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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

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Abstract

Ecosystem responses to climate change can exert positive or negative feedbacks on climate, mediated in part by slow-moving factors such as shifts in vegetation community composition. Long-term experimental manipulations can be used to examine such ecosystem responses, but they also present another opportunity: inferring the extent to which contemporary climate change is responsible for slow changes in ecosystems under ambient conditions. Here, using 23 years of data, we document a shift from nonwoody to woody vegetation and a loss of soil carbon in ambient plots and show that these changes track previously shown similar but faster changes under experimental warming. This allows us to infer that climate change is the cause of the observed shifts in ambient vegetation and soil carbon and that the vegetation responses mediate the observed changes in soil carbon. Our findings demonstrate the realism of an experimental manipulation, allow attribution of a climate cause to observed ambient ecosystem changes, and demonstrate how a combination of long-term study of ambient and experimental responses to warming can identify mechanistic drivers needed for realistic predictions of the conditions under which ecosystems are likely to become carbon sources or sinks over varying timescales.

Keywords: climate change, ecosystem–climate feedback, long-term observation, shrub encroachment, snowmelt, soil carbon model, vegetation, warming experiment

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Introduction

In the western United States, recent data suggest a trend toward earlier snowmelt (Hidalgo *et al.*, 2009; Pederson *et al.*, 2011, 2013) and toward woody plant encroachment into montane meadows and grasslands (Archer *et al.*, 1994; Breshears *et al.*, 2005; Archer, 2010). Such shifts in vegetation cover have the potential to alter carbon sources and sinks (Pacala *et al.*, 2001; Schwalm *et al.*, 2012). Hence, understanding the causal links between local climate and vegetation and between those factors and carbon cycling is increasingly important for predicting both the future structure and functioning of ecosystems. Because of climate–ecosystem feedback (Lashof *et al.*, 1997), it is also important for predicting the climates that regions of the planet will experience in the future. Trend data alone, however, in the form of temporal correlations in climatic, vegetational, and carbon cycle variables, are not sufficient to establish and quantify the causal mechanisms needed for predictive modeling.

Disentangling past woody encroachment trends caused by climate effects from effects of past land use and fire management presents a challenge for predicting ecological feedbacks to climate in the future (Archer *et al.*, 1994). Controlled experimental manipulation provides a well-established approach to inferring causal relationships in ecology (Underwood, 1997), but such experiments may introduce unrealistic environmental conditions. Purely observational studies provide the means of studying systems under actual climate variability, but are limited in their ability to infer controlling mechanisms. The combination of experimental manipulation and long-term observational studies in the same ecosystem can be a particularly powerful way to take advantage of the benefits of each approach and thereby make reliable predictions about future ecosystem response to climate change (Carpenter, 1998; Dunne *et al.*, 2004; Harte & Kueppers, 2012). Greater confidence in predictions is obtained when the findings

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from these two approaches corroborate one another. Whereas purely observational studies cannot determine that climate change is the cause of observed ecosystem trends, our combined study of ambient and manipulated plots can.

Here, we report results from combining measured ecosystem responses to a long-term climate manipulation experiment with data from direct observation of long-term ambient trends in unheated plots. A previous study (Harte *et al.*, 2006) that examined plot responses to a 5-year drought provided model-based evidence that an observed decline in soil carbon in heated plots might be a transient effect, to be followed by a recovery of soil carbon. Here, we show, with eight additional years of data from the experiment, that the predicted reversal of soil carbon loss in the heated plots, a 23-year downward trend in soil carbon in the ambient plots, and an ambient-plot shift in plant community composition that tracks the faster heated-plot vegetation shifts have occurred.

The experimental study site is a subalpine meadow, and both the manipulation and the observations were carried out over the past 23 years (see Materials and methods, and Appendix S1). We focus on four response variables in the study site: date of snowmelt, aboveground biomass of the two dominant vegetation forms, forbs and shrubs, and soil organic carbon. We examine the consistency between observed ambient-plot trends in each of these variables and their responses to experimental warming. We further identify the dominant processes governing these trends and, from them, predict the future carbon source–sink dynamics of the study site under continuing warming. Generalizing from this study, we characterize the critical data needed to determine future trends in stored carbon in other types of ecosystems.

Materials and methods

Our warming experiment is conducted at the Rocky Mountain Biological Laboratory, Gunnison, CO, USA (lat. 38°57′29″; long. –106°59′22″; elev. 2920 m). In 1989, ten 3 m × 10 m plots were established in an ungrazed montane meadow (the 'Warming Meadow'). Above five of the plots, overhead infrared radiators have been on night and day, and throughout the year, since January 06, 1991, casting a downward heat flux at the surface of ~15 watts m^{-2} prior to June 1993, and 22 watts m^{-2} subsequently. Each plot spans a 10 m microclimate gradient with the upper zone of each plot flat and relatively dry, a steeper and dry middle zone, and a more moist, flat lower zone. Soil temperature and moisture are measured and logged every 2 h at 5, 12, 25 cm depth in each zone. The microclimatic effect of experimental heating throughout the growing season has been to warm the top 15 cm of soil by ~2 °C and dry it by 10–20% (gravimetric basis) during the growing season, and to prolong the snow-free season at each end by an average of ~2 weeks.

Vegetation in the upper zone of the plots, which this report focuses on, consists of one dominant woody shrub, *Artemisia tridentata* (sagebrush), ~40 species of perennial forbs, including *Erigeron speciosus* (fleabane) and *Delphinium nelsonii* (larkspur), and 16 species of graminoids, including *Festuca thurberi* (a bunch grass). Aboveground biomass (AGB) of forbs and shrubs is estimated visually approximately every ten days during the growing season, by counting the occupied fraction of 225 gridded cells on a 75 × 75 cm quadrat, and using a regression of coverage vs. measured AGB obtained off-site. For sagebrush, areal coverage measurements are based only on foliage, most of which is shed at the end of the growing season, not on woody stems, and thus is a measure of annual production. For forbs, annual production is determined from the growing season peak value of AGB with a correction factor to account for the annual succession of forb species (Saleska *et al.*, 2002). Soil organic carbon (SOC) is measured in four cores (10 cm long, 1.7 cm diameter) extracted from the upper zone of each plot in early June and early August each year (1). Carbon content is determined from mass loss upon ignition at 430 °C after confirmation that results are tightly correlated with results from CN analysis (Europa Scientific) as described in (Saleska *et al.*, 2002). Snowmelt date is calculated as the date logged soil temperature rises above 2 °C at 12 cm depth. All analyses are carried out on data averaged over all five plots within treatments. All the above, and additional, details about the site, the experimental design and methods, and the microclimatic effects of heating have been described (Harte *et al.*, 1995; Shaw & Harte, 2001; Saleska *et al.*, 2002; Dunne *et al.*, 2004).

To project forward in time the magnitude of soil carbon in the plots, we adapted the decomposition-weighted productivity (DWP) model, which simulates the effect of plant community composition on soil carbon dynamics (Saleska *et al.*, 2002). This model treats the soil organic carbon pool as the sum of components, each regulated by the productivity and litter quality of a different functional group of plants. In the specific application to the meadow-warming experiment, these groups are forbs, shrubs, and graminoids. For a mathematical description of the model, details regarding model parameterization, and results of a validation test of the model, see Appendix S1.

A linear mixed model, fitted with restrictive maximum likelihood methods, was used to determine whether heated and ambient plots were following similar trends over time while accounting for autocorrelation of plots over time. Effect of treatment, year, and treatment by year were treated as fixed effects, while plot was treated as a random effect. When model residuals were evaluated for normality and homoscedasticity, some transformations were made to datasets (Shrub[ln(x)+1]; Forb[sqrt(x)]; $Carbon_{93\text{-}06}$[ln(x)]; $Carbon_{07\text{-}13}$[1/(x)]; $Carbon_{91\text{-}13}[(x)^{-3}]$). These changes improved homoscedasticity and made no qualitative change to significance values. More weight was placed on creating homoscedastic than on creating perfectly normal residuals, as mixed models tend to be more robust to non-normal than to heteroscedastic residuals (Zuur *et al.*, 2009).We hypothesized that we would see significant effects of treatment and year separately, but no significant combined effect of treatment by year, where treatments followed parallel, but offset, trends over time.

Results

Observations over 23 years show a significant effect of heating on snowmelt date and a significant trend toward earlier snowmelt on both heated and ambient plots (Fig. 1, Table S1). The five exceptionally dry winters in the Rockies corresponding to the 2000–2004 widespread drought (Hidalgo *et al.*, 2009; Pederson *et al.*, 2011, 2013) and the exceptionally dry winter of 2012 are clearly visible in the melt date record.

We tested a number of multiple regression models to explain date of snowmelt. In the most parsimonious model (Table S1), plot number (a surrogate for southerly aspect), year, and heating treatment each significantly advanced date of snowmelt. A year-by-treatment interaction was marginally significant ($P = 0.066$), indicating that the heating advance of snowmelt increased over time, as is evident in Fig. 1.

By 1993, the third year of experimental warming, forb AGB was lower in heated plots than in ambient plots and slowly decreased over time in both heated and ambient plots (Fig. 2a). After 1993, the only time that heated-plot exceeded ambient-plot forb AGB was in 2002, the year of earliest melt in the 23-y record. The fitted slope of the temporal decline in forb AGB in the heated plots is approximately 50% greater than the slope for the control plots. Despite this, a linear mixed-model analysis showed a significant effect for year but not treatment or treatment by year (Tr: $P = 0.66$, Yr: $P < 0.0001$, Tr:Yr: $P = 0.085$) (Table S2). Serially removing insignificant effects did not qualitatively change the model result (Tr: $P = 0.2243$; Yr: $P < 0.0001$).

In a response opposite to that of forbs, shrub AGB increased over time in both heated and ambient plots and at three times the rate in heated plots compared to ambient plots (Fig. 2b). However, the ambient- and heated-plot temporal trend lines for shrub AGB diverged somewhat and showed a significant effect treatment by year (Tr: $P < 0.643$, Yr: $P < 0.0001$, Tr:Yr: $P < 0.0001$) (Table S3).

Snowmelt date explained approximately 50% of the interannual variability in both forb and shrub AGB (Fig. 3) when heated and ambient plot data are combined. Treatment differences in slopes of forb and shrub AGB vs. melt date were not significantly different.

Soil organic carbon (SOC) decreased in the heated plots compared to the ambient plots after the onset of heating and then, after reaching a minimum, slowly increased; ambient-plot SOC slowly decreased during the 23 years (Fig. 4a). The increase in heated-plot SOC from 1994 to 2013 was significant ($y = 0.033x + 3.88$; $t = 2.79$; $P = 0.006$). The decrease in the ambient plots was marginally significant ($y = -0.048+5.71$; $t = -1.784$; $P = 0.078$). A linear mixed model looking at overall effect of treatment and year, with plot added as a random effect, showed a significant interaction of treatment by year ($P = 0.01$; Table S4). Results were further broken down into early effects (1993–2006) and late treatment effects (2007–2013); previous analysis had already shown a statistically significant treatment effect

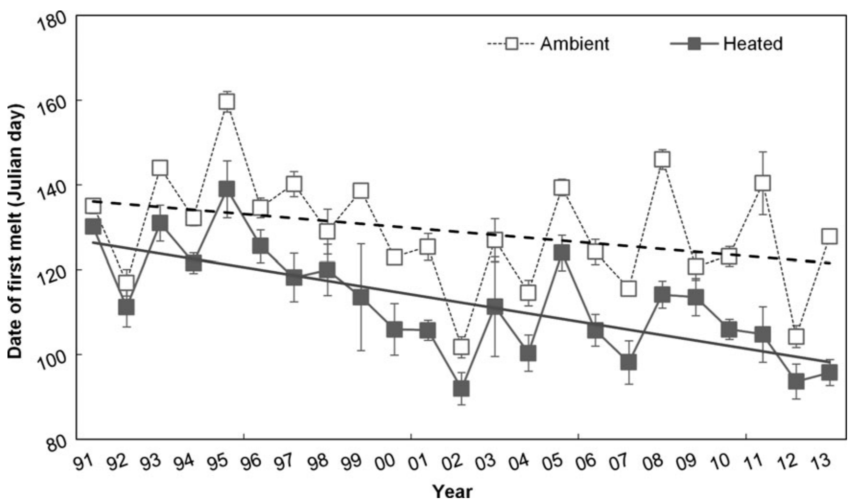

Fig. 1 Date of snowmelt averaged over five replicates in each treatment, plotted against year. Error bars are ± standard errors. Multiple regression analysis (Table S1) shows that heating advanced snowmelt by an average of 7.7 days ($P < 0.04$), plus an interaction effect that advanced melt by an additional 0.5 days per year ($P < 0.07$). Long-term climate trends are advancing ambient snowmelt at a rate of 0.74 days per year ($P < 0.0002$).

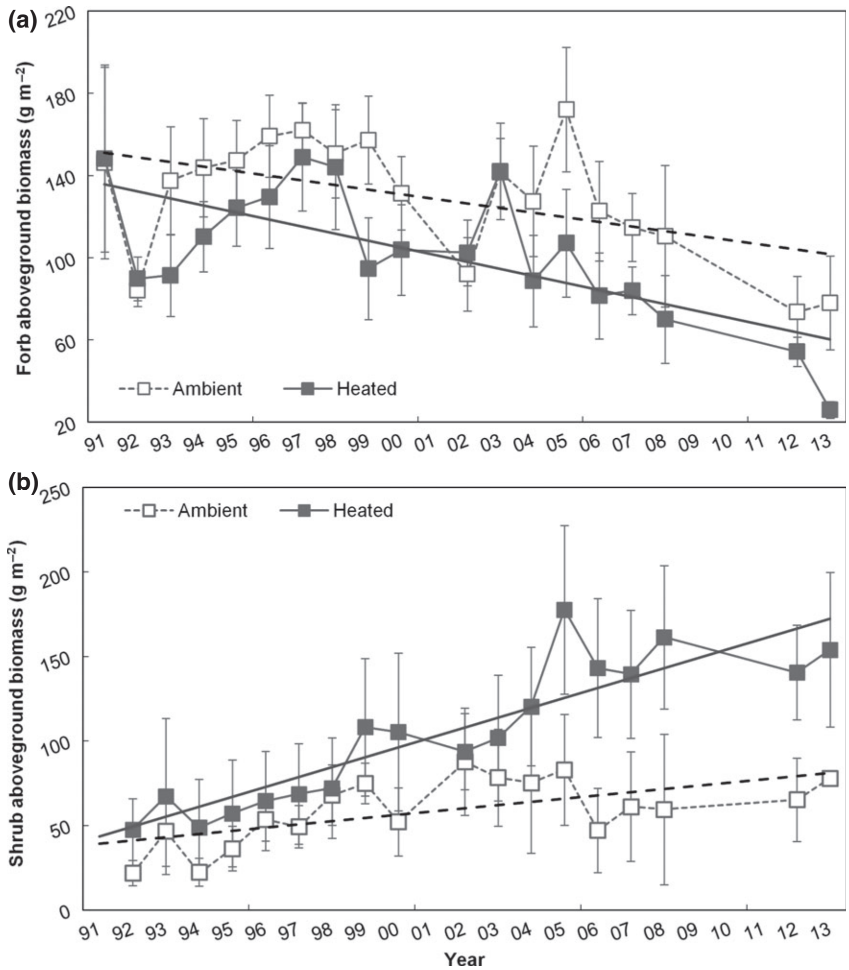

Fig. 2 The figure shows aboveground biomass averaged over five replicates in each treatment, plotted against year for (a) forbs, (b) shrubs. Error bars are ± standard errors. Regression lines are calculated from all replicates all years for each treatment for (a) forbs (Forb Ambient Biomass = −2.23 Year since 1990 + 153.2; Adjusted R^2 = 0.056; P = 0.012); (Forb Heated Biomass = −3.49 Year since 1990 + 139.6; Adjusted R^2 = 0.15, P < 0.0001) and b. shrubs (Shrub Ambient Biomass = 1.78 Year since 1990+38.42; Adjusted R^2 = 0.031; P < 0.054) (Shrub Heated Biomass = 5.69 Year since 1990 + 38.91; Adjusted R^2 = 0.17; P < 0.001).

(Harte *et al*., 2006), and reanalysis confirmed this through a statistically significant treatment-by-year effect (P = 0.029; Table S5). In the later time period, however, there was no significant interaction of treatment by year, and when the insignificant interaction effect was removed, there was a significant effect of year (P = 0.0047) but no significant effect of treatment (P = 0.871) (Table S6), as apparent in the visible convergence of the SOC data in Fig. 4a.

Discussion

The pattern of SOC response in the heated plots is complex and of particular interest because of its potential relevance to climate feedback (Lashof *et al*., 1997). As had been predicted in previous studies (Saleska *et al*., 2002; Harte *et al*., 2006), as forb AGB decreased and shrub AGB increased, SOC in the heated plots was expected to first decrease then eventually rebound. This initial decrease in heated-plot SOC was explained by the lower intrinsic rate of shrub litter productivity (in units of inverse time) relative to that of forbs. The delayed increase in heated-plot SOC was predicted because shrub litter was shown to form a more recalcitrant SOC than does forb litter (Shaw & Harte, 2001), and thus, increasing shrub production should result in SOC with a longer turnover time. The effect of changing soil microclimate on the rate of mineralization of SOC was shown to be negligible because the warming and drying effects of the heating manipulation on carbon mineralization rates canceled (Saleska *et al*., 2002).

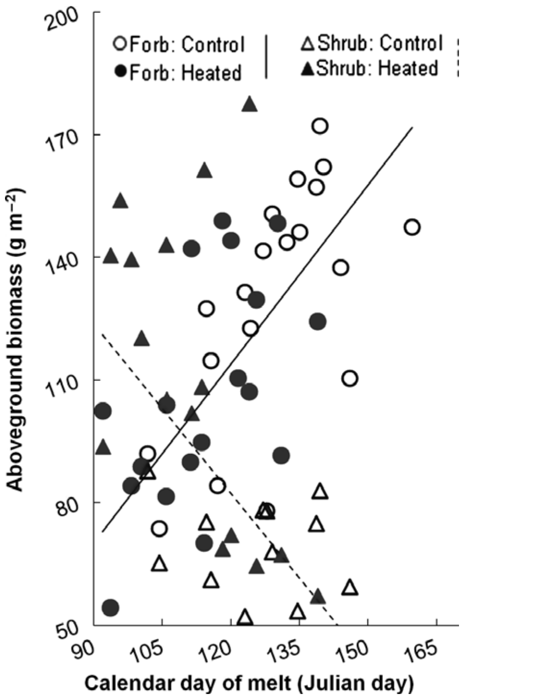

Fig. 3 Forb and shrub aboveground biomass averaged over five replicates in each treatment, plotted against date of snowmelt. (Forb Biomass = 1.46 Day of Melt −61.58, $R^2 = 0.47$, $P < 0.001$; Shrub Biomass = −1.38 Day of Melt +248.39, $R^2 = 0.3077$, $P < 0.001$).

In particular, we had predicted, based on available data through 1998, that by the end of the second decade of the experiment, the SOC levels in the heated plots would increase to approximately their preheating level (Saleska *et al.*, 2002). The prediction was based on a simple carbon mass balance model (Appendix S1) with input driven by observed annual plant production and output (carbon mineralization) given by an empirically determined function of soil temperature and moisture, multiplied by a SOC quality factor that differed for forbs and shrubs and was also empirically determined. The model accurately predicts ambient SOC values across an elevational and vegetation cover gradient (Figure S1).

At the time of that prediction, we did not consider the effect of already-occurring climate change on the ambient vegetation and SOC. Overall, a significant trend toward earlier snowmelt on heated and ambient plots was detected (Fig. 1 and Table S1), reflective of the broad-scale long-term climate trends in the American west toward dryer conditions and reduced snowpack (Hidalgo *et al.*, 2009; Pederson *et al.*, 2011, 2013). An analysis of variance for both forb and shrub data suggested that while treatments were significantly different from each other, when the treatment-by-year effect was considered they followed similar trends over time. Comparison of the slopes of AGB over time showed that the control-plot trend was not significantly different from the heated-plot trend in forbs.

A difference in the slope of the melt date data in control and heated plots may be caused by an albedo effect. In particular, because the dominant shrub, sagebrush, has aboveground overwintering stems and foliage, with relatively low albedo, that extend above the snowpack in spring during snowmelt, it is reasonable to conjecture that the enhanced shrub growth actually has promoted earlier melt in the immediate vicinity of sagebrush plants, possibly explaining the marginally significant ($P = 0.066$) difference in slopes in Fig. 1, and in turn, through a positive feedback, contributing to the enhanced shrub growth shown in Fig. 2b.

If the model applied in Saleska *et al.* (2002) to explain the heated-plot SOC response is driven by advancing melt date in the ambient plots, then it also predicts the observed drop in ambient-plot SOC as a consequence of the drop in annual ambient-plot forb production driven by that advancing ambient melt date. The model output is shown in Fig. 4b, with chosen parameter values indicated in the caption. Despite its simplicity, the model does predict the approximate behavior of the SOC levels in the ambient and heated plots, although it does not attempt to capture the stochastic behavior evident in the data and underestimates somewhat the magnitude of the drop in the ambient-plot SOC levels. It predicts the observed steep drop and then the beginning of a slow recovery in the heated-plot levels, leading to a near equality between heated- and ambient-plot SOC toward the end of the second decade of the experiment.

The model predicts that in roughly 50 years after the start of the experiment, the heated-plot SOC will have risen to and leveled out at about 15% above the initial value at the start of the experiment. Under continuing advance of snowmelt, the ambient-plot SOC level is projected to reach a minimum in about three or four decades from now at a value roughly 20% below the initial value and then slowly rise to the initial value in approximately a century. Over the even longer term, it should rise to approximately the same asymptotic value that the heated plots achieve.

The key finding that SOC first declines and then slowly recovers is the consequence of the fact that the increase in productivity of the plants favored by warming (sagebrush) is less than the decrease in the productivity of the plants that are disfavored (forbs), but they also produce more recalcitrant SOC. It is likely that in other types of ecosystems, with plants having different traits, these same two governing influences (rate of litter input to the soil and litter quality) will result in different outcomes for SOC.

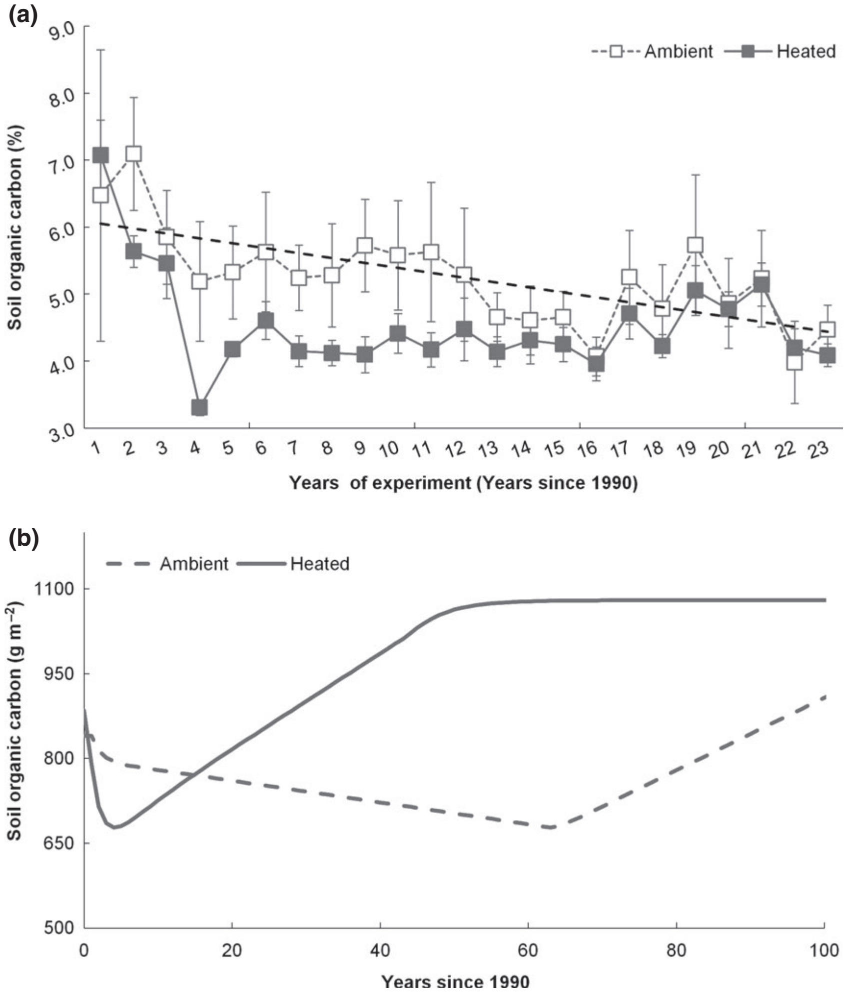

Fig. 4 Figure 4a shows percent soil organic carbon averaged over five replicates in heated and ambient plots, plotted against year. Standard errors for ambient plots and heated plots in each year average ~0.40% and 0.21%. Figure 4b shows 100-year soil carbon simulation (details in Appendix S1). For the forbs, the parameters used are $P = 2.5$ and $\mu_* k = 0.5$. For the shrubs, $P = 0.6$ and $\mu_* k = 0.2$ (see Appendix S1 for explanation of how model parameters are empirically determined). (Ambient Soil Organic Carbon = −0.07 Year since 1990+6.13; $R^2 = 0.49$).

A basis for interpreting the findings of this study may be found in the worldwide 'leaf economics spectrum' (Reich *et al.*, 1997; Wright *et al.*, 2004) or 'plant economics spectrum' (Reich, 2014). In this framework, correlations among key functional traits arise from a fundamental trade-off between leaf life span and specific leaf area (due to high resource investment per leaf area required to maintain longer-lived leaves) (Lloyd *et al.*, 2013; Osnas *et al.*, 2013) and are thus consistently arrayed along a global 'fast–slow' plant economic spectrum (Reich, 2014) that coordinates trade-offs in resource acquisition across gradients of resource availability. Earth system models (Moorcroft *et al.*, 2001; Thornton & Zimmerman, 2007; Bonan *et al.*, 2012; Kim *et al.*, 2012) increasingly use plant economic spectrum relations to simulate process rates associated with different plant functional types, but few models yet use plant hydraulic traits in the context of simulating water cycling (Reich, 2014), or propagate leaf traits to their afterlife effects on litter decomposition and soil carbon storage (but see Brovkin *et al.*, 2012).

In our experimental system, however, water is the dominant limiting resource whose availability is further limited by advancing snowmelt dates caused by experimental manipulation and regional warming, and propagation of leaf traits to afterlife effects on litter decomposability was a key driver of observed soil carbon changes. Although leaf hydraulic traits and water resources were not the focus of the original leaf economic spectrum (Reich *et al.*, 1997; Wright *et al.*, 2004), it is clear that 'fast' traits that promote high growth potential also require large water flux rates (Brodribb *et al.*, 2007; Blonder *et al.*, 2011; Sack *et al.*, 2013), and evidence suggests that slow traits promote drought tolerance (see many studies cited in Reich, 2014).

Thus, we should expect that plants from the 'slow leaf' end of the trait spectrum (shrub leaves with thick, low SLA leaves, and long life spans, also associated with low productivity and low nitrogen) should be favored under dry conditions relative to the 'fast leaf' end of the forb plant leaves (with high SLA, short life spans, high productivity, and high nitrogen). Based on the global trait spectrum, we may expect associated predictable patterns of climate feedbacks: Where water (or other) resources become more limited (as in this experiment), we expect 'slow leaf' plants to become more successful, and where resources are abundant (or become more so, in contrast to this experiment), we should expect warming to reinforce traits at the fast turnover end of the spectrum, leading to short-term carbon storage that gives way to longer term carbon losses.

Spatial or structural variation in communities can also induce more complex responses that advantage taxa at several points along the fast–slow spectrum, confounding these first-order expectations (Reich, 2014). For example, in vertically structured canopies, increased resource availability may initially stimulate increases in LAI, which in turn increase limitation in the light resource below the canopy, hence advantaging 'slow turnover' taxa in the understory.

This work thus lends further empirical support to the common sense suggestion (Reich, 2014) that inclusion of plant hydraulic traits and water resources is an opportunity for further improving earth system model simulations, and to the initial efforts (Brovkin *et al.*, 2012) in the global earth system modeling literature to use leaf traits to predict their afterlife effects on litter decomposition and soil carbon storage.

Another warming-induced transition under a warming climate record is from spruce-fir-dominated forest to pine domination, as suggested by pollen records (Anderson *et al.*, 2000); this may be an example of a transition from high production rate of long-lived litter to lower production rate of shorter-lived litter, and thus, under continuing warming, the DWP model would predict both short- and long-term SOC decline. A quantitative prediction would require acquisition of additional data to determine the parameters in the model, and this has not been performed, but the robust qualitative conclusion that can be drawn is that such a climate-induced forest transition would likely result in a positive carbon cycle feedback in the near and longer term. More detailed ecosystem models might, of course, give divergent results.

In summary, over 23 years, heated plots showed an advancement of snowmelt date, a decrease in forb aboveground biomass, an increase in shrub aboveground biomass, and an initial loss of soil organic carbon followed by a partial recovery. Ambient plots exhibited the same trends, but at a slower rate. SOC in the ambient plots has yet to show any sign of reversal and recovery. By identifying the linkages between melt date and vegetation and between vegetation and carbon cycling, we conclude that the decrease in ambient-plot soil carbon observed at our field site will likely continue for a few more decades, reach a minimum, and then rise, though at a slow rate.

The trends we observed over the last decade in the ambient plots are consistent with broader scale observations throughout western North America that indicate a reduction in carbon uptake due to recent drought (Hidalgo *et al.*, 2009; Pederson *et al.*, 2011, 2013) as well as an increase in shrub production (Archer *et al.*, 1994; Breshears *et al.*, 2005; Archer, 2010). Ability to attribute observed temporal trends in ecological data to climate change is limited by incomplete understanding of relevant mechanisms. We have shown that long-term observations of ecosystem change, combined with results from a controlled climate manipulation experiment and a simple, empirically parameterized model, can provide considerable insight into how the carbon budget of an ecosystem will respond in the future to continuing warming. The approach we have taken should be generalizable to other ecosystems for which comparable data can be obtained, allowing forecasting of longer term responses of soil carbon budgets to climate change. Loss or gain of soil organic carbon is especially relevant to global warming because of the potential for significant carbon cycle feedback to the climate.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 The structure, parameterization, and validation of the DWP model.
Figure S1 Comparison of predicted and observed soil organic carbon.
Tables S1–S6 Results of statistical analyses