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Uneven rate of plant turnover along elevation in grasslands

Patrice Descombes[1,2]*, Pascal Vittoz[3], Antoine Guisan[3,4], Loïc Pellissier[1,2]

[1]Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, CH-8092 Zürich, Switzerland
[2]Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland
[3]University of Lausanne, Institute of Earth Surface Dynamics, Géopolis, CH-1015 Lausanne, Switzerland
[4]University of Lausanne, Department of Ecology and Evolution, Biophore, CH-1015 Lausanne, Switzerland

* Corresponding author: Patrice Descombes, patrice.descombes@wsl.ch

Keyword

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Abstract

Plant taxonomic and phylogenetic composition of assemblages are known to shift along environmental gradients, but whether the rate of species turnover is regular or not (e.g., accelerations in particular sections of the gradient) remains poorly documented. Understanding how rates of assemblage turnover vary along gradients is crucial to forecast where climate change could promote the fastest changes within extant communities. Here we analysed turnover rates of plant assemblages along a 2500 m elevation gradient in the Swiss Western Alps. We found a peak of turnover rate between 1800 m and 2200 m indicating an acceleration of grassland compositional changes at the transition between subalpine and alpine belts. In parallel, we found a peak in phylogenetic turnover rate in Poales between 1700 m and 1900 m and Super-Rosids between 1900 m and 2300 m. Our results suggest that changes in abiotic or biotic conditions near the human-modified treeline constitute a strong barrier for many grassland plant species, which share analogous elevation range limits. We propose that this vegetation zone of high ecological transitions over short geographical distances should show the fastest community responses to climate change from the breakdown of barrier across ecotones.

Introduction

Since species survive and reproduce within bounded abiotic conditions (Hutchinson 1957; Soberón 2007), the composition of species assemblages changes along environmental gradients. Clines in temperature or moisture are generally associated with strong species compositional changes, such as in plants (Gentry 1988; Pellissier et al. 2010; de Bello et al. 2013), animals (Sanders 2002; Graham et al. 2009; Longino and Colwell 2011; Pellissier et al. 2012) and even microorganisms (Pellissier et al. 2014a). However, few studies so far investigated the rate of assemblage turnover along environmental gradients (Mena and Vázquez-Domínguez 2005; Bach et al. 2007; Jankowski et al. 2009; Jankowski et al. 2013). If all species show idiosyncratic response to abiotic conditions, a constant rate of compositional turnover is expected along the entire environmental gradient (Gleason 1926; Bach et al. 2007). In contrast, if a large proportion of species shares similar environmental limits, referred as “range boundary clumping” (Clements 1916; Leibold and Mikkelson 2002), a peak in the turnover component of beta-diversity would be expected in this section of the gradient (Mena and Vázquez-Domínguez 2005).

Elevation gradients are among the most studied environmental clines in ecology since they provide large variations in abiotic conditions over very short distances (Körner 2007). In the Alps and other mountain ranges in temperate climate, the climate shifts toward more stressful conditions for plant growth with increasing elevation (Körner 2003) and clines in species alpha- and beta-diversity can be observed (Körner 2000; Dubuis et al. 2011; Pellissier et al. 2013a). Species richness decreases (Körner 2000; Vittoz et al. 2010) and lowland species are replaced by high elevation specialists (Körner 2000; Theurillat et al. 2003). Gradients in environmental conditions along elevation can also be confounded with change in human land uses and disturbances, and in the intensity of biotic processes, especially around the treeline (Pottier et al. 2013). Yet, the rate of compositional changes along elevation remains poorly studied (Odland and Birks 1999; Jankowski et al. 2013). Jankowski et al. (2013) investigated compositional changes of trees and birds in tropical mountains of the Peruvian Andes and showed distinct peaks in plant and bird turnover rates along elevation. At a functional level, Ndiribe et al. (2013b) demonstrated the importance of climate and land-use factors in shaping patterns of functional and phylogenetic beta-diversity, and Pellissier et al. (2010) highlighted that dominant functional traits expressed in communities in the Swiss Alps change more rapidly around the treeline. Repeated beta-diversity comparisons between pairs of plots experiencing a small difference in elevation allows us to evaluate the evenness of the nestedness and turnover components of beta-diversity along elevation.

Complementing measures of taxonomic beta-diversity, phylogenetic beta-diversity provides additional insights into the mechanisms underlying diversity patterns along environmental gradients by considering phylogenetic relatedness among species (Graham and Fine 2008; Pellissier et al. 2013b). Phylogenetic community ecology is tightly linked to the concept of niche conservatism, the tendency of closely related species to retain the same environmental niche (Wiens et al. 2010). Phylogenetic turnover of assemblages along environmental gradients is expected to reflect niche-related processes, especially environmental filtering of lineages (Graham and Fine 2008). Phylogenetic diversity patterns have been observed to change along elevation (Culmsee and Leuschner 2013; Ndiribe et al. 2013a; Pellissier et al. 2013b), but the absence of relationships were also documented in other studies (Bryant et al. 2008; Chalmandrier et al. 2015). Large phylogenetic distances associated to low trait conservatism between species in assemblages can blur ecological signals (Kembel and Hubbell 2006; Godoy et al. 2014). Thus, focusing on patterns within specific clades might provide more detailed information. If niche boundaries are phylogenetically conserved, or clumped in particular clades, the rate of phylogenetic turnover along elevation should not be constant but present irregularities in sections of the elevation gradient (Ndiribe et al. 2013a).

Taxonomic beta-diversity variation along environmental gradients can be further decomposed into a turnover and a nestedness component (Baselga 2010). Nestedness of species assemblages occurs when the species composition of sites with smaller numbers of species are subsets of the composition at richer sites (Wright and Reeves 1992; Ulrich and Gotelli 2007), and reflects species loss as a consequence of processes promoting the disaggregation of assemblages into its subsets (Gaston et al. 2000). In contrast, assemblage turnover implies the replacement of some species by others across community pairs, and results predominantly from a shift in environmental conditions (Qian et al. 2005). Decomposing beta-diversity into turnover and nestedness components provides complementary information on the processes shaping the assembly of communities (Baselga and Leprieur 2015).

Here, we investigate the gamma- and alpha-diversity, and the turnover and nestedness components of beta-diversity of plant communities in grasslands along a 2500 meters elevation gradient in the Western Swiss Alps with a special emphasis on the evenness of the turnover rate. We computed beta-diversity of pairs of plots separated by an elevation smaller than 20 meters and decomposed it into turnover and nestedness components (Baselga 2010). Using a species-level phylogeny of the regional flora, we further investigated phylogenetic turnover of Poales, Super-Asterids and Super-Rosids clades along elevation. In the case of idiosyncratic response of species to shifting environmental conditions along the elevation gradient, we should observe a flat relationship between turnover rate and elevation. In contrast, if species share similar range limits, a higher turnover rate should be observed in portions of the gradient. Documenting turnover rates along elevation gradients is particularly relevant in the context of climate change. Sections of the gradient with higher turnover rate indicate the presence of a strong barrier across different ecosystems, which might be lifted by climate change.

Methods

Study area and data collection

The study area, covering approximately 700 km^2, is located in the Western Alps of Switzerland (canton de Vaud) and exhibits an elevational gradient ranging from 375 m to 3200 m with a soil parent material that is mainly calcareous (46°10′–46°30′ N; 6°50′–7°10′ E; Fig. 1). The region has a temperate climate with mean annual temperature between 8 °C at 375 m and -5°C at 3200 m and with annual sum of precipitation between 1200 mm and 2600 mm (Bouët 1985). Below the treeline (i.e. 1900 m; lowered by a few 100 meters through centuries of human activities; Gehrig-Fasel et al. 2007), most of the open vegetation areas are used for grazing and/or mowing, often with regular fertilization, whereas the areas in alpine belt are occupied by alpine grasslands and glaciers with much lower levels of human disturbance, except cattle grazing in summer on the most accessible areas. The species data have been collected in open and non-woody vegetation areas only (i.e. grasslands, meadows, rocks and screes; see Fig. S1 to see how open areas and selected plots are distributed along the elevation gradient) using a balanced random stratified sampling design (Hirzel and Guisan 2002) relying on slope, elevation and aspect (see Fig. S2 to see how the selected plots are distributed in the ecological space). Since slope, elevation and aspect are proxies for contrasted ecological conditions, this design allows us to collect data from the full range of vegetation types present along the elevation gradient. The vegetation sampling includes 912 sites surveyed exhaustively on 2 x 2 m squares across the whole gradient between 2002 and 2009 (for more details see Dubuis et al. 2011) and which had similar topography. Species cover was visually estimated according to a 7-level scale.

Alpha- and gamma-diversity

To investigate how the local species pools vary along elevation gradient, we computed the total number of species encountered in sampled plant communities within 20 m elevation bands centred on each 10 m elevation steps. This represents the local gamma-diversity defined for each elevation section. In this study, we only used elevation as ecological gradient (see Körner 2007) since this gradient is highly correlated to abiotic factors such as degree-days (Spearman's correlation: $r = -0.997$; Fig. S2) or precipitation (Spearman's correlation: $r = 0.959$; Fig. S2), and also associated with shifts in biotic conditions such as reduced competition at higher elevation (e.g. Michalet et al. 2006; Michalet et al. 2015), a decrease in herbivore pressure (e.g. Reynolds and Crossley 1997; Garibaldi et al. 2011; Pellissier et al. 2014b) or a gradient of land use by humans (see above).

In addition, within each of the 20 m elevation sections, we computed the mean number of species found in communities as a measure of local average alpha-diversity in each elevation band. Comparing alpha- and gamma-diversity and their deviation along elevation, a measure of beta-diversity (Tuomisto 2010), provide information on the intensity of environmental and human mediated filtering processes within each elevation band. The range of 20 m was selected because it constitutes a good compromise between resolution of the elevation bands and number of possible comparisons between pairs of vegetation plots. However, to ensure that our conclusions were non sensitive to the choice of threshold, we also ran the analyses with a range of 10 m and a range of 50 m. Because land use might influence plant alpha- and gamma-diversity patterns (e.g. Fischer et al. 2008; Niedrist et al. 2009), we also related number of open areas (see Fig. S1) and diversity of vegetation types (see Fig. S3) to the alpha- and gamma-diversity within each of the 20 m elevation bands. Plots were grouped with a hierarchical clustering and the groups were attributed to a vegetation type, according to the classification of Delarze and Gonseth (2008), on the basis of their respective differential species.

Community taxonomic turnover and nestedness of beta-diversity

We computed beta-diversity of all plant species, Poales (i.e. Cyperaceae, Juncaceae and Poaceae), Super-Asterids (i.e. Apiales, Asterales, Caryophyllales, Dipsacales, Ericales, Gentianales, Lamiales and Santalales) and Super-Rosids (i.e. Brassicales, Celastrales, Fabales, Geraniales, Malpighiales, Malvales, Rosales and Saxifragales) between all pairs of communities with an elevation difference lower than 20 m and partitioned the total beta-diversity (Jaccard dissimilarity index, β_{jac}) into turnover (Turnover component of Jaccard dissimilarity, β_{jtu}) and nestedness-resultant dissimilarity (Nestedness-resultant component of Jaccard dissimilarity, β_{jne}) by using the package “betapart” (Baselga 2012; Baselga and Orme 2012) in R (R Development Core Team, www.R-project.org). β_{jtu} and β_{jne} vary between 0 and 1, where high values indicate greater dissimilarity in species composition and low values indicate greater proportion of shared species. In the absence of nestedness (i.e. species between pairs of communities are completely different), β_{jtu} is equal to β_{jac} and equal to 1. The difference between β_{jtu} and β_{jac} is a measure of the nestedness component of beta-diversity. In the absence of turnover (i.e. species of a community are a subset of a richer community), β_{jne} is equal to β_{jac} and is influenced by differences in species richness. We related the β_{jtu} and β_{jne} values to the mean elevation of each pair of plots using a linear model including both a linear and a quadratic term. Any deviation from an intercept-only model, either with a linear or non-linear slope, would indicate a non-constant turnover and nestedness rate along elevation. We also investigated how the spatial distance between pairs of plots varies between elevation bands along the elevation gradient by relating the horizontal distance separating each pair of plots with their mean elevation and their taxonomic turnover (β_{jtu}). Because land use might influence plant beta-diversity patterns (Ndiribe et al. 2013b), we also related elevation and habitat variables (i.e. number of open areas, diversity of vegetation types) to the mean taxonomic turnover (β_{jtu}) within 20 m elevation bands by using an ordinary least squares regression (OLS) model and quantified the relative importance of elevation vs. habitat variables for explaining beta-diversity variation with a variance partitioning analyses (see Appendix S1 for methodological details on the OLS models and variable partition analyses). Finally, we extracted the elevation minima and maxima of each plant species from the 912 plots. We related these range limits to the elevation gradient in order to explain how range boundaries could influence dissimilarities in species composition.

Community phylogenetic turnover of beta-diversity

We tested the phylogenetic signal in species distribution along the elevation gradient (the median elevation at which the species occurred), by pruning from a published phylogeny of the 231 most frequent and abundant plant species in our study area (Ndiribe et al. 2013a). We calculated Blomberg’s K statistic with the “phylosignal” function as implemented in the “picante” R package (Blomberg et al. 2003; Kembel et al. 2010), as our measure of phylogenetic signal. We calculated Blomberg’s K across all species and in three angiosperm clades: Poales, Super-Asteridsand Super-Rosids. Blomberg’s K statistic compares the observed distribution of the trait values to expectations under a Brownian motion model of trait evolution. K values close to 1 indicate trait evolution consistent with a Brownian motion model of evolution, while K values close to 0 indicate a random distribution of trait values with respect to the phylogeny (Blomberg et al. 2003). We tested the significance of this test by comparing the observed K value to a null distribution generated by comparing 999 randomisations of trait values across the tips of the phylogenetic tree (Kembel et al. 2010).

We computed phylogenetic turnover of beta-diversity of all plant species, Poales, Super-Asterids and Super-Rosids between pairs of plots with an elevation difference lower than 20 m, using the mean pairwise distance (MPD) implemented in the “comdist” function in the “picante” R package (Kembel et al. 2010). We related the mean elevation of each pair of plots with their phylogenetic turnover value and tested for the existence of shifts in rates of phylogenetic turnover using a linear model including quadratic terms. In order to visualize the contribution of families to communities along elevation, we calculated the proportion of species occurrences and the proportion of species cover of the dominant plant clades of Poales, Super-Asterids and Super-Rosids (i.e. Poaceae, Cyperaceae, Asteraceae, Fabaceae, Apiaceae, Saxifragaceae) for 200 m elevation bands.

Results

Alpha- and gamma-diversity

We found that the gamma-diversity within the 20-meters elevation bands showed a hump-shaped curve, with a peak between 1500 and 1900 m (Fig. 2a). Similarly, the mean alpha-diversity of communities within each elevation band showed a hump-shaped curve, but with a peak between 1100 and 1500 m (Fig. 2a). We observed a strong relationship between the gamma- and the mean alpha-diversity (Spearman’s correlation: $r = 0.632$), indicating that a larger gamma-diversity is associated with a higher mean alpha-diversity of communities, but the relationship showed higher discrepancies in some section of the gradient (Fig. 2a). Differences between gamma- and mean alpha-diversities are overall larger at lower elevation, but with a peak around 1400-2100 m (maximum difference: 222 at 1820 m). Note that the difference between gamma and alpha diversity in elevation bands of 20 m is another measure of beta-diversity (Tuomisto 2010), and showed only weak correlation with the turnover component of beta diversity calculated between pairs of plots with less than 20 m of difference in elevation (Spearman’s correlation: $r = 0.212$). Finally, we also observed a strong relationship between the gamma-diversity and the number of open areas (Spearman’s correlation: $r = 0.750$) and the diversity of vegetation types ($r = 0.786$), indicating that larger open areas and areas with diverse vegetation types sustain higher gamma-diversity. The relationships with alpha-diversity were weaker for number of open areas ($r = 0.585$) and the diversity of vegetation types ($r = 0.285$).

Community taxonomic turnover and nestedness of beta-diversity

Overall, beta-diversity between pairs of plots along elevation is mainly generated by species turnover (β_{jtu}; mean: 0.80, sd: 0.17; Fig. 2b), while the contribution of nestedness to overall dissimilarity was much lower (β_{jne}; mean: 0.06, sd: 0.10; Fig. 2b). We found that the turnover (β_{jtu}) and nestedness (β_{jne}) components of beta-diversity were uneven along elevation (β_{jtu}: linear s= $4.8*10^{-4}$, quadratic s= $-1.2*10^{-7}$, β_{jne}: linear s= $-2.6*10^{-4}$, quadratic s= $7.9*10^{-8}$; Fig. 2b). Including quadratic terms improved the models for turnover (AIC difference: -229.8) and nestedness (AIC difference: -260.7) supporting the existence of a hump-shaped relationship. The rate of community turnover was highest (greatest dissimilarity in proportion of unshared species) in the elevation section between 1800 and 2200 m, while elevation ranges with the highest nestedness (greatest dissimilarity in proportion of shared species) were below 1200 m and above 2200 m. We found a weak correlation between the Euclidian geographic distance separating pairs of plots with their mean elevation (Spearman's correlation: r = -0.232) and with their taxonomic turnover (β_{jtu}; Spearman's correlation: r = 0.080), suggesting that shift in spatial distance along elevation does not explain the observed pattern of beta-diversity. We also found a weak relationship between mean beta-diversity (β_{jtu}) and the number of open areas (Spearman's correlation: r = 0.363), alpha-diversity (r = -0.231) and gamma-diversity (r = 0.165) in elevation bands of 20 m along the elevation gradient. Elevation was the only significant parameter in the model (OLS model: estimate = 0.460, t-value = 4.093, p-value < 0.001) explaining the variation in taxonomic turnover (β_{jtu}). When partitioning the explained variance of mean beta-diversity (R^2 = 0.21) among elevation and habitat variables (i.e. number of open areas and diversity of vegetation types) in the OLS model, elevation displayed the strongest independent effect, with a higher independent proportion of explained variance (11.7 %) than habitat variables (0.0%).

The turnover (β_{jtu}) component of beta-diversity was also uneven along elevation for Poales (β_{jtu}: linear s= $6.7*10^{-4}$, quadratic s= $-1.8*10^{-7}$; Fig. 3a), Super-Rosids (β_{jtu}: linear s= $3*10^{-4}$, quadratic s= $-6.2*10^{-8}$; Fig. 3a) and Super-Asterids (β_{jtu}: linear s= $6.5*10^{-4}$, quadratic s= $-1.9*10^{-7}$; Fig. 3a). Including quadratic terms improved the models for Poales (AIC difference: -154.9), Super-Rosids (AIC difference: -10.8) and Super-Asterids (AIC difference: -292), supporting the existence of a hump-shaped relationship. However, Super-Rosids show a weaker hump-shaped relationship than Poales and Super-Asterids (Fig. 3a). The rate of community turnover was highest in the elevation section between 1700 and 2000 m for Poales, between 2000 and 2400 m for Super-Rosids and between 1600 and 1900 m for Super-Asterids (Fig. 3a).

The distribution of the species elevation maxima follows a hump-shaped curve with a peak between 2000 m and 2200 m (Fig. 4). In contrast, the distribution of the species elevation minima shows a plateau between lowland and 1600 m and decreases rapidly between 1800 and 2400 m (Fig. 4). The important decrease of the minimum range values around 2000 m indicates that many species have their lower range limit around this elevation. As a result, many high and low elevation species have their lower and higher elevation limit near 2000 m respectively.

Community phylogenetic turnover of beta-diversity

We found a weak phylogenetic signal of niche conservatism (i.e. species-specific median of elevation distribution) across all plant species from the phylogeny (Blomberg's K: K = 0.095, n = 231, Z-score = -2.411, p-value = 0.002), in Poales (Blomberg's K: K = 0.174, n = 48, Z-score = -1.649, p-value = 0.022), Super-Rosids (Blomberg's K: K = 0.251, n = 50, Z-score = -1.589, p-value = 0.003) and Super-Asterids (Blomberg's K: K = 0.101, n = 122, Z-score = -1.194, p-value = 0.1). Only Super-Asterids showed a non-significant difference of Blomberg's K compared to a null distribution across the phylogeny, suggesting that the plant niche of Super-Asterids does not follow patterns of phylogenetic inertia.

The turnover rate in phylogenetic beta-diversity was more even along elevation across all plant species from the phylogeny (All plant species: linear s= $2.6*10^{-2}$, quadratic s= $-7.2*10^{-6}$) than the turnover rates in phylogenetic beta-diversity of Poales, Super-Rosids and Super-Asterids which were more uneven along elevation (Poales: linear s= 0.188, quadratic s= $-5.5*10^{-5}$, Super-Rosids: linear s= 0.138, quadratic s= $-3.3*10^{-5}$, Super-Asterids: linear s= $-4.5*10^{-2}$, quadratic s= $1.5*10^{-5}$; Fig. 3b). Including quadratic terms improved the models of phylogenetic beta-diversity for all clades (AIC difference; All plant species = -179.3, Poales = -1646.4, Super-Rosids = -257.6, Super-Asterids = -233.6), supporting the existence of a non-linear relationship. The turnover rate in phylogenetic beta-diversity showed a strong hump-shaped pattern in Poales (peak between 1700-1900m) and Super-Rosids (peak between 1900-2300m), while turnover rate in Super-Asterids was more even along elevation (Fig. 3b). The explained variance in the relationship between phylogenetic beta-diversity and elevation was higher in Poales ($R^2 = 0.236$) and Super-Rosids ($R^2 = 0.164$) than Super-Asterids ($R^2 = 0.056$) or across all plant species from the phylogeny ($R^2 = 0.035$).

Plant clades show different patterns of distribution and dominance along elevation (Fig. 5, S4, S5, S6). Plant communities between 800 and 2800 m show a global decrease in the species proportion of Poales (from 28.6 % at 1300 m to 11.6 % at 2700 m; Fig. 5) along elevation, with an increase in Super-Rosids (from 21 % at 1500 m to 65.7 % at 2900 m; Fig. 5) and a contrasting pattern for Super-Asterids (minimum = 14.8 % at 2900 m, maximum = 47.3 % at 2100 m; Fig. 5). However, Poales species dominate plant communities in term of relative cover (i.e. bare soil and rock excluded; range: 42.8 - 58.7 %; Fig. S5) compared to Super-Rosids (range: 14.5 - 25 %; Fig. S5) and Super-Asterids (range: 19.9 - 32.5 %; Fig. S5), except in the highest bands. In Poales, Poaceae species dominate plant communities of low elevation and show a constant decrease of their relative cover from 900 m (57.3 %) to 2700 m (31.3 %; Fig. S5), while Cyperaceae species show a constant increase of their relative cover from 900 m (1.4 %) to 2700 m (16.6 %; Fig. S5). In Super-Rosids and Super-Asterids, Fabaceae species have a higher relative cover at low elevations (10.4 % at 900 m; Fig. S5), Asteraceae and Apiaceae species at mid-elevations (11.8 % at 1900 m and 5.9 % at 1500 m, respectively; Fig. S5) and Saxifragaceae species dominate in relative cover plant communities of very high elevations (17.8 % at 2700 m, 91.4 % at 2900 m; Fig. S5). Yet, the net breakpoint in the dominance of Saxifragaceae species above 2800 m is partly due to the smaller plot sampling and the small number of species occurring at this elevation, with a more regular transition when the real cover (i.e. bare soil and rock included) is considered (Fig. S6).

Overall, we found that the results were not sensitive to the resolution of elevation section considered, whether it is 10, 20 or 50 meters (Fig. S7, S8).

Discussion

Measures of species turnover are essential tools to investigate assemblage shifts along environmental gradients (Williams 1996), and particularly along elevation gradients which are commonly used as proxies of shifts in abiotic (see Körner 2007) and biotic conditions (Reynolds and Crossley 1997; Michalet et al. 2006; Körner 2007; Pellissier et al. 2014b; Michalet et al. 2015). Using this analytical tool, we showed that turnover rate along elevation in grassland communities is not constant but peaks around 1800-2200 m, corresponding approximately to the regional treeline (1900 m, Gehrig-Fasel et al. 2007). The juxtaposition of highly dissimilar assemblages, large difference between gamma- and mean alpha-diversity (maximum between 1400-2100 m), and the high diversity of vegetation types (Fig. S3) indicate a singular ecological transition in this narrow elevation band (Fig. 2, 3, S3). This supports the hypothesis that across regional species pool in the Western Swiss Alps, many plant species share the same upper or lower elevation range limit (Fig. 4) and display "range boundary clumping" (Leibold and Mikkelson 2002). Human disturbances and current land management have probably favoured the mosaic of habitats occurring at mid-elevation. However, from the habitat data available, we found no evidence that the larger open areas or the higher diversity of vegetation types observed at mid elevation explain the observed taxonomic and phylogenetic turnover near the treeline. Together, our results document the singularity of grassland taxonomic and phylogenetic turnover at the border between the subalpine and alpine belts. Our study suggests that, like trees, this ecotone (Theurillat et al. 2003) constitutes a strong barrier for some herbaceous plant clades, even after centuries of land use (Tinner and Theurillat 2003). Despite grazing having shaped a continuum of open vegetation types across the subalpine and alpine belts, which should have since long allowed species exchanges along the elevation gradient (Vittoz et al. 2009), our results indicate the persistence of this ecotone.

The transition from the subalpine to the alpine belts, where the turnover was the most acute, is associated with several changes in the abiotic environment, including more stressful temperatures and a shorter growing season (Körner 2007). Enduring stressful abiotic conditions in the alpine belt requires particular and often convergent adaptations (Pellissier et al. 2010), including a lower stature (Körner 2003), a decreasing specific leaf area (Salinas et al. 2011) associated to slower growth rates (Whittaker 1956). Plant distribution may also be limited by other abiotic factors in the alpine belt, including strong wind, ground instability, the type of underground rock (i.e. calcareous or siliceous), or frost during the growing season, which can result in functionally distinct plant communities at high compared to low elevations (Diaz and Cabido 1997). While clumped minima and maxima elevation range values observed around the treeline is expected to be partially controlled by abiotic factors (Diaz and Cabido 1997), changes in biotic interactions might also modulate plant range limit at the subalpine-alpine ecotone. In symmetry to the stressful abiotic conditions limiting lowland species in the alpine belt, higher competition among plant species (Choler et al. 2001; Alexander et al. 2015) and higher insect herbivore pressure on poorly defended alpine species in the subalpine belt likely limits the growth of small alpine plant species (Galen 1990; Bruelheide and Scheidel 1999; Pellissier et al. 2012; Pellissier et al. 2014b). However, high grazing pressure by cows or sheep in subalpine pastures can also reduce plant competition and favour the establishment of alpine plants at lower elevation (Vittoz et al. 2009). Moreover, higher species richness could also be favoured at intermediate position along environmental severity gradients as a result of decreasing inter-specific competition and increasing stress-tolerance with elevation (Michalet et al. 2006; Holmgren and Scheffer 2010; Verwijmeren et al. 2013; Michalet et al. 2015) favouring the mixture of low competitive species and high elevation stress-tolerant species (Michalet et al. 2015). Our results contrast with a study in Norway where no major discontinuity in species richness, composition or turnover was observed at the forest-limit ecotone (Odland and Birks 1999).

Taxonomic turnover component of beta-diversity was associated to uneven phylogenetic turnover rate along elevation. Poales and Super-Rosids showed a significant but weak phylogenetic conservatism of species range and an acceleration of phylogenetic turnover with a peak reached around 1900 m for both clades (Fig. 3b). This corroborates the finding of Ndiribe et al. (2013) showing singular phylogenetic diversity patterns in Liliopsida (i.e. incl. Poales) along elevation. Several Poales and Super-Rosids lineages showed a preference either for the montane-subalpine or for the alpine environment, shaping the higher lineage turnover at the subalpine-alpine ecotone. For instance, the species in the genus *Carex* (Cyperaceae) show a preference for mid-elevation environments (i.e. 1300 – 2500 m; Fig. 5, Fig. S5), the species in the genus *Saxifraga* (Saxifragaceae) show a preference to colder environment above the treeline (i.e. > 2100 m; Fig. 5, S5) and the species in the Fabaceae family show a preference for lower elevation environments (i.e. < 2300 m; Fig. 5, S5). Many *Carex* species are tolerant to low temperatures (Körner 2003) and can be dominant and diversified in communities above the treeline (Grabherr 1989; Körner 2003). Conversely, Poaceae generally dominate grasslands below treeline (Fig. S5). In different regions, phylogenetic patterns in Liliopsida distinct from coexisting Magnolopsida have been reported along environmental gradients (Silvertown et al. 2001; Cahill et al. 2008). For instance, Cahill et al. (2008) observed that the intensity of competition showed a stronger phylogenetic signal in Liliopsida than Magnolopsida, as a consequence of higher niche conservatism in Liliopsida. Moreover, phylogenetic turnover is not always associated to functional turnover, due to possible convergence of traits between phylogenetically distinct species groups (Godoy et al. 2014). The lower phylogenetic conservatism of Super-Asterids range suggests that most lineages contain species that are distributed both above and below the treeline, explaining the constant lineage turnover rate along elevation (Fig. 3b; Chalmandrier et al. 2015). This constant phylogenetic turnover contrasts with the observed peak of taxonomic turnover at mid-elevation for Super-Asterids (Fig. 3), indicating that taxonomic turnover is not always associated to phylogenetic turnover. Similarly, Ndiribe et al. (2013a) found prevailing patterns of phylogenetic overdispersion in three families of the Super-Asterids clade (i.e. Apiaceae, Lamiaceae and Asteraceae families), indicating that closely related species diversified to occupy communities in contrasting environmental conditions, or that close relatives co-occur less often than expected. The low niche conservatism observed in Super-Asterids could be due to strong rates of evolution occurring in this clade favouring niche differentiation (Cooper et al. 2010) or the lack of high/low elevation specialized clades (i.e. lack of species in the Fabaceae and Saxifragaceae families, respectively), which may in part be attributed to their life-history traits (Ndiribe et al. 2013a). For instance, species of the Lamiaceae family have evolved phenolic compounds providing herbivore resistance and favouring their persistence in communities in contrasted environmental conditions (Grøndahl and Ehlers 2008).

Compared to gamma-diversity, the peak in alpha-diversity occurs at a lower elevation around 1100-1500 m, indicating that plant community richness is not necessary strictly associated to a higher species richness in a local pool. Alpha-diversity seems to reflect the disturbances occurring on plant communities at both ends of the elevation gradient, with more intensive land use (pastures, fertilization) at low elevation increasing plant exclusion by competition (Eriksson et al. 1995; Foster and Gross 1998) and limiting the diversity of vegetation types (Fig. S3) and severe environmental conditions at high elevation allowing the growth of few stress tolerant species. Before the intensification of agriculture, beginning around 60 years ago, dry and oligotrophic grasslands were more frequent below 1100 m (Lachat et al. 2010) and a similar analysis would have probably not resulted in so steep decline of alpha-diversity at low elevations. These grasslands are very species rich but are now very rare in the landscape at low elevations. A higher intensity of land use may also explain the lower gamma-diversity occurring at low elevation, which tends to homogenise the composition of plant communities. The land use at low elevation and the high elevation stress could explain the higher nestedness pattern below 1200 m and above 2200 m. In alpine habitat, communities with lower species richness are more frequently a subset of richer alpine communities. Since alpine habitats are supposed to be more stochastic due to stronger temporal variations in environmental conditions such as solifluction or landslides, some communities may suffer random loss of species shaping nestedness in the alpine belt (Körner 2003). Nestedness below 1200 m is probably the result of the intensive land use (i.e. pasturing, grazing, mowing, and fertilization), which limits plant composition to the more competitive species, subset of richer lowland communities.

Climate change is currently increasing temperature in the Alps with rapid detectable changes in alpine plant communities (Pauli et al. 2012). Based on the present study, we can expect that the same temperature rise along the elevation gradient may not trigger the same amount of turnover rate in communities. In the transition between the subalpine and alpine belts, distinct flora are juxtaposed and only a strong ecological barrier appears to keep them apart. Climate change may lift the existing barrier across the subalpine-alpine ecotone, allowing for the upward movement and invasion of more competitive subalpine plants in the alpine grasslands, shaping novel assemblages and potentially causing local extinction of species in those communities (Alexander et al. 2015). Monitoring scheme investigating plant community changes along wide elevation gradients are required to evaluate the speed of changes (Vittoz et al. 2010). While the absence of change in the turnover rate of phylogenetic beta-diversity along elevation were documented (Bryant et al. 2008; Chalmandrier et al. 2015), our study reports a strong species turnover between the subalpine and alpine vegetation belts and suggests that climate change might, in turn, have an uneven impact on species' range shifts across the elevation gradient.

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Supporting information

Additional supporting information in the online version of this article (see „Supplementary Material”) contains the following:

Appendix S1. Methodological details about OLS models and variable partition analyses

Fig. S1 Number of open areas and plots along the elevation gradient in the study area.

Fig. S2 Principal Components Analysis of sampled plot location in the environmental space.

Fig. S3 Number of vegetation types along the elevation gradient.

Fig. S4 Proportion of the main vascular plant clades in elevation bands of 200 m.

Fig. S5 Mean relative cover of the main vascular plant clades in elevation bands of 200 m.

Fig. S6 Mean cover of the main vascular plant clades in elevation bands of 200 m.

Fig. S7 Diversity changes along the elevation gradient obtained by comparing plant communities of the same elevation (± 10 m & ± 50 m).

Fig. S8 Diversity changes and relationship between elevation and plant relatedness in plant community turnover of the same elevation (± 10 m & ± 50 m) for 3 plant clades.

Figures

Fig. 1 Location of the study area in the western Alps of Switzerland. The red dots represent vegetation sampling sites and green areas represent forests ecosystems. The light grey line shows the limits of study area. The dark grey line shows the 800 m isoline.

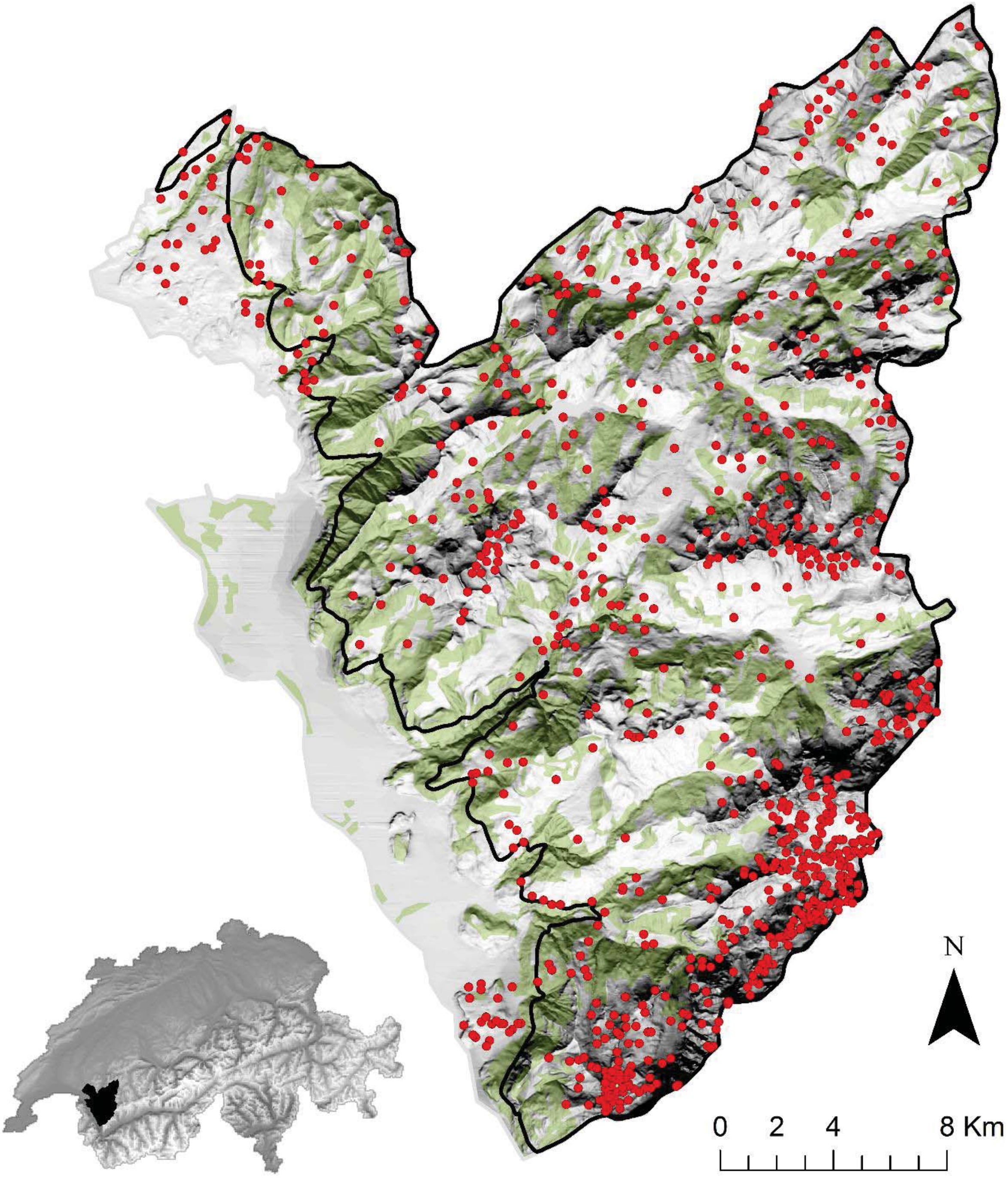


Fig. 2 Diversity changes along elevation gradients obtained by comparing plant communities within 20 m elevation bands as a measure of (a) mean community diversity (black points; mean alpha-diversity), total species richness (green points; gamma-diversity) and (b) proportion of species turnover (black points; turnover component of beta-diversity) and nestedness (green points; nestedness component of beta-diversity). Curves represent the quadratic relationships. Dashed lines represent the 5 and 95 percentiles.

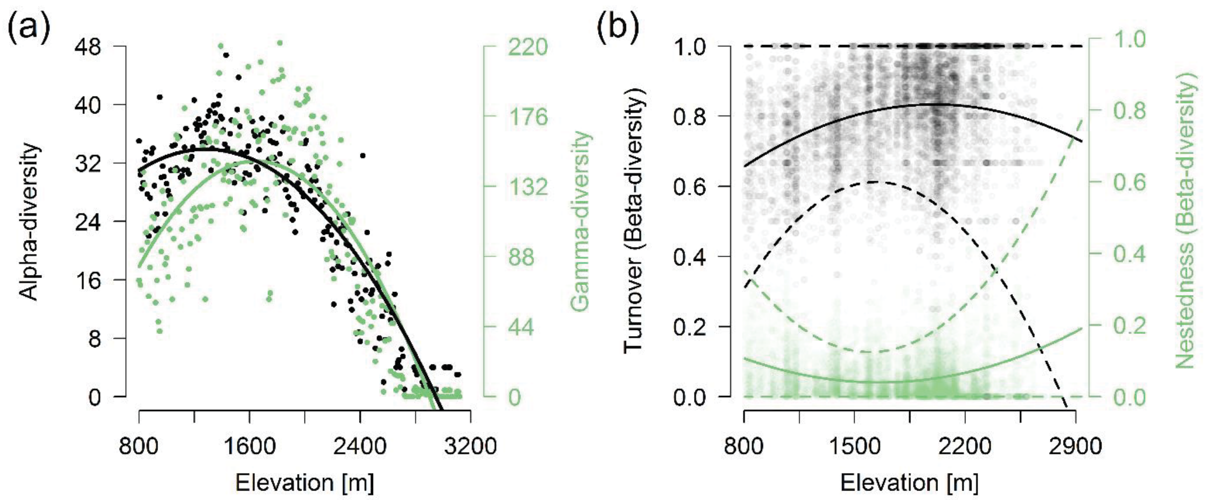


Fig. 3 Relationship between elevation and (a) proportion of plant species turnover (turnover component of beta-diversity) and (b) phylogenetic plant relatedness calculated as the mean pairwise distance (MPD) separating taxa in pairs of plant inventories of the same elevation (range 20 m) for Super-Asterids (black points), Super-Rosids (blue points) and Poales (red points) clades. Curves represent the quadratic relationships.

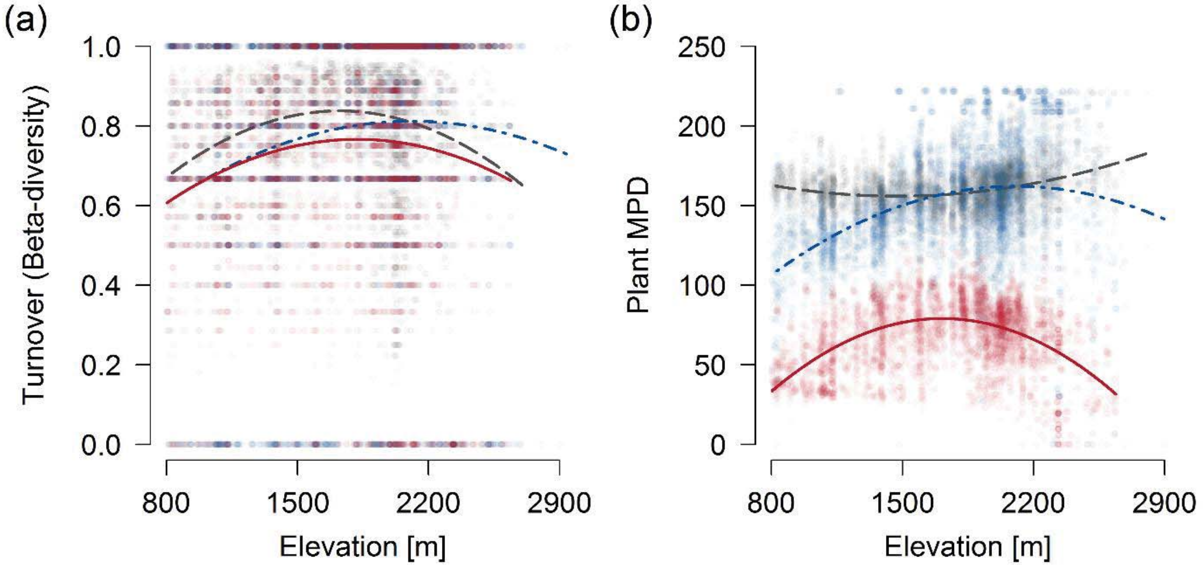


Fig. 4 Distribution of the minimum (black) and maximum (grey) elevation of the species ranges in elevation bands of 20 m for each 10 m along the elevation gradient in the study area. Curves were fitted with a GAM function.

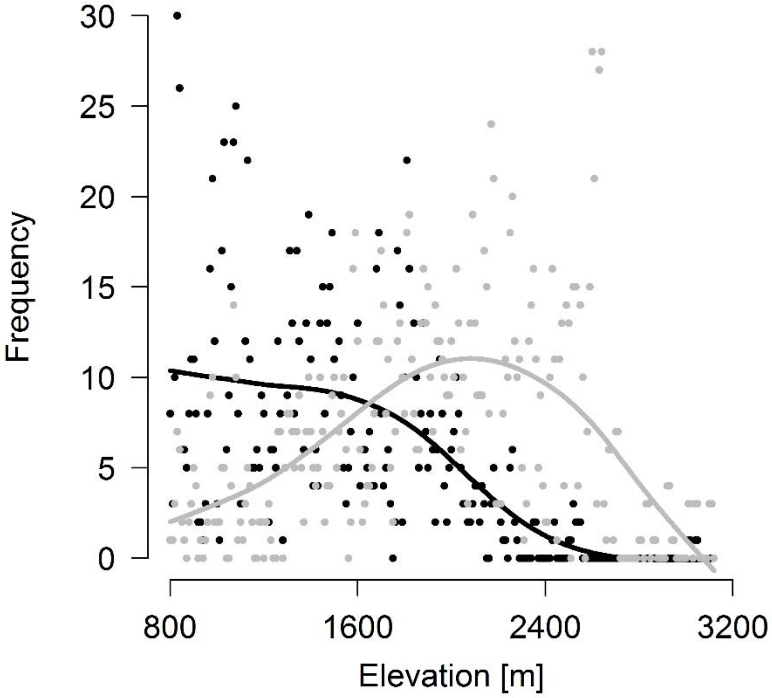
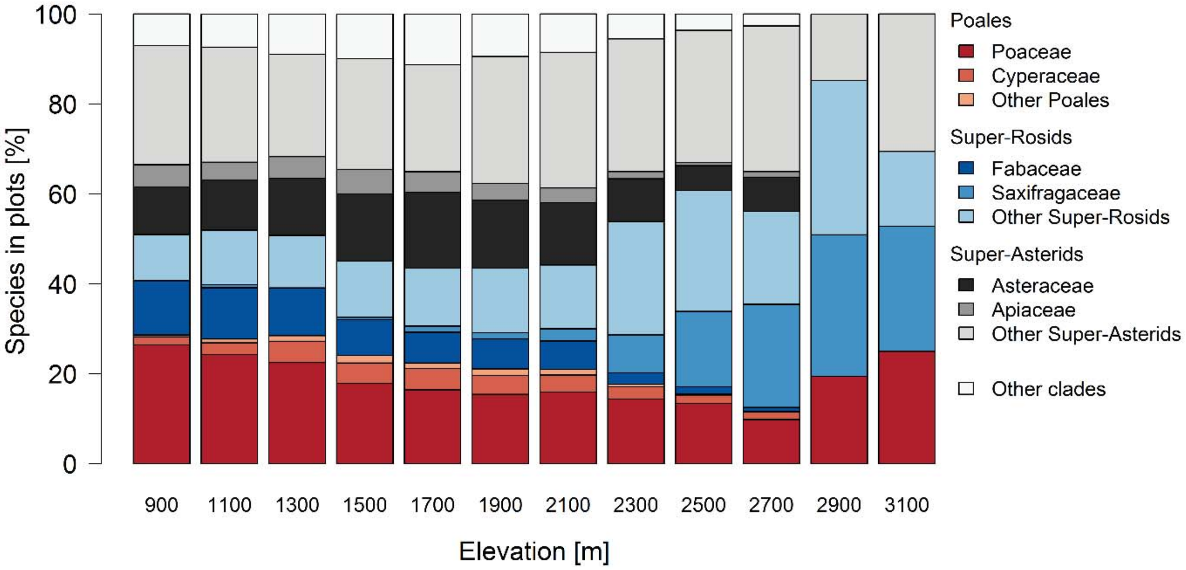


Fig. 5 Mean proportion of occurrences of the main vascular plant clades in plant communities in elevation bands of 200 m. Each color represents the mean proportion of the plant clade in plant communities for the corresponding elevation band. The different shades of red-orange correspond to Poales, the blue shades to Super-Rosids and the grey-black shades to Super-Asterids.



Research article for *Alpine Botany*

Uneven rate of plant turnover along elevation in grasslands

Patrice Descombes[1,2]*, Pascal Vittoz[3], Antoine Guisan[3,4], Loïc Pellissier[1,2]

[1]Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, CH-8092 Zürich, Switzerland
[2]Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland
[3]University of Lausanne, Institute of Earth Surface Dynamics, Géopolis, CH-1015 Lausanne, Switzerland
[4]University of Lausanne, Department of Ecology and Evolution, Biophore, CH-1015 Lausanne, Switzerland

* Corresponding author: Patrice Descombes, patrice.descombes@wsl.ch

Supplementary materials

Appendix S1. Methodological details about OLS models and variable partition analyses

OLS models

We compared the turnover component of beta-diversity to elevation and habitat variables (frequency of open areas and diversity of vegetation types) by using an ordinary least squares regression (OLS) model and including all predictor variables and quadratic terms to account for non-linear relationships. The proportion of variation in the turnover component of beta-diversity explained by the OLS models was quantified with the coefficient of determination (R^2).

Variable partition analyses

In addition, we quantified the relative importance of elevation vs. habitat variables (i.e. frequency of open areas and diversity of vegetation types) for explaining beta-diversity variation by using a variance partitioning analyses (Borcard et al., 1992). This analysis decomposes the proportion of variation in beta-diversity explained by the full OLS model (R^2) into two sources of variation by means of partial regressions (Legendre, 2012): (i) variation due to the independent effect of the elevation variable, (ii) variation due to the independent effect of habitat variables, and (iii) variation due to the combined effect of elevation and habitat variables. When partitioning the explained variance of beta-diversity ($R^2 = 0.21$), among elevation and habitat variables in OLS full models, elevation displayed the strongest independent effect, with a higher independent proportion of explained variance (11.7 %) than habitat variables (0.0%).

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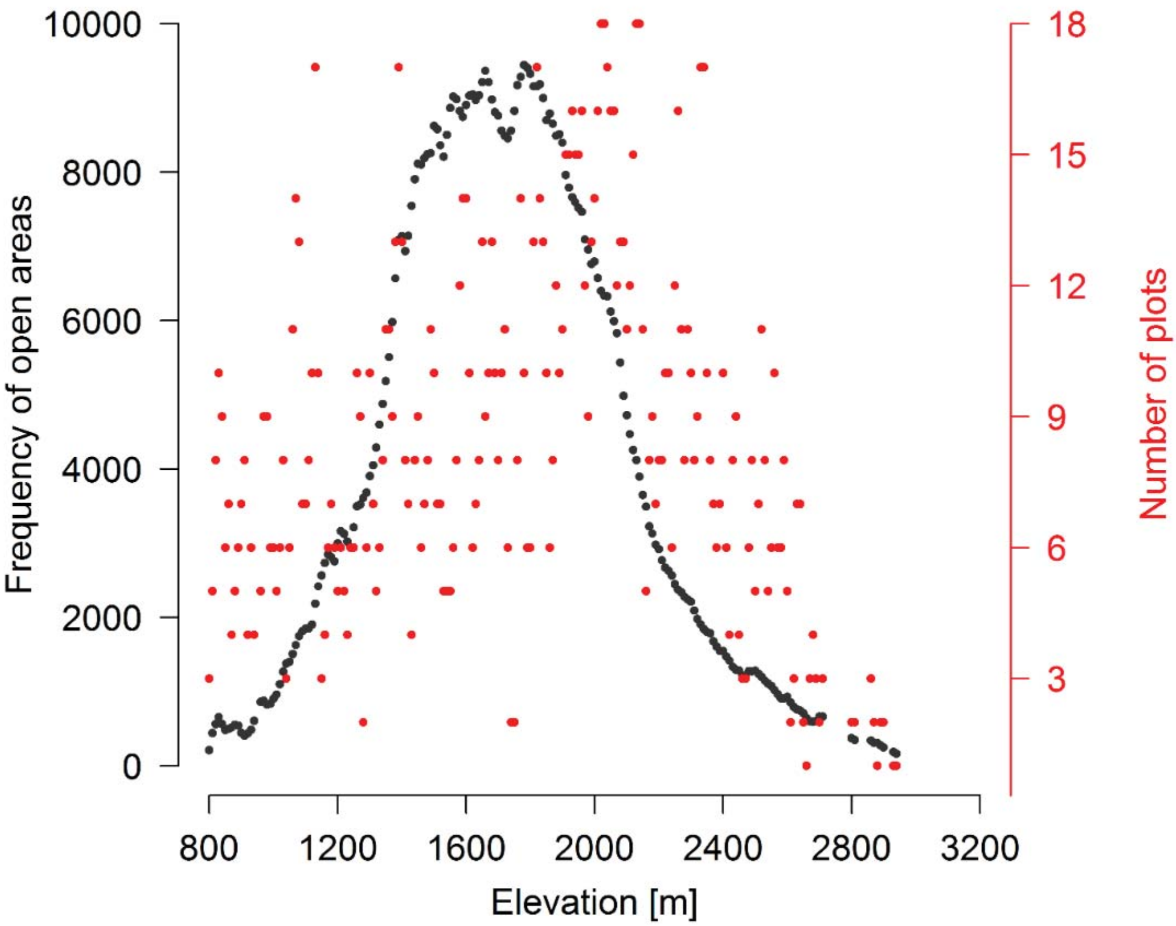

Fig. S1 Number of open areas (black points) and plots (red points) in elevation bands of 20 m for each 10 m along the elevation gradient in the study area. The unit of open areas is the number of pixels in elevation bands at a resolution of 25 m.

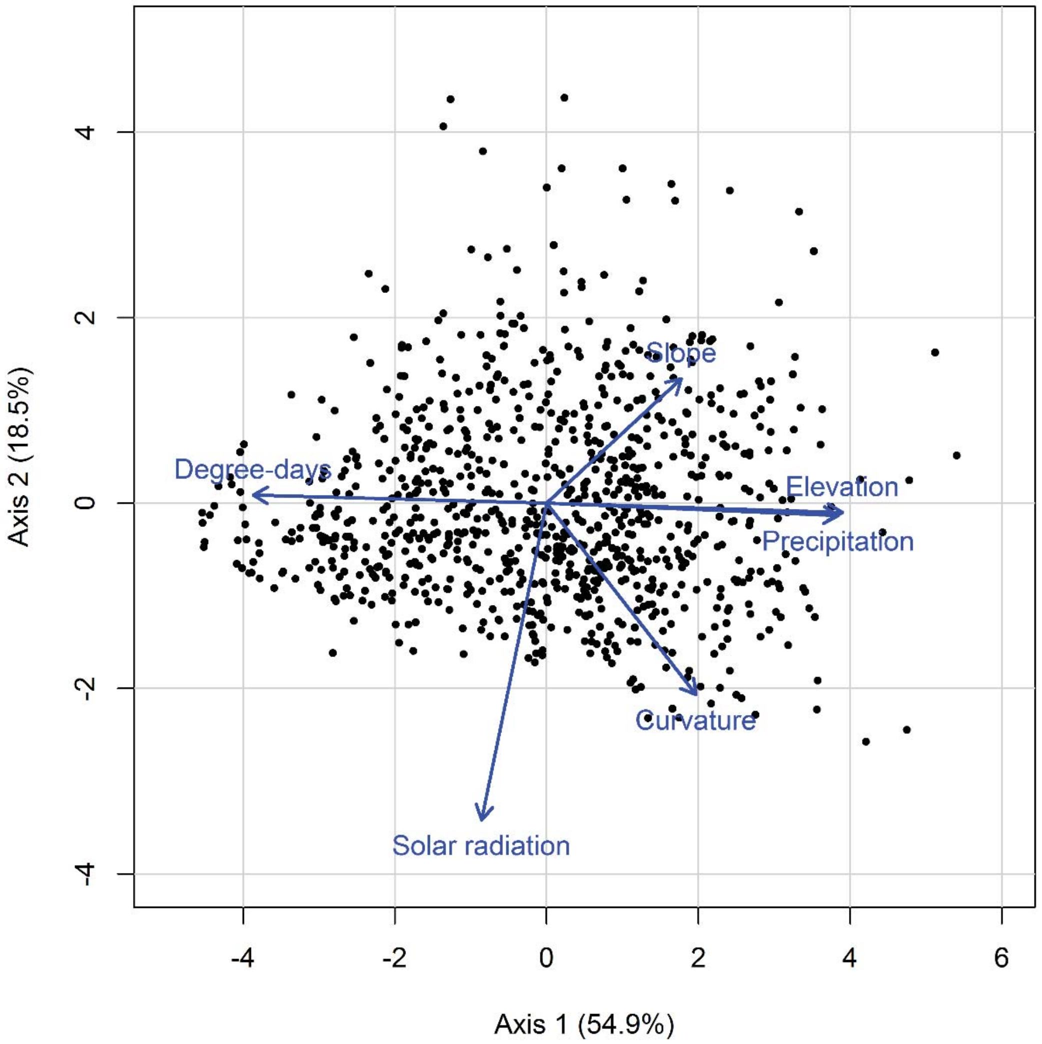

Fig. S2 Principal Components Analysis based on plot location (points) related to six environmental variables (blue arrows): elevation, annual sum of precipitation, annual sum of degree-days (better factor than mean temperature to explain plan distribution; Zimmermann and Kienast 1999), annual sum of solar radiation, curvature (related to shape of land, with negative values for concave areas, positive values for convex areas and 0 for flat areas or regular slopes) and slope. The two first axes of the initial PCA explained 73.4 % of the total variance (axis 1, 54.9 %; axis 2, 18.5 %). The length of the vectors represents the magnitude of the correlation between the variables and the axes.

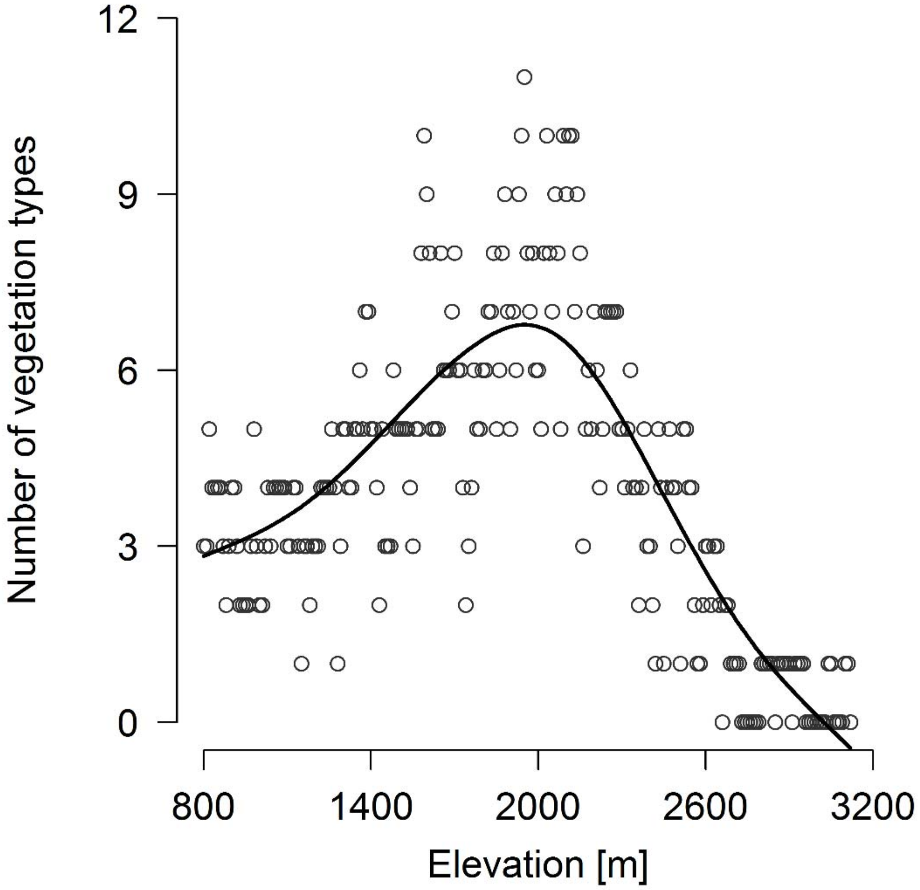

Fig. S3 Number of vegetation types among inventoried plots, within 20 m elevation bands centered on each 10 m elevation steps along the elevation gradient in the study area. The plots were grouped with a hierarchical clustering and the groups were attributed to a vegetation type, according to the classification of Delarze and Gonseth (2008), on the basis of their respective differential species. The curve was fitted with a GAM function.

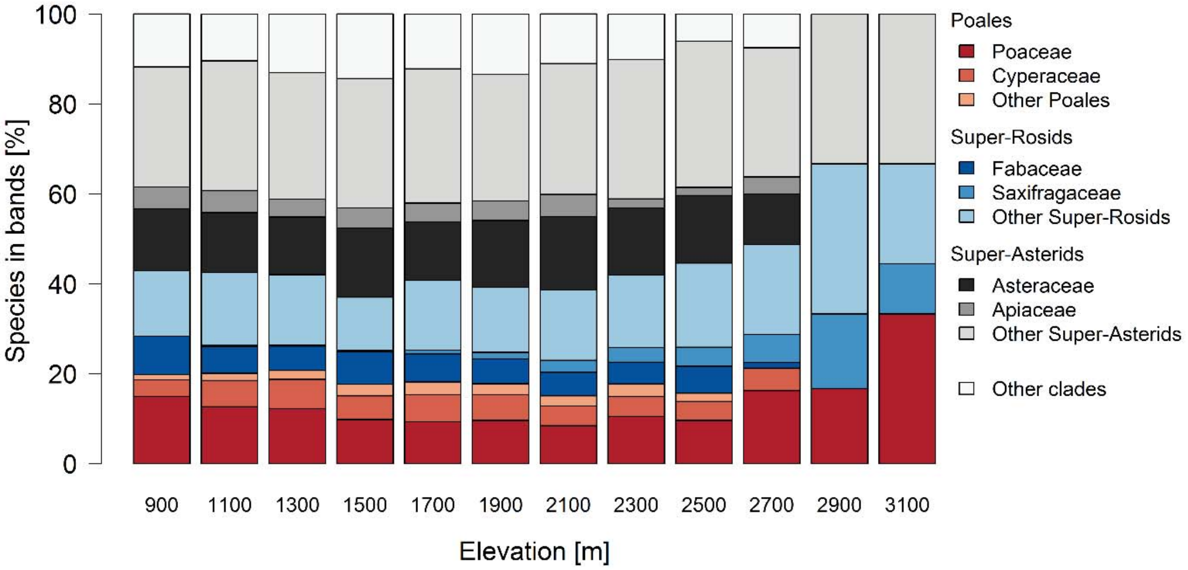

Fig. S4 Proportion of the main vascular plant clades in the species pool (gamma-diversity) in elevation bands of 200 m. The different shades of red-orange correspond to Poales, the blue shades to Super-Rosids and the grey-black shades to Super-Asterids.

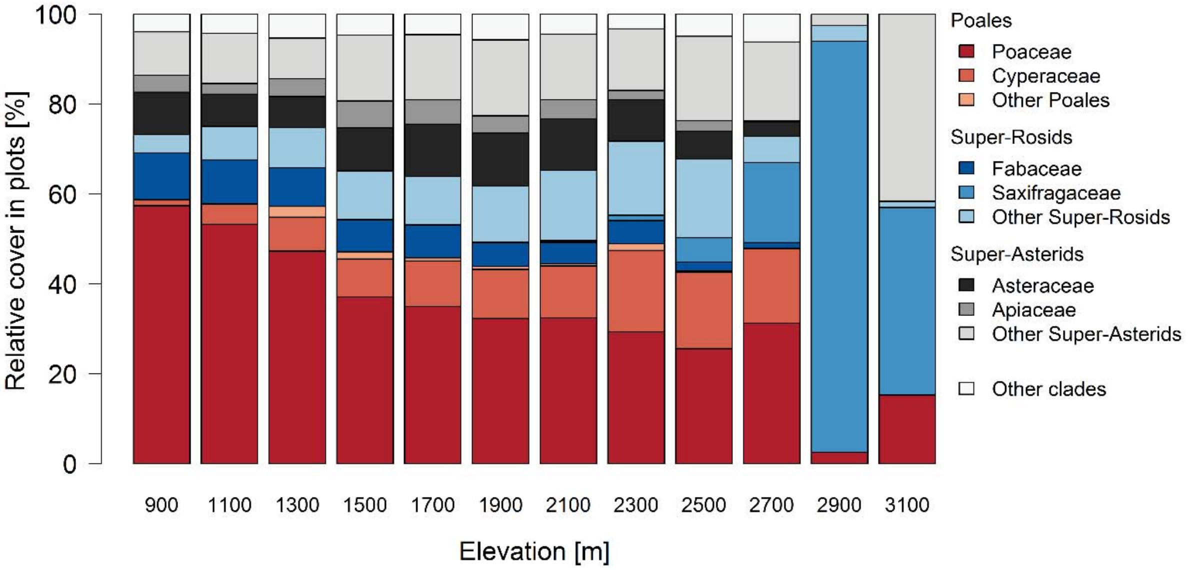

Fig. S5 Mean relative cover (bare soil and rock excluded) of the main vascular plant clades in plant communities in elevation bands of 200 m. See Fig. S5 for the real mean cover of the main vascular plant clades in plant communities when taking in account bare soil and rock. The different shades of red-orange correspond to Poales, the blue shades to Super-Rosids and the grey-black shades to Super-Asterids.

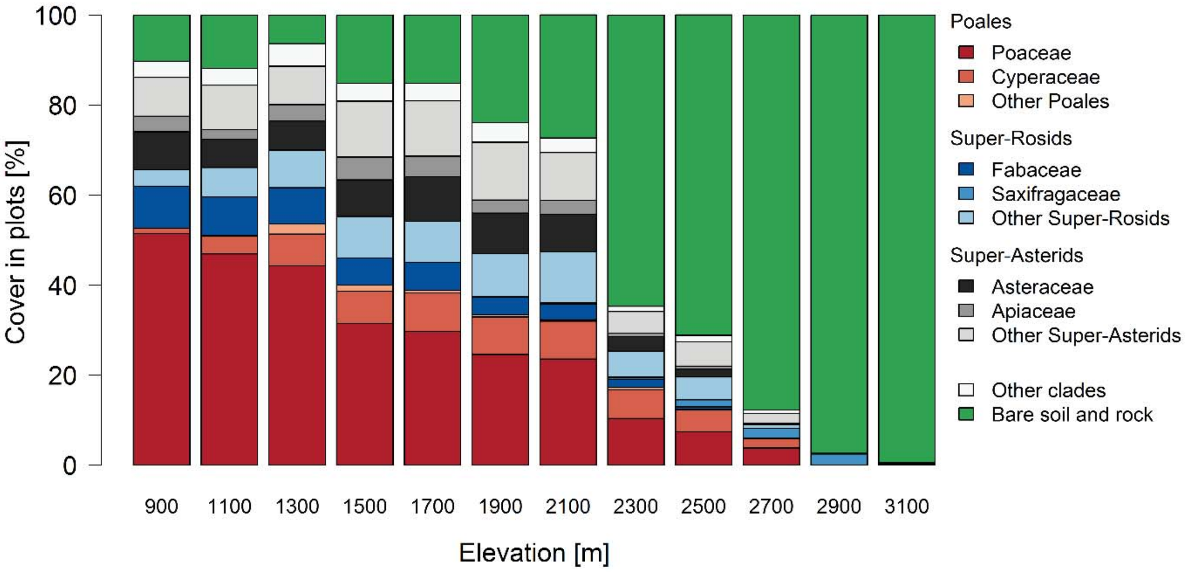

Fig. S6 Mean cover of the main vascular plant clades and cover of bare soil and rock in plant communities in elevation bands of 200 m. The different shades of red-orange correspond to Poales, the blue shades to Super-Rosids and the grey-black shades to Super-Asterids.

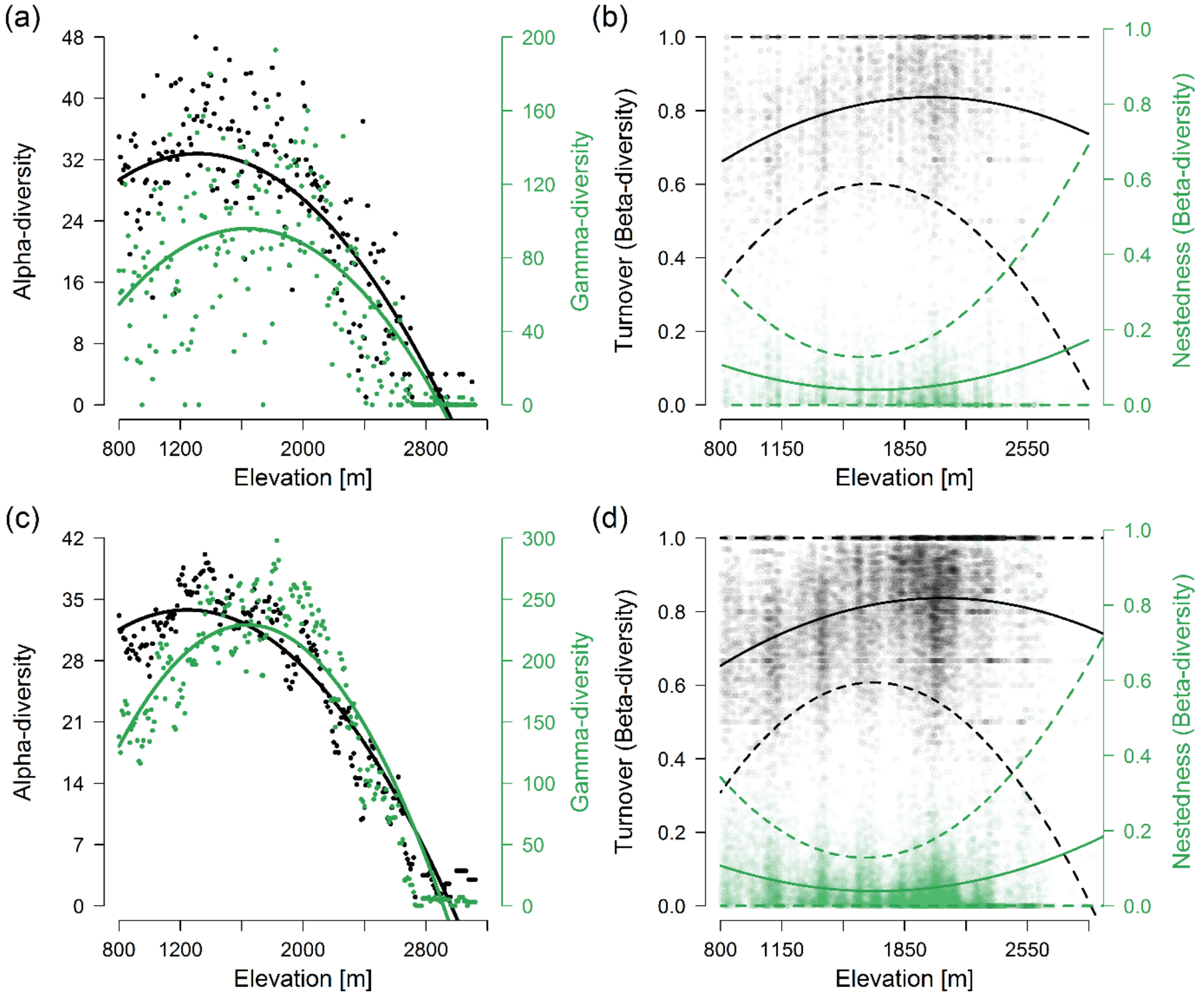

Fig. S7 Diversity changes along the elevation gradient obtained by comparing plant communities of the same elevation (range; a and b: 10 m; c and d: 50 m) as a measure of (a and c) mean community diversity (black points; mean alpha-diversity), total species richness (green points; gamma-diversity) and (b and d) proportion of species turnover (black points; turnover component of beta-diversity) and nestedness (green points; nestedness component of beta-diversity). Curves represent the quadratic relationships. Dashed lines represent the 5 and 95 percentiles.

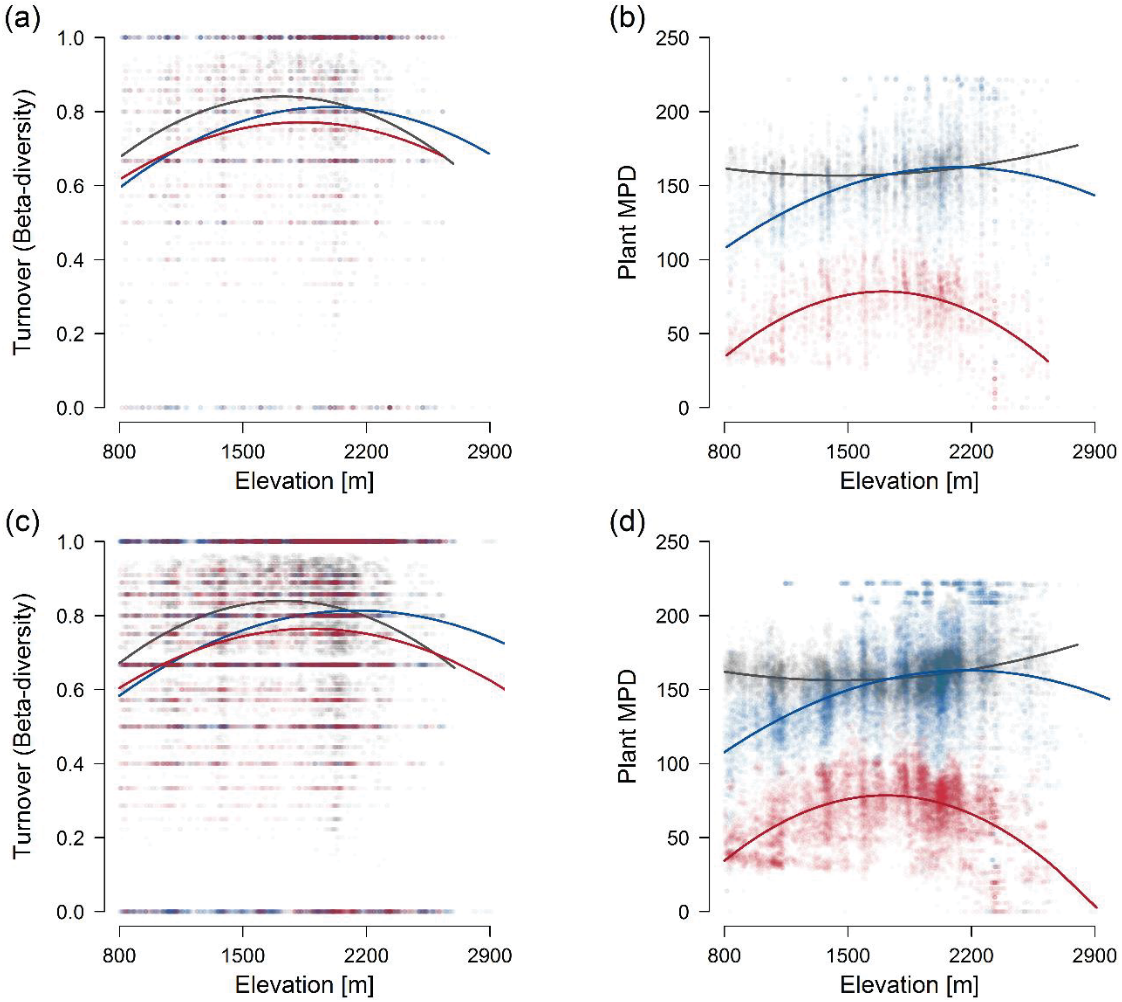

Fig. S8 Relationship between elevation and (a and c) proportion of plant species turnover (turnover component of beta-diversity) and (b and d) phylogenetic plant relatedness calculated as the mean pairwise distance (MPD) separating taxa in pairs of plant inventories of the same elevation (range; a and b: 10 m, c and d: 50 m) for Super-Asterids (black points), Super-Rosids (blue points) and Poales (red points) clades. Curves represent the quadratic relationships.

References

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Zimmermann NE, Kienast F (1999) Predictive mapping of alpine grasslands in Switzerland : Species versus community approach. J Veg Sci 10:469–482. doi: 10.2307/3237182