

Spatial scale and intraspecific trait variability mediate assembly rules in alpine grasslands

Loïc Chalmandrier^{1,2*}, Tamara Münkemüller^{1,2}, Marie-Pascale Colace^{1,2}, Julien Renaud^{1,2}, Serge Aubert³, Bradley Z. Carlson^{1,2}, Jean-Christophe Clément^{1,2,4}, Nicolas Legay^{1,2}, Gilles Pellet³, Amélie Saillard^{1,2}, Sébastien Lavergne^{1,2} and Wilfried Thuiller^{1,2}

¹Laboratoire d'Écologie Alpine (LECA), University of Grenoble Alpes, F-38000 Grenoble, France; ²Laboratoire d'Écologie Alpine (LECA), CNRS, F-38000 Grenoble, France; ³Station Alpine Joseph Fourier, UMS CNRS 3370, Université Joseph Fourier, Grenoble 1, BP 53, 38041 Grenoble cedex 9, France; and ⁴CARTELE, Université Savoie Mont Blanc - INRA, 73376 Chambéry, France

Summary

1. Assembly of grassland communities has long been scrutinized through the lens of functional diversity. Studies generally point to an overwhelming influence of climate on observed patterns of functional diversity, despite experimental evidence demonstrating the importance of biotic interactions. We postulate that this is because most observational studies neglect both scale dependencies of assembly processes and phenotypic variation between individuals. Here, we test for changes in the importance of abiotic filtering and biotic interactions along a stress gradient by explicitly accounting for different scales. In addition to quantifying intraspecific trait variability (ITV), we also vary the two components of spatial scale, including grain (i.e. community size) and extent (i.e. the geographical area that defines the species pool).

2. We sampled 20 grassland communities in ten sites distributed along a 975-m elevation gradient. At each site, we measured seven functional traits for a total of 2020 individuals at different spatial grains. We related community functional diversity metrics to the main environmental gradient of our study area, growing season length (GSL), and assessed the dependence of these relationships on spatial grain, spatial extent and ITV.

3. At large spatial grain and extent, the imprint of environmental filtering on functional diversity became more important with increasing stress (i.e. functional diversity decreased with shorter GSL). At small spatial grain and extent, we found a convex relationship between functional diversity and GSL congruent with the hypothesis that competition is dominant at low-stress levels while facilitative interactions are dominant at high-stress levels (i.e. high functional diversity at both extremes of the stress gradient). Importantly, the effect of intraspecific variability on assembly rules was noticeable only at small spatial grain and extent.

4. Synthesis. Our study reveals how the combination of abiotic stress and biotic interactions shapes the functional diversity of alpine grasslands at different spatial scales, and highlights the importance of phenotype variation between individuals for community assembly processes at fine spatial scale. Our results suggest that studies analysing trait-based assembly rules but ignoring ITV and focusing on a single spatial scale are likely to miss essential features of community diversity patterns.

Key-words: competition, facilitation, functional diversity, grassland, intraspecific variability, spatial extent, spatial grain, stress

Introduction

Community ecology aims to understand the processes shaping the structure and composition of communities. A long tradition of studies has provided insights into the rules determining the local coexistence of species within assemblages (Cody & Diamond 1975). However, an important remaining issue is that patterns of diversity are inherently dependent on the spatial scale of the study (Levin 1992; Chave 2013;

Münkemüller *et al.* 2014) and on the taxonomic level at which organisms are considered (as individuals, populations, species, genera, etc.). Thus, analysing resulting diversity patterns across scales can give a more complete picture of these processes and improve our understanding of community assembly rules (Kraft & Ackerly 2010; Albert *et al.* 2011; Weiher *et al.* 2011).

Trait-based approaches represent a promising avenue for improving our understanding of community assembly processes (McGill *et al.* 2006). Functional traits measure morphological, physiological or phenological features that impact

*Correspondence author. E-mail: loic.chalmandrier@usys.ethz.ch

the fitness of individuals via their effects on growth, reproduction and survival in given environments (Violle *et al.* 2007). Because they are related to species' niches (Thuiller *et al.* 2004), the variability of these traits within communities (i.e. functional diversity) is assumed to reflect the imprint of assembly rules such as environmental filtering or competitive interactions. One approach to disentangling the relative contributions of different assembly rules is to measure the deviance of observed functional diversity from the expected distribution under a model of random assembly. Typically, this null model is based on random combinations from a species pool: the set of species present in the region due to biogeographical and historical processes (Ricklefs 2004; Hardy 2008; Chalmandrier *et al.* 2013). Differences between observed and null patterns of functional diversity are then interpreted in the light of theoretical frameworks (e.g. Spasojevic, Copeland & Suding 2014) and the most likely set of assembly rules is inferred. However, diversity patterns and the associated conclusions depend heavily on the spatial scale of the study and the resolution at which functional traits are measured within communities.

Spatial scale has two components (Wiens 1989): (i) grain (e.g. the plot area of the sampled community) and (ii) extent [e.g. the geographical area that contains the communities (plots) under study] that, in the case of diversity pattern studies, defines the species pool to which community structure is compared (Cornell & Harrison 2014). In terms of assembly rules, a fine grain is deemed to be more appropriate for detecting the signature of biotic interactions, considering that individuals are then close enough to directly interact with each other. At large grain, the aggregation of individuals due to local processes (such as biotic interactions or local environmental heterogeneity) is more likely to be averaged out and community diversity becomes more representative of the impact of large-scale environmental filtering (Kraft & Ackerly 2010; Thuiller *et al.* 2014, 2015; Yang *et al.* 2014). A study with a large spatial extent often includes a broad range of environmental conditions and thus a species pool with a wide range of trait values. Thus, the comparison of local communities to this species pool is more likely to reflect the filtering of species along environmental gradients. A study with a small spatial extent, instead, reflects local pools of species or individuals possessing suitable traits to survive within the same local abiotic conditions (de Bello *et al.* 2012). Small spatial extent therefore can negate the influence of large-scale gradients and can potentially reveal the signal of local assembly processes (Chalmandrier *et al.* 2013). Combining both spatial scale features, a large-scale study (e.g. large grain and large spatial extent) should thereby reinforce the detection of climatic gradients' effects on community assembly, while small spatial scales (e.g. small grain and small spatial extent) should be better suited to detect the signature of biotic interactions (Vamosi *et al.* 2009; Gross *et al.* 2013).

Beyond the description of diversity patterns, comparing community structure across spatial grain and extent can also help to address some of the major flaws of diversity pattern analyses. First, different assembly rules can lead to similar observed diversity patterns (Mayfield & Levine 2010;

HilleRisLambers *et al.* 2012). For example, competitive hierarchy and abiotic filtering are both predicted to result in functionally convergent communities (Kraft *et al.* 2014). However, if these assembly rules operate at different spatial scales, varying spatial scale may help to distinguish one process from the other. Secondly, local communities are often the result of multiple interacting assembly rules. For instance, in communities occurring along stress gradients, the 'stress-gradient hypothesis' predicts that communities at the high end of the stress gradient will be structured by facilitation (Michalet *et al.* 2006). However, these stressed communities are also structured by strong abiotic filtering, which can obscure the signal of facilitation. By studying diversity pattern across spatial scales, we are more likely to detect both processes and have a more complete picture of the processes influencing community structure.

Finally, in functional trait studies, species are traditionally considered to be functionally homogeneous entities (i.e. no phenotypic difference), thus assuming that intraspecific trait variability (ITV) is negligible compared to interspecific trait variability. However, recent works question this assumption and show that ITV can significantly affect patterns of community functional diversity (Albert *et al.* 2010, 2012; Siefert 2012). One may expect that trait–environment relationships (how a single trait responds to a given environmental gradient) will appear more clearly when considering ITV since ecological processes act on individual and not on species *per se* (Jung *et al.* 2010; Cianciaruso *et al.* 2012; Kichenin *et al.* 2013). Consequently, ITV is today more commonly integrated in biodiversity studies, and hypotheses have been formulated regarding the situations when its quantification is more relevant (Siefert *et al.* 2015), particularly: (i) for the study of certain functional traits like vegetative height that are inherently very variable within species (Kazakou *et al.* 2014) and (ii) at small spatial scales where species turnover is limited and intraspecific variability accounts for most of the functional turnover (Albert *et al.* 2011). However, to our knowledge, the importance of ITV has rarely been tested while simultaneously varying the spatial grain and the spatial extent.

Here, we investigated the functional diversity of 20 sub-alpine and alpine plant communities along an elevation gradient accounting for spatial grain, extent and ITV. We tested three hypotheses in our study. (i) At large spatial scale (e.g. large grain and extent), we anticipate plant community functional diversity to respond primarily to abiotic stress due to landscape-scale climatic gradients. We expect that this effect should cause communities to appear functionally convergent (i.e. co-occurring individuals are more similar than expected under random assembly) in the more stressful conditions of high-elevation sites. (ii) At small spatial scale (e.g. small extent and grain), we expect functional diversity to be shaped to a greater degree by biotic interactions and to be overall more divergent than at large spatial scale (Gross *et al.* 2013). As the studied communities are set along an elevation gradient, we expect to find a pattern congruent with the aforementioned 'stress-gradient hypothesis' (Michalet *et al.* 2006). In terms of functional traits, competition at the lower end of the

stress gradient should result in limiting similarity and thus functional divergence. At the high end of the gradient, facilitation should also lead to functional divergence because individuals with traits that are poorly suited to local abiotic conditions are locally facilitated by individuals with contrasting adaptive traits (Michalet *et al.* 2006; Gross *et al.* 2009). We thus expect an overall convex relationship between functional diversity and the stress gradient. (iii) Finally, we make the hypothesis that the inclusion of ITV is more relevant for inferring community assembly processes at a small spatial scale where species turnover is less pervasive than at large spatial scale (Albert *et al.* 2011; Siefert *et al.* 2015).

Materials and methods

STUDY SITE

The study was conducted in the central French Alps (45.12°N, 6.40°E) (Fig. 1). Ten sites were studied along a continuous 975-m elevation gradient (1750–2725 m) in a cow-grazed pasture. Subalpine grasslands dominated the bottom of the gradient while sparsely vegetated alpine meadows characterized higher elevations.

The ten sites were evenly distributed along the elevation gradient (on average 100-m elevation difference apart from each other and separated by a geographical distance of 340 m on average) on the same south-facing slope. Thus, all sites were situated on a single environmental gradient that encompassed two major alpine drivers: temperature and radiation (de Bello *et al.* 2013). In each site, we placed two non-overlapping plots of 10 × 10 m a few metres apart

from each other in homogeneous vegetation. Within each plot, we studied plant communities at four grain sizes using two orthogonal transects per plot and point-contact sampling (see below for more detail). Overall, we thus collected data for 80 communities situated in 20 plots, which were nested in 10 sites (Fig. 1). We conducted a phytosociological survey during peak productivity (mid-July, 2012) that indicated the presence of 199 species across the studied plots, with an average richness of 47.9 species per plot (ranging from 32 to 67).

DATA

Four nested grain sizes

In each quadratric plot, we sampled plant individuals along two transects that followed its diagonals (Fig. 1). The sampling protocol of individuals was designed in such a way that we obtained four spatially nested communities with decreasing grain sizes. Small communities were entirely nested in larger communities, and all nested communities had the same centre. At the small grain size (1.25 × 1.25 m), we sampled one individual every 8.75 cm along both plot transects; at the first intermediate grain size (2.5 × 2.5 m), we sampled one individual every 17.5 cm; at the second intermediate grain size (5 × 5 m), we sampled one individual every 35 cm and; at the large grain size (10 × 10 m), we sampled one individual every 70 cm (Fig. 1). This sampling design allowed us to considerably reduce the sampling effort, as the four nested communities were partially characterized by the same individuals. For example, two communities from the same plot at consecutive spatial grains shared half of sampled individuals. Furthermore, the number of considered individuals per community was constant across scales (41 individuals). In

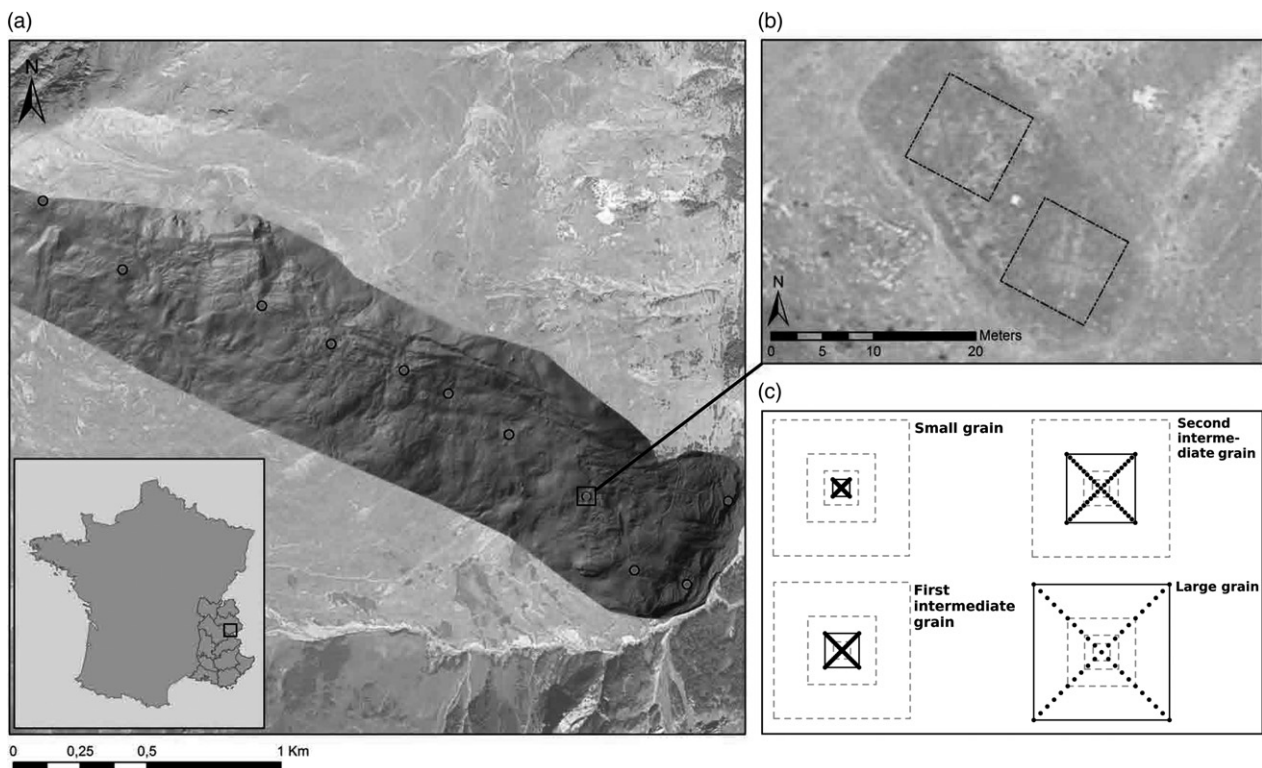


Fig. 1. Overview of the study area. (a) Large extent, where dots indicate the position of the sites. (b) Small extent: an example site containing two 10 × 10 m plots. (c) Within plots, black points show the positions of the sampled plant individuals according to the grain size: 1.25 × 1.25 m (upper left corner); 2.5 × 2.5 m (upper right corner); 5 × 5 m (bottom left corner); 10 × 10 m (bottom right corner).

total, this procedure resulted in the sampling of 2020 individuals from 137 species (as compared to the 199 species observed in the study area, meaning that 62 species were too rare to be detected with our design). We sampled on average 16.15, 17.45, 18.65 and 19.85 species in the communities defined by increasing grain sizes (1.25 × 1.25 m, 2.5 × 2.5 m, 5 × 5 m vs. 10 × 10 m). Information about the number of individuals sampled per species and its link to *in situ* species' abundance is available in Appendix S1 in the Supporting Information.

Functional traits

For each sampled individual, we identified the species and measured seven functional traits. (i) Vegetative height is the distance between the highest photosynthetic organ and the ground, which is associated with plant competitive vigour (Violle *et al.* 2009); (ii) specific leaf area (SLA) is the one-sided area of a fresh leaf divided by its oven-dry mass. SLA is usually correlated positively with relative growth rate and negatively with short leaf life span (Hunt & Cornelissen 1997; Reich *et al.* 1999). (iii) Leaf dry matter content (LDMC) is the oven-dried mass of a leaf divided by its water-saturated fresh mass. It was measured using the partial rehydration method, which has been proven to give results similar to the full rehydration method (Vaieretti *et al.* 2007). LDMC is related to the average density of leaf tissues and tends to scale negatively with SLA. (iv) Leaf nitrogen concentration (LNC) is the total amount of nitrogen per unit of dry leaf mass, which quantifies the allocation of available nitrogen to photosynthetic enzymes in leaf chloroplasts (Reich *et al.* 1999; Pérez-Ramos *et al.* 2012). (v) Leaf carbon concentration (LCC) is the total amount of carbon per unit of leaf dry mass and represents investment in structural tissues (Poorter & Bergkotte 1992). (vi) Leaf carbon isotopic ratio ($\delta^{13}\text{C}$) provides a time-integrated measure of stomatal conductance (Farquhar, O'leary & Berry 1982). (vii) Leaf nitrogen isotopic ratio ($\delta^{15}\text{N}$) reflects the isotope signature of nitrogen sources of the plant but also the type of mycorrhization. As such, it provides a measure of the plant's nitrogen acquisition strategy (Dawson *et al.* 2002; Hobbie & Högberg 2012).

To obtain reliable leaf trait estimates for SLA and LDMC, we collected a single non-senescent, non-grazed, non-frozen, well-developed leaf per individual (Cornelissen *et al.* 2003). For some individuals that had very small leaves and should thus lead to biased measures of area (ex. *Galium mollugo*), we selected a larger number of leaves. This was done case by case but consistently through the gradient. Non-photosynthetic tissue (e.g. petiole) was removed from the leaves before measurement. We measured leaf area using a portable laser leaf scanner (CID Bio-science Inc., Camas, WA, USA). We performed at least three measurements per sample to detect a potential scanner error. For LNC, LCC, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, dried and marble-ground leaf samples of 1–2 mg were analysed at the individual level with a continuous-flow isotope ratio mass spectrometer (Delta V Advantage; Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (Flash EA1112; Thermo Scientific, Milan, Italy) at La Rochelle University-UMR CNRS LIENS.

Environmental variables

We quantified changes in environmental conditions across the elevation gradient by measuring growing season length (GSL). GSL, defined here as the number of days without snow cover and with air temperatures above 0 °C, is known to be an important driver of grassland functional assembly (Violle *et al.* 2015). In alpine ecosystems, variation in snow cover duration along elevation and mesotopographic gradients is a key

driver of plant distribution and community composition (Evans *et al.* 1989; Choler 2005; Carlson *et al.* 2015). To account for this parameter, we estimated growing season energy budgets, as mediated by snow cover duration, using a remote sensing-based snow distribution model calibrated to Landsat 7 and 8 imagery. Daily air temperature values for each plot were obtained from the SAFRAN meteorological model developed by Météo France for the French Alps (Durand *et al.* 2009). For 5 years falling between 2000 and 2014, daily maps of snow cover at 15 m resolution were used to estimate the number of snow-free days with a daily mean air temperature over 0 °C between snow melt-out and August 15. GSL was then averaged across years and extracted for the studied sites. More methodological details and validation results for the snow cover model are available in Carlson *et al.* (2015). We calculated an average GSL of 85.6 days per year and a variation between 40.2 and 115 days per year. Given the uniform south-facing slope of our study area, variation in GSL was strongly negatively related to elevation (cor = -0.94; $P < 0.001$). It was further related to environmental variables measured in the field: GSL was positively correlated to mean annual temperature (cor = 0.83, $P < 0.001$), yearly number of frost days (cor = 0.86, P -value < 0.001), soil ammonium concentration (cor = 0.60, P -value = 0.005) and nitrate concentration (cor = 0.54, P -value = 0.013).

Because of this, plants at high-elevation communities face multiple sources of stress beside a short GSL such as cold stress (albeit less frost risk because of the snow cover), lower soil resources or lower CO₂ partial pressure. High-elevation plants are known to have particular traits that help them to cope with these abiotic stress factors: for instance, smaller stature that prevents heat dispersion, higher LDMC and lower SLA that reflects a conservative ecological strategy (stress-tolerant and slow-growing) or a higher stomatal conductance to cope with lower CO₂ partial pressure that leads to a higher foliar $\delta^{13}\text{C}$ (Körner 2003; de Bello *et al.* 2013; Kichenin *et al.* 2013).

ANALYSIS

Diversity indices

We calculated the functional diversity of each community with and without accounting for ITV. To account for ITV, we calculated the functional distance matrix for all sampled individuals. Since measured functional traits were only moderately correlated (the strongest correlation was between LDMC and foliar $\delta^{13}\text{C}$: $r = 0.44$, $P < 0.001$), we kept all traits for the analysis. First, we centred and scaled each functional trait and then used Euclidean distance to calculate pairwise functional distances between individuals. To calculate the functional distance between individuals while ignoring intraspecific variability, we replaced each individual trait value by the mean trait value of the species over the whole study area before calculating the functional distance matrix as described above. The resulting two functional distance matrices (with and without intraspecific variability) were then divided by the maximum distance value across both matrices to allow for direct comparison of functional diversity metrics.

We used the equivalent number of Rao's quadratic entropy (Rao 1986) to calculate the diversity ${}^{\alpha}D_{ij}$ of community j belonging to site i , at a given grain size:

$${}^{\alpha}D_{ij} = \left[1 - \frac{1}{N^2} \sum_{k=1}^N \sum_{l=1}^N d_{kl}\right]^{-1} \quad \text{eqn 1}$$

with N , the number of individuals in the community j belonging to site i (i.e. 41) and d_{kl} the Euclidean functional distance between individual k and l belonging to community j belonging to site i .

Spatial extent and null models

At each sampled spatial grain size, we used two different null models to account for two different spatial extents. First, we wanted to know whether observed functional diversity deviated from a null expectation in which individuals are randomly distributed within the landscape regardless of their functional traits or their taxonomy. For this purpose, we defined a 'landscape null model' in which we randomized species across the entire landscape. We will refer to the use of this null model as 'large extent'. For each grain size, null distributions were generated by randomly assigning without replacement 41 individuals from the 2020 sampled individuals in the landscape to each of the 20 plots. Secondly, we wanted to know whether observed functional diversity deviated from a null expectation in which individuals are randomly distributed within sites regardless of their functional traits or their taxonomy (de Bello *et al.* 2012). For this purpose, we defined a 'site null model' in which we randomized species only within sites. We will refer to the use of this null model as 'small extent'. For a given grain size, null distributions were generated for each plot by randomly assigning, without replacement, 41 individuals from the 202 individuals sampled at the site level. This constrained null model operates on a smaller spatial extent than the landscape null model (where 41 individuals are assigned to a plot from the 2020 individuals sampled at the landscape level), because individuals are randomized within sites rather than across the landscape. The sampling size of the null model is also smaller which is known to affect its power in the case of phylogenetic diversity studies (Kraft *et al.* 2007). We, however, tested a similar null model on simulated communities in a previous study and found that this is much less an issue in functional diversity studies (Chalmandrier *et al.* 2013). Each null model was run 10 000 times. Standard effect sizes (SES) represent deviations of functional diversity from random expectations. SES are defined as the observed functional diversity value minus the mean of the functional diversity values under the null hypothesis divided by the standard deviation of the functional diversity values under the null hypothesis. A negative SES value indicates that functional diversity is lower than expected if individuals were randomly distributed in the plot (or landscape). Conversely, a positive SES value indicates that functional diversity is higher than expected if individuals were randomly distributed in the plot (or landscape). We assessed the significance of deviations of observed functional diversity from null model distributions by identifying the proportion of random values that fell below the observed diversity value. If this rank value was below 0.05, then functional diversity for a given plot was considered significantly low; if it was higher than 0.95, functional diversity for a given plot was considered significantly high.

For example, we marked a community in Fig. 4 (with an arrow) that is changing diversity patterns when analysed at a small vs. large extent. At a large spatial extent, the SES is significantly negative (SES = -2.77, rank = 0.00). Such trait clustering is usually interpreted as a signal of environmental filtering. In contrast, at a small spatial extent, the SES is strongly positive (SES = 1.70, rank = 0.96). Such trait overdispersion can be interpreted as a signal of niche-partitioning competition or facilitation acting as a secondary assembly rule at the scale of the site.

Multimodel inference

We calculated the SES of functional diversity for each of the 20 plots, both with and without ITV, for the four spatial grains (small, first intermediate, second intermediate and large) and the two spatial extents considered (i.e. landscape vs. site null models). We then analysed the

dependency of SES of functional diversity on GSL, spatial grain, spatial extent and ITV. To do so, we developed a set of mixed models that included plots nested within sites as random effects. Fixed effects included the following: (i) scaled GSL and the square of it (GSL²), in order to test whether low as well as high stress (induced by short GSL) resulted in functional divergence (hypothesis 2 from the introduction); (ii) ITV ('ITV' vs. 'noITV'); (iii) spatial grain (proportional to the logarithm of community area); and (iv) spatial extent. We included two- and three-way interaction terms between GSL, one of the two spatial scale components and ITV. The logic behind this interaction effect was to explicitly test whether the community response to environmental gradients was dependent on the spatial scale components and on ITV.

We used an information theory approach to evaluate all the possible linear mixed models including all or a subset of terms (Burnham & Anderson 2002). Models were then ranked according to corrected Akaike information criterion (AICc), and their relative importance (RI) was evaluated using AICc weights. We retained models with a cumulated AICc weight of 0.95 (Johnson & Omland 2004). The RI of each fixed effect in the confidence set was calculated as the sum of the AICc weights over all of the models in which it appeared. We further calculated average parameter estimates and significance terms for fixed effects for the retained set of models. We reran the entire procedure for various sets of contrasts to ensure that our conclusions regarding the significance of the slope of SES of functional diversity against GSL in each context (small spatial scale, large spatial scale and inclusion of ITV) were appropriate. All analyses were conducted using R version 3.0.2 (R Core Development Team 2012) using the packages: NLME (Pinheiro *et al.* 2007) and MuMIn (Bartoń 2012).

COMPLEMENTARY ANALYSES

Estimating functional diversity using multiple traits has been criticized. Since traits may represent different niche axes, the aggregated information may obscure certain assembly rules (Spasojevic & Suding 2011). We thus repeated the same analysis described above but on single-trait diversity measures. Results are presented in Appendix S2 and are summarized in the main text and in Table 1.

We considered that a significant relationship between the SES of functional diversity and GSL² could emerge from a linear relationship with an underlying environmental gradient with a concave or convex relationship to GSL. In our study area, a good candidate was soil organic content which displayed a high correlation to GLS² (-0.86). We thus rerun the analysis described above but replacing GLS² by soil organic matter content to account for this potential bias. Results are presented in Appendix S3.

Results

EFFECTS OF SPATIAL GRAIN AND EXTENT

Both spatial extent and grain strongly influenced SES of functional diversity (hereafter 'functional diversity'), with functional diversity decreasing with increasing extent (extent: *z*-value: 8.224, RI = 1.00; Figs 2 and 3). While functional diversity was, in general, not significantly different from random expectations at small extent (site null model), we observed significant functional convergence at a larger extent (Fig. 4). Single-trait analyses revealed that this pattern was mainly driven by Height, SLA and LNC, as well as foliar $\delta^{15}\text{N}$ when ITV was considered (Table 1).

The effect of spatial grain on functional diversity was smaller but nevertheless significant. At a small grain size, individuals co-occurred with functionally more similar individuals than at a larger grain size (z -value: 5.006, $RI = 1.00$; Figs 2 and 3). Single-trait analyses revealed that this pattern was mainly driven by Height, LDMC and LNC (Table 1).

EFFECTS OF INTRASPECIFIC TRAIT VARIABILITY

The inclusion of ITV did not influence functional diversity in a consistent way (Figs 2 and 3). However, ITV was always included in the most parsimonious linear models and thus had a high RI ($RI = 1.00$). Across models, ITV was always

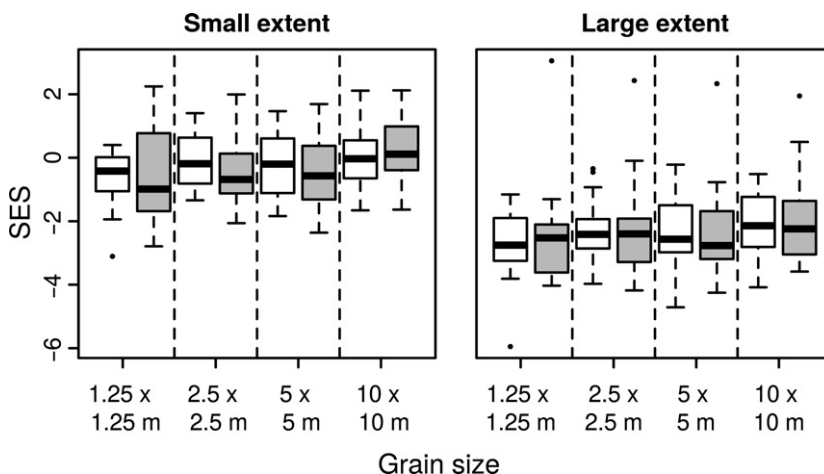
Table 1. Summary of the congruence of functional diversity patterns for individual traits. We classified traits as ‘driving traits’ if they had a significant pattern (P -value < 0.05) going in the same direction as the multitrait functional diversity pattern and ‘countering traits’ if they showed a significant pattern going into the opposite direction. More complete results for the single-trait models are available in Appendix S2

Main conclusions	Driving trait	Countering trait
Functional diversity decreased with finer grain	Height, LDMC, LNC	/
Functional diversity decreased with increasing spatial extent	Height, SLA, LNC, $\delta^{15}N^*$	/
Functional diversity increased with growing season length (GSL) at large spatial extent and grain	Height, SLA, LCC*	LDMC, $\delta^{15}N^\dagger$
Functional diversity had a convex relationship to GSL at small spatial grain and extent	LDMC	/

LCC, Leaf carbon concentration; LDMC, Leaf dry matter content; LNC, leaf nitrogen concentration; SLA, specific leaf area

*Relationship only when intraspecific trait variability is included.

†See Appendix S2.



Functional α -diversity

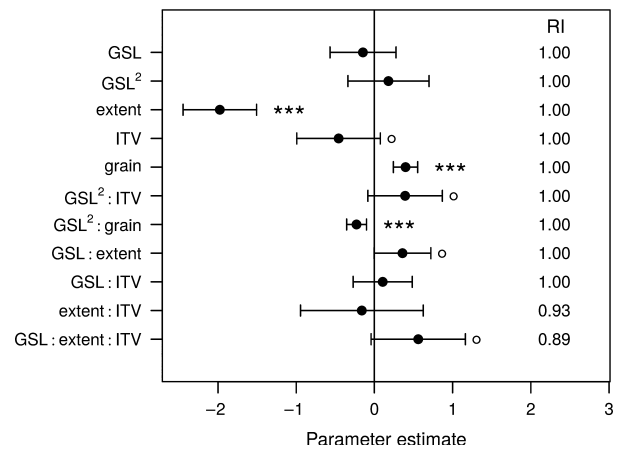


Fig. 3. Average parameter estimates and 95% confidence intervals for fixed effects for retained models of plot-level functional diversity. Relative importance (RI) is the sum of AIC weights of models in which a given predictor appears. Results are shown only for predictors with $RI > 0.8$. GSL: growing season length (scaled). ITV, inclusion of ITV.

Fig. 2. Influence of spatial extent, grain and intraspecific trait variability (ITV) on the standard effect size of functional diversity (SES). SES represents the deviation of functional diversities of a plot at a given grain size from its null distributions: random assembly from the site pool (small extent) or random assembly from the landscape pool (large extent). A negative (resp. positive) SES value indicates that functional diversity is lower (resp. higher) than expected from its null distribution. White boxes: not including ITV; grey boxes: including ITV.

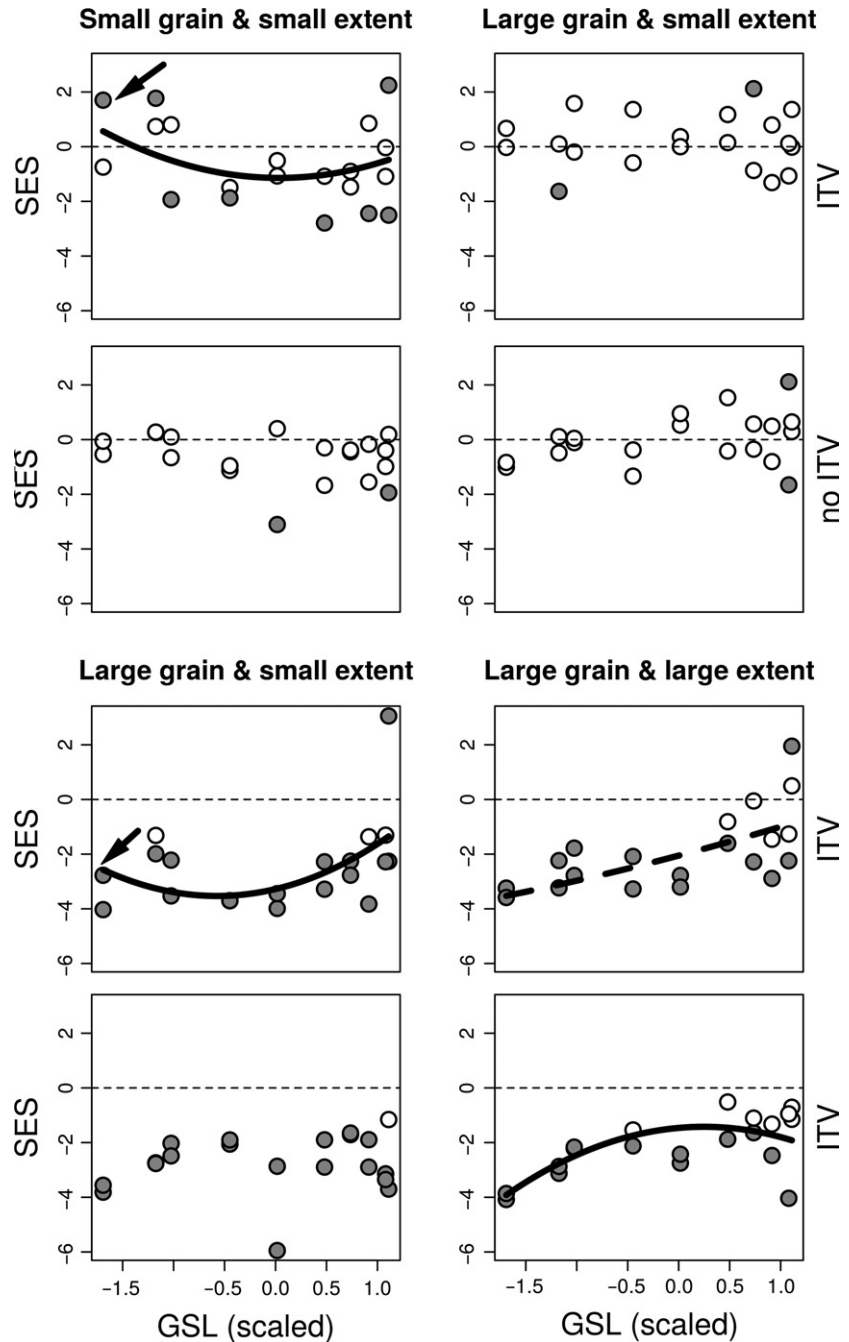


Fig. 4. Standardized effect size (SES) of community functional diversity as a function of growing season length (GSL). A negative (resp. positive) SES value indicates that functional diversity is lower (resp. higher) than expected from its null distribution at a given spatial extent. We displayed four spatial settings: small grain (1.25×1.25 m) and small extent (top left panels); small grain (1.25×1.25 m) and large extent (bottom left panels); large grain (10×10 m) and small extent (top right panels); large grain (1.25×1.25 m) and large extent (bottom right panels). Filled circles represent significantly low (rank lower than 0.05) or high (rank above 0.95) functional diversity. The polynomial curves were obtained from the averaged coefficient estimates given by the model averaging procedure. If non-significant, the curve is absent. If the coefficient of degree 2 was not significant (indicating a linear relationship), the line is dashed.

RI = 1.00; GSL^2 : grain z -value: 3.477, RI = 1.00), and accounting for ITV, only strengthened this pattern and made the relationship nonlinear (GSL :extent:ITV z -value: 2.560, RI = 0.89; GSL^2 :extent:ITV z -value: 2.361, RI = 0.54). Single-trait analyses revealed that Height, SLA and LCC (when ITV was included) were driving this pattern (Table 1, Appendix S2). In contrast, functional diversity based on LDMC and foliar $\delta^{15}N$ decreased with GSL (Table 1, Appendix S2).

At small spatial grain and extent, GSL did not significantly influence functional diversity when ITV was not included (GSL^2 z -value: 0.572, RI = 1.00; GSL z -value: 0.572, RI = 1.00). When ITV was included, GSL displayed a

convex relationship with GSL (Figs 3 and 4) with a degree 2 coefficient marginally different from 0 (z -value: 1.806, RI = 1.00). Complementary analysis revealed that soil organic matter was not responsible for this pattern (Appendix S3). Single-trait analyses showed that the convex relationship between functional diversity and GSL was driven by LDMC (Appendix S2, GSL^2 z -value: 2.104, RI = 1.00) and did not depend on ITV (maximal RI of ITV coefficients: 0.64).

Discussion

Our study highlights the importance of considering both spatial grain and extent as well as ITV when studying functional

diversity patterns of grassland communities. We found that (i) at large spatial extent and grain, functional diversity is reduced when GSL decreased, suggesting an increasing pressure of environmental filtering when abiotic stress increases; (ii) at small spatial grain and extent, functional diversity has a convex relationship with GSL (i.e. more functional divergence for low- and high-stress levels) suggesting a shift from dominant competition in favourable conditions to dominant facilitation in highly stressful conditions; and (iii) the inclusion of ITV was mainly important at small spatial scales.

STRONG ENVIRONMENTAL FILTERING AT LARGE SPATIAL SCALE

Spatial grain and extent strongly influenced observed functional diversity patterns. At large spatial grain and extent, many communities appeared functionally more similar than expected by chance. In agreement with previous studies (de Bello *et al.* 2013; Hulshof *et al.* 2013), we found that communities tended to be more functionally convergent in sites at upper elevations experiencing a brief snow-free period. This result strongly supports our first hypothesis. Indeed, while other factors, such as competitive hierarchy and local environmental heterogeneity, could explain the observed patterns (Kraft *et al.* 2014), our study gives compelling evidence that large-scale abiotic filtering through GSL is the major driver of community assembly at large spatial scales. We found that (i) functional convergence is only overwhelmingly observed at large spatial extent and does not vary strongly with spatial grain (if local environmental heterogeneity or competitive hierarchy was the major drivers, we would expect even stronger functional convergence at the smallest grain size); and (ii) the effect of spatial extent is strongest for communities experiencing a brief growing season. This strong, large-scale environmental filter can be explained by the fact that stressful conditions at high elevations require specific functional traits or combinations of traits that result in reduced trait variability (Height, SLA, LCC, Table 1). These large-scale findings support the more general hypothesis about stronger effects of environmental filters under stressful conditions (Currie *et al.* 2004) and are in line with results for similar ecosystems (de Bello *et al.* 2013).

Two traits showed contrasting patterns relative to the overall trend of increasing convergence with increasing stress: diversity of LDMC and foliar $\delta^{15}\text{N}$ increased with increasing stress (decreasing GSL). This phenomenon has been observed before (de Bello *et al.* 2013) but has to our knowledge, so far not been sufficiently explained in the literature. We thus propose hypotheses that would need to be tested in future works. In addition to the classical trade-off opposing fast-growing and stress-intolerant species to slow-growing and stress-tolerant species (Díaz *et al.* 2016), LDMC is also related to palatability for herbivores (Deraison *et al.* 2015; Ibanez, Arène & Lavergne 2016). We can speculate that the higher variability in LDMC at higher elevations is due to a release from grazing pressure due to low herbivore richness and abundance (Descombes *et al.* 2016). Foliar $\delta^{15}\text{N}$ has been

associated with nitrogen acquisition strategies in subarctic plants (Hobbie & Höglberg 2012). In our study site, available mineral nitrogen stocks decrease with GSL (see Materials and methods). A possible interpretation is thus that the low available nitrogen forced individuals to diversify in nitrogen acquisition strategies resulting in higher $\delta^{15}\text{N}$ diversity. This mechanism has been experimentally detected in high-elevation communities before (Ashton *et al.* 2010), but further studies are needed to access the importance of this mechanism across elevation gradients.

SHIFTS BETWEEN DIFFERENT TYPES OF BIOTIC INTERACTIONS AT SMALL SPATIAL SCALE

At small spatial grain and extent, we observed functional diversity patterns that were congruent with the stress-gradient hypothesis (Michalet *et al.* 2006), with more functional divergence at both low- and high-stress levels (i.e. long vs. short GSLs). At the low stress end of our gradient, communities tended to be functionally divergent, a pattern that was consistent with the hypothesis that competition should favour the local coexistence of plant individuals with dissimilar traits (Kraft, Godoy & Levine 2015). However, some communities showing significant functional convergence were observed at intermediate to long growing seasons at small but not at large spatial grains (Fig. 4). Hierarchical competition or local abiotic filtering can explain this pattern. Competition theory predicts that coexistence can be favoured by both stabilizing niche differences and equalizing fitness among individuals (Adler, Ellner & Levine 2010), and it is likely that the interplay between both mechanisms leads to variable outcomes of plant competition within competitive subalpine communities. Alternatively, it is also possible that some unmeasured local environmental gradients (such as soil nitrogen, Darrouzet-Nardi & Bowman 2011) promoted the co-occurrence of similar individuals at a small spatial grain in these particular communities.

Communities with a short growing season displayed high functional diversity at small spatial scales but – in contrast – low functional diversity at large spatial scales (Fig. 4). This can be interpreted as the overlay of two assembly rules: the aforementioned abiotic stress that resulted in strong functional convergence and the impact of biotic interactions among plant neighbours that resulted in functional divergence. While a divergent functional diversity pattern can also be interpreted to be the result of limiting similarity, in stressful environments facilitation is known to be the most important form of biotic interaction (Choler, Michalet & Callaway 2001; Callaway *et al.* 2002). Accordingly, high functional diversity at upper-elevation sites can be interpreted to be a consequence of facilitative interactions among plant individuals, with stress-intolerant plant individuals co-occurring with stress-tolerant plants, which creates the local environmental conditions necessary for their persistence (Michalet *et al.* 2006; McIntire & Fajardo 2014). In terms of functional traits, this translates into facilitated and facilitating individuals having a dissimilar set of functional traits linked to stress

tolerance (such as LDMC which displayed the same pattern, Table 1) and ultimately into a high functional diversity within the community (Gross *et al.* 2009). Further experimental evidence within our study area, however, would be necessary in order to confirm our interpretation of observed functional diversity patterns.

ACCOUNTING FOR ITV: A MATTER OF SCALE, NUMBER AND TYPE OF TRAITS

Our results show that accounting for ITV when studying assembly rules is important in specific conditions. As we expected, including ITV did not significantly influence the detection of assembly processes at large spatial extent and was not required to detect the response of functional diversity to the GSL gradient. This result can be explained by the important species turnover across mountainous landscapes coupled with a strong functional turnover in response to climatic gradients (Chalmandrier *et al.* 2015). Consequently, at this spatial scale, intraspecific functional variability is likely to have a negligible effect on overall functional diversity patterns (Siefert, Fridley & Ritchie 2014; Lajoie & Vellend 2015).

Strikingly, at small spatial extent and fine grain where biotic interactions are likely to have a more prominent influence, the inclusion of ITV was essential to detect the convex relationship between functional diversity and GSL. Specifically, when ignoring ITV, diversity was underestimated in functionally divergent communities (Fig. 4, see also Siefert 2012). The importance of ITV at small scale supports findings from other studies demonstrating that plant species cope with competitive and facilitative interactions through phenotypic plasticity (Violle *et al.* 2009; Gubsch *et al.* 2010; García-Cervigón *et al.* 2015). More generally, the importance of accounting for ITV is highly dependent on spatial scale (Albert *et al.* 2011; Siefert *et al.* 2015). Finally, consideration of ITV was not equally important for all functional traits. Functional diversity based on leaf 'chemical' traits was more likely to be influenced by ITV than morphological traits (Siefert *et al.* 2015). We argue that the strong variability of soil nitrogen content between sites (between 15.20 and 62.3 $\mu\text{g g}^{-1}$ dw) and elevations (which alters CO₂ partial pressure) can explain the high intraspecific variability of leaf chemical traits in our study.

Conclusion

Our study demonstrates that carefully planned field surveys and accompanying multiscale diversity analyses of functional traits help to disentangle the effects of multiple assembly rules. We found support for the stress-gradient hypothesis in alpine and subalpine plant communities: low-stress communities are mainly driven by competition while high-stress communities are driven by strong environmental filters and facilitative interactions. Moreover, our results demonstrate that steep climate gradients can mask the influence of biotic interactions when small spatial scales and ITV are ignored (Choler, Michalet & Callaway 2001; Gross

et al. 2009). Beyond the scope of alpine ecosystems, our study stresses the importance of studying diversity patterns across multiple spatial scales (e.g. Gross *et al.* 2013). Together with a unified diversity framework, such an explicit consideration of scale should pave the way to better detect local assembly rules that are masked at larger spatial scale (e.g. facilitation in communities under strong abiotic filtering) or to disentangle assembly rules that have similar impacts on community structure but do not operate at the same spatial scale (e.g. large-scale abiotic filtering and competitive hierarchy).

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Data accessibility

Data can be accessed through the Dryad Data Repository <http://dx.doi.org/10.5061/dryad.8b3h0> (Chalmandrier *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Number of sampled individuals per species.

Appendix S2. Relationship between community single-trait diversity and growing season length.

Appendix S3. Is soil organic matter content also driving functional diversity?