RESEARCH ARTICLE

Inferring community assembly processes from functional seed trait variation along elevation gradient

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Abstract

1. Assembly of plant communities has long been scrutinized through the lens of trait-based ecology. Studies generally analyse functional traits related to the vegetative growth, survival and resource acquisition and thus ignore how assembly rules may affect plants at other stages of their life cycle, particularly when seeds disperse, persist in soil and germinate.

2. Here, we analysed an extensive dataset of 16 traits for 167 species measured in-situ in 36 grasslands located along an elevation gradient and studied the impact of abiotic filtering, biotic interactions and dispersal on traits reflecting different trait categories: plant vegetative growth, germination, dispersal and seed morphology. For each community, we quantified community-weighted means (CWMs) and functional diversity (FD) for all traits and established their relationships to mean annual temperature.

3. The seed traits were weakly correlated with vegetative traits. Therefore, these traits constituted independent axes of plant phenotypical variation that could be affected differently by community assembly rules. Abiotic filtering impacted mostly vegetative traits and to a lesser extent seed germination and morphological traits. Increasing low-temperature stress in upland sites selected for short-stature, slow-growing and frost-tolerant species that produce small quantities of small seeds with high degree of dormancy, high temperature requirements for germination and low germination speed.

4. Biotic interactions, specifically competition in the lowlands and facilitation in uplands, also filtered some functional traits in the studied communities. The benign climate in lowlands seems to promote plant with competitive strategies that include fast growth and resource acquisition (vegetative growth traits) and early and fast germination (germination traits), whereas the effects of facilitation on the vegetative and germination traits were cancelled out by the strong abiotic filtering.

5. The changes in the main dispersal vector from zoochory to anemochory along the elevation gradient strongly affected the dispersal and the seed morphological trait structure of the communities. This may be explained by stronger vertical

turbulence and moderate warm upwinds and low grazing intensity in the uplands that select for light and non-round shaped seeds with lower terminal velocity and endozoochorous potential.

6. *Synthesis.* We demonstrate that, in addition to vegetative traits, seed traits can substantially contribute to functional structuring of plant communities along environmental gradients. Thus, the 'hard' seed traits related to germination and dispersal are critical to detect multiple, complex community assembly rules. Consequently, such traits should be included in core lists of plant traits and, when applicable, be incorporated into the analysis of community assembly.

1 | INTRODUCTION

Now more than ever, ecologists are striving to understand the processes shaping the structure and composition of biological communities along environmental gradients (Cody et al., 1975; Cornwell & Ackerly, 2009; Weiher & Keddy, 1999). Disentangling the community assembly rules, that is, the ecological processes selecting for or against species from the regional species pool and determining local community composition (Keddy, 1992), is crucial both for explaining current biodiversity patterns and for predicting their future changes over the course of global change (D'Amen et al., 2017; Götzenberger et al., 2012; Newbold, 2018). In this context, trait-based approaches provide fundamental tools allowing for a better understanding of community assembly rules (McGill et al., 2006). These approaches assume that functional traits, that is 'morphological, physiological, phenological or behavioral characteristics impacting individuals' fitness via their effects on growth, reproduction and survival' (Violle et al., 2007), mediate species' ecological niches and interactions (Pillar et al., 2021). Therefore, community functional trait composition should reflect the outcome of key assembly rules: abiotic filtering, dispersal and biotic interactions (de Bello et al., 2013; Spasojevic & Suding, 2012).

The common agreement is that multiple traits related to different organs and/or ontogenetic stages (Dayrell et al., 2018; Kleyer & Minden, 2015) should be considered, because they relate to different ecological niche axes (Craine et al., 2012; Grime et al., 1997; Laughlin, 2014; Leishman & Westoby, 1992). This is particularly important when analysing community assembly along complex environmental gradients (e.g. elevation, latitude), as traits evolve in response to various abiotic and biotic conditions and therefore might have multiple functions (Kergunteuil et al., 2018). Yet a closer look at the published literature reveals that most of the studied traits relate to vegetative growth, survival and resource acquisition (e.g. leaf, root and whole-plant traits), while regeneration and dispersal traits are rarely considered (E-Vojtkó et al., 2020; Jiménez-Alfaro et al., 2016; Rosbakh et al., 2018). Thus, including floral, gametophyte, seed and seedling traits may provide additional, unique information about different plant functions and should maximize our understanding

of trait-based community assembly (E-Vojtkó et al., 2020; Jiménez-Alfaro et al., 2016; Laughlin, 2014; Rosbakh et al., 2018).

Ecological theory predicts that a plant species cannot be part of the community unless it possesses seed traits that are optimized to the local assembly processes (Grubb, 1977; Poschlod et al., 2013). Even if the local environmental conditions are suitable for adult plant growth and survival ('adult niche' sensu Grubb, 1977), a species' long-term persistence is defined by its ability to produce viable seeds that can successfully disperse, persist, germinate and produce viable seedlings ('regeneration niche'; Grubb, 1977). A few scarce studies have demonstrated that variability in seed traits is not random in plant communities (e.g. Fernández-Pascual et al., 2017; Rosbakh, Phartyal, et al., 2020; Soons et al., 2017). This suggests that seed traits, similarly to vegetative traits, may relate directly or indirectly to fitness and niche differences among species (Kraft et al., 2015) and may contribute to species coexistence in competitive environments (Poschlod et al., 2013). However, this remains largely unverified empirically. Only a relatively small number of traits linked to either dispersal (e.g. Johnson et al. (2018) or establishment (e.g. Rosbakh, Phartyal, et al., 2020) have been studied, thus neglecting germination and seed persistence in soil (Poschlod et al., 1998). Moreover, these are mainly 'soft' traits (Weiher & Keddy, 1999), which carry several, often independent, functions. For example, seed mass, widely considered as one of the major functional trait axes separating plant strategies (Díaz et al., 2016) can reflect abiotic filtering effects on dispersal (i.e. large seeds have lower potential of epizoochory; Römermann et al., 2005), germination (large seedlings from large seeds perform better at the germination stage; Leishman & Westoby, 1994), persistence in the soil (smaller seeds persist longer in soil; Hodkinson et al., 1998) and competition (e.g. Cadotte, 2017; Huang et al., 2020). In other words, such a trait is likely influenced by many interacting assembly processes and it may be difficult to infer assembly rules from its analysis. In contrast, studying instead a bunch of 'hard traits' may help to disentangle the respective impact of individual assembly processes.

Here, we compare the role of seed traits (germination, dispersal and seed morphology) in the assembly of mountain grassland communities. Traits related to vegetative growth were also used in this study to

access whether seed traits may partially reflect plant ecological strategies unrelated to the seed and seedling stages in plant life cycle. We analysed an extensive dataset of 16 traits for 167 species measured in 36 grasslands located along a steep elevation gradient. Specifically, we tested whether variation in two key metrics of community functional structure (community-weighted means (CWMs) and functional diversities (FDs); Ricotta & Moretti, 2011) was significantly driven by elevation. These metrics can accurately capture the mechanisms that shape community assembly (Kraft et al., 2015): the CWMs largely relate to dominant species and fitness differences, whereas FD is often used as a surrogate for niche partitioning (complementarity) and species coexistence (Cadotte, 2017; Kraft et al., 2015). First, we expected to detect strong effects of abiotic filtering on vegetative and seed community trait composition along the elevation gradient. Harsher abiotic stress in upland sites should cause a significant shift in plant strategies towards stress–adaptation and a stronger exclusion of maladapted species (Chalmandrier et al., 2017; de Bello et al., 2013). This should be reflected in a CWM shift with elevation and a stronger trait convergence (low FD) in upland compared to lowland communities (Figure 1).

Because temperature controls similarly growth and development in seedlings and adult plants, abiotic filtering should have comparable effects on both vegetative and seed germination traits. Specifically, we expected the upland communities to be assembled from slow-growing, frost-tolerant and short-stature species as an adaptation to short growing seasons with high probability of frost injuries (Chalmandrier et al., 2017; de Bello et al., 2013). As for the seed traits, we expected upland communities to be dominated by

species with a regeneration strategy that minimize risks of seedling establishment in cold climates (e.g. dormant seeds with a high-temperature requirement for germination and slow germination speed (Fernández-Pascual et al., 2021; Rosbakh & Poschlod, 2015). Furthermore, the short growth period with overall low temperatures coupled with frequent and severe frost events should favour the assemblage of species with lighter seeds and lower seed production in upland compared to lowland communities (e.g. Inouye, 2008; Steinacher & Wagner, 2013).

Second, we expected communities to be structured by biotic interactions shifting from competition in lowlands to facilitation in uplands (Choler et al., 2001; Maestre et al., 2009). Competition for limiting resources in the lowland sites should promote hierarchical competition or niche partitioning, resulting in trait convergence or divergence respectively (Kraft et al., 2015; Münkemüller et al., 2020). Conversely, higher levels of facilitation to cope with abiotic stress should result in trait divergence in the uplands (McIntire & Fajardo, 2014). This shift should be manifested not only in vegetative traits (Chalmandrier et al., 2017), but also in seed germination traits, as seedling establishment can be strongly affected by biotic interactions with adult plants (e.g. Kos & Poschlod, 2007; Thompson & Grime, 1983). In particular, if seed germination traits relate to niche differences among species, this should promote niche partitioning and should lead to high functional trait divergence under the high level of competition in the lowlands. There, in grasslands with dense and tall vegetation, seedlings grow in gaps (spatial niches) with comparatively low competition for available resources, especially light (Thompson & Grime, 1983). Additionally,
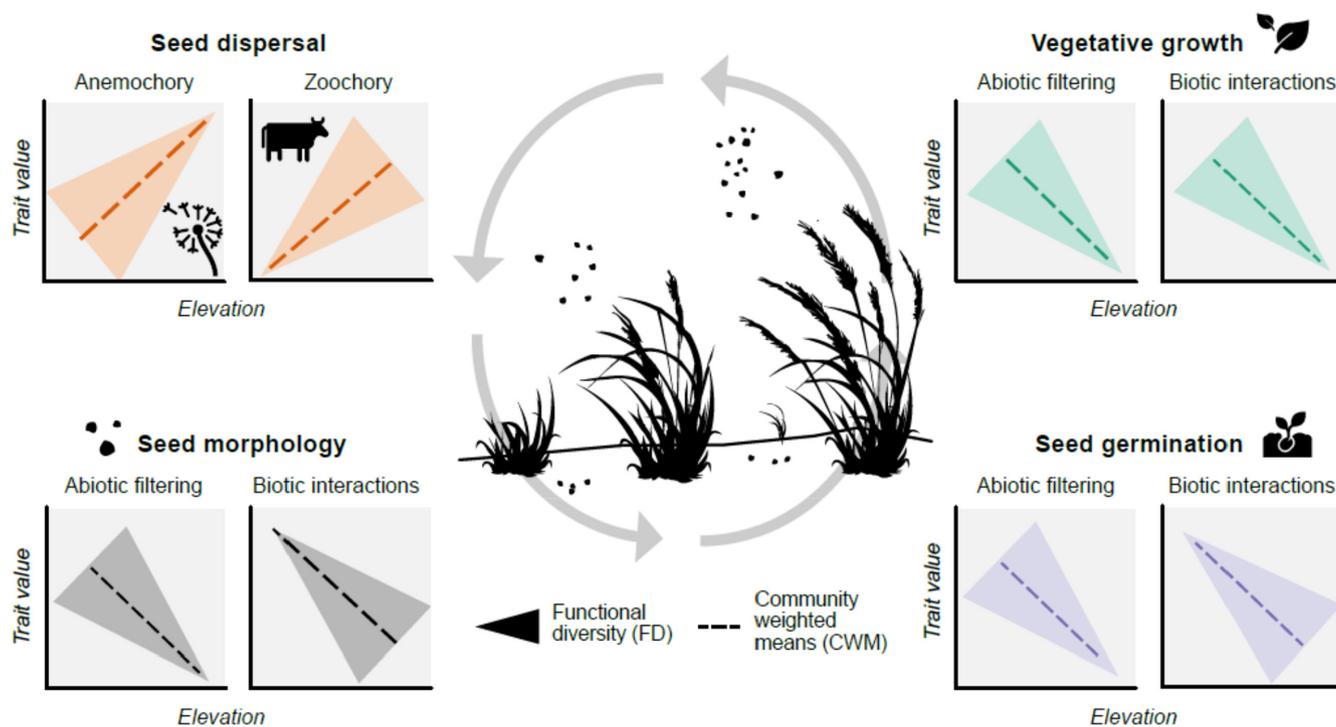
FIGURE 1 Graphical summary of expected community-weighted means (CWMs) and functional diversity of vegetative and seed traits of grasslands along the elevation gradient. The dashed lines indicate anticipated changes in CWMs (i.e. trait values of dominant species) caused by environmental filtering and/or biotic interactions gradient from competition in lowlands to facilitation in uplands. The shaded area indicates changes in functional diversity due to shifts in niche partitioning and coexistence patterns, related to the increasing elevations.

early germination, may increase the likelihood of seedling establishment by preceding the peak of vegetation growth (Forbis, 2010; Kardol et al., 2013). Alternatively, amelioration of abiotic stress by neighbours (i.e. facilitation) at high elevations (Choler et al., 2001) might allow the establishment of stress-sensitive seedlings in the vicinity of stress-resistant plants resulting in a higher functional diversity. Seed size and production were expected to be affected by the above-mentioned biotic processes in the same manner (Figure 1). Finally, if seed germination traits relate to fitness differences among species (Kraft et al., 2015), this should promote hierarchical competition and lead to functional convergence in lowland sites as species need to exhibit the same competitive traits to establish in those competitive environments. As germination traits are also constrained by abiotic stress in the uplands, we should observe a shift in CWM with elevation and functional convergence throughout the gradient.

Third, we anticipated that the shift in the main dispersal vector with elevation would affect community assembly in grasslands (Figure 1). Specifically, lowland communities should be dominated by species better adapted to zoochory, due to the higher frequency and intensity of grazing (Pellissier et al., 2010). In upland communities, species should be adapted to anemochory, due to frequent and intense vertical wind turbulences (Tackenberg & Stöcklin, 2008). Dispersal strategy was further expected to affect the diversity of plant dispersal traits. We predicted that the decreasing connectivity among upland grasslands (Körner, 2007) would lead to a stronger functional convergence in dispersal traits due to strong abiotic filtering on species' dispersal ability (i.e. only good dispersers could persist in patchy alpine vegetation). In contrast, seed dispersal traits in lowland communities were expected to be divergent, due to better habitat connectivity and a larger number of available dispersal vectors. Finally, changes in seed morphological traits at the community level should reflect the shift in the main dispersal strategy from zoochory to anemochory. Specifically, upland communities were expected to be assembled with species with light, elongated or flat seeds with comparatively large projection, a set of traits favouring dispersal by wind along longer distances (Fenner et al., 2005; Thomson et al., 2011).

2 | MATERIALS AND METHODS

2.1 | Study system

Field work was carried out in the eastern part of the Bavarian Alps (Germany), from 2009 to 2021. The region has a typical alpine relief, with steep mountain peaks composed of Triassic lime and dolomite rocks. The climate is montane with high mean annual precipitation rates (1500–2000 mm/year; Marke et al., 2013) and an elevation-driven decrease in mean annual air temperatures with a lapse rate of *c.* −0.6°C/100 m of elevation. The non-forest vegetation is largely represented by species-rich calcareous grasslands on nutrient-poor soils. In lowlands, grasslands are dominated by graminoids (e.g. *Arrhenatherum elatius*, *Helictotrichon pubescens*, *Carex flacca*) and tall forbs (e.g. *Buphthalmum salicifolium*, *Centaurea jacea*). As elevation

increases, they are replaced by sedges (e.g. *Carex firma*, *C. sempervirens*), dwarf shrubs (e.g. *Vaccinium vitis-idaea* and *Silene acaulis*) and short-stature herbs (e.g. *Ligusticum mutellina*, *Ranunculus montanus*, *Soldanella alpina*). Until the 1950s, the lowland grasslands were intensively grazed by domestic cattle and/or used for hay-making. Nowadays, the grasslands at elevations 600–1600 above sea level (a.s.l.) are used for low-intensity cattle grazing, whereas the subalpine and alpine grasslands above *c.* 1700 m a.s.l. are occasionally grazed by sheep or wild ungulates such as the alpine ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*).

2.2 | Data collection

2.2.1 | Plant composition and environmental characteristics of the study sites

Plant community composition was collected in 2009 in 36 grasslands located along an elevation gradient from 656 to 2363 m a.s.l. that reflected mainly a strong variation in mean annual temperature (Appendices S1 and S2). In each grassland, the vegetation was surveyed in ten 2 × 2 m² plots per site during the peak of the growing season, which was elevation specific. In each plot, the abundance of all vascular species was estimated based on six percentage classes: <0.1%, 1%–5%, 5%–25%, 25%–50%, 50%–75% and 75%–100%. The relative abundance of a species at a site was then calculated as the mean value of its abundance in all plots. In total, we recorded 379 species in all the sites.

2.3 | Trait data

We sampled the most representative species in the local communities: we did not consider species present in fewer than three sites and with a maximum abundance of <3% across all sites. In total, we collected vegetative and seed traits for 167 species. Species with measured trait data accounted for more than 80% of the total abundance of each community, allowing for a reliable estimate of functional diversity (de Bello et al., 2013; Pakeman & Quested, 2007).

Each species was sampled at the site where it was the most abundant (15%–87.5%) following Rosbakh and Poschlod (2015). Fully ripened fruits and seeds (hereafter 'seeds') were collected at maturity in these 'optimal' sites during the growing seasons 2009–2020. Because of low seed quantity and/or quality, the seeds of several species were collected from populations located close to the 'optimal' sites under similar environmental conditions. Seeds were collected from a large number of randomly chosen individuals growing at a minimal 2 m distance from each other. After collection, seeds were air-dried for several days, cleaned of flower/fruit debris, and kept dry in a cold room at 4°C prior to the trait measurements from 6 to 24 weeks. If not specified otherwise, the trait measurements followed the standardized protocols (Kleyer et al., 2008; Perez-Harguindeguy et al., 2016). Because it was

work intensive to measure traits in multiple populations per species, we neglected intraspecific trait variability: trait values within species were considered to be 'fixed', that is, a single mean trait value was assigned per species measured under the species' optimal ecological conditions.

2.4 | Vegetative traits

We measured canopy height (CH), specific leaf area (SLA), leaf nitrogen content (LeafN) and foliar frost sensitivity (FoliarFS) for each species. All measurements were made in situ in the 'optimal' growing sites as described above.

2.5 | Seed germination traits

We considered dormancy type, initial temperature of germination, germination speed and germination synchrony as traits representing the different aspects of the plant regeneration strategy. Every species was characterized in terms of type of seed dormancy (sensu Baskin & Baskin, 2004) based on published data in (Baskin & Baskin, 2014; Rosbakh, Baskin, et al., 2020; Rosbakh & Poschlod, 2015) and the authors' unpublished data on the seed germination ecology of the study species. Dormancy type is a categorical variable with six classes: non-dormancy (ND), physical dormancy (PY), physiological dormancy (PD), morphological dormancy (MD), morphophysiological dormancy (MPD, i.e. MD+PD) and combinational dormancy (CD, i.e. PY+PD). The seeds of a high proportion (82%) of the study species were categorized as dormant, of which 74% had a component of PD that was further subcategorized into three levels (non-deep, intermediate and deep) depending on the depth of dormancy (Baskin & Baskin, 2014). Only 7% of study species possessed PY and none of them had MD or CD. To make the species comparable with each other, a relative weighted score was given to each species based on the type/depth of dormancy. Ultimately, we described species' dormancy type with five categories: ND, PY, non-deep PD/MPD, intermediate PD/MPD and deep PD/MPD. Each was associated with a relative rank score of 0, 0.25, 0.5, 0.75 and 1 respectively (DormRank).

The remaining seed germination traits were obtained from experiments under controlled conditions (see Rosbakh and Poschlod (2015) for further details). In brief: seeds with PD were either cold moist stratified at 4°C for 6 weeks or treated with 0.1% gibberellin acid prior to the germination experiment to alleviate the dormancy. Seeds of eight species were mechanically scarified to overcome physical dormancy. Seeds were left to germinate for 6 weeks along a temperature gradient (10/2, 14/6, 18/10, 22/14, 26/18, 30/22°C, 14/10 h photoperiod), which represents the germination conditions (from cool spring to warm summer) in the studied plant communities along the elevation gradient. Seed germination was scored regularly; the viability of non-germinated seeds was checked through inspection of embryos. The seed germination data were used to calculate:

1. Minimal temperature of seed germination (T5): lowest temperature at which 5% of all seeds germinated (Rosbakh & Poschlod, 2015);
2. Germination speed calculated as mean germination time in days (MGT; Lozano-Isla et al., 2019) with lower values reflecting faster seed germination;
3. Germination synchrony calculated as the germination synchronization index (Lozano-Isla et al., 2019), with values close to one indicating that all seeds germinate at the same time (more synchronized germination), while values close to zero indicate that at least two seeds germinated at a different time (less synchronized germination).

2.6 | Seed dispersal traits

We assumed that anemochory, epi- and endo-zoochory were the most important seed dispersal vectors in the study system (Pellissier et al., 2010; Poschlod et al., 2005; Tackenberg & Stöcklin, 2008). We measured seed terminal velocity (TV; m/s) as a proxy for species' wind-dispersal potential, with lower values indicating longer dispersal distances. TV was calculated from hand stopped falling times from a height of 2 m with a correction for the initial acceleration phase (Tackenberg & Stöcklin, 2008).

Epizoochory was estimated as seed attachment potential to the fur of cattle and sheep (EpiCow and EpiSheep, %), two of the most common domestic grazers in the study system. The values range from 0% to 100%, with higher values indicating potentially longer dispersal distances by the corresponding animals (Römermann et al., 2005). EpiSheep values correlate closely with seed attachment potential to ibex and chamois fur (S. Rosbakh, unpubl. results) and can thus be used as proxies for epizoochory by these two species.

Species capacity for endozoochory (EndoZoo) is based on dung germinating seed surveys in the study area (Poschlod and Rosbakh, unpubl. results) and published data on comparable systems using similar approach (Albert et al., 2015). Briefly, the method includes fresh dung collection in the field followed by its cultivation in a greenhouse and identification of all plants emerging from the samples. It is a semi-quantitative variable with three levels: 1—seed endozoochorous dispersal is frequent (viable seeds are found in more than half of all samples) and/or in large numbers (>100 germinable seeds/kg of dry dung); 0.5—endozoochory is rare (viable seeds are present in less than 50% of dung samples) and/or in small numbers (<100 germinable seeds per kg of dry dung); 0—viable seeds are not found in the dung samples.

2.7 | Seed morphological traits

Seed mass (SeedMass, mg), seed shape (SeedShape) and seed projection (SeedPr; mm^2) were also included in our study to provide additional mechanistic explanations of seed dispersal trait variability along the elevation gradient. Seed mass (SeedMass) is the average mass of a single seed extrapolated from the weights of three samples of 100 seeds each. Seed shape (SeedShape) is the variance of

seed length, width and height; it is a dimensionless value that varies between zero in perfectly round seeds and 0.2 in disk- or needle-shaped seeds (Knevel, 2005). Seed projection, the one-side area of a seed, was measured by scanning seeds on a flatbed scanner with resolution of 1200 dpi followed by seed area measurements with the help of ImageJ software (Schneider et al., 2012). Although, strictly speaking, seed production (average number of seeds produced per ramet of 10 randomly selected individuals; SeedN) is not a morphological trait, it was included in this category for the sake of brevity.

2.8 | Data analysis

To estimate and visualize the relationship between plant traits, we analysed the correlation matrix between functional traits using phylogenetic generalized least squares (pGLS) regression models and conducted a phylogenetic principal component analysis (pPCA) on the species-trait matrix. The pGLS and pPCA are based on a large dated phylogeny of the European flora (Durka & Michalski, 2012).

To analyse the change in the functional structure of communities, we estimated community-weighted means (CWMs) and functional diversity (FD; Ricotta & Moretti, 2011). The CWM of a community is the average trait value weighted by species relative abundance. It mainly reflects the trait value of the dominant species in a community and thus describes the main adaptation strategy to local environmental conditions (de Bello et al., 2021). FD reflects trait convergence or divergence (i.e. a decrease or increase in trait diversity compared to a null expectation) and was calculated using Rao's quadratic entropy (Rao, 1982).

We tested whether observed functional diversity deviated from the null expectation that communities are a random sample of species from the regional pool. For each community, null functional diversity distributions were generated by permuting the columns (species) of the site-by-species abundance matrix. We then computed the standard effect sizes (SES) to evaluate the deviations of observed functional diversity values from random expectations. SES are calculated as the observed functional diversity value minus the mean of the null functional diversity values divided by the standard deviation of the null functional diversity values. A negative SES value indicates that functional diversity is convergent, that is, lower than expected according to the null hypothesis. Conversely, a positive SES value indicates that functional diversity is divergent, that is, higher than the null hypothesis would indicate. We further assessed the significance of functional diversity SES by identifying the proportion of random values that fell below the observed diversity value. If this rank value was below 0.05, functional diversity in that plot was considered significantly low; if it was higher than 0.95, functional diversity in that plot was considered significantly high.

The change in community CWM and FD values with elevation was estimated with the help of a degree 2 polynomial regression because a trait–environment relationship can be nonlinear (Bernard-Verdier et al., 2012; Kergunteuil et al., 2018). Where the quadratic term was not significant, this term was removed. Model assumptions were met in all cases. All statistical analyses were conducted in the R statistical environment (R Core Development Team, 2021).

3 | RESULTS

3.1 | Trait–trait relationships

Vegetative and seed traits were weakly correlated with each other (Appendix S3); the strongest correlations among them were between leaf frost sensitivity and mean germination time (negative relationship, $r^2 = 0.17$). Collinearity between seed germination and seed dispersal traits was also relatively low, with the strongest correlation between the dormancy rank and terminal velocity ($r^2 = 0.09$, $p < 0.05$).

Several morphological traits were significantly correlated with dispersal traits. The following were observed: a moderate negative correlation between seed shape and terminal velocity and potential for endozoochory ($r^2 = 0.19$ and $r^2 = 0.20$) respectively. Seed projection was also negatively moderately correlated with terminal velocity ($r^2 = 0.19$). Seed mass displayed a moderate negative and positive relationships with attachment potential to sheep fur ($r^2 = 0.18$) and terminal velocity ($r^2 = 0.16$). The latter was also strongly negatively correlated with seed projection ($r^2 = 0.48$).

Importantly, we also detected several significant, from low to moderate, correlations within the group of traits, a pattern that supports our trait categorization scheme. In the vegetative trait group, SLA was significantly, positively correlated with canopy height ($r^2 = 0.05$)). Similarly, leaf nitrogen content displayed a positive, although weak, significant relationship with canopy height and specific leaf area ($r^2 = 0.03$ and $r^2 = 0.06$ respectively).

In contrast, the traits within the germination/establishment trait groups showed stronger correlations. Mean germination time (MGT) was positively moderately correlated with dormancy rank ($r^2 = 0.21$) and minimal temperature of seed germination ($r^2 = 0.40$); this trait was also negatively correlated with synchrony of germination (SYN; in all cases $p < 0.05$). Furthermore, dormancy rank and MGT displayed a positive, yet weak significant relationship ($r^2 = 0.11$), whereas this trait was weakly negatively correlated with SYN ($r^2 = 0.1$).

Among seed dispersal traits, seed attachment potentials to cattle and sheep furs were positively moderately correlated ($r^2 = 0.24$); the former trait also displayed significant positive, yet weak, relationship with potential for endozoochory ($r^2 = 0.10$).

The pPCA on species-trait matrix is presented in the Appendix S4.

3.2 | Variation of community-weighted means with elevation

The community-weighted means (CWMs) of almost all traits changed significantly along the elevation gradient, albeit with differences in explained variance (Figure 2). Vegetative traits showed the strongest variation with elevation: CWM of canopy height, SLA and foliar frost sensitivity showed a sharp linear decrease with elevation ($r^2 = 0.67$,

0.80 and 0.81, respectively, $p < 0.001$). The variation in CWM for leaf nitrogen content followed the same pattern; however, the amount of variance explained by this relationship was moderate ($r^2 = 0.25$, $p = 0.002$).

As regards to germination traits, the CWMs of dormancy rank, minimum germination temperature and mean germination time displayed a significant, positive relationship with the elevation gradient with a moderate amount of explained variance ($r^2 = 0.22$, 0.28 and 0.30, respectively, all $p < 0.001$). The CWM for germination synchrony did not exhibit a significant relationship with elevation (Figure 2; $r^2 = 0.04$, $p = 0.27$).

CWM values for both seed terminal velocity and endozoochory rate decreased in a sharp manner with increasing elevation (Figure 2; $r^2 = 0.65$ and 0.70, respectively, both $p < 0.001$). The CWM for the sheep epizoochory rate was high across the entire gradient (86% on average) and weakly increased with increasing elevation (Figure 2; $r^2 = 0.15$, $p = 0.02$). The CWM for cow epizoochory did not vary significantly with elevation (Figure 2; $r^2 = 0.03$, $p = 0.27$).

The CWM for seed mass and seed number per ramet displayed a significantly negative relationship with elevation, the explained variance of the latter being larger (Figure 2; $r^2 = 0.27$, $p = 0.002$ and $r^2 = 0.51$, respectively, $p < 0.001$). The CWM values for seed shape significantly but moderately increased with increasing elevation (Figure 2; $r^2 = 0.21$, $p = 0.02$). The CWM for seed projection showed a concave, significant relationship with the elevation (Figure 2; $r^2 = 0.22$, $p = 0.005$).

3.3 | Variation in functional diversities along the elevation gradient

The standard effect sizes (SES) of the functional diversity of vegetative traits were mostly non-random along the gradient (Figure 3). The proportion of communities with negative SES values (trait convergence) was higher for canopy height and SLA (Figure 3), whereas for leaf nitrogen content (LeafN) and foliar frost sensitivity (FoliarFS) the majority of the communities had positive SES values (trait divergence; Figure 3). Mean SES for frost sensitivity was −0.17 across communities and 16% of communities displayed significant diversity (rank below 0.05). SES of canopy height decreased nonlinearly with increasing elevation (Figure 3; $r^2 = 0.56$, $p < 0.001$), indicating that species in upland communities had more similar trait values than their lowland counterparts. In contrast, SES of FoliarFS showed the opposite pattern: they were convergent in the lowlands, increased with elevation, resulting in comparatively strong trait divergence in upland communities (Figure 3; $r^2 = 0.29$, $p = 0.004$). Furthermore, the SES of SLA showed a significant, slightly concave relationship with elevation (Figure 3; $r^2 = 0.19$, $p = 0.03$), with stronger trait convergence in upland and lowland plant communities compared to the middle part of the gradient. Finally, the SES of Leaf N did not vary significantly with elevation (Figure 3; $r^2 = 0.12$, $p = 0.12$).

Standard effect sizes of germination traits were mostly divergent throughout the elevation gradient (Figure 3), except for DormRank
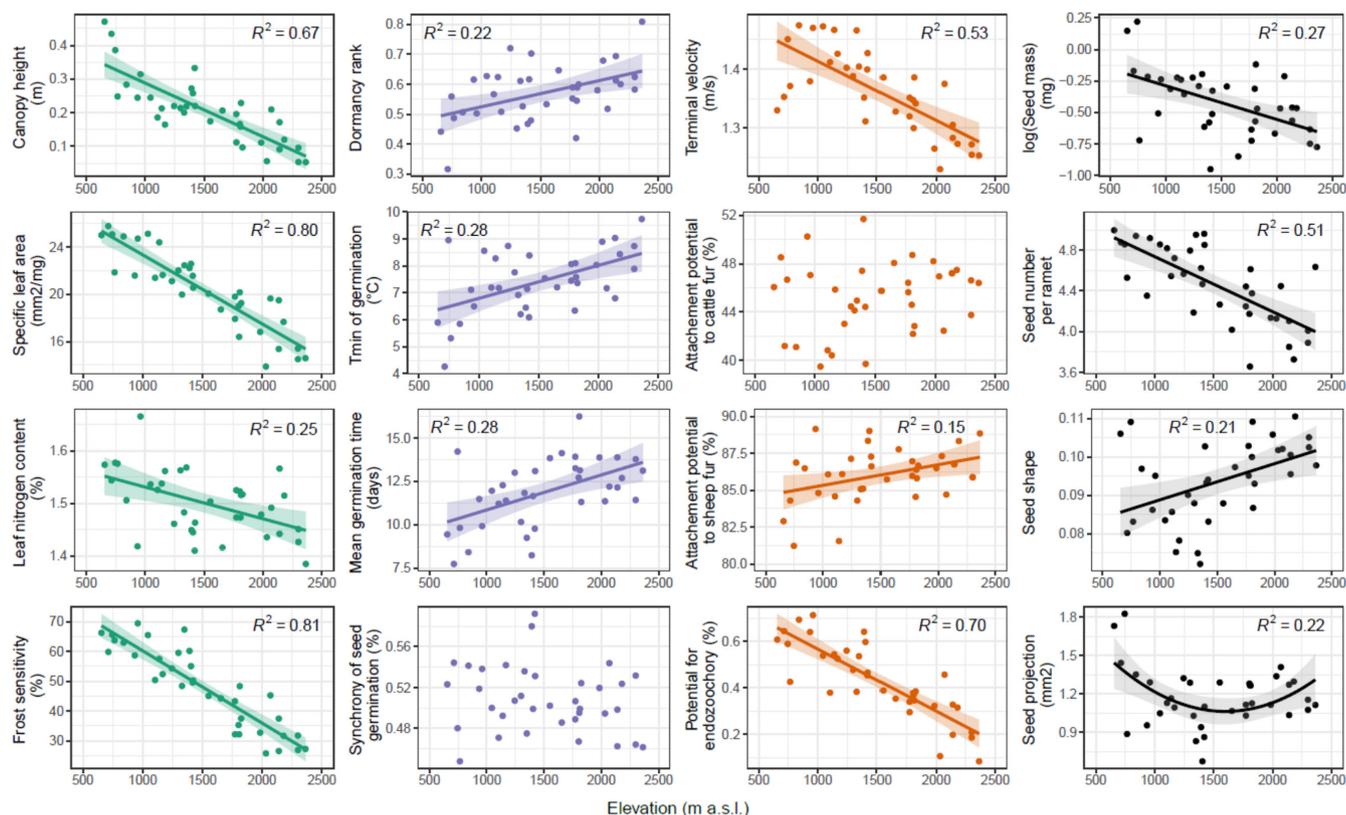
FIGURE 2 Variation in community-weighted means (CWMs) of 16 traits with elevation deduced from linear regressions. Circles in the panels are CWMs of the 36 studied grasslands. Full lines indicate significant relationships ($p < 0.05$), the shaded areas denote the 95% confidence interval of the fitted CWM values.
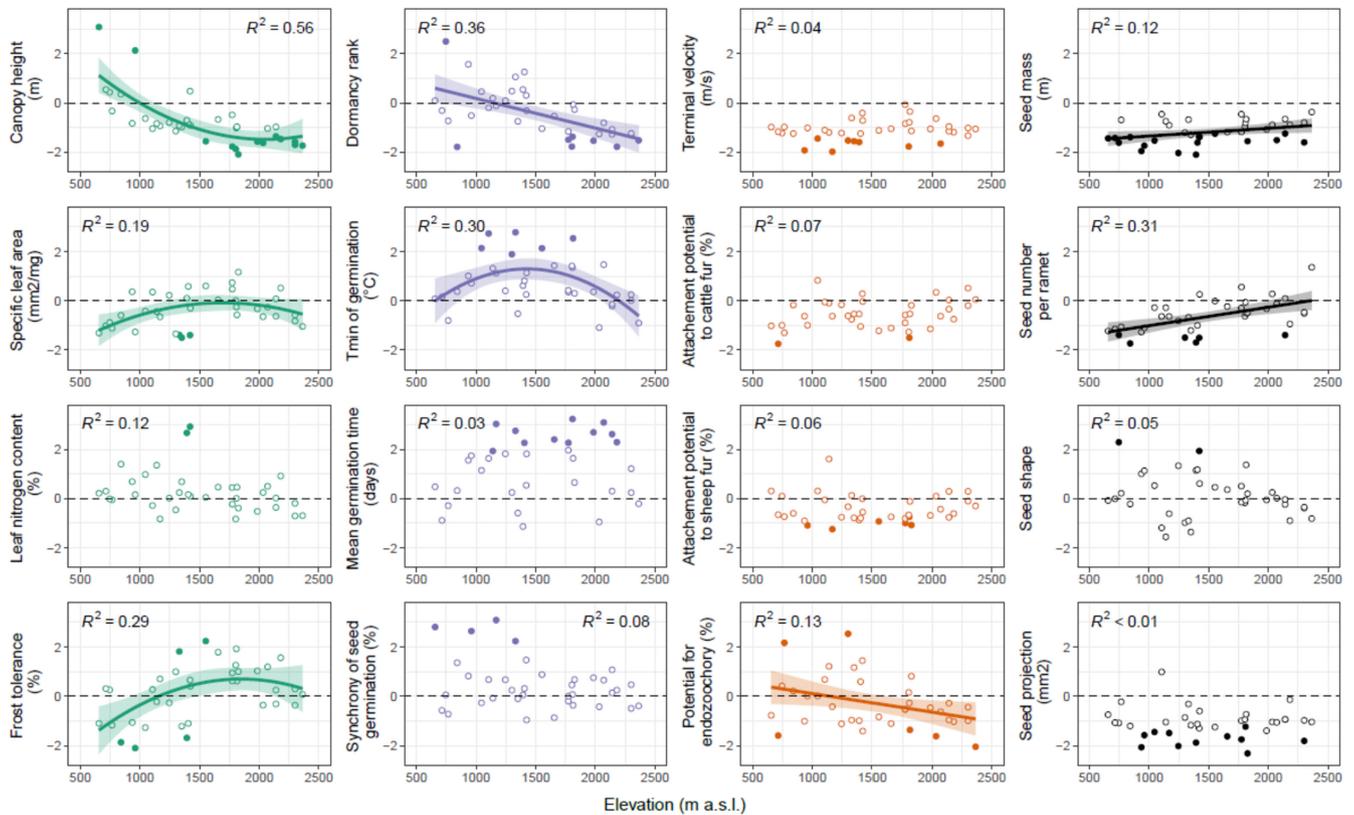
FIGURE 3 Variation in functional diversity (FD) of the 16 traits with elevation. Circles in the panels indicate standard effect sizes (SES) of the study traits in 36 study grasslands. Negative and positive SES values indicate a narrower and broader trait range than expected respectively. Filled circles represent significantly low (rank lower than 0.05) or high (rank above 0.95) functional diversity. Full lines indicate significant relationships ($p < 0.05$), the shaded areas denote the 95% confidence interval of the fitted SES values.

FD values that were predominantly convergent. Significant changes in FD were only found for DormRank and T5. As regards the former, SES decreased linearly with elevation ($r^2 = 0.36$, $p = 0.002$; Figure 3), changing the functional trait signature of the communities from functional divergence to convergence. As regards the latter, the FD of T5 varied moderately with elevation ($r^2 = 0.20$, $p = 0.03$; Figure 3), with more divergent communities in the middle part of the gradient (i.e. concave relationship).

Dispersal trait functional diversities were almost exclusively convergent throughout the elevation gradient (Figure 3). Among dispersal traits, only the FD of EndoZoo varied significantly with elevation (positive, weak relationship; $r^2 = 0.13$, $p = 0.03$; Figure 3).

The functional diversities of seed morphological traits along the elevation gradient followed a clear convergence pattern, except for SeedShape that did not show any clear tendency towards convergence or divergence within the communities. Elevation had a significant, negative effect on FD values of SeedMass and SeedN ($r^2 = 0.12$, $p = 0.04$, and $r^2 = 0.31$, $p < 0.001$), indicating stronger convergence of the traits in the lowland communities.

4 | DISCUSSION

Regeneration has always been considered a fundamental aspect of plant community ecology (Grime et al., 1981; Grubb, 1977;

Keddy, 2010), yet it has been largely neglected in studies of community assembly (Jiménez-Alfaro et al., 2016; Poschlod et al., 2013; Saatkamp et al., 2019). We provide the first comprehensive evidence that little-studied regenerative (seed) functional traits are important determinants of plant community structure in addition to vegetative traits. Specifically, we show that seed traits are only weakly linked to vegetative traits and may constitute independent axes of plant phenotypical variation. We then show that abiotic conditions, biotic interactions and dispersal act differently on the functional traits of plants related to different life stages and that this ultimately shape the structure of mountain grassland communities.

4.1 | Elevation strongly filters plant communities

Confirming our expectations, abiotic conditions have a prominent impact on functional composition of mountain grassland communities in regards to both vegetative and seed traits. Mean values of vegetative traits (i.e. CWMs) shifted strongly (or moderately in the case of leaf nitrogen content) with elevation (Figure 2). Specifically, the increasing abiotic stress towards upland sites seemed to select for short-stature species (Bucher & Rosbakh, 2021; de Bello et al., 2021; Pellissier et al., 2010), and to filter out tall-stature species (as shown by the convergent functional diversity of height in upland sites). This highlights the critical importance of small stature for

plants to cope with abiotic stress, as this allows heat accumulation near the ground during the short growing season (Körner, 2021). The shift in the mean trait values of SLA and leaf N also mirrors the shift of leaf-economic strategies with elevation from fast-growing species with rapid nutrient acquisition in lowland sites (high SLA and leaf N values) to slow-growing and nutrient-conservative species (low SLA and leaf N values in upland sites, Rosbakh et al., 2015; Spasojevic & Suding, 2012). Finally, plants were more frost-resistant in upland sites, which may show the importance of this trait to cope with frost events at higher elevations that may occur even during the vegetation season in summer. In contrast to canopy height, the functional diversity of this trait was not convergent in cold sites, possibly indicating that despite the strong climatic stress, other ecological processes may maintain the presence of stress-sensitive species (see below).

The considerable effects of abiotic filtering on grassland community assembly were also detected when analysing seed trait variation along the elevation gradient. Community-weighted means for three out of four seed germination traits (degree of dormancy, temperature requirement for germination and germination speed) presented a clear response to elevation, albeit less strong than for vegetative traits (Figure 2). We attribute these patterns to the shifts in seed germination strategies with elevation-related abiotic stress. Low-temperature stress (e.g. frequent, severe frost events) at high elevation selects species that produce seeds with a high degree of dormancy, high temperature requirements for germination and low germination speed (Baskin & Baskin, 2014; Fernández-Pascual et al., 2021; Rosbakh & Poschlod, 2015). Furthermore, the increasing convergence in seed dormancy with elevation implies that plant communities in upland sites are largely assembled from species with similar high degrees of seed dormancy. Together these patterns indicate that elevation-related stress select for species that can postpone germination to more suitable conditions for seedling establishment via mechanisms of seed physiological dormancy (Baskin & Baskin, 2014). Specifically, these species require a long cold stratification periods necessary to break physiological dormancy. This prevents seeds from germinating shortly after dispersal in late summer–early autumn, whereas high base temperatures of germination and slow germination speeds postpone germination of non-dormant seeds to late spring–early summer, when severe frost events are less frequent (Rosbakh, Margreiter, et al., 2020; Rosbakh & Poschlod, 2015).

The decrease in CWMs for seed size and seed production with elevation suggested that species in upland communities produce fewer and lighter seeds than species in lowland communities. This can be attributed to the harsh climatic conditions at high elevation that are stressful for sexual reproduction (Figure 2). A short growth period coupled with frequent and severe frost events considerably limits pollination, fertilization and seed maturation (Lundemo & Totland, 2007; Rosbakh & Poschlod, 2016; Steinacher & Wagner, 2013), thereby filtering out species that require more resources to produce large quantities of heavy seeds. Alternatively, the prevalence of species producing light seeds in alpine communities could reflect the increasing role of anemochory with elevation (see below).

4.2 | Shifts in biotic interactions from lowlands to uplands filter vegetative and seed traits

The stress gradient hypothesis predicts that increasing stress should lead to a shift of biotic interactions from competition to facilitation (Maestre et al., 2009). Our results partially align with this hypothesis and further suggest how functional traits may underpin this mechanism in mountain plant communities.

As expected, the relatively benign climate in low-elevation grasslands seem to promote plants with competitive strategies that favor fast growth and resource acquisition (comparatively high CWM values for canopy height, SLA and leaf N; Figure 2). Likely because of the weak trade-off between those traits and frost resistance, species from the lowlands invest less in protecting their leaves against negative temperatures (high CWMs for frost sensitivity in lowlands; Figure 2). The convergent FD values in those grasslands further suggest that frost-resistant plants are excluded from these communities, likely due to their comparatively low competitiveness (Bucher & Rosbakh, 2021). In contrast, the high FD for canopy height indicates that both small and tall plants can co-occur, suggesting that some degree of niche partitioning associated with this trait maintains species coexistence in those competitive environments (Münkemüller et al., 2020). Surprisingly, in upland communities, the functional diversities of SLA and frost sensitivity were higher than in the lowland communities. This suggests that some species with high foliar frost sensitivity and/or high SLA can persist there despite the strong abiotic stress. We attribute this pattern to the high number of available thermic niches that characterize topographically complex environments at high elevation (Scherrer & Körner, 2011) or to facilitative interactions among co-occurring species, with stress-resistant species creating favourable local environments for the persistence of stress-sensitive species (Cavieres & Badano, 2009; Choler et al., 2001).

Similar to vegetative traits, germination traits in the lowlands seem to be constrained by high levels of competition. Species in the lowlands tend to germinate after a comparatively short stratification period (low T5 community-weighted means) and display a high germination speed (low MGT community-weighted means) that allows seedling establishment in early spring before the closure of dense vegetation cover (Figure 2). Additionally, the functional diversity of T5, MGT and SYN was divergent in low- to mid-elevation grasslands (Figure 3). This suggests that niche partitioning stabilizes the coexistence of multiple regeneration and temporal niches (Bernard-Verdier et al., 2012; Grubb, 1977). In the uplands, this pattern vanishes and may indicate that the increasing abiotic filtering (which promotes trait convergence, see above) overrides the signal of biotic interactions.

Interestingly, seed mass and seed production FD were convergent throughout the entire elevation gradient (Figure 3), a pattern that may be attributed to the effects of both abiotic and biotic filtering on the functional structure of communities. In the uplands, seed trait convergence could be related to the impact of abiotic filtering (see above), but in the lowlands, seed trait convergence might reflect hierarchical competition favouring plants producing large seeds and/or in large

numbers, two traits that ensure regeneration in dense, tall grassland vegetation (Jakobsson & Eriksson, 2000; Leishman & Westoby, 1994).

4.3 | Seed dispersal traits and community assembly

The relationship between community functional trait structure and dispersal is traditionally less studied in mountain grasslands than the impact of abiotic and biotic filtering. There are, however, evidences that dispersal ability determines species capacity to colonize patches of suitable habitat and maintain sink populations beyond the limits of their abiotic niche (Dullinger et al., 2012; Isabelle et al., 2012).

Ours results suggest that the change of predominant dispersal vector with elevation plays an important role in community assembly via its effects on seed dispersal traits. The strong decreases in average seed terminal velocity and potential for endozoochory with elevation point to a clear shift in the main plant dispersal strategy from endozoochory in lowland sites to anemochory in upland sites (Figure 2). In lowland sites, the higher rate of endozoochory may be due to the long history of grazing by domestic animals (Gilck & Poschlod, 2021; Poschlod, 2014) that may have favoured the immigration and persistence of endozoochorous plants. In upland sites, lower seed terminal velocity and flatter seeds (higher values of seed shape) indicate that seeds of many plants are likely dispersed by the intense vertical turbulence (Tackenberg & Stöcklin, 2008) and moderate warm upwind (Tackenberg, Poschlod, & Kahmen, 2003) that allow effective dispersal over long distances in patchy alpine vegetation (Tackenberg, Poschlod, & Bonn, 2003).

Epizoochory rates are remarkably higher for sheep than for cattle, suggesting that the former are an effective seed dispersal vector along the entire elevation gradient (Figure 2). We also detected a weak yet significant increase in seed attachment potential to sheep fur with elevation (Figure 2). This pattern can be explained by traditional sheep grazing in upland grasslands or similar properties of sheep and wild ungulates' fur to collect and retain seeds during dispersal (S. Rosbakh, unpubl. data). Because upland grasslands are mainly grazed by wild ungulates, the corresponding communities might have been assembled with species better adapted to this seed dispersal vector.

Both epizoochory rates and seed terminal velocity are correlated with seed mass, seed shape and seed projection across species. In consequence, the shift in seed dispersal strategies along the elevation gradient can also be seen in the community patterns of seed morphological traits (Figure 2). As previously shown, wind-dispersed seeds tend to be light and non-round in shape (e.g. elongated or winged seeds; Appendix S3), two traits that positively affect terminal velocity values (Fenner et al., 2005; Thomson et al., 2011). As for epizoochory by sheep, light diaspores with an elongated shape facilitate 'anchoring' in animal fur (Römermann et al., 2005). As seen previously, large seed mass may be favoured in the lowlands by competitive interactions. The joint impact on the competitive filter in the lowlands on one hand and the wind and epizoochory dispersal filter in the uplands on the other hand may explain why the functional diversities of seed

mass, seed shape, sheep and cattle epizoochory, and terminal velocity are consistently convergent along the elevation gradient.

4.4 | Conclusions and implications

Our study reveals that in addition to vegetative traits, regenerative seed functional traits can substantially contribute to plant community assembly along environmental gradients. We demonstrate that a combined study of vegetative traits and seed germination, dispersal and morphology traits in plant community ecology is critical for the detection of multiple, complex community assembly rules. Specifically, we find that in mountain grasslands located along a steep environmental gradient (1) abiotic filtering mostly impacts vegetative traits and to a lesser extent, seed germination and morphological traits, (2) biotic interactions, specifically competition, had an effect on all traits but act in different ways and (3) the shift in the main dispersal vector affect the structure of dispersal traits and by extension, of seed morphological traits. These findings lend support to the recent claim that plant trait research should consider multiple traits representing different ecological niche axes, that is, different organs and/or ontogenetic stages (Craine et al., 2012; Kleyer & Minden, 2015; Laughlin, 2014). Therefore, along with other authors (Jiménez-Alfaro et al., 2016; Saatkamp et al., 2019), we advocate that 'hard' seed traits related to germination and dispersal should be included in core lists of plant traits, and when applicable, be incorporated into analyses of community assembly. In this context, further research is needed to estimate the potential contribution of intraspecific variability to seed trait variation along environmental gradients, a task requiring large sampling and measuring effort, as our study did not account for this aspect.

Our work has important implications not only for studies on community assembly rules, but also for land use and climate change research and for conservation/restoration ecology. As regards the former, our results indicate that CWM and FD of seed traits can be effective in anticipating vegetation changes in upland grassland communities: the fast rise of temperatures in mountain ecosystems (Lamprecht et al., 2018; Rumpf et al., 2019) may lead to a relaxation of the low-temperature filtering of germination traits of warm-adapted species, resulting in an altered composition of communities in upland sites (i.e. increase in frequency and abundance of species from lower elevations). As regards the latter, the detected patterns in dispersal trait variation can support some nature conservation and/or restoration decisions. The functional structure and composition of lowland grasslands seem strongly dependent on cattle grazing. Therefore, to conserve plant biodiversity in existing grasslands or re-establish abandoned ones, we recommend maintaining or re-introducing grazing at the historic levels, if applicable.

AUTHORS' CONTRIBUTIONS

S.R. conceived the study and performed the experiments; S.R. and S.P. compiled the dataset; S.R. and L.C. analysed the dataset; S.R.

and L.C. wrote the first version of the manuscript. All the authors helped in critically revising the manuscript and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

Data used for the statistical analysis are achieved at Zenodo https://doi.org/10.5281/zenodo.6638739 (Sergey et al., 2022).

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