Title: Community turnover by composition and climatic affinity across scales in an alpine system

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Short title: Alpine plant community-climate relationships with elevation

ABSTRACT

Premise of the study: Examining community turnover across climate gradients at multiple scales is vital to understanding biogeographic response to climate change. This approach is especially important for alpine plants in which the relative roles of topographic complexity and non-climatic or stochastic factors vary across spatial scales.

Methods: We examined the structure of alpine plant communities across elevation gradients in the White Mountains, California. Using community climatic niche means (CCNMs) and measures of

community dissimilarity, we explored the relationship between community composition and elevation gradients at three scales: the mountain range, individual peaks, and within elevation contours.

Key Results: At the mountain range scale, community turnover and CCNMs showed strongly significant relationships with elevation, with an increase in the abundance of cooler and wetter-adapted species at higher elevations. At the scale of a single peaks, we found weak and inconsistent relationships between CCNMs and elevation, but variation in community composition explained by elevation increased. Within the elevation contours, the range of CCNMs was weakly positively correlated with turnover in species identity, likely driven by microclimate and other site-specific factors.

Conclusions: Our results suggest that there is strong environmental sorting of alpine plant communities at broad scales, but microclimatic and site-specific, non-climatic factors together shape community turnover at finer scales. In the context of climate change, our results imply that community-climate relationships are scale-dependent, and predictions of local alpine plant range shifts are limited by a lack of topoclimatic and habitat information.

Key words: alpine ecology; climatic niche mean; elevation gradient; GLORIA; Great Basin; beta diversity; species turnover; community assembly; White Mountains

INTRODUCTION

Mountain environments contain important ecosystems and are heralds of species distribution shifts in response to climate change (Körner, 2003). Pronounced warming at higher elevations exacerbates this potential for mountains to exhibit early signs of biotic responses to climate change (Pepin et al., 2015). Species have responded by generally moving upslope in response to warming

(Parmesan and Yohe, 2003; Lenoir et al., 2008; Pauli et al., 2012; Millar et al., 2015; Smithers et al., 2018; Malanson et al., 2019), with this upslope advance having accelerated in recent years (Steinbauer et al., 2018). However, it is increasingly recognized that climate change expectations of wholesale upward or poleward shifts of species distributions are overly simplistic (Lenoir and Svenning, 2015), especially in topographically complex landscapes (Rapacciuolo et al., 2014). Further, alpine species, often cool-adapted and long-lived, may be both directly sensitive to temperature change due to their physiology and indirectly sensitive due to competitive exclusion by species recruiting from lower elevations (Alexander et al., 2015; Rumpf et al., 2018). Predicting how these direct and indirect impacts of climate change will together shape future communities requires a better understanding of how complex mountain landscapes shape community assembly.

A long-standing debate in community ecology is whether community assembly is repeatable and predictable. If environmental filtering shapes community assembly, then there should be repeated, deterministic patterns of community composition across similar climatic and geologic conditions (Clements, 1916, 1936). On the other hand, less predictable, or stochastic, processes in the form of chance colonization, random extinction, ecological drift, and dispersal limitation could be more important in explaining patterns of community assembly (Gleason, 1927; Slatkin, 1974). While this debate has often been waged as either deterministic or stochastic forces being the driver of community assembly, it is more likely that communities are structured by both processes (Chase and Myers, 2011). In the context of climate change, this debate can be further distilled to a debate about whether climatic or non-climatic factors structure community assembly. The relative importance of deterministic climatic factors versus deterministic non-climatic or stochastic factors (hereafter referred to as non-climatic factors) can change depending on the system or scale at which we examine it. In alpine systems, the relative importance of these factors in shaping plant communities is particularly unclear, and this

knowledge gap limits our ability to predict the rate and magnitude of plant community change in alpine systems in response to climate warming.

A first step to understanding the relative importance of these factors in shaping plant communities is to examine how communities are currently distributed across multiple scales of climatic complexity. In mountain systems, scales for describing plant community response to climate change can range from a single elevation at one location to an entire mountain range. Elevation is a useful geographic feature when studying deterministic and stochastic effects on community assembly because at different scales of elevation range, the relative importance of each process may change. Across an entire mountain range, the physical isolation of mountaintops may amplify the stochastic processes of dispersal and colonization as low-lying areas between suitable high-elevation habitat can create geographic barriers to species movement (Dirnböck et al., 2011). However at the scale of a single peak where dispersal is likely not limiting, the deterministic process of environmental filtering may play a larger role with high community turnover across steep climate gradients driven by elevation (Körner, 2003, 2007). Lastly, small-scale topographic complexity in the alpine zone can also drive variation in community composition (Van de Ven et al., 2007; Scherrer and Körner, 2011; Lenoir et al., 2013; Winkler et al., 2016). At this microclimatic scale, community variation within an elevation contour may be high where topographic complexity is high; the variety of potential habitats may deterministically facilitate close proximity of species and communities with a variety of climatic niches. However, within an elevation contour, other factors such as the geology, habitat stability (e.g., scree moves more than bedrock) or species interactions may also play a large role in community variation (Graae et al., 2018).

Comparing different types of community characteristics allows us to disentangle how climatic and non-climatic processes are shaping the community across scales. Community climatic niche affinities are metrics of the community (similar to any community-weighted mean traits) derived from climatic conditions found across the component species' regional distributions (Landolt et al., 2010; Scherrer and

Körner, 2011; Lenoir et al., 2013). At broad scales, plant species ranges are largely determined by a suite of environmental factors, with many of those factors climatically based. The suite of climatic factors that a species can tolerate can be referred to as its climatic niche affinity, and climatic tolerances of the community can be described using the combined climatic niche affinities of its component species. When considering community climatic niche affinities, environmental filtering processes may drive species turnover. Conversely, stochastic processes such as the timing of species arrival into the community may drive community similarity metrics based on species composition alone (Fukami et al., 2005). Similar patterns of climatic niche affinities and community composition across elevation for a single scale would indicate that deterministic processes are driving much of the community turnover. For a counter example, if the range of climatic niche affinities encompassed within elevation contours is not correlated with turnover in the community composition (ie., where species turnover is high, the range of climatic niche affinity values among species is low), this points to non-climatic factors shaping the community variation at this scale. These types of comparisons could be scaled up to look at different elevation bands on a single peak, among peaks in a mountain range, or even among mountain ranges.

Management of large areas of public lands for resilience with a changing climate challenges us to understand how communities will shift both locally and regionally (Pecl et al., 2017). Examining relationships between plant communities and climate gives key insights into the potential for species and communities to respond to climate change by tracking their climatic niche across different scales and may inform whether moving upslope in elevation is a predictable method for species to remain in their climatic niche in response to climate change. Evaluating changes in biodiversity and species distributional shifts requires long-term monitoring across multiple scales (Gottfried et al., 2012). The Global Observation Research Initiative in Alpine Environments (GLORIA) is an international collaboration assessing global distributional shifts of alpine plant species in response to changing climate (http://www.gloria.ac.at/). This international program was founded to provide cost-effective, universal

monitoring protocols and a unifying network to investigate the rate and magnitude of the changes in alpine communities through time and spatial patterning at local, regional, and global scales (Grabherr et al., 2010). This network has led to key findings about the vulnerability of montane systems to changing climate, including upward distributional shifts of many alpine species and loss of cool-adapted species in mountains (Pauli et al., 2007, 2012; Gottfried et al., 2012; Lamprecht et al., 2018; Rumpf et al., 2018; Steinbauer et al., 2018). The North American chapter was founded in 2004 (Millar and Fagre, 2007) with installations in California and Montana, and now has installations in many mountain regions of North America. As part of this effort, GLORIA Great Basin (www.gloriagreatbasin.org) established a series of downslope transects on five peaks in the White Mountains, California (Fig. 1) extending from alpine mountaintops into the subalpine zone to monitor community changes in the local species pool at the individual mountain and at the mountain range scale.

In this study, we evaluate the role of climatic versus non-climatic processes in explaining plant community turnover across elevation gradients at three scales in the White Mountains, California, USA: across an entire mountain range, within each of five peaks spread across the mountain range, and within elevation contours of each peak (Fig. 1). We use metrics of community climatic niche means and community composition to examine relationships among species turnover, community niche affinities, and elevation across scales. Consistent with environmental filtering, community climatic niche affinities may be highly dependent on the elevation gradient, with the presence and abundance of cooler and wetter-adapted species (dependent on their climatic niche) increasing with elevation, especially with climate metrics that vary the most predictably across the elevation gradient, such as temperature and precipitation. For this system specifically, previous work has found that community climate affinities are representative of local climatic niche means derived from microclimate field data (Oldfather and Ackerly 2019). However, given that the relative importance of deterministic and stochastic processes may vary with spatial scale and the level of community organization under consideration (Fukami et al., 2005), the

relationships between elevation and climatic niche affinities may be strongest at broader spatial scales, while the relationship between elevation and community composition may be stronger at smaller scales (i.e., within a single peak). Specifically, we propose the following hypotheses (see Fig. 2 for a conceptual diagram).

1) At broad spatial scales (mountain range), non-climatic or stochastic processes will drive more variation in species composition and turnover than climatic or deterministic processes. Based on this, we predict that elevation as a proxy for deterministic changes explains more variation in species composition and turnover within each peak than across the entire range.

2) At broad spatial scales, climatic filters will be more important in explaining plant community variation in climatic niche space than non-climatic or stochastic differences. We predict that elevation will be better at predicting community climatic niche affinities at large spatial scales (mountain range) than at smaller scales (individual peak), where microclimate within an elevation may obscure this relationship

3) At the smallest scales (within elevation contour on a single peak), microclimate, habitat differences, and other unmeasured factors facilitate niche partitioning, thereby driving patterns of community assembly. We predict a positive relationship between the range of community climatic niche affinities and species turnover within elevation contours.

METHODS

Study Area—The White Mountains are a cold and dry mountain range along the California-Nevada border at the western margin of the Great Basin in the eastern rain-shadow of the Sierra Nevada (Powell and Klieforth, 1991). At the White Mountains Research Center's Barcroft Station (3800 m), mean annual precipitation is approximately 455 mm and mean annual temperature is -1.7 ^{o}C (Western Regional Climate Center). Most of the precipitation in the range comes as winter snow,

although monsoonal rain events also occur during the summer. The alpine zone ranges in elevation from treeline at roughly 3500 m to the top of White Mountain Peak at 4300 m. The alpine flora in the White Mountains is made up of obligate alpine species, lower montane species, and cold-desert species associated with the Sierra Nevada, Great Basin, and Rocky Mountains (Rundel et al., 2008).

Field Surveys—We sampled alpine community composition along elevation gradients using 100-meter belt transects on five peaks in the White Mountains: White Mountain Peak (WMT), Mount Barcroft (BAR), Sheep Mountain East (SME), Patriarch Grove South (PGS), and Campito Mountain (CPT) (Bishop, 2011). On each peak, the first transect was established on the southeast aspect (east aspect for Campito Peak), 35 vertical meters below the summit. Two, 50m x 1m belt transects were extended from this central point following the elevation contour to create a 100-meter x 1-meter belt transect at one elevation. Additional 100m x 1m transects were established on each peak in intervals of 25 vertical meters below the previous transect on the same aspect (Fig. 1). While transects were placed at this fixed 25 m interval, peaks had differing numbers of transects based on the total distance between upper treeline and the top of the peak. Transects were established across 3 consecutive years from 2011-2013 (Table 1). Sampling was conducted in mid-July to best correspond with flowering timing of most alpine plant species in the White Mountains. Each transect was divided into ten continuous, 10m x 1m segments. In each segment, we recorded the presence of every species. In addition, we assessed cover of plant species and substrate (rock, scree, litter, bare ground) along the entire transect using a point-intercept method with 40 points per 10m x 1m segment. A pair of points was located at every half-meter along the transect, with the points in each pair 0.5 m apart (0.25 m from the center of the belt transect). The substrate or plant species was recorded as a “hit” if a point intersected with it.

Community Metrics—To investigate how communities varied across spatial gradients, we used community-weighted climatic niche means (CCNM) and community composition. A CCNM is the abundance-weighted mean of each component species' average species niche space across its range (De Frenne et al., 2013). For community composition we used the Bray-Curtis dissimilarity metric of β diversity, which incorporates both species presence and relative abundance (Anderson et al., 2011). Our measure of abundance used for both metrics was the number of segments in which it was found for each transect. We consider how these two community metrics change across three nested scales: the elevation gradient of the entire mountain range, the elevation gradient of a single peak, and within a single elevation contour of a peak.

A CCNM is a property of a single community, or in our specific case, a transect for mountain range- and peak-scale analyses and a 10m segment within transects for the elevation contour-scale analysis. We focused on the following climatic measurements as they are likely major structuring factors for alpine plant communities: climatic water deficit, mean annual precipitation, July maximum temperature, and January minimum temperature. Climatic water deficit is an integrative measure of how much energy availability (temperature) exceeds water supply (precipitation), with higher values indicating hotter, drier conditions, and lower values indicating cooler, wetter conditions. July maximum and January minimum temperatures were calculated mean daily high and low temperatures of the month, respectively. Using a recently compiled database of California herbarium specimens derived from the Consortium of California Herbaria as well as additional natural history museums and herbaria (Baldwin et al., 2017), we extracted locations from all vouchered specimens in the database for each surveyed species. We used those database locations to extract 30-year (1961-1990) means for climatic water deficit, mean annual precipitation, maximum July temperature, and minimum January temperature from the TerraClimate gridded dataset (Abatzoglou et al., 2018), which is itself an amalgamation of the WorldClim dataset (Fick and Hijmans, 2017) and other data. After culling the

213 herbaria records to one record per species per grid cell to reduce sampling bias, we extracted the four
214 mean climate values for each species, representing the mean climatic niche of the species for each
215 climate metric (Appendix S1; see Supplemental Data with this article). This 30-year period was chosen as
216 the temporal range of most likely establishment for the majority of the generally long-lived individual
217 plants sampled. For each transect on each of the five peaks, we calculated a weighted mean of the mean
218 climatic niche value of each species present in that transect. The mean was weighted by the abundance
219 of each species in that community, in our case the number of segments in which it was found when the
220 community was defined as the whole transect and the number of point-intercept hits when the
221 community was defined as the 10m x 1m segments within the transect. The abundance weighting allows
222 more dominant species to have a larger effect on the community's CCNM. This final calculation produces
223 one CCNM value for each climate metric in each community, allowing for examination of how the
224 overall climatic niche of the community changes across the elevation gradients or ranges within
225 elevation contours.

226 To examine community patterns within the elevation contours we used two metrics to
227 represent how species identity and climatic niches vary across the contour: β diversity and CCNM range.
228 We calculated per-transect β diversity as the total species richness in each transect divided by the mean
229 species richness across the 10 segments within each transect (Whittaker, 1960; Anderson et al., 2011).
230 Therefore, the minimum possible value is a β diversity of 1, which would indicate that every species in
231 the whole transect is represented within each segment of that transect. This metric gives a measure of
232 the amount of species variation that can be found within a single elevational band. The range of CCNM
233 within a single transect was determined by calculating the CCNM per segment, and then subtracting the
234 minimum from the maximum of each transect for each climate variable. The CCNM range gives a
235 measure of how variable the climatic niches of the communities are along the elevation contour; a low
236 range indicates that elevation is predominantly driving any variation in the climatic niche of the

237 communities, and a high range indicates that microclimate may be shaping the patterns of community
238 climatic niches across the landscape as well.
239
240 ***Statistical Analyses***—In order to quantify the community turnover explained by the elevational
241 gradient at the scale of the mountain range and all peaks separately, we performed permutation-based
242 MANOVAs using the 'adonis' function (1000 permutations) in the vegan package (Oksanen et al., 2008).
243 We built separate MANOVAs for the entire mountain range and for each of the peaks. For each of these
244 models, the dependent variable is a Bray-Curtis dissimilarity matrix (with the matrix rows representing
245 single transects) and the independent variable is elevation across either the entire mountain range or
246 across each peak, respectively. To visualize these relationships, we performed an ordination based on
247 non-metric dimensional scaling (NMDS) that included community data from each peak across the entire
248 White Mountain range.
249 To examine how CCNMs changed across the entire mountain range, we constructed linear
250 mixed effects models for each of the four CCNMs (climatic water deficit, mean annual precipitation,
251 maximum July temperature, and minimum January temperature) as the response variable, elevation as
252 the predictor variable, and with a random intercept effect of peak. We compared models with and
253 without a quadratic term for elevation and used Akaike's Information Criterion (AIC) to choose the
254 model with the best fit. We used a Bonferroni-corrected significance threshold of P=0.0125 for each of
255 the four models representing the different CCNM responses across all the peaks to account for multiple
256 testing. For each of the four CCNMs, we also built linear models for each peak with CCNM as the
257 response variable and elevation as the predictor variable. We used a Bonferroni-corrected significance
258 threshold of P=0.01 for each of the five models representing, for each CCNM, the CCNM response for
259 the five different peaks.

To examine community composition and species turnover at the scale of each elevation contour, we used linear models to determine whether the range in CCNM within an elevation contour (transect) significantly explained variation in β diversity. All analyses were performed using R version 3.6.0 (R Core Team, 2018). Data manipulation and visualization were performed using the R packages dplyr (Wickham et al., 2019), sf (Pebesma, 2018), and ggplot2 (Wickham, 2016).

RESULTS

Community Composition—We observed a total of 123 species in 70 genera and 25 families across the entire mountain range, with individual peak species richness ranging from 50-69 (Table 1). Across the mountain range, elevation explained 30% of the variation in community composition ($P < 0.001$, Fig. 3). When looking at each peak independently, there was an approximate 10-20% increase in the community variation explained by elevation (BAR 42% $P < 0.001$, CPT 37% $P = 0.012$, PGS 40% $P = 0.002$, SME 42% $P < 0.001$, WMT 52% $P < 0.001$). The NMDS ordination visualizes these relationships by reducing the community dimensionality into 2 dimensions. These ordinations show a clear range-wide relationship between the first axis (NMDS1) and elevation (95%, $P < 0.001$), as indicated by the arrow. Therefore, species such as *Erigeron vagus* are associated with higher elevation sites and *Erigeron tener* is associated with lower elevation sites. Within the summits, the community composition had stronger, but unique relationships with elevation; the ellipses that encompass the standard deviation of points associated with each summit line up well with the first axis and vary across the second axis (NMDS2).

Community-weighted Climatic Niche Mean—All CCNM metrics (climatic water deficit, mean annual precipitation, maximum July temperature, and minimum July temperature) showed highly significant linear relationships with elevation at the mountain range scale ($P < 0.001$ for all metrics, Fig. 4, Appendix S2). For each CCNM at the mountain range scale, the non-quadratic model performed best.

Climatic water deficit, maximum July temperature, and minimum January temperature CCNMs showed a negative relationship with elevation while mean annual precipitation showed a positive relationship with elevation. Collectively, these results indicate that the presence and abundance of species with cooler, wetter niches increased with elevation. At the individual mountain scale, the relationships between the CCNM and elevation were weak, inconsistent, or absent (Fig. 4, Appendix S2).

Variation in community composition and CCNMs across elevation contours—The mean β diversity per transect across the elevation contours was 2.1 [range, 1.3-3.2]. A β diversity of 2 indicates that, on average across the segments of the transect, there are twice as many species represented in the whole transect than in each segment. The mean of the ranges of CCNM per transect across the elevation contours were climatic water deficit: 173 mm [0 - 465], mean annual precipitation: 15.3 mm [0 - 47.9], maximum July temperature: 1.61°C [0 - 3.88], and minimum January temperature: 2.01°C [0 - 5.75]. Interestingly, this range is slightly lower, but similar in magnitude as the range of CCNM values observed across the entire mountain range (Fig. 5).

For CCNMs based on mean annual precipitation and maximum July temperature, the CCNM range was significantly and positively correlated with the per-transect β diversity (mean annual precipitation: adjusted R^2 = 0.138, P = 0.003; maximum July temperature: adjusted R^2 = 0.073, P = 0.027; Fig. 5). For climatic water deficit and minimum January temperature, there was no significant relationship between CCNM range and per-transect β diversity (climatic water deficit: adjusted R^2 = -0.016, P = 0.683; minimum January temperature: adjusted R^2 = -0.014, P = 0.590).

DISCUSSION

Investigating the dynamics of community turnover across climate gradients is a fruitful avenue for understanding where and how species distributions may shift with a changing climate (Scherrer and

308 Körner, 2011; Lenoir et al., 2013). Across the entire mountain range, both community metrics (climate-
309 derived CCNM and composition-derived Bray-Curtis dissimilarity) exhibited strong relationships with
310 elevation, but the relationships between CCNM and elevation at the individual peak scale was weak and
311 inconsistent (Figs. 3, 4). In contrast, there was a stronger relationship between elevation and community
312 composition at the scale of the individual peak relative to the entire mountain range (Fig. 3). Lastly, the
313 range of community climatic niche means was positively, but weakly correlated with the per-transect β
314 diversity (Fig. 5). Below, we discuss in more depth how the processes that shape alpine plant
315 distributions and community assembly vary across scales and explore potential impacts for using these
316 community metrics for predicting the effects of climate change on mountain communities.
317
318 ***Community Composition and Turnover Across Scales***—Elevation was a strong predictor of
319 community dissimilarity and CCNM across the entire White Mountain range (Figs. 3, 4), suggesting that
320 elevation structures both community composition and niche affinities across broad spatial scales.
321 However, we found varying responses to elevation between the two community metrics at the scale of
322 individual peaks. Consistent with our first hypothesis, more variation in community composition was
323 explained by elevation at the individual peak scale relative to the entire range despite a lower elevation
324 range within each individual summit relative to the mountain range. At the mountain range scale, non-
325 climatic differences between peaks (e.g., biotic interactions or geology) or stochastic differences likely
326 reduce the community variation explainable by elevation. Community dissimilarity has a strong, but
327 unique relationship with elevation within each summit (Fig. 3), which muddles the broader-scale
328 relationship between elevation and dissimilarity across summits.
329 At the scale of individual peaks, the elevation gradient may encompass variation in additional factors
330 besides climate, such as available space, underlying changes in geology, biotic interactions, and
331 microtopography. These non-climatic factors may influence patterns of species dissimilarity across the

elevation gradients within each peak. Dispersal limitation may also weaken the relationship between elevation and community composition at the scale of the entire mountain range (Dirnböck et al., 2011). If stochastic processes such as dispersal shape community assembly, then community dissimilarity should not vary predictably across environmental gradients. But if deterministic processes such as environmental filtering shape community assembly, community dissimilarity will not vary predictably across spatial gradients (Chase and Myers, 2011). In our study, elevation encompasses both spatial and climatic gradients limiting our ability to assess the relative importance of stochastic vs. deterministic processes in shaping species (Fig. 1; Appendix S3). Nonetheless, if dispersal limitation is reduced within individual peaks relative to among peaks across the range, elevation may be more predictive of variation in community composition within peaks as species are filtered with respect to the climatic conditions across the gradient (Svenning and Sandel, 2013; Graae et al., 2018).

Climatic Niche Means Across Scales—If climatic filtering is primarily responsible for shaping community assembly, then the presence and abundance of cooler, wetter-adapted species should increase with elevation, particularly at the scale of the entire mountain range. Indeed, we found that CCNMs based on all four climate metrics were significantly related to elevation at the mountain range scale (Fig. 4). Encouragingly, these relationships at this scale all also matched the predicted patterns of climatic niche means and elevation based on how the actual climate is predicted to vary across elevation gradients (Appendix S4). Species associated with cooler and wetter conditions were found more often and/or in higher abundance at higher elevations (Fig. 4). We also found support for our second hypothesis that elevation should more strongly predict climatic niche affinities at large spatial scales (mountain range) than at smaller scales (individual peak). Despite the strong, consistent relationship between CCNMs and elevation across the entire mountain range, dependent on the peak and the climate variable used to quantify CCNM, there were variable results for whether elevation was

356 predictive of community niche affinities for individual peaks. Therefore, at finer scales, elevation is less
357 consistently predictive of the climatic niche means of communities. This may be due to the reduced
358 range of elevation change, and therefore climatic variation, within each summit, allowing non-climatic
359 factors to play a larger role in community assembly. Within elevation contours, the range of community
360 climatic niche affinities influenced variation in species turnover with the CCNMs based on July maximum
361 temperatures and precipitation (Fig. 5), suggesting that for at least these climate metrics, microclimate
362 may facilitate niche partitioning and species coexistence at the within-contour scale. Future studies
363 should more formally examine the mechanisms of how microclimate drives patterns of community
364 assembly across these three spatial scales.

365 One caveat of our methodology is that the peaks were surveyed over the course of three years.
366 Interannual variation in weather could certainly have affected our ability to successfully identify all
367 species present in the transects. While we attempted to survey during peak flowering of the majority of
368 plant species in the White Mountains, it is also possible that different temperatures and precipitation
369 amounts in the three years could have changed the species abundances or even shifted that peak
370 phenological period outside of our sampling period. Since a given peak was surveyed in a single year,
371 this potential issue could only affect the mountain range-scale analyses.

372 An important caveat of our use of CCNMs is that due to data availability, we quantified CCNMs
373 with species' occurrences from California distributions, not the species' global distributions. For many
374 species, California encompasses the range of climatic conditions that the species experience across their
375 ranges. For other species, however, the occurrences in California are a subset of the species' larger
376 distribution, and hence their climatic niches. Niche estimates are likely particularly inaccurate for species
377 whose western range limits are found in eastern California. Further, all CCNM calculations assumed no
378 variation among populations across species ranges and thus do not account for the possibility that the
379 populations surveyed in the White Mountains may have different climatic niches relative to those found

380 in other parts of the species range. CCNMs also disregard influences of fine-scale climate on species'
381 distributions due to the coarse resolution of the climatic and herbarium specimen data (Bramer et al.,
382 2018), potentially helping to explain the weaker and less consistent relationships found between
383 elevation and CCNMs within each peak relative to across the entire mountain range.
384
385 ***Drivers of Community Variation Within Elevation Contours***—The maximum range in CCNMs observed
386 within a single elevation contour was on par with the overall maximum range of CCNM values observed
387 across the entire mountain range. This points to at least some role of microclimate in shaping species
388 distributions and community assembly. Surprisingly, we found CCNM differences within elevation
389 contours that were equivalent to those found across 100 m in elevation. While in general, species are
390 expected to move upslope in response to warming, at the local scale there will likely be suitable
391 microclimate within the same elevation. Species movement may be lateral or even downslope in order
392 to track newly suitable microclimate. These findings are supported by research in alpine plant biology
393 which has found that microclimate has a large influence on species' distributions (Körner, 2003).
394 However, the range of community climatic niche means was positively, but weakly, correlated with the
395 β diversity within elevation contour (Fig. 5), indicating minor support for our third hypothesis.
396 Therefore, other non-climatic processes are also shaping the species turnover within the elevation
397 contour. As dispersal limitation at this scale is unlikely, two major potential factors that may be instead
398 be shaping community distributions are habitat type (e.g., presence of moveable scree) and species
399 interactions. In addition to microclimate, substrate type (rock, scree, organic soil) likely heavily influence
400 species distributions, as well as species' responses to climate change (Kulonen et al., 2018). Species
401 interactions directly, or in conjunction with habitat type and microclimate, can also influence species
402 distributions at fine spatial scales (Alexander et al., 2015; Blonder et al., 2018; Graae et al., 2018). For
403 example, lower elevation species may be more competitive on organic soils than on rock or scree

404 whereas higher elevation obligate alpine plants potentially have more adaptive traits (e.g., contractile
405 roots) for persisting on the dynamic scree habitat (Kulonen et al., 2018). As we build our temporal
406 dataset, future studies will examine whether interactions between habitat segregation and elevation
407 influence species and community responses to climate change over time.
408
409 ***Conclusions/Implication for Climate Change Research***—Our findings suggest that the effects of
410 elevation on community niche affinities and community dissimilarity varies with spatial scale. At the
411 scale of the entire mountain range, there is climatic filtering across the elevation gradient, with an
412 increase in the presence and abundance of cool, wet-adapted species at higher elevations. Within
413 individual peaks and elevation contours, however, the signal of climatic filtering breaks down. This
414 points to differences in how climatic and non-climatic factors may shape species composition at
415 different scales. At broad spatial scales, deterministic climate appears to be a main driver of plant
416 community assembly since the large, consistent elevation gradient can mask stochastic factors such as
417 chance colonization and extinction and non-climatic factors like geology. At smaller scales where
418 dispersal is less limiting and microsite climatic variation is common even within the same elevation
419 contour, synoptic climatic factors appear less important than non-climatic factors in structuring
420 community. We did not directly measure those non-climatic factors, but they are likely to be related to
421 habitat and substrate type.
422 Since climatic niche metrics are often used for quantifying community responses to climate
423 change, it is important to understand their relative strengths in explaining community turnover across
424 scales. The breakdown of correlations between CCNM and elevation at finer-scales, even though species
425 turnover based on identity is still explained by elevation at this scale, suggests an important caveat for
426 using climate-based community measures at these scales. Perhaps we would not find this pattern if our
427 climate data used to calculate the species climatic niches were at finer resolutions, which is supported

by the positive correlation per-transect β diversity and range of CCNM within a transect. However, this correlation is weak indicating that higher resolutions may not be sufficient to understand species distributions at these micro-topographic scales. Within the context of climate change, predictions of local alpine plant range shifts will be limited by availability of topoclimatic, as well as habitat, information.

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Author Contributions

Brian Smithers, Meagan Oldfather, and Michael Koontz participated in data collection, data processing, analysis, and in the writing of the manuscript.

Jim Bishop and Catie Bishop created the downslope transect protocol, participated in data collection, data processing, and in editing of the manuscript.

Jan Nachlinger participated in data collection, data processing, and in the editing of the manuscript.

Seema Sheth participated in data processing, analysis and in the writing of the manuscript.

Data Accessibility

Data and R code from the project are available on the GLORIA Great Basin website (https://www.gloriagreatbasin.org/documents-archives) as well as in a permanent Figshare repository (DOI: 10.6084/m9.figshare.8968793). Due to the long-term nature of plot monitoring, we have not collected voucher specimens from within the plots however when voucher specimens from outside the plot were collected, the specimens were housed at the White Mountain Research Center, Owens Valley Station.

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Supporting Information

Additional Supporting Information may be found online in the supporting information section at the end of the article.

Appendix S1: Climatic Niche Means (CNMs) for each species observed among all peaks.

Appendix S2: Model results for each of the climate metrics on each of the peaks and for all peaks combined.

Appendix S3: Average climate variables for each transect.

Peak	Sample Year	Elevation (m)	Soil Type	Aspect	# Transects	Richness
White Mountain Peak (WMT)	2012	3971-4296	Igneous	SE	14	50
Mount Barcroft (BAR)	2011	3625-3950	Igneous	SE	14	69
Sheep Mountain (SME)	2011	3475-3725	Dolomitic	SE	11	57
Campito Mountain (CPT)	2013	3325-3500	Quartzitic	E	8	51
Patriarch Grove South (PGS)	2012	3299-3478	Dolomitic	SE	8	51

Table 1: Sampled peaks and associated data in the White Mountains, CA. Total richness is the number of unique species found on each peak.

FIGURE LEGENDS

Figure 1. Geographic extent and terrain of the study area in the White Mountains, east of the Sierra Nevada mountain range in California (red diamond in inset). Points mark the centers for each transect, with 50m long and 1m wide belt transects extending on either side of these center points following the elevation contour. Terrain is rendered as a hillshade using the ⅓ arc second (~10m) digital elevation model from the USGS National Elevation Dataset with a sun angle of 40 degrees and a sun direction of 270 degrees. WMT = White Mountain Peak, BAR = Mount Barcroft, SME = Sheep Mountain East, PGS = Patriarch Grove South, and CPT = Campito Mountain. All transects are centered along the southeast aspect of each peak, except Campito Mountain (CPT), which is centered on the east aspect.

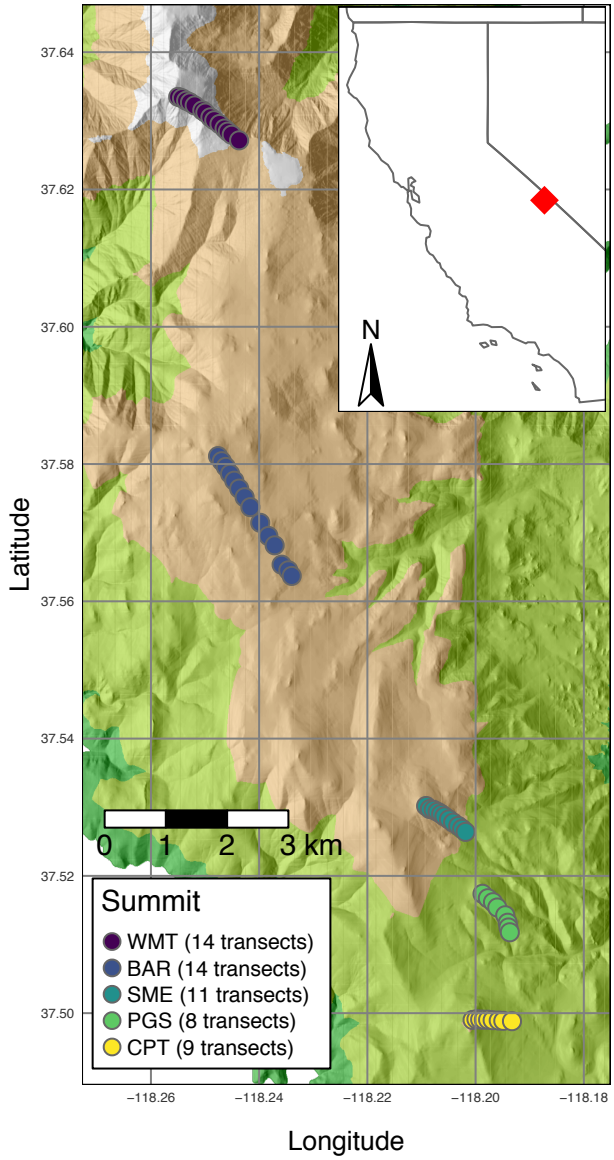
Figure 2. Conceptual figure illustrating the three presented hypotheses and the three scales of analysis: mountain range, summit, and within elevation contours. Species identity is represented by differing plant morphology and climatic niche affinity is represented by color. The first and second hypotheses

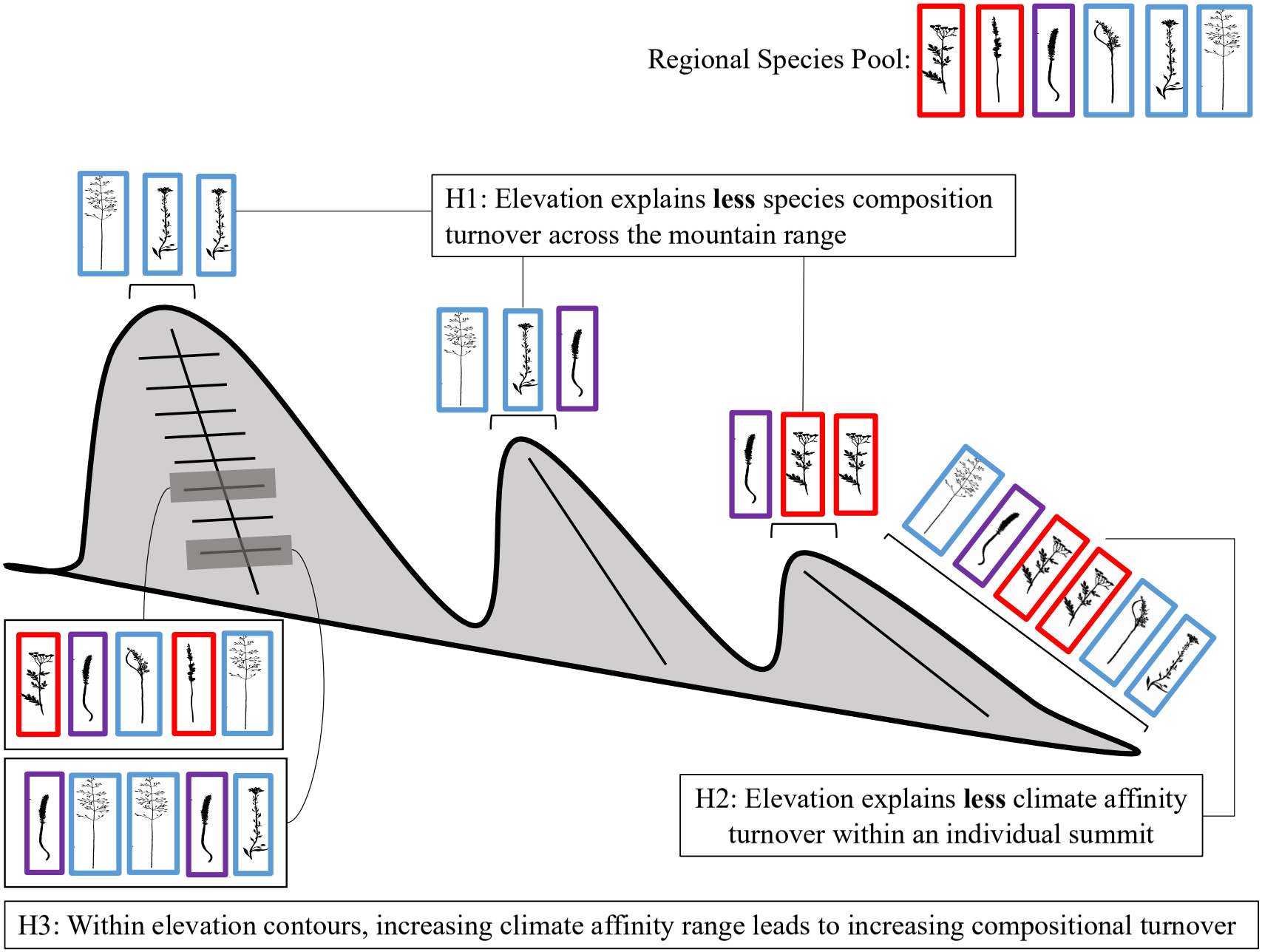
625 (H1, H2) require comparisons of the general patterns of community turnover across the elevation
626 gradient (for species identity and climatic niche affinity) between the mountain range and summit
627 scales. Across the mountain range, we hypothesize predictive changes in the climatic niche affinity, but
628 less so in species identity, across the elevation gradient. Within an individual summit, we hypothesize
629 predictive changes in species identity, but less so in the climatic niche affinity of those species, across
630 the elevation gradient. The third hypothesis (H3) focuses on comparing communities within elevation
631 contours (single scale) and we show the hypothesized positive correlation between the turnover in
632 species identity and range of climatic niche affinity.
633
634 Figure 3. Non-metric dimensional scaling (NMDS) ordination of Bray-Curtis dissimilarity. The arrow
635 indicates the directional influence of elevation. In the event of species name overlap, only the more
636 common species is shown here, but all species were included in the analysis.
637
638 Figure 4: Community-weighted Climatic Niche Means for (A) Climatic Water Deficit (CWD), (B) Mean
639 Annual Precipitation (MAP), (C) Average July maximum temperature (July T_{max}), and (D) Average January
640 minimum temperature (Jan T_{min}) along the elevation gradient. The black solid lines represent the linear
641 model fit for the entire range, all of which showed highly significant trends ($P < 0.001$). Shaded areas
642 represent the standard error around the linear model. Each point is 1 transect and is color-coded by
643 peak. Peaks with a significant ($P < 0.05$) relationship between CCNM and elevation are shown with a
644 solid line, and those with a non-significant ($P > 0.05$) relationship are shown with a dashed line.
645
646 Figure 5. Relationship between community climatic niche mean (CCNM) range and per-transect β
647 diversity. Climate metrics with a significant ($P < 0.05$) relationship between CCNM range and β diversity

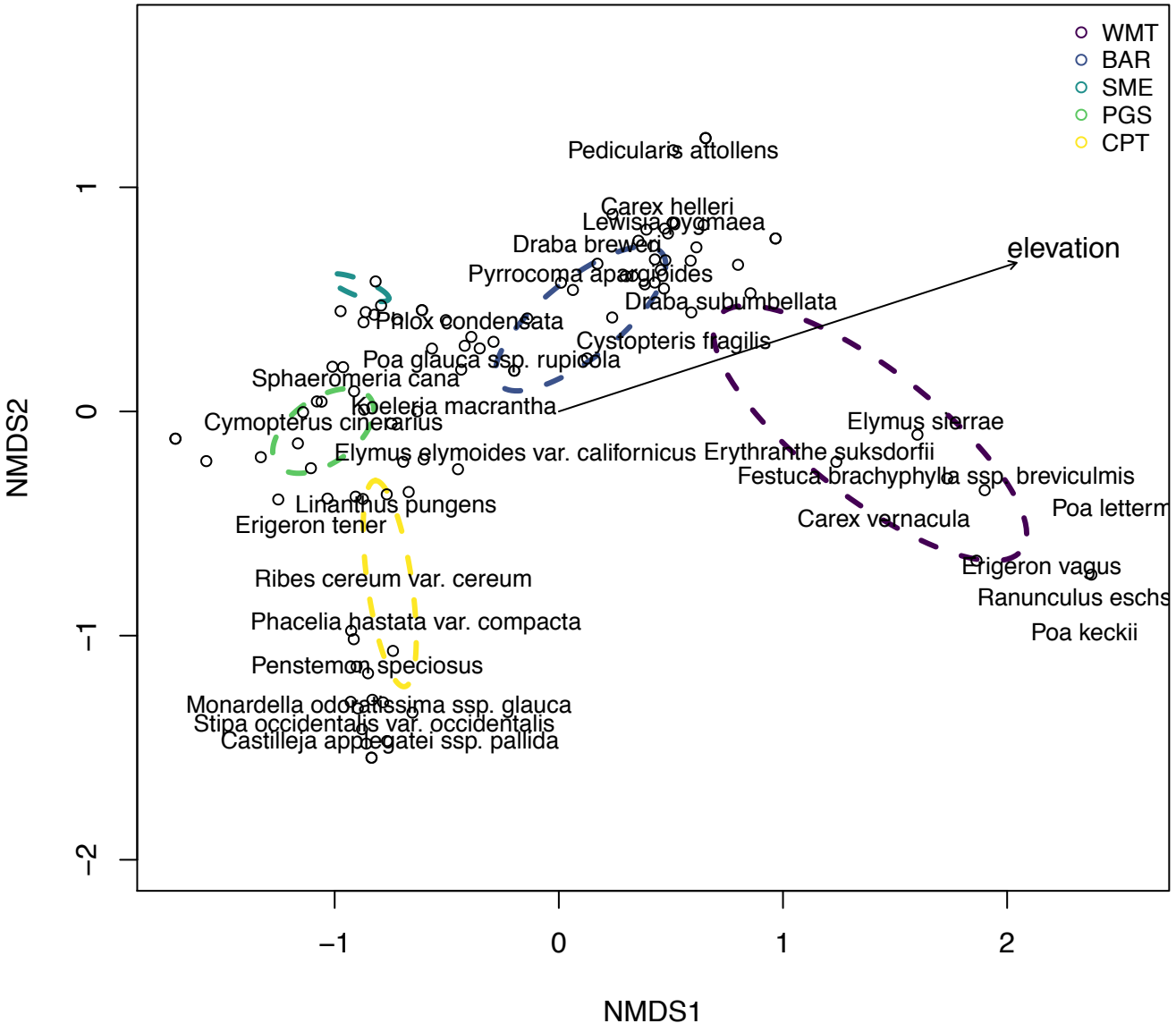
648 per transect are shown with a solid line, and those with a non-significant ($P > 0.05$) relationship are

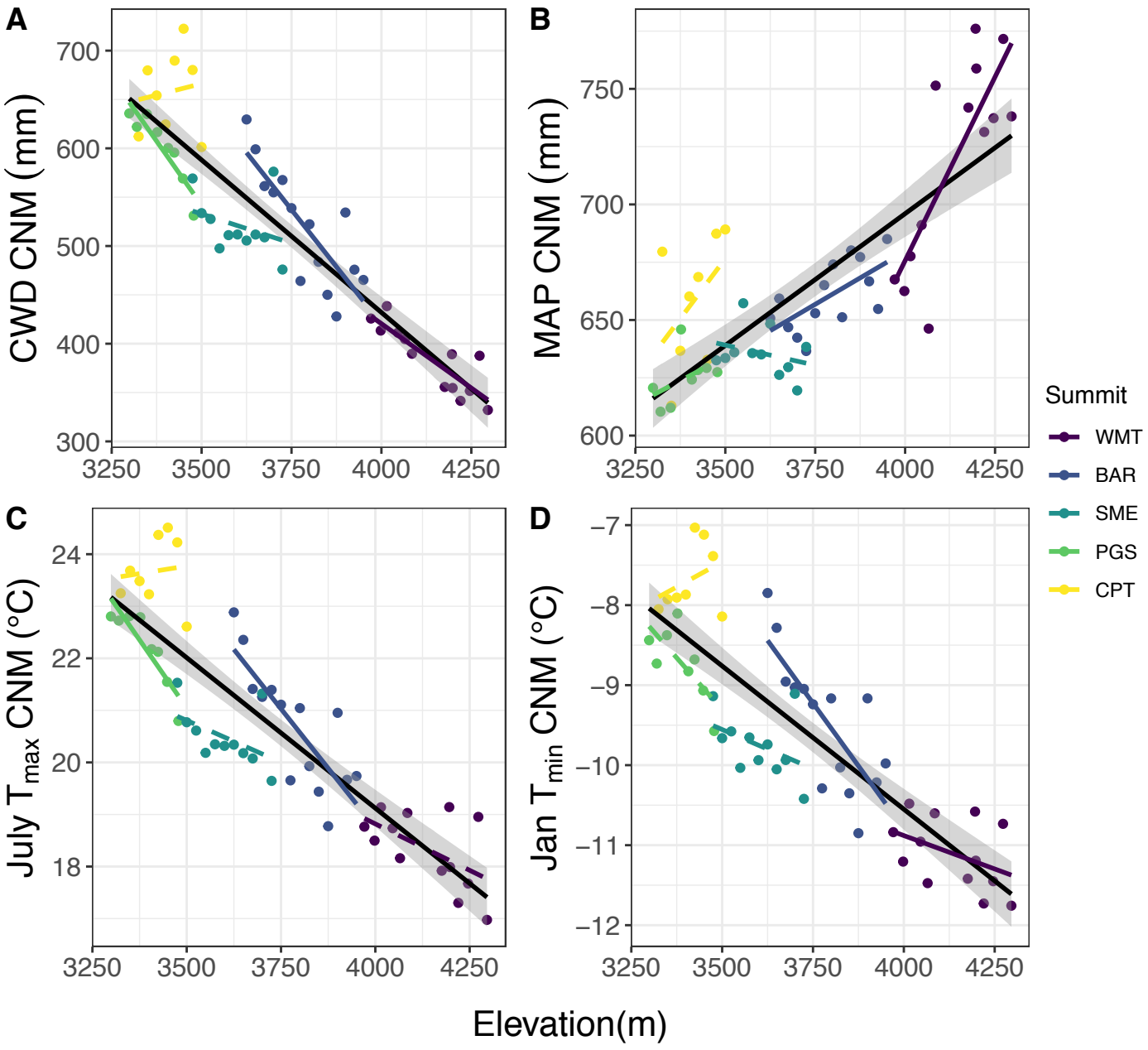
649 shown with a dashed line.

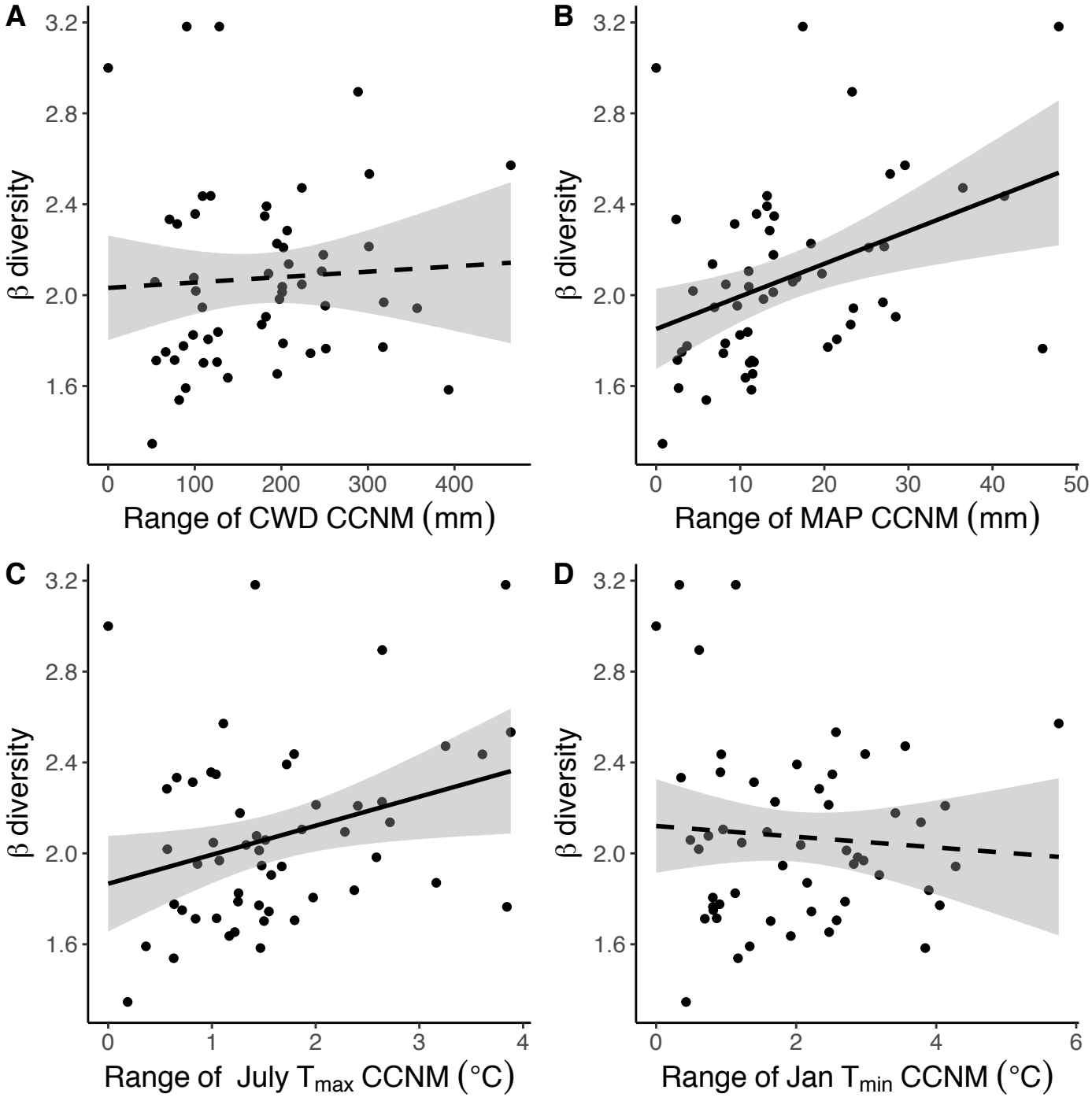
650


37.64
37.62
37.60
37.58
37.56
37.54
37.52
37.50
Latitude
−118.26
−118.24
−118.22
−118.20
−118.18
Longitude
N
0
1
2
3 km
Summit
WMT (14 transects)
BAR (14 transects)
SME (11 transects)
PGS (8 transects)
CPT (9 transects)


Regional Species Pool:
H1: Elevation explains **less** species composition turnover across the mountain range
H2: Elevation explains **less** climate affinity turnover within an individual summit
H3: Within elevation contours, increasing climate affinity range leads to increasing compositional turnover


WMT
BAR
SME
PGS
CPT
elevation
Pedicularis attollens
Carex helleri
Lewisia pygmaea
Draba breweri
Pyrrocoma apargioides
Draba subumbellata
Phlox condensata
Cystopteris fragilis
Poa glauca ssp. rupicola
Sphaeromeria cana
Koeleria macrantha
Cymopterus cinerarius
Elymus elymoides var. californicus
Erythranthe suksdorfii
Festuca brachyphylla ssp. breviculmis
Elymus sierrae
Poa letterm
Carex vernacula
Linanthus pungens
Erigeron tener
Erigeron vagus
Ranunculus eschs
Poa keckii
Ribes cereum var. cereum
Phacelia hastata var. compacta
Penstemon speciosus
Monardella odoratissima ssp. glauca
Stipa occidentalis var. occidentalis
Castilleja applegatei ssp. pallida
NMDS2
NMDS1
1
0
−1
−2
−1
0
1
2


A
B
C
D
CWD CNM (mm)
MAP CNM (mm)
July T_{max} CNM (°C)
Jan T_{min} CNM (°C)
Elevation(m)
Summit
WMT
BAR
SME
PGS
CPT


A
B
C
D
β diversity
3.2
2.8
2.4
2.0
1.6
0
100
200
300
400
Range of CWD CCNM (mm)
10
20
30
40
50
Range of MAP CCNM (mm)
1
2
3
4
Range of July T_{max} CCNM (°C)
6
Range of Jan T_{min} CCNM (°C)