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**Lags in phenological acclimation of mountain grasslands
after recent warming**

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1 Introduction

2 Climate warming is altering the biodiversity and functioning of mountain grasslands. Plant
3 communities will not immediately restructure to adjust to new air and soil temperatures and
4 associated changes in growing season length and snow cover (Carlson et al., 2017; Choler,
5 2015; Gobiet et al., 2014) but will show a number of transient responses (Hastings et al., 2018)
6 that are susceptible to lag behind climate warming (Alexander et al., 2018). Plastic responses of
7 plant phenotypes are prone to be triggered before species' abundance distributions and, finally,
8 community composition change (Nicotra et al., 2010). By monitoring these transient dynamics,
9 we can identify the short-term acclimation lags, i.e. the difference between the current state to
10 the one completely accustomed to a new climate, that can temporarily impair ecosystem
11 functions and services and can serve as early-warning signals of long-term degradations.
12 Quantifying and characterizing acclimation lags in addition to the responses to warming is
13 pivotal to understand how strongly adjusting plant species and communities are still
14 underperforming in comparison to well-adapted ones, how prone they are to be replaced and
15 outcompeted by better adapted ones, and how strongly ecosystem processes are impaired (Ryo
16 et al., 2019; Ström et al., 2011)

17

18 Among plastic responses to warming, plant phenology is one of the first to be triggered (Bellard
19 et al., 2012; Parmesan & Hanley, 2015; Shen et al., 2015). Phenology refers to the timing and
20 duration of events in species' plant growth and reproduction over the year including budburst,
21 flowering, seed production and browning. Phenology strongly affects demographic performance,
22 community assembly and functions (Ackerly et al., 2000; Richardson et al., 2013). As climate
23 warming does not only result in higher mean temperatures but also in changed snow cover

24 regimes and earlier starts and longer durations of growing seasons, it will affect different
25 aspects of plant phenology in different periods of the season. In the short-term, phenology can
26 allow acclimation of plant communities, notably for their main functions such as productivity
27 (Carlson et al., 2017; Piao et al., 2019). However, many questions on the transient responses
28 of mountain plant phenology to warming remain open: Do early or late season phenological
29 stages acclimate the fastest? How much time does it require to close acclimation lags? Are
30 species plastic in their responses or does acclimation require a restructuring of community
31 composition? It will depend on the answers to these questions which species and ecosystem
32 functions can prevail under climate warming. Therefore, we need to effectively measure
33 phenological responses to realistic warming scenarios and use informative phenological
34 indicators and ways to characterize acclimation lags.

35

36 Plant phenology and its response to warming climate is a globally long-studied phenomenon
37 with different experimental methods and at different organism levels (Piao et al., 2019; Winkler
38 et al., 2019; Wolkovich et al., 2012). For mountain grasslands, experimental warming showed
39 an advancement in greening, flowering and fruiting but a delayed browning at community-level
40 (Meng et al., 2019). However, even so community-level phenological responses often resemble
41 species-specific responses to warming (Diez et al., 2012), species with different characteristics
42 still show idiosyncratic responses (Arft et al., 1999; Dunne et al., 2003; Li et al., 2016; Smith et
43 al., 2012; S. P. Wang et al., 2014). Yet, it has been suggested that responses can potentially be
44 generalized at the growth form-level (Arft et al., 1999; Dunne et al., 2003; Oberbauer et al.,
45 2013). For example, graminoids and forbs are prone to give different responses as they differ in
46 functional and reproductive strategies (Reich et al., 2003; Shen et al., 2015; Siebenkäs et al.,
47 2015).

48

49 Both at community level and at species level, a plethora of indicators have been suggested to
50 track changes in phenology for different periods in the season and to approximate different
51 demographic processes (Table 1). Consequently these indicators can respond differently to
52 warming. Therefore, a comprehensive study of warming effects and acclimation lags requires
53 not only to combine species and community level measures but also to integrate different
54 indicators to have the most complete overview on phenological changes. Here, we refer to
55 indicators that capture the start, end or pace of phenological stages as proxies for the timing of
56 plant growth and reproduction (Time-related indicators, Table 1) and we refer to indicators that
57 capture the length of phenophases (e.g. length of greening or flowering) and the number of
58 individuals passing to a certain phenophase as proxies of demographic performance
59 (Performance-related indicators, Table 1).

60

61 For time-related indicators, warming generally leads to an earlier and quicker onset of
62 phenophases in early-season while late-season responses are much more variable (Parmesan
63 & Hanley, 2015). We are not aware of acclimation lag studies but expect faster acclimation to
64 warming in the early season as it has been shown that plants are plastic in adjusting the leaf-out
65 to changes in snow cover dynamics (Choler, 2015; Körner, 1999). In contrast, high mountain
66 grassland plants are adapted to short growing seasons and we expect that adjusting to longer
67 season lengths may be more difficult than to start the season earlier. For performance-related
68 indicators, warming leads to more plant growth but also more idiosyncratic species-specific
69 responses, e.g. to either decreases or increases in reproductive performance (Aldridge et al.,
70 2011; Carlson et al., 2017; Liu et al., 2012; Li et al., 2016). Additionally, while climate warming
71 might generally improve conditions for plant growth, it often is associated with lower snow cover

72 protection and more frequent exposure to freezing events due to early snowmelt which may limit
73 some species (Choler, 2015). In contrast to time-related indicators, we expect
74 performance-related indicators to be more limited by physiological constraints, to be less plastic
75 and thus, be much slower in adjusting (Baptist et al., 2010).

76

77 Hitherto, warming studies have mainly focussed on a single type of indicator (Aldridge et al.,
78 2011; Li et al., 2016; Meng et al., 2019; S. P. Wang et al., 2014; T. Wang et al., 2014) (but see
79 counter examples: (H. Wang et al., 2020; S. Wang et al., 2014). and quantified phenological
80 changes as a response to warming (i.e. the warming effect) (Piao et al., 2019; Shen et al., 2015;
81 Wolkovich et al., 2012) but rarely measured acclimation lags (Ryo et al., 2019). Measuring
82 acclimation lags is a challenge as it requires to identify the adjusted community state after
83 complete acclimation (Visser & Both, 2005).

84

85 Here, we suggest a combination of a transplant experiment with a conceptual framework to
86 measure transient warming and cooling effects and acclimation lags in mountain grasslands
87 (Fig. 1). We added cooling effects to test for reciprocity and to find out whether the acclimation
88 to new thermal conditions in mountain grasslands is generally a slow phenomenon (Crous,
89 2019). Our reciprocal transplant experiment along an elevation gradient simulates three degrees
90 of warming and longer growing seasons hence, a realistic warming scenario for the Alps for this
91 century (see projections for RCP4.5 and 8.5 scenarios: Jacob et al., 2014; Vorkauf et al., 2021).
92 We transplanted alpine communities 500m downwards to subalpine conditions to simulate
93 climate warming (Fig. 1A, AlpineWarmed) and, reciprocally, we transplanted subalpine
94 communities 500m upwards (Fig. 1A, SubalpineCooled). We controlled for transplantation
95 effects at both sites with control plots (Fig. 1A, AlpineControl and SubalpineControl, resp.). We

96 suggest measuring warming (or cooling) effects by comparing AlpineControl to AlpineWarmed
97 plots (or SubalpineControl to SubalpineCooled plots, Fig. 1C).
98
99 To measure acclimation lags we assume that plants in control plots are in equilibrium with
100 climatic conditions. To justify this assumption despite ongoing climate change, we argue that i)
101 the historical climate warming is a slow and long-term phenomenon compared to the
102 experimental manipulation and thus negligible in comparison (Appendix Table S3), and ii) the
103 ongoing climate change has not induced yet a trend of longer growing seasons even though this
104 is an expected phenomenon (Jacob et al., 2014; J. Wang et al., 2021). Moreover, results would
105 only be more extreme if we would have transplanted communities from long-term climate
106 equilibrium. Acclimation lags can then be measured by comparing where the state of
107 AlpineWarmed plots (or SubalpineCooled plots) is relative to the shortest trajectory of
108 acclimation which we define here as the shortest distance between states of AlpineControl and
109 Subalpine Control plots (Fig. 1B, D). We suggest two measurements (Fig. 1D): Acclimation lags
110 can be big either because little acclimation has been achieved yet and the still to cover distance
111 is much larger than the distance already covered (deficient acclimation) and/or because
112 transient adjustments deviate in direction from the shortest trajectory to complete acclimation
113 (deviating acclimation). Theoretically, we expect that in the very long-term lags will close and
114 compared plots will be indistinguishable.
115 Combining a species to community scale approach, a multi index approach for phenology and
116 our conceptual framework, we asked whether: i) mountain grassland phenology completely
117 acclimated in timing and performance over three years of warming; ii) the lag in acclimation was
118 due to deficient and/or divergent warming effects and iii) the transient responses to warming
119 and cooling were symmetric.

120 **Methods**

121 *Experimental Design*

122 The experiment was implemented close to the Col du Lautaret (45°02'04"N 06°24'18"E) in the
123 French Alps in September 2016 (Fig. 1.A). The transplantation sites are the subalpine site
124 "Lautaret" (45°04'00"N 06°41'90"E) at 1920 m altitude and the alpine site "Galibier" (45°05'44"N
125 06°40'06"E) at 2450 m altitude. Sites are close to each other (~2km airline distance), have a
126 similar orientation (South-East at alpine and South-South-West at subalpine site), bedrock
127 (base-riched flysch) and soil (dystric cambisols). During the observation-period (autumn 2016 -
128 autumn 2019), average annual soil temperature at the subalpine site was 3.2°C warmer than at
129 the alpine site (and days with similar temperatures at the two sites were very rare), average July
130 soil temperature was 3.1 °C warmer and snow free season was 58.7 days longer (Table S1, Fig.
131 2.A). At the subalpine site, plant communities were mainly dominated by the graminoids
132 *Patzkea paniculata*, *Carex sempervirens*, *Festuca nigrescens* and the forbs *Centaurea uniflora*,
133 *Helianthemum nummularium*, and *Meum athamanticum* (Appendix Fig. S13). At the alpine site,
134 plant communities were mainly dominated by the graminoids *Carex sempervirens*, *Festuca*
135 *nigrescens*, *Poa alpina* and the forbs *Potentilla aurea*, *Trifolium alpinum*, and *Geum montanum*
136 (Appendix Fig. S13). Overall, the dominant graminoid species in AlpineControl and
137 SubalpineControl plots makeup to 22.5% and 26.5% of relative abundance, respectively. All
138 plant communities were dominated by perennial species.

139

140 In 2016, to simulate the effect of warming on alpine grasslands, we transplanted 10 replicates
141 4m² blocks of vegetation with at least 20 cm of their intact belowground parts and the
142 surrounding soils from the alpine to the subalpine site (AlpineWarmed plots in the following). For

143 transport, each block was cut in 4 x 1m² subblocks that were re-assembled in their original
144 composition when re-planted. To simulate the effect of cooling on subalpine communities, 10
145 intact 4 m² blocks of vegetation and soils were transplanted from the subalpine to the alpine site
146 (SubalpineCooled plots). To control for the transplantation stress, we also horizontally
147 transplanted 10 intact 1m² blocks at both the subalpine and the alpine sites (SubalpineControl
148 plots and AlpineControl plots, respectively). Around the turfs we placed water permeable root
149 barriers to avoid root ingrowth from the natural vegetation around the plots. At both sites, cattle
150 and sheep were kept out by electric fences.

151 *Defining the growing season*

152 We considered the start and end of phenological events always relative to the start of the
153 growing season and the end of growing season, respectively (Table S1). **This choice assures**
154 **that i) plots in different sites and years are comparable and ii) we compare the direct**
155 **phenological response rather than the differences in calendar dates** (Johansson et al., 2013).
156 We defined the start (end) of the growing season as the first date when the NDVI based on
157 MODIS (Moderate Resolution Imaging Spectroradiometer) remote-sensed data was above
158 (below) 0.1 and the locally measured daily soil temperature was above (below) 1 °C (Choler,
159 2015, 2018) (Fig. 2). For the remote-sensing data (RS-based NDVI), we downloaded the
160 MOD09Q1 surface reflectance products corresponding to tile h18.v4 (40–50° N, 0–15.6° E) from
161 the Land Processes Distributed Active Archive Center (LP DAAC). We used surface reflectance
162 in the red and near-infrared to calculate the 250m-resolution NDVI **8-days** times series
163 corresponding to the two sites. The RS-based NDVI time series data were BISE (Best Index
164 Slope Extraction) corrected, gap-filled with cubic spline interpolation and smoothed using the
165 Savitzky-Golay filter (Choler, 2015). For the local soil temperature measurements, we equipped

166 the two sites with standalone soil temperature data loggers (Hobo pendant UA, Onset Computer
167 Corporation, Bourne, MA) buried at 5 cm below ground. We smoothed daily soil temperature
168 time series with cubic spline interpolation.

169 *On site measurements and phenological indicators*

170 **Community-level**

171 We tracked the phenology at community-level using NDVI as a measurement of greening and a
172 proxy for photosynthetic activity and plant growth (Myneni & Williams, 1994) (Fig. 2.C). We
173 measured NDVI (Normalized Difference Vegetation Index) in each treatment subblock
174 (10 x 4 x 1 m² subblocks for AlpineWarmed and for SubalpineCooled) and in each control block
175 (10 x 1 m² blocks for AlpineControl and SubalpineControl) with three measurement repetitions
176 once (twice at maximum growth) per week during the growing seasons of the years 2017, 2018
177 and 2019. We took the measurements with a Decagon ProCheck spectral reflectance sensor for
178 NDVI with 630 nm (red) and 800 nm (near-infrared) spectral irradiance. The measurements
179 were taken at clear sky from 11am to 2pm during the same day for both sites. We derived
180 indicators from the NDVI curves over the growing season independently for each year,
181 treatment subblocks, control blocks and replicates. We gap-filled the time series (i.e. the other
182 days of the week) using cubic smoothing spline interpolation and smoothed using
183 Savitzky-Golay filter (Choler, 2015).

184

185 Based on these time series, we calculated several indicators. These indicators were based on
186 the definition of seasons within the whole growing season: i) early-season as the period starting
187 from the onset of the growing season to the last day when the NDVI values were below the 90%
188 of the maximum NDVI, ii) mid season as the period when the NDVI values stayed above 90% of

189 the maximum NDVI, iii) late-season as the period between the first day where NDVI values
 190 dropped below 90% of the maximum NDVI until the offset of the growing season. The threshold
 191 choice (e.g. 80% of the maximum NDVI) did not affect the results (unpublished). While the start
 192 and end of growing seasons were identified with MODIS remote-sensed data, we got to capture
 193 the unique phenological dynamics in plant growth of each plot repetition by i) starting NDVI
 194 measurements right after the snow melt when the field site was accessible, ii) identifying the
 195 maximum NDVI based on field measurements for each plot.

196

197 We calculated time-related indicators as (Table 1): i) the days from the start of growing season
 198 until 90% of the maximum plant growth (greening days), ii) greening speed as the rate of
 199 increase in the NDVI values (i.e. from 0.1 of onset value to 90% of maximum NDVI value)
 200 during early-season (Eq.2), iii) ratio of mid-season days to growing season days, iv) days after
 201 90% of the maximum plant growth until the end of growing season (browning days), v) browning
 202 speed as the rate of decrease in the NDVI values (from 90% of maximum NDVI value to 0.1 of
 203 offset value) during late-season (Eq.3).

204

$$205 \quad \textit{Greening speed} = \left| \frac{0.9 \times \textit{maxNDVI} - 0.1}{\textit{Greening days}} \right| \quad \textbf{(eqn 1)}$$

206

207

$$208 \quad \textit{Browning speed} = \left| \frac{0.1 - 0.9 \times \textit{maxNDVI}}{\textit{Browning days}} \right| \quad \textbf{(eqn 2)}$$

209

210 We calculated performance-related indicators as proxies for biomass production and plant
 211 growth as the areas under NDVI curves for each season (Table 1): i) early plant growth, ii)

212 mid-season plant growth, iii) late plant growth and iv) annual (i.e. whole growing season) plant
213 growth.

214 ***Species-level***

215 We tracked the phenology of focal dominant species (Appendix Table S2) in one sub-block of
216 each treatment block (20 x 1 m² sub-blocks in total) and in each control block (20 x 1 m² blocks
217 in total) every week during the growing seasons of 2017, 2018 and 2019. The selected
218 dominant species for the blocks with subalpine origin (SubalpineControl and SubalpineCooled)
219 were *Patzkea paniculata*, *Carex sempervirens*, *Festuca nigrescens*, *Centaurea uniflora*,
220 *Helianthemum nummularium*, and *Meum athamanticum*. The selected species for the blocks
221 with alpine origin (AlpineWarmed and AlpineControl) were *Carex sempervirens*, *Festuca*
222 *nigrescens*, *Poa alpina*, *Potentilla aurea*, and *Trifolium alpinum*, *Geum montanum*. We focus
223 here on the flowering, fruiting and dissemination phases as they reflect both early- and
224 late-season plant growth and reproduction phenologies. For each treatment subblock and
225 control block and each species, we determined the phenophases of 10 randomly selected
226 individuals (or the maximum number of individuals available when less than 10, see Appendix
227 TableS2 for percentage of observations when less than 10 individuals were observed). During
228 the peak of the growing season, we increased the frequency of NDVI and phenology
229 measurements to two times a week.

230

231 To reduce observation bias, we determined the start of the phenophase for a species as the
232 average of i) the last date when no individuals of the given species in the given phenophase
233 were observed and ii) the first date when the individuals of the given species in the given
234 phenophase were observed (vice versa for the end of phenophase) (Li et al., 2016). **In case this**

235 averaging is not possible for the fact that the start or end of a phenophase were exactly the start
236 or the end of the observation period on the field, the latter dates were taken.

237

238 We calculated time-related indicators as the days from the start of the growing season until the
239 mean date of the phenophase (Table 1) (Moussus et al., 2010).

240

241 We calculated performance-related indicators as (Table 1): i) the maximum ratio of individuals in
242 the phenophase to the number of sampled individuals (maximum 10) and ii) length of the
243 phenophase as the number of days between the onset and the end of the phenophase. (Li et
244 al., 2016). We excluded the length of the dissemination period from our study as we could not
245 collect the data over the whole dissemination period.

246 *Statistical analyses*

247 For our sets of phenological indicators (community- vs. species-level and time vs. performance
248 related), we analyzed four different treatment effects (Fig. 1.C): i) a warming effect by comparing
249 AlpineWarmed to AlpineControl plots, ii) a cooling effect by comparing SubalpineCooled to
250 SubalpineControl plots, iii) an acclimation lag after warming by comparing SubalpineControl to
251 AlpineWarmed plots, and iv) an acclimation lag after cooling by comparing AlpineControl to
252 SubalpineCooled plots. We conducted all the statistical analyses on R (R Core Team, 2017).

253

254 First, we tested the different treatment effects for each phenology indicator independently using
255 linear mixed effects models (*nlme* R package). At the community-level, we took the median of
256 the measurement repetitions to avoid including measurement errors due to the handheld NDVI
257 sensor. We considered treatment (custom contrast setting of above-explained comparisons, Fig.

258 1.C) and year as fixed effects and subplot identity nested in plot identity as random effect. At the
259 species-level, we accounted for treatment, year and functional group (forbs or graminoids) as
260 fixed effects and block and species identity as random effects. As we conducted multiple tests,
261 we adjusted the p-values with multivariate t-distribution adjustment within the *emmeans*
262 package in R (Lenth, 2016). Here, we discuss the common responses of forbs and graminoids,
263 and report the species-specific responses in the Appendix (Fig. S1).

264

265 Secondly, in order to summarize results for timing vs. performance related phenological
266 indicators, we performed six different Principal Component Analyses (PCA) for time-related vs.
267 performance-related indicators for communities, forbs and graminoids. We visualized the first
268 two components of each PCA in the Appendix (Figs S4-6). For further analyses we determined
269 the number of significant principal components (PC) with Horn's parallel analysis in the R
270 package *paran* (Dinno, 2018; Franklin et al., 1995) (Appendix Fig. S12). As a result, we retained
271 the first two PCs For community-level PCAs two PCs were necessary to well capture the
272 variation, for species-level PCAs one PC was sufficient. Then calculated i) the multidimensional
273 acclimation lag (here "multidimensional" refers to the multiple indicators and the one or two PC
274 axes describing their variation) as the percentage of the remaining acclimation relative to the
275 complete acclimation (Fig. 1.D), ii) the deviation from the shortest acclimation trajectory as the
276 angle between the shortest acclimation trajectory and the warming effect (Fig. 1.D) with the
277 shortest acclimation trajectory being the euclidean distance between AlpineControl and
278 SubalpineControl plots In the case of two significant PCs (i.e. community level), we calculated
279 the euclidean distances with the *dist* function within the *stats* package and the angles with the
280 *Angle* function within the *LearnGeom* package in R (Briz-Redón & Serrano-Aroca, 2018). In the

281 case of a single significant PC (i.e. species level), angles were set either to 0° (i.e. on the
282 acclimation trajectory) or to 180° (opposite direction of the acclimation trajectory).

283

284 For interpretation, we speak of “acclimation lag” or “deficient warming effect” if we found a
285 significant difference between SubalpineControl and AlpineWarmed or AlpineControl and
286 SubalpineCooled and of “complete acclimation” otherwise. We speak of a divergent warming or
287 cooling effect if the observed trajectory deviates from the shortest trajectory of complete
288 acclimation. Importantly, acclimation lags can be much higher than 100% when the distance to
289 the optimally adapted community is not narrowing down over time but is instead increasing
290 during the transient dynamics. This can either happen when the adjustment response goes in a
291 “wrong” direction or when the adjustment response goes in the “right” direction but then
292 overshoots largely. We consider that the acclimation lags in warming and cooling are
293 symmetrical when they have almost the same (i.e. maximum 10% difference) multidimensional
294 acclimation lag.

295 Results

296 *Was phenology completely acclimated after three years of warming?*

297 In a first step, we summarized results for the six sets of indicators (Table 1, combinations of
298 community, forbs, graminoids with time-related and performance-related) and depending on
299 whether at least one indicator per set showed a significant acclimation lag, we give further
300 details in upcoming sections.

301 After three years of warming, the phenology of communities and focal species did not
302 completely acclimate, with the exception of graminoids (Fig. 3). For time-related indicators (Fig.
303 3.A), we observed complete acclimation to warming in most cases, especially during

304 early-season and flowering. However, late-season phenology (i.e. days after max plant growth)
305 for communities and fruiting phenophase for forbs showed a significant acclimation lag.
306 For performance-related indicators (Fig. 3.B), we observed significant acclimation lags under
307 warming except for the graminoids. Both annual and mid-season plant growth for communities
308 and flowering phenophase (i.e. both flowering length and max % flowering) for forbs failed to
309 reach complete acclimation.

310 ***Was the warming effect on phenology deficient and/or divergent?***

311 Both deficient and divergent warming effects were responsible for the observed acclimation lags
312 (Fig. 4). However, lag size and deviation angle were dependent on the focal organism level and
313 phenological indicators.

314

315 For time-related indicators, the community-level acclimation lag was relatively small, 10%, and
316 deviated only slightly from the shortest trajectory, 5° (Fig. 4). With warming and longer season
317 length (Figs 2 & Table S1), alpine community plant growth in the early-season slowed down and
318 communities took longer to reach their maximum plant growth (compared to AlpineControl). In
319 late-season, communities decreased browning speed and increased browning days (i.e. days
320 after max plant growth) but failed to acclimate to the complete use of the late-season which
321 constitutes the major part of the acclimation lag. Interestingly, plant communities could only
322 acclimate their greening speed to longer season length in the third year but failed to do so in the
323 first two years after transplantation (Appendix Fig. S6.A). At the species-level, forbs did not only
324 fail to close the acclimation lag due to the absence of any warming effect (Figs 3A, 4), **but they**
325 **even increased the lag by responding in the “wrong” direction (i.e. 180° away from the shortest**

326 **trajectory to complete acclimation.** Specifically, fruiting for the AlpineWarmed species started
327 earlier than for the SubalpineControls in all three years after the transplantation.

328

329 For performance-related indicators, the community-level acclimation lag was relatively large,
330 26%, but deviated only moderately from the shortest trajectory, 15° (Fig. 4). Thus, even if
331 communities could increase their performance during early- and late-season, their
332 underperformance in the most important mid-season resulted in an important acclimation lag
333 (Fig. 3). In addition, this acclimation lag tended to increase over years (Appendix Fig. S7.A).

334 **Forbs showed an even bigger acclimation lag (685%) because they responded in the “right”**
335 **direction but exceeded far beyond the acclimation state. Notably, such large lags occur because**
336 **the original distance between the phenology of alpine and subalpine plants was small and the**
337 **response is measured relative to this original distance (Fig. 4).** This was especially the case for
338 reproduction in the indispensable flowering stage (length **of flowering period** and number of
339 individuals **reaching this phenophase**) (Fig. 3).

340 ***Were acclimation lags in warming and cooling symmetric?***

341 Acclimation lags in warming and cooling were not always symmetric. However, the strongest
342 acclimation lags caused by warming (i.e. performance-related indicators for communities and
343 forbs and time-related indicators for forbs) were symmetric for cooling (Fig. 4, Appendix Figs S4
344 & S5).

345 For time-related indicators, cooling caused a larger acclimation lag and stronger deviation from
346 the shortest trajectory than warming at the community-level. Forbs were on the shortest
347 acclimation trajectory after cooling **in contrast to their deviating response to warming response**
348 but the sizes of acclimation lags were similar (Fig. 4).

349 For performance-related indicators, at the community-level, acclimation lags and deviations
350 from shortest trajectories were comparable for warming and cooling (Fig. 4 & Appendix Fig.
351 S5.A). After cooling, annual and mid-season plant-growth could acclimate completely but early-
352 and late-season plant growth failed to acclimate (Appendix Fig. S3.B). Forbs suffered even
353 more from cooling than from warming and this was true for lag size and deviation from shortest
354 trajectories. This trend holds for graminoids even though their acclimation lags were not
355 significant.

356 **Discussion**

357 The phenology of mountain grasslands **is known to** strongly respond to climate change but so
358 far little was known about remaining acclimation lags. Here, we built on our conceptual
359 framework and a reciprocal transplant experiment to unravel whether phenological responses to
360 warming and cooling follow the shortest trajectories to complete acclimation and how big
361 remaining lags to complete acclimation are. We found that important aspects of phenology did
362 not acclimate after three years of warming. This suggests that the projected climate warming is
363 exceeding the limits of phenological plasticity of the here studied grasslands. This was
364 especially true for indicators that are key for demographic performance and thus success. Forbs
365 and overall community phenology were most affected, while graminoids coped overall well with
366 climate changes. **Importantly, even though we observed strong warming effects, they were not**
367 **strong enough to lead to complete acclimation and we also found that transient dynamics**
368 **largely deviated from the shortest trajectory to acclimation, especially for forbs. Finally, the**
369 **symmetry between acclimation lags under warming and cooling underlines that important**
370 **phenological processes adjust too slowly. This might indicate that the functioning of mountain**
371 **grasslands under the threat of climate change can be reversible in the short-term.**

372 ***Timing of phenological events***

373 Earlier works found that climate warming led to earlier phenology (experimental warming: Meng
374 et al., 2018, 2019; review on existing studies: Parmesan & Hanley, 2015; review on alpine
375 ecosystem: Winkler et al., 2019) and faster plant growth (H. Wang et al., 2020). In apparent
376 contradiction, our climate warming experiment promoted later phenology (i.e. later maximal
377 plant growth, later starts of fruiting and dissemination periods of graminoids) and slower
378 early-season increase of growth (i.e. slower greening speed). These warming effects allowed
379 complete acclimation of the early- and mid-season timing of phenology to subalpine conditions
380 for graminoids and communities. One major reason for this difference with other studies is that
381 we used the growing season start and not calendar days as a reference (Johansson et al.,
382 2013). Our main arguments for this choice are that the snow-free growing season is a major
383 driver of alpine ecosystems (Choler 2015), that plants physiologically respond to the first frost
384 free days and that thus the comparison among study sites is ecologically less meaningful when
385 it is based on calendar days. Another reason for our results is that with our *in situ* transplant
386 experiment, we did not only manipulate temperature but also the expected accompanying
387 changes in snow cover and growing season length (Choler 2015). In fact, once we calculated
388 the warming effect on greening days based on calendar days, we found an advancement too
389 (i.e. 24.85, with $p < .001$ according to two sample t-test) but this reflects mainly the
390 advancement of snow melt.

391

392 Our results are consistent with apparent strategies of alpine communities: alpine conditions
393 force plants to squeeze life cycles in shorter growing seasons (Körner, 1999) and induce faster
394 plant growth right after the snow melt that is later in the year and thus, plants experience higher

395 air temperatures directly after the snowmelt (Jonas et al., 2008). Yet, with warming and longer
396 growing seasons (just as in subalpine conditions), snowmelt is earlier, the protective effect of
397 snow cover is lost and thus, lower air temperatures are accompanied by potential spring
398 freezing events that together slow down plant growth in the early-season and can kill flower
399 buds and leaves of frost-sensitive species (Choler, 2018; D. Inouye, 2000; D. W. Inouye, 2008).
400 For the end of the growing season, we found in concordance with H. Wang et al. (2020) that
401 plant communities could not sustain the high mid-season plant growth rates. Potential
402 explanations are warming-associated increases of drought stress (H. Wang et al., 2020) (i.e.
403 even though the air-borne estimated water balance of precipitation and evapotranspiration is
404 comparable between sites, *unpublished results*) or inherent allocation trade-offs (Johansson et
405 al., 2013).

406

407 In sum, alpine plant communities adjusted well to warmer conditions and higher uncertainties at
408 the beginning of the growing season but could not fully achieve their adaptation to faster cycles
409 at the end of the growing season.

410 ***Phenological indicators linked to performance***

411 In our experiment, the warming of grasslands increased yearly plant community growth (i.e.
412 photosynthetic activity approximated by NDVI curves) which is consistent with several earlier
413 studies (Cao et al., 2015; Carlson et al., 2017; S. Wang et al., 2012; Yang et al., 2019) but in
414 contradiction to H. Wang et al. (2020). Our observed yearly increase was due to increased early
415 and late plant growth, despite reduced mid-season plant growth. While our early-season results
416 coincide with those of H. Wang et al. (2020), they differ for the mid and late-season (i.e. no
417 change and decrease). Reasons might be the fact that they i) could only record for 2°C of

418 warming and ii) defined early- and late-seasons on the basis of months rather than considering
419 yearly differences in seasonal dynamics (i.e. interannual differences in start and end of growing
420 season). Here, we suggest that i) when 3°C is exceeded, a negative warming effect can be
421 imposed on mid-season community performance and ii) it is important to consider interannual
422 differences in identifying the seasons and warming effects on them.

423

424 Interestingly, in our experiment these strong warming effects were mostly due to short-term
425 responses of the communities, such as phenotypic plasticity, and not due to compositional
426 changes of plant communities. As most species in our observed grasslands were perennials,
427 limited species turnover took place in the first three years after transplantation (Appendix Fig.
428 S8).

429

430 Going a step further than merely describing the warming effect, we also showed that the
431 significant increase of growth was not sufficient to close the acclimation lag completely. In other
432 words, better-adapted grassland species originating from the subalpine area take better
433 advantage of the more favorable climate and grow better over the year. In line with these
434 results, it has already been shown that a positive demographic response to warming is not
435 always able to prevent extinction (Sheth & Angert, 2018). The reason for the remaining
436 acclimation lag is probably functional traits of subalpine communities (e.g. height, **Specific leaf**
437 **area**) being better adapted to the favorable climate than those of alpine communities.

438

439 The community-wide warming effects on growth do not necessarily translate into increased
440 reproductive performance at the species-level (Doak & Morris, 2010). Earlier studies found
441 idiosyncratic warming effects on reproductive performance at the species-level. Some found an

442 increase (Iler et al., 2019; Kudernatsch et al., 2008; Li et al., 2016), no change at all (Dorji et al.,
443 2020) or a decrease (Aldridge et al., 2011; Gugger et al., 2015; Liu et al., 2012) depending on
444 species and ecosystem and others identified species-specific responses (S. Wang et al., 2014;
445 Winkler et al., 2019). In our study, we could relate the species-specific responses to growth
446 forms with forbs failing to acclimate to warmer conditions (i.e. shorter flowering period, fewer
447 individuals flowering) but alpine graminoids performing as well as subalpine graminoids under
448 warmer, subalpine climate. This is in line with independent Ellenberg indicator values (i.e.
449 categorical values indicating the species' abiotic niche; (Bartelheimer & Poschlod, 2016)
450 suggesting that the dominant forbs in our study system are much less tolerant to variation in
451 temperature (and moisture) than the dominant graminoids (Appendix Fig. S9). Specifically, we
452 argue that problems of forbs to acclimate could be linked to: i) disrupted vernalization (i.e. flower
453 bud formation depends on low temperatures, especially during winter; (Liu et al., 2012), ii) more
454 allocation of resources to somatic growth than to reproduction (Johansson et al., 2013; Liu et
455 al., 2012), iii) shading created by graminoids that have the potential to grow taller than forbs.
456

457 The observed acclimation lag of forbs in flowering performance is prone to cascade to the other
458 trophic levels, specifically to associated pollinators (Gezon et al., 2016) and thus to further
459 disrupt functioning of warmed alpine communities. In addition, responses specific to growth form
460 may also cause a community composition shift in favor of graminoids. This is in line with a
461 recent global review on the ecological flexibility of graminoids in their climate and habitat
462 range, their success in establishment and dispersal and ecological competitiveness due to their
463 functional and physiological traits (Linder et al., 2018). Yet, such shift in communities also risks
464 the well-being of the whole multitrophic network and ecosystem functioning through further
465 reduction of pollination services (Burkle et al., 2013; Gezon et al., 2016). In our study site, we

466 already found indications of a significant acclimation lag on pollinator diversity after three years
467 of warming (Appendix Fig. S10).

468

469 The short-term community-level and growth form-specific **results point** to expected long-term
470 responses of mountain grasslands (Pironon et al., 2017), including range shifts and
471 restructuring of communities. With warming, we know that some plant communities will be able
472 to track their climatic niche and some will not, either due to migration failures or absence of
473 niche space on mountain tops (Alexander et al., 2015, 2016; Matteodo et al., 2013). In a
474 scenario where subalpine plant communities can track their climate but alpine communities
475 remain within their current niche, alpine species may not be able to increase their demographic
476 performance either in plant growth or in reproduction fast enough and will thus be outcompeted
477 by the subalpine species (Alexander et al., 2015, 2016). The increase in community plant
478 growth and the competitive exclusion of slower-growing alpine species will also change
479 plant-soil feedbacks. According to the “fast-slow” plant economics spectrum, faster growth is
480 associated to more exploitative plant traits (and thus, functional strategies), especially under
481 favorable environmental conditions (Martinez-Almoyna et al., 2020; Reich, 2014). Such an
482 aboveground functional strategy shift towards the faster part of the economic spectrum will
483 affect the microorganisms involved in plant litter composition (e.g. higher bacteria:fungi ratio),
484 will change their ecosystem functions (e.g. faster nutrient cycling) and will then feedback to the
485 plant communities, potentially further accelerating changes (Bardgett & Wardle, 2010).

486 ***Divergent warming effects***

487 It has been recently highlighted that perturbations to an ecosystem's steady state can trigger
488 transient responses of ecological relevance (Mari et al., 2017). The question is not only how long it

489 will take until the new steady state is reached but also how strongly responses are initially amplified
490 before decaying towards a final state. Here we demonstrate that warming effects, especially on the
491 phenology of alpine forbs, can be not only divergent (Ryo et al., 2019) but can lead phenology far
492 away from any acclimation. In line with a previous long-term study (Wu et al., 2012), we found a
493 similar but weaker response at the community-level. Overall, determining the divergent
494 responses can inform us on the long-term trajectory of the warming effect, and can serve as an
495 early warning signal for negative impacts on ecosystem functioning (Scheffer et al., 2009). For
496 example, fine scale NDVI measurements on communities are relatively easy to implement and
497 according to our results, monitoring only for community productivity can serve for early detecting
498 shifts in communities and ecosystem functioning.

499 ***Symmetry between acclimation lag after warming and cooling***

500 We found most of the acclimation lags after warming and cooling to be symmetric, indicating
501 **some plasticity in phenological responses to climate change that is however not sufficient for**
502 **short-term acclimation to realistic warming scenarios. We conclude that** slow phenological
503 acclimation to new thermal conditions is a general phenomenon for mountain plant
504 communities. Notably, for some phenological indicators (i.e. timing of community growth and
505 flowering performance of forbs), the acclimation lag after cooling was significantly wider than for
506 warming. It has been suggested earlier that for mountain grasslands, physiological limits at the
507 cold thermal range edge are much more pronounced than at the warm edge (Pellissier et al.,
508 2013). In addition, it has been shown that a major driver of the warm edge is competition
509 (Alexander et al., 2015), which has not yet started to act at its full force in our experiment.
510 However, decrease in flowering performance both with warming and cooling indicate that
511 flowering phenology is highly sensitive at both ends of the thermal limits (Li et al., 2016; S. P.
512 Wang et al., 2014).

513

514 The question of symmetry might also have practical implications. With the advancing research
515 on climate warming, the reversibility of the warming effect at many levels is still an open debate
516 (Scheffer et al., 2001). The symmetric response between acclimation lag after warming and
517 cooling can also inform us on the reversibility of the impacts of warming. Here, it seems like
518 most of the warming impacts especially on aboveground productivity and flowering performance
519 can be reversible in the short-term. However, we also acknowledge that these observed
520 transient responses might be buffered by the ones at different levels or can even lead to other
521 cascading effects or critical transitions.

522

523 ***Conclusion and perspectives***

524 With our reciprocal transplant experiment on mountain grasslands, we revealed that community
525 and species-level phenological responses to climate warming were not enough for their
526 complete acclimation to their new conditions in the short-term, except for graminoids. These
527 phenological acclimation lags probably impair other ecosystem functions, such as pollination
528 and plant-soil feedbacks. Short-term acclimation lags, and especially strong deviations from
529 acclimation trajectories, may also hint at long-term impairment of ecosystem functions and
530 restructuring of communities. This emphasizes the importance of characterizing the size and
531 direction of acclimation lags in upcoming global change research.

532

533 *BB, WT and TM conceived the ideas and designed methodology; PC substantially helped with the*
534 *interpretation of the results and design of the conceptual framework; AS and TM organized the fieldwork;*
535 *MPC, JR, AS and TM established the protocol; JR managed the database; BB, RDV, JR and MPC*

536 collected the data; BB analysed the data; BB, WT and TM led the writing of the manuscript. All authors
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538

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549

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807

Table 1: Grouping of phenological indicators and their representation at different levels. **Shading indicates the focal organism level.** (g: indicator related to plant growth; r: indicator related to reproductive period)
(Please refer to the main text for further explanation of their calculation and interpretation)

		Indicators	Level	
			Community-level	Species-level
Phenology	Time-related	Days after max plant growth	g	
		Days before max plant growth	g	
		Greening speed	g	
		Browning speed	g	
		Ratio mid-season days	g	
		Days until mean flowering day		r
		Days until mean fruiting day		r
		Days until mean dissemination day		g
	Performance-related	Annual plant growth	g	
		Early plant growth	g	
		Mid-season plant growth	g	
		Late plant growth	g	
		Flowering length		r
		Fruiting length		r
		Max % flowering		r
		Max % fruiting		r
		Max % dissemination		g

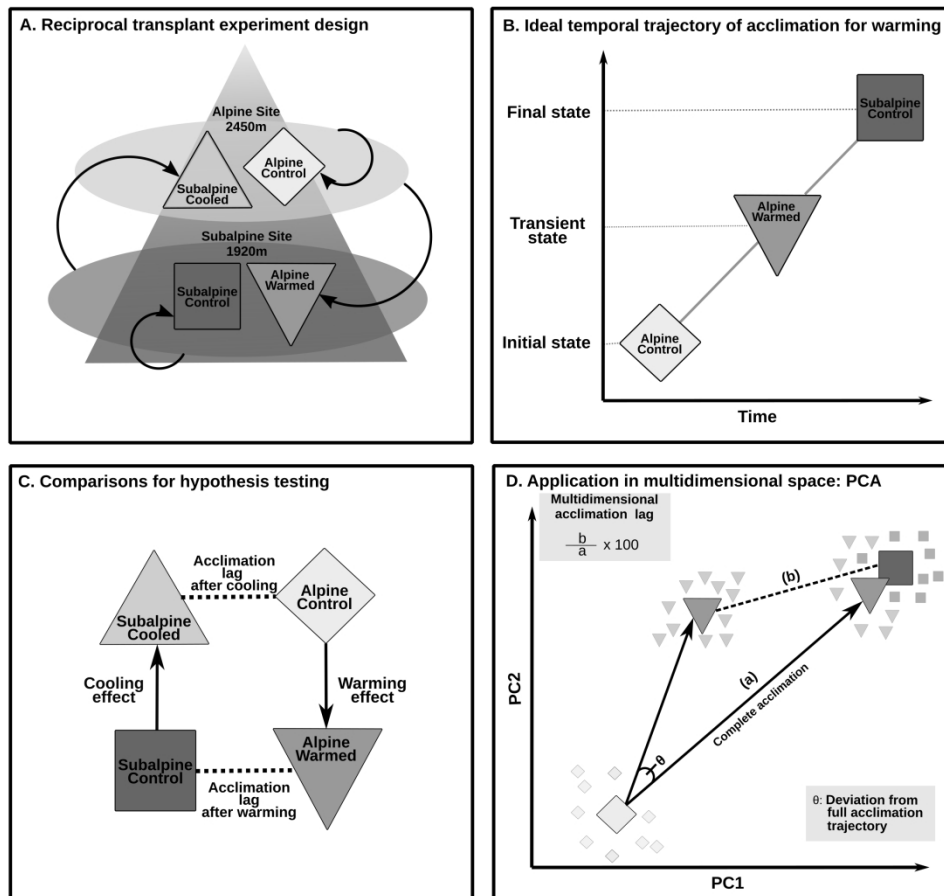


Fig. 1: (A) Schematic representation of the reciprocal transplant experiment. Arrows indicate the destination of the transplantation.

(B) Ideal temporal trajectory of acclimation to warming and the representation of the states (initial, transient and final) of the transplanted plots under the assumption that initial (final) states are at equilibrium under alpine (subalpine) conditions. (C) Treatment effects and associated comparisons of plots (custom contrast setting). Arrows indicate cooling or warming effects. Dotted lines indicate acclimation lags.

For the warming effect, AlpineWarmed is contrasted to AlpineControl. For the cooling effect, SubalpineCooled is contrasted to SubalpineControl. For the acclimation lag after warming, SubalpineControl is contrasted to AlpineWarmed. For the acclimation lag after cooling, AlpineControl is contrasted to SubalpineCooled. (D) Application of the framework to real data based on a Principal Component Analysis (PCA) in order to identify a warming effect, an acclimation lag, and a deviation from the full acclimation trajectory.

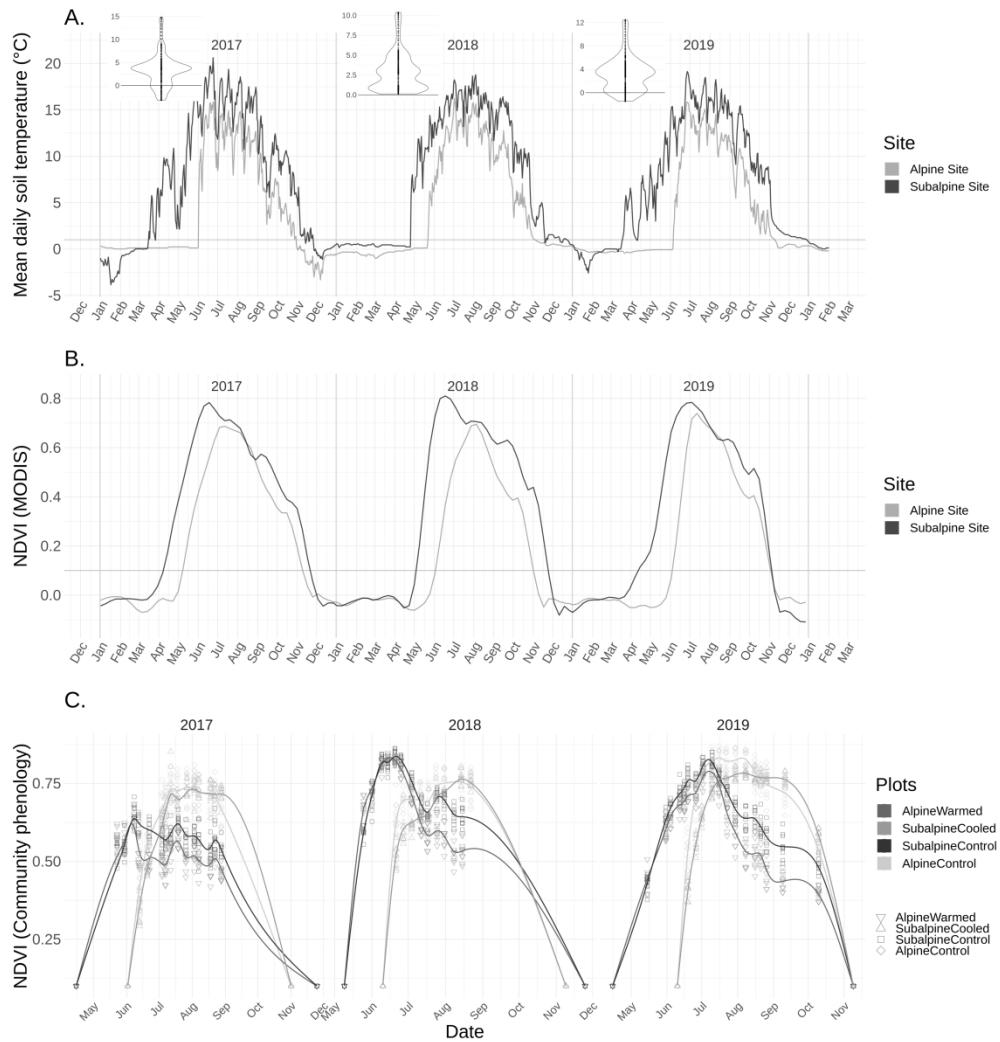


Fig. 2: (A) Soil temperature with daily soil temperature differences between the two sites for each year in the violin plots, (B) NDVI from MODIS remote-sensed data and (C) on-site NDVI plot measurements of alpine and subalpine sites. (A) and (B) were used to identify the growing seasons. (C) Transparent data points are on-site NDVI measurements for each plot. NDVI curves are daily means of interpolated and smoothed on site NDVI measurements for each treatment and control plots. (See main text Methods for details)

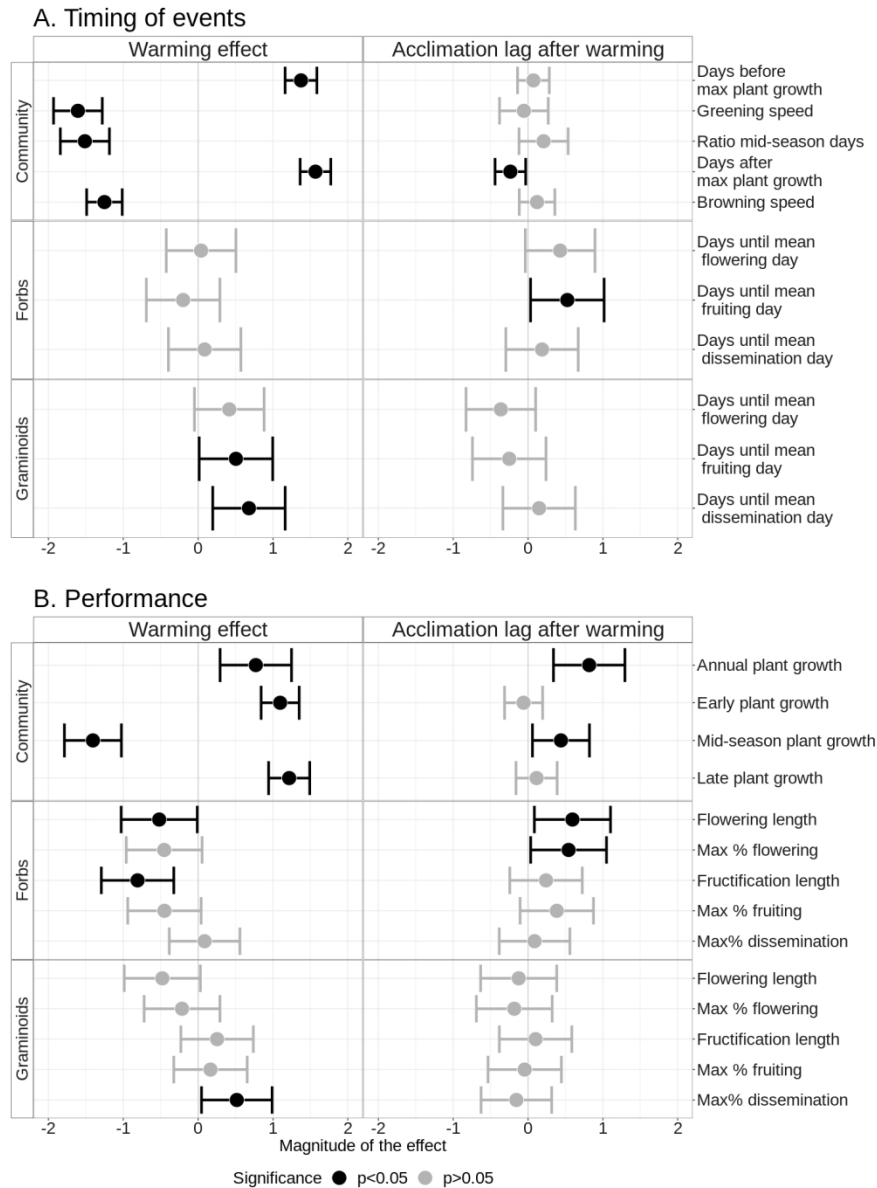


Fig. 3: Standardized effect sizes as the magnitude of warming effect and acclimation lag after warming at each focal organism level (community-level, species-level forbs and graminoids) for (A) timing of events and (B) performance related phenological indicators. Significant results are shown in black. Error bars represent 95% confidence intervals. Warming effect: AlpineWarmed-AlpineControl. Acclimation lag after warming: SubalpineControl-AlpineWarmed. For time-related indicators, positive warming effects indicate delayed phenology.

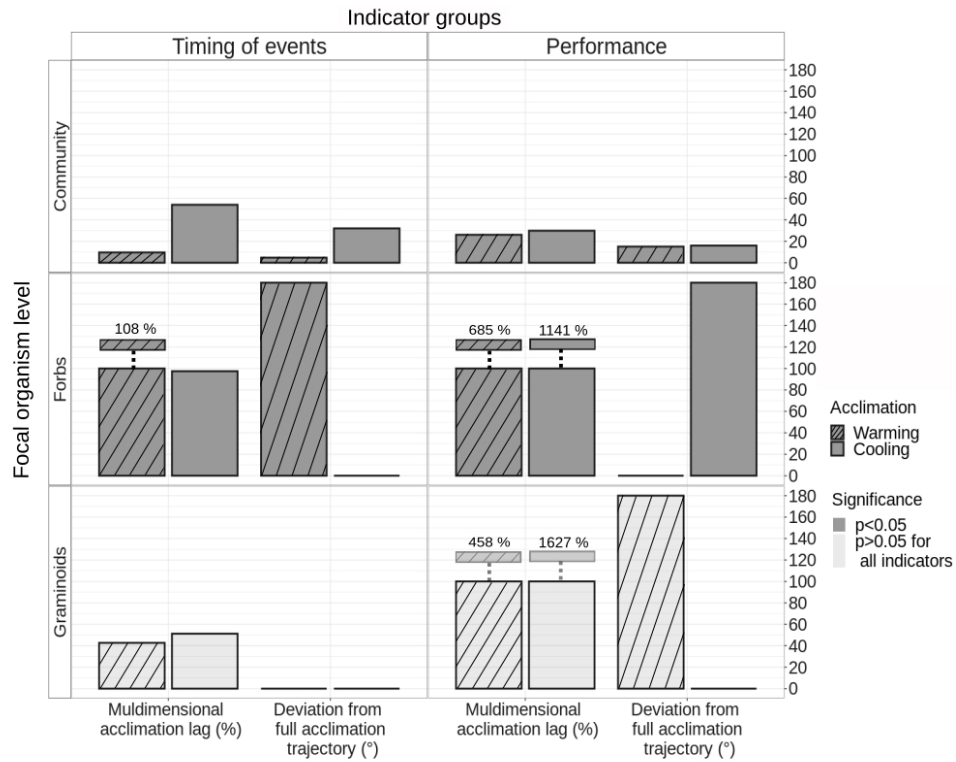


Fig. 4: Multidimensional acclimation lag and the deviation from full acclimation trajectory for both indicator groups (timing of events and performance) and all organism levels (community-level, species-level forbs and graminoids). Acclimation for warming and for cooling are shown in stripes and solid bars, respectively. When all the indicators fully acclimate, they are shown in light grey (insignificant acclimation lag in the contrast analysis, see Figure 2).

Table S1: Soil temperature, growing season (GS) lengths, start and end dates of alpine and subalpine sites

Year	Site	Soil temperature (°C)	Soil temperature (°C)	GS length	Season start	Season end
		annual	july			
2017	alpine	3.74	12.35	152	2017-06-02	2017-11-01
2017	subalpine	7.16	16.02	224	2017-04-15	2017-11-25
2018	alpine	4.42	13.85	152	2018-06-10	2018-11-09
2018	subalpine	7.34	16.66	200	2018-05-09	2018-11-25
2019	alpine	3.88	13.40	152	2019-06-10	2019-11-09
2019	subalpine	7.14	16.17	208	2019-04-15	2019-11-09

Table S2: Focal species' descriptive table

Species	Growth form	Origin	Flower onset	Observations (%) <10 individuals	Cover class	Ellenberg moisture indicator	Ellenberg moisture indicator variation	Ellenberg temperature indicator	Ellenberg temperature indicator variation
<i>Geum montanum</i> L.	forb	alpine	May	66.83	2	3.0	small variation (I)	1.5	small variation (I)
<i>Potentilla aurea</i> L.	forb	alpine	June	2.51	3	2.5	small variation (I)	1.5	large variation (II)
<i>Trifolium alpinum</i>	forb	alpine	June	1.13	4	2.5	small variation (I)	1.5	small variation (I)
<i>Poa alpina</i> L.	graminoid	alpine	June	2.13	2	3.5	large variation (II)	1.5	large variation (II)
<i>Carex sempervirens</i> Vill.	graminoid	both	June	1.32	4	2.0	small variation (I)	1.5	small variation (I)
<i>Festuca nigrescens</i> Lam.	graminoid	both	June	2.32	4	2.5	large variation (II)	2.5	large variation (II)
<i>Centaurea uniflora</i>	forb	subalpine	July	10.65	3	2.0	small variation (I)	2.0	small variation (I)
<i>Helianthemum nummularium</i> (L.) Miller	forb	subalpine	June_May	4.64	2	2.0	small variation (I)	1.5	small variation (I)
<i>Meum athamanticum</i> Jacq.	forb	subalpine	May	1.63	3	2.5	small variation (I)	2.5	small variation (I)
<i>Patzkea paniculata</i> (L.) G. H. Loos	graminoid	subalpine	June	7.02	4	2.0	small variation (I)	3.0	small variation (I)

***Flower onset** according to the local plant functional trait database *Androsace* (Thuiller et al., unpublished)

****Observations (%)**: Percentage of observations when only less than 10 individuals are recorded over the total number of observations along the whole growing season.

*****Cover class** according to Braun-Blanquet classes (2: 6-25%, 3: 26-50%, 4: 51-75% cover). Inventories were done at each site in 2016.

Thuiller *et al.* (unpublished) *Androsace* Plant Functional Traits Database, Laboratoire d'Ecologie Alpine, 38610 Gières, France
 Braun-Blanquet J., Roussine N. & Nègre R., (1952) Les groupements végétaux de la France méditerranéenne. Dir. Carte Group.
 Vég. Afr. Nord, CNRS, 292 p.

Table S3: Changes in annual air and soil temperature (°C) and in community-level phenological indicators (NDVI). Historical changes are between 1960-2016 for temperature and between 2000-2016 for phenological indicators. Experimental changes are between 2016 observed data and average of three-years experimental outputs. The last column shows how much change was already taken due to ongoing climate warming in comparison to the experimental warming. The sign difference indicates that the changes are in different directions.

Indicator	Historical change (HC)	Experimental change (EC)	HC relative to EC (%)
Annual air temperature	1.20000	NA	NA
Annual soil temperature	0.80000	3.20000	25.00
Growing Season Length	0.73383	48.61855	1.51
Annual plant growth	4.78956	17.90705	26.75
Early plant growth	4.35445	4.22724	103.01
Late plant growth	-1.14368	18.68990	-6.12
Mid-season plant growth	1.65843	-4.93400	-33.61
Greening speed	-0.00121	0.00056	-216.07
Browning speed	0.00098	-0.00218	-44.95
Greening days	7.30226	6.56413	111.24
Browning days	-6.94135	49.42147	-14.05
Mid-season ratio	-0.00087	-0.09379	0.93

*Daily mean air temperature data were extracted from SAFRAN–CROCUS–MEPRA meteorological model developed by Météo-France for the French Alps. NDVI data were extracted from MODIS remote sense time series data for historical changes. Changes were calculated from predicted values of a linear model between indicator values and years. Remote sense data were prepared and phenological indicators were calculated in the same way as it was elaborated on the main manuscript. Annual air temperature for EC is missing as the experimental measurements have gaps in the data to damaged probes on the field site.

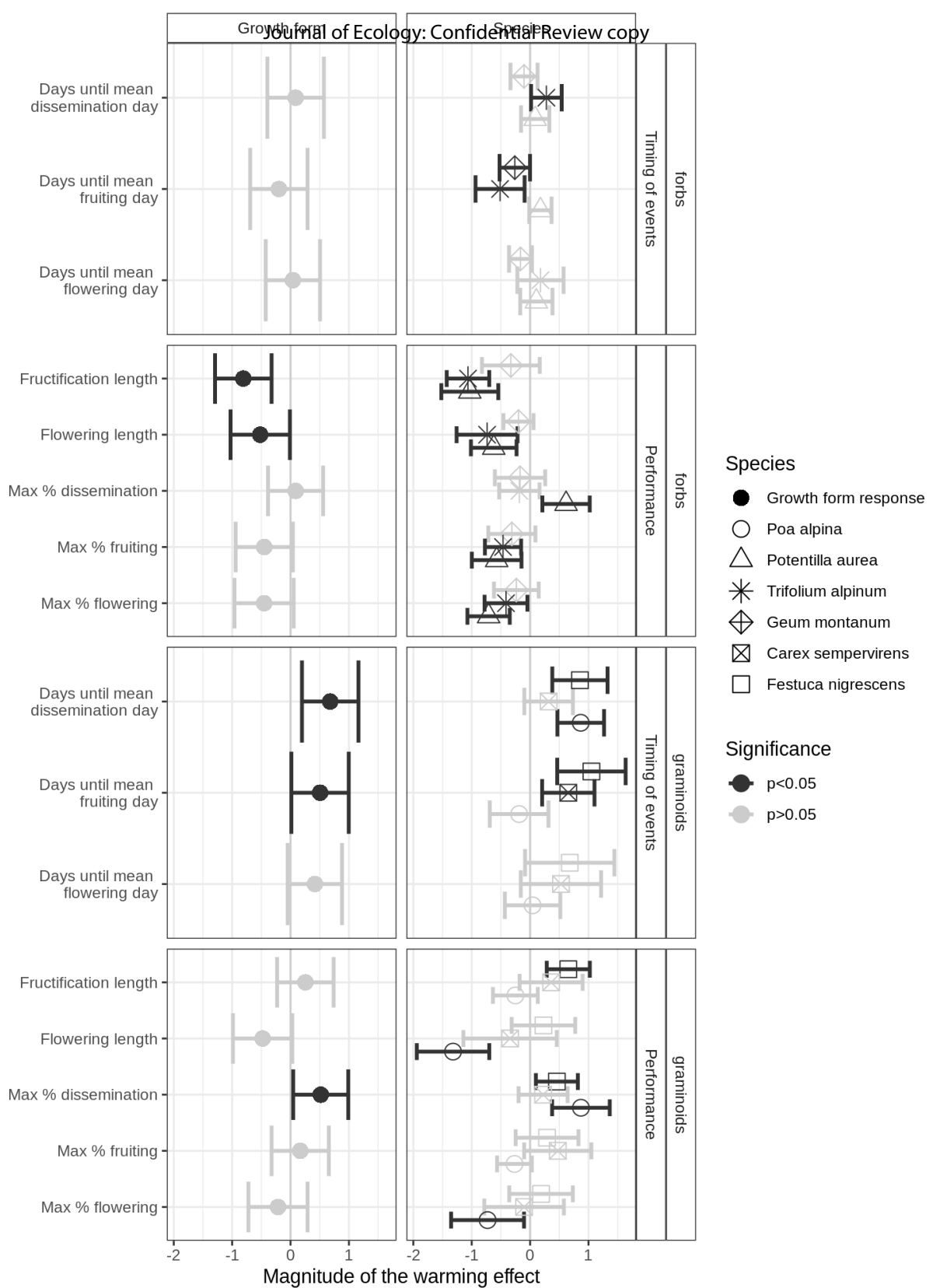


Figure S1: Standardized effect sizes as the magnitude of warming effect for timing and performance related indicators and for each growth form and each species. Significant results are shown in black. Error bars represent 95% confidence intervals. Warming effect: AlpineWarmed-AlpineControl.

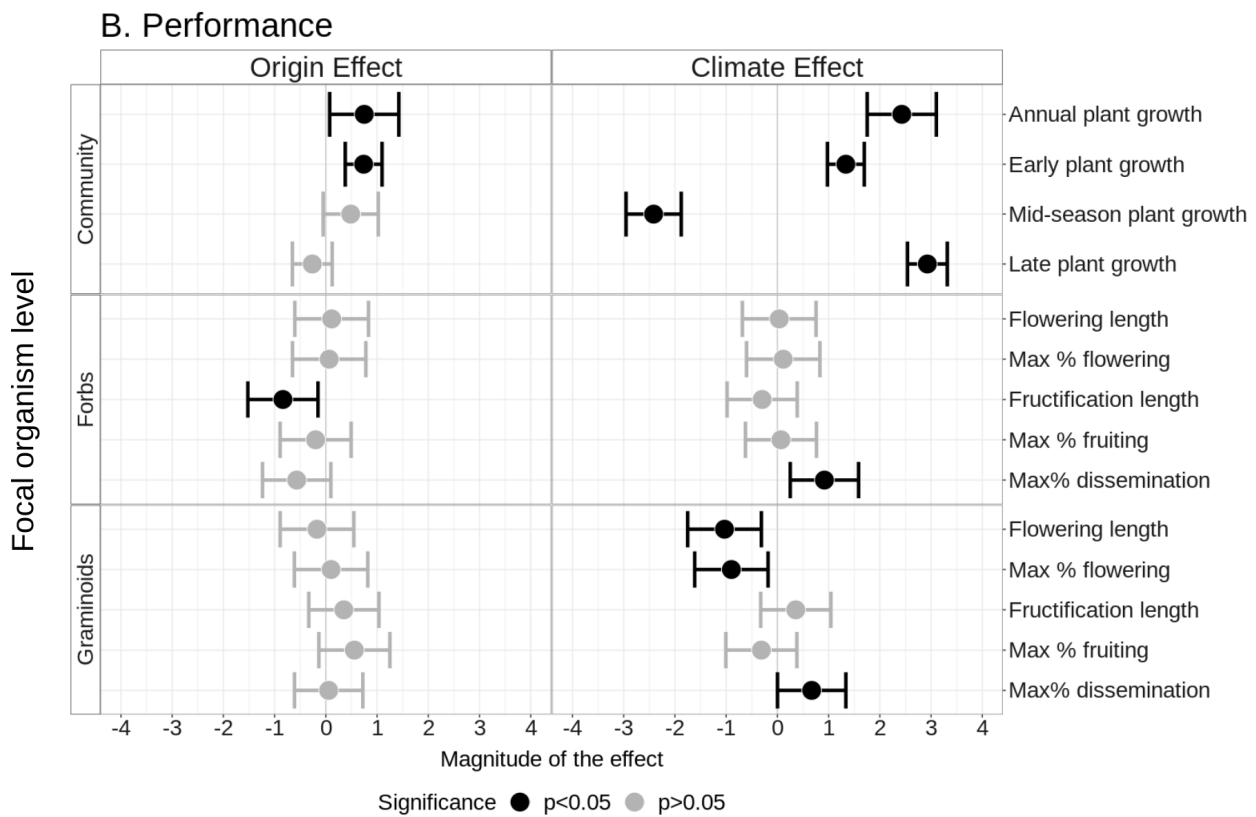
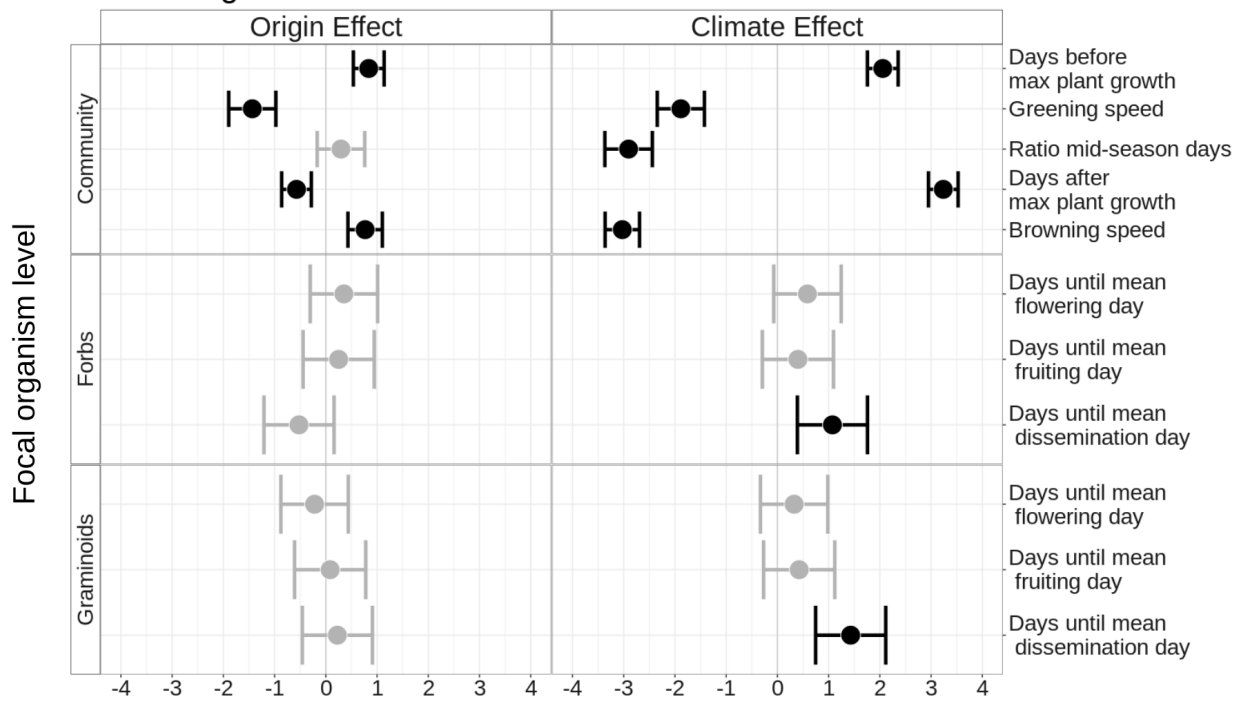
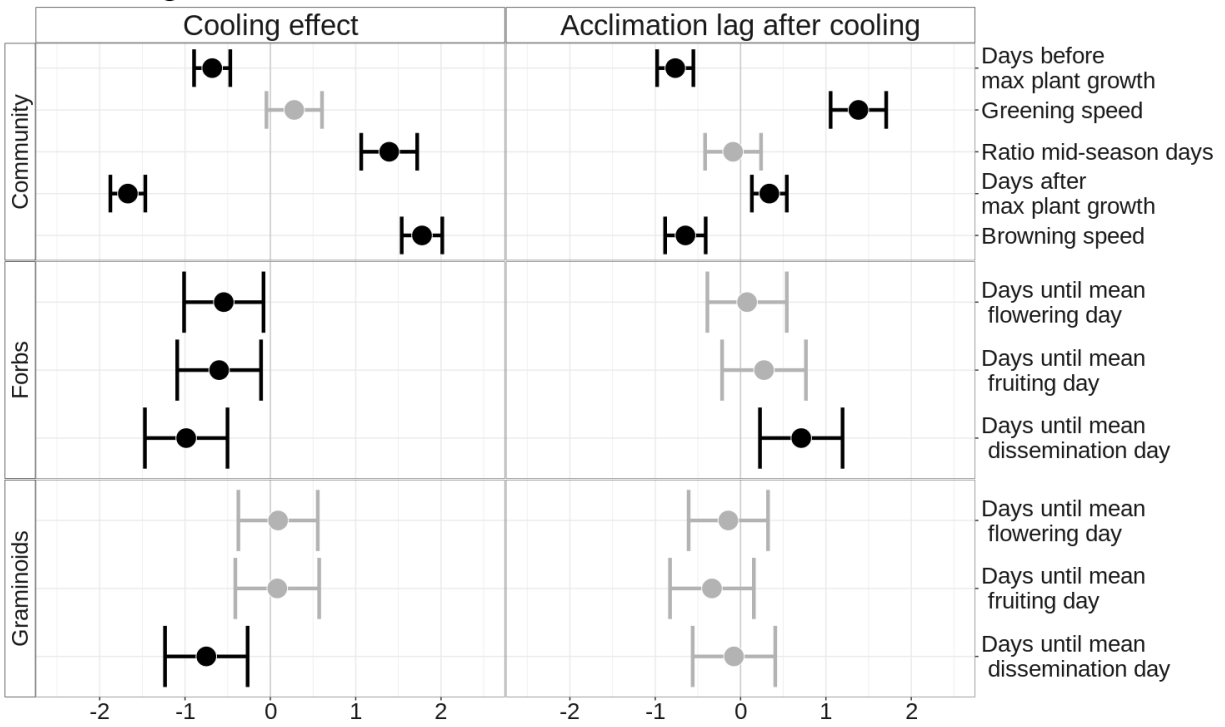


Figure S2: Standardized effect sizes as the magnitude of origin and climate effects at each focal organism level (community level, species level forbs and graminoids) for **(A)** timing of events and **(B)** performance related phenological indicators. Significant results are shown in black. Error bars represent 95% confidence intervals. Origin effect: Subalpine origin - Alpine origin; Climate effect: Subalpine site - Alpine site.



B. Performance

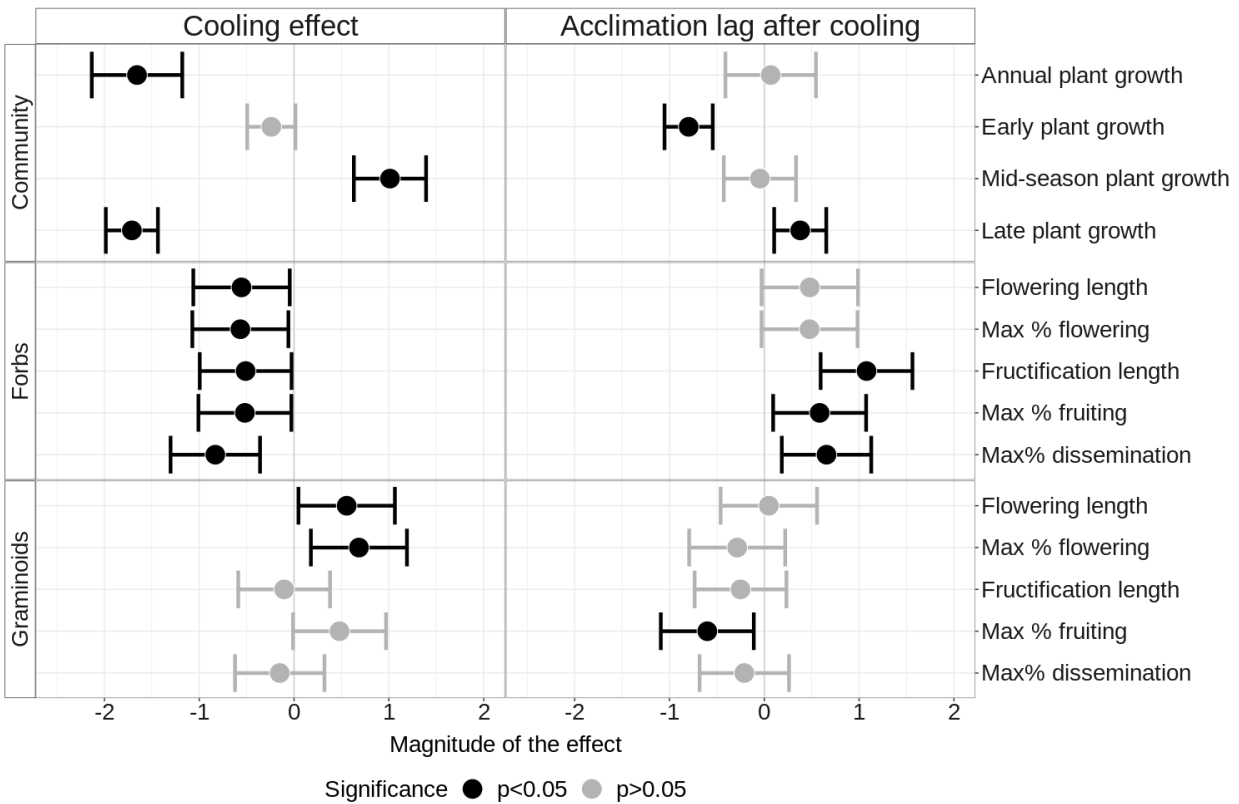
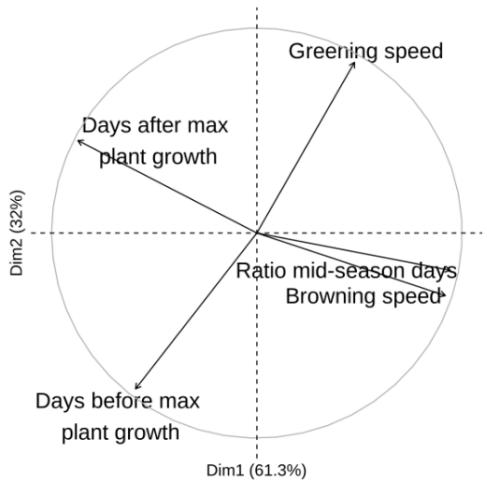
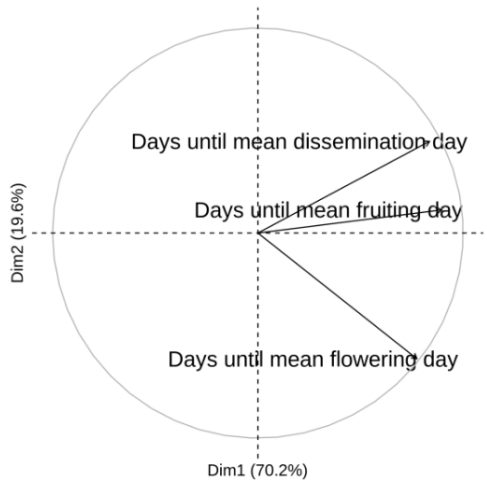


Figure S3: Standardized effect sizes as the magnitude of cooling effect and acclimation lag after cooling at each focal organism level (community level, species level forbs and graminoids) for **(A)** timing of events and **(B)** performance related phenological indicators. Significant results are shown in black. Error bars represent 95% confidence intervals. Warming effect: AlpineWarmed-AlpineControl. Acclimation lag after warming: SubalpineControl-AlpineWarmed.

A) Community



B) Forbs



C) Graminoids

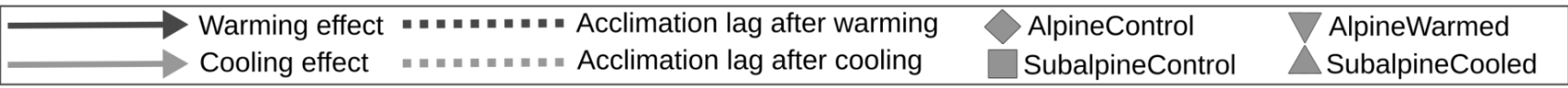
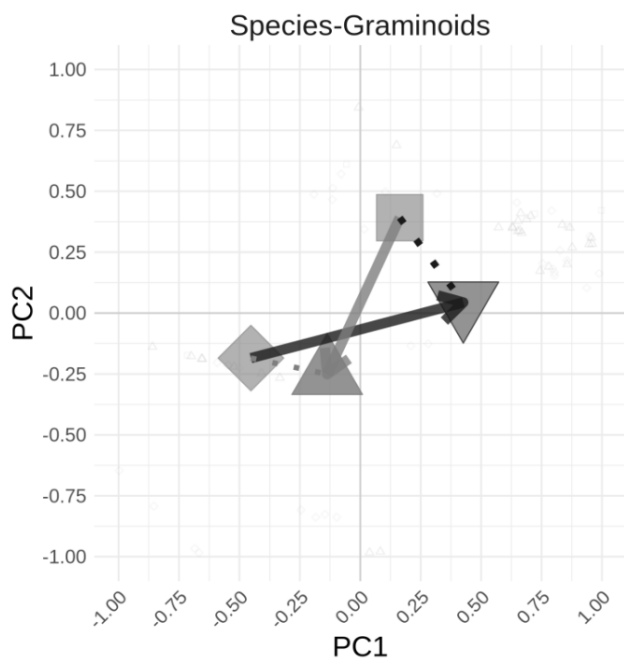
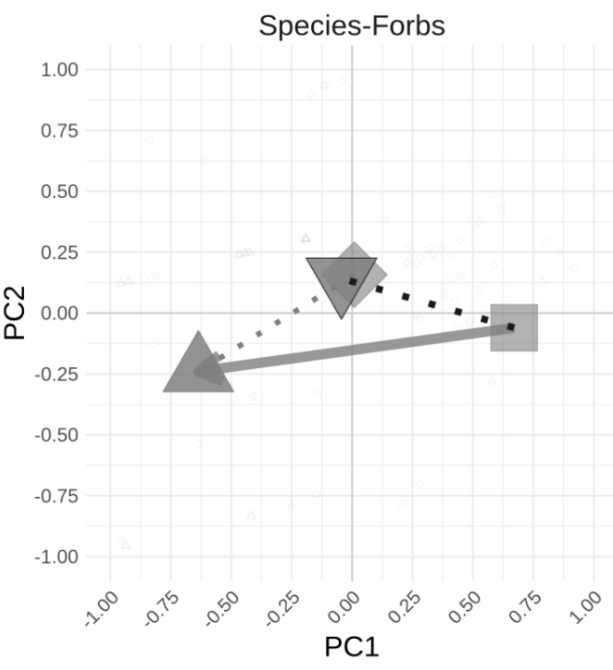
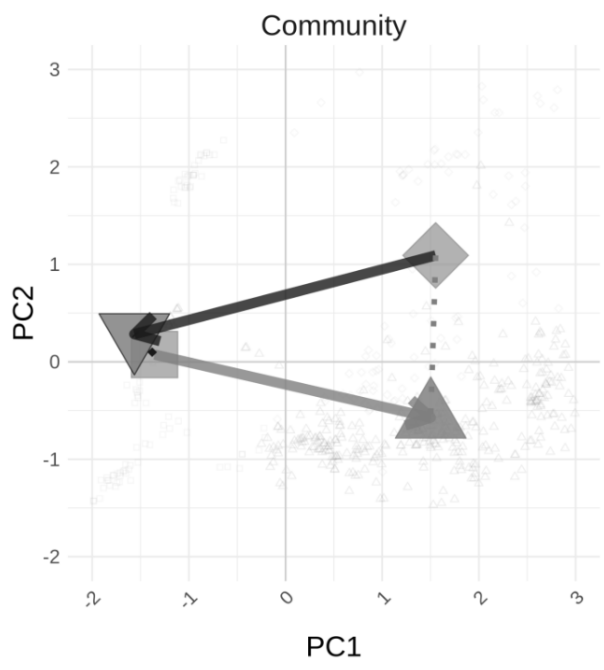
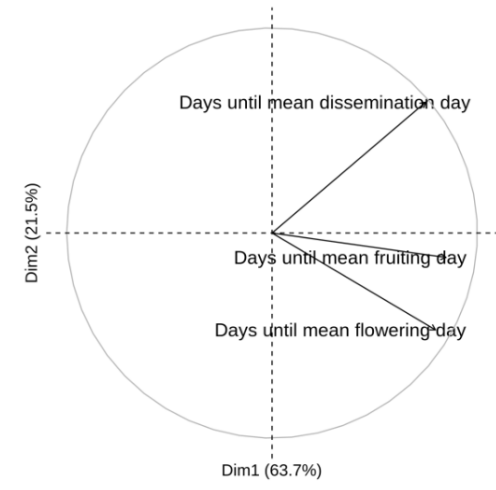
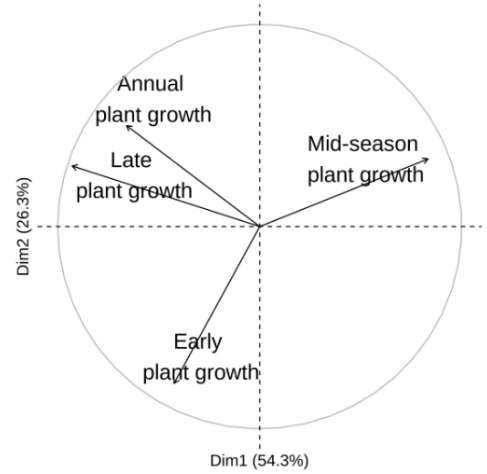
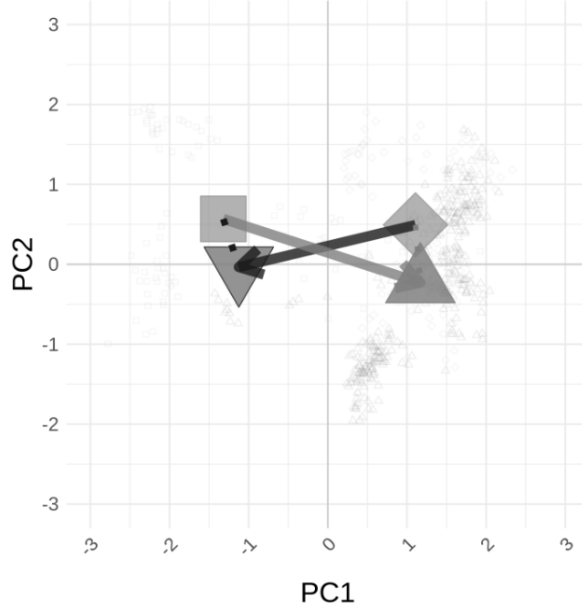


Figure S4: Differences in timing related phenological indicators (plotted in a two-dimensional PCA space) between two treatments and controls (AlpineWarmed, SubalpineCooled, AlpineControl and SubalpineControl) at the community (A) and the species level (forbs (B) and graminoids (C)). Straight arrows highlight warming (AlpineWarmed-AlpineControl) or cooling effect (SubalpineCooled-SubalpineControl) and dotted lines the acclimation lag after warming (SubalpineControl-AlpineWarmed) or cooling (AlpineControl-SubalpineCooled). Here, the responses over 3 years were shown (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed, triangle: SubalpineCooled). For further analyses, the first two PCs were selected from (A) and only the first PC from (B) and (C).

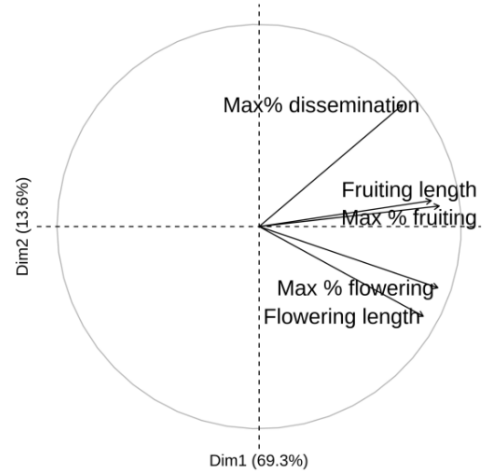
A) Community



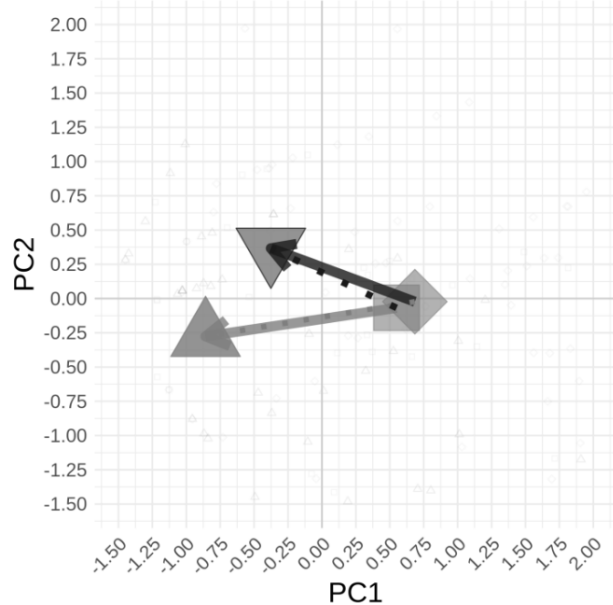
Community



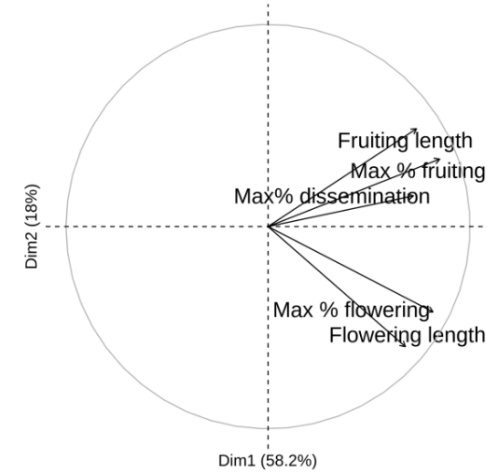
B) Forbs



Species-Forbs



C) Graminoids



Species-Graminoids

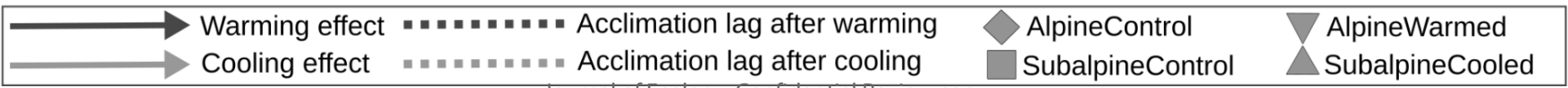
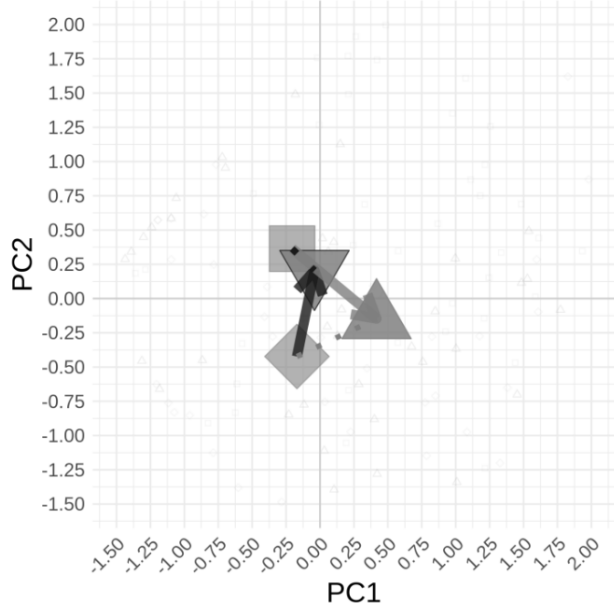
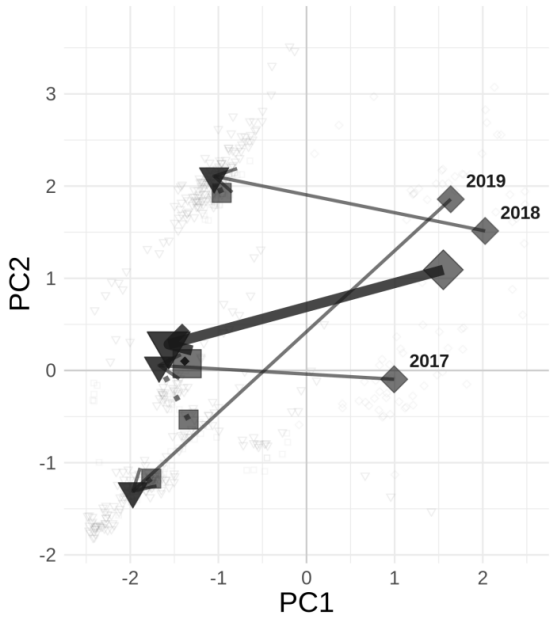
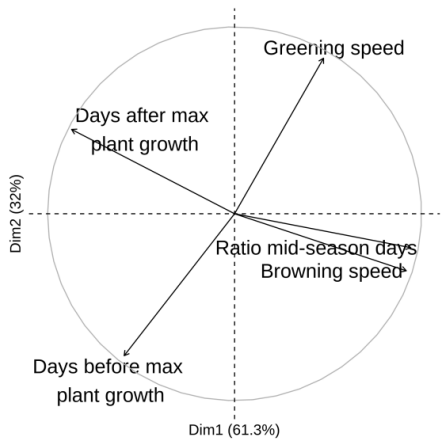
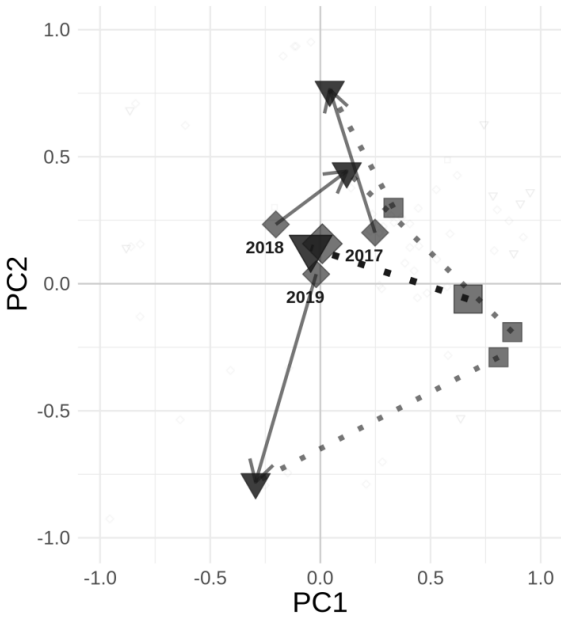
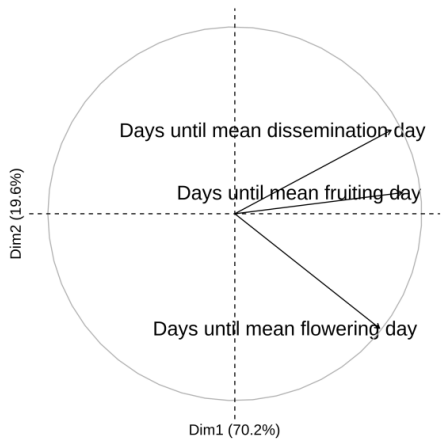


Figure S5: Differences in performance related phenological indicators (plotted in a two-dimensional PCA space) between two treatments and controls (AlpineWarmed, SubalpineCooled, AlpineControl and SubalpineControl) at the community (A) and the species level (forbs (B) and graminoids (C)). Straight arrows highlight warming (AlpineWarmed-AlpineControl) or cooling effect (SubalpineCooled-SubalpineControl) and dotted lines the acclimation lag after warming (SubalpineControl-AlpineWarmed) or cooling (AlpineControl-SubalpineCooled). Here, the responses over 3 years were shown (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed, triangle: SubalpineCooled). For further analyses, the first two PCs were selected from (A) and only the first PC from (B) and (C).

A) Community



B) Forbs



C) Graminoids

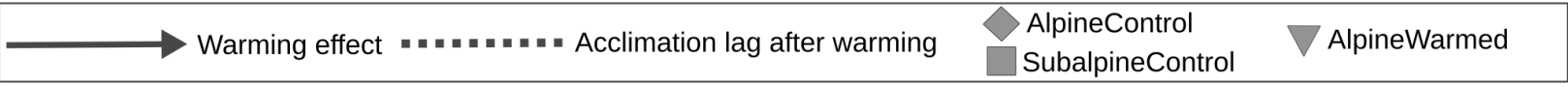
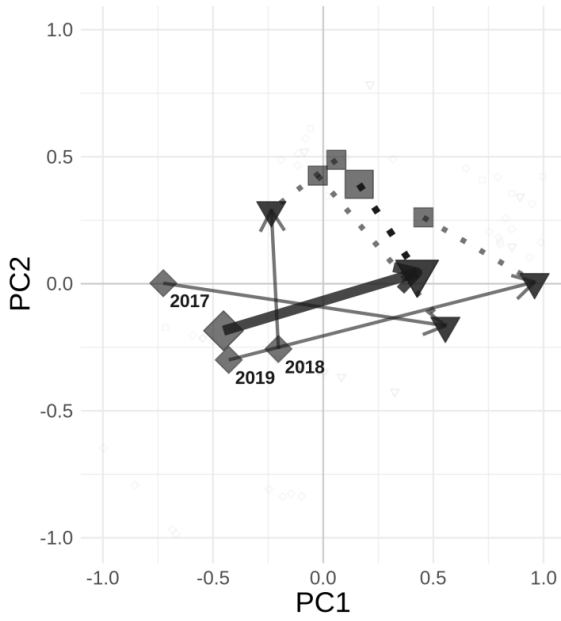
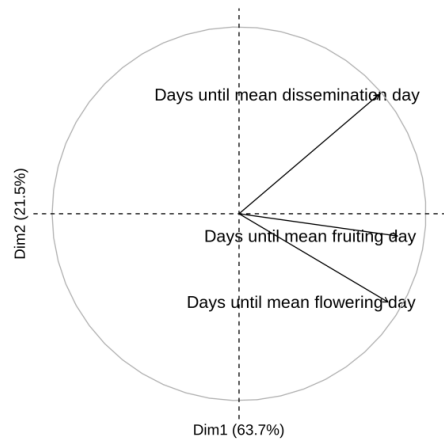
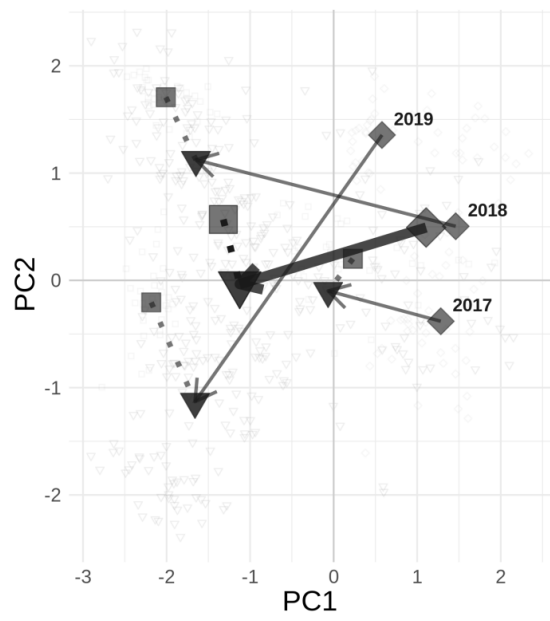
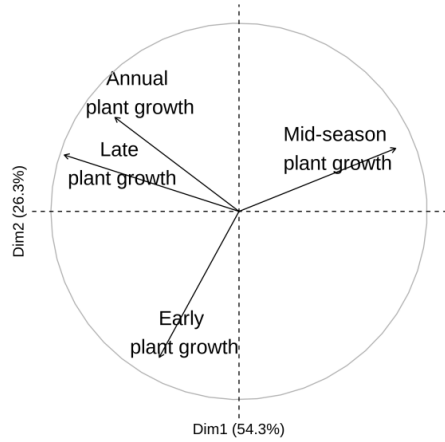
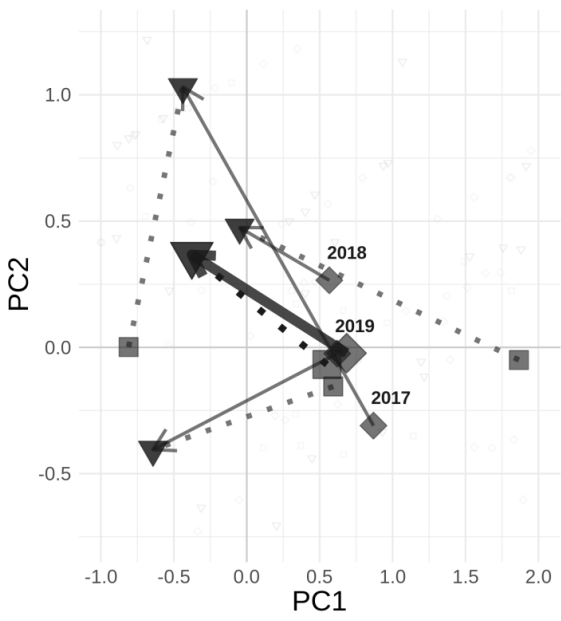
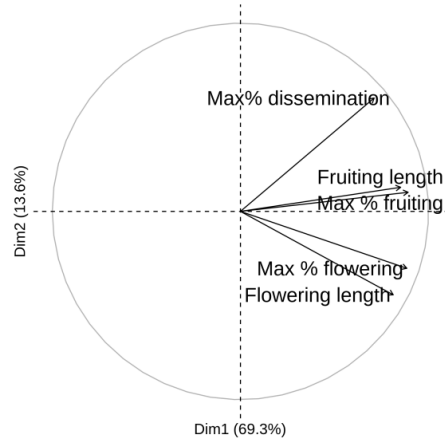


Figure S6: Differences in timing related phenological indicators (plotted in a two-dimensional PCA space) between the three treatments (AlpineWarmed, AlpineControl and SubalpineControl) at the community (A) and the species level (forbs (B) and graminoids (C)). Straight arrows highlight warming effect (AlpineWarmed-AlpineControl) and dotted lines the acclimation lag after warming (SubalpineControl-AlpineWarmed). Thicker lines indicate the overall response for three years. Thinner lines indicate annual response. (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed). For further analyses, the first two PCs were selected from (A) and only the first PC from (B) and (C).

A) Community



B) Forbs



C) Graminoids

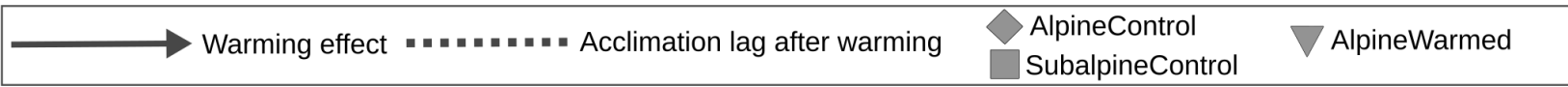
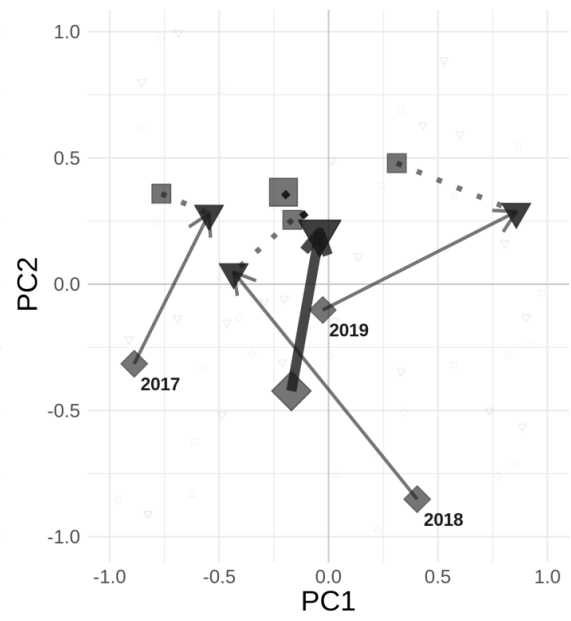
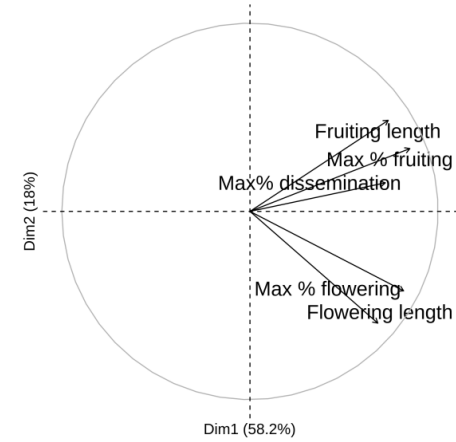


Figure S7: Differences in performance related phenological indicators (plotted in a two-dimensional PCA space) between the three treatments (AlpineWarmed, AlpineControl and SubalpineControl) at the community (A) and the species level (forbs (B) and graminoids (C)). Straight arrows highlight warming effect (AlpineWarmed-AlpineControl) and dotted lines the acclimation lag after warming (SubalpineControl-AlpineWarmed). Thicker lines indicate the overall response for three years. Thinner lines indicate annual response. (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed). For further analyses, the first two PCs were selected from (A) and only the first PC from (B) and (C).

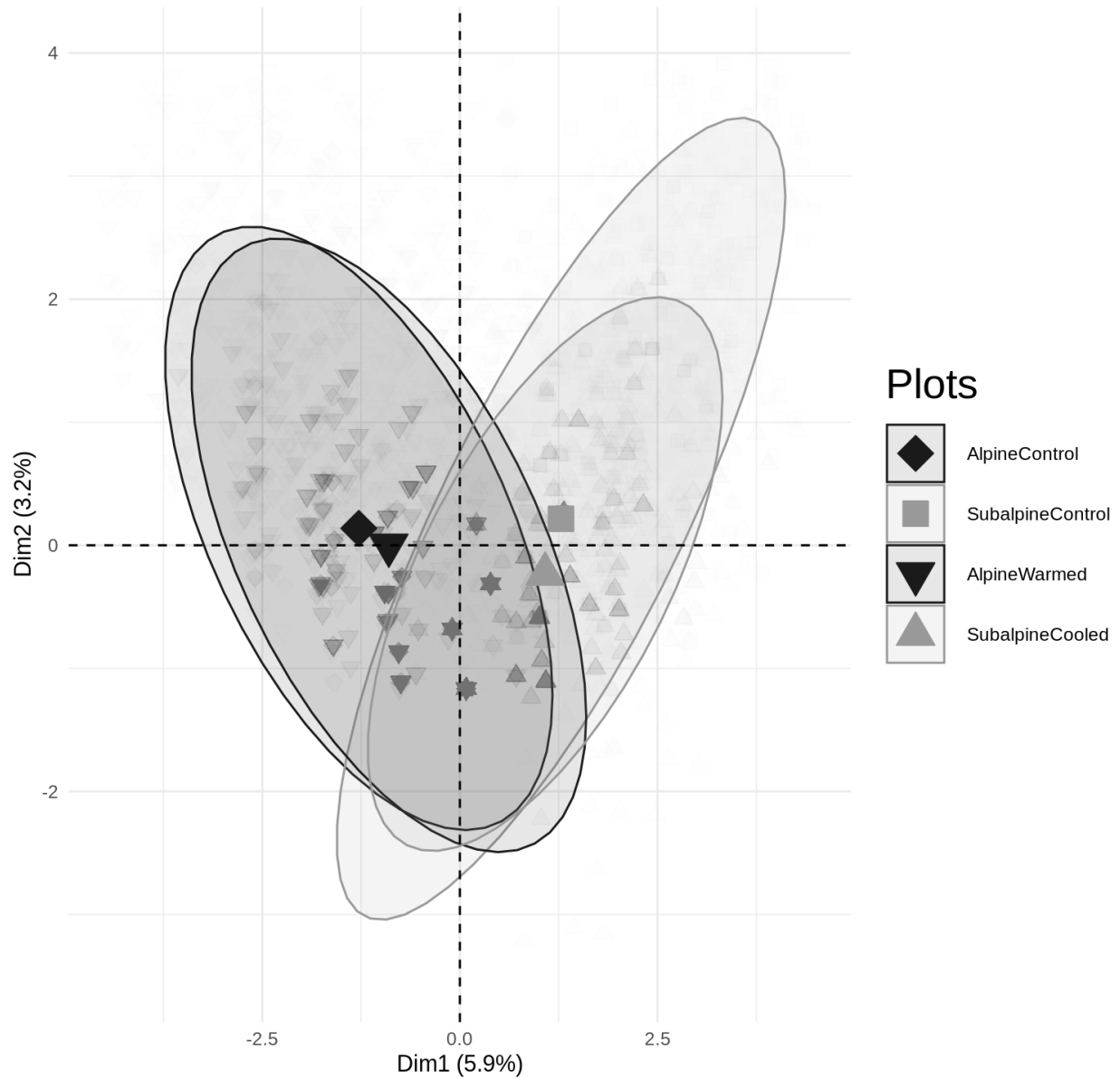


Figure S8: Principal component analysis (PCA) of community composition from abundance data collected in 2018 of dominant species in both alpine and subalpine sites. (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed, triangle: SubalpineCooled).

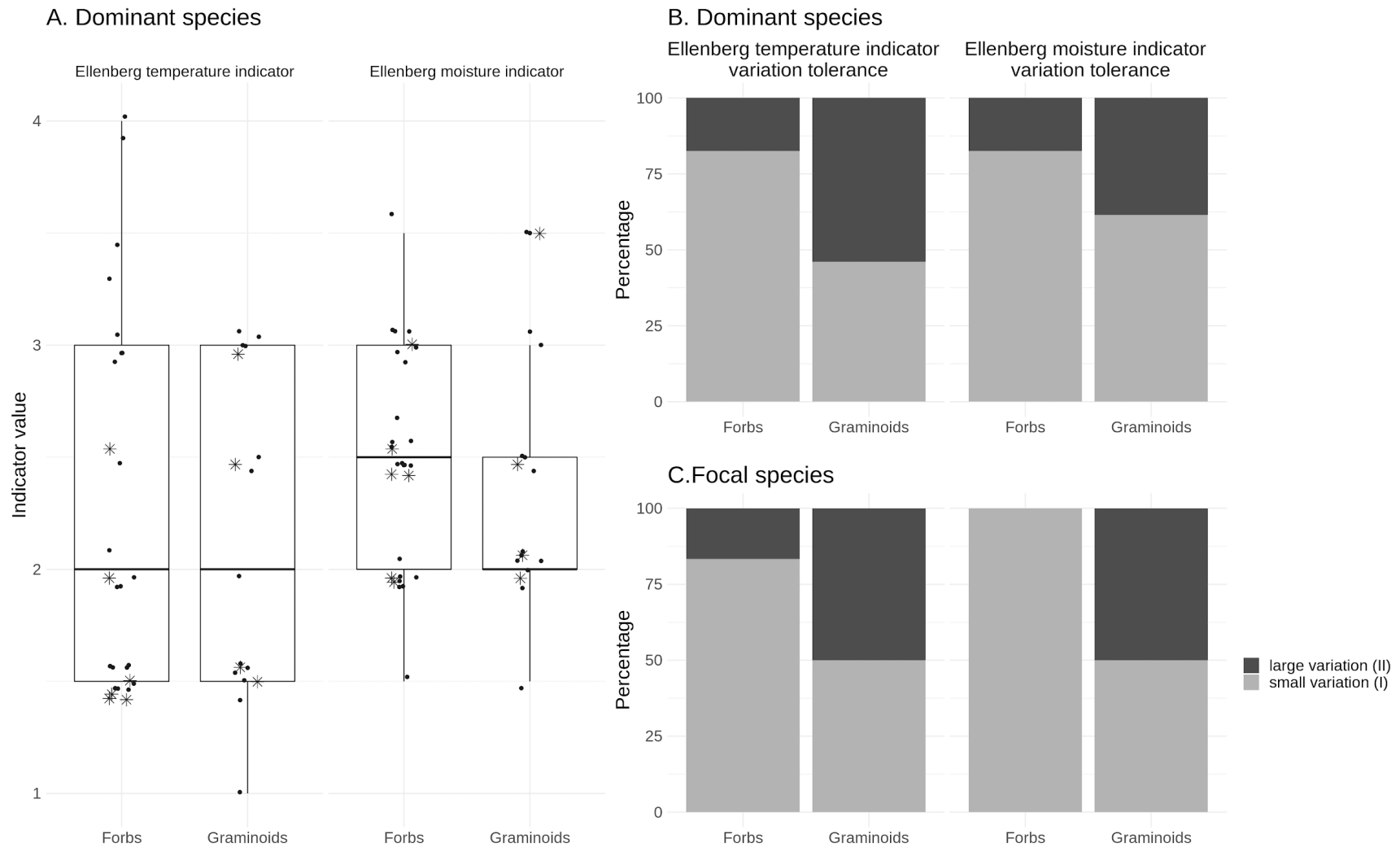


Figure S9: (A) Ellenberg temperature and moisture indicator values of dominant species in alpine and subalpine site. The values of the focal species are shown in star. Percentages of number of species that can tolerate small or large variation in their Ellenberg temperature and moisture indicator values (B) for dominant species in both sites and (C) for focal species in the study.

Appendix S10: Cascading acclimation lag: From phenological indicators to flower visiting insects

Grassland phenology can have strong impacts on pollination services. As we found that warmed alpine forbs' communities flowered less often, for shorter time periods and tendentially earlier than subalpine forbs' communities (Figure 2), we asked whether this had any cascading effect on flower visiting behavior of insects.

To answer this question we observed insects visiting flowers in the AlpineWarmed, AlpineControl and SubalpineControl plots between June and September in 2019. Observations were limited to conditions favourable for insect visits, i.e. between 10:00 and 13:00 and only if it was warm enough, not too cloudy (either $> 13^{\circ}\text{C}$ if less than half of the sky was covered with clouds or $> 15^{\circ}\text{C}$ otherwise) and not too windy (maximum 29.5 km/h). Each week (and twice at the peak of growing season) we spent 10 minutes at each of 8 randomly chosen replicates of each treatment to observe flower visits (summing up to a total of 1400 observation minutes). We counted all insects that visited a flower within a 1 m² focal area during this standardized time period. We only identified main insect groups following the guidelines of the public science UK PoMS, Pollinator Monitoring Scheme (<https://www.ceh.ac.uk/our-science/projects/pollinator-monitoring>) because the observations were done by non-expert interns.

Pollinator visits per minute were generally quite low (AlpineControl: 0.34, AlpineWarmed: 0.04, SubalpineControl:0.2, SubalpineCooled: 0.32). We found strong site-specific effects on pollinator communities, with more flies and small insects ($<3\text{mm}$) in AlpineControl plots and more *Coleoptera* and *Hymenoptera* species in SubalpineControl plots. Overall, AlpineControl plots tended to attract slightly more visits than SubalpineControl plots. Due to these site specific differences, we focus on acclimation lags comparing AlpineWarmed and SubalpineControl plots that are at the same site and thus available to the same pollinator community. Our main results show that the flowers in AlpineWarmed plots were visited by a significantly less diverse group of insects and also had a tendency to be overall less visited than the SubalpineControl plots (Figure S10).

As AlpineWarmed and Subalpine Control plots are at the same location (randomly placed at the site) and have been observed at the same moment, differences in flower visiting insects are clearly due to plot-level vegetation differences. We conclude that reduced flower numbers, shorter flowering periods and premature flowering are among the main drivers of impaired flower visiting of insects creating a cascading acclimation lag from plant phenology to insect pollination.

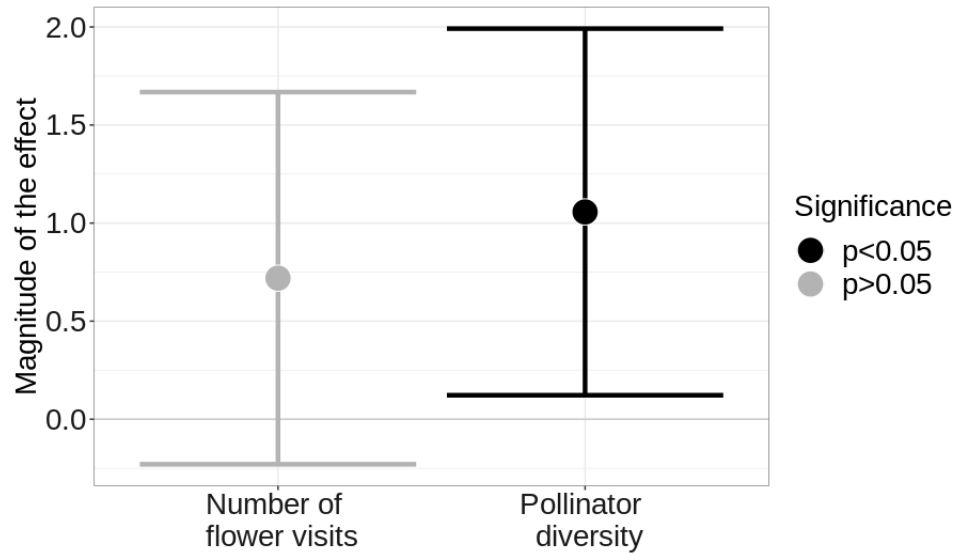


Figure S.10: Acclimation lags after warming (Standardized effect sizes of the difference between SubalpineControl and AlpineWarmed). Significant results are shown in black. Error bars represent 95% confidence intervals.

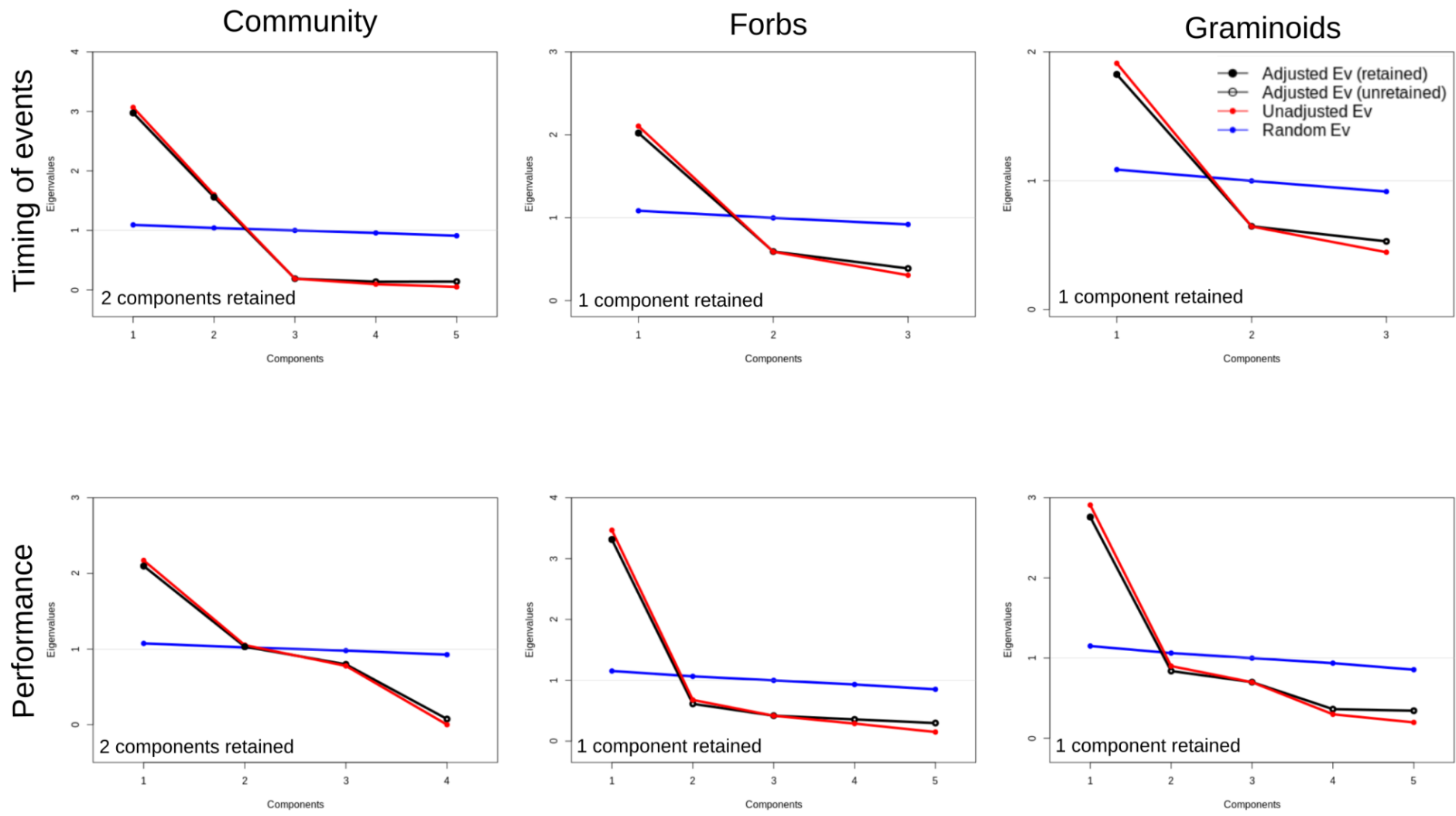


Figure S12: Results from Horn's parallel analysis to select the number of principal components from each PCA (Appendix Figure S4-7).

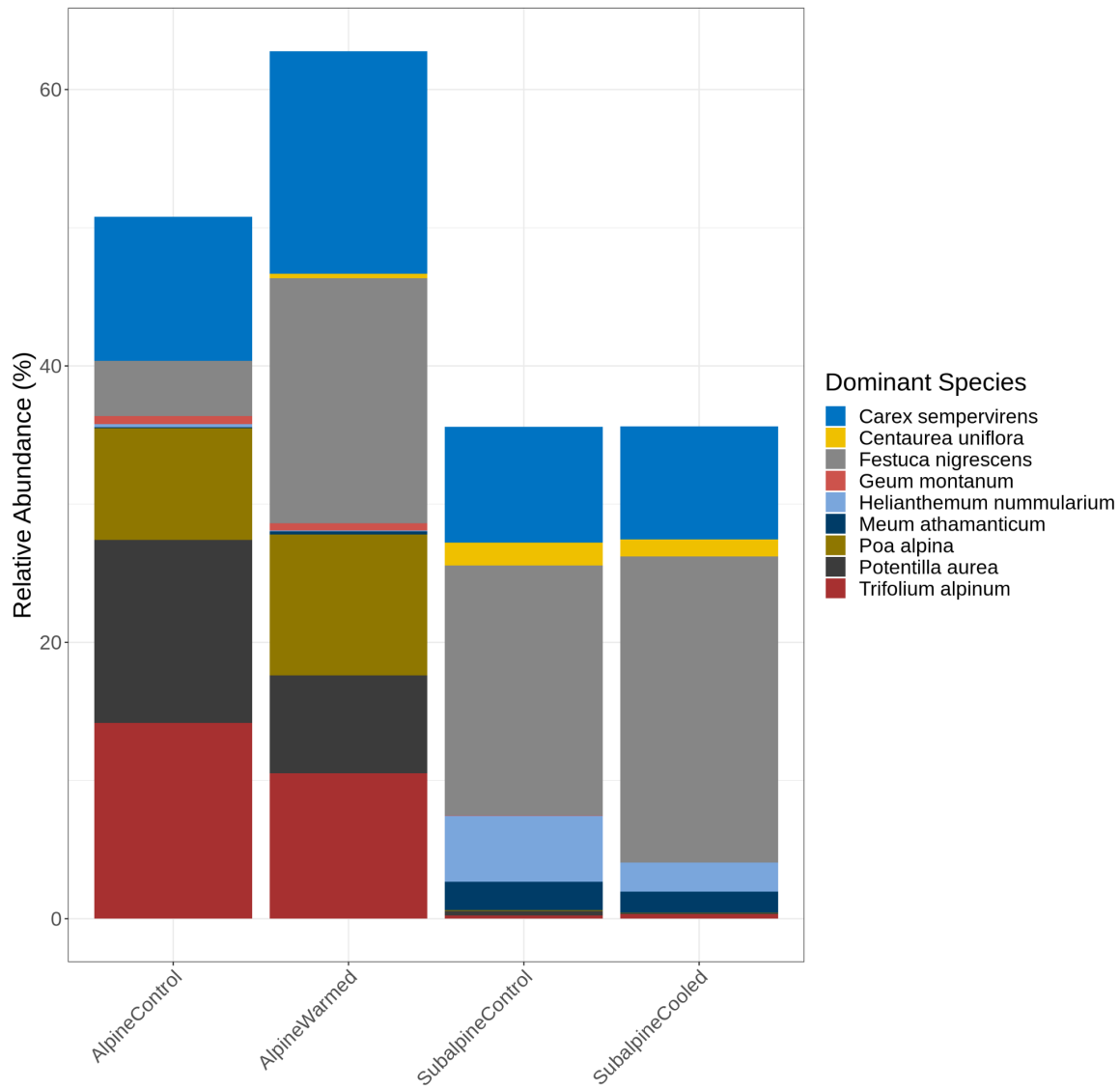


Figure S13: Relative abundances (%) of dominant species in the different experimental plots. These are calculated from a separate dataset of species abundances collected in 2018, i.e. two years after the transplantation.