

**Ecosystem impacts of climate change: Snowmelt timing, species diversity, and plant productivity**

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### Abstract:

A 14 year warming experiment being conducted in a subalpine meadow has resulted in several physical changes, including advanced date of snowmelt, a decrease in soil moisture, and increased soil temperature in heated plots versus control plots. These microclimate changes have led to a shift in plant community composition towards dominance of sagebrush (*Artemisa tridentata*) at the expense of herbaceous forb plant species. Among the forb species, deep rooted species have not been as adversely affected as shallow rooted species. Within the experimental warming plots, there is also a positive, although non-significant, correlation between snowmelt timing and species richness with earlier melting plots having lower species richness. Using observational data along a naturally-occurring snowmelt gradient, this study attempted to identify if the relationships between snowmelt timing and species richness and community composition hold true across a larger meadow area, and if snowmelt timing correlates to other important ecosystem process such as plant productivity and soil carbon storage. We also looked for evidence in support of a hypothesized link between plant diversity and ecosystem function. Snowmelt timing did not correlate with species richness, aboveground biomass, or soil organic carbon, although it was correlated with community composition, with earlier snowmelt leading to a greater proportion of shallow rooted forbs and a greater presence of sagebrush. Species richness did not correlate with aboveground biomass or soil organic carbon, however plant community composition did show some significant correlation with <sup>1</sup> ecosystem functioning. Sagebrush was present only in early melting plots, and plots with sagebrush had significantly higher soil organic carbon than plots without sagebrush. Forb composition was significantly correlated with aboveground biomass, with plots containing more deep rooted forbs having higher aboveground biomass.

### Introduction

Among the main areas of concern regarding global warming are the biotic changes it may produce, including changes to plant community composition. In particular, researchers are interested in climate-induced changes in plant species distributions and abundances, and of the consequences of these changes on ecosystem function (de Valpine and Harte 2001). An ongoing warming experiment in a subalpine meadow in the Colorado Rocky Mountains has documented several physical differences between warmed and control plots, including earlier

date of snowmelt, increased soil temperature, and decreased soil moisture (Harte et al. 1995). The plant community has also changed in response to the experimental warming treatment with a shift in species dominance towards sagebrush (*Artemisa tridentata*) at the expense of forb species, whose above ground biomass decreased in warmed plots versus control plots (Harte and Shaw 1995). Not all forb species have responded equally to the experimental warming, with shallow rooted forb species being more negatively affected than deeper tap-rooted forb species (de Valpine and Harte 2001). In addition to plant composition and physical changes, there has also been evidence of a positive feedback to climate warming: in the warmed plots, soil carbon in the form of organic matter substantially decreased on the order of  $\sim 200 \pm 150 \text{ g C/m}^2$  (Saleska et al. 2002). It is not clear whether an earlier date of snowmelt, drier soils, or warmer soils drives these observed shifts in the plant community composition in the warming experiment, however snowmelt timing tends to be the best explanatory variable for many observed changes in the warming meadow experiment. And while the experiment has not documented an effect of heating on plant species diversity, unpublished data from a natural snowmelt gradient that exists within the warming meadow experimental plots does show a non-significant ( $p = 0.12$ ) correlation between increased species diversity and later snowmelt date (Fig. 1 – J. Harte unpublished data).

In addition to potentially affecting species diversity and community composition, snowmelt timing may also correlate with other ecosystem processes, namely soil carbon and plant productivity, both directly by increasing the length of the growing season and indirectly through the hypothetical relationship between species diversity and ecosystem productivity. Intuitively, length of growing season should have an impact on plant productivity, especially within species, and studies have theorized a link between plant species diversity and ecosystem productivity via resource niche complementarity (Tilman et al. 2001). However, field observations and experiments have demonstrated mixed results concerning the link between species diversity and plant productivity (Tilman et al. 2001, Wardle et al. 1997, Hooper and Vitousek 1997). To better understand the extent to which snowmelt timing affects plant community composition and ecosystem processes, and whether there is a strong correlation between diversity and ecosystem functioning in our system, we looked for the following relationships using observational data from a subalpine meadow:

- 1) The relationship between snowmelt timing and diversity (species richness and composition), productivity, and soil organic carbon;
- 2) The relationship between species richness and productivity and soil carbon;
- 3) The relationship between species composition (in terms of changes in forb species and the presence of sage) and productivity and soil organic carbon.

A better understanding of the effect of snowmelt will tell us whether patterns that occur in the warming meadow also occur across the landscape, and it may allow us to differentiate the effect of snowmelt timing from the effects of soil moisture, soil temperature, and other factors. Looking for relationships between plant diversity/composition and ecosystem processes will contribute to the ongoing debate as to what effect diversity has on ecosystem function by providing further evidence that diversity either does or does not affect ecosystem function.

## Methods

The study was conducted at the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, CO USA (38°53'N, 107°02'W) at an elevation of 2920m. We used data collected in the spring of 2001 of the approximate snowmelt dates of patches in the meadow to establish 29 2m by 2m plots, each subdivided into 16 0.5m by 0.5m quadrats, along a naturally occurring snowmelt gradient. There were 13 early melt plots with melt dates ranging from the 117<sup>th</sup> and 128<sup>th</sup> Julian days, and there were 16 late melt plots, all of which melted out after the 131<sup>st</sup> Julian day.

We compiled plant species richness data by surveying species presence/absence in each quadrat of each plot. We conducted species surveys twice during the summer, once in late June and once in late July, in order to ensure that we observed all species regardless of their flowering phenology.

To assess aboveground plant productivity, all aboveground plant material from three randomly selected 0.5m by 0.5m quadrats from each plot was clipped, dried, and weighed. Clipping was conducted at approximately peak biomass. Because all herbaceous plants in our system completely senesce each fall, peak standing biomass is considered to be a conservative estimate of aboveground plant productivity. Data from the three quadrats were used to estimate total plot aboveground plant productivity.

We measured soil organic carbon content of each plot by collecting one soil core (1.8 cm diameter and 10 cm deep) from each of the three quadrats in which above ground biomass was measured. Rocks and roots were removed from the samples and the samples were dried for 24-48 hours at 105°C. The dried samples were weighed and then burned at 430°C, and then weighed again. The mass lost on combustion was used to calculate organic carbon content. Soil moisture was measured using the same sized cores, with moisture measured as the amount of water lost per gram of <2mm soil after drying the soil for 24 hours at 105°C.

Using the gathered data on species richness, aboveground biomass, soil moisture, and soil carbon we looked for patterns between snowmelt timing and plant diversity, composition, productivity, and soil carbon; between plant diversity/composition and productivity and soil carbon; and between sagebrush presence and diversity/composition, productivity, and soil carbon. These relationships were analyzed using both ANOVA and regression techniques in the JMP-IN statistical package (SAS Institute 2003). All results are presented as the mean  $\pm$  standard error.

## Results

### *Snowmelt timing*

There was no detectable difference in species richness between early and late snowmelt plots. Early snowmelt plots had a mean species richness of  $17.6 \pm 0.88$  [mean  $\pm$  s.e.], while late snowmelt plots had a mean species richness of  $17.7 \pm 0.79$  (Table 1,  $p=0.95$ ). Mean aboveground biomass differed between early and late plots,  $153.56 \text{ g/m}^2 \pm 13.84$ , versus  $172.16 \text{ g/m}^2 \pm 12.48$ , but this difference was non-significant (Table 1,  $p=0.33$ ). There was no general trend between plant composition and date of snowmelt when all of the plots are included ( $p=0.92$ ,  $r^2=0.0004$ ), but when one extreme outlier that had almost no deep forb biomass is removed the correlation becomes significant ( $p=0.04$ ,  $r^2=0.15$ ) with earlier plots containing more shallow rooted forbs than late plots. Soil organic carbon did not differ significantly: the mean soil organic carbon for the early plots was  $8.28\% \pm 0.6\%$  and was  $7.34\% \pm 0.5\%$  for the late plots (Table 1).

### *Plant species richness and composition*

There was no correlation between species richness and aboveground biomass (Fig. 2,  $p=0.22$ ,  $r^2=0.06$ ). There was a correlation between plant composition and aboveground biomass via the ratio of percent shallow forbs to percent deep forbs, with plant communities containing more deep rooted forbs producing more aboveground biomass (Fig. 3,  $p=0.03$ ,  $r^2=0.17$ ). The ratio of shallow to deep rooted forbs was not, however, significantly correlated with soil organic carbon ( $p=0.44$ ).

#### *Presence of Sagebrush*

Sagebrush was only present in five of the early melt plots, and none of the late melt plots: the mean Julian snowmelt date of plots containing sagebrush was  $123.2 \pm 2.24$  and the mean Julian snowmelt date of plots without sagebrush was  $129.5 \pm 1.05$  (Table 1,  $p=0.02$ ). The presence of sagebrush did not significantly influence species richness ( $p=0.47$ ), with a mean species richness in sagebrush plots of  $17.5 \pm 1.31$ , and a mean species richness in non-sagebrush plots of  $18.6 \pm 0.61$  (Table 1). Mean aboveground biomass for plots with and without sagebrush were  $174.81 \pm 22.507 \text{ g/m}^2$  and  $161.53 \pm 10.49 \text{ g/m}^2$  respectively, but this difference was non-significant (Table 1,  $p=0.60$ ). Mean percent soil organic carbon (SOC) did differ significantly ( $p=0.005$ ) with  $10.162\% \pm 0.87\%$  SOC in plots with and  $7.295\% \pm 0.41\%$  SOC in plots without sagebrush (Table 1). The ratio of the mean percentage of shallow rooted forb biomass and the mean percentage of deep rooted forb biomass was  $0.81 \pm 0.11$ , for plots with sagebrush and  $1.23 \pm 0.05$ , for plots without sagebrush, but this difference was non-significant ( $p=0.41$ ).

#### *Regression analysis*

Several regressions were performed in order to determine if correlations exist between date of snowmelt, species richness, aboveground biomass, and soil organic carbon. Date of snowmelt did not correlate with species richness (Fig. 4,  $p=0.80$ ,  $r^2=0.07$ ), soil organic carbon (Table 1,  $p=0.23$ ,  $r^2=0.11$ ), or aboveground biomass (Table 1,  $p=0.37$ ,  $r^2=0.03$ ). Species richness did not correlate with soil organic carbon (Table 1,  $p=0.37$ ,  $r^2=0.03$ ) or plant community composition (in terms of percentage shallow rooted forbs,  $p=0.88$ ,  $r^2=0.001$ ). Soil organic carbon did not have a functional effect on species richness (Table 1,  $p=0.37$ ,  $r^2=0.03$ ), but above ground biomass did have a marginally significant effect on SOC (Table 1,  $p=0.08$ ,  $r^2=0.11$ ).

## Discussion

In complex ecosystems, elucidating mechanisms that drive certain ecosystem processes can be difficult. Observational studies are especially prone to this difficulty—in an unmanipulated environment it is not always possible to isolate the multitude of factors that can influence ecosystem processes and parameters such as plant productivity, soil microclimate, plant community composition and nutrient cycling. This complexity may be responsible for the lack of significant results and our inability to detect theorized links between snowmelt timing, diversity, and productivity.

For snowmelt timing, the results may have been non-significant for several reasons, including a snowmelt gradient that was not comprehensive or expansive enough, or that some variable other than snowmelt timing—amount of sunlight received, soil moisture, soil temperature, or other soil microclimatic conditions—may be driving the observed results from the warming experiment.

This study does lend some further insight as to what may be driving one of the observed changes in the warming experiment. Plots with sagebrush had significantly higher SOC than plots without sagebrush. This result mirrors observed changes in the warming experiment, where the warmed plots have experienced both a drop in SOC and an increase in the prevalence of sage brush. This study reinforces predictions made earlier by Saleska et al. (2002) that the drop in SOC in the heated plots is transient, and that SOC will eventually recover to the same, or as this study suggests even surpass, the SOC level of the control plots.

Although patterns of SOC and sagebrush presence did follow a prediction from a modelling study (Saleska et al. 2002), other relationships that we expected to find were not significant in our study. For example, we did not find a correlation between soil moisture, which decreased significantly in warmed plots, and shifts in plant community composition, the prevalence of sagebrush, or SOC levels. This suggests that soil moisture may not be responsible for observed changes in those particular parameters in the warming experiment. We also did not find evidence to support the relationship between snowmelt timing and species diversity that was suggested by the non-significant trend within the warming plots.

Since plant species richness was not correlated with productivity or other ecosystem processes, this study does not support the theorized link between diversity and ecosystem function. However, this is an observational study, and because the system was not manipulated

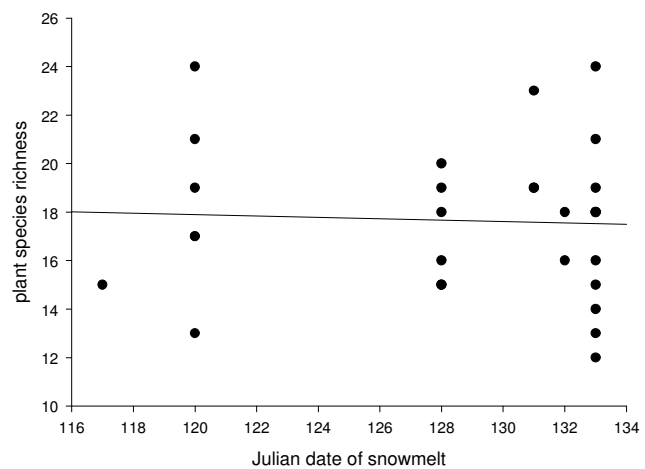
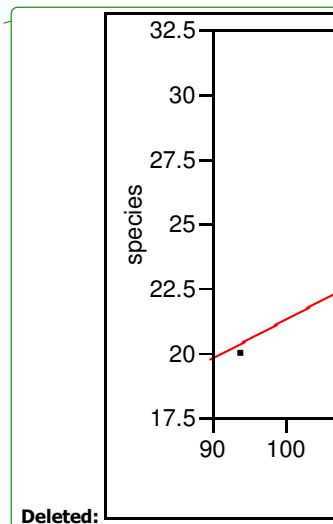
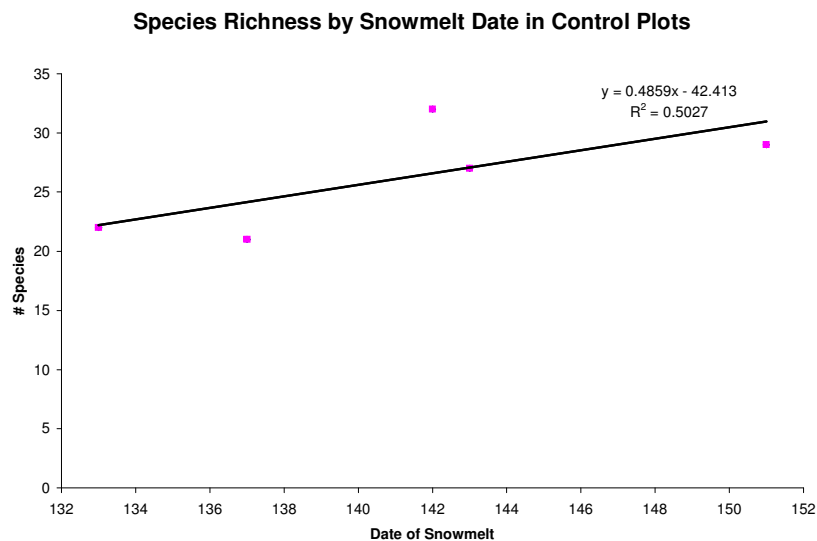
it is still possible that a relationship exists between diversity and ecosystem function, but due to the nature of this study the signal of this relationship may have been obscured by other co-occurring processes.

Although our observation study did not reveal most of the patterns we expected to find, this does not necessarily mean that these relationships do not exist, just that they may not be solely responsible for processes in the ecosystem. To isolate the potential presence of these relationships, further experiments that control for more variables are needed to reinforce the findings of this study, or to reveal relationships that may have remained hidden due to confounding variables. A more comprehensive snowmelt gradient may be necessary, or snowmelt may need to be manipulated in order to better understand how ecosystems may respond to future climate warming.

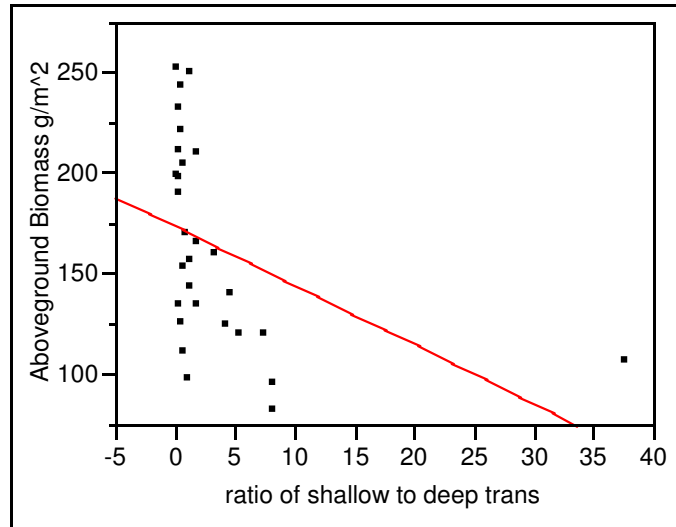
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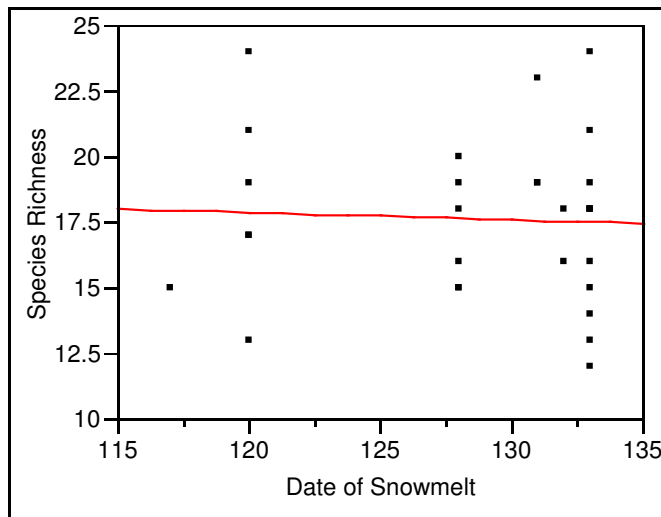
**Fig. 1** – Unpublished data from warming meadow, Harte 1998.  $y = 0.15 \cdot x + 5.16$   $r^2 = 0.19$   $p = 0.12$



**Fig. 2** Linear regression of Julian date of snowmelt by plant species richness  
 $y = -0.028 \cdot x + 21.28$   $r^2 = 0.002$   $p = 0.80$



**Fig. 3** Linear regression of plant composition by aboveground biomass.  
 $y = -2.93x + 173.54$   $r^2=0.17$   $p=0.03$



**Fig. 4** Linear regression of species richness by date of snowmelt.  
 $y = -0.028x + 21.28$   $r^2=0.002$   $p=0.80$

**Table 1.** Statistical analyses, n=29 for all tests [except for tests with and without sagebrush as explained in the Methods section].

|                                         | Snowmelt timing          |        |         |                |         |                              |  |
|-----------------------------------------|--------------------------|--------|---------|----------------|---------|------------------------------|--|
|                                         | Early                    | S.E.   | Late    | S.E.           | F-Ratio | Probability > F <sup>a</sup> |  |
| Mean Julian date of snowmelt            | 123.462                  | 0.839  | 132.500 | 0.757          | 63.9905 | < 0.0001                     |  |
| Species richness                        | 17.615                   | 0.881  | 17.688  | 0.794          | 0.0037  | 0.9520                       |  |
| Aboveground biomass (g/m <sup>2</sup> ) | 153.552                  | 13.843 | 172.158 | 12.478         | 0.9967  | 0.3270                       |  |
| Percent shallow rooted forb biomass     | 48.531%                  | 0.072  | 44.971% | 0.065          | 0.1644  | 0.6883                       |  |
| Percent deep rooted forb biomass        | 31.325%                  | 0.062  | 47.430% | 0.056          | 3.2557  | 0.0823                       |  |
| Percent organic carbon in soil          | 8.282%                   | 0.006  | 7.335%  | 0.005          | 1.2142  | 0.2802                       |  |
|                                         | Presence of Sage         |        |         |                |         |                              |  |
|                                         | Yes                      | S.E.   | No      | S.E.           | F-Ratio | Probability > F <sup>a</sup> |  |
| Mean Julian date of snowmelt            | 123.200                  | 2.222  | 129.542 | 1.014          | 6.7388  | 0.0151                       |  |
| Species richness                        | 17.458                   | 1.407  | 18.600  | 0.642          | 0.541   | 0.4667                       |  |
| Aboveground biomass (g/m <sup>2</sup> ) | 174.807                  | 22.610 | 161.528 | 10.320         | 0.2854  | 0.5975                       |  |
| Percent organic carbon in soil          | 10.162%                  | 0.009  | 7.295%  | 0.004          | 9.2911  | 0.0051                       |  |
| Percent shallow rooted forb biomass     | 31.058%                  | 0.111  | 49.795% | 0.051          | 2.2634  | 0.1441                       |  |
| Percent deep rooted forb biomass        | 38.374%                  | 0.107  | 40.533% | 0.049          | 0.003   | 0.9547                       |  |
|                                         | Regression               |        |         | r <sup>2</sup> | p       |                              |  |
| AGB by date of snowmelt                 | AGB = -39.19 + 1.58*date |        |         | 0.03           | 0.370   |                              |  |
| AGB by species richness                 | AGB = 97.26 + 3.77 *SR   |        |         | 0.06           | 0.2184  |                              |  |
| AGB by soil organic carbon              | AGB = 107.68 + 7.62*SOC  |        |         | 0.11           | 0.0768  |                              |  |
| Species richness by date of snowmelt    | SR = 21.28 – 0.028*date  |        |         | 0.002          | 0.7993  |                              |  |
| Soil organic carbon by date of snowmelt | SOC = 19349 – 0.091*date |        |         | 0.05           | 0.2343  |                              |  |
| Species richness by soil organic carbon | SR = 15.75 + 24.53*SOC   |        |         | 0.03           | 0.327   |                              |  |

<sup>a</sup> df = 28 for all tests