Title: Community turnover by composition and climate 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; plant ecology; species distribution; topography; 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). Mountain geometry generally, but not always, also means that species will face decreasing land area as they track their climatic niche to higher elevations (Elsen and Tingley, 2015). 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 climate 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. Importantly, 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 climatologic 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 gradients, 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 larger role (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). When considering community climatic niche affinities, environmental filtering processes may drive species turnover. Conversely, community similarity metrics based on species composition alone may be more dependent on the stochastic order and timing of species arrivals into the community (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 change 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: across an entire mountain range, within each of five peaks spread across the mountain range, and within elevation contours of each peak, in the White Mountains, California, USA (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 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. 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 raw community composition and elevation may be stronger at smaller scales (i.e., within a single peak). Specifically, we propose the following hypotheses.

1) At broad spatial scales (mountain range), non-climatic or stochastic differences will be more important in explaining variation in species composition and turnover. We predict that elevation explains less variation in species composition and turnover across the entire range versus within each peak.

2) At broad spatial scales, climatic factors as environmental filters will be more important in explaining plant community variation in climatic niche space. 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).

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).

166 ***Field Surveys***—We sampled alpine community composition along elevation gradients using 100-
167 meter belt transects on five peaks in the White Mountains: White Mountain Peak (WMT), Mount
168 Barcroft (BAR), Sheep Mountain East (SME), Patriarch Grove South (PGS), and Campito Mountain (CPT)
169 (Bishop, 2011). On each peak, the first transect was established on the southeast aspect (east aspect for
170 Campito Peak), 35 vertical meters below the summit. Two, 50m x 1m belt transects were extended from
171 this central point following the elevation contour to create a 100-meter x 1-meter belt transect at one
172 elevation. Additional 100m x 1m transects were established on each peak in intervals of 25 vertical
173 meters below the previous transect on the same aspect (Fig. 1). Transects were established across 3
174 consecutive years from 2011-2013 (Table 1). Each transect was divided into ten continuous, 10m x 1m
175 segments. In each segment, we recorded the presence of every species. We assessed cover of plant
176 species and substrate (rock, scree, litter, bare ground) along the entire transect using a point-intercept
177 method with 40 points per 10m x 1m segment. A pair of points was located at every half-meter along
178 the transect, with the points in each pair 0.5 m apart (0.25 m from the center of the belt transect). The
179 substrate or plant species was recorded as a "hit" if a point intersected with it.
180
181 ***Community Metrics***—To investigate how communities varied across spatial gradients, we used
182 community-weighted climatic niche means (CCNM) and community composition. A CCNM is the
183 abundance-weighted mean of each component species' average species niche space across its range (De
184 Frenne et al., 2013). For community composition we used the Bray-Curtis dissimilarity metric of β
185 diversity, which incorporates both species presence and relative abundance (Anderson et al., 2011). Our
186 measure of abundance used for both metrics was the number of segments in which it was found for
187 each transect. We consider how these two community metrics change across three nested scales: the
188 elevation gradient of the entire mountain range, the elevation gradient of a single peak, and within a
189 single elevation contour of a peak.

190 A CCNM is a property of a single community, or in our specific case, a transect for mountain
191 range- and peak-scale analyses and a 10m segment within transects for the elevation contour-scale
192 analysis. Any climate metric can be used to quantify a community's CCNM. We focused on the following
193 climatic measurements as they are likely major structuring factors for alpine plant communities: climatic
194 water deficit (CWD), mean annual precipitation (MAP), July maximum temperature (July T_{max}), and
195 January minimum temperature (Jan T_{min}). CWD is an integrative measure of how much energy
196 availability (temperature) exceeds water supply (precipitation), with higher values indicating hotter,
197 drier conditions, and lower values indicating cooler, wetter conditions. Using a recently-compiled
198 database of California herbarium specimens derived from the Consortium of California Herbaria as well
199 as additional natural history museums and herbaria (Baldwin et al., 2017), we extracted locations from
200 all vouchered specimens in the database for each surveyed species. We used those database locations
201 to extract 30-year (1961-1990) mean climate values for CWD, MAP, July T_{max}, and Jan T_{min} from the
202 TerraClimate gridded dataset (Abatzoglou et al., 2018), which is itself an amalgamation of the WorldClim
203 dataset (Fick and Hijmans, 2017) and other data. After culling the herbaria records to one record per
204 species per grid cell to reduce sampling bias, we extracted the four mean climate values for each
205 species, representing the mean climatic niche of the species for each climate metric (Appendix S1; see
206 Supplemental Data with this article). This 30-year period was chosen as the temporal range of most
207 likely establishment for the majority of the generally long-lived individual plants sampled. For each
208 transect on each of the five peaks, we calculated a weighted mean of the mean climatic niche value of
209 each species present in that transect. The mean was weighted by the abundance of each species in that
210 community, in our case the number of segments in which it was found when the community was
211 defined as the whole transect and the number of point-intercept hits when the community was defined
212 as the 10m x 1m segments within the transect. The abundance weighting allows more dominant species
213 to have a larger effect on the community's CCNM. This final calculation produces one CCNM value for

214 each climate metric in each community, allowing for examination of how the overall climatic niche of
215 the community changes across the elevation gradients or ranges within elevation contours. For this
216 system, regional CCNM values are representative of local climatic niche means derived from
217 microclimate field data (Oldfather and Ackerly, in press).

218 To examine community patterns within the elevation contours we used two metrics to
219 represent how species identity and climatic niches vary across the contour: β diversity and CCNM range.
220 We calculated per-transect β diversity as the total species richness in each transect divided by the mean
221 species richness across the 10 segments within each transect. Therefore, the minimum possible value is
222 a β diversity of 1, which would indicate that every species in the whole transect is represented within
223 each segment of that transect. This metric gives a measure of the amount of species variation that can
224 be found within a single elevational band. The range of CCNM within a single transect was determined
225 by calculating the CCNM per segment, and then subtracting the minimum from the maximum of each
226 transect for each climate variable. The CCNM range gives a measure of how variable the climatic niches
227 of the communities are along the elevation contour; a low range indicates that elevation is
228 predominantly driving any variation in the climatic niche of the communities, and a high range indicates
229 that microclimate may be shaping the patterns of community climatic niches across the landscape as
230 well.

231

232 ***Statistical Analyses***—To examine how CCNMs changed across the entire mountain range, we
233 constructed linear mixed effects models for each of the four CCNMs (CWD, MAP, July T_{max}, and Jan T_{min})
234 as the response variable, elevation as the predictor variable, and with a random intercept effect of peak.
235 We compared models with and without a quadratic term for elevation and used Akaike's Information
236 Criterion (AIC) to choose the model with the best fit. For each of the four CCNMs, we also built linear
237 models for each peak with CCNM as the response variable and elevation as the predictor variable.

238 In order to quantify the community turnover explained by the elevational gradient at the scale
239 of the mountain range and all peaks separately, we performed permutation-based MANOVAs using the
240 'adonis' function (999 permutations) in the vegan package (Oksanen et al., 2008). We built separate
241 MANOVAs for the entire mountain range and for each of the peaks. For each of these models, the
242 dependent variable is a Bray-Curtis dissimilarity matrix (with the matrix rows representing single
243 transects) and the independent variable is elevation across either the entire mountain range or across
244 each peak, respectively. To visualize these relationships, we performed an ordination based on non-
245 metric dimensional scaling (NMDS) that included community data from each peak across the entire
246 White Mountain range.
247 To examine community composition and species turnover at the scale of each elevation
248 contour, we used linear models to determine whether the range in CCNM within an elevation contour
249 (transect) significantly explained variation in β diversity. All analyses were performed using R version
250 3.6.0 (R Core Team, 2018). Data manipulation and visualization were performed using the R packages
251 dplyr (Wickham et al., 2019), sf (Pebesma, 2018), and ggplot2 (Wickham, 2016).
252
253 RESULTS
254 ***Community Composition***—We observed a total of 123 species in 70 genera and 25 families across the
255 entire mountain range, with individual peak species richness ranging from 50-69 (Table 1). Species
256 richness increased with elevation at PGS, and steeply declined with elevation at WMT, but did not vary
257 linearly with elevation on the remaining peaks (Appendix S2).
258 Across the mountain range, elevation explained 30% of the variation in community composition
259 ($P < 0.001$, Fig. 2). When looking at each peak independently, there was an approximate 10-20%
260 increase in the community variation explained by elevation (BAR 42% $P < 0.001$, CPT 37% $P = 0.013$, PGS
261 40% $P < 0.001$, SME 42% $P < 0.001$, WMT 52% $P < 0.001$). The NMDS ordination visualizes these

262 relationships by reducing the community dimensionality into 2 dimensions. First, the ordinations show a
263 clear range-wide relationship between the first axis (NMDS1) and elevation (95% $P < 0.001$), as indicated
264 by the arrow. Therefore, species such as *Erigeron vagus* are associated with higher elevation sites
265 and *Erigeron tenor* is associated with lower elevation sites. Within the summits, the community
266 composition had stronger, but unique relationships with elevation; the ellipses that encompass the
267 standard deviation of points associated with each summit line up well with the first axis and vary across
268 the second axis (NMDS2).
269
270 ***Community-weighted Climatic Niche Mean***—All CCNM metrics (CWD, MAP, Jan T_{min}, and July
271 T_{max}) showed highly significant linear relationships with elevation at the mountain range scale ($P < 0.001$
272 for all metrics, Fig. 3, Appendix S3). For each CCNM at the mountain range scale, the non-quadratic
273 model performed best. CWD, Jan T_{min}, and July T_{max} CCNMs showed a negative relationship with
274 elevation while annual precipitation (MAP) showed a positive relationship with elevation. Collectively,
275 these results indicate that the presence and abundance of species with cooler, wetter niches increased
276 with elevation. At the individual mountain scale, the relationships between the CCNM and elevation
277 were weak, inconsistent, or absent (Fig. 3, Table S2). On some of the peaks, the CCNM trend ran counter
278 to the range-wide trend, although those peak-scale countertrends were insignificant.
279
280

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 ranges of CCNM per transect across the elevation contours were CWD 173 mm [0 - 465], MAP 15.3 mm [0 - 47.9], July T_{max} 1.61°C [0 - 3.88], and Jan T_{min} 2.01°C [0 - 5.75]. Interestingly, this variation is slightly lower, but similar in magnitude as the range of CCNM values observed across the entire mountain range (Fig. 3).

For CCNM MAP and July T_{max}, the CCNM range was significantly and positively correlated with the per-transect β diversity (MAP: adjusted R^2 = 0.138, P = 0.003; July T_{max}: adjusted R^2 = 0.073, P = 0.027; Fig. 4). For CWD and Jan T_{min}, there was no significant relationship between CCNM range and per-transect β diversity (adjusted R^2 = -0.016, P = 0.683; Jan T_{min}: 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 Körner, 2011; Lenoir et al., 2013). Using a detailed alpine plant community dataset across steep elevation and climate gradients, we investigated how climate associations shape species distributions and community assembly across multiple scales over which range shifts have been predicted and quantified. Across the entire mountain range, both community metrics (climate-derived CCNM and composition-derived Bray-Curtis dissimilarity) exhibited strong relationships with elevation, but the relationships between CCNM and elevation at the individual peak scale was weak and inconsistent (Figs. 2, 3). In contrast, there was a stronger relationship between elevation and community composition at

304 the scale of the individual peak relative to the entire mountain range (Fig. 2). Lastly, the range of
305 community climatic niche means was positively, but weakly correlated with the per-transect β diversity
306 (Fig. 4). Below, we discuss in more depth how the processes that shape alpine plant distributions and
307 community assembly vary across scales and explore potential impacts for using these community
308 metrics for predicting the effects of climate change on mountain communities.
309
310 ***Community Composition and Turnover Across Scales***—Elevation was a strong predictor of
311 community dissimilarity and CCNM across the entire White Mountain range (Figs. 2, 3), suggesting that
312 elevation structures both community composition and niche affinities across broad spatial scales.
313 However, we found varying responses to elevation between the two community metrics at the scale of
314 individual peaks. Consistent with our first hypothesis, more variation in community composition was
315 explained by elevation at the individual peak scale relative to the entire range despite decreased
316 elevation range within each individual summit relative to the mountain range. At the mountain range
317 scale, non-climatic differences between peaks (e.g., biotic interactions or geology) or stochastic
318 differences likely reduce the community variation explainable by elevation. Community dissimilarity has
319 a strong, but unique relationship with elevation within each summit (Fig. 2), which muddles the broader-
320 scale relationship between elevation and dissimilarity across summits.
321 At the scale of individual peaks, the elevation gradient may encompass variation in additional
322 factors besides climate, such as available space, underlying changes in geology, biotic interactions, and
323 microtopography. Thus, these additional non-climatic factors may influence patterns of species
324 dissimilarity across the elevation gradients within each peak. Further, dispersal limitation is another
325 potentially important non-climatic factor that may weaken the relationship between elevation and
326 community composition at the scale of the entire mountain range (Dirnböck et al., 2011). On the one
327 hand, if stochastic processes such as dispersal effects explain community assembly, then species

328 dissimilarity should be invariant across environmental gradients such as elevation. On the other hand, if
329 deterministic processes such as environmental filtering are more important in shaping community
330 assembly, then species turnover should be invariant across spatial gradients (Chase and Myers, 2011).
331 Because elevation across the entire mountain range encompasses both spatial and climatic gradients
332 (Fig. 1; Appendix S4), then our ability to assess the relative importance of stochastic vs. deterministic
333 processes in shaping species turnover may be limited. Nonetheless, if dispersal limitation is reduced
334 within individual peaks relative to among peaks across the range, then variation in community
335 composition within peaks may be better explained by elevation as species are filtered with respect to
336 the climatic conditions across the gradient (Svenning and Sandel, 2013; Graae et al., 2018).
337
338 ***Climatic Niche Means Across Scales***—If climatic filtering is primarily responsible for shaping
339 community assembly, then the presence and abundance of cooler, wetter-adapted species should
340 increase with elevation, particularly at the scale of the entire mountain range. Indeed, we found that
341 CCNMs based on all four climate metrics were significantly related to elevation at the mountain range
342 scale (Fig. 3). Encouragingly, these relationships at this scale all also matched the predicted patterns of
343 climatic niche means and elevation based on how the actual climate is predicted to vary across elevation
344 gradients (Appendix S4). Species associated with cooler and wetter conditions were found more often
345 and/or in higher abundance at higher elevations (Fig. 3). We also found support for our second
346 hypothesis that elevation should more strongly predict climatic niche affinities at large spatial scales
347 (mountain range) than at smaller scales (individual peak). Despite the strong, consistent relationship
348 between CCNMs and elevation across the entire mountain range, dependent on the peak and the
349 climate variable used to quantify CCNM, there were variable results for whether elevation was
350 predictive of community niche affinities for individual peaks. Therefore, at finer scales, elevation is less
351 consistently predictive of the climatic niche means of communities. This may be due to the reduced

range of elevation change, and therefore climatic variation, within each summit, allowing non-climatic factors to play a larger role in community assembly. Within elevation contours, the range of community climatic niche affinities influenced variation in species turnover with the CCNMs based on July maximum temperatures and precipitation (Fig. 4), suggesting that for at least these climate metrics, microclimate may facilitate niche partitioning and species coexistence at the within-contour scale. Future studies should more formally examine the mechanisms of how microclimate drives patterns of community assembly across these three spatial scales.

One important caveat of our use of CCNMs is that due to data availability, we quantified CCNMs with species' occurrences from California distributions, not the species' global distributions. For many species, California encompasses the range of climatic conditions that the species experience across their ranges. For other species, however, the occurrences in California are a subset of the species' larger distribution, and hence their climatic niches. Niche estimates are likely particularly inaccurate for species whose western range limits are found in eastern California. Further, all CCNM calculations assumed no variation among populations across species ranges and thus do not account for the possibility that the populations surveyed in the White Mountains may have different climatic niches relative to those found in other parts of the species range. CCNMs also disregard influences of fine-scale climate on species' distributions due to the coarse resolution of the climatic and herbarium specimen data (Bramer et al., 2018), potentially helping to explain the weaker and less consistent relationships found between elevation and CCNMs within each peak relative to across the entire mountain range.

Drivers of Community Variation Within Elevation Contours—The maximum range in CCNMs observed within a single elevation contour was on par with the overall maximum range of CCNM values observed across the entire mountain range. This points to at least some role of microclimate in shaping species distributions and community assembly. We found CCNM differences within elevation contours that

were equivalent to those found across 100 m in elevation! While in general, species are expected to move upslope in response to warming, at the local scale there will likely be suitable microclimate within the same elevation. Species movement may be lateral or even downslope in order to track newly suitable microclimate. These findings are supported by research in alpine plant biology which has found that microclimate has a large influence on species' distributions (Körner, 2003). However, the range of community climatic niche means was positively, but weakly, correlated with the β diversity within elevation contour (Fig. 4), indicating minor support for our third hypothesis. Therefore, other non-climatic processes are also shaping the species turnover within the elevation contour. As dispersal limitation at this scale is unlikely, two major potential factors that may be instead be shaping community distributions are habitat type (e.g., presence of moveable scree) and species interactions. In addition to microclimate, substrate type (rock, scree, organic soil) likely heavily influence species distributions, as well as species' responses to climate change (Kulonen et al., 2018). Species interactions directly, or in conjunction with habitat type and microclimate, can also influence species distributions at fine spatial scales (Alexander et al., 2015; Blonder et al., 2018; Graae et al., 2018). For example, lower elevation species may be more competitive on organic soils than on rock or scree whereas higher elevation obligate alpine plants potentially have more adaptive traits (e.g., contractile roots) for persisting on the dynamic scree habitat (Kulonen et al., 2018). As we build our temporal dataset, future studies will examine whether interactions between habitat segregation and elevation influence species and community responses to climate change over time.

Conclusions/Implication for Climate Change Research—Our findings suggest that the effects of elevation on community niche affinities and community dissimilarity varies with spatial scale. At the scale of the entire mountain range, there is climatic filtering across the elevation gradient, with an increase in the presence and abundance of cool, wet-adapted species at higher elevations. Within

individual peaks and elevation contours, however, the signal of climatic filtering breaks down. This points to differences in how climatic and non-climatic factors may shape species composition at different scales. At broad spatial scales, deterministic climate appears to be a main driver of plant community assembly since the large, consistent elevation gradient can mask stochastic factors such as chance colonization and extinction and non-climatic factors like geology. At smaller scales where dispersal is less limiting and microsite climatic variation is common even within the same elevation contour, synoptic climatic factors appear less important than non-climatic factors in structuring community. We did not directly measure those non-climatic factors, but they are likely to be related to habitat and substrate type. Since climatic niche metrics are often used for quantifying community responses to climate change, it is important to understand their relative strengths in explaining community turnover across scales. The breakdown of correlations between CCNM and elevation at finer-scales, even though species turnover based on identity is still explained by elevation at this scale, suggests an important caveat for using climate-based community measures at these scales. Perhaps we would not find this pattern if our 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 to come).

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Peak	Sample Year	Elevation (m)	Soil Type	Aspect	# Transects	Total 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

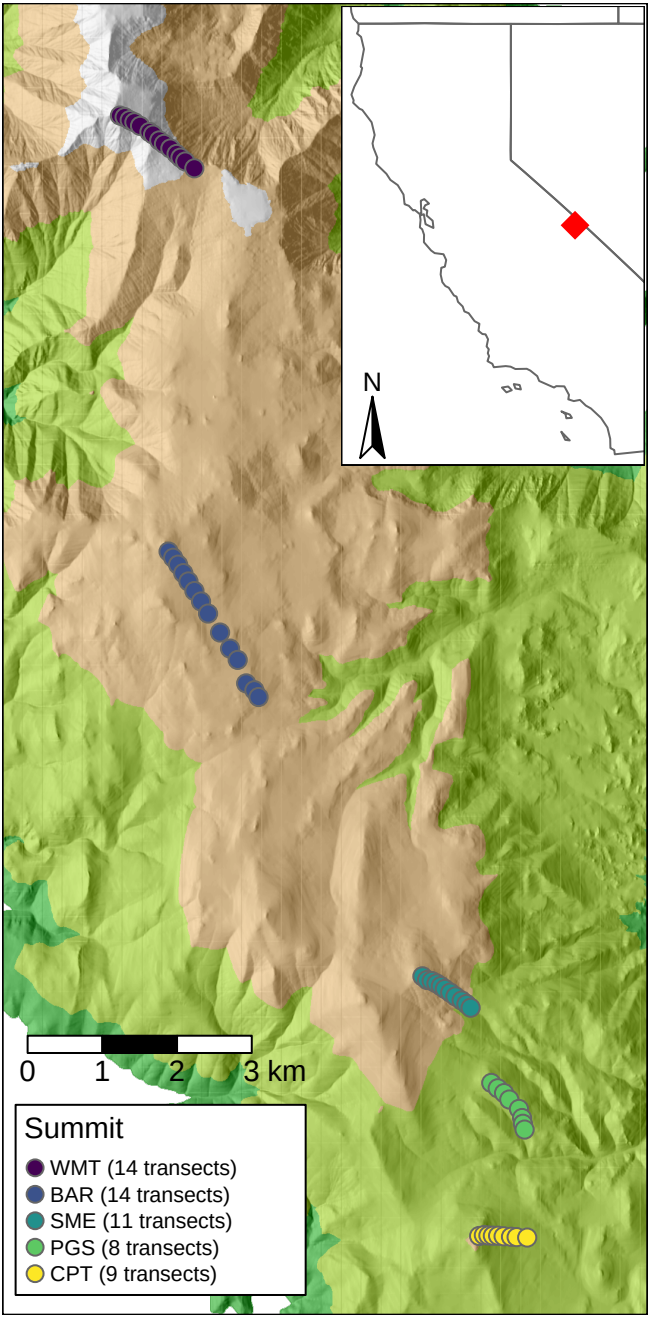
Figure 1. Geographic extent and terrain of the study area in the White Mountains, east of the Sierra Nevada mountain range in California (red diamond in inset). Points mark the centers for each transect, with 50m long and 1m wide belt transects extending on either side of these center points following 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

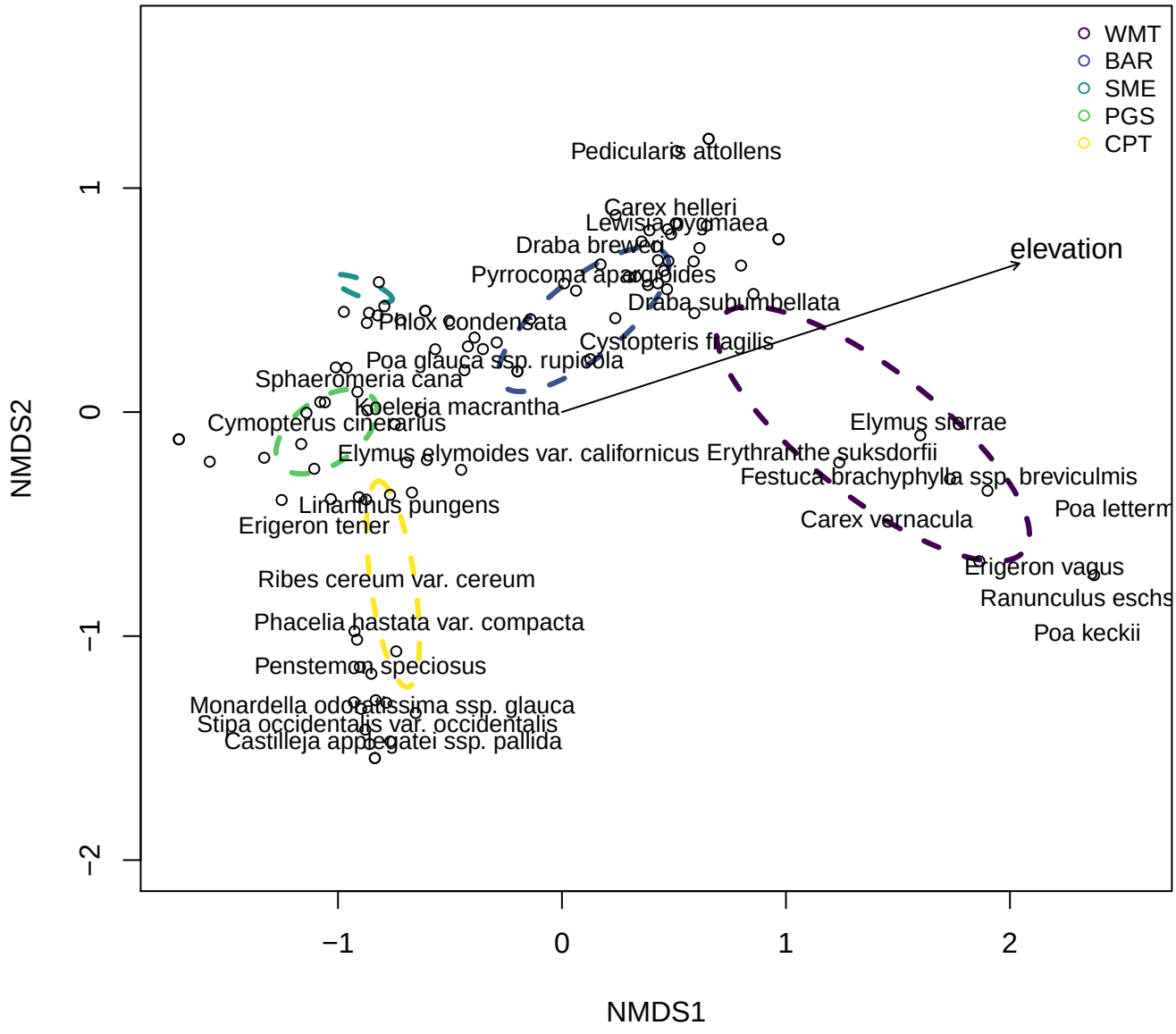
270 degrees. WMT = White Mountain Peak, BAR = Mount Barcroft, SME = Sheep Mountain East, PGS = Patriarch Grove South, and CPT = Campito Mountain. All transects are centered along the southeast aspect of each peak, except Campito Mountain (CPT), which is centered on the east aspect.

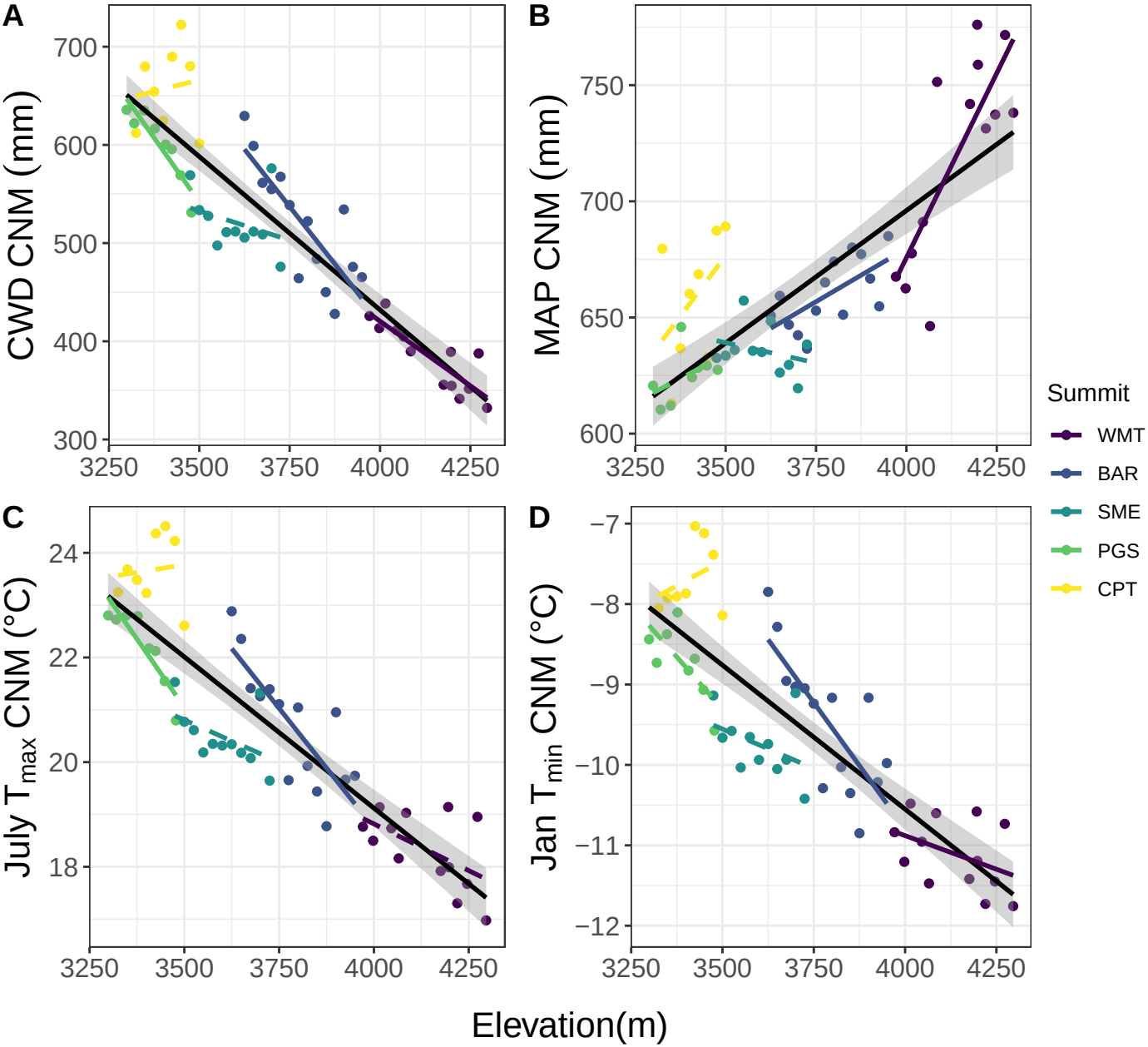
Figure 2. Non-metric dimensional scaling (NMDS) ordination of Bray-Curtis dissimilarity. The arrow indicates the directional influence of elevation. In the event of species name overlap, only the more common species is shown here, but all species were included in the analysis.

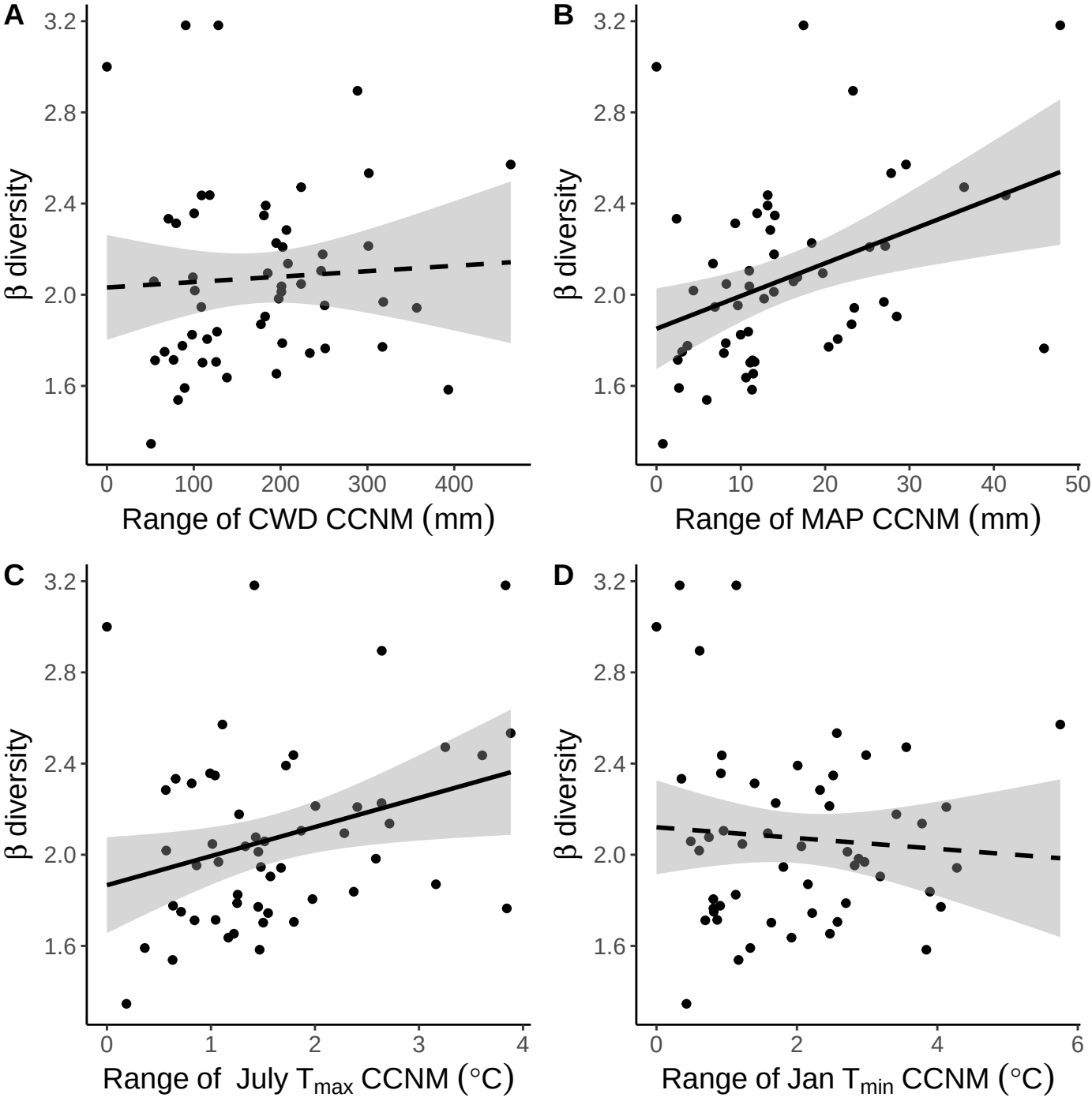
Figure 3: Community-weighted Climatic Niche Means for (A) Climatic Water Deficit (CWD), (B) Mean Annual Precipitation (MAP), (C) Average July maximum temperature (July T_{max}), and (D) Average January minimum temperature (Jan T_{min}) along the elevation gradient. The black solid lines represent the linear model fit for the entire range, all of which showed highly significant trends ($P < 0.001$). Shaded areas represent the standard error around the linear model. Each point is 1 transect and is color-coded by peak. Peaks with a significant ($P < 0.05$) relationship between CCNM and elevation are shown with a solid line, and those with a non-significant ($P > 0.05$) relationship are shown with a dashed line.

Figure 4. Relationship between community climatic niche mean (CCNM) range and per-transect β diversity. Climate metrics with a significant ($P < 0.05$) relationship between CCNM range and β diversity per transect are shown with a solid line, and those with a non-significant ($P > 0.05$) relationship are shown with a dashed line.


N
0
1
2
3 km
Summit
WMT (14 transects)
BAR (14 transects)
SME (11 transects)
PGS (8 transects)
CPT (9 transects)


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
Elymus sierrae
Erythranthe suksdorfii
Festuca brachyphylla ssp. breviculmis
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
CWD CNM (mm)
700
600
500
400
300
3250
3500
3750
4000
4250
B
MAP CNM (mm)
750
700
650
600
C
July T_{max} CNM (°C)
24
22
20
18
D
Jan T_{min} CNM (°C)
−7
−8
−9
−10
−11
−12
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)