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The responses of montane shrubs to spatial and temporal climate variation in the Rocky Mountains: predicting plant responses to climate change

Ellen McCullough[1,2]

[1]Stanford University, PO Box 15380, Stanford CA 94309 USA (ellen.mccullough@stanford.edu)
[2]Rocky Mountain Biological Laboratory, PO Box 519, Crested Butte, CO, USA

Abstract– Anthropogenically induced global climate change is expected to alter global mean temperatures by 3-5 °C over the next century. This study addresses the potential effects of anticipated climate change on several woody shrub species in the Rocky Mountains. Three species were harvested along an elevational gradient, which varied spatially in climate factors such as snowmelt date and air temperature. The annual growth rings of each plant were measured and matched with the corresponding climate conditions on the year of their formation, which provided data on plant responses to temporal climate variability. Date of snowmelt was the only climate factor that loosely explained interannual growth ring variation, but this was not significant. Elevation explained variation in lifetime growth rates for some species. However, elevation did not explain levels of interannual variability. This study concludes that the effects of elevation and interannual climate variation on annual growth rates are probably dampened by a variety of unknown mechanisms.

Key words: dendrochronology, climate change, sagebrush, serviceberry, snowberry, elevational gradients, montane shrubs.

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Anthropogenic greenhouse gas inputs are expected to alter global mean temperatures by 3-5 °C over the next century (IPCC 2001a). Human induced climate changes are likely to have important implications for the plants growing in the Rocky Mountains. Global climate models have predicted that, by 2050, temperatures will probably be higher and snow levels reduced in the Rocky Mountains, resulting in an earlier spring snowmelt, longer growing season, and drier soil conditions (IPCC 2001b). Small-scale climate manipulation experiments have supported this prediction. Such experiments have found that induced radiation that alters soil temperature by as little as 1.5 °C has a multitude of effects on ecosystem characteristics such as date of snowmelt, soil moisture, and growth rates of different species (Harte and Shaw 1995; Price and Waser 1998; Perfors *et al.* 2003).

Different types of experiments have used elevational gradients as a means of predicting ecosystem responses to climate change (Dunne *et al.* 2003). Plant distributions along altitudinal gradients are often determined by various climatological factors, such as temperature, length of growing season (as determined by snow cover), wind exposure, and water availability. Climate also varies through space along an elevational gradient due to the adiabatic lapse rate, which describes temperature decreases of 6-10 °C per 1000m gain in elevation. Therefore, elevation can be used to infer species' responses to a range of climate conditions, because of the climate variability that occurs along elevational gradients.

This study focused on three shrubby species of the Rocky Mountains, each with a different elevational range (Table 1). In order to assess the effects of climate factors on plant growth, growth ring

analysis was used to reconstruct data on plant growth for a number of years. The growth rings revealed plant growth rates over a temporally varying climate, just as the elevational gradients revealed growth rates over a spatially varying climate. While previous studies have linked manipulated temperature increases with higher growth rates using growth ring analysis (Perfors *et al*. 2003), this study instead used natural interannual climatological variations to determine past plant responses.

After calculating annual growth ring widths for the three subject species of this study, I attempted to determine which climatological factors (among growing season length, snowmelt date, annual and monthly precipitation levels, air temperature, and heating degree days between May and June[3]) have been the most important determinants of plant growth and restrictors of elevational range. Specifically, I tested the following two hypotheses:

Hypothesis 1: Date of snowmelt is more influential than other environmental factors in explaining annual departures from expected growth rates. Because snowmelt date determines the length of the growing season and greatly affects soil moisture levels, it has been shown to play an important role in plant phenology (Harte and Shaw 1995; Dunne *et al*. 2003). Data supporting this hypothesis will suggest that plants should respond to climate change if the change alters winter precipitation levels and spring snowmelt dates.

Hypothesis 2: Interannual variance in growth rates will be greatest for a species when it is at an elevation close to its elevational limit. As plants respond to a varying environmental factor, it is expected that growth rates will be highest where the factor is most favorable and that growth will be lower and more variable at the limits of the environmental factor. If data support this hypothesis, variance could be a tool in predicting the magnitude of a species' response to climate change based on its location within its elevational range. According to this reasoning, plants might shift their elevational ranges upward in response to earlier snowmelt dates.

Materials and Methods

Three species were harvested for this study (see Table 1) in three meadows along the East River in Gothic, Colorado. Sites were established by Dunne *et al*. (2003) because of their comparability in all aspects except elevation. The lower site is at the SE base of Mt. Crested Butte (el. 2770 m), the middle site is at RMBL just north of the Gothic townsite (latitude 38º53' W, longitude 107º02' N, el. 2940 m), and the upper site is towards the top of Red Rock Mountain (el. 3190 m - Fig. 1). *Artemisia tridentata* is the dominant species in each of the three meadows, and they have similar slopes, substrates, and grazing history (*ibid*). Each species of this study is found throughout the range spanned by these three montane meadows. However, *Artemisia* does not extend far above the top meadow while *Amelianchier pumila* does not extend far below the lowest meadow. *Symphoricarpos oreophilus* could not be found in the middle site, although it grows in both of the other sites.

Five plants of each species were collected at each study site (40 plants in all). Plants were selected if they appeared to be old (as judged by stem thickness) and therefore would contain growth

Table 1. Organisms studied.

Shrub species	Common name	Family	Local elevational range
Artemisia tridentata	Sagebrush	*Asteraceae*	plains - montane
Symphoricarpos oreophilus	Mountain Snowberry	*Caprifoliaceae*	plains - subalpine
Amelanchier pumila	Serviceberry	*Rosaceae*	montane - subalpine

[3]Heating degree days measure the cumulative number of degrees in a period of time by which the mean temperature falls below 18.3 °C.

data for a longer time period. Within each meadow, plants were harvested from an area spanning the entire meadow, so that no two plants of the same species were harvested too close to each other and that the plants grew in a variety of slopes, aspects, and substrates. At the time of harvest, data on the location and growing conditions of each plant (i.e. slope, aspect, substrate, close competitive neighbors, location within meadow) were recorded.

In the lab, the lower portion of the stem of each plant was sawed off and smoothed with very fine sandpaper to reveal the growth rings. Five radii were drawn from the center to the outside of each cross section, and the width of each ring at each radius was measured using a caliper and a microscope. All five of the measurements for each ring width were averaged to estimate plant growth for every year of the plant's life span.

Statistical Analysis– First, plant age factors were separated out of absolute ring width measurements through age detrending (Ferguson 1964). For each plant, annual ring width data were plotted against time. Based on lifelong patterns of growth that were common to each species, a type of function was determined for each species that best described how annual ring widths varied with the plant's age. Each plant was then fit to a specific function corresponding to the function type for its species, and the best-fit function was used to calculate annual deviations from expected growth rates. These deviations were normalized and expressed as a fraction of their expected ring width values. For *Artemisia*, a plant's growth pattern was best expressed by a downward facing parabola (see Fig. 2a). For *Amelianchier* and *Symphoricarpos*, the first few years of ring width data on each plant were omitted, and analysis was focused on the growth in the plant's later years, when the annual ring widths were more stable and clustered around a flat line. Because the first few years of growth were highly variable between plants and followed a variety of patterns, mean ring width values of the later, constant stage of plant growth were used, and annual deviations from each plant's flat mean value were analyzed (see Figs. 2b, c).

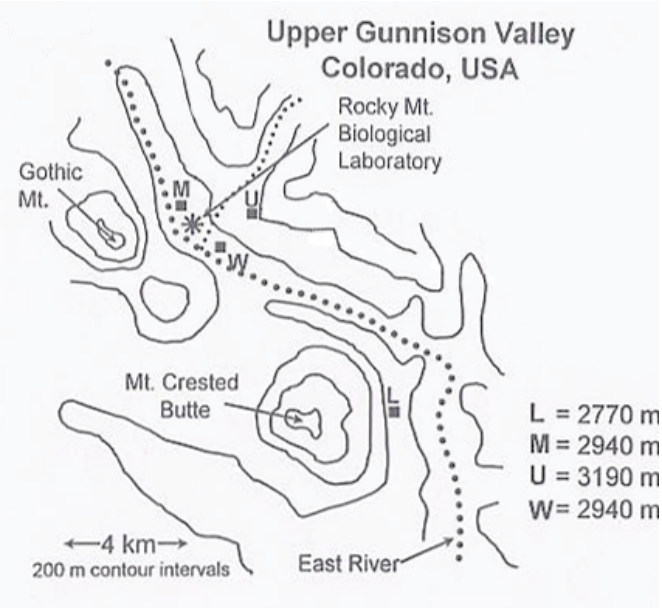


Fig. 1. Map of study sites at the Rocky Mountain Biological Laboratory. The warming meadow (W)was the location of Perfors *et al*. (in press) and Harte & Shaw (1995). All three sites (L: Lower; M: Middle; U: Upper) occurred along the East River watershed on an elevational gradient spanning 500 m. (modified from Dunne *et al*. 2003).

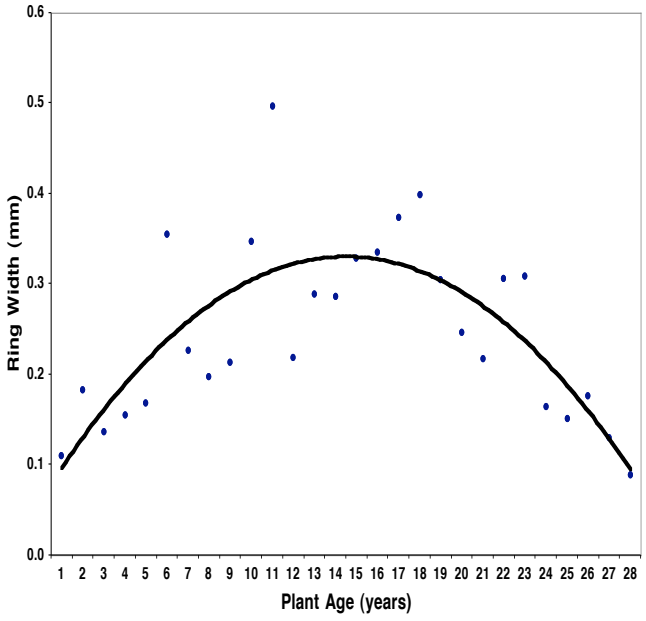


Fig. 2a. Annual growth ring widths of *Artemisia* and a polynomial best fit curve. This graph represents the entire life span of one plant. The data points mark the widths of its growth rings every year of its life. Distances between observed ring widths and expected ring widths reflect annual ring width deviates.

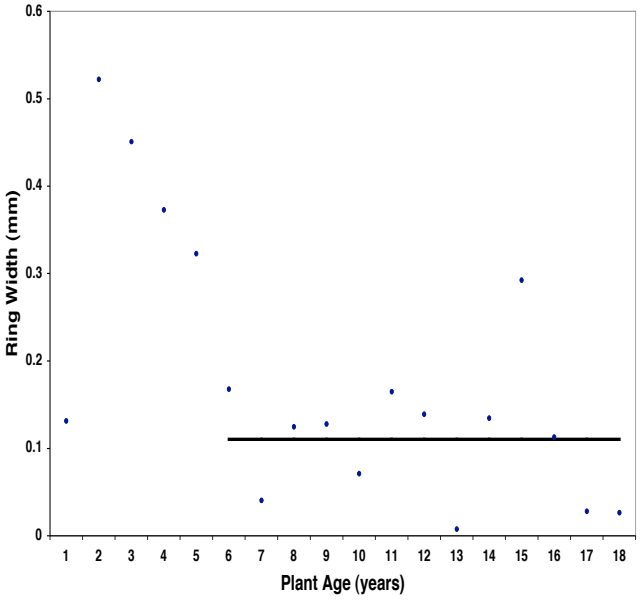


Fig. 2b. Annual growth ring widths of one *Amelianchier* plant. The best-fit curve represents the mean value of the ring widths from age 6 to the present, the portion of the curve where growth rates stabilized. Distances from observed values to the expected mean value represent annual growth deviates.

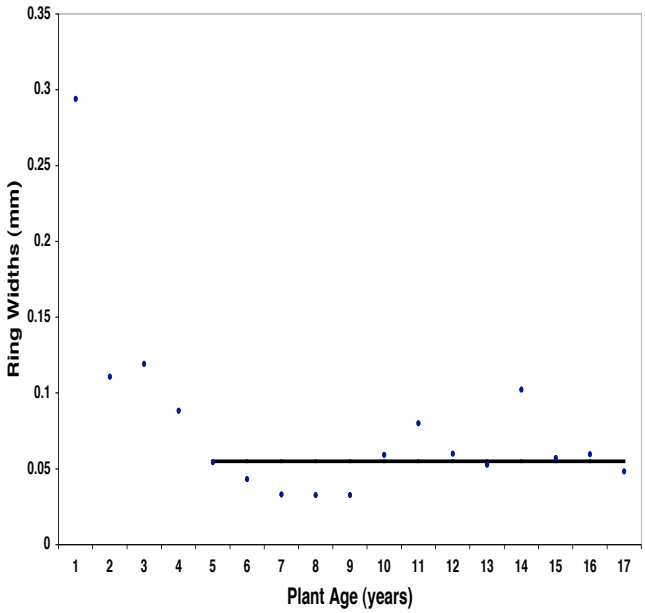


Fig. 2c. Annual growth ring widths of *Symphoricarpos*. See Fig. 2b for explanation of curve-fitting procedure.

In order to assess responses of individual plants to interannual climate variability, a series of average annual growth ring widths for each species was calculated (n = 40). Next, climate conditions were assigned to each year and site. Temperature and precipitation data from Crested Butte (9 miles away) were taken from the National Oceans and Atmosphere Administration National Climatic Data Center (NOAA 2002), while snowmelt and growing season length data came from the Rocky Mountain Biological Laboratory (billy barr, unpublished data – Fig. 3). Regression analysis was used to determine how ring widths responded to the various climate conditions. A separate regression was performed for each species. Where data were taken remotely and could not be inferred between sites (*i.e.* air temperature and total precipitation), regression was separated by site as well as species.

The second hypothesis regarding interannual growth ring variability was tested with two methods. For each *Artemisia* plant, the root mean square of the normalized annual deviates from the expected, curve-fit values were calculated. One-way ANOVA was performed to determine whether the populations of root mean squares differed between sites. For each *Symphoricarpos* and *Amelianchier* plant, a coefficient of variation was calculated based on the absolute values of the deviations from expected mean annual growth ring width. A T-test was used to compare means between the elevational sites for each species, just as was done with *Artemisia*.

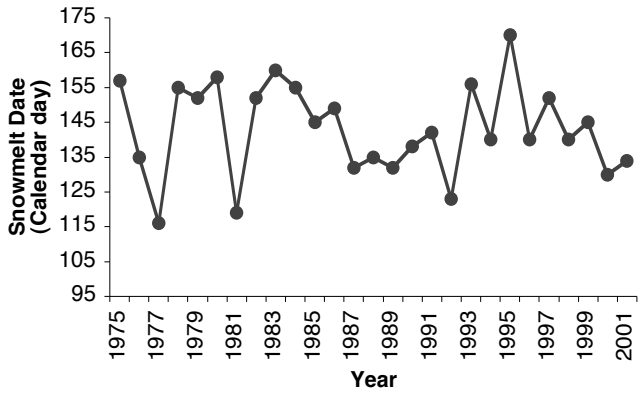


Fig. 3. Snowmelt dates measured from the townsite of Gothic between 1975 and 2001 (b. barr, unpublished data).

Finally, the parameters of the best fit curves for each species were examined for differences between sites. Differences between the maximum values of the parabola were tested for *Artemisia*, and differences in mean values of the final, flat portion of the curve were tested for *Amelianchier* and *Symphoricarpos*.

Results

Monthly and annual precipitation levels, mean monthly temperatures, heating degree days, date of snowmelt, and growing season length (difference between first autumn snowfall and spring snowmelt date) were tested as independent factors that could potentially influence annual growth ring deviates. Date of snowmelt was the only factor that seemed to explain growth ring variation. However, snowmelt date did not ever explain a significant amount of interannual growth ring variation. Accurate climate data were only available in each site for a span of three years, though. Data for other years were inferred from off site weather stations, at RMBL and in Crested Butte. Even when only the three years of accurate data were used, snowmelt date did not significantly explain interannual growth ring variation (see Figs. 4a and 4b).

Variance did not differ between sites for any species. Interannual ring width variation, when expressed as a fraction of expected values, was very similar between elevational sites for each species (*Artemisia*: $F_{2,14} = 0.158$, $P = 0.856$; *Amelianchier*: $T_8 = 1.33$, $P = 0.219$; *Symphoricarpos*: $T_8 = 0.201$, $P = 0.846$).

The maximum values of the parabolas that fit *Artemisia* growth curves decreased significantly as elevation increased (ANOVA; $F_{2,10} = 6.266$, $P = 0.023$) (Fig. 5). However, the age of the plant when this maximum value was reached did not differ between the two sites (F test; $F_{2,10} = 0.430$, $P = 0.665$). This suggests that the amount of annual growth was greater at the lower site while the time required to reach maximum growth rates was the same between sites. The mean value of the final, flat portion of the growth curve was marginally greater in the lower site for *Amelianchier* (T test; $T_8 = 1.958$, $P = 0.0859$). Additionally, the number of years required for the plant to reach the flat portion of its growth curve was greater in the upper elevation site than the lower one (T test; $T_8 = 2.449$, $P = 0.040$), signifying a lengthening of the amount of time to reach maturity at the lower site, where mature growth rates were lower. With *Symphoricarpos*, neither the mature growth rate nor the number of years required to reach maturity differed between sites (T test; $T_8 = 0.590$, $P = 0.571$ and $T_8 = 0.688$, $P = 0.511$, respectively).

Fig. 4a. *Artemisia* response to snowmelt variation. In years with later snowmelt dates, *Artemisia* grew more. This effect was marginally significant ($r^2 = 0.399$, $P = 0.068$). Snowmelt data were derived from local weather stations at each of the three sites taken between 1996 and 1998.

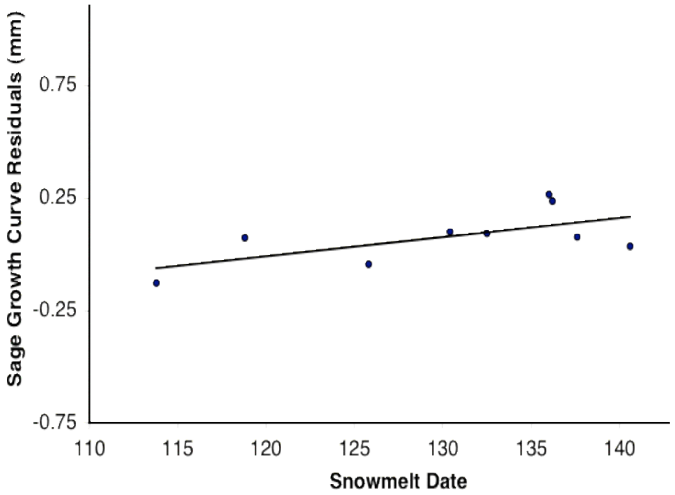
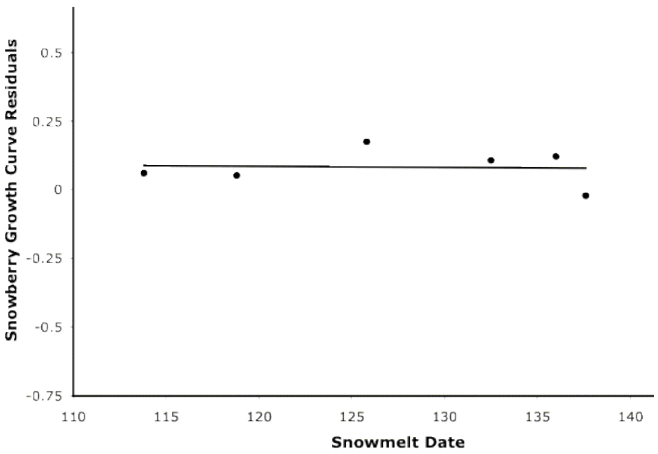


Fig. 4b. Response of *Symphoricarpos* to snowmelt variation. Snowmelt date did not explain variations in growth rate of *Symphoricarpos* between 1996 and 1998 ($r^2 = 0.003$, $P = 0.917$).



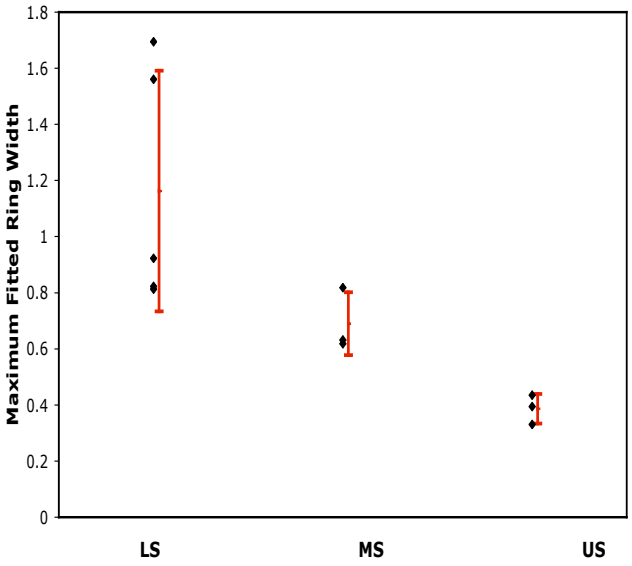


Fig. 5. Effect of site on maximum fitted growth curve values in *Artemisia*. This figure shows that growth rates decreased as elevation increased for *Artemisia* ($F_{2,10}$ = 6.266, P = 0.023). The parameter for growth rate was the maximum value of the fitted growth curve parabola for each individual plant (see Fig. 2a). The error bars mark one standard deviation above and below the mean.

Discussion

Neither hypothesis was supported by the experimental data. First, individual plants did not show a greater amount of interannual variation when they were found closer to their elevational limits (i.e. the upper site for *Artemisia* and the lower site for *Symphoricarpos*). There are several possible explanations for these results. For instance, perhaps the elevational gradient used in this experiment (< 500m) was simply not large enough, and a greater span could yield significant results. It is also possible that perceived elevational limits were not actual limits. Because plant distributions along an elevational gradient are determined by so many factors, there do not exist locally relevant elevational range data for any of these three species. Therefore, it was difficult to determine local elevational limits due to a lack of literature and difficulty in confirming observations. If, for instance, the lower site did not represent the lower limit of *Symphoricarpos*, then one would not expect to see greater interannual growth ring variation at that site for that species.

Finally, interannual growth ring variation could have been lower than anticipated because the different populations have become locally adapted to their conditions. Experiments using *Achillea* have shown that individual plant sizes decrease along an elevational gradient. However, when the plants from the lower end of the gradient were grown in the alpine zone, they were shorter than the plants that originally came from the alpine zone, and they did not flower. Conversely, the plants from the upper end did not grow as tall as the plants from the lower end when they were grown together at the lower site (Clausen *et al.* 1948). Local adaptation could lead to a dampening of elevational effects. This could be resolved by using a reciprocal transplant experiment as well as a common garden to separate genetic and environmental differences between populations. However, such an experiment would require many years to complete due to the slow growth rates of these woody species.

Date of snowmelt was the only factor that seemed to explain any interannual growth ring variance. Since overall growth rates were higher at the lower site where snow melts earlier, I expected plant growth rates to increase as winter precipitation levels decrease and snow melt occurs even earlier in the season, as GCM models have predicted for the Rocky Mountains. Qualitatively, this suggests that, as climate changes, *Artemisia* plants at high altitudes will begin to look more like their low elevation counterparts (*i.e.* much larger). This might affect many small and large scale ecological characteristics of high elevation meadows, such as nutrient cycling, food availability, habitat, carbon sequestration and surface albedo. Perfors *et al.* (2003) showed that overall growth rates of *Artemisia* increased in plants found in heated plots compared to those in control plots. In that study, snowmelt date explained growth variability between plots and within plots (each plot had a dry, higher portion and a moist, lower portion), but it did not explain interannual growth rate variability.

Interannual differences in growth rates were not explained as well by snowmelt date as were overall (*i.e.* lifetime) differences. This could have occurred if the shrubby species showed a lag time between favorable or unfavorable climatic

conditions and biomass accumulation through some sort of buffering mechanism.

Due to a lack of clearly delineated elevational effects on growth rates and interannual growth variation, it is hard to make a prediction about how shrubby species of montane ecosystems will respond to a different climate. Paleological data have shown shifts in species ranges among island mountain chains in the Great Basin. However, on the shorter time scale that is expected from anthropogenically induced climate changes, these range shifts might not serve as a mechanism of prediction. Because of the implied changes in growth rates due to earlier snowmelt, we might expect *Artemisia* to reach larger sizes in the higher elevations as climate conditions become more favorable. This might result in competitive exclusion of other species currently found in the higher elevations, with effects rippling throughout the food web. Since mountains are conically shaped, an upward shift in elevation rage also signifies a decrease in available habitat area.

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