Hemispheric and Continental Scale Patterns of Similarity in Mountain Tundra

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**DOI:** [https://doi.org/10.17077/u06a-840z](https://doi.org/10.17077/u06a-840z)
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Acknowledgments. AJB was funded by the Rural and Environment Science and Analytical Services Division of the Scottish Government.
Abstract

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

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

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

Key words: alpine; beta diversity; climate, distance; oroarctic
Background and objectives

The biodiversity of mountain tundra, encompassing both alpine and oroarctic tundra (the latter is tundra at high latitudes where the effects of elevation differentiate it from arctic tundra; Virtanen et al. 2016) is globally higher than expected (Körner 2000). Mountain tundra diversity is also regarded as threatened due to anthropogenic climate warming, and several studies document recent changes in high elevation plant diversity (e.g., Britton et al. 2009, Spasojevic et al. 2013, Lesica and Crone 2017, Steinbauer et al. 2018). These observations imply that patterns and processes underlying mountain plant assemblages may be spatially structured, producing strong heterogeneity in possible plant responses to climate change (e.g., Anthelme et al. 2014).

Therefore, although first described by von Humboldt and Bonpland (1805), and despite a growing body of observations on the patterns of alpha and beta diversity (respectively, the diversity of species at local sites and the change in species composition among such sites) on environmental gradients in mountains (e.g., Kikvidze et al. 2005, Löffler and Pape 2008, Li et al. 2011, Elmendorf et al. 2012, Gritsch, Dirnböck and Dullinger 2016, Harbert and Cooper 2017, García-Gutiérrez et al. 2018), a better understanding of the large-scale spatial variation in mountain plant assemblages is crucial to better dissect possible climate-plant relations and responses to future climate change.

The importance of changing scales is now a central principle of physical geography (Meentemeyer 1989, Walsh et al., 1997, Malanson et al., 2017) (we use scale in the most common way, as equivalent with extent, and so large scale covers larger areas). McGill (2010) argued that understanding scale dependence was needed to explain biogeographic patterns. He highlighted four controls on the distributions of species: climate, species interactions, habitat, and dispersal. Although he hypothesized climate and dispersal as operative and possibly equally
important at both the smallest and largest scales, climate operates at small scale only as
microclimate, and microclimate is the result of the macroclimate being modified by habitat and
the organisms themselves (plants in most cases). At the scale of the globe, climate does not
differentiate distributions because climates repeat in patterns determined by gradients of latitude
and continentality, and so climate effects are confined to continental to hemispheric scales.
Dispersal can make a difference at small scale through a mass effect, but it dominates processes
at the largest, global, scale. This sequence in which processes would dominate the structuring of
species patterns on a gradient of increasing spatial scale would then be simplified: biotic
interactions – habitat – climate – dispersal. Furthermore, without observations in the past, our
understanding at larger scales is inferred from long-term biogeographic patterns (e.g., Douda et
al. 2018) that are represented by geographic distance and isolation; these serve as a proxy for
observations of dispersal.

Large-scale compositional patterns in mountain vegetation reflect historical speciation-
extinction dynamics (Hewitt 1996, Hoorn et al. 2013), Tertiary continental dynamics (Wolfe
1987), regional extinction-immigration dynamics (Riebesell 1982, Hadley 1987, Harris 2007),
large-scale climatic niche processes (Virtanen et al. 2016), and spatial processes related to
geographic distance (Taylor 1977, Malanson, Cheney and Kinney 2015, Clarke et al. 2018). As a
result, the relationship of mid-latitude alpine tundra to arctic tundra is not a simple gradient of
difference with latitude (e.g., Billings 1973, Virtanen and Eurola 1997, Virtanen et al. 2016).
Moreover, studies find that plant community relations to environment vary with the scale of
analysis (e.g., Kim et al. 2012), including alpine communities (e.g., Suding et al. 2015,
Chalmandrier et al. 2017). The relevance of geographic scale for local and regional diversity was
illustrated by Malanson, Fagre and Zimmerman (2016, 2018), who showed that the drivers of
beta and alpha diversity differed among four regions across the Rocky Mountains in the USA. In summary, due to their topographic complexity, steep environmental gradients, and mix of habitat types, mountain tundra varies as much within geographic units (valleys and slopes) as among them. The explanations for the beta diversity at continental scales may be related to climate, but biogeographic history and the geographic separation of mountain tundra regions should also play a role.

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

Here, we take a first step towards improving knowledge of the large-scale biogeographic patterns of mountain tundra assemblages and how they relate to space (geographic distance) and climate. We compiled data from Europe and North America and examined variation in plant community composition in oroarctic and mid-latitude mountain tundra as it is related to variation in climatic variables and geographic distance. Variation in concert with climate is expected because energy and water resources, and their relevant variables such as temperature and soil moisture, are important dimensions of species distribution or niche. We believe that geographic distance matters because it is a proxy for processes that have occurred in the past that we cannot observe; these include responses to past climate changes and disequilibria (e.g., Douda et al.
2018), including dispersal (Malanson et al. 2017). For example, Muster et al. (2009) revealed
that genetic links between Scandinavian, Alp, and Carpathian spiders could be explained either
by low rates of current dispersal or high dispersal rates at the Last Glacial Maximum (LGM), and
patterns of plant endemism and refugia also reflect disequilibria (e.g., Patsiou et al. 2014,
Smycka et al. 2017). Plant community composition could reflect responses to past climatic
conditions (e.g., Kammer, Schöb and Choler 2007), extending to the LGM, where niche
constraints have not had time to be fully expressed.

Our main aim was to address intercontinental patterns in similarity in mountain tundra
vegetation in relation to spatial and climatic variables. Many environmental factors differ across
the mountain regions studied here. These include the environmental templates determined by the
geological processes of mountain building and the millennia of erosion under different climatic
regimes. We focused on distance and climatic difference as the potential factors that would
differentiate the floras in order to examine such factors at the broad scale in the context of the
framework provided by McGill (2010). The other factors that differentiate these mountain
regions, such as differences in substrates and soils, equally differentiate mountains within
regions and properly are within the domain of habitat differentiation at smaller scales as
hypothesized by McGill (2010). We contend that specific geographic characteristics will alter
the relationships with distance and climate; e.g., oroarctic communities will be more similar to
each other relative to those at mid-latitudes than distance or climate would dictate (cf. Virtanen
et al. 2016), and extremes of climate or isolation will lessen similarity due to endemism. Because
mountain tundra exists in a narrow range of temperatures, we also expected that water (e.g.
precipitation) rather than temperature would be principally responsible for climatic
differentiation. Additionally, we recognize a potential difference in responses for vascular and
bryophyte taxa, because bryophytes disperse via spores, as opposed to the varied and larger propagules of vascular plants, which leads to less geographic isolation over (possibly longer) evolutionary time (cf. Ledent et al. 2019). We expect:

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

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

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

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

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

### Methods

#### Data sources and selection

Species data

We used records of species presence in multiple vegetation plots (relevés) from 13 regions in Europe and North America (Figure 1, Table 1; these data are publicly accessible at ir.uiowa.edu). The regions were defined based on how earlier datasets were published; but each covers a section of a mountain range within 1º of latitude and longitude. We chose these regions
because they had extensive coverage in numbers of plots for their areas, the data collection methods were comparable, and in most cases consistently followed the Braun-Blanquet methodology in the field (and in all cases used a visual estimate of percent cover in quadrats, which we simplified to species presence). Places that were not considered were those that did not use quadrats for sampling, compiled presence for entire ranges or communities rather than by plot, or reported summaries only (e.g., syntaxa). We further excluded the sites from Virtanen et al. (2016) that they had identified as arctic, and for Scotland we excluded those vegetation types described by Averis et al. (2004) as non-montane and plots at elevations less than 675 m, which Birse (1976, 1980) set as the lower limit of alpine vegetation. Because the observations were made at different times, all nomenclature was updated to currently accepted taxonomy using the Taxonomic Name Resolution Service at iPlant Collaborative (http://tnrs.iplantcollaborative.org); for unresolved species, we retained the original nomenclature. We removed lichens from the analyses because their response to climate may be the inverse of vascular species (Walker et al. 2006) and their taxonomic comparability in the several data sources was low. We then divided the observations into vascular and bryophyte datasets because we expected the two types of plants to respond differently to climate (Molau and Alatalo 1998). We discarded records where only the genus was identified because for comparing regions these would bias the results toward greater than actual similarity. Our final dataset contained 397 bryophytes and 1814 vascular species on 4829 plots.

In order to have balanced comparisons in the analyses but retain the breadth of observations, we reduced the data to 200 plots per region where more plots were available in a region. To sample 200 plots from a larger pool, we ran detrended correspondence analysis (DCA; using PC-ORDv6), an eigenvector ordination that represents the order of similarity on its
primary axis, on the data for each region, and then sampled 200 plots via a regular systematic
selection along that axis so that the full range of plant communities would be represented. The
plots were approximately evenly distributed along this axis because the Braun-Blanquet
classification method, not used here, works better with that type of field sample. The final data
set included 2507 plots for vascular plants (with 1733 species) and 1751 plots for bryophytes
(with 361 species; the Betic, Cantabria, and Yosemite vicinity data had no bryophyte records).

Climate data

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

Geographic distance and spatial variables

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

Analyses

We used a Multi-Response Permutation Procedure (MRPP; McCune and Grace 2002),
with Sørenson (1948) similarity, to test for differences between continents, between latitudinal
(oroarctic and mid-latitude) regions, and among continent-by-latitude regions. MRPP is an alternative to discriminant analysis that avoids parametric assumptions. Sørenson similarity, the proportion of species abundance shared between pairs of observations to their summed abundance, has characteristics relative to shared species that makes it a preferred representation (McCune and Grace 2002, Austin 2013).

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

We ordinated the plot-species data by nonmetric multidimensional scaling (NMDS). We determined the number of ordination axes to analyze by examining the correlation between the distances among all pairs of plots in the dimensions of ordination space with the Sørenson similarity matrix and increased the number of axes as long as the increase in correlation was greater than 0.05; we ended using four axes (for visualization, we used the first three dimensions). We regressed the means of the plot positions of each region on the four ordination axes with the bioclimatic variables and the Moran eigenvectors scores. After examining all 36
bivariate plots for nonlinear patterns, we used General Linear Models (GLMs) to fit stepwise models (0.05 to enter, 0.10 to remove; cf. Draper and Smith 2014) with an overall $R^2$ and per-variable contribution. We used these metrics to estimate the relative importance of the climatic and geographic variables.

**Results**

**Bioclimates and geographic distances for regions**

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

**Regions, similarity and distance**

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

Table 5 shows the mean Sørenson similarity for all pairs of regions. The correlation between the average similarity of all pairs and the distances between them was $r = -0.468$ ($p < 0.001$ by Mantel test; 13 regions, $n = 78$) for the vascular species and $r = -0.406$ ($p < 0.016$; 10 regions, $n = 45$) for the bryophytes. The relationship of similarity among pairs of regions to distances among pairs of regions was exponential for the vascular species and linear for the bryophytes (Figure 3). Although a number of positive-residual points appeared to be outliers,
their removal did not improve the regression $R^2$; these apparent outliers were pairs of oroarctic regions. The 78 pairs appeared to be divided into two less definitive groups: those between and those within continents (distances greater than and less than 4500 km, respectively). When the data were divided in that way, the relation of similarity to distance was much stronger between than within continents (Figure 3,c-h). The vascular species in Europe still had a weak relationship, but the European bryophytes and both vascular plants and bryophytes in North America had no significant relations with distance (Figure 3,e-h); however, some $R^2$ were relatively high and the possibility of a relationship exists. Also, although several regressions were significant, the plots revealed triangular patterns wherein the full range of similarities occurred at the shortest distances with less similarity at the longest. These observations match our first and second expectations.

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

Ordination and General Linear Models

In addition to stress (vascular, 21.9; bryophyte, 23.1), we examined the competence of the NMDS ordination by correlating the distances between all pairs in ordination space with the similarity matrix reduced by that ordination, increasing the number of axes until the increment in
was less than 0.05. This method produced ordinations for both vascular and bryophyte groups with four axes, with correlations with the similarity matrix of 0.444 and 0.452, for vascular and bryophytes respectively (p < 0.001 for both).

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

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

Discussion

Large-scale, biogeographic elevational and latitudinal patterns in mountain vegetation have previously been thought to be primarily driven by climate (with the temporal change in species distributions also associated with climatic changes). Our analyses tackled this question and provide new evidence that location can supersede climate in the determination of large-scale
biogeographic patterns in mountain species assemblages. First, distance is a consistent factor in
the differentiation of these assemblages or floras. Second, geographic regions are differentiated.
Distance matters primarily between rather than within continents. The relative importance of
distance, as seen in the patterns of similarity, in accounting for the variance in observed patterns
of beta diversity is indicative of processes at larger spatial and temporal scales. The triangular
patterns indicate that multiple factors may operate at smaller scales while geographic connection
through dispersal is the dominant process at larger scales. The triangular pattern is more evident
for vascular species because the similarity is higher at shorter distances, specifically for oroarctic
pairs, while it has a tighter distribution at the longest distances. Evolutionary differentiation of
floras and disequilibrium of communities in flux following Holocene climate changes would
weaken the link between current climates and similarity and reflect past connections through
dispersal. If these links are true, our results support the contention of McGill (2010) that
dispersal supersedes climate in determining community differentiation at the largest spatial
scales.

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

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

Isolation is more than simple distance.

Whereas Virtanen et al. (2016) thought that the differences between the oroarctic and
mid-latitude tundra in Europe were in part attributable to climate and perhaps to differences in
relief, our addition of Scottish and Alaskan oroarctic regions provides additional insight. While
distance alone matters, the oroarctic connection between Europe and Alaska indicates that the
relationship to the circumarctic low elevation tundra may play a role in the similarity among
oroarctic regions. Also, the central Brooks Range has rugged topography like that of the Rocky
Mountains or the Alps, but this region is not strongly differentiated from the other, less rugged, oroarctic regions, suggesting that complexity of relief is probably less important in differentiating mountain tundra. Cooper (1989) suggested that high elevation tundra in Alaska is a good analog for widespread Beringian tundra of the Last Glacial Maximum, which accords with this conclusion.

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

Another specific geographic comparison can be made between the Mediterranean-climate regions of California and Spain (the YNP and BET regions). These two have the lowest warm-season precipitation, yet they are the most dissimilar pair. They are both toward the southwestern extremes of their continents and have no mountain ranges farther in that direction (although some connections to the Atlas Mountains may exist for BET and to the Sierra Madre for YNP). Thus they are relatively isolated in both climate and geographic space. Both ranges are relatively high in endemic species (Faverger 1972, Malanson, Zimmerman and Fagre 2015). For BET this is probably because of its isolation but for the Sierra Nevada of California it may also be attributable to its large area.
Patterns of vegetation change observed in relation to past or present climate change should be interpreted in light of regional and specific characteristics of place. Similar degrees of change in the oroarctic and mid-latitude alpine tundra vegetation may signify different impacts, given differences in functional types and responses to climate (Bruun et al. 2006). These differences might even extend to greater geographic specificity, as where Lesica and McCune (2004) have pointed out changes for arctic-centered species at their southern range limit in Glacier National Park, Montana. Changes in locations with more endemic species, e.g., in BET, should perhaps be weighted more in terms of impact assessment.

Mountain tundra is undergoing changes that could threaten its unique character (e.g., Britton et al. 2009). It is also potentially threatened by rising treelines in some areas and by rising low-elevation arctic tundra in others (e.g., Vanneste et al. 2017). Controversial ideas about mitigation include assisted migration - moving plants poleward to track their geographically shifting climatic niche (e.g., Abeli et al. 2014, Ramírez-Amezcu et al. 2016, Pykälä 2017). For the mountain tundra examined here, this idea must face simple problems of uncertainty before the complex ones related to ethics. Brooker et al. (2018) have shown that it may be particularly difficult to translocate some mountain tundra species because of our inadequate knowledge of their niche and the difficulty of identifying climatically-suitable locations within topographically complex mountain landscapes. At larger scales, mountain tundra is already near the end of the global temperature gradient. Little area exists where it is now too cold for tundra plants but where substrates exist to support any in a warmer future. Retreating glaciers would nominally provide space, but the threshold switch from ice to ice-free may not leave the needed range of temperature in its wake. Additionally, the rate of warming is expected to be greater at higher latitudes (Serreze et al. 2000), further limiting the feasibility of poleward migration. Even within
ranges, elevation-dependent warming (Rangwala and Miller 2012) will limit the amount of new
area to which alpine plants could migrate (with or without assistance). Given that mountain
tundra does not align on simple climatic gradients, it is not clear that any region could or should
be a target for translocations from any other. When considering assisted migration of mid-
latitude tundra species, the oroarctic regions may already be too threatened to serve as a suitable
receptor region. Given its distinct floristic character and that oroarctic tundra is faced with the
potential for greater warming, less active mitigation and more protection (e.g., Thuiller et al.
2014) may be a better strategy.

Conclusions

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

The relevance of biogeographic theory to the conservation in a changing climate is also
dependent on the details of biogeography, such as latitudinal gradients, as well as on scale. Given
the potential problems that global climate change poses for mountain tundra, approaches to
mitigation should be considered. Although biogeographic theory is relevant to all five of the
approaches categorized by Malanson et al. (2019), the patterns revealed here further limit the
efficacy of the most fraught approach, assisted migration. When the implications of local context 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.

<table>
<thead>
<tr>
<th>Code</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation (m)</th>
<th>Climate</th>
<th>Relief</th>
<th>initial#</th>
<th>#used-v</th>
<th>#used-b</th>
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Locations and sources: ALP, Swiss Alps, Braun-Blanquet (1926); BET, Betic Range, including the Sierra Nevada, 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 Area, 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).
Table 2. The climate variables used; Annual; Warm – warmest quarter; Cold – coldest quarter; Wet – wettest quarter; Dry – driest quarter; T – mean temperature (°C); P – mean precipitation (mm). Data for three points in each region were drawn from the CHELSA downscaled product.

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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).

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Dist3   700  956  801  2997 1048  1376  746  1805  654  1287  1253     

684

685

686
Table 4. Multiple Response Permutation Procedure (MRPP) effect size, $A$ (chance-corrected metric showing differences in comparisons). The comparison was between continents, latitudes, and their combination; continents – Europe, EU, and North America, NA; latitudes – midlatitude, ML, and oroarctic, OA. The separation between groups is significant in all comparisons with $p < 0.000001$.

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

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

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

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Total strength, contribution:

| Geography | 1.90  | 0.95  |
| Region    | 0.11  | 0.75  |
| Distance  | 1.79  | 0.20  |
| Climate   | 0.84  | 0.42  |
| Precipitation | 0.83 | 0.42  |
| Temperature| 0.01  | <0.00 |
| Summed AdjR² (of 4.0) | 3.14 | 1.27 |
Figure 1. The locations of the 13 regions identified in Table 1 shown on an azimuthal equidistant projection.
Figure 2. The mean Sørenson similarity metrics of all the pairs of plots between regions graphed against the distance (km) between them. For the vascular species, similarity-distance relations were fit with an exponential equation, while the bryophyte relations were linear. The p values were calculated using a Mantel randomization. The triangles symbols in a are the oroarctic regions.
Figure 3. Nonmetric multidimensional scaling (NMDS) results plotted in two dimensions for a reduced set of plots for visualization only. Regions are grouped by continent (Europe – EU; North America – NA) and latitude zone (ML – midlatitude; OA – oroarctic).