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Research

Climatic filtering and temporal instability shape the phylogenetic diversity of European alpine floras

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Alpine ecosystems are hotspots of biodiversity despite their cold climates. Here we investigate spatial patterns in the phylogenetic diversity (i.e. the degree of species relatedness) of European alpine floras and quantify the influence of climatic conditions since the late Pleistocene and historical climatic instability in shaping these patterns. We collected species-pool data for 22 alpine regions in central and southern Europe and calculated phylogenetic diversity within and between regions using two metrics sensitive to terminal branching in the phylogeny. We regressed phylogenetic diversity against macroclimatic variables representing seasonal extremes between the Last Glacial Maximum (LGM; 21 000 years BP) and the present at 1000-year intervals. We found the lowest phylogenetic diversity in the Carpathians and the central Alps, and the highest in the north-eastern and southern Iberian Peninsula. Phylogenetic diversity decreased with temperature seasonality and low winter temperature. While the effect of temperature seasonality was relatively constant over time, the influence of winter temperature decreased after the LGM. We also found that phylogenetic diversity decreased with historical climatic instability. Between regions, phylogenetic diversity was mainly explained by current climatic distance rather than geographic distance, suggesting that alpine floras were primarily driven by species sorting along climatic gradients. Our results confirm the role of environmental filtering in shaping the current phylogenetic diversity of alpine floras, resulting in more closely related lineages in regions with relatively cold and unstable climates. We also highlight the importance of explicitly incorporating climatic variation through time to better understand the processes structuring the current biodiversity of alpine floras.

Keywords: alpine grasslands, angiosperms, high mountains, Holocene, macroecology, Pleistocene

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Introduction

Alpine habitats represent the outpost of plant life in the mountains between the tree and snow lines (Körner 2021). Present-day biodiversity in alpine habitats results from the combined effects of ecological and evolutionary processes that occurred mainly during the late Tertiary and Quaternary (Kadereit et al. 2004). While alpine species are exposed to extreme environmental stress, including low temperatures and infertile soils, past diversifications and adaptations have determined the patterns of ecological strategies across their phylogeny (Nagy and Grabherr 2009, Körner 2021). Ecological and evolutionary processes are recognized as drivers of contemporary assemblages in alpine floras (Jiménez-Alfaro et al. 2021a, Testolin et al. 2021), but we still lack a clear picture of how these processes interact to determine the phylogenetic diversity (i.e. the degree of species relatedness) of these floras across broad geographical scales.

The diversity and composition of alpine floras are related to a variety of biogeographic processes, from historical climatic fluctuations (including glaciation and deglaciation cycles) to species dispersal routes and allopatric speciation events that occurred mainly during the Pleistocene (2.6 Ma–11.7 ka BP) (Schmitt 2009, Muellner-Riehl et al. 2019, Körner 2021). Glacial periods caused the extinction of cold-sensitive species that occasionally found refuge in suitable habitats, such as ice-free glacier margins, deep valleys or *nunataks* (Hewitt 1999, Pan et al. 2020). Furthermore, interglacial warming led to local extinctions of cold-adapted species due to physiological constraints and the expansion of forests and more competitive species (Birks 2008, 2019). Climate warming after the Last Glacial Maximum (LGM; ~21 ka BP) triggered upward shifts of cold-adapted species (Birks and Willis 2008) and, at the beginning of the Holocene (~11.7 ka BP), alpine habitats reached similar extents as today (Tinner and Theurillat 2003). Environmental constraints during the Holocene ultimately shaped current taxonomic similarities among alpine regions (Jiménez-Alfaro et al. 2021a). However, we do not know to what extent macroclimatic constraints since the late Pleistocene explain the phylogenetic diversity of the present-day alpine floras.

Patterns of phylogenetic diversity of contemporary biotic assemblages are expected to reflect niche-based species dynamics (Webb et al. 2002). At large spatial scales, strong environmental filtering can lead to patterns of phylogenetic clustering (i.e. low phylogenetic diversity) (Qian and Sandel 2017, Lososová et al. 2021) if closely related species retain their niche-related traits (Wiens and Graham 2005). At finer spatial scales and in the presence of niche conservatism, facilitation between close relatives (Sargent and Ackerly 2008) or competitive hierarchy (Mayfield and Levine 2010) can also entail phylogenetic clustering, whereas biotic interactions can lead to phylogenetic overdispersion (i.e. high phylogenetic diversity) (Webb et al. 2002). However, niche conservatism is not always the rule, as ecological convergence among distantly related species can occur due to adaptation to similar environmental conditions (Freckleton and Jetz 2009). Patterns of phylogenetic diversity can also reflect geographical isolation (Weigelt et al. 2015), speciation (Guevara et al. 2016) and migration (Feng et al. 2014), making it challenging to generate predictions at large spatial scales.

Although alpine ecosystems are exposed to low temperatures globally, seasonality and continentality differ substantially among regions (Testolin et al. 2020). Harsh environmental conditions in alpine regions constrain the range of ecological adaptations of plants (Kraft et al. 2015). If niches are fully conserved in the phylogeny, only specific lineages with inherited adaptations will occur in alpine regions with harsher environmental conditions (e.g. summer drought), leading to phylogenetic clustering (Webb et al. 2002). Conversely, more benign environmental conditions (e.g. lower seasonality) should result in greater niche differentiation and promote a greater diversity of lineages (phylogenetic overdispersion) with a broader range of adaptations. Furthermore, paleoclimatic stability may promote diversification across geological time scales and support the persistence of specific lineages (Eiserhardt et al. 2015). More climatically unstable alpine regions, such as those covered by ice sheets during the LGM, contain species that were able to recolonize after local extinctions (Kissling et al. 2012). Therefore, higher climatic instability should also lead to phylogenetic clustering if niches are conserved across the phylogeny. Conversely, more stable alpine regions should comprise a mixture of distantly related taxa, which could diversify to occupy a broader range of environments and persist longer over evolutionary time.

Patterns of phylogenetic diversity within alpine regions (i.e. gamma-diversity) can be complemented by examining the shared evolutionary history between alpine regions (i.e. beta-diversity) (Swenson 2011). Large-scale patterns of between-region phylogenetic diversity can be explained by environmental differences and geographic distances, which reflect past and present environmental filtering and dispersal limitations, respectively (Nekola and White 1999, Qian et al. 2020). If environmental filtering acts on phylogenetically conserved niches adapted to contrasting environmental conditions, then phylogenetic diversity between alpine regions should be low (i.e. high lineage turnover) (Jin et al. 2015). Conversely, if closely related species have different climatic and habitat preferences, then phylogenetic diversity between alpine regions should be high (i.e. low lineage turnover). Consequently, studying patterns of phylogenetic diversity between alpine regions offers multiple opportunities to elucidate the processes behind contemporary patterns of biodiversity.

Here we describe spatial patterns in the phylogenetic diversity of European alpine floras (within and between regions) and examine the role of environmental filtering since the LGM in shaping these patterns. Besides the expected impact of past climatic constraints on present-day phylogenetic diversity, we also evaluate the legacy effects of different post-glacial periods, assuming that past climates exerted stronger constraints on plant diversity than contemporary climates through selective extinction or recolonization (Eiserhardt et al. 2015). By analyzing legacy effects on present-day phylogenetic diversity, we may be able to estimate when major changes in the distribution of alpine floras occurred. We hypothesize that strong environmental selection pressures and historical climatic instability have played an important role in shaping the present-day phylogenetic diversity of European alpine floras (Weiher and Keddy 1995, Jablonski et al. 2006, Kissling et al. 2012). Specifically, we aim at 1) quantifying the phylogenetic diversity of alpine floras in central and southern Europe and 2) examining how phylogenetic diversity relates to changes in macroclimate since the LGM and historical climatic instability.

Material and methods

European alpine floras

We used the regional alpine floras compiled by Jiménez-Alfaro et al. (2021b) for central and southern Europe. The dataset consists of complete lists of vascular plants sampled in alpine habitats (above the tree line) in 23 mid-latitude mountain regions (Fig. 1; Supporting information). These regions share a common biogeographical history with glacial–interglacial cycles that caused similar distributional shifts and local extinction processes, leading to the isolation and speciation of related species lineages (Nagy and Grabherr 2009). Original data come from vegetation databases integrated into the European Vegetation Archive (EVA; Chytrý et al. 2016), representing the regional diversity of alpine grasslands (for more details on data collection, cleaning and attributes, see Appendix S1 in Jiménez-Alfaro et al. 2021a). The authors classified the species lists into alpine specialists (species restricted to alpine habitats) and generalists (species that also occur at lower elevations). We subset the data to analyze only the regional floras of alpine angiosperm specialists, as they represent species lineages that have adapted to and evolved in alpine habitats. In total, we analyzed 791 alpine angiosperm species. Species names were standardized according to The Plant List (<www.theplantlist.org>).

Phylogenetic data

We created a phylogeny by linking the species in our dataset to the most recent mega-phylogeny for seed plants implemented in the R package 'V.PhyloMaker' (Jin and Qian 2019). This mega-phylogeny contains more than 70 000 species derived from the mega-trees produced by Zanne et al. (2014) and Smith and Brown (2018). We used the 'scenario 3' approach to add missing species (~45%) and genera (~4%) to the phylogeny. In this scenario, branch lengths of added taxa in a family are determined by placing nodes evenly between dated nodes and tips within the family. Missing species are added at the mid-point of their genus branch, and missing genera are added at the mid-point of their family branch (for details, see Qian and Jin 2016, Jin and Qian 2019). Using a phylogeny constructed under this scenario is equivalent to a phylogeny fully resolved at the species level, as long as all families and most genera are resolved (Qian and Jin 2020).

Macroclimatic data

We extracted six variables for temperature and precipitation with a resolution of 30 arc-seconds from Divíšek (2021): temperature seasonality, mean temperature of the warmest quarter (hereafter mean summer temperature), mean temperature of the coldest quarter (mean winter temperature), precipitation seasonality, precipitation of the warmest quarter (summer precipitation) and precipitation of the coldest quarter (winter precipitation). These macroclimatic variables were calculated based on the downscaled and debiased monthly temperature and precipitation simulations from the community climate system model ver. 3 (CCSM3; Collins et al. 2006) as provided by the PaleoView software (Fordham et al. 2017). The downscaling procedure was based on the delta-change method (Ramirez Villejas and Jarvis 2010). As baseline climatic data, the dataset uses monthly temperature and precipitation grids for 1940–1989 from the CHELSA database (Karger et al. 2017). A detailed description of the dataset, including the downscaling method used, can be found in the technical specification of the dataset (Divíšek 2021). We downloaded each variable for 22 time windows between the present-day and the LGM (21 ka BP) at intervals of 1000 years. We selected these variables to account for maximum climatic variation among alpine regions and the effects of seasonal extremes.

For each raster layer, we extracted data that corresponded to the current extent of the alpine regions (Supporting information). Then, we calculated the mean of all raster values within each alpine region to obtain a single measure per variable and region. We extracted the raster data using the R package 'raster' (Hijmans 2021).

Mean summer and winter temperatures and summer precipitation were strongly correlated ($|r| > 0.7$) (Supporting information). All alpine regions showed similar temporal trends for the temperature variables. Mean summer and winter temperatures increased steadily since the LGM, while temperature seasonality increased between the LGM and 17 ka BP and decreased thereafter (Supporting information). In contrast, alpine regions showed contrasting temporal trends in precipitation variables. Overall, winter precipitation generally decreased since the LGM, while summer precipitation decreased between 21 and 17 ka BP and steadily increased thereafter. Precipitation seasonality generally decreased in alpine regions since the LGM but peaked between 18 and 15 ka BP.

As a measure of historical climatic instability, we calculated the variance of each macroclimatic variable across the 22 time windows for each alpine region. Higher values of these measures indicate more unstable climatic conditions since the LGM, while lower values indicate more stable climatic conditions. We excluded temperature and precipitation seasonality from these calculations because these variables are coefficients of variation, and their temporal variance is difficult to interpret. We also excluded climatic instability, measured as the variance of summer precipitation, from subsequent analyses because this variable was strongly correlated with mean winter temperature ($r = -0.78$) and current summer precipitation ($r = 0.97$), and any association with phylogenetic diversity could be spurious. All other climatic instability variables had correlation coefficients < |0.63| with macroclimatic variables (Supporting information).

Data analyses

Phylogenetic diversity metrics

We performed statistical analyses in R ver. 4.1.0 (<www.r-project.org>). We estimated the within-region (gamma) phylogenetic diversity of the flora of each alpine region by calculating the phylogenetic mean nearest taxon distance (MNTD). MNTD is the mean branch length distance between each species and its phylogenetically nearest neighbor in the region's flora (Webb et al. 2002). For between-region (beta) phylogenetic diversity, we calculated D_{nn}, the between-assemblage analog of MNTD, which calculates the mean nearest taxon distance separating species in two regions (Swenson 2011). We calculated all phylogenetic diversity metrics using the R package 'PhyloMeasures' (Tsirogiannis and Sandel 2017).

We used MNTD and D_{nn}, which are sensitive to the variation at terminal phylogenetic levels, because we expected the signature of recent (Quaternary) processes of extinction and speciation to be stronger in young lineages (Kadereit et al. 2004, Schmitt 2009, Birks 2019). Indeed, alpine floras consist of more closely related species than the respective regional floras and include some families that have evolved tolerance to low temperatures (Qian et al. 2021) (Supporting information). Therefore, post-glacial abiotic constraints should filter ecological strategies that have diversified recently, and recent diversification should not result in large niche shifts among co-existing species (Supporting information). Nonetheless, we also report the results at deeper (or basal) phylogenetic levels in Supporting information for comparison with the results at terminal phylogenetic levels and to provide a complete picture of phylogenetic diversity patterns in European alpine floras.

Because MNTD and D_{nn} are correlated with species richness, we standardized their values (MNTD.ses and D_{nn}.ses) to make them comparable among sites (Pavoine and Bonsall 2011). To standardize the observed MNTD and D_{nn} to the values expected given the observed species richness, we first randomized the species presence/absence in the regions × species matrix, keeping species richness in the regions and species frequency across all regions, thus without changing row and column totals (Gotelli 2000). For randomizations, we used the 'Curveball algorithm' (Strona et al. 2014), which can uniformly sample the set of all possible matrix configurations and requires notably less computational effort than other available methods, allowing large matrices to be randomized quickly. Then, we recalculated MNTD and D_{nn} to obtain simulated values for these metrics. We repeated this step 999 times to get the distribution of simulated MNTD and D_{nn} values. Finally, we calculated MNTD.ses and D_{nn}.ses as (observed value − mean of simulated values)/standard deviation of simulated values. Positive MNTD.ses and D_{nn}.ses indicate higher phylogenetic diversity than under random expectation (overdispersion), whereas negative MNTD.ses and D_{nn}.ses indicate lower phylogenetic diversity than under random expectation (clustering).

The use of standardized effect sizes of MNTD and D_{nn} significantly reduces but does not eliminate the effect of species richness on these metrics (Pearson's $r = -0.2$ between MTND.ses and species richness; Pearson's $r = -0.21$ between D_{nn}.ses and differences in species richness) (Sandel 2018). Specifically, holding the strength of filtering constant, assemblages composed of more species have larger absolute index values. This bias can be eliminated by rarefying all assemblages to the lowest species richness found in the dataset, but this comes with a loss of information and increased error. We explored this possibility by sub-setting each regional pool 1000 times and calculating their average rarefied MNTD and D_{nn} values. We found that the rarefied values were strongly correlated with the standard metrics ($r > 0.7$). For simplicity and to avoid the loss of information due to rarefaction, we used the standard MNTD.ses and D_{nn}.ses values.

In a preliminary evaluation of MNTD.ses of alpine regions, we found that the Balkan range had extremely low MNTD.ses compared to the other regions (Supporting information). We found this pattern was due to the higher proportion of Poales in this alpine region compared to the other regions (Supporting information). If a particular lineage, such as Poales, is overrepresented at a given site, MNTD.ses decreases because phylogenetic distances are calculated mainly between close relatives. Therefore, we decided to exclude the Balkan range from the analyses because we could not determine whether this pattern was due to eco-evolutionary processes or preferential sampling of specific habitats or species groups (e.g. graminoids) (see Supporting information for more details).

To examine variation in lineage composition among alpine regions, we calculated phylogenetic dissimilarities (Supporting information) between sites using the Simpson-derived pairwise index (phylo-β_{sim}) in the R package 'betapart' (Baselga and Orme 2012). Phylo-β_{sim} and D_{nn}.ses are both measures of phylogenetic beta-diversity. However, while phylo-β_{sim} accounts for phylogenetic turnover (lineage replacement) between sites, D_{nn}.ses reflects species relatedness at terminal phylogenetic levels. Furthermore, phylo-β_{sim} is independent of taxon richness. We used Phylo-β_{sim} and non-metric multidimensional scaling (NMDS) to visualize phylogenetic dissimilarities between regions in three-dimensional space.

Models predicting phylogenetic diversity

Our data were spatially structured. Therefore, we used spatial simultaneous autoregressive (SAR) models (Kissling and Carl 2007) in the R package 'spdep' (*lagsarlm* function; Bivand et al. 2013) to predict MNTD.ses as a function of individual macroclimatic variables in each time window (from 21 to 0 ka BP) and historical climatic instability. SAR models account for spatial autocorrelation by adding a spatial weight matrix that specifies the neighborhood of each site and the relative weight of each neighbor. The spatial weight matrices were defined by successively fitting a SAR model and testing different distances between neighbors ranging from 100 to 500 km from a given region at intervals of 50 km.

We tested for spatial autocorrelation in the residuals of each model using Moran's *I* in the R package 'ape' (Paradis and Schliep 2019). While we found significant spatial autocorrelation in the residuals of non-spatial models (i.e. ordinary least square regressions) and SAR models with short neighboring distances (< 300 km), the residuals for SAR models with a neighboring distance ≥ 300 km did not show significant spatial autocorrelation. Therefore, we used 300 km as the neighboring distance in our SAR models. We obtained the standardized regression coefficient and error for each macroclimatic predictor in the models to compare the effects on a common scale (Zuur et al. 2007). Given our relatively small sample size, we did not introduce more than one variable at a time in the models.

We performed multiple regression on distance matrices (MRM) in the R package 'ecodist' (Goslee and Urban 2007) to predict D_{nn}.ses as a function of individual macroclimatic variables in each time window while controlling for the effect of geographic distance. We calculated geographic distance as cost distance, prioritizing mid-elevation corridors and penalizing coastal areas and the highest summits to optimize mountain dispersal routes (Jiménez-Alfaro et al. 2021a). We used 999 permutations to determine statistical significance in each regression (Legendre et al. 1994). We obtained the standardized regression coefficient and error for each macroclimatic predictor in the models to compare the effects on a common scale.

We also used generalized dissimilarity modeling (GDM) in the R package 'gdm' (Fitzpatrick et al. 2020) to separate the explained variance in D_{nn}.ses into three parts: explained uniquely by current climatic distance (considering all macroclimatic variables simultaneously), explained uniquely by geographic distance and explained by geographically structured variation in the current climate (i.e. variance jointly explained by climatic and geographic distance). GDM can accommodate the non-linearity of ecological datasets over large extents and deal with multicollinearity among predictors (Ferrier et al. 2007, Glassman et al. 2017).

Results

Spatial patterns in the regional phylogenetic structure

We found the highest phylogenetic diversity in the Iberian Peninsula, particularly in the East and West Pyrenees, North Iberia and the Baetic System (Fig. 1a). These regions contained more distantly-related lineages than other European alpine regions under a random expectation. In contrast, we found the lowest phylogenetic diversity of alpine floras in the Carpathians and the central Alps. These regions contained more closely related lineages than under a random expectation compared to other European alpine regions.

Alpine floras from the central and western Alps and the Carpathians were phylogenetically similar to each other, but consistently dissimilar from the Mediterranean alpine floras (Fig. 1b). Although some alpine regions were grouped according to major geographic areas (e.g. the Iberian Peninsula, the Alps and the Carpathians) in the ordination space, others were relatively isolated (e.g. the south Hellenides and the central Apennines).

Macroclimatic drivers of the phylogenetic diversity of alpine floras

Temperature seasonality, mean winter temperature and summer precipitation strongly influenced the phylogenetic

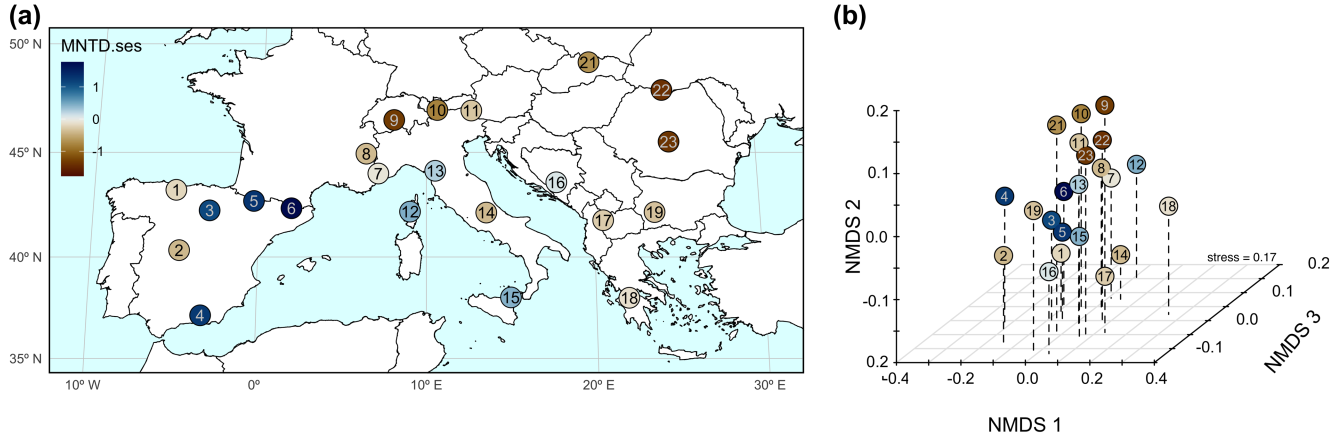

Figure 1. Spatial patterns in the phylogenetic diversity of European alpine floras (a). Positive MNTD.ses (blue) indicate high phylogenetic diversity (co-occurrence of distantly related species). In contrast, negative MNTD.ses (brown) indicate low phylogenetic diversity (co-occurrence of closely related species). Non-metric multidimensional scaling (NMDS) of alpine regions based on Simpson's pairwise phylogenetic dissimilarities (phylo-β_{sim}) (b). Colors correspond to MNTD.ses. An animated version of (b) can be found at <https://gifyu.com/image/Sx2iw>. The alpine regions are: 1) Cantabrian; 2) Central System; 3) N Iberian; 4) Baetic system; 5) W Pyrenees; 6) E Pyrenees; 7) Maritime Alps; 8) W Alps; 9) WC Alps; 10) EC Alps; 11) E Alps; 12) Corsica; 13) N Apennines; 14) C Apennines; 15) S Apennines; 16) Dinarides; 17) Scardo Pindic Mountains; 18) S Hellenides; 19) Rhodope-Rila; 21) W Carpathians; 22) E Carpathians; 23) S Carpathians (Supporting information).

diversity (MNTD.ses) of the present-day alpine floras (Fig. 2). Phylogenetic diversity was higher in areas with lower temperature seasonality, warmer winters and lower summer precipitation (Fig. 2; Supporting information). While the effect of temperature seasonality on present-day phylogenetic diversity was relatively constant over time, the effects of mean winter temperature and summer precipitation slightly increased towards the Pleistocene. Within-region phylogenetic diversity was also positively related to precipitation seasonality between 14 and 17 ka BP (Fig. 2). Historical climatic instability, measured as the variance in mean winter temperature, was negatively associated with within-region phylogenetic diversity (Fig. 3; Supporting information). This association remained significant after controlling for the effects of individual macroclimatic variables (Supporting information).

Geographical and current climatic distances together explained 65% of the variance in between-region phylogenetic diversity, measured as D_{nn}.ses (Fig. 4). Current climatic distance uniquely explained 45% of the variance in D_{nn}.ses, while geographic distance uniquely explained 4%. While the influence of summer temperature on present-day D_{nn}.ses of alpine floras was relatively constant for all periods since the LGM, we found the strongest effect of mean winter temperature between 11 and 17 ka BP (Fig. 2; Supporting information). The effect of summer precipitation on D_{nn}.ses was stronger during the Holocene, and the effect of precipitation seasonality varied considerably over time.

Discussion

Using comprehensive data on the regional distribution of alpine angiosperm plants, we revealed contrasting spatial patterns of phylogenetic diversity in European alpine regions. Variations in past and present macroclimate and historical climatic instability determined the within- and between-region phylogenetic relatedness of contemporary alpine floras. The congruence between phylogenetic diversity and climatic variation indicates that the present-day phylogenetic structure of alpine floras reflects the imprint of species assembly related to climatic preferences. Our findings also provide evidence that past climatic conditions complement current climatic conditions in shaping the diversity of European alpine floras and that these effects can be traced back at least to the Last Glacial Maximum (LGM; ~21 ka BP). We stress the need to combine phylogenetic and trait-based approaches to gain insights into the processes structuring alpine floras.

Within-region phylogenetic diversity

We found that phylogenetic clustering among close relatives was greater in the Carpathians and the central Alps than in other mountain ranges. This finding seems to be associated with larger current and historical climatic instability in these regions and consequently greater physiological stress. Increased temperature seasonality and lower mean winter

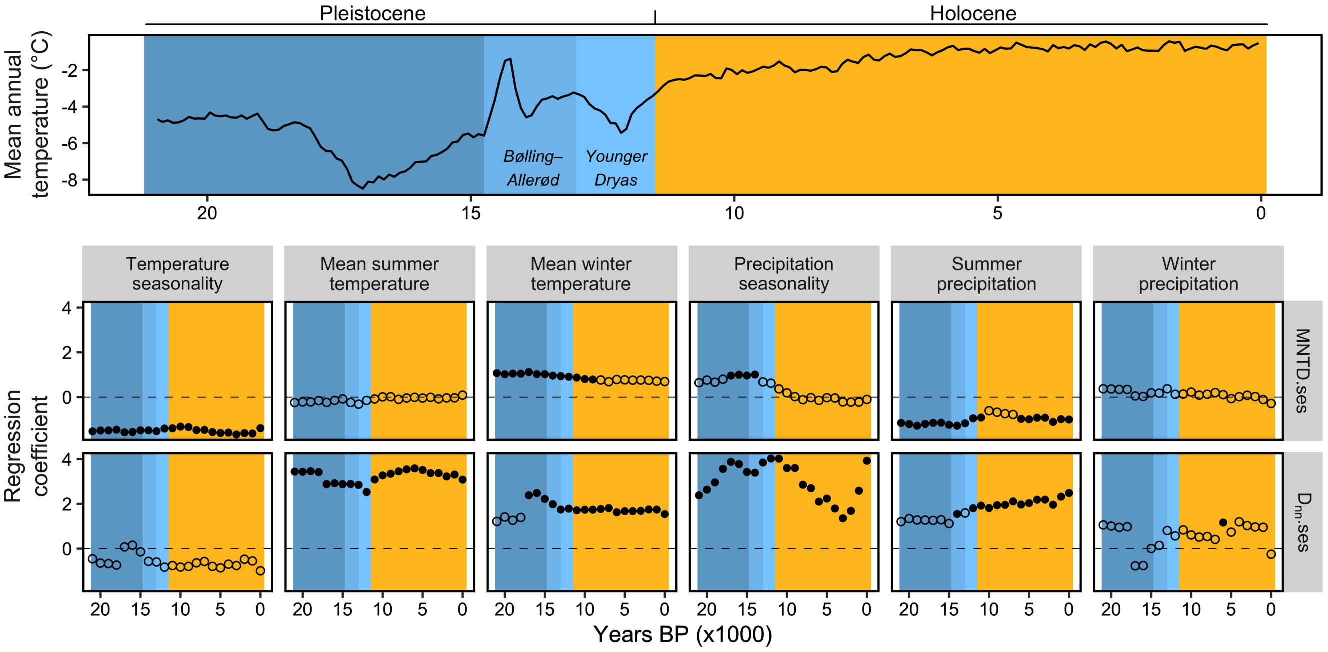

Figure 2. Influence of present-day and past climate on the phylogenetic diversity of European alpine floras. The upper panel shows the mean annual temperature across all European alpine regions based on the downscaled CCSM3 model. The lower panels show the temporal variation in the effect (i.e. regression coefficients) of different macroclimatic variables on MNTD.ses (within-region phylogenetic diversity) and D_{nn}.ses (between-region phylogenetic diversity) of alpine floras between the LGM (21 ka BP) and the present-day (0 BP). Empty and filled points show non-significant ($p \geq 0.05$) and significant ($p < 0.05$) regression coefficients, respectively. Regression coefficients for MNTD.ses derive from SAR models, and regression coefficients for D_{nn}.ses derive from MRM.

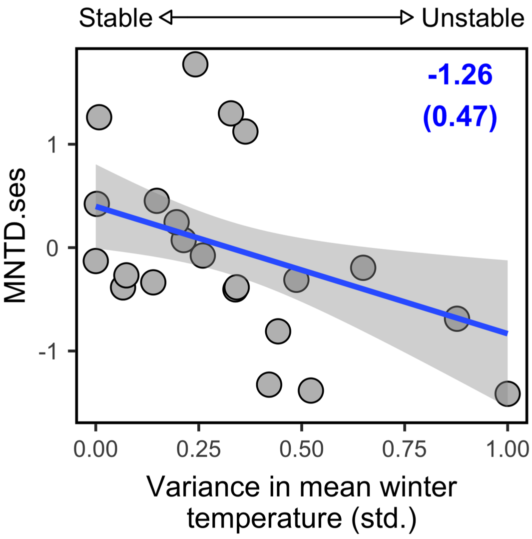

Figure 3. Bivariate relationship between historical climatic instability calculated as the variance of mean winter temperature in 1000-year time windows between the LGM (21 ka BP) and the present-day (0 BP) and MNTD.ses (within-region phylogenetic diversity) of European alpine floras. The regression line corresponds to the relationship after controlling for spatial autocorrelation. The standardized partial regression coefficient and error (in brackets) are in blue. We only show the relationship for the variable with a significant ($p < 0.05$) effect on MNTD.ses (see Supporting information for complete results). std. = standardized.

temperature may have filtered the regional pools towards a narrow set of suitable trait values of specific lineages, allowing them to cope with strong abiotic constraints. These findings point out the fundamental influence of selective environmental pressures at terminal phylogenetic levels (Webb et al. 2002, Kraft et al. 2015) and could also explain why these relatively low-diverse regions have a consistently similar phylogenetic composition.

Although our study system is characterized by relatively low temperatures (Testolin et al. 2020), mean winter temperature, which positively correlates with the length of the winter (Choler 2015), was positively associated with the phylogenetic diversity of alpine floras. However, the main influence of mean winter temperature corresponded to the LGM, with smaller effects in the following and more recent time windows. Notably, large areas in the central Alps were glaciated during the LGM, and post-glacial recolonization was reduced in some poorly dispersing and stress-intolerant lineages (Svenning and Skov 2004, Kissling et al. 2012). Both the effects of environmental filtering and limited post-glacial recolonization on the floras of the Carpathians and the central Alps may have been amplified by recent and repeated speciations (Hughes and Atchison 2015). These speciations did not entail large niche shifts among species and could have been favored by the availability of free but hostile environments and sympatric speciation (Dixon et al. 2009).

Alpine floras with the highest phylogenetic diversity were found in the north-eastern and southern Iberian Peninsula. The north-eastern Iberian alpine regions showed a phylogenetic composition between the Carpathians/Alps and other alpine regions in the Mediterranean Basin or Atlantic seaboard (e.g. Corsica, central Apennines or the Cantabrian range). The location of these Iberian regions in geographically and climatically transitional areas, together with less severe and more stable climates, may have promoted the persistence of more distantly related lineages than expected at random. These findings support the view of the mountain systems of the Iberian Peninsula as current interglacial refugia for cold-adapted plants from which recolonization occurred (Hewitt 1999, Birks and Willis 2008, Feliner 2011). Moreover, these highly diverse Iberian alpine regions host several endemics adapted to cold and dry conditions that are now found almost exclusively in the highest mountains of this area (e.g. species of the genera *Colchicum*, *Thymelaea* and *Genista*; Supporting information). Therefore, phylogenetic overdispersion in these alpine regions could reflect a mixture of lineages adapted to different degrees of aridity.

Variation in precipitation seasonality around the Bølling–Allerød period (14–17 ka BP) more strongly influenced present-day phylogenetic diversity within regions than any other period. During that time, climatic oscillations led to an abrupt warm and moist interstadial period (Hoek 2009) that accentuated differences in precipitation seasonality between temperate (i.e. the Alps and Carpathians) and Mediterranean alpine regions (Supporting information). In contrast to the environmental filtering hypothesis, we found floras with more distantly related lineages in areas with drier summers. We suggest that summer precipitation is not low enough to act as a filter because European alpine areas generally receive high precipitation and intercept humidity from the fog.

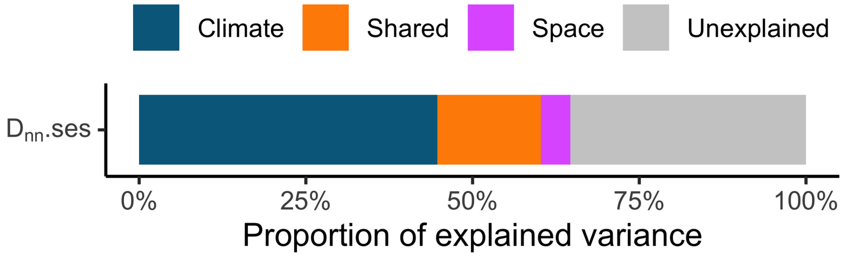

Figure 4. Proportion (%) of variance in D_{nn}.ses explained uniquely by current climatic distance (climate), by geographically structured climate variation (shared), uniquely by geographic distance (space), and by neither climatic nor geographic distance (unexplained). The explained variation was calculated based on the results of the GDM.

Summer temperatures are also generally lower than at lower elevations, resulting in sufficient residual moisture from rainy or snowy winters and springs. Nonetheless, our study system is characterized by a north–south gradient from temperate alpine regions with wetter summers to Mediterranean mountains with drier summers (Pauli et al. 2012). Since we did not control for the effects of other macroclimatic variables in our models, summer precipitation can capture the effects of continental temperature gradients, an explanation supported by the strong negative correlation between summer precipitation and temperature variables.

Between-region phylogenetic diversity

We found that between-region phylogenetic diversity was more strongly associated with climatic differences between regions than with geographic distance. After accounting for the effects of climatic differences, geographic distance alone explained only 4% of the variation in phylogenetic diversity between regions. This finding indicates that patterns of phylogenetic relatedness between alpine floras were primarily driven by species sorting along climatic gradients, as suggested by the environmental filtering hypothesis, rather than by dispersal limitation of recently evolved species. Therefore, while extreme seasonality and historical climatic instability filtered regional alpine pools to a narrow set of closely related species, current climatic differences between alpine regions prevent the exchange of regionally-adapted species. Moreover, the effect of climatic differences on between-region phylogenetic diversity was stronger at shallow than at deep phylogenetic levels (Supporting information), indicating the influence of environmental filtering at the terminal branches of the phylogeny. These results are consistent with previous regional studies of angiosperm plants in the US (Jin et al. 2015), China (Qian et al. 2020) and Brazil (Massante and Gerhold 2020).

Alpine regions with more different summer and winter temperatures had more distantly related species pools. However, this trend was less important during the LGM for winter temperature. The reason is that during that period, the mean winter temperature was more homogeneous among alpine regions and only the Carpathians and, to a lesser extent, the central Alps differed consistently from the other alpine regions (Supporting information). Therefore, alpine regions in the LGM were mainly concentrated towards the upper end of the winter temperature gradient (Supporting information), which reduced the effect of temperature differences during the LGM on phylogenetic and niche dissimilarities.

This pattern is also evident for summer precipitation because this variable partially captures the effect of extreme seasonal temperature, as discussed in the previous section. Consequently, increasing differentiation in winter temperature between alpine regions at the end of the Pleistocene likely favored higher turnover among closely related species. As we found for within-region phylogenetic diversity, the effect of precipitation seasonality on present-day phylogenetic diversity between regions was the lowest around 3 and 21 ka BP when differences in precipitation regimes were greatly reduced. These concurrent findings within and between regions reinforce the idea that today's phylogenetic diversity patterns are driven mainly by the distinct biogeographical history of the central European and Mediterranean alpine regions.

Because our study is based on observational data, we cannot ensure whether harsh environments filter species based on their life-history traits or whether these harsh environments, could, for instance, favour the co-occurrence of closely-related species that compete with other species (Cadotte and Tucker, 2017). In our study, we address environmental filtering as an environmental influence derived from several processes, which can only partially reflect the sieve of species selection. Furthermore, while our findings highlight the key role of climatic filtering in selecting closely-related species with similar ecological strategies, niche conservatism can be weak in some lineages (Pavoine and Bonsall 2011). Trait values can vary at different rates across lineages, and convergent evolution of similar traits can occur in distantly related lineages, loosening the relationship between phylogeny and function (Webb et al. 2002, Freckleton and Jetz 2009). We suggest that trait-based approaches with a particular focus on stress-tolerance traits can be helpful in further testing our conclusions and identifying mechanisms that underpin the evolutionary assembly of species pools in European alpine regions.

Conclusions

Our study highlights the role of climatic filtering and historical climatic instability in structuring the phylogenetic diversity of present-day European alpine floras. We have shown that the pre-Holocene climate complements the present-day climate in shaping the current phylogenetic diversity of these floras. The contrasting biogeographical histories of central European and Mediterranean alpine regions explain phylogenetic diversity patterns at shallow phylogenetic levels. Our findings also suggest that considering climate variability over time, rather than as isolated episodes, can improve our understanding of the role of ecological and evolutionary processes in shaping contemporary biodiversity. We further conclude that macroecology and biogeography studies should incorporate historical climate variation to better understand spatial patterns of regional diversity. This view may provide a broader framework for conserving regional assemblages under a mixed evolutionary and ecological perspective.

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Author contributions

Josep Padullés Cubino: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Milan Chytrý**: Conceptualization (equal); Funding acquisition (lead); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Jan Divíšek**: Conceptualization (equal); Methodology (equal); Resources (equal); Writing – review and editing (equal). **Borja Jiménez-Alfaro**: Conceptualization (equal); Data curation (equal); Methodology (equal); Writing – review and editing (equal).

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Data availability statement

All the data sets used are publicly available and referenced in Material and methods.

Supporting information

The Supporting information associated with this article is available with the online version.

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