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Plant functional and phylogenetic turnover correlate with climate and land use in the Western Swiss Alps

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Abstract

Aims
Understanding the relative importance of historical and environmental processes in the structure and composition of communities is one of the longest quests in ecological research. Increasingly, researchers are relying on the functional and phylogenetic β-diversity of natural communities to provide concise explanations on the mechanistic basis of community assembly and the drivers of trait variation among species. The present study investigated how plant functional and phylogenetic β-diversity change along key environmental and spatial gradients in the Western Swiss Alps.

Methods
Using the quadratic diversity measure based on six functional traits—specific leaf area, leaf dry matter content, plant height, leaf carbon content, leaf nitrogen content and leaf carbon to nitrogen content alongside a species-resolved phylogenetic tree—we relate variations in climate, spatial geographic, land use and soil gradients to plant functional and phylogenetic turnover in mountain communities of the Western Swiss Alps.

Important Findings
Our study highlights two main points. First, climate and land-use factors play an important role in mountain plant community turnover. Second, the overlap between plant functional and phylogenetic turnover along these gradients correlates with the low phylogenetic signal in traits, suggesting that in mountain landscapes, trait lability is likely an important factor in driving plant community assembly. Overall, we demonstrate the importance of climate and land-use factors in plant functional and phylogenetic community turnover and provide valuable complementary insights into understanding patterns of β-diversity along several ecological gradients.

Keywords: ecological gradients, functional and phylogenetic β-diversity, plant community turnover, Rao's quadratic entropy index (Q), Western Swiss Alps

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INTRODUCTION

Traits inherited through the evolution of lineages define the capacity of species to survive in communities within a given environment, and also have an influence on the phylogenetic community structure (Graham *et al.* 2009). Despite the recent use of phylogenetic approaches in ecology to understand how species assemble into communities, most studies have generally focused on ecosystem functioning and community diversity (Cadotte *et al.* 2008; Cavender-Bares *et al.* 2009; Flynn *et al.* 2009). Yet, in several ecosystems, the diversity among communities plays a fundamental role in ecological community structure and is influenced through various forms of habitat modification such as human land use (Vellend *et al.* 2007; Hofer *et al.* 2008; Kessler *et al.* 2009). The effects of land use often complement environmental drivers (e.g. climatic, edaphic) and may lead to a cascade of negative effects on biodiversity, such as the loss of trait diversity (Flynn *et al.* 2009). Importantly, the loss of trait diversity may directly alter the evolutionary history of species communities, if the specific traits favouring species' response to external conditions are phylogenetically conserved, and tend to occur in phylogenetically clustered communities (Helmus *et al.* 2010; Knapp *et al.* 2008). In this context, investigating the functional and phylogenetic β-diversity of communities can provide better insights into the main factors that drive variation in the composition of ecological communities. However, thus far, only a few studies have investigated the impacts of both environmental (including human land use) and spatial factors on community phylogenetic structure (Wiens *et al.* 2010).

Non-random community structure have been postulated to arise through deterministic processes (e.g. environmental filtering and density-dependent interactions) driven by environmental change (Cavender-Bares *et al.* 2009; Webb *et al.* 2002). However, a clear detection of these processes requires sound knowledge of the functional and phylogenetic variations among communities (Pellissier *et al.* 2013; Swenson 2011). Functional traits are considered to provide valuable information about a species ecological niche because they arose in a given environment associated with particular selective pressures (Lavorel *et al.* 2007). They have thus been widely used to investigate community assembly by identifying the key traits that are robust indicators of ecological strategies (Swenson *et al.* 2011; Westoby *et al.* 2002). However, measured traits are not necessarily those creating patterns of diversity or affecting species' response to particular environmental conditions, at least not fully (Cavender-Bares *et al.* 2009; Flynn *et al.* 2009). Therefore, in complement to functional diversity, investigating changes in phylogenetic diversity along broad ecological gradients can yield additional useful information on the ecological and evolutionary processes that shape community structure (Graham and Fine 2008; Webb *et al.* 2002).

Both functional and phylogenetic diversity can be partitioned into within-community (α), among-community (β) and regional (γ) diversity components (Graham and Fine 2008; Meynard *et al.* 2011; Ricotta and Szeidl 2009; Whittaker 1972). In contrast to the other components of diversity, β-diversity (i.e. the compositional turnover among communities; Whittaker 1972) integrating both functional and phylogenetic diversity has received very little attention in studies of species distributions and assemblage formation (Devictor *et al.* 2010). Rather, most studies have relied on species β-diversity, which is limited by assigning equal weight among taxa and ignoring phylogenetic branch lengths (Graham and Fine 2008; Swenson 2011). Furthermore, a complete turnover in the species composition between two communities may correspond to little or no turnover in the functional or phylogenetic community turnover (Graham and Fine 2008; Meynard *et al.* 2011; Swenson *et al.* 2011). The low number of studies may have persisted because of the difficulty in separating patterns of functional and phylogenetic β-diversity (Graham and Fine 2008). Thus, where available, spatial geographic distances have been used in concert with environmental distances to better understand the patterns of compositional β-diversity (Legendre *et al.* 2005) and reveal which pure spatial or environmental variations best predict community dissimilarity (Condit *et al.* 2002; Legendre *et al.* 2005; Whittaker 1972).

Functional β-diversity measures the turnover between communities by estimating the functional dissimilarity among species across space (Swenson 2011; Swenson *et al.* 2011). Phylogenetic β-diversity measures the phylogenetic distance among communities across space (Graham and Fine 2008). As a measure linked to phylogenetic composition, phylogenetic β-diversity provides evolutionary explanations for patterns of β-diversity along ecological gradients, and possibly reveals the lineages that largely drive these patterns (Dinnage 2009; Graham and Fine 2008). In general, the measurement of β-diversity is very important in biodiversity and ecological modelling studies (Devictor *et al.* 2010; Mokany *et al.* 2011) because it can capture complex interactions along ecological gradients and eliminate the subjectivity associated with community delimitation (Graham and Fine 2008; Graham *et al.* 2009).

Here, we investigate variations in the functional and phylogenetic β-diversity of plant communities along broad ecological gradients in the Western Swiss Alps. We use a comprehensive dataset comprising six functional leaf traits, a well-resolved species-level phylogeny, and four sets of ecological gradients namely climatic variables (temperature, moisture, solar radiation), spatial geographic distances, seven land-use variables (exploited meadow, middle intensity meadow, unfertilized meadow, pasture, unfertilized pasture, high mountain pasture, unexploited area) and soil properties (soil pH, soil phosphorus, soil nitrogen). These variables were carefully chosen for their potential significant role in mountain plant distributions (Dubuis *et al.* 2012; Pellissier *et al.* 2013; Randin *et al.* 2009). In particular, land use is an important factor in plant community assembly (Hofer *et al.* 2008; Vellend *et al.* 2007), and growing evidence suggests that it may influence nonrandom patterns of phylogenetic community structure (Flynn *et al.* 2009; Knapp *et al.* 2008). Thus, given that these variables may be important in driving plant distributions, we expect high functional and phylogenetic turnover rates in plant communities across space. We used two different measures of β-diversity to relate functional and phylogenetic β-diversity patterns to the ecological gradients. Specifically, we asked two main questions. First, do functional and phylogenetic β-diversity biodiversity facets exhibit similar representation of compositional turnover in mountain communities? Second, what is the relationship between the β-diversity facets (functional and phylogenetic β-diversity) and climate, spatial, land use and soil gradients?

MATERIALS AND METHODS

Study area

The study area is a 700-km^2 region located in the Western Swiss Alps (Fig. 1). Elevation of the area ranges from 375 to 3210 m a.s.l. The mean annual temperature and precipitation vary from 8°C to −5°C and from 1200 mm to 2600 mm, respectively (Bouët

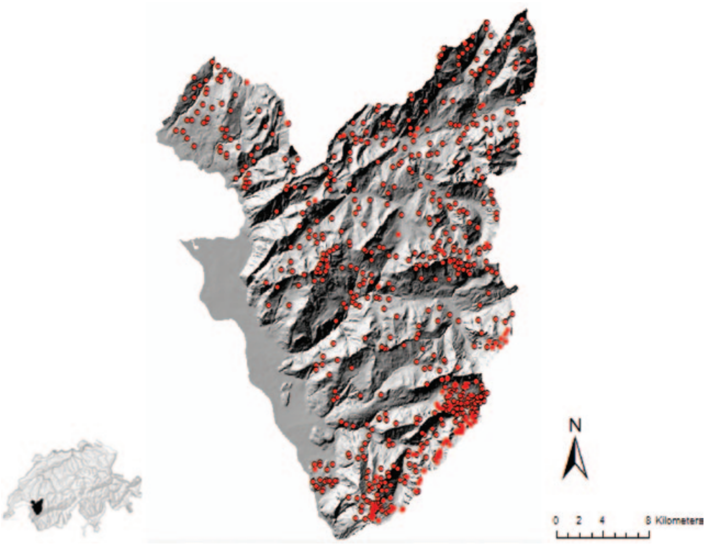

Figure 1: geographical location of the study area in the Western Alps of Canton de Vaud, Switzerland. The red dots represent the 693 sampled plots in the area.

1985). The soil parent material is typically calcareous. In this region, the highlands are predominantly occupied by important glaciers and alpine grasslands. At lower elevations, the vegetation structure is heavily influenced by land use, with open non-forested areas commonly used for agriculture. Diverse vegetation types characterize the vegetation structure along the elevation belts, but fertilized pastures and meadows are common from the forelands to the subalpine areas and unfertilized, grazed grasslands in subalpine and alpine areas (Randin *et al.* 2009).

Field sampling

The community data comprised 693 4-m^2 plots sampled between May and September of 2002–10. The plots were selected from open non-forested areas following a stratified random sampling based on elevation, slope and aspect (Hirzel and Guisan 2002). The sampling was centred on plot surfaces of 4 m^2 (Fig. 1). Each plot was separated by at least 200 m from other plots to minimize spatial autocorrelation (Randin *et al.* 2009). Plant species were exhaustively inventoried from the plots, and the species cover was estimated using the simplified cover scheme of Vittoz and Guisan (2007): <0.1, 0.1–1, 1–5, 5–15, 15–25, 25–50, 50–75 and >75%. The median values of these classes: 0.05, 0.5, 3, 10, 20, 37.5, 62.5 and 82.5% were used to estimate species abundances. These percentages were chosen to provide more reliable estimates and appropriate values for the statistical analyses of the vegetation cover in this mountain region. For further analyses, we retained 231 of 260 most locally frequent and abundant vascular plant species with >20 occurrences (i.e. number of individuals) in the plots.

Preparation of DNA samples

Total DNAs were extracted from silica-dried leaf materials of 160 species collected from the study area, using Qiagen's DNA kit (Qiagen, Hilden, Germany). CTAB protocols (Doyle and Doyle 1987) were used for about 14 of these 160 species with strong chemical inhibiting compounds. To ensure thorough pulverisation, leaf samples were ground with 2 pellet balls using a standard pulverizing machine for 60 s and 30 Hz. The plastid *rbcL* gene (ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit) was amplified by polymerase chain reaction (PCR) using standard forward and reverse primers for angiosperm species (Olmstead *et al.* 1992). Reactions were performed on ice in 50 μl volumes, each containing 33.6 μl of sterile water, 10.0 μl of 10× DNA polymerase buffer 3.0μl of dNTP (10 mM), 1.0 μl of each primer (10 μM), 0.4 μl of *Taq* DNA polymerase (Bioline, London, UK) and 1.0 μl of aqueous dilution of DNA. PCR amplification was carried out on an Applied Biosystems GeneAmp 2700 thermal cycler (Applied Biosystems, CA, USA) using an initial denaturation of 2 min at 94°C followed by 34 cycles of 60 s at 94°C, 60 s at 50°C of annealing time, 2 min at 72°C of extension and a final extension of 7 min at 72°C.

Resultant PCR products were run on 1.2% agarose gels and stained with ethidium bromide before viewing in GeneSnap (Syngene, USA). They were purified using a Qiaquick PCR purification kit (Qiagen, Hilden, Germany) before the sequencing reaction. Cycle sequencing of the purified PCR products were done with the forward and reverse primers in both directions, an additional primer 20R (5´-TGCATTGC [A/G] CGGTG [A/G] ATGTG-3´) was designed to capture most of the internal sections of the *rbcL* gene. Reactions were performed on ice in 10 μl volumes, each contained 5.0 μl of sterile water, 2.0 μl of sequence terminator ABI Big Dye version 3.1 (Applied Biosystems, CA, USA; sequencing kit manual), 1.0 μl of each primer and 2.0 μl of cleaned PCR product. Sequencing reaction was done on an initial denaturation of 3 min at 96°C; 30 cycles of 15 s at 96°C, 15 s at 50°C and 90 s at 60°C. Cycle sequencing products were visualized on an ABI 3100 DNA sequencer (Applied Biosystems, CA, USA). Sequences were later checked for identity by Basic Local Alignment Search Tool search for highly similar sequences using the National Center for Biotechnology Information online blast facility. Forward and reverse contigs were edited and assembled with DNA Baser version 3× (DNA Baser, Heracle Biosoft) before exported for alignment. This study generated 160 fresh DNA sequences using the *rbcL* gene. We augmented the data to obtain a full plant phylogeny of 231 species by downloading 73 *rbcL* (including two outgroups) and 123 *matK* sequences from published sources in GenBank (Table S1). The sequence alignment generated as part of this study is deposited in the Dryad repository (doi:10.5061/dryad.q0fh6734) and in GenBank (accession nos. KF602071-KF602251).

Phylogenetic reconstructions

Plant phylogenetic relationships were inferred from the molecular data obtained for the 231 sampled species. Sequences were aligned in SEAVIEW (Gouy *et al.* 2010) and rooted on two gymnosperm outgroups: *Abies alba* Mill. and *Picea abies* (L.) H. Karst. (Table S1). The final concatenated matrix consisted of 3092 nucleotide base pairs. We used the GTR + Γ model of sequence evolution to infer the phylogenetic tree as determined by the software jMODELTEST (Posada 2008) based on the Akaike Information Criterion.

Phylogenetic reconstructions were performed using two Bayesian methods. First, a phylogram was constructed using MrBAYES (Ronquist *et al.* 2012). Two independent analyses that included four Metropolis-coupled Markov chains (MCMC) starting at different random trees were run for 30 million generations each, sampling trees every 1000 generations. Default priors were used for all model parameters. Convergence of the two independent MCMC runs was assessed from the effective sampling size (ESS) of the model parameters and the log likelihood values in the TRACER software (Drummond and Rambaut 2007). A burn-in of 10 000 sampled trees was applied, before an all-compatible majority consensus tree was reconstructed from the remaining 20 000 sampled trees. Second, a time-calibrated tree was constructed in BEAST (Drummond and Rambaut 2007) using nine published fossils (Magallón and Castillo 2009; Table S2). All priors for the fossils were drawn from lognormal distributions, with means and standard deviations set to reflect the 95% confidence intervals in the fossil records. We used a Yule model for the tree prior and the searches used an uncorrelated relaxed molecular clock. Analyses were run for 80 million generations, sampling parameters and trees every 1000 generations. Convergence of the two independent runs was assessed as for the MrBAYES analyses from the ESS of the model parameters and log likelihood values in Tracer. A burn-in of 40 000 trees was applied, before reconstructing the dated tree from the remaining 40 000 trees. The resulting trees from MrBAYES and BEAST (Figs S1 and S2) were highly congruent with the Angiosperm Phylogeny Group (2009) classification, but we chose the time-calibrated tree for further analyses.

Plant functional traits

We used six plant functional traits that represent important syndromes of resource-use and competitive strategies. These traits were leaf carbon content (C), leaf nitrogen content (N), the ratio between leaf carbon and nitrogen content (C/N), leaf dry matter content (LDMC) measured as the ratio of leaf dry mass to its water-saturated fresh mass (in mm g^{-1}), specific leaf area (SLA) measured as the ratio of leaf surface to its dry mass (in mm^2 mg^{-1}), and plant height (H in cm) measured as the distance between the top of the photosynthetic tissue and the ground. C and N are linked to plant photosynthetic rates and nutrient cycling processes. LDMC is linked to the average density of leaf tissue and leaf lifespan. SLA is linked to relative growth rate and photosynthetic ability. H is linked to plant competitive ability and above-ground biomass (Cornelissen *et al.* 2003). LDMC, SLA and H are well documented for important plant ecological strategies, and their crucial role in mediating community assembly (e.g. Ackerly and Cornwell 2007; Westoby *et al.* 2002).

LDMC, SLA and H were gathered for all 231 species, while C, N and C/N were measured for 220 plant species, and we pruned the 11 species without these measures from the inferred phylogenetic tree. To better understand the spatial congruence between functional and phylogenetic β-diversity, we measured the degree of tree-wide phylogenetic signal in the six traits using K of Blomberg *et al.* (2003) in the R package PICANTE (Kembel *et al.* 2010).

Climate, spatial, land use and soil gradients

Climatic data were derived from the Swiss national meteorological stations for temperature degree-days (DDEG), moisture index (MIND) and solar radiation (SRAD), using a digital elevation model at 25 m resolution. We calculated DDEG from spatially interpolated daily temperatures based on the sum of days multiplied by temperature above 0°C, whereas MIND was calculated as the monthly average of daily water balance (precipitation–evapotranspiration). SRAD was calculated as the sum of the monthly average of daily global solar radiation in ArcGIS 10 following Randin *et al.* (2009). These variables are expected to have important ecophysiological significance for mountain plant species and are well correlated with the upper distribution limit of plant communities (Randin *et al.* 2009).

For each plot location, we extracted the values of climatic variables from the corresponding climatic layer. The spatial variable was represented by the geographic coordinate position (GEO) of each plot. The land use (LU) data consisted of seven different land management categories. These data were obtained by directly interviewing local farmers in the study area, and reclassifying the information on a raster grid in ArcGIS 10 (full details are in Randin *et al.* 2009). The land-use types (exploited meadow, middle intensity meadow, unfertilized meadow, pasture, unfertilized pasture, high mountain pasture and unexploited area) were classified according to the activity conducted on the sampled surface (Fig. 2; Table 1). This data was available for 340 of the 693 communities and was used to quantify the proportion of plant families in each land management category.

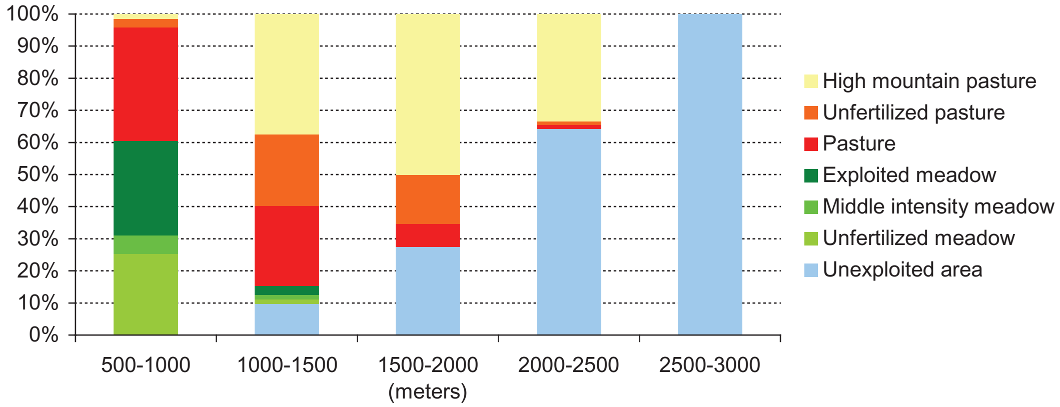

Figure 2: categories of land use at the 340 sampled sites grouped by elevation range. *High mountain pasture*: unfertilized pasture that is grazed only during summer by relatively low numbers of cattle. *Exploited meadow*: fertilized meadow that is used for hay production, generally mown two or three times a year and sometimes grazed in autumn. *Middle intensity meadow*: meadow that is lightly fertilized (with manure or compost) and mown once a year. *Unfertilized meadow*: unfertilized meadow that is mown once a year in July. *Pasture*: pasture that is grazed by cattle of various kinds, usually fertilized and sometimes mown. *Unfertilized pasture*: unfertilized pasture that is found at low and middle elevation. *Unexploited area*: area that is not exploited due to rocks, rock fall or other factors. Data obtained from Randin *et al.* (2009).

Table 1: land use data consisting of seven different land management practices in the Western Swiss Alps (Data obtained from Randin *et al.* (2009))

Land use class	Description	Number of plots
Exploited meadow	Meadow principally exploited for hay production, generally mown two or three times a year, fertilized and sometimes grazed in autumn.	23
Middle intensity meadow	Lightly fertilized (manure or compost) meadow, mown once a year.	5
Unfertilized meadow	Unfertilized meadow, mown once a year in July.	19
Pasture	Pasture grazed by cattle of different kinds, usually fertilized, sometimes mown with varying intensity.	51
Unfertilized pasture	Unfertilized pasture, at low or middle elevation.	34
High mountain pasture	Pastured grazed only during summer in subalpine–alpine areas, unfertilized, low intensity of cattle grazing.	105
Unexploited area	Unexploited (rocks, rock fall).	103

Lastly, three soil variables namely soil pH, total soil phosphorus (soil P) and total soil nitrogen (soil N) content were measured from the first 10 cm of the top organo-mineral horizon in 190 communities in the study area (see Dubuis *et al.* 2012).

Plant functional and phylogenetic β-diversity

To understand the influence of each trait on β-diversity, we measured functional β-diversity for each functional trait, and phylogenetic β-diversity using the modified version of Rao's quadratic entropy index (*Q*; Leinster and Cobbold 2012; Rao 1982; Ricotta and Szeidl 2009) published in de Bello *et al.* (2010). The statistical architecture of *Q* allows the computation of β-diversity by the additive partitioning of the total diversity in an area and the comparison of the observed values to an appropriate null model (see de Bello *et al.* 2010; Pellissier *et al.* 2013). A null model was used to determine if β-diversity deviated from the expectations of a random assembly (Kraft *et al.* 2011; Pellissier *et al.* 2013). This approach is increasingly used to differentiate functional and phylogenetic community structure from randomly assembled communities, especially when an elevation gradient is considered (Kraft *et al.* 2011). *Q* was computed using null distributions (Gotelli and Graves 1996) that reshuffled the names on the phylogeny and the functional distance matrix 9999 times (Kembel *et al.* 2010). The randomization procedure evaluated the effect of the phylogeny and functional traits but fixed species prevalence and species richness, thereby preserving the important properties over the study area (Pellissier *et al.* 2013). The null distributions generated for functional and phylogenetic β-diversity were then compared with the observed functional and phylogenetic β-diversity among communities to detect significantly dissimilar pairs of communities (>95th percentile). In this analysis, species with more similar functional trait values and phylogenetic relatedness are placed close to each other, generating a smaller value in comparison to species that have less similar trait values or phylogenetic relationships. The functional and phylogenetic dissimilarities were generated from the estimation of $\beta_{\text{Norm-prop}}$ (see de Bello *et al.* 2010), which is rescaled from 0 to 1 based on increasing dissimilarity between pairs of communities.

We related the functional and phylogenetic dissimilar pairs of communities measured with *Q* to variations in climate (DDEG, MIND and SRAD), spatial (GEO), land use (LU) and soil (soil pH, soil P and soil N content) gradients measured with Euclidean distances. We assessed if dissimilar pairs of communities significantly varied along these gradients using Mantel tests (e.g. Pellissier *et al.* 2013; Swenson 2011) and 9999 permutations. Mantel correlations may yield much smaller absolute values than regular correlation coefficients on the same raw data, however, the Mantel test is more appropriate for partitioning the variation in community composition along environmental and spatial gradients (Dutilleul *et al.* 2000; Legendre *et al.* 2005). As partial Mantel test is similarly suited to the analysis of the variation in β-diversity among communities (Legendre *et al.* 2005), we used this method to assess the independence of functional and phylogenetic β-diversity along the ecological gradients, including the explanatory overlap among the four most representative ecological variables on β-diversity. Pearson's product-moment correlations analyzed for comparisons with the Mantel and partial Mantel tests are provided in the supplementary data (Tables S3, S4 and S5). Finally, we related these four ecological variables to β-diversity using constrained analysis of principal coordinates (CAP) implemented in the "vegan" R library. We tested the significance of the relationship using Monte Carlo permutation tests randomized 2000 times. We then plotted the results of the CAP analysis using coloured dots to represent each land-use category. All statistical analyses were performed in R (R Development Core Team 2012).

RESULTS

Phylogenetic reconstructions

The two Bayesian inferences produced highly congruent topologies (Figs S1 and S2; Ndiribe *et al*., unpublished data). The chronogram, in particular, was well supported with nodes fully congruent with the Angiosperm Phylogeny Group tree (2009). A total of 71% nodes showed posterior probabilities ≥95%. Deep nodes were well supported in comparison with a few terminal nodes, e.g. the terminal nodes belonging to some members of Asteraceae, Cyperaceae, Lamiaceae and Poaceae. Overall, our results retrieved the monophyly in the angiosperm families and genera.

Phylogenetic signal

The phylogenetic signal in the six traits, as measured with K of Blomberg *et al.* (2003), showed estimated K values that were all less than one (Table 2) and corresponded to a convergent pattern of evolution (K of Blomberg *et al.* 2003; Kembel *et al.* 2010). However, *P* values for the two traits C and N were higher than 5%, which indicates that despite the low phylogenetic signal, trait evolution is nevertheless higher than expected following a random distribution of traits on the phylogeny. For the 231 species, LDMC had the highest signal (K = 0.33, $P < 0.001$), followed by SLA (K = 0.13, $P < 0.001$) and H (K = 0.10, $P < 0.001$). For the 220 species, C/N had the highest signal (K = 0.14, $P < 0.001$), followed by N (K = 0.09, $P = 0.08$), and C (K = 0.07, $P = 0.45$).

Table 2: **phylogenetic signal in functional traits measured with K of Blomberg *et al.* (2003; K < 1 signify low phylogenetic signal, while K > 1 signify high phylogenetic signal)**

Functional trait	K value	*P* value
LDMC	0.33	0.001
SLA	0.13	0.001
Plant height (H)	0.10	0.001
Leaf carbon to nitrogen content (C/N)	0.14	0.001
Leaf nitrogen (N)	0.09	0.08
Leaf carbon (C)	0.07	0.45

β-Diversity and ecological variation

Functional and phylogenetic β-diversity showed significant correlations with each other in H and LDMC, but not with the other traits. We also identified functional turnover that was statistically independent of phylogenetic turnover in H (Table 3). Functional and phylogenetic β-diversity showed the most significant correlations with climatic temperature (DDEG) and moisture (MIND), land use (LU) and spatial (GEO) variables but were poorly correlated with soil nitrogen and phosphorus (soil N and soil P) (Fig. S3; Table 3). For functional turnover, we found that H and SLA traits were most influenced by DDEG, MIND, GEO and LU factors, in contrast to LDMC, which was the least response variable for functional turnover. The other traits (N, C and C/N) ranked intermediate in their performance along these gradients. Overall, plant functional turnover exhibited the highest response in H and SLA, followed by N and C/N (Fig. S3; Table 3). Similarly, for phylogenetic turnover, we found that phylogenetic β-diversity was most influenced by DDEG, MIND, GEO and LU factors (Table 3). These results were also corroborated by the partial Mantel tests (Tables 4 and 5).

The effect of land use on functional and phylogenetic β-diversity

Phylogenetic β-diversity in complement to most functional β-diversity variables suggests that land use (LU) is an important driver of plant community structure (Table 3). For instance, even though the three land management categories (middle intensity meadow, exploited meadow and pasture) are practiced in a few communities (Table 1), they still exhibited the highest proportional representation (0.89, 0.88 and 0.82, respectively; Fig. S4) of plant families in the area. Furthermore, the CAP results from the 340 LU communities showed an overall significant effect of climate (DDEG and MIND) and spatial (GEO) variables on functional and phylogenetic β-diversity (Fig. 3; Table S6). This analysis corroborates the importance of climatic variables (mainly DDEG, MIND and GEO) in driving functional and phylogenetic

Table 3: **correlations between each functional β-diversity and phylogenetic β-diversity (hereafter β-PD) variable assessed with Mantel tests**

	β-PD	N	C	C/N	LDMC	SLA	H
Mantel *r*							
N	−0.02 (ns)						
C	−0.04 (ns)	−0.02 (ns)					
C/N	−0.05 (ns)	0.57***	−0.08 (ns)				
LDMC	0.14***	0.17***	−0.03 (ns)	0.25***			
SLA	0.01 (ns)	0.32***	−0.04 (ns)	0.35***	0.19***		
H	0.20***	0.06***	−0.11 (ns)	0.08***	0.01 (ns)	0.23***	
DDEG	0.14***	0.13***	0.02 (ns)	0.13***	−0.01 (ns)	0.33***	0.36***
MIND	0.15***	0.09***	−0.08 (ns)	0.09***	0.01 (ns)	0.26***	0.37***
SRAD	0.04**	−0.02 (ns)	−0.05 (ns)	−0.03 (ns)	0.02 (ns)	−0.01 (ns)	0.03*
GEO	0.08***	0.04***	−0.01 (ns)	0.04**	−0.01 (ns)	0.15***	0.15***
Soil N	0.03 (ns)	−0.03 (ns)	−0.01 (ns)	0.02 (ns)	0.04 (ns)	0.06 (ns)	0.04 (ns)
Soil pH	0.01 (ns)	−0.06 (ns)	−0.01 (ns)	−0.02 (ns)	0.01 (ns)	−0.02 (ns)	0.08 **
Soil P	0.03 (ns)	−0.01 (ns)	0.04 (ns)	0.01 (ns)	0.01 (ns)	−0.01 (ns)	−0.03 (ns)
LU	0.07***	0.05***	0.03***	0.05***	−0.02 (ns)	0.12 ***	0.10***

Abbreviations: N = leaf nitrogen, C = leaf carbon, C/N = leaf carbon-nitrogen content, H = plant height, soil N = total soil nitrogen content, soil pH, soil P = total soil phosphorus content.
The Mantel *r* statistic and *P* values were calculated following 9999 permutations.
Mantel *r* values ≥ 0.10 are presented in bold while significant *P* values are asterisked.

Table 4: **co-variation between β-diversity and the ecological variables assessed with partial Mantel tests**

	N	C	C/N	LDMC	SLA	H
Co-variable (β-PD)						
Mantel *r*						
DDEG	**0.13*****	−0.04 (ns)	**0.14*****	−0.03 (ns)	**0.33*****	**0.34*****
MIND	**0.10*****	−0.07 (ns)	**0.11*****	−0.01 (ns)	**0.26*****	**0.35*****
SRAD	−0.02 (ns)	−0.05 (ns)	−0.02 (ns)	0.02 (ns)	−0.01 (ns)	0.02*
GEO	0.04 ***	−0.01 (ns)	0.04***	−0.02 (ns)	**0.15*****	**0.14*****
Soil N	−0.03 (ns)	−0.01 (ns)	0.01 (ns)	0.03 (ns)	0.06 (ns)	0.01 (ns)
Soil pH	−0.06 (ns)	−0.01 (ns)	−0.02 (ns)	−0.01 (ns)	−0.02 (ns)	0.08**
Soil P	−0.01 (ns)	0.03 (ns)	−0.02 (ns)	0.01 (ns)	−0.01 (ns)	−0.03 (ns)
LU	0.05***	0.04***	0.06***	−0.03 (ns)	**0.12*****	0.09***

The partial Mantel statistic provides the correlation between the functional β-diversity and ecological variable, when the effects of phylogenetic β-diversity are controlled.
Mantel *r* values ≥ 0.10 are presented in bold, while significant *P* values are asterisked.
The complete variable names are given in Table 3.

turnover in this region. Finally, the partial Mantel tests suggest that LU may parallel climatic factors in partly influencing plant community turnover (e.g. correlations of phylogenetic β-diversity ($r = 0.08$, $P = 0.004$) and H ($r = 0.37$, $P = 0.001$) with DDEG). In fact, dissimilar pairs of communities may be found under different LU but similar temperature and moisture conditions (Table 5). Overall, among the eight abiotic variables investigated, solar radiation and soil properties were the weakest explanatory variables for plant functional and phylogenetic β-diversity.

DISCUSSION

In this study, we investigated patterns of functional and phylogenetic β-diversity along key ecological gradients of the Western Swiss Alps to understand the turnover among plant communities, and detect the key factors that drive this process in mountainous landscapes. Our results lead to two main points. First, climatic temperature and moisture (DDEG and MIND) and land use (LU) gradients are significantly related to plant functional and phylogenetic turnover, despite the relatively low *r* values provided by the Mantel test (Dutilleul

Table 5: co-variation between the β-diversity and the four most important ecological variables assessed with partial Mantel tests

Variable	Co-variable	β-PD	N	C	C/N	LDMC	SLA	H
Mantel r								
DDEG	LU	0.06**	0.08***	0.08***	0.06***	−0.02 (ns)	−0.18 (ns)	**0.26*****
LU	DDEG	−0.02 (ns)	0.01 (ns)	−0.02 (ns)	−0.02 (ns)	0.01 (ns)	−0.03 (ns)	−0.03 (ns)
GEO	LU	0.02 (ns)	0.02 (ns)	−0.01 (ns)	−0.01 (ns)	0.01 (ns)	−0.08 (ns)	0.08***
LU	GEO	−0.01 (ns)	0.03**	0.01 (ns)	0.01 (ns)	0.01 (ns)	−0.07 (ns)	0.04***
GEO	DDEG	0.04***	−0.01 (ns)	−0.03 (ns)	−0.03 (ns)	0.02 (ns)	0.06***	0.05***
DDEG	GEO	**0.12*****	0.08***	0.08***	0.06***	−0.02 (ns)	**0.30*****	**0.33*****
MIND	LU	**0.12*****	0.05***	0.09***	0.02 (ns)	−0.07 (ns)	−0.19 (ns)	**0.22*****
LU	MIND	−0.04 (ns)	0.01 (ns)	−0.02 (ns)	−0.01 (ns)	0.03**	−0.03 (ns)	−0.02 (ns)
MIND	DDEG	0.07***	0.01 (ns)	−0.07 (ns)	0.01 (ns)	0.03**	0.02 (ns)	**0.17*****
DDEG	MIND	0.04***	0.08***	0.02 (ns)	0.08***	−0.03 (ns)	**0.21*****	**0.13*****
GEO	MIND	0.05***	0.02**	0.01 (ns)	0.02 (ns)	−0.01 (ns)	**0.11*****	0.08***
MIND	GEO	**0.13*****	0.09***	−0.08 (ns)	0.09***	0.01 (ns)	**0.23*****	**0.35*****

The partial Mantel statistic provides the correlation between the β-diversity and ecological variable, while controlling for the effects of a second ecological variable (co-variable).

Overall, the most correlated variables are H and SLA with DDEG and MIND.

Partial Mantel *r* values ≥ 0.10 are presented in bold, while significant *P* values are asterisked.

The complete variable names are given in Table 3.

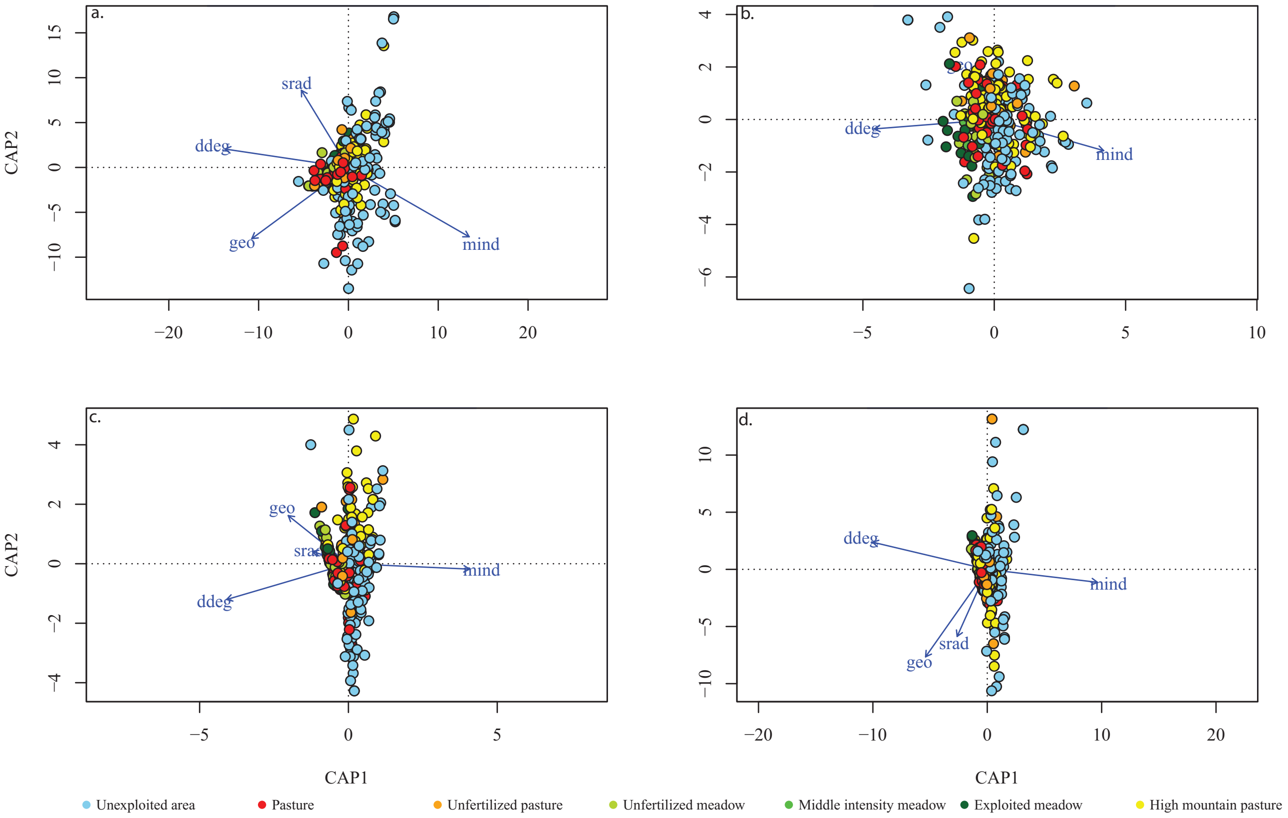

Figure 3: constrained analysis of principal coordinates for: **a.** phylogenetic β-diversity, **b.** β Leaf nitrogen, **c.** β Specific leaf area, and **d.** β Plant height measured with Rao's quadratic index (*Q*). ddeg = temperature degree-days, mind = moisture index, geo = geographic distances and srad = solar radiation.

et al. 2000; Legendre *et al.* 2005). This highlights the potential importance of global change factors (i.e. climate and LU change) in plant community turnover (Winter *et al.* 2009). Second, we show that functional and phylogenetic β-diversity are not redundant (maximum correlation: $Q = 0.20$), but useful complementary measures of biodiversity. The use of both measures alongside models of trait evolution can provide better explanations for patterns of community β-diversity.

β-Diversity and ecological variation

Our study on plant community turnover in a temperate mountain region provides empirical evidence for how functional and phylogenetic β-diversity—and thus the β structure of plant communities—vary across space as a function of change in environmental and spatial drivers. The significant correlation between functional and phylogenetic β-diversity and most ecological variables indicate that the key drivers of plant distributions and diversity in this region (Randin *et al.* 2009; Vittoz *et al.* 2008) also influence the β-diversity among communities. Among the eight ecological variables investigated, climatic temperature and moisture (DDEG and MIND), land use (LU) and spatial geographic distances (GEO) were the most important predictors of plant community turnover. The high degree of similarity exhibited between phylogenetic β-diversity and most functional β-diversity variables, particularly along similar DDEG, MIND and LU gradients (Fig. S3), confirm previous studies that have shown these gradients to be key drivers of plant species distributions and assembly in mountainous regions (Randin *et al.* 2009; Riedo *et al.* 2001; Vittoz *et al.* 2008). Climate, in particular, is widely acknowledged as an important predictor of plant species distributions (Guisan *et al.* 2006; Pottier *et al.* 2013) and is involved with the production of both local- and large-scale patterns of biodiversity (Devictor *et al.* 2010; Jankowski *et al.* 2009; Meynard *et al.* 2011).

The effect of climate (DDEG and MIND) on β-diversity above that of spatial distances (GEO) further confirms that climatic variables in themselves are highly spatially structured (Legendre *et al.* 2005), and throughout the study area, geographic distances tend to be short within given homogeneous species pools. Overall, β-diversity patterns showed the weakest correlations with soil nutrient properties. This may arise because total fractions of soil nutrients are generally poor indicators of plant community turnover (Dubuis *et al.* 2012; Paoli *et al.* 2006), but likely more robust predictors of microbial community structure (Kuramae *et al.* 2012; Shahnavaz *et al.* 2012). Soil pH in particular was not correlated with functional and phylogenetic β-diversity (except H) as measured with Q but showed a few high correlations with phylogenetic β-diversity and within functional β-diversity, LDMC and H traits. This difference suggests that soil pH likely overwhelms the effects of other, less stressful soil conditions (Shahnavaz *et al.* 2012), especially as total fractions of soil nitrogen and soil phosphorus remained poorly correlated with plant functional and phylogenetic β-diversity.

The effect of land use on functional and phylogenetic β-diversity

The significant effect of land use (LU) on phylogenetic β-diversity and most functional β-diversity traits (Tables 3 and 4) suggests that plant species respond to LU drivers, with cumulative impacts on the functional and phylogenetic structure of species' communities (Knapp *et al.* 2008). The LU predictor further indicate that functional and phylogenetic turnover may be largely mediated through environmental filtering (Knapp *et al.* 2008) because turnover largely reflects deterministic processes that are environmentally structured (Condit *et al.* 2002). Land-use intensification putatively mediated through environmental filtering has already been shown to cause a decrease in the functional diversity of animal communities (Flynn *et al.* 2009). Here, in conjunction with climatic predictors (Fig. 3), the effect of LU on β-diversity was mainly driven by the most evolutionarily labile traits (H and SLA). Therefore, it can be hypothesized that climate and LU would result in relatively dissimilar effects on functional and phylogenetic β-diversity in environmentally filtered communities that emerge from convergent traits (Cavender-Bares *et al.* 2009; Webb *et al.* 2002).

In mountainous areas, the substantial disparity in regional environmental conditions and anthropogenic (e.g. LU) pressure (Körner 2007) suggests that plant functional and phylogenetic community turnover would equally show differences in response to the effects of homogenization (Vellend *et al.* 2007; Winter *et al.* 2009). Land-use intensification (e.g. pasturing, heavy fertilization and mowing) may only contribute marginally to functional and phylogenetic homogenization (Vellend *et al.* 2007) if these effects are embedded within the effects of the environment (Winter *et al.* 2009). These effects will however again depend on the degree of trait conservatism (vs lability) and on the species represented in the plant communities of interest. For example, less frequent plant families (e.g. Geraniaceae and Liliaceae) with minimal representation across the LU categories (mainly middle intensity meadow, pasture and exploited meadow), unlike Poaceae, Asteraceae and Fabaceae (highly frequent) may be more severely affected by land-use intensification and therefore contribute greatly to functional and phylogenetic homogenization.

β-Diversity and trait evolution

The overall low phylogenetic signal in traits (i.e. K values <1) suggests that high evolutionary trait lability rather than conservatism drives species sorting along the ecological gradients (Webb *et al.* 2002; Whittaker 1972) and equally indicate that convergent adaptations to colder conditions occur in this temperate mountainous environment (Körner 2003; Pellissier *et al.* 2013). Our results strongly indicate that high trait variation associated with environmental conditions mostly drive community turnover in this region (Pellissier *et al.* 2013). For instance, LDMC with the highest phylogenetic signal (and most conserved overall) exhibited the weakest correlations with the ecological variables, unlike H, which showed the least phylogenetic signal but the most significant correlations with the ecological variables.

On this basis, we affirm that LDMC is not a key trait for enhancing plant species adaptations to unpredictable environmental conditions in high elevation areas, especially as it was the least response variable for plant functional turnover. As studied here, multiple functional β-diversity facets in concert with phylogenetic β-diversity can prove a powerful approach in revealing which traits may be under selection in given environmental conditions. Although, the low phylogenetic signal in traits observed here may have undermined the congruence between the functional and phylogenetic β-diversity of communities, our results nevertheless stress the importance of jointly considering multiple functional and phylogenetic β-diversity in investigations of β-diversity and community phylogenetic structure, in order to clearly reveal the community turnover not captured by either facets, or by the use of a single trait. Finally, our results highlight the importance and benefits of considering several ecological gradients in investigating the turnover of plant communities.

CONCLUSIONS AND FUTURE PERSPECTIVES

The present study assessed the functional and phylogenetic turnover of plant communities along several mountain ecological gradients. Our assessments were based on a well-sampled dataset evaluated using the methodological approach provided by *Q*, in combination with phylogenetic signal in traits. We have shown that plant functional and phylogenetic turnover were better predicted by climate (temperature and moisture) and land use (LU) gradients, in contrast to solar radiation and total soil nutrient gradients. We further demonstrated the importance of evolutionarily labile traits in driving plant community turnover—and particularly convergent adaptations toward low plant height (H) at high elevations in mountain regions. Our study is also applicable to other ecosystems, because we illustrate that by combining functional and phylogenetic β-diversity facets, we can gain new insights into the key drivers of biodiversity patterns across space (Graham and Fine 2008; Winter *et al.* 2009). Nevertheless, the sound understanding of the global distribution of biodiversity may require the consideration of global change factors (i.e. climate and LU) in a similar integrative assessment but in diverse ecosystems.

SUPPLEMENTARY MATERIAL

Supplementary material is available at Journal of Plant Ecology online.

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