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# Floristic similarity, diversity, and endemism as indicators of refugia characteristics and needs in the West

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1 Floristic similarity, diversity, and endemism as indicators of refugia characteristics and  
2 needs in the West

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22 **ABSTRACT**

23 The floras of mountain ranges, and their similarity, beta diversity, and endemism, are indicative  
24 of processes of community assembly; they are also the initial conditions for coming disassembly  
25 and reassembly in response to climate change. As such, these characteristics can inform  
26 thinking on refugia. The published floras or approximations for 42 mountain ranges in the three  
27 major mountain systems (Sierra-Cascades, Rocky Mountains, and Great Basin ranges) across  
28 the western USA and southwestern Canada were analyzed. The similarity is higher among the  
29 ranges of the Rockies while equally low among the ranges of the Sierra-Cascades and Great  
30 Basin. Mantel correlations of similarity with geographic distance are also higher for the Rocky  
31 Mountains. Endemism is relatively high, but is highest in the Sierra-Cascades (due to the Sierra  
32 Nevada as the single largest range) and lowest in the Great Basin, where assemblages are  
33 allochthonous. These differences indicate that the geologic substrates of the Cascade  
34 volcanoes, which are much younger than any others, play a role in addition to geographic  
35 isolation in community assembly. The pattern of similarity and endemism indicates that the  
36 ranges of the Cascades will not function well as stepping stones and the endemic species that  
37 they harbor may need more protection than those of the Rocky Mountains. The geometry of the  
38 ranges is complemented by geology in setting the stage for similarity and the potential for  
39 refugia across the West. Understanding the geographic template as initial conditions for the  
40 future can guide the forecast of refugia and related monitoring or protection efforts.

41

42

## 43 INTRODUCTION

44 Alpine tundra, the primarily herbaceous vegetation found above treeline, is the product  
45 of adaptations of species to a low-energy climate (e.g. Matteodo et al. 2013) and the sorting and  
46 assemblage of species, including their interactions (e.g., Cavieres et al. 2014), within that  
47 climate (Körner 2003; Nagy and Grabherr 2009). That sorting and assemblage has occurred  
48 since the Last Glacial Maximum on (likely; see Elsen and Tingley 2015) increasingly smaller  
49 and more isolated areas as the alpine tundra biome has moved upslope on mountains (Harris  
50 2007). Thus mountain geography will likely have determined the assembly of the extant alpine  
51 communities and will continue to do so as climate continues to change. Because ongoing  
52 climate change is affecting biological and physical systems in mountain regions at rates higher  
53 than global averages (e.g., Cannone et al. 2007) and because some have projected areal  
54 losses of the climatic regime associated with alpine tundra (Diaz and Eischeid 2007; Ackerly et  
55 al. 2010), the need to understand the relations of floras and their geographic context in the  
56 potential response of alpine tundra to climate change is reinforced (Malanson et al. 2007).  
57 Rapid change in alpine floras and the potential loss of species makes it especially important to  
58 monitor and, if possible, protect these locations. Monitoring and protection can be informed by  
59 the study of refugia (e.g., Morelli et al. 2012).

60 The characteristics of places that make a good refugium or that indicate the need for a  
61 refugium will vary with focus. Ashcroft (2010) noted that thinking on refugia differs with spatial  
62 focus between in situ refugia versus refugia as part of a system of stepping stones and between  
63 micro- and macro-refugia. We focus on the broad regional geography of refugia and thus on  
64 both in situ and distributed refugia. In Ashcroft's (2010) definition, refugia are taxon specific, but  
65 here we examine geographies for multiple taxa. Thus a good in situ refugium would be diverse  
66 in habitat and species and thus large. A good stepping stone refuge would be accessible, but  
67 also have the diversity of habitat to support different taxa.

68           Our purpose is to set the context for monitoring or protection by identifying mountain  
69 ranges in the western USA and southwestern Canada in terms of the criteria for refugia function  
70 and need. We examine the floristic similarity, beta diversity, and endemism of plant taxa.  
71 Endemism of mountain ranges will be inversely related to similarity, and thus the relation of  
72 richness to beta diversity is uneven. These observations are relevant to alpine refugia because  
73 the assembly of alpine communities is likely the result of processes starting with past refugia,  
74 and can inform our thinking on those patterns and processes. Identification of the role of factors  
75 such as isolation, can help to identify where refugia might exist or fail as climate continues to  
76 change into the future. This is in line with the approach outlined by Keppel et al. (2012) in that  
77 we examine biogeography – ecology – patterns if one includes the template of changing climate  
78 and geology as part of biogeography.

79           Here, we examine the floristic patterns within regions in order to determine constraints  
80 on future response to climate change. We follow Billings (1978) with similar analyses and some  
81 of the same data. We identify patterns of similarity and relate these to the isolation across the  
82 major mountain systems and for individual ranges in the western USA and immediately adjacent  
83 Canada – hereafter “the West”. Harris (2007) used similar data to infer the role of refugia in the  
84 present assemblage of alpine plant species. Wagner et al. (2014) and Malanson et al. (2015)  
85 have reported evidence for relatively recent assemblage of plant communities in this region.

86           Research on local patterns and dynamics of alpine tundra demonstrate variability  
87 relative to climatic constraints or drivers rather than a similar general response (e.g., Vonlanthen  
88 et al. 2006, Randin et al. 2009, Kudo et al. 2010). Malanson and Fagre (2013) have argued that  
89 such studies need a broader context in order to interpret the observations because a  
90 background rate of change, in the absence of climate change, is expected (following the theory  
91 of island biogeography) but unknown. Malanson et al. (2011, 2015) examined such context by  
92 comparing the similarity within and between a few hundred alpine sites in Colorado and

93 Montana and for ranges across the West. In the first instance, distance and climate differences  
94 were confounded, but as much difference in community composition existed within as between  
95 the regions. In the second instance, distance was more correlated than climate differences with  
96 community similarity, indicating that the geographic history of these ranges, possibly over the  
97 past 20,000 yr, was most important in determining the assemblage of species. However, that  
98 analysis did not examine detailed spatial relations of individual ranges that might indicate how  
99 alpine communities might change in the future given the current spatial distribution.

## 100 **Phytogeography of alpine tundra in western North America**

101         The phytogeography of the three major mountain systems in the West, the Rocky  
102 Mountains, the Sierra Nevada-Cascades (here we include the coastal ranges of the Olympics  
103 and southwestern Canada, although not defined separately), and the Great Basin ranges  
104 (Figure 1), developed over tens of millions of years following uplift of the ranges in a generally  
105 warmer climate. But as the planet cooled –with fluctuations – floras would have moved north  
106 and south as well as up and down slopes, and differences in floras developed due to  
107 connections to broader global Arcto-Tertiary geoflora; in the Pliocene, however, adaptations to  
108 local environments started to differentiate the alpine flora across the region (Axelrod 1948,  
109 1957, Axelrod & Raven, 1985, Wolfe 1987). Schofield (1969) described the phytogeography of  
110 the region broadly. He noted the connections of the alpine floras to that of the Arctic, but also to  
111 a non-Arctic “circumalpine” distribution; Nagy and Grabherr (2009) reported some data derived  
112 from Bliss (1985) on chorology. Within the region Schofield (1969) described an important  
113 disjunction as the Western American Bivalent Alpine that he argued was a direct result of  
114 glaciations having eradicated continuous distributions leaving the current pattern as a result of  
115 recovery from refugia. We discuss three regions, because the Great Basin ranges are the  
116 possible connection between the other two (Billings 1978). The three regions have somewhat  
117 different geological and biogeographical histories. Recently, Elsen and Tingley (2015) reported

118 that mountain ranges vary in the amount of area at different elevations, giving different shapes  
119 to graphs of this distribution. For the mountain ranges in this study, all fall into their “diamond”  
120 shape category, but for the highest elevations species studied here the shape is effectively a  
121 pyramid, with decreasing area at higher elevations effectively limiting the potential response of  
122 species to climate change, given known species-area relations (not to mention that higher  
123 elevation areas tend to be bare rock on which it may take millennia for soils to develop).

#### 124 *Rocky Mountains*

125 The Rocky Mountains are a chain of ranges, and more clearly a part of the continuous  
126 cordillera of the western hemisphere running from Patagonia to Alaska. Here, we consider the  
127 section from New Mexico to Alberta. This section extends some 2000 km and reaches 500 km  
128 in width. The majority of the Rocky Mountain system originated from the late Cretaceous and  
129 early Paleocene periods in the Laramide Orogeny. Major thrusting from the west was followed  
130 by folding of this crustal material (USGS:  
131 <http://geomaps.wr.usgs.gov/parks/province/rockymtn.html>). The geology, and thus the  
132 substrate for ecosystems, is varied. In some ranges, sedimentary rocks are exposed, while  
133 others are primarily granitic; extrusive igneous rocks are present locally.

134 The climate of the Rocky Mountains is continental, with average monthly minimum and  
135 maximum temperatures in the alpine zone of  $-7^{\circ}$  and  $4^{\circ}$  and an average annual precipitation of  
136 1000 mm (source: interpolated by DAYMET at [daymet.ornl.gov](http://daymet.ornl.gov)).

137 Peet (1988) described 11 forest types that, with the exception of riparian zones and seral  
138 stages form a complex mosaic of imprecise elevational and latitudinal bands. These bands  
139 correspond to those described by Merriam (1898). Above these, alpine tundra occurs. Billings  
140 (1978) noted that many of the alpine plant species that occur in this region are also present in  
141 the Arctic due to a more continuous series of ranges allowing easier dispersal from the north.  
142 Another factor cited by Billings (1978) are the abundant early and late snowbeds that provided a

143 broad environmental gradient related to Arctic conditions (Billings 1978). Hadley (1987) reported  
144 patterns for the Rocky Mountains extending from southern New Mexico to the Beartooth Range  
145 in Montana. He too found that dispersal from one alpine region to another, and diffusion  
146 through historic migration corridors, have both contributed to the current geographical  
147 distribution of plants species found in the Rocky Mountain range.

#### 148 *Cascades – Sierra Nevada*

149         The Cascades-Sierra Nevada cordillera consists of the North Cascades, the Cascade  
150 volcanoes, and the Sierra Nevada range. This cordillera extends as long north – to – south as  
151 does the Rockies, but is narrower and less continuous. The entire area was composed of  
152 terranes accreted to the North American plate (USGS:  
153 <http://geomaps.wr.usgs.gov/parks/province/pacifmt.html>). In the North Cascades paleozoic  
154 rocks, following uplift and erosion, were overlain by volcanic activity within the last 35 million  
155 years. Between the North Cascades and the Sierra Nevada the Cascade volcanoes stretch as  
156 a series of stratovolcanic cones. The current mountains are less than 1.5 M yr in age, but  
157 earlier peaks in the region formed 35 M yr ago. In addition to basalts and andesites, pumices  
158 and other pyroclastic substrates are common. Set to the west of this line, the Trinity Alps are  
159 largely granitic. The Sierra Nevada range is the result of uplift beginning in the Miocene but  
160 most significant in the Pliocene and Pleistocene periods. Much of the current range is the result  
161 of a large tilted fault uplifted since 5 M yr ago, but the rocks are primarily granites of Mesozoic  
162 age.

163         The climate of the Sierra-Cascades is moderated by the Pacific Ocean and while cold  
164 the average monthly minimum and maximum temperatures in the alpine zone are -4° and 6°  
165 and an average annual precipitation of 2000 mm (source: interpolated by DAYMET at  
166 [daymet.ornl.gov](http://daymet.ornl.gov)). Only two ranges having less precipitation than the wettest in the Rockies,



167 and ranging from just above 500 mm in parts of the Sierra Nevada to over 3700 mm on  
168 Vancouver Island.

169         Although vegetation zones were lower during the Pleistocene, the Cascade volcano  
170 region results in significant disconnection of alpine environments along the cordillera, while the  
171 Sierra Nevada is the single largest contiguous extent of alpine environment. The environment  
172 varies across the range with latitude to a greater degree than in the Rockies because the  
173 precipitation gradient is marked. Alpine endemics are commonly found within this range,  
174 especially compared to the Rocky Mountains, because the Cascades are more isolated  
175 (Billings, 1978). Taylor (1977) examined the flora of the Sierra-Cascades. He found distance to  
176 account for more of the dissimilarity than did difference in climate. His regressions did not  
177 account for the lack of independence in dissimilarity and distance matrices, but the difference in  
178  $R^2$  (.67 for distance, .42 for actual evapotranspiration) supports the general conclusion.

#### 179 *Great Basin Ranges*

180         Most of the ranges within the Great Basin originated between the Oligocene to the  
181 Pleistocene (Billings 1978; USGS: <http://geomaps.wr.usgs.gov/parks/province/basinrange.html>).  
182 Stretching of the crust resulted in a series of fault-block mountain ranges oriented north-south,  
183 with some accompanying volcanism. These ranges are spatially dispersed between the  
184 western outliers of the Rocky Mountains (the Wasatch Mountains) and the Sierra Nevada,  
185 themselves also fault blocks. The peaks are lower than those of the other ranges

186         The climate of the Great Basis is influenced by the rainshadow of the Sierra-Cascades.  
187 The average monthly minimum and maximum temperatures in the alpine zone are  $-6^{\circ}$  and  $7^{\circ}$   
188 and an average annual precipitation of 700 mm (source: interpolated by DAYMET at  
189 [daymet.ornl.gov](http://daymet.ornl.gov)).

190 Not as high as the two other systems and on isolated ranges, the alpine environments  
191 are more clearly islands. This condition was the focus of Billings' (1978) study, in which he  
192 examined dissimilarity across these ranges as well and their floristic associations with the other  
193 larger systems. For two transects across the Great Basin, he found that distance was not an  
194 important factor affecting floristic similarity, but north-south correlations indicated directions of  
195 colonization. Although small, the central Great Basin ranges have greater environmental  
196 diversity than the Rockies or Cascades because these ranges experienced more rapid  
197 evolutionary changes (Axelrod & Raven 1985). Billings (1978) reported high endemism for the  
198 Great Basin ranges as a group because these mountains are more isolated; otherwise they are  
199 more similar to the Rocky Mountains, despite the Sierra–Nevada being closer.

200 A recurring question in studies of the diversity and associations of alpine floras  
201 worldwide is the importance of refugia. Here, we use the term generally and do not distinguish  
202 macro-, micro-, in-situ, nunatak, peripheral, lowland, etc. types (sensu Holderegger and Thiel-  
203 Egenter, 2009). Most of this new discussion is motivated by the ability to analyze individual  
204 species phylogeography; what is clear is that alpine plant communities have assembled from a  
205 variety of different locations as climate changed and mountain summits became habitable for  
206 these species but not for others (e.g., DeChaine & Martin 2005a). These studies are an  
207 important component of the larger questions on refugia in biogeography (e.g., Ashcroft 2010),  
208 including those on alpine fauna (e.g., DeChaine & Martin 2005b).

## 209 **MATERIALS AND METHODS**

### 210 **Study Areas**

211 We reduced the 56 mountain areas in the West used by Malanson et al. (2015). For  
212 more spatial detail, they used some specific study sites, but here we emphasize the broad  
213 similarity across entire ranges and so combine some of their sites and use more complete floras  
214 (e.g., where they used three sample areas in the Sierra Nevada, we use a single flora for the

215 entire range). The mountain ranges, geographic coordinates, and data sources for each study  
216 area are shown in Table 1. Species were included in this study if they were recorded as being  
217 in “alpine” locations in the source documents. These locations will have been above the  
218 timberline but may have included krummholz or dwarf conifers, which were excluded from the  
219 study. The quality of these data depend on proficiency and consistency of other scientists,  
220 which may vary. Moreover, the taxonomy is subject to constant revision. All species names  
221 were updated and reconciled to the Integrated Taxonomic Information System ([www.itis.gov](http://www.itis.gov)) in  
222 November, 2013. The data are included as Appendix 1.

223           We calculated the geographic distances between all possible pairs of alpine sites using  
224 the haversine method (Sinnott 1984). This calculation accounts for the shape of the earth as an  
225 approximate ellipsoid. The range of distances is large, with the closest mountains (Mesa Seco  
226 and Gunnison North) 17 km apart and the farthest (Vancouver Island and Carson National  
227 Forest) 2187 km.

228           Our interests are in the differences in community composition and in endemism among  
229 mountain ranges. For the floras on the 42 ranges we calculated the Sorenson (1948) similarity  
230 between all pairs based on species presence. We calculated the average similarity for all 903  
231 pairs, the average of all similarity for the three mountain systems, and the average within the  
232 three systems. Using the similarity and distance measures, we calculated the Mantel  
233 correlation for the whole, the systems, and within systems. We also counted the number of  
234 quasi-endemic species for each range (quasi- because we do not have all records of all alpine  
235 areas in the West, this issue is acute for our most northern sites in southern Alberta and British  
236 Columbia where ranges close to the north will likely share species). To assess the effects of  
237 isolation, we plotted the similarity versus the distance to the two closest neighbors for each  
238 range for each system, not repeating pairs. We fitted a simple exponential regression to these

239 patterns and qualitatively assessed the ranges with large residuals. We calculated beta  
240 diversity, using  $\beta = \gamma/\alpha$  for the three ranges separately.

## 241 **RESULTS**

### 242 **Similarity**

243 Similarity across the West is not high (Table 2, rows 1-2). Similarity ranged from 0 to  
244 0.71. As expected, the Rocky Mountains have much higher average similarity. The similarities  
245 of the Great Basin and Sierra-Cascades systems are the same within as for those systems  
246 compared with the entire West, but the similarity within the Rocky Mountains is higher. The  
247 ranges of the Great Basin are more similar to those nearby: to the Sierra Nevada (for those to  
248 the west) or to the Rockies (for those to the east). The ranges of the Great Basin have a  
249 scattered geography in contrast to that of the two cordilleras.

250 The Mantel correlations of similarity with distance are highest in the Rockies and lowest  
251 in the Great Basin (Table 2, row 3). In the Rockies, where the ranges are relatively close (there  
252 are over twice as many ranges over the same latitudinal range in the Rockies as in the Sierra-  
253 Cascades) and aligned north-south, the relationship with distance is stronger. The low  
254 correlation in the Great Basin is indicative of the weak spatial organization within this group.

255 When similarities are plotted against distance, low similarity in the Great Basin is notable  
256 (Figure 2). The Deep Creek and Ruby ranges, although separated by only 151 km, have a  
257 similarity of only 0.10. The Henry and Tushar mountains, at 123 km, are similar to only 0.18.  
258 Still in the Great Basin, the White and Wassuk ranges have similarities of only .07 and 0.09 to  
259 the Sierra Nevada, 101 and 121 km distant, but the overall breadth of the Sierra Nevada  
260 explains some of this; the White and Wassuk are less than 0.10 similar to any other Great Basin  
261 range as well. In the Sierra Cascades, the small and isolated Vancouver Island alpine has  
262 similarities of 0.07, 0.12, and 0.13 with its nearest neighbors in the North Cascades, Garibaldi

263 Peak, and the Olympics. Mt. Shasta has similarities of 0.07 and 0.10 with the neighboring  
264 Sierra Nevada and the Trinity Alps. Mt. Jefferson and Three Sisters are also close and of low  
265 similarity, 0.17. In contrast, the Olympics and Mt. Rainier are quite similar at 0.52 while  
266 separated by 180 km and Puget Sound. In the Rockies, the similarities between the Wasatch  
267 and Uinta ranges and between the Absaroka and Bighorn are relatively low at 0.21 and 0.15  
268 and 97 and 180 km., respectively.

### 269 **Endemism and diversity**

270 The Sierra-Cascades has high endemism as a system and a high average per range  
271 (Table 2, row 4) primarily because the Sierra-Nevada is the largest single range, spanning some  
272 400 km. The Rockies have high endemism as a system but a low average per range because  
273 these species are spread throughout the many ranges, not concentrated. The Great Basin is,  
274 however, the surprise because it has relatively few endemic species. These individually  
275 isolated ranges are not so individualistic in composition.

276 The diversity across the ranges is also as expected (Table 2, rows 5-6). The Rockies  
277 have more species than the Sierra-Cascade and Great Basin systems combined. Beta diversity  
278 is also highest in the Rockies, while it is similar between the others. To examine specific  
279 geographic effects, we calculated beta diversity for the Sierra-Cascades without the dominant  
280 Sierra-Nevada and for the Rocky Mountains including only the main front of the cordillera –  
281 excluding the ranges of western Colorado, Utah, Idaho, and northeastern Wyoming that are out  
282 of line. Beta diversity drops by 25% (from 6.25 to 4.69) in the Sierra-Cascades and by 21% in  
283 the Rockies (from 5.80 to 4.56). The Sierra Nevada substantially determines the regional  
284 diversity pattern of its cordillera because of its endemism – and its size. The alignment of  
285 ranges in the Rocky Mountains is somewhat less important even though some of the ranges  
286 excluded – the Bighorn, Uinta, and Wasatch – are among those with lowest similarity.

### 287 **DISCUSSION**

288           The geometry of the ranges is magnified by the geology in setting the stage for similarity  
289 and the potential for refugia. While similarity is correlated with distance, some of the residuals  
290 may be explained by geology, although we did not explore the diversity of geologic substrates  
291 thoroughly. Many of the ranges have mixed substrates, but some observations – the low  
292 similarities of Mt. Shasta and the White Mountains – could be related to their substrates. Time  
293 is another factor: Mt. Shasta has erupted several times in the past 10,000 years, the last being  
294 about 200 years ago  
295 ([http://volcanoes.usgs.gov/volcanoes/mount\\_shasta/mount\\_shasta\\_geo\\_hist\\_5.html](http://volcanoes.usgs.gov/volcanoes/mount_shasta/mount_shasta_geo_hist_5.html)), but all  
296 volcanoes in the Cascades and the Olympics have had some recent activity while leaving some  
297 areas unchanged.

298           Similarity does not tell all we need to know about refugia, and cannot be interpreted  
299 directly. For example, here the Sierra Nevada has low overall similarity to other ranges, while  
300 by itself may constitute a number of possible microrefugia or an in situ macrorefugium (see Rull  
301 (2009) for the basics of microrefugia, Mee and Moore () for further implications, and Gentili et al.  
302 (2015) for alpine discussion) for given its diversity and endemism (the extent of the area above  
303 treeline that is bare rock or areas with minimal soil may lower this possibility).

304           The distribution of endemic species is more puzzling. The low endemism in the Great  
305 Basin indicates that these flora have not had time for autochthonous development. Although  
306 spatially isolated the alpine areas are relatively small and further within-island isolation that is  
307 important for adaptive radiation is less likely (cf. Gehrke and Linder 2014). The degree of  
308 endemism in the Sierra-Cascades and the Rocky Mountains, with the caveat that some of these  
309 species may be on ranges not included in the study, indicate that adaptations to local  
310 environments may have occurred as the ranges of alpine species moved to higher elevations  
311 during the past 20,000 years. This adaptability could play a role in response to future climate  
312 change. Such adaptability is only beginning to be explored (e.g., Massatti and Knowles 2014).

313 Diversity leads to high similarity, except where it does not. The Sierra Nevada and the  
314 White Mountains in California both have high diversity and low similarity – and high endemism.  
315 For our data both were surveyed relatively recently (Rundel 2008; Rundel et al. 2011) and we  
316 believe these are reliable. The Sierra Nevada is the largest range, and the White Mountains are  
317 geologically distinct. However, other ranges are also geologically distinct.

318 Which ranges would make good refugia? Ideally, ranges that are diverse, similar to  
319 others, and not isolated would make the best refugia (cf. Ashton 2010). The best examples of  
320 these are in the Rocky Mountains. Of these, the Absarokas, with the highest diversity (352  
321 species), high similarity (0.27), and close to neighbors (94 km, 143 km, 150 km, and 180 km to  
322 surrounding ranges) are a good example. Additionally, the Absarokas are geologically diverse.  
323 Because of its size and diversity, the Sierra Nevada will probably serve as a refugium for those  
324 species it contains. However, it may not serve a habitat from which species can migrate given  
325 the gap in distance and geology to the more northern peaks and ranges.

326 Which ranges or floras indicate the need for refugia or protection? The Cascade ranges,  
327 without the Sierra Nevada, are low in similarity and diversity and high in endemism and  
328 isolation, with the possible exception of Mt. Rainier. On the other hand, the Trinity Alps, which  
329 are not geologically part of the Cascade chain, are also relatively in need. Mt. Shasta stands  
330 out among these as in need of protection, or at least monitoring, in part because so much of its  
331 area is recently disturbed by volcanism and would not support many species. As a worst case,  
332 for species adapted to specific combinations of geologic substrate and climate no future  
333 geography may exist.

334 The Great Basin ranges present a different logic. While the endemism and low similarity  
335 of the White Mountains may indicate a need for protection, they are not isolated. In contrast,  
336 some of the other Great Basin ranges are isolated and dissimilar but have low endemism.  
337 These conditions would indicate that it is the communities on these ranges that are potentially

338 threatened with change. Given the likelihood of individualistic responses to climate change,  
339 current community structure is not as important as individual species existence in planning  
340 monitoring or protection. However, the dissimilar communities in these ranges probably indicate  
341 narrow ranges of climate and other habitat dimensions in these small alpine areas.

342 In the Rocky Mountains, because of their geography, being east of the main cordillera,  
343 endemism, and low similarity, the Bighorn Mountain flora may be most in need of protection.  
344 The ranges of Idaho, west of the cordillera and geologically similar to those of the Great Basin  
345 (the geographic boundaries used are by convention and are arguable), present a similar  
346 potential problem.

347 For the West, we have described the context within which species will respond to  
348 ongoing climate change. We have been able to use current patterns of similarity, beta diversity,  
349 and endemism to identify ranges in the West that are likely to serve as refugia and some that  
350 are likely to need protection or at least monitoring. Within ranges, more detailed focus on the  
351 most threatened habitats is still needed (e.g., Malanson et al. 2012). For the West, Further work  
352 on phylogeography and species traits, especially dispersal mechanisms, is warranted for these  
353 mountain ranges and can contribute to eco-evolutionary theory (Graham et al. 2014; Massatti  
354 and Knowles 2014).

355 Our reasoning and analyses differ from the guidance given by Ashcroft (2010) and in  
356 thinking about refugia because we are asking primarily about mountains and their geography  
357 and biogeography instead of focusing on organisms per se. We realize that in the end the  
358 determinants of refugia will be organism-specific and require an organism focus, perhaps at fine  
359 geographic scale (e.g., Patsiou et al. 2014; Gentili et al. 2015), but our analysis indicates that at  
360 a broad level a geographic analysis can provide guidance. Similarity, beta diversity, and  
361 endemism can focus efforts of science and management on locations, within which organisms  
362 will live or not. After all refugia are, or will be, places. This approach, based in the tradition of



363 Billings (1978), is still a useful complement to the frontiers of phylogeography reported  
364 elsewhere in this issue.

365

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553

554 Table 1. The 42 mountains or ranges used in the study, with their location and the source of the  
 555 species data.

556	<u>Site</u>	<u>Province/State</u>	<u>System</u>	<u># Species</u>	<u># Endemics</u>	
557	<u>Source</u>					
558	3Sisters	Oregon	Sierra-Cascades	25	4	Van
559	Vechten, 1960					
560	Absaroka	Wyoming	Rockies	352	24	RMH*
561	Bighorn	Wyoming	Rockies	87	12	RMH
562	MtBaldy	Montana	Rockies	151	11	
563	Bamberg & Major, 1968					
564	Carson	New Mexico	Rockies	160	12	RMH
565	Cascades	Washington	Sierra-Cascades	95	11	
566	Douglas, 1971; del Moral, 1979					
567	DeepCreek	Utah	Great Basin	29	3	
568	McMillan, 1948					
569	EagleCap	Oregon	Great Basin	18	3	
570	Johnson, 2004					
571	FlintCreek	Montana	Rockies	117	14	
572	Bamberg & Major, 1968					
573	GunnisonN	Colorado	Rockies	274	9	RMH
574	GunnisonS	Colorado	Rockies	274	14	RMH
575	GlacierNP	Montana	Rockies	229	41	Damm,
576	2001					

577	Garibaldi	British Columbia	Sierra-Cascades	53	5	Archer,
578	1963					
579	GrosVentre	Wyoming	Rockies	215	7	RMH
580	Henry	Utah	Great Basin	27	0	Neese,
581	1981					
582	Lemhi, etc	Idaho	Rockies	149	38	
583	Caicco, 1983; Moseley, 1983, 1985;					
584						U
585						rbancz
586						yk,
587						1993
588	IndianPeaks	Colorado	Rockies	212	8	
589	Komarkova, 1979					
590	MedicineBow	Wyoming	Rockies	252	33	
591	Billings, 1988; Lukas et al., 2012					
592	Mosquito	Colorado	Rockies	230	10	RMH
593	MesaSeco	Colorado	Rockies	94	2	
594	Johnson, 1970					
595	MtJefferson	Oregon	Sierra-Cascades	45	1	
596	Ingersoll, 1991					
597	Olympics	Washington	Sierra-Cascades	117	7	Bell &
598	Bliss, 1973; Belsky & del Moral, 1982					
599	ParkRang	Colorado	Rockies	88	3	RMH

600	Rainier	Washington	Sierra-Cascades	137	18	
601	Edwards, 1980					
602	RockyMtnNP	Colorado	Rockies	92	7	
603	Willard, 1979					
604	Ruby	Nevada	Great Basin	32	0	Loope,
605	1970					
606	SanJuan	Colorado	Rockies	223	15	RMH
607	Shasta	California	Sierra-Cascades	41	14	Cooke,
608	1940					
609	Sierra	California	Sierra-Cascades	371	169	Rundel
610	SanFrancisco	Arizona	Great Basin	47	3	Little,
611	1941					
612	NRockies	Alberta	Rockies	180	48	Beder,
613	1967; Bryant, 1968; Trottier, 1972					
614	SWColorado	Colorado	Rockies	169	2	RMH
615	Tetons	Wyoming	Rockies	64	2	RMH
616	Trinity	California	Sierra-Cascades	21	2	
617	Ferlatte, 1974					
618	Tushar	Utah	Great Basin	167	7	Taye,
619	1995					
620	Uinta	Utah	Rockies	99	13	
621	Hayward, 1952; Ostler et al., 1982; St. Clair,					

622						
623						1984
624	VancouverIsl	British Columbia	Sierra-Cascades	42	15	Ogilvie
625	and Ceska, 1984					
626	Wasatch	Utah	Rockies	134	16	Arno et
627	al., 1977					
628	Wassuk	Nevada	Great Basin	32	5	Bell
629	and Johnson, 1980					
630	White	California	Great Basin	120	3	Rundel
631	et al., 2008					
632	WindRiver	Wyoming	Rockies	243	5	RMH
633	Yellowstone	Wyoming	Rockies	201	11	RMH

634

635 \*RMH: online source of the Rocky Mountain Herbarium

636 (<http://rmh.uwyo.edu/research/floristics.php>)

637

638

639 Table 2. Similarity, Mantel correlations, endemism and diversity of the 42 ranges and within the

640 three major mountain systems in the West.

641		All	Sierra-Cascades	Great Basin	Rockies
642	1 Similarity, all	0.19	0.13(0.15)	0.11(0.16)	0.22(0.17)
643	2 Similarity, internal		0.13(0.11)	0.11(0.08)	0.30(0.20)
644	3 Mantel r (all, internal)	-.51	-.34	-.29	-.47
645	4 Endemic Species (%)	45	39	14	34
646	5 Richness	1398	592	344	1036
647	6 Beta diversity		6.25	5.83	5.80

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652  
653 Figures

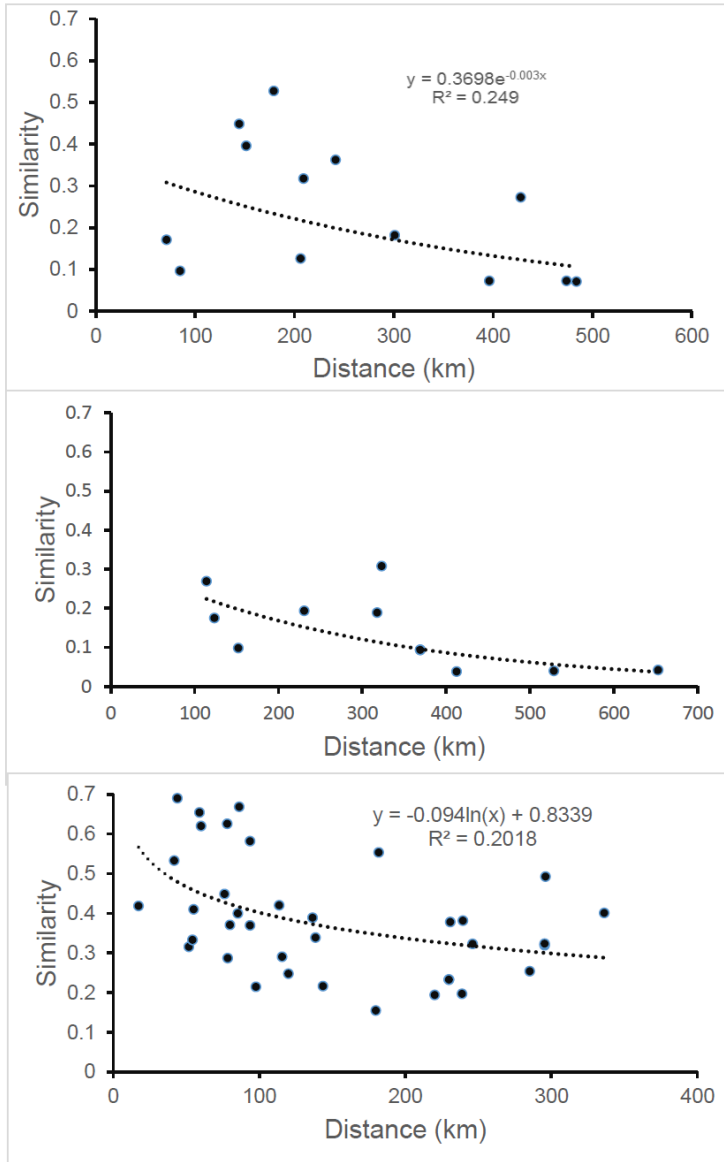
654 Figure 1. The pattern of alpine areas in the Sierra-Cascades (and Coast Ranges), the Great  
655 Basin ranges, and the Rocky Mountains, based on distributions of *Sibbaldia procumbens* and  
656 *Oreamnos americanus* (mountain goat) at GBIF.org, courtesy of Mike Jones, University of  
657 Massachusetts.



658  
659  
660



661 Figure 2. Similarities of nearest two neighbors plotted against distance and fit with an  
662 exponential function. Large residuals are analyzed qualitatively in the text.



663