5 scenario, and up to 3 weeks under the more aggressive RCP 8.5 scenario, by the end of the century (Extended Data Table 3). By comparison, for the shrub layer, active season extension may approach 3 weeks under RCP 4.5, and 6 weeks under RCP 8.5, by the end of the century (Extended Data Table 3).

These calculations, conducted using autumn 2015 and spring 2016 temperature sensitivities derived from PhenoCam data, are intended for illustrative purposes; using sensitivities from other years would result in some difference in the calculated values, but would not substantially change the overall inference. However, because the phenological temperature sensitivities derived from the ground observations are in some cases higher than those from the PhenoCam data, extrapolation based on mean (across species) phenophase-specific temperature sensitivities in Table 1, or species-specific phenophase- specific temperature sensitivities in Extended Data Tables 4 or 5, would potentially lead to even more dramatic estimates of active season extension under future warming.

Supplementary Note 4

FLUXNET analysis of relationships between temperature and the seasonality of photosynthesis

We re-analyzed data from a previously published synthesis study[6] to evaluate relationships between temperature and the seasonality of photosynthesis in evergreen conifer forests. The objectives of this analysis were two-fold. First, we sought to investigate whether our estimates of the temperature sensitivity of spring green-up and autumn green-down for *Picea*, derived from camera G_{CC}, were compatible in both sign and magnitude with estimates of the temperature sensitivity of the switching "on" and "off" of photosynthetic uptake in conifer forests in spring and autumn. In other words, we asked whether it is reasonable to conclude that a longer "green" period driven by warmer temperatures might also imply a longer photosynthetically active period for the dominant tree species? Second, we wanted to investigate whether the experimental responses to SPRUCE temperature treatments were more consistent with the spatial patterns (across sites) or the interannual patterns (within sites) of temperature sensitivity, given that spatial patterns mostly represent equilibrium responses and the interaction of multiple covarying factors, while interannual variation may reflect more rapid but potentially transient responses to external forcing[6,7].

Briefly (for full details see Richardson *et al*., 2010, ref. 6) we used eddy covariance measurements of forest-atmosphere CO_2 flux, measured by eddy covariance, from $n = 12$ evergreen conifer sites (86 site-years of data) included in V2 of the FLUXNET "La Thuile" dataset (http://www.fluxdata.org). In this dataset, 30-minute measurements of the net ecosystem exchange (NEE) of CO_2 have been standardized, gap-filled and partitioned to respiration and photosynthesis using a common set of algorithms, and then aggregated to daily integrals. We included those temperate and boreal evergreen-dominated sites which had not been recently

disturbed or heavily managed, and which passed several basic quality-control filters. For each site-year of data, we extracted transition dates characterizing the "start" and "end" of photosynthetic uptake (defined by a threshold value of 2 g C m^{-2} d^{-1}) with curve-fitting methods. Similarly, for each site-year of data we calculated mean spring and autumn temperature as the air temperature during the ± 30 days surrounding the site-level mean (across all years for a site) "start" and "end" transition date. For our analysis of spatial patterns, we calculated site-level means for both transition dates and mean annual air temperature. For our analysis of interannual patterns, we calculated transition date anomalies and air temperature anomalies from the site-level means for each site-year of data.

This analysis showed, not surprisingly[8–10], that warmer temperatures were associated with an earlier start, and a later end, to the photosynthetic uptake period in evergreen conifer forests. This was true both across sites, in relation to spatial variation in mean site temperature, and within sites, in response to interannual variation in spring and autumn temperature. Across sites, we found that the start of the photosynthetic uptake period was advanced by 7.3 ± 0.8 days per 1 °C increase in mean annual temperature, while the end of the photosynthetic uptake period was delayed by 4.7 ± 0.5 days per 1 °C increase in mean annual temperature (Extended Data Figure 3 a, b). The response to interannual variation in temperature tended to be smaller: at individual sites, we found that the start of the photosynthetic uptake period was advanced by 3.5 ± 0.7 per 1°C anomaly in mean springtime temperature, and the end of the photosynthetic uptake period was delayed by 1.6 ± 0.5 d per 1°C anomaly in mean autumn temperature (Extended Data Figure 3 c, d). Our results from SPRUCE (Figure 2 and Extended Data Table 2), indicating that for *Picea* spring green-up was advanced by between 1.6 ± 0.3 (in 2016) and 2.1 ± 0.5 (in 2017, excluding frost-damaged trees in the two +9.0 °C enclosures) days per 1°C of warming, while

autumn senescence was delayed by between 1.2 ± 0.2 (in 2015) and 2.5 ± 0.5 (in 2016) days per 1°C of warming, were therefore consistent in magnitude with the within-site sensitivity to interannual variation in temperature, but not the across-site sensitivity to spatial variation in temperature.

Supplementary Note 5

2016 ground observations of vegetation phenology

From phenological ground observations in 2016, we extracted transition dates for a selection of spring and early summer phenophases for a range of woody and herbaceous species (Extended Data Table 4). We analyzed these data using the linear temperature model and breakpoint temperature model, with the observed phenological transition date as the *y* variable and the mean air temperature differential (ΔT) as the *x* variable. We did not use the linear temperature and CO_2 model because elevated CO_2 treatments were not turned on until June 2016, by which time the phenological transitions under consideration were largely complete.

Across eight species and a total of 23 different species-phenophase combinations, we found that spring phenological transitions were in all cases advanced with increasing warming (Extended Data Table 4); all estimated temperature sensitivities were significantly different from zero at $P < 0.05$, with $P < 0.001$ for 19 of 23 cases. In 14 of 23 cases, we identified a breakpoint temperature model t^* parameter that improved model fit, but the mean (± 1 standard deviation) temperature threshold was typically quite high (6.6 ± 1.4 °C). And, in all but one case (leaf growth by *Chamaedaphne*; ΔAICc = -1.7), there was stronger support (ΔAICc > 0) for the linear temperature model than the breakpoint temperature model.

2017 ground observations of vegetation phenology

In 2017, phenological ground observations were conducted weekly from March through December, on the same species that had been previously observed in 2016. From these observations we estimated a total of 44 species-phenophase transition date combinations, including both vegetative and reproductive phenology, and spring and autumn events (Extended

Data Table 5). We used the same modeling framework—the linear temperature model and the breakpoint temperature model—applied to the spring 2016 ground observations. However, because the elevated CO_2 treatments were turned on in June 2016, and therefore may have influenced phenology in 2017, we also considered a linear model incorporating temperature (measured ΔT), CO_2 (two levels, ambient and elevated), and the CO_2 x temperature interaction, effects.

For the linear temperature model, the T effect was significant at $P \leq 0.05$ in all but a handful (7 of 44) of cases (Extended Data Table 5). For two of these (fall buds present on *Chamaedaphne* and *Picea*), the same transition date was recorded for all enclosures and hence the T effect had a slope of zero, suggesting photoperiod control. In four other instances, model RMSE was very large (20 days or larger), suggesting that either these phenophases may have been difficult to evaluate visually, or factors beyond temperature and photoperiod may be involved. By comparison, the T effect was significant at $P < 0.01$ or better in the vast majority (29 of 44) cases. These results show consistent patterns of spring events—such as onset of shoot growth, onset of leaf greening or leaf growth, onset of flowering, onset of fruiting—all being advanced by the warming treatments. Termination of flowering was in most (but not all) instances also advanced with increasing temperature, but generally to a lesser degree than the onset of flowering, indicating an increase in the duration of flowering with warming. By comparison, events associated with senescence, including folding, coloration and dropping of foliage, consistently occurred later with increasing temperature. For *Rhododendron*, a late-season flowering event was observed in 9 of 12 plots; the last date these flowers were observed in each plot was also found to occur later with increasing temperature.

With the linear temperature and CO_2 model, we found only the weakest evidence for a CO_2 effect on phenology in 2017. In just 1 of 44 cases (termination of flowering by *Kalmia polifolia*) was the CO_2 effect significant at $P < 0.05$, and for this species and phenophase both the CO_2 effect and the CO_2 x T interaction effect were both significant at $P < 0.01$. This was the only case where ΔAICc was lower for the linear temperature and CO_2 model than for the simpler temperature-only model.

With the breakpoint temperature model, we successfully identified a t^* value in 23 of 44 cases. However, in only 12 cases did AIC_C indicate greater support ($\Delta AICc < 0$) by the data for the breakpoint temperature model over the linear temperature model, and in only 5 cases was the breakpoint temperature model strongly supported ($\Delta AICc < -2.0$) over the linear temperature model. For the 12 cases where the breakpoint temperature model was better supported than the linear temperature model, the mean (±1 SE) t^* was 4.8 ± 1.5 °C. For only 4 of 12 cases was $t^* <$ 4.0 °C.

Comparison of 2016 and 2017 results, and overall conclusions

There were 17 phenophase-species combinations for which corresponding observations were made in both 2016 and 2017. For these 17, we found that the estimated phenological temperature sensitivities (derived from the slope of the linear temperature model) were well-correlated between the two years ($r = 0.71$, $P < 0.01$). For example, onset dates of shoot elongation and leaf growth in *Chamaedaphne* were the most temperature-sensitive phenological events (approx. 4-5 days advancement per 1°C warming) in spring 2016 and again in spring 2017. By comparison, flowering dates for *Chamaedaphne*, *Eriophorum* spp., and *Maianthemum*

were comparatively temperature-insensitive (approx. 1-2 days advancement per 1 °C warming) in spring 2016 and again in spring 2017.

For the breakpoint temperature model, we successfully identified t^* values in both spring 2016 and spring 2017 for 9 phenophase-species combinations. Mean t^* values for these were very similar between the two years (6.3 ± 2.1 °C in 2016, 6.2 ± 1.6 °C in 2017). And, for the one instance (onset of *Chamaedaphne* leaf growth) where ΔAICc was < 0 in both 2016 and 2017, t^* values were similar in 2016 (5.2 ± 0.8 °C) and 2017 (6.3 ± 1.0 °C). However, in general the t^* values estimated from the spring 2016 data were not well-correlated with the t^* values estimated from the spring 2017 data for the same phenophase-species combinations (r = -0.15, P = 0.70). This may be because of the generally weak support for the breakpoint temperature model in both years (most ΔAICc > 0), and consequently the relatively poorly constrained values of t^*. There was also some inconsistency between years; for example, there were two instances where t^* values were identified in 2016 (but were not identified in 2017), and four instances where t^* values were identified in 2017 (but were not identified in 2016).

Mean January-June enclosure air temperatures were similar between 2016 and 2017 (about 3 °C in the ambient environment plots, see Extended Data Table 1), but the timing of "warm spells" and "cold spells" was different, and for much of the spring in 2017, degree-days above 0 °C were accumulated more rapidly than in 2016. Analyses that integrate multiple years of phenological observations, and account for year-to-year differences in the timing of warmer vs. colder weather, may be necessary to more definitively estimate robust t^* thresholds. Nevertheless, as with the camera data, these analyses clearly show that (1) there are relatively few cases where there is strong evidence that photoperiod will constrain the phenological

response to warming; and (2) where there is evidence for a photoperiod effect, it is expected to be a factor only at relatively high levels of warming.

Supplementary Note 6

The 2016 Spring Frost Event

The vegetation damage from the 2016 spring frost event in the warmest plots was triggered by unusually warm conditions during winter and early spring (Extended Data Figure 4 a). For northern Minnesota (state Climate Division 2), the period of January–March was the 5th warmest of the last 122 years, with a mean air temperature (–6.8 °C) that was 4.9 °C above the long-term mean. This warm weather resulted in the onset of green-up (as estimated from G_{CC} using a 25% seasonal amplitude threshold) of existing *Picea* foliage by the end of March in all enclosures. For the *Larix*, new needles were just beginning to break through the bud scales by the end of the first week of April in all but the two unheated enclosures and the two ambient environment plots.

The warm weather continued through April 8. By this time, the two experimental +9.0 °C enclosure—plots 17 and 10—had accumulated 665 ± 19 degree-days (0 °C base temperature), since January 1. This was four times as many degree-days as were accumulated in the two unheated enclosures—plots 6 and 19—over the same period (161 ± 7 degree-days). Indeed, in the +9.0 °C enclosures, it had been more than a month since minimum temperatures dropped below –2.5 °C, which is a commonly-used temperature threshold for frost damage of de-hardened tissue[11]. By comparison, in the unheated enclosures, daily minimum temperatures had been below freezing on all but a dozen nights in the previous three months.

Early in the morning of April 9, ambient air temperatures dropped to a near-record low for that date of –15 °C. Temperatures in the two unheated enclosures dropped to –12.0 ± 0.3 °C (Extended Data Figure 4 b), and the two +9.0 °C enclosures experienced below-freezing temperatures, with temperatures reaching –4.6 °C in plot 17, and –3.1 °C in plot 10. Highly

variable temperatures over the following four days may have contributed to the resulting damage, as temperatures rose by almost 20 °C on April 10 before again dropping below freezing (even in the +9 °C enclosures) on April 12 (Supplementary Figure 4 b).

Foliage mortality was observed in the both the +9.0 °C (plots 10 and 17) and +6.75 °C (plots 8 and 16) enclosures. In plot 17, for example, the signs of frost damage were almost immediately obvious for *Larix*, while for *Picea* the transition from green to brown was somewhat more gradual (Extended Data Figure 4 c). By April 20, foliage mortality of these species was estimated to reach 50%. Overall, the damage to *Larix* and *Picea* in plot 17 was particularly dramatic (Extended Data Figure 4 d-f). Later in the spring, foliar loss approached 100% for some *Picea* but not others, indicating loss of multiple foliar cohorts. However, not all of the *Larix* and *Picea* in the warmest plots displayed damage: some trees remained visibly healthy and did not lose significant amounts of foliage, indicating potential genetic differences in the sensitivity of winter dehardening to temperature. Trees in enclosures that received less experimental warming suffered little or no damage, despite experiencing colder minimum temperatures. The patterns of damage evident at SPRUCE point to warm temperatures—rather than photoperiod—as the environmental signal driving de-hardening.

By early May, *Larix* re-flushed from epicormic buds, while *Picea* (which typically retains foliage for up to 5–7 years) flushed from overwintering terminal buds that were not damaged. There are obvious carbon and nutrient losses associated with the shedding of damaged foliage[12], yet spring frost events have historically been infrequent enough that mature woody plants typically carry sufficient reserves to tolerate occasional light damage[13,14]. At SPRUCE, the premature foliar senescence in the frost-damaged tree species led to significant nutrient inputs into the plot. Damage was significant enough to prevent normal retranslocation of foliar nitrogen

during senescence. Nitrogen content (% dry matter) in the frost-damaged litter was 70% greater for *Picea* and 100-500% greater for *Larix* than normal autumn senescent litter (Extended Data Table 6). This has implications for both the trees, and the broader ecosystem nutrient budgets. Some studies have noted that in cases of severe or recurring frost damage, future growth rates and survivorship may be affected[15], and this is being tracked at SPRUCE. The long-term impacts of the 2016 spring frost on *Picea* and *Larix* vigor are not yet clear. But, without photoperiod serving to check premature de-hardening, these trees may be predisposed to more frequent frost damage under warmer climate regimes.

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