ARTICLE

Macrosystems Ecology

Explanation of beta diversity in European alpine grasslands changes with scale

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Abstract

The importance of environmental difference among sites and dispersal limitations of species to the explanation of diversity differs among biological systems and geographical regions. We hypothesized that climate and then dispersal limitation will predominantly explain the similarity of alpine vegetation at increasing distances between pairs of regions at subcontinental extent. We computed the similarity of all pairs of 23 European mountain regions below 50° N after dividing the species lists of each region by calcareous or siliceous substrates. Distance decay in similarity was better fitted by a cubic polynomial than a negative exponential function, and the fit was better on calcareous than on siliceous substrate. Commonality analysis revealed that the proportion of explanation of beta diversity by climatic difference had unimodal patterns on a gradient of increasing distance between

regions, while explanation by dispersal limitation had consistently rising patterns on both substrates. On siliceous substrate, dispersal limitation explained more of the variation in beta diversity only at longer distances, but it was predominant at all distances on calcareous substrate. The steeper response to distance at <1600 km and >2600 km may indicate dispersal limitation at different temporal scales, and the uptick in the response to distance at the longest distances may reflect how isolated some regions have been before and since the last glacial maximum.

INTRODUCTION

Beta diversity is fundamentally connected to spatial scale (Qian & Ricklefs, 2012). Although it has multiple definitions (Tuomisto, 2010), beta diversity quantifies the variability in species composition across space. Beta diversity is known to increase with distance through the so-called distance decay of similarity, which is mainly driven by dispersal limitation, environmental variation, and niche-width differences (Nekola & White, 1999), but these drivers differ among studies across latitudes, biogeographical realms, and the mobility of organisms (Soininen et al., 2007). Although Soininen et al. (2007) concluded that beta diversity is scale-dependent, that is, effect size changes with study extent, how the relative importance of the drivers changes across distance has not been as intensively investigated. McGill (2010) provided a framework of a more specific switch among causes, with biotic interactions, local habitat, climate, and dispersal changing in their relative importance along a lineal gradient of spatial scale (i.e., increasing distance) from submeter to global.

Despite its importance, few studies have addressed the framework of how the relative importance of drivers changes with lineal distance as proposed by McGill (2010). Instead, most examinations of environmental difference and geographic distance have done so at a single scale (e.g., Fluck et al., 2020; Stehn & Roland, 2018) or compared regions (e.g., Bahram et al., 2013; Qian & Ricklefs, 2007). Those that did address distance gradients took an indirect approach by changing the grain of analysis (Keil et al., 2012, for multiple taxa across Europe; Kadowaki & Inouye, 2015, in an experimental fungivorous community; Batista et al., 2021, for Atlantic Forest bats). More directly, Cáceres et al. (2014), using Mantel correlograms, reported that distance decay was most important at middle distances for birds and mammals in southwestern Brazil. However, none of these studies directly examined the relative importance of distance versus other drivers of beta diversity as distance increased.

In this study, we examined the beta diversity (i.e., the turnover in community composition), of the alpine grasslands of 23 mountain regions of southern and central Europe (south of 50° N). In addition to inter-range distances of 95–3300 km, the study area has notable variations in precipitation, temperature, and seasonal differences that reflect differences in Mediterranean and mid-latitude climates. Moreover, alpine grasslands are more sensitive to climate than more topographically controlled alpine communities (Berauer et al., 2019). However, the ecological patterns of plant communities are contingent on their history and geography (cf. Ricklefs et al., 1999). Indeed, the diversity of alpine plant communities is contingent on their development from refugia at the last glacial maximum (LGM) (e.g., Dullinger et al., 2012; Normand et al., 2011; Schönswetter et al., 2005; Tordoni et al., 2020). Additionally, calcareous and siliceous substrates have been identified as distinct habitats for European alpine vegetation (Gigon, 1987; Michalet et al., 2002; Pittarello et al., 2017), and the differences may affect responses to climate change (Alvarez et al., 2009; Niklas et al., 2021). These constraints are seen in differences in interpretations among studies (e.g., Chalmandrier et al., 2017; Lenoir et al., 2010).

We hypothesized that the relative importance of different drivers in explaining beta diversity will change across spatial scales (Figure 1). Specifically, we expected that climatic difference would be relatively more important than dispersal limitation in describing the similarity of regional species pools (i.e., all species observed in the alpine grassland habitats of the 23 mountain ranges) at shorter distances (i.e., <1000 km), while, except for successional sequences, dispersal limitation would be increasingly important as the distance increases up to interprovincial differentiation at global scale (but here at >2000 km). We assumed that distance is a surrogate for dispersal limitation (cf. Langenheder & Lindström, 2019; Qian & Ricklefs, 2012), and we examined the similarity of pairs of regions relative to climatic differences and
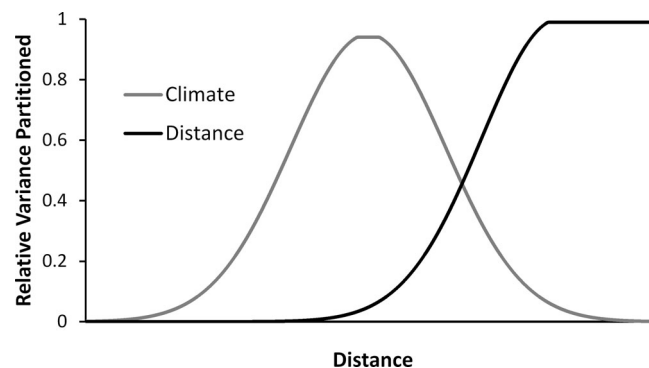
FIGURE 1 The form of the hypothesized switch in contribution to variance in beta diversity explained by variables representing climatic difference and dispersal limitation at increasing distance between observations (cf. McGill, 2010). The distance units are not specified because the relationship will change among biological systems and geographical regions

distance at increasing increments of distance between pairs of regions.

## METHODS

Location and data

We analyzed species pools in the alpine habitats of 23 mountain regions in southern and central Europe (Figure 2). These data were prepared by Jiménez-Alfaro, Abdulhak, Attorre, Bergamini, Carranza, Chiarucci, Ćušterevska, et al. (2021) and Jiménez-Alfaro, Abdulhak, Attorre, Bergamini, Carranza, Chiarucci, Ćušterevska, Dullinger, et al. (2021) using 16,804 relevés (vegetation plots) that were above local treeline and further screened to eliminate those of wetlands, rock outcrops, and early seral stages to focus on alpine grasslands. All relevés are stored in the European Vegetation Archive (Chytrý et al., 2016). We used taxonomic data rather than phylogenetic or functional differences, which can provide different insights (e.g., Zhang et al., 2013) because it is more complete in our region and involves fewer choices (cf. Testolin, Carmona, et al., 2021). For these legacy data, the sampling intensity in the 23 regions was not strictly even. However, for our purposes, it is important that the sampling captured close to 100% of the species, which was demonstrated by Jiménez-Alfaro, Abdulhak, Attorre, Bergamini, Carranza, Chiarucci, Ćušterevska, Dullinger, et al. (2021) and further supported in preliminary analyses (Appendix S1).

We divided the relevés by whether the vegetation indicated calcareous or siliceous substrates. Preliminary analyses with the substrates combined revealed a weak relationship of similarity with distance and environmental difference in simple multiple regression ($R^2 = 0.06$; Appendix S1). Accordingly, we divided regional species pools into calcareous and siliceous subsets—except for Corsica, which is only siliceous, and the Northern Iberian Range, which we excluded from the calcareous group because only two relevés were so identified and the range is primarily volcanic in origin. We used TWINSPAN (Two-Way Indicator Species Analysis; Hill, 1979) as a divisive classification method. Following the phytosociological interpretation of data collectors, the division by TWINSPAN matched assignment to a substrate in the original data for 87% of plots from the calcareous group and 97% of the siliceous group. TWINSPAN classification was also consistent with an expert-based system used for the classification of European habitat types (Chytrý et al., 2020), in which 74% and 94% of the plots from TWINSPAN groups 1 and 2 were assigned to calcareous and siliceous bedrocks, respectively. From these data, we derived regional species presence.

To sample climate data for the regions, we excluded 1146 of the relevés because the recorded elevations differed by more than 500 m from the GTOPO30 DEM; this position error would lead to erroneous climate attributions. We then identified 4098 unique 30-arcsecond grid cells (c. 1 km) within which one or more of the 15,658 relevés were located based on recorded latitude and longitude floored at two decimal places. We extracted 19 bioclimatic variables from CHELSA (Climatologies at High Resolution for the Earth's Land Surface Areas; Karger et al., 2017, 2018) for each cell. We discarded the monthly variables for high and low temperature and precipitation because they are highly correlated with the quarterly variables; we discarded the temperatures for the wettest and driest quarters because slight differences in precipitation in a single month can switch an observation season; and we further reduced the data to five temperature and five precipitation variables by eliminating isothermality and temperature and precipitation seasonality, which are less meaningful biologically. This left 12 bioclimatic variables for further analyses.

The geographic distance among regions was based on the cost-distance estimates provided by Jiménez-Alfaro et al. (2021; see their appendix S4) for the same mountain regions. These distances, in kilometers, were generated by weighting cells by elevation and computing minimum distances with these weights. These distances reflect the most plausible dispersal routes at intermediate elevations, excluding artifact total distances across the sea, as a proxy for both historical and recent dispersal events (Jiménez-Alfaro, Abdulhak, Attorre, Bergamini, Carranza, Chiarucci, Ćušterevska, Dullinger, et al., 2021).
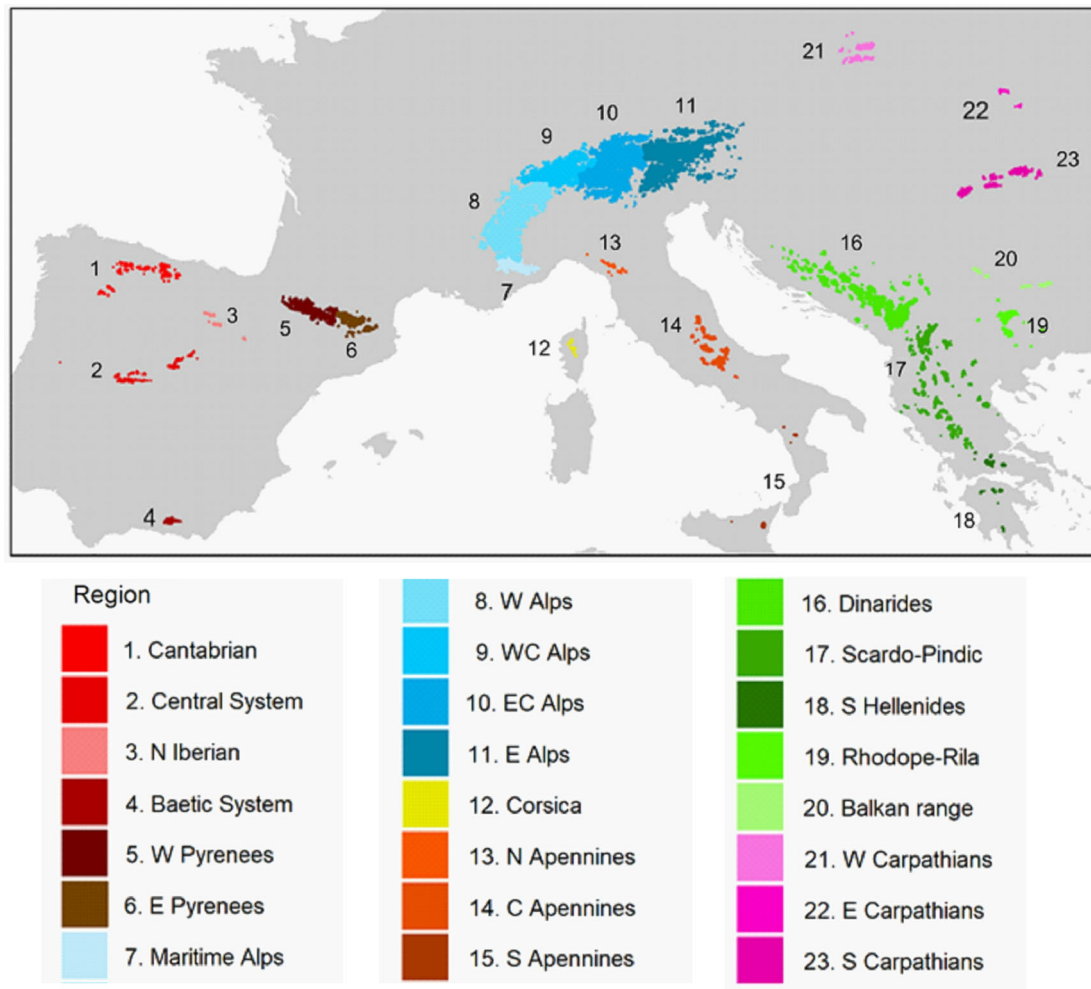
FIGURE 2 Location and extent of the 23 alpine regions of southern and central Europe

Analyses

To assess the relative importance of climate and distance at different spatial scales, we examined *similarities* among regions relative to the *differences* in their climate and the *distances* between them. For difference/distance relationships, we expected a constraining relationship rather than one underlying driver of the process. We calculated the Beta-Simpson (Bsim; β_{sim} in Baselga & Laprieur, 2015) index of similarity between pairs of regions using 'betapart' (Baselga & Orme, 2012). Beta-Simpson captures the turnover or replacement component of the Sorenson index of similarity; being a useful indicator of beta diversity because it minimizes differences due to richness (Baselga & Laprieur, 2015). We did not analyze the nestedness component of similarity because it should not be informative when the sampling units are spatially separated, and in preliminary analyses, it had no relationship with distance (Appendix S1).

Choosing a single climatic indicator that best accounts for the compositional similarities among the regions minimizes bias toward a distance-based explanation. Therefore, we used principal components analysis (PCA) of the 12 selected climate variables (PC-ORD v.7, McCune & Mefford, 2016) for the 4098 cells. We calculated the differences among the centroids of the regions determined from the cell scores on the axes with significant ($p < 0.0001$) eigenvalues determined by comparison to randomizations.

Topographic diversity could also affect the compositional turnover between regions. It is reasonable to suppose that more topographically rugged regions (e.g., the Alps vs. the Apennines) may harbor more microhabitats (cf. Dagnino et al., 2020), which could affect beta diversity. To assess the role of topography on defining patterns of beta diversity, in preliminary analyses, we examined regressions of Bsim with the differences in maximum and range in elevation among the relevés for each region (these ranged from 2040 and 420 m in the northern Apennines to 3370 and 1220 m in the Baetic system and the east-central Alps). No relationship between topographic

complexity and beta diversity was evident ($R^2 < 0.01$ or less, $p > 0.10$ for both substrates), and it was not considered further. Likewise, Bsim was not related to the difference in the size of the regional species pools in univariate regressions ($R^2 < 0.01$, $p > 0.20$ for calcareous substrate and $R^2 < 0.02$, $p > 0.03$ for siliceous substrate).

We first examined the decay in similarity with distance for Bsim on both types of substrate because this approach has been informative in the past (e.g., Nekola & White, 1999; Soininen et al., 2007). We determined the best-fitting simple function for this relationship by comparing linear, exponential, and cubic polynomial functions with the Akaike information criterion corrected for small sample sizes (AIC$_c$). In preliminary analyses, no relationship of decay in Bsim with the differences in climatic variables was evident over the full range of distance (Appendix S1), and we did not consider these further. The distance-decay analysis, however, did not address the question of whether explanation changes with scale, and to that end, we divided the distance gradient into increments and partitioned the variance in regressions.

In sequential analyses, we increased the distance in equal increments to assess the importance of distance relative to climatic variables in determining community similarity. With the shortest and farthest distance at 95 and 3306 km (in cost-distance), we examined 10 increments of increasing distance: 95–417, 95–738, 95–1059, 95–1380, 95–1701, 95–2022, 95–2343, 95–2664, 95–2985, and 95–3306 km. This approach differs from distinct bins in Mantel correlograms that are sensitive to bin boundaries. We modeled the change in similarity with distance with a negative exponential function and with a cubic polynomial function. The former is most common in theory and observation (Antão et al., 2019); however, McGill (2010) suggested that the role of distance may increase at the longest distances.

To assess the relative importance of climate and distance as the distance increments increased, we used commonality analysis because it partitions the variance in regressions such that unique and shared variance components are revealed and thus the contributions of distance and climate can be disentangled (Ray-Mukherjee et al., 2014); many of the studies cited above comparing environmental difference and distance effects on beta diversity used other regression-based or Mantel correlation-based methods to partition variance. Commonality analysis also reveals suppressor variables, which are more common in shared contributions. We regressed Bsim of all regional pairs in all distance classes on the two independent variables and both variables individually (distance between the centroids in PCA of climate variables and cost-distance; except at the shortest distance increment and for climate on calcareous substrate at the

second increment, all regressions had $p < 0.01$ as determined by randomization tests where Bsim was permuted). We then determined the unique and shared proportions of variance explained. We used adjusted R^2 as a measure of variance explained and set this to zero for all regressions with nonsignificant F ($p > 0.01$), based on comparisons with randomizations. For graphical display of the commonality analysis results, we show the total variance partitioned to each of the two independent variables by summing their unique contribution with 1/2 of their shared contributions; this apportionment is an approximation because the shared variance cannot be further divided.

Although examining change in the importance of distance on a gradient of distance is the common structure for distance-decay analyses, it might not be the most rigorous test given that distance and environmental gradients may not be the same. As a guardrail for the main analyses, we examined the pattern of explanation of Bsim over a gradient of increasing difference in climate, and we determined whether distance remained an important predictor. The commonality analysis paralleled that for the distance gradient, but we used 10 increments of increasing difference between the centroids of the regions in climatic PCA space instead of geographic distance.

RESULTS

Climatic difference

The variables reveal substantial differences in bioclimates among the 4098 cells (maximum difference of >15° and >800 mm in growing season temperature and precipitation) and differentiate the mid-latitude and Mediterranean regions (Appendix S2: Table S1). Three PCA axes were significant based on calculated eigenvalues compared to randomizations, and they accounted for 33%, 27%, and 17% of the variance (Appendix S2: Table S2). The eigenvectors were correlated with both temperature and precipitation gradients: the first with those of hot quarters, the second with those of cold quarters, and the third with their seasonality (Appendix S2: Table S3).

Distance decay

Similarity declined with distance (Figure 3). Distance decay could be fitted with a negative exponential function that was in the same range as reported by Antão et al. (2019) as a general result across taxa and resolutions. However, model selection using AIC$_c$ indicated that a polynomial fit was more parsimonious and better met model assumptions, with AIC$_c$ weights 11 and 2 times higher than those for

exponential models (Appendix S3: Table S1). The cubic polynomials improved the least-squares fit because the slope of decay appears to accelerate rather than become level at the longest distance (Figure 3).

Variance partitioned

The pattern of explanation of Bsim by climatic difference and distance over increasing distances differed between substrates (Appendix S3: Tables S1,S2,S3). Distance explained more of the variation in Bsim than did the difference in climate at all distances on calcareous substrates. Moreover, the proportion explained by distance increased at longer distances between regions (Figure 4a; Table 1). The contribution of distance rose with distance except for leveling or decline at approximately 1600–2400 km, which is related to the form of the distance decay (Figure 3). The explanation by climate peaked at intermediate, but still long, distance. On siliceous substrate, the explanation by climate difference was greater than that by distance at <1400 km with a peak at 95–738 km (Figure 4b). Distance had a minor suppression effect at the shortest distance increment, wavered, and

then increased consistently above 1000 km. Most of the contributions of distance and climatic differences were unique (Table 1).

Changing the analytical framework to gradients of climate difference revealed consistent greater explanation by distance, not climate difference, although they became more similar at greater differences (Appendix S1: Table S3). The two substrates had similar patterns (Figure 5; Table 2). These results indicate that the importance of distance in explaining the variance in Bsim is not simply an artifact of using a distance gradient.

DISCUSSION

Environmental difference versus dispersal limitation

We assessed whether the proportions of explanation of beta diversity by climatic difference and dispersal limitation changed with increasing distance in the alpine vegetation of southern and central Europe. Dispersal limitation, using distance as a surrogate measure, explained most of the variation in beta diversity, but the
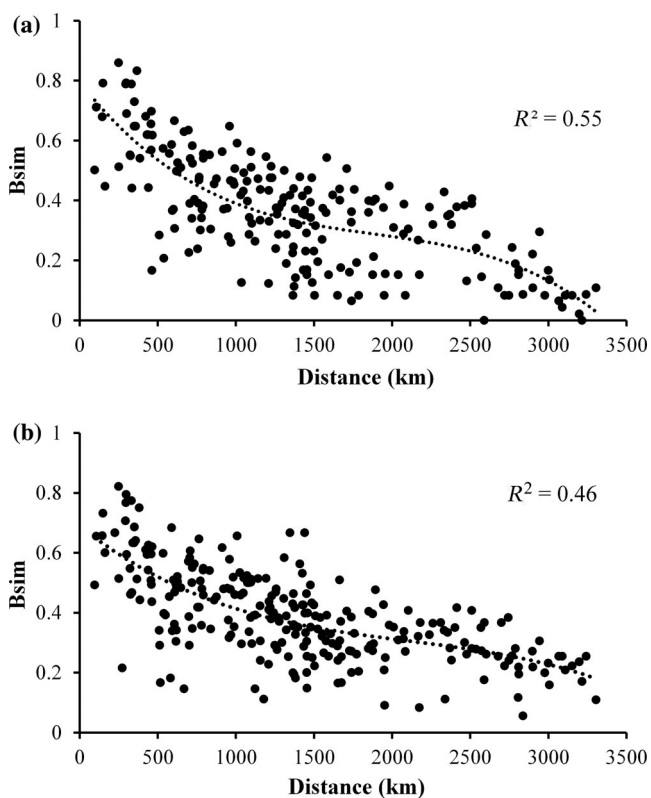
FIGURE 3 The distance decay of similarity (Bsim) for the calcareous (a) and siliceous (b) observations, with modeled cubic functions
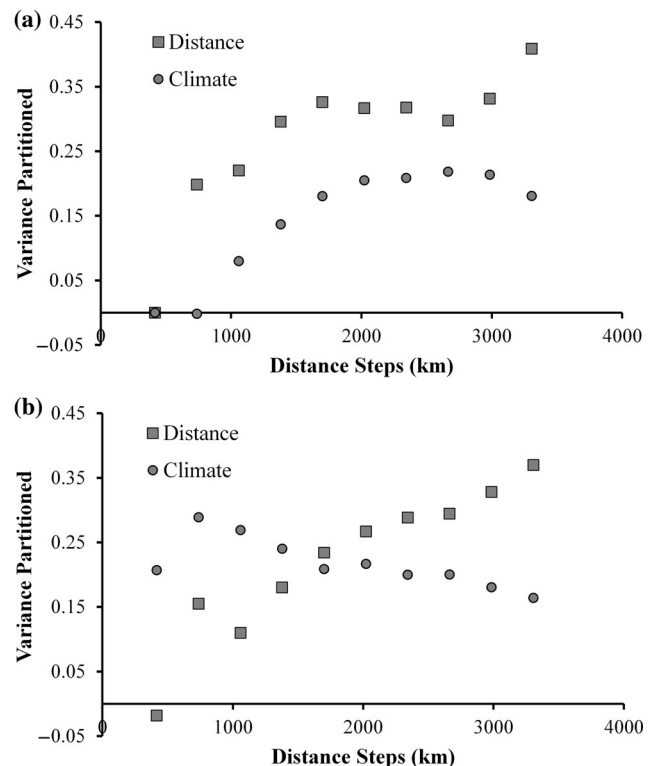
FIGURE 4 The sum of the unique and proportions of the shared explained variances partitioned in commonality analysis to climate and distance variables at incrementally increasing distances; (a) calcareous and (b) siliceous substrates

TABLE 1 Results of commonality analysis partition of variance of the explanation of Beta-Simpson (Bsim) on calcareous and siliceous substrates for the unique contributions of distance, climatic difference, and their shared portion at increasing extents (zero if regressions were all nonsignificant)

| Contributors	Distance (km)									
	95–416	95–737	95–1058	95–1379	95–1700	95–2021	95–2342	95–2663	95–2984	95–3305
Calcareous										
Distance	0	0.197	0.181	0.231	0.238	0.230	0.245	0.229	0.237	0.323
Climate	0	−0.003	0.041	0.073	0.093	0.119	0.136	0.150	0.119	0.095
Shared	0	0.003	0.078	0.129	0.176	0.173	0.146	0.137	0.190	0.171
Siliceous										
Distance	−0.036	0.094	0.083	0.130	0.163	0.193	0.230	0.246	0.273	0.323
Climate	0.189	0.229	0.242	0.190	0.137	0.142	0.141	0.151	0.125	0.117
Shared	0.036	0.121	0.054	0.101	0.143	0.149	0.117	0.098	0.111	0.094
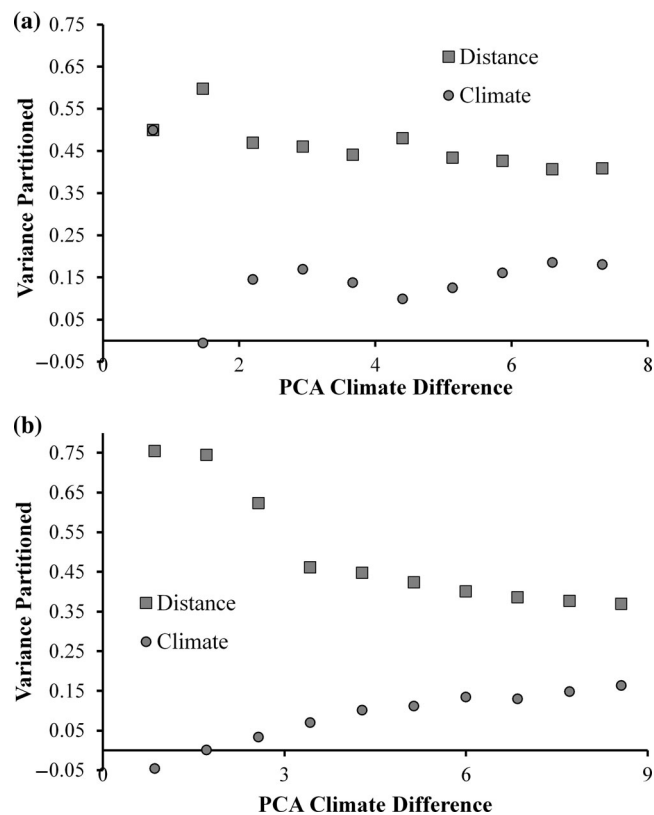
FIGURE 5 The sum of the unique and proportions of the shared explained variances partitioned in commonality analysis to climate and distance variables at incrementally increasing climatic difference represented by distance among regional centroids in three principal components analysis (PCA) dimensions; (a) calcareous and (b) siliceous substrates

pattern differed between the calcareous and siliceous substrates. For the range of distances that we examined, the climatic difference had a unimodal pattern of explanation, but it exceeded the explanation of geographic distance at shorter distances only on the siliceous substrate.

The explanation contributed by geographic distance increased over the range of distances. Our hypothesis, as represented in Figure 1, was thus partly supported. The change in relative explanation between climatic difference and geographic distance elucidates the framework proposed by McGill (2010) by directly addressing a hypothesis based on a gradient of distance.

The cubic polynomial revealed that the distance decay of similarity was steeper at the shortest distances and again at the longest ones. Similarly, the response of explained variance changed more at either end of the distance gradient. At short distances, the effect of isolation among neighbors within larger groupings (e.g., the Alps) is already evident. At middle distances, stepping-stone regions exist in various directions, which reduces the increase in isolation. At the longest distances, the potential acceleration in the explanation of Bsim, which was more definitive on calcareous substrate, indicates the effects of dispersal limitation separating the distant regions over a longer period. An alternative explanation is that the closer alpine areas of Western Europe may have been less isolated or shared refugia at the LGM, and so are now more similar than the current distance would represent.

Our finding of the importance of dispersal limitation on a gradient of distance agrees with that of Dullinger et al. (2012), who showed that the spatial distribution of alpine species is strongly determined by dispersal limitation even within a single region such as the Eastern Alps, and with that of Jiménez-Alfaro, Abdulhak, Attorre, Bergamini, Carranza, Chiarucci, Ćušterevska, Dullinger, et al. (2021), who reported effects of isolation on alpha diversity for our 23 mountain regions. The results are also consistent with a greater determination of alpine plant species richness by spatial factors than by the macroclimate as reported by Testolin, Attorre, et al. (2021) for global ecoregions.

TABLE 2 Results of commonality analysis partition of variance of the explanation of Beta-Simpson (Bsim) on calcareous and siliceous substrates for the unique contributions of distance, climatic difference, and their shared portion at increasing climatic difference (using as the gradient the range of distances between the centroids of the regions in the volume of the three significant eigenvectors of PCA of the climate variables; zero if regressions were all nonsignificant)

Contributors	Climate difference (PCA space)									
	0–0.73	0–1.47	0–2.20	0–2.93	0–3.67	0–4.40	0–5.13	0–5.86	0–6.60	0–7.33
Calcareous										
Distance	0	0.593	0.370	0.356	0.396	0.439	0.382	0.342	0.313	0.323
Climate	0	−0.011	0.045	0.064	0.093	0.058	0.073	0.077	0.091	0.095
Shared	0	0.011	0.200	0.210	0.090	0.083	0.105	0.169	0.189	0.171
Siliceous										
Distance	0.709	0.746	0.586	0.422	0.411	0.378	0.329	0.333	0.330	0.323
Climate	−0.092	0.003	−0.004	0.031	0.065	0.066	0.063	0.077	0.101	0.117
Shared	0.092	−0.003	0.075	0.078	0.073	0.092	0.144	0.106	0.096	0.094

Abbreviation: PCA, principal components analysis.

System constraints

At LGM, many of these regions would have had nearby refugia with continuous distributions of alpine climate and related vegetation that are now isolated at higher elevations (Schönswetter et al., 2005). However, the spatial relationships and species pools would have differed, thus individualizing their influences on current alpha and beta diversity (Médail & Diadema, 2009). For example, Tordoni et al. (2020) found that the effects of refugia on current patterns of alpha and beta diversity differed among ranges in the southeastern Alps. The influence of refugia requires further investigation.

Our results contrast with—but do not contradict—the conclusion of Normand et al. (2011) that dispersal limitation was secondary to climatic effects in the postglacial structuring of European vegetation. This may be explained by the limited range of low-temperature conditions in alpine systems (Körner, 2003; Testolin et al., 2020). However, alpine systems may be a useful contrast of distance and climate effects because they occupy much of the global range of precipitation (Testolin et al., 2020) (our precipitation data span 500–3000 mm annually at 1-km cell resolution, given the inclusion of both mid-latitude and Mediterranean climates) and alpine plants appear to be sensitive to temperature differences (Fazlioglu & Wan, 2021).

Our focus was on distance, but because we divided the observations between calcareous and siliceous substrates, we can report on differences for two distinct alpine habitats dominated by different species pools. The substrates correspond to edaphic differences (e.g., Adamczyk et al., 2019; Boscutti et al., 2014; Škornik et al., 2021), but their effects are at the habitat and biotic interaction scales in McGill's (2010) framework. In forest vegetation, drought-intolerant species grow better on siliceous than calcareous substrates (Michalet et al., 2002), which could reduce sensitivity to climatic differences. The stronger role for distance as an explanatory variable on the calcareous substrates may be related to glacial and postglacial history because both glaciation and refugia on the calcareous substrates were more widespread than those on the siliceous substrates at LGM (Schönswetter et al., 2005). The larger species pool and potentially higher endemism on the calcareous substrates would also contribute to the steeper distance decay and a greater role for distance in beta diversity. Further study of the geographic distributions of these substrates is needed.

Caveats and conclusions

We did not examine beta diversity within regions because many of the relevés co-occur with others in the same 1-km^2 cell, and we did not include biotic interactions or habitat variables, which are not well-differentiated at the regional scale. At the shorter distances conceptualized by McGill (2010), Scherrer et al. (2019) differentiated biotic interactions and habitat filtering in spatial coexistence within local (4 m^2) plant communities, and Usinowicz and Levine (2021) found that competition negated climate amelioration among alpine species. Although numerous studies have identified differences in plant community composition in response to variation in alpine habitat, often in relation to the topography (e.g., Jiménez-Alfaro et al., 2014; Malanson et al., 2012), topographic complexity is an indicator, not a driver, of plant community composition and thus does not fit in the conceptual

framework of changing drivers on a gradient of distance. Furthermore, Chauvier et al. (2021) reported that differences in land use affected the distributions of individual species in the Alps, and land use in alpine habitats could vary both within and among regions. It is also likely that ecological patterns other than taxonomic beta diversity, such as those of functional traits, will have different scaling relations with climate and dispersal limitation (e.g., Ndiribe et al., 2014; Zhang et al., 2013).

The forms of distance decay and explanation of beta diversity over distance among mountain ranges of southern and central Europe indicate that the relative importance of climatic constraints and dispersal limitation depends on the isolation of the ranges, but the processes are mediated by the differences among substrates. More information at finer scales, between those of Scherrer et al. (2019) and this study, could reveal additional effects of climate or add habitat effects as proposed by McGill (2010). The importance of dispersal limitation seen here implies that plant community composition and diversity may not be in equilibrium with a continually changing climate and that the effects of future climate changes will be difficult to anticipate (cf. Malanson et al., 2019).

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
All authors with the exception of George P. Malanson, Elizabeth R. Pansing, and Riccardo Testolin contributed original data to EuroVeg. The problem was conceived and the data analyzed by George P. Malanson and Elizabeth R. Pansing, with advice from Riccardo Testolin and Borja Jiménez-Alfaro. The manuscript draft was written by George P. Malanson, and all authors contributed to revisions and the submitted draft.

DATA AVAILABILITY STATEMENT
The vegetation data (Jiménez-Alfaro, Abdulhak, Attorre, Bergamini, Carranza, Chiarucci, Ćušterevska, et al., 2021) are available from Dryad: https://doi.org/10.5061/dryad.0cfxpnw1h. The climate data (Karger et al., 2018) are available from Dryad: https://doi.org/10.5061/dryad.kd1d4. Derived data (a table of beta similarity, distances, and climatic differences; Malanson and Jiménez-Alfaro, 2022) are available from Dryad: https://doi.org/10.5061/dryad.8w9ghx3nz.

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