UNIVERSITY OF CALIFORNIA, SAN DIEGO

Plant Community Responses to Recent and Future Climate Change in California's White Mountains

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Biology

by

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2014

The Dissertation of Your Full Legal Name is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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Chapter 1, in full, is a reprint of the material as it appears in: Kopp, C. W., and E. E. Cleland. 2014. Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range. Journal of Vegetation Science 25:135–146. The dissertation author is the primary investigator and author of this paper.

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ABSTRACT OF THE DISSERTATION

Plant Community Responses to Recent and Future Climate Change in California's White Mountains

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Rapid climate change has resulted in shifts in the distribution and abundance of organisms along with changes in timing of biological events (phenology). Such shifts could be the result of direct responses to changes in the environment, or indirect responses resulting from altered biotic interactions between species. In this compilation I investigate the effects of recent and future climate change on the high elevation plant

community of California's White Mountains. Chapter 1 investigates if there have been shifts in distribution and abundance of alpine and sub-alpine plant species along an elevational gradient in the White Mountains during the last half-century. Chapter 2 tests how sagebrush encroachment affects alpine plant species and how the plant community responds to experimental removal at three sites along an elevation gradient. Sagebrush presence was expected to lower the abundance of co-occurring alpine plant species and, conversely, sagebrush removal was expected to increase cover of co-occurring species, especially at lower elevations with more favorable growing conditions. Chapter 3 tests how plant species respond to warming and if these responses vary by elevation and the presence of sagebrush. It was expected that alpine species at the lower (warm) margins of their range would respond negatively to warming, with potentially positive responses at high elevations, and that the presence of sagebrush might dampen these responses. Finally, Chapter 4 evaluates how experimental warming and sagebrush presence or absence interact to influence the phenology of photosynthetic biomass production, and flowering of the cushion plant, *Trifolium andersonii*, and the grass, *Koeleria macrantha*, at two elevations. Observational findings of this work were that several species in the White Mountains have experienced changes in distribution and abundance over the past half-century. Experimental findings show that climate change is having direct (via warming) and indirect (via species interactions) effects on both individual species cover and phenology and community composition as a whole.

CHAPTER 1

Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range

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Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range

Christopher W. Kopp & Elsa E. Cleland

Keywords
Alpine plants; *Artemisia rothrockii*; Climate change; Cushion plants; *Eriogonum ovalifolium*; Great Basin; Multivariate analysis; *Phlox condensata*; Species ranges; *Trifolium andersonii*; White Mountains

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Abstract

Question: Have there been shifts in abundance and distribution of alpine and sub-alpine plant species along an elevational gradient in an arid North American mountain range during the last half-century?

Location: Elevational gradient in the White Mountains, California, USA (37°30′ N, 118°10′ W).

Methods: We conducted a 49-yr re-survey of plant species distribution and abundance in areas originally surveyed in 1961. Species abundance data were collected along line transects between elevations of 2900 and 4000 m. We evaluated the degree of plant community shift over time across elevations; specifically, we expected species ranges to shift upward such that species peak abundances would be observed higher in elevation in 2010 than in 1961. To address this expectation we conducted a permutational multivariate linear model analysis with elevation, soil type and year as factors. We further performed single-species analyses to evaluate how focal species contributed to the multivariate community-level shifts between 2010 and 1961, and how these varied across elevations and soil types. Growing season climate data (June 1 through October 31) collected between 1961 and 2010 were analysed to quantify the change in annual mean temperature and precipitation at this site.

Results: We found that *Artemisia rothrockii* increased in abundance at the upper reaches of its distribution between the 2010 and 1961 surveys. Additionally, we recorded significant declines in abundances in the lower elevation ranges of three alpine cushion plants: *Trifolium andersonii, Phlox condensata* and *Eriogonum ovalifolium*. These shifts coincided with a 0.98 °C increase in mean growing season temperatures and a 53 mm decrease in mean annual precipitation between 1961 and 2010.

Conclusions: These results suggest that rising temperatures and decreasing precipitation are negatively impacting alpine plant species while promoting expansion of sub-alpine species, possibly signalling the transition of this alpine plant community to sagebrush steppe.

Introduction

The study of species distributions along environmental gradients is a cornerstone of plant ecology (Schimper 1903; MacArthur 1972; Whittaker 1975). Species ranges are often defined by their bioclimatic envelope (Elith & Leathwick 2009; Sexton et al. 2009), and with rising temperatures predicted in the coming decades (Meehl et al. 2007) species are expected to shift their distributions pole-ward and upward in elevation to track their climatic niche (reviewed in Thuiller et al. 2008). This is supported by fossil records that indicate species have responded to past climate change by expanding their ranges into newly suitable habitats, while declining in portions of their range that were no longer environmentally suitable (Cronin & Schneider 1990; Wright et al. 1993; Williams et al. 2001 Parshall 2002; Calcote 2003; Gray et al. 2006). Consistent with these past patterns, rapid pole-ward and upward range expansions have been observed for many species worldwide in recent decades (Hughes 2000; McCarty

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2001; Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003; Parmesan 2006; Chen et al. 2011), although upward elevational shifts have been more readily apparent (Kullman 2002; Klanderud & Birks 2003; Beckage et al. 2008; Holzinger et al. 2008; Kelly & Goulden 2008; Lenoir et al. 2008; le Roux & McGeoch 2008; Bergamini et al. 2009; Van Bogaert et al. 2011; Pauli et al. 2007). There is growing confidence that these shifts are the result of increasing global temperatures and shifts in precipitation regimes (Rosenzweig et al. 2008; Maclean & Wilson 2011).

Mountainous ecosystems are predicted to experience a greater magnitude of climate change than other systems (Giorgi et al. 1997), and alpine floras will likely be sensitive indicators of climate change, with particularly evident shifts in species distributions (Spicer & Chapman 1990; Doak & Morris 2010). Different mechanisms could lead to shifting distributions at upper vs lower elevational range margins, however. Species ranges are jointly influenced by biotic interactions and environmental constraints, with the assumption that increased stress is exerted at the margins of a species' distribution (reviewed by Sexton et al. 2009). In particular, upper elevational or latitudinal range margins are often thought to be determined by species physiological tolerances to low temperature stress, while biotic interactions are thought to play a larger role in determining lower elevational or latitudinal margins (MacArthur 1972). Further, species interactions are likely to vary along elevational gradients; according to the 'stress gradient hypothesis', at lower elevations where abiotic stress is lower, competition exerts a greater influence, while facilitation ameliorates increased abiotic stress at high elevations (Callaway et al. 2002). As a result, competition might hasten declining abundances at the lower elevational range margin of a species, while facilitation could potentially hasten establishment near the species' upper range margin.

The hypothesized range shifts of alpine species in response to climate change may be further constrained by barriers to long-distance dispersal between isolated mountain ranges (Dullinger et al. 2004) and edaphic factors such as soil specialization (Damschen et al. 2010). As global temperatures continue to rise there is increasing concern that species will be unable to colonize newly suitable habitats quickly enough to keep pace with declining climatic suitability within their current ranges (Loarie et al. 2009). This is particularly true for slow-growing, long-lived species (Davis 1989) common in alpine ecosystems, for which there is likely to be a long lag-time between climatic shifts and distributional responses, potentially facilitating a 'crash' in abundance as species become susceptible to disease or low recruitment under sub-optimal climatic conditions (Breshears et al. 2005; van Mantgem & Stephenson 2007). Finally, if species in montane ecosystems respond individualistically to climate change rather than 'marching' together up-slope, the result could be novel species interactions (Brooker et al. 2007), altered community structure and potentially higher rates of local extinction of already rare species.

North America's Great Basin, with its numerous isolated mountain ranges, provides an ideal natural laboratory in which to examine species responses to recent climatic change. It is projected that boreal habitats in this region may ascend at a rate as high as 167 m for every 1 °C increase in mean temperature, such that a 3 °C increase in temperature could result in a 66% to 90% loss of boreal range extent and a 20% to 50% loss of species (Murphy & Weiss 1992). This scenario could result in localized extinctions for alpine species, many of which are endemic, display strong soil affinities and are confined to high mountain peaks (Van de Ven et al. 2007). In this study, we documented shifts in plant species abundances along elevational transects on three distinct soil types first described by Mooney et al. (1962). Specifically, we asked whether: (1) focal plant species in sub-alpine and alpine zones experience similar shifts in abundances and elevational ranges over time; (2) abundance and/or range shifts are similar across soil types, indicating a role of edaphic factors in limiting species range shifts; and (3) biotic interactions mediate shifting species abundances over time, specifically whether alpine species had higher declines in abundance at their lower range margins in zones where sub-alpine species are expanding their upper range margins.

Methods

Study area

The White Mountains are on the western edge of Basin and Range Province and lie within the rain shadow of the Sierra Nevada Mountains, USA. This relatively narrow mountain range has a steep elevation gradient, ranging from 1220 m at its base in the Owens Valley to 4344 m at the summit of White Mountain Peak. Winter snow accounts for much of the mountain range's precipitation. Precipitation varies with elevation, ranging from 456 $mm \cdot yr^{-1}$ at Barcroft Station (3800 m) to 142 $mm \cdot yr^{-1}$ at Bishop Airport in Owens Valley (1250 m). Temperature also varies with elevation, with a mean annual temperature of −1.7 °C at Barcroft Station, compared to 13.3 °C in Bishop (Hall 1991). The steep gradient of elevation results in five distinct plant communities: cold desert (1220–1980 m), montane (1980–2900 m), sub-alpine (2900–3500 m), alpine (3500–4000 m), and high alpine (4000–4344 m) (Rundel et al. 2008). Our study spanned the sub-alpine and alpine vegetation zones. Historically, these zones have been characterized as having perennial prostrate cushion plants that are generally expected to have relatively little

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inter-annual fluctuation in abundance. Common species include *Phlox condensata* (A. Gray) E.E. Nelson, *Trifolium andersonii* A. Gray, *Eriogonum ovalifolium* Nutt. and *Arenaria kingii* (S. Watson) M.E. Jones, along with the grasses *Koeleria macrantha* (Ledeb.) Schult., *Elymus elymoides* (Raf.) Swezey and various *Poa* species. Shrub species have not historically been present in alpine zones in the White Mountains, but *Artemisia rothrockii* A. Gray (sagebrush) has been the dominant shrub species in the sub-alpine. Primary soil types within the White Mountains are derived from quartzite, dolomite and granite and many plant species are strongly soil specific (Mooney et al. 1962).

The White Mountains have a long history of land use in the form of mining, livestock grazing and recreation. Inyo National Forest (Bishop, CA) records indicate that ca. 40 000 head of domestic sheep were grazed annually throughout the White Mountains from ca. 1890 to 1923. The first officially documented stocking rates show that between 10 000 and 14 380 AUMs (animal unit months) were grazed in the mid-1920s. A transition to primarily cattle grazing occurred in the mid-1930s and sheep grazing permanently ceased after 1952. Between 1923 and the late-1950s the US Forest Service implemented sustainable resource management strategies that resulted in greatly reduced stocking rates (McElroy 1964; Harold 1966). These management directives were, and continue to be, aimed toward multiple land-use types that maintain and improve water resources along with the scenic and recreational value of the White Mountains, with special attention paid toward the Bristlecone pine (*Pinus longaeva* D.K. Bailey). Grazing of cattle at moderate stocking rates of ca. 500 AUMs continued until ca. 1992 at elevations as high as 3650 m and is still permitted in eastern drainages below 2900 m in the Inyo National Forest.

Climate data

Growing season temperature data (1 June through 31 October) collected between 1961 and 2010 at the White Mountain Research Center Barcroft facility (3800 m; WMRC 2010) were analysed to determine variations in daily mean, maximum and minimum temperatures. Long-term precipitation data at this station is unreliable due to missing and incomplete data, as well as issues with blowing snow. Therefore, precipitation data from the PRISM Climate Mapping Program (PRISM Climate Group 2013) were analysed in order to understand regional changes in precipitation during the period between surveys.

Vegetation surveys

We compared species distributions and abundances in 2010 against species distributions and abundances recorded by Harold Mooney and colleagues in 1961 (Mooney et al. 1962). Mooney surveyed 113 transects in both forested and open areas on Barcroft, Sagehen and Cottonwood granitic plutons, Campito Formation quartzite and Reed Formation dolomite in areas south of White Mountain Peak (Mooney et al. 1962; H.A. Mooney, pers. comm.). Our survey was conducted in July and August 2010 on these soil types, with 26 transects on granite, 23 transects on quartzite and 13 transects on dolomite, giving a total of 62 transects (Appendix S1). Our survey contained fewer transects because we did not resurvey the forested areas from Mooney et al. (1962). Transects were surveyed at elevational increments of ca. 150 m on north-, south-, east- and west-facing slopes, unless no slope with a particular aspect existed. Transects were 50 m in length, placed parallel to the contour of the slope, and located at elevations between 2895 and 4010 m on granitic soil, between 2895 and 3810 m on quartzitic soil and between 3050 and 3810 on dolomitic soil. In accordance with methods used in Mooney et al. (1962), survey areas were chosen randomly, but placement of each transect was subjectively determined based on elevation, substrate uniformity, exposure and homogeneity of vegetation. Individual plants and cover types intercepted along each transect were measured to the nearest centimeter. Additionally, general visual surveys were conducted during the summer months of 2010, 2011 and 2012 to identify isolated individuals of *A. rothrockii* at the upper range margins of sagebrush in the White Mountains.

Data analysis

All statistical analyses were conducted using the R software environment (R Foundation for Statistical Computing, Vienna, AT). Change in climate over time was evaluated with linear models, where each climate variable was predicted by year.

We were unable to relocate the original transect-level data from the 1961 survey. Thus, the average number of individuals of each species encountered per 25 m of transect was extracted from figures in the original Mooney et al. (1962) manuscript (Appendix S1), using the digitizing software TechDig. This yielded comparable data by elevation and soil type for seven common species that were observed in 1961 and 2010. These species were *Arenaria kingii*, *Artemisia rothrockii*, *Eriogonum gracilipes*, *E. ovalifolium*, *Koeleria macrantha*, *Phlox condensata* and *Trifolium andersonii*.

To evaluate our hypothesis that the elevational distribution of species has changed over time, and evaluate whether these shifts vary among soil types, we conducted a permutational multivariate linear model analysis (PERMANOVA; Anderson 2001; McArdle & Anderson 2001)

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using the adonis function within the vegan package. First, a distance matrix was calculated based on Bray–Curtis dissimilarity among samples; each sample represented the abundances of the seven focal species averaged across transects at a given elevation and soil type. We chose to use Bray–Curtis dissimilarity because it has been shown to capture species turnover along environmental gradients (Faith et al. 1987) and because shared zero abundances do not contribute to increasing similarity between samples. Elevation (continuous), Soil type (categorical) and Year (categorical) were included in the linear model, in addition to all possible interactions of the three factors. The distance matrix was then permuted 999 times and pseudo-F statistics were calculated for each term in the model. We expected that Elevation and Soil type would explain significant variation in species composition, based on natural history knowledge of the area (Mooney et al. 1962; Rundel et al. 2008), in addition to an Elevation*Soil type interaction, because some species have higher elevational range margins on granite than on other soil types, potentially because these darker soils retain more heat due to their lower albedo as compared with dolomite or quartzite soils (Mooney et al. 1962). A significant effect of Year would indicate a shift in community composition (relative species abundances) over time. Significant Year*Elevation and Year*Soil type effects would indicate significant changes in community composition over time at some elevations and soil types but not others.

To evaluate how each of the focal species contributed to the multivariate community-level shifts between 2010 and 1961, and how these varied across elevations and soil types, *z*-scores were calculated for individual species abundances averaged across transects at each elevation in 2010. A statistically significant change over time was defined as a species' abundance in 1961 that fell outside of 2 SD ($z = \pm 2$) of the 2010 mean.

Results

Precipitation and temperatures

Daily mean growing season temperatures at Barcroft increased 0.02 °C·yr^{-1} ($R^2 = 0.11$, $P = 0.03$) between 1961 and 2010. Daily minimum temperatures were largely responsible for this increase as they rose 0.03 °C·yr^{-1} ($R^2 = 0.23$, $P = 0.001$), while daily maximum temperatures did not change. Yearly precipitation at Barcroft Station decreased 4.97 mm·yr^{-1} between 1961 and 2010 ($R^2 = 0.12$, $P = 0.01$; Fig. 1).

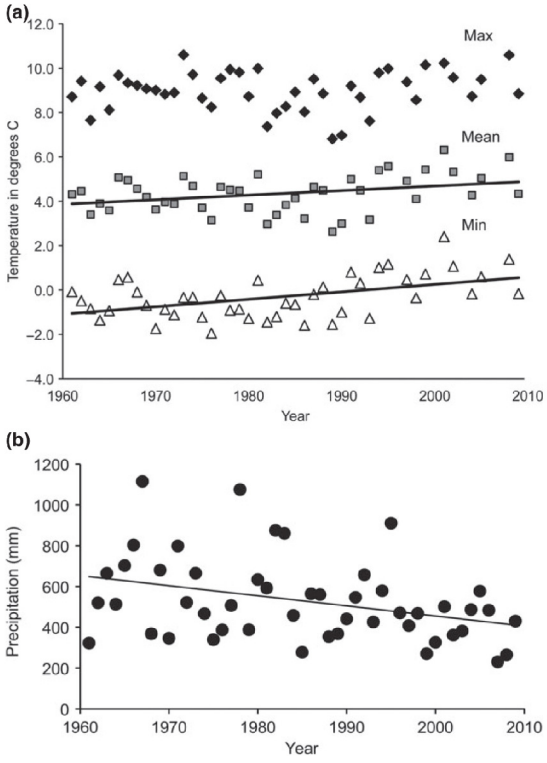

Fig. 1. Daily mean 1 June through 31 October temperatures (**a**) at Barcroft Station (3800 m) increased 0.98 °C between 1961 and 2010. Daily minimum temperatures were largely responsible for this increase as they rose 0.03 °C·yr^{-1} while daily maximum temperatures increased only 0.008 °C·yr^{-1}. Yearly precipitation at Barcroft Station (**b**) decreased 4.97 mm·yr^{-1} between 1961 and 2010.

Multivariate community response

The seven plant species that we were able to compare to Mooney et al. (1962) comprised 24.9 ± 2.2% (±SE) of taxa at each elevation on granitic soils, 24.1 ± 2.7% of taxa on quartzitic soils and 25.5 ± 2.9% of taxa on dolomitic soils. Although this represents only about a quarter of the total species diversity at the site, the focal species are all relatively abundant and accounted for 52.1 ± 3.9% of total cover (estimated as line density) at each elevation on granite, 57.4 ± 5.1% of cover on quartzite and 61.2 ± 5.3% of cover on dolomite. As expected, significant variation in species composition ($P < 0.001$) was explained by Elevation ($F_{1,39} = 23$), Soil type ($F_{2,39} = 13.9$) and their interaction ($F_{2,39} = 5.4$). Species composition also changed over time (Year $F_{1,39} = 3.7$), and the magnitude of change varied by Elevation (Year*Elevation, $F_{1,39} = 3.5$, $P = 0.005$) but not by Soil type or their three-way interaction.

To visualize how elevation and soil type influenced the degree of community composition change over time in the multivariate analysis, we plotted the Bray–Curtis dissimilarity between 1961 and 2010 against elevation for each soil type (Fig. 2). On granitic substrates, dissimilarity in

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community composition between 1961 and 2010 (temporal turnover) tended to increase with elevation, except at the highest elevation (3950 m), where there was little community turnover over time. On quartzitic substrates there was relatively similar turnover in community composition across elevation. In contrast, on dolomite the highest turnover occurred at the lowest elevations and the least turnover occurred at high elevations. To understand how individual species and their responses at different elevations contributed to this overall community shift, the results for each focal species are detailed in the following sections.

Sagebrush

Only one focal species, *Artemisia rothrockii*, experienced widespread increases in abundance over time on granite and quartzite substrates, where it is now the most abundant species below 3650 m in both the sub-alpine and alpine zones. This species, identified as *A. arbuscula* Nutt. in Mooney et al. (1962), was also the only species that appeared to increase its elevational range margin between surveys. *A. rothrockii* had upper range margins of 3500 m in 1961 on both granitic and dolomitic soils, but the margin rose to 3650 m in 2010 on granitic soils. On quartzitic soils, a dark soil with a low albedo, *A. rothrockii* had an upper range margin at 3650 m, the upper bounds of this soil type in the White Mountains, in both 1961 and 2010. The higher range margin on quartzitic soils in 1961 is possibly due to lower albedo on this dark soil. At these new range margins, 2010 abundance values were not significantly different from zero values recorded in 1961 (granite, $z = 1.44$, $P = 0.07$; dolomite, $z = 0.50$, $P = 0.31$) due to a patchy invasion front; there were transects at this elevation with zero abundance of sagebrush in 2010, and others with high abundance. On both granite and quartzite there were some minor, but significant, adjustments in abundance at several elevations along the gradient, resulting in abundance values more regularly distributed across the gradient in 2010 than in 1961. On dolomite, where *A. rothrockii* abundance was low in both 1961 and 2010, there were no significant changes in abundance between the survey years, although no populations were observed at 3050 m in 2010 (Fig. 3a; raw data in Appendix S3).

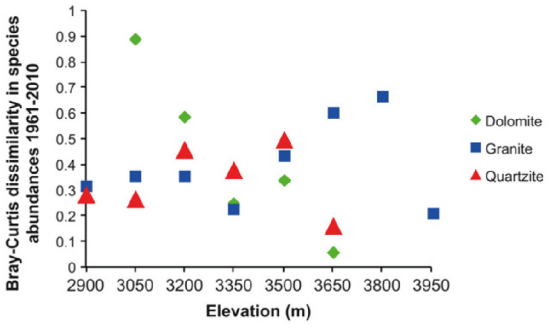

Fig. 2. Bray–Curtis dissimilarity in species abundances for seven species surveyed in the White Mountains on granite, quartzite and dolomite in 1961 and 2010.

Cushion plants

Three species, *Phlox condensata*, *Trifolium andersonii* and *Eriogonum ovalifolium*, experienced decreased abundances on both granitic and quartzitic soils in 2010 compared to 1961. On quartzite there were significant declines in abundance at elevations of peak 1961 abundance for these three species and, as a result, abundances throughout their entire ranges in 2010 were minimal relative to 1961 abundances. On granitic soils, where there is wider elevational distribution of these species, significant declines in abundance were observed in 2010 at the central portions of these species ranges, while low abundances were maintained at the lower portions of their ranges and peak abundances were maintained at the upper bounds of the survey. These declines in abundance at the central portions of cushion plant ranges in 2010 resulted in abundances similar to those observed at the lower portions of their ranges in 1961. Two of these species, *T. andersonii* and *E. ovalifolium*, were not recorded on dolomite in 1961 but had populations with low abundance recorded at 3200 m (*T. andersonii*; 0.25 plants·25 m^{-1}, $z = 0.71$, $P = 0.24$) and 3500 m (*E. ovalifolium*; 1.63 plants·25 m^{-1}, $z = 0.50$, $P = 0.31$) in 2010. On dolomite, *P. condensata* showed minimal shifts in abundance in the core of its range between 1961 and 2010. However, a population of *P. condensata* (29.67 plants·25 m^{-1}, $z = 0.95$, $P = 0.17$) was recorded 300 m below the 1961 lower range margin (3350 m), although no plants were observed 150 m below the 1961 boundary in 2010 (Fig. 3b,c,c; raw data in Appendix S3). Additionally, one cushion plant, *Arenaria kingii*, showed no significant range or abundance shifts on either granitic or quartzitic soils and had only minor abundance shifts on dolomitic soils (Fig. 3g; raw data in Appendix S3).

While we found significant declines in large segments of *P. condensata*, *T. andersonii* and *E. ovalifolium* ranges, populations of another cushion plant, *E. gracilipes*, displayed more complex, but largely insignificant, shifts between 1961 and 2010. On dolomite, *E. gracilipes* had significantly lower abundance at 3500 m ($z = -1.72$, $P = 0.04$) in 2010, while at 3050 and 3200 m, populations were intercepted by our survey in 2010 but not in the 1961 survey. There were no populations of *E. gracilipes* recorded on quartzite in 1961, while there were plants of this species observed at 2900 m (6.2 plants·25 m^{-1}, $z = 3.84$,

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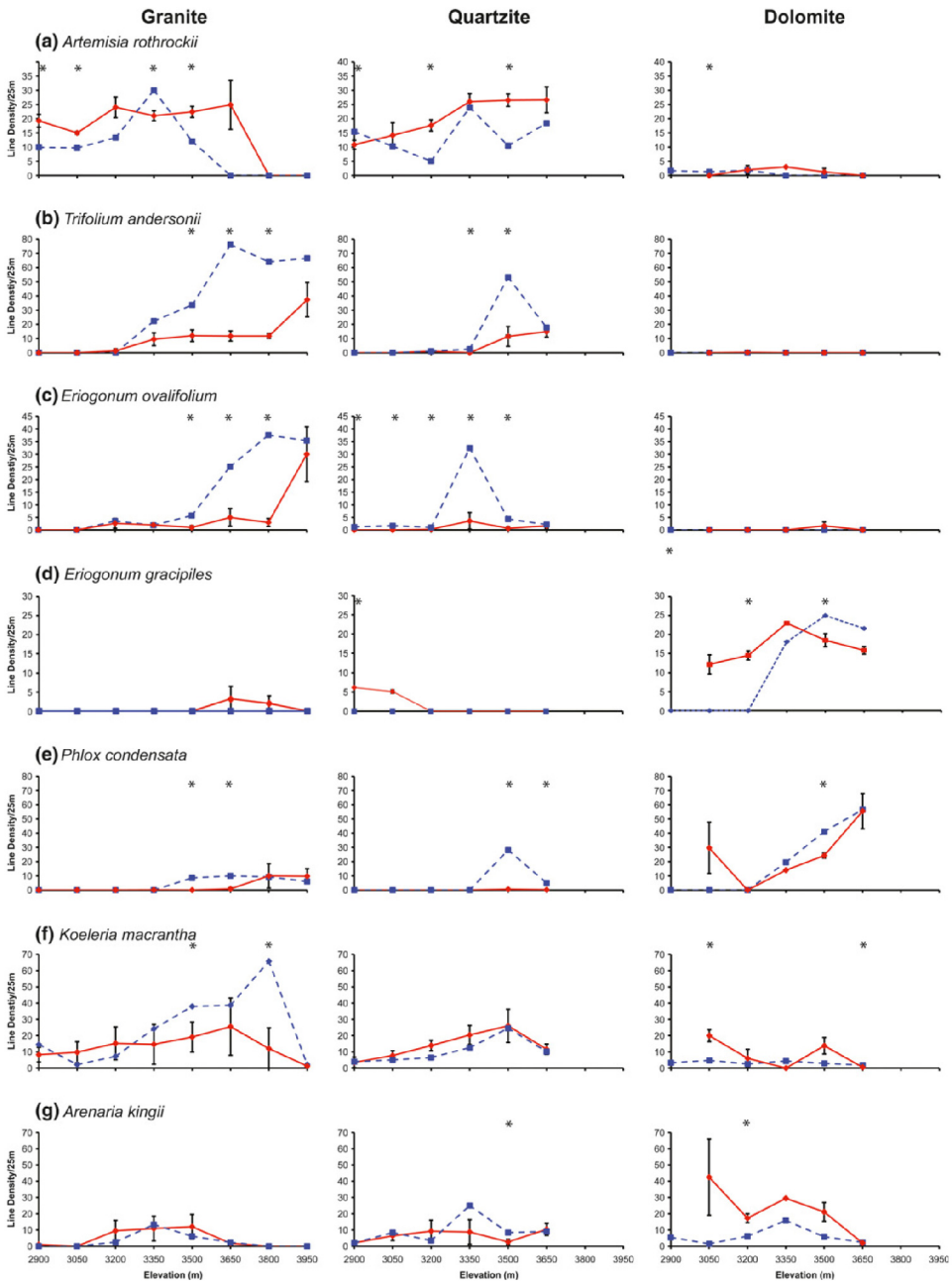

Fig. 3. Distribution and abundance in 1961 (blue dashed) and 2010 (solid red) for seven species (*Artemisia rothrockii* (**a**), *Trifolium andersonii* (**b**), *Eriogonum ovalifolium* (**c**), *Eriogonum gracilipes* (**d**), *Phlox condensata* (**e**), *Koeleria macrantha* (**f**) and *Arenaria kingii* (**g**)) surveyed in the White Mountains in these years. Elevations with no data points were not surveyed. Significant differences in abundance between sampling years at specific elevations are denoted by *.

$P < 0.01$) and 3050 m (5.1 plants·25 m^{-1}, $z = 0.50$, $P = 0.31$) in 2010. This species was also not recorded on granite in 1961, but populations were intercepted at 3650 m (3.3 plants·25 m^{-1}, $z = 0.5$, $P = 0.31$) and 3800 m (2.0 plants·25 m^{-1}, $z = 0.5$, $P = 0.31$) in 2010 (Fig. 3d; raw data in Appendix S3).

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Bunchgrassses

Mooney et al. (1962) included data for *Poa glauca* Valh and *K. macrantha*, both perennial bunchgrasses. Due to identification problems in the field, we do not consider *P. glauca* here. However, *K. macrantha* had mostly minimal shifts in abundance on granitic and quartzitic soils, and sporadic, largely insignificant, adjustments on dolomite (Fig. 3f; raw data in Appendix S3).

Discussion

Analyses seeking to quantify range shifts by comparing historical and contemporary data sets are often restricted by data limitations (Tingley & Beissinger 2009). In many cases, data on historical species presence or abundance at various elevations can be gleaned from figures in publications, but these coarse data are challenging to compare to present distributions using traditional statistical techniques. Here, we compared mean species abundances in 1961 to sampled distributions in 2010 using a permutational multivariate model. This technique enabled us to document (1) a statistically significant shift in dominant plant species composition over time along an elevational transect in the White Mountains, and (2) variable magnitude of changes, dependent on elevation but not soil type. These changes coincided with an overall 0.98 °C increase in growing season temperatures and a 53 mm decrease in mean annual precipitation between 1961 and 2010 at this location.

It is widely assumed that species ranges will shift poleward and upward in elevation in response to rising temperatures associated with climate change (Sexton et al. 2009); an increase in abundances near the upper latitudinal or elevation range margin of a species could logically precede such range expansions. Of the seven focal species we were able to compare between surveys, only one, *A. rothrockii*, increased in abundance in the upper portions of its elevational range in the White Mountains. Comparisons of photos taken in the same location in 1993 and 2012 support this finding, showing that *A. rothrockii* is now present where it was not previously documented at an elevation of 3593 m (Fig. 4). Shifts in species range limits are more difficult to establish than changes in abundance, because isolated individuals near the upper elevational range margins are unlikely to be sampled using the line transect method employed in this study. However, additional observations provide strong evidence that *A. rothrockii* has advanced upwards in elevation. Floristic accounts of Lloyd & Mitchell (1973) indicate that this species was found at elevations as high as 3800 m in the 1960s. Flowering plants of *A. rothrockii* can now be observed as high as 3993 m, and a second-year seedling of this species was observed at an elevation of 4102 m in 2012 on granitic substrates, 293 m higher than a herbarium specimen collected in 1964 by Mitchell and La Marche at 3809 m, a few kilometers to the north (Consortium of California Herbaria 2013). This new elevation record far surpasses any previous observations for this species, suggesting that *A. rothrockii* is establishing a foothold in the high-alpine areas of the White Mountains. Upward range expansion of individual species at rates as high as 37.5 m·decade^{-1} have been observed worldwide (Kullman 2002; Klanderud & Birks 2003; Beckage et al. 2008; Holzinger et al. 2008; Kelly & Goulden 2008; Lenoir et al. 2008; le Roux & McGeoch 2008; Van Bogaert et al. 2011). The upward expansion rate of as much as 30 m·decade^{-1} by *A. rothrockii* in the White Mountains is consistent with these findings, but the 293 m increase in elevational range exceeds previous projections for the Great Basin, predicting that species will ascend at a rate of 167 m for every 1 °C increase in mean annual temperature (Murphy & Weiss 1992).

In contrast with sagebrush, the bunchgrass *K. macrantha* declined in abundance at high elevation. This species has wide geographic and climatic distributions across the northern hemisphere. It is found from sea level to 4400 m in the Himalaya and grows in areas with precipitation ranging from 300 mm to 2000 mm and temperature extremes ranging from −50 to 39 °C (Dixon 2000). Thus, in the White Mountains, *K. macrantha* is at its climatic margin for precipitation and, therefore, may be particularly sensitive to periods of severe drought at this location.

Five of the seven focal species considered in this study were cushion plants; these prostrate wildflowers are characteristic components of alpine floras. Three of these species, *E. ovalifolium*, *P. condensata* and *T. andersonii*, experienced significant and widespread declines at the lower portions of their ranges but no corresponding increase in abundance in their upper elevational ranges, especially on granitic and quartzitic soils. While there have been numerous documented range expansions, to our knowledge only five other studies have documented recent declines of plant species abundances at their lower elevational or latitudinal range peripheries (Klanderud & Birks 2003; Lesica & McCune 2004; Kelly & Goulden 2008; Damschen et al. 2010; Krushelnycky et al. 2013). Declines in some species could be indirectly caused by species interactions, specifically via competition with species that are increasing in abundance at their upper elevational or latitudinal range margins. In the White Mountains, cushion plants declined in zones where *A. rothrockii* expanded its elevational range or increased in abundance, but this was likely not due to negative interactions with *A. rothrockii* because declines also occurred where *A. rothrockii* was not present or did not change in abundance between survey

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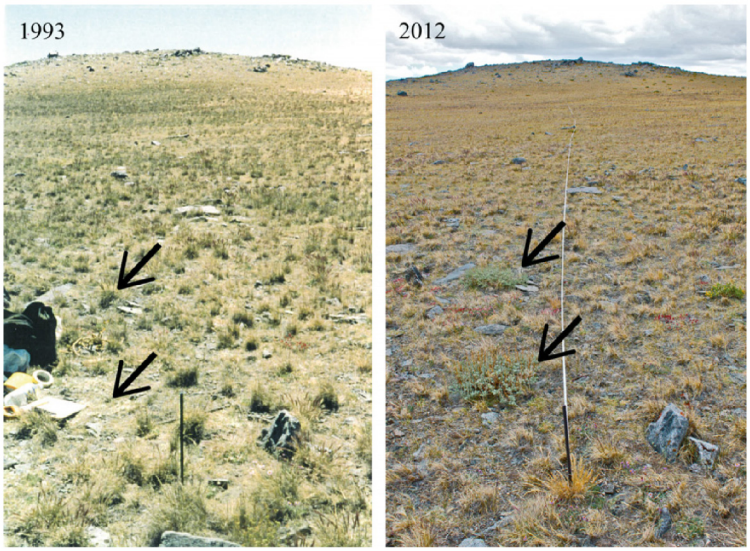

Fig. 4. Comparisons of photos taken in the same location in 1993 (left) and 2012 (right) show that *Atremisia rothrockii* is now present where it was not previously documented at an elevation of 3593 m. (1993 photo by Steven Travers)

years. Although it is clear that *E. ovalifolium*, *P. condensata* and *T. andersonii* are experiencing declines in abundance in the lower portions of their ranges (Fig. 3b,c,e), it is not clear how long these declines have been underway. Data from 1961 indicate that these species were encountered in minimal abundances at the lowest reaches of their ranges and our data show a widening of this zone of low abundance. If declines in abundance continue, these cushion plants may face localized population extinctions throughout the White Mountains.

Populations of another cushion plant, *E. gracilipes*, displayed mostly insignificant changes in distribution and abundance between 1961 and 2010, except for an apparent expansion of populations into lower elevations than previously documented. In the White Mountains, *E. gracilipes* is generally found in isolated populations, and it is possible that populations of this species may have been missed by the 1961 survey, making this downward range expansion a sampling artifact. However, downward range expansions could be the result of other factors, such as changes in precipitation patterns. In the Sierra Nevada mountain range, just to the west of the White Mountains, Crimmins et al. (2011) documented downward shifts in species optimum elevations over the last 80 yr, and attributed this shift to an alleviation of water stress at lower elevations, where rising precipitation exceeded an increase in evaporative demand associated with rising temperatures. Since precipitation declined in the White Mountains between surveys (Fig. 1), this mechanism is unlikely to explain the increase in abundance of this focal species in the lower portion of its elevational range, because water stress is likely to have increased rather than decreased over time.

Although we saw differences across elevations, our analysis did not find significant differences among soil types in terms of abundance responses over time. Our findings are consistent with those from a similar re-survey study in Oregon's Siskiyou Mountains, which found differential responses of species abundances at their northern vs southern range margins, and similar levels of community shift across soil types (Damschen et al. 2010). The Siskiyou re-survey also found that rare edaphic endemics, restricted to particular soil types, had greater declines than widespread species. In the present study, we were restricted to common species documented in the original Mooney et al. (1962) publication. Thus, while we infer similar degrees of community reorganization among soil types, we cannot conclude whether rare soil endemics in the region have experienced similar responses.

Since our study is observational, we cannot definitively conclude that climate was the primary cause of the observed shifts in plant community composition. However, our observations of overall shifts in species composition paired with increased shrub abundance are consistent with findings from experimental warming studies in arctic and alpine systems. For instance, the International Tundra Experiment (ITEX) found that increasing mean temperatures by 1–3 °C with passive warming structures resulted in rapid declines of species diversity and evenness and increases in shrub height and cover in alpine and arctic

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communities (Walker et al. 2006). A radiant heating experiment in an alpine meadow in Colorado found similar results, with enhanced growth and recruitment of sagebrush and decreased production of forbs in response to artificial warming (Harte & Shaw 1995). In the Colorado experiment, warming induced earlier snowmelts (Harte & Shaw 1995) and early snowmelt dates at this location have been shown to expose several alpine plant species to more frequent early-season frost mortality, resulting in decreased flower and seed production (Inouye 2008). In addition, New Zealand alpine plant species normally protected by late-season snow banks showed decreased frost tolerance compared to those found in exposed areas, subjecting them to potential spring and summer frost damage (Bannister et al. 2005). Consistent with these observations, species with affinities for extreme late-melting snowbeds in Norway have declined over time, again associated with warming during the same time period (Klanderud & Birks 2003). Increased temperatures and decreased annual precipitation in the White Mountains have likely resulted in longer snow-free periods and may help explain declines in cushion plants as a result of decreased seed production and recruitment due to frost damage (Doak & Morris 2010). An expanded growing season could also facilitate the spread of *A. rothrockii*, since growing season length is positively correlated with survival, growth and abundance of other species within this genus (Galen & Stanton 1995; Hou & Romo 1998; Perfors et al. 2003). However, initial establishment of *A. rothrockii* may be associated with wet El Niño years producing conditions that enhance seed production, germination and seedling survival, resulting in abundant local seed supply that makes establishment events more likely in subsequent years around these isolated invasions (Bauer et al. 2002). Continued declines of cushion plants coupled with encroachment by *A. rothrockii* could result in the transformation of high-elevation plant communities in the White Mountains from alpine fell-field to sagebrush steppe.

The substantial decline in abundance of cushion plants across elevational bands with widths of 300 m (*P. condensata*) to 450 m (*E. ovalifolium* and *T. andersonii*) at the lower portion of their ranges should be viewed with significant conservation concern. In addition to the direct influence of climate change, shifts in fire and grazing regimes should also be considered when interpreting these results. Although there is no modern account of wildfire at the elevations sampled and no records of blazes between sampling dates (California Department of Forestry & Fire Protection 2010), shifts in grazing regimes may have played a role in the observed shifts in plant community composition.

Historical accounts of pre-European settlement in the inter-mountain western United States suggest that plant communities had higher densities of grasses and less dense stands of sagebrush, particularly in mountain ranges and drainages (Christensen & Johnson 1964). With settlement of this region came an era of intense overgrazing by livestock, primarily sheep and cattle. The impacts of intensive grazing in the western United States have included loss of biodiversity and decreased densities of a wide variety of taxa (Fleischner 1994). Long-term studies of sagebrush steppe recovery after abandonment of intensive grazing indicate that historical plant communities may not return to pre-grazed assemblages (West et al. 1984), and that sagebrush may actually increase in cover and dominance once grazing is abandoned (Anderson & Holte 1981; West et al. 1984). While the impact of livestock grazing on cushion plants is not well studied, forb species in arid North American ecosystems have generally been found to respond neutrally to overgrazing while grasses largely respond negatively (Jones 2000). The 1961 survey occurred 38 yr after intense grazing by domestic sheep had ended, and cattle grazing was largely curtailed, and ultimately ended in much of the survey area, since the original survey. Therefore, if species such as cushion plants were negatively affected by late-nineteenth and early-twentieth century overgrazing then we would expect to see these species maintain or increase in abundance between surveys, instead of experiencing declines.

In conclusion, while our results are consistent with the expectation that plant species will have the largest responses to environmental change at the peripheries of their ranges (Sexton et al. 2009), there was large variation among species in how their abundances shifted over time. Only sagebrush displayed the expected increase in abundance in the upper portion of its elevational range, while three alpine cushion plants declined in the lower portions of their range, another alpine cushion plant appeared to have a downward elevational range shift, and a bunchgrass declined in the upper portions of its elevational range. The complex shifts we observed call attention to the need for future experimentation to identify the environmental and biotic mechanisms associated with shifting abundance and range distributions of unique species inhabiting this arid mountain range. Future studies should focus on the role of multiple drivers of environmental change in addition to warming in order to identify the mechanisms associated with declines of sensitive alpine species, as well as the potential role of biotic interactions with species such as sagebrush that are experiencing rapid range expansions.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Original species distribution and abundance data from Mooney et al. (1962).

Appendix S2. List of transect GPS locations.

Appendix S3. Summary statistics comparing 1961 (Mooney et al. 1962) and 2010 species data.

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Chapter 1, in full, is a reprint of the material as it appears in: Kopp, C. W., and E. E. Cleland. 2014. Shifts in plant species elevational range limits and abundances observed over nearly five decades in a western North America mountain range. Journal of Vegetation Science 25:135–146. The dissertation author is the primary investigator and author of this paper.

CHAPTER 2

Community response to sagebrush encroachment and removal along an arid elevation gradient

Abstract: Shrub encroachment into grasslands and other herbaceous-dominated communities is an issue of management concern in many ecosystems worldwide, and is often associated with changes in the existing herbaceous plant community. The stress gradient hypothesis predicts that shrub impacts on herbaceous species will be environmentally dependent, varying from facilitative in stressful environments to inhibitory in more favorable environments. In California's White Mountains, *Artemisia rothrockii* (sagebrush) has been historically abundant at mid-elevations but has more recently encroached into higher elevation alpine habitats. This study evaluated how sagebrush encroachment affects alpine plant species and how the plant community responded to experimental removal at three sites along an elevation gradient. Sagebrush presence was expected to lower the abundance of co-occurring alpine plant species, and conversely sagebrush removal was expected to increase cover of co-occurring species, especially at lower elevations with more favorable growing conditions. Instead, the results of this study were more nuanced, revealing mostly inhibitory effects of sagebrush that varied with elevation and metric of community change. Where sagebrush had more recently colonized at high elevations, cover and richness of co-occurring species was lower under shrubs, a response driven by a decline in grasses. Total cover and richness was otherwise unaffected by sagebrush at lower elevations and was not impacted by its

removal at any elevation. Analysis of species composition, however, showed that both sagebrush presence and removal had the greatest influence on community composition at lower elevations, with significant dissimilarity between sagebrush removal and non-removal treatments, and convergence in species composition in open and removal plots. These results demonstrate that while sagebrush has important influences on herbaceous species composition in the White Mountains, they are only partially consistent with the predictions of the stress gradient hypothesis; the largely inhibitory influences of sagebrush were most evident at low elevations when examining species composition, and greatest at high elevation when examining aggregated community cover.

Introduction

The global repositioning of species in response to past climatic adjustments is a process documented in fossil and pollen records (Cronin and Schneider 1990, Wright et al. 1993, Williams et al. 2001, Parshall 2002, Calcote 2003, Gray et al. 2006) and is a phenomenon that is currently being driven in response to anthropogenically triggered rapid climate change (Parmesan and Yohe 2003). These current range adjustments allow for real-time monitoring of species interactions in environments formerly novel to one or more species. Woody species, predominantly shrubs, have been found to be particularly responsive to changing climate (Walker et al. 2006) and their range expansions could have significant impacts on ecosystems (Eldridge et al. 2011). Therefore, experiments testing community response to recent shrub encroachment are important for understanding how ecosystems will appear and function in the future.

A recent synthesis of the impacts of shrub encroachment on ecosystem structure found that in arid environments, grasslands are susceptible to ecosystem degradation in response to shrub encroachment, with declines in cover of grasses a common result (Eldridge et al. 2011). Where shrubs have encroached into alpine environments, the stress gradient hypothesis predicts that in these temperature stressed high elevation regions, the presence of a shrub could act as a facilitator to other species (Bertness and Callaway 1994). In arid environments, however, increasing elevation can intensify temperature stress while ameliorating moisture stress, complicating predictions of species interactions along elevation gradients (Michalet et al. 2014). Determining how a widespread and range expanding plant species in an arid environment interacts with other plant species along an elevation gradient could grant insights into what abiotic factors are governing the system and into future plant communities under climate change.

In California's White Mountains, an arid mountain range on the western edge of North America's Great Basin, rising temperatures and declining precipitation have corresponded with lower abundance of several alpine cushion plant species and the upward advancement of *Artemisia rothrockii* (sagebrush) (Kopp and Cleland 2014) (Chapter 1). Where sagebrush is actively colonizing alpine habitats it forms "shrub islands", similar to those formed by *Prosopis ruscifolia* in Argentina's Wet Chaco region (Cabral et al. 2003) and by *Cornus drummondii* in Kansas' (USA) tallgrass prairie region (Lett and Knapp 2005). The development of these shrub islands results in habitat modifications such as changes in light, soil moisture, nutrient concentrations and moderation of temperatures. When woody species encroach into previously shrub free communities, they produce a positive feedback loop resulting in enhanced establishment

of same-species propagules (Germino and Smith 1999, 2000, Germino et al. 2002, D'Odorico et al. 2013). Therefore, the encroachment of sagebrush has the potential to transform the composition of alpine plant communities that it spreads into.

In ecosystems that have been altered by shrub encroachment, can the plant community return to its previous stable state if the shrub species is removed? Several neighbor removal experiments have attempted to answer this question. In California's Sierra Nevada, the removal of sagebrush at a recently encroached site (Bauer et al. 2002) along a gradient of increasing soil moisture resulted in increased herbaceous cover along the gradient (Berlow et al. 2003). In addition, the removal of sagebrush resulted in increased soil moisture in a sagebrush steppe community in the northern Great Basin (Inouye 2006). Globally, the removal of shrubs in mountain systems generally result in response patterns similar to those predicted by the stress gradient hypothesis (Bertness and Callaway 1994), with non-shrub co-occurring species increasing at low elevations and decreasing at high elevations in response to shrub removal (Choler et al. 2001, Callaway et al. 2002). However, trends opposite to the stress gradient hypothesis have been observed across an elevation gradient in the Chilean Andes (Cavieres et al. 2006) where opposing stress gradients of aridity and temperature can produce unpredictable species interactions (Michalet et al. 2014).

This study evaluated how sagebrush encroachment has influenced the alpine plant community in the White Mountains as well as the plant community response to sagebrush removal across an elevation gradient. Lower elevations have higher overall plant cover (Chapter 3) and higher photosynthetic biomass (Chapter 4), indicating more favorable growing conditions at lower elevations. Sagebrush encroachment was hypothesized to

reduce cover of co-occurring alpine plant species and, hence, the removal of sagebrush was expected to have a positive effect on co-occurring species cover, especially at lower elevations where environmental conditions are more favorable to plant growth. Finally, species' responses to sagebrush presence and removal were expected to be reflected in plant water stress, with release from sagebrush competition resulting in decreased water stress, consistent with past sagebrush removal experiments.

Methods

Study System

The White Mountains are located in California on the western edge of the Basin and Range Province and lie within the rain shadow of the Sierra Nevada. The location of this mountain range in a transition zone between the maritime influence of the Pacific Ocean and the interior continental influence of North America results in a cold, arid climate. Winter snow accounts for much of the yearly precipitation, which varies with elevation, ranging from 456 mm/yr at Barcroft Station (3800 m; 37° 34' 59" N, 118° 14' 14" W) to 327 mm/yr at Crooked Creek Station (3094 m; 37° 29' 56" N, 118° 10' 19" W). Temperature declines with increasing elevation, with a mean annual temperature of -1.7°C at Barcroft Station, and 0.9°C at Crooked Creek Station (Hall 1991).

Initial survey

Artemisia rothrockii, which is closely related to *A. tridentata*, is actively encroaching at the high-elevation site (Chapter 1) and forms approximately 10 m diameter colonies, or "shrub islands" in recently invaded sites. To determine if the

presence of sagebrush alters the alpine plant community here, in June 2011 cover was measured within these islands and immediately outside of them by placing 1-m^2 quadrats along transects running perpendicular across the islands and outside of them. At each of four islands surveyed, four plots were established inside the islands and four plots outside of the islands for a total of 32 plots at the high-elevation site.

Shrub removal experiment

Following these initial observations at the high elevation site, a shrub removal experiment was established at three elevations to evaluate the response of alpine and sub-alpine plant communities to sagebrush removal. High-elevation plots were located at 3700 m (37° 34’ 12” N, 118° 14’ 21” W), mid-elevation plots were located at 3100 m (37° 29’ 52” N, 118° 10’ 31” W) and low elevation plots were located at 2900 m (37° 21’ 45 N, 118° 11’ 15” W). In June and July 2011, 1-m^2 plots were established on granitic (high- mid-elevation sites) and quartzitic (low-elevation site) derived soils. At low- and mid-elevation sites, plots with and without sagebrush were chosen making sure there was appreciable cover of both grasses and forbs within the plots. The low- and mid- elevation sites contained six open (no sagebrush present), six shrub and six removal plots. In the shrub removal plots, the sagebrush was cut at the base of the stem and removed. *Artemisia rothrockii* is a species that can re-sprout and so plots that had experienced re-sprouting were trimmed back yearly.

Pre-treatment species cover data were collected for each plot in June 2011. In June of 2012 and 2013 (at the peak of each growing season), species cover was visually

estimated in each plot using a 1x1 m quadrate with 10x10 cm partitions in order to record individual species cover responses to treatments.

Leaf water potential

To measure treatment effects on plant water stress, pre-dawn leaf water potential data were collected in 2013 using a Pressure Chamber Instrument (PMS Instrument Company, Albany, OR, USA). Three sample leaves from each species with sufficient available leaf material from each plot were measured prior to sunrise (0430 – 0530).

Data analysis

Statistical analyses were conducted using the statistical programming language R, version 3.0.3 (R Core Development Team, 2013). To determine if there was a significant difference in cover of species within and outside of high-elevation sagebrush islands, cover values were compared with a t-test. To determine how species composition responded across elevation and among treatments in response to sagebrush removal, a permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) was conducted on Bray-Curtis dissimilarities among plots using the 'adonis' function in the R vegan package (Oksanen et al. 2013). Bray-Curtis dissimilarity was chosen because it has been shown to capture species turnover along environmental gradients (Faith et al. 1987). Elevation, treatment and year were included as factors in the linear model, in addition to all possible interactions of these three factors. The distance matrix was then permuted 999 times and pseudo-F statistics were calculated for each term in the model. Canonical Analysis of Principle coordinates (CAP) was employed as an ordination method to

visually display the treatment effects on species composition (Anderson and Willis 2003). Finally, the responses of aggregate community responses (species richness and cover of grasses, forbs, and total cover) were evaluated with linear models where year, elevation and shrub treatment were factors and pre-treatment cover as a covariate.

Results

Plant community response to recent sagebrush encroachment

At 3700 m there was significantly higher total cover of non-sagebrush species in un-colonized than in sagebrush-colonized fell field (t_{17}=4.23, p<0.01). When grouped together, grasses had significantly less cover in shrub islands than un-encroached alpine fell field (Fig 2.1; t_{14}=4.68, p<0.01). Individually, the grass species *Stipa pinetorum* (t_{15}=3.19, p<0.01), *Elymus elymoides* (t_{15}=3.80, p<0.01) and *Koeleria macrantha* (t_{15}=2.55, p=0.02) had greater cover outside of the shrub islands. Unlike the grasses, there was not a significant difference in the cumulative cover of forb species between sagebrush colonized and un-colonized alpine fell field (Fig. 2.1; t_{21}=1.15, p=0.26). Individually, there was significantly more cover of *Eriogonum ovalifolium* in open fell field (t_{15}=2.48, p=0.03) while the other cushion plant, *Trifolium andersonii*, had no significant difference in cover between encroached and un-encroached fell field (t_{15}=0.52, p=0.61).

Plant community response to sagebrush removal

PERMANOVA analysis of Bray–Curtis dissimilarities in species abundances among plots found there were significant effects of Elevation ($F_{2,134}$=98.96, p<0.01),

Sagebrush ($F_{2,134}$=2.28, p<0.01) and an Elevation*Sagebrush interaction ($F_{4,134}$=2.97, p<0.01) (Table 2.1a). Pairwise comparisons found significant differences between Open and Sagebrush (t=2.35, p<0.01) and Open and Removal treatments (t=2.14, p<0.01) at 3700 m (Table 2.1b). At that elevation, species in Open plots were divergent from both Removal and Sagebrush treatments generally along the CAP1 axis (Table 2.2, Fig. 2.2). At 3100 m there was a significant difference between Open and Sagebrush treatments (t=1.75, p=0.01) but no significant difference between Open and Removal treatments (t=1.36, p=0.11) or Removal and Sagebrush treatments (Fig. 2.2; t=1.47, p=0.07). At 2900 m there were significant differences between Open and Sagebrush (t=1.76, p=0.05) and Removal and Sagebrush treatments (t=1.96, p=0.02) with divergence between Removal and Sagebrush treatments, with Open plots falling in closer alignment with Shrub plots than Removal plots (Table 2.2, Fig. 2.2).

Aggregate community responses

There were significant Elevation ($F_{2,120}$=19.4, p<0.01), Sagebrush ($F_{2,120}$=8.80, p<0.01), Year ($F_{1,120}$=10.1, p<0.01) and Elevation*Sagebrush ($F_{4,120}$=6.29, p<0.01) effects on total plot cover (Table 2.3). Open plots had greater cover than Sagebrush and Removal plots at 3700 m while there were significant pairwise differences at lower elevations (Fig. 2.3). Similar effects and patterns were present for total grass cover (Table 2.3, Fig. 2.3). For forb cover, there were significant Elevation ($F_{2,120}$=43.0, p<0.01), Year ($F_{1,120}$=7.13, p=0.01) and Elevation*Year ($F_{2,120}$=4.27, p=0.03) (Table 2.3) with the greatest forb cover at 3100 m (Fig. 2.3). The effect of year is attributed to generally equal declines in cover across treatments from 2012 to 2013 as a result of drought conditions

over the course of the experiment. Year over year differences between treatments were not appreciable and so data is presented as averages across years. For species richness, there were significant effects of Elevation ($F_{2,120}$=10.3, p<0.01) and Sagebrush ($F_{2,120}$=7.45, p<0.01) (Table 2.3) with generally greater species richness in Open plots at higher elevations than Sagebrush and Removal plots (Fig. 2.3).

Leaf Water Potential

Due to insufficient available plant material I was unable to sample leaf water potential for all species at all sites and no samples were measured from the 2900 m site. Of the samples measured, there were no significant effects of Elevation, Sagebrush or their interaction for individual species or when all samples were grouped together (Table 2.4).

Discussion

The encroachment of shrubs into grasslands has often been attributed to fire suppression or changes in grazing regime (Eldridge et al. 2011). However, in the White Mountains it appears that neither of these factors is contributing to the expansion of sagebrush into high alpine habitats. Instead, long-term rises in temperature and declines in precipitation are likely responsible (Chapter 1). At high elevations, sagebrush expansion appears to be inhibiting growth of the common grass species, with neutral effect on the cover of cushion plants, the dominant forbs in this system (Fig. 2.1). Findings here are consistent with studies of shrub encroachment in other alpine systems that have also resulted in decreased cover of co-occurring species (Wookey et al. 2009,

Brandt et al. 2013). These findings suggest that the declines of cushion plants reported in Chapter 1 are not tied to sagebrush expansion but instead are the result of long-term warming and drying, especially considering that declines in these species occurred at higher elevations where sagebrush has not yet established robust populations.

There were no strong cover responses to sagebrush removal across the elevation gradient. Since species in this experiment are long-lived perennials, it may take several years until significant responses are detectable. Further, this experiment was conducted during a period of drought and species may not have responded as strongly as they would under weather conditions with average precipitation. Other experiments that have removed neighboring species across elevation gradients have found that target species (those that are left after removal) responded negatively to the removal of neighbors at high elevations but positively at lower elevations (Callaway et al. 2002) while experiments that have removed sagebrush have found increased cover of co-occurring plant species in response to its removal (Berlow et al. 2003, Inouye 2006). In California's Sierra Nevada, herbage cover increased one year after the removal of sagebrush at a location where this species had recently established (Bauer et al. 2002). Specifically, herbage cover increased linearly with increasing soil moisture when sagebrush was removed, although all removal sites experienced positive responses regardless of soil moisture (Berlow et al. 2003). While the stress gradient hypothesis is often thought of in terms of increasing facilitation with increasing elevation (Bertness and Callaway 1994), in xeric systems opposing gradients of aridity and temperature can result in unpredictable species interactions (Michalet et al. 2014). Along the White Mountains elevation gradient, water limitation may have a strong influence on competitive interactions, with facilitation

or even neutral interactions at lower, drier elevations and competition at higher, wetter elevations. However, there was no significant water stress response detected across treatments (Table 2.4), suggesting that competition for water is not directly responsible for the observed responses to sagebrush presence. Further, increased temperatures have, at least in the short-term, largely negative effects on the plant community but sagebrush appears to buffer these effects (Chapter 3). Regardless of sagebrush's ability to buffer co-occurring species against rising temperatures, it may be allelopathy by sagebrush that is driving the responses observed by grasses along the elevation gradient.

While there was minimal response of vegetative cover to sagebrush removal, there were changes in community composition. At lower elevation sites, analysis of species composition shows divergence in species composition between removal and shrub plots. At both these sites, open plots tended to overlap with species dispersion between both shrub and removal treatments. This pattern is most pronounced at 2900 m and has a weaker signature at 3100 m (Fig. 2.2b&c). At the highest elevation, however, removal and shrub treatments have considerable overlap with strong divergence from open plots. However, there is some overlap between removal and open treatments, suggesting that species composition in removal plots is moving toward increased similarity to open plots (Fig. 2.2a). This pattern from low to high elevation may be indicative of species along this gradient evolving to withstand sagebrush's allelopathic properties (Weaver and Klarich 1977, Groves and Anderson 1981). At 3700 m, where sagebrush is a recent arrival, there is a strong negative response by grass species (Fig. 2.1) but this is not apparent at lower elevations where sagebrush has been present for much longer. Though research on this subject is limited, an experiment examining native

grass species grown in competition with *Centaurea maculosa,* an invasive species in North America that exudes allelopathic compounds, found that naïve grass populations performed poorly compared to experienced populations (i.e. have persisted in the presence of *C. maculosa* over a prolonged period) (Callaway et al. 2005). In the White Mountains, sagebrush has the strongest effect on community composition at the upper margin of its range, suggesting a strong negative effect that has been overcome through selection for tolerance to sagebrush's allelopathic compounds at lower elevations. Future research should test if evolved adaption to the presence of sagebrush has occurred across the White Mountains elevation gradient. Further, the impact of allelopathy by sagebrush on forb species has not received extensive study and literature on the subject is depauperate. However, our observations suggest that forb species in the White Mountains are not inhibited by the presence of sagebrush and that declines in cushion plants described in Chapter 1 are being driven primarily by long-term climatic trends. Future research should aim to isolate the impact that volatile organic compounds exuded by sagebrush have on forb species in order to confirm the lack of negative effects on this functional group observed in our experiment.

Based on the patterns observed here, the encroachment of sagebrush into the White Mountains' alpine zone is having a negative effect on the grass species found there. While the removal of sagebrush did not have strong effects on species' cover, removal did have a significant effect on community composition at the lowest elevation. These results demonstrate that while sagebrush has important influences on herbaceous species composition in the White Mountains, they are only partially consistent with the predictions of the stress gradient hypothesis. However, evolved resistance to allelopathy

by sagebrush may be an important driver of community response to sagebrush presence, and more study of it effects across elevationally distributed plant populations is needed.

Table 2.1. (a) Results from PERMANOVA analysis of Bray–Curtis dissimilarities abundance data with year and elevation, treatment and year as fixed variables, permutated 999 times. (b) Pairwise comparisons of Bray–Curtis dissimilarities abundances of open, sagebrush and removal treatments at 3700 m, 3100 m and 2900 m.

(a)	*DF*	*Pseudo-F*	*p*
Elevation	2,134	98.96	**<0.01**
Shrub	2,134	2.28	**<0.01**
Year	1,134	1.72	0.06
Elevation:Sagebrush	4,134	2.97	**<0.01**
Elevation:Year	2,134	1.38	0.13
Sagebrush:Year	2,134	0.20	1.00
Elevation:Sagebrush:Year	4,134	0.21	1.00

(b)	3700 m		3100 m		2900 m	
	t	*p*	*t*	*p*	*t*	*p*
Open:Sagebrush	2.35	**0.01**	1.75	**0.01**	1.76	**0.05**
Open:Removal	2.14	**0.01**	1.36	0.11	1.96	**0.02**
Sagebrush:Removal	0.34	0.99	0.07	1.47	1.12	0.31

Table 2.2. Correlation values of species abundances and canonical analysis of principal coordinates (CAP) axis scores.

	3700 m		3100 m		2900 m	
Species	CAP1	CAP2	CAP1	CAP2	CAP1	CAP2
Allium atrorubens	0.00	0.00	0.00	0.00	0.00	0.00
Androsace septentrionalis	0.00	0.00	0.23	0.13	0.31	0.08
Antenaria rosea	0.18	-0.03	0.00	0.00	0.00	0.00
Arabis holboellii	0.00	0.00	0.00	0.00	0.01	0.18
Arabis lemmonii	0.00	0.00	-0.11	0.04	0.09	-0.03
Arenaria kingii	-0.19	0.06	0.00	0.00	0.33	-0.04
Astragalus oophorus	0.00	0.00	0.00	-0.45	-0.12	-0.07
Castilleja applegatei	0.00	0.00	0.00	0.00	0.32	0.09
Chenopodium berlandieri	0.00	0.00	0.00	0.00	0.00	0.00
Chrysothamnus viscidiflorus	-0.10	0.18	0.00	0.00	0.00	0.00
Cryptantha flavoculata	0.00	0.00	-0.10	-0.12	0.00	0.00
Draba oligosperma	-0.10	0.01	0.00	0.00	0.00	0.00
Elymus elymoides	-0.64	-0.27	-0.67	0.13	0.60	-0.41
Erigeron pygmeus	-0.38	-0.21	0.00	0.00	0.00	0.00
Eriogonum gracilipes	0.00	0.00	0.00	0.00	0.39	0.55
Eriogonum ovalifolium	-0.49	-0.08	0.00	0.00	0.00	0.00
Eriogonum umbelatum	0.00	0.00	-0.36	-0.41	0.00	0.00
Erysimum argillosum	0.00	0.00	0.08	-0.07	-0.04	0.04
Koeleria macrantha	-0.41	-0.07	0.12	-0.34	0.18	0.06
Lewisia rediviva	0.00	0.00	0.00	0.00	-0.14	0.06
Linanthus nuttallii	-0.13	0.23	-0.77	0.33	0.00	0.00
Linanthus pungens	-0.37	-0.41	0.09	-0.06	0.06	0.02
Mimulus suksdorfii	0.00	0.00	0.00	0.00	0.00	0.00
Monarda odoratissima	0.00	0.00	0.08	-0.08	0.00	0.00
Muhlenbergia richardsonis	-0.44	0.39	0.00	-0.01	-0.11	-0.52
Oryzopsis hymenoides	0.00	0.00	0.02	-0.23	0.00	0.00
Penstemon heterodoxis	-0.07	0.13	0.00	0.00	0.00	0.00
Phlox condensata	0.04	0.21	0.00	0.00	0.00	0.00
Phlox longifolia	0.00	0.00	0.00	0.00	-0.36	0.03
Poa seconda	0.07	-0.08	0.00	0.00	-0.05	0.03
Potentilla pseudosericea	-0.23	-0.09	0.00	0.00	0.00	0.00
Pyrrocoma apargioides	-0.16	0.10	0.00	0.00	0.00	0.00
Silene bernardina	0.00	0.00	0.00	0.00	0.15	0.18
Stipa comata	0.00	0.00	0.37	0.02	0.42	-0.21
Stipa pinetorum	-0.56	0.26	0.47	0.54	0.47	0.39
Townsendia scapigera	-0.11	-0.03	0.00	0.00	0.00	0.00
Trifolium andersonii	0.13	0.09	0.25	0.39	0.00	0.00

Table 2.3. Results from ANOVA comparing responses by elevation, sagebrush presence, year and their interactions for total cover, total grass cover, total forb cover and species richness.

	Total Cover			Total Grass		Total Forb		Richness	
	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Elevation	2,120	19.38	**<0.01**	100.83	**<0.01**	43.02	**<0.01**	10.27	**<0.01**
Sagebrush	2,120	8.80	**<0.01**	18.92	**<0.01**	2.78	0.07	7.45	**<0.01**
Year	1,120	10.11	**<0.01**	5.15	**0.03**	7.13	**0.01**	2.97	0.09
Elevation:Sagebrush	4,120	6.29	**<0.01**	17.57	**<0.01**	1.20	0.32	0.97	0.43
Elevation:Year	2,120	2.85	0.06	2.31	0.10	4.27	**0.02**	2.55	0.08
Sagebrush:Year	2,120	0.79	0.46	1.41	0.25	0.23	0.79	0.03	0.97
Elevation:Sagebrush:Year	4,120	0.29	0.88	1.09	0.36	0.20	0.94	0.03	1.00

Table 2.4. Results from ANOVA comparing leaf water potential by elevation, sagebrush and their interaction. There were no significant effects of elevation or sagebrush presence on leaf water potential values.

	Combined species			All Grass			*Stipa pinetorum*			*Elymus elymoides*			*Trifolium andersonii*		
	DF	*F*	*p*	DF	*F*	*p*	DF	*F*	*p*	DF	*F*	*p*	DF	*F*	*p*
Elevation	1,42	2.11	0.15	1,41	3.38	0.07									
Sagebrush	2,42	1.01	0.37	2,41	0.91	0.41	2,37	0.89	0.42	2,22	0.71	0.50	2.13	0.11	0.89
Elevation:Sagebrush	2,42	0.25	0.78	2,41	0.20	0.82									

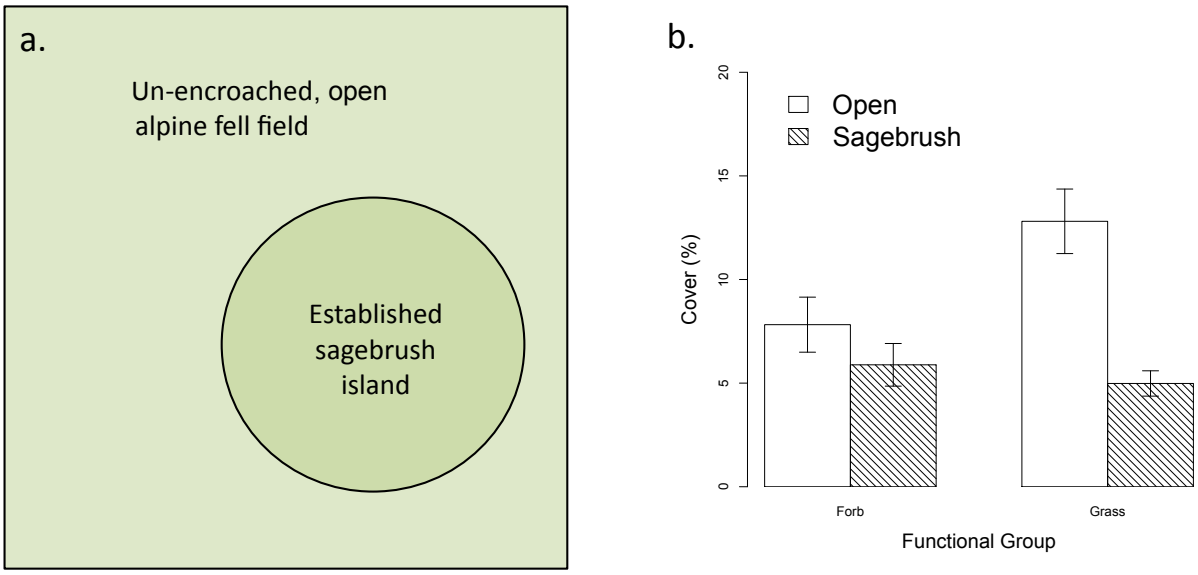

Figure 1.1. a) Diagram of shrub "islands" in sagebrush encroached alpine fell field. b) Vegetative cover of grass and forb functional groups in sagebrush encroached (shrub) and un-encroached (open) alpine fell field at 3700 m.

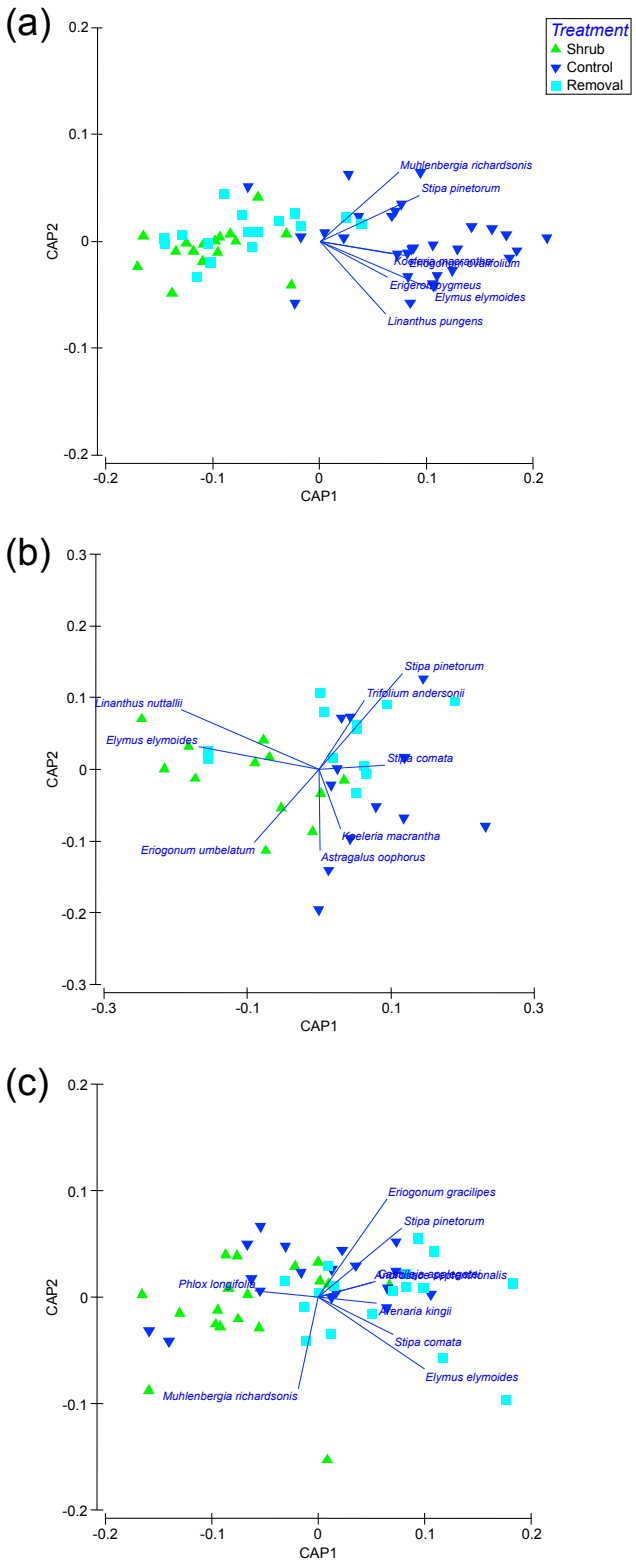

Figure 1.2. Canonical analysis of principal coordinates of Open, Shrub and Removal treatments at (a) 3700 m, (b) 3100 m and (c) 2900 m.

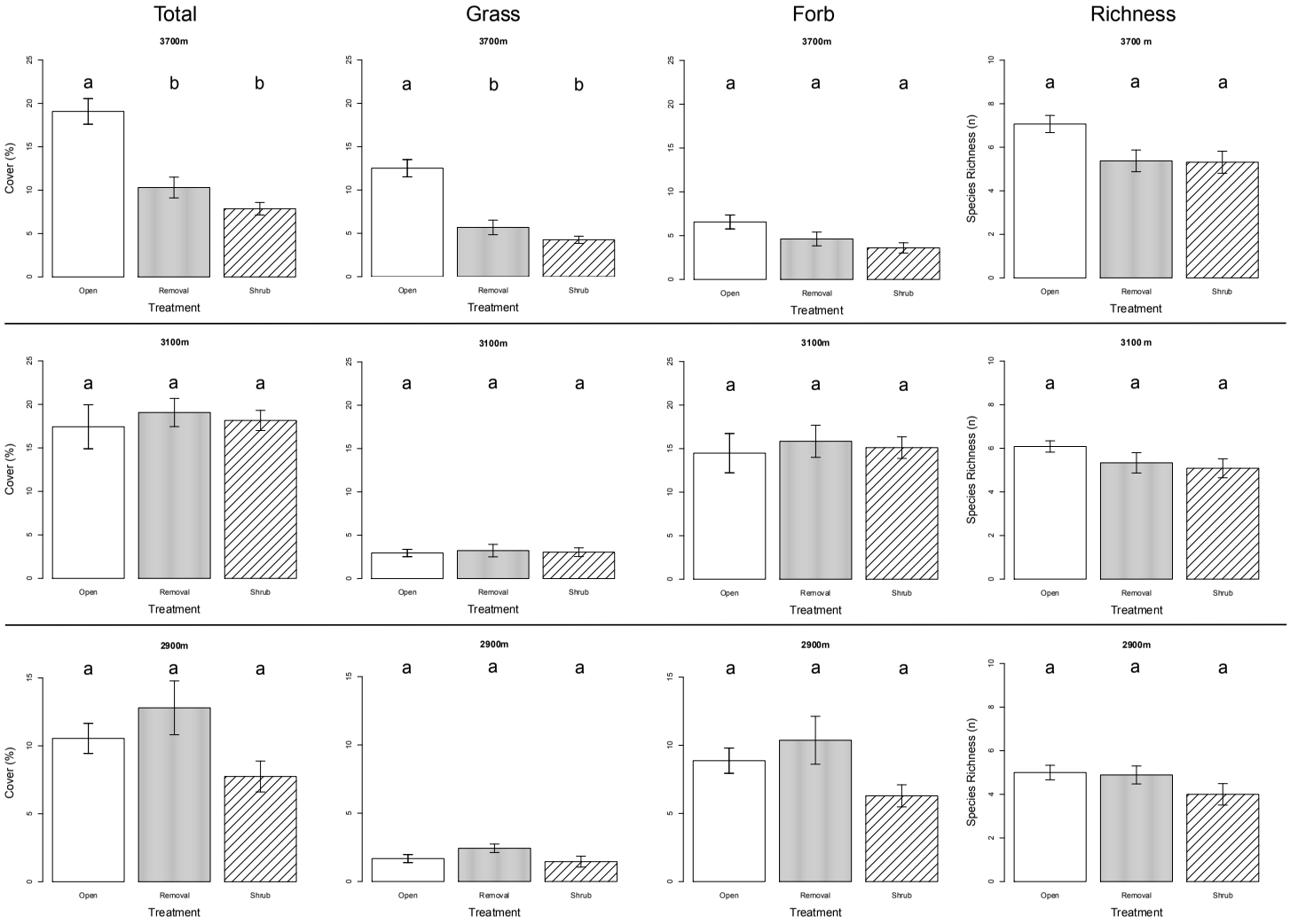

Figure 2.3. Columns 1, 2 and 3: Mean total, grass and forb cover across open, removal and shrub treatments at 3700 m, 3100 m, and 2900 m. Column 4: Mean species richness across open, removal and shrub treatments at 3700 m, 3100 m, and 2900 m.

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CHAPTER 3

Plant community response to warming across an elevation gradient in an arid North American Mountain range

Abstract: Rapid climate change has resulted in shifts in the distribution and abundance of organisms. Such shifts could be the result of direct responses to changes in the environment, or indirect responses resulting from altered biotic interactions among species. For instance, experimental warming often increases shrub abundance; shrubs can have either facilitative or inhibitory influences on understory species depending on environmental context, and hence increased shrub abundance could initiate important indirect effects of warming on plant communities. Understanding how rapidly changing climate will influence the outcomes of these relationships is a subject that has received limited attention but is important for constructing predictive models. In California's White Mountains, where sagebrush has encroached into alpine areas over the past half-century, an artificial warming experiment was conducted using open top warming chambers at two elevations to test how plant species respond to warming and if these responses varied by elevation and the presence of sagebrush. It was expected that alpine species at the lower (warm) margins of their range would respond negatively to warming, with potentially positive responses at high elevations, and that the presence of sagebrush might dampen these responses. Experimental warming achieved an increase of 2.5 - 3.5 C and decreased overall plant cover, especially at the lower elevation site. A strong decline in forb abundance with warming drove the overall cover response at the lower elevation.

Forbs also declined under sagebrush at the low elevation but there was no interaction with warming, suggesting the forb decline under warming was a direct response to the environmental change. In contrast, grasses at this elevation increased in cover with warming only under sagebrush, indicating they may have responded indirectly to warming via competitive release following decline of the forbs, which dominated biomass at that elevation. Similarly, at the high elevation site species richness increased with warming only under sagebrush, again where overall cover declined, suggesting sagebrush encroachment at high elevations can modify community responses to rising temperatures. Mechanistically, the indirect influences of sagebrush were not explained by a separate shading treatment, or by measures of plant water stress. These results are only a snapshot of potential responses to warming in a community of slow-growing perennial plants, but suggest that alpine plant communities in arid environments could experience significant change over a relatively short period in response to rapid warming, due to a combination of direct responses to warming, and indirect responses mediated by altered species composition

Introduction

In recent decades climate has changed worldwide (Socker et al. 2013), and in the southwestern U.S. the future climate is predicted to become both warmer and drier (Seager et al. 2007). Plant communities are already responding to climate change through earlier timing of plant activity and shifts in species ranges poleward in latitude and upward in elevation (Walther et al. 2002, Walther 2003, Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006, Lenoir et al. 2008, Walther 2010, Socker et al. 2013). These

range shifts have largely corresponded to model predictions (Thomas et al. 2004, Thuiller 2004, Brooker et al. 2007), whereby species shifts are assumed to be direct responses to a shifting environment, and their movements track their "climatic niche." As species rearrangements occur, however, shifts in species composition could result in novel species interactions and indirect effects on species abundances and community composition (Davis et al. 1998, Brooker 2006, Saccone et al. 2009). For instance, in arid ecosystems facilitation by nurse plants could act as a shield to beneficiary species against increasingly harsh conditions (Cavieres et al. 2014).

The stress gradient hypothesis predicts that along gradients of increasing abiotic stress, plant interactions shift from competitive to facilitative (Bertness and Callaway 1994). In mountain environments the stress gradient hypothesis is usually considered in terms of temperature stress; i.e. for any given species competition dominates at low elevations and facilitation at high elevations. This prediction has largely held true in mesic environments (Maestre et al. 2009). However, in xeric environments opposing stress gradients of temperature and precipitation are present. In such environments, facilitation by drought-tolerant species is important at lower elevations due to increased water stress. Shrubs are often important facilitators in such environments and their response to stress contributes greatly to plant-plant interactions across opposing stress gradients. As a result, at lower elevations in arid environments, the importance of facilitation by drought-tolerant species may help to mitigate the negative impacts of climate change but at higher elevations facilitation by cold-tolerant species may weaken under warming conditions (Michalet et al. 2014). To predict future changes in plant communities it is important to understand if individual species along a gradient of stress

respond negatively, positively or neutrally to direct abiotic shifts as well as indirectly through biotic interactions as a result of climate change (Angert et al. 2013, Cavieres et al. 2014). Here, we test the response of plant communities to warming with and without the presence of shrubs in a xeric mountain environment.

In California's White Mountains (USA) it is predicted that suitable habitat will shift upward and shrink (Murphy and Weiss 1992, Ackerly et al. 2010) in response to predicted temperature rise (Socker et al. 2013) resulting in shifting plant species distributions (Van de Ven et al. 2007, Ackerly et al. 2010). A recent resurvey in the White Mountains showed that, in correlation with a 1 °C increase in temperature over 49-years, there have been significant changes in the distribution and abundance of several plant species there (Murphy and Weiss 1992, Ackerly et al. 2010, Kopp and Cleland 2014). Models should allow policy makers a greater level of confidence when formulating strategies to preserve biodiversity in the face of continued climate change. However, the use of experimental tools to empirically test biotic responses to future environmental conditions remains important in testing the reliability of models. In that vein, models need to account for indirect responses of individual species to climate change in the form of both shifting and novel biotic interaction (Cavieres et al. 2014). Along with the growing catalog of documented biotic responses to climate change there is also a robust dataset of experimental work demonstrating potential biological responses to future climate change. The International Tundra Experiment has employed a uniform protocol using passive open top warming chambers (Molau 1996) to simulate projected future temperatures and study the response of Arctic and alpine plant communities to warmer conditions. These passive warming studies have produced significant short-term

(Walker et al. 2006) and long-term (Elmendorf et al. 2012) plant community responses. However, it has also been found that responses can vary from species to species within a community (Klanderud 2008) and species specific responses could affect competitive and facilitative interactions (Cavieres and Sierra-Almeida 2012). Warming experiments conducted along gradients of abiotic stress can help elucidate under what conditions competitive and facilitative interactions influence responses to climate change.

The response of plant communities to warming has been studied over a broad geographic range but, to our knowledge, has received little attention in arid alpine or sub-alpine locations in North America. An artificial warming experiment was conducted using open top warming chambers at two elevations in California's White Mountains with the expectation that plant species would respond individually to warming and their response would vary by elevation and the presence of sagebrush. Specifically, it was expected that alpine species at the lower margin of their elevation range would respond negatively to warming but that the presence of sagebrush could moderate these responses. Conversely, it was expected that at higher elevations alpine species near the upper edge of their elevational range would respond positively to warming, and that sagebrush encroachment would dampen these responses through competitive inhibition. Further, two potential mechanism for indirect effects of sagebrush on understory species were evaluated; an artificial shading treatment was established to mimic the influence of shading by shrubs, and plant pre-dawn water-potential measurements were taken to evaluate how the presence of sagebrush influenced understory species access to soil moisture.

Methods

An artificial warming experiment was carried out in California's White Mountains, USA. The White Mountains are located on the western edge of North America's Basin and Range Province and lie within the rain shadow of the Sierra Nevada Mountains. The regional climatology is cold and arid with winter snow accounting for much of the yearly precipitation. Total precipitation varies with elevation, ranging from 456 mm/yr at Barcroft Station (3800 m) to 327 mm/yr at Crooked Creek Station (3094 m). Temperature is also strongly dependent on elevation, with a mean annual temperature of -1.7 °C at Barcroft Station, and 0.9 °C at Crooked Creek Station (Hall 1991).

The response of alpine plant communities to warming was tested at two locations in the White Mountains. High elevation plots were located at 3700 m (37° 34.1' N, 118° 14.3' W), while low elevation plots were located at 3100 m (37° 29.9' N, 118° 10.3' W). In late-June and early-July 2011 1-m^2 plots were established on granitic derived soils at both sites. At each elevation, plots were arranged in a randomized design with 4 replicate plots of each of the 5 treatments: warmed with *Artemisia rothrockii* (Warmed Sagebrush) and without (Warm) established sagebrush plants, shaded without sagebrush (Shade), and controls with sagebrush (Sagebrush) and without (Open) established sagebrush plants for a total of 20 plots at each site. Plots were selected based on species composition, abundance, and cover of commonly shared species at each site. Warming chambers were constructed following Molau (1996) and were made of 5 oz clear Crystalite fiberglass (thickness = 1.1 mm, light transmission = 90%) (Ridout Plastics Company Inc., San Diego, CA, USA). Chambers were 1-m diameter and were held in place year round by fastening the base of the chambers to 152 mm spike nails.

Throughout the experiment, surface temperatures within plots (three plots per treatment at each site, n=30) were monitored using iButton temperature loggers (Maxim Integrated Products, Sunnyvale, CA, USA). To shield against solar radiation, the temperature loggers were attached to the interior of 5.1 cm diameter by 7.6 cm long white PVC pipe. In order to determine treatment effects on plant water stress, pre-dawn (0430–0530) leaf water potential data were collected in late-May and early-June 2013 using a Pressure Chamber Instrument (PMS Instrument Company, Albany, OR, USA). At the beginning of the experiment, and at the peak of each growing season, species cover was visually estimated in each plot using a 1-m^2 gridded quadrat in order to measure individual species responses to treatments. Finally, to measure changes in growth of sagebrush, marked stems were tagged and measured for elongation and changes in diameter at the same time species cover was recorded. Sagebrush height was also recorded at that time.

Data analysis

Statistical analysis was conducted using the statistical programming language R version 3.0.3 (R Core Development Team, 2014). The effectiveness of the warming chambers were assessed using linear mixed models where plot was included as a random factor to account for repeated measures, and Elevation, Warming and Sagebrush were included as fixed factors. Responses of percent cover and species richness to treatments were evaluated using linear models with Elevation, Warming, Sagebrush and Year as factors and a preteatment measure of cover or richness as a covariate. Tukey's honest significant differences of least-squared means were performed as post-hoc tests. Pre-

dawn water potential was replicated within plots, and species varied between elevations, hence these data were analyzed using linear mixed models where plot was included as a random factor, and Warming and Sagebrush presence were fixed factors, analyzed separately for each elevation. The Shading treatment was compared separately to Open and Sagebrush treatments via t-tests.

Results

Temperature manipulation

The effect of warming chambers on temperature varied by elevation and depended on the presence of sagebrush within plots (Table 3.1). Warming chambers increased yearly mean temperatures by 2.5 °C compared to Open plots (Fig. 3.1a; Table 3.1) at 3100 m while the increase was 3.5 °C (Fig. 1b; Table 3.1) at 3700 m. Warmed Sagebrush plots were 2.0 °C warmer than control Sagebrush plots (Fig. 1a; Table 3.1) at 3100 m and 2.8 °C warmer (Fig. 3.1b; Table 3.1) at 3700 m. At 3100 m Shaded plots were 0.5 °C warmer than Sagebrush plots (Fig. 3.1a; Table 3.1) while there was no temperature difference between Shaded and Sagebrush treatments ($p=0.54$) at 3700 m (Fig. 3.1b, Table 3.1).

The overall mean differences in temperatures between warming and control treatments were not consistent across a 24-hour period. Mean daily minimum temperatures in summer 2012 occurred just prior to sunrise and were 2.0 °C colder in Warmed plots compared to Open plots at 3100 m (Fig. 3.1c) while Warmed plots were 0.1 °C warmer than Open at 3700 m (Fig. 3.1d). Mean daily maximum temperatures were

7.0 °C and 4.7 °C warmer in Warmed than Open at 3100 m (Fig. 3.1c) and 3700 m (Fig. 3.1d), respectively.

Community level responses

There was no warming ($F_{1,12}$=0.56, p=0.47) or year ($F_{1,12}$=1.15, p=0.30) effect on total cover of sagebrush. Attempts to monitor stem elongation by sagebrush were unsuccessful due to a high rate of marked stem breakage. However, there was no significant Warming ($F_{1,12}$=0.01, p=0.92) or Elevation ($F_{1,12}$=3.20, p=0.10) effect on sagebrush height. For total plot cover, there were significant Elevation ($F_{4,51}$=2.95, p=0.03) Warming ($F_{4,51}$=6.39, p>0.01), Sagebrush ($F_{4,51}$=6.33, p<0.01), Year ($F_{1,51}$=22.2, p<0.01) and Elevation*Sagebrush ($F_{2,51}$=5.84, p=0.01) effects (Table 3.2a). Overall, total vegetative cover was lower in Warmed plots than Open at both elevations with lower cover in Sagebrush plots compared to Open plots at 3100 m. At 3100 m, Warmed Sagebrush plots had significantly less cover than unwarmed open plots (p<0.01) (Fig. 3.2). For total grass cover there were significant Elevation ($F_{4,51}$=13.8, p<0.01), Warming ($F_{4,51}$=5.48, p<0.01), Sagebrush ($F_{4,51}$=4.40, p<0.01), Elevation*Warming ($F_{2,51}$=5.54, p=0.01) and Elevation*Warming*Sagebrush ($F_{1,51}$=5.97, p=0.02) effects. Greater cover of grasses at 3700 m (Fig. 3.2) accounted for the Elevation effect. Generally, there was less cover in Warmed plots than Open, with the exception of Warmed Sagebrush at 3100 m, which had significantly greater cover than unwarmed Sagebrush plots (Fig. 3.2; p=0.04). Forbs experienced significant Elevation ($F_{4,51}$=5.89, p<0.01), Warming ($F_{4,51}$=5.91, p<0.01), Sagebrush ($F_{4,51}$=8.32, p<0.01), Year ($F_{1,51}$=16.5, p<0.01) and Elevation*Sagebrush ($F_{4,51}$=8.11, p<0.01) effects on cover (Table 3.2a). Warming

generally decreased forb cover and at 3100 m there was less cover of forbs in Sagebrush plots compared to Open plots (Fig. 3.2). Finally, there was significantly lower species richness at 3100 m (Table 3.2a; $F_{1,25}$=7.24, p=0.01).

At 3700 m, shading generally did not have an effect on vegetative cover with the exception of forbs, which had greater cover in Open plots compared to Shade (t=2.26, p=0.05) and marginally greater cover than Sagebrush plots (t=1.88, p=0.08) (Table 3.2b; Fig. 3.3). Sagebrush had lower total, grass and forb cover in Sagebrush plots at 3100 m (Table 3.2b; Fig. 3.3). There was no effect of shading on species richness at 3700 m but at 3100 m there was greater species richness in shaded plots compared to open plots (t=3.53, p<0.01) (Table 3.2b; Fig. 3.3).

Leaf Water Potential

There were no significant differences in pre-dawn water potential in response to warming or sagebrush presence at either elevation (Table 3.3a). At 3100 m there were significant differences in grass leaf water potential between Shade and Open treatments (t=6.23, p<0.01) and Shade and Sagebrush treatments (t=4.53, p<0.01) while at 3700 m there was a significant differences in grass leaf water potential between Shade and Open treatments (t=2.99, p<0.01) (Table 3.3b).

Discussion

The overall level of warming produced by open top chambers in the White Mountains matched the level of warming predicted to occur over the next century in California and western-Nevada (Ackerly et al. 2010) and was similar to warming

produced by passive warming devices in other studies (Walker et al. 2006). While open top chambers effectively raised overall mean temperatures (Fig. 3.1a; Table 3.1), several studies that have utilized open top chambers report that the level of heating can be uneven with minimal overnight heating and enhanced maximum temperatures occurring in some studies (Godfree et al. 2011). Temperatures in warmed plots (no sagebrush) at 3100 m showed the greatest departures from controls with minimum temperatures 2.0 °C colder at night and 10.6 °C warmer during the day. In contrast, warmed plots at 3700 m had 0.1 °C warmer minimum temperatures compared to control (Fig. 3.1b; Table 3.1). The discrepancy in minimum temperatures between elevations may be explained by overnight wind patterns. The 3100 m site is in a protected area with light overnight winds (*Western Regional Climate Center* 2014). Without mixing of the atmosphere, particularly in the protected space within an open top chamber, cold air settling results in greater cooling within the chamber. While this effect on wind also occurs at 3700 m, the breezier environment at that elevation (*Western Regional Climate Center* 2014) maintains more mixing and thus less overnight cooling in warmed plots. Warmed sagebrush treatments at both elevations were warmer than control sagebrush plots at night, likely the result of sagebrush canopy creating an insulated layer that was enhanced by the open top chambers. Overall, while the warmed plots (no sagebrush) at 3100 m produced colder overnight temperatures compared to control, the remainder of warmed plots had minimum temperature warming levels similar to what has been observed in other experiments (Godfree et al. 2011).

The open top chambers also produced extreme daytime warming, up to 10.6 °C warmer than controls (Table 3.1; Fig. 3.1a). Similar, yet not as extreme, patterns have

been observed in southern Africa (Musil et al. 2005). One possible explanation for our chambers producing this level of enhanced warming is the high elevation and high amount of cloudless conditions that prevail. During summer months there are rarely days with continuous cloud cover and when clouds do develop they do not usually obscure the sun for prolonged periods. With this high level of solar radiation, temperatures within chambers can reach considerable levels. A global meta-analysis showed that plant responses to experimental warming are less than those observed due to rising temperatures over time, suggesting that artificial warming may not fully represent realistic patterns of climate warming (Wolkovich et al. 2012). Hence, while the warming treatment in this experiment was effective at raising mean temperatures, artifacts associated with lower nighttime temperatures and extreme daytime high temperatures introduce important caveats to the results presented here.

After two years there was less vegetative cover in warmed treatments compared to controls at both 3100 and 3700 m (Fig. 3.2). Especially at the lower elevation site, this response was driven by a decline in the forbs that dominate biomass at this elevation. This suggests that the strong declines in cushion plants observed over time at this elevation (Chapter 1) are more likely a direct response to warming as opposed to an indirect inhibitory response to sagebrush encroachment. Other warming studies using open top chambers have found that plant communities can respond to warming over a relatively short time period, although long-term trends for grass species in these studies have been positive rather than negative (Walker et al. 2006). Further, there is often a lack of positive growth response by forb species to warming (Harte and Shaw 1995, Price and Waser 2000, Jägerbrand et al. 2009). The lack of a positive growth response by sagebrush

to warming was unexpected since upward encroachment in elevation by this species in the White Mountains is positively correlated with long-term increases in temperature (Chapter 1). However, other studies in North American montane systems have observed mixed responses by sagebrush to warming (Price and Waser 2000, Perfors et al. 2003) and shrubs in other arctic and alpine tundra communities have not shown significant positive cover responses until the fourth year of warming (Walker et al. 2006). Further monitoring of this experiment will be needed to establish the directional response of sagebrush to warming in the White Mountains.

Contrary to initial expectations, the presence of sagebrush did not appear to buffer the plant community, at least in the short-term, against rapid climate change. As a result, it appears that species in this arid community are responding directly to climate warming. However, the upward encroachment of sagebrush in response to a lengthening of the growing season displaces grass species in recently colonized areas (Chapter 2). This suggests that grasses are directly (through warming) and indirectly (through sagebrush encroachment) affected by climate change in alpine habitats. The opposite (positive) response by grasses to warming at 3100 m may be the result of grasses taking advantage of competitive release via loss of forb cover. This suggests that cushion plants in the White Mountains do not facilitate other species, at least at lower elevations. In the Andes, where cushion plants act as nurse plants for other species, this facilitative relationship between these cushion plants and other species is weaker at lower elevations (Schöb et al. 2013). While grasses did not increase in response to forb declines in warmed treatments at 3700 m, species richness did increase marginally in warmed sagebrush treatments at that elevation. These patterns suggest that at lower elevations forbs, principally *T.*

andersonii, competitively exclude other species and the loss of this species allows grasses to fill this newly opened space. At 3700 m, where cover decreased in response to warming, there was an increase in species richness in warmed shrub plots (Fig. 3.2). The release from competition coupled with facilitation by sagebrush may explain this response.

In xeric systems, where there are opposing stress gradients (temperature and aridity), the outcome of species interactions in the face of changing climate are unpredictable and species dependent (Michalet et al. 2014). The outcomes of this experiment, as well as results detailed in Chapter 2, appear to demonstrate the complexity of species interactions across the arid elevation gradient in the White Mountains, with sagebrush acting both as a competitor to grasses but also a potential facilitator for new species at high elevations where temperature is low and precipitation higher. At lower elevations, *T. andersonii* appears to be outcompeting grass species, but with this decline, grasses are able to fill the space vacated by this cushion plant. Finally, *T. andersonii* is a species that has experienced significant declines in cover over the past half-century in the White Mountains (Chapter 1) and the negative response to experimental warming suggests that this species will experience continued declines, with the most substantial losses at the lower margins of its range.

Warming experiments have been shown to produce drier soil conditions (Rustad et al. 2001) and individual species rooting depth is important in responses to soil moisture availability (Sala et al. 1989). Overall, shade, shrub and warmed plots were the most water stressed at 3100 m while shade and shrub plots were the most water stressed at 3700 m. For grass species, the lowest leaf water potential values were in shaded plots

(Fig. 3.4) and this corresponds to a positive growth response in this treatment (Fig. 3.3). However, the flush of growth in these plots by shallowly rooted species results in greater leaf surface area for which water can be transpired, drawing down soil moisture and resulting in water stress as the plants mature. Grasses growing under shrubs will benefit from shading alleviating water stress during peak growing season but for plants that rely on deeper soil moisture they will have to compete directly with sagebrush for water. For *T. andersonii*, the greatest amount of water stress was in sagebrush and warmed (no sagebrush) plots, although there was not an overall treatment effect. *Trifolium andersonii* is a species that has both deep tap root as well as shallow, spreading adventitious roots that allow it to take advantage of both deep soil moisture along with temporary shallow surface soil moisture (Rundel et al. 2005). Water stress in sagebrush plots indicates *T. andersonii* may be competing with deep-rooted sagebrush for water while water stress in warmed plots without sagebrush may indicate that warming has resulted in decreased surface and deep soil moisture.

These experimental findings and the observational findings presented in Chapter 1 provide affirmation of predictive models showing shrinking habitat and species distributions in the Great Basin and White Mountains (Murphy and Weiss 1992, Van de Ven et al. 2007, Ackerly et al. 2010). The findings presented here are by no means what the end result of rising temperatures in the White Mountains will produce. The period that produced the data presented here was warm and abnormally dry and this may have potentially masked treatment responses by the slow growing perennial species studied in this experiment due to overall drought stress across treatments. It will be important to observe community responses over a longer period that includes greater interannual

climatic variation. However, these findings coupled with long-term changes in the plant community (Chapter 1) indicate that plant communities in the White Mountains and Great Basin face an uncertain future.

Table 3.1. (a) September 2011 through August 2012 mean temperatures by treatment along with June through August daily mean, minimum and maximum temperatures at 3100 m and 3700 m. (b) Results from ANOVA of the linear mixed models comparing September 2011 through August 2012 mean temperatures by elevation, warming, sagebrush presence and their interactions. (c) Results form t-tests comparing September 2011 through August 2012 mean temperatures between open, sagebrush and shading treatments at 3100 m and 3700 m.

(a)

		12 Month Daily Mean		June-August Daily Mean		June-August Daily Mean Minimum		June-August Daily Mean Maximum	
Elevation	Treatment	Temperature (°C)	StErr	Temperature (°C)	StErr	Temperature (°C)	StErr	Temperature (°C)	StErr
3100 m	Open	8.84	0.06	12.93	0.15	0.13	0.15	24.91	0.16
	Warm	11.37	0.09	16.31	0.19	-1.88	0.16	35.48	0.24
	Shade	8.86	0.07	13.10	0.16	-0.79	0.16	25.61	0.16
	Sagebrush	8.40	0.06	12.67	0.16	-0.41	0.16	24.70	0.14
	Warm Sagebrush	10.43	0.07	15.10	0.17	0.11	0.14	31.87	0.21
3700 m	Open	7.37	0.06	11.75	0.13	1.10	0.10	22.70	0.15
	Warm	10.87	0.07	16.10	0.17	1.22	0.10	33.38	0.25
	Shade	6.79	0.05	10.61	0.11	2.39	0.09	19.65	0.12
	Sagebrush	6.82	0.05	11.32	0.13	1.31	0.10	22.35	0.15
	Warm Sagebrush	9.58	0.06	14.49	0.15	2.89	0.10	27.37	0.20

(b)	*DF*	*F*	*p*
Elevation	1,16	5.02	**0.04**
Warming	1,16	86.00	**<0.01**
Sagebrush	1,16	8.79	**0.01**
Elevation:Warming	1,16	2.39	0.14
Elevation:Sagebrush	1,16	0.25	0.62
Warming:Sagebrush	1,16	0.69	0.42
Elevation:Warming:Sagebrush	1,16	0.12	0.74

(c)	3100 m		3700 m	
	t	*p*	*t*	*p*
Open:Sagebrush	8.11	**<0.01**	10.55	**<0.01**
Open:Shade	0.13	0.90	10.36	**<0.01**
Sagebrush:Shade	7.78	**<0.01**	0.72	0.47

Table 3.2. (a) Results from ANOVA of the linear models comparing total species cover, total grass cover, total forb cover and species richness responses by elevation, warming, sagebrush presence and their interactions. (b) Results form t-tests comparing total species cover, total grass cover, total forb cover and species richness responses between open, sagebrush and shading treatments at 3100 m and 3700 m.

(a)		Total Cover		Grass Cover		Forb Cover		Richness	
	DF	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Elevation	4,51	2.95	**0.03**	13.84	**<0.01**	5.89	**<0.01**	3.21	**0.02**
Warming	4,51	6.39	**<0.01**	5.48	**<0.01**	5.91	**<0.01**	1.80	0.14
Sagebrush	4,51	6.33	**<0.01**	4.40	**<0.01**	8.32	**<0.01**	4.76	**<0.01**
Year	1,51	22.15	**<0.01**	2.47	0.12	16.45	**<0.01**	0.10	0.76
Elevation:Warming	2,51	0.26	0.77	8.18	**<0.01**	0.69	0.50	1.95	0.15
Elevation:Sagebrush	2,51	5.84	**0.01**	3.25	0.05	8.11	**<0.01**	2.18	0.12
Warming:Sagebrush	2,51	0.95	0.39	5.54	**0.01**	0.66	0.52	3.56	**0.04**
Elevation:Year	1,51	0.90	0.35	0.83	0.37	0.13	0.72	0.72	0.40
Warming:Year	1,51	0.15	0.70	0.05	0.82	0.03	0.85	0.72	0.40
Sagebrush:Year	1,51	1.32	0.26	0.03	0.85	2.90	0.09	0.02	0.88
Elevation:Warming:Sagebrush	1,51	0.51	0.48	5.97	**0.02**	1.11	0.30	3.88	**0.05**
Elevation:Warming:Year	1,51	0.03	0.86	0.17	0.69	0.29	0.59	0.64	0.43
Elevation:Sagebrush:Year	1,51	1.56	0.22	0.07	0.79	1.75	0.19	0.02	0.89
Warming:Sagebrush:Year	1,51	0.62	0.44	0.62	0.44	1.12	0.30	0.02	0.89
Elevation:Warming:Sagebrush:Year	1,51	0.13	0.72	0.01	0.91	0.17	0.68	0.24	0.62

(b)	Total Cover				Forb Cover				Grass Cover				Richness			
	3700 m		3100 m		3700 m		3100 m		3700 m		3100 m		3700 m		3100 m	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Open:Sagebrush	0.18	0.86	2.86	**0.01**	1.88	0.08	3.51	**<0.01**	1.79	0.10	4.78	**<0.01**	0.17	0.87	1.57	0.14
Open:Shade	0.58	0.57	0.78	0.45	2.26	**0.05**	0.78	0.46	1.41	0.18	2.51	**0.02**	0.00	1.00	3.53	**<0.01**
Sagebrush:Shade	0.42	0.68	1.37	0.20	0.11	0.92	1.80	0.09	0.34	0.74	3.10	**0.01**	0.3	0.77	1.62	0.13

Table 3.3. (a) Results from ANOVA of the linear mixed models comparing leaf water potential of *Trifolium andersonii* at 3100 m by warming, sagebrush and their interaction along with leaf water stress of grasses by elevation, warming, sagebrush presence and their interactions. (b) Results form t-tests comparing leaf water potential responses of *Trifolium andersonii* and grasses between open, sagebrush and shading treatments at 3100 m and 3700 m.

(a)	*Trifolium andersonii*		Grass	
	$F_{1,13}$	*p*	$F_{1,25}$	*p*
Elevation			83.27	**<0.01**
Warm	0.35	0.56	0.00	0.95
Sagebrush	0.01	0.92	1.74	0.20
Elevation:Warm			0.23	0.63
Elevation:Shrub			0.81	0.38
Warm:Sagebrush	4.16	0.06	0.82	0.37
Elevation:Warm:Sagebrush			0.06	0.81

(b)	*Trifolium andersonii*		Grass			
	3100 m		3100 m		3700 m	
	t	*p*	*t*	*p*	*t*	*p*
Open:Sagebrush	1.74	0.10	1.07	0.30	1.41	0.16
Open:Shade	1.11	0.28	6.23	**<0.01**	2.99	**<0.01**
Sagebrush:Shade	2.45	0.03	4.53	**<0.01**	1.40	0.17

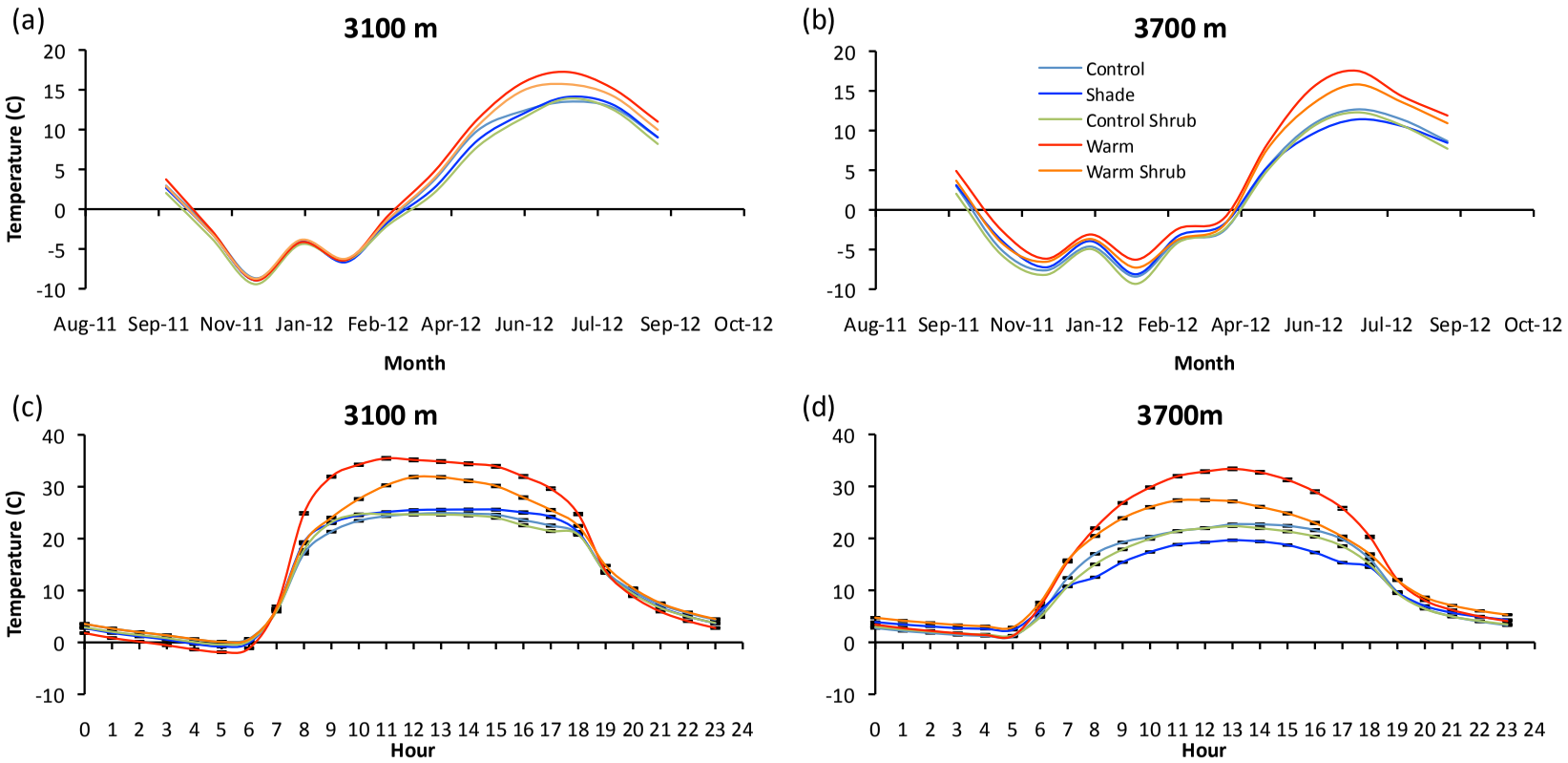

Figure 3.1. Daily mean temperatures from September 2011 to August 2012 for (a) 3100 m and (b) 3700 m along with hourly mean temperatures during summer 2012 at (c) 3100 m and (d) 3700 m.

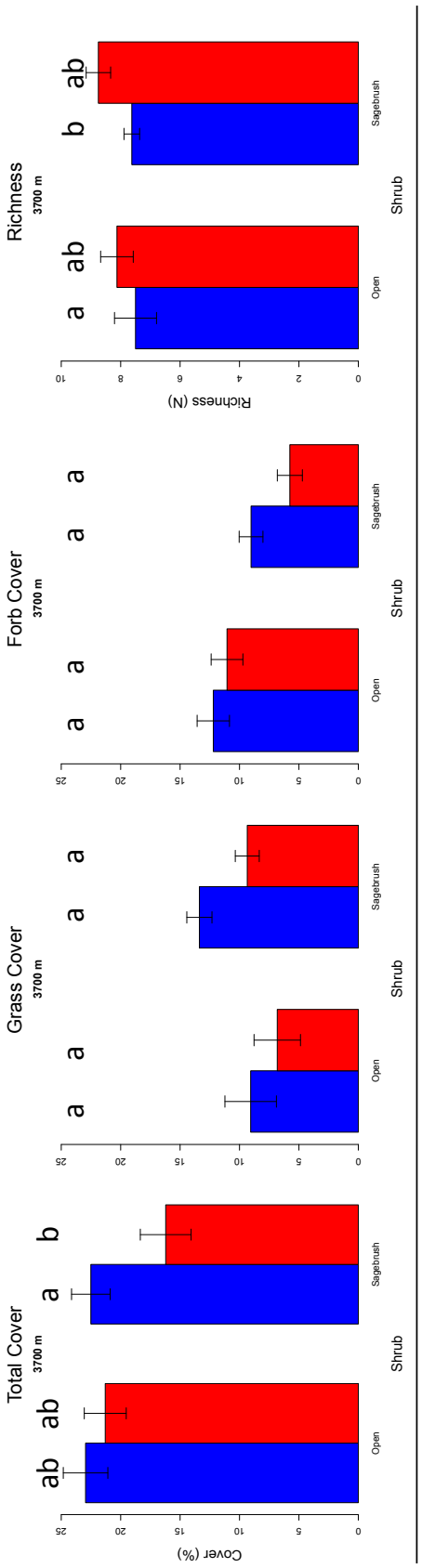

Figure 3.2. Mean total, grass and forb cover along with species richness across open and shrub treatments in response to artificial warming or control at 3700 m and 3100 m. Letters signify significant differences between treatments.

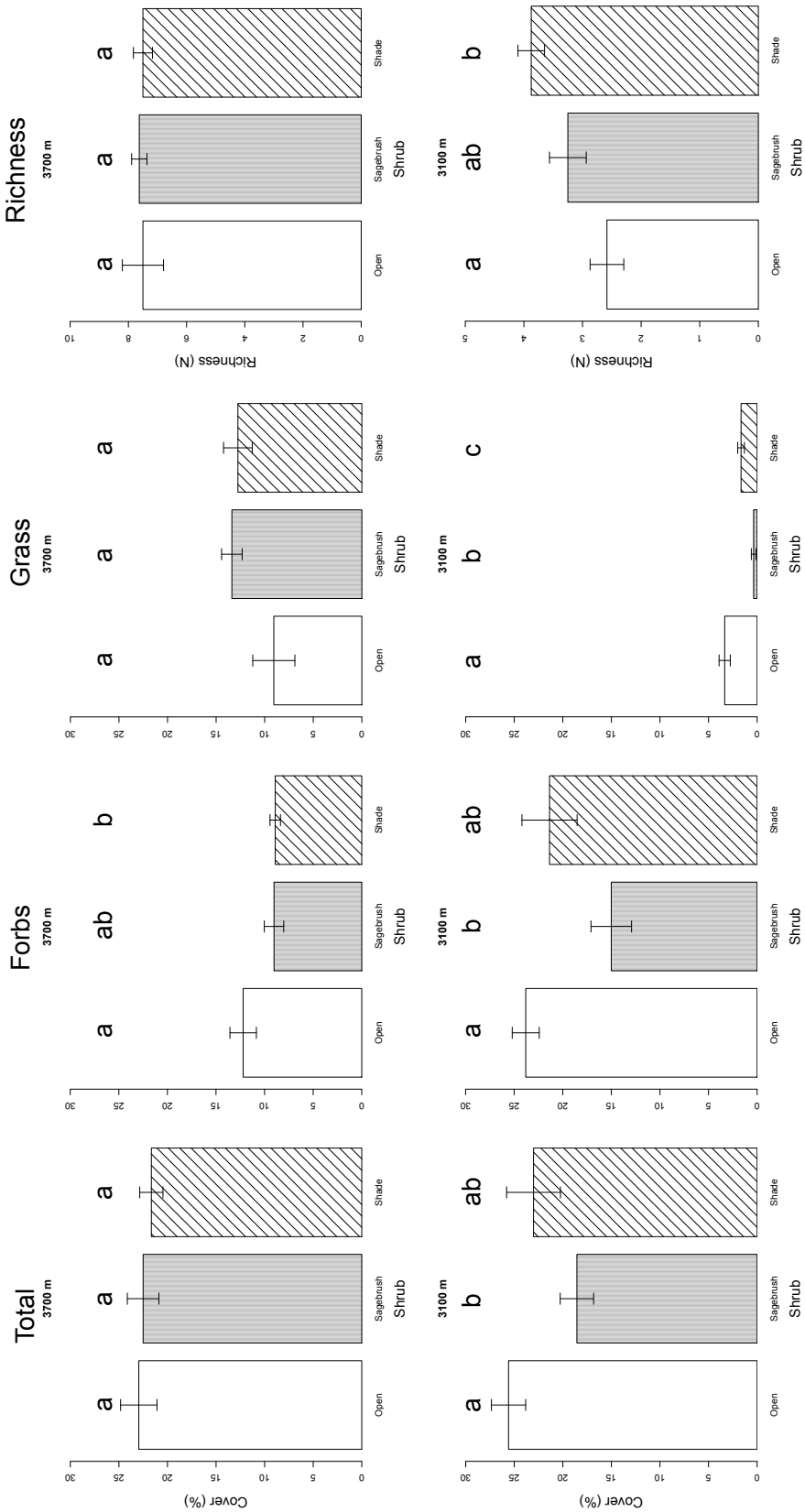

Figure 3.3. Columns 1, 2 and 3: Mean total, grass and forb cover along with species richness across open, sagebrush and shade treatments at 3700 m and 3100 m. Letters signify significant differences between treatments.

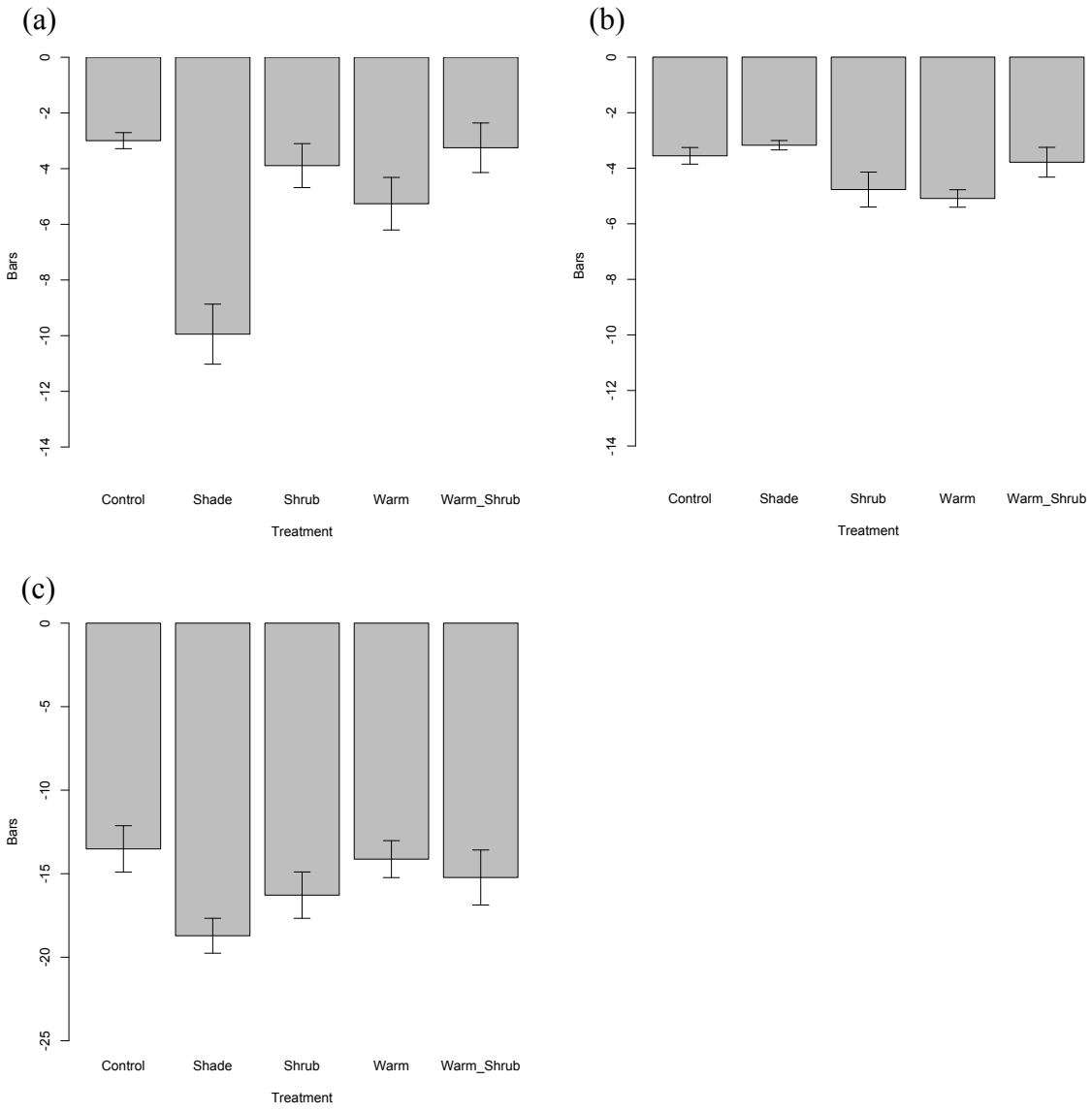

Figure 3.4. Pre-dawn leaf water potential values for grasses at 3100 m (a) and 3700 m (b) along with *Trifolium andersonii* at 3700 m (c).

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CHAPTER 4

Phenological response to warming altered by a range expanding shrub species; an example of indirect effects of warming mediated by species interactions

Abstract: Shifts in plant species ranges and phenology observed worldwide in recent decades are recognized as sensitive indicators of species responses to climate change, and are generally assumed to be the direct consequence of rising temperatures. Phenology can also be influenced by species interactions, and hence indirect effects of climate change on phenology could arise via range shifts and altered species composition. In an arid North American mountain range, sagebrush (*Artemisia rothrockii)* has experienced a rapid upward elevational range expansion into alpine areas previously dominated by prostrate species. Here, I describe how experimental warming and sagebrush presence or absence interacted to influence the phenology of photosynthetic biomass production (as estimated by normalized difference vegetation index (NDVI)), and flowering of the cushion plant, *Trifolium andersonii*, and the grass, *Koeleria macrantha*, at two elevations. The timing of peak canopy greenness was not influenced by warming, but occurred later in the presence of sagebrush, reflecting the late phenology of this species relative to the remainder of the community. Warming increased canopy greenness overall but did not affect the timing of peak NDVI. In contrast, species-level flowering phenology was strongly accelerated by warming, but delayed in the presence of sagebrush. Warming caused *T. andersonii* and *K. macrantha* to experience as much as 11-day advancements in initial and peak flowering dates, but the presence of sagebrush lessened these phenological advancements. Further, total flower production of *T. andersonii* was bolstered by warming, but less so in the

presence of sagebrush. Delays in flowering in artificially shaded plots provide evidence that shading by sagebrush is likely the mechanism acting to delay flowering of the understory species. These data demonstrate that species interactions can modify phenological responses to climate change, and suggest that indirect effects of rising temperatures via shifting species ranges and interactions may even overwhelm the direct effects of rising temperatures on phenology.

Introduction

As the responses of plant communities to global warming have become better understood, two main patterns have emerged. First, plant species have shown the ability to advance their range margins both upward in elevation and poleward in latitude (Parmesan 2006). In arctic and alpine regions shrubs have been particularly responsive, both expanding their ranges over time (Sturm et al. 2001, Myers-Smith et al. 2011), and increasing in abundance in response to experimental warming (Walker et al. 2006). Second, spring phenology (i.e., the timing of biological events such as leaf emergence or flowering) has become earlier (Walther et al. 2002, Root et al. 2003, Parmesan 2006). While advanced spring phenology is often observed in response to warming, there is significant variation among species in the magnitude and even direction of phenological responses, with isolated cases of delayed phenology with warming (Menzel et al. 2006). This suggests that other factors besides temperature are likely influencing flowering phenology.

Species interactions, for instance, can influence phenology. Some deciduous forest species have evolved to accelerate their phenology in early spring in order to avoid

light inhibition from canopy shading (Uemura 1994). Further, understory individuals of deciduous tree species have been found to experience advanced spring phenology compared to canopy individuals within the same species (Augspurger and Bartlett 2003). The encroachment of shade producing shrubs into arctic and alpine environments in response to rising temperatures (Sturm et al. 2001, Myers-Smith et al. 2011) has the potential to alter the phenology of high-light adapted species. However, to our knowledge, phenological responses to recent colonization of shrubs or under conditions of enhance warming have not been observed.

In California's White Mountains, *Artemisia rothrockii* (sagebrush) has expanded its range margin upward in elevation over the past half-century during a period when local temperatures increased and precipitation decreased (Kopp and Cleland 2014) (Chapter 1). In order to test how plants in areas recently encroached by sagebrush respond phenologically to warming we conducted an artificial warming experiment. Shading treatments were also imposed to mechanistically evaluate how shading by overstory shrubs might influence phenology. In response to warming, we hypothesized that the date of first flowering and peak flowering would be earlier than control but that the presence of sagebrush could alter species level phenology and species level reproductive output via shading.

Methods

We conducted an artificial warming experiment in California's White Mountains, USA. The White Mountains are located on the western edge of North America's Basin and Range Province and lie within the rain shadow of the Sierra Nevada Mountains and

are in a transition zone between the maritime influence of the Pacific Ocean and the continental influence of North America resulting in a cold and arid climate. Winter snow accounts for much of the yearly precipitation, which varies with elevation, ranging from 456 mm/yr at Barcroft Station (3800 m) to 327 mm/yr at Crooked Creek Station (3094 m). Temperature is also strongly dependent on elevation, with a mean annual temperature of -1.7 °C at Barcroft Station, and 0.9 °C at Crooked Creek Station (Hall 1991).

The response of alpine plant communities to warming was tested at two locations in the White Mountains. High elevation plots were located at 3700 m (37° 34.1' N, 118° 14.3' W), while low elevation plots were located at 3100 m (37° 29.9' N, 118° 10.3' W) (Fig. 4.1). In late-June and early-July 2011 1-m^2 plots were established on granitic derived soils at both sites. At each elevation, plots are arranged in a randomized design with 4 replicate plots of each of the 5 treatments: (1) shaded without *Artemisia rothrockii* (Shade), (2) warmed with established *A. rothrockii* plants (Warmed Sagebrush) (3) without established *A. rothrockii* plants (Warm) and (4) controls with established *A. rothrockii* plants (Sagebrush) and (5) without established *A. rothrockii* plants (Open) for a total of 20 plots at each site. Plots were selected based on species composition, abundance, and cover of commonly shared species at each site. Warming chambers were constructed following (Molau 1996) and were made of 5 oz clear Crystalite fiberglass (thickness = 1.1 mm, light transmission = 90%) (Ridout Plastics Company Inc., San Diego, CA, USA). Chambers were 1-m diameter and were held in place year round using 152 mm spike nails. These chambers increased temperatures between 2.5 °C and 3.5 °C compared to control (Chapter 3).

Between May 13, 2013 and July 20, 2013, the normalized difference vegetation index (NDVI) in the center 0.5 m^2 of each plot was monitored using a Cropscan Multispectral Radiometer (Cropscan Inc., Rochester, MN, USA). NDVI measures greenness of vegetation based on the difference between the maximum absorption of radiation in the blue and red spectral band and the maximum reflection of radiation in the near-infrared spectral band (Rouse et al. 1974). Measurements were taken at weekly intervals between 11 AM and 1 PM on sunny days.

Beginning in early-May, 2013, flower production of *Trifolium andersonii* and *Koeleria macrantha* were monitored on alternating days at both 3100 m and 3700 m. At each sampling time, total fully bloomed flowers of *T. andersonii* and newly produced flower heads of *K. macrantha* were quantified. Since *T. andersonii* can remain in bloom for several days before wilting, there were some individual flowers that were counted on multiple days.

Data analysis

Statistical analysis was conducted using the statistical programming language R, version 3.0.3 (R Core Development Team, 2014). Date of first flowering, date of maximum flower production, total flowers quantified on peak flowering date, peak NDVI and date of peak NDVI were determined and compared across treatments using linear models and compared via Type II Anova with Treatment (warm vs. unwarmed), Elevation and Sagebrush presence as factors. *Koeleria macrantha* was only found in sufficient plots for analysis at the higher elevation, and hence flowering phenology and total flower production for this species was analyzed with a model including only

Treatment and Sagebrush as factors. The Shade treatment was compared against unwarmed Open and Sagebrush controls at each elevation via Welch's Two Sample t-test.

Results

NDVI

There were significant Elevation ($F_{1,26}$=22.9, p<0.01), Warming ($F_{1,26}$=9.58, p=0.01) and Sagebrush ($F_{1,26}$=10.35, p<0.01) effects on maximum NDVI across elevations (Table 4.1) with significant Warming ($F_{1,26}$=10.4, p=0.01) and Sagebrush ($F_{1,26}$=7.51, p=0.02) effects at 3100 m (Table 4.1). At both elevations there were greater NDVI values for Sagebrush plots, with the highest values at 3100 m (Fig. 4.1). There were no significant differences between the Shade treatment and Open or Sagebrush treatments at 3700 m and only a marginally higher NDVI values in Shade compared to Open plots at 3100 m (Table 4.4, Fig. 4.1; t=-2.19, p=0.06).

First flowering date

For *T. andersonii,* there were significant Elevation ($F_{1,23}$=77.1, p<0.01), Warming ($F_{1,23}$=9.58, p=0.01), Sagebrush ($F_{1,23}$=10.4, p<0.01) and Warming*Sagebrush ($F_{1,23}$=4.61, p=0.04) effects on date of first flowering across elevations (Table 4.2). At both elevations, *T. andersonii* in Warmed plots flowered approximately 6 days earlier than Open and Warmed Sagebrush treatments, and 10 (3100 m) or 11 (3700 m) days earlier than in Sagebrush plots (Fig. 4.2). The strongest effects of Shading on first flower date of *T. andersonii* were at 3700 m where flowers did not appear in Shaded plots until approximately 11 days after flowering began in Open (t=-3.00, p=0.03) and Sagebrush

plots (t=-2.43, p=0.06). For *K. macrantha,* there was a significant Sagebrush ($F_{1,11}$=10.5, p=0.01) effect (Table 4.3) with plots containing sagebrush flowering later than plots without sagebrush (Fig. 4.3). Shading did not have any significant effects on date of first flowering of *K. macrantha* compared to Open and Sagebrush treatments (Table 4.4).

Peak flowering date

Warming strongly accelerated peak flowering dates for *T. andersonii* (Table 4.2; $F_{1,26}$=39.6, p<0.01). For *K. macrantha*, the presence of sagebrush delayed peak flowering (Table 4.3; Fig. 4.3; $F_{1,12}$=5.40, p=0.04). The strongest effect of the shading treatment was on peak flowering date of *K. macrantha,* with peak flowering occurring approximately 9 days later in Shaded plots than Open plots (t=-9.00, p<0.01) and approximately 6 days later than Sagebrush plots (Table 4.4; t=-6.57, p=0.01).

Maximum flowers

There was a significant Elevation*Warming effect on maximum flower production for *T. andersonii* (Table 4.3; $F_{1,26}$=7.66, p=0.01). While there were no significant Warming or Sagebrush effects at 3700 m (Table 4.3), at 3100 m there were significant Warming ($F_{1,14}$=12.6, p<0.01), Sagebrush ($F_{1,14}$=14.2, p<0.01) and a marginal Warming*Sagebrush effect ($F_{1,14}$=4.21, p=0.06) (Table 4.3). Here, Warmed Sagebrush plots produced substantially fewer flowers than other treatments (Fig. 4.2). There was a significant Warming effect on maximum flower production by *K. macrantha* (Table 4.3; $F_{1,12}$=9.39, p=0.01) with Open plots producing more flowers than other treatments (Fig. 4.3).

Discussion

Maximum canopy greenness increased in response to warming and in plots where sagebrush was present, with the highest values at 3100 m. The greater production at the lower elevation is likely attributable to more moderate conditions found there (i.e. warming, longer growing season). Further, plots with sagebrush, which is active later in the season, experienced later peaks in greenness at both elevations. While neither warming nor shading had an impact on the phenology of NDVI, they did affect timing of flowering for the target species of this study.

In the absence of sagebrush, warming advanced flowering phenology of both *T. andersonii* and *K. macrantha* by as much as 11 days (*T. andersonii* first flowering date in warm vs. open at 3100 m). This magnitude of phenological advancement is consistent with other warming experiments that have found advances in the onset of flowering dates in the range of 1.9-3.3 days per °C of warming (Arft et al. 1999). The presence of sagebrush, however, lessened the advancement of phenology in response to warming by *T. andersonii*, and delayed flowering phenology overall for *K. macrantha*, demonstrating that species interactions can influence phenological responses to climate change. The warming treatment increased temperatures less in plots with sagebrush than in plots without sagebrush (Chapter 3), hence decreased warming may be a mechanism that partially explains the lessened advancement of flowering phenology when warming was combined with sagebrush presence. Artificial shading had only slight effects on temperatures compared to open and sagebrush treatments (Chapter 3) but nonetheless delayed phenology suggesting that light limitation may also be an important cue for flowering in this system.

Together, these findings suggest that shade-producing species could substantially modify phenological responses to rising temperatures if these species establish in communities containing species adapted to high light. The delay of flowering due to shade shown here is counter to findings that canopy shading can accelerate spring green-up of deciduous forest species (Augspurger and Bartlett 2003). Many alpine and arctic tundra species rely on light cues related to snowmelt to initiate growth and flowering (Körner 2003, Wipf and Rixen 2010). It is therefore possible that in our study system light inhibition by shrubs acts as a substitute for light inhibition by snow cover on tundra plants, delaying flowering. With a lengthening of the growing season in tundra environments as a result of climate change, the establishment of shade producing shrubs could decrease the possibility of phenological mismatch with mutualistic pollinators. Future research should focus on the effect of shading by shrubs on phenology in other alpine and arctic tundra plant communities.

Other studies have found that species that phenologically "track" climate change by flowering earlier with rising temperatures also tend to have higher performance under warmer conditions, compared to species with less flexible phenology (Cleland et al. 2012). In this experiment the most common focal species, *T. andersonii*, displayed greater flower production in warmed plots (Fig. 4.2). However, seedpod formation by *T. andersonii* only occurred in four plots across treatments and elevations (data not shown), suggesting there was poor pollination. Flower production is only one measure of performance and recruitment via sexual reproduction may not be of critical importance for a long-lived clonal species like *T. andersonii.* However, between 1961 and 2010, *T. andersonii* experienced significant declines in abundance in the study area (Chapter 1).

Further, cover of this species has declined across treatments (except for shaded treatments) at 3100 m since the establishment of this experiment in 2011, with the greatest declines occurring in warmed treatments (Chapter 3). It is possible that this species is now flowering out of sync with the phenology of its pollinators (Kudo and Ida 2013), but without long-term observations of both plant and pollinator phenology this remains conjecture. Longer-term monitoring in this experiment will be important; prior warming experiments in alpine environments that have monitored multiple fitness categories have found that reproductive fitness tends to increase in later years of the experiment, possibly the result of depletion of stored plant reserves (Arft et al. 1999).

As the responses of arctic and alpine plant communities to climate change have become better understood, two main paradigms have emerged; warming tends to promote shrub encroachment (Sturm et al. 2001, Myers-Smith et al. 2011) and also leads to an advancement of spring phenology (Walther et al. 2002, Root et al. 2003, Parmesan 2006). Here, for the first time, we show that a range expansion by one species can alter the phenological response to increased temperatures by another. These findings demonstrate the importance of shifts in species composition, particularly shrub encroachment, in mediating indirect effects of climate change on plant communities.

Table 4.1. Results from ANOVA comparing responses of NDVI to warming and sagebrush presence across elevation for maximum flowers and peak day of year.

	Maximum		Peak Day of Year	
	$F_{1,26}$	p	$F_{1,26}$	p
Elevation	22.93	**<0.01**	2.13	0.16
Warming	9.39	**0.01**	0.00	0.96
Sagebrush	10.16	**<0.01**	16.57	**<0.01**
Elevation*Warming	2.31	0.14	0.47	0.50
Elevation*Sagebrush	0.81	0.38	0.00	0.96
Warming*Sagebrush	0.91	0.35	1.33	0.26
Elevation*Warming*Sagebrush	2.44	0.13	0.24	0.63

Table 4.2. Results from ANOVA comparing responses of *Trifolium andersonii* to warming and sagebrush across elevation, warming and sagebrush for date of first flower, date of peak flowering and maximum flowers.

	DOY First Flower		DOY Peak Flowering		Maximum Flowers	
	$F_{1,23}$	p	$F_{1,26}$	p	$F_{1,26}$	p
Elevation	77.13	**<0.01**	2.58	0.12	2.53	0.12
Warming	9.58	**0.01**	31.58	**<0.01**	3.52	0.07
Sagebrush	10.35	**<0.01**	0.03	0.86	12.49	**<0.01**
Elevation*Warming	0.05	0.83	1.83	0.19	7.66	**0.01**
Elevation*Sagebrush	0.04	0.84	0.31	0.58	2.27	0.14
Warming*Sagebrush	4.61	**0.04**	0.15	0.70	3.96	0.06
Elevation*Warming*Sagebrush	0.15	0.70	0.24	0.63	0.50	0.49

Table 4.3. Results from ANOVA comparing responses by *Koeleria macrantha* to warming and sagebrush of date of first flower, date of peak flowering and maximum flowers 3700 m.

	DOY First Flower		DOY Peak Flower		Maximum Flowers	
	$F_{1,11}$	p	$F_{1,12}$	p	$F_{1,12}$	p
Warming	10.46	**0.01**	2.64	0.13	9.39	**0.01**
Sagebrush	3.40	0.09	5.40	**0.04**	0.23	0.64
Warming*Sagebrush	0.60	0.46	0.15	0.71	1.48	0.25

Table 4.4. Shading, open and sagebrush treatment comparative responses of peak NDVI date, maximum NDVI, date of first flowering, peak flowering date and maximum flower production.

			Shade vs. Open		Shade vs. Sagebrush	
			t	*p*	*t*	*p*
NDVI	Peak DOY	3100 m	-0.49	0.64	0.85	0.43
		3700 m	-0.75	0.49	0.66	0.53
	Maximum NDVI	3100 m	-2.19	0.06	1.26	0.27
		3700 m	0.27	0.80	1.46	0.21
Trifolium andersonii	First Flower DOY	3100 m	-0.71	0.51	-2.52	0.07
		3700 m	-3.00	**0.03**	-2.43	**0.06**
	Peak Flowering	3100 m	1.74	0.13	1.37	0.20
		3700 m	2.30	0.10	0.41	0.70
	Maximum Flowers	3100 m	2.00	0.10	1.79	0.11
		3700 m	0.65	0.55	2.04	0.13
Koeleria macrantha	First Flower DOY	3700 m	-1.14	0.31	-0.61	0.56
	Peak Flowering DOY	3700 m	-6.57	**0.01**	-9.00	**<0.01**
	Maximum Flowers	3700 m	-2.15	0.10	-2.03	0.12

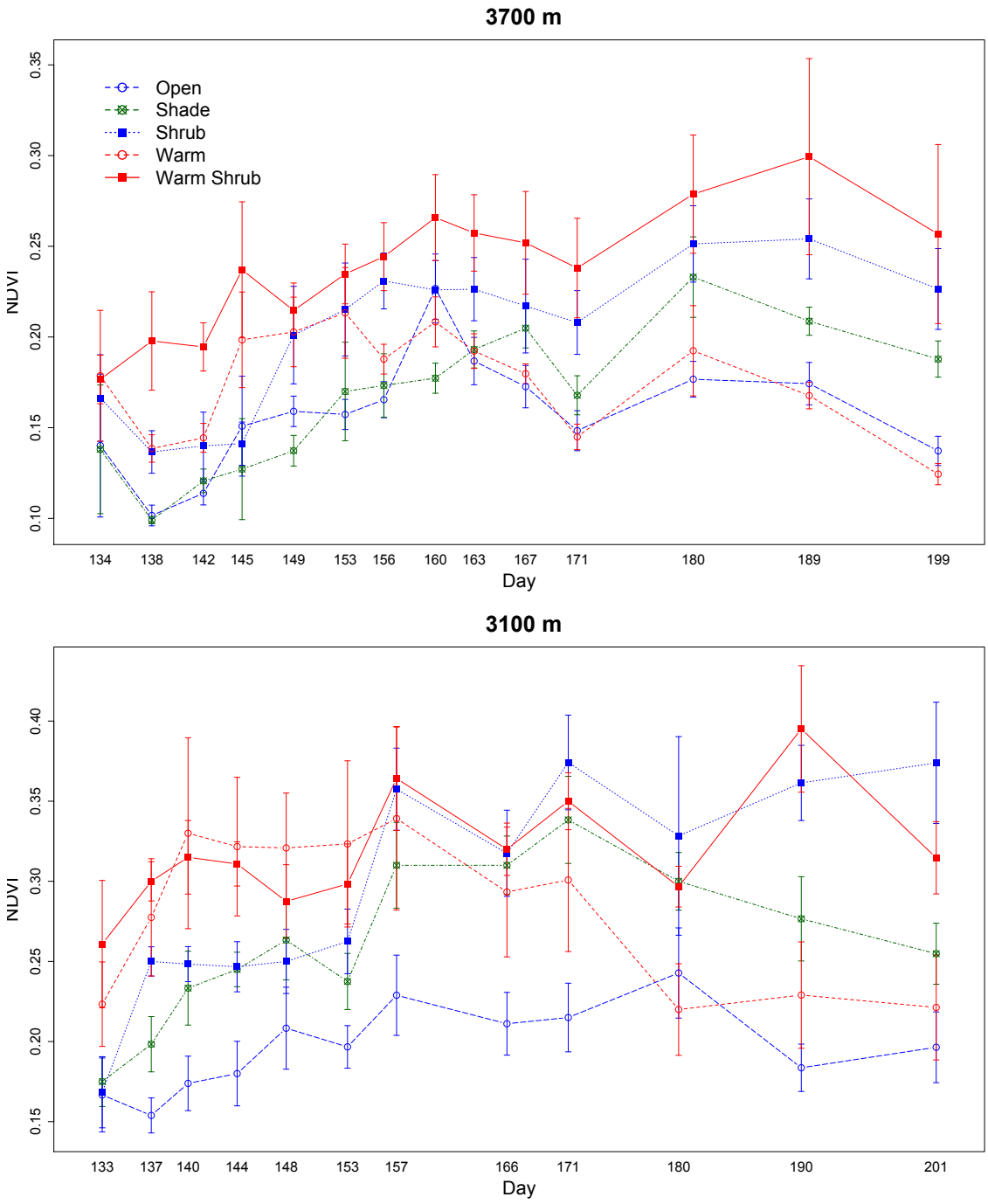

Figure 4.1. NDVI values across treatments and day of year at 3700 m (top) and 3100 m (bottom).

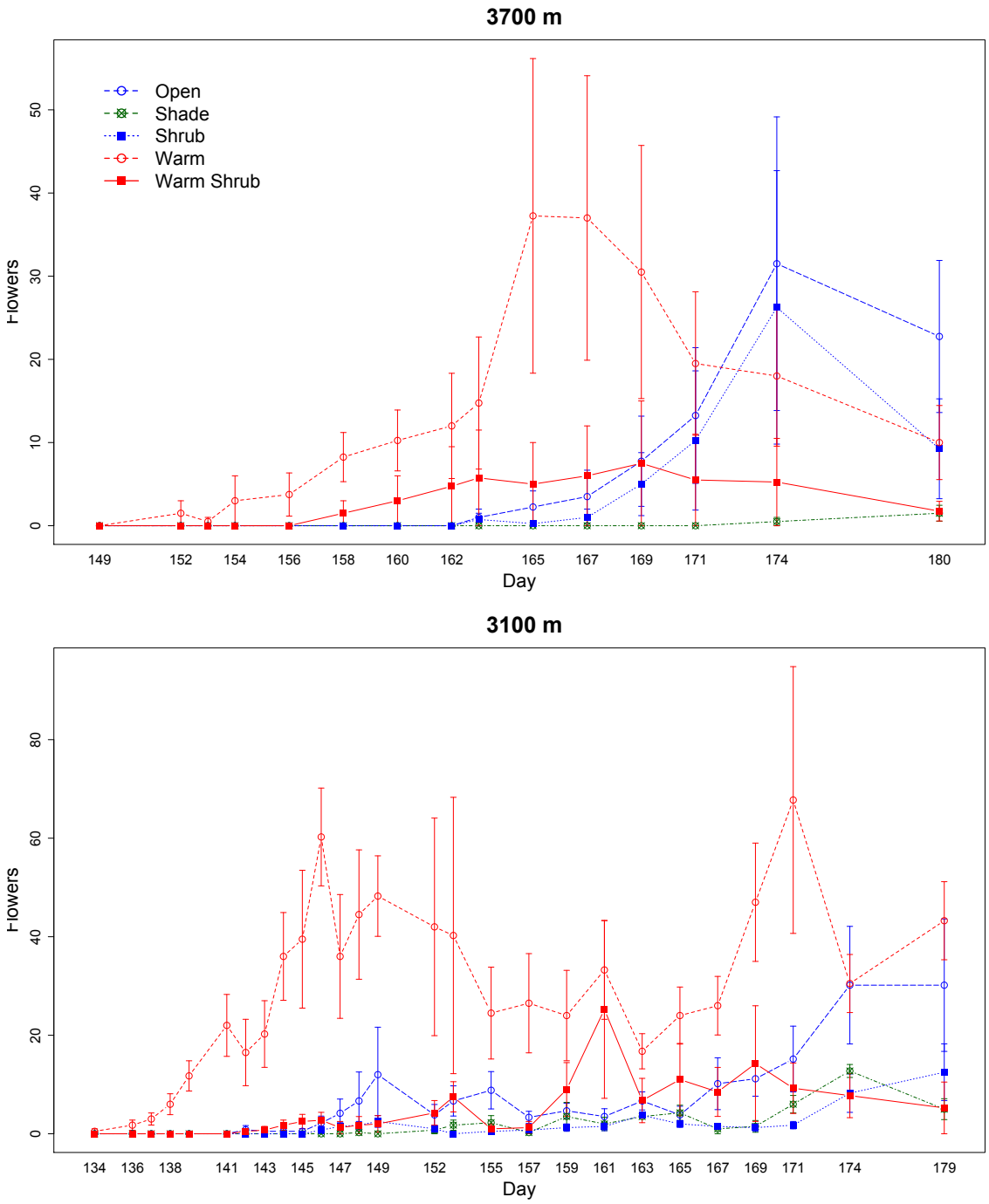

Figure 4.2. Daily flower production of *Trifolium andersonii* across treatments at 3700 m (top) and 3100 m (bottom).

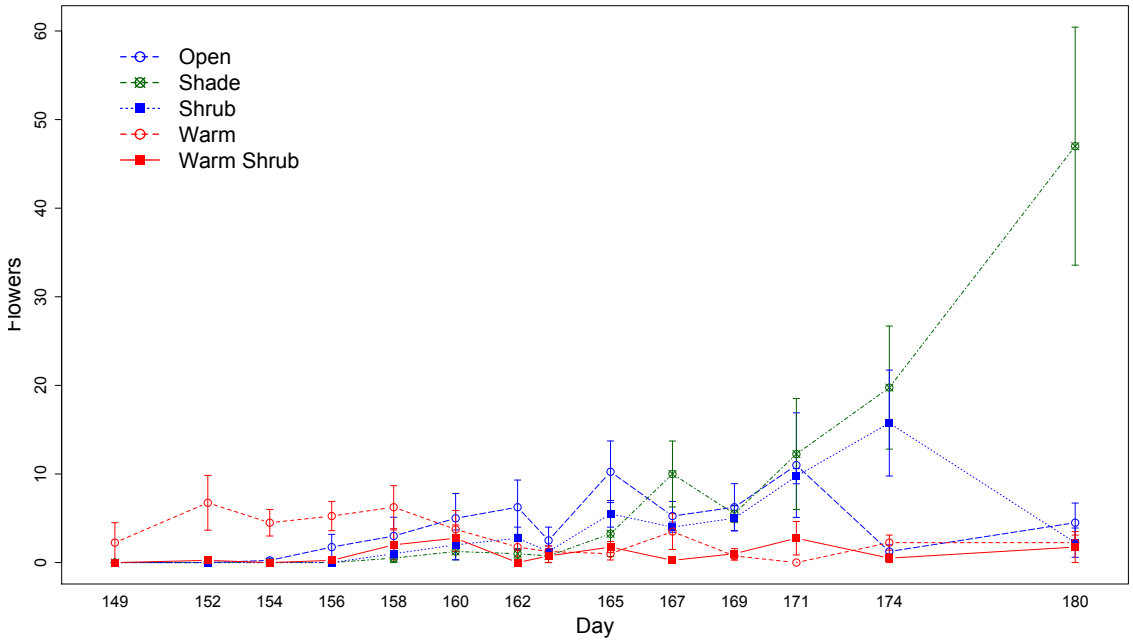

Figure 4.3. Daily flower production of *Koeleria macrantha* across treatments at 3700 m.

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