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Climate and Species Traits Shape Responses of Alpine Flora in the US Rocky Mountains to a Changing World

Analysis of Five GLORIA Sites across the Southern Rockies

A field crew collects vegetation data at a GLORIA site in Rocky Mountain National Park in 2019.
NPS / ERIN BORGMAN

Climate and species traits shape responses of alpine flora in the US Rocky Mountains to a changing world: Analysis of five GLORIA sites across the southern Rockies

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Abstract

The Global Observation Research Initiative in Alpine Environments (GLORIA) is a world-wide network of sites dedicated to monitoring changes in alpine flora near mountain tops. In this project we analyzed data collected at 5 sets of GLORIA monitoring sites in the Rocky Mountains of the western USA. Each site was visited between 2 and 4 times in the years spanning 2003 to 2021. These sites include four National Parks (Great Sand Dunes National Park and Preserve, Rocky Mountain National Park, Yellowstone National Park, and Glacier National Park) and one wilderness area in the Pecos Wilderness within Santa Fe National Forest. We focused on testing the climatic sensitivity of the alpine flora as a whole, and the relative responsiveness of plant species based upon their commonness or rarity, their geographic ranges, and other aspects of their life forms and of site characteristics.

We find that across all sites and species there is strong evidence for turnover of the flora in the GLORIA sampling areas, with rare species disproportionately increasing over time and common species generally declining. We also find that graminoids and shrubs have increased more than forbs, as has been found or suggested in other studies. Multiple climate variables have significant influence on changes in plant cover. In particular, higher annual precipitation increases abundance, on average. Lower growing season precipitation, higher growing degree days (reflecting both warmer temperatures and more days of higher temperatures), and higher mean temperatures also lead to increasing abundance. Also, species with lower latitudinal ranges tended to increase more over time, while species with more northerly ranges often declined. Within these general trends there are substantial differences between species, as indicated by random species-level effects, but there were no strong patterns in these effects that would suggest additional generalizations between species groups.

Beyond our findings regarding the drivers of alpine plant dynamics, we examined factors that could potentially add bias or uncertainty to the data sets and made recommendations regarding data collection going forward. Among these suggestions are: 1) that all the NPS GLORIA teams consider consulting with previous species lists when performing field surveys; 2) that redundant temperature data loggers be deployed by at least two team members at each plot; and 3) that a careful training protocol be developed to better standardize cover estimation across parks and censuses. We expand on these recommendations at the end of report.

List of Terms and Acronyms

GLORIA-related and other ecological terms and definitions

AET: Actual evapotranspiration.

Aspect: Indicates cardinal direction of study plot slopes.

gdd: Growing degree-days. It is a measure of heat accumulation often used to predict plant growth and development during the growing season. In this multi-species study we intentionally use a simplified version of the standard definition of growing degree days, and sum the number of days with air temperatures above 0°C as our measure of gdd.

Habit: Plant growth form (e.g., graminoid, forb, shrub, etc.)

Park: Indicates the 5 focal study areas (4 national parks, 1 wilderness area) included in these analyses.

Perennation: Distinguishes annuals from perennials and for perennials classifies by placement of overwintering shoot meristems (belowground, aboveground, or on erect woody stems).

PET: Potential evapotranspiration.

Plot: 1 × 1-m plot in which percentage cover estimates are made.

PRISM (Parameter-elevation Regressions on Independent Slopes Model) interpolated climate data: https://prism.oregonstate.edu/

SOI: Species of special interest. SOI lists were acquired from various stake holders.

Species cover: Visual estimates of species level % cover of surveyed area. Values used are aggregated from 1 × 1-m plots to Park-summit-aspect level.

Summit: Unique categorical identifier for each summit in each park. The study includes a total of 20 unique summits (4 per park).

Summit-aspect: Unique categorical identifier for data from a particular aspect on a given summit. The dataset contains a total of 80 unique summit-aspects.

Summit-transition: Unique categorical identifier for data from a particular summit during a unique transition period.

Taxonomic unit: Broad taxonomic group (monocot, dicot, or gymnosperm).

Total plant cover: Total vascular plant cover estimated from the sum of species cover (described above).

Transition: Time period between two consecutive surveys.

Statistical and modeling-related terms

AIC (Akaike information criterion): A metric often used to select the best model from a set of similar statistical models (linear mixed effect models in this report). AICc is a modified form of AIC that is used to account for sample size.

climPC mod: Used in text as climPC model, indicating a model using climate PCA axes 1 and 2 as explanatory variables.

climPC1: Axis 1 from principal component analysis of climate variables.

climPC2: Axis 2 from principal component analysis of climate variables.

climVar mod: Used in text as climVar model, indicating a model using separate climate data (e.g., annual precipitation, maximum temperature) as explicit explanatory variables.

latmean1090: Used in text as short hand for mean species latitude. The mean of each species' North American latitudinal range between 10% and 90% values of full range. Based on points in GBIF database, cropped to polygon of North America.

max.gs.tmean: Also used in text as gs.tmean. The mean growing season temperature.

min.gdd: Also used in text as gdd. Growing degree days.

min.gs.ppt: Also used in text as gs.ppt. Growing season precipitation.

min.wy.ppt: Also used in text as wy.ppt. Water year precipitation.

sitelat: Also used in text as summit latitude. Summit-specific latitude.

snowdays: The number of days with snow cover with respect to water years.

Introduction

Climate Change effects on species and ecosystems

Evidence continues to accumulate of ongoing climate change, with alterations of many aspects of seasonal and annual climate in most parts of the world (IPCC 2022). In addition, extreme climate events have been changing in frequency and intensity, with these shifts also largely in concordance with climate model predictions. Understanding how climate changes will alter the composition and functioning of ecological communities is a major focus of current applied and basic ecology. Observed ecological impacts that have been persuasively linked to climate change include range shifts, alteration of phenology, disease outbreaks, and altered plant-herbivore dynamics (Parmesan and Yohe 2003, Grabheer et al 1994, Strum et al 2015, Parmesan and Hanley 2015, Parmesan et al. 2022). However, efforts to document climate change effects have also shown many muted or counter-intuitive effects. For example, many species have not shown predicted changes in elevational ranges or abundance patterns, even in regions with clear climate change (Moritz et al. 2008, Parmesan and Hanley 2015).

One likely reason for these mixed results is the sparsity of high-quality, long-term data with which to document climate change effects and to separate these effects from other fluctuations in population numbers and community composition. Most studies documenting the ecological effects of climate change are either based on low precision data, such as simple presence/absence surveys, or on more detailed data taken over smaller spatial and temporal ranges, as is true of most demographic studies (Parmesan and Hanley 2015, Morris and Doak 2001, data from Morris et al. 2020). In addition, most ecological data collection targets only one or a handful of species, limiting the ability to make community-wide assessments of climate effects.

The Global Observation Research Initiative in Alpine Environments (GLORIA) is an unusual effort to assemble high resolution data on many co-occurring species over relatively long periods of time and across wide geographic areas (Pauli et al. 2015). The initiative targets alpine plant communities at mountain summits, includes approximately 130 sites spread across six continents, and is based on the collection of plant and temperature data taken every five to ten years. Here, we use GLORIA data collected in the U.S. Rocky Mountains (https://www.nps.gov/subjects/mountains/gloria.htm) across four national parks (Great Sand Dunes National Park and Preserve, Rocky Mountain National Park, Yellowstone National Park, and Glacier National Park) and one wilderness area (Pecos Wilderness) in the Santa Fe National Forest to test for climate sensitivity of alpine flora in the Rocky Mountains of the continental US.

The Rocky Mountains alpine tundra houses a diverse set of species and is an integral part of the national parks and wilderness area included in this study. The alpine ecosystem, a major scenic and scientific feature at these parks, contains rare and endemic plant species and supports diverse wildlife. These fragile alpine ecosystems across the Mountain West are already experiencing changing conditions. Temperatures have increased in the northern Rocky Mountains at a higher rate than the global average (Pederson et al. 2010) and several arctic and boreal species at the southern margin of their geographic ranges are declining in and around Glacier National Park (Lesica and

Crone 2017). To best manage these systems in the face of these ongoing changes, land managers need to better understand if alpine floras are being broadly impacted by climate change as well as what drives the patterns in alpine vegetation changes, plant vulnerability, and resilience to stressors.

Past work on vegetation and climate change in alpine ecosystems

Alpine ecosystems have been proposed to be especially sensitive to climate change for two reasons. First, in part due to elevation-dependent warming, there have been rapid changes in climate documented in some alpine areas. Second, there is a presumption that climate conditions are particularly important in shaping species occurrences and distributions in these harsh environments. Taken together, climate effects are generally thought to be more impactful to alpine species, relative to biotic interactions or other effects, than is true for species in many other ecosystems (Doak and Morris 2010, Louthan et al. 2015, Morris et al. 2020, Mamantov et al. 2020, Lodetti et al. 2024).

Multiple studies have shown that specific alpine plants are sensitive to climate conditions and may be responding to changing climate (e.g., Grabherr et al.1994, Doak and Morris 2010, Oldfather et al. 2021). These projects often use annual data to show changes in either abundance or demographic rates and how these are influenced by climate drivers. However, by focusing on small numbers of species (typically one species in only a handful of populations) they are insufficient to draw broader conclusions about climate sensitivity of whole alpine communities or to document the extent of climate change effects already ongoing in alpine communities.

Multi-species studies often take an alternative approach of documenting abundances and changes in abundance for large suites of taxa. However, for it to be feasible to gather data on dozens to hundreds of taxa in alpine habitats, multi-species studies must, in one way or another, reduce the total sampling effort per species, relative to studies in more accessible habitats or those focused on a small number of taxa. In the GLORIA program, the extensive field efforts are made manageable by sampling only every five to ten years and with sampling restricted to fairly small plots on each focal summit. Past work done as part of GLORIA and similar studies have documented several signs of climate change, but have largely focused on community level changes, rather than attributes of species that can predict which species might increase and which will decline as a result of climatic changes (summarized in Lodetti et al. 2024; but see, for example Porro et al. 2019). Here we analyze GLORIA data from the five locations across the U.S. Rocky Mountains to better understand both community- and species-level responses to climate change, and in particular which species features are the most important predictors of changing abundance. While other similar analyses have focused on the idea of “winning” vs “losing” taxa (e.g., Lodetti et al. 2024), here we take a more nuanced approach to predicting a gradient of responses.

While the GLORIA project is focused on climate change, other anthropogenic effects can also influence plant community dynamics and could confound analyses of climate effects. In the U.S. Rockies perhaps the most widespread additional impact is likely to be atmospheric deposition of anthropogenically derived nutrients, in particular nitrogen (Bowman et al. 2014, Baron et al. 2000). As in other ecosystems (Pardo et al. 2011), nitrogen deposition can alter multiple aspects of the ecological functioning of alpine plant communities, with effects potentially impacting overall biomass, productivity, and species composition. While these effects are possible, and nitrogen inputs to alpine systems are clearly elevated in parts of our study area (Baron et al. 2000), there are currently limited data indicating strong effects on alpine plant composition or population-level dynamics. In particular, the most direct test of these effects, done in Rocky Mountain National Park, found that a single species, out of the 43 species present in the experimental plots, showed a significant response to nitrogen addition (Bowman et al. 2012). In spite of this limited response, spatial trends in deposition rates may confound some aspects of climate change in this study region.

Specific project objectives

In this study we used GLORIA-collected plant abundance and temperature logger data from 20 focal summits (four GLORIA summits in each of five parks) visited between two and four times in the years spanning 2003 to 2021. We supplemented field data with species distribution and life history data and additional estimates of climate conditions between surveys. We endeavor to address three broad questions:

1. Is there evidence of shifting species abundance patterns that would imply climate change effects on alpine plant communities across the U.S. Rocky Mountains?
2. Is overall plant abundance changing on summits and do any changes correspond to climate conditions?
3. What aspects of local climate, other site attributes, and species' traits predict changing abundances, and can any effects seen be used to infer which species are most at risk due to ongoing climate change?

Our particular goal in all these questions is to assess species and community responses to climate that can inform management of alpine ecosystems by the National Park Service. We also aimed to establish a process for making climate sensitivity assessments, so they can be repeated or adjusted in the future with these or similar data and for other biological components of park flora. Finally, by closely examining the data collected as part of the GLORIA surveys, we assess ways that future data collection could be either improved or standardized across parks and survey periods.

Methods

GLORIA vegetation data sets

GLORIA vegetation and soil temperature data for Great Sand Dunes National Park and Preserve (GRSD), Rocky Mountain (ROMO) and Yellowstone (YELL) national parks, and Pecos Wilderness (PECO) are available on the National Park Service website (https://irma.nps.gov/DataStore/Reference/Profile/2297334) and for Glacier National Park (GLAC) through the USGS ScienceBase database (https://www.sciencebase.gov/catalog). Vegetation and soil temperature data for all five parks were gathered according to GLORIA protocol (Pauli et al., 2015). Note that we refer to the 5 study locations as parks, though one (PECO) is a wilderness area within a National Forest. Table 1 shows the years when vegetation data were gathered for each park, as well as the number of transition periods, or time periods between two surveys when the observed changes in abundance occur. Hereafter we simply refer to these as "transitions." Below we briefly explain how temperature and vegetation data were cleaned and aggregated for analyses. More detailed methods can be found in the Supplementary Methods (Appendix A). Code for data cleaning and analyses can be found on the National Park Service website (https://irma.nps.gov/DataStore/Reference/Profile/2306683).

Table 1. Years of 1-m^2 species percent cover vegetation surveys for each park and the number of transitions to date. Transitions are the time periods between consecutive surveys.

Park	Survey years	Transitions
Glacier National Park, MT (GLAC)	2003/2004, 2009, 2014, 2019	3
Yellowstone National Park, WY (YELL)	2011, 2016	1
Rocky Mountain National Park, CO (ROMO)	2010, 2014, 2019	2
Great Sand Dunes National Park and Preserve, CO (GRSD)	2009, 2015, 2020	2
Pecos Wilderness, NM (PECO)	2016, 2021	1

The GLORIA field protocols leave some room for interpretation and some choice about exactly which types of vegetation data to gather. Consequently, GLORIA field crews in each of the five parks took slightly different field approaches for some types of data collection, which resulted in variation in each dataset with respect to the types of plant occurrence and abundance gathered as well as different data recording methods (see Pauli et al. 2015: GLORIA Manual 5th Ed.). We did preliminary analyses of the different types of data collected (see below) and found that the 1-m^2 quadrat species-level percent cover visual estimates were most consistently collected across all five parks, using comparable field and data recording protocols, making it the most reliable for the present study. These analyses also showed that other data types (e.g., broadly binned, ordinal abundance data in larger areas on each summit aspect (see Appendix A: Summit area sections) or point count data within quadrats) did not have meaningful or reliable correspondence within or across parks, nor did it provide higher resolution information with which to estimate changing abundances. Additionally, the 1-m^2 species-level data were the most informative and detailed data collected, especially about changes in less abundant species, which represent the majority of species at all sites. We therefore performed all statistical analyses on these species-level 1-m^2 quadrat visual cover estimates data. See Supplementary Methods (Appendix A) for more discussion about discrepancies between plant cover data gathered using point-intercept counts and visual cover estimates as well as a comparison of recorded data to quadrat photos in PECO.

GLORIA 1-m^2 percent cover data contain species-specific percent cover estimates for up to four 1-m^2 quadrats (collectively called a "quadrat cluster") at each focal summit-aspect. On each summit-aspect, the four quadrats in a quadrat cluster are placed at the corners of a 3-m × 3-m grid (Figure 1). Ideally there are four quadrats in a quadrat cluster, but in many cases, data were missing from one or more of the quadrats. (See Pauli et al. 2015 for details of the ideal GLORIA site setup.) Rather than directly using data from individual quadrats, we averaged percent cover estimates within each summit-aspect's quadrat cluster to create a single percent cover estimate per species per summit-aspect per survey (see Appendix A: Figure 25 for histograms of aggregated values). The aggregated estimates of cover at the beginning and end of a transition were then used to assess changes in abundance. Recall that "transition" refers to the time period between two consecutive surveys and encompasses the time period over which any observed changes in abundances would have occurred. Averaging percent cover estimates at the summit-aspect level removed a great deal of random variation in abundance estimates and also corresponded to the finest scale measurement of climate data from buried Pendant temperature recorders, one of which is deployed on each aspect of each summit.

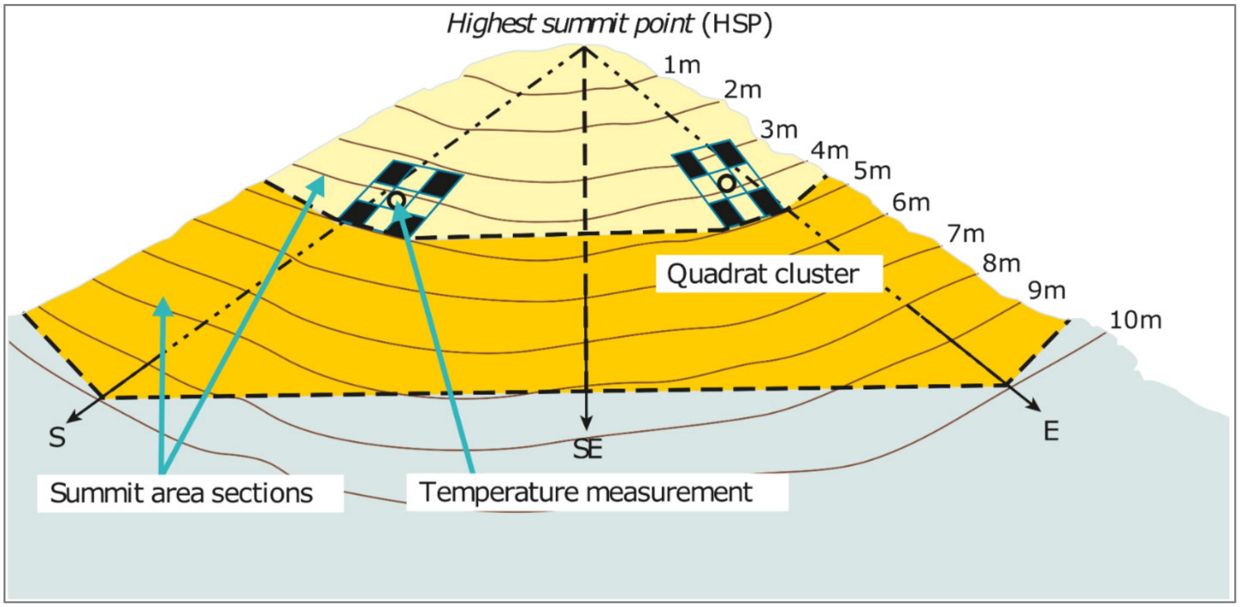

Figure 1. Field plot design for alpine monitoring following GLORIA methods. This plot layout is replicated on each of the four summits in a target region. The design is centered on the highest point on the summit and extends to 10 m in elevation below the highest point. From Pauli et al. 2015. GLOBAL OBSERVATION RESEARCH INITIATIVE IN ALPINE ENVIRONMENTS

The broad patterns of abundance changes were similar across all parks, but GLAC had substantially lower variability in abundances across time than that seen in other parks. One particular component of data collection methods at resurveys may have had important effects on why results differed between GLAC and all other parks. The GLORIA protocols stipulate that when estimating species occurrence and abundance during a survey, the teams should not consult information from the past survey, so as not to bias their estimates. However, the GLAC surveyors decided referencing species lists from past surveys, though not the estimated abundances, would likely decrease observation errors (this is a common approach to vegetation sampling outside of GLORIA surveys). This difference in methods, along with consistency in field crew between the resurveys, may help explain the dramatically lower variation in cover estimates for GLAC sites and may also be impacting other results (see below).

Data cleaning overview

We compiled data from all parks into one dataset. This involved removing subspecies and varieties designations, which helped to reduce uncertainties associated with subspecies-level identification and helped with comparison of species across parks (see Appendix A for more detail). After aggregating data to the species-level, we compiled a comprehensive list of species occurring across all parks. Table 2 and Table 3 show the number of species occurring in each park and their overlap in occurrence across parks, respectively.

Table 2. Number of plant species observed in GLORIA plots by park (not including lichen, ferns, or clubmosses).

Region	Number of species
Glacier National Park (GLAC)	89
Yellowstone National Park (YELL)	97
Rocky Mountain National Park (ROMO)	100
Great Sand Dunes National Park (GRSD)	82
Pecos Wilderness (PECO)	63
Total	242

Table 3. The number of common and unique species across the five parks included in the study. Values along the diagonal indicate the number of species unique to that park. Values above the diagonal indicate the number of species shared by park pairs. The five parks share only seven species in common.

	Park Code				
Park Code	GLAC	YELL	ROMO	GRSD	PECO
GLAC	41	39	30	26	15
YELL	–	61	34	32	21
ROMO	–	–	30	57	39
GRSD	–	–	–	14	39
PECO	–	–	–	–	18

Species information

Traits

We generated a set of attributes for all species that may explain changes in abundance over time (Appendix D: Table 16). With 242 species, many of which are not well studied, these attributes had to be simple and easy to score with only general knowledge. Many other relevant traits would be desirable to use in our analyses but cannot be accurately scored for more than a handful of species (e.g., extent of below-ground clonality, leaf thickness, root-shoot allocation, mean lifespan). We settled on three traits plus a high-level taxonomic classification, as outlined in Table 4, some of which have been identified in past alpine plant analyses as potential predictors of climate change effect (Porro et al. 2019).

Table 4. Species traits used in analyses and the number of observations in the analysis dataset with each trait. An observation is a survey at a given summit-aspect of a species with the trait.

Category	Species Trait	Number of Observations
Perennating	Below Ground	3,842
	Above Ground	499
	Woody	57
	Annual	3
Leaves	Deciduous	4,043
	Evergreen	358
Habit	Forb	3,302
	Graminoid	1,042
	Shrub	54
	Tree	3
Taxonomic unit	Dicot	3,325
	Monocot	1,073
	Gymnosperm	3

Species geographic ranges

Given that the geographical range of a species is likely to be a reflection, at least in part, of its climatic tolerances, we sought to characterize each species' geographical range using information from herbarium records in the Integrated Digitized Biocollections (iDigBio.org) database (GBIF 2022; Powers 2024). The iDigBio database contained multiple records that included occurrence locations (spatial coordinates) for all species in the species list except *Tetraneuris brandegeei*, which only had one herbarium record. As this study focused on climate change impacts on alpine communities in the western United States, we filtered specimen records for those within North America. To do this, we cropped a point shapefile generated using spatial coordinates from the herbarium records with a shapefile of North America. This ensured that erroneous points were removed (i.e., points over the Pacific Ocean) as well as points outside of North America that would be less relevant to species' latitudinal ranges as they pertain to this study. The clipped species coordinates were then used to develop several geographical range values that characterize the species latitudinal ranges within North America: minimum, maximum, and mean latitude plus the same set of summary statistics for all points within the 10th and 90th percentile of latitude values for a species. These latter statistics controlled for extreme outliers that would otherwise have substantial effects on each of the range metrics.

Climate data

Mean daily soil temperature

Hourly soil temperature data (°C) was collected at all summit-aspects in all parks with shallowly buried temperature data loggers (Pendent loggers from Onset Corp). Data from temperature loggers were uploaded and subsequently run through QA/QC processes, then published as cleaned hourly soil temperature readings. Substantial blocks of missing temperature data occurred in most parks, and we developed an approach to estimate these missing values in order to avoid reducing the overall data set (see Appendix A). We aggregated these hourly temperature data to mean daily temperature by taking the mean of all hourly readings within each 24-hour period. When there were fewer than 20 hourly temperature readings within a 24-hour period we treated this as missing temperature data, as that number of missing hourly readings could substantially influence daily estimates. For analyses, data were further aggregated to be consistent with the temporal resolution (5-year) of vegetation data. See Appendix A for a more detailed description of temperature data cleaning, interpolation, and aggregation.

Water balance model data

We used mean monthly temperature and monthly precipitation sums as inputs to a Thornthwaite-type monthly water balance model (Lutz et al. 2010) to infer each summit-aspects' soil water availability and annual snow-free period. The model requires geographical information about each summit-aspect including slope angle and aspect, latitude and longitude, and elevation. It also requires historic daily temperature and precipitation data for each site, including 10 years of burn-in data for model calibration, which we acquired from the PRISM database using summit coordinates. With this information the water balance model provides daily estimates of snowpack depth, growing degree days, and potential and actual evapotranspiration, which we incorporated into our final analysis dataset (see below).

Soil chemistry

Soil chemistry data were available for four of the five parks but not for GLAC. This data gap limited the usefulness of the soil chemistry information for our full analyses. Moreover, there was extremely high variation in nitrogen concentrations (and other values) across the samples (Appendix A: Figure 29), to the extent that we questioned the accuracy of the data. As a result, we asked an alpine soil researcher to examine the data, and she felt that some of the values, especially several values for two measures of nitrogen concentrations (NH_4-N and total N) and one potassium value (total P), seemed outside reasonable bounds.

To further test the accuracy of the GLORIA soil samples and to look for evidence of patterns in nitrogen levels across the parks, we examined two other data sets. First, we compared soil nitrogen concentrations from the GLORIA samples to weekly values from surveys of soil N from the National Atmospheric Deposition Program National Trends Network (hereafter NADP) (https://nadp.slh.wisc.edu/networks/national-trends-network/) taken from sites closest to the summits in each park. We found that many GLORIA samples had values far exceeding those reported in this standardized program (Appendix A: Figure 30). However, the NADP samples also indicated a trend in soil nitrogen levels, with much lower concentrations in YELL and GLAC than in the three southerly parks (Appendix A: Figure 31). The same trend may be reflected in the GLORIA soil chemistry data, though with few samples overall and none from GLAC, it is hard to make the same northerly vs. southerly site comparison.

We also looked for patterns in regional nitrogen deposition rates using information from the Rocky Mountain Regional Snowpack Chemistry Monitoring Study (https://www.usgs.gov/centers/colorado-water-science-center/science/rocky-mountain-regional-snowpack-chemistry-monitoring). While no sampling sites in this program were at the GLORIA summits or at similar elevations, we could ask if there were strong and consistent differences in deposition rates between the five park regions that could be used in the interpretation of our results. Specifically, we identified the five snowpack deposition sites closest to each summit within a park (many of these sites were duplicates across the four GLORIA summits in each park) and then asked whether there were consistent differences in deposition of ammonium (NH_4) or nitrate (NO_3) over the years of sampling, which ranged between one and thirty. We found that there is substantial within-park variation in deposition rates (Appendix A: Figure 32), but also some patterns of between-park variation that are broadly similar to the NADP soil data. Especially for NO_3, there is strong tendency for lower latitude parks to have higher deposition rates. We also tested the significance of these park level differences using mixed linear models, with either NO_3 or NH_4 concentrations as functions of the fixed effects of water year and park, with a random effect of snow deposition station. For both NO_3 and NH_4 we see significant park differences (NH_4, F-value = 15.6; NO_3, F-value = 37.8). However, for NH_4 the marginal r^2 (fraction of variation explained by the fixed effects of the model) is only 0.16, while for NO_3 it is 0.42. These results suggest that while there is real regional variation in deposition rates, these are not consistent enough within regions to add to our predictive models for plant abundance changes. Nonetheless, we consider the possible effects of deposition rates in driving some of our results, as presented below.

Analysis datasets

Species-level data

We compiled a final dataset of changes in species cover using data described above: species abundances for each transition on each summit-aspect, as well as climate, species traits, and geographical range information. Since our goal was to predict changes in species abundance over the 5-year transitions, summit-aspect level time-variant climate data were aggregated into 5-year summaries corresponding to the time between survey years (Table 5). For example, we included 5-year mean growing season temperatures (for each summit-aspect) which were found by taking the mean of annual growing season temperatures. Five-year aggregated data was based either on the water year averages (i.e., mean number of snow free days and mean water year precipitation) or on growing season averages (mean annual growing season temperature, mean growing season precipitation). We included 3 different summary statistics for each time-varying climate metric: the mean of the annual data over the transition, the annual minimum value, and the annual maximum value. Table 5 shows a summary of attributes included in the dataset used for analyses. In the final dataset we also included the first two principal components from a principal component analysis of all climate variables (see Results). We refer to these principal components as climPC1 and climPC2 below.

Table 5. Attributes included as predictors in models for species abundance. This list includes all categories of effects included as fixed effects in our statistical models. For each climate variable, three alternative summary statistics were tested (mean, maximum, or minimum over a five-year transition).

Attribute type	Attribute name	Start/end date for annual summaries
Climate (time-variant)	Mean growing season temperature (ºC)	July 1st–September 25th
	Total growing season precipitation (mm)	June 1st–September 25th
	Total water year precipitation (mm)	October 1st–September 30th
	Growing degree days (gdd)	October 1st–September 30th
	Number of days with snow cover (snow days)	October 1st–September 30th
	Growing season potential evapotranspiration (PET, mm)	July 1st–September 25th
	Growing season actual evapotranspiration (AET, mm)	July 1st–September 25th
Species and summit (time-invariant)	Latitudinal range (based on 10th to 90th percentiles) (degrees latitude)	–
	Perennating	–
	Habit	–
	Leaves	–
	Start cover	–
	Site latitude	–

Total vegetation cover data set

In addition to looking at changes in individual species cover we analyzed changes in total vascular plant cover over time. To estimate total vascular plant cover we summed species-level cover estimates within each 1-m^2 quadrat, then found the mean of the summed values within quadrat clusters (i.e., summit-aspects). Note that the summed total vascular plant cover values can exceed 100% due to overlapping canopy layers.

In four of the parks, teams directly estimated total vascular plant cover data using both visual estimation and point-intercept field methods. However, given the lack of such data at GLAC and concerning patterns in the data for the other parks that indicated strong observer effects, we decided the aggregation method described above would be the most reliable and consistent measure of total cover. The same climate and summit variables described in the species-level data were used in analyses of changes in total vascular plant cover.

Analysis methods

Trends and aggregation of climate data

We first tested for temperature trends using linear regressions to establish whether climate had substantially changed over the GLORIA study period in each park or had shifted over the 30 years from 1990–2020. Using all climate variables described under Analysis Datasets above, we next performed a Principal Components Analysis (PCA) to reduce these high dimensional descriptions of climate to simpler aggregate climate indices for use in some predictive models.

Tests for community turnover

We began our analyses of ecological dynamics by looking for evidence of broad patterns of community change or turnover, such as species in some parks becoming rarer or more abundant. These analyses were not designed to test for specific effects driving these changes, but to assess broad evidence for non-random patterns of change in species abundances. Specifically, we fit mixed linear models to predict change in abundance of each species (the difference between ending and starting cover) across each five-year transition. The only fixed effect in these models was starting cover, while random effects included transition number within a park and species ID. We fit these models to the entire data set and to separate subsets of the data for each park. In addition to these main models, we also conducted several tests to examine whether patterns seen in the data were likely to be the result of observation errors, changes in identification of species by the survey teams, or other artifacts.

Modeling species-specific abundance changes

Most of our results come from fitting and interpreting species-level models of changing abundance, as predicted by species traits and summit-aspect level climate. We used linear mixed effects models to analyze climate impacts on species abundances across the five parks. We present results from two slightly different models: one which uses the first two principal components from the climate principal component analysis as explanatory variables (see Results) and another which uses individual climate variables as explanatory variables. See Appendix A for full model selection details.

Modeling changes in total vascular plant cover

In addition to analyzing changes in individual species cover over time, we looked for changes in total vascular plant cover. This model selection process closely follows methods described for species-specific changes in abundance (see Appendix A for additional details).

Models for species of special interest

Park staff identified 39 species and species groups of particular interest based on cultural, ecological, or restoration importance (see Results). We had adequate data to analyze trends for 19 of these species of interest (SOI); other species had very limited occurrence data that would not support analysis of their changing cover values or lacked data entirely. For each SOI with adequate data, we fit the two species-level global models (climPC and climVar models) using data only for that SOI. Additional details can be found in Appendix B.

Data quality analysis

We performed a targeted set of analyses to uncover patterns in the data that would indicate inaccuracies or bias in the occurrence and abundance estimates. With only a single estimate per species per survey year in each quadrat there are no straightforward statistical tests to directly quantify data accuracy, but we examined the data in several ways to look for evidence of substantial issues. While we looked for some persistent issues with these analyses, note that in the Supplementary Methods (Appendix A) we also outline several data cleaning procedures used to improve problems that may arise from inconsistent species identification.

Results and Discussion

Temperature trends between parks

PRISM temperature summaries show that mean annual temperatures have been rising across all five parks since 1990 (Figure 2). However, the strength of these trends varies considerably, and temperature trends throughout the GLORIA study periods for each park have not all reflected longer-term temperature increases. In particular, GLAC has a weaker pattern of increase in the long term, and also shows an average decrease in mean annual temperatures from 2003 to 2019, adding useful context to some of the results discussed below. All other parks show average increases in mean annual temperature since 1990 and through their respective study periods, though the rate of increase differs between the longer-term and study period trends. Note that temperature data gathered *in situ* with temperature data loggers shows similar trends but is impacted by data in initial survey years beginning in August and by missing data.

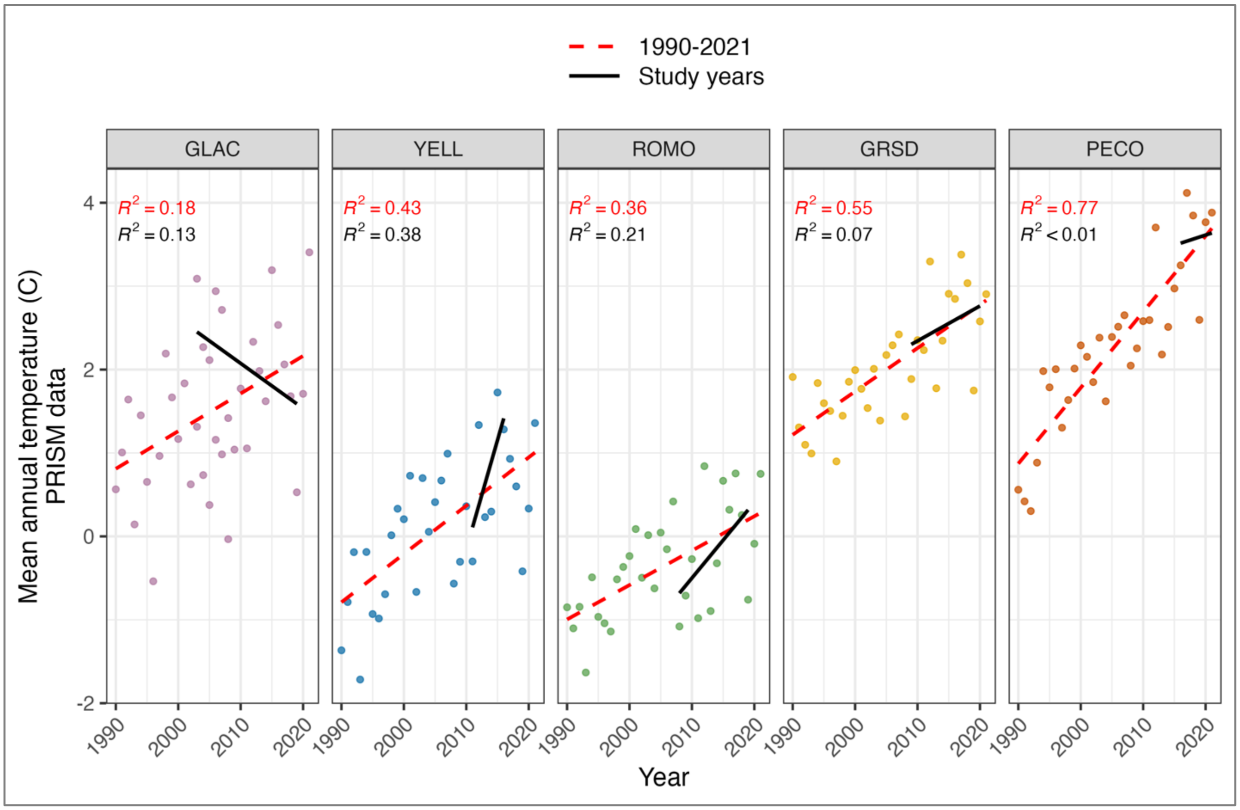

Figure 2. Temporal trends of mean annual temperature at each park based on daily PRISM data. Data points show the annual mean of daily mean temperatures across all four summits in each park. Dashed red lines show trends from January 1st, 1990 to September 7th, 2021. Shorter solid black lines show trends through study years for each park. All parks show increases in mean annual temperature since 1990. All parks, except GLAC, also show average increases through their respective GLORIA study periods, though the rate of increase differs between the longer-term and study period trends and shows less consistency. NPS

Climate principal component analysis

We performed a principal component analysis (PCA) on the full set of climate variables described in Analysis Datasets above. In combination, principal components 1 and 2 (PC1 and PC2) explained 70% of variation in the climate data (Figure 3). PC1 captured 50.6 % of the variation and is driven by variables for water availability and stress, with PC1 values positively correlated with total water year precipitation. PC2 captured 19.6% of the variation and is most associated with variables related to growing season temperatures, precipitation, and length. Specifically, positive PC2 values correspond to warmer temperatures and higher growing season precipitation.

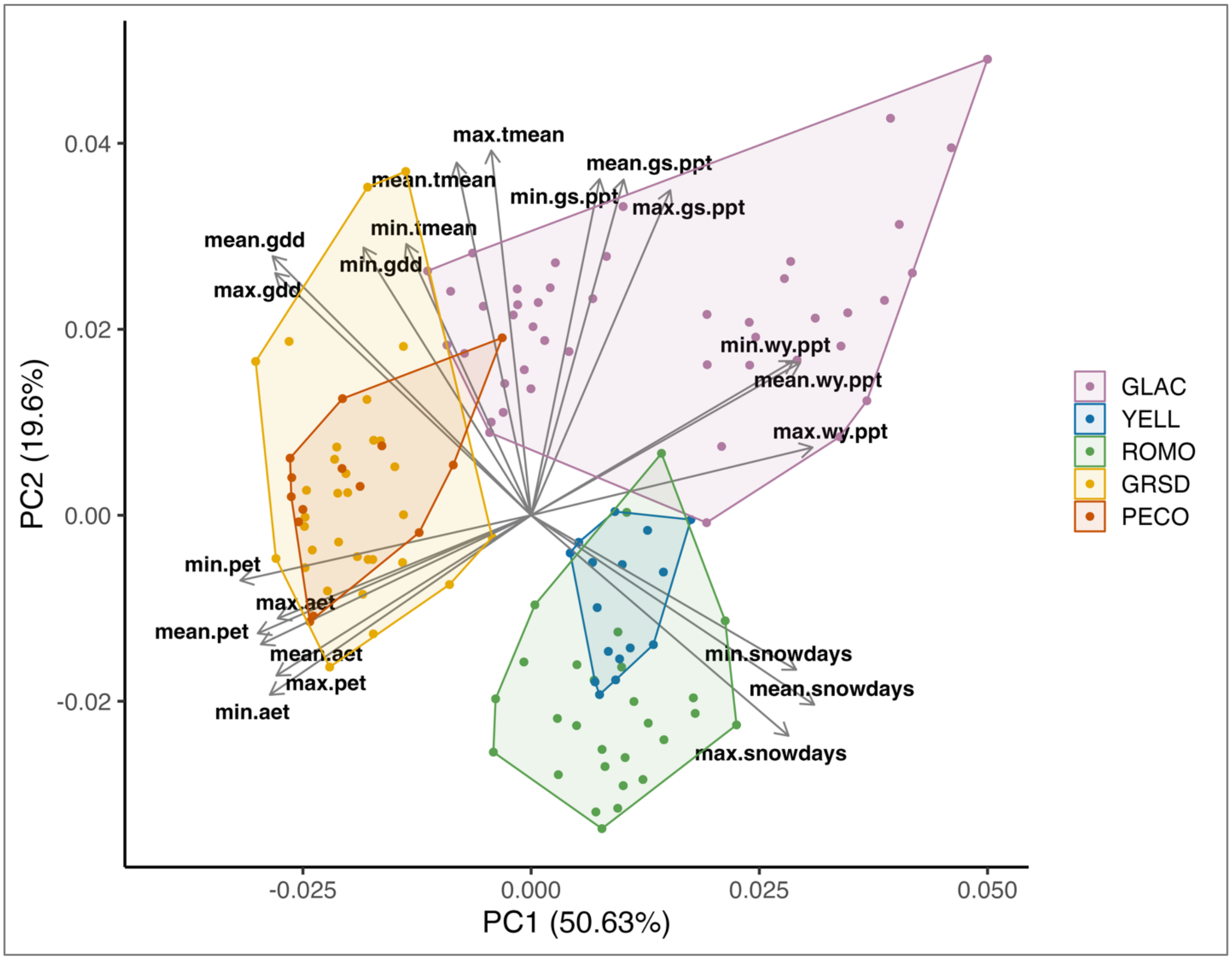

Figure 3. Results of principle components analysis of all summary climate variables considered in analyses. Data points for each annual summit-aspect are shown with color indicating the park. Loadings of climate variables on the two PC axes are also shown. PC1 is positively associated with precipitation values, especially water year precipitation, and snow days. PC1 is also negatively associated with PET and AET, indicating water stress. PC2 is mostly strongly and positively associated with temperature, growing degree days, and growing season precipitation. NPS

Community turnover

Our first analyses looked for evidence of community-level change and turnover. The data showed a striking pattern of turnover in species abundances over the five-year transition periods. In particular, we saw a clear tendency for species with initially low cover values (hereafter referred to as “rare” for simplicity) or that were initially absent from summit-aspects, to increase in abundance, while initially more abundant species disproportionately declined (Figure 4). In a linear mixed model of change in abundance (difference between starting and ending cover values) regressed on starting abundance, and with random effects for transition and species, the coefficient for starting abundance was -0.203 ($p < 2 \times 10^{-16}$).

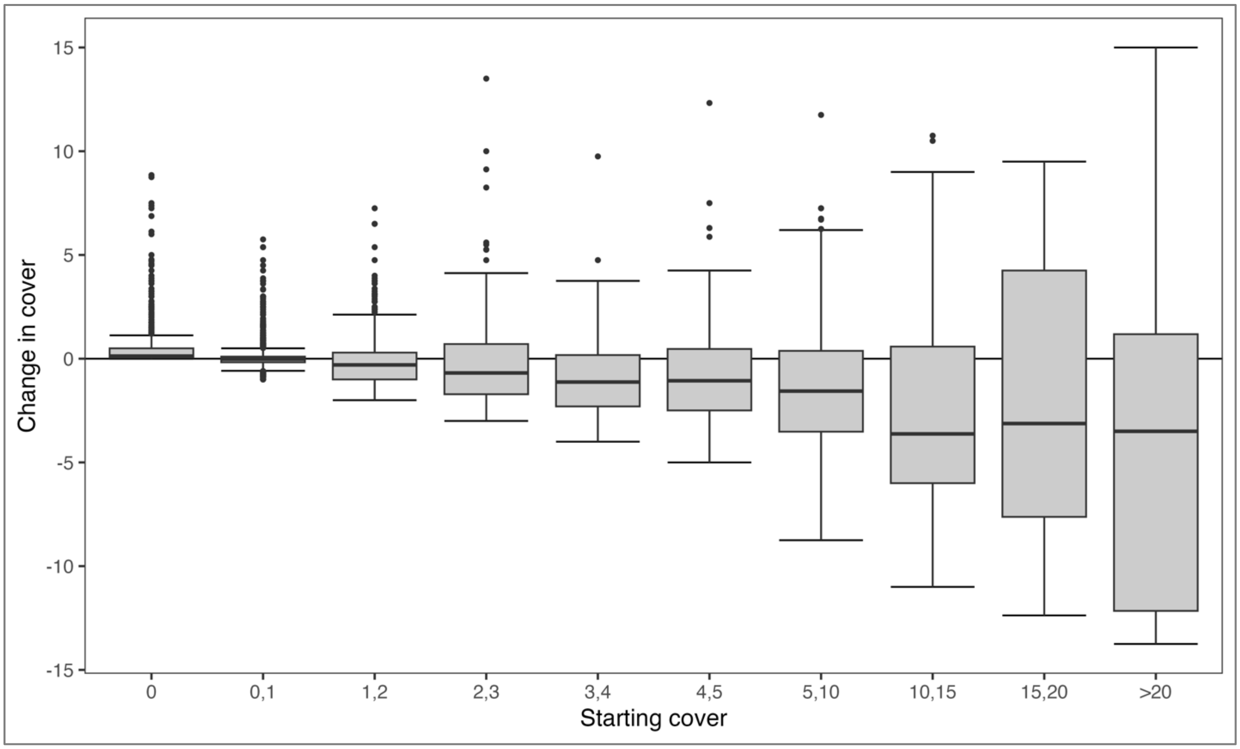

Figure 4. The change in species cover declines with starting cover values across all parks and transitions. Both axes show aspects of percent cover (change in percent cover on the y axis and starting percent cover on the x axis). Cover change is the difference between ending and starting cover on a given slope-aspect and for a given species over a single transition period. Starting cover labels indicate the range of starting cover values used to construct each boxplot, with more common species (those with higher starting cover) towards the right of the x axis, and those which started with zero cover shown to the far left. Note the non-linear scaling of these bins, which reflects the skewed distribution of cover values seen in all parks. The results show species with initially low cover (0%, 0–1%, 1–2%) generally increased between GLORIA surveys, while species with initially high cover (10–15%, 15–20%, >20%) generally decreased. NPS

This pattern is consistent with expectations of community change with ongoing climate change, has been seen or suggested in studies of other plant communities (Jackson and Sax 2009, Gibson-Reinemer et al. 2015), and has been suggested as a signal of alpine communities undergoing climate change (Schuchardt et al. 2023, Lamprecht et al. 2018, Alexander et al. 2017). If abiotic conditions are shifting away from those that favor past and current community dominants, these common species should decline and other species that were formally absent or rare may increase in abundance. This pattern should be particularly strong in GLORIA data, where plots are directly adjacent to summits. In these settings, rare or absent species that subsequently increase are likely to be lower-elevation species, while initially abundant taxa are more likely to be near their optimal climate conditions initially, but to be increasingly mis-matched with local conditions as climate changes. In contrast, at a summit few species that are initially rare are likely to be at the lower edge of their elevational range, and thus to decrease further with warming conditions.

While this interpretation of the apparent turnover in species abundances is reasonable, there are also several sampling issues that could contribute to, and perhaps solely generate, the observed pattern of turnover. To test for these effects, we did several additional analyses:

1. One plausible reason for the overall pattern could be that species starting at zero can only increase. Increases from zero can be real colonization or could be due to changes in classification by the surveyors. However, we found that the turnover pattern is essentially unchanged if we remove all transitions that go from zero cover to a positive value (starting cover coefficient = -0.174, $p < 2 \times 10^{-16}$).
2. Another spurious effect could be changing classification of difficult taxa. The two genera we hypothesized to be the most problematic were Potentilla and Poa. However, removing these from the analyses, in addition to removing species transitions starting with zero, still did not alter the pattern of community turnover (starting cover coefficient = -0.159, $p < 2 \times 10^{-16}$).
3. Another possible effect is that as time progressed, identification became more stable and that fluctuations in rare taxa would decline. We therefore performed an analysis in which we included the transition number as a fixed effect. Note that PECO and YELL have only a single transition, and only GLAC has three transitions, leading to a relatively weak ability to test for this effect. Still, this model also supported a strong negative effect of starting abundance on change in cover (coefficient = -0.470, $p < 2 \times 10^{-16}$). The model also shows a negative effect of transition number on abundance change (coefficient = -0.261, $p = 0.04$) along with a positive interaction between transition number and starting abundance (coefficient = 0.200, $p < 2 \times 10^{-16}$). Together, these results suggest that changes in abundance generally weaken over subsequent transitions, but that the pattern of community turnover still is supported.

The results of the above tests lead us to conclude that the trend in community turnover is not generated by variations in plant identification by surveyors but is a real pattern in the GLORIA data.

We also looked at the generality of the community turnover pattern by dividing the data from different parks and conducting separate analyses, again using starting abundance as a fixed effect, and including random effects for transition and species. The only park that did not show a significant negative coefficient for starting cover (p values from 0.015 to $< 2 \times 10^{-16}$) was GLAC (Figure 5). GLAC is also the park with by far the lowest changes in abundances. However, even for GLAC, a spearman rank correlation between starting cover and change in cover was negative and significant

($\tau = -0.185$, $p = 6.1 \times 10^{-15}$). Similarly, when data was divided by aspect (N, S, E, and W), we found the same turnover pattern on all aspects (starting abundance p-values from 0.0003 to $p < 2 \times 10^{-16}$).

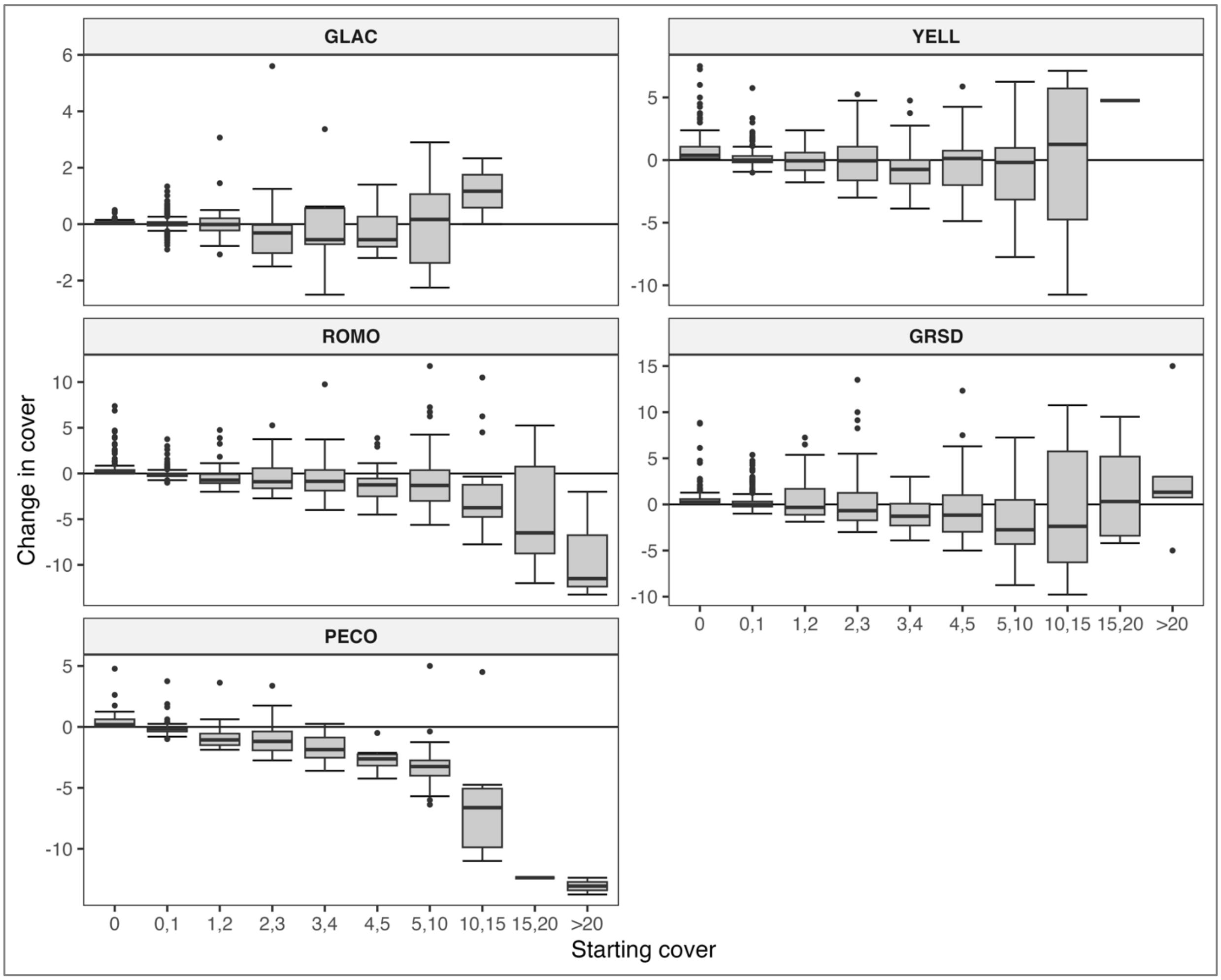

Figure 5. The change in species cover with starting cover is shown separately for each park. Cover change is the simple difference between ending and starting cover on a slope-aspect. X axis labels indicate the range of starting values included in each boxplot; note the non-linear scaling of these bins. GLAC is the only park for which there is not a significant decline in cover change with increasing starting cover. NPS

Together these results suggest that climate change is already having substantial impacts on community dynamics across study sites. The weaker turnover pattern at GLAC may be because this park has experienced less directional climate change effects than have the other parks over their study periods (Figure 2) or may result from the more consistent and conservative approach to assessing abundance changes used by GLAC research team. It could also be due to the low nitrogen deposition in this region (although the similarly low deposition at YELL doesn't correspond to low turnover).

Changes in species abundances

Climate drivers of changing abundance

The model selection process (described in Appendix A) revealed which independent variables were retained in the best-supported models, or in other words which variables were best able to predict changes in species abundances. The climate variables retained in the best-supported model using explicit climate variables were: the annual minimum growing degree day value across each transition (henceforth simply termed gdd), the annual minimum value of growing season precipitation (henceforth gs.ppt), the annual minimum value of water year precipitation (henceforth wy.ppt), and the maximum value of mean growing season temperatures across each transition (henceforth gs.tmean). These were used in all subsequent modeling of species abundance.

Before presenting patterns in how these climate predictors influenced changes in species abundance, it is worth summarizing how they correlate with one another as well as with park and summit latitudes. As shown in Figure 6, gdd and gs.tmean are moderately positively correlated (0.246), as are wy.ppt and gs.ppt (0.538), while gdd and wy.ppt are negatively correlated (-0.417). wy.ppt has the strongest, and most positive, relationship with summit latitude (0.729), while other climate variables, including gs.tmean, do not show simple latitudinal gradients (Figure 6). Similar to these results, climPC1, which is associated with water year precipitation and water availability, is strongly positively correlated (0.694) with latitude, but climPC2, which represents growing season temperature, precipitation, and length, does not show a clear latitudinal trend (Figure 7).

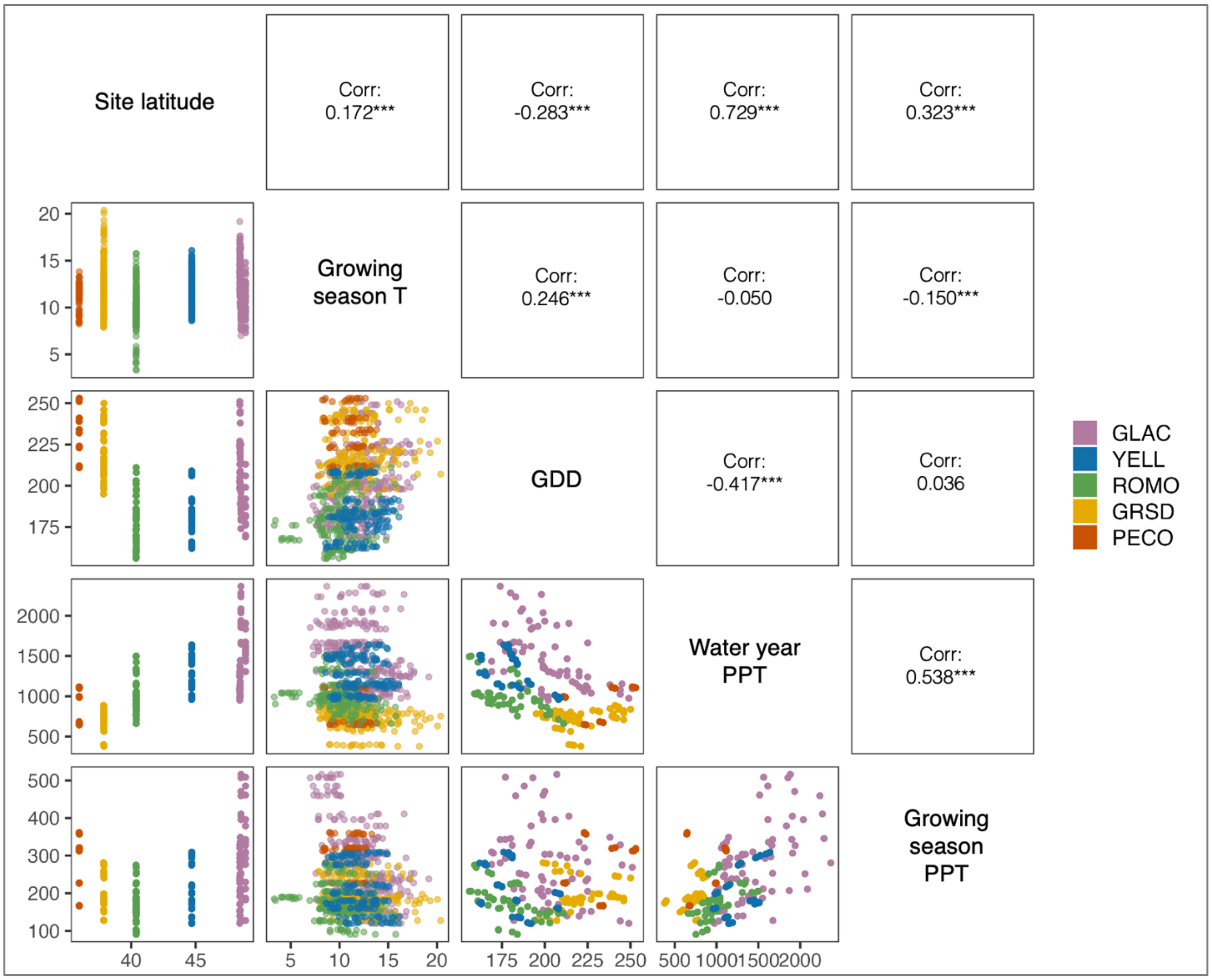

Figure 6. Relationship of climate variables to latitude and park. Bivariate scatterplots (lower left panels) are color-coded by park, and overall Pearson correlations are shown (upper right panels). Each data point corresponds to annual data at a given peak-aspect. In scatterplots (lower left) x- and y-axis ranges correspond to the range of values observed for each variable. Units for each variable are described in Methods, Table 5. For correlations, *** Designates p-values <0.001. Growing Degree Days (GDD, the number of days with air temperatures above freezing during the growing season) and Growing Season Temperature mean are moderately positively correlated, as are Water Year PPT and Growing Season PPT, while GDD and Water Year PPT are negatively correlated. Water Year PPT has the strongest, and most positive, relationship with summit latitude. NPS

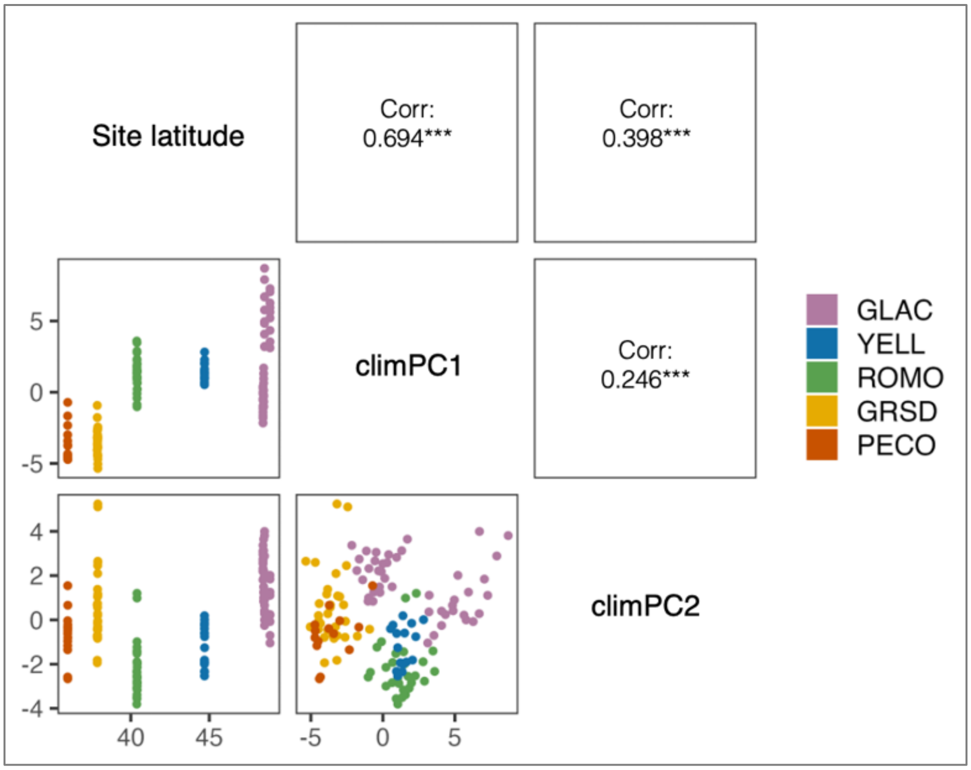

Figure 7. The relationship of climate PC1 and PC2 to latitude and park. See *Support for turnover in species abundances* section below for further explanation of data presentation. For correlations, *** designates p-value < 0.001. ClimPC1, which is associated with water year precipitation and water availability, is strongly positively correlated with latitude, but climPC2, which represents growing season temperature, precipitation, and length, does not show a clear latitudinal trend. NPS

Variables selected in the best-supported models

Our model fitting framework identified the best-supported model structures that either included climate PC axes 1 and 2 (climPC1 and climPC2), or explicit climate variables. We first summarize results from the climate PCA model, then turn to the more complex models using explicit climate variables.

Overall model fit was good for the best-supported models that used aggregated climate PCA variables (henceforth, climPC models). The model with the lowest AICc had marginal and conditional R^2 values of 0.661 and 0.710, respectively. This model included starting cover and three species-specific predictors (habit, perennating mode, and mean species latitudinal range (latmean1090 and its square, latmean1090^2)), as well as both PC climate variables and summit latitude (Figures 8 and 9). Multiple interactions were also included, as were random intercepts for transition and species, and random slopes for both climPC variables, indicating that the effect of climPC variables differed substantially among species (Appendix C: Table 14). While several alternative models had low delta-AICc values (Appendix C: Table 11), all had quite similar predictive variables as the top model.

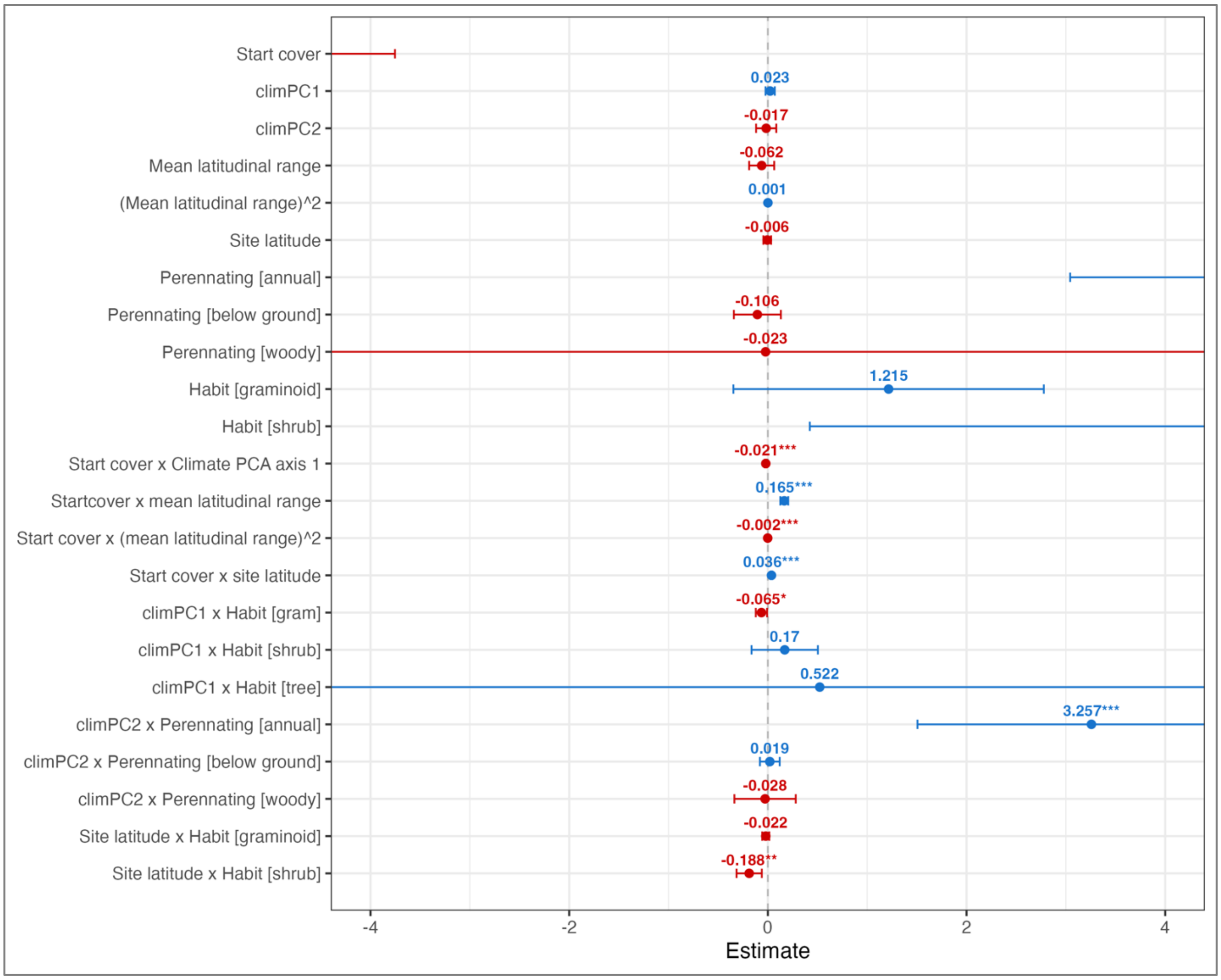

Figure 8. Coefficients for fixed effects in the best-supported climPC model. For each coefficient, the mean and 95% confidence limits (CLs) are shown. Coefficients with positive mean estimates are shown in blue, while those with negative mean estimates are in red. Note that the scale of the figure cuts off some means and CLs, but this scale is needed to see most of the best constrained values. See Table 14 (Appendix C) for values. All coefficients with 95% CLs not overlapping zero can be individually considered as statistically significant. These include start cover, perennating (annual), and habit (shrub), as well as the following interactions: start cover × climPC1, start cover × mean latitudinal range., start cover × mean latitudinal range^2, start cover × summit latitude, and climPC2 × perennating (annual). However, all displayed coefficients are in the best supported predictive model, indicating support for their effects even if they have CLs overlapping zero. NPS

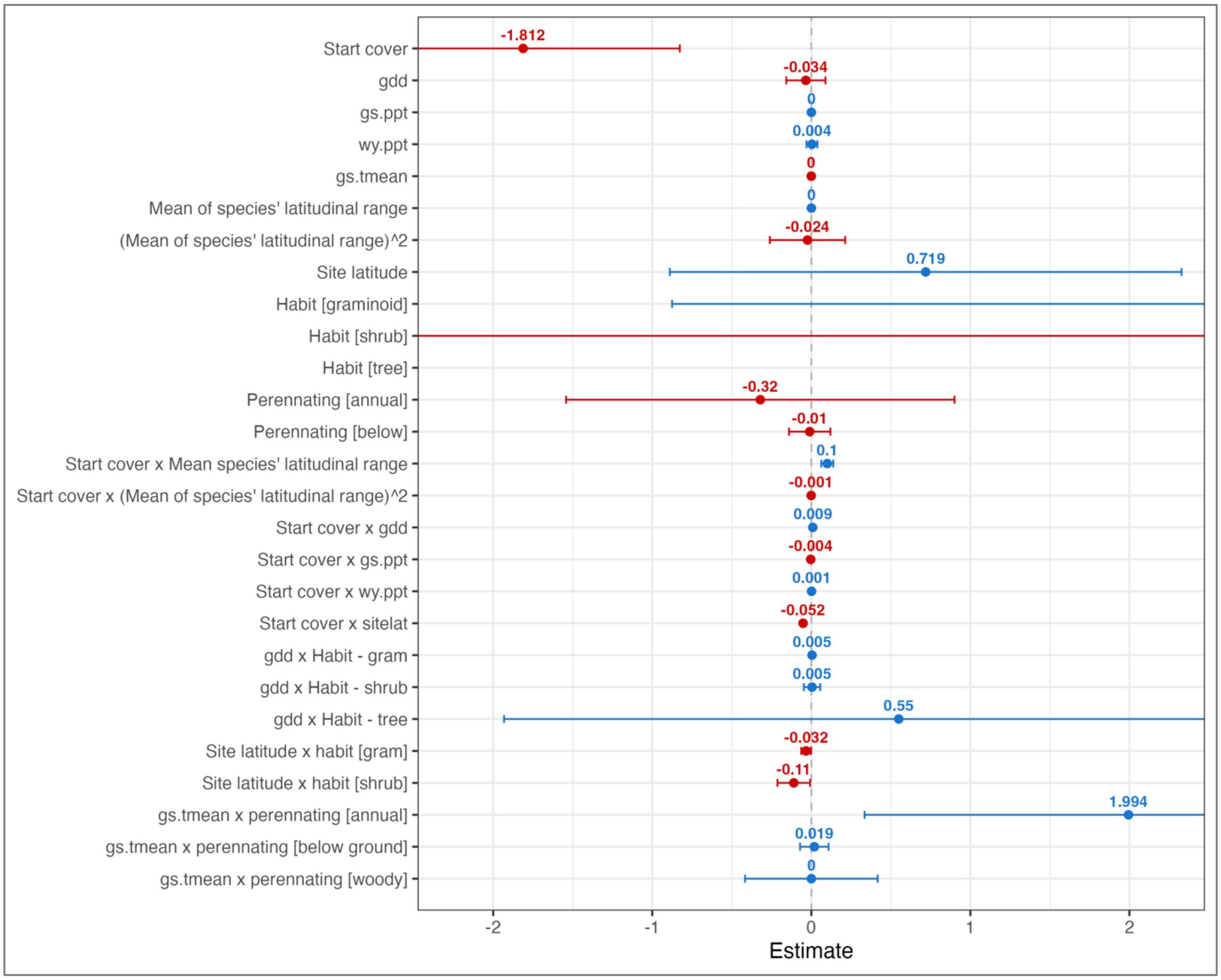

Figure 9. Coefficients for fixed effects in the best supported climate variables models. For each coefficient, the mean and 95% confidence limits (CLs) are shown. Coefficients with positive mean estimates are shown in blue, while those with negative mean estimates are in red. Note that the scale of the figure cuts off some means and CLs, but this scale is needed to see most of the best constrained values. See Table 14 (Appendix C) for all values. All coefficients with 95% CLs not overlapping zero can be considered as individually statistically significant. These include: start cover and perennating (annual), as well as the following interactions: start cover × mean spp. lat., start cover × mean spp. lat.^{2}, and start cover × summit latitude. However, all displayed coefficients are in the best supported predictive model, indicating support for their effects even if they have CLs overlapping zero. NPS

The best-supported model with explicit climate variables (henceforth, climVar models) included the same species and summit variables seen in the climPC model. It also includes main effects and some interactions of the four climate variables discussed above (gs.tmean, wy.ppt, gs.ppt, and gdd; Figure 9). The best model also included random intercepts for transition and species, as well as random slopes for all four climate variables, indicating that the effects of climate differed meaningfully among species (Appendix C: Table 14). Using explicit climate variables resulted in a modest increase in explanatory power over the climPC models, with marginal and conditional R^2 of 0.707 and 0.750, respectively. As with the climPC models, highly supported alternative models were very similar in structure (Appendix C: Table 12).

The complexity of the best-supported models, and in particular the support for multiple interactions, makes a simple description of all the supported effects difficult. Nonetheless, several effects stand out from an examination of the model coefficients. We summarize some of the clearest and most important predictions below.

Support for turnover in species abundances

The climPC and climVar models both predict that increases in cover (the difference between starting and ending cover) will be largest for species with lower starting cover, and that change in cover will be negative, on average, for species with the highest starting cover (Figure 10). This result supports what was found using the far simpler community turnover models (Figure 4): species with low starting abundance tended to increase while initially more abundant species decreased, again suggesting that this is a robust finding.

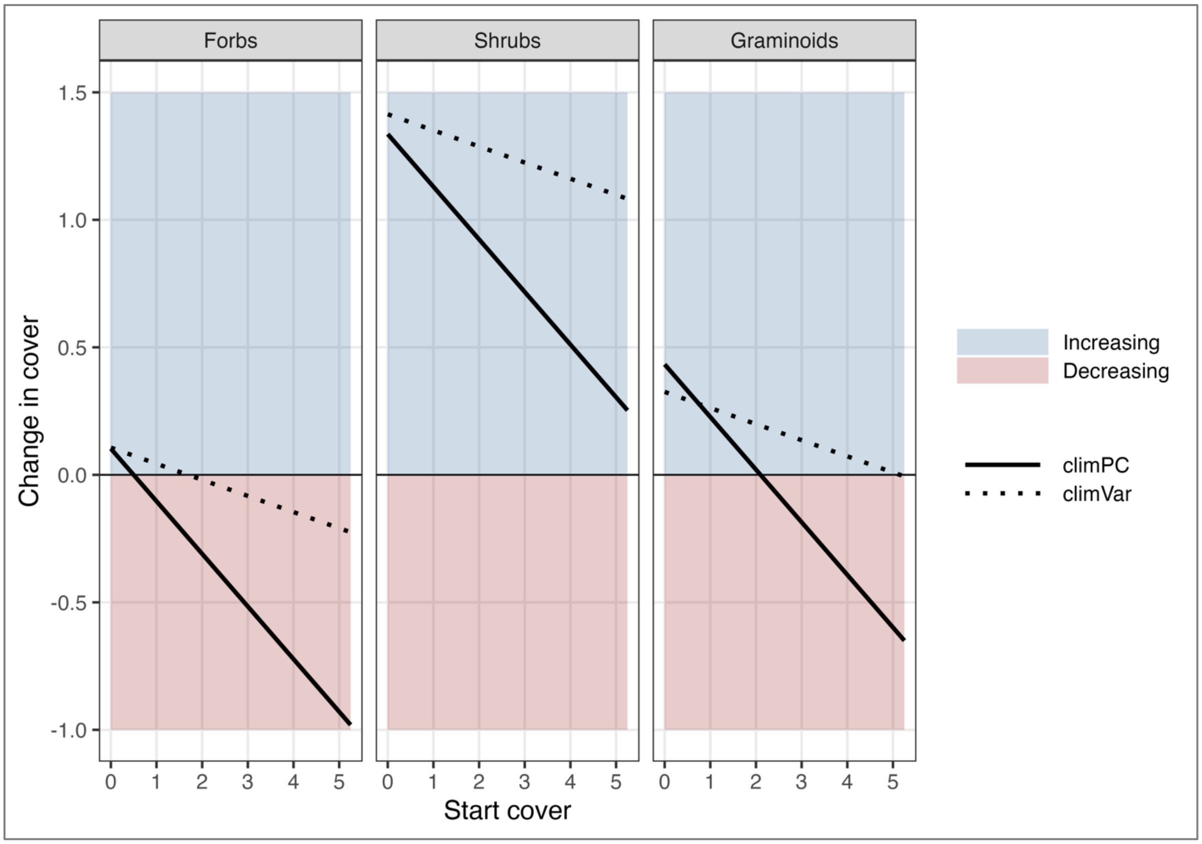

Figure 10. Mean predicted changes in total percent cover of below-ground perennating forbs, shrubs and graminoids as a function of total percent starting cover values ranging from 0% to 5%. Portions of the prediction lines above the y-axis zero value (blue background) indicated predicted increases in cover, and portions of the line below the y-axis zero value indicated predicted decreases in cover. All predictions are made using median values of climate variables, mean spp. latitudinal range., and summit latitude. Forbs are predicted to decrease in both models except in instances where the starting cover is <1–2%; shrubs are predicted to increase in cover regardless of their starting cover in both models; and graminoids are predicted to increase in the climVar model and decrease when the starting cover is >2% in the climPC model. In all cases, relative increases in cover are largest for species with lower starting cover. NPS

Effects of species traits on changing abundance

The pattern of less common species becoming more abundant, and vice versa for common species, is mediated by other variables, including species traits and summit latitude. Since the great majority of plant taxa in the GLORIA study plots are forbs, with either above- or below-ground perennation, to illustrate these patterns, we plot change in cover for these groups as a function of starting cover and latitude (Figure 11). Model predictions show that both increases in rarer species and declines of abundant species will be most pronounced at southerly parks, and these patterns apply to forbs with both above- and below-ground perennation. At northerly sites there is not a strong signature of species turnover, with all species predicted to increase. It is possible that this pattern of greater turnover in the south is at least partially attributable to higher nitrogen deposition in the southernly regions, although it is not clear why this would directly lead to the pattern of higher increases in low abundance species that we see, rather than unstructured changes in composition. It is also possible that in the southerly regions lower elevation species that are adapted to greater drought stress are disproportionately increasing at the GLORIA sites as climate change shifts high elevation sites into climate regimes with greater water stress.

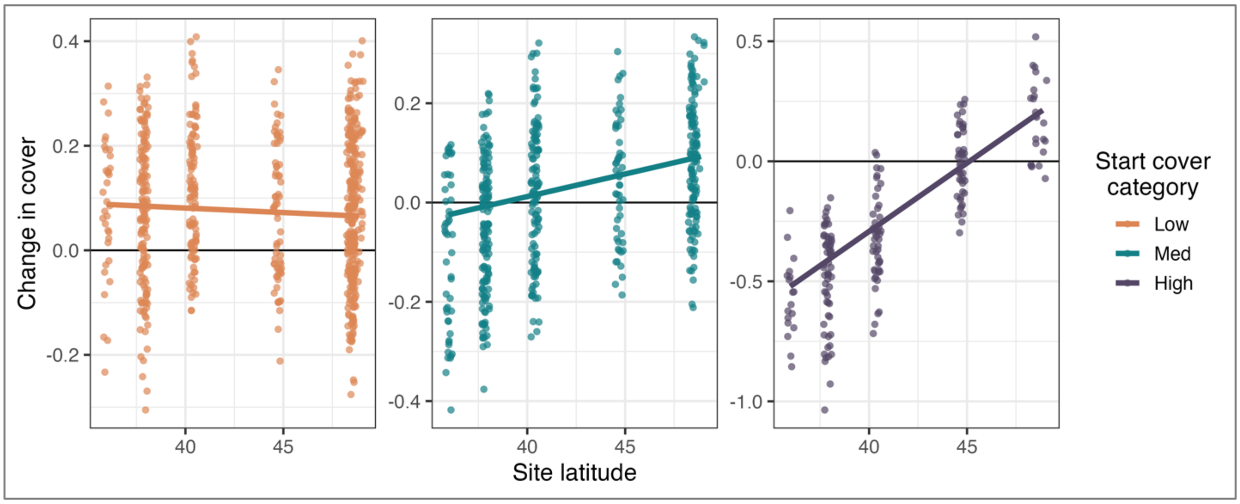

Figure 11. Predicted difference between ending and starting cover across summit latitudes, for above- and below-ground perennating forbs and stratified by starting cover. Note the different scaling for the y-axis of each plot. Predictions are generated using median values of all other predictors and are from the climPC model. Low, Medium, and High starting cover values were set to 0.125%, 0.425%, 1.75%, reflecting the 25%, 50%, and 80% quantiles of % cover values for forbs, excluding 0-values. Each point indicates change for an individual species on a particular summit aspect over one transition. Model predictions show that both increases in rarer forbs and declines of abundant forbs will be most pronounced at southerly parks. NPS

Interactions of starting cover and latitude

The mean latitude of a species geographical range also interacts with starting cover to influence change in abundance (Figure 12). The best climPC model predicts that low to medium abundance species with mean latitude ranges between 50–60 degrees (near the US-Canada border to approx. Anchorage, AK), would be roughly stable in cover, while the few species in our sample with even more northerly range centers would decline. These patterns apply to all but the most abundant species, for which there is a prediction that species with both northerly and southerly distributions may do poorly. However, there are few of these abundant species and this pattern may be an artifact of the quadratic functional form used for latitude. While these patterns are not simple, their overall message is that species with more southerly range centers show stronger turnover in abundances, with strong increases of rarer species and strong declines of abundant ones. Species with a more northerly mean range show less pattern in their population trends, and in particular lower effects of abundance in driving different population trends.

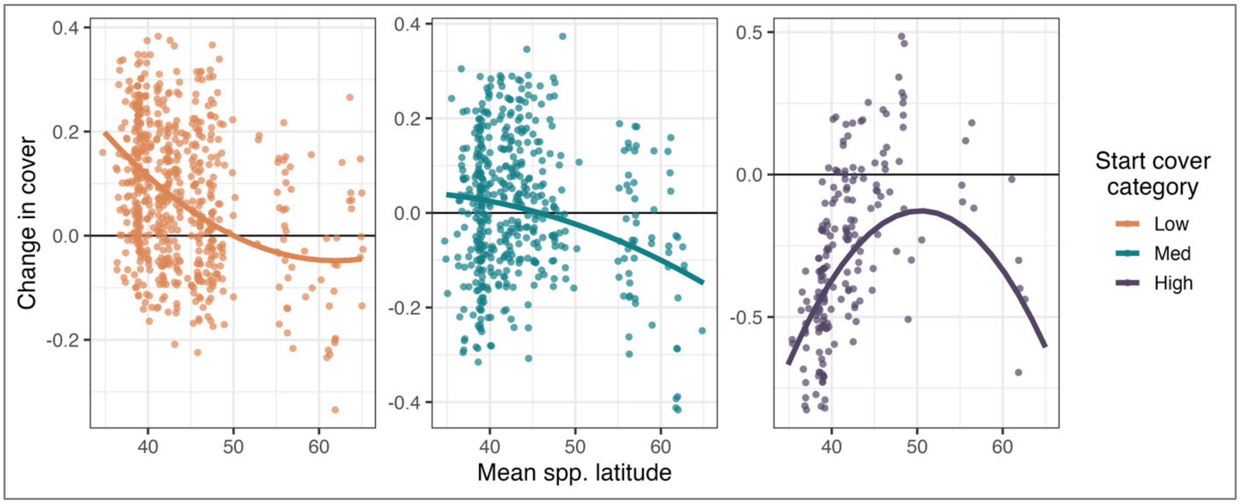

Figure 12. Predicted difference between ending and starting cover for above and below ground forbs for species with different mean range latitudes, stratified by starting cover. Note the different scaling for the y-axis of each plot. Predictions are generated using median values of all other predictors, are from the climPC model, and use low, medium, and high starting cover values of 0.125%, 0.425%, 1.75%, reflecting the 25%, 50%, and 80% quantiles of % cover values for forbs. Species with a more southerly mean range (~40–50 degrees latitude) show stronger turnover in abundances, with strong increases of rarer species and strong declines in initially abundant ones. Low to medium abundance species with mean latitude ranges between 50–60 degrees are predicted to be roughly stable in cover, while those with more northerly ranges would decline. NPS

Influences of climate on changing abundance

Both climPC and climate variable models also support climate effects on changing abundance, often with strong interactive effects of starting cover. The best-supported climPC model predicts strong effects of climPC1 (the principal component largely driven by variables for water availability and stress), with low and medium abundance plants increasing with higher climPC1 values, and more moderate effects on plants with high starting values (Figure 13). Remembering that climPC1 is positively correlated with latitude (Figure 6), there are two effects driving larger increases in cover of most species at more northerly sites: climate effects and a latitude effect independent of climate.

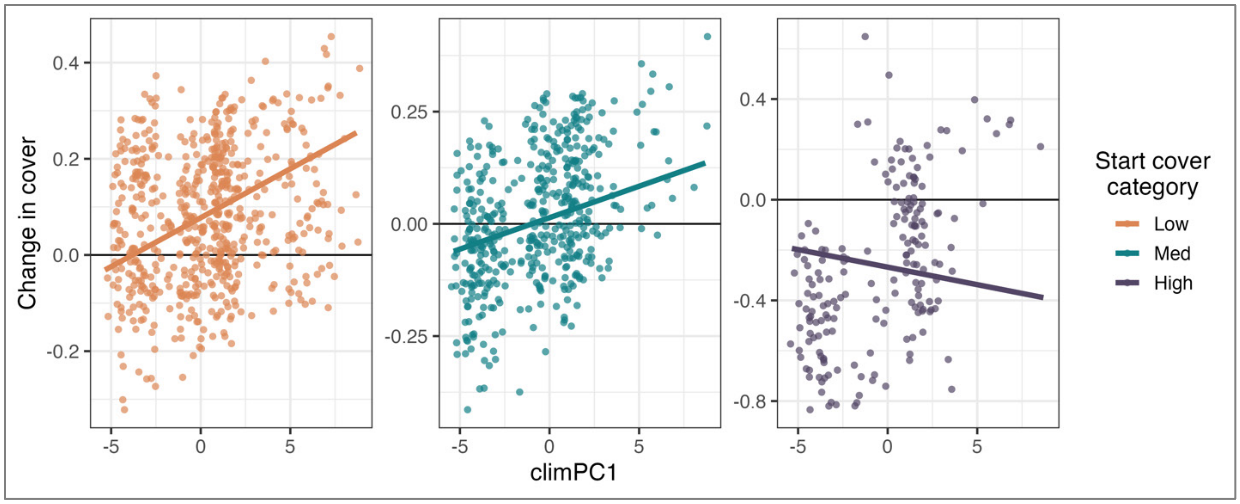

Figure 13. Predicted difference between ending and starting cover across climPC1 values, for above and below ground forbs and stratified by starting cover. Note the different scaling for the y-axis of each plot. Predictions are generated using median values of all other predictors and are from the climPC model. Low, Medium, and High starting cover values were set to 0.125%, 0.425%, 1.75%, reflecting the 25%, 50%, and 80% quantiles of % cover values. Recalling that PC1 values are positively correlated with total water year precipitation, low and medium abundance plants increase with higher climPC1 values, with more moderate effects on plants with high starting values. NPS

Similarly, in the climVar model, there are substantial effects of three of the climate variables on changing cover, with some substantial interactions with start cover. Increased water year precipitation (wy.ppt) is predicted to positively influence cover change regardless of starting cover (Figure 14). In contrast, higher growing season precipitation (gs.ppt) is predicted to have generally negative effects on cover changes, but with little effect on low abundance species and stronger effects for more abundant species (Figure 14). Finally, more growing degree days (gdd) are predicted to positively influence cover change across starting abundances, although again with far stronger effects on more abundant species (Figure 14).

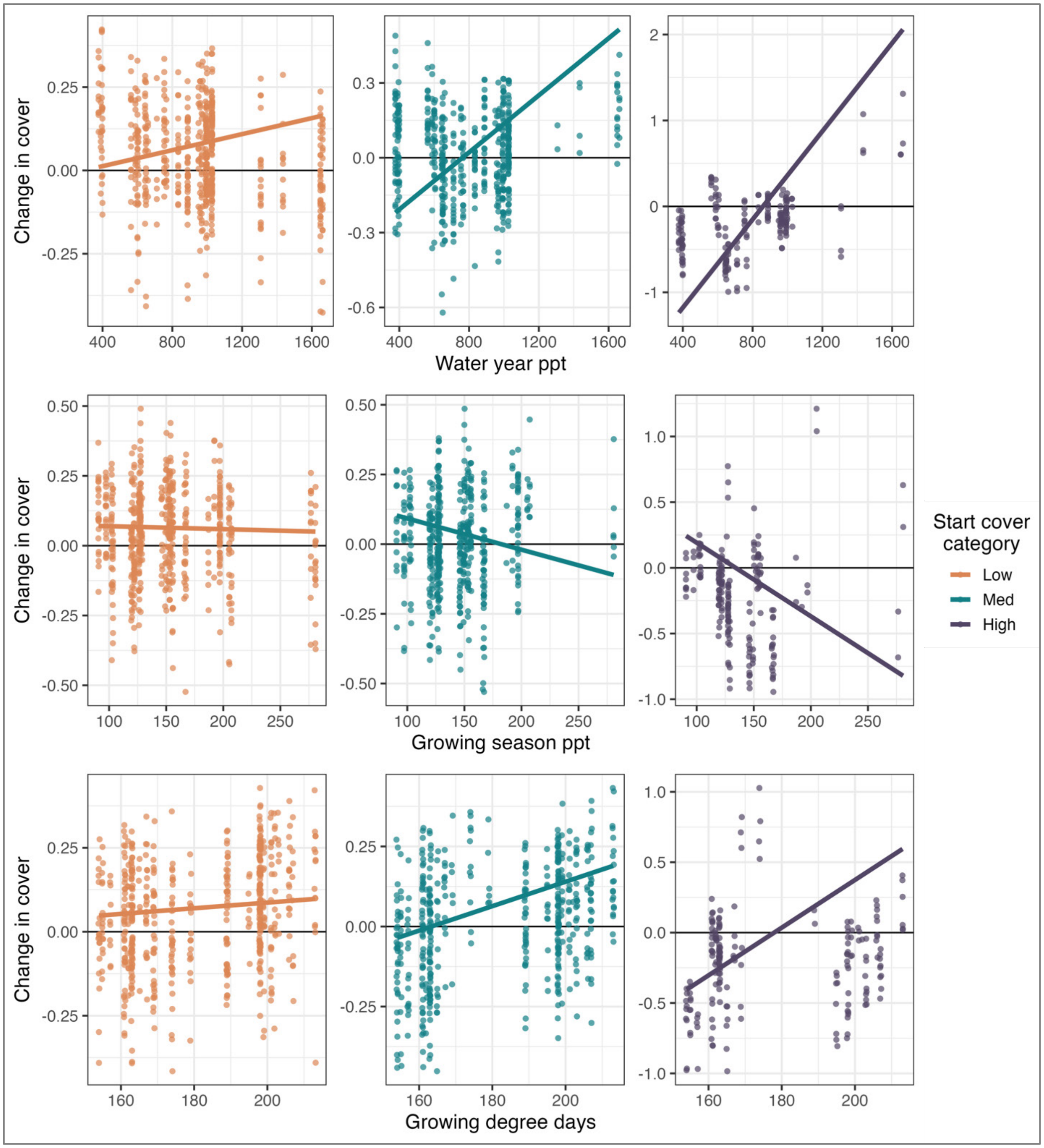

Figure 14. Predicted difference between ending and starting cover across climate variables, for above and below ground forbs and stratified by starting cover. Note the different scaling for the y-axis of each plot. Predictions are generated using median values of all other predictors and are from the climVar model. Low, Medium, and High starting cover values were set to 0.125%, 0.425%, 1.75%. Effects of water year precipitation (wy.ppt), growing season precipitation (gs.ppt), and growing degree days (gdd) are shown in these panels. Species with all starting abundances are predicted to benefit from increasing water year precipitation and growing degree days but are predicted to be negatively influenced by increasing growing season precipitation, especially for more abundant species. All three climate variables have quite modest influence on rarer species and more pronounced effects on more abundant ones. NPS

<u>Shrubs and graminoids generally increase, unlike other groups</u>

Both shrubs and graminoids increased more than did other plant groups (Figure 10), although for both groups, these effects are predicted to vary across latitudes (Figure 15). For graminoids, lower abundance species are predicted to increase most in parks at lower latitudes and higher abundance species are predicted to increase more at high latitudes. However, unlike for forbs, for almost all taxa and sites, graminoids increased in cover (Figure 15). Shrubs have far less data but show similar patterns to those seen for graminoids (Figure 15). These patterns may partly be accounted for by high nitrogen deposition at southerly regions, although past studies of nitrogen effects show mixed responses from graminoids (Bowman et al. 2012) and all three southern regions have very similar nitrogen deposition rates, but differ in graminoid and shrub increases.

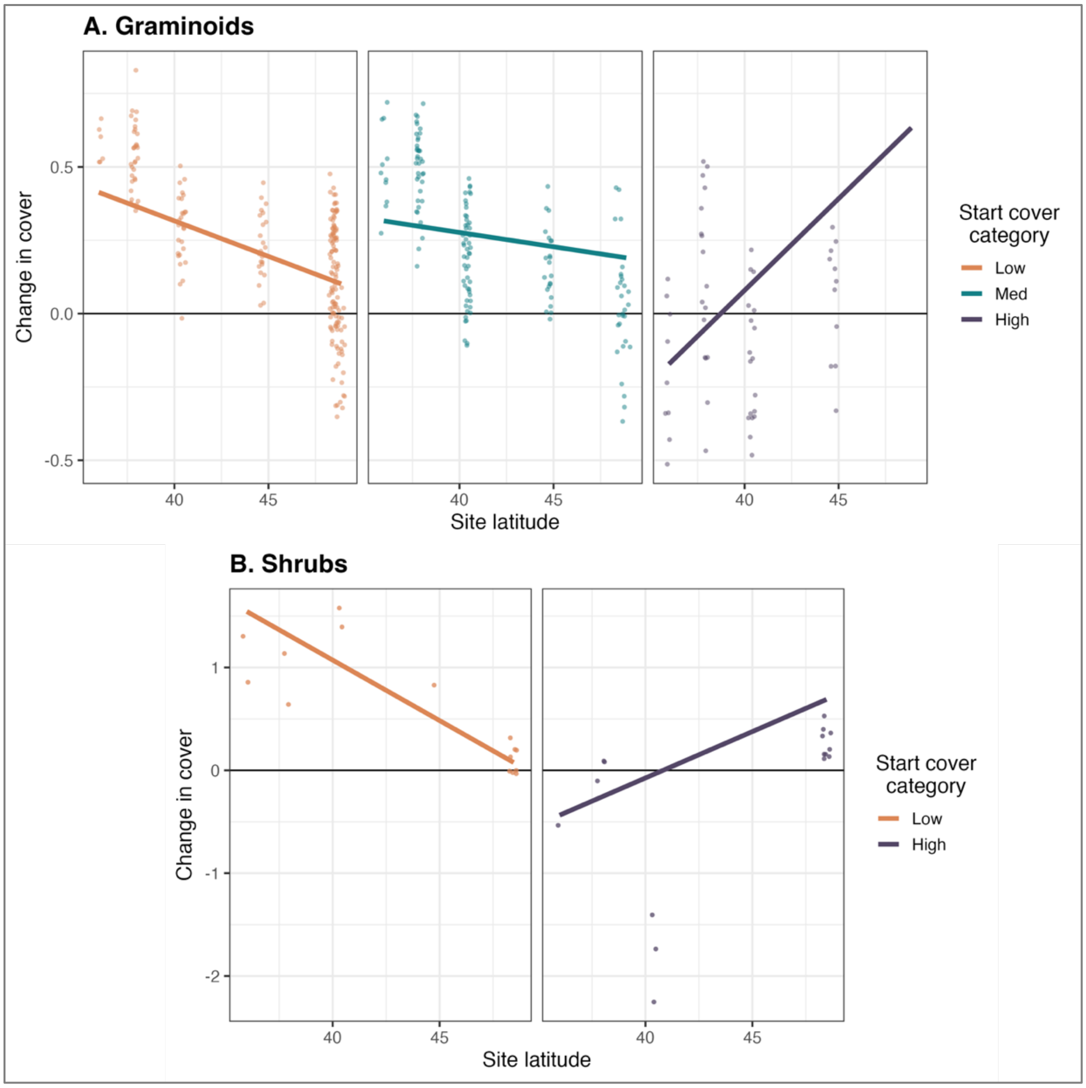

Figure 15. Predicted changes in cover of graminoids and shrubs, as functions of starting cover and latitude, stratified by starting cover. Due to the limited occurrences of shrubs, we show only two starting cover categories, low and high, which have average start cover values of 2.1% and 5.4%. Graminoids and shrubs increased cover in almost all cases, though to varying degrees across latitudes. NPS

Species specific effects

Beyond these fixed effects, our models included random species effects, with both random intercepts and random climate variable slopes. A total of 32 species had at least one significant random mode (estimated random effect for that species), as indicated by 95% confidence intervals that did not overlap zero, for either the best climPC or best climVar model (Appendix C: Table 10). "Significance" in a random intercept model implies that a given species' predicted change in cover is estimated to be notably different (higher or lower) than the models' average predicted change in cover. There are 11 significant random intercept modes for the climPC model and three for the climVar model. More interesting are the large number of significant modes for random climate variable slopes (Appendix C: Table 10). Significant random slopes indicate greater or lesser responsiveness to changes in a climate effect, depending on the sign of the overall slope, and relative to model averages. If the mean intercept or slope of all species is positive, a negative random slope means lower than average effect, while a positive random effect means a greater than average effect. The opposite is true if the mean intercept or slope is negative. The results suggest that several taxa are more responsive to gs.tmean (growing season mean temperature) and gdd than are species on average, while there are several taxa less responsive to wy.ppt (water year precipitation) than the average. However, we do not see good general correspondence between the two models. For example, species with positive modes (value for a random effect) for climPC1 generally do not show positive modes for wy.ppt, which loads positively onto this PC axis (Figure 3). Similarly, modes for gs.tmean (which loads positively on PC2) and gdd (which loads negatively on PC2) do not show effects consistent with those for PC2 itself.

One reason for these inconsistencies may be that taxa-specific random slope modes generally have negative correlations with intercept modes, especially for the climPC model (Appendix C). While this is not unusual for random effects, it means that, for example, a lower positive slope between cover and a climate variable is often compensated for by a higher intercept. To better show predicted performance of species with significant random effects for intercepts or slopes, we have plotted their predicted change in cover when starting from low abundance for forbs and graminoids (Figures 16–18). While there are too many of these relationships to fully summarize, we illustrate their interpretation with one example:

- Predictions from the climPC model show *Paronychia pulvinata* (Rocky Mountain nailwort) performing best at the lowest values of both climPC1 and climPC2 (Figure 16). For this high elevation fellfield cushion plant, this makes sense, suggesting that compared to most species, it performs better in cold and exposed conditions. We see comparable effects on *P. pulvinata* with gs.tmean, with better performance with lower gs.tmean. However, the species also performs better with higher gdd. This seeming contradiction is probably due to this fellfield plant preferring long snowfree periods but cool growing seasons, reflected in high gdd in spite of low gs.tmean (Figure 16).

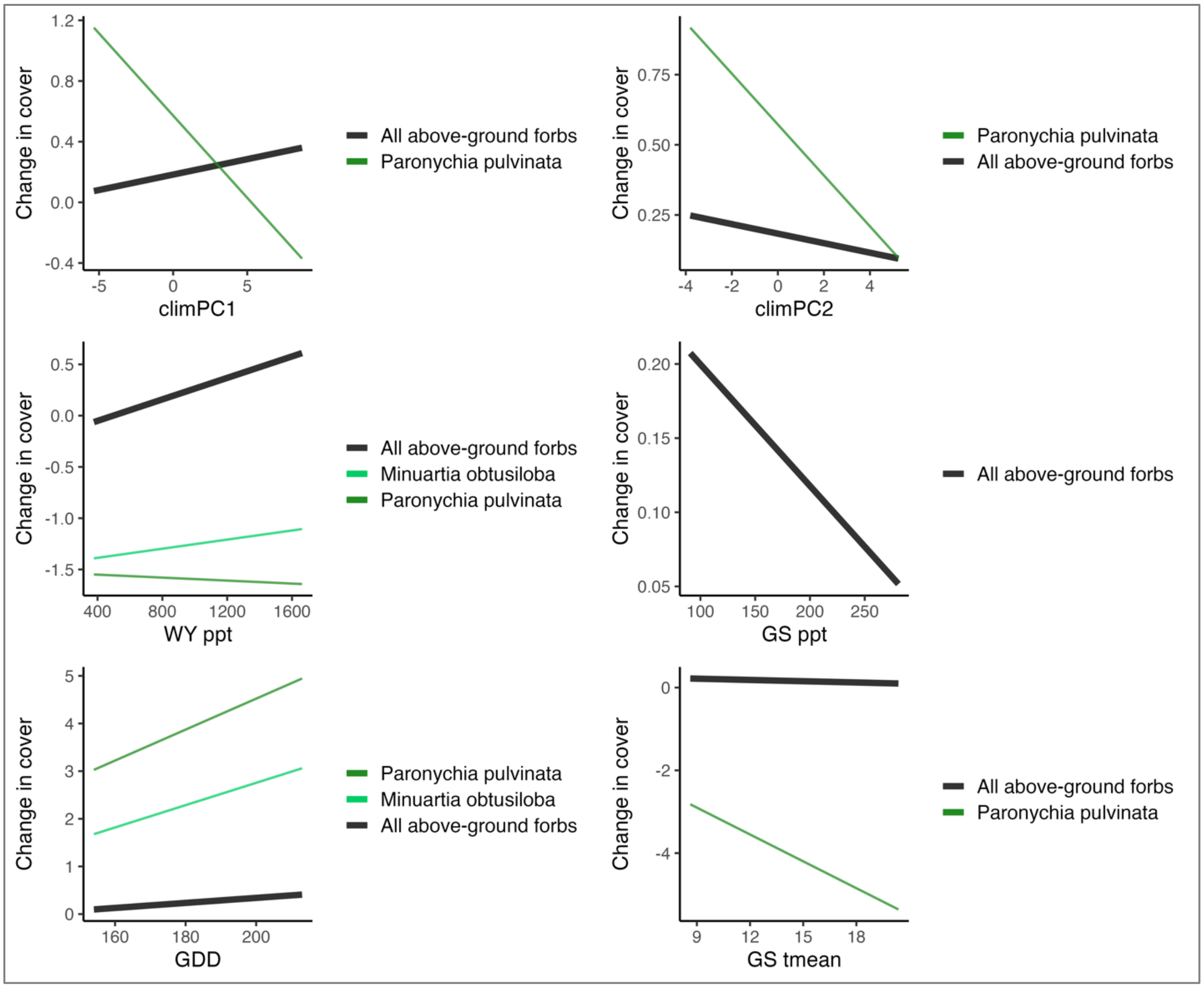

Figure 16. Estimated responses to climate variables (see Figure 3 for PC1 and PC2 descriptions) for above-ground perennating forb species with significant conditional modes. All predictions are made using low starting cover (0.125%), the range of observed values for the climate variable on the x-axis, and median values for all other predictors. To best indicate which line corresponds to each species, the list of species in each panel's legend are shown in order of the predicted changes in cover (slope of species lines) on the far right of each panel, from most positive to most negative. The mean response of all above-ground forbs is shown with a thick black line. Predictions from the climPC model show *Paronychia pulvinate* performing best at the lowest values of both climPC1 and climPC2, and showing strong effects of both gdd and gs.tmean. This result suggests compared to most species, it performs better in cold and exposed conditions with long growing seasons. NPS

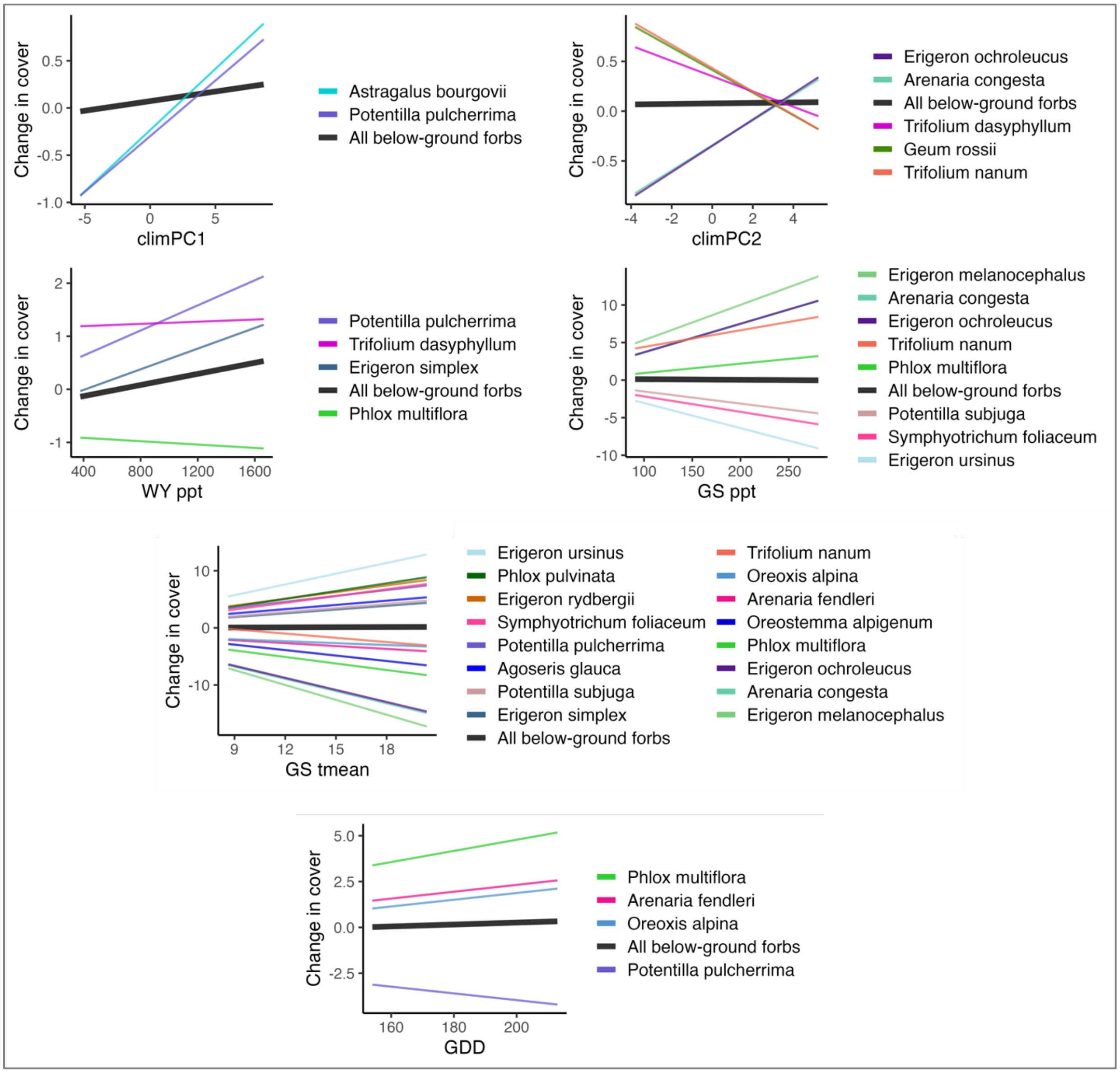

Figure 17. Estimated responses to climate variables for below-ground forb species with significant conditional modes. All predictions are made using low starting cover (0.125%), the range of observed values for the climate variable on the x-axis, and median values for all other predictors. To best indicate which line corresponds to each species, the list of species in each panel's legend are shown in order of the predicted changes in cover (slope of species lines) on the far right of each panel, from most positive to most negative. The mean response of all below-ground forbs is shown with a thick black line. Though below-ground perennating forbs show little mean response to many climate variables, the random effects of different individual species suggest that some are strongly influenced by them. For example, change in abundance of *Erigeron ursinus* is predicted to be positively associated with growing season mean temperature and negatively associated with growing season precipitation, while *Erigeron melanocephalus* shows the opposite pattern. NPS

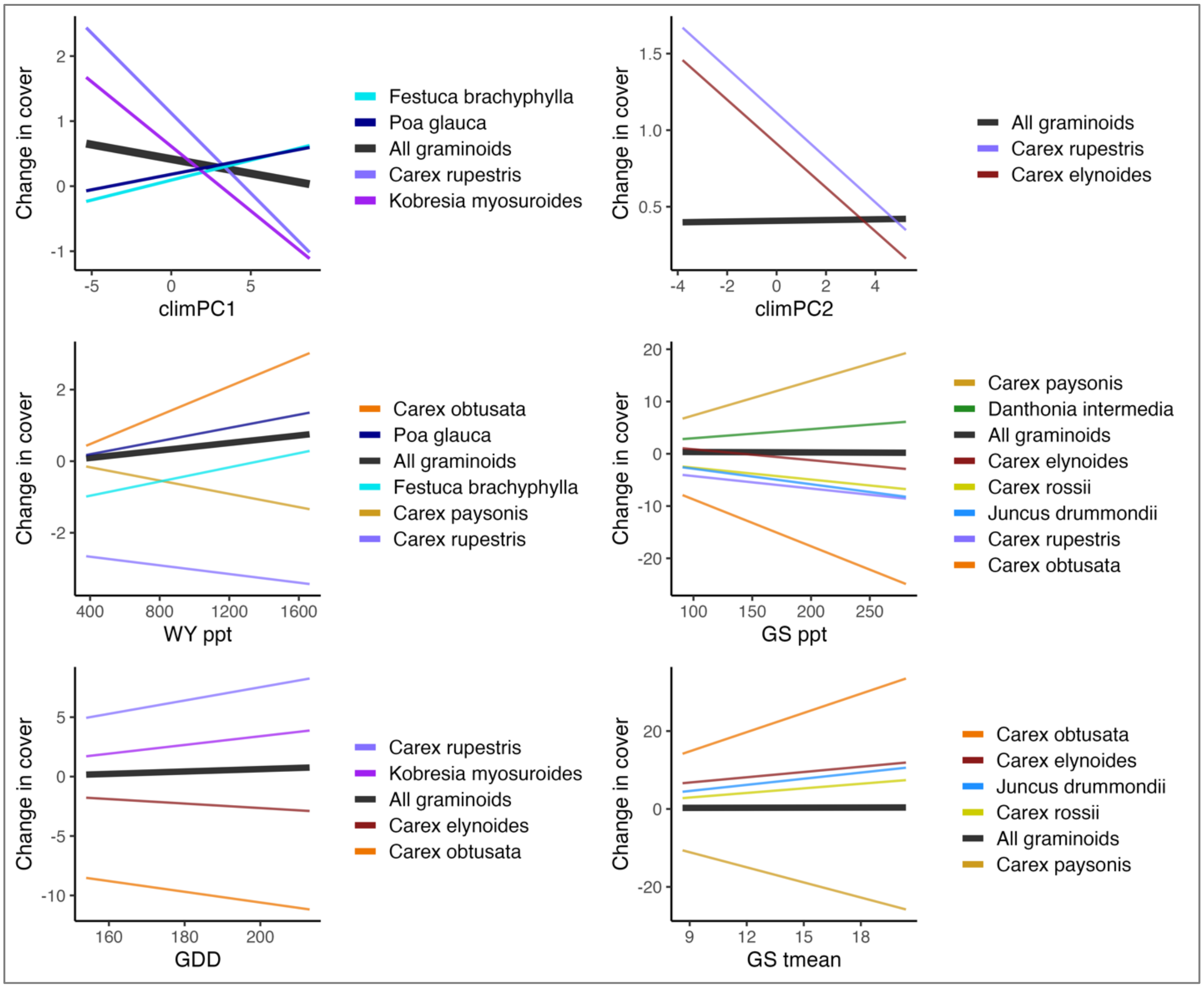

Figure 18. Estimated responses to climate variables for graminoid species with significant conditional modes. All predictions are made using low starting cover (0.125%), the range of observed values for the climate variable on the x-axis, and median values for all other predictors. To best indicate which line corresponds to each species, the list of species in each panel's legend are shown in order of the predicted changes in cover (slope of species lines) on the far right of each panel, from most positive to most negative. The mean response of all graminoids is shown with a thick black line. Though graminoids show little mean response to many climate variables, the random effects of different individual species suggest that some are strongly influenced by them. For example, change in abundance of *Carex obtusata* is predicted to be positively associated with water year precipitation and growing season mean temperature. NPS

Below-ground perennating forbs show little mean response to growing season mean temperature (gs.tmean), but the random effects of different individual species suggest that some are strongly positively, and some strongly negatively, influenced by temperature (Figure 17). The same is also true for graminoids, with graminoids overall showing little mean response to many climate variables, but random effects of individual species are influenced by climate (Figure 18).

It is likely that many other species also have divergent responses to environmental drivers, but limited data on most species means that the power to detect these effects is low for all but the most abundant and widely distributed species.

Changes in total plant cover

Across time, there were substantial changes in total plant cover at the GLORIA sites, with different patterns in each park (Figure 19). The two more northerly parks showed stable total cover, while the other three parks had larger shifts. In ROMO, cover declined sharply from 2010 to 2014 but then was stable. In PECO, with only two surveys, cover estimates declined sharply from 2016 to 2021. And at GRSD the middle survey of the three found substantially higher cover. We analyzed models to look for effects of climate and other factors in explaining these changes, but in the section *Observer effects on estimates of changing abundance*, below, also discuss the possibility of observer effects being the primary driver of these large changes.

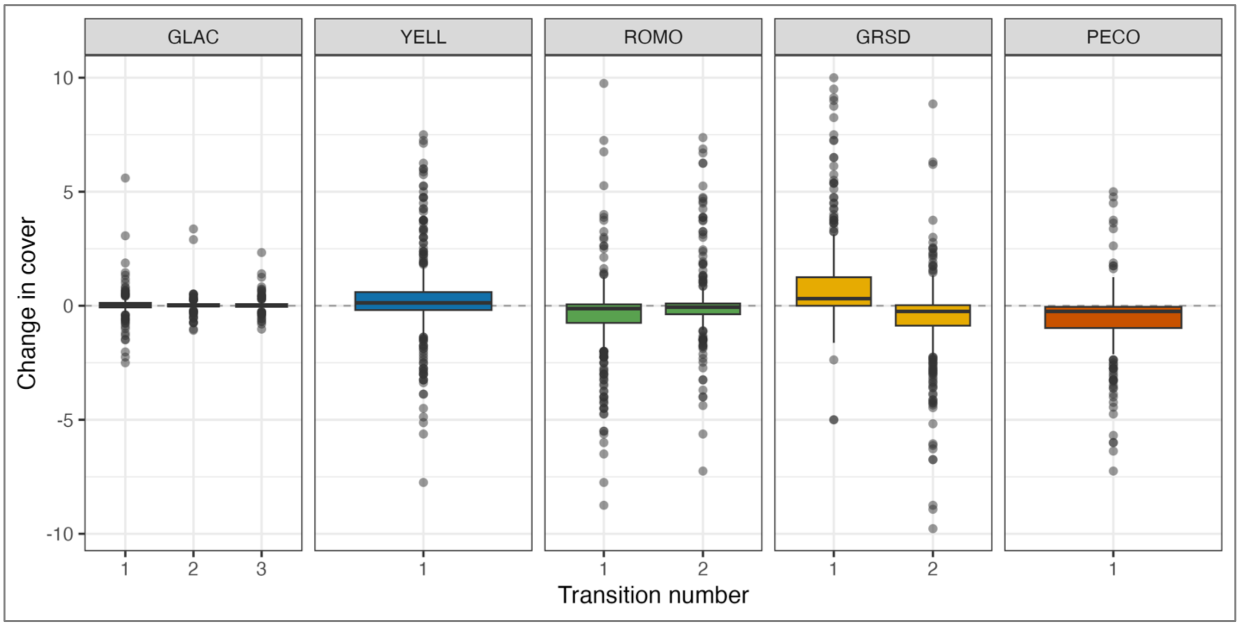

Figure 19. Distribution of change in species' abundance, measured as percent cover, across each transition in each park. While most parks and transitions show boxplots centered very close to 0, at GRSD there is a more unusual pattern of increase of most species over the first transition, followed by declines over the second transition. NPS

Models for total plant cover show similar patterns of climate and latitude effects as do those focused on individual plant species, although there are also some differences (Figure 20; Appendix C: Table 15). The best climPC model for total cover shows a negative effect of climPC1 and, like that for species abundance models, negative climPC2 effects. The interaction of climPC1 and start cover is also positive in the total cover model, while it is negative in the species model. Site latitude also differs, with positive effects in the species model and negative effects on total cover. However, the interaction of starting cover and summit latitude is positive in both models. Park was also retained as a fixed effect in the vascular plant cover model, although none of the individual park coefficients were significantly different from zero. The other coefficients in this model also all have very small coefficients and most have confidence limits overlapping zero, suggesting low ability to explain shifts in plant cover.

Results from the top climate variable models for species and total cover are generally well-aligned (Figure 21; Appendix C: Table 15). For total cover, growing season precipitation had positive, while water year precipitation had negative, effects in both models. The interactions of these variables with start cover were also the same. The best total cover model retained snow cover days and did not include growing degree days, unlike the species model. However, these two variables are strongly and negatively correlated (Figure 3), indicating that the two models include very similar effects. The climate variable model for total cover also retained park as a fixed effect, with YELL, GRSD, and ROMO having significant and positive coefficients, indicating substantial differences from GLAC, the reference level of the park variable. Overall, the climVar model results indicate that in spite of differences between species in climatic effects, species-level effects of climate on abundance changes are consistent enough to sum into similar patterns at the entire community level.

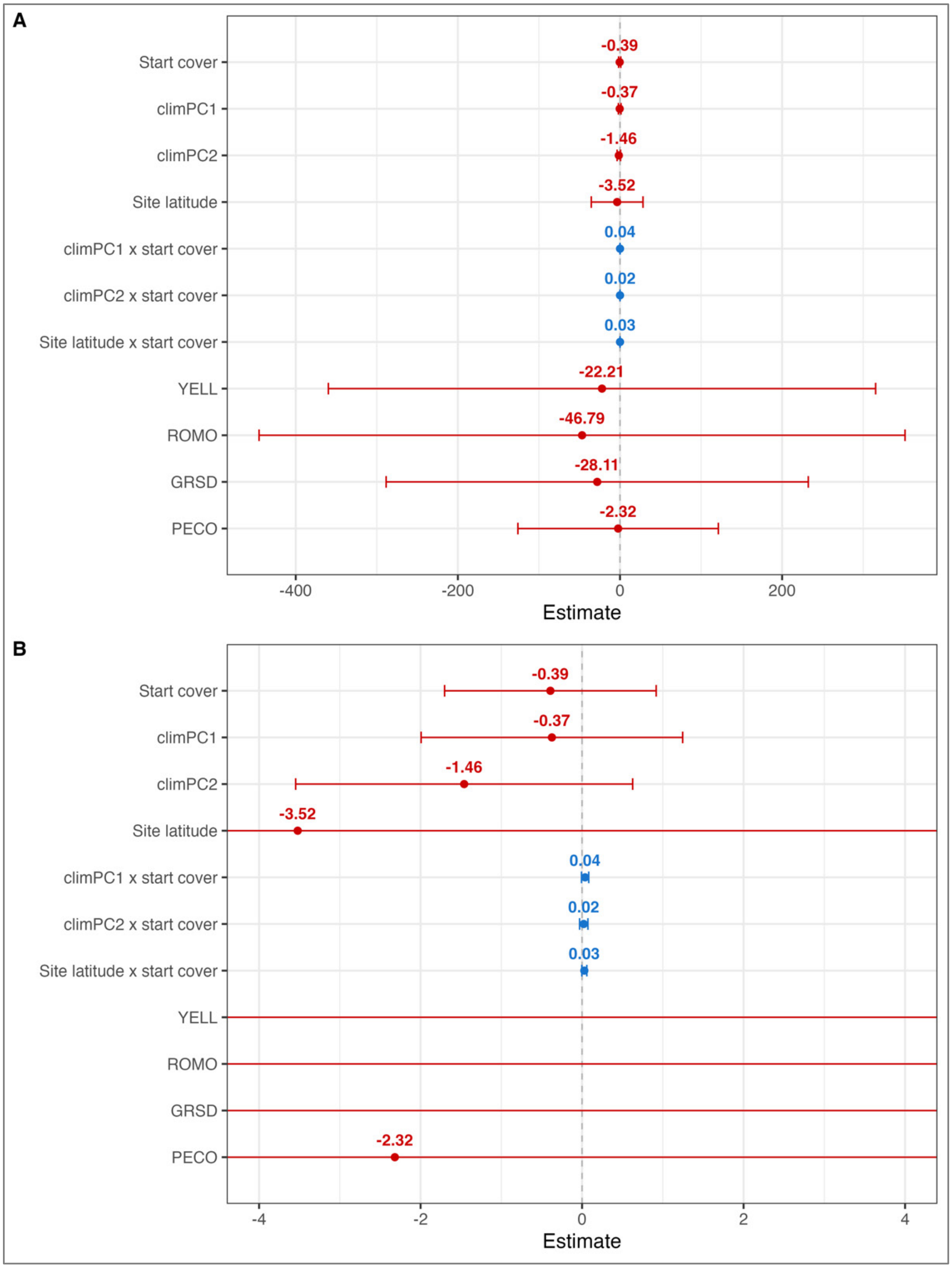

Figure 20. Estimated fixed effects coefficients from the best-supported climPC model, predicting total vascular plant cover. In Panel A the full range of coefficient estimates are shown. In Panel B the same results are shown but with a smaller x-axis range to visualize the values of better-supported coefficients. While none of the coefficients are significantly different from zero, all displayed coefficients are in the best supported predictive model, indicating support for their effects even if they have confidence limits overlapping zero. NPS

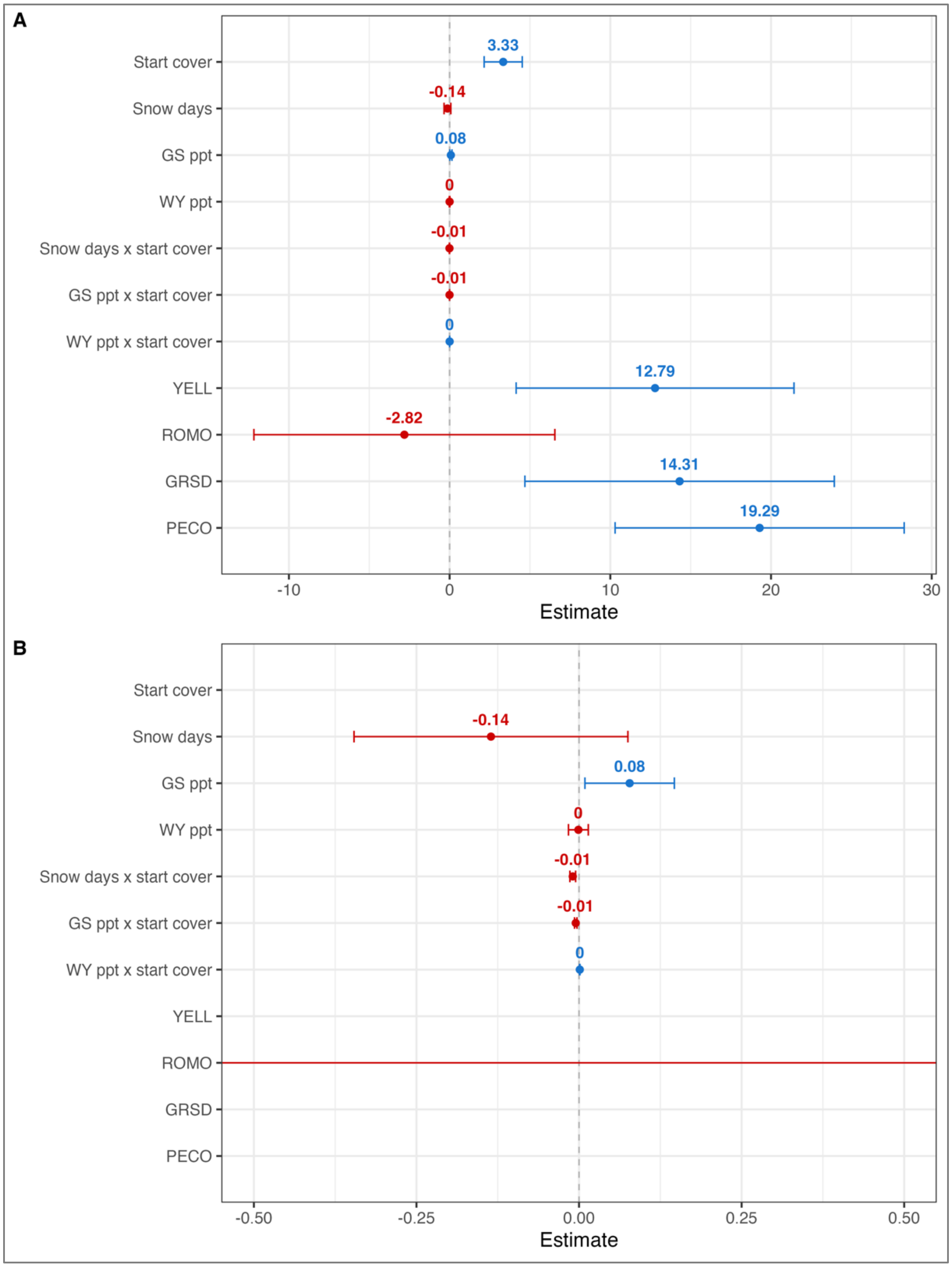

Figure 21. Estimated fixed effect coefficients from the best-supported models predicting total vascular plant cover using climate variables. In Panel A the full range of coefficient estimates are shown. Panel B shows the same results but with a smaller range along the x-axis to visualize the values of better-supported coefficients. Note that coefficients for YELL, GRSD, and PECO are outside of the range of x-axis values shown in Panel B. Significant positive effects include start cover, YELL, GRSD, PECO, and GS ppt, while significant negative effects include snow days × start cover, growing season precipitation (gs.ppt) × start cover, and water year precipitation (wy.ppt) × start cover. NPS

Species of special interest (SOI)

General trends in SOI groups paralleled those seen across all taxa, with, on average, declines in almost all groups in ROMO and PECO, and more mixed declines and increases in the other three parks (compare Figure 22 to Figure 9). Examining the raw patterns of change shows that a few taxa declined, on average, in GLORIA study sites across all parks where they occurred (Figure 22). No SOI increased on average in all parks (Figure 23). However, when considering population changes in different slope-aspects within each park, there was less sign of consistent declines or increases. No SOI with more than one transition in a park showed only increases or decreases. We found consistent declines of four SOI in ROMO, but for all these there were only two data points (*Achillea millefolium*, *Oxyria digyna, Polygonum viviparum, Salix petrophila*). Two SOI showed consistent declines in PECO: *Castilleja* spp., with seven observations, and *Sedum lanceolatum* with three.

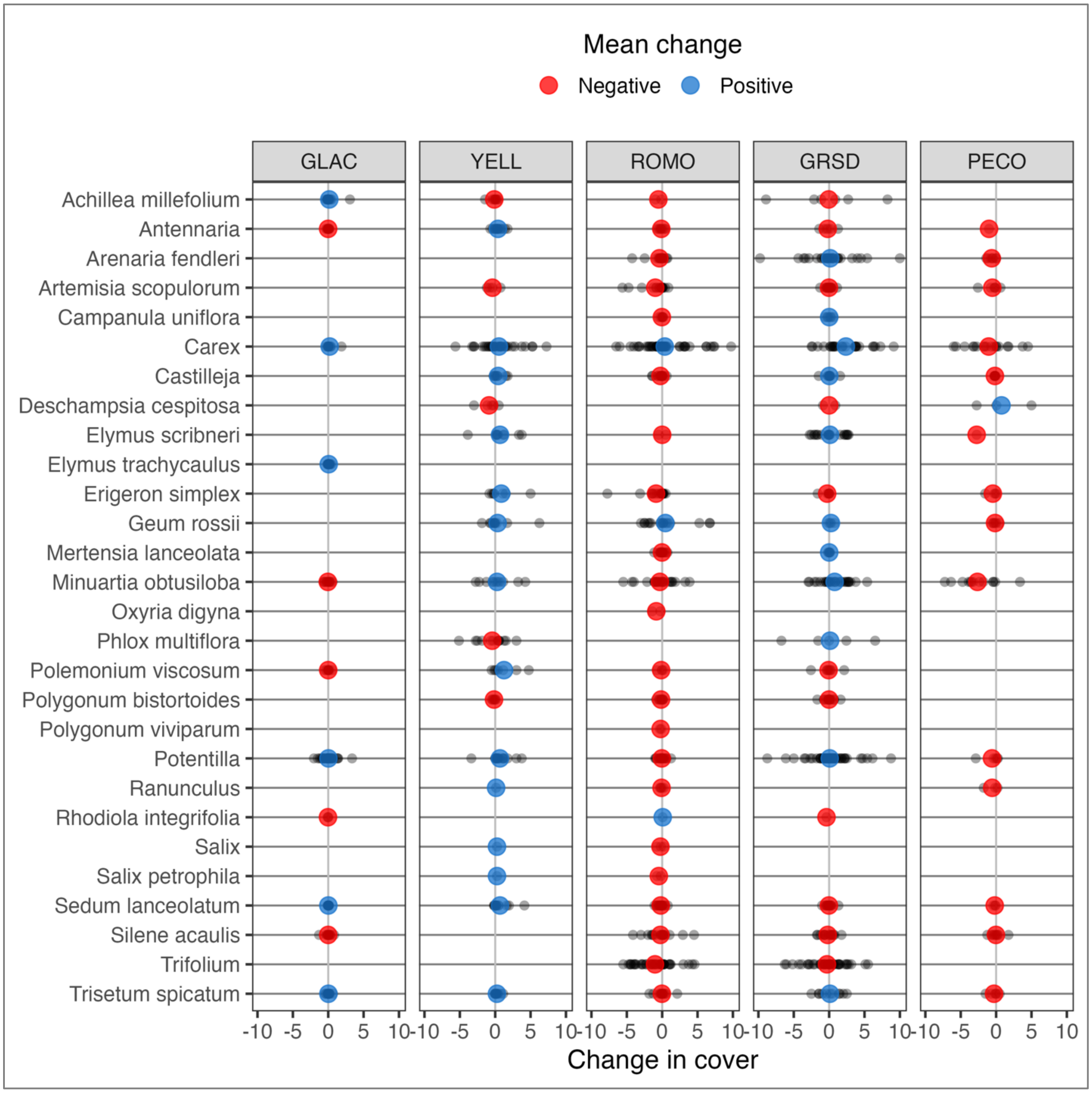

Figure 22. Changes observed in species of interest arranged by park. Each small grey point is a single average change on a given summit-aspect over one five-year transition. Large dots indicate the mean change for each species in each park, with blue indicating average increases and red average decreases. General trends in SOI groups show, on average, declines in almost all groups in ROMO and PECO, and more mixed declines vs increases in the other three parks. NPS

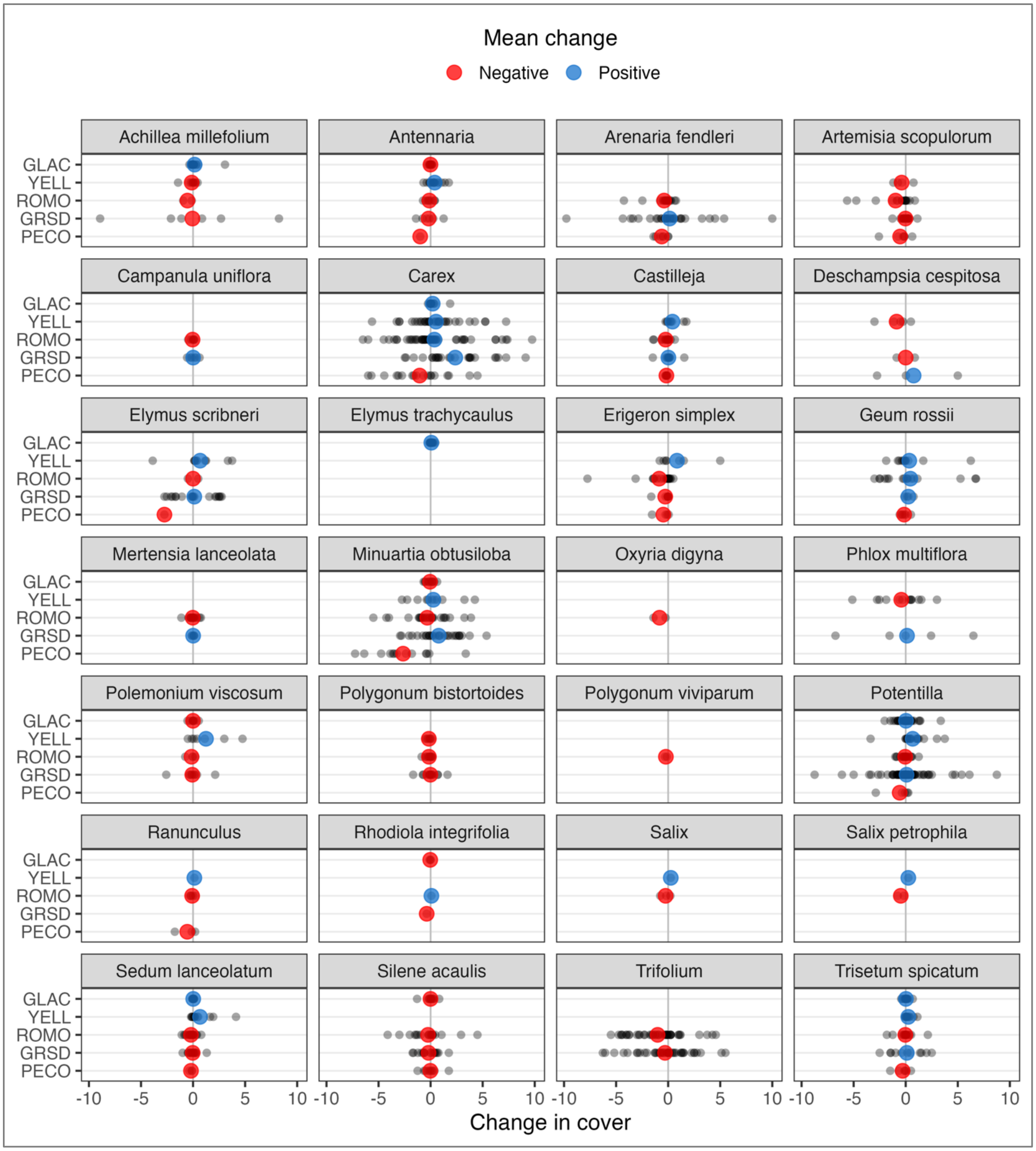

Figure 23. Changes observed in species of interest in each park. Each small grey point is a single average change on a given summit-aspect over one five-year transition. Large dots indicate the mean change for each species in each park, with blue indicating average increases and red average decreases. NPS

Fitting climate variable models separately to each SOI helped to reveal which taxa have similar or strongly varying responses to geographic and climate variables, relative to the entire ensemble of species. Not surprisingly, the much more limited data for each SOI leads to simpler top predictive models, although for most species 3–5 predictors were selected, as were some interactions with start cover (Appendix B: Table 9).

Overall, the best-supported models for individual SOI show qualitatively similar effects of summit latitude and climate to those seen for the general species models. In particular, most taxa have the same coefficient sign for each climate variable and for latitude as seen for the mean of all species, indicating the direction of effect of climate and latitude were similar for SOI and most other species (Appendix B: Table 9 vs. Appendix C: Table 14). None of the species showed a consistent pattern of mismatch with the overall species responses. For example, *Antennaria* has the opposite response to gdd and gs.ppt from that seen in the general model, but the same sign of response for wy.ppt and gs.tmean.

To better visualize predicted change in cover of the SOI, we plotted predictions of changing cover as a function of each driver variable in the best-supported models for the species, holding all other variables at constant mean values. These figures are included in Appendix B. Perhaps the most interesting result from these models is that the two SOI that show the most general declines and had enough data to fit predictive models (*Silene acaulis* and *Polygonum bistortoides*) do not have predicted patterns of change that match climate change effect predictions. For example, *Silene acaulis* is predicted to increase at lower latitudes and there is no latitude effect for *Polygonum bistortoides*. There is also no gs.tmean effect for either species. These results suggest that other non-climate drivers of change may be important drivers of these species, or possibly that other climate effects may outweigh those that we could quantify.

Observer effects on estimates of changing abundance

With surveys conducted only every five years, often by changing field crews, there is strong potential for several types of error to occur, all of which could influence the results of analyses of changes in species abundance with respect to climate or biotic factors. An especially worrisome problem we might expect to see is dramatic changes in abundance estimates due to changing observers rather than true changes in cover. Given the data collection methods, there is no straightforward statistical test that can quantify the extent of this problem, but we visually examined the data to look for patterns that might indicate observer issues. For each summit-aspect, we looked at changes in cover across all surveys in the data set (Figure 24). Only GRSD appears to show a pattern that is clearly worrisome, with many species increasing from 2009 to 2015 on all summit-aspects and then declining again 5 years later. We found no evidence that the climate was radically different over the two transitions, nor were there differences between aspects or other summit characteristics that would explain these changes. It is worth noting that PECO also shows broad declines in abundance over the single transition of data, though mean annual soil temperatures across PECO sites show an analogous decline, indicating a potential link between abundance and climate trends. To test the influence of these potential sources of variation on the overall models, we reran all our models without GRSD and PECO and found no significant difference in the results, suggesting that these possible problems do not account for the significant effects we describe above.

To uncover other evidence of possible effects of observer error, we also looked at patterns in total cover quadrat per survey and plotted these patterns for each park (see Figure 19, above). For all parks besides GLAC, we see a large range of total vascular plant cover values with some broad trends in the direction of change in total plant cover from one survey to another. While these may reflect real changes in abundance, they could also be caused by observer differences between surveys or shifting interpretations of cover estimate rules.

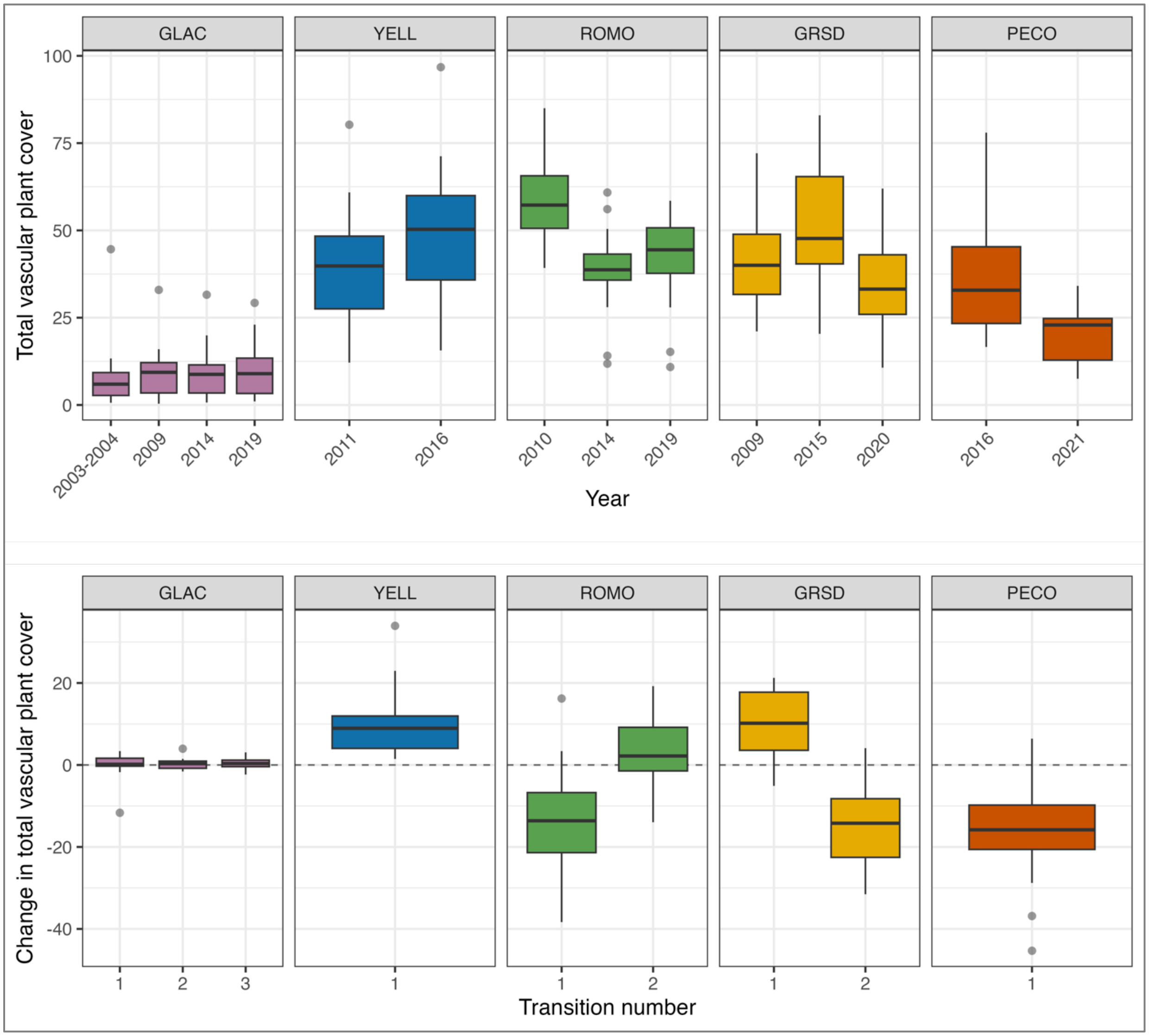

Figure 24. Changes in total plant cover at each park. Top row: distributions of total cover on each summit-aspect for each census year. Bottom row: the percentage change in total plant cover over each transition for each summit-aspect. While there is no consistent change across all parks, there are marked shifts in estimated cover for all parks except GLAC. NPS

Summary and Conclusions

We first summarize our ecological results, and then propose recommendations for future monitoring and management based on these results.

Ecological results

We found that the GLORIA data combined across five parks and multiple transitions is powerful enough to allow estimation of several patterns in species change over time, as well as the factors influencing these changes. While the data sets available at this point allow meaningful interpretation, it is important to remember that the total temporal span of the data spans only 5 (PECO) to 15 (GLAC) years. Additionally, the summit top sites included in GLORIA studies do not reflect the full range of conditions or the full range of species that characterize alpine habitats across any of the five parks.

The most pervasive pattern we found was that of species turnover, with more common species mostly declining and less common species increasing across the five-year transitions between GLORIA surveys. In general, this turnover pattern is consistent with predictions that changing abiotic conditions will result in shifting suitability (and perhaps competitive abilities) of plants, so that formerly dominant species will decline and other, formerly less abundant taxa, will increase. In other contexts, especially at midpoints on mountainsides, this pattern would be less apparent, as rarer species at a site would include those that were suited both to warmer and cooler conditions or similarly divergent aspects of other environmental gradients. However, because GLORIA sites are exclusively in close proximity to summits, the vast majority of rare species at a site are likely to be those formerly most suited to lower elevations. Thus, the turnover pattern we observe conforms to what would be expected if shifting climate regimes are driving changes in species abundance. We also note that while nitrogen deposition into alpine ecosystems may contribute to shifts in relative abundances, there would not be an expectation that these effects would drive the overall pattern of turnover that we see, with differential effects on most common vs. most rare species.

A major goal of our work was to uncover the most important drivers of changes in population abundance across surveys. Our models to test for different drivers of changing abundance yield several important relationships:

1. Model predictions imply that warmer drier conditions may alleviate growth limitations imposed by low growing season temperatures, and are in general beneficial, despite cooler, wetter conditions being the historic norm. Growing degree days (gdd, the number of days with air temperatures above 0°C) and water year precipitation (wy.ppt, or total annual precipitation) both positively influence abundance, while growing season precipitation (gs.ppt) has negative effects. Growing season mean temperature (gs.tmean) has a negative, but non-significant effect, as judged by the confidence limits of its coefficient, although it is retained in the best-supported predictive model. Together, these effects suggest that warmer conditions during the entire span of likely plant activity is important for performance (captured by gdd), while higher temperatures in the middle of the growing season (gs.tmean)

are less important in determining plant abundance. Similarly, the contrasting effects of gs.ppt and wy.ppt imply that precipitation during the non-growing season has positive effects for changing cover, while growing season precipitation alone has negative effects, possibly by limiting gdd. These results make sense in light of species turnover, suggesting that the positive effects of warming conditions are benefiting most species, which are generally rarer and increasing precisely due to changing conditions. While here we summarize findings from the climate variable models, the climPC models largely confirm the same patterns of effects.

2. The other site-specific driver of changing abundance is summit latitude. We find substantial effects of latitude, showing that factors that are separate from climate but that also vary geographically are also having important effects in changing plant abundance. Latitude has a positive effect on changing abundance in the climPC models, but a stronger and negative effect in the climate variable models. This difference in latitude effects is due to how these models include different climate effects, since in the models, latitude effects are separate from differences in climate between the study sites, which are correlated with latitude (Figure 3). Since climate is also included in the models, latitude effects should be interpreted separately from climate as measured during the study. So, for example, latitude is positively correlated with wy.ppt, which itself has a positive effect on abundance. Thus, the negative effect of latitude does not imply that changes in abundance will be lower in more northerly parks, but rather that after accounting for climatic differences, plant abundance does not increase as much in the north. The differing sign of effects in the two classes of models is therefore likely to reflect the differing climate effects captured by other variables in these models (with more precision in the estimation of climate effects in the climate variable models). While interpreting latitude effects is complex, it is important to remember that other spatially structured variables besides climate can contribute to latitudinal patterns and should not be assumed to arise solely from climatic differences.
3. We found that shrubs and graminoids increase more than species with other morphologies, especially more than forbs, which comprise most alpine plants found at the GLORIA sites. In addition, both do better at lower latitudes and in the case of graminoids, with higher gdd. These patterns all conform to expectations from other studies (Porro et al. 2019) and seem probable with warming and drying conditions, which should favor woody species and those with faster growth in warmer, more water-stressed environments. These results suggest that graminoids and shrubs are more positively affected by ongoing shifts in climate or are simply able to respond more rapidly to these shifts than are other species also favored by these conditions. In either case, they reflect high sensitivity to climate changes for these groups.
4. The last well-supported major driver of changing abundance is the geographic range of a species, summarized as the midpoint of a species' western North American range. For most species—all but the few abundant ones—having a more northerly mid-range is related to declining abundance, while the most southerly ones are predicted to on average be increasing. This pattern is in keeping with the idea of shifting climates favoring species that are best adapted to warmer and potentially more water-stressed conditions than have historically been experienced at the GLORIA sites. The predicted effects of latmean1090, our

measure of mid-latitudinal range, is complicated by the support for linear and squared effects, and their interaction with starting cover. The effect of the squared term in these models leads to the prediction that rare species with extremely northerly range centers will also fare somewhat better, while abundant species with intermediate range centers will do markedly better than either southerly or northerly ones. We suspect that these complicated patterns are due to the limitations of the simple functional form we used to model latitude effects. In addition, very few species had extremely high or low mid-latitudes, making inference at the edges of the relationship less certain. The overall result, including that it is not a simple pattern favoring species with lower-latitude ranges, conforms to that seen in broad surveys of climate change effects on species ranges (e.g., Parmesan and Yohe 2003, Parmesan and Hanley 2015).

In addition to general models for species-level changes, we also examined patterns and drivers of total vascular plant cover and significant individual differences in species as well as patterns of change in species of interest (SOI) identified by NPS personnel. Unsurprisingly, analysis of species with significant random effects in our general models showed that many responded quite differently to climate than indicated by the mean species response, showing that species-specific responses need to be researched and accounted for in planning any detailed management actions. For example, we see only a small number of SOI that have uniformly declined across all parks or that showed extreme sensitivity to climate variables. Even within single parks, SOI with more than one occurrence generally showed a mixed pattern of increase and decrease (Figure 22 and Figure 23), although several taxa declined at all sites where they occurred in PECO and ROMO. However, we caution that there are significant issues with statistical power that make the detection of species-specific patterns difficult with the data available. Many species were rare and occurred on few summit-aspects. In addition, while temperature loggers give summit-aspect level climate data, all other climate variables are summit-level, weakening the ability to tease out their effects.

Recommendations for future monitoring and management

Our scientific findings and analysis of observation errors and other data collection issues suggest recommendations for future data collection and some management considerations. Specifically:

- **Limit sources of variation in data during resurveys**: At all study sites but Glacier, we observed a great deal of variation in cover estimates that seemed likely to arise in part from observer differences. One reason for the markedly lower variance in cover estimates at Glacier is certainly that the same field crew sampled the site for all surveys. They used photos to recreate the quadrat plots meticulously to ensure 1m^2 frames were placed exactly as before. They also consulted their previous species lists for each quadrat at resurveys to avoid missing anything seen before or unknowingly changing a species identification. Despite GLORIA protocols specifying that no consultation with past data be made, the time between resurveys as well as challenging identification of some species are contravening considerations. Since it is not always possible to have the same individuals resurvey plots, an extra effort should also be made to develop a specific training program that all observers would use immediately before doing GLORIA surveys to calibrate their estimations of cover.

- **Prevent missing soil temperature data**: We suggest that NPS teams add procedures to prevent lapses in soil temperature datasets. We encountered multiple instances of significant gaps in soil temperature data. The 5-year time interval for GLORIA surveys makes failure or improper launching of temperature loggers more problematic than for studies with higher study site replication and shorter resurvey intervals. Given the costs of information loss from missing summit-aspect climate data, we suggest that NPS consider taking two steps in deploying loggers in the future:
    - We suggest that two loggers be deployed at each aspect, rather than just one. While this doubles the cost for the actual devices, they are inexpensive compared to the time and information costs of missing data.
    - We suggest that for each pair of loggers, one is downloaded and relaunched or replaced by one team member, while the other is serviced by a different team member. This would reduce the chances of mistakes in deployment due to misunderstanding of the proper procedure and would minimize loss of data for a given site. An alternative would be to ask a researcher to visit the sites a month or more after each survey to check that the loggers are operating correctly. However, this will lead to more site trampling and more personnel time.
- **Collect different data to improve inference about summit-aspect climate**: In the future, collection of more summit-aspect level climate data, or use of topographic information to improve the use of interpolated microclimate conditions (Lutz et al. 2010) would lead to greater power to discern climate change vulnerability for individual taxa or groups of species. Examples of data that could be collected include soil moisture and irradiance, both of which would aid in the estimation of plant-relevant microclimate features.
- **Collection of usable soil nutrient data**: It would be extremely valuable to collect site-specific soil data, especially information that is most applicable to plant growing conditions. Perhaps the most feasible way to do so would be to deploy resin strips to measure available soil nutrients. Resin strips are inexpensive and can be deployed over several months or a year in alpine systems to characterize available nutrients (e.g., Simpson et al. 2019). While deployment for a year would yield valuable information, they must be collected before all strips are fully saturated, so would require collection before a five-year resurvey.
- **Establish additional study plots to test the generality of the pattern of declining trends in common species:** One of the strongest patterns we see in the GLORIA data is falling cover of more common species. However, GLORIA sites are not a representative sample of alpine habitats, making it important to determine how broad this pattern is. Understanding this pattern also has implications for the best species to use in restoration programs. We suggest establishing study plots stratified by aspect and elevation and using these to monitor dominant species only. This will limit the time needed to perform monitoring and thus could make the project feasible. Data from such a project allow tests of whether individual species' elevational ranges are predictive of their abundance trends in each park. This data collection

could also estimate the local elevational ranges of species found in GLORIA plots, which would allow better interpretation of changes in abundance.

- **Analyze other types of GLORIA data to test the patterns found in quadrat data:** In particular, analyzing the summit area section data (Figure 1) would be a reasonable next step. The summit area section data consist of abundance classes in bands 0–5 and 5–10 meters from the summit and are designed to capture upslope movement of plant species. It would be interesting to see if the turnover effect described here is also signaled in those data. If similar patterns are not identifiable with the coarser abundance estimates used in the summit-area section methodology, we would suggest that park personnel consider modification of these methods, especially employing finer scale estimates of abundance of less abundant species.
- **Consider broad patterns of species change in restoration and management decisions**: Our results confirmed that woody species and graminoid abundance are more likely to increase than other plant groups, patterns also suggested in other studies (Porro et al. 2019). This pattern implies that species from these groups should be avoided in restoration projects to reduce their increasing dominance. At least for shrubs, direct control of densities in alpine areas might also be warranted in the future.
- **Focused monitoring of particular species:** Our results suggest that some groups of species, as well as particular species, may be at the highest risk of decline and should be targeted for restoration or monitoring. In particular, Appendix C: Table 10, Figure 16, Figure 17, and Figure 18 summarize species that are predicted to have the greatest deviations from general patterns of change, given climate, location, and morphological group. Similarly, in Appendix B: Table 9 we summarize patterns of change and sensitivity to climate for the SOI. Considering these results in relation to a park's specific climate futures could generate a list of species of particular interest for further study. At least some subset of these species would be good targets for more focused monitoring efforts going forward, including work to better understand how they are impacted by climate and what conditions might provide refugia for them within different parks.
- **Repeat data analyses as more data are gathered:** Refitting the best climPC and climVar models that we found in this work, to see how consistent and well-defined the results are, would be valuable. Indeed, repeating these analyses with even one more survey per park would allow far greater power to test for climate and climate change effects on the alpine flora. While the effort to collect GLORIA data is substantial, more data, especially taken as climate change effects continue to manifest, will allow more meaningful analyses to be done. At a minimum, this would involve running only two models and using the work done here to simplify the task of reanalysis.

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Appendix A: Supplementary Methods

Data cleaning and prep

Aggregating 1-m^2 visual percent cover estimates from quadrats to summit-aspects

Before analysis, we went through several steps to make cleaner and more comparable data sets. As is explained below, the steps needed to error check the data and fill in data gaps (especially climate data) were far more extensive than anticipated at the onset of the project.

First, we removed subspecies and varieties designations. Aggregating data to the species level allows for easier comparison of trends across parks, removes uncertainty surrounding subspecies-level identification, and alleviates challenges that subspecies data poses for defining species ranges (see below). To do so, we removed any suffix from each species scientific name (i.e., *Poa glauca* ssp. *rupicola* became *Poa glauca*), then averaged the 1-m^2 percent cover estimates by species within each survey on each summit-aspect. Nomenclature for all vegetation data followed the Integrated Species Taxonomic Information System (www.itis.gov), which can be cross walked to multiple other local nomenclature schema.

Second, we checked field notes and examined the data sets for clear changes in species identification, including use of different synonymous names in different parks or survey periods. We made corrections to the data sets to address these issues when they were clear. However, some changes in identification, especially of difficult taxa such as *Potentilla* and *Poa* species, may have occurred but were not documented or obvious from scrutiny of the data.

Another aspect of data cleaning involved standardization of the taxa included in the data sets. Information on lichens, ferns, and clubmosses was not collected consistently across surveys or parks, so we removed information for all these taxa from all data sets. As a result, our dataset is on “total vascular plant cover” and does not include fern or clubmoss cover.

Finally, we had to make a standard decision about which zero occurrences counted as data. Given that most species are limited to a subset of summit-aspects, and that many are only found in one or two parks, percent cover estimates of zero (i.e., not present) do not provide useful information regarding the local factors driving abundance trends. Also, most of our analyses focus on changes in cover between censuses, so pairs of zero occurrences that span a transition are also not useful to include. Given these considerations, we added zeros to quadrat-level (1-m^2) percent cover data for any species that occurred on a summit at some point through the study period but did not have percent cover data recorded during a given survey. For example, if percent cover data was recorded for species A in three of four quadrats in a quadrat cluster on a given summit-aspect, then a zero value for percent cover was added for the fourth plot on that summit-aspect. Likewise, if non-zero percent cover data was recorded for a species within a 1-m^2 plot in one survey year but not others, then we added a zero value to percent cover data for that species in the other years of data for that summit-aspect. To further refine the addition of the important zero-values, we then removed instances when a species had zero-values in percent cover estimates for two consecutive surveys (i.e., wasn’t present for two consecutive surveys).

In some instances, not all four plots on a summit aspect were censused. We accounted for these instances by only using data from surveyed plots to calculate the mean species abundance value used in the analyses. If none of the plots were surveyed, we listed all data for that year and summit-aspect as missing.

Using the cleaned-up data sets, we created a comprehensive list of all species present in all parks, hereafter referred to as the "species list." Table 2 and Table 3 show the number of species in each park represented in the cleaned and aggregated dataset used for analyses. Table 16 (in Appendix D) lists all species in the species list, the number of transitions analyzed, the parks in which they had at least one occurrence, and the traits assigned to them from Table 4. Figure 25 shows a histogram of aggregated values after averaging percent cover estimates within each summit-aspect's quadrat cluster to create a single percent cover estimate per species per summit-aspect per survey.

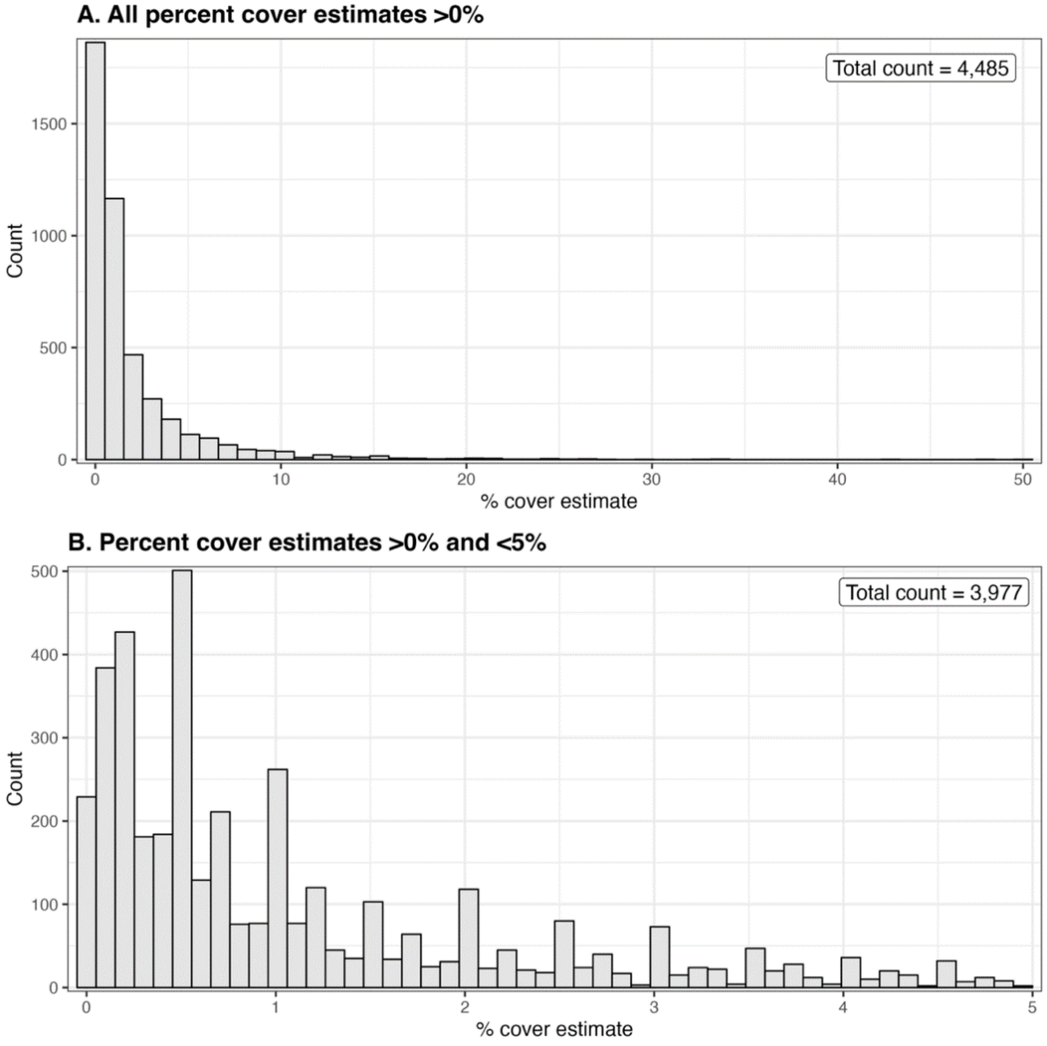

Figure 25. Histogram of percent cover estimates aggregated to summit-aspect estimates (quadrat cluster-level). Most cover values were between 0 and 1%. This pattern of few common and many rare to somewhat rare species is typical of virtually all community data. NPS

Understanding observer errors in vegetation data

We did some analyses of the quadrat-level point count data to ask whether notable changes seen in percent cover data were artifactual and why. However, point count data are not able to capture changes in abundance of rare species. These data we are also absent from Glacier National Park (NP) entirely, as well as early survey years in Rocky Mountain NP and Great Sand Dunes National Park and Preserve, making use of these data instead of cover estimates impractical.

To gain a better qualitative understanding of the degree to which changes in total cover may be attributable to observer error, we examined photos of PECO quadrats from 2016 and 2021, and compared the photos to visual cover estimates and point-intercept count data. Examination of photos showed that for some quadrats, large shifts in total plant cover did not correspond to any perceivable change in plant cover visible in photos (Figure 26), although for others there is a reasonable correspondence (not shown). We also asked across all transitions and years how well correlated changes in total point counts and total plant cover estimates are in each park (Figure 27). Unfortunately, the correspondence appears fairly low, with a correlation of r = 0.80 in YELL from 2011 to 2016 down to 0.44 in ROMO from 2014 to 2019. Overall, we were left feeling that some substantial observer effects have occurred, and that they likely have fairly strong effects on estimated abundances.

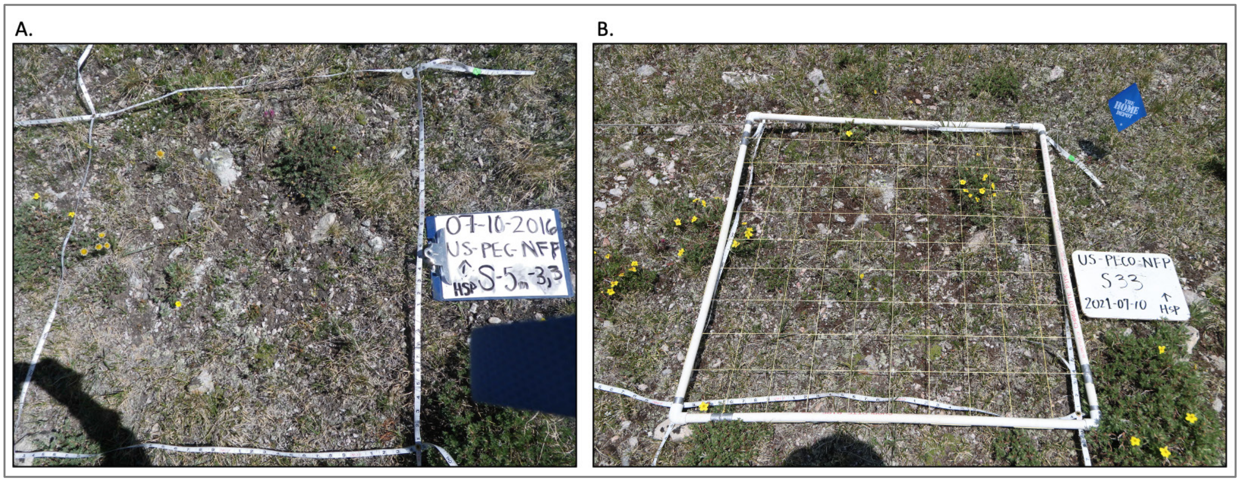

Figure 26. Photos of study plots illustrating inconsistent cover estimates. Panels A and B are of the same 1 × 1-m quadrat at PECO. The photo in panel A was taken in 2016 and the photo in panel B was taken in 2021. Recorded data estimates 58% vascular plant cover in 2016 and only 28% cover in 2021, however comparison of these photos does not support this 30% decrease in vascular plant cover over the 5-year period. NPS

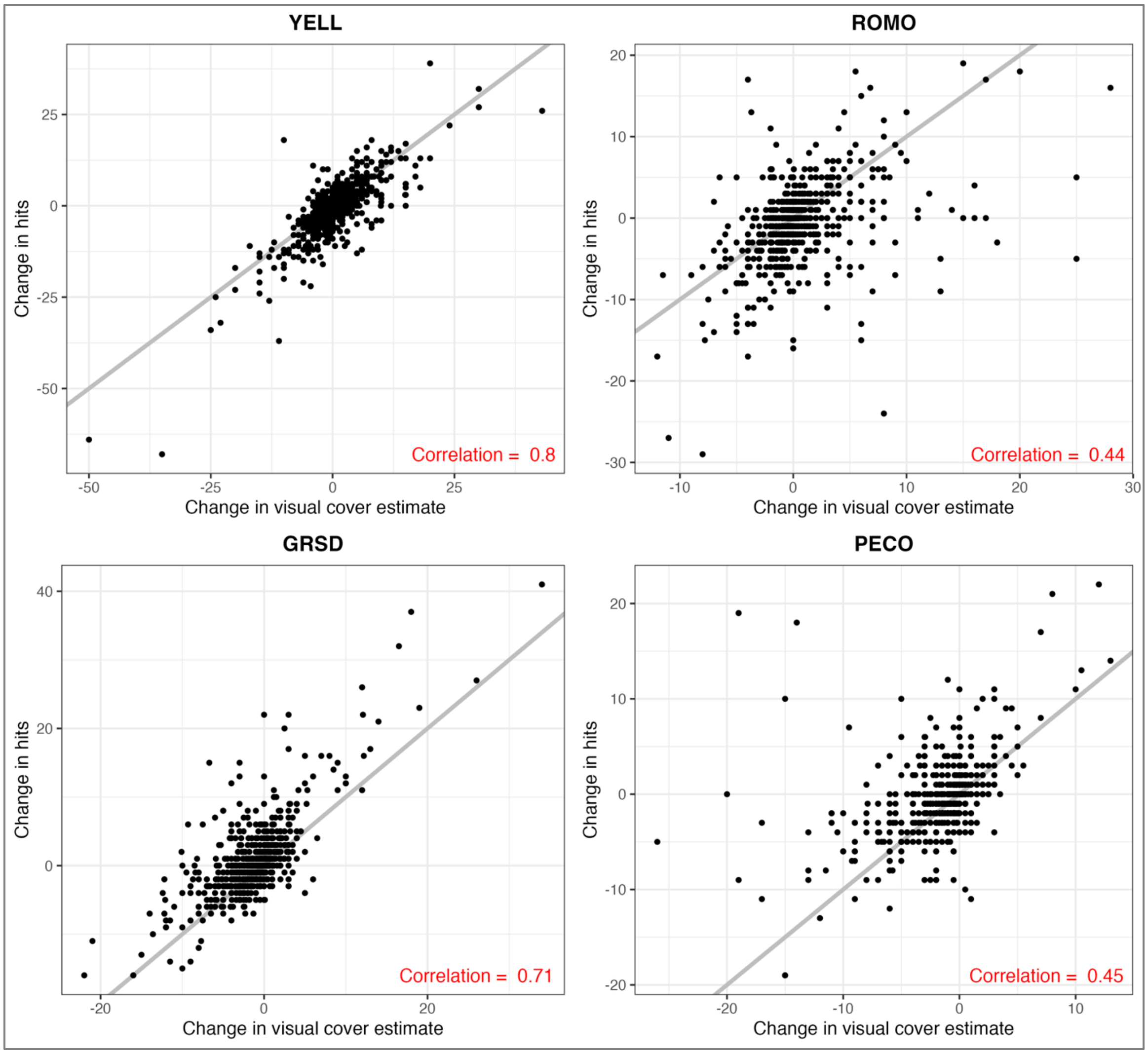

Figure 27. Comparison of estimated changes in species-level abundance using visual percent cover (x-axis) and point-intercept (y-axis) methods. Red values in bottom right of panels show the correlation in change cover estimates between the two methods. Each point is change in abundance estimates for one summit-aspect across a single transition. NPS

Given these issues, we explored whether our results changed substantially when we excluded data that was potentially less reliable. To address this, we reran the best selected explanatory model, described in *Drivers of changing abundance*, leaving out either the PECO or GRSD data and excluding data on three particularly problematic taxa, *Poa* spp., *Carex* spp., and *Potentilla* spp. The results of these models, fit to reduced data sets, largely corresponded to the model fit to all data (Appendix C: Table 13), suggesting that while observer errors (misidentified species and high/low cover estimates) are nontrivial issues in the data sets, they are not unduly changing the basic conclusions we would draw from the analyses. All results described in the main text are generated using the full data set.

Soil temperature data (Climate data)

Hourly soil temperature data (°C) was collected at all sites in all parks with shallowly buried temperature data loggers. Data from temperature loggers were uploaded and subsequently run through QA/QC processes, then published as cleaned hourly soil temperature readings. We first aggregated hourly temperature data to mean daily soil temperature by taking the mean of all hourly readings within each 24-hour period. When there were fewer than 20 hourly temperature readings within a 24-hour period we treated this as missing temperature data, as that number of missing readings could influence daily temperature average estimates.

There were many time periods with missing data in all parks except PECO (Figure 28). In most cases, for a given time period, data was missing for a subset of a site (summits or summit-aspects) within a park. However, nearly a year's worth of hourly temperature data was missing at all sites in GRSD from 2013-09-18 to 2014-08-29.

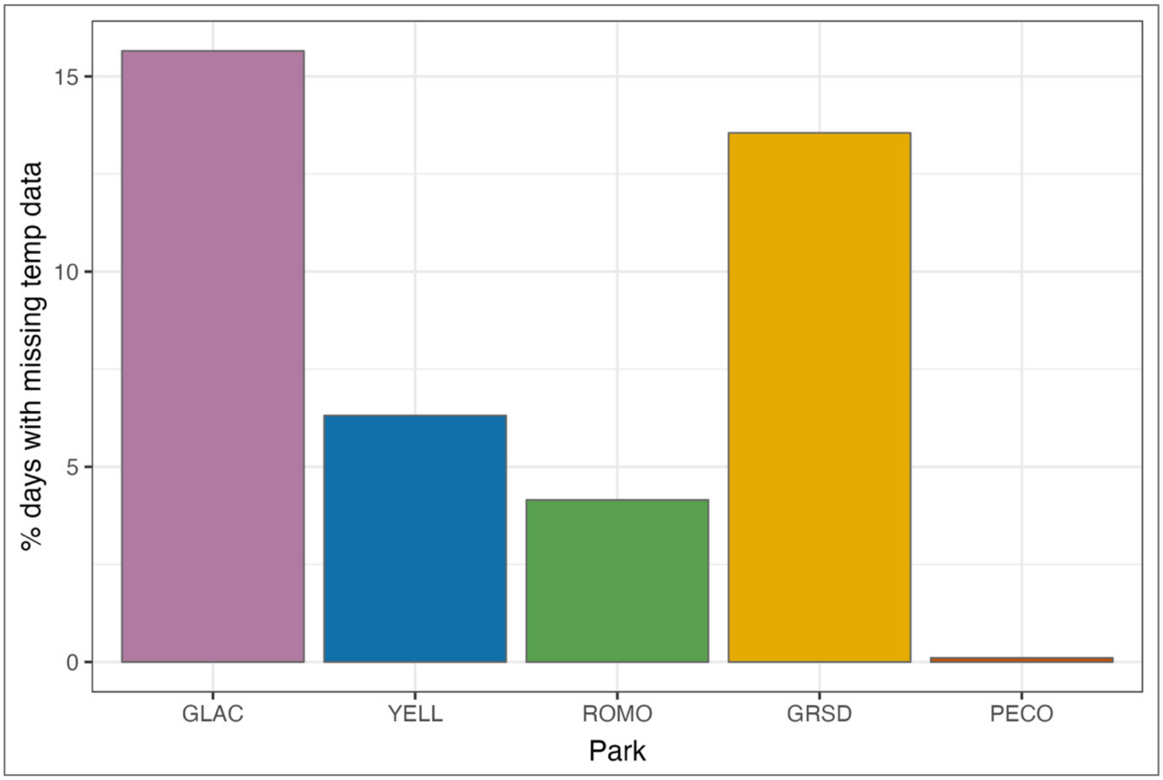

Figure 28. Percent of days across park-specific study periods that did not have an adequate number of individual hourly temperature readings (≥ 20 obs.) to generate reasonable mean daily temperature estimates. NPS

We interpolated missing summit-aspect level soil temperature data using non-missing soil temperature from surrounding sites and PRISM climate data (PRISM, 2014). We first created global linear models that predicted non-missing temperature for the focal summit-aspect using non-missing temperature data for surrounding summit aspects, and including day of year, day of year^2, and PRISM temperature data for the focal summit as explanatory variables. We then used the "dredge" function from R’s MuMIn package (Barton, 2023) to select the subset of variables from the global model that best predicted mean daily temperature. The best model for each summit-aspect was selected using AICc values and then used to fill in the missing temperature values.

To deal with GRSD’s year of missing temperature data in addition to other sporadically missing data, we first interpolated missing values for the park for all periods *except* the missing year (2013-09-18 to 2014-08-29), following the same steps described above. We re-fit summit-aspect level linear models using observed and interpolated daily mean temperature values as the dependent variable, and PRISM mean daily temperature values and day of year as predictor variables. We then used R’s “dredge” function (MuMIn package) to compare models fit with all combinations of predictor variables and used the best model (lowest AICc) to predict mean daily temperature values for the missing year for each summit-aspect.

Soil chemistry data

Figure 29 shows extremely high variation in nitrogen concentrations across the samples. Figure 30 and Figure 31 show comparisons of soil chemistry values in the GLORIA soil chemistry data package to values in NADP National Trends Network datasets. Figure 32 shows substantial within-park variation in deposition rates, but also some patterns of between-park variation that are broadly similar to the NADP soil data.

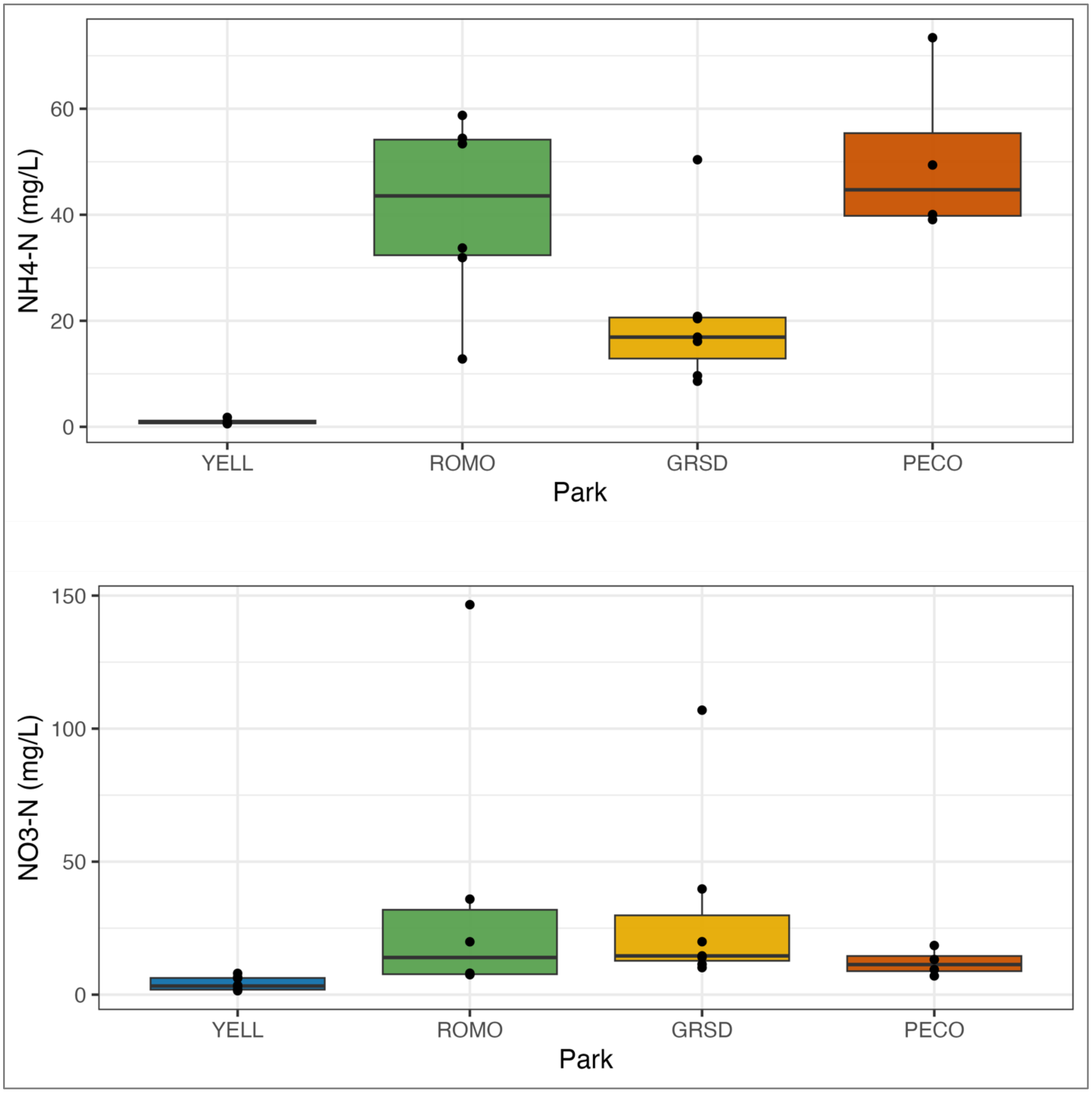

Figure 29. Box plots of NH_4-N and NO_3-N values from the GLORIA soil chemistry data package. Black points show individual data values. There was extremely high variation in nitrogen concentrations (and other values) across the samples. NPS

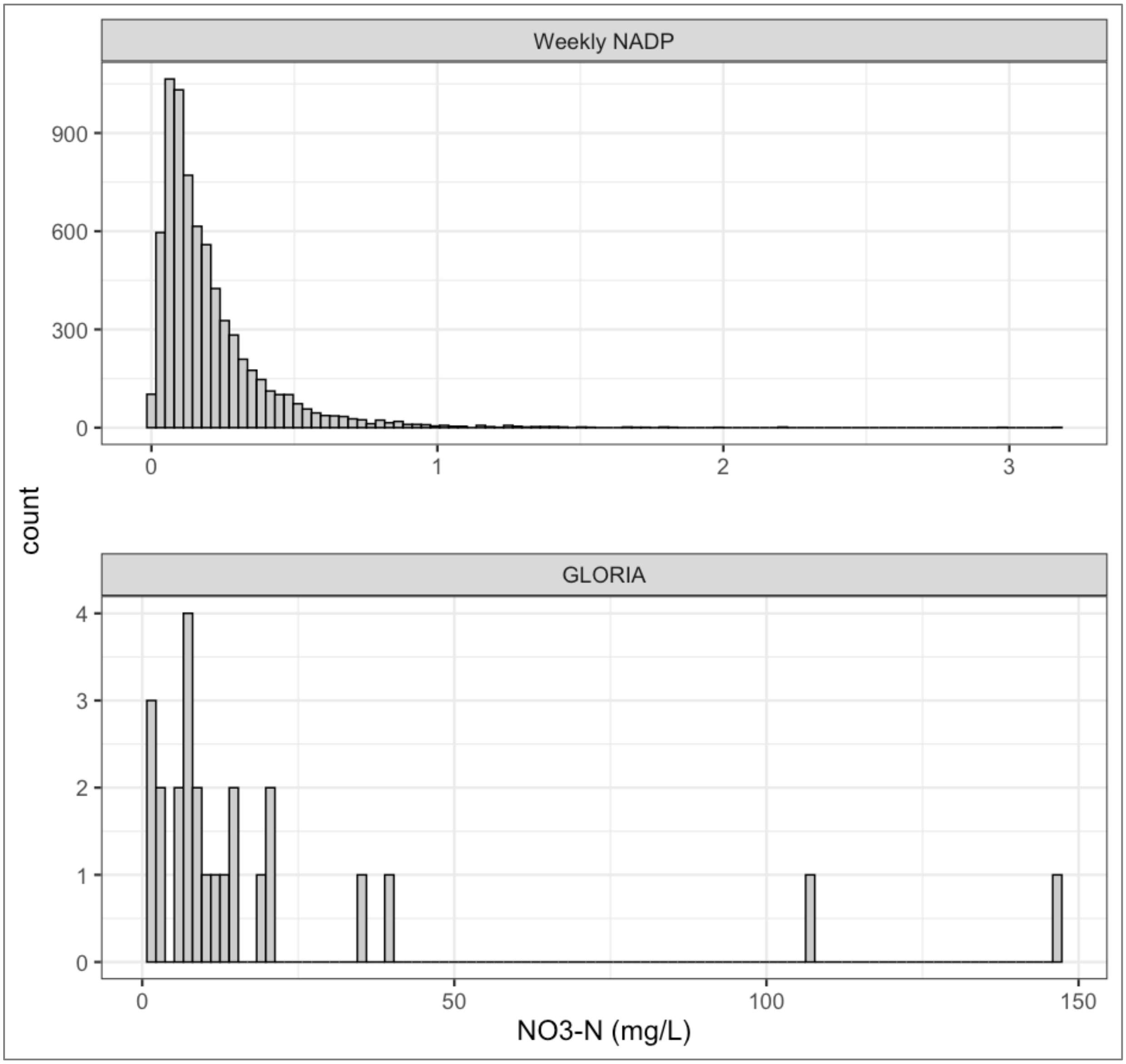

Figure 30. Comparison of NO_3-N values in the GLORIA soil chemistry data package to values in NADP National Trends Network datasets. Data from both sources has been through a QA/QC process. Note the very different extents on the x-axes of the two histograms, with NADP data spanning a far narrower range than GLORIA data. Weekly NADP data were downloaded for a single site close to each GLORIA field site included in this study (5 total). Weekly NADP soil sample collection for each of the five comparison sites began in the early 1980s. NPS

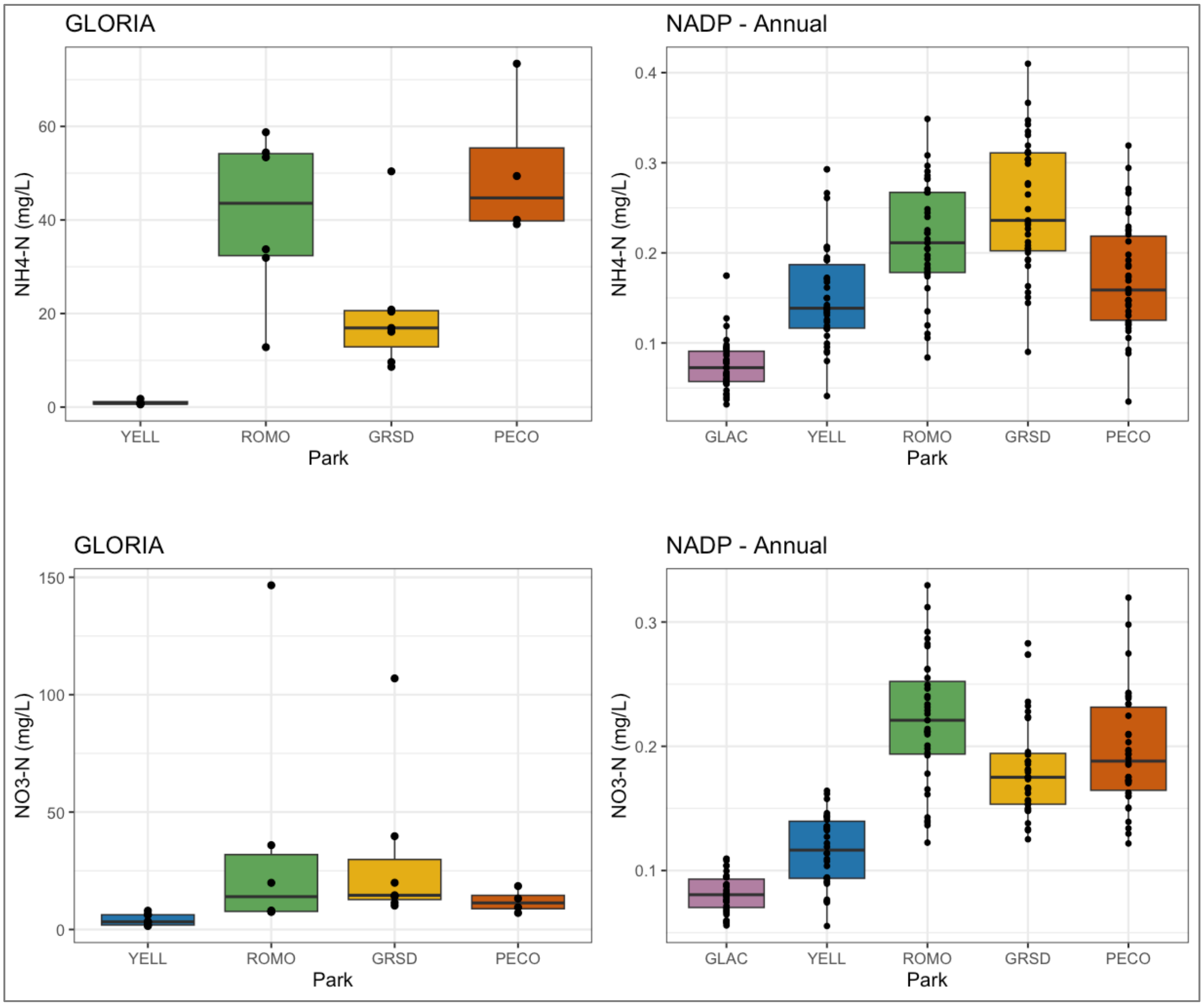

Figure 31. NO_3-N and NH_4-N concentrations found in GLORIA and NADP soil samples. Note the different scales used between GLORIA and NADP estimates. NPS

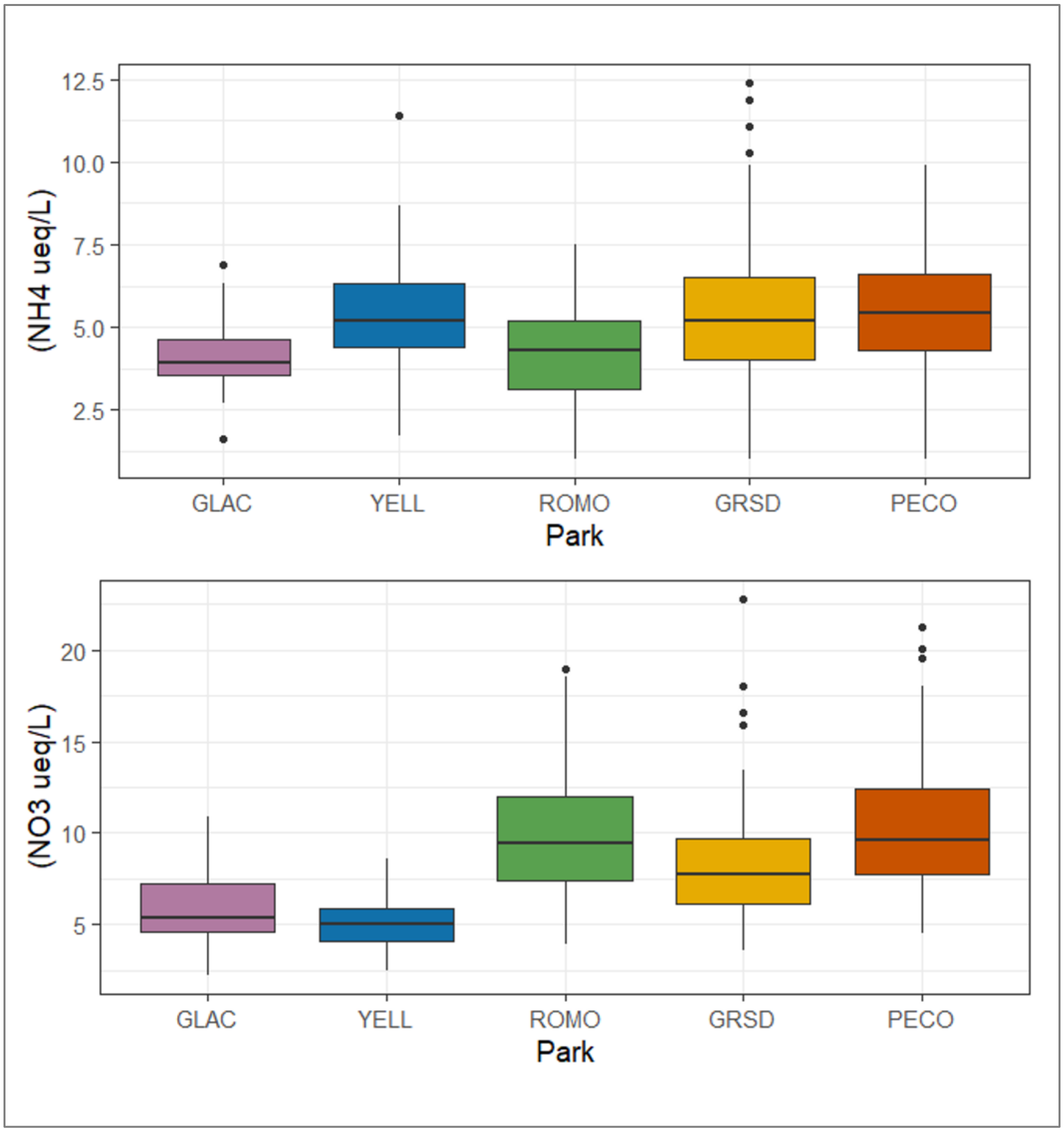

Figure 32. NH_4 and NO_3 deposition rates at Rocky Mountain Regional Snowpack Chemistry Monitoring study sites near GLORIA summits included in this study. There is substantial within-park variation in deposition rates and patterns of between-park variation that are broadly similar to the NADP soil data. NPS

Summit area sections

In addition to 1-m^2 percent cover data, each park recorded species-level categorical abundance data in upper and lower summit area sections (SAS). Upper and lower SASs are five and 10 vertical meters from each summit's highest point, respectively. ROMO, PECO, GRSD, and YELL recorded SAS data according to Table 6. During their 2003/2004 and 2009 surveys, GLAC recorded SAS abundance values using letter character symbols (i.e., r! = rare, r = rare, etc.) or percent cover numerical estimates (i.e., 0.001%), according to earlier GLORIA protocol. Due to inconsistencies in this data across parks, and the categorical rather than quantitative nature of the information, we chose not to use it in the analyses we performed in this study.

Table 6. Summit area section abundance categories.

Abundance category	Description
100	Very rare (1–4 individuals, or 1 well developed perennial individual)
200	Rare (5–19 individuals or 2–9 well developed perennial individuals)
300	Rare to scattered
400	Scattered (20–49 individuals, or 10–29 well developed perennial individuals)
500	Scattered to common
600	Common (more than above but less than 50% cover)
700	Common to dominant
800	Dominant (more than 50% cover)

Model Selection

Modeling species-specific abundance changes

The best predictive model was selected following the general methods outlined in Zuur et al. (2009), which involves finding the optimal random effect structure first, followed by the best fixed effect structure. Given the number of predictor variables, we needed to simplify our selection process in several ways, as described below. Most importantly, we used model selection at some stages that replaced the full set of climate variables with the first two principal components from a climate PCA and at other stages we limited the suite of explicit climate variables so as to not include multiple, highly correlated predictor variables. In all these model steps, we standardized the scaling of all continuous predictors to improve model fit and to best meet linear model assumptions. While we used rescaling of predictors to perform model selection, we then refit the best supported models with predictors on their natural scales and present results using these more easily interpreted versions of the models.

Random effect selection

We began by selecting the best random effect structure. We considered random intercepts for species, park-summit-aspect, and summit-transition, random slopes for species' latitudinal ranges, and climPC1 and 2 with respect to species. Linear mixed models were fit for all combinations of the potential random effects and using the most complex fixed effect structure, including all main fixed effects and interactions that were of interest (Table 7). The models were fitted using maximum likelihood and AICc values were compared to select the optimal random effect structure.

Fixed effects selection with climate principal components

To determine the optimal fixed effect structure, we input a fitted model with the random effect structure selected as described above and with a global model with all species traits, climPC1 and 2, and selected interactions (Table 7) into the *dredge* function in the R environment. We fixed the random effects already supported and selected the model with the lowest AICc value from this output.

Explicit climate variable selection

After identifying the optimal fixed and random effect structure using the climPC models, we replaced the two climate principal component fixed effects selected for the climate PC model with explicit climate variables. To perform model selection on these fixed effects, we first grouped highly correlated climate variables, then created all combinations of variables across the four resulting groups. The four groups were: A) transition-level (5-year) minimum, mean, and maximum values for mean annual growing season temperature; B) mean annual growing season precipitation; C) the mean number of days with snow cover within water years (Oct 1–Sept 30) and the mean number of growing degree days within water years; and D) mean annual water year precipitation, and mean annual water year potential and actual evapotranspiration. We then fit mixed effect models by substituting in only one variable from each set of climate variables for climate PCs 1 & 2 (i.e., [start cover × climPC1] became [start cover × (mean growing season temperature + mean growing season precipitation]). We also let the number of climate variables range from one to four, such that not all climate variable groups were represented in all combinations. We fit each model using maximum likelihood and compared their AICc values. Finally, once the optimal set of explicit climate variables were selected, we ran this model through R's *dredge* function to determine the best fixed effect structure, given the selected set of explicit climate variables. We refit the best model using relative maximum likelihood to obtain fixed and random effect parameter estimates. Table 7 describes the sequence of model selection steps.

Table 7. Sequence of model selection steps, with a summary of the global models tested and the best-supported model structures. Steps 1 and 2 refer to model selection using the climate PC variables, while steps 3–5 refer to model selection using the suite of explicit climate variables (see Table 5).

Model selection step	**Input—Global Model**	**Output—Best-fit model**
1. Random effect structure selection	End Cover ~ Start cover × (mean latitudinal range + [mean latitudinal range]^2) + (start cover + mean latitudinal range + [mean latitudinal range]^2 + perennating + leaves + habit) × (climPC1 + climPC2 + site latitude) + Random effects	End Cover ~ Start cover × (mean latitudinal range + [mean latitudinal range]^2) + (start cover + mean latitudinal range + ([mean latitudinal range]^2 + perennating + leaves + habit) × (climPC1 + climPC2 + site latitude) + (1 | transition) + (climPC1 + climPC2 | species)
2. Fixed effect structure selection	End Cover ~ Start cover × (mean latitudinal range + [mean latitudinal range]^2) + (start cover + mean latitudinal range + [mean latitudinal range]^2 + perennating + leaves + habit) × (climPC1 + climPC2 + site latitude) + (1 | transition) + (climPC1 + climPC2 | species)	End cover ~ Start cover × (climPC1 + mean latitudinal range + [mean latitudinal range]^2 + summit latitude) + climPC2 × perennating + habit × (climPC1 + summit latitude) + (1 | transition) + (climPC1 + climPC2 | species)
3. Explicit climate variable selection (with random slopes removed for computational feasibility) [A]	End cover ~ Start cover × (climate variables + mean latitudinal range + [mean latitudinal range]^2 + summit latitude) + climate variables × perennating + habit × (climate variables + summit latitude) + (1 | transition)	End cover ~ Start cover × (gs.tmean + wy.ppt + gs.ppt + gdd + mean latitudinal range + [mean latitudinal range]^2 + summit latitude) + (gs.tmean + wy.ppt + gs.ppt + gdd) × perennating + habit × site latitude + (gs.tmean + wy.ppt + gs.ppt + gdd) × habit + (1 | transition)
4. Refit random slope structure with explicit climate variables	End cover ~ Start cover × (gs.tmean + wy.ppt + gs.ppt + gdd + mean latitudinal range + [mean latitudinal range]^2 + summit latitude) + (gs.tmean + wy.ppt + gs.ppt + gdd) × perennating + habit × site latitude + (gs.tmean + wy.ppt + gs.ppt + gdd) × habit + (1 | transition)	End cover ~ Start cover × (gs.tmean + wy.ppt + gs.ppt + gdd + mean latitudinal range + [mean latitudinal range]^2 +summit latitude) + (gs.tmean + wy.ppt + gs.ppt + gdd) × perennating + habit × site latitude + (gs.tmean + wy.ppt + gs.ppt + gdd) × habit + (1 | transition) + (gs.tmean + wy.ppt + gs.ppt + gdd | species)
5. Dredge fixed effect structure after refitting random slopes	End cover ~ Start cover × (gs.tmean + wy.ppt + gs.ppt + gdd + mean latitudinal range + [mean latitudinal range]^2 +summit latitude) + (gs.tmean + wy.ppt + gs.ppt + gdd) × perennating + habit × site latitude + (gs.tmean + wy.ppt + gs.ppt + gdd) × habit + (1 | transition) + (gs.tmean + wy.ppt + gs.ppt + gdd | species)	End cover ~ Start cover × (mean latitudinal range + [mean latitudinal range]^2 + gdd + gs.ppt + wy.ppt +summit latitude) + habit × (gdd +summit latitude) + perennating × gs.tmean + (1 | transition) + (gs.tmean + wy.ppt + gs.ppt + gdd | species)

[A] “Climate variable” refers to the climate variables described in the Appendix A: Supplementary Methods subsection “Explicit climate variable selection.”

Modeling changes in total vascular plant cover

The model selection process for total vascular plant cover was very similar to that for species-specific models, and is therefore described briefly here, highlighting the minor differences.

First, with the most complex fixed effect structure including the two climate principal components, we compared three combinations of two possible random intercept terms, park-summit-aspect and summit-transition, to determine the best random effect structure. We then ran the resulting model through *dredge* to determine the best fixed effect structure from the global model incorporating climate principal components. Neither climate principal component was included in the best model.

As with species-specific models above, we replaced climate principal components with explicit climate variables. Given that neither climate principal component was selected in the best model described above, we replaced explicit climate variables for climate principal components in the model with the most complex fixed effect structure. The same four groups of highly correlated climate variables were used here as in the species-specific model. We fit mixed effects models with the optimal random effect structure, the most complex fixed effect structure using all combinations of explicit climate variables from the four groupings using maximum likelihood and selected the best model by comparing AICc values. We then ran the model with the lowest AICc value though the *dredge* function to find the optimal fixed effect structure. We refit the best model using relative maximum likelihood to obtain fixed and random effect parameter estimates.

Appendix B: Species of special interest

Species of interest model selection

We had adequate data to analyze trends for 19 species or groups in the species of interest (SOI) list we received from park personnel (Table 8). Other species had very limited occurrence data that would not support analysis of their changing cover values (<20 transitions or change cover estimates in the analysis dataset) or lacked data entirely. For each SOI with adequate data, we fit the two species-level global models (climPC and climVar models) using data only for that SOI. The structure of the two best global models were adjusted to account for lack of variation in species-level predictor variables in these single species models. We then ran models fitted to each SOI's data through the *dredge* function to determine which predictor variables were important in explaining observed changes in percent cover for the SOI. Table 9 shows the coefficients of best-supported models for each SOI.

Table 8. List of species of interest identified by park staff, based on cultural, ecological, or restoration importance, denoted by an "X."

Common name (species, genus, or group)	Scientific name	Cultural	Restoration	Ecological	Notes
American bistort	*Polygonum bistortoides*	X	X	N/A	Included
Pussytoes	*Antennaria* spp.	N/A	X	N/A	Included
Alpine sagebrush	*Artemisia scopulorum*	N/A	X	N/A	Included
Sedge	*Carex* spp.	N/A	X	N/A	Included
Slender wheatgrass	*Elymus trachycaulus*	N/A	X	N/A	Included
Spreading wheatgrass	*Elymus scribneri*	N/A	X	N/A	Included
Onestem fleabane	*Erigeron simplex*	N/A	X	N/A	Included
Fendler's sandwort	*Arenaria fendleri*	X	N/A	N/A	Included
Ross' avens	*Geum rossii*	N/A	X	X	Included
Prairie bluebells	*Mertensia lanceolata*	X	N/A	N/A	Included
Paintbrush	*Castilleja* spp.	X	N/A	N/A	Included
Twinflower sandwort	*Minuartia obtusiloba*	N/A	X	N/A	Included
Moss campion	*Silene acaulis*	X	X	N/A	Included
Sticky polemonium	*Polemonium viscosum*	N/A	N/A	X	Included
Stone crop	*Sedum lanceolatum*	X	N/A	N/A	Included
Clover	*Trifolium* spp.	N/A	X	N/A	Included
Spike trisetum	*Trisetum spicatum*	N/A	X	N/A	Included
Yarrow	*Achillea millefolium*	X	N/A	N/A	Included
Cinquefoil	*Potentilla* spp.	N/A	N/A	X	Included
Rock spikemoss	*Selaginella densa*	X	N/A	N/A	Not enough data
Alpine bistort	*Polygonum viviparum*	X	N/A	N/A	Not enough data

Table 8 (continued). List of species of interest identified by park staff, based on cultural, ecological, or restoration importance, denoted by an "X."

Common name (species, genus, or group)	Scientific name	Cultural	Restoration	Ecological	Notes
Arctic bellflower	*Campanula uniflora*	X	N/A	N/A	Not enough data
Tufted hairgrass	*Deschampsia cespitosa*	X	X	N/A	Not enough data
Flowery phlox	*Phlox multiflora*	X	N/A	N/A	Not enough data
Alpine mountain sorrel	*Oxyria digyna*	N/A	X	N/A	Not enough data
Ledge stonecrop	*Rhodiola integrifolia*	N/A	X	N/A	Not enough data
Alpine willow	*Salix petrophila*	X	N/A	X	Not enough data
Willow	*Salix* spp.	X	N/A	N/A	Not enough data
Rocky Mountain blue columbine	*Aquilegia saximontana*	N/A	N/A	X	Not present in data
Copper-scale sedge	*Carex chalciolepis*	N/A	X	N/A	Not present in data
Chokecherries	*Aronia/Prunus* spp.	X	N/A	N/A	Not present in data
Mountain avens	*Dryas octopetala*	N/A	X	X	Not present in data
Gooseberries	*Ribes montigenum*	X	N/A	N/A	Not present in data
Graylocks four-nerve daisy	*Hymenoxys/Rydbergia grandiflora*	N/A	X	X	Not present in data
King's crown	*Sedum roseum*	X	N/A	N/A	Not present in data
Mountain death camus	*Zigadenus elegans*	X	N/A	N/A	Not present in data
Osha	*Ligusticum porteri*	X	N/A	N/A	Not present in data
Shortfruit willow	*Salix brachycarpa*	N/A	N/A	X	Not present in data
Serviceberry	*Amelanchier* spp.	X	N/A	N/A	Not present in data
Buttercup	*Ranunculus*	N/A	N/A	X	Not enough data

Table 9. Coefficients of best-supported models for each species of interest (SOI). The first row in the table shows the coefficients for the general species models for comparison. Blue cells indicate positive effects, while red indicates negative effects. The similarity of sign and magnitude of most SOI coefficients to that of the overall model (shown in the first row) indicates that the drivers of changing abundance for most SOI were comparable to those for rest of the flora surveyed.

SOI	**Intercept**	**Start cover**	**gdd**	**gs.ppt**	**wy.ppt**	**gs.tmean**	**Site lat.**	**Mean spp. lat**	**Mean spp. lat.^{2}**	**Habit – shrub**	**Start cover × gdd**	**Start cover × site lat**	**Start cover × wy.ppt**	**Start cover × gs.ppt**	**Start cover × mean spp. lat^2**	**Perennating-woody × gs.temp**
Main species cover model	1.3365	−1.812	0.0041	−0.0003	0.0003	−0.0102	−0.0238	−0.0344	0.0003	4.9881	0.0093	−0.0518	0.0014	−0.0038	−0.0009	0.0003
Antennaria spp.	3.3684	−0.1542	−0.0296	−0.0019	0.0001	0.1478	N/A	N/A	N/A	N/A	N/A	N/A	0.0013	N/A	N/A	N/A
Polemonium viscosum	−0.985	5.0152	0.0061	N/A	N/A	N/A	N/A	N/A	N/A	N/A	−0.0228	N/A	N/A	N/A	N/A	N/A
Potentilla spp.	−10.4793	0.5542	0.0059	−0.0006	0.0014	0.0549	−0.1271	0.5825	−0.0061	−1.6574	−0.0083	N/A	0.001	N/A	0.0003	0.2272
Trisetum spicatum	−0.1743	2.2094	0.0119	N/A	N/A	N/A	−0.0348	N/A	N/A	N/A	−0.0122	N/A	N/A	N/A	N/A	N/A
Trifolium spp.	−3.2037	−4.4968	0.0029	0.0164	0.0011	0.002	N/A	N/A	N/A	N/A	0.02	N/A	0.0027	N/A	N/A	N/A
Castilleja spp.	−3.4161	0.2652	−0.0073	0.0121	0.0009	0.2345	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Silene acaulis	0.9013	2.191	0.021	0.0065	0.0039	N/A	−0.2094	N/A	N/A	N/A	N/A	N/A	N/A	−0.0096	N/A	N/A
Sedum lanceolatum	1.6986	−19.5346	0	N/A	N/A	N/A	−0.0379	N/A	N/A	N/A	0.0204	0.4101	N/A	N/A	N/A	N/A
Graminoids	2.437	0.2133	0.0091	0.001	0.0009	−0.037	−0.0984	N/A	N/A	N/A	0.0152	−0.0461	0.0009	−0.006	N/A	N/A
Minuartia obtusiloba	1.1035	1.7701	0.045	0.0095	0.0067	N/A	−0.3505	N/A	N/A	N/A	N/A	N/A	N/A	−0.0082	N/A	N/A
Polygonum bistortoides	−0.4288	−5.5764	0.0022	−0.0054	−0.0002	N/A	0.0218	N/A	N/A	N/A	0.0425	−0.2662	0.0073	0.0349	N/A	N/A
Carex spp.	−2.6446	1.7197	0.0702	−0.0047	0.0072	0.4059	−0.4581	N/A	N/A	N/A	N/A	N/A	N/A	−0.007	N/A	N/A
Arenaria fendleri	−3.0042	−18.2226	0.0045	0.0153	0.0009	N/A	N/A	N/A	N/A	N/A	0.0692	N/A	0.0077	0.0133	N/A	N/A
Geum rossii	−0.9776	3.3237	N/A	0.011	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	−0.0193	N/A	N/A
Mertensia lanceolata	−0.0114	−2.5372	N/A	N/A	0.0001	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.0045	N/A	N/A	N/A
Achillea millefolium	11.8948	−3.2826	N/A	N/A	N/A	N/A	−0.2476	N/A	N/A	N/A	N/A	0.0904	N/A	N/A	N/A	N/A
Artemisia scopulorum	0.1322	0.5992	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Elymus trachycaulus	0.0732	0.9532	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Erigeron simplex	−5.3106	0.2203	N/A	N/A	N/A	N/A	0.1396	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

Plots are shown for each species of special interest with enough data to develop individual species models (Figures 33–53). The top left plot for all species shows observed changes in cover by starting cover values with data points and trend lines. All additional plots correspond to explanatory variables selected in the main model for each species and show the predicted change in cover (y-axis) across the range of observed values for the explanatory variable on the x-axis, with any additional variables set to their median observed value.

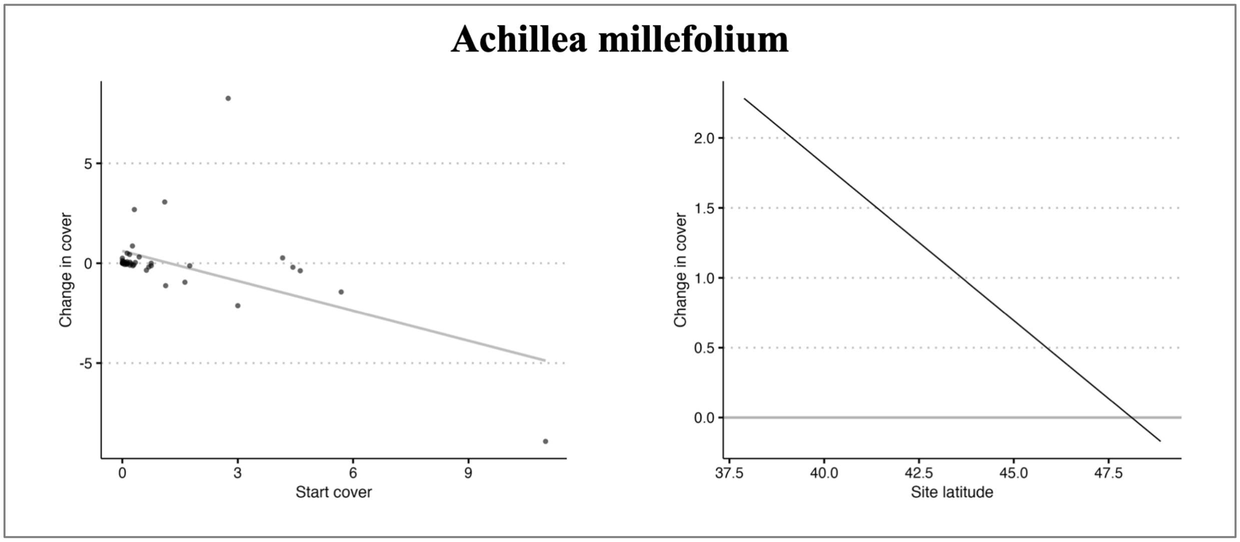

Figure 33. Observed changes in cover (y-axis) by starting cover values (x-axis, left) and site latitude (right) for *Achillea millefolium*. Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated negatively with start cover and site latitude. NPS

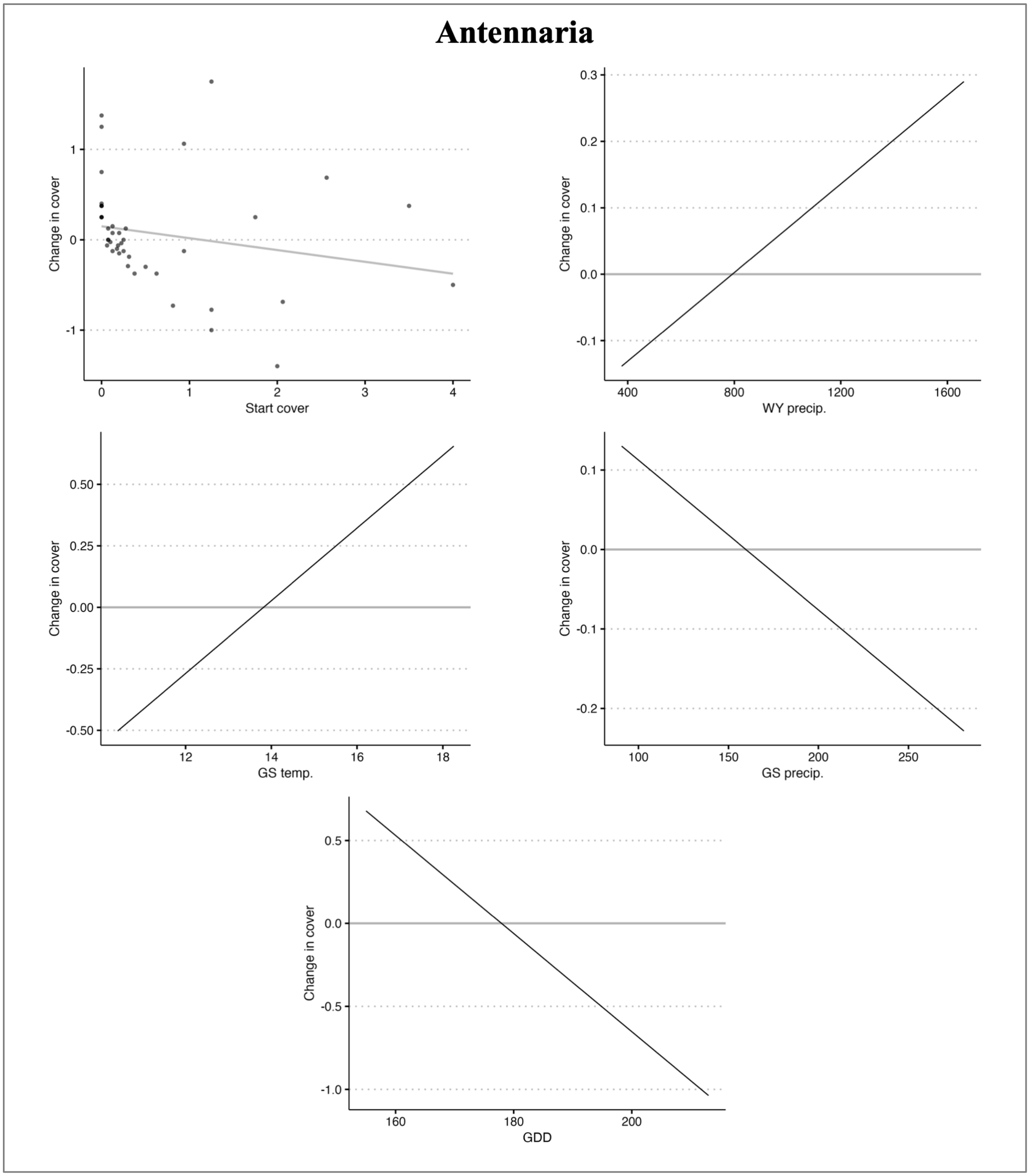

Figure 34. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Antennaria* spp. Dots represent data points and lines are linear regression fits. Change in abundance in these taxa were associated positively with water year precipitation and growing season temperature and negatively with growing season precipitation and growing degree days. NPS

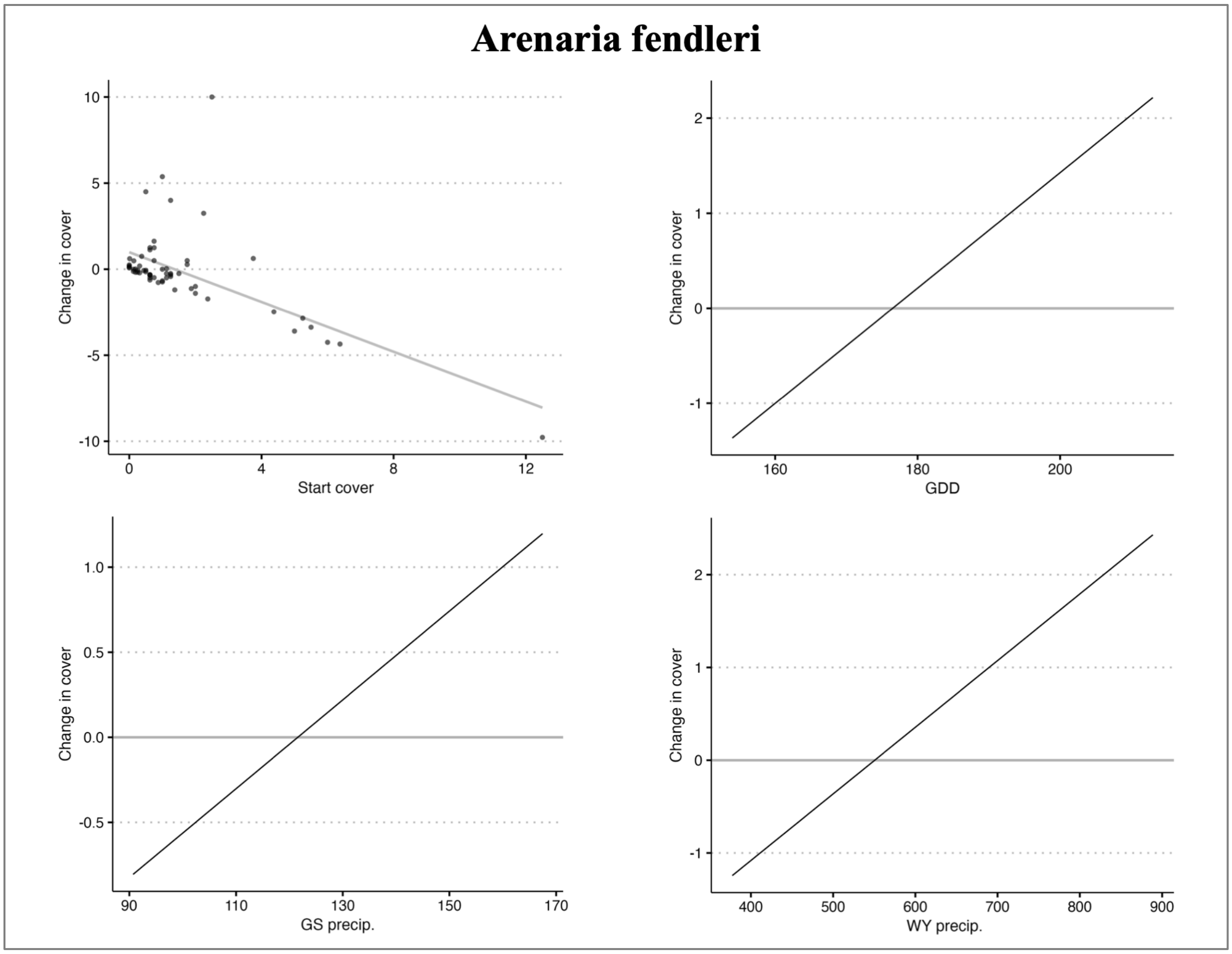

Figure 35. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Arenaria fendleri.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with growing degree days, growing season precipitation, and water year precipitation and negatively with start cover. NPS

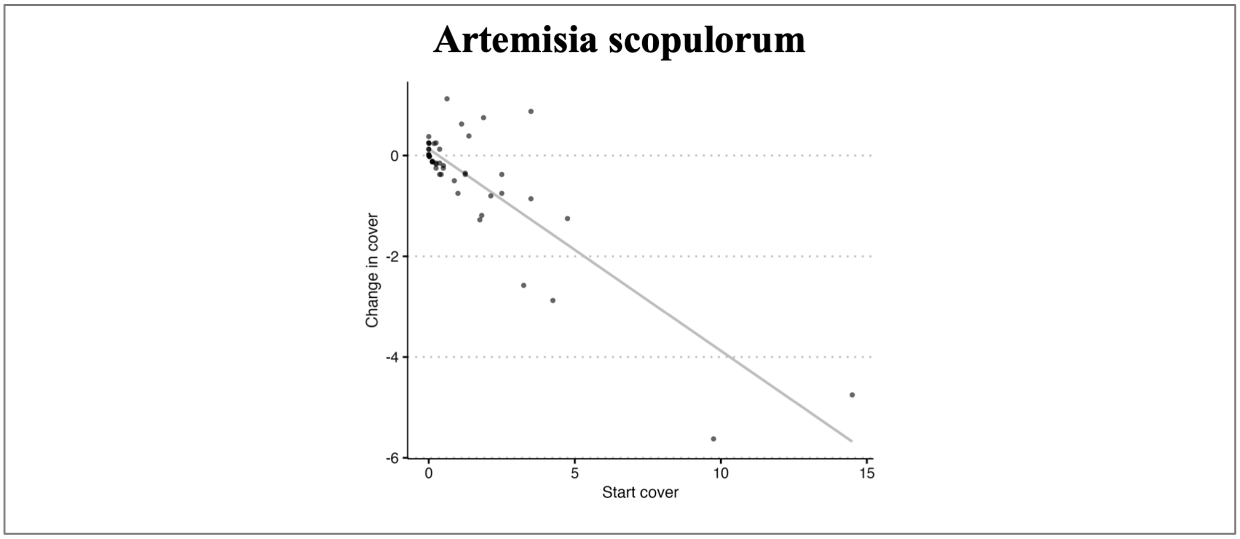

Figure 36. Observed changes in cover (y-axis) by start cover (x-axis) for *Artemisia scopulorum.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated negatively with start cover. NPS

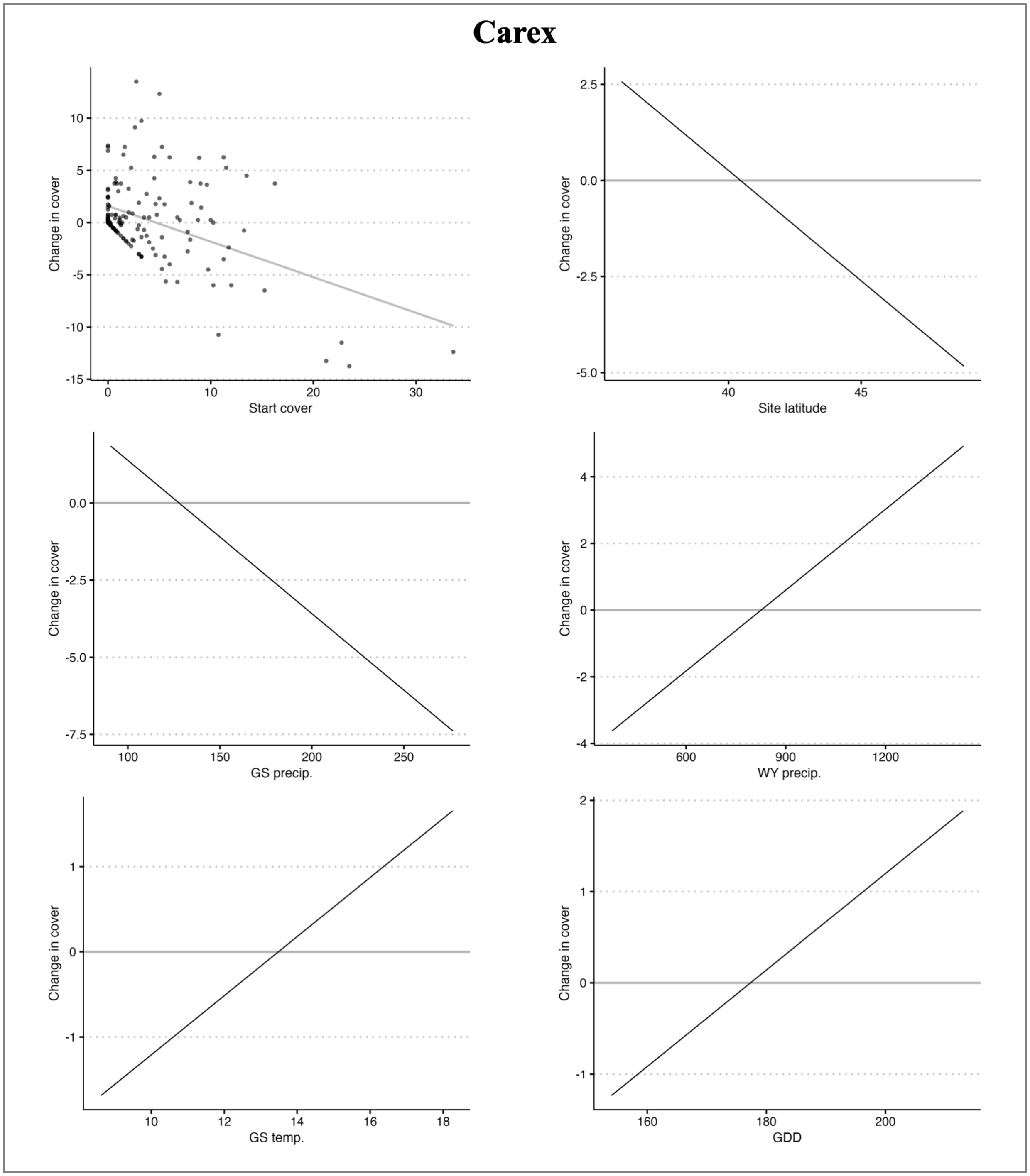

Figure 37. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Carex* spp. Dots represent data points and lines are linear regression fits. Change in abundance in *Carex* spp. were associated positively with water year precipitation, growing season temperature, and growing degree days and negatively with start cover, site latitude, and growing season precipitation. NPS

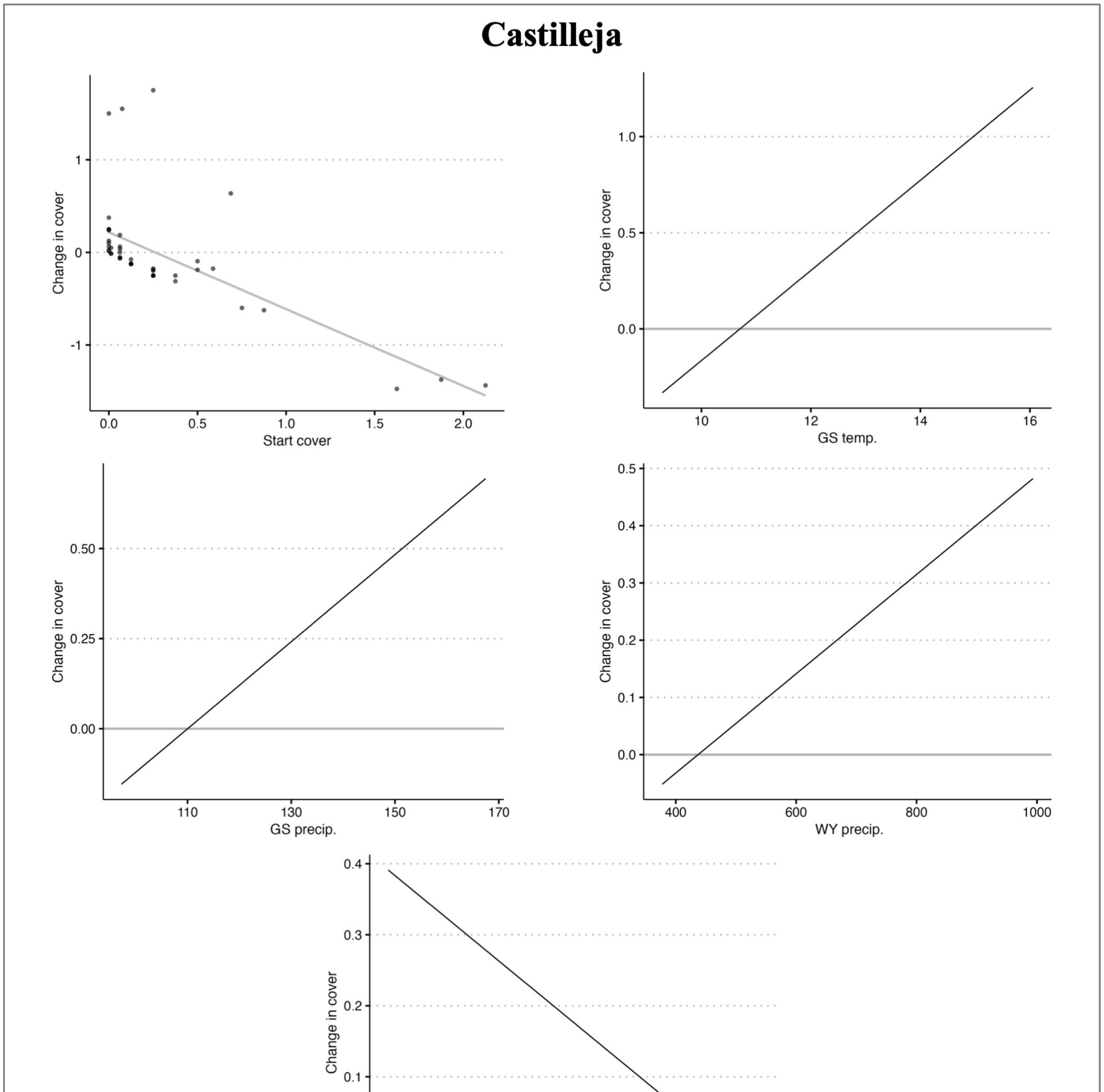

Figure 38. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Castilleja* spp. Dots represent data points and lines are linear regression fits. Change in abundance in these taxa were associated positively with growing season temperature, growing season precipitation, and water year precipitation and negatively with start cover and growing degree days. NPS

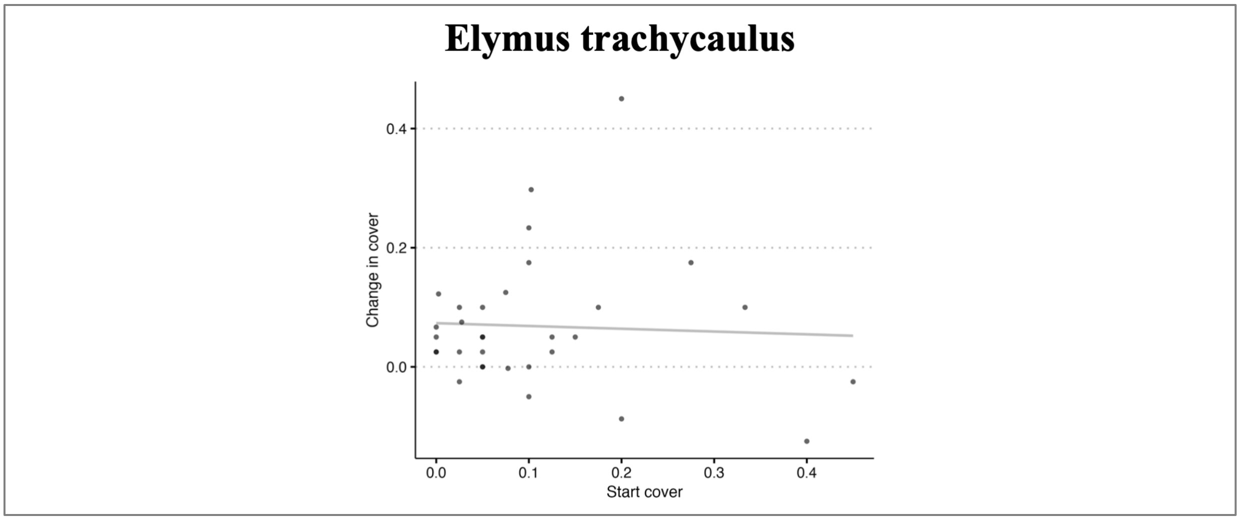

Figure 39. Observed changes in cover (y-axis) by start cover (x-axis) for *Elymus trachycaulus.* Dots represent data points and lines are linear regression fits. There was little difference in the change in abundance of this species related to start cover. NPS

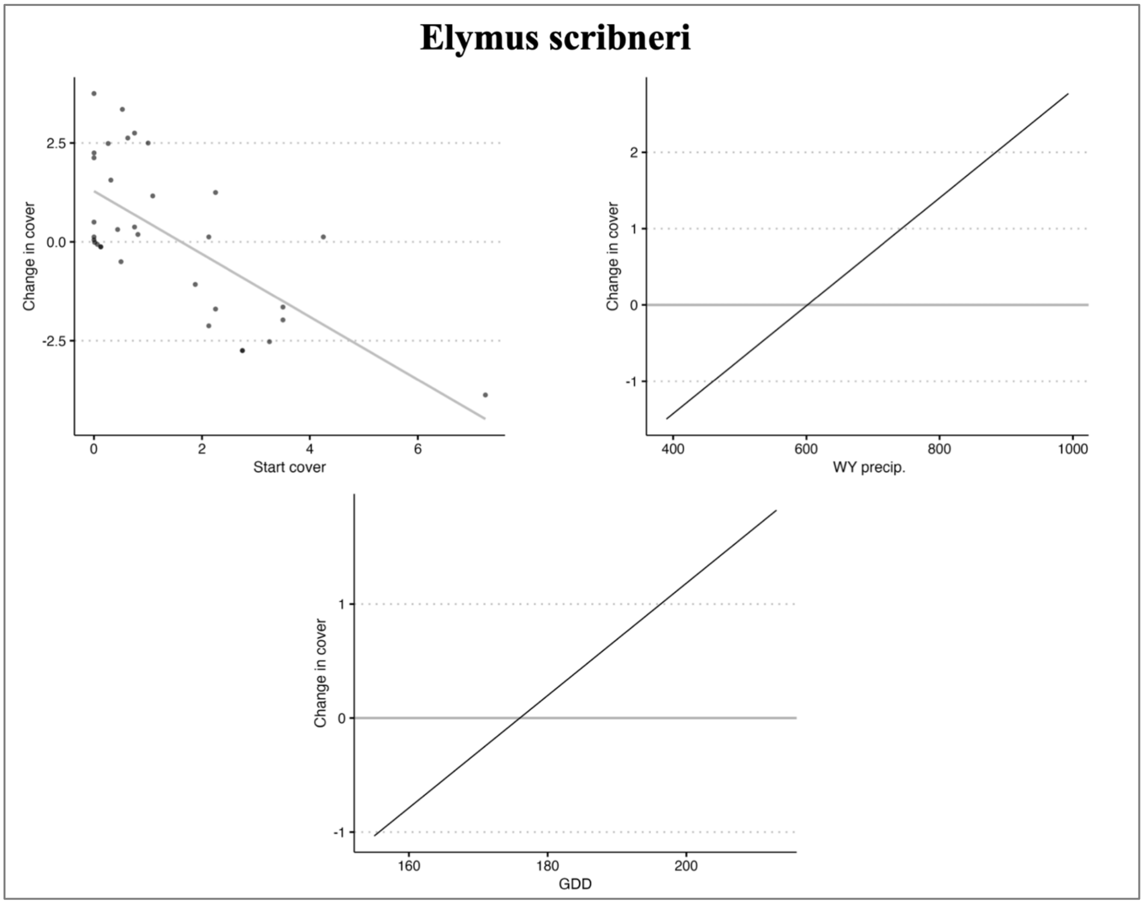

Figure 40. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Elymus scribneri.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with water year precipitation and growing degree days and negatively with start cover. NPS

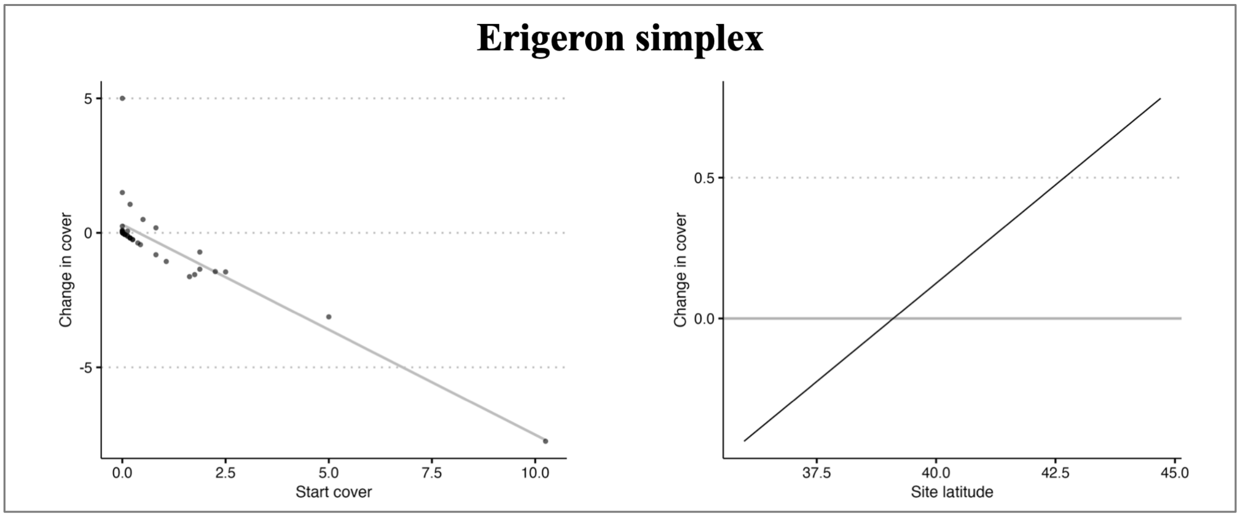

Figure 41. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Erigeron simplex.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with site latitude and negatively with start cover. NPS

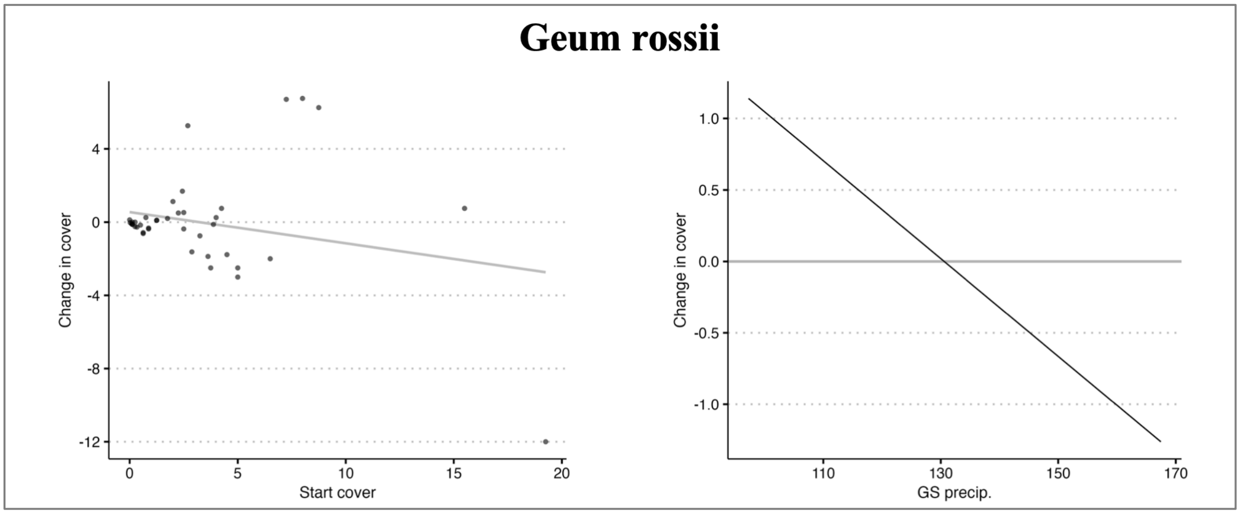

Figure 42. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Geum rossii.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated negatively with start cover and growing season precipitation. NPS

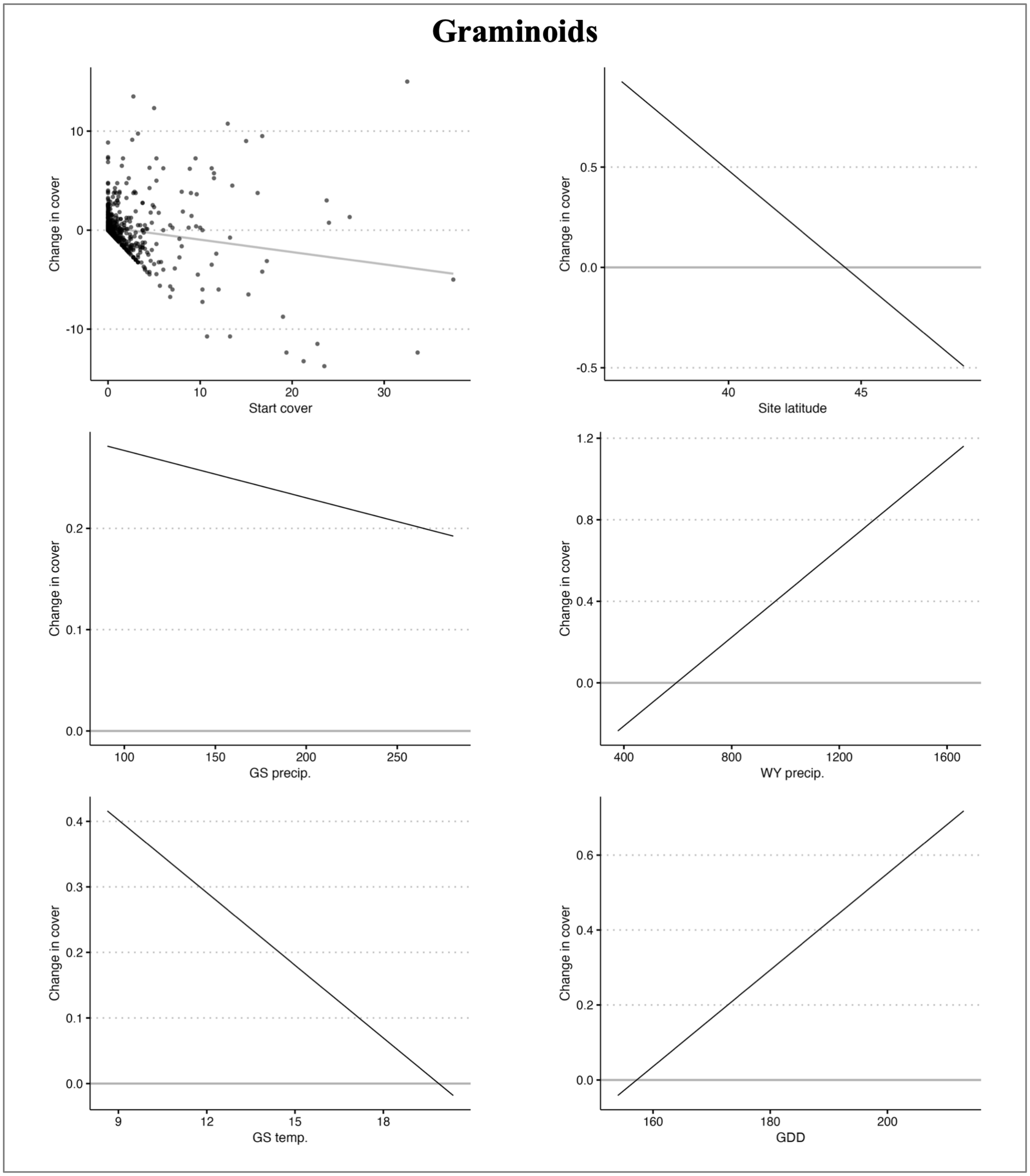

Figure 43. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for graminoids. Dots represent data points and lines are linear regression fits. Change in abundance in this group was associated positively with water year precipitation and growing degree days and negatively with start cover, site latitude, growing season precipitation, and growing season temperature. NPS

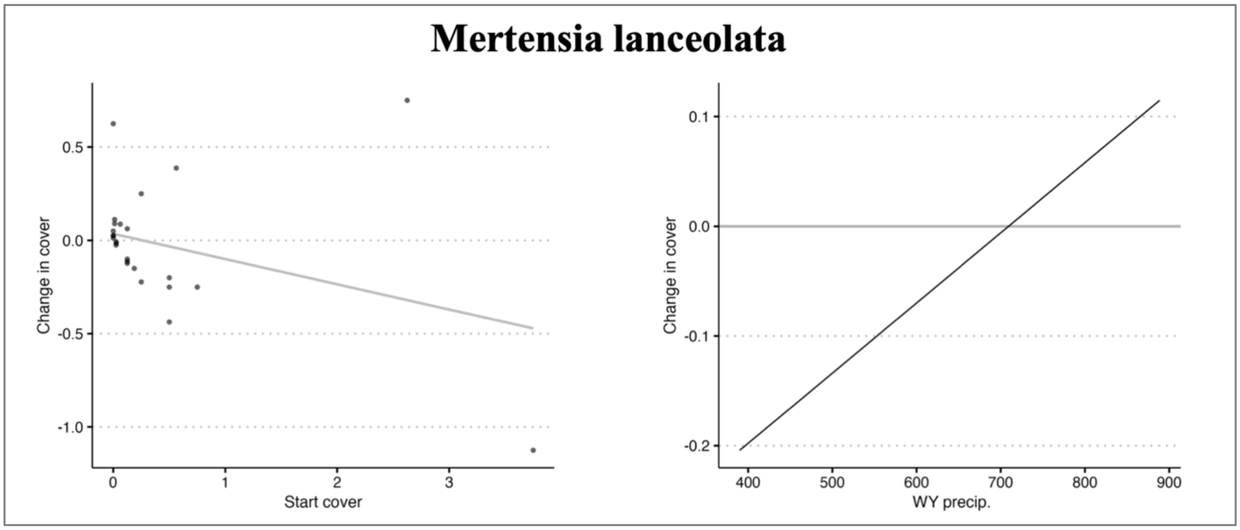

Figure 44. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Mertensia lanceolata.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with water year precipitation and negatively with start cover. NPS

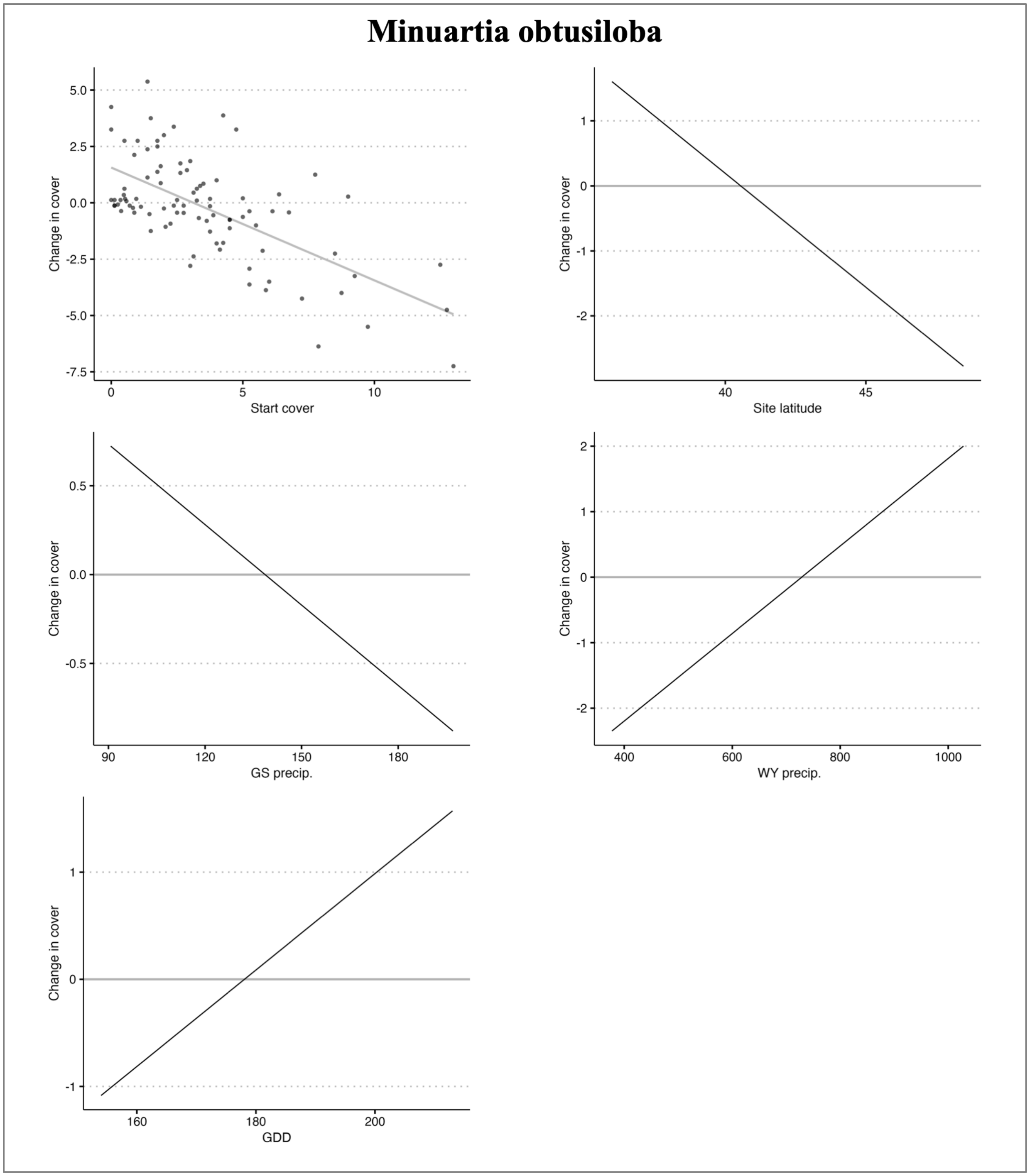

Figure 45. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Minuartia obtusilada.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with water year precipitation and growing degree days and negatively with start cover, site latitude, and growing season precipitation. NPS

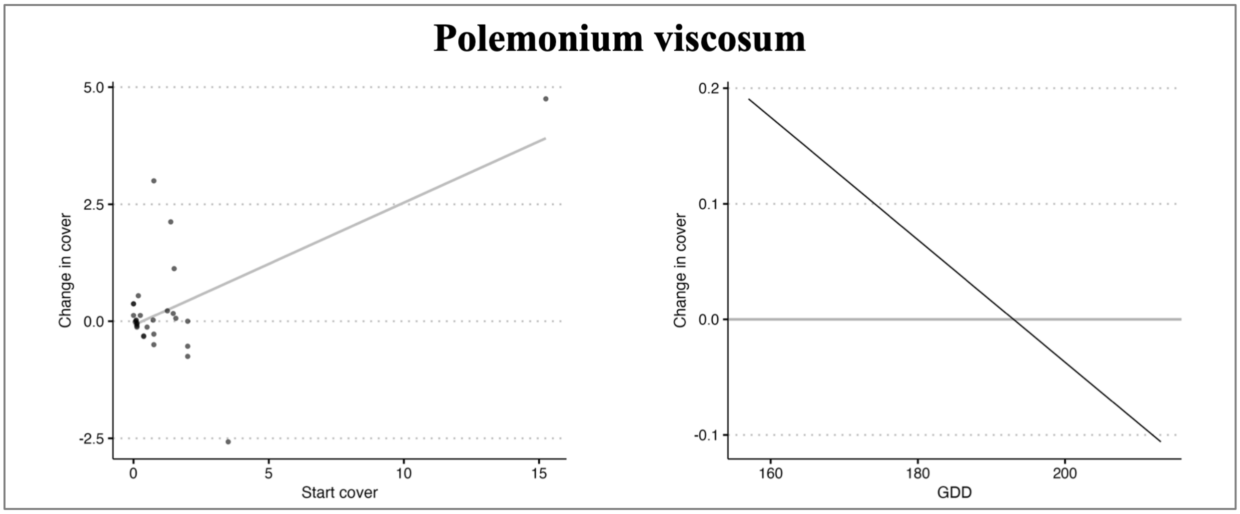

Figure 46. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Polemonium viscosum.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with start cover (unlike most other species) and negatively with growing degree days. NPS

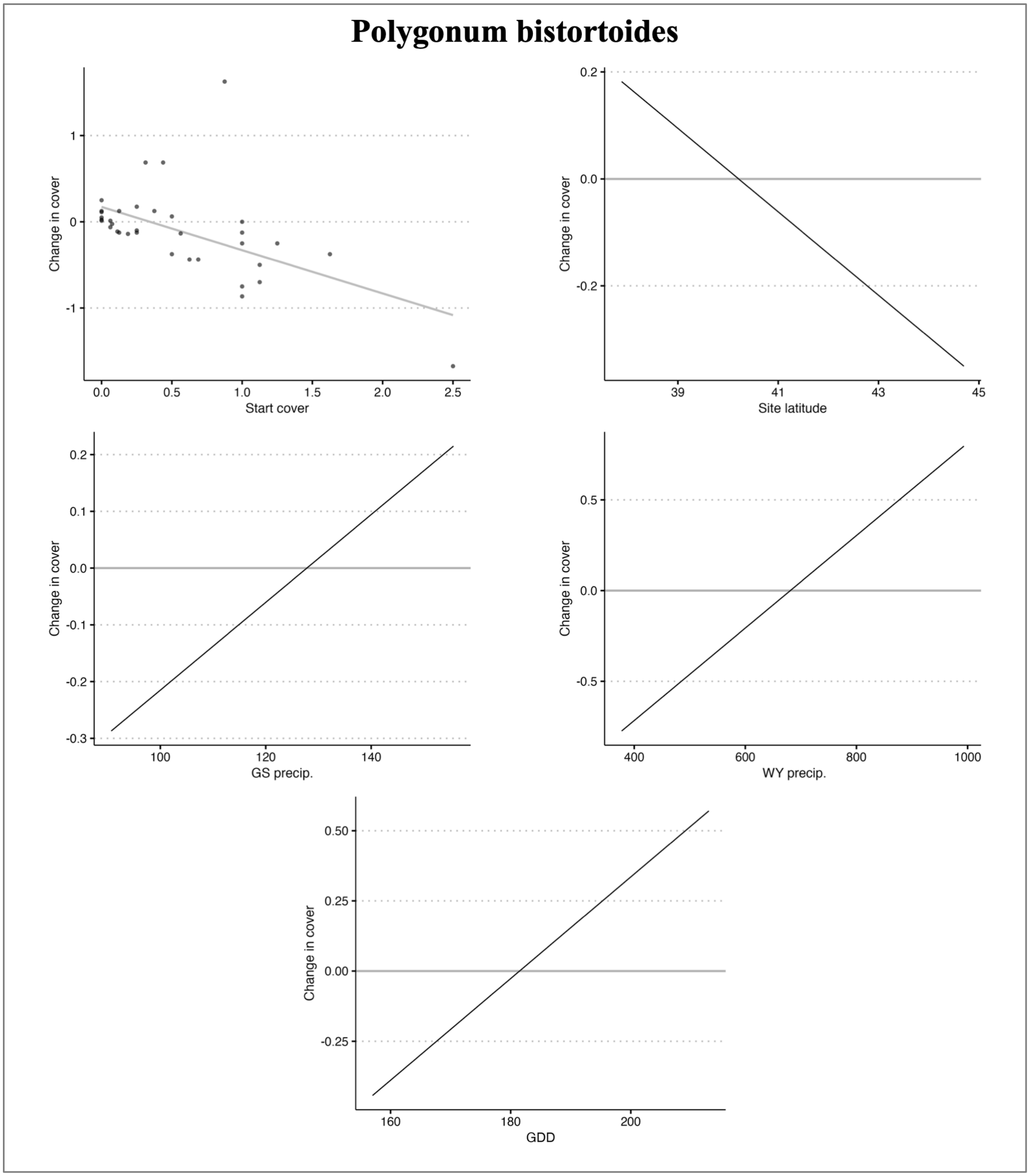

Figure 47. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Polygonum bistortoides.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with growing season precipitation, water year precipitation, and growing degree days and negatively with start cover and site latitude. NPS

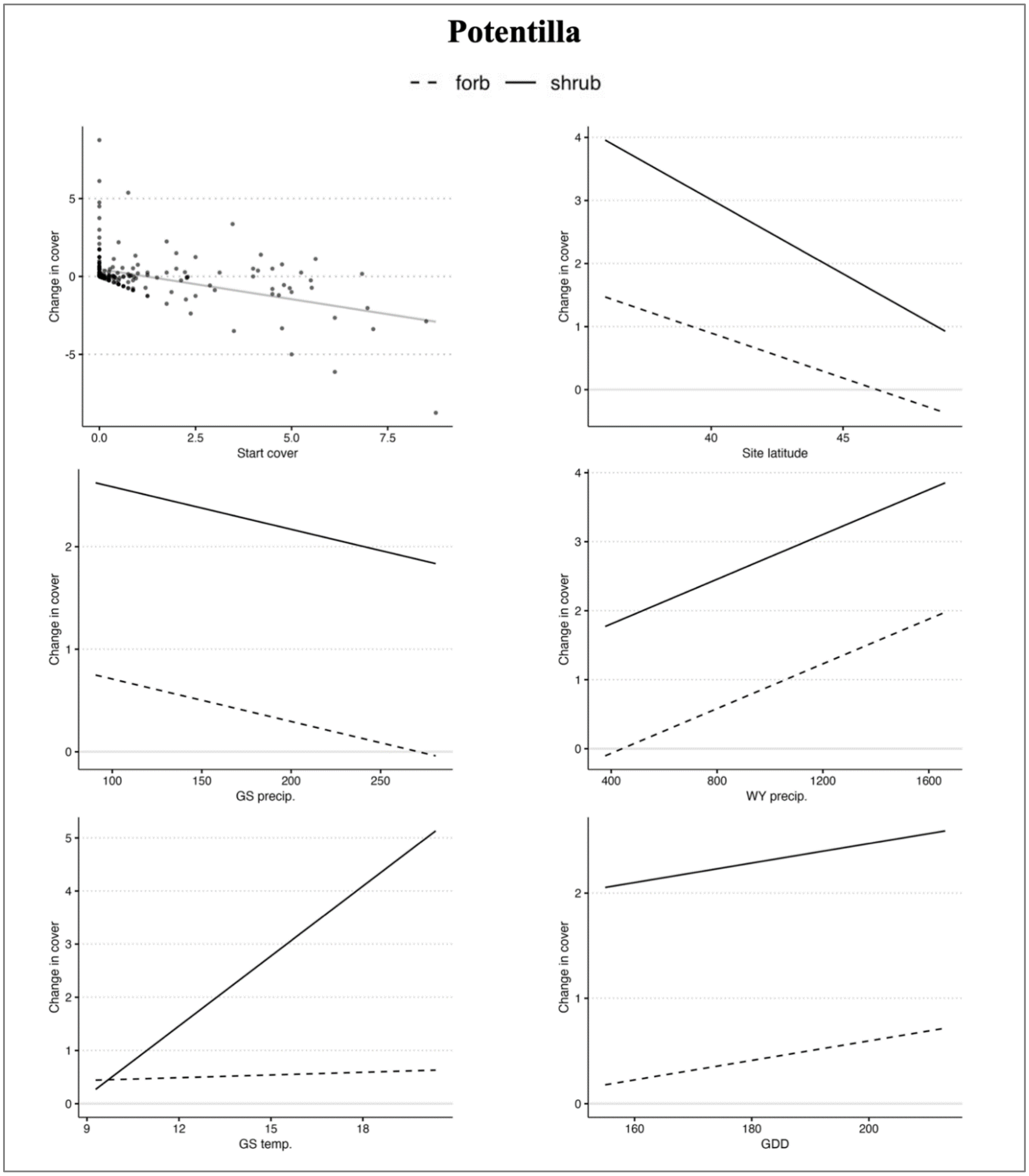

Figure 48. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Potentilla* spp. In the top left panel, dots represent data points, and the line represents the linear regression fit for change cover versus starting cover for the whole genus. In all other panels, dashed lines represent regression fits for forb species (11 species) and solid lines represent the single shrub species (*Potentilla fruticosa*). Change in abundance in these taxa were associated positively with water year precipitation, growing season temperature, and growing degree days and negatively with start cover, site latitude, and growing season precipitation. NPS

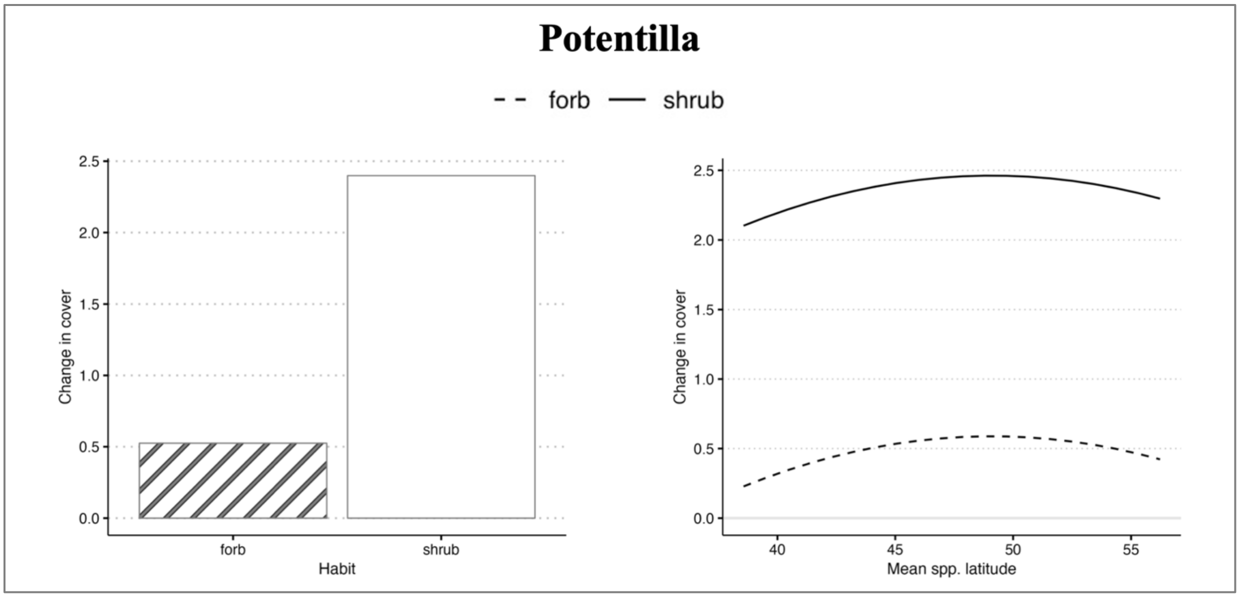

Figure 49. The left panel shows changes in *Potentilla* spp. cover as a function of habit, and the right panel shows changes in cover as a function of mean species latitude (geographical range). Dashed and solid lines in the right panel represent forbs and shrubs, respectively. NPS

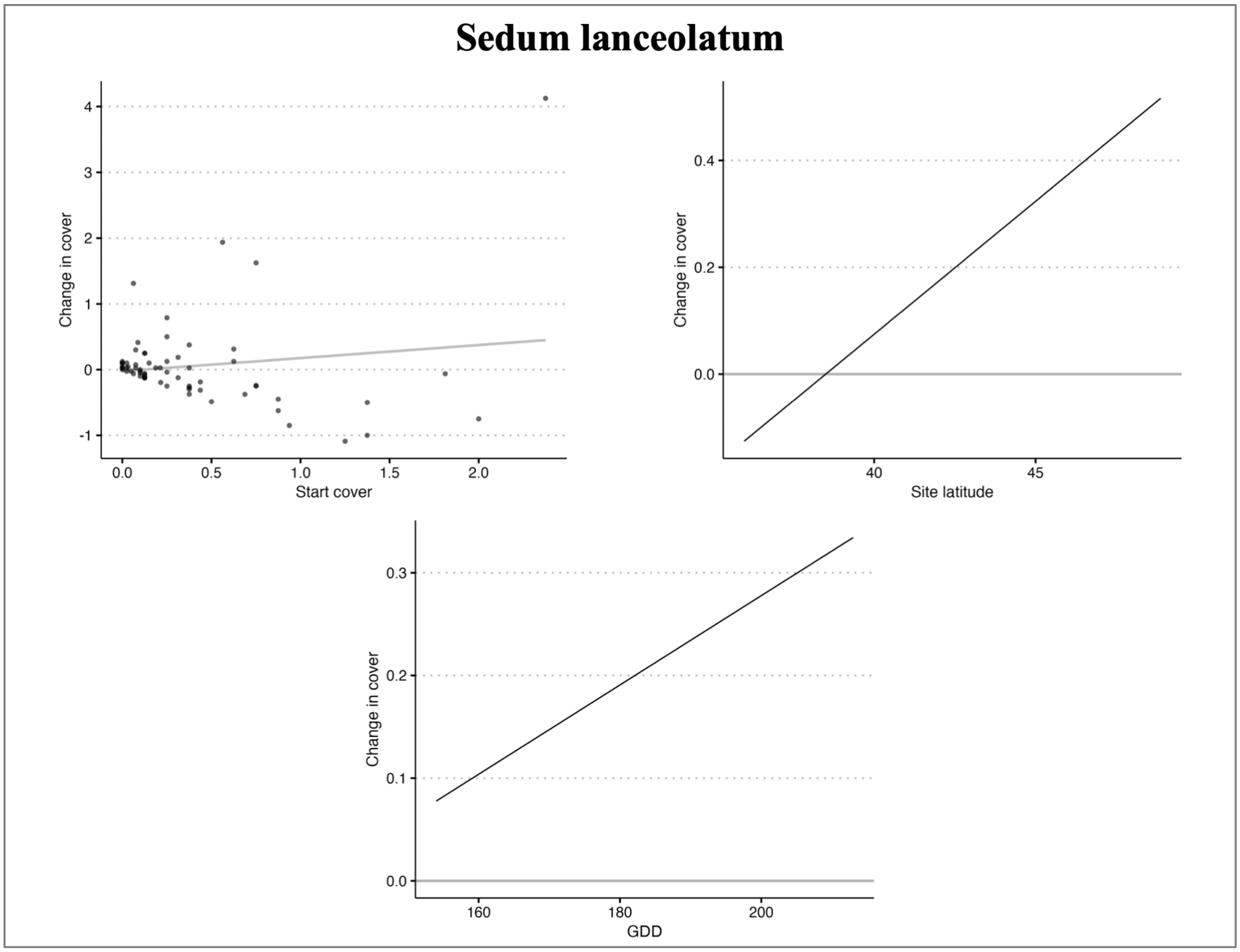

Figure 50. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Sedum lanceolatum.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with site latitude and growing degree days and, to a lesser extent, start cover. NPS

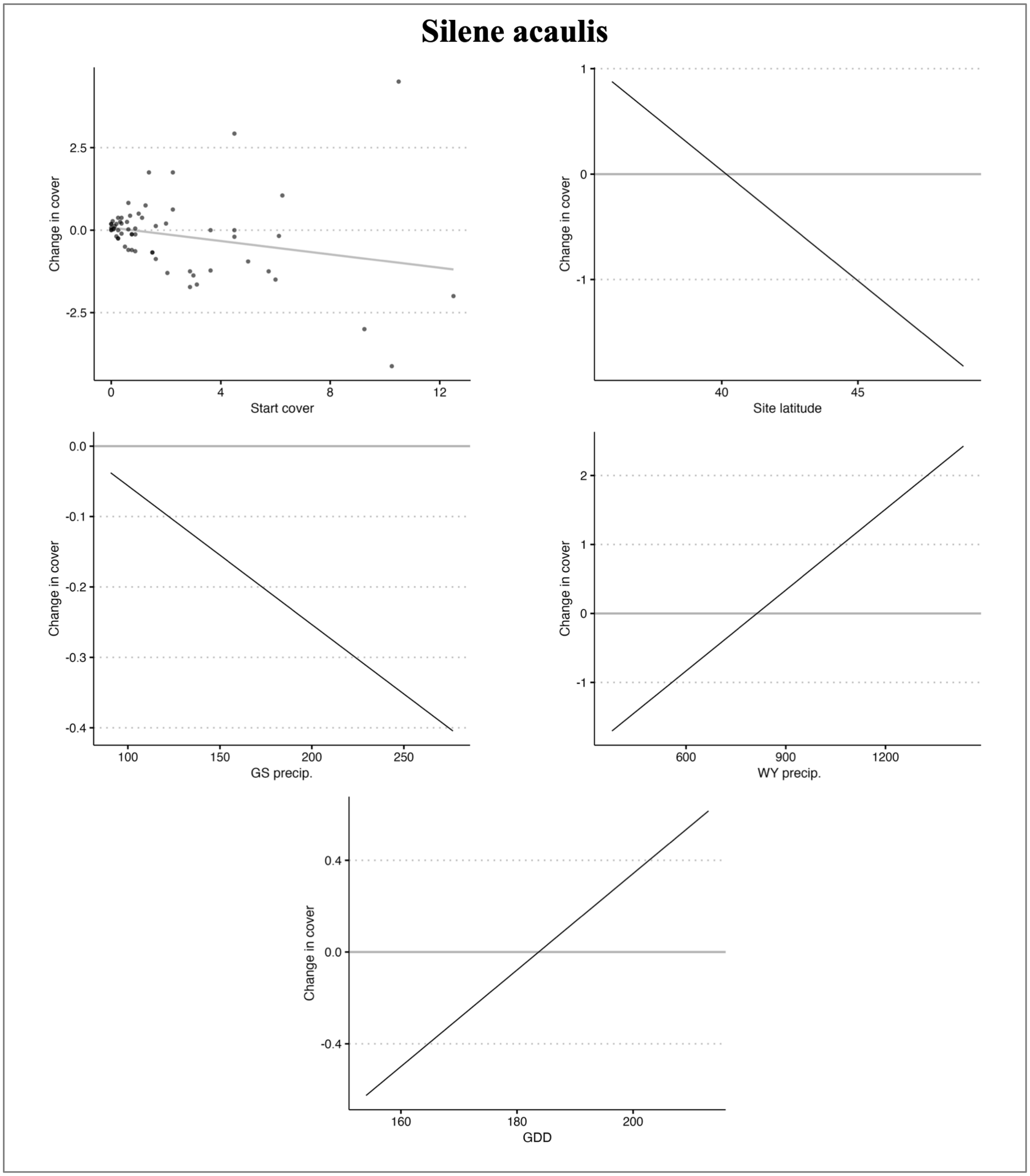

Figure 51. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Silene acaulis.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with water year precipitation and growing degree days and negatively with start cover, site latitude, and growing season precipitation. NPS

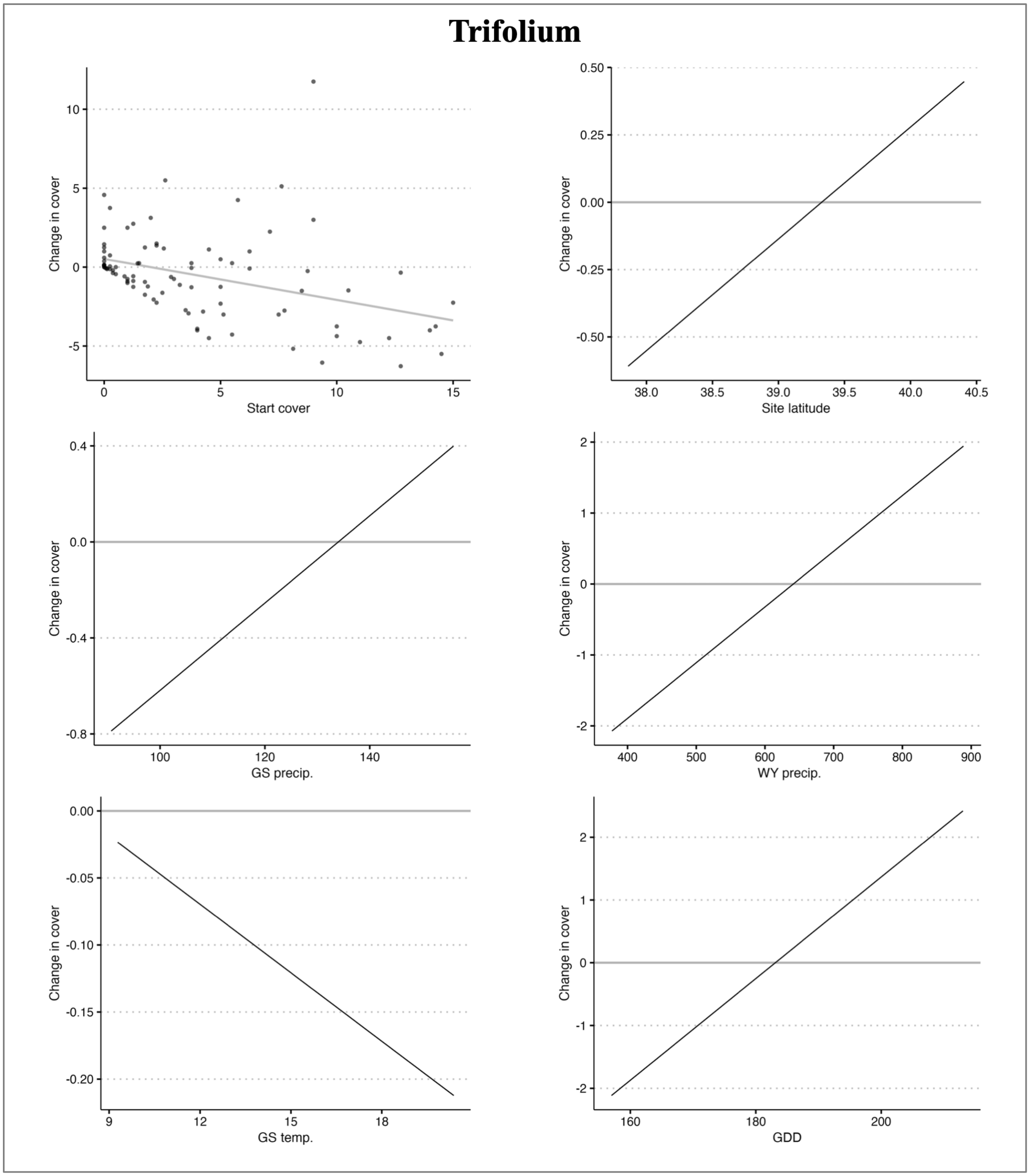

Figure 52. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Trifolium* spp. Dots represent data points and lines are linear regression fits. Change in abundance in these taxa were associated positively with site latitude, growing season precipitation, water year precipitation, and growing degree days and negatively with start cover and growing season temperature. NPS

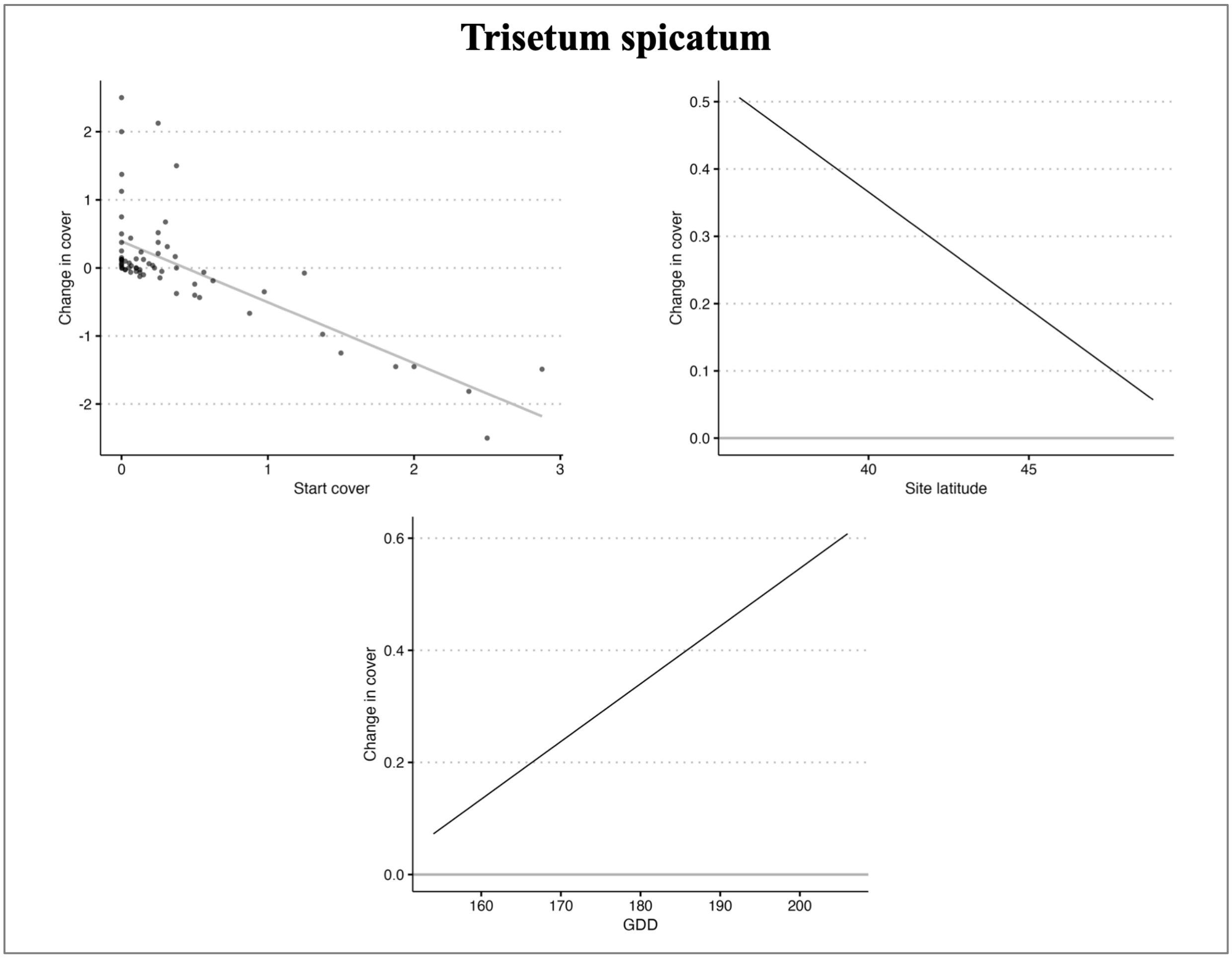

Figure 53. Observed changes in cover (y-axis) by various explanatory variables (x-axis) for *Trisetum spicatum.* Dots represent data points and lines are linear regression fits. Change in abundance in this species was associated positively with growing degree days and negatively with start cover and site latitude. NPS

Appendix C: Supplementary Results

Change in species abundance models

Species random effects

Figure 54 and Tables 10–14 show supplementary results related to species random effects.

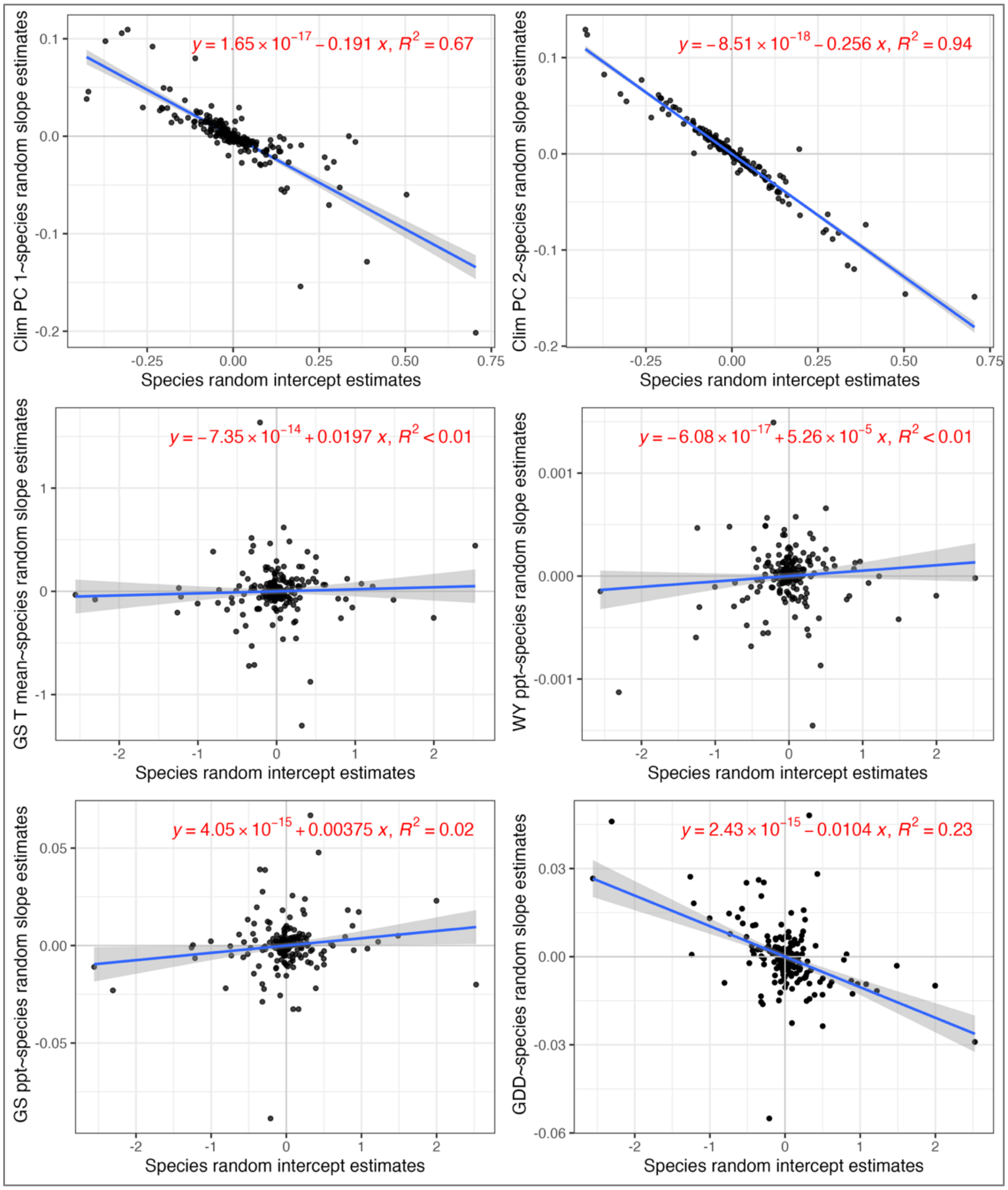

Figure 54. Correlations between random intercept and random slope modes for all taxa, including those without significant condition modes. For most climate variables, there is a negative correlation between the random slope mode and the random intercept mode, indicating a lower positive slope between cover and a climate variable is often compensated for by a higher intercept. NPS

Table 10. Random intercept and slope values for species that showed one or more significant random effects in either the climPC or climVar models. Random estimates with 95% credible intervals not overlapping zero are bolded and the table cell is colored blue (positive) or red (negative).

Species	climPC model intercept	climVar model intercept	climPC1	wy.ppt	gs.ppt	climPC2	gs.t mean	gdd
climPC model	2.145	–	0.023	–	–	−0.017	–	–
climVar model	–	1.337	–	0.000	0.000	–	−0.010	0.004
Agoseris glauca	0.097	0.325	−0.015	0.000	−0.009	−0.027	0.238	−0.014
Arenaria congesta	−0.421	−0.351	0.046	−0.001	0.039	0.124	−0.723	0.026
Arenaria fendleri	0.156	−0.629	−0.053	0.000	0.006	−0.029	−0.178	0.013
Astragalus bourgovii	−0.307	−0.126	0.109	0.000	0.005	0.055	−0.123	0.006
Carex elynoides	0.504	2.526	−0.060	0.000	−0.020	−0.146	0.442	−0.029
Carex obtusata	0.310	−0.210	−0.053	0.001	−0.089	−0.082	1.635	−0.055
Carex paysonis	0.132	0.321	−0.012	−0.001	0.067	−0.040	−1.301	0.048
Carex rossii	−0.009	−0.807	−0.003	0.000	−0.022	0.005	0.384	−0.009
Carex rupestris	0.705	−2.307	−0.202	−0.001	−0.023	−0.149	−0.079	0.046
Danthonia intermedia	−0.018	0.818	0.006	0.000	0.018	0.003	−0.260	0.001
Erigeron melanocephalus	0.278	0.430	−0.071	−0.001	0.048	−0.063	−0.877	0.028
Erigeron ochroleucus	−0.426	−0.283	0.038	−0.001	0.039	0.129	−0.713	0.025
Erigeron rydbergii	0.293	0.392	−0.026	0.000	−0.022	−0.089	0.383	−0.013
Erigeron simplex	−0.170	−0.064	0.021	0.000	−0.007	0.049	0.210	−0.012
Erigeron ursinus	0.147	0.092	−0.003	0.001	−0.033	−0.049	0.618	−0.023
Festuca brachyphylla	−0.324	−1.242	0.106	0.000	0.000	0.062	0.032	0.001
Geum rossii	0.336	0.406	0.000	0.000	−0.011	−0.116	0.091	0.004
Juncus drummondii	0.057	−0.318	−0.005	0.000	−0.029	−0.017	0.517	−0.015
Kobresia myosuroides	0.196	−2.557	−0.154	0.000	−0.011	0.005	−0.034	0.027
Minuartia obtusiloba	0.078	−1.215	−0.029	0.000	−0.007	−0.013	−0.053	0.018
Oreostemma alpigenum	−0.153	−0.050	0.015	0.000	0.018	0.045	−0.328	0.011
Oreoxis alpina	0.093	−1.004	−0.029	0.000	0.002	−0.019	−0.119	0.013
Paronychia pulvinata	0.389	−1.261	−0.129	−0.001	−0.001	−0.074	−0.206	0.027
Phlox multiflora	−0.047	−0.514	−0.007	−0.001	0.013	0.019	−0.389	0.025
Phlox pulvinata	−0.035	−0.297	0.003	0.001	−0.022	0.011	0.442	−0.016
Poa glauca	−0.234	−0.057	0.092	0.000	0.004	0.038	0.030	−0.008
Potentilla pulcherrima	−0.371	0.501	0.097	0.001	−0.010	0.082	0.332	−0.024
Potentilla subjuga	−0.048	−0.112	0.001	0.000	−0.015	0.016	0.231	−0.004
Symphyotrichum foliaceum	0.095	−0.320	−0.016	0.000	−0.020	−0.026	0.385	−0.013

Table 10 (continued). Random intercept and slope values for species that showed one or more significant random effects in either the climPC or climVar models. Random estimates with 95% credible intervals not overlapping zero are bolded and the table cell is colored blue (positive) or red (negative).

Species	**climPC model intercept**	**climVar model intercept**	**climPC1**	**wy.ppt**	**gs.ppt**	**climPC2**	**gs.t mean**	**gdd**
Trifolium dasyphyllum	0.273	1.487	−0.033	0.000	0.005	−0.079	−0.083	−0.003
Trifolium nanum	0.355	1.998	−0.006	0.000	0.023	−0.120	−0.257	−0.010
Vaccinium scoparium	0.198	0.163	−0.009	0.000	−0.033	−0.064	0.483	−0.009

Table 11. Dredge results for climPC models of changes in species cover. Models shown are those with delta AICc values < 2, in increasing order of delta AICc from left to right. The highlighted column 1 indicates the best model. Cells with a plus sign (“+”) indicate the inclusion of multi-level categorical factors, while an en dash (“–“) indicates that a factor was not included in the best supported model.

Predictors	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Start cover	2.603	2.600	2.597	2.600	2.604	2.596	2.597	2.603
climPC1	−0.028	−0.059	−0.045	−0.024	−0.028	0.023	−0.038	−0.006
climPC2	–	–	–	–	–	−0.031	–	–
Site latitude	0.167	0.167	0.144	0.148	0.170	0.145	0.130	0.135
Mean spp. lat.	0.136	0.145	0.145	0.138	0.134	0.145	0.158	0.133
Mean spp. lat.^{2}	−0.097	−0.125	−0.122	−0.102	−0.096	−0.122	−0.128	−0.096
Perennating	+	+	+	+	+	+	+	+
Habit	+	+	+	+	+	+	+	+
Leaves	–	–	–	–	+	–	–	–
Start cover × summit lat.	0.411	0.412	0.408	0.408	0.412	0.408	0.405	0.412
Start cover × mean spp. lat.	0.569	0.567	0.566	0.568	0.569	0.565	0.568	0.569
Start cover × mean spp. lat.^{2}	−0.424	−0.421	−0.420	−0.422	−0.424	−0.420	−0.421	−0.423
Start cover × climPC1	−0.138	−0.137	−0.132	−0.134	−0.138	−0.134	−0.131	−0.139
climPC1 × Mean spp. lat.^{2}	−0.035	–	–	−0.026	−0.035	–	–	−0.035
climPC1 × per.	+	+	+	+	+	–	+	+
climPC1 × hab	–	–	+	+	–	+	+	–
climPC2 × per.	–	–	–	–	–	+	–	–
Site lat × per.	–	–	–	–	–	–	+	+
Site lat. × habit	+	+	+	+	+	+	–	+
AICc	12046.00	12046.54	12046.75	12047.43	12047.57	12047.62	12047.88	12047.94
delta AICc	0.00	0.54	0.75	1.43	1.57	1.62	1.88	1.95

Table 12. Dredge results from climVar models predicting changes in species cover. Models shown are those with delta AICc values < 2, in increasing order of delta AICc from left to right. The highlighted column 1 indicates the best model. Cells with a plus sign (“+”) indicate the inclusion of multi-level categorical factors, while an en dash (“–“) indicates that a factor was not included in the best supported model.

Predictors	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Start cover	2.488	2.505	2.484	2.486	2.483	2.49	2.487	2.488	2.485
tmean	−0.025	−0.031	−0.032	−0.036	−0.022	−0.067	−0.016	−0.027	−0.026
gdd	0.279	0.296	0.298	0.293	0.279	0.356	0.29	0.312	0.276
wy.ppt	0.623	0.619	0.564	0.612	0.563	0.623	0.659	0.661	0.615
gs.ppt	−0.221	−0.223	−0.223	−0.222	−0.221	−0.222	−0.222	−0.223	−0.221
Site latitude	−0.379	−0.374	−0.377	−0.368	−0.378	−0.378	−0.426	−0.427	−0.373
Mean spp. lat.	0.056	0.064	0.056	0.06	0.05	0.064	0.068	0.077	0.054
Mean spp. lat.^{2}	−0.051	−0.053	−0.049	−0.051	−0.048	−0.053	−0.056	−0.058	−0.05
Perennating (Per.)	+	+	+	+	+	+	+	+	+
Habit (Hab.)	+	+	+	+	+	+	+	+	+
Start cover × summit latitude	−0.558	−0.578	−0.568	−0.568	−0.567	−0.559	−0.565	−0.566	−0.568
Start cover × tmean	−0.051	–	−0.057	−0.056	−0.054	−0.055	−0.05	−0.054	−0.053
Start cover × gdd	0.593	0.578	0.604	0.603	0.6	0.595	0.593	0.597	0.599
Start cover × gd.ppt	−0.538	−0.54	−0.54	−0.54	−0.541	−0.536	−0.536	−0.535	−0.541
Start cover × wy.precip	1.047	1.058	1.064	1.063	1.06	1.049	1.052	1.055	1.06
Start cover × mean spp. lat.	0.396	0.405	0.393	0.394	0.392	0.398	0.396	0.396	0.393
Start cover × mean spp. lat.^{2}	−0.219	−0.225	−0.215	−0.216	−0.215	−0.22	−0.218	−0.219	−0.216
Habit × summit latitude	+	+	+	+	+	+	–	–	+
Habit × tmean	+	–	–	–	+	–	+	–	+
Habit × gdd	+	+	+	+	+	+	+	+	+

Table 12 (continued). Dredge results from climVar models predicting changes in species cover. Models shown are those with delta AICc values < 2, in increasing order of delta AICc from left to right. The highlighted column 1 indicates the best model. Cells with a plus sign (“+”) indicate the inclusion of multi-level categorical factors, while an en dash (“–“) indicates that a factor was not included in the best supported model.

Predictors	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Habit × wy.ppt	–	–	–	+	–	–	+	+	+
Perennating × tmean	+	+	+	+	+	+	+	+	+
Perennating × gdd	–	–	–	–	–	+	–	–	–
Perennating × wy.ppt	–	–	+	–	+	–	–	–	–
AICc	11640.57	11641.38	11641.74	11642.01	11642.07	11642.12	11642.24	11642.43	11642.45
delta AICc	0.00	0.81	1.17	1.45	1.50	1.55	1.67	1.86	1.89

Table 13. Comparison of model coefficients when all data is included, without *Potentilla*, *Poa*, and *Carex* species data, without GRSD data, and without PECO data. Each of the excluded subsets of the data were suspected to potentially contain errors that could drive patterns in model results that could indicate false patterns in species' cover changes. However, qualitative results of the models were largely unaffected by exclusion of these data subsets. Almost no changes involved a change of sign of the best estimate of a parameter (Est.), with the majority of changes being in the range of confidence limits (CL).

	All data		**No Potentilla, Poa, or Carex**		**no GRSD**		**no PECO**	
Predictors	***Est.***	***CL***	***Est.***	***CL***	***Est.***	***CL***	***Est.***	***CL***
Intercept	**1.21** [A]	**1.00 to 1.43** [A]	**1.28** [A]	**1.10 to 1.47** [A]	**0.97** [A]	**0.76 to 1.19** [A]	**1.24** [A]	**1.00 to 1.48** [A]
Start cover	**2.18** [A]	**2.11 to 2.25** [A]	**2.29** [A]	**2.21 to 2.37** [A]	**2.22** [A]	**2.05 to 2.39** [A]	**2.18** [A]	**2.10 to 2.25** [A]
Mean spp. lat.	0.02	−0.08 to 0.12	0.03	−0.06 to 0.12	0.03	−0.08 to 0.14	0.05	−0.06 to 0.16
Mean spp. lat.^{2}	−0.03	−0.09 to 0.03	**−0.08** [A]	**−0.14 to −0.02** [A]	−0.04	−0.10 to 0.02	−0.03	−0.09 to 0.04
min gdd	**0.27** [A]	**0.10 to 0.45** [A]	**0.27** [A]	**0.10 to 0.44** [A]	−0.06	−0.23 to 0.11	**0.21** [A]	**0.02 to 0.41** [A]
min gs.ppt	**−0.18** [A]	**−0.31 to −0.04** [A]	**−0.15** [A]	**−0.28 to −0.01** [A]	**−0.15** [A]	**−0.22 to −0.09** [A]	−0.12	−0.27 to 0.03
min wy.ppt	**0.61** [A]	**0.33 to 0.90** [A]	**0.54** [A]	**0.26 to 0.82** [A]	**0.24** [A]	**0.10 to 0.38** [A]	**0.59** [A]	**0.30 to 0.88** [A]
Site lat.	**−0.37** [A]	**−0.64 to −0.10** [A]	**−0.33** [A]	**−0.59 to −0.07** [A]	0.09	−0.09 to 0.27	**−0.43** [A]	**−0.72 to −0.15** [A]
habit [gram]	**0.25** [A]	**0.10 to 0.39** [A]	0.08	−0.07 to 0.23	**0.21** [A]	**0.00 to 0.42** [A]	**0.25** [A]	**0.08 to 0.41** [A]
habit [shrub]	**1.02** [A]	**0.33 to 1.71** [A]	**5.65** [A]	**2.09 to 9.22** [A]	0.55	−0.37 to 1.46	**1.42** [A]	**0.66 to 2.19** [A]
habit [tree]	0.62	−18.71 to 19.96	0.03	−17.44 to 17.50	−0.8	−18.36 to 16.77	−0.23	−19.53 to 19.06
perennating [annual]	**1.90** [A]	**0.25 to 3.55** [A]	**1.87** [A]	**0.36 to 3.38** [A]	**2.29** [A]	**0.67 to 3.90** [A]	**1.92** [A]	**0.26 to 3.59** [A]
perennating [below]	−0.12	−0.32 to 0.08	**−0.16** [A]	**−0.32 to −0.00** [A]	0.01	−0.19 to 0.21	−0.11	−0.33 to 0.10
max gs.tmean	−0.02	−0.17 to 0.13	−0.03	−0.18 to 0.12	0.06	−0.11 to 0.22	−0.02	−0.19 to 0.14
Start cover × mean spp. lat.	**0.27** [A]	**0.19 to 0.34** [A]	**0.28** [A]	**0.22 to 0.35** [A]	0.06	−0.03 to 0.16	**0.29** [A]	**0.21 to 0.37** [A]
Start cover × mean spp. lat.^{2}	**−0.11** [A]	**−0.16 to −0.06** [A]	**−0.27** [A]	**−0.35 to −0.19** [A]	−0.02	−0.09 to 0.04	**−0.12** [A]	**−0.18 to −0.07** [A]
Start cover × min gdd	**0.42** [A]	**0.35 to 0.49** [A]	**0.43** [A]	**0.37 to 0.50** [A]	**0.51** [A]	**0.32 to 0.70** [A]	**0.39** [A]	**0.32 to 0.47** [A]

[A] Bold text indicates statistical significance.

Table 13 (continued). Comparison of model coefficients when all data is included, without Potentilla, Poa, and Carex species data, without GRSD data, and without PECO data. Each of the excluded subsets of the data were suspected to potentially contain errors that could drive patterns in model results that could indicate false patterns in species' cover changes. However, qualitative results of the models were largely unaffected by exclusion of these data subsets. Almost no changes involved a change of sign of the best estimate of a parameter (Est.), with the majority of changes being in the range of confidence limits (CL).

	All data		**No Potentilla, Poa, or Carex**		**no GRSD**		**no PECO**	
Predictors	***Est.***	***CL***	***Est.***	***CL***	***Est.***	***CL***	***Est.***	***CL***
Start cover × min gs.ppt	**−0.34**[A]	**−0.41 to −0.27**[A]	**−0.31**[A]	**−0.38 to −0.24**[A]	**−0.35**[A]	**−0.42 to −0.29**[A]	**−0.31**[A]	**−0.39 to −0.24**[A]
Start cover × min wy.ppt	**1.00**[A]	**0.85 to 1.14**[A]	**0.89**[A]	**0.76 to 1.02**[A]	**0.81**[A]	**0.65 to 0.97**[A]	**1.03**[A]	**0.88 to 1.17**[A]
Start cover × Site lat.	**−0.54**[A]	**−0.68 to −0.41**[A]	**−0.48**[A]	**−0.62 to −0.34**[A]	**−0.42**[A]	**−0.59 to −0.24**[A]	**−0.61**[A]	**−0.77 to −0.46**[A]
min gdd × habit [gram]	**0.16**[A]	**0.01 to 0.32**[A]	0.09	−0.08 to 0.26	0.09	−0.14 to 0.32	0.14	−0.02 to 0.30
min gdd × habit [shrub]	−0.08	−1.02 to 0.85	**5.66**[A]	**0.91 to 10.42**[A]	−1.23	−3.16 to 0.69	−0.76	−1.83 to 0.32
min gdd × habit [tree]	0.09	−28.84 to 29.03	−1.34	−27.71 to 25.04	−2.48	−28.73 to 23.77	−1.46	−30.36 to 27.43
Site lat. × habit [gram]	**−0.16**[A]	**−0.29 to −0.04**[A]	−0.06	−0.19 to 0.07	−0.13	−0.31 to 0.06	**−0.17**[A]	**−0.32 to −0.03**[A]
Site lat. × habit [shrub]	−0.42	−0.87 to 0.04	−0.61	−2.55 to 1.33	0.22	−1.21 to 1.65	**−0.5**[A]	**−0.98 to −0.01**[A]
perennating [annual] × max gs.tmean	**4.61**[A]	**2.25 to 6.97**[A]	**4.62**[A]	**2.52 to 6.72**[A]	**4.53**[A]	**2.40 to 6.67**[A]	**4.61**[A]	**2.26 to 6.96**[A]
perennating [below] × max gs.tmean	0.03	−0.12 to 0.18	0.04	−0.11 to 0.19	−0.04	−0.21 to 0.12	0.03	−0.14 to 0.19
perennating [woody] × max gs.tmean	0.03	−0.71 to 0.77	0.67	−0.86 to 2.19	0.26	−0.52 to 1.03	0.31	−0.46 to 1.08

[A] Bold text indicates statistical significance.

Table 14. Model coefficients for climPC and climVar models of change in species cover.

	climPC model		climVar model	
Predictors	**Estimates**	**p**	**Estimates**	**p**
(Intercept)	2.15	0.202	1.34	0.725
Start cover	−4.81	**<0.001** [A]	−1.81	**<0.001** [A]
climPC1	0.02	0.335	–	–
Mean spp. lat.	−0.06	0.332	−0.03	0.584
Mean spp. lat.^{2}	0	0.404	0	0.682
Site lat.	−0.01	0.753	−0.02	0.844
climPC2	−0.02	0.743	–	–
Perennating [annual]	5.83	**<0.001** [A]	−24.2	**0.017** [A]
Perennating [below]	−0.11	0.38	−0.32	0.607
Perennating [woody]	−0.02	0.994	–	–
Habit [gram]	1.22	0.127	0.72	0.381
Habit [shrub]	8.79	**0.04** [A]	4.99	0.096
Start cover × climPC1	−0.02	**<0.001** [A]	–	–
Start cover × mean spp. lat.	0.17	**<0.001** [A]	0.1	**<0.001** [A]
Start cover × mean spp. lat.	0	**<0.001** [A]	0	**<0.001** [A]
Start cover × summit lat.	0.04	**<0.001** [A]	−0.05	**<0.001** [A]
climPC2 × perennating [annual]	3.26	**<0.001** [A]	–	–
climPC2 × perennating [below]	0.02	0.702	–	–
climPC2 × perennating [woody]	−0.03	0.858	–	–

[A] Bold text indicates statistical significance.

Total vascular plant cover models

Table 15 shows supplementary results related to total vascular plant cover.

Table 15. Comparison of fitted coefficients from the best-supported models predicting change in total vascular plant cover using climate PC axes (climPC model) and climate variables (climVar model).

	climPC model		**climVar model**	
Predictors	**Estimates**	**p**	**Estimates**	**p**
Intercept	173.73	0.83	12.74	0.53
Starting plant cover	−0.39	0.56	**3.33** [A]	**<0.001** [A]
climPC1	−0.37	0.65	–	–
climPC2	−1.46	0.17	–	–
Site latitude	−3.52	0.83	–	–
YELL	−2.32	0.97	**19.29** [A]	**<0.001** [A]
ROMO	−28.11	0.83	**14.31** [A]	**<0.001** [A]
GRSD	−22.21	0.90	**12.79** [A]	**<0.001** [A]
PECO	−46.79	0.82	−2.82	0.56
Starting plant cover × climPC1	0.04	0.10	–	–
Starting plant cover × climPC2	0.02	0.43	–	–
Starting plant cover × summit latitude	0.03	0.08	–	–
Snow days	–	–	−0.14	0.21
gs.ppt	–	–	0.08	0.03
wy.ppt	–	–	−0.001	0.90
Starting plant cover × snow days	–	–	**−0.01** [A]	**<0.001** [A]
Starting plant cover × gs.ppt	–	–	**−0.01** [A]	**<0.001** [A]
Starting plant cover × wy.ppt	–	–	**0.00** [A]	**<0.001** [A]

[A] Bold text indicates statistical significance.

Appendix D: Species List

Table 16 lists all species in the dataset and the parks in which they occur.

Table 16. List of all species in dataset and the parks in which they occur. N refers to the sample size across parks where found and leaves were evergreen (E) or deciduous (D).

Species	Parks	N	Tax. unit	Habit	Perennating	Leaves
Abies lasiocarpa	ROMO	1	gymno	tree	woody	E
Achillea millefolium	GLAC, GRSD, ROMO, YELL	40	dicot	forb	below	D
Agoseris aurantiaca	PECO, ROMO	4	dicot	forb	below	D
Agoseris glauca	GLAC, YELL	31	dicot	forb	below	D
Agrostis humilis	GLAC, YELL	3	monocot	gram	below	D
Agrostis variabilis	GLAC	4	monocot	gram	below	D
Allium geyeri	GRSD, YELL	7	monocot	forb	below	D
Androsace chamaejasme	GRSD, PECO	29	dicot	forb	below	D
Androsace septentrionalis	GLAC, GRSD, ROMO, YELL	45	dicot	forb	below	D
Anemone drummondii	GLAC	1	dicot	forb	below	D
Anemone multifida	GLAC	3	dicot	forb	below	D
Antennaria alpina	GLAC	3	dicot	forb	below	E
Antennaria media	ROMO, YELL	16	dicot	forb	below	E
Antennaria microphylla	YELL	2	dicot	forb	below	E
Antennaria parvifolia	PECO	1	dicot	forb	below	E
Antennaria rosea	GRSD, ROMO	7	dicot	forb	below	E
Antennaria umbrinella	GLAC, YELL	14	dicot	forb	below	E
Arabis drummondii	GRSD, ROMO	4	dicot	forb	below	D
Arabis lemmonii	GLAC, YELL	4	dicot	forb	below	D
Arabis lyallii	YELL	5	dicot	forb	below	D
Arabis pycnocarpa	YELL	1	dicot	forb	below	D
Arenaria congesta	YELL	6	dicot	forb	below	D
Arenaria fendleri	GRSD, PECO, ROMO	60	dicot	forb	below	D
Arnica angustifolia	GLAC	7	dicot	forb	below	D
Arnica ovata	GLAC	3	dicot	forb	below	D
Arnica rydbergii	ROMO	1	dicot	forb	below	D
Artemisia arctica	ROMO	12	dicot	forb	below	D
Artemisia borealis	GLAC	12	dicot	forb	below	D
Artemisia scopulorum	GRSD, PECO, ROMO, YELL	47	dicot	forb	below	D
Astragalus alpinus	YELL	6	dicot	forb	below	D
Astragalus australis	GLAC, YELL	10	dicot	forb	below	D

Table 16 (continued). List of all species in dataset and the parks in which they occur. N refers to the sample size across parks where found and leaves were evergreen (E) or deciduous (D).

Species	Parks	N	Tax. unit	Habit	Perennating	Leaves
Astragalus bourgovii	GLAC	7	dicot	forb	below	D
Astragalus kentrophyta	YELL	5	dicot	forb	below	D
Avenula hookeri	GLAC	3	monocot	gram	below	D
Besseya alpina	PECO, ROMO	4	dicot	forb	below	D
Besseya wyomingensis	GLAC, YELL	29	dicot	forb	below	D
Boechera divaricarpa	GLAC	2	dicot	forb	below	D
Boechera pendulina	YELL	8	dicot	forb	below	D
Bromus pumpellianus	GLAC	6	monocot	gram	below	D
Bupleurum americanum	GLAC	12	dicot	forb	below	D
Calamagrostis purpurascens	GLAC, GRSD, PECO, ROMO, YELL	41	monocot	gram	below	D
Campanula rotundifolia	GLAC, GRSD, ROMO	21	dicot	forb	below	D
Campanula uniflora	GRSD, ROMO	13	dicot	forb	below	D
Carex albonigra	GLAC, ROMO	7	monocot	gram	below	D
Carex arapahoensis	ROMO	5	monocot	gram	below	D
Carex atrosquama	GLAC, YELL	5	monocot	gram	below	D
Carex elynoides	PECO, ROMO, YELL	20	monocot	gram	below	D
Carex haydeniana	YELL	2	monocot	gram	below	D
Carex heteroneura	PECO, YELL	6	monocot	gram	below	D
Carex microptera	ROMO, YELL	5	monocot	gram	below	D
Carex nardina	GLAC	3	monocot	gram	below	D
Carex obtusata	ROMO	1	monocot	gram	below	D
Carex pachystachya	ROMO	1	monocot	gram	below	D
Carex paysonis	YELL	4	monocot	gram	below	D
Carex phaeocephala	ROMO, YELL	7	monocot	gram	below	D
Carex pyrenaica	ROMO	2	monocot	gram	below	D
Carex rossii	GRSD, ROMO	6	monocot	gram	below	D
Carex rupestris	GLAC, GRSD, PECO, ROMO, YELL	70	monocot	gram	below	D
Carex scopulorum	YELL	1	monocot	gram	below	D
Castilleja haydenii	GRSD, PECO	17	dicot	forb	below	D
Castilleja nivea	YELL	5	dicot	forb	below	D
Castilleja occidentalis	PECO, ROMO	16	dicot	forb	below	D
Castilleja puberula	ROMO	2	dicot	forb	below	D
Castilleja pulchella	YELL	4	dicot	forb	below	D
Cerastium arvense	GLAC, ROMO, YELL	27	dicot	forb	below	D

Table 16 (continued). List of all species in dataset and the parks in which they occur. N refers to the sample size across parks where found and leaves were evergreen (E) or deciduous (D).

Species	Parks	N	Tax. unit	Habit	Perennating	Leaves
Cerastium beeringianum	GRSD, YELL	12	dicot	forb	below	D
Chionophila jamesii	ROMO	2	dicot	forb	below	D
Claytonia megarhiza	GRSD, PECO, ROMO	7	dicot	forb	below	D
Crepis nana	GLAC	3	dicot	forb	below	D
Cryptantha sobolifera	GLAC	10	dicot	forb	below	D
Danthonia intermedia	ROMO	6	monocot	gram	below	D
Danthonia parryi	GRSD	2	monocot	gram	below	D
Deschampsia cespitosa	GRSD, PECO, YELL	10	monocot	gram	below	D
Douglasia montana	GLAC	11	dicot	forb	below	D
Draba aurea	GRSD, PECO, ROMO, YELL	24	dicot	forb	below	D
Draba breweri	GRSD, ROMO	7	dicot	forb	below	D
Draba crassa	GRSD, YELL	8	dicot	forb	below	D
Draba crassifolia	YELL	4	dicot	forb	below	D
Draba grayana	ROMO	5	dicot	forb	below	D
Draba helleriana	PECO	4	dicot	forb	below	D
Draba incerta	GLAC, YELL	28	dicot	forb	below	D
Draba lonchocarpa	GLAC, ROMO	18	dicot	forb	below	D
Draba oligosperma	YELL	1	dicot	forb	below	D
Draba paysonii	GLAC	25	dicot	forb	below	D
Draba praealta	GLAC	3	dicot	forb	below	D
Draba spectabilis	PECO	4	dicot	forb	below	D
Draba streptocarpa	GRSD, PECO, ROMO	40	dicot	forb	below	D
Elymus scribneri	GRSD, PECO, ROMO, YELL	33	monocot	gram	below	D
Elymus trachycaulus	GLAC	32	monocot	gram	below	D
Erigeron compositus	GLAC, YELL	27	dicot	forb	below	D
Erigeron melanocephalus	PECO	2	dicot	forb	below	D
Erigeron nivalis	GLAC	1	dicot	forb	below	D
Erigeron ochroleucus	YELL	12	dicot	forb	below	D
Erigeron peregrinus	ROMO	4	dicot	forb	below	D
Erigeron pinnatisectus	GRSD, PECO, ROMO	35	dicot	forb	below	D
Erigeron rydbergii	YELL	8	dicot	forb	below	D
Erigeron simplex	GRSD, PECO, ROMO, YELL	37	dicot	forb	below	D
Erigeron ursinus	YELL	4	dicot	forb	below	D
Eriogonum androsaceum	GLAC	18	dicot	forb	below	D
Eriogonum arcuatum	GRSD	3	dicot	forb	below	D

Table 16 (continued). List of all species in dataset and the parks in which they occur. N refers to the sample size across parks where found and leaves were evergreen (E) or deciduous (D).

Species	Parks	N	Tax. unit	Habit	Perennating	Leaves
Eriogonum flavum	GRSD	3	dicot	forb	below	D
Eriogonum hookeri	YELL	3	dicot	forb	annual	D
Eriogonum jamesii	GRSD	6	dicot	forb	below	D
Eriogonum ovalifolium	GLAC, YELL	13	dicot	forb	below	D
Eritrichium nanum	GRSD, PECO, ROMO, YELL	38	dicot	forb	below	D
Erysimum capitatum	GRSD, ROMO	9	dicot	forb	below	D
Festuca baffinensis	GLAC, ROMO	6	monocot	gram	below	D
Festuca brachyphylla	GLAC, GRSD, PECO, YELL	60	monocot	gram	below	D
Festuca idahoensis	GLAC, YELL	4	monocot	gram	below	D
Festuca minutiflora	GRSD, ROMO	30	monocot	gram	below	D
Festuca saximontana	GLAC	6	monocot	gram	below	D
Gentiana algida	ROMO	1	dicot	forb	below	D
Gentiana parryi	PECO	1	dicot	forb	below	D
Gentianella tenella	GRSD	2	dicot	forb	below	D
Geum rossii	GRSD, PECO, ROMO, YELL	39	dicot	forb	below	D
Geum triflorum	GLAC, YELL	6	dicot	forb	below	D
Helictotrichon mortonianum	ROMO	12	monocot	gram	below	D
Heterotheca pumila	GRSD	7	dicot	forb	below	D
Heuchera parvifolia	GLAC, GRSD, PECO	21	dicot	forb	below	D
Hieracium gracile	PECO	1	dicot	forb	below	D
Juncus drummondii	ROMO	2	monocot	gram	below	D
Kobresia myosuroides	GRSD, ROMO	30	monocot	gram	below	D
Koeleria macrantha	YELL	1	monocot	gram	below	D
Koenigia islandica	ROMO	2	dicot	forb	below	D
Lewisia pygmaea	ROMO, YELL	8	dicot	forb	below	D
Linum lewisii	GLAC, YELL	5	dicot	forb	below	D
Lloydia serotina	GRSD, PECO, ROMO	19	monocot	forb	below	D
Lomatium cous	YELL	8	dicot	forb	below	D
Lupinus alpestris	YELL	1	dicot	forb	below	D
Lupinus depressus	GLAC, YELL	23	dicot	forb	below	D
Lupinus wyethii	YELL	1	dicot	forb	below	D
Luzula spicata	GLAC, GRSD, PECO, ROMO, YELL	55	monocot	gram	below	D
Mertensia alpina	YELL	2	dicot	forb	below	D
Mertensia lanceolata	GRSD, ROMO	25	dicot	forb	below	D
Mertensia oblongifolia	GLAC	9	dicot	forb	below	D

Table 16 (continued). List of all species in dataset and the parks in which they occur. N refers to the sample size across parks where found and leaves were evergreen (E) or deciduous (D).

Species	Parks	N	Tax. unit	Habit	Perennating	Leaves
Minuartia austromontana	GLAC	8	dicot	forb	above	D
Minuartia macrantha	GRSD	9	dicot	forb	above	D
Minuartia nuttallii	GLAC	21	dicot	forb	above	D
Minuartia obtusiloba	GLAC, GRSD, PECO, ROMO, YELL	91	dicot	forb	above	D
Minuartia rubella	GLAC, GRSD, ROMO	14	dicot	forb	above	D
Myosotis alpestris	YELL	10	dicot	forb	below	D
Myosotis asiatica	GLAC	10	dicot	forb	below	D
Oreostemma alpigenum	YELL	7	dicot	forb	below	D
Oreoxis alpina	GRSD, PECO, ROMO	61	dicot	forb	below	D
Oxyria digyna	ROMO	2	dicot	forb	below	D
Oxytropis sericea	GLAC, YELL	22	dicot	forb	below	D
Packera cana	GLAC, YELL	15	dicot	forb	below	D
Packera cymbalaria	GLAC	5	dicot	forb	below	D
Paronychia pulvinata	GRSD, PECO, ROMO	49	dicot	forb	above	E
Pedicularis cystopteridifolia	YELL	5	dicot	forb	below	D
Pedicularis parryi	GRSD	4	dicot	forb	below	D
Penstemon ellipticus	GLAC	6	dicot	forb	below	D
Penstemon whippleanus	PECO, ROMO	5	dicot	forb	below	D
Phacelia hastata	GRSD, YELL	3	dicot	forb	below	D
Phacelia sericea	GLAC	14	dicot	forb	below	D
Phlox condensata	GRSD	22	dicot	forb	below	D
Phlox multiflora	GRSD, YELL	18	dicot	forb	below	D
Phlox pulvinata	YELL	8	dicot	forb	below	D
Physaria saximontana	GLAC	2	dicot	forb	below	D
Picea engelmannii	ROMO	2	gymno	tree	woody	E
Poa abbreviata	ROMO	2	monocot	gram	below	D
Poa alpina	GLAC, GRSD, ROMO, YELL	40	monocot	gram	below	D
Poa arctica	GLAC, GRSD, ROMO	37	monocot	gram	below	D
Poa cusickii	GLAC, ROMO, YELL	11	monocot	gram	below	D
Poa glauca	GLAC, GRSD, PECO, ROMO, YELL	98	monocot	gram	below	D
Poa interior	GLAC	9	monocot	gram	below	D
Poa reflexa	ROMO	2	monocot	gram	below	D
Poa secunda	GLAC, GRSD, YELL	26	monocot	gram	below	D
Polemonium pulcherrimum	GLAC, YELL	13	dicot	forb	below	D

Table 16 (continued). List of all species in dataset and the parks in which they occur. N refers to the sample size across parks where found and leaves were evergreen (E) or deciduous (D).

Species	Parks	N	Tax. unit	Habit	Perennating	Leaves
Polemonium viscosum	GLAC, GRSD, ROMO, YELL	29	dicot	forb	below	D
Polygonum bistortoides	GRSD, ROMO, YELL	35	dicot	forb	below	D
Polygonum douglasii	GLAC	4	dicot	forb	below	D
Polygonum viviparum	ROMO	2	dicot	forb	below	D
Potentilla concinna	GRSD, PECO, ROMO	25	dicot	forb	below	D
Potentilla diversifolia	GLAC, GRSD, ROMO, YELL	34	dicot	forb	below	D
Potentilla fruticosa	GLAC, GRSD, PECO	26	dicot	shrub	woody	D
Potentilla glandulosa	YELL	4	dicot	forb	below	D
Potentilla gracilis	PECO	1	dicot	forb	below	D
Potentilla multisecta	YELL	1	dicot	forb	below	D
Potentilla nivea	GLAC, GRSD, ROMO	38	dicot	forb	below	D
Potentilla ovina	GLAC, GRSD, ROMO, YELL	26	dicot	forb	below	D
Potentilla pulcherrima	GRSD	10	dicot	forb	below	D
Potentilla rubricaulis	GLAC, GRSD	32	dicot	forb	below	D
Potentilla saximontana	GLAC	7	dicot	forb	below	D
Potentilla subjuga	GRSD, ROMO	22	dicot	forb	below	D
Primula angustifolia	GRSD, PECO, ROMO	45	dicot	forb	below	D
Pseudocymopterus montanus	PECO	2	dicot	forb	below	D
Pulsatilla patens	YELL	3	dicot	forb	below	D
Ranunculus adoneus	ROMO	4	dicot	forb	below	D
Ranunculus eschscholtzii	ROMO	1	dicot	forb	below	D
Ranunculus eximius	YELL	1	dicot	forb	below	D
Ranunculus macauleyi	PECO	1	dicot	forb	below	D
Ranunculus macounii	PECO	2	dicot	forb	below	D
Rhodiola integrifolia	GLAC, GRSD, ROMO	5	dicot	forb	below	D
Rhodiola rhodantha	GRSD, PECO	7	dicot	forb	below	D
Salix nivalis	ROMO	1	dicot	shrub	woody	D
Salix petrophila	ROMO, YELL	3	dicot	shrub	woody	D
Saxifraga bronchialis	GLAC, PECO	10	dicot	forb	above	E
Saxifraga caespitosa	GLAC	6	dicot	forb	above	E
Saxifraga cernua	PECO	2	dicot	forb	below	D
Saxifraga chrysantha	GRSD, PECO, ROMO	4	dicot	forb	above	E
Saxifraga flagellaris	GRSD, PECO	8	dicot	forb	above	E
Saxifraga rhomboidea	GRSD, PECO, ROMO, YELL	19	dicot	forb	below	D
Saxifraga rivularis	ROMO	1	dicot	forb	below	D

Table 16 (continued). List of all species in dataset and the parks in which they occur. N refers to the sample size across parks where found and leaves were evergreen (E) or deciduous (D).

Species	Parks	N	Tax. unit	Habit	Perennating	Leaves
Sedum lanceolatum	GLAC, GRSD, PECO, ROMO, YELL	66	dicot	forb	above	E
Senecio amplectens	PECO	2	dicot	forb	below	D
Senecio crassulus	YELL	1	dicot	forb	below	D
Senecio fremontii	YELL	1	dicot	forb	below	D
Senecio integerrimus	YELL	3	dicot	forb	below	D
Senecio lugens	YELL	1	dicot	forb	below	D
Senecio serra	YELL	1	dicot	forb	below	D
Senecio taraxacoides	PECO	2	dicot	forb	below	D
Sibbaldia procumbens	PECO, ROMO	9	dicot	forb	below	D
Silene acaulis	GLAC, GRSD, PECO, ROMO	61	dicot	forb	above	E
Smelowskia calycina	GLAC, YELL	41	dicot	forb	below	D
Solidago multiradiata	GLAC, YELL	24	dicot	forb	below	D
Solidago nana	GRSD	6	dicot	forb	below	D
Solidago simplex	GRSD, PECO, ROMO	8	dicot	forb	below	D
Stellaria americana	GLAC	8	dicot	forb	below	D
Stellaria longipes	GLAC, ROMO	9	dicot	forb	below	D
Symphyotrichum foliaceum	YELL	11	dicot	forb	below	D
Taraxacum ceratophorum	GLAC	6	dicot	forb	below	D
Taraxacum officinale	GRSD, ROMO, YELL	5	dicot	forb	below	D
Taraxacum scopulorum	GLAC	3	dicot	forb	below	D
Tetraneuris acaulis	GRSD	16	dicot	forb	below	D
Tetraneuris brandegeei	GRSD, PECO	21	dicot	forb	below	D
Tetraneuris grandiflora	PECO, ROMO	14	dicot	forb	below	D
Thlaspi montanum	GRSD, ROMO	14	dicot	forb	below	D
Tonestus lyallii	ROMO	8	dicot	forb	below	D
Tonestus pygmaeus	GRSD, PECO, ROMO	56	dicot	forb	below	D
Townsendia parryi	GLAC	2	dicot	forb	below	D
Trifolium dasyphyllum	GRSD, ROMO	44	dicot	forb	below	D
Trifolium nanum	GRSD, ROMO	35	dicot	forb	below	D
Trifolium parryi	ROMO	10	dicot	forb	below	D
Trisetum spicatum	GLAC, GRSD, PECO, ROMO, YELL	66	monocot	gram	below	D
Trisetum wolfii	YELL	1	monocot	gram	below	D
Vaccinium scoparium	PECO, ROMO	4	dicot	shrub	woody	D

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