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To flee or not to flee: how range dynamic of alpine species are changing through time

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To flee or not to flee: how range dynamic of alpine species are changing through time

By

LiAn Makana Noonan

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Master's Thesis

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LiAn Makana Noonan

June 20, 2023

To flee or not to flee: how range dynamic of alpine species are changing through time

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
LiAn Makana Noonan
June 20, 2023

Abstract

In response to anthropogenic climate change, alpine floras in particular have been forecasted to shift their ranges upslope and north, yet recent analyses have shown otherwise. While a handful of floras have been found to track the trajectory of predictive models, most floristic elements have remained in their historical ranges despite a changing climate. Therefore, to improve the accuracy of models predicting range shifts, I address the following questions: (1) are mountain floras spatially structured through time; and (2) how are range dynamics of mountain floras changing through time. To address these questions, this study analyzed the herbarium records of 46 endemic alpine flora found in the Sierra Nevada Ranges of California. A permutational multivariate analysis of variance (PERMANOVA) was used to test the association between spatial similarities and similarities in collection time and/or elevation. The effect size of time and each environmental parameter (latitude, longitude, and elevation) were used to assess how range dynamics of alpine floras have changed over the past century. While the occurrence of some floras were found to be spatially structured and were considered to have been distributed latitudinally, longitudinally, and/or elevationally in relation to time, a majority of floras (89%) were found remaining in their historical ranges. Our results were found to be similar to recent analyses, suggesting the ranges of alpine floras have not tracked climate change as forecasted. If the rate of climate change is to follow the proposed trajectory, then species distribution models need to include the current distribution of species to accurately reflect future distributions and ultimately influence conservation decisions.

Acknowledgements

I would also like to recognize my students, instructors, and peers from Biology 101, 204, and Bellingham Technical College who not only developed my confidence in public speaking but also taught me how to speak up in tough times. Furthermore, I'd like to especially thank Dr. Carrie Schwarz and Dr. Merrill Peterson for the advice they've given. You both have inspired me with your dedication to furthering higher level education and your humility. Thank you two for being the pillars keeping me standing these past few years.

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Introduction

Anthropogenic climate change has reportedly triggered range shifts of many alpine floras through time (**Parmesan & Yohe, 2003**). Range shifts are among the most well documented response of species to a changing climate, but researchers have yet to settle on the extent to which species move in congruence with changes in climatic variables and ultimately establish themselves in new habitats. Research on elevational range shifts have focused on (1) species expansion into new terrain upslope, commonly known as the leading edge, and (2) species contractions at lower elevations downslope, referred to as the rear edge. Such range dynamics remain complex as they highlight the independent nature or range shifts. That is, shifts in elevational range edges such as the leading and rear edges, are not always synchronous (**Kelly & Goulden, 2008**) nor in the same direction (**Lenoir et al., 2010**). Therefore, understanding the independent response of species to changes in environmental parameters such as latitude, longitude, and elevation through time would provide us with a better understanding of the current direction of alpine floras. However, to date very few studies have quantified how range dynamics of alpine species are changing over time.

Some studies focused on species distribution modeling have predicted that species will shift their range when modeled alongside climate variables under different warming scenarios (**Loarie et al., 2009**). These studies forecast that range shifts will occur based on climate and habitat suitability and often project shifts in species occurrences poleward and/or towards higher elevations (**Lenoir et al., 2008; Parmesan & Yohe, 2003; Rixen et al., 2014; Rumpf et al., 2018a; Walther et al., 2005; Wershow & DeChaine, 2018**). While it is true that some species ranges have shifted in correspondence with the predictive models, recent empirical and observation-based studies have found that species respond idiosyncratically to range shifts

(**Lenoir et al., 2010; Rumpf et al., 2018a; Rumpf et al., 2018b**). In other words, the distribution of species have shifted counterintuitively to the predicted models or have experienced little to no shifts in range (**Alexander et al., 2018; Dullinger et al., 2012a; Dullinger et al., 2012b**). A resurvey of 1,576 vegetation plots in the European Alps found the average increase in species abundance of the 183 species recorded was more pronounced than the average range limit expansion upslope (**Rumpf et al., 2018a**). Although there were a few species found to shift ranges upslope at both leading and rear edges, the majority were found to be centered around little to no elevational change. The average lack of change in elevation might be explained by the increase in the abundance of species within their historical ranges. Such proliferation, also known as the process of in-filling, indicates species may not be shifting range and instead maintained their historical locations. Alternatively, species may also experience a lag effect, where species have been documented to persist in their environment despite the displacement of suitable habitat.

High mountain regions inclusive of the alpine zone are arguably the region most threatened by changing climate (**Beniston, 2003**) and therefore provide an ideal system to study how alpine floras have been spatially structured through time. The isolating conical shape of the mountain top paired with accelerated rate in which high mountain species experience climatic change make the alpine zone a model system for studying the impact of anthropogenic climate change on the spatial structure of species over time. Furthermore, the unique topography (**Boucher, 2015; Wallis, 2016**) and spatial heterogeneity (**Ackerly, 2010**) of alpine zones generate a high degree of endemism. Endemics are surrogates for biodiversity (**Capers et al., 2013; Lenoir et al., 2008; Pauli et al., 1996; Walker et al., 2001**) as they are restricted to a specific area or habitat (**IUCN, 2018**) and therefore inform us of the overall health of

ecosystems, particularly structural changes over time. Alpine endemic species have adapted well to the inhospitable climates of high mountain regions but may also have a reduced tolerance to changes in climate (**Brooks et al., 2006; de Lima et al., 2020; Myers et al., 2000; Thomas, 2011**). Such characteristics advocate the use of endemic alpine species as representatives in understanding the relationship between environmental parameters such as latitude, longitude, and elevation through time. To assess the relationship between environmental parameters and time, I must first define the alpine zone.

The alpine zone has been loosely defined as the area that consists of vegetation found above the tree line (**Körner, 2003**) but should be specifically defined for the purpose of this study. Following a conservative approach used by Sharsmith (1940) and Rundel (2011), the lower elevational limit of the alpine zone was defined at 3300m to account for tree line ecotones and elevational maximum specific to the Sierra Nevada Mountain range. Previous approaches to delimiting the alpine zone have included (1) setting tree line ecotones as lower elevational limits (**Billings, 1978**), (2) using set elevations (**Rundel, 2011; Sharsmith, 1940**), and/or (3) other characteristics of the habitat surrounding a specified flora (**Testolin et al., 2020**). While each of these methods were applied to individual studies, variations in geographical characteristics and microclimates across latitudes have resulted in a lack of a ubiquitous classification for the alpine zone (**Körner, 2003**). The alpine zone of California was initially set with a lower elevational limit of 3500m (**Sharsmith, 1940**); however, the Northern Sierra Nevada range does not meet the lower elevational threshold. To avoid omitting fragmented communities of alpine species or concurrently lower dispersing species, this study will adopt the elevational boundary of 3300m (Figure 1). Alpine species found strictly within the alpine zone (therefore maintaining an elevational standing above 3300m) and alpine species centered within the alpine zone with

potential distribution at lower elevations will be considered alpine species for this study

(**Körner, 2003**). We include central species with a lower elevational margin distribution, as they

may be indicators of in-filling. Omitting species with lower margin distributions entirely would

reduce the assessment power of the extent of elevations associated with species occurrences.
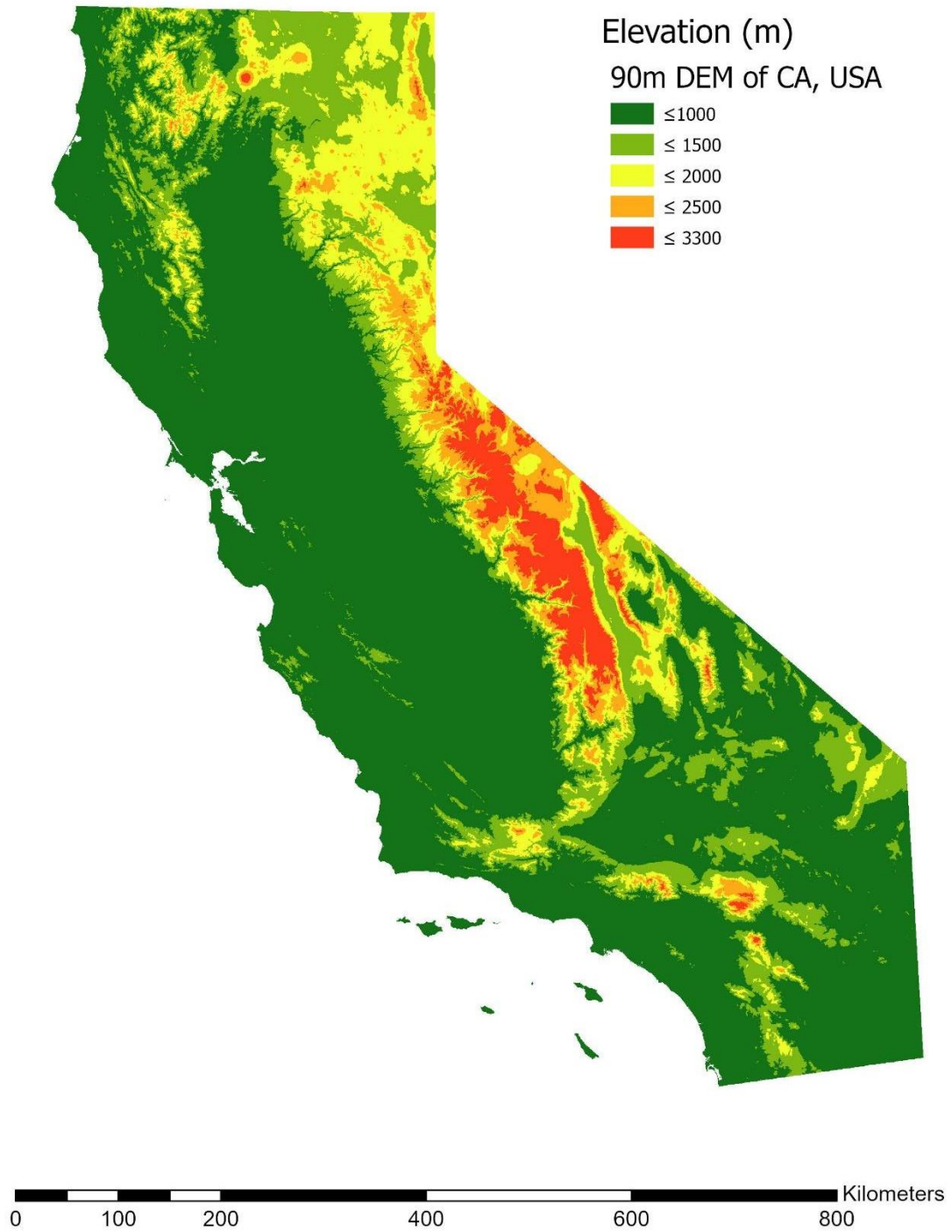
Figure 1. *A digital elevation model (DEM) of the elevational ranges of California where the lower elevational threshold of 3300m is highlighted in red.*

The Sierra Nevada ranges are ideal for studying whether flora have been spatially structured though time as this range hosts a majority of endemic flora in California. As of 1978, approximately 30% of the flora found in California were considered endemic to the state (**Raven & Axelrod, 1978**). The Sierra Nevada ranges are representative of 15% of the overall endemic flora found within the state, thus accounting for half of the endemic flora found within California (**Shevock, 1997**). Summatively, the Sierra Nevada ranges (1) geographically span approximately 25% of California, (2) account for half of the total endemic flora within the state, and (3) are projected to be currently experiencing range shifts and contractions (**Loarie et al., 2008**). Therefore, my study will use flora that are endemic to the alpine zones of the Sierra Nevada ranges of California to understand whether flora are spatially structured through time. While some studies may differentiate levels of endemism such as true or near (**de Lima et al., 2020**), delineating the classification of endemics is not imperative to my study and will be referred to collectively as endemic. The flora will be deemed endemic in accordance with the Jepson Manual, where native species confined to a specific geographic area (**Baldwin et al., 2012**) are considered endemic.

Over the last century the climate of the Sierra Nevadas has changed and may be informative of whether floristic elements have tracked climate over time (**Halofsky, 2021; Pauli et al., 2012; Wuebbles, 2017**). Annual average temperatures in the Southwest United States have reportedly increased approximately 1.6 degrees Fahrenheit between the years of 1901 and 2016 (**Vose et al., 2017**) and continues to rise with elevation. In turn, the average increase in temperature has resulted in an increasing proportion of winter precipitation delivered as rain rather than as snow (**Knowles et al., 2006**), further reducing snowpack in many parts of the Sierra Nevada range. The accumulation of snow is integral to the floral population in the alpine

zone in particular as snowpack provides insulation from winter temperature extremes and stores water which slowly melts and supports populations in the spring and summer (**Dettinger et al., 2018; Körner, 2003**). As such, the climate conditions of the Sierra Nevada ranges may reflect the occurrences of species through time.

Based on the documented change of climate parameters in the Sierra Nevada over the last century and its forecasted trajectory, this study will utilize historical and contemporary herbaria collections of endemic alpine flora distributed within the Sierra Nevada range to address the following questions. First, are herbaria collections of endemic alpine flora spatially structured through time? Second, how are range dynamics of alpine species changing over time? To address these questions, I used cataloged herbarium records from the Consortia of California Herbaria 2 (CCH2) (**CCH2 Portal, 2023**) to form a species occurrence dataset which I will analyze to determine the biogeographic response of alpine floras to climate change.

Methods

To determine whether endemic alpine floristic elements are spatially structured and fundamentally understand how range dynamics of these species have changed over the past century I ran a permutational multivariate analysis of variance (PERMANOVA) and a Pearson's product-moment correlation analysis. A permutational analysis of variance (PERMANOVA) was used to test the associations between the spatial similarity of herbaria collections and the similarity of collection time and/or elevation. To assess how range dynamics of alpine floras are changing through time I used a Pearson's product-moment correlation to determine the strength of the relationship between time and the environmental parameters: latitude, longitude, and elevation. The results of the Pearson's product-moment correlation were transformed into Cohen's d to calculate the effect size of time and each environmental parameter to ultimately assess the range dynamics of endemic alpine floras over the past century.

Species selection and dataset development

Species were selected from a comprehensive checklist (**Rundell, 2011**) of 46 species endemic to the alpine zones of the Sierra Nevada ranges in California (**Baldwin et al., 2012**). Species identified broadly as Californian endemics were excluded from the study, as they do not have as steep a limitation on geographic expansion as presented in the Sierra Nevada ranges. Of the 46 species selected for this study, the number of unique herbarium records per species ranged from 2 records (representative of the species *Leptosiphon oblanceolatus* (Brand) J. M. Porter & L. A. Johnson (Polemoniaceae)) to 188 records (representative of the species *Lilium kelleyanum* Lemmon (Liliaceae)) and averaged 58 unique herbarium records per species (Table 1). This comprehensive species list (**Rundell, 2011**) was selected as it provided a recent detailed analysis

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of the floristic richness and associated biogeographic relationships of species currently present within the alpine zone of the Sierra Nevada ranges.

To retrieve the historical species distribution data, I downloaded species occurrence records (hereafter referred to as herbaria records) from the Consortia of California Herbaria (CCH2) (**CCH2 Portal, 2023**). The genus and species of selected flora were input into the CCH2, producing records of each unique herbaria specimen. Unique herbarium specimen records will be used accordingly to define an individual record of a specific species with a unique catalog number and symbiota ID in the CCH2 Herbarium. Any discrepancies in binomial nomenclature were included in the summative caption next to taxa cataloged in the CCH2 herbarium. The binomial nomenclature followed in this study (**Rundell, 2011**) was in line with species identified in *The Jepson Manual, 2nd Edition* (**Baldwin et al., 2012**). The summary of unique herbarium records for each species (excluding cultivated and captivate occurrences) were downloaded using the Symbiota Native structure. Each of the unique herbaria records of the 46 selected species (Table 1) were cataloged in a dataset and manually filtered for inaccuracies and discrepancies. Inaccuracies included extreme outliers in minimum elevation and/or coordinate locations. Discrepancies included improper elevational metrics, differing binomial nomenclature and/or differing families, which were amended to align with the Jepson manual, 2nd ed. (**Baldwin et al., 2012**). The original herbaria image was referenced in the case of either inaccuracies or discrepancies. If there was a lack of ubiquity between the image and the cataloged data, the data contained within the image label was used. If the image was illegible, the sample was removed from the study. After collating the records, my study included a total of 46 species across 18 families (Table 1).

Table 1. *The number of unique herbarium records of 46 endemic alpine species with their associated range in minimum elevation in meters and range of the years collected. Nomenclature follows Baldwin et al. (2012) and the data was gathered from the CCH2 Portal (2023).*

Family	Scientific Name	Range of Minimum Elevation (m)	Range of Years Collected	Number of Unique Herbaria Records per Species
Apiaceae	*Lomatium torreyi*	914 – 3446	1895 – 2021	65
Apiaceae	*Oreonana clementis*	1585 – 3901	1895 – 2019	61
Asteraceae	*Erigeron elmeri*	1520 – 3354	1902 – 2010	44
Asteraceae	*Hazardia whitneyi var. whitneyi*	304 – 3169	1894 – 2018	67
Asteraceae	*Hulsea vestita subsp. vestita*	1402 – 3410	1895 – 2015	86
Asteraceae	*Oreostemma peirsonii*	2316 – 3733	1933 – 2019	23
Asteraceae	*Orochaenactis thysanocarpha*	1524 – 3415	1897 – 2019	112
Boraginaceae	*Cryptantha circumscissa var. rosulata*	2591 – 3659	1949 – 2008	9
Boraginaceae	*Phacelia eisenii*	1249 – 3352	1896 – 2019	76
Boraginaceae	*Phacelia orogenes*	1768 – 3048	1888 – 1983	21
Brassicaceae	*Boechera pygmaea*	2103 – 3433	1904 – 2018	24
Brassicaceae	*Draba cruciata*	2400 – 3963	1904 – 2002	29
Brassicaceae	*Draba lemmonii*	2501 – 4418	1878 – 2013	176
Brassicaceae	*Draba longisquamosa*	3169 – 4267	1897 – 2009	26
Brassicaceae	*Draba sharsmithii*	3049 – 3780	1935 – 2006	16
Brassicaceae	*Draba sierrae*	2985 – 4115	1929 – 1998	42
Brassicaceae	*Streptanthus gracilis*	1706 – 3414	1900 – 1981	19
Cyperaceae	*Carex congdonii*	1070 – 3901	1904 – 2020	141
Cyperaceae	*Trichophorum clementis*	2556 – 3810	1928 – 2013	100
Fabaceae	*Astragalus monoensis var. ravenii*	3316 – 3688	1956 – 1988	12
Fabaceae	*Lupinus covillei*	2225 – 3293	1863 – 2020	52
Fabaceae	*Lupinus gracilentus*	2552 – 3200	1929 – 2015	20

Table 1. Continued.

Family	Scientific Name	Range of Minimum Elevation (m)	Range of Years Collected	Number of Unique Herbaria Records per Species
Fabaceae	*Trifolium macilentum var. dedeckerae*	2133 – 3418	1931 – 2015	41
Fabaceae	*Trifolium monanthum subsp. tenerum*	1402 – 3186	1905 – 2019	15
Juncaceae	*Luzula orestera*	2134 – 3584	1900 – 2019	95
Lamiaceae	*Monardella beneolens*	2000 – 3598	1896 – 2020	27
Liliaceae	*Lilium kelleyanum*	516 – 4012	1903 – 2017	188
Montiaceae	*Lewisia disepala*	1402 – 2316	1938 – 1996	16
Orobanchaceae	*Castilleja praeterita*	2240 – 3478	1898 – 2019	69
Poaceae	*Calamagrostis muiriana*	2484 – 3718	1895 – 2013	94
Poaceae	*Poa stebbinsii*	365 – 3642	1900 – 2018	72
Poaceae	*Stipa kingii*	1990 – 3536	1900 – 2014	93
Polemoniaceae	*Ipomopsis aggregata subsp. bridgesii*	1524 – 3048	1900 – 2016	60
Polemoniaceae	*Leptosiphon oblanceolatus*	3361 – 3505	1966 – 2019	2
Polemoniaceae	*Phlox dispersa*	2438 – 4286	1937 – 2019	24
Polemoniaceae	*Polemonium eximium*	2000 – 4417	1863 – 2017	102
Polygonaceae	*Eriogonum nudum var. scapigerum*	2743 – 3718	1895 – 2020	53
Polygonaceae	*Eriogonum ovalifolium var. caelestinum*	1890 – 3672	1962 – 2020	14
Polygonaceae	*Eriogonum polypodum*	2297 – 3421	1905 – 2019	37
Polygonaceae	*Eriogonum spergulinum var. pratense*	1829 – 3353	1942 – 2013	31
Polygonaceae	*Eriogonum wrightii var. olanchense*	3298 – 3567	1950 – 1978	7
Primulaceae	*Dodecatheon subalpinum*	2545 – 3292	1917 – 2009	16
Ranunculaceae	*Aquilegia pubescens*	1982 – 3962	1889 – 2018	177
Rosaceae	*Ivesia muirii*	2591 – 3700	1900 – 2019	73
Rosaceae	*Ivesia pygmaea*	335 – 4150	1864 – 2019	81
Rubiaceae	*Galium hypotrichium subsp. subalpinum*	2546 – 3689	1919 – 2021	44

Data filtration

The dataset containing all of the unique herbarium records of each species was filtered to a subset and include only the following relevant parameters included in the primary data source: family, scientific name, genus, subgenus, species, subspecies, year, month, day, state, county, latitude (lat), longitude (long), datum (specific map projection), minimum elevation (minel) in meters (m), maximum elevation (max) in meters (m), and the verbatim elevation (units preserved to match initial record regardless of proper metric), which were then assessed for incomplete cases. Any individual herbarium record containing an incomplete case for either year, latitude, and/or longitude were removed from the dataset.

Samples with missing elevational data were interpolated to improve the accuracy and resolution of the dataset. The function 'SpatialPoints' from the 'sp' R package version 1.5-1 (**Pebesma & Bivand, 2005**) was used to list and conform the coordinate reference system (World Geodetic System, WGS84 represented as European Petroleum Survey Group, ESPG:4326) of the coordinates of all herbarium records to the standard Global Positioning System (GPS). The function 'get_elev_point' from the package 'elevatr' (**Hollister, 2021**) was used to reference each coordinate (latitude and longitude) and return an elevation for each coordinate. The correlation between the interpolated elevations and the elevations provided by the CCH2 herbarium were compared using Pearson's correlation, which measures the relationship between two variables, and resulted in a strong and significant positive linear correlation (r = 0.904, $p < 0.001$) (Figure S1). The interpolated elevations replaced missing elevations and increased the sample size by 611 unique herbarium records. The elevations of unique herbarium records with previously recorded elevations were not replaced and were retained. Any unique herbarium record with an elevation that fell above of the elevational range

of Mount Whitney, which is topographically referred to as the highest geographical point in California sitting at 4418m (**Britannica, 2023**), were replaced with the interpolated values to exclude outliers.

Species with 20 or more unique herbarium records were considered having met the sample size for a Permutational Multivariate Analysis of Variance (PERMANOVA) for this study. The determined sample size of 20 or more unique herbarium records per species was selected as it is large enough to include differences between groups with a high confidence, but small enough to process the data given practically. Based on the sample size baseline, 10 species were eliminated from the 46. The following are the species which were removed from the study based on sample size *Cryptantha circumscissa* (Hook. & Arn.) I. M. Johnst. var. *rosulata* J. T. Howell (Boraginaceae), *Draba sharsmithii* Rollins & R. A. Price (Brassicaceae), *Streptanthus gracilis* Eastw. (Brassicaceae), *Astragalus monoensis* Barneby var. *ravenii* (Barneby) Isely (Fabaceae), *Trifolium monanthum* A. Gray *subsp. tenerum* (Eastw.) J.M. Gillett (Fabaceae), *Lewisia disepala* Rydb. (Montiaceae), *Leptosiphon oblanceolatus* (Brand) J. M. Porter & L. A. Johnson (Polemoniaceae), *Eriogonum ovalifolium* Nutt. var. *caelestinum* Reveal (Polygonaecae), *Eriogonum wrightii* Torr. ex Benth. var. *olanchense* (J. T. Howell) Reveal (Polygonaceae), *Dodecantheon subalpinum* Eastw. (Primulaceae) (Table 1).

Are herbaria collections of endemic alpine flora spatially structured through time?

To determine whether herbaria collections of endemic alpine flora were spatially structured through time, I ran a permutational multivariate analysis of variance (PERMANOVA) on the 36 species with at least 20 occurrences. A PERMANOVA was used to test for associations between the spatial similarity of herbaria collections and the similarity of collection time and/or minimum elevation using the model formula geo ~ year * minel (**Anderson et al., 2017**). Spatial similarity was calculated using the Euclidean distance between the geographic locations of species occurrences (longitude and latitude). The PERMANOVA was done using the 'adonis2' function in the 'Vegan' R package version 2.6-2 (**Oksanen et al., 2022**). Alternative formula structure was tested in the 'adonis2' function to evaluate whether the order of variables significantly influenced results and the order of variables did not show significant variation between tests (Table S2, Table S3). Significance of model parameters were determined using $1e^6$ permutations and a Benjamini-Hochberg (BH) correction test was applied to the *p*-values obtained through the PERMANOVA (Table S1) using the 'p.adjust' function in base R version 4.1.2 (**R Core Team, 2021**).

How are range dynamics of alpine species changing through time?

For each of the 36 species with at least 20 occurrences, a Pearson's product-moment correlation was used to determine the strength of the relationship between time and the environmental parameters latitude, longitude, and elevation. The correlation between time and environmental parameters were represented using the 'pairs.panels' function in the 'psych' package version 2.3.3 (**Revelle, 2023**).

The results from Pearson's product-moment correlation (rho) were transformed into Cohen's d using the function 'r2d' from the 'psych' package version 2.3.3 (**Revelle, 2023**) to calculate the effect size of time and each environmental parameter. Cohen's d values across all species were then modeled as a violin plot to display the effect size of each environmental parameter and to assess the potential range dynamics of endemic alpine flora over approximately the past 100 years. All statistical analyses in this study were conducted using R statistical software version 4.1.2 (**R Core Team, 2021**). All data and code will be made freely available in the supplementary information.

Results

Are herbaria collections of endemic alpine flora spatially structured through time?

Over half of the species (20 of 36) were found to be spatially structured through time and/or elevation (Table 2, Figure 2, Figure 3) based on the PERMANOVA results (*p.adjust <* 0.05). The results for five of these species (*Draba longisquamosa* O. E. Schulz (Brassicaceae)*, Hazardia whitneyi* var. *whitneyi* (A. Gray) Greene (Asteraceae)*, Oreostemma peirsonii* (Sharsm.) G. L. Nesom (Asteraceae)*, Orochaenactis thysanocarpha* (A. Gray) Coville (Asteraceae)*,* and *Phacelia orogenes* Brand (Boraginaceae)) were found to have a significant association with time (Table 2), but the strength of the association was found to be species dependent. For example, the spatial structure of *O. peirsonii* was found to be strongly associated with time ($R^2 = 0.358$, *p.adjust <* 0.01) (Figure 2b) whereas the spatial structure of *O. thysanocarpha* was not as strongly associated with time ($R^2 = 0.078$, *p.adjust <* 0.01) (Figure 2c). Sixteen species were found lacking a significant association (*p.adjust >* 0.05) with elevation, while those with significant associations varied in strength. The spatial structure of *P. orogenes* was highly associated with elevation ($R^2 = 0.648$, *p.adjust <* 0.001) (Figure 3d). *H. whitneyi* var. *whitneyi* also displayed a significant association ($R^2 = 0.226$, *p.adjust <* 0.001) (Figure 3a), but with less separation than *P. orogenes*. An interactive effect was found between time and elevation within the distribution of *O. peirsonii* ($R^2 = 0.112$, *p.adjust <* 0.05) (Table 2), indicating elevation is dependent upon time of collection (Figure 2b, Figure 2c).

Table 2. *Analysis of the association between the location of collection and time or elevation was run using a Permutational Multivariate Analysis of Variance (PERMANOVA) and supported by the reported Benjamini-Hochberg (BH) correction. Represented pseudo-F value.*

	p.adjust values (BH Pr(>F))			Pseudo F Ratio (F)			Percent Coefficient of Variation (R^2)		
Species	Yr	Minel	Yr:Minel	Yr	Minel	Yr:Minel	Yr	Minel	Yr:Minel
Aquilegia pubescens	0.815	0.598	0.512	0.292	0.393	2.091	0.002	0.003	0.016
Boechera pygmaea	0.4	**0.002**	0.847	1.871	**18.209**	0.199	0.049	**0.476**	0.005
Calamagrostis muiriana	0.716	**0.002**	0.772	0.772	**35.588**	0.28	0.006	**0.281**	0.002
Carex congdonii	0.815	**0.002**	0.703	0.258	**36.523**	0.721	0.001	**0.211**	0.004
Castilleja praeterita	0.244	**0.002**	0.711	2.6	**165.886**	0.699	0.011	**0.708**	0.003
Draba cruciata	0.815	0.132	0.512	0.471	3.027	1.41	0.016	0.101	0.047
Draba lemmonii	0.815	**0.002**	0.074	0.306	**48.397**	7.273	0.001	**0.212**	0.032
Draba longisquamosa	**0.022**	**0.046**	0.512	**7.615**	**4.974**	1.785	**0.209**	**0.137**	0.049
Draba sierrae	0.229	**0.002**	0.512	3.656	**16.179**	1.711	0.061	**0.272**	0.029
Erigeron elmeri	0.874	0.181	0.768	0.197	2.36	0.35	0.005	0.055	0.008
Eriogonum nudum var. *scapigerum*	0.241	0.074	0.749	3.239	4.706	0.493	0.056	0.082	0.009
Eriogonum polypodum	0.815	**0.002**	0.512	0.543	**23.735**	1.485	0.009	**0.404**	0.025
Eriogonum spergulinum var. *pratense*	0.985	0.506	0.772	0.008	0.459	0.186	0	0.017	0.007
Galium hypotrichium subsp. *subalpinum*	0.798	0.246	0.749	0.605	1.806	0.514	0.015	0.044	0.013
Hazardia whitneyi var. *whitneyi*	**0.009**	**0.002**	0.512	**25.959**	**26.441**	1.827	**0.221**	**0.226**	0.016
Hulsea vestita subsp. *vestita*	0.798	0.278	0.88	0.576	1.363	0.051	0.007	0.016	0.001
Ipomopsis aggregata subsp. *bridgesii*	0.953	**0.002**	0.512	0.055	**33.716**	1.413	0.001	**0.37**	0.015
Ivesia muirii	0.965	0.931	0.88	0.014	0.023	0.063	0	0	0.001
Ivesia pygmaea	0.106	0.164	0.772	4.781	2.265	0.38	0.057	0.027	0.004
Lilium kelleyanum	0.798	**0.002**	0.333	0.521	**159.163**	3.469	0.002	**0.465**	0.01

Table 2*. Continued.*

Species	*p.adjust* values (BH Pr(>F))			Pseudo F Ratio (F)			Percent Coefficient of Variation (R^2)		
	Yr	Minel	Yr:Minel	Yr	Minel	Yr:Minel	Yr	Minel	Yr:Minel
Lomatium torreyi	0.46	**0.002**	0.512	1.484	**12.485**	1.48	0.019	**0.163**	0.019
Lupinus covillei	0.09	**0.002**	0.512	6.07	**60.233**	2.048	0.052	**0.518**	0.018
Lupinus gracilentus	0.716	**0.002**	0.814	0.79	**18.367**	0.258	0.022	**0.519**	0.007
Luzula orestera	0.874	0.273	0.675	0.173	1.577	0.848	0.002	0.018	0.01
Monardella beneolens	0.874	0.086	0.074	0.133	4.015	8.195	0.004	0.114	0.232
Oreonana clementis	0.229	**0.002**	0.88	2.832	**32.121**	0.115	0.031	**0.349**	0.001
Oreostemma peirsonii	**0.009**	**0.002**	**0.037**	**208.693**	**290.28**	**66.101**	**0.358**	**0.498**	**0.113**
Orochaenactis thysanocarpha	**0.009**	**0.002**	0.074	**15.552**	**67.526**	7.453	**0.078**	**0.34**	0.038
Phacelia eisenii	0.244	0.345	0.749	2.703	1.106	0.491	0.035	0.014	0.006
Phacelia orogenes	**0.009**	**0.002**	0.512	**20.207**	**71.203**	1.505	**0.184**	**0.648**	0.014
Phlox dispersa	0.965	**0.019**	0.333	0.019	**19.106**	4.823	0	**0.435**	0.11
Poa stebbinsii	0.244	0.275	0.658	2.662	1.475	0.98	0.036	0.02	0.013
Polemonium eximium	0.254	0.131	0.711	2.75	3.022	0.696	0.026	0.029	0.007
Stipa kingii	0.815	0.09	0.308	0.387	3.472	3.512	0.004	0.036	0.036
Trichophorum clementis	0.031	**0.002**	0.847	9.693	**32.657**	0.139	0.07	**0.236**	0.001
Trifolium macilentum var. *dedeckerae*	0.229	0.341	0.308	3.188	1.137	4.269	0.07	0.025	0.094
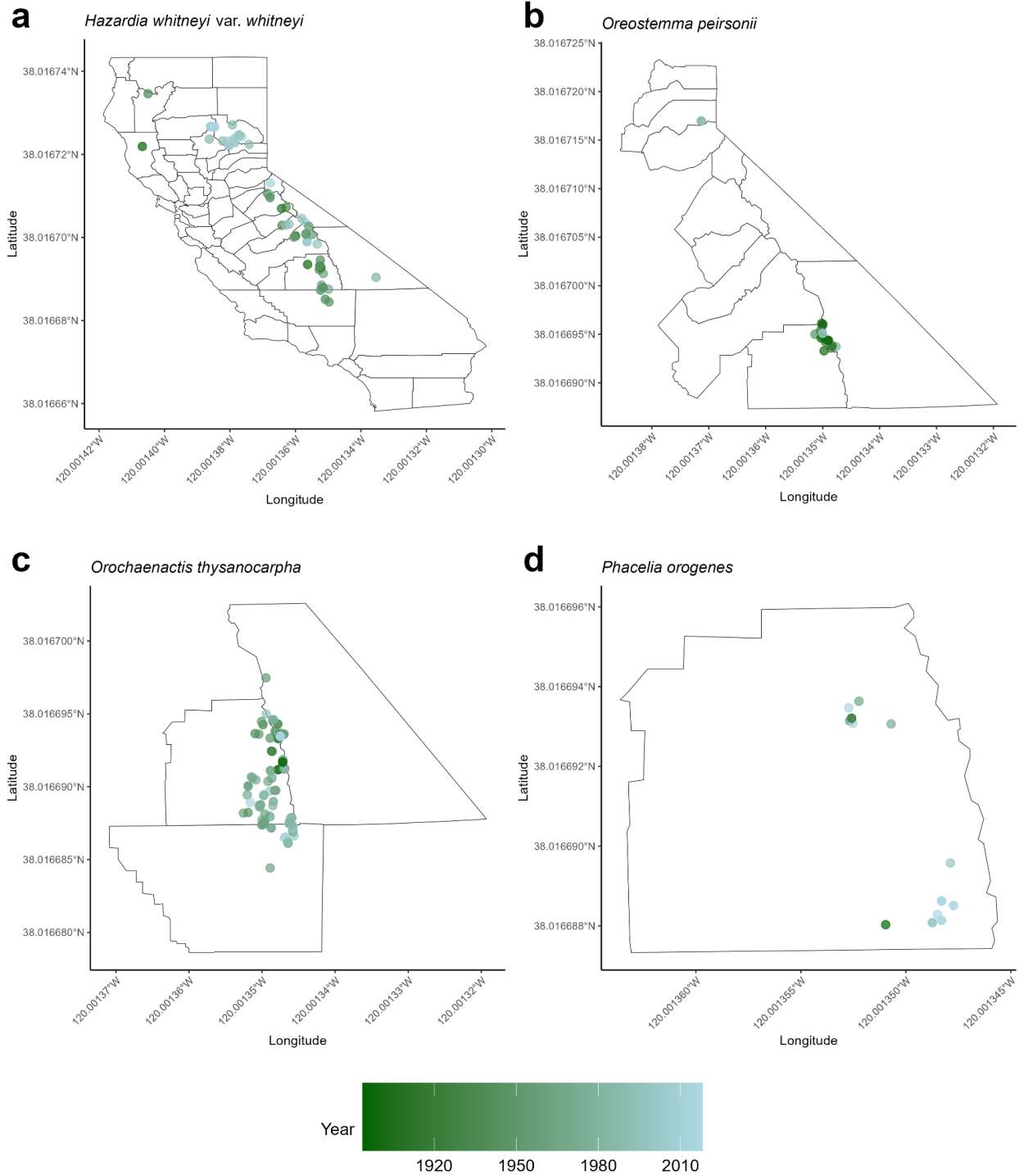
Figure 2*. The spatial structure of (a) H. whitneyi var. whitneyi, (b) O. peirsonii, (c) O. thysanocarpha, and (d) P. orogenes through time. Early collections are modeled in dark green while recent collections are modeled in light blue. Species distributions experiencing a heavy overlap between collection years model a low amount of clustering associated with time, whereas a clear separation in collection years model a high amount of clustering.*
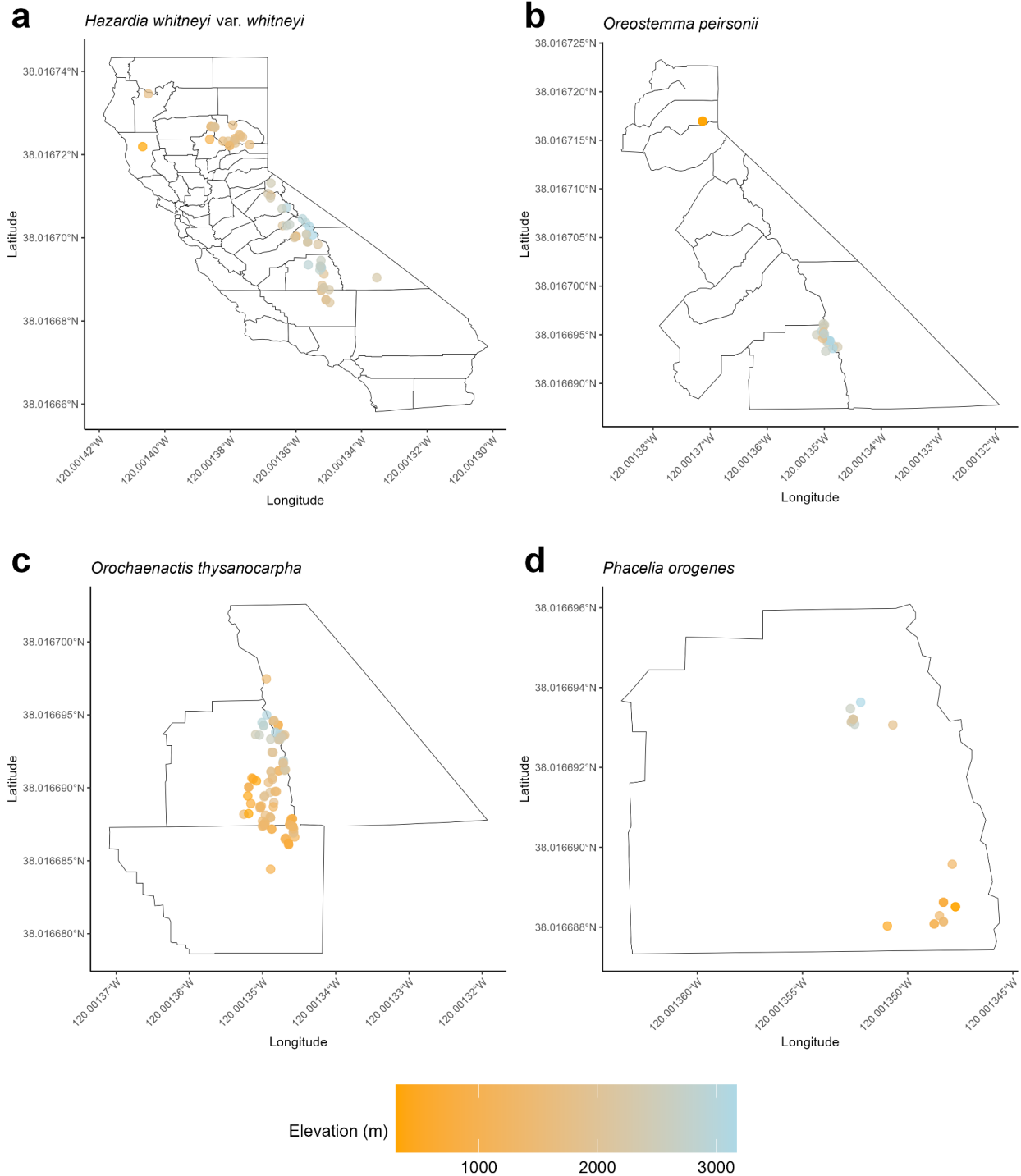
Figure 3. *The spatial structure of (a) H. whitneyi var. whitneyi, (b) O. peirsonii, (c) O. thysanocarpha, and (d) P. orogenes associated with elevation. Lower elevations are modeled in orange while higher elevations are modeled in light blue. Species distributions experiencing a heavy overlap in color points model a low amount of clustering associated with elevation, whereas a clear separation in elevation is modeled through separation in colors.*

How are range dynamics of alpine species changing through time?

Nearly a quarter (8 of 36) of the longitude of sample collections within a species were found to be either positively or negatively correlated with time (Table S4). Of those species, five (*Castilleja praeterita* Heckard & Bacig. (Orobanchaceae)*, Eriogonum nudum* Douglas ex Benth. var. *scapigerum* (Eastw.) Jeps. (Polygoniaceae)*, O. thysanocarpha, P. orogenes,* and *Polemonium eximium* Greene (Polemoniaceae)) had a positive correlation with time. A positive correlation between longitude, as seen in *P. orogenes* (Figure 4), indicates the occurrences of these species over time is correlated with an Eastward distribution of occurrences (r = 0.557, *p* < 0.01). The remaining three species (*H. whitenyi* var. *whitneyi, O. peirsonii,* and *Trichophorum clementis* (M. E. Jones) S. G. Sm. (Cyperaceae)) had a negative correlation with time, indicating a Westward distribution of occurrences. For example, *H. whitneyi* var. *whitneyi* displayed a negative correlation between longitude and time (r = -0.367, *p* < 0.001) (Figure 4).

A sixth (6 of 36) of the species demonstrated a correlation between time and the latitude of sample collections within a species (Table S4) which indicates a poleward distribution over time, or the measure of distance North or South moving further from the equator. *O. thysanocarpha* was the only species of the five with a negative correlation (r = -0.275, *p* < 0.01) and was therefore the only species with a Southward distribution (Figure 4, Table S4). The four other species (*D. longisquamossa, H. whitneyi* var. *whitneyi, O. peirsonii,* and *T. clementis*) were positively correlated with latitude and were distributed in a Northward direction (Table S4).

Four of the 36 species exhibited a correlation between time and the elevation of sample collections within a species (Table S4), where a positive correlation indicates a distribution higher in elevation and a negative correlation represents a distribution in lower elevations in relation to time. *Phacelia eisenii* Brandegee (Boraginaceae) was the only species with a higher

distribution when correlated with time (r = 0.336, $p < 0.01$). The remaining three species were found to have a negative correlation with time (*Carex congdonii* L. H. Bailey (Cyperaceae)*, H. whitenyii* var. *whitenyii*, and *O. thysanocarpha*), representing a distribution lower in elevation relative to time (Table 4).
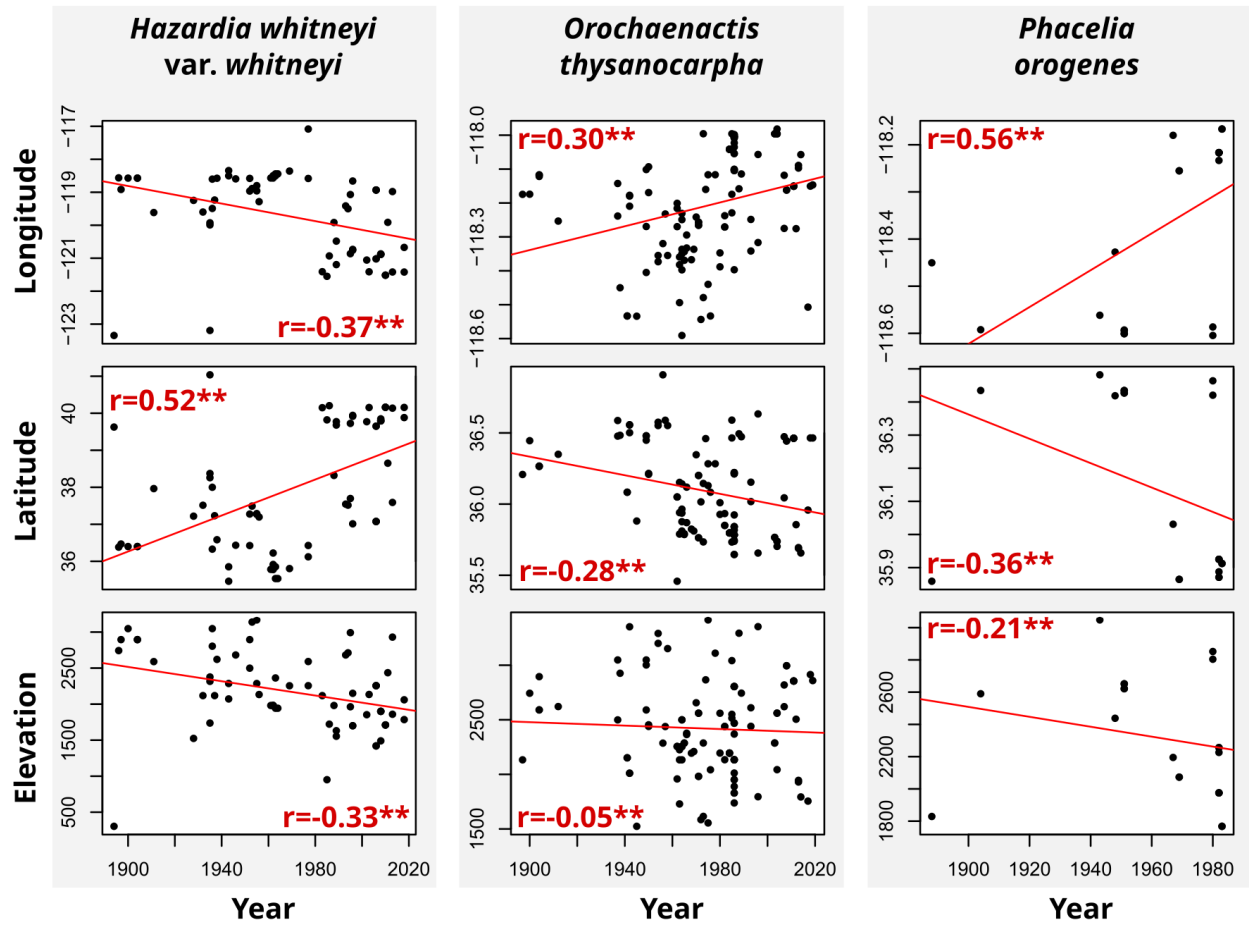
Figure 4. Correlation plots modeling the strength of association between time, latitude, longitude, and/or minimum elevation of the occurrences of (a) O. thysanocarpha, (b) H. whitneyi var. Whitneyi and (c) P. orogenes. Pearson's correlation coefficients and significance codes are reported in red (* < 0.05, ** < 0.01, *** < 0.001.)

Among the three parameters (Figure 5), a third of the species (12 of 36) were found to have a significant effect size (Cohen's d). Of those species, five were found to have a large enough effect size (d > 0.8) to have a strong association between time and parameter (Table S5). Four species (*D. longisquamosa, H. whitneyi* var. *whitenyi,* and *O. peirsonii*) were found to have a large and significant effect size and one species, *Boechera pygmaea* (Rollins) Al-Shehbaz (Brassicaceae) (d = 0.846, *p* < 0.05), was found to have a large effect size but was not significant (Table S5). The time of species occurrences of *P. orogenes* and longitude had a large and positive effect size (d = 1.342, *p* < 0.01), indicating a strong Eastward distribution (Figure 4). Both *H. whitenyi* var. *whitneyi* (d = 1.231, *p* < 0.001) and *D. longisquamossa* (d = 1.145, *p* < 0.01) had a large and positive effect size associated with latitude (Figure 5), indicating time had a strong influence on the Northward distribution of these two species. *O. peirsonii* had a large effect size associated with each parameter, longitude, latitude, and minimum elevation (d = -1.491, *p* < 0.01; d = 1.495, *p* < 0.01; d = -1.165, *p* < 0.01 respectively). The effect size indicated that the species occurrences of *O. peirsonii* had a strong Northwest distribution but with a decline in elevation (Figure S4). However, the average effect size of the 36 species were found to be insignificant (*p* < 0.05) and/or small (d < 0.8) (Table S5).
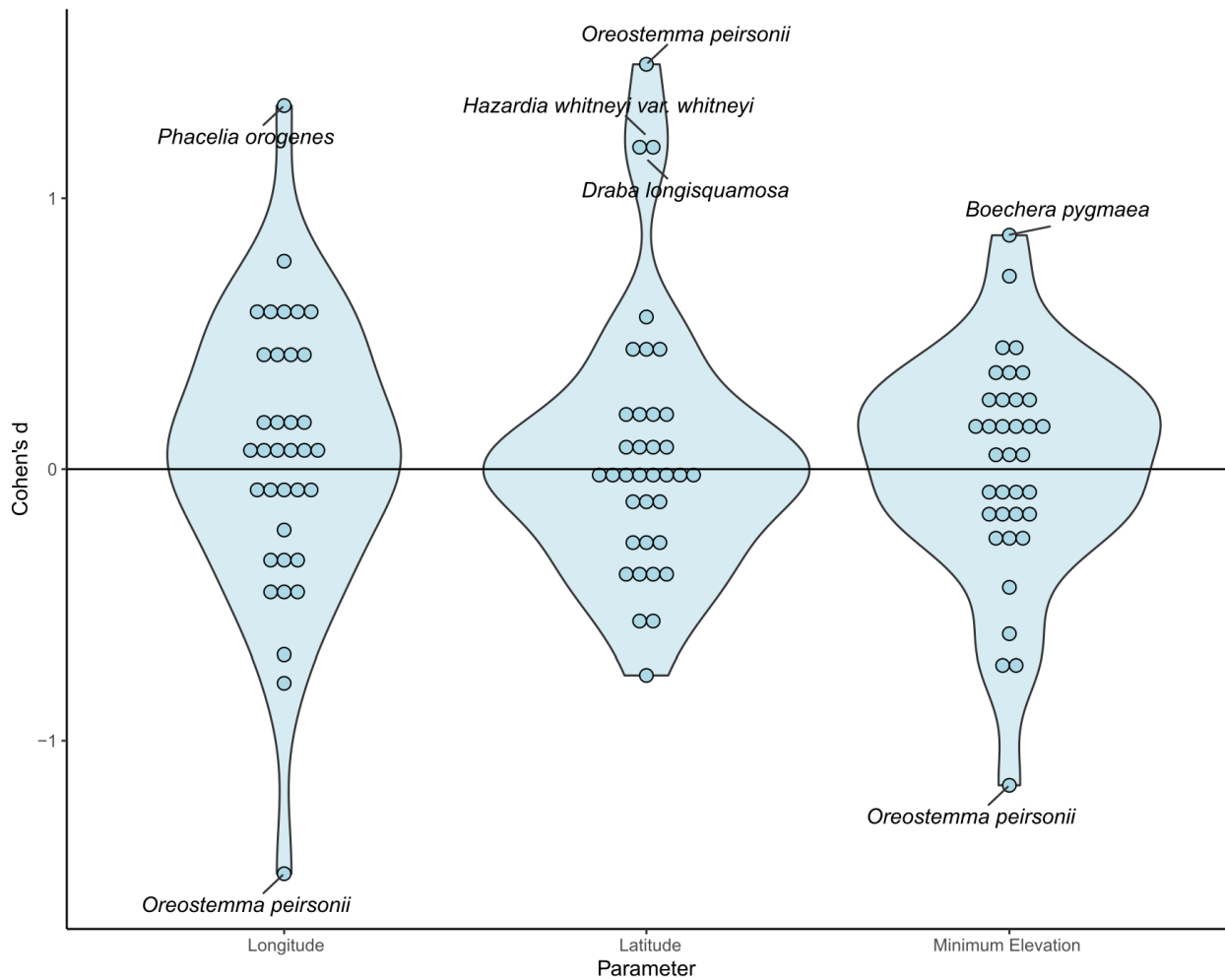
Figure 5. *The effect size (Cohen's d) of the association between time and environmental parameters (latitude, longitude, and elevation) influencing species occurrences. The points represent each of the 36 species and their correlation density. Species with an effect size larger than 0.8 are labeled. Positive and negative effect sizes indicate the directionality of the relationship.*

Discussion

My data demonstrates that some species are spatially structured (Table 2) and have

occurred directionally and/or elevationally in correlation with time (Table S4). It is important to

emphasize that, although I did find approximately four species (*P. orogenes, O. peirsonii, H.*

whitneyi var. *whitneyi,* and *D. longisquamosa*) with a strong enough effect size to be considered

directionally distributed, the remaining 32 species distributions cannot be considered

directionally distributed. Based on species distribution models, most species need to shift their

ranges North and upward in elevation to track suitable habitat. Instead, my data revealed very

few species (approximately 11%) were associated with the parameters related to directionality

(Figure 5). The inconsistency between the Northward and upslope distributions forecasted by

older models (**Chen et al., 2011; Hughes, 2000; Lenoir et al., 2008; Pauli et al., 1996;**

Parmesan & Yohe, 2003; Walther et al., 2005) were similar to recent findings (**Auld et al.,**

2021; Cannone & Pignatti, 2014; Lenoir et al., 2010; Lenoir & Svenning, 2014; Niskanen et

al., 2019; Rumpf et al., 2018a; Harsch et al., 2009). Such disjunct between models and more

recent studies further necessitate understanding the biogeographic history of species in order to

improve forecasting capabilities.

My findings showed that over half of the species (20 of 36) were spatially structured

through time and/or elevation (Table 2). Consequently, not all species were associated with both

the main effects of elevation and time. For example, *C. praeterita* was distributed across a strong

localized elevational gradient. This gradient is due to the increase in elevation from the Kennedy

meadows in Tulare County that connect to the summit of Olancha peak in Inyo County (Figure

S3). *C. praterita* is therefore spatially structured by the geography of the landscape. Furthermore,

of the species which were spatially structured, none of them were independently structured by

time. The lack of structure determined by time alone shows that the geography of the landscape

was a large factor in the distribution of species over time. For example, *D. longisquamosa* primarily occurred along the county lines of Fresno, Tulare, and Inyo, in which collections were found to have a similar elevational profile (Figure S3). This may explain the lower association between distribution and elevation but does not explain the stronger association between distribution and time (Figure S2). The association between the distribution of *D. longisquamosa* and time may be attributed to the collection of species no longer occurring in historical locations spatially (Figure S2, Figure S4), likely nodding to a change in occurrences through time.

A majority of species were found to be either idiosyncratically distributed or were found to have no spatiotemporal relationship with latitude, longitude, and/or elevation. Although five species (*H. whitneyi* var. *whitneyi*, *O. peirsonii, T. clementis, D. longisquamosa,* and *I. pygmaea*) were found to have a Northward distribution over time, only three (*H. whitneyi* var. *whitneyi*, *O. peirsonii,* and *D. longisquamosa*) were found to have a strong enough effect size to be considered directionally distributed (Figure 5). Furthermore, *O. peirsonii* was found to be the only species with a considerable elevational effect size and contrary to model predictions, *O. peirsonii* was distributed downslope (Figure 4, Figure 5). The remaining 32 species (88.89%) were not found to be directionally distributed and may be explained as maintaining themselves within their historical locations through either (1) an in-filling process (**Rumpf et al., 2018a**) or (2) distributions lagging behind climate (**Alexander et al., 2018**), where species are not yet displaying changes due to reasons such as dispersal limitations (**Alexander et al., 2018**).

To address the species lacking spatial structure and/or significant directional distribution, some studies have focused on an in-filling process and lagged responses of species to climate through time. For example, a few studies found that species were shifting their populations into other communities (**Cannone & Pignatti, 2014; Rumpf et al., 2018a**), contributing to the in-

filling process. The species were found to independently radiate in different directions, which may explain the lack of spatial structuring of some of the species in my PERMANOVA analyses (Table 2). The lack of spatial structure of some of the species may also be attributed to lagged responses to climate change. A study conducted by Alexander et al. (2018) studied the lags and the range shifts of plants relative to climate and found there were two plausible responses relative to this study that might explain the lack of spatial structure and directionality seen in my study. First, a dispersal lag (**Alexander et al., 2018**) was defined as the ability of species to track climate temporally and across an elevational gradient (**Svenning & Sandel, 2013**). My results show only one species, *O. peirsonii,* of the four were found to have a large enough effect size to be considered significant (Figure 5, Table S5), indicating that around 97% (36 of 37) species did not change elevational direction over time. As such, unsuitable habitat or species-specific dispersal capabilities (**Dullinger et al., 2012a; Dullinger et al., 2012b; Rumpf et al., 2018a**) may explain the inability of species to disperse into both higher and lower elevations. Second, an extinction lag, which measured the ability of species to persist at rear edges, may have also occurred (**Alexander et al., 2018**). *C. congdonii* demonstrated that species were found to be collected at both high and low elevations both recently (Figure S4). Should *C. congdonii* have followed the significant downslope trend, there would not have been occurrences at higher elevations in the recent collections, yet they are still present. This persisted response of species may be due to acclimatory abilities and/or pocket refugium (**Malanson et al., 2015; Wershow & DeChaine, 2018**) allowing species to temporarily remain within the habitat. Alternatively, any combination of the aforementioned lags could be co-occurring and contribute to the lack of spatial structure and ultimately the inability to determine directional distribution through time.

Recent analyses of alpine flora have found that a handful of species have responded to climate change by shifting their ranges upslope, but the remaining species were found to have experienced no change in range through time. One study tested range dynamics using historical vegetation plots which were resampled (**Rumpf et al., 2018a**). This study found that range responses were primarily species-specific but displayed a trend where range limits and averages generally shifted upslope (**Rumpf et al., 2018a**). The overall change in elevation in terms of range size, optima, and leading and rear edges were found to remain largely unchanged. Another study combined herbaria, historic observations, and collected species to test elevational shifts, range contractions, and upslope shifts in leading and rear edges (**Auld et al., 2022**). Similar to the results of my study, they found movement in both directions relative to elevational shifts (although downlope shifts were found to be insignificant post-multiple hypothesis testing adjustment). Interestingly, they found that upslope shifts in leading and rear edges did display a primarily upslope shift, which contrasts downslope distribution through time of *O. peirsonii* (Figure 5, Figure S4). Yet overall, a majority of the species experienced no significant shifts in average elevation (58%), upper edge (72%), and lower edge (69%) over time (**Auld et al., 2022**).

Recent studies analyzing resampled transects, historic collections, and recent occurrences alike suggest that species ranges are moving individualistically through time but species on average are not moving at all. While the lack of spatial structuring and directionality in distribution might be due to the aforementioned reasons, I cannot discount that sampling biases associated with herbaria collecting (such as biases with respect to collection accessibility) and/or a lack of publication/digitization of collected species may have contributed to the results. A study was conducted which tested the sampling bias associated with herbaria data and found

numerous biases associated with collections from large scale digitizations (**Daru et al., 2018**).

My dataset was sourced from a consortium of different herbaria with collections from multiple contributors, which remedies some of the temporal biases which assumes species may be under collected in specific regions (**Daru et al., 2018**). Despite these caveats, herbaria are regarded as informative as long as the primary data has been extensively reviewed (**Loiselle et al., 2008**).

My case study novelly used herbaria data to show that endemic alpine flora are spatially structured through time (Figure 2, Figure 3, Table 2), their distributions are directionally associated with time (Figure 4, Table S4), and endemic alpine flora are on average not found to be changing distributions directionally (Figure 5, Table S5). Understanding the idiosyncratic responses of species will be important in reevaluating models and ultimately contribute to new management strategies surrounding areas of conservation priority and/or species of concern. That said, a suggestion for future models is to incorporate the empirical data preserved in historic records as a predictor variable in modeling habitat suitability or range dynamics. While integrating individual species responses to climate may be difficult to apply to a broader geographic scale or across multiple species, it is imperative independent species models are first used to forecast future distributions most accurately. Once a framework has been introduced to predictively model species at the level of an individual, phenological similarities or shared characteristics may be used to standardize shared models across species less tediously. Although there is still much research that needs to be directed towards understanding the individualistic responses of range dynamics within alpine species, the publication, digitization, and overall improvement of accessibility to herbaria records would improve our understanding of how alpine flora are changing through time.

References

Ackerly, D. D., Loarie, S. R., Cornwell, W. K., Weiss, S. B., Hamilton, H., Branciforte, R., & Kraft, N. J. B. (2010). The geography of climate change: implications for conservation biogeography. Diversity and Distributions, 16(3), 476-487. 10.1111/j.1472-4642.2010.00654.x

Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders, N. J., & Pellissier, L. (2018). Lags in the response of mountain plant communities to climate change. *Global Change Biology*, *24*(2), 563-579. 10.1111/gcb.13976

Anderson, M. J. (2017). Permutational Multivariate Analysis of Variance (PERMANOVA). *Wiley StatsRef: Statistics Reference Online*, 1-15. 10.1002/9781118445112.stat0784115

Auld, J., Everingham, S. E., Hemmings, F. A., & Moles, A. T. (2022). Alpine plants are on the move: Quantifying distribution shifts of Australian alpine plants through time. *Diversity and Distributions*, *28*(5), 943-955. 10.1111/ddi.13494

Baldwin, B. G., Goldman, D. H., Keil, D. J., Patterson, R., Rosatti, T. J., & Wilken, D. (Eds.). (2012). *The Jepson Manual: Vascular Plants of California* (2nd ed.). University of California Press.

Beniston, M. (2003). Climatic change in mountain regions: a review of possible impacts. *Climate Variability and Change in High Elevation Regions: Past, Present & Future. Advances in Global Change Research*, *15*, 5-31. https://doi.org/10.1007/978-94-015-1252-7_2

Billings, W. D. (1978). Alpine phytogeography across the Great Basin. *Great Basin Naturalist Memoirs*, (2), 105-117. http://www.jstor.org/stable/23376561

Boucher, F. C., Zimmermann, N. E., & Conti, E. (2015). Allopatric speciation with little niche divergence is common among alpine Primulaceae. *Journal of Biogeography*, *43*(3), 591-602. 10.1111/jbi.12652

Brooks, T. M., Mittermeier, R. A., Da Fonesca, G. A. B., Gerlach, J., Hoffman, M., Lamoreux, J. F., Mittermeier, C. G., Pilgrim, J. D., & Rodrigues, A. S. L. (2006). Global biodiversity conservation priorities. *Science*, *313*(5783), 58-61. 10.1126/science.1127609

Capers, R. S., Kimball, K. D., McFarland, K. P., Jones, M. T., Lloyd, A. H., Munroe, J. S., Fortin, G., Mattrick, C., Goren, J., Sperduto, D. D., & Paradis, R. (2013). Establishing Alpine Research Priorities in Northeastern North America. *Northeastern Naturalist*, *20*(4), 559-577. https://www.jstor.org/stable/43288160

Cannone, N., & Pignatti, S. (2014). Ecological responses of plant species and communities to climate warming: upward shift or range filling processes? *Climatic Change*, *123*(2), 201-214. https://doi-org.ezproxy.library.wwu.edu/10.1007/s10584-014-1065-8

CCH2 Portal. (2023). Specimen Data from the Consortium of California Herbaria. Retrieved from https://www.cch2.org/portal/

Chen, I.-C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024-1026. 10.1126/science.1206432

Daru, B. H., Park, D. S., Primack, R. B., Willis, C. G., Barrington, D. S., Whitfeld, T. J. S., Seidler, T. G., Sweeney, P. W., Foster, D. R., Ellison, A. M., & Davis, C. C. (2018). Widespread sampling biases in herbaria revealed from large-scale digitization. *The New Phytologist*, *217*(2), 939-955. https://www.jstor.org/stable/90016953

de Lima, R. A. F., Souza, V. C., de Siqueira, M. F., & ter Steege, H. (2020). Defining endemism levels for biodiversity conservation: Tree species in the Atlantic Forest hotspot. *Biological Conservation*, *252*. 10.1016/j.biocon.2020.108825

Dettinger, M., Alpert, H., & Battles, J. (2018). *Sierra Nevada summary report. California's fourth climate change assessment* [Publication No. SUMCCCA4-2018-004. Sacramento, CA: State of California. 94 p.].

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnböck, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J.-C., Psomas, A., Schmatz, D. R., Silc, U., … Hülber, K. (2012a). Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, *2*, 619-622. 10.1038/nclimate1514

Dullinger, S., Willner, W., Plutzar, C., Englisch, T., Schratt-Ehrendorfer, L., Moser, D., Ertl, S., Essl, F., & Niklfeld, H. (2012b). Post-glacial migration lag restricts range filling of plants in the European Alps. *Global Ecology and Biogeography*, *21*, 829-840. 10.1111/j.1466-8238.2011.00732.x

Halofsky, J. E., Peterson, D. L., Buluc, L. Y., & Ko, J. M. (2021). *Climate Change Vulnerability and Adaptation for Infrastructure and Recreation in the Sierra Nevada* [General Technical Report]. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 275 p.

Harsch, M. A., Hulmn, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, *12*(10), 1040-1049. https://doi.org/10.1111/j.1461-0248.2009.01355.x

Hollister, J.W. (2021). elevatr: Access Elevation Data from Various APIs. R package version 0.4.1. https://CRAN.R-project.org/package=elevatr/

Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Biological Sciences*, *105*(33), 11823-11826. https://doi.org/10.1073/pnas.0802891105

Knowles, N., Dettinger, M. D., & Cayan, D. R. (2006). Trends in snowfall versus rainfall in the western United States. *Journal of Climate*, *19*(18), 4545-4559. https://doi.org/10.1175/JCLI3850.1

Körner, C. (2003). *Alpine plant life: functional plant ecology of high mountain ecosystems* (2nd ed.). Springer Berlin Heidelberg.

Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N. E., Dullinger, S., Pauli, H., Willner, W., & Svenning, J.-C. (2010). Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, *33*(2), 295-303. 10.1111/j.1600-0587.2010.06279.x

Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, *320*(5884), 1768-1771. 10.1126/science.1156831

Lenoir, J., & Svenning, J. C. (2014). Climate-related range shifts - a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15-28. https://doi-org.ezproxy.library.wwu.edu/10.1111/ecog.00967

Loarie, S. R., Carter, B. E., Hayhoe, K., McMahon, S., Moe, R., Knight, C. A., & Ackerly, D. D. (2008). Climate change and the future of California's endemic flora. *PLoS ONE*, *3*(6), e2505. https://doi.org/10.1371/journal.pone.0002502

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*, 1052-1055. https://doi.org/10.1038/nature08649

Loiselle, B. A., Jorgensen, P. M., Consiglio, T., Jimenez, I., Blake, J. G., Lohmann, L. G., & Montiel, O. M. (2008). Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes? *Journal of Biogeography*, *35*, 105-116. 10.1111/j.1365-2699.2007.01779.x

Malanson, G. P., Zimmerman, D. L., & Fagre, D. B. (2015). Floristic similarity, diversity and endemism as indicators of refugia characteristics and needs in the West. *Biodiversity*, *16*(4), 1-10. 10.1080/14888386.2015.1117989

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853-858. 10.1038/35002501

Niskanen, A. K. J., Niittynen, P., Aalto, J., Väre, H., & Luoto, M. (2019). Lost at high latitudes: Arctic and endemic plants under threat as climate warms. *Biodiversity Research*, *25*(5), 809-821. 10.1111/ddi.12889

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., de Caceres, M., Durand, S., …
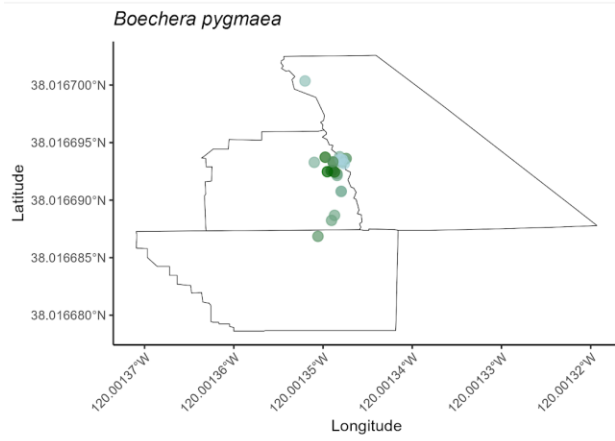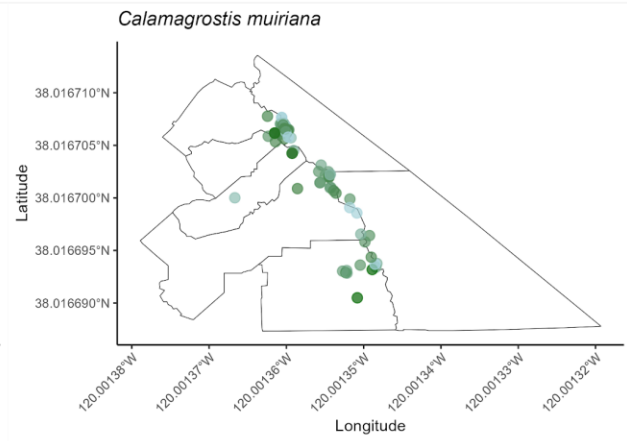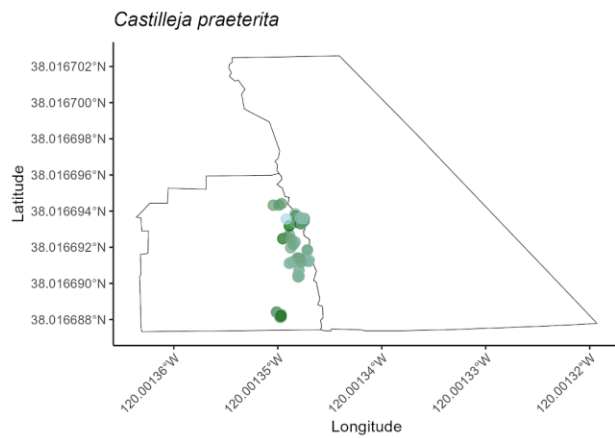
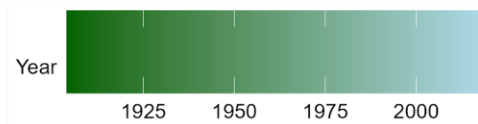Weedon, J. (2022). Vegan: community ecology package. R package version 2.6-2. https://CRAN.Rproject.org/package=vegan

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*, 37-42. https://doi.org/10.1038/nature01286

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B., Coldea, G., Dick, J., Erschbamer, B., Calzado, R. F., Ghosn, D., Holten, J. I., Kanka, R., Kazakis, G., Kollar, J., Larsson, P., Moiseev, P., Moissev, D., Molau, U., … Grabbherr, G. (2012). Recent plant diversity changes on Europe's mountain summits. *Science*, *336*(6079), 353-355. 10.1126/science.1219033

Pauli, H., Gottfried, M., & Grabherr, G. (1996). Effects of climate change on mountain ecosystems - upward shifting of alpine plants. *World Resources Review*, *8*(3), 382-390.

Pebesma, E. J., & Bivand, R. S. (2005). Classes and methods for spatial data in R. *R News*, *5*(2), 9-13.https://cran.r-project.org/doc/Rnews/

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.R-project.org/

Raven, P. H., & Axelrod, D. I. (1978). *Origin and Relationships of the California Flora*. California Native Plant Society, Berkeley, CA.

Revelle, W. (2023). *psych: Procedures for Psychological, Psychometric, and Personality Research*. R package version 2.3.3. https://CRAN.R-project.org/package=psych

Rixen, C., Wipf, S., Frei, E. R., & Stöckli, V. (2014). Faster, higher, more? Past, present and future dynamics of alpine and arctic flora under climate change. *Alpine Botany*, *124*(2), 77-79. 10.1007/s00035-014-0141-z

Rumpf, S. B., Hülber, K., & Klonner, G. (2018a). Range dynamics of mountain plants decrease with elevation. *Biological Sciences*, *115*(8), 1848-1853. https://doi.org/10.1073/pnas.1713936115

Rumpf, S. B., Hülber, K., Zimmermann, N. E., & Dullinger, S. (2018b). Elevational rear edges shifted at least as much as leading edges over the last century. *Global Ecology and Biogeography*, *28*(4), 533-543. https://doi-org.ezproxy.library.wwu.edu/10.1111/geb.12865

Rundel, P. W. (2011). The diversity and biogeography of the alpine flora of the Sierra Nevada, California. *Madroño*, *58*(3), 153-184. https://www.jstor.org/stable/10.2307/26476397

Sharsmith, C. (1940). A contribution to the history of the alpine flora of the Sierra Nevada. Ph.D. Dissertation, University of California, Berkeley, CA.

Shevock, J. R. (1997). *Status of the Sierra Nevada: The Sierra Nevada Ecosystem Project* (Vol. 2). U.S. Department of the Interior, U.S. Geological Survey. https://pubs.usgs.gov/dds/dds-43/VOL_II/VII_C24.PDF

Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, *100*(7), 1266-1286. 10.3732/ajb.1200469

Testolin, R., Attorre, F., & Jiménez-Alfaro, B. (2020). Global distribution and bioclimatic characterization of alpine biomes. *Ecography*, *43*(6), 779-788. 10.1111/ecog.05012

Thomas, C. (2011). Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology and Evolution*, *26*(5), 216-221. 10.1016/j.tree.2011.02.006

Vose, R. S., Easterling, D. R., & Kunkel, K. E. (2017). Temperature changes in the United States [In: Wuebbles, D.J.; Fahey, D.W.; Hibbard, K.A.; et al., eds. Climate science special report. Fourth national climate assessment, Volume I. Washington, DC: U.S. Global Change Research Program: 185–206.].

Walker, M. D., Gould, W. A., & Chapin III, F. S. (2001). Scenarios of biodiversity changes in arctic and alpine tundra. *Global Biodiversity in a Changing Environment*, *152*, 83-100. 10.1007/978-1-4613-0157-8_5

Wallis, G. P., Waters, J. M., Upton, P., & Craw, D. (2016). Transverse alpine speciation driven by glaciation. *Trends in Ecology & Evolution*, *31*(12), 916-926. 10.1016/j.tree.2016.08.009

Walther, G.-R., Beißner, S., & Burga, C. A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, *16*(5), 541-548. 10.1111/j.1654-1103.2005.tb02394.x

Wershow, T. S., & DeChaine, E. G. (2018). Retreat to refugia: Severe habitat contraction projected for endemic alpine plants of the Olympic Peninsula. *American Journal of Botany*, *105*(4), 760-778. 10.1002/ajb2.1042

Wuebbles, D.J.; Fahey, D.W.; Hibbard, K.A.; Dokken, D.J.; Stewart, B.C.; and Maycock, T.K.; USGCRP. (2017): Climate Science Special Report: Fourth National Climate Assessment, Volume I. U.S. Global Change Research Program, Washington, DC, USA, 470 pp. 10.7930/J0J964J6.
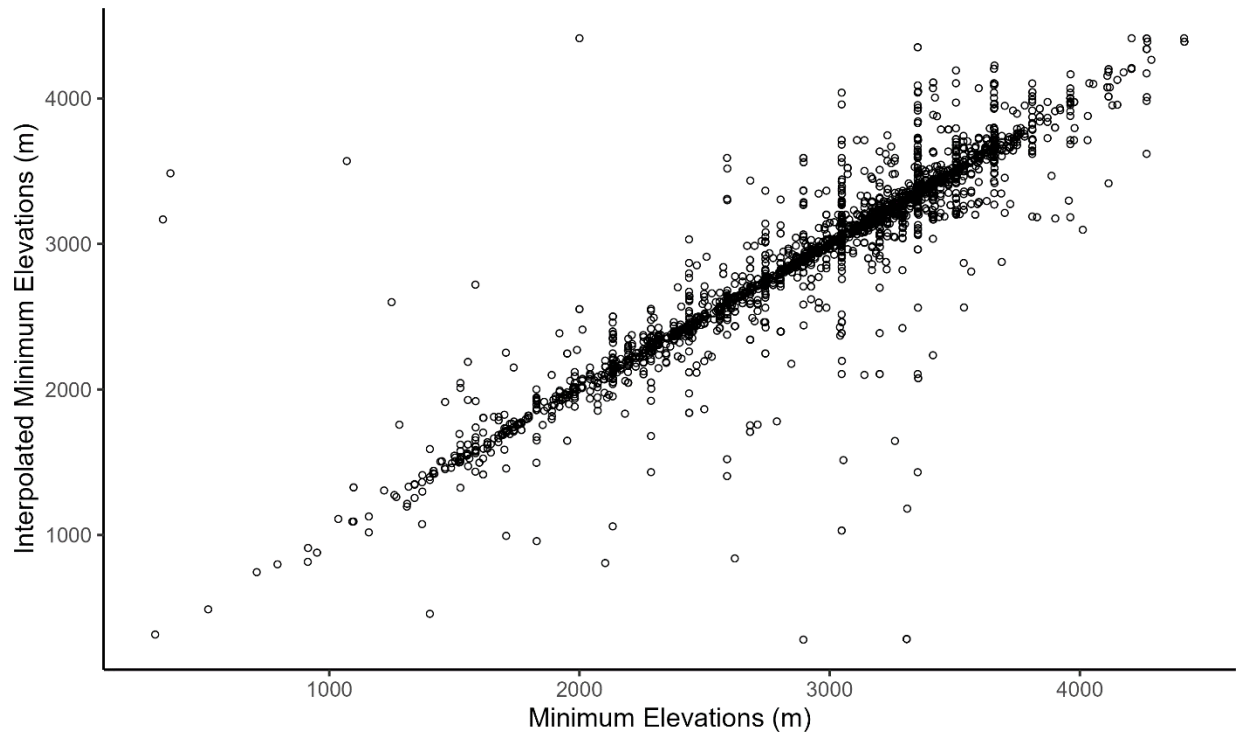
Figure S1*. Figure S1. Correlation (r=0.904) between interpolated elevations and actual elevations provided by the data uploaded to the CCH2 herbarium.*

a

Boechera pygmaea

b

Calamagrostis muiriana

c

Castilleja praeterita

d

Draba lemmonii

Year

1925   1950   1975   2000
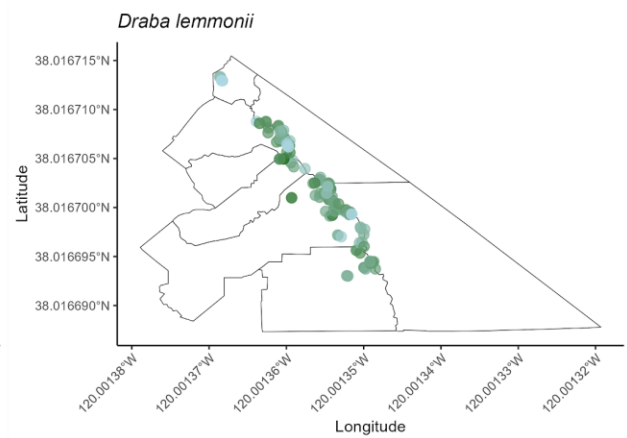
***Figure* S2**. *The spatial structure of species (a-p) through time. Early collections are modeled in dark green while recent collections are modeled in light blue. Species distributions experiencing a heavy overlap between collection years model a low amount of clustering associated with time, whereas a clear separation in collection years model a high amount of clustering.*

e *Draba longisquamosa*

f *Draba sierrae*

g *Eriogonum polypodum*

h *Ipomopsis aggregata* var. *bridgesii*

Year

Figure S2. Continued.

38

i *Lilium kelleyanum*

j *Lomatium torreyi*

k *Lupinus covillei*

l *Lupinus gracilentus*

Year

Figure S2. Continued.

m *Carex congdonii*

n *Oreonana clementis*

o *Phlox dispera*

p *Trichophorum clementis*

Year

1925   1950   1975   2000

Figure S2. *Continued.*

40

a

Boechera pygmaea

b

Calamagrostis muiriana

c

Castilleja praeterita

d

Draba lemmonii

Elevation (m)

2500   3000
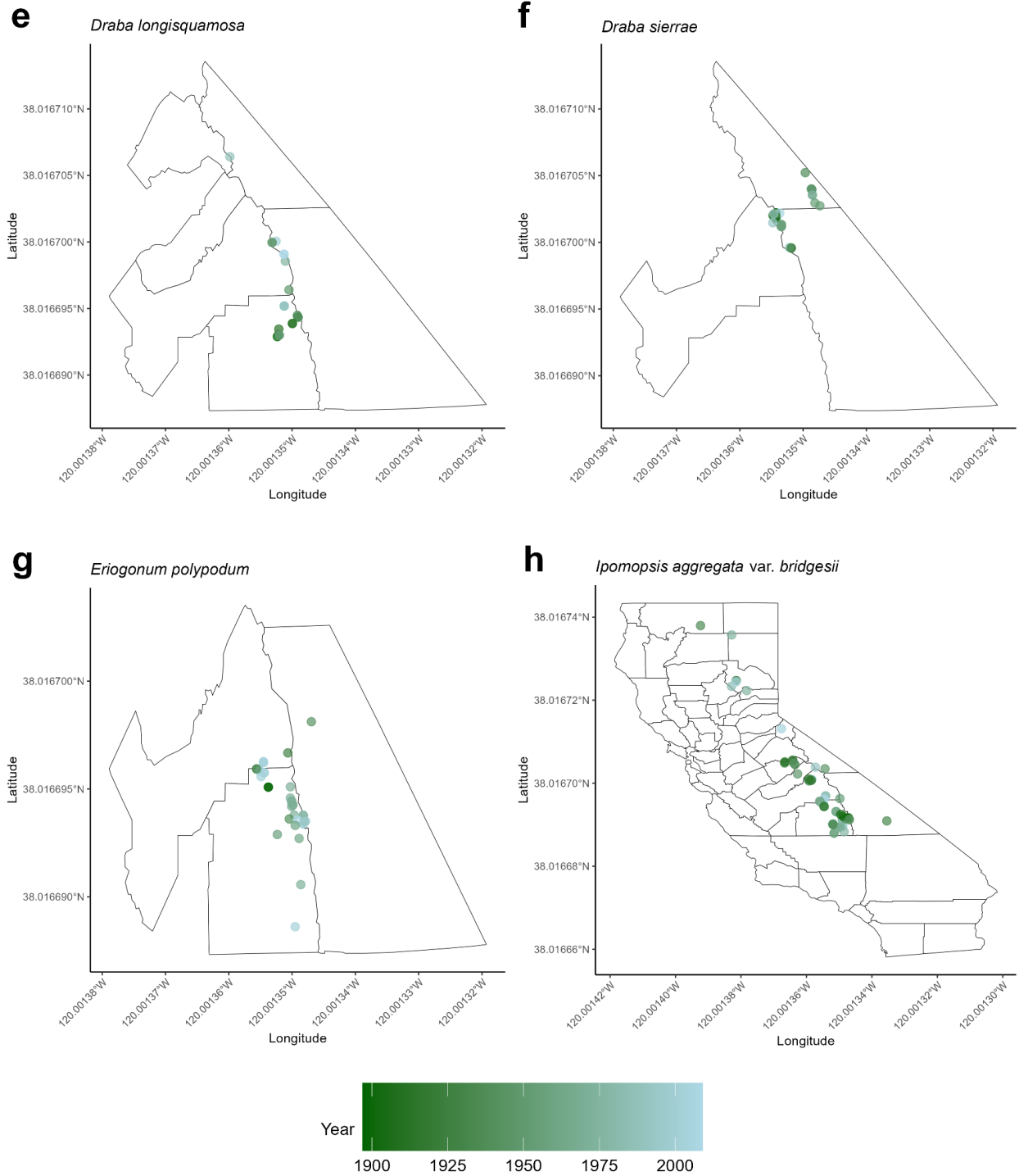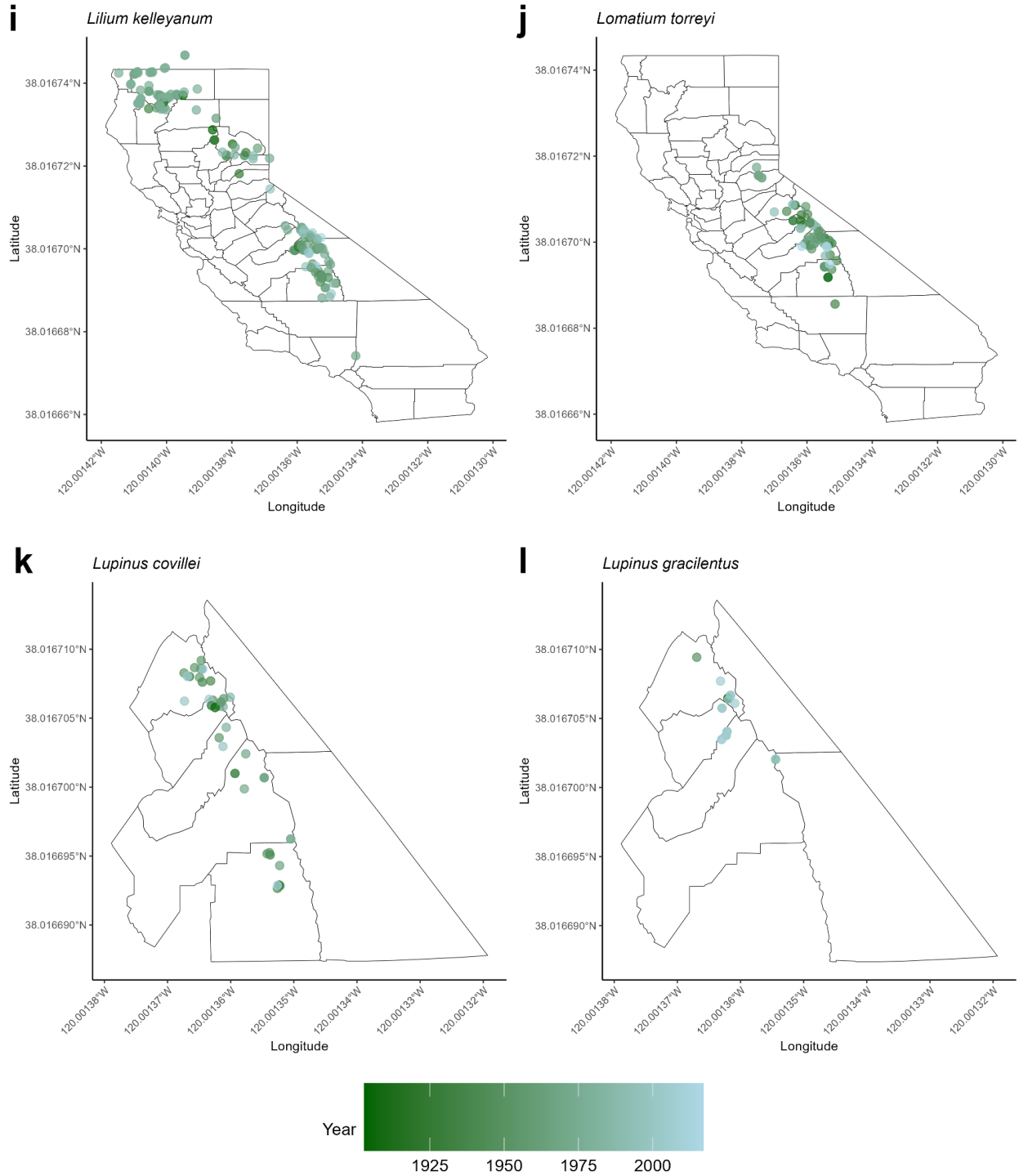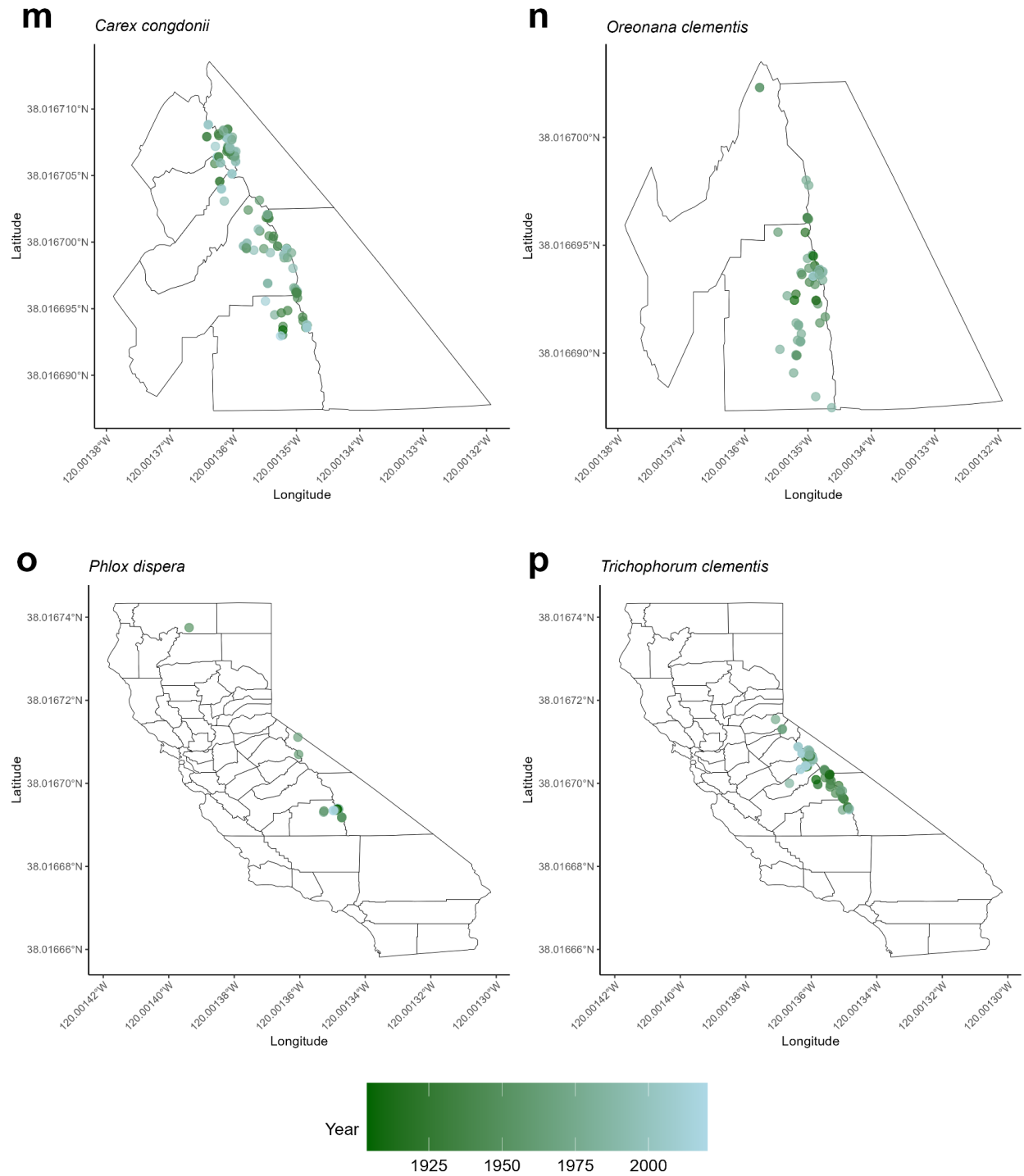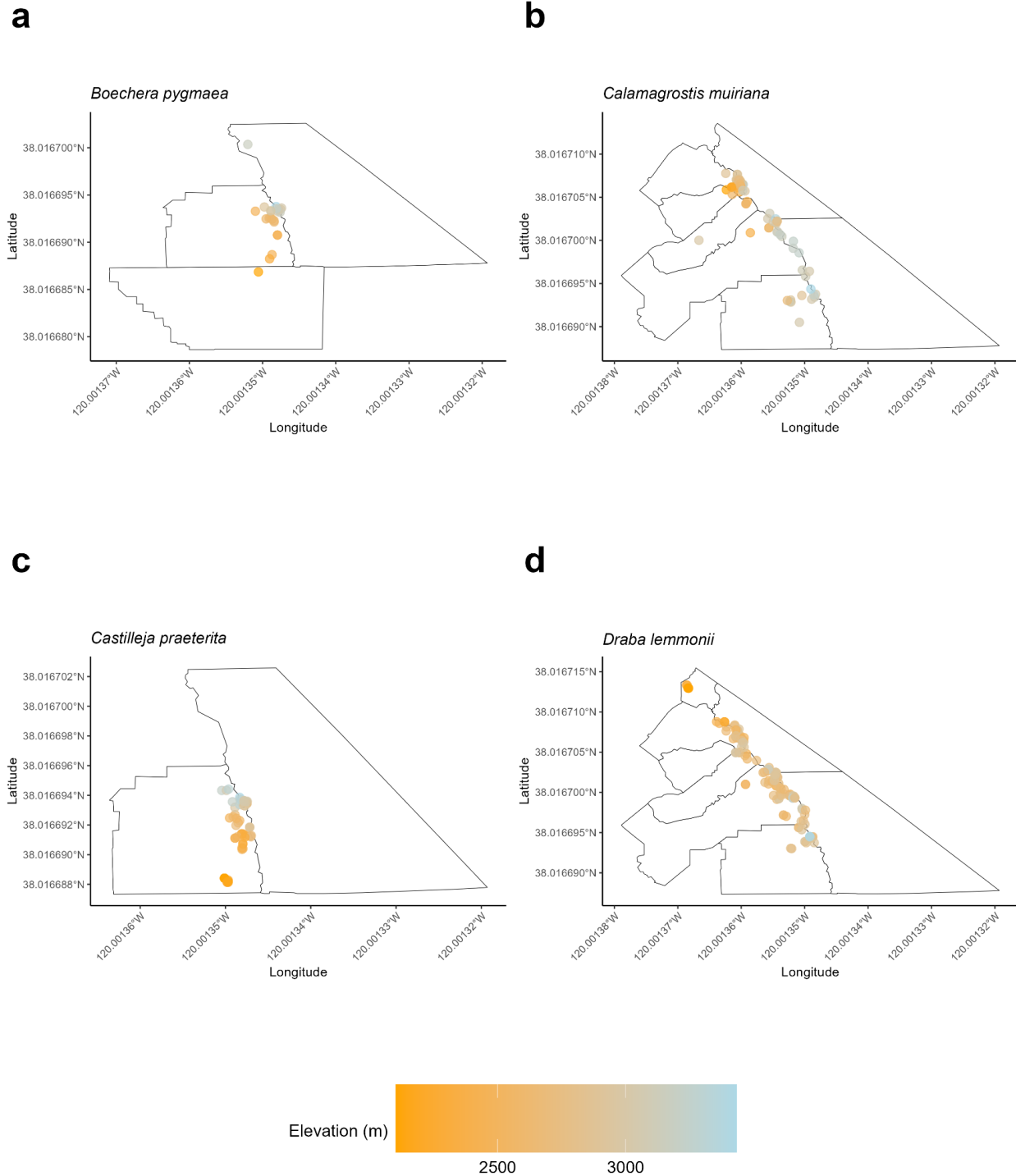
Figure S3*. The spatial structure of species (a-p) associated with elevation. Lower elevations are modeled in orange while higher elevations are modeled in light blue. Species distributions experiencing a heavy overlap in color points model a low amount of clustering associated with elevation, whereas a clear separation in elevation is modeled through separation in colors.*

e *Draba longisquamosa*

f *Draba sierrae*

g *Eriogonum polypodum*

h *Ipomopsis aggregata* var. *bridgesii*

Elevation (m)

3250 3500 3750 4000 4250

Figure S3*. Continued.*

i *Lilium kelleyanum*

j *Lomatium torreyi*

k *Lupinus covillei*

l *Lupinus gracilentus*

Elevation (m)

Figure S3. Continued.

43

m *Carex congdonii*

n *Oreonana clementis*

o *Phlox dispera*

p *Trichophorum clementis*

Elevation (m)

2000   3000
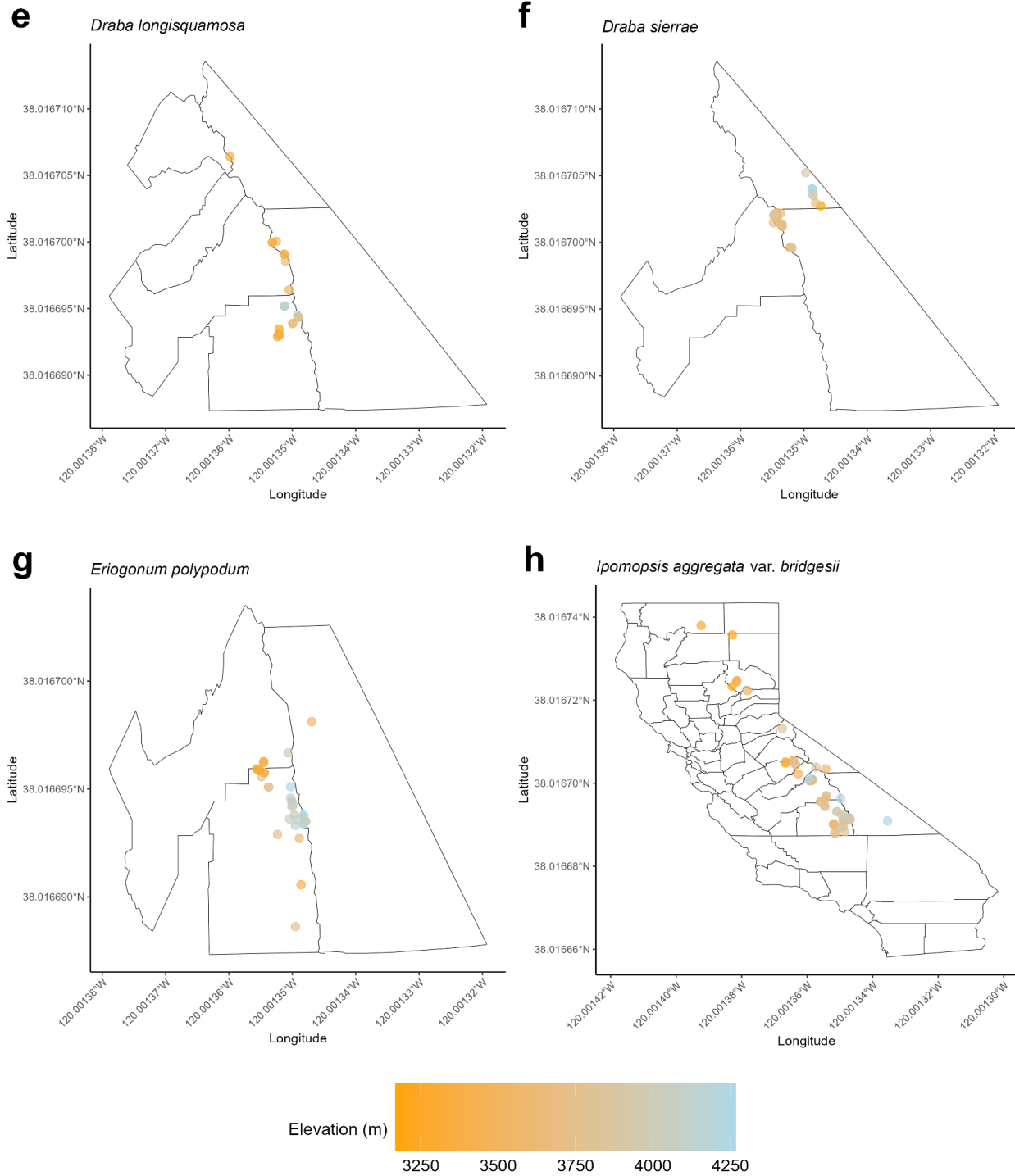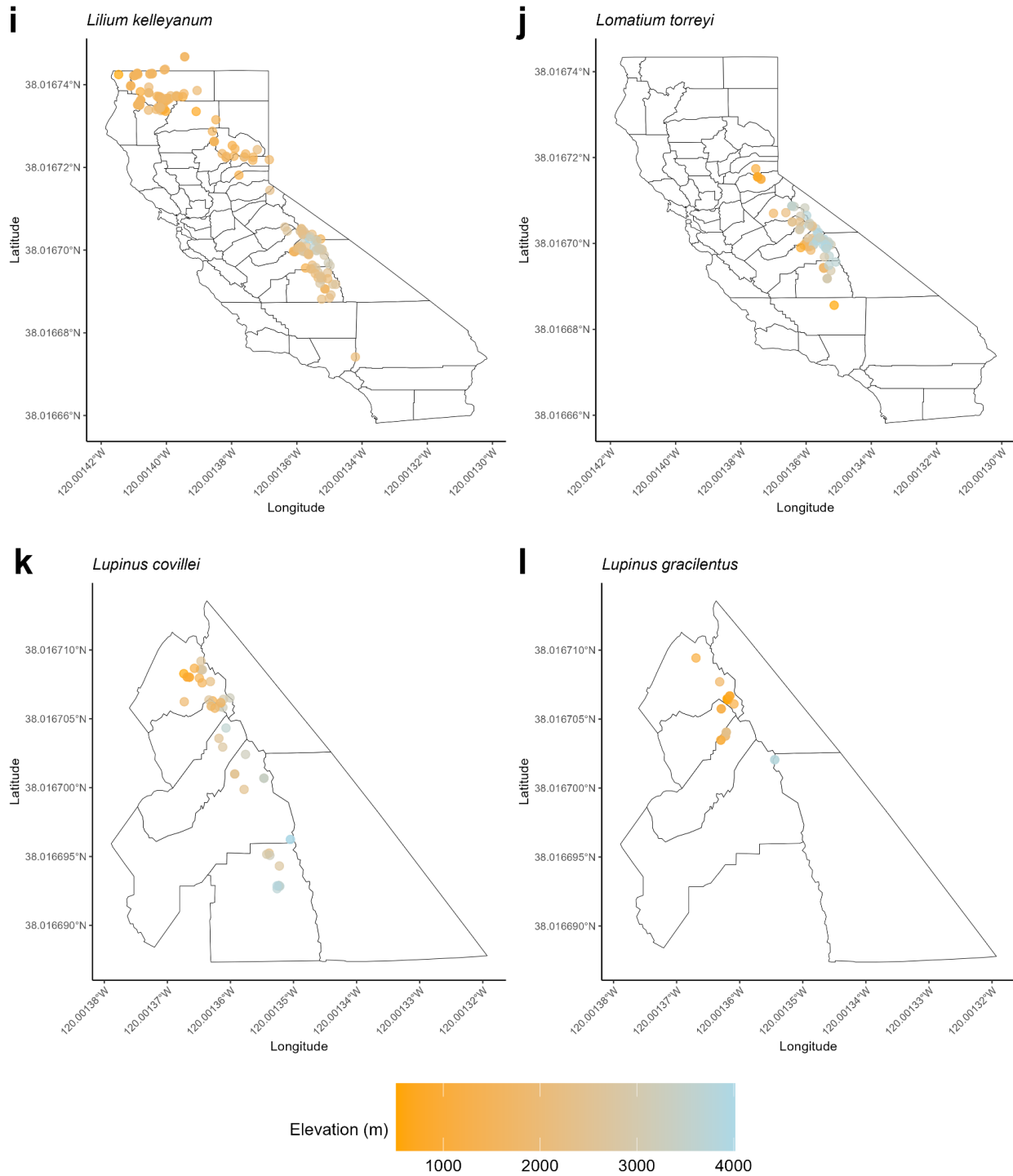
Figure S3. *Continued.*
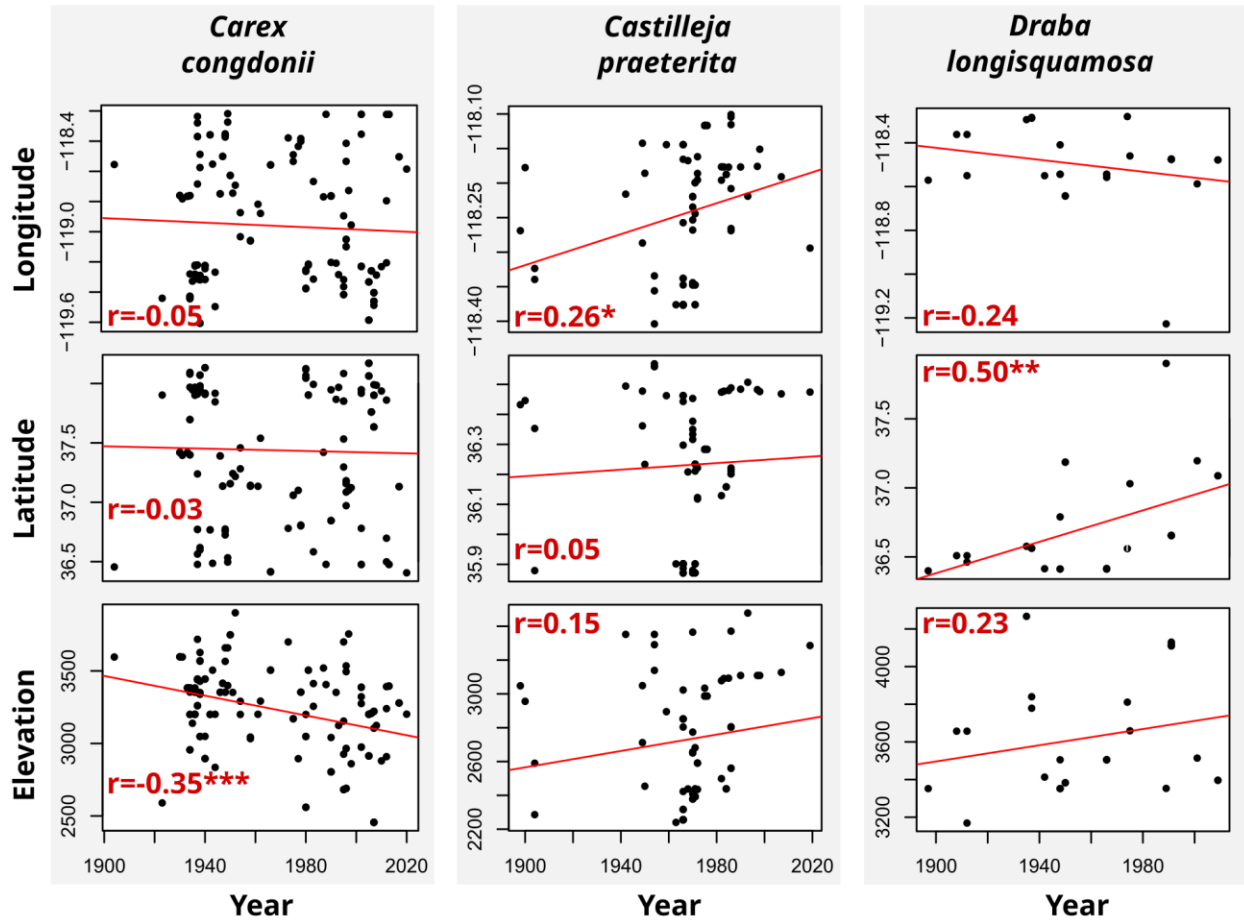
Figure S4*. Correlation plots modeling the strength of association between time and cardinal direction (longitude and latitude) and/or minimum elevation of species occurrences. Correlation values and significance codes are reported in red (* < 0.05, ** < 0.01, *** < 0.001).*
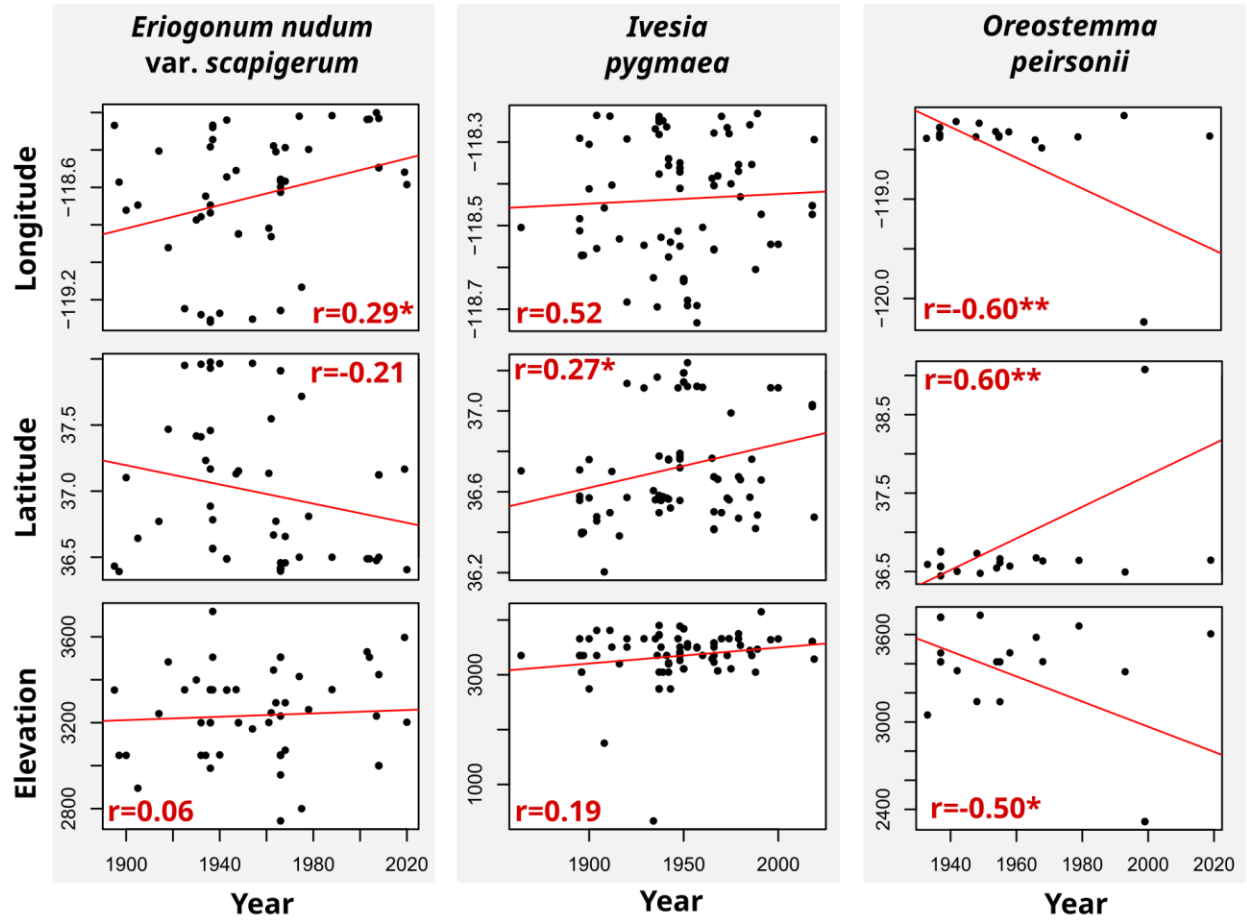
Figure 4. *Continued*

Figure 4. *Continued*

47

Table S1. *An analysis of the association between the location of collection and time or elevation was run on each of the 36 species which met the designated sample size (n ≥ 20). The Permutational Analysis of Variance (PERMANOVA) and Benjamini-Hochberg (BH) corrected p-values of significance (p.adjust < 0.05) for the 36 species are indicated in bold.*

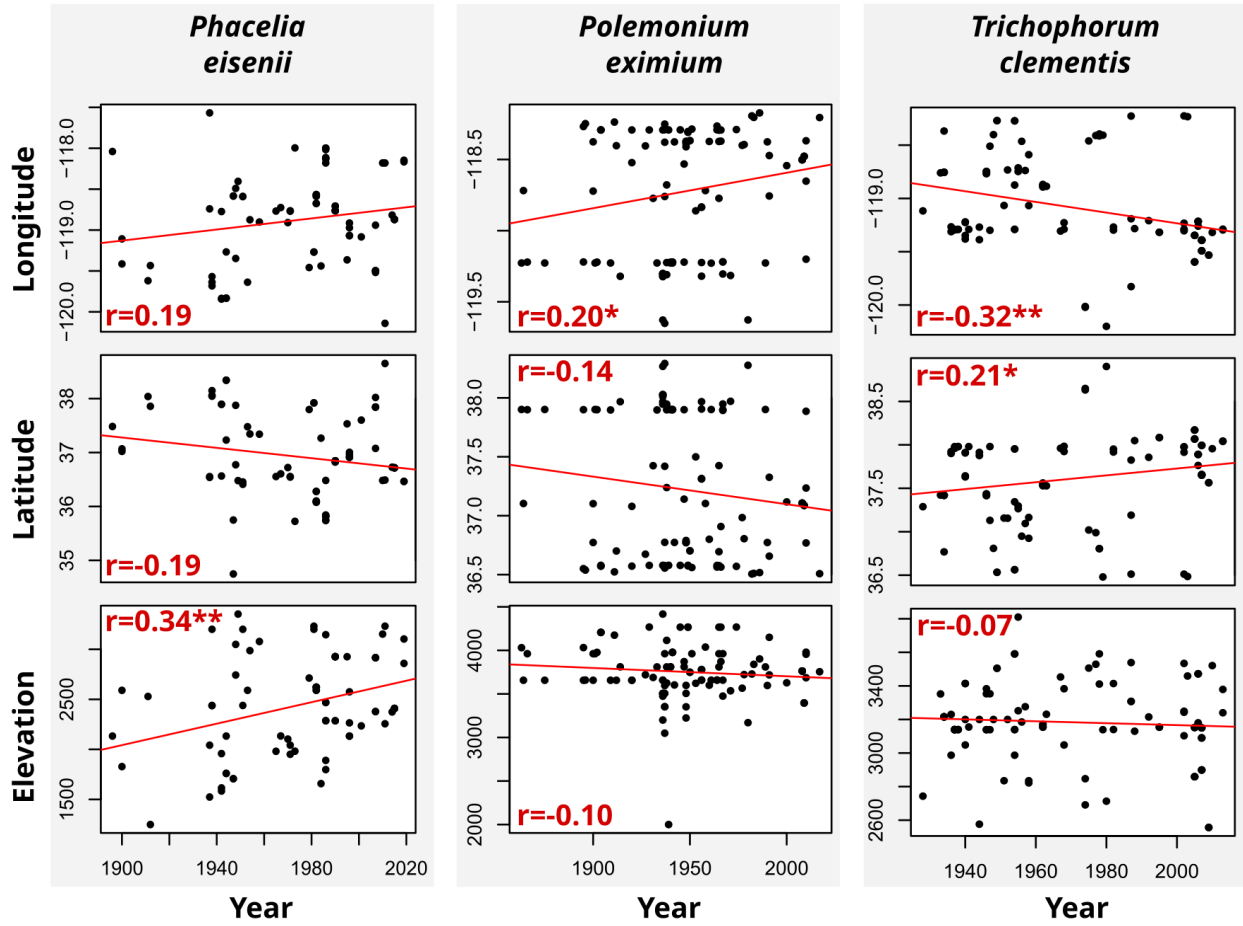| Species	Pr(>F) Yr	Pr(>F) Minel	Pr(>F) Yr:Minel	BH Pr(>F) Yr	BH Pr(>F) Minel	BH Pr(>F) Yr:Minel
Aquilegia pubescens	0.637	0.566	0.141	0.815	0.598	0.512
Boechera pygmaea	0.184	**0.001**	0.755	0.4	**0.002**	0.847
Calamagrostis muiriana	0.387	**0.001**	0.642	0.716	**0.002**	0.772
Carex congdonii	0.637	**0.001**	0.399	0.815	**0.002**	0.703
Castilleja praeterita	0.098	**0.001**	0.442	0.244	**0.002**	0.711
Draba cruciata	0.575	0.089	0.22	0.815	0.132	0.512
Draba lemmonii	0.57	**0.001**	**0.008**	0.815	**0.002**	0.074
Draba longisquamosa	**0.003**	0.025	0.184	**0.022**	**0.046**	0.512
Draba sierrae	0.06	**0.001**	0.19	0.229	**0.002**	0.512
Erigeron elmeri	0.733	0.132	0.581	0.874	0.181	0.768
Eriogonum nudum var. *scapigerum*	0.078	0.042	0.526	0.241	0.074	0.749
Eriogonum polypodum	0.554	**0.001**	0.237	0.815	**0.002**	0.512
Eriogonum spergulinum var. *pratense*	0.985	0.465	0.622	0.985	0.506	0.772
Galium hypotrichium subsp. *subalpinum*	0.492	0.186	0.504	0.798	0.246	0.749
Hazardia whitneyi var. *whitneyi*	**0.001**	**0.001**	0.184	**0.009**	**0.002**	0.512
Hulsea vestita subsp. *vestita*	0.455	0.233	0.866	0.798	0.278	0.88
Ipomopsis aggregata subsp. *bridgesii*	0.85	**0.001**	0.249	0.953	**0.002**	0.512
Ivesia muirii	0.939	0.931	0.846	0.965	0.931	0.88
Ivesia pygmaea	**0.023**	0.115	0.647	0.106	0.164	0.772
Lilium kelleyanum	0.496	**0.001**	0.066	0.798	**0.002**	0.333

Table S1. *Continued.*

Species	Pr(>F) Yr	Pr(>F) Minel	Pr(>F) Yr:Minel	BH Pr(>F) Yr	BH Pr(>F) Minel	BH Pr(>F) Yr:Minel
Lomatium torreyi	0.224	**0.001**	0.218	0.46	**0.002**	0.512
Lupinus covillei	**0.017**	**0.001**	0.161	0.09	**0.002**	0.512
Lupinus gracilentus	0.368	**0.001**	0.704	0.716	**0.002**	0.814
Luzula orestera	0.741	0.214	0.365	0.874	0.273	0.675
Monardella beneolens	0.756	0.051	**0.007**	0.874	0.086	0.074
Oreonana clementis	**0.067**	**0.001**	0.88	0.229	**0.002**	0.88
Oreostemma peirsonii	**0.001**	**0.001**	**0.001**	**0.009**	**0.002**	0.037
Orochaenactis thysanocarpha	**0.001**	**0.001**	**0.007**	**0.009**	**0.002**	0.074
Phacelia eisenii	0.088	0.308	0.525	0.244	0.345	0.749
Phacelia orogenes	**0.001**	**0.001**	0.237	**0.009**	**0.002**	0.512
Phlox dispersa	0.92	**0.01**	0.072	0.965	**0.019**	0.333
Poa stebbinsii	0.099	0.223	0.338	0.244	0.275	0.658
Polemonium eximium	0.11	0.085	0.431	0.254	0.131	0.711
Stipa kingii	0.639	0.056	**0.05**	0.815	0.09	0.308
Trichophorum clementis	**0.005**	**0.001**	0.778	**0.031**	**0.002**	0.847
Trifolium macilentum var. *dedeckerae*	0.068	0.295	**0.043**	0.229	0.341	0.308

Table S2. BH corrected p.adjust values for the individual effects of 'year' for five formulas. Significant values are in bold for comparison.

Species	geo~yr*min	geo~min*yr	geo~yr:min	geo~yr+min +yr:min	geo~min+yr +min:yr
Aquilegia pubescens	0.731	0.766	0.767	0.730	0.765
Boechera pygmaea	0.310	0.642	0.621	0.309	0.696
Calamagrostis muiriana	**0.029**	0.054	0.061	**0.029**	0.051
Carex congdonii	0.169	0.075	0.069	0.169	0.074
Castilleja praeterita	0.194	0.227	0.226	0.192	0.193
Draba cruciata	0.731	0.897	0.899	0.730	0.870
Draba lemmonii	0.731	0.768	0.775	0.730	0.771
Draba longisquamosa	**0.036**	**0.014**	**0.015**	**0.036**	**0.017**
Draba sierrae	0.151	0.177	0.187	0.153	0.168
Erigeron elmeri	0.802	0.897	0.899	0.801	0.870
Eriogonum nudum var. scapigerum	0.164	0.205	0.199	0.162	0.193
Eriogonum polypodum	0.731	0.650	0.657	0.730	0.708
Eriogonum spergulinum var. pratense	0.992	0.996	0.996	0.992	0.990
Galium hypotrichium subsp. subalpinum	0.207	0.171	0.187	0.207	0.168
Hazardia whitneyi var. whitneyi	**0.000**	**0.013**	**0.013**	**0.000**	**0.012**
Hulsea vestita subsp. vestita	0.654	0.739	0.767	0.653	0.722
Ipomopsis aggregata subsp. bridgesii	0.903	0.766	0.767	0.903	0.765
Ivesia muirii	**0.000**	**0.001**	**0.001**	**0.000**	**0.001**
Ivesia pygmaea	0.096	0.152	0.151	0.097	0.157
Lilium kelleyanum	0.731	0.739	0.767	0.730	0.722

Table S2. *Continued*

Species	geo~yr*min	geo~min*yr	geo~yr:min	geo~yr+min +yr:min	geo~min+yr +min:yr
Lomatium torreyi	0.350	0.574	0.577	0.351	0.572
Lupinus covillei	0.085	**0.012**	**0.013**	0.085	**0.012**
Lupinus gracilentus	0.580	0.642	0.621	0.580	0.722
Luzula orestera	0.151	0.338	0.340	0.153	0.352
Monardella beneolens	0.802	0.739	0.767	0.801	0.722
Oreonana clementis	0.164	0.574	0.577	0.162	0.570
Oreostemma peirsonii	0.311	0.897	0.899	0.312	0.826
Orochaenactis thysanocarpha	**0.000**	**0.002**	**0.003**	**0.000**	**0.001**
Phacelia eisenii	0.193	0.171	0.178	0.192	0.168
Phacelia orogenes	**0.000**	**0.022**	**0.027**	**0.001**	**0.026**
Phlox dispersa	0.934	0.897	0.899	0.934	0.905
Poa stebbinsii	0.109	0.128	0.137	0.109	0.135
Polemonium eximium	0.151	0.128	0.137	0.151	0.135
Stipa kingii	0.731	0.739	0.767	0.730	0.722
Trichophorum clementis	0.151	0.128	0.151	0.153	0.135
Trifolium macilentum var. dedeckerae	0.164	0.171	0.187	0.162	0.168

Table S3. *BH corrected p.adjust for the individual effects of 'minimum elevation' for five formulas. Significant values are in bold for comparison.*

Species	geo~yr*min	geo~min*yr	geo~yr:min	geo~yr+min +yr:min	geo~min+yr +min:yr
Aquilegia pubescens	0.750	0.739	0.752	0.748	0.739
Boechera pygmaea	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Calamagrostis muiriana	0.157	0.088	0.162	0.162	0.089
Carex congdonii	0.099	0.213	0.101	0.096	0.214
Castilleja praeterita	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Draba cruciata	0.126	0.129	0.132	0.133	0.128
Draba lemmonii	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Draba longisquamosa	0.056	0.153	0.055	0.053	0.153
Draba sierrae	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Erigeron elmeri	0.165	0.160	0.162	0.166	0.161
Eriogonum nudum var. scapigerum	0.059	**0.048**	0.057	0.058	**0.048**
Eriogonum polypodum	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Eriogonum spergulinum var. pratense	0.223	0.254	0.213	0.222	0.255
Galium hypotrichium subsp. subalpinum	0.178	0.254	0.203	0.178	0.255
Hazardia whitneyi var. whitneyi	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Hulsea vestita subsp. vestita	0.293	0.254	0.290	0.295	0.255
Ipomopsis aggregata subsp. bridgesii	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Ivesia muirii	0.722	0.203	0.729	0.727	0.203
Ivesia pygmaea	0.163	0.083	0.162	0.166	0.084
Lilium kelleyanum	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**

Table S3. Continued

Species	geo~yr*min	geo~min*yr	geo~yr:min	geo~yr+min +yr:min	geo~min+yr +min:yr
Lomatium torreyi	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
Lupinus covillei	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Lupinus gracilentus	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
Luzula orestera	**0.002**	**0.004**	**0.000**	**0.002**	**0.004**
Monardella beneolens	0.096	0.103	0.137	0.096	0.103
Oreonana clementis	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Oreostemma peirsonii	0.122	0.156	0.137	0.163	0.156
Orochaenactis thysanocarpha	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Phacelia eisenii	0.338	0.542	0.342	0.337	0.542
Phacelia orogenes	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Phlox dispersa	**0.018**	**0.021**	**0.008**	**0.019**	**0.020**
Poa stebbinsii	0.584	0.254	0.584	0.594	0.255
Polemonium eximium	0.477	0.604	0.476	0.491	0.603
Stipa kingii	0.093	0.093	0.100	0.094	0.093
Trichophorum clementis	**0.027**	**0.029**	**0.029**	**0.026**	**0.029**
Trifolium macilentum var. dedeckerae	0.338	0.324	0.365	0.337	0.325

Table S4. *Pearson's correlation results between time and longitude, latitude, and minimum elevation across the 36 species which met the sample size requirement (n=20). Pearson's correlation coefficients and significance codes are reported in red (* < 0.05, ** < 0.01, *** < 0.001).*

Species	Longitude	Latitude	Minimum Elevation
Aquilegia pubescens	0.095	0.003	0.040
Boechera pygmaea	0.358	0.197	0.396
Calamagrostis muiriana	-0.023	0.094	0.099
Carex congdonii	-0.054	-0.026	-0.351***
Castilleja praeterita	0.259*	0.050	0.146
Draba cruciata	-0.202	-0.083	-0.291
Draba lemmonii	-0.026	0.042	-0.138
Draba longisquamosa	-0.239	0.497**	0.226
Draba sierrae	0.288	0.056	0.058
Erigeron elmeri	-0.112	-0.016	-0.090
Eriogonum nudum var. *scapigerum*	0.292*	-0.212	0.060
Eriogonum polypodum	0.056	-0.139	-0.037
Eriogonum spergulinum var. *pratense*	0.032	0.005	-0.099
Galium hypotrichium subsp. *subalpinum*	-0.154	0.110	0.212
Hazardia whitneyi var. *whitneyi*	-0.367**	0.524***	-0.328**
Hulsea vestita subsp. vestita	-0.041	0.091	0.107
Ipomopsis aggregata subsp. bridgesii	-0.024	0.025	0.045
Ivesia muirii	0.019	0.008	0.158
Ivesia pygmaea	0.052	0.270*	0.193
Lilium kelleyanum	0.033	-0.044	0.096
Lomatium torreyi	-0.177	0.109	-0.069
Lupinus covillei	-0.216	0.234	0.131
Lupinus gracilentus	-0.163	-0.130	-0.047
Luzula orestera	0.069	-0.025	0.090
Monardella beneolens	0.211	-0.037	0.145
Oreonana clementis	0.066	-0.202	-0.150
Oreostemma peirsonii	-0.598**	0.599**	-0.503*
Orochaenactis thysanocarpha	0.298**	-0.275**	-0.048
Phacelia eisenii	0.189	-0.188	0.336**
Phacelia orogenes	0.557**	-0.355	-0.213
Phlox dispersa	0.014	-0.024	0.073
Poa stebbinsii	0.225	-0.168	0.169
Polemonium eximium	0.198*	-0.139	-0.103
Stipa kingii	0.106	-0.030	-0.041
Trichophorum clementis	-0.323**	0.214*	-0.067
Trifolium macilentum var. *dedeckerae*	0.262	-0.265	0.008

Table S5. *Cohen's d results between time and longitude, latitude, and minimum elevation across the 36 species which met the sample size requirement (n=20). Effect size and significance codes are reported in red (* < 0.05, ** < 0.01, *** < 0.001).*

Species	Longitude	Latitude	Minimum Elevation
Aquilegia pubescens	0.190	0.006	0.079
Boechera pygmaea	0.768	0.403	0.864
Calamagrostis muiriana	-0.046	0.189	0.199
Carex congdonii	-0.108	-0.053	-0.750***
Castilleja praeterita	0.537*	0.099	0.295
Draba cruciata	-0.413	-0.166	-0.608
Draba lemmonii	-0.051	0.084	-0.278
Draba longisquamosa	-0.493	1.145**	0.463
Draba sierrae	0.600	0.112	0.116
Erigeron elmeri	-0.225	-0.033	-0.181
Eriogonum nudum var. *scapigerum*	0.610*	-0.435	0.120
Eriogonum polypodum	0.111	-0.280	-0.073
Eriogonum spergulinum var. *pratense*	0.064	0.010	-0.199
Galium hypotrichium subsp. *subalpinum*	-0.311	0.222	0.434
Hazardia whitneyi var. *whitneyi*	-0.788**	1.231***	-0.694**
Hulsea vestita subsp. *vestita*	-0.082	0.182	0.216
Ipomopsis aggregata subsp. *bridgesii*	-0.048	0.050	0.090
Ivesia muirii	0.039	0.016	0.320
Ivesia pygmaea	0.105	0.562*	0.392
Lilium kelleyanum	0.066	-0.088	0.193
Lomatium torreyi	-0.361	0.219	-0.138
Lupinus covillei	-0.443	0.482	0.264
Lupinus gracilentus	-0.330	-0.262	-0.095
Luzula orestera	0.139	-0.050	0.181
Monardella beneolens	0.431	-0.075	0.293
Oreonana clementis	0.132	-0.413	-0.303
Oreostemma peirsonii	-1.491**	1.495**	-1.165*
Orochaenactis thysanocarpha	0.625**	-0.573**	-0.097
Phacelia eisenii	0.384	-0.383	0.712**
Phacelia orogenes	1.342**	-0.759	-0.436
Phlox dispersa	0.028	-0.048	0.146
Poa stebbinsii	0.461	-0.341	0.343
Polemonium eximium	0.403*	-0.280	-0.207
Stipa kingii	0.213	-0.059	-0.082
Trichophorum clementis	-0.683**	0.438*	-0.134
Trifolium macilentum var. *dedeckerae*	0.543	-0.549	0.016