ALPINE PLANT COMMUNITY SHIFTS OVER A 30 YEAR PERIOD IN SEQUOIA AND KINGS CANYON NATIONAL PARKS, CALIFORNIA

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ABSTRACT

Alpine plant community shifts over a 30-year period in Sequoia and Kings Canyon National Parks, California

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Plants of alpine regions around the world are threatened by climate warming. In alpine regions, climate warming has been predicted to cause ‘greening’ and plant community shifts towards species from warmer climates. However, slow growth rates coupled with limited dispersal in alpine habitats may lead to considerable lags in community level responses. Here we took advantage of a historical survey conducted on 105 plots in the alpine of Sequoia and Kings Canyon National Parks, in the Sierra Nevada mountains of California, USA. We found that over a 30-year period, plots display, on average, a 21% increase in herbaceous plant cover, a 25% increase in species richness, and the community shifts towards species with affinities for higher maximum summer temperatures.

Keywords: climate change, alpine, plants, community shifts, elevation
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1. INTRODUCTION

1.1 Background

The alpine region of California is a biodiversity hotspot (Baldwin et al. 2017). It makes up less than 2% of the land area in the state, with most of the alpine regions concentrated in the central and southern Sierra Nevada. Alpine habitat, defined as occurring at elevations above tree line, is a harsh place to exist. Covered by snow for over half the year with little rainfall, extreme winds, and intense light exposure during a limited growing season, plants specialize to survive this stressful environment.

As temperatures continue to rise (Solomon et al. 2007), species in the high alpine environments are increasingly at risk of losing their habitat (Parmesan 2006) and resurveys in Europe, Asia, and the Rocky Mountains of North America are already detecting significant plant community shifts away from the facilitative growing environment typically found there to a more competitive one (Callaway 2002). In California, models are projecting a 50-90% loss of alpine habitat by 2100 (Hayhoe et al. 2018), however we currently lack data in California’s Sierra Nevada alpine to test whether these model predictions are accurate locally. The need for local scale data is becoming increasingly clear as at least a few observational studies have seen a wide variety of species responses (Engler et al. 2011).

Generally, models and some analyses suggest that species will move up in elevation to track suitable climate (Chen et al. 2011), however in the alpine there is not much or no elevation to gain. Many species grow as mat or cushion plants, which are characterized as slow-growing, long-lived, prostrate species (Kopp and Cleland 2014). These are also called nurse plants, since cushion species create a facilitative environment, acting as incubators for seedlings to grow up under and near them, soil stability, and wind protection (Cavieres et al. 2014). With a change in species, dominance structure and community dynamics, including increased competition and decreased facilitation among alpine species, will occur (Gottfried et al. 2012). Over time, this, in addition to warming temperatures, has the potential to dramatically alter the alpine vegetation community of the Sierra Nevada, possibly leading to the extirpation of the charismatic cushion plants historically found there.
Understanding species and community responses to temperature changes are critical for managing biodiversity in rare ecosystems. In this study, we use a resurvey approach to assess changes in alpine plant communities in Sequoia and Kings Canyon National Parks over a roughly thirty-year period (surveys originally took place between 1986 and 1993). We look specifically at whether there have been changes in herbaceous and woody cover, herbaceous species richness, and community climate niche affinity.

1.1.1 Predicted changes in herbaceous and woody cover

Historically, alpine habitats have been dominated by short, slow growing herbaceous perennials that are poor competitors (Kopp and Cleland 2014). In a warming environment, taller woody shrubs are predicted to expand upwards in elevation and colonize these sites, perhaps becoming dominant members of the community (Baruah et al. 2017). Synthesizing multiple studies over both short term (4 years) and long term (100 years) of shrub expansion from the Canadian Arctic, Alaska, the European Artic and Greenland, Myers-Smith et al. (2011) found evidence of shrub expansion in all these places. Interestingly, herbaceous cover has also increased in these sites and, as yet, there is no evidence that alpine specialists are decreasing (Kullman 2010, Kopp and Cleland 2014). However, this observation might be expected if there is a lag time in the response of alpine specialists. Slow growing cushion plants may be able to survive in the short term, but not long term, on stored energy reserves, while slowly being shaded by overtopping woody species. Another explanation may be that the longer summer growing season associated with a warming climate may lead to an overall increase in vegetation (both woody and herbaceous), in these historically sparsely vegetated habitats. This phenomenon is referred to as the ‘greening’ of the alpine and has already been observed in the French Alps (Carlson et al. 2017).

1.1.2 Predicted changes in species richness

When considering changes in species richness within the alpine, it is useful to first consider the limiting factors of species range shifts in response to climate warming (Alexander et al. 2018). Changing climate can be mitigated if plants are able to migrate to regions of suitable climate. However, dispersal limitation, or low rates of dispersal, would mean that plants have
difficulty tracking their climate niche. The second limitation is population establishment, or the lack of suitable conditions within the dispersal range that affect germination and establishment of new migrants. New sites might lack the below and above ground biotic mutualists (e.g., mycorrhizal fungi and pollinators) needed, despite suitable abiotic conditions for adult plants. A third limiting factor is the long time scale of extinction. Even when population growth rates turn negative, it may take years or decades for populations to go extinct, especially for slow growing, long lived, taxa such as alpine cushion plants. Overall, these three limiting factors may lead to considerable time lags in a species ability to track their climate niche and for scientists to detect meaningful changes (Alexander et al. 2018). In the absence of these time lags, species richness is predicted to generally increase within alpine communities. While alpine specialists may well go extinct, thus reducing overall richness, the longer growing season and more hospitable growing environment is predicted to lead to an influx of more colonizing species from lower elevations potentially resulting in an overall increase in richness.

Though some studies have shown an increase in overall species richness in alpine communities (Steinbauer et al. 2018), results are varied and potentially place dependent. In Europe between 2001-2008, species richness increased at northern alpine summits, but decreased at southern Mediterranean mountain summits (Pauli et al. 2018). The authors speculate that greater precipitation in the north has allowed for more recent germination and establishment of taxa from lower elevations. In the south however, where precipitation is much lower, reduced establishment paired with some extirpation of alpine specialists may be occurring. Between 1999-2017 in the Artic tundra of Canada, no changes in species richness were observed over the nearly 20-year study (Meyer-Smith 2018).

1.1.3 Predicted changes in community climate affinity

In addition to assessing shifts in species richness and abundance, there is great interest in whether species are tracking their climate niches within the alpine. Very few studies have examined this to date and those that did have found a variety of responses.

Becker-Scarpitta et al. (2019) took a community level approach asking whether communities were shifting towards sets of species from warmer and drier regions. Climate means
of individual species across their geographic distribution were averaged to calculate a community temperature index of co-occurring species (DeVictor et al. 2008, Becker-Scarpitta et al. 2019).

Under a warming climate, alpine assemblages have been found experimentally to shift from species that are, on average, from wet and cool climates to species that are, on average, from warmer and drier climates (Oldfather and Ackerly 2019). However, at the same time, Becker-Scarpitta et al. (2019) found no evidence of a shift at their three study sites in Quebec Province, Canada over a 40-year period. In another long-term study of alpine vegetation (42 years) in Italy, Evangelista et al. (2016) found that the alpine plant community had increased in thermophilic plant frequency. This is the start of a process called ‘thermophilization’, or the declining of cold-adapted plants and the increase of warm adapted ones (Gottfried et al. 2012).

A recent study in the White Mountains, California used a similar approach, however they only had one snapshot in time, not a resurvey (Smithers et al. 2019). They found that within the alpine zone, low elevation plots contained more warm adapted species on average, while the high elevation plots contained more cold adapted species. This result suggests that alpine communities are currently filtering species based on species’ climate affinities, and that given climate warming, we might expect to see shifts towards more warm affinity species over time.

1.2 Alpine habitat in Sequoia and Kings Canyon National Parks

In the southern Sierra Nevada mountains, Sequoia and Kings Canyon National Parks make up a large chunk of uninterrupted high elevation habitat. 83% of these parks is over 2100 meters in elevation (Graber et al. 1993) and over 40% of the land area in these parks is classified as alpine terrain (non-forested areas at or above 3000 meters elevation). The alpine region of Sequoia and Kings Canyon National Parks is home to 385 vascular plant species (Rundel 2011), thirty of which are listed as California Native Plant Society special status species (Huber et al. 2013). The plant community is composed of mostly herbaceous, perennial forbs and graminoids, including the iconic alpine cushion plants, and contains very few woody or annual taxa (Rundel 2011). Perennial clump forming grasses, sedges and rushes are another common component of this community, as they can grow and reproduce quickly during the short growing seasons in the alpine.
1.3 Climate change within Sequoia and Kings Canyon National Parks

There are very few high elevation weather stations located in the Sierra Nevada which makes it challenging to know precisely how temperature and precipitation has changed over the last thirty years. Furthermore, the variable topography, slope, and aspect of high elevation environments make extrapolations from lower elevation weather stations less reliable (Körner 2003). However, there are studies suggesting that temperatures at higher elevations are changing at a faster rate than lowland areas (Pepin et al. 2015).

The weather station most applicable to the southern Sierra Nevada alpine is located at Emerald Lake (2813 meters) in Sequoia National Park. Emerald Lake is 100 meters lower than previously studied alpine National Resource Inventory (NRI) plots and 664 meters lower than the average alpine NRI plot elevation. After extracting temperature and precipitation data from this station (published in Sardo et al. 2019), we found that since 1983 the average annual temperature has increased by 0.63 °C per decade with summer rates increasing by 1°C per decade (Figure 1). Meanwhile, precipitation has been highly variable with no apparent trends. In total, this amounts to a 1.9°C increase in annual temperature and a 3.0°C summer temperature increase between 1983 and 2015.
1.4 Natural Resource Inventory: A baseline for characterizing change

To monitor the vegetation found within Sequoia and Kings Canyon National Parks, the National Park Service started a National Resource Inventory (NRI) project in 1985 (Graber et al. 1993). 0.1-hectare circular plots were established throughout the park, including 201 plots in alpine habitat, with the idea that they would be regularly resurveyed. However, due to funding constraints, most plots have not been revisited since their initial establishment. One of the primary objectives stated in Graber et al. (1993), was to use the NRI plots to establish a baseline for monitoring vegetation change over time. The current study aims to do exactly that: monitor change, if any, in alpine vegetation since these plots were initially established approximately 30 years ago.

Twenty-five plots in the Siberian Outpost and Boreal Plateau regions of Sequoia National Park were resurveyed in 2012 by Cathy Bell (Bell 2012), thirteen of which fall in alpine habitat. One of the main study objectives of Bell (2012), in addition to monitoring vegetation change, was to determine the feasibility of relocating the NRI plots. Her technical report contains extensive
methodological detail and suggestions for future surveyors, which provided much insight to the current study. While we did not include her data in the present study, we have made it available online in the digital archive, DigitalCommons@CalPoly.

1.5 Study Objectives

In this study, we resampled 105 of the NRI alpine plots in Sequoia and Kings Canyon National Parks (SEKI). These plots were established and originally sampled between 1986-1993. Our primary goal was to assess change, if any, in the following aspects of alpine plant communities in this region:

1. herbaceous and woody vegetation cover
2. species richness
3. community climate affinity

In addition, we provide photos and accurate GPS coordinates for the plots (not collected during the original surveys), to assist future generations studying and managing these rare habitats.
2. MATERIALS AND METHODS

2.1 Summary

Historical plots were resampled following the methods in Graber et al. 1993 and Bell 2012. In total, we sampled 105 of 201 plots that occur above 2950 meters elevation and had no trees present in the historical survey taller than or equal to 1.3 meters (Figure 2). We did not sample all plots for the following reasons: 1) we were unable to relocate a plot after searching for it in the field or 2) time constraints prevented us from searching for and sampling a plot. Thus, the 105 plots in this study represent a haphazard sample of the 201 NRI plots occurring above 2950 meters with no trees present in the historic survey.
2.2 Plot relocation and set up

The original plots were set up prior to the National Park Service acquiring GPS units and were mapped using rough coordinates from 15-minute maps. Each plot was marked with a quarter sized round tag glued to a rock and/or a stainless-steel stake (each with the plot number) and photos were taken in the four cardinal directions from the plot center. We relocated these plots using the rough coordinates and the photographs. Once the plot markers were found, a 17.8-meter measuring tape was laid out in each of the cardinal directions. The circular plot...
boundary was marked by 8 pin flags to mark the boundaries during our resurvey. Figure 3 shows the basic plot layout. A GPS point and four updated cardinal direction photos were taken at each plot center. These were labeled with the plot number, cardinal direction, and year (i.e., 104_E_2019). These photos are contained in the digital supplement. At select plots that had an associated historical soil sample, we obtained a soil sample using a hori hori and measured the soil depth.

2.2.1 Whole plot

Inside this 17.8-meter radius circle, we identified and recorded all vascular plant species. The total time spent exploring the whole plot was variable and we searched until we thought we had examined the entire area of the plot and until we were not encountering any new species. If we were unable to identify a plant, we would either take a snippet of the plant and/or try to locate the same species outside the plot for collection and later identification. If a plant was too immature to identify, we would record it as “seedling” or “immature grass” for example.

2.2.2 Transect lines

Meter tapes were positioned along the north and east lines from plot center using a compass to the plot edge (17.8 m long) and served as our two transects. We recorded cover as either Herb, Rock, Bare, or the species of woody plant, including shrubs and trees (see woody plant definitions see below) for each centimeter along the transect. If herbs were present in the understory of a woody plant, we recorded both and therefore, total cover for each transect could be greater than 1780 cm. We did not record the substrate under woody plant or herbs. We defined the cover category of Rock was classified as any rock over 10 cm in any dimension. If it was smaller than 10 cm, we called it Bare ground. We recorded total centimeters covered by each category but not the exact centimeter position on which it fell. For example, if, in a 5 cm stretch there was one centimeter of herb and the rest was bare ground, we would record that as one centimeter herb and four centimeters bare.
2.2.3 Quadrats

Following the historical survey methods, we surveyed more intensely at 1, 5, and 15 meters along the north and east transects using a 1-meter square frame or quadrat. We engineered a lightweight flexible 1 m² quadrat out of parachute cord with patches of fabric at each corner to 1) demarcate the corners, and 2) allow us to place a small rock on the corners to hold the quadrat in place. Within each quadrat, each vascular plant species was identified and recorded. If we were unable to identify a plant, we would either take a snippet of the plant and/or try to locate the same species outside the plot for collection and later identification. We measured percent cover of each species. Effort was made at the start of every season to standardize our ocular cover estimates by using cards that represented 1% cover with different dispersal rates illustrated with the corresponding percent cover. We also frequently had two observers making and comparing estimates to improve our accuracy. In addition to cover for each species, we recorded the absolute percent cover of each species in the 1 m² quadrat. We also recorded percent Rock, Bare, Soil Lichen, and Crustose Lichen.

![Plot boundary](image)

Figure 3: The layout of a plot showing the two transect lines and the six quadrats. Based on the original figures in Graber et al. 1993 and Bell 2012.
2.2.4 Plots

2.2.4.1 Plots surveyed

We had remarkable success relocating plots despite the lack of accurate GPS information. We failed to relocate only a handful of plots that we searched for. The original photos taken from plot center in each cardinal direction proved invaluable. We printed multiple copies of these photos so that every team member was able to contribute to the search effort. While we did not record our search times, it generally took 1-2 hours to locate plot center. This was and hiking times to get into the areas was by far the most time-consuming part. In some cases, the metal tag glued to rock at plot center was missing, however, residual glue on the rock remained. See example photos in Figure 4.

A)
Figure 4: Example plot photos. A) Stainless steel marker for plot 254 with meter tapes running the north and east transect lines from plot center. B) Cardinal direction photos from plot center of plot 134 in 1986 and C) in 2019.

2.2.4 Plots unable to relocate or fully sample

We searched for plot 433 and were unable to find it, possibly due to rock fall. Plot 249 was under snow and unable to be fully surveyed.

2.2.4.3 Year to year variation in plot data

To determine the extent of yearly variation in the plots driven by variation in seasonal growth, we selected twelve plots in Dusy Basin to resurvey two years in a row: 2018 and 2019. These plots were chosen for their relatively ease to access and because they were clustered near each other reducing our hiking time. These plots were NRI plots: 259, 262, 265, 266, 267, 268, 269, 270, 271, 272, 273, 274.

2.3 Fieldwork

2.3.1 Field preparation

To prepare for the field work, we did substantial training. This included once a week meeting for four months during school to discuss gear, food, first aid, general backpacking protocol, literature on alpine vegetation, and plant identification. We made extensive use of plant collections made in the previous year to study the morphology of alpine species.

Members of the field crew took a Wilderness First Aid course. We recommend meeting with Park Service employees including Sylvia Haultain prior to any resampling effort to learn the protocol and do a sample plot together. However, due to scheduling conflicts we were not able to meet with Haultin. The field crew of four hiked into Rae Lakes in the early season in 2018 go over the protocol, learn plant species, practice ocular estimates, and sample one practice plot all together, as it was too early to key out any grass species.
In the second season, the crew spent one day at an alpine graminoid workshop led by Dena Grossenbacher at Cal Poly. We undertook one training trip where we resurveyed three plots all together to standardize our observations (plot numbers 134, 131, 139).

2.3.2 Trips

Plots in this study were located many kilometers from trailheads and thus were only accessible via overnight backpacking trips. We organized each trip to maximize the number of potential plots encountered during a given backpack trip, and to minimize hiking distance whenever possible. Most trips lasted around 5 days and we were able to survey 5 – 15 plots per trip.

2018 Trip details

Rae Lakes


Notes: Training Trip. We used Rae Lakes Ranger Station as base. The crew hiked over Kearsarge and Glen Pass in one day (which we would not advise if crew is unused to altitude). The next day and a half were spent training on ocular cover estimates and plant id. The crew then hiked out with the rest of the third day and into the evening.

Upper Basin/Pinchot

August 8-19, 2018: 20 plots surveyed. 1 plot not located (433). Dena Paolilli, Dena Grossenbacher, Charlie Gibbons, Ella Abelli-Amen, Courtney Tuskan

Notes: The crew hiked in 4 miles up Taboose Pass trail in the evening on the first night to avoid the warm temperatures at the low elevation Taboose Pass trailhead. The next morning, we continued up to Bench Lake Ranger Station. We had sent food caches in with the ranger at the beginning of the season. We spent a night at the station and then set up a base camp for 6 days in Upper Basin. After finishing the Upper Basin plots, we headed back to the ranger station to pick up food and then over Pinchot Pass for 2 nights.

Wanda Lake/Darwin Basin

Notes: The crew hiked in over Lamarck Col from the North Lake trailhead and headed to Wanda Lake first. We spent one night there and headed to McClure Ranger Station where we had also cached food at the start of the season. We spent one night there and headed to Darwin Basin the next day where we spent the remainder of the nights. We hiked out in one day via Lamarck Col.

Dusy Basin
August 31-September 3, 2018: 12 plots surveyed. Dena Grossenbacher, Charlie Gibbons, Ella Abelli-Amen, Courtney Tuskan, Joel Smith

Notes: The crew hiked in on one day and spend the three nights in the same camping spot in Upper Dusy.

2019 Trip details

Siberian Outpost

Notes: This was a training trip. We hiked in from the Cottonwood Pass trailhead to Siberian Outpost in one day. We did the three plots all together to calibrate our ocular cover estimates. Many flowers were blooming however it was a little early for the grasses, sedges, and rushes. We hiked out over Cottonwood as well.

Siberian Outpost

Notes: We were lucky to have Alison Colwell join us on this trip. We hiked in from the Cottonwood Pass trailhead to the Rock Creek Ranger Station where we had food cached. From there we went towards Funston Lake and the Boreal Plateau. From there we made our way back towards the Siberian Outpost and out over Cottonwood Pass.

Lake South America/Wright Lakes
Notes: Jenn Yost joined us on this trip. We started hiking from the Sheppard Pass trailhead in the evening to avoid the heat from the Owens Valley. We spent that night below Sheppard Pass and hiked to the Tyndall Ranger Station that night to pick up food we cached. From there, we hiked to Lake South America where we stayed for 3 nights before hiking back by Tyndall Ranger Station on our way to Wright Lakes. We spent 2 nights at Wright Lakes and then hiked all the way out over Sheppard’s Pass on the last day.

Martha Lake
Notes: This trip was the deepest we got into the backcountry. It involved the most off trail hiking and was about 26 miles to get into the area where the plots were. We came in from the North Lake trailhead over Piute Pass. From there we joined the John Muir Trail to the Godard Canyon Trail. We had packers meet us with a food cache at the top of that trail. From there we spent a night before going over an unnamed pass descended into an unnamed basin where we based for the rest of the plots. We hiked out in two days from there.

Dusy Basin
Notes: We hiked in from the Bishop Pass trailhead at South Lake to Upper Dusy Basin.

Granite Basin
September 5-7, 2019: 8 plots surveyed. Dena Paolilli, Charlie Gibbons, Kieran Althaus, Karen Bach
Notes: We hiked in over Granite Pass and spent two nights finding plots in area with less use trails than other places we’d been before.

Tablelands
September 8-11, 2019: 7 plots surveyed. Charlie Gibbons, Kieran Althaus, Karen Bach, Reed Kenny
Notes: The crew hiked in from the Pear Lake trailhead and camped past Pear Lake in the Tablelands.

*2020 Trip details*

Mineral King

August 13-17, 2020: 5 plots surveyed. Dena Paolilli, Ella Abelli-Amen, Matt Murray

Notes: We almost just went with two of us, but we were able to recruit a strong hiker and beginning botanist. This was key as the more able bodies looking for the plots, the quicker it goes finding them. We started from the White Chief trailhead in Mineral King. After two nights in the White Chief area and surveying the plots in there, we hiked back down almost to the trailhead and forked over to the Franklin Pass. We spent the remaining two nights on the south side of Franklin Pass and then hiked out.

**2.3.3 Plant identification and collections**

We collected plant specimens when we were unsure of identification or as a voucher. These specimens were always collected from outside the circumference of the plot in order to avoid impacting the plot for future study. When performing collections, we put plant specimens into a small cardboard field press (8.5 x 6.5 inches) in newspaper labeled with date, plot number, and our tentative identification (if known). For short trips, plants were sometimes left in plastic ziploc bags with the plot and date written on them and transferred to a full-size press upon exiting the backcountry.

Plant identification of specimens was done at Cal Poly by Dena Paolilli and Dena Grossenbacher. *Carex* samples were all sent to Dean W. Taylor to determine the vast majority to species (immature Carex are often not able to be determined to species). *Poa* samples were all sent to Rob Soreng, the author of the Flora of North America *Poa* treatment, for identification. Difficult Asteraceae specimens were determined by Dave Keil, and *Boechera* and *Phlox* were identified by Alison Colwell. In total, we deposited 166 plant specimens at the Robert F. Hoover Herbarium (OBI) at Cal Poly State University, San Luis Obispo. There are approximately 50 remaining specimens that will be mounted and deposited within the year.
2.4 Variables used in data analyses

2.4.1 Estimating herb species richness

Herbs were defined as any non-woody vascular plant species as defined in the original surveys. However, between 1986 and 1991 some species were variously treated as herbs or as woody shrubs. We therefore excluded these questionable species in both the herb and woody classification (for more information see below in woody richness).

Herb richness was calculated as the total number of herbs within each 1m² quadrat. We used the quadrat sampling, rather than the whole plot species lists, due to the greater likelihood that similar search effort was spent on quadrats in historic and contemporary surveys. Because the whole plot area totals 995 square meters it was difficult to detect all species within the plot with there was higher variance between observers and time spent searching.

We were unable to estimate woody species richness changes due to the original sampling protocol and the problems in classification of woody plants. In 1991 during the original surveys, the crews realized they were not consistent on what they were designating a woody plant or an herb. To standardize they defined the following list that would be counted as woody plants:

*Penstemon davidsonii*
*Penstemon newberryi*
*Phyllodoce breweri*
*Vaccinium nivictum (Vaccinium cespitosum)*

Plants that were treated as herbs:

*Apocynum* sp.
*Chrysopsis breweri*
*Eriogonum umbellatum*
*Eriogonum wrightii*
*Leptodactylon pungens (Linanthus pungens)*
*Penstemon* sp.
Since the original data only reports herb or shrub, we have no way of knowing which species they were referring to in the various historical data sheets. For our study we wrote down the individual woody species in the quadrats to avoid this confusion in the future. Prior to 1991, and the definition above, it is unknown what fell into that category.

To account for this in our model, we isolated the questionable plants (*Penstemon davidsonii, Penstemon newberryi, Phylloco broweri, Vaccinium nivictum (cespitosum*)) that could previously have been listed as shrub but should count as herb. If they were named in the historic survey, they were included in the woody category. If they were not specifically mentioned by name, measurement of that species was added to the herb category.

The following species were consistently classified as woody plants in contemporary surveys:

Artemisia ludoviciana ssp. incompta
Artemisia norvegica ssp. saxatilis
Artemisia rothrockii
Chrysothamnus parryi ssp. vulcanicus
Ericameria discoidea
Ericameria suffruticosa
Holodiscus microphyllus var. microphyllus
Jamesia americana var. rosea
Kalmia polifolia
Leptodactylon pungens
Monardella glauca
Penstemon davidsonii var. davidsonii
Penstemon newberryi var. newberryi
Phlox diffusa
Phylloco broweri
Pinus albicaulis
Pinus contorta ssp. murrayana
Ribes cereum
**Ribes montigenum**
**Salix arctica**
**Salix orester**
**Salix planifolia ssp. planifolia**
**Spiraea densiflora**
**Vaccinium caespitosum**

2.4.2 *Estimating percent herb cover*

For each plot, we estimated percent herb cover as the sum of the total recorded centimeter cover for each of the two transect lines divided by the total distance (1780 cm x 2).

We chose to use our transect data (line intercept method) rather than quadrat data (ocular cover method) for estimating cover because of the high degree of observer error in ocular cover estimates found in other studies (Vittoz et al. 2010, Klimeš et al. 2001, Vittoz and Guisan 2007). Ocular cover estimates are often highly variable between different observers and even the same observer on different days. In contrast, the line intercept method has been shown to be less likely to suffer from observer error (Vittoz et al. 2010).

2.4.3 *Estimating percent woody cover*

We used the same coding to refine the “woody” category as described above in estimating woody species richness. We estimated percent woody cover as the sum of the total recorded centimeter cover for each of the two transect lines divided by the total distance (1780 cm x 2).

2.4.4 *Estimating community climate affinity*

For all species that occurred within 1X1 meter quadrats, global occurrence data was obtained from the Global Biodiversity Information Facility database (www.gbif.org). We removed occurrences that were in the ocean, with the word “garden” in the site description, any cultivated records and any duplicate records that had identical latitude and longitude values. Thus, the final set of occurrences for each species represents the global native and non-native occurrences for that taxon. For each occurrence, climate data was then extracted from the WorldClim-Global Climate Data database (www.worldclim.com). We chose to focus on four variables: maximum
temperature of the warmest month, minimum temperature of the coldest month, precipitation of the driest month, and precipitation of the wettest month. We chose these four variables due to the potential for wide variability in temperatures throughout the year and for the potential in a changing climate for species stress tolerances to be based on the lowest and highest temperatures (Kopp and Cleland 2014). For each species, we then calculated the mean climate value for each of the four variables. For each quadrat, the 'community climate affinity' was calculated as the mean of all the species means for those species occurring within the quadrat for each of the four climate variables (Figure 5).

Figure 5: The concept of community climate affinity methods. We extracted the occurrence data of each species found in example plot j from global occurrence records. In this illustration we started with species B, represented by a blue square. We obtained climate data (maximum temperature of the warmest month shown here) for each of those places where species B has been known to occur. This was averaged and the combined average of all species climate affinities found in plot j serves as the community climate affinity for that specific climate variable (in this case, maximum temperature of the warmest month).

2.5 Data analysis

All statistical analyses were performed in R version 3.5.2 (R Development Core Team 2018) using the R package “lme4” (Bates et al. 2015). Violin plots were made using “ggplot”
All data and R scripts are included are digitally archived at DigitalCommons@CalPoly.

### 2.5.1 Assessing change in herb and woody cover

To test whether there was a change in woody plant and herb cover over the 30-year period, we used two separate linear mixed models for the two response variables: herb cover and woody cover. In both models, plot was treated as a random effect and visit (historic =1, contemporary=2) was a fixed effect, and summed cover of the two transect lines in the plot as the response variable.

### 2.5.2 Assessing change in herb species richness

To test whether there was a change in species richness over the 30-year period, we used a generalized linear mixed model using the “glmer” function with a Poisson error distribution and quadrat nested within plot as a random effect, visit as the dependent variable, and with richness as the predictor variable.

### 2.5.3 Assessing change in community climate affinity

To test whether there was a change in community climate affinity over the 30-year period, we used four separate linear mixed models (one for each of the climate variables) with quadrat nested within plot as a random effect, visit as the dependent variable, and one of the four climate variables as the predictor.

### 2.5.4 Assessing contemporary year to year variation versus long term change

For the 12 plots revisited twice, one year apart (all in Dusy Basin), we repeated the analyses described above except that ‘visit’ had three levels (visit 1= historic, visit 2 = 2018, visit 3 =2019). In cases where the overall effect of visit was significant, we performed multiple pairwise comparisons to determine which visits were significantly different (function ‘glht’ from R package multcomp, Hothorn et al. 2008).
3. RESULTS

3.1 Overview

A total of 222 species were found across all quadrats sampled (n=623) across 105 plots with an average of 4.14 species per quadrat. The plots, each containing six quadrats, varied in species richness from 0-18 across all quadrats. No non-natives were detected in any of the plots. The plots, each containing six quadrats, varied in species richness from 0-18 across all quadrats. No non-natives were detected in any of the plots. The ten most abundant herb species, measured as the percent of quadrats they were found in, were: Juncus parryi (70%), Carex breweri (64%), Carex filifolia (42%), Antennaria media (40%), Selaginella watsonii (40%), Eriogonum incanum (39%), Carex spectabilis (22%), Carex rossii (21%), Elymus elymoides (19%), Solidago multiradiata (15%), and Lupinus breweri (15%). Of the 14 plots with trees, Pinus albicaulis and Pinus contorta, were the only two tree species found with Pinus albicaulis about 3 times more abundant than Pinus contorta. The five most abundant woody species in terms of percent cover along the transects were Pinus albicaulis (1.27%), Salix orestra (0.478%), Holodiscus discolor var microphyllus (0.395%), Phyllococe breweri (0.394%), and Pinus contorta (0.156%). The following species were only found in one quadrat across all plots: Boechera lemonni, Cirsium occidentale, Cryptantha nubigena, Danthonia unispicata, Dodecatheon jeffreyi, Draba oligosperma, Mimulus suksdorfi, Polygonum shastense, Sedum lanceolatum, Stipa occidentale, Streptanthus tortuosus, Thalictrum fendleri, and Viola macloskeyi.

3.2 Herb and woody cover

Herb cover ranged between 0-85% across all plots (Figure 6). Overall, herb cover increased 21% on average between the historic (11.83%) and contemporary time periods (14.34%) (linear mixed model, f= 9.75, df = 103, P= 0.002).

The percent woody cover ranged from 0-40% per plot. The historic average woody cover was 2.2% of transect lines surveyed per plot. While we measured woody plants to be 3.4% of contemporary cover, there was no significant change between visits (linear mixed model, f= 1.75, df = 103, P=0.188).
Figure 6: Box plots of herbaceous cover. The mean amount of cover is shown in red. A) Box plot of herbaceous cover in all alpine National Resource Inventory plots in Sequoia and Kings Canyon National Parks (n=105) from historic (1986-1993) to contemporary (2018-2020) surveys. Herb cover increased by 21% (P=0.002). B) Box plot of the change in percent herbaceous cover between historic and contemporary surveys.
Figure 7: Box plots of woody cover. The mean amount of cover is shown in red. A) Box plot of woody cover in all alpine National Resource Inventory plots in Sequoia and Kings Canyon National Parks (n=105) from historic (1986-1993) to contemporary (2018-2020) surveys. Woody cover did not change (P=0.188). B) Box plot of the change in percent woody cover between historic and contemporary surveys.

3.3 Herb species richness

The number of herb species per 1 m quadrats ranged from 0 - 18 across both historic and contemporary surveys (Figure 7). Between historic and contemporary sampling, herb richness quadrats increased by 25%, from 3.26 species historically to 4.14 contemporarily (generalized linear mixed model, z=8.146, P< 0.001).
Figure 8: Box plots of herb species richness in all alpine National Resource Inventory plots (n=105) in Sequoia and Kings Canyon National Parks. A) Total herb species richness from historic (1986-1993) and contemporary (2018-2020) surveys. B) The difference in total species richness from historic to contemporary. The mean number of herb species is shown in red. Species richness increased 25% from 3.26 to 4.14 (P< 0.001).

3.4 Community climate affinity

Comparing the community climate affinities for the maximum temperature of the warmest month for each quadrat we found contemporary climate affinities for maximum temperature had increased by 2% from 20.73°C to 21.19°C (linear mixed model, t = 4.157, df = 381, P< 0.001).

The contemporary community climate affinity for the minimum temperature of the coldest month did not change from the historic (linear mixed model, t = 1.48, df = 785, P = 0.14).

The mean community climate affinity for precipitation of the wettest month did not change across visits (linear mixed model, t = -0.32, df = 398, P = 0.75).

The contemporary mean community climate affinity for precipitation of the driest month did not change from the historic levels, 22.62 and 22.06 respectively (linear mixed model, t = -1.85, df = 363, P = 0.065).
Figure 9: Violin plots of community climate affinity for four chosen climatic variables in all alpine National Resource Inventory plots (n=105) in Sequoia and Kings Canyon National Parks from historic (1986-1993) to contemporary (2018-2020) surveys. The mean community climate affinities are shown in red. A) The mean community climate affinity for maximum temperature increased across visits (P<0.001). B) The community climate affinity for the minimum temperature of the coldest month did not change from the historic (P=0.14). C) The mean community climate affinity for precipitation of the wettest month also did not change (P=0.75). D) The community climate affinity for the driest month did not change from the historic values (P=0.065).
3.5 Assessing contemporary year to year variation in Dusy Basin

3.5.1 Herb and woody cover

For 12 plots that were visited three times (once historically, and twice contemporarily in 2018 and 2019) we found an overall effect of sample visit on herb cover, Figure 9A (linear mixed model, ANOVA, chisq=16.091, df = 2, P = 0.0003). Posthoc tukey comparisons revealed a significant difference in herb cover between historical and both contemporary visits (2018: P<0.001, 2019: P = 0.0279), but not between the two contemporary visits (P=0.349).

There was no change in woody cover across visits, Figure 9B (linear mixed model, ANOVA, chisq= 1.0992, df=2, P=0.577).

Figure 10: Box plots of herbaceous and woody cover in Dusy Basin alpine National Resource Inventory plots (n=12) in Sequoia and Kings Canyon National Parks from historic (1986-1993) to contemporary (2018-2019) surveys. The mean amount of cover is shown in red. A) There was an increase in herb cover by visit (P<0.01) and B) no change in woody cover.

3.5.2 Herb species richness

For these same 12 plots we found an overall effect of sample visit on herb species richness (linear mixed model, ANOVA, chisq=25.061, df = 2, P < 0.001). Posthoc tukey
comparisons revealed a significant difference in herb cover between historical and both contemporary visits (P<0.001), but not between 2018 and 2019 (P=0.67).

Figure 11: Box plot of herb species richness in Dusy Basin alpine National Resource Inventory plots (n=12) in Sequoia and Kings Canyon National Parks from historic (1986-1993) to contemporary (2018-2019) surveys. The mean number of herb species found in quadrats is shown in red.

3.5.3 Community climate affinity

Sample visit influenced the community climate affinity for mean maximum temperature of the warmest month, Figure 11A (linear mixed model, ANOVA, chisq= 7.96, df=2, P=0.019). There was an increase, shown through posthoc tukey comparisons, in affinity for maximum temperature of the warmest month between historic and both contemporary visits (P<0.001) but not between the two contemporary surveys (P=0.743).
Figure 12: Violin plots of community climate affinity for four chosen climatic variables in Dusy Basin alpine National Resource Inventory plots (n=12) in Sequoia and Kings Canyon National Parks from historic (1986-1993) to contemporary (2018-2019) surveys. Community climate affinity means are shown in red. A) The mean community climate affinity for maximum temperature increased across visits (P<0.001). B) The community climate affinity for the minimum temperature of the coldest month did not change from the historic (P=0.74). C) The mean community climate affinity for precipitation of the wettest month changed from historic values to 2019 (P=0.007) but between the other years. D) The community climate affinity for the driest month did not change from the historic values (P=0.1).

There was no change in community climate affinity for the minimum temperature of the coldest month between visits, Figure 11B (linear mixed model, ANOVA, chisq= 0.5918, df=2, P=0.74).
The community affinity for mean precipitation of the wettest month decreased (linear mixed model, chisq=9.988, df= 2, P= 0.007) from 130.89 mm historically to 2019 by 7.51 mm (linear mixed model, z=-3.154, P=0.005) with no change between 2018 and 2019, Figure 11C (linear mixed model, z=-1.373, P=0.355).

The contemporary 2019 mean community climate affinity for precipitation of the driest month did not change from the historic levels, 23.57 and 25.32 respectively, Figure 11D (linear mixed model, ANOVA, chisq= 4.6, df = 2, P = 0.1).
4. DISCUSSION

4.1 Overview

Long term observational studies such as this are the only glimpse into changes in these remote alpine vegetation communities and are rare in the United States. Though an overall greening effect has been found in some cases in Europe, alpine habitat there experiences additional pressures such as grazing and more off-trail human impact than the high elevation areas of Sequoia and Kings Canyon National Parks. Studies had been done in the White Mountains, the mountain range east of these Parks, and found an increase in cover along with a decrease in species richness.

Over a 30-year period, we found that alpine plant communities in Sequoia and Kings Canyon became greener with more total plant cover, more species rich, and communities have shifted towards species that are on average from regions with warmer summer temperatures. These observations go against model projections that alpine plants are in decline and that plants typically found there will soon be gone. However, our observations are in line with the lag between establishment and extinction, thus the alpine species may still be gone soon. Further monitoring and experiments, outlined below, will need to be done.

4.2 Herb and woody cover

Herb cover has increased in the high elevations of Sequoia and Kings Canyon National Parks over the last 30 years. The explanation for this result could be two-fold. First, warmer, longer summers may have allowed alpine plants to produce more biomass. While alpine taxa are generally considered slow growing, under the right conditions (i.e., warmer temperatures) they may grow more quickly and retain that growth year-to-year as seen in the plots we resurveyed two contemporary years in a row. Secondly, colonization and establishment of new taxa in these plots may have caused an overall increase in herbaceous cover. Unfortunately, the original survey method for herb cover along transects (line intercept method) did not assess cover of individual species and instead lumped all herb cover into a single number, so we are not able to distinguish between these two possibilities in the present study.
Woody cover is generally quite low in the Sierra Nevada alpine (Rundel 2011) and our results reflected that: woody cover was on average less than 4% of plots in both historic and contemporary surveys. While the absolute increase in woody cover has so far been small (1.6% increase), if the rate of change were to increase in the future this has the potential to dramatically alter the alpine landscape towards a more competitive community dynamic and the shading out of the low growing cushion plants.

A caveat with resurvey studies like ours involving just two time points separated by several decades, is that it is unknown whether patterns observed reflect an overall trend or simply represent year to year variation. Because the original plot surveys spanned a ten-year interval (1986 – 1993) which contained both wet and dry years, this is less likely driving our overall results. To explore this further, we also estimated contemporary year-to-year variation (2018 vs 2019) in a subset of plots (n=12). We found no significant difference in herb cover between 2018 and 2019, while both contemporary years had greater herb cover than the historic surveys. This implies that the increase has occurred in response to the changing conditions over the last 30 years and was not a result of annual variation in temperature or precipitation. This makes sense considering the long-lived slow-growing habit of alpine species such as the cushion plants and the low number of annual plants found in the alpine zone. Alpine vegetation communities in California likely experience reduced year to year change in cover relative to low elevation vegetation which experiences dramatic changes in cover depending on the sample year.

**4.3 Herb species richness**

In addition to finding an overall greening effect, we found that species richness also increased. Potentially, there are several non-mutually exclusive explanations for this. First, it could be that species from lower elevations dispersed and colonized the alpine over the last 30 years, thus increasing the overall number of species within our plots. Secondly, it could be that we are witnessing the extinction lag of the alpine specialists, which are slow to be extirpated following the arrival of more competitive species from lower elevations, in which case we expect the number of species to be reduced in the future. Finally, it could be that the increase in richness is due not to recent dispersal, but rather to a large preexisting seed bank of both alpine and lower
elevation species. In this case, the higher temperatures of the last 30 years may have created the conditions necessary for these seeds to germinate and establish.

Again, a caveat regarding species richness is that the changes over the 30-year period may simply reflect year to year variation that does not reflect an overall directional change. We however found no evidence to support year to year effects on richness. In our subsample of 12 plots, we found no significant difference in richness between 2018 and 2019, but both contemporary years had higher richness than the historical surveys. This suggests that the increased richness is not a temporary effect and instead has been growing steadily over time.

4.4 Community climate affinity

We found that community climate affinity for maximum temperatures of the warmest month increased over this 30-year period. As this result was also reflect in our year-to-year assessment, with significant change between historic and both contemporary years community affinities for maximum temperature and no change between 2018 and 2019, this further suggests an influx of lower elevation species that are used to warmer temperatures over the 30-years. Given that the summer temperatures are at increasing at a faster rate (1°C per decade) than the overall annual temperature, this trend seems likely to continue.

The concept of community climate affinities, although a relatively new one, could be helpful in monitoring changes in plant communities over time at a more subtle level than simply looking at species richness. Our results are consistent with an overall increase of warmer affinity plant species in the alpine, i.e., the process of thermophilization whereby warm-adapted species increase within a community and cold-adapted species decrease. While our current analysis does not fully distinguish between these two processes, future analyses will aim to disentangle the relative drivers of the community climate shifts – colonization of warm-adapted species versus extirpation of cold-adapted species. We predict that most likely our results are driven by the former, and that given extinction lag times of cold-adapted species we are not yet observing the latter.

4.5 Further steps: Improving reproducibility, management implications, and the fate of alpine plants
We encountered many difficulties in reconciling past data with our current surveys, mainly due to limitations in the analyses we could accomplish given the historical data. For example, we had no way of standardizing effort in our plot surveys. We did not know how much time was spent searching as each plot, how much time between last species and next species, nor did we have a systematic approach to walking through each plot. Details such as these, if they were documented, would likely increase the accuracy of year-to-year comparisons. Another limitation was the lack of species-specific herb data on the transects and woody data in the quadrats in the historic surveys. Future resurveys will be able to compare more directly to this data as well as Cathy Bell's.

There is much data to be gained from quadrat photos. In 2018 and 2019, we took Cathy Bell's suggestion and took photos from above directed down at the quadrats. However, afterwards we noticed that several were from a different angle or slightly from the side. Having a selfie stick or some other device that could hold the camera above the quadrat at a set height and angle in a variety of conditions may be useful in obtaining photographs for comparison.

A common garden experiment as has been done in Europe could be helpful to study what continually increasing warm temperatures and the introduction of more woody species will do to a typically herb and graminoid habitat at high elevations. This could help narrow the range on where the tipping point potentially is leading to the extirpation of alpine cushion plants and other high elevation specialists.

Given the small but significant changes we found in herb cover, species richness, and community climate affinity for the maximum temperature of the warmest month, close monitoring of the alpine in future is in order. In addition, collecting seeds and/or in situ propagation of cuttings from alpine species would be wise. Land managers will have to make difficult decisions if alpine species start to die off.

The establishment of low elevation species, including more woody plants, could lead to the extirpation of historic alpine plants. Alternatively, these alpine specialist species, perennial grasses, sedges, rushes, and cushion plants, may find suitable niches in the differing topography of alpine habitat and disperse to cold micro-refugia at a similar elevation or even a lower one with
the appropriate slope and aspect. Yet another option could be that typical high elevation species are adaptable and able to track the climate thus persisting in warmer and warmer temperatures.

4.6 Conclusion

Over the last 30-years, we found that alpine plots in Sequoia and Kings Canyon National Parks in California, USA have increased in both herbaceous and woody plant cover, as well as species richness, and the community assemblage has shifted towards species with affinities for higher maximum summer temperatures. With the rarity of alpine habitat in California and the potential of dramatic changes with continuing increasing temperatures, further monitoring of this fragile habitat is advised.

REFERENCES


