

1 **Inferring community assembly processes from functional seed trait variation along tem-**
2 **perature gradient**

3

4 Rosbakh Sergey¹, Chalmandrier Loïc^{2,3}, Phartyal Shyam^{1,4} and Poschlod Peter¹

5

6 ¹ Ecology and Conservation Biology, University of Regensburg, D-93040 Regensburg, Germany

7 ² Theoretical Ecology, Faculty of Biology and Pre-Clinical Medicine, University of Regensburg,

8 D-93040 Regensburg, Germany

9 ³ Centre for Integrative Ecology, University of Canterbury, School of Biological Sciences,

10 Christchurch Canterbury 8041, New Zealand

11 ⁴ Nalanda University, School of Ecology and Environment Studies, Rajgir, India

12

13 Corresponding author: Sergey Rosbakh, sergey.rosbakh@ur.de, ORCID: [https://orcid.org/0000-](https://orcid.org/0000-0002-4599-6943)

14 [0002-4599-6943](https://orcid.org/0002-4599-6943)

15

16

17

18

19 Running title: Functional seed traits along temperature gradient

20 **Abstract**

- 21 1. Assembly of plant communities has long been scrutinized through the lens of trait-based
22 ecology. Studies generally analyze functional traits related to the vegetative growth, sur-
23 vival and resource acquisition and thus ignore how ecological processes may affect plants
24 at other stages of their lifecycle, particularly when seeds disperse, persist in soil and ger-
25minate.
- 26 2. Here, we analyzed an extensive data set of 16 traits for 167 species measured in-situ in 36
27 grasslands located along an elevational gradient and compared the impact of abiotic fil-
28tering, biotic interactions and dispersal on traits reflecting different trait categories: plant
29 vegetative growth, germination, dispersal, and seed morphology. For each community,
30 we quantified community weighted mean (CWM) and functional diversity (FD) for all
31 traits and established their relationships to mean annual temperature.
- 32 3. The seed traits were weakly correlated to vegetative traits and thus constituted independ-
33ent axes of plant phenotypical variation that were affected differently by the ecological
34 processes considered. Abiotic filtering impacted mostly the vegetative traits and to a less-
35er extent on seed germination and morphological traits. Increasing low-temperature stress
36 towards colder sites selected for short-stature, slow-growing and frost-tolerant species
37 that produce small quantity of smaller seeds with higher degree of dormancy, high tem-
38perature requirements for germination and comparatively low germination speed.
- 39 4. Biotic interactions, specifically competition in the lowlands and facilitation in uplands,
40 also filtered certain functional traits in the study communities. The benign climate in low-
41 lands promoted plant with competitive strategies including fast growth and resource ac-
42quisition (vegetative growth traits) and early and fast germination (germination traits),
43 whereas the effects of facilitation on the vegetative and germination traits were cancelled
44 out by the strong abiotic filtering.

45 5. The changes in the main dispersal vector from zoochory to anemochory along the gradi-
46 ent strongly affected the dispersal and the seed morphological trait structure of the com-
47 munities. Specifically, stronger vertical turbulence and moderate warm-upwinds com-
48 bined with low grazing intensity selected for light and non-round shaped seeds with low-
49 er terminal velocity and endozoochorous potential.

50 6. *Synthesis*. We clearly demonstrate that, in addition to vegetation traits, seed traits can
51 substantially contribute to functional structuring of plant communities along environmen-
52 tal gradients. Thus, the ‚hard‘ seed traits related to germination and dispersal are critical
53 to detect multiple, complex community assembly rules. Consequently, such traits should
54 be included in core lists of plant traits and, when applicable, be incorporated into analysis
55 of community assembly.

56

57 **Key words:** assembly, convergence, community, competition, dispersal, divergence, facilitation,
58 filtering, germination, seed, trait

59

60

61

62

63

64

65

66

67 **Introduction**

68 Now more than ever, ecologists are striving to understand the processes shaping the structure and
69 composition of biological communities along ecological gradients (Cody et al. 1975; Cornwell
70 und Ackerly 2009; Weiher und Keddy 1999). Disentangling the community assembly rules, i.e.
71 the ecological processes selecting for or against species from the regional species pool and de-
72 termining local community composition (Keddy 1992), is crucial both for explaining current
73 biodiversity patterns and for predicting their future changes over the course of global change
74 (D'Amen et al. 2017; Götzenberger et al. 2012; Newbold 2018).

75 In this context, trait-based approaches provide fundamental tools allowing a better understand-
76 ing of community assembly processes (McGill et al. 2006). These approaches assume that func-
77 tional traits, that is ‘morphological, physiological, phenological or behavioral characteristics im-
78 pacting individuals’ fitness via their effects on growth, reproduction and survival’ (Violle et al.
79 2007) mediate species’ ecological niches and interactions (Pillar et al. 2021). Therefore, commu-
80 nity functional trait composition should reflect the outcome of key assembly rules: abiotic filter-
81 ing, dispersal and biotic interactions (Bello et al. 2013; Spasojevic und Suding 2012).

82 The common agreement is that multiple traits related to different organs and/or ontogenetic stag-
83 es (Dayrell et al. 2018; Kleyer und Minden 2015) should be considered, because they relate to
84 different ecological niche axes (Craine et al. 2012; Grime et al. 1997; Laughlin 2014; Leishman
85 und Westoby 1992). This is particularly important when predicting community assembly along
86 complex environmental gradients (e.g. elevation, latitude), as traits evolve in response to various
87 abiotic and biotic conditions and therefore might have multiple functions (Kergunteuil et al.
88 2018). Yet a closer look at the published literature reveals that the prevailing majority of the ex-
89 amined employed traits relate to vegetative growth, survival and resource acquisition (e.g. leaf,
90 root and whole-plant traits), while regeneration and dispersal traits are rarely considered

91 (E Vojtkó et al. 2020; Jiménez-Alfaro et al. 2016; Rosbakh et al. 2018). Thus, including floral,
92 gametophyte, seed and seedling traits, which provide additional, unique information about dif-
93 ferent plant functions, in the current research agenda is intended to maximize our understanding
94 of trait-based community assembly (E Vojtkó et al. 2020; Jiménez-Alfaro et al. 2016; Larson
95 und Funk 2016; Laughlin 2014; Poschlod et al. 2013; Rosbakh et al. 2018).

96 Ecological theory predicts that a plant species cannot be a part of the community if it possesses
97 seed traits that are not optimised to the processes ruling the local community assembly process
98 (Grubb 1977; Poschlod et al. 2013). Even if the environmental conditions are suitable for adult
99 plant growth and survival ('adult niche' *sensu* Grubb 1977), the species' long-term persistence in
100 the community is ultimately defined by its ability to produce viable seeds that can successfully
101 disperse, persist, germinate and produce vital seedlings ('regeneration niche'; Grubb 1977). Sev-
102 eral studies, albeit very scarce, have demonstrated that variability in seed traits related to disper-
103 sal, germination and seedling establishment is not random in plant communities (e.g.
104 (Fernández-Pascual et al. 2017; Lebrija-Trejos et al. 2010; Rosbakh et al. 2020c; Soons et al.
105 2017). This suggests that seed traits are, similarly to adult plant traits, important for explaining
106 co-existence patterns and assembly rules in plant communities (Poschlod et al. 2013). However,
107 this remains largely unverified empirically. Surprisingly, community seed trait composition has
108 been assessed only using a relatively small number of traits mostly related to either dispersal
109 (e.g. (Johnson et al. 2018) or establishment (e.g. (Rosbakh et al. 2020c), thus neglecting germi-
110 nation and seed persistence in soil (Poschlod et al. 1998). Moreover, these are mainly 'soft'
111 traits, easy-to-measure plant characteristics with low predictive power (Weiher und Keddy
112 1999), which carry several, often independent, functions. For example, seed mass, one of the
113 most frequently studied seed traits in functional ecology (Larson und Funk 2016), can reflect
114 abiotic filtering effects on germination (large seedlings from large seeds perform better at the

115 germination stage; (Leishman und Westoby 1994), but also persistence in the soil (smaller seeds
116 persist longer in soil; (Hodkinson et al. 1998)).

117 In this paper, we explore the role of vegetative growth, germination (establishment), dispersal
118 and seed morphological traits in the assembly of mountain grasslands. We analyzed an extensive
119 data set of 16 traits for 167 species measured in 36 grasslands located along a steep temperature
120 gradient. Specifically, we tested whether variation in two key metrics of community functional
121 structure (community-weighted trait mean values (CWM) and functional diversities (FD); (Ri-
122 cotta und Moretti 2011)) was significantly driven by the steep temperature gradient.

123 First, based on previous research in similar settings (Bello et al. 2013; Chalmandrier et al. 2017),
124 the increase in low-temperature stress as site altitude rose was expected to cause a significant
125 shift in plant strategies towards stress-adaptation and a stronger selection of maladapted species.
126 This strong abiotic filtering at high elevation should lead to a shift in the CWMs along the tem-
127 perature gradient and a stronger trait convergence (low FD) in upland communities compared to
128 their lowland counterparts. Because ambient temperatures control growth and development in
129 seedlings and adult plants in a similar manner, we anticipated that abiotic filtering would have
130 comparable effects on both vegetative and seed germination traits. Specifically, for the seed traits
131 we expected the upland communities to be dominated by species with a risk-averse regeneration
132 strategy aiming to minimize risks of seedling establishment in cold climates (e.g. dormant seeds
133 with a high temperature requirement for germination and slow germination speed (Fernández-
134 Pascual et al. 2021; Rosbakh und Poschlod 2015). Given that the high levels of low-temperature
135 stress at high elevations (short growth period with overall low temperatures coupled with fre-
136 quent and severe frost events) negatively affect seed production resulting in low seed quality and
137 quantity (e.g. (Inouye 2008; Steinacher und Wagner 2013)), we further expected alpine grass-
138 lands to be assembled by species with comparatively lighter seeds and lower seed productivity.

139 Second, we expected to observe patterns congruent with the stress gradient hypothesis, which
140 states that biotic interactions in plant communities change with the level of abiotic stress
141 (Maestre et al. 2009). The comparatively benign conditions seen in low-elevation grasslands
142 should promote hierarchical competition or niche partitioning, resulting in trait convergence or
143 divergence, respectively (Münkemüller et al. 2020). Conversely, higher levels of facilitation in
144 colder sites were anticipated to result in trait divergence (McIntire und Fajardo 2014). The shift
145 from competition in lowland grasslands to facilitation in alpine ones should be manifested not
146 only in vegetative traits, but also in traits related to seed germination, as seedling establishment
147 can be strongly affected by biotic interactions with adult plants (e.g. (Kos und Poschlod 2007;
148 Thompson und Grime 1983). In particular, we anticipated high functional divergence in seed
149 germination traits because of temporal and spatial niche partitioning under high levels of compe-
150 tition, which in our study system are confined to lowlands. There, in grasslands with dense and
151 tall vegetation, seedlings can establish themselves in gaps (spatial niches) with comparatively
152 low competition for available resources, especially light (Thompson und Grime 1983). Addition-
153 ally, early germination, before the onset of vegetative growth of the dominant species, could also
154 considerably increase chances for seedling establishment (Forbis 2010; Kardol et al. 2013). Al-
155 ternatively, amelioration of low-temperature stress by neighbors (i.e. facilitative interactions) at
156 high elevations (Choler et al. 2001) might lead to a large number of spatial niches available for
157 seedling establishment resulting in a higher divergence of the seed germination traits. Seed size
158 and production were expected to be affected by the abovementioned biotic processes in the same
159 manner.

160 Third, we expected to observe shifts in seed traits congruent with the change in the main disper-
161 sal vector along the temperature gradient. The warm, lowland communities should be dominated
162 by species better adapted to zoochory, due to the higher frequency and intensity of grazing
163 (Pellissier et al. 2010). At the colder end of the gradient we anticipated species adapted to

164 anemochory to dominate the communities, due to frequency and intensity of vertical wind turbu-
165 lences (Tackenberg und Stöcklin 2008). Dispersal processes were further expected to affect the
166 diversity of plant dispersal traits. We predicted that the decreasing connectivity among montane
167 grassland as elevation increases (Körner 2007) would lead to stronger convergence in dispersal
168 traits in upland communities due to strong abiotic filtering effects on species' dispersal ability
169 (i.e. only good dispersers could persist in patchy alpine vegetation). In contrast, seed dispersal
170 traits in lowland communities were expected to be divergent, due to better habitat connectivity
171 and a larger number of various dispersal vectors available. Finally, we anticipated that the
172 changes in seed morphological traits at the community level would also reflect the shift in the
173 main dispersal strategy from zoochory to anemochory. Specifically, upland communities were
174 expected to be assembled by species with light, elongated or flat seeds with comparatively large
175 projection, a set of traits favoring dispersal by wind along longer distances (Fenner et al. 2005;
176 Thomson et al. 2011).

177

178 **Materials and methods**

179 *Study system*

180 Field work was carried out in the eastern part of the Bavarian Alps (Germany), from 2009 to
181 2020. The region has the typical alpine relief, with steep mountain peaks composed of Triassic
182 lime and dolomite rocks. The climate is typically montane with high mean annual precipitation
183 rates (1500-2000 mm/year; (Marke et al. 2013)) and an altitudinal decrease in mean annual air
184 temperatures with a lapse rate of ca. $-0.6^{\circ}\text{C}/100$ m of elevation. The non-forest vegetation is
185 largely represented by species-rich calcareous grasslands on nutrient-poor soils. In lowlands,
186 grasslands are dominated by graminoids (e.g. *Arrhenatherum elatius*, *Helictotrichon pubescens*,

187 *Carex flacca*) and tall forbs (e.g. *Bupthalmum salicifolium*, *Centaurea jacea*). As elevation in-
188 creases, they are replaced by sedges (e.g. *C. firma*, *C. sempervirens*), dwarf shrubs (e.g.
189 *Vaccinium vitis-idaea* and *Silene acaulis*) and short-stature herbs (e.g. *Ligusticum mutellina*,
190 *Ranunculus montanus*, *Soldanella alpina*). Until the 1950s, the lowland grasslands were inten-
191 sively grazed by domestic cattle and/or used for hay-making. Nowadays, the grasslands at eleva-
192 tions 600-1600 above sea level (a.s.l.) are used for, or managed by, low-intensity cattle grazing,
193 whereas the subalpine and alpine grasslands above ca. 1700 m a.s.l. are occasionally grazed by
194 sheep or wild ungulates such as the alpine ibex (*Capra ibex*) and chamois (*Rupicapra*
195 *rupicapra*).

196 *Data collection*

197 *Plant composition and environmental characteristics of the study sites*

198 Plant community composition was collected in 2009 in 36 grasslands located along an elevation
199 gradient from 656 to 2363 m a.s.l. In each grassland, the vegetation was surveyed in ten 2 x 2
200 plots per site during the peak of the growing season, which was elevation specific. In each plot,
201 the abundance of all vascular species was estimated based on six percentage classes: <0.1%,
202 1%–5%, 5%–25%, 25%–50%, 50%–75% and 75%–100%. The relative abundance of a species
203 at a site was then calculated as the mean value of its abundance in all plots. In total, we recorded
204 379 species in all the sites.

205 *Site temperature characteristics*

206 Due to the remoteness and low accessibility of the study area, the only available data on site
207 temperature conditions was mean annual air temperature at 2 meters above soil surface (MAT).
208 The air temperature data were obtained from 20 weather stations located in the study area at ele-

209 vations ranging from 360 to 1919 m a.s.l. MAT at each station was calculated for the period
210 2000–2008; from these data, lapse rates between elevation and MAT in the study region were
211 calculated (-0.33 °C/100 m of elevation) to define the MAT in each studied grassland. Although
212 MAT is criticised for its inability to reflect the complex thermal patterns of vegetation, especially
213 above the tree-line (Scherrer et al. 2011), we found it to be a good predictor for local temperature
214 conditions, and further weakly correlated with other ecological gradients (e.g. soil moisture and
215 nutrients) in the study system (Rosbakh und Poschlod 2021). The MAT of the studied grasslands
216 ranged between 1.8 and 7.3 °C.

217 *Trait data*

218 We sampled the most representative species in the local communities. More specifically, we did
219 not consider species present in fewer than three sites and with a maximal abundance of <3%
220 across all sites. In total, we collected vegetative and seed traits for 167 species. Species with
221 measured trait data accounted for more than 80% of the total abundance of each community,
222 allowing for a reliable estimate of functional diversity (Bello et al. 2013; Pakeman und Quested
223 2007).

224 Each species was sampled at the site where it was the most abundant following the approach
225 described in Rosbakh and Poschlod (2015). Fully ripened seeds and fruits (hereafter ‘seeds’)
226 were subsequently collected at maturity in these ‘optimal’ sites during the growing seasons
227 2009–2020. Because of low seed quality and/or quantity, the seeds of several species were col-
228 lected from populations located close to the ‘optimal’ sites. Seeds were collected from a large
229 number of randomly chosen individuals growing at a distance from each other. After collection,
230 seeds were air-dried for several days, cleaned of flower/fruit debris, and kept dry in a cold room
231 at 4 °C prior to the trait measurements. If not specified otherwise, the trait measurements fol-
232 lowed the standardized protocols (Kleyer et al. 2008; Perez-Harguindeguy et al. 2016). The trait

233 values within species were considered to be ‘fixed’, i.e. a single mean trait value was assigned
234 per species measured under the species' optimal ecological conditions. Therefore, our study does
235 not consider potential intraspecific trait variation.

236 *Vegetative traits*

237 To compare the detected community assembly rules for the seed traits to those for vegetative
238 traits, we also measured canopy height (CH), specific leaf area (SLA), leaf nitrogen content
239 (LeafN) and foliar frost sensitivity (FoliarFS) for each species. All measurements were made *in*
240 *situ* in the ‘optimal’ growing sites as described above.

241 *Seed germination traits*

242 We considered dormancy type, initial temperature of germination, germination speed and germi-
243 nation synchrony as the traits that represent different aspects of the seed regeneration strategy.
244 Every species was characterized in terms of type of seed dormancy (*sensu* (Baskin und Baskin
245 2004)) based on published data in (Baskin und Baskin 2014; Rosbakh et al. 2020a; Rosbakh und
246 Poschlod 2015) and the authors’ unpublished data on the seed germination ecology of the study
247 species. Dormancy type is a categorical variable with six classes: non-dormancy (ND), physical
248 dormancy (PY), physiological dormancy (PD), morphological dormancy (MD),
249 morphophysiological dormancy (MPD, i.e. MD+PD), and combinational dormancy (CD, i.e.
250 PY+PD). The seeds of a high proportion (82%) of the study species were categorized as
251 dormant, of which 74% had a component of PD that was further subcategorized into three levels
252 (non-deep, intermediate and deep) depending on the depth of dormancy (Baskin und Baskin
253 2014). Only 7% of study species possessed PY and none of them had MD or CD. Thus, to make
254 the species comparable with each other, a relative weighted score was given to each species
255 based on the type/depth of dormancy. Ultimately, this led to the species’ allocation to five cate-

256 gorical variables: ND, PY, non-deep PD/MPD, intermediate PD/MPD, and deep PD/MPD with a
257 relative rank score of 0, 0.25, 0.5, 0.75 and 1, respectively (DormRank).

258 The remaining seed germination traits were obtained from germination experiments under con-
259 trolled conditions (see (Rosbakh und Poschlod 2015) for further details). In brief: seeds with PD
260 were either cold moist stratified at 4°C for six weeks or treated with 0.1% gibberellin acid prior
261 to the germination experiment to alleviate the dormancy. Seeds of eight species were mechani-
262 cally scarified to overcome physical dormancy. Seeds were germinated for 6 weeks along a tem-
263 perature gradient (10/2, 14/6, 18/10, 22/14, 26/18, 30/22 °C, 14/10h photoperiod), which repre-
264 sents the germination conditions (from cool spring to warm summer season) in the plant com-
265 munities along the elevation gradient that the seeds may encounter. Seed germination was scored
266 regularly; the viability of non-germinated seeds was checked through inspection of embryos. The
267 seed germination data were used to calculate:

268 1) minimal temperature of seed germination (T5): lowest temperature at which 5 % of all seeds
269 germinated (Rosbakh und Poschlod 2015);

270 2) germination speed calculated as mean germination time in days (MGT; (Lozano□Isla et al.
271 2019)) with lower values reflecting faster seed germination;

272 3) germination synchrony calculated as the germination synchronization index (Lozano□Isla et
273 al. 2019), with values close to one indicating that germination of all seeds occurs at the same
274 time (more synchronized germination), while values close to zero indicate that seed germination
275 of at least two seeds occurred at a different time (less synchronized germination).

276 *Seed dispersal traits*

277 We assumed that anemochory, epi- and endo-zoochory are the most important seed dispersal
278 vectors in the study system (Pellissier et al. 2010; Poschlod et al. 2005; Tackenberg und Stöcklin

279 2008). We used seed terminal velocity (TV; m/s) as a proxy for species' capacity for dispersal by
280 wind, with lower values indicating longer dispersal distances. TV was calculated from hand
281 stopped falling times from a height of 2 m with a correction for the initial acceleration phase.
282 The height of 2 m was chosen to minimize the effect of reaction time on the hand stopped falling
283 times (Tackenberg und Stöcklin 2008).

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

290 Species capacity for endozoochory (EndoZoo) is based on dung germinating seed surveys in the
291 study area (Poschlod and Rosbakh, unpublished results) and published data on comparable sys-
292 tems (Albert et al. 2015). It is a semi-quantitative variable with three levels: 1 – seed
293 endozoochorous dispersal is frequent (viable seeds are found in more than half of all samples)
294 and/or in large numbers (>100 germinable seeds/kg of dry dung); 0.5 – endozoochory is rare
295 (viable seeds are present in less than 50% of dung samples) and/or in small numbers (<100
296 germinable seeds per kg of dry dung); 0 – viable seeds are not found in the dung samples.

297 *Seed morphological traits*

298 Seed mass (SeedMass, mg), seed shape (SeedShape) and seed projection (SeedPr; mm²) were
299 also included in our study to provide additional mechanistic explanations of seed dispersal trait
300 variability along the MAT gradient. Seed mass (SeedMass) is the average mass of a single seed
301 extrapolated from the weights of three samples of 100 seeds each. Seed shape (SeedShape) is the
302 variance of seed length, width and height; it is a dimensionless value that varies between zero in

303 perfectly round and 0.2 in disk- or needle-shaped seeds (Knevel 2005). Seed projection, a one-
304 side are of a seed, was measured by scanning seeds on a flatbed scanner with resolution of 1200
305 dpi followed by seed area measurements with the help of ImageJ software (Schneider et al.
306 2012). Although, strictly speaking, seed production (average number of seeds produced per
307 ramet of 10 randomly selected individuals; SeedN, pcs) is not a morphological trait, it was in-
308 cluded in this category for the sake of brevity.

309 *Data analysis*

310 To estimate and visualize the relationship between studied plant traits, we analyzed the correla-
311 tion matrix between functional traits using the package *corrplot* (Wei et al. 2017) and conducted
312 a principal component analysis (PCA) on the species-trait matrix.

313 To analyze the change in the functional structure of communities, we estimated community
314 weighted mean values (CWMs) and functional diversity (FD)(Ricotta und Moretti 2011). The
315 CWM of a community is the average trait value weighted by species-relative abundance. It gen-
316 erally quantifies the trait value of the dominant species in a community and thus describes the
317 dominating species' adaptation strategy to given environmental conditions (Bello et al. 2021).
318 FD reflects trait convergence or divergence (i.e. a decrease or increase in trait dissimilarity com-
319 pared to random expectation) and is calculated using Rao's quadratic entropy (Rao 1982).

320 Additionally, we tested whether observed functional diversity deviated from the null expectation
321 that communities are a random sample of species from the regional pool. For each community,
322 null functional diversity distributions were generated by permuting the columns (species) of the
323 site-by-species abundance matrix. We then computed the standard effect sizes (SES) to evaluate
324 the deviations of observed functional diversity values from random expectations. SES are calcu-
325 lated as the observed functional diversity value minus the mean of the null functional diversity
326 values divided by the standard deviation of the null functional diversity values. A negative SES

327 value indicates that functional diversity is convergent, i.e. lower than expected according to the
328 null hypothesis. Conversely, a positive SES value indicates that functional diversity is divergent,
329 i.e. higher than the null hypothesis would indicate. We further assessed the significance of func-
330 tional diversity SES by identifying the proportion of random values that fell below the observed
331 diversity value. If this rank value was below 0.05, functional diversity in that plot was consid-
332 ered significantly lower; if it was higher than 0.95, functional diversity in that plot was consid-
333 ered significantly higher.

334 The changes in community CWM and FD values with MAT were estimated with the help of a
335 polynomial regression (e.g. $FD \sim MAT + MAT^2$) because a trait–environment relationship can
336 be nonlinear (Bernard-Verdier et al. 2012; Kergunteuil et al. 2018). Where the quadratic term
337 was not significant, this term was removed. Model assumptions were met in all cases. All
338 statistical analyses were conducted in the R statistical environment (R Core Development Team
339 2021).

340

341 **Results**

342 *Trait-trait relationships*

343 Vegetative and seed traits were weakly correlated with each other (Appendix 1); the strongest
344 correlations were between leaf N and seed projection ($r=0.29$, $t=3.9$, $p<0.001$); and canopy
345 height and potential for endozoochory ($r=0.24$, $t=3.2$, $p=0.002$). Collinearity between seed
346 germination and seed dispersal traits was also relatively low, with the strongest correlation
347 between dormancy rank and potential for endozoochory at $r=-0.22$ ($t=-2.9$, $p=0.004$). Several
348 morphological traits were significantly correlated with dispersal traits. The following were
349 observed: a positive moderate correlation between terminal velocity and seed mass ($r=0.44$,

350 $t=6.2$, $p<0.001$) and moderate negative correlations between terminal velocity and seed shape
351 ($r=-0.44$, $t=-6.3$, $p<0.001$), between seed attachment potential to cow fur and terminal velocity
352 ($r=-0.23$, $t=-3.4$, $p<0.001$), and between seed attachment potential to sheep fur and seed mass
353 ($r=-0.27$, $t=-4.2$, $p<0.001$) and seed projection ($r=-0.60$, $t=-9.7$, $p<0.001$).

354 Importantly, we also detected a number of significant, from low to moderate, correlations within
355 the group of traits, a pattern that supports our trait categorisation scheme. In the vegetative trait
356 group, SLA was significantly, positively correlated with canopy height, leaf nitrogen and frost
357 sensitivity ($r=0.23$, $r=0.33$, $r=0.21$, respectively; in all the cases $p<0.005$). Similarly, canopy
358 height and foliar frost sensitivity displayed a positive, though weak, significant relationship
359 ($r=0.16$, $t=3.0$, $p=0.003$).

360 In contrast, the traits within the germination/establishment trait groups showed stronger
361 correlations. Dormancy rank was positively, moderately correlated with minimal temperature of
362 seed germination and germination speed ($r=0.34$, $r=0.48$, $t=4.3$ and 5.7 respectively; in both
363 cases $p<0.001$) and negatively, weakly ($r=-0.27$, $t=-3.7$, $p<0.001$) with synchrony of
364 germination, suggesting that dormant seeds tended to germinate under comparatively high
365 temperatures, in a slow and asynchronous manner.

366 Among seed dispersal traits, terminal velocity and seed attachment potential to cattle fur were
367 negatively correlated ($r=-0.35$, $t=-3.4$, $p<0.001$). The former trait also displayed a significant,
368 positive correlation ($r=0.40$, $t=5.5$, $p<0.001$) with seed attachment potential to sheep fur.

369 *Variation of community weighted means along the temperature gradient*

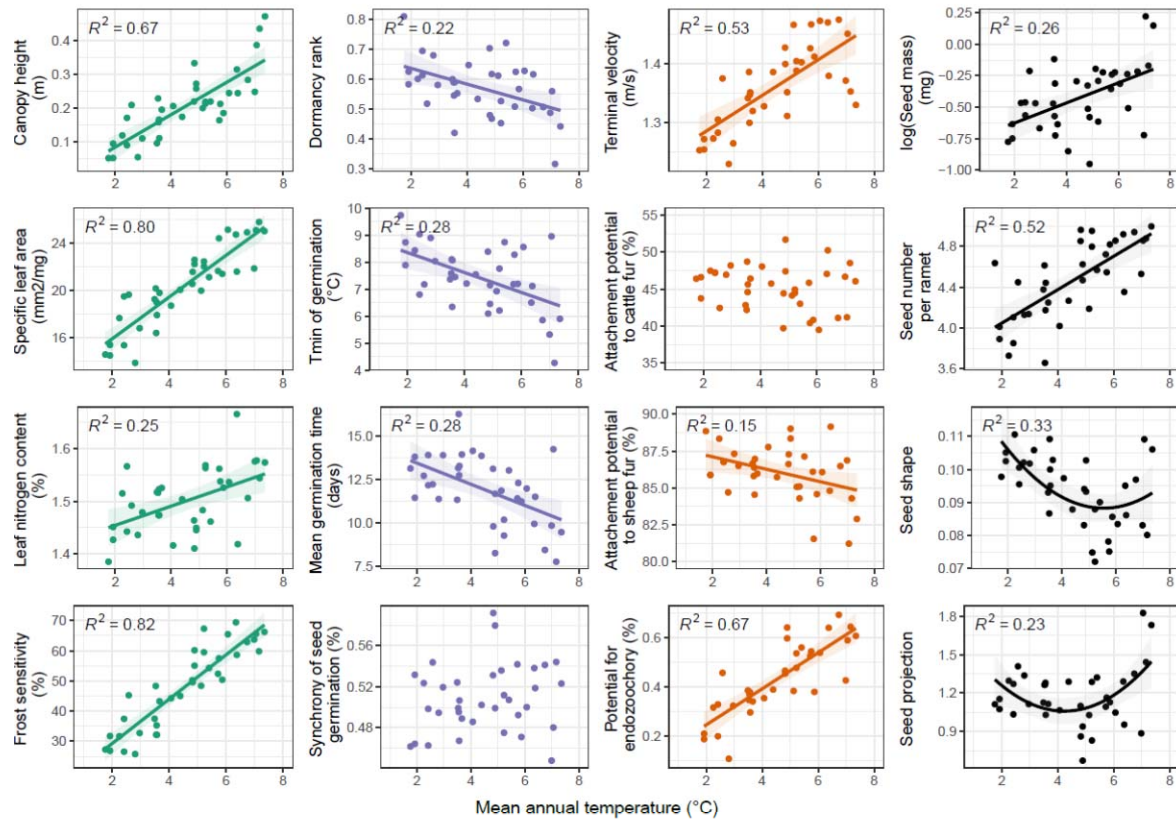
370 The community weighted means (CWM) of almost all traits changed significantly along the gra-
371 dient of mean annual temperature (MAT), with differences as to the nature of the relationship
372 and the explained variance (Figure 2). Vegetative traits showed the strongest variation with

373 MAT; community-average values for canopy height, SLA and foliar frost sensitivity showed a
374 sharp linear increase with temperature ($R^2 = 0.66, 0.80$ and 0.82 , respectively, $p < 0.001$). The
375 variation in CWM for leaf nitrogen content followed the same pattern; however, the amount of
376 variance explained by this relationship was moderate ($R^2 = 0.25$, $p = 0.002$).

377 As regards germination traits, the CWMs of dormancy rank, minimum germination temperature
378 and mean germination time displayed a significant, negative relationship with the MAT gradient
379 with a moderately similar power ($R^2 = 0.22, 0.28$ and 0.28 , respectively, all $p < 0.001$). In ecologi-
380 cal terms, these patterns suggest that species in upland communities tend to produce dormant
381 seeds with a high temperature requirement for germination and relatively low germination speed.
382 The CWM for germination synchrony did not exhibit a significant relationship with MAT gradi-
383 ent (Figure 1; $R^2 = 0.03$, $p = 0.29$).

384 CWM values for both seed terminal velocity and endozoochory rate increased in a sharp manner
385 with increasing temperature (Figure 2; $R^2 = 0.62$ and 0.70 , respectively, both $p < 0.001$). This pat-
386 tern indicates that communities at the warm end of the gradient are dominated by species with
387 high rates of endozoochory, while communities at the cold end of the gradient are dominated by
388 species with high rates of anemochory. The CWM for the sheep epizoochory rate was high
389 across the entire temperature gradient (86% on average) but significantly and weakly decreased
390 with increasing MAT (Figure 1; $R^2 = 0.15$, $p = 0.02$), suggesting a moderately lower potential for
391 sheep epizoochory in lowland plant communities. The CWM for cow epizoochory did not vary
392 significantly along the temperature gradient (Figure 1; $R^2 = 0.03$, $p = 0.27$).

393



395 Figure 2. Variation in community weighted mean of 16 traits with mean annual temperatures.
 396 Full lines indicate significant relationships ($p < 0.05$).

397

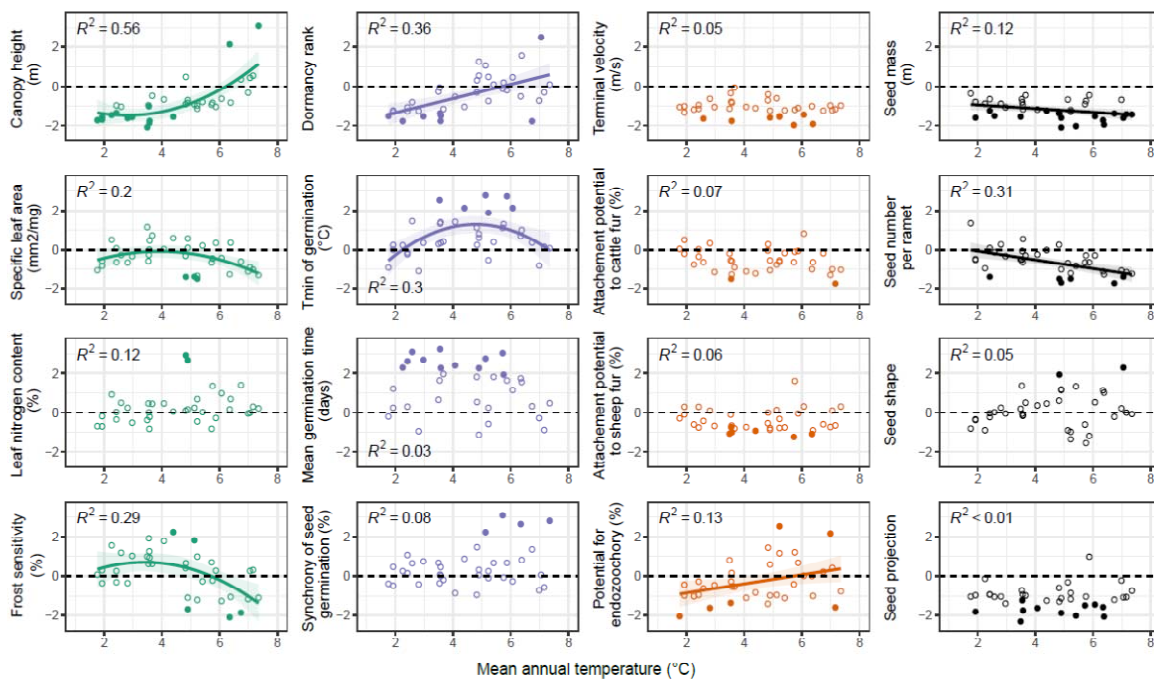
398 The CWM for seed mass and seed number per ramet displayed a significantly negative relation-
 399 ship with the gradient of MAT, the strength of the former relationship being considerably strong-
 400 er (Figure 2; $R^2 = 0.26$, $p = 0.003$ and $R^2 = 0.52$, respectively, $p < 0.001$). The CWM values for seed
 401 shape significantly but moderately increased with decreasing MAT in a non-linear manner (Fig-
 402 ure 1; $R^2 = 0.323$, $p = 0.02$). The CWM for seed projection showed a concave, significant relation-
 403 ship with the MAT gradient (Figure 1; $R^2 = 0.23$, $p = 0.02$), indicating a tendency for seeds with
 404 comparatively large surfaces to be found at both ends of the gradient.

405 *Variation in functional diversities along the temperature gradient*

406 The functional diversities of vegetative traits were mostly non-random along the gradient (Figure
407 3). The proportion of communities with negative SES values (trait convergence) was higher for
408 canopy height and SLA (Figure 3), whereas for LeafN and foliar frost sensitivity (FoliarFS) the
409 majority of the communities had positive SES values (trait divergence; Figure 2). Mean standard
410 effect size for frost sensitivity was -0.17 across communities and 16% of communities displayed
411 significant diversity (rank below 0.05). FD of canopy height strongly decreased with decreasing
412 MAT in a non-linear manner (Figure 3; $R^2 = 0.56$, $p < 0.001$), indicating that species in upland
413 communities had more similar trait values than their lowland counterparts. In contrast, FD of
414 FoliarFS showed the opposite pattern: being convergent in the lowlands, trait diversity increased
415 towards the cold end of the MAT gradient, resulting in comparatively strong trait divergence in
416 upland communities (Figure 3; $R^2 = 0.29$, $p = 0.004$). Furthermore, the functional diversity for
417 SLA showed a significant, slightly concave relationship with MAT (Figure 3; $R^2 = 0.20$,
418 $p = 0.02$), with stronger trait convergence in upland and lowland plant communities as compared
419 to their more divergent counterparts from the middle part of the gradient. Finally, FD for Leaf N
420 did not vary significantly across the temperature gradient (Figure 3; $R^2 = 0.12$, $p = 0.13$).

421 For germination, functional diversities were mostly divergent throughout the temperature gradi-
422 ent (Figure 3), except for DormRank FD values that were predominantly convergent. Significant
423 changes in FD were only found for DormRank and T5. As regards the former, SES decreased
424 linearly with decreasing MAT ($R^2 = 0.36$, $p < 0.001$; Figure 3), changing the functional trait signa-
425 ture of the communities from trait divergence to convergence. As regards the latter, the FD of T5
426 varied moderately with MAT ($R^2 = 0.3$, $p = 0.03$; Figure 3), with more divergent communities in
427 the middle part of the gradient as compared to its ends (i.e. concave relationship).

428 Dispersal trait functional diversities were almost exclusively convergent throughout the tempera-
 429 ture gradient (Figure 3). Among dispersal traits, only the FD of EndoZoo varied significantly
 430 with MAT (negative, weak relationship; $R^2 = 0.13$, $p=0.03$; Figure 3).
 431 The functional diversities of seed morphological traits along the gradient of MAT followed a
 432 clear convergence pattern. FD values of SeedShape did not show any clear tendency towards
 433 convergence or divergence within the communities. MAT had a significant, positive effect on
 434 FD values of SeedMass and SeedN ($R^2 = 0.12$, $p=0.04$, and $R^2 = 0.31$, $p<0.001$), indicating
 435 stronger convergence of the traits in the communities in warmer sites.



436

437 Figure 3. Variation in functional trait diversity (FD) of sixteen traits with mean annual tempera-
 438 tures. Full lines indicate that the FD-MAT relationship was significant according to the linear
 439 regressions ($p < 0.05$). Negative and positive standard effect size (SES) indicate a narrower and
 440 broader trait range than expected, respectively. Filled circles represent significantly low (rank
 441 lower than 0.05) or high (rank above 0.95) functional diversity.

442 **Discussion**

443 Regeneration has always been considered a fundamental aspect of plant community ecology
444 (Grime et al. 1981; Grubb 1977; Keddy 2010), yet it has been largely neglected in studies of
445 community assembly (Jiménez-Alfaro et al. 2016; Poschlod et al. 2013; Saatkamp et al. 2019).
446 In this study, we show that seed traits are only weakly linked to vegetative traits and thus consti-
447 tute independent axes of plant phenotypical variation that may be affected differently by ecologi-
448 cal processes. We thus provide the first comprehensive evidence that little-studied seed
449 functional traits are important determinants of plant community structure in addition to
450 vegetative functional traits. Specifically, we demonstrate that abiotic conditions, biotic interac-
451 tions and dispersal acting differently on the functional traits of plants at different stages of their
452 life cycle and ultimately shape the structure of mountain grassland communities.

453 *Temperature strongly filters plant communities*

454 Confirming our expectation, abiotic conditions have a prominent impact on dominant vegetative
455 traits of mountain grassland communities. Community weighted means of vegetative traits shift-
456 ed strongly (or moderately in the case of leaf nitrogen content) along the temperature gradient
457 (Figure 2). Specifically, the increasing low-temperature stress towards higher sites seemed to
458 select for short-stature species (Bello et al. 2013; Bucher und Rosbakh 2021; Pellissier et al.
459 2010), and to further filter out tall species (based on the convergent functional diversity of height
460 in those sites). This shows the critical importance of small stature for plants to cope with abiotic
461 stress, as this allows heat accumulation near the ground during the short growing season (Körner
462 2021). The shift in the mean trait values of SLA and leaf N also mirrors the shift of leaf-
463 economics strategies along the temperature gradient from fast-growing species with fast nutrient
464 acquisition in warmer sites (high SLA and leaf N values) to slow-growing and nutrient-

465 conservative species (low SLA and leaf N values in cooler sites (Rosbakh et al. 2015; Spasojevic
466 und Suding 2012). Finally, plants were more frost resistant in colder sites, showing the im-
467 portance of that trait for coping with frost events, which at higher elevations can occur even dur-
468 ing the summer months. In contrast to plant height, the functional diversity of these traits was not
469 convergent in cold sites, possibly indicating that despite the strong climatic stress, other ecologi-
470 cal processes may promote the coexistence of species with different trait values (see below).

471 Community weighted means for three out of four seed germination traits (degree of dormancy,
472 temperature requirement for germination and germination speed) presented a clear response to
473 the temperature gradient, but those relationships were less strong than for vegetative growth
474 traits (Figure 2). We attribute these shifts in CWM to the effects of abiotic filtering on germina-
475 tion strategies in alpine environments. Low-temperature stress (e.g. frequent, severe frost events)
476 at the colder end of the gradient selects for plants that produce seeds with a higher degree of
477 dormancy, high temperature requirements for germination and comparatively low germination
478 speed (Baskin und Baskin 2014; Fernández-Pascual et al. 2021; Rosbakh und Poschlod 2015).
479 Furthermore, there was an increasing convergence in seed dormancy with decreasing tempera-
480 tures, which implies that plant communities in the colder sites are largely assembled from spe-
481 cies with similarly high degrees of seed dormancy that are able to postpone seed germination to
482 more favorable conditions for seedling establishment in late spring – early summer via mecha-
483 nisms of seed physiological dormancy (Baskin und Baskin 2014). These adaptations aim to
484 match seed germination timing with the most suitable environmental conditions to maximize
485 establishment success. Specifically, longer cold stratification periods necessary to break physio-
486 logical dormancy prevent seeds from germinating shortly after dispersal, whereas high base tem-
487 peratures of germination and slow germination speeds postpone germination of non-dormant

488 seeds to late spring-early summer, characterized by a comparatively low probability of severe
489 frost events (Rosbakh et al. 2020b; Rosbakh und Poschlod 2015).

490 The decrease in CWMs for seed size and seed production along the lower temperature gradient
491 suggested that species in alpine communities produce a small quantity of lighter seeds. This can
492 be explained by the presence of harsh climatic conditions that are stressful for sexual reproduc-
493 tion (Figure 2). A short growth period coupled with frequent and severe frost events considerably
494 limits pollination, fertilization and seed maturation (Lundemo und Totland 2007; Rosbakh und
495 Poschlod 2016; Steinacher und Wagner 2013), thereby filtering out species that require more
496 resources to produce a large quantity of heavy seeds. Alternatively, the dominance of light seeds
497 in alpine communities could reflect the increasing role of anemochory along the elevational gra-
498 dient (see below).

499 *Shifts in biotic interactions from lowlands to uplands filter vegetative and seed traits*

500 The stress gradient hypothesis predicts that the increasing stress along the elevational gradient
501 should lead to a change in biotic interactions from competition to facilitation (Maestre et al.
502 2009). Our results are partially congruent with this hypothesis and further suggest that in addi-
503 tion to abiotic filtering, biotic interactions can also filter certain functional traits in mountain
504 plant communities.

505 As expected, the relatively benign climate in low-elevation grasslands promotes plants with
506 competitive strategies including fast growth and resource acquisition (comparatively high CWM
507 values for canopy height, SLA and leaf N; Figure 2). Likely because of the moderate trade-off
508 between those traits and frost resistance, species from the lowlands also invest less in protecting
509 their leaves against negative temperatures (high CWMs for frost sensitivity in lowlands; Figure
510 2). The convergent FD values in lowland grasslands further suggest that frost-resistant plants are

511 excluded from these communities, most likely due to their comparatively low competitiveness
512 (Bucher und Rosbakh 2021). In contrast, the high FD for canopy height may indicate that both
513 small and tall plants are able to co-occur, suggesting that some degree of niche partitioning asso-
514 ciated with this trait maintains species coexistence in those benign but competitive environments
515 (Münkemüller et al. 2020). Surprisingly, in upland communities, the functional diversities of
516 SLA and frost sensitivity are higher than in the lowland communities. This suggests that some
517 species with high foliar frost sensitivity and high SLA can persist despite the strong abiotic
518 stress. We attribute this pattern to a comparatively higher number of available thermic niches in
519 topographically more complex higher elevations (Scherrer und Körner 2011) or to increasing
520 facilitation among co-occurring species, with frost-resistant species creating local environmental
521 conditions for the persistence of frost-tender species (Cavieres und Badano 2009; Choler et al.
522 2001).

523 Similarly to vegetative traits, seedling establishment in the lowlands seems to be constrained
524 mainly by higher levels of competition. Dominant species in the lowlands tend to possess differ-
525 ent regeneration strategies including germination after a comparatively short stratification period
526 (low T5 community weighted mean values) and high germination speed (low MGT community
527 weighted mean values) that allows germination in early spring before the closure of dense vege-
528 tation cover (Figure 2). Although the germination traits of dominant species tend to shift across
529 the temperature gradient, there is strong divergent functional diversity of T5, MGT and SYN in
530 low to mid-elevation grasslands (Figure 3). This suggests that niche partitioning stabilizes the
531 coexistence of multiple regeneration and temporal niches (Grubb 1977, Bernard-Verdier 2012).
532 In the uplands, this pattern vanishes and may indicate that the increasing abiotic filtering (which
533 promotes trait convergence, see above) overrides the signal of biotic interactions.

534 Another interesting finding of our study is the strong convergence of FD values for seed mass
535 and seed production throughout the entire gradient (Figure 3), a pattern that can be attributed to
536 both abiotic and biotic filtering effects on the functional community composition structure.
537 While in the uplands trait convergence could be related to the impact of abiotic filtering (see
538 above), in the lowlands, the convergence of the traits might reflect the hierarchical competition
539 favoring plants producing comparatively large seeds in large numbers, two traits necessary to
540 ensure regeneration in dense, tall grassland vegetation (Jakobsson und Eriksson 2000; Leishman
541 und Westoby 1994).

542 *Seed dispersal traits and community assembly*

543 The relationship between community functional trait structure and the dispersal ecology of
544 mountain vegetation is traditionally less studied than the impact of abiotic and biotic filtering.
545 There is, however, evidence that dispersal ability determines species capacity to colonize patches
546 of suitable habitat and maintain sink populations beyond the limits of their abiotic niche
547 (Dullinger et al. 2012; Isabelle et al. 2012). Our results demonstrate that seed dispersal traits are
548 also involved in community assembly. The most striking result is the strong decrease in
549 community mean seed terminal velocity and potential for endozoochory along the temperature
550 gradient (Figure 2). These distinct changes in dominant trait values point to a clear shift in the
551 dispersal strategy from endozoochory in lowland sites to anemochory in higher elevation
552 grasslands. This is likely due to the prevalence of opposite dispersal vectors at both ends of the
553 temperature gradient. In warmer sites, the higher rate of endozoochory may be due to the long
554 history of grazing by domestic animals (Gilck und Poschlod 2021; Poschlod 2014) that may have
555 favored the immigration and persistence of endozoochorous plant. In colder sites, the lower
556 terminal velocity and higher values of seed shape indicate that many plants are likely dispersed
557 by the intense vertical turbulence (Tackenberg und Stöcklin 2008) and moderate warm upwind

558 (Tackenberg et al. 2003a) in the upland habitats that allow effective dispersal over long distances
559 in patchy alpine vegetation (Tackenberg et al. 2003b).

560 Rates of epizoochorous potential are remarkably higher for sheep than for cattle, suggesting that
561 the former are an effective seed dispersal vector available in all grassland communities along the
562 entire gradient (Figure 2). We also detected a weak yet significant increase in seed attachment
563 potential to sheep fur along the temperature gradient (Figure 2). This pattern can be explained by
564 traditional sheep grazing in upland grasslands or similar properties of sheep and wild ungulates'
565 fur as regards collecting and retaining seeds during dispersal (S. Rosbakh, unpublished data).
566 Because it is mainly upland grasslands that are grazed by wild ungulates, the corresponding
567 communities might have been assembled by species better adapted to this type of seed dispersal.

568 Both epizoochory rates and seed terminal velocity are correlated with seed mass, seed shape and
569 seed projection across species. In consequence, the shift in seed dispersal strategies along the
570 temperature gradient can also be seen in the community patterns of seed morphological traits
571 (Figure 2). As previously shown, wind-dispersed seeds tend to be light and non-round in shape
572 (e.g. elongated or winged seeds; Appendix 1), two traits that positively affect terminal velocity
573 values (Fenner et al. 2005; Thomson et al. 2011). As for epizoochory by sheep, light diaspores
574 with an elongated shape facilitate 'anchoring' in animal fur (Römermann et al. 2005). As seen
575 previously, seed mass may be filtered in the lowlands by competitive interactions. The joint
576 impact on seed mass of the competitive filter in the lowlands and the wind and epizoochory
577 dispersal filter in the highlands may indicate why the functional diversity of seed mass, seed
578 shape, sheep and cattle epizoochory, and terminal velocity are consistently convergent along the
579 temperature gradient.

580

581 *Conclusions and implications*

582 Our study reveals that in addition to vegetation traits, seed traits can also substantially contribute
583 to functional structuring of plant communities along environmental gradients. We clearly
584 demonstrate that a combined study of vegetative traits and seed germination, dispersal and mor-
585 phology traits in plant community ecology is critical for the detection of multiple, complex
586 community assembly rules. Specifically, we find that in montane grassland located along a steep
587 temperature gradient 1) abiotic filtering mostly impacts vegetative traits and to a lesser extent,
588 seed germination and morphological traits, 2) biotic interactions, specifically competition, were
589 also found to have an effect on all types of traits but in different ways and 3) the changes in the
590 main dispersal vector affect the structure of dispersal traits and by extension, morphological
591 traits. These findings lend empirical support to the recent argument that plant trait research
592 should consider multiple traits representing different ecological niche axes, i.e. different organs
593 and/or ontogenetic stages (Craine et al. 2012; Kleyer und Minden 2015; Laughlin 2014). There-
594 fore, along with (Jiménez-Alfaro et al. 2016; Saatkamp et al. 2019) we advocate that ‘hard’
595 seed traits related to germination and dispersal should be included in core lists of plant traits and,
596 when applicable, be incorporated into analyses of community assembly.

597 The detected community-level seed trait responses to changing temperature have important im-
598 plications not only for studies on the community assembly process, but also for land use and cli-
599 mate change research and conservation/restoration ecology. As regards the former, our results
600 indicate that CWM and FD of seed traits can be effective in predicting vegetation changes in
601 upland grassland communities. For example, the fast temperature rise in mountain ecosystems
602 (Lamprecht et al. 2018; Rumpf et al. 2019) may lead to relaxation of low-temperature stress fil-
603 tering effects on the seed dormancy, initial temperature of germination and germination speed
604 trait values of warm-adapted species, resulting in an altered composition of communities in cold

605 sites (i.e. increase in frequency and abundance of species from lower elevations). As regards the
606 latter, the detected patterns in dispersal trait variation can support some nature conservation
607 and/or restoration decisions. The functional structure and composition of lowland grasslands
608 seem to be strongly dependent on or affected by the cattle grazing dominant here. Therefore, to
609 conserve plant biodiversity in existing grasslands or re-establish abandoned ones, we recommend
610 maintaining or re-introducing grazing at the historic levels, as applicable.

611

612 **Acknowledgments**

613 We thank the numerous students and research assistants who helped with the trait measurements.
614 SP is grateful to the Alexander von Humboldt Foundation, Germany for his Humboldt Experi-
615 enced Researcher Fellowship. SR and PP were partially supported by the FORKAST project
616 (TP12 Poschlod). LC acknowledges funding from the European Union's Horizon 2020 research
617 and innovation programme under Marie Skłodowska-Curie agreement No 840946 (Project
618 "CLIMB").

619

620 **Author contributions**

621 SR conceived the study and performed the experiments; SR and SP compiled the dataset; SR and
622 LC analyzed the dataset. SR and LC wrote the first version of the manuscript. All the authors
623 helped in critically revising the manuscript and gave final approval for publication.

624

625 **Data availability statement**

626 Should the manuscript be accepted for publication, the data will be archived at Zenodo.

627

628 **Appendix**

629 Appendix 1. Trait-trait correlation plot and matrix (Pearson's correlation coefficient).

630 Appendix 2. Principal component analysis of species-trait data.

631

632

633

634

635

636

637

638

639

640

641

642

643

644

645

646

647

648

649

650

651

652

653

654

655

656 **References**

- 657 Albert, Aurélie; Auffret, Alistair G.; Cosyns, Eric; Cousins, Sara A. O.; D'hondt, Bram;
658 Eichberg, Carsten et al. (2015): Seed dispersal by ungulates as an ecological filter: A trait-based
659 meta-analysis. In: *Oikos* 124 (9), S. 1109–1120.
- 660 Baskin, Carol C.; Baskin, Jerry M. (2014): *Seeds*. Second Edition: Elsevier.
- 661 Baskin, Jerry M.; Baskin, Carol C. (2004): A classification system for seed dormancy. In: *Seed*
662 *science research* 14 (1), S. 1–16.
- 663 Bello, Francesco de; Carmona, Carlos P.; Dias, André T. C.; Götzenberger, Lars; Moretti,
664 Marco; Berg, Matty P. (2021): *Handbook of trait-based ecology: from theory to R tools*:
665 Cambridge University Press.
- 666 Bello, Francesco de; Lavorel, Sandra; Lavergne, Sébastien; Albert, Cécile H.; Boulangeat,
667 Isabelle; Mazel, Florent; Thuiller, Wilfried (2013): Hierarchical effects of environmental filters
668 on the functional structure of plant communities: a case study in the French Alps. In: *Ecography*
669 36 (3), S. 393–402. DOI: 10.1111/j.1600-0587.2012.07438.x.
- 670 Bernard-Verdier, Maud; Navas, Marie-Laure; Vellend, Mark; Violle, Cyrille; Fayolle, Adeline;
671 Garnier, Eric (2012): Community assembly along a soil depth gradient: contrasting patterns of
672 plant trait convergence and divergence in a Mediterranean rangeland. In: *Journal of ecology* 100
673 (6), S. 1422–1433. DOI: 10.1111/1365-2745.12003.
- 674 Bucher, Solveig Franziska; Rosbakh, Sergey (2021): Foliar summer frost resistance measured
675 via electrolyte leakage approach as related to plant distribution, community composition and
676 plant traits. In: *Functional Ecology* 35 (3), S. 590–600. DOI: 10.1111/1365-2435.13740.
- 677 Cavieres, Lohengrin A.; Badano, Ernesto I. (2009): Do facilitative interactions increase species
678 richness at the entire community level? In: *Journal of ecology* 97 (6), S. 1181–1191. DOI:
679 10.1111/j.1365-2745.2009.01579.x.
- 680 Chalmandrier, Loïc; Münkemüller, Tamara; Colace, Marie-Pascale; Renaud, Julien; Aubert,
681 Serge; Carlson, Bradley Z. et al. (2017): Spatial scale and intraspecific trait variability mediate
682 assembly rules in alpine grasslands. In: *Journal of ecology* 105 (1), S. 277–287.
- 683 Choler, Philippe; Michalet, Richard; Callaway, Ragan M. (2001): Facilitation and competition
684 on gradients in alpine plant communities. In: *Ecology* 82 (12), S. 3295–3308. DOI:
685 10.1890/0012-9658(2001)082[3295:FACOGI]2.0.CO;2.
- 686 Cody, Martin L.; MacArthur, Robert H.; Diamond, Jared M. (1975): *Ecology and evolution of*
687 *communities*: Harvard University Press.
- 688 Cornwell, William K.; Ackerly, David D. (2009): Community assembly and shifts in plant trait
689 distributions across an environmental gradient in coastal California. In: *Ecological Monographs*
690 79 (1), S. 109–126.

- 691 Craine, Joseph M.; Wolkovich, Elizabeth M.; Gene Towne, E.; Kembel, Steven W. (2012):
692 Flowering phenology as a functional trait in a tallgrass prairie. In: *New phytologist* 193 (3), S.
693 673–682. DOI: 10.1111/j.1469-8137.2011.03953.x.
- 694 D’Amen, Manuela; Rahbek, Carsten; Zimmermann, Niklaus E.; Guisan, Antoine (2017): Spatial
695 predictions at the community level: from current approaches to future frameworks. In: *Biological*
696 *Reviews* 92 (1), S. 169–187. DOI: 10.1111/brv.12222.
- 697 Dayrell, Roberta L. C.; Arruda, André J.; Pierce, Simon; Negreiros, Daniel; Meyer, Pablo B.;
698 Lambers, Hans; Silveira, Fernando A. O. (2018): Ontogenetic shifts in plant ecological
699 strategies. In: *Functional Ecology* 32 (12), S. 2730–2741. DOI: 10.1111/1365-2435.13221.
- 700 Dullinger, S.; Willner, W.; Plutzer, C.; Englisch, T.; Schratt-Ehrendorfer, L.; Moser, D. et al.
701 (2012): Post-glacial migration lag restricts range filling of plants in the European Alps. In:
702 *Global Ecol Biogeogr* 21 (8), S. 829–840. DOI: 10.1111/j.1466-8238.2011.00732.x.
- 703 Eñ Vojtkó, Anna; Bello, Francesco; Durka, Walter; Kühn, Ingolf; Götzenberger, Lars (2020):
704 The neglected importance of floral traits in trait-based plant community assembly. In: *Journal*
705 *of Vegetation Science* 31 (4), S. 529–539. DOI: 10.1111/jvs.12877.
- 706 Fenner, Michael K.; Fenner, Michael; Thompson, Ken (2005): The ecology of seeds: Cambridge
707 University Press.
- 708 Fernández-Pascual, Eduardo; Carta, Angelino; Mondoni, Andrea; Cavieres, Lohengrin A.;
709 Rosbakh, Sergey; Venn, Susanna et al. (2021): The seed germination spectrum of alpine plants: a
710 global meta-analysis. In: *New phytologist* 229 (6), S. 3573–3586. DOI: 10.1111/nph.17086.
- 711 Fernández-Pascual, Eduardo; Pérez-Arcoiza, Adrián; Prieto, José Alberto; Díaz, Tomás E.
712 (2017): Environmental filtering drives the shape and breadth of the seed germination niche in
713 coastal plant communities. In: *Annals of Botany* 119 (7), S. 1169–1177. DOI:
714 10.1093/aob/mcx005.
- 715 Forbis, T. (2010): Germination phenology of some Great Basin native annual forb species. In:
716 *Plant Species Biology* 25 (3), S. 221–230. DOI: 10.1111/j.1442-1984.2010.00289.x.
- 717 Gilck, Fridtjof; Poschold, Peter (2021): The history of human land use activities in the Northern
718 Alps since the Neolithic Age. A reconstruction of vegetation and fire history in the Mangfall
719 Mountains (Bavaria, Germany). In: *The Holocene* 31 (4), S. 579–591. DOI:
720 10.1177/0959683620981701.
- 721 Götzenberger, Lars; Bello, Francesco de; Bråthen, Kari Anne; Davison, John; Dubuis, Anne;
722 Guisan, Antoine et al. (2012): Ecological assembly rules in plant communities—approaches,
723 patterns and prospects. In: *Biological Reviews* 87 (1), S. 111–127. DOI: 10.1111/j.1469-
724 185X.2011.00187.x.
- 725 Grime, J. P.; Mason, G.; Curtis, A. V.; Rodman, J.; Band, S. R. (1981): A Comparative Study of
726 Germination Characteristics in a Local Flora. In: *Journal of ecology* 69 (3), S. 1017. DOI:
727 10.2307/2259651.
- 728 Grime, J. P.; Thompson, K.; Hunt, R.; Hodgson, J. G.; Cornelissen, J. H. C.; Rorison, I. H. et al.
729 (1997): Integrated Screening Validates Primary Axes of Specialisation in Plants. In: *Oikos* 79
730 (2), S. 259. DOI: 10.2307/3546011.

- 731 Grubb, Peter J. (1977): The maintenance of species richness in plant communities: the
732 importance of the regeneration niche. In: *Biological Reviews* 52 (1), S. 107–145.
- 733 Hodkinson, D. J.; Askew, A. P.; Thompson, K.; Hodgson, J. G.; Bakker, J. P.; Bekker, R. M.
734 (1998): Ecological correlates of seed size in the British flora. In: *Functional Ecology* 12 (5), S.
735 762–766.
- 736 Inouye, David W. (2008): Effects of climate change on phenology, frost damage, and floral
737 abundance of montane wildflowers. In: *Ecology* 89 (2), S. 353–362. DOI: 10.1890/06-2128.1.
- 738 Isabelle, Boulangeat; Pauline, Philippe; Sylvain, Abdulkhak; Roland, Douzet; Luc, Garraud;
739 Sébastien, Lavergne et al. (2012): Improving plant functional groups for dynamic models of
740 biodiversity: at the crossroads between functional and community ecology. In: *Glob Change Biol*
741 18 (11), S. 3464–3475. DOI: 10.1111/j.1365-2486.2012.02783.x.
- 742 Jakobsson, Anna; Eriksson, Ove (2000): A comparative study of seed number, seed size,
743 seedling size and recruitment in grassland plants. In: *Oikos* 88 (3), S. 494–502. DOI:
744 10.1034/j.1600-0706.2000.880304.x.
- 745 Jiménez-Alfaro, Borja; Silveira, Fernando A. O.; Fidelis, Alessandra; Poschod, Peter;
746 Commander, Lucy E. (2016): Seed germination traits can contribute better to plant community
747 ecology. In: *Journal of Vegetation Science* 27 (3), S. 637–645.
- 748 Johnson, Anna L.; Borowy, Dorothy; Swan, Christopher M. (2018): Land use history and seed
749 dispersal drive divergent plant community assembly patterns in urban vacant lots. In: *J Appl Ecol*
750 55 (1), S. 451–460. DOI: 10.1111/1365-2664.12958.
- 751 Kardol, Paul; Souza, Lara; Classen, Aimée T. (2013): Resource availability mediates the
752 importance of priority effects in plant community assembly and ecosystem function. In: *Oikos*
753 122 (1), S. 84–94. DOI: 10.1111/j.1600-0706.2012.20546.x.
- 754 Keddy, Paul A. (1992): Assembly and response rules: two goals for predictive community
755 ecology. In: *Journal of Vegetation Science* 3 (2), S. 157–164.
- 756 Keddy, Paul A. (2010): *Wetland ecology: principles and conservation*: Cambridge University
757 Press.
- 758 Kergunteuil, Alan; Descombes, Patrice; Glauser, Gaetan; Pellissier, Loïc; Rasmann, Sergio
759 (2018): Plant physical and chemical defence variation along elevation gradients: a functional
760 trait-based approach. In: *Oecologia* 187 (2), S. 561–571.
- 761 Kleyer, Michael; Bekker, R. M.; Knevel, I. C.; Bakker, J. P.; Thompson, K.; Sonnenschein, M. et
762 al. (2008): The LEDA traitbase: a database of life-history traits of the Northwest European
763 flora. In: *Journal of ecology* 96 (6), S. 1266–1274.
- 764 Kleyer, Michael; Minden, Vanessa (2015): Why functional ecology should consider all plant
765 organs: An allocation-based perspective. In: *Basic and Applied Ecology* 16 (1), S. 1–9. DOI:
766 10.1016/j.baae.2014.11.002.
- 767 Knevel, Irma C. (2005): The LEDA traitbase collecting and measuring standards of life-history
768 traits of the Northwest European Flora: Univ., Community and Conservation Ecology Group.

- 769 Körner, Christian (2007): The use of ‘altitude’ in ecological research. In: *Trends in ecology &*
770 *evolution* 22 (11), S. 569–574. DOI: 10.1016/j.tree.2007.09.006.
- 771 Körner, Christian (2021): Alpine plant life: functional plant ecology of high mountain
772 ecosystems.
- 773 Kos, Martijn; Poschod, Peter (2007): Seeds use temperature cues to ensure germination under
774 nurse-plant shade in xeric Kalahari savannah. In: *Annals of Botany* 99 (4), S. 667–675. DOI:
775 10.1093/aob/mcl293.
- 776 Lamprecht, Andrea; Semenchuk, Philipp Robert; Steinbauer, Klaus; Winkler, Manuela; Pauli,
777 Harald (2018): Climate change leads to accelerated transformation of high-elevation vegetation
778 in the central Alps. In: *New phytologist* 220 (2), S. 447–459. DOI: 10.1111/nph.15290.
- 779 Larson, Julie E.; Funk, Jennifer L. (2016): Regeneration: an overlooked aspect of trait-based
780 plant community assembly models. In: *Journal of ecology* 104 (5), S. 1284–1298. DOI:
781 10.1111/1365-2745.12613.
- 782 Laughlin, Daniel C. (2014): The intrinsic dimensionality of plant traits and its relevance to
783 community assembly. In: *Journal of ecology* 102 (1), S. 186–193.
- 784 Lebrija-Trejos, Edwin; Pérez-García, Eduardo A.; Meave, Jorge A.; Bongers, Frans; Poorter,
785 Lourens (2010): Functional traits and environmental filtering drive community assembly in a
786 species-rich tropical system. In: *Ecology* 91 (2), S. 386–398. DOI: 10.1890/08-1449.1.
- 787 Leishman, Michelle R.; Westoby, Mark (1992): Classifying plants into groups on the basis of
788 associations of individual traits—evidence from Australian semi-arid woodlands. In: *Journal of*
789 *ecology* 80 (3), S. 417. DOI: 10.2307/2260687.
- 790 Leishman, Michelle R.; Westoby, Mark (1994): The role of seed size in seedling establishment
791 in dry soil conditions—experimental evidence from semi-arid species. In: *Journal of ecology* 82
792 (2), S. 249. DOI: 10.2307/2261293.
- 793 Lozano-Isla, Flavio; Benites-Alfaro, Omar E.; Pompelli, Marcelo F. (2019): GerminaR: An R
794 package for germination analysis with the interactive web application “GerminaQuant for R”.
795 Wiley Online Library.
- 796 Lundemo, Sverre; Totland, Ørjan (2007): Within-population spatial variation in pollinator
797 visitation rates, pollen limitation on seed set, and flower longevity in an alpine species. In: *Acta*
798 *Oecologica* 32 (3), S. 262–268. DOI: 10.1016/j.actao.2007.05.007.
- 799 Maestre, Fernando T.; Callaway, Ragan M.; Valladares, Fernando; Lortie, Christopher J. (2009):
800 Refining the stress-gradient hypothesis for competition and facilitation in plant communities. In:
801 *Journal of ecology* 97 (2), S. 199–205. DOI: 10.1111/j.1365-2745.2008.01476.x.
- 802 Marke, T.; Strasser, U.; Kraller, G.; Warscher, M.; Kunstmann, Harald; Franz, H.; Vogel, M.
803 (2013): The Berchtesgaden National Park (Bavaria, Germany): a platform for interdisciplinary
804 catchment research. In: *Environmental earth sciences* 69 (2), S. 679–694.
- 805 McGill, Brian J.; Enquist, Brian J.; Weiher, Evan; Westoby, Mark (2006): Rebuilding
806 community ecology from functional traits. In: *Trends in ecology & evolution* 21 (4), S. 178–185.

- 807 McIntire, Eliot J. B.; Fajardo, Alex (2014): Facilitation as a ubiquitous driver of biodiversity. In:
808 *New phytologist* 201 (2), S. 403–416. DOI: 10.1111/nph.12478.
- 809 Münkemüller, Tamara; Gallien, Laure; Pollock, Laura J.; Barros, Ceres; Carboni, Marta;
810 Chalmandrier, Loïc et al. (2020): Dos and don'ts when inferring assembly rules from diversity
811 patterns. In: *Global Ecol Biogeogr* 29 (7), S. 1212–1229. DOI: 10.1111/geb.13098.
- 812 Newbold, Tim (2018): Future effects of climate and land-use change on terrestrial vertebrate
813 community diversity under different scenarios. In: *Proceedings of the Royal Society B:*
814 *Biological Sciences* 285 (1881), S. 20180792. DOI: 10.1098/rspb.2018.0792.
- 815 Pakeman, Robin J.; Quested, Helen M. (2007): Sampling plant functional traits: What proportion
816 of the species need to be measured? In: *Applied Vegetation Science* 10 (1), S. 91–96. DOI:
817 10.1111/j.1654-109X.2007.tb00507.x.
- 818 Pellissier, Loïc; Fournier, Bertrand; Guisan, Antoine; Vittoz, Pascal (2010): Plant traits co-vary
819 with altitude in grasslands and forests in the European Alps. In: *Plant Ecology* 211 (2), S. 351–
820 365.
- 821 Perez-Harguindeguy, Natalia; Diaz, Sandra; Garnier, Eric; Lavorel, Sandra; Poorter, Hendrik;
822 Jaureguiberry, Pedro et al. (2016): Corrigendum to: new handbook for standardised measurement
823 of plant functional traits worldwide. In: *Australian Journal of botany* 64 (8), S. 715–716.
- 824 Pillar, Valério D.; Sabatini, Francesco Maria; Jandt, Ute; Camiz, Sergio; Bruelheide, Helge
825 (2021): Revealing the functional traits linked to hidden environmental factors in community
826 assembly. In: *Journal of Vegetation Science* 32 (1), e12976. DOI: 10.1111/jvs.12976.
- 827 Pöschl, P.; Kiefer, S.; Tränkle, U.; Fischer, S.; Bonn, S. (1998): Plant species richness in
828 calcareous grasslands as affected by dispersability in space and time. In: *Applied Vegetation*
829 *Science* 1 (1), S. 75–91. DOI: 10.2307/1479087.
- 830 Pöschl, Peter (2014): Kulturlandschaft, Landnutzungswandel und Vielfalt–Mechanismen und
831 Prozesse der Entstehung und Entwicklung unserer Kulturlandschaft und die Notwendigkeit einer
832 Genbank für Wildpflanzen für Ernährung und Landwirtschaft (WEL). In: *POSCHLOD, P. et al.:*
833 *Handbuch Genbank WEL, Hoppea, Sonderband*, S. 7–40.
- 834 Pöschl, Peter; Abedi, Mehdi; Bartelheimer, Maik; Drobnik, Juliane; Rosbakh, Sergey;
835 Saatkamp, Arne (2013): Seed ecology and assembly rules in plant communities. In: *Vegetation*
836 *ecology* 2, S. 164–202.
- 837 Pöschl, Peter; Tackenberg, Oliver; Bonn, Susanne (2005): Plant dispersal potential and its
838 relation to species frequency and coexistence. In: *Vegetation ecology*, S. 147–171.
- 839 R Core Development Team (2021): R: a language and environment for statistical computing.
840 Vienna, Austria: R Foundation for Statistical Computing.
- 841 Rao, C. Radhakrishna (1982): Diversity and dissimilarity coefficients: A unified approach. In:
842 *Theoretical Population Biology* 21 (1), S. 24–43. DOI: 10.1016/0040-5809(82)90004-1.
- 843 Ricotta, Carlo; Moretti, Marco (2011): CWM and Rao's quadratic diversity: a unified framework
844 for functional ecology. In: *Oecologia* 167 (1), S. 181–188. DOI: 10.1007/s00442-011-1965-5.

- 845 Römermann, Christine; Tackenberg, Oliver; Poschlod, Peter (2005): How to predict attachment
846 potential of seeds to sheep and cattle coat from simple morphological seed traits. In: *Oikos* 110
847 (2), S. 219–230.
- 848 Rosbakh, Sergey; Baskin, Carol C.; Baskin, Jerry M. (2020a): Nikolaeva et al.'s reference book
849 on seed dormancy and germination.
- 850 Rosbakh, Sergey; Margreiter, Vera; Jelcic, Bernardica (2020b): Seedlings of alpine species do
851 not have better frost-tolerance than their lowland counterparts. In: *Alpine Botany* 130 (2), S.
852 179–185.
- 853 Rosbakh, Sergey; Pacini, Ettore; Nepi, Massimo; Poschlod, Peter (2018): An unexplored side of
854 regeneration niche: seed quantity and quality are determined by the effect of temperature on
855 pollen performance. In: *Frontiers in Plant Science* 9, S. 1036. DOI: 10.3389/fpls.2018.01036.
- 856 Rosbakh, Sergey; Phartyal, Shyam S.; Poschlod, Peter (2020c): Seed germination traits shape
857 community assembly along a hydroperiod gradient. In: *Annals of Botany* 125 (1), S. 67–78.
- 858 Rosbakh, Sergey; Poschlod, Peter (2015): Initial temperature of seed germination as related to
859 species occurrence along a temperature gradient. In: *Functional Ecology* 29 (1), S. 5–14.
- 860 Rosbakh, Sergey; Poschlod, Peter (2016): Minimal temperature of pollen germination controls
861 species distribution along a temperature gradient. In: *Annals of Botany* 117 (7), S. 1111–1120.
862 DOI: 10.1093/aob/mcw041.
- 863 Rosbakh, Sergey; Poschlod, Peter (2021): Plant community persistence strategy is
864 elevation-specific. In: *Journal of Vegetation Science* 32 (3), e13028. DOI: 10.1111/jvs.13028.
- 865 Rosbakh, Sergey; Römermann, Christine; Poschlod, Peter (2015): Specific leaf area correlates
866 with temperature: new evidence of trait variation at the population, species and community
867 levels. In: *Alpine Botany* 125 (2), S. 79–86.
- 868 Rumpf, Sabine B.; Hülber, Karl; Wessely, Johannes; Willner, Wolfgang; Moser, Dietmar;
869 Gattringer, Andreas et al. (2019): Extinction debts and colonization credits of non-forest plants
870 in the European Alps. In: *Nature Communications* 10 (1), S. 4293. DOI: 10.1038/s41467-019-
871 12343-x.
- 872 Saatkamp, Arne; Cochrane, Anne; Commander, Lucy; Guja, Lydia K.; Jimenez-Alfaro, Borja;
873 Larson, Julie et al. (2019): A research agenda for seed-trait functional ecology. In: *New*
874 *phytologist* 221 (4), S. 1764–1775. DOI: 10.1111/nph.15502.
- 875 Scherrer, Daniel; Körner, Christian (2011): Topographically controlled thermal-habitat
876 differentiation buffers alpine plant diversity against climate warming. In: *Journal of*
877 *biogeography* 38 (2), S. 406–416.
- 878 Scherrer, Daniel; Schmid, Samuel; Körner, Christian (2011): Elevational species shifts in a
879 warmer climate are overestimated when based on weather station data. In: *International Journal*
880 *of Biometeorology* 55 (4), S. 645–654. DOI: 10.1007/s00484-010-0364-7.
- 881 Schneider, Caroline A.; Rasband, Wayne S.; Eliceiri, Kevin W. (2012): NIH Image to ImageJ:
882 25 years of image analysis. In: *Nature Methods* 9 (7), S. 671–675. DOI: 10.1038/nmeth.2089.

- 883 Soons, Merel B.; Groot, G. Arjen; Cuesta Ramirez, M. Teresa; Fraaije, Rob G. A.; Verhoeven,
884 Jos T. A.; Jager, Monique (2017): Directed dispersal by an abiotic vector: wetland plants
885 disperse their seeds selectively to suitable sites along the hydrological gradient via water. In:
886 *Functional Ecology* 31 (2), S. 499–508. DOI: 10.1111/1365-2435.12771.
- 887 Spasojevic, Marko J.; Suding, Katharine N. (2012): Inferring community assembly mechanisms
888 from functional diversity patterns: the importance of multiple assembly processes. In: *Journal of*
889 *ecology* 100 (3), S. 652–661. DOI: 10.1111/j.1365-2745.2011.01945.x.
- 890 Steinacher, Gerlinde; Wagner, Johanna (2013): The progamic phase in high-mountain plants:
891 from pollination to fertilization in the cold (Plants, 2).
- 892 Tackenberg, O.; Poschlod, P.; Kahmen, S. (2003a): Dandelion seed dispersal: the horizontal
893 wind speed does not matter for long-distance dispersal - it is updraft! In: *Plant Biology* 5 (5), S.
894 451–454. DOI: 10.1055/s-2003-44789.
- 895 Tackenberg, Oliver; Poschlod, Peter; Bonn, Susanne (2003b): Assessment of wind dispersal
896 potential in plant species. In: *Ecological Monographs* 73 (2), S. 191–205. DOI: 10.1890/0012-
897 9615(2003)073[0191:AOWDPI]2.0.CO;2.
- 898 Tackenberg, Oliver; Stöcklin, Jürg (2008): Wind dispersal of alpine plant species: A comparison
899 with lowland species. In: *Journal of Vegetation Science* 19 (1), S. 109–118. DOI: 10.3170/2007-
900 8-18338.
- 901 Thompson, K.; Grime, J. P. (1983): A comparative study of germination responses to diurnally-
902 fluctuating temperatures. In: *J Appl Ecol* 20 (1), S. 141. DOI: 10.2307/2403382.
- 903 Thomson, Fiona J.; Moles, Angela T.; Auld, Tony D.; Kingsford, Richard T. (2011): Seed
904 dispersal distance is more strongly correlated with plant height than with seed mass. In: *Journal*
905 *of ecology* 99 (6), S. 1299–1307. DOI: 10.1111/j.1365-2745.2011.01867.x.
- 906 Violle, Cyrille; Navas, Marie-Laure; Vile, Denis; Kazakou, Elena; Fortunel, Claire; Hummel,
907 Irène; Garnier, Eric (2007): Let the concept of trait be functional! In: *Oikos* 116 (5), S. 882–892.
- 908 Wei, Taiyun; Simko, Viliam; Levy, Michael; Xie, Yihui; Jin, Yan; Zemla, Jeff (2017): Package
909 ‘corrplot’. In: *Statistician* 56 (316), e24.
- 910 Weiher, Evan; Keddy, Paul (1999): Assembly rules as general constraints on community
911 composition. In: *Ecological assembly rules: perspectives, advances, retreats*, S. 251–271.