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Hemispheric and Continental Scale Patterns of Similarity in Mountain Tundra

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24 **Abstract**

25 Understanding the full range of biodiversity patterns from local to global scales, through the
26 study of the drivers of multiscale plant community composition and diversity, is a current goal of
27 biogeography. A synthetic understanding of to what extent vegetation compositional patterns are
28 produced by biotic factors, geography or climate and how these patterns vary across scales is
29 needed. This lack hinders prediction of the effects of climate change in global vegetation.

30 Variation in community composition is examined in relation to climatic difference and
31 geographic distance at hemispheric and continental scales. Vascular plants and bryophytes in 13
32 mountain regions were analyzed; eight in Europe and five in North America, nine mid-latitude
33 and four oroarctic. Species composition differed between continents and between oroarctic and
34 mid-latitude regions. Patterns of paired regional similarity with distance were significant for all
35 pairs and intercontinental pairs, but not for those within Europe and North America. Climatic
36 variables accounted for most of the variance in vegetation patterns revealed by General Linear
37 Models of ordinations, but geographic variables, of Moran eigenvectors and latitudinal zones,
38 were also important and significant. The effects of geography were typically twice as strong for
39 vascular plants as for bryophytes. The importance of geography at these scales suggests that past
40 evolutionary and ecological processes are as important as current fit to any climatic niche.

41 Interpretation of observations of the impacts of global climate change should recognize
42 geographic context and phylogeny, and policies to mitigate them, such as assisted migration,
43 should be cautious.

44

45 *Key words: alpine; beta diversity; climate, distance; oroarctic*

46

47 **Background and objectives**

48 The biodiversity of mountain tundra, encompassing both alpine and oroarctic tundra (the
49 latter is tundra at high latitudes where the effects of elevation differentiate it from arctic tundra;
50 Virtanen et al. 2016) is globally higher than expected (Körner 2000). Mountain tundra diversity
51 is also regarded as threatened due to anthropogenic climate warming, and several studies
52 document recent changes in high elevation plant diversity (e.g., Britton et al. 2009, Spasojevic et
53 al. 2013, Lesica and Crone 2017, Steinbauer et al. 2018). These observations imply that patterns
54 and processes underlying mountain plant assemblages may be spatially structured, producing
55 strong heterogeneity in possible plant responses to climate change (e.g., Anthelme et al. 2014).
56 Therefore, although first described by von Humboldt and Bonpland (1805), and despite a
57 growing body of observations on the patterns of alpha and beta diversity (respectively, the
58 diversity of species at local sites and the change in species composition among such sites) on
59 environmental gradients in mountains (e.g., Kikvidze et al. 2005, Löffler and Pape 2008, Li et al.
60 2011, Elmendorf et al. 2012, Gritsch, Dirnböck and Dullinger 2016, Harbert and Cooper 2017,
61 García-Gutiérrez et al. 2018), a better understanding of the large-scale spatial variation in
62 mountain plant assemblages is crucial to better dissect possible climate-plant relations and
63 responses to future climate change.

64 The importance of changing scales is now a central principle of physical geography
65 (Meentemeyer 1989, Walsh et al., 1997, Malanson et al., 2017) (we use scale in the most
66 common way, as equivalent with extent, and so large scale covers larger areas). McGill (2010)
67 argued that understanding scale dependence was needed to explain biogeographic patterns. He
68 highlighted four controls on the distributions of species: climate, species interactions, habitat,
69 and dispersal. Although he hypothesized climate and dispersal as operative and possibly equally

70 important at both the smallest and largest scales, climate operates at small scale only as
71 microclimate, and microclimate is the result of the macroclimate being modified by habitat and
72 the organisms themselves (plants in most cases). At the scale of the globe, climate does not
73 differentiate distributions because climates repeat in patterns determined by gradients of latitude
74 and continentality, and so climate effects are confined to continental to hemispheric scales.
75 Dispersal can make a difference at small scale through a mass effect, but it dominates processes
76 at the largest, global, scale. This sequence in which processes would dominate the structuring of
77 species patterns on a gradient of increasing spatial scale would then be simplified: biotic
78 interactions – habitat – climate – dispersal. Furthermore, without observations in the past, our
79 understanding at larger scales is inferred from long-term biogeographic patterns (e.g., Doua et
80 al. 2018) that are represented by geographic distance and isolation; these serve as a proxy for
81 observations of dispersal.

82 Large-scale compositional patterns in mountain vegetation reflect historical speciation-
83 extinction dynamics (Hewitt 1996, Hoorn et al. 2013), Tertiary continental dynamics (Wolfe
84 1987), regional extinction-immigration dynamics (Riebesell 1982, Hadley 1987, Harris 2007),
85 large-scale climatic niche processes (Virtanen et al. 2016), and spatial processes related to
86 geographic distance (Taylor 1977, Malanson, Cheney and Kinney 2015, Clarke et al. 2018). As a
87 result, the relationship of mid-latitude alpine tundra to arctic tundra is not a simple gradient of
88 difference with latitude (e.g., Billings 1973, Virtanen and Eurola 1997, Virtanen et al. 2016).
89 Moreover, studies find that plant community relations to environment vary with the scale of
90 analysis (e.g., Kim et al. 2012), including alpine communities (e.g., Suding et al. 2015,
91 Chalmandrier et al. 2017). The relevance of geographic scale for local and regional diversity was
92 illustrated by Malanson, Fagre and Zimmerman (2016, 2018), who showed that the drivers of

93 beta and alpha diversity differed among four regions across the Rocky Mountains in the USA. In
94 summary, due to their topographic complexity, steep environmental gradients, and mix of habitat
95 types, mountain tundra varies as much within geographic units (valleys and slopes) as among
96 them. The explanations for the beta diversity at continental scales may be related to climate, but
97 biogeographic history and the geographic separation of mountain tundra regions should also play
98 a role.

99 Understanding the processes influencing alpine tundra beta diversity across multiple
100 scales is important for anticipating the effects of ongoing climatic change (Socolar et al. 2016).
101 Potential mitigation, such as assisted migration (fourth among five categories of increasing
102 intervention outlined by Malanson et al. 2019), would depend on biogeographic insights (Hewitt
103 et al. 2011, Abeli et al. 2014). Factors that make anticipation and thus mediation problematic,
104 however, include uncertainty about the relative importance of climate as a determinant of beta
105 diversity given the varying spatial and temporal context and relatively high beta diversity
106 (Opedal, Armbruster and Graae 2015, Stivrins et al. 2016).

107 Here, we take a first step towards improving knowledge of the large-scale biogeographic
108 patterns of mountain tundra assemblages and how they relate to space (geographic distance) and
109 climate. We compiled data from Europe and North America and examined variation in plant
110 community composition in oroarctic and mid-latitude mountain tundra as it is related to variation
111 in climatic variables and geographic distance. Variation in concert with climate is expected
112 because energy and water resources, and their relevant variables such as temperature and soil
113 moisture, are important dimensions of species distribution or niche. We believe that geographic
114 distance matters because it is a proxy for processes that have occurred in the past that we cannot
115 observe; these include responses to past climate changes and disequilibria (e.g., Douđa et al.

116 2018), including dispersal (Malanson et al. 2017). For example, Muster et al. (2009) revealed
117 that genetic links between Scandinavian, Alp, and Carpathian spiders could be explained either
118 by low rates of current dispersal or high dispersal rates at the Last Glacial Maximum (LGM), and
119 patterns of plant endemism and refugia also reflect disequilibria (e.g., Patsiou et al. 2014,
120 Smycka et al. 2017). Plant community composition could reflect responses to past climatic
121 conditions (e.g., Kammer, Schöb and Choler 2007), extending to the LGM, where niche
122 constraints have not had time to be fully expressed.

123 Our main aim was to address intercontinental patterns in similarity in mountain tundra
124 vegetation in relation to spatial and climatic variables. Many environmental factors differ across
125 the mountain regions studied here. These include the environmental templates determined by the
126 geological processes of mountain building and the millennia of erosion under different climatic
127 regimes. We focused on distance and climatic difference as the potential factors that would
128 differentiate the floras in order to examine such factors at the broad scale in the context of the
129 framework provided by McGill (2010). The other factors that differentiate these mountain
130 regions, such as differences in substrates and soils, equally differentiate mountains within
131 regions and properly are within the domain of habitat differentiation at smaller scales as
132 hypothesized by McGill (2010). We contend that specific geographic characteristics will alter
133 the relationships with distance and climate; e.g., oroarctic communities will be more similar to
134 each other relative to those at mid-latitudes than distance or climate would dictate (cf. Virtanen
135 et al. 2016), and extremes of climate or isolation will lessen similarity due to endemism. Because
136 mountain tundra exists in a narrow range of temperatures, we also expected that water (e.g.
137 precipitation) rather than temperature would be principally responsible for climatic
138 differentiation. Additionally, we recognize a potential difference in responses for vascular and

139 bryophyte taxa, because bryophytes disperse via spores, as opposed to the varied and larger
140 propagules of vascular plants, which leads to less geographic isolation over (possibly longer)
141 evolutionary time (cf. Ledent et al. 2019). We expect:

142 1: Similarity in plant communities among regions will be more related to geographic distance
143 than to climate; this relationship will be stronger for intercontinental than intracontinental
144 distances.

145 2: Patterns of similarity will be modified so that oroarctic communities will be more similar than
146 mid-latitude communities, after accounting for distance and climate.

147 3: Vascular species will have stronger relations with distance than bryophytes.

148 4: Among climate variables, similarity among regions will be more related to precipitation than
149 to temperature.

150 This knowledge is essential for understanding the similarities and dissimilarities in processes
151 underlying the beta-diversity of plant communities at continental to hemispheric scale (e.g.,
152 Jimenez-Alfaro et al. 2018). It would also provide a base for investigating how diversity arises
153 and is maintained in terms of the importance of current niches and past changes.

154

155 **Methods**

156 *Data sources and selection*

157 Species data

158 We used records of species presence in multiple vegetation plots (relevés) from 13
159 regions in Europe and North America (Figure 1, Table 1; these data are publicly accessible at
160 ir.uiowa.edu). The regions were defined based on how earlier datasets were published; but each
161 covers a section of a mountain range within 1° of latitude and longitude. We chose these regions

162 because they had extensive coverage in numbers of plots for their areas, the data collection
163 methods were comparable, and in most cases consistently followed the Braun-Blanquet
164 methodology in the field (and in all cases used a visual estimate of percent cover in quadrats,
165 which we simplified to species presence). Places that were not considered were those that did not
166 use quadrats for sampling, compiled presence for entire ranges or communities rather than by
167 plot, or reported summaries only (e.g., syntaxa). We further excluded the sites from Virtanen et
168 al. (2016) that they had identified as arctic, and for Scotland we excluded those vegetation types
169 described by Averis et al. (2004) as non-montane and plots at elevations less than 675 m, which
170 Birse (1976, 1980) set as the lower limit of alpine vegetation.

171 Because the observations were made at different times, all nomenclature was updated to
172 currently accepted taxonomy using the Taxonomic Name Resolution Service at iPlant
173 Collaborative (<http://tnrs.iplantcollaborative.org>); for unresolved species, we retained the
174 original nomenclature. We removed lichens from the analyses because their response to climate
175 may be the inverse of vascular species (Walker et al. 2006) and their taxonomic comparability in
176 the several data sources was low. We then divided the observations into vascular and bryophyte
177 datasets because we expected the two types of plants to respond differently to climate (Molau
178 and Alatalo 1998). We discarded records where only the genus was identified because for
179 comparing regions these would bias the results toward greater than actual similarity. Our final
180 dataset contained 397 bryophytes and 1814 vascular species on 4829 plots.

181 In order to have balanced comparisons in the analyses but retain the breadth of
182 observations, we reduced the data to 200 plots per region where more plots were available in a
183 region. To sample 200 plots from a larger pool, we ran detrended correspondence analysis
184 (DCA; using PC-ORDv6), an eigenvector ordination that represents the order of similarity on its

185 primary axis, on the data for each region, and then sampled 200 plots via a regular systematic
186 selection along that axis so that the full range of plant communities would be represented. The
187 plots were approximately evenly distributed along this axis because the Braun-Blanquet
188 classification method, not used here, works better with that type of field sample. The final data
189 set included 2507 plots for vascular plants (with 1733 species) and 1751 plots for bryophytes
190 (with 361 species; the Betic, Cantabria, and Yosemite vicinity data had no bryophyte records).

191 Climate data

192 Because several of the regions did not have georeferenced plot data, we chose three
193 representative locations within each study area. The locations were midway between treeline and
194 summits. Using the latitude and longitude for these three points in the CHELSA climate dataset
195 (Karger et al. 2017; these are at 30-arcsecond resolution for 1979-2013), we took the average for
196 key bioclimatic variables: mean annual temperature, warmest quarter and coldest quarter mean
197 temperatures, and the annual and wettest, driest, warmest, and coldest quarter mean precipitation.

198 Geographic distance and spatial variables

199 We used the haversine method to calculate the great circle distances, in kilometers,
200 between points in the middle of each region. We calculated the mean distance among regions and
201 the summed distance to the three nearest neighbors as an indicator of isolation. Following Peres-
202 Neto and Legendre (2010) for dealing with distances among an array of points, we calculated
203 Moran spatial eigenvectors by applying principle coordinates analysis to the matrix of distances
204 between pairs of regions (also known as principle coordinate neighbor matrices).

205 *Analyses*

206 We used a Multi-Response Permutation Procedure (MRPP; McCune and Grace 2002),
207 with Sørensen (1948) similarity, to test for differences between continents, between latitudinal

208 (oroarctic and mid-latitude) regions, and among continent-by-latitude regions. MRPP is an
209 alternative to discriminant analysis that avoids parametric assumptions. Sørensen similarity, the
210 proportion of species abundance shared between pairs of observations to their summed
211 abundance, has characteristics relative to shared species that makes it a preferred representation
212 (McCune and Grace 2002, Austin 2013).

213 We calculated the Sørensen (1948) similarity among all possible pairs of plots in our
214 data; We then calculated the mean similarity among the pairs of regions. We regressed the
215 similarity between pairs of regions on the distances between them, testing for significance of the
216 correlation using the randomization method proposed by Mantel (1967) (this analysis meets the
217 limiting criteria, similarity questions to which spatial eigenvectors do not apply, proposed by
218 Legendre et al. 2015). After preliminary analyses, we used an exponential fit for the vascular
219 species and a linear fit for the bryophytes. From the resulting patterns, we separated the pairs into
220 those between continents (long distances) and within continents and calculated and plotted
221 regressions. We then did the same for the within-continent pairs split between Europe and North
222 America. We also examined the differences in patterns and in the differences between vascular
223 and bryophyte similarities for the pairs of regions.

224 We ordinated the plot-species data by nonmetric multidimensional scaling (NMDS). We
225 determined the number of ordination axes to analyze by examining the correlation between the
226 distances among all pairs of plots in the dimensions of ordination space with the Sørensen
227 similarity matrix and increased the number of axes as long as the increase in correlation was
228 greater than 0.05; we ended using four axes (for visualization, we used the first three
229 dimensions). We regressed the means of the plot positions of each region on the four ordination
230 axes with the bioclimatic variables and the Moran eigenvectors scores. After examining all 36

231 bivariate plots for nonlinear patterns, we used General Linear Models (GLMs) to fit stepwise
232 models (0.05 to enter, 0.10 to remove; cf. Draper and Smith 2014) with an overall R^2 and per-
233 variable contribution. We used these metrics to estimate the relative importance of the climatic
234 and geographic variables.

235 **Results**

236 *Bioclimates and geographic distances for regions*

237 The data for the bioclimatic and geographic variables are shown in Tables 2 and 3. One
238 significant Moran eigenvector was found, and it appears to differentiate the more clustered
239 European ranges from those in North America.

240 *Regions, similarity and distance*

241 The MRPP (Table 4) revealed significant differences between the continents, the
242 latitudes, and the continent-by-latitude groupings; the low p values indicate the distinct
243 differences, although the magnitudes are small because within-group heterogeneity is high. The
244 greatest dissimilarity for vascular communities was between the European and North American
245 oroarctic, which contrasted with their low effect for bryophytes. For bryophytes, the mid-latitude
246 communities had the smallest dissimilarity while both of these continents differed from the North
247 American oroarctic.

248 Table 5 shows the mean Sørensen similarity for all pairs of regions. The correlation
249 between the average similarity of all pairs and the distances between them was $r = -0.468$ ($p <$
250 0.001 by Mantel test; 13 regions, $n = 78$) for the vascular species and $r = -0.406$ ($p < 0.016$; 10
251 regions, $n = 45$) for the bryophytes. The relationship of similarity among pairs of regions to
252 distances among pairs of regions was exponential for the vascular species and linear for the
253 bryophytes (Figure 3). Although a number of positive-residual points appeared to be outliers,

254 their removal did not improve the regression R^2 ; these apparent outliers were pairs of oroarctic
255 regions. The 78 pairs appeared to be divided into two less definitive groups: those between and
256 those within continents (distances greater than and less than 4500 km, respectively). When the
257 data were divided in that way, the relation of similarity to distance was much stronger between
258 than within continents (Figure 3,c-h). The vascular species in Europe still had a weak
259 relationship, but the European bryophytes and both vascular plants and bryophytes in North
260 America had no significant relations with distance (Figure 3,e-h); however, some R^2 were
261 relatively high and the possibility of a relationship exists. Also, although several regressions
262 were significant, the plots revealed triangular patterns wherein the full range of similarities
263 occurred at the shortest distances with less similarity at the longest. These observations match
264 our first and second expectations.

265 The patterns differed between the vascular and bryophyte species. The triangular
266 relationship is more distinct, as indicated by the exponential relationship, for the vascular
267 species. The vascular similarity is higher at the shorter distances, specifically for oroarctic pairs,
268 while it has a tighter distribution at the longest distance. This geographic effect is also seen in the
269 difference in similarity between the vascular and bryophyte species: the greatest vascular minus
270 bryophyte differences are SOS versus SCT and NOS (0.0497 and 0.0281, respectively) while
271 CBR versus SCT and SOS (-0.0220 and -0.0179) are among the greatest bryophyte>vascular
272 differences (Table 6). These observations meet our second and third expectations.

273 *Ordination and General Linear Models*

274 In addition to stress (vascular, 21.9; bryophyte, 23.1), we examined the competence of
275 the NMDS ordination by correlating the distances between all pairs in ordination space with the
276 similarity matrix reduced by that ordination, increasing the number of axes until the increment in

277 r was less than 0.05. This method produced ordinations for both vascular and bryophyte groups
278 with four axes, with correlations with the similarity matrix of 0.444 and 0.452, for vascular and
279 bryophytes respectively ($p < 0.001$ for both).

280 The visualization of the ordination showed that the plots within each region were
281 clustered together: mid-latitude European plots are neighbors, mid-latitude North American plots
282 are neighbors, and the oroarctic plots are neighbors that separate the mid-continental European
283 and North American plots (Figure 4).

284 The GLMs revealed significant relationships for the mean positions of the 13 regions on
285 all four ordination axes for the vascular plant data, and on two of the four for the bryophyte data
286 (Table 7). For vascular species, the geographic factors of regionalization and distance were
287 important for all four axes, and geography accounted for more than double the variance in the
288 combined four ordination axes than the climatic variables. Of the latter, precipitation accounted
289 for almost all the contribution. For the bryophytes, overall GLMs were weaker, with no
290 significant variables for two of the four axes. Climate accounted for 44% of the contribution of
291 geography, with wet quarter precipitation the only significant climatic variables. For bryophytes,
292 the strongest individual relationship was for latitude, i.e., either mid-latitude or oroarctic, and
293 NMDS3 (74.7% contribution). These observations meet all four of our expectations.

294

295 **Discussion**

296 Large-scale, biogeographic elevational and latitudinal patterns in mountain vegetation
297 have previously been thought to be primarily driven by climate (with the temporal change in
298 species distributions also associated with climatic changes). Our analyses tackled this question
299 and provide new evidence that location can supersede climate in the determination of large-scale

300 biogeographic patterns in mountain species assemblages. First, distance is a consistent factor in
301 the differentiation of these assemblages or floras. Second, geographic regions are differentiated.
302 Distance matters primarily between rather than within continents. The relative importance of
303 distance, as seen in the patterns of similarity, in accounting for the variance in observed patterns
304 of beta diversity is indicative of processes at larger spatial and temporal scales. The triangular
305 patterns indicate that multiple factors may operate at smaller scales while geographic connection
306 through dispersal is the dominant process at larger scales. The triangular pattern is more evident
307 for vascular species because the similarity is higher at shorter distances, specifically for oroarctic
308 pairs, while it has a tighter distribution at the longest distances. Evolutionary differentiation of
309 floras and disequilibrium of communities in flux following Holocene climate changes would
310 weaken the link between current climates and similarity and reflect past connections through
311 dispersal. If these links are true, our results support the contention of McGill (2010) that
312 dispersal supersedes climate in determining community differentiation at the largest spatial
313 scales.

314 The distance-similarity and climatic relations differed between vascular plants and
315 bryophytes, with greater uncertainty in the latter. The findings qualitatively agree with the
316 findings of Nekola and White (1999), who found that vascular plants had 1.5-1.9 times higher
317 distance decay rates than bryophytes. Our results rather suggest that at hemispheric-
318 intercontinental scales, the difference is typically at least two times higher. The reasons for lower
319 similarity decay rates of bryophytes may be due to their longer evolutionary history and thus
320 generally wide geographic ranges, species persistence in microsites due to broad physiological
321 tolerances, or high migration rates. For example, Ledent et al. (2019) reported that the role of

322 extra-continental migrants in European bryophyte community assembly since the LGM greatly
323 exceeded that of other plants.

324 Our results further indicate a novel pattern in that the difference in the decay rate between
325 vascular plants and bryophytes is geographically dependent. At intercontinental scale both
326 vascular plants and bryophytes show a decay in similarity, but at the continental scale, bryophyte
327 decay rates, in contrast to those for vascular species, are not significant in Europe, where our
328 eight ranges are less isolated than the five in North America. The pattern may reflect the minimal
329 dispersal limitation at these scales (too few points for North America prohibit inference) and the
330 differentiation of bryophytes between the mid-latitude and oroarctic latitudes regardless of
331 distance. Moreover, Lenoir et al. (2012) reported that the similarity decay rate of vascular plants
332 was about two times greater than that of bryophytes across a ~4500 km gradient of high latitude
333 tundra, but for our four oroarctic regions (with only six points) the decay rate is two orders of
334 magnitude greater for vascular plants. This geographic effect is also seen in the difference in
335 similarity between the vascular and bryophyte species: the greatest vascular-minus-bryophyte
336 differences are SOS versus SCT and NOS (0.0497 and 0.0281, respectively) while CBR versus
337 SCT and SOS (-0.0220 and -0.0179) are among the greatest bryophyte>vascular differences.
338 Isolation is more than simple distance.

339 Whereas Virtanen et al. (2016) thought that the differences between the oroarctic and
340 mid-latitude tundra in Europe were in part attributable to climate and perhaps to differences in
341 relief, our addition of Scottish and Alaskan oroarctic regions provides additional insight. While
342 distance alone matters, the oroarctic connection between Europe and Alaska indicates that the
343 relationship to the circumarctic low elevation tundra may play a role in the similarity among
344 oroarctic regions. Also, the central Brooks Range has rugged topography like that of the Rocky

345 Mountains or the Alps, but this region is not strongly differentiated from the other, less rugged,
346 oroarctic regions, suggesting that complexity of relief is probably less important in
347 differentiating mountain tundra. Cooper (1989) suggested that high elevation tundra in Alaska is
348 a good analog for widespread Beringian tundra of the Last Glacial Maximum, which accords
349 with this conclusion.

350 Among the climatic factors, differences in precipitation explained much of the pattern of
351 relations among both the vascular and bryophyte communities. Precipitation might be expected
352 to be a stronger factor than temperature, given the narrow range of the latter that defines
353 mountain tundra, and this finding complements the finding of Kikvidze et al. (2005) that
354 precipitation had the greater direct influence on alpha diversity in a global comparison. The
355 weaker climatic relations of the bryophytes echo the observations of Lang et al. (2012) for arctic
356 tundra. The bryophytes tend to be restricted to wetter sites, which minimizes the effects of
357 variation in regional precipitation.

358 Another specific geographic comparison can be made between the Mediterranean-climate
359 regions of California and Spain (the YNP and BET regions). These two have the lowest warm-
360 season precipitation, yet they are the most dissimilar pair. They are both toward the southwestern
361 extremes of their continents and have no mountain ranges farther in that direction (although
362 some connections to the Atlas Mountains may exist for BET and to the Sierra Madre for YNP).
363 Thus they are relatively isolated in both climate and geographic space. Both ranges are relatively
364 high in endemic species (Faverger 1972, Malanson, Zimmerman and Fagre 2015). For BET this
365 is probably because of its isolation but for the Sierra Nevada of California it may also be
366 attributable to its large area.

367 Patterns of vegetation change observed in relation to past or present climate change
368 should be interpreted in light of regional and specific characteristics of place. Similar degrees of
369 change in the oroarctic and mid-latitude alpine tundra vegetation may signify different impacts,
370 given differences in functional types and responses to climate (Bruun et al. 2006). These
371 differences might even extend to greater geographic specificity, as where Lesica and McCune
372 (2004) have pointed out changes for arctic-centered species at their southern range limit in
373 Glacier National Park, Montana. Changes in locations with more endemic species, e.g., in BET,
374 should perhaps be weighted more in terms of impact assessment.

375 Mountain tundra is undergoing changes that could threaten its unique character (e.g.,
376 Britton et al. 2009). It is also potentially threatened by rising treelines in some areas and by
377 rising low-elevation arctic tundra in others (e.g., Vanneste et al. 2017). Controversial ideas about
378 mitigation include assisted migration - moving plants poleward to track their geographically
379 shifting climatic niche (e.g., Abeli et al. 2014, Ramírez-Amezcuca et al. 2016, Pykälä 2017). For
380 the mountain tundra examined here, this idea must face simple problems of uncertainty before
381 the complex ones related to ethics. Brooker et al. (2018) have shown that it may be particularly
382 difficult to translocate some mountain tundra species because of our inadequate knowledge of
383 their niche and the difficulty of identifying climatically-suitable locations within topographically
384 complex mountain landscapes. At larger scales, mountain tundra is already near the end of the
385 global temperature gradient. Little area exists where it is now too cold for tundra plants but
386 where substrates exist to support any in a warmer future. Retreating glaciers would nominally
387 provide space, but the threshold switch from ice to ice-free may not leave the needed range of
388 temperature in its wake. Additionally, the rate of warming is expected to be greater at higher
389 latitudes (Serreze et al. 2000), further limiting the feasibility of poleward migration. Even within

390 ranges, elevation-dependent warming (Rangwala and Miller 2012) will limit the amount of new
391 area to which alpine plants could migrate (with or without assistance). Given that mountain
392 tundra does not align on simple climatic gradients, it is not clear that any region could or should
393 be a target for translocations from any other. When considering assisted migration of mid-
394 latitude tundra species, the oroarctic regions may already be too threatened to serve as a suitable
395 receptor region. Given its distinct floristic character and that oroarctic tundra is faced with the
396 potential for greater warming, less active mitigation and more protection (e.g., Thuiller et al.
397 2014) may be a better strategy.

398

399 **Conclusions**

400 Fundamental theory in biogeography is based on changes in scale, and disentangling the
401 roles of abiotic, biotic, and dispersal drivers as they vary with scale continues to be a frontier of
402 research. For hemispheric patterns of mountain tundra, the effects of climatic differences are
403 superseded by those of geographic distance at the most extensive scale, as examined here for the
404 first time. More quantification of the form of the transitions among drivers along a gradient of
405 scale is needed, however, with attention to smaller scales where local habitat factors are likely to
406 be important. The specifics of geography, such as isolation, also matter – as well-known since
407 Darwin and Wallace.

408 The relevance of biogeographic theory to the conservation in a changing climate is also
409 dependent on the details of biogeography, such as latitudinal gradients, as well as on scale. Given
410 the potential problems that global climate change poses for mountain tundra, approaches to
411 mitigation should be considered. Although biogeographic theory is relevant to all five of the
412 approaches categorized by Malanson et al. (2019), the patterns revealed here further limit the

413 efficacy of the most fraught approach, assisted migration. When the implications of local context
414 and scale are recognized, the balance among mitigation choices may shift.

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Table 1. The regions used, showing the codes referred to in the text, their central locations and elevations, general climate type, relative relief, and the number of plots in the original data, and the reduced number used in the calculations.

Code	Latitude	Longitude	Elevation (m)	Climate	Relief	initial#	#used-v	#used-b
ALP	46.62N	8.41E	2950	continental	high	167	167	94
BET	37.05N	3.37W	3200	Mediterranean	low	347	200	n/a
CAN	43.19N	4.96W	2100	maritime	high	577	200	n/a
CBR	69.28N	143.82W	2200	continental	high	438	200	200
GNP	48.72N	113.63W	2400	continental	high	525	200	200
IPA	40.06N	105.59W	3600	continental	high	481	200	200
YNP	44.25N	10.41E	2000	Mediterranean	low	305	200	200
NOS	69.04N	20.86E	1000	maritime	low	235	200	200
CBR	42.41N	2.21E	2650	Mediterranean	high	340	200	146
SBC	50.11N	123.22W	2000	maritime	high	152	151	128
SCT	57.07N	3.67W	1300	maritime	low	540	200	200
SOS	61.66N	7.02E	1900	maritime	low	368	200	200
YNP	37.96N	119.32W	3650	Mediterranean	high	188	188	n/a

Locations and sources: ALP, Swiss Alps, Braun-Blanquet (1926); BET, Betic Range, including the Sierra Nevada, Spain, EuroVeg.org; CAN, Cantabrian Range, Spain, EuroVeg.org; CBR central Brooks Range, Alaska, Arctic Vegetation Archive (geobotany.uaf.edu); GNP, Glacier National Park, Montana, Damm (2001); IPA, Indian Peaks National Monument, Colorado, Komarkova (1979); NAP, Northern Apennines, Italy, Petraglia & Tomaselli (2007); NOS, northern Scandinavia, Norway, EuroVeg.org; PYR, eastern Pyrenees, Spain, France, Andorra, Braun-Blanquet (1948); SBC, southern British Columbia, Archer (1963), Brett, Klinka and Qian (2001); SCT, Scotland, Birse (1976, 1980); SOS, southern Scandinavia, Norway, EuroVeg.org; YNP, Yosemite vicinity, Sierra Nevada, California, Pemble (1970).

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674 Table 2. The climate variables used; Annual; Warm – warmest quarter; Cold – coldest quarter;
 675 Wet – wettest quarter; Dry – driest quarter; T – mean temperature (°C); P – mean precipitation
 676 (mm). Data for three points in each region were drawn from the CHELSA downscaled product.

Region	AnnualT (°C)	WarmT (°C)	ColdT (°C)	AnnualP (mm)	WetP (mm)	DryP (mm)	WarmP (mm)	ColdP (mm)
ALP	-2.8	6.2	-11.3	979	389	143	389	160
BET	1.4	10.8	-5.3	591	248	17	17	232
CAN	3.9	10.5	-1.3	1584	583	185	185	345
CBR	-11.7	7.1	-27.3	423	248	42	167	73
GNP	0.5	11.9	-9.6	952	325	159	169	251
IPA	-2.7	8.2	-12.1	679	236	115	209	121
NAP	2.8	12.4	-5.6	1049	373	184	213	249
NOS	-2.0	8.5	-11.6	727	246	105	194	203
PYR	0.0	8.5	-7.3	955	308	166	272	193
SBC	0.6	9.5	-7.8	2501	1161	201	202	1125
SCT	3.6	9.3	-1.4	1462	481	251	311	721
SOS	-2.7	7.1	-11.5	974	333	158	332	236
YNP	0.6	12.1	-6.5	837	446	43	43	444

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Table 3. The distances (km) between pairs of regions, the single significant Moran
 eigenvector based on principle coordinates analysis of that matrix, the average distance
 to all 12 other regions (Dist12, km), and the summed distance to the three nearest
 neighbors (Dist3, km).

	ALP	BET	CAN	CBR	GNP	IPA	NAP	NOS	PYR	SBC	SCT	SOS	YNP
ALP	0	1439	1117	6913	8030	8371	306	2583	678	8285	1420	1674	
BET	1439	0	696	7765	8250	8335	1409	3851	762	8682	2228	2826	
CAN	1117	696	0	7068	7646	7809	1240	3236	590	8045	1547	2197	
CBR	6913	7765	7068	0	2805	3934	7222	4596	7284	2403	5609	5276	
GNP	8030	8250	7646	2805	0	1155	8332	6397	8085	709	6613	6646	
IPA	8371	8335	7809	3934	1155	0	8650	7105	8328	1767	6988	7200	
NAP	306	1409	1240	7222	8332	8650	0	2824	693	8616	1731	1949	
NOS	2583	3851	3236	4596	6397	7105	2824	0	3150	6452	1794	1037	
PYR	678	762	590	7284	8085	8328	693	3150	0	8438	1683	2159	
SBC	8285	8682	8045	2403	709	1767	8616	6452	8438	0	6884	6829	
SCT	1420	2228	1547	5609	6613	6988	1731	1794	1683	6884	0	791	
SOS	1674	2826	2197	5276	6646	7200	1949	1037	2159	6829	791	0	
YNP	9248	9409	8837	3783	1280	1206	9581	7685	9301	1385	7865	7939	
Moran1	-10204	-9630	-9431	9526	14082	14303	-10420	-4683	-10303	14598	-7410	-6878	
Dist12	4172	4638	4169	5388	5496	5904	4379	4226	4263	5708	3763	3877	
Dist3	700	956	801	2997	1048	1376	746	1805	654	1287	1253		

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 686

687 Table 4. Multiple Response Permutation Procedure (MRPP) effect size, A (chance-corrected
 688 metric showing differences in comparisons). The comparison was between continents, latitudes,
 689 and their combination; continents – Europe, EU, and North America, NA; latitudes – midlatitude,
 690 ML, and oroartic, OA. The separation between groups is significant in all comparisons with $p <$
 691 0.000001.

	<u>Vascular A</u>	<u>Bryophyte A</u>
692		
693 2 continents	0.010	0.011
694 2 latitudes	0.013	0.013
695 Continent by latitudes		
696 EU-ML vs. NA-ML	0.010	0.020
697 EU-ML vs. NA-OA	0.025	0.025
698 EU-ML vs. EU-OA	0.019	0.014
699 NA-ML vs. NA-OA	0.027	0.029
700 NA-ML vs. EU-OA	0.024	0.022
701 NA-OA vs. EU-OA	0.040	0.015

702

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704

705 Table 5. Mean Sørensen floristic similarity between regions for vascular species (upper
 706 triangular; 78 pairs) and bryophytes (lower triangle; 45 pairs); the diagonal is the within-region
 707 similarity calculated using both taxa (for YNP it is 0.540). The mean is from all possible pairs of
 708 plots between the pairs of regions. Sørensen similarity is the proportion of species abundance
 709 shared to the total abundance of each pair of plots. The similarities between regions are low, as
 710 are the within-region similarities.

711

	ALP	BET	CAN	CBR	GNP	IPA	NAP	NOS	PYR	SBC	SCT	SOS
ALP	0.0821	0.0024	0.0098	0.0106	0.0059	0.0072	0.0187	0.0235	0.0163	0.0020	0.0087	0.0081
BET		0.5963	0.0186	0.0014	0.0002	0.0002	0.0077	0.0005	0.0048	0.0005	0.0079	0.0079
CAN			0.7862	0.0016	0.0021	0.0010	0.0211	0.0056	0.0148	0.0002	0.0253	0.0253
CBR	0.0095			0.1414	0.0239	0.0106	0.0137	0.0357	0.0032	0.0017	0.0040	0.0040
GNP	0.0125			0.0039	0.0940	0.0131	0.0037	0.0096	0.0048	0.0088	0.0014	0.0014
IPA	0.0089			0.0029	0.0538	0.0221	0.0011	0.0066	0.0021	0.0033	0.0020	0.0020
NAP	0.0063			0.0180	0.0056	0.0066	0.1663	0.0151	0.0174	0.0039	0.0444	0.0444
NOS	0.0125			0.0248	0.0053	0.0073	0.0301	0.0926	0.0084	0.0024	0.0481	0.0481
PYR	0.0443			0.0083	0.0070	0.0124	0.0215	0.0226	0.0592	0.0016	0.0114	0.0114
SBC	0.0101			0.0047	0.0130	0.0164	0.0088	0.0104	0.0052	0.0669	0.0014	0.0014
SCT	0.0011			0.0231	0.0015	0.0021	0.0263	0.0263	0.0203	0.0072	0.1475	0.1475
SOS	0.0081			0.0310	0.0045	0.0057	0.0268	0.0311	0.0225	0.0063	0.0299	0.0299

712

713

714 Table 6. The difference in the Sørensen similarity, calculated as vascular – bryophyte, between
 715 the communities for the pairs of regions that had both taxa.

716

	ALP	CBR	GNP	IPA	NAP	NOS	PYR	SBC	SCT
CBR	0.0020								
GNP	-0.0057	0.0221							
IPA	-0.0033	0.0057	-0.0340						
NAP	0.0105	-0.0017	0.0017	0.0002					
NOS	0.0110	0.0098	0.0078	0.0035	-0.0046				
PYR	-0.0343	-0.0042	-0.0013	-0.0050	0.0020	-0.0125			
SBC	-0.0060	-0.0014	0.0056	0.0035	0.0010	0.0009	-0.0033		
SCT	0.0218	-0.0220	0.0012	0.0016	0.0226	0.0233	0.0079	-0.0042	
SOS	0.0106	-0.0179	0.0032	0.0005	0.0251	0.0281	-0.0101	-0.0019	0.0497

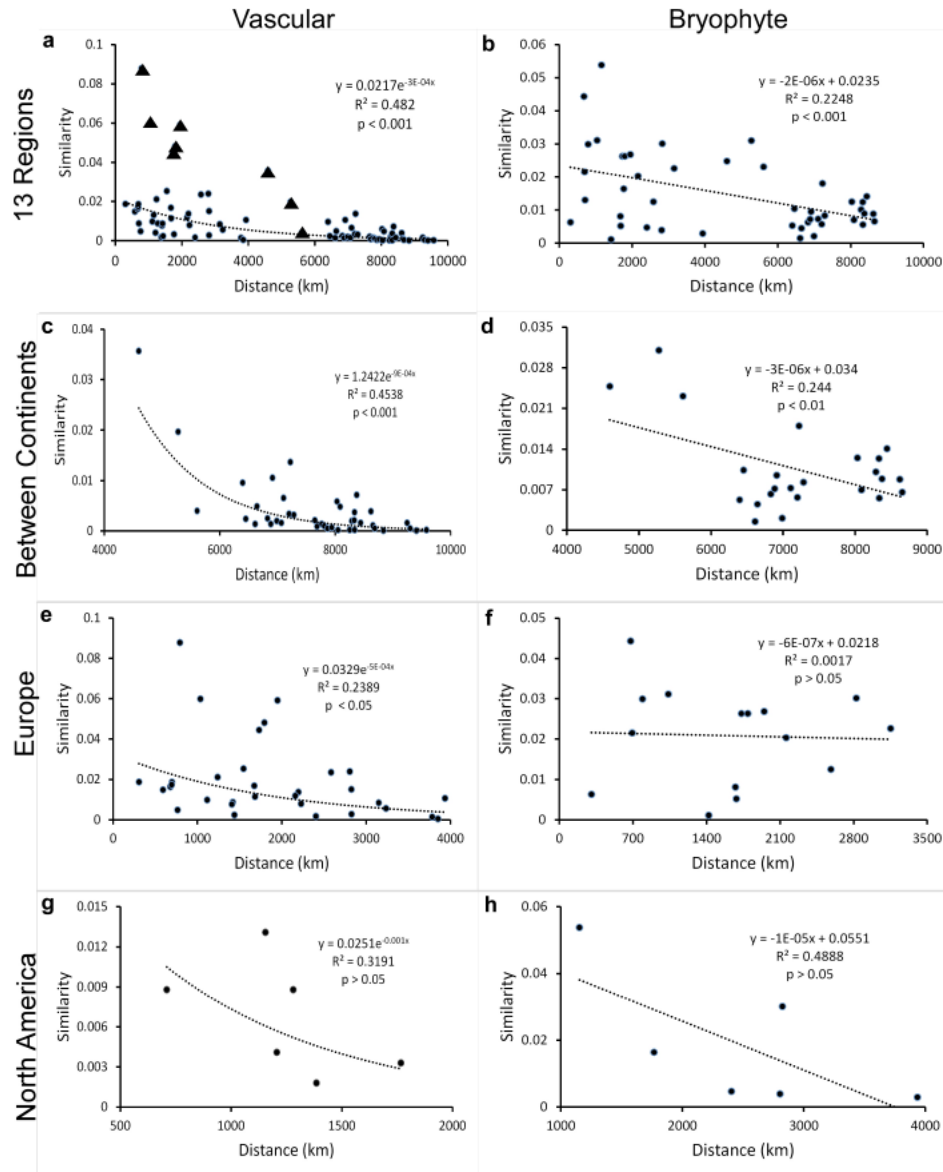
717
 718

719 Table 7. General Linear Models of the four nonmetric multidimensional scaling (NMDS)
 720 ordination axis centroids of the regions on the geographic and climatic variables for the vascular
 721 and bryophyte species. Geographic: continent (Europe and North America); latitude (mid-
 722 latitude and oroarctic); significant Moran eigenvector – Moran1; distance to all 12 others –
 723 Dist12; and distance to three nearest neighbors – Dist3. Climatic: by time (mean Annual or
 724 Cold, Warm, Dry or Wet quarter) P – precipitation; T – temperature. Not entering any model:
 725 AnnualP, AnnualT, WarmT, DryP.

	<u>Vascular</u>			<u>Bryophyte</u>		
728	NMDS1	Contribution	p	no terms in the model		
729	Moran1	0.469	<0.000			
730	Dist3	0.359	0.001			
731	Error	0.173				
732	Adjusted R ²		0.793			
733						
734	NMDS2	Contribution	p	no terms in the model		
735	Dist12	0.610	0.010			
736	WarmP	0.243	0.002			
737	Error	0.146				
738	Adjusted R ²		0.824			
739						
740	NMDS3	Contribution	p	Contribution	p	
741	ColdP	0.480	0.005	Latitude	0.747 <0.000	
742	Dist12	0.139	0.036	Moran1	0.195 0.025	
743	Error	0.382		Error	0.059	
744	Adjusted R ²		0.542		0.925	
745						
746	NMDS4	Contribution	p	Contribution	p	
747	Moran1	0.545	<0.000	WetP	0.417 0.044	
748	Dist3	0.208	0.087	Error	0.584	
749	Continent	0.111	<0.000			
750	WarmP	0.108	0.011			
751	ColdT	0.014	0.005			
752	ColdP	0.002	0.038			
753	Error	0.011				
754	Adjusted R ²		0.977		0.344	
755						
756	Total strength, contribution:					
757	Geography	1.90		0.95		
758	Region	0.11		0.75		
759	Distance	1.79		0.20		
760	Climate	0.84		0.42		
761	Precipitation	0.83		0.42		
762	Temperature	0.01		<0.00		
763	Summed AdjR ² (of 4.0)		3.14		1.27	
764						
765						
766						

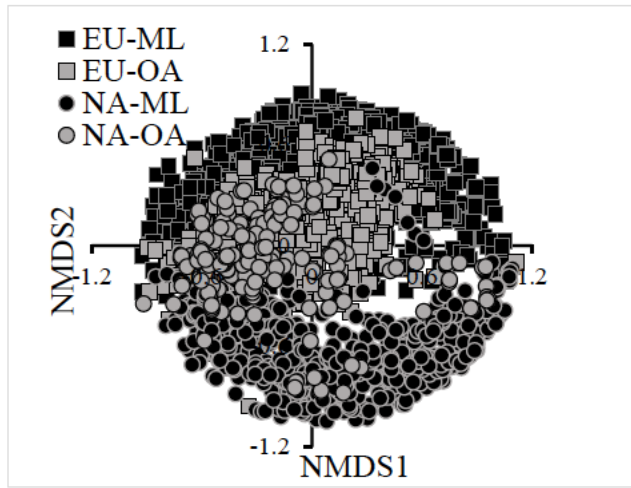


767
768 Figure 1. The locations of the 13 regions identified in Table 1 shown on an azimuthal
769 equidistant projection.



770
 771 Figure 2. The mean Sørensen similarity metrics of all the pairs of plots between regions graphed
 772 against the distance (km) between them. For the vascular species, similarity-distance relations
 773 were fit with an exponential equation, while the bryophyte relations were linear. The p values
 774 were calculated using a Mantel randomization. The triangles symbols in **a** are the oroarctic
 775 regions.

776



777
 778 Figure 3. Nonmetric multidimensional scaling (NMDS) results plotted in two dimensions for a
 779 reduced set of plots for visualization only. Regions are grouped by continent (Europe – EU;
 780 North America – NA) and latitude zone (ML – midlatitude; OA – oroarctic).

781
 782

783