

## RESEARCH ARTICLE

# Lags in phenological acclimation of mountain grasslands after recent warming

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## Abstract

1. In the current biodiversity crisis, one of the crucial questions is how quickly plant communities can acclimate to climate warming and longer growing seasons to buffer the impairment of community functioning. Answering this question is pivotal especially for mountain grasslands that experience harsh conditions but provide essential ecosystem services to people.
2. We conducted a reciprocal transplant experiment along an elevation gradient (1,920 m vs. 2,450 m) in the French Alps to test the ability of plant species and communities to acclimate to warming and cooling. For 3 years, we measured weekly the timing of phenological events (e.g. start of flowering or greening) and the length of phenological stages linked to demographic performance (e.g. lengths of flowering or greening periods).
3. We found that warming (and cooling) changed the timing of phenological events strongly enough to result in complete acclimation for graminoids, for communities in early and mid-season, but not at all for forbs. For example, warming resulted in later greening of communities and delayed all phenophases of graminoids. Lengths of phenological stages did not respond strongly enough to climate change to acclimate completely, except for graminoids. For example, warming led to an acclimation lag in the community's yearly productivity and had a strong negative impact on flowering of forbs. Overall, when there was an acclimation failure, responses to cooling were mostly symmetric and confirmed slow acclimation in mountain grasslands.
4. *Synthesis.* Our study highlights that phenological plasticity cannot prevent disruption of community functioning under climate warming in the short term. The failures to acclimate after 3 years of warming signals that species and communities underperform and are probably at high risk of being replaced by locally better-adapted plants.

## KEYWORDS

climate change, global change ecology, mountain grasslands, NDVI, phenology, reciprocal transplant, transient dynamics, warming experiment

## 1 | INTRODUCTION

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

Among plastic responses to warming, plant phenology is one of the first to be triggered (Bellard et al., 2012; Parmesan & Hanley, 2015; Shen et al., 2015). Phenology refers to the timing and duration of events in species' plant growth and reproduction over the year including budburst, flowering, seed production and browning. Phenology strongly affects demographic performance, community assembly and functions (Ackerly et al., 2000; Richardson et al., 2013). As climate warming does not only result in higher mean temperatures but also in changed snow cover regimes and earlier starts and longer durations of growing seasons, it will affect different aspects of plant phenology in different periods of the season. In the short term, phenology can allow acclimation of plant communities, particularly for their main functions such as productivity (Carlson et al., 2017; Piao et al., 2019). However, many questions on the transient responses of mountain plant phenology to warming remain open: Do early- or late-season phenological stages acclimate the fastest? How much time is required to close acclimation lags? Are species plastic in their responses or does acclimation require a restructuring of community composition? It will depend on the answers to these questions which species and ecosystem functions can prevail under climate warming. Therefore, we need to effectively measure phenological responses to realistic warming scenarios and use informative phenological indicators and ways to characterize acclimation lags.

Plant phenology and its response to warming climate is a globally long-studied phenomenon with different experimental methods and at different organism levels (Piao et al., 2019; Winkler et al., 2019; Wolkovich et al., 2012). For mountain grasslands, experimental warming showed an advancement in greening, flowering and fruiting but a delayed browning at community level (Meng et al., 2019). However, even so community-level phenological

responses often resemble species-specific responses to warming (Diez et al., 2012), species with different characteristics still show idiosyncratic responses (Arft et al., 1999; Dunne et al., 2003; Li et al., 2016; Smith et al., 2012; Wang, Meng, et al., 2014). Yet, it has been suggested that responses can potentially be generalized at the growth-form level (Arft et al., 1999; Dunne et al., 2003; Oberbauer et al., 2013). For example, graminoids and forbs are likely to give different responses as they differ in functional and reproductive strategies (Reich et al., 2003; Shen et al., 2015; Siebenkäs et al., 2015).

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

For time-related indicators, warming generally leads to an earlier and quicker onset of phenophases in early-season while late-season responses are much more variable (Parmesan & Hanley, 2015). We are not aware of acclimation lag studies but expect faster acclimation to warming in the early season as it has been shown that plants are plastic in adjusting the leaf out to changes in snow cover dynamics (Choler, 2015; Körner, 1999). In contrast, high mountain grassland plants are adapted to short growing seasons and we expect that adjusting to longer season lengths may be more difficult than to start the season earlier. For performance-related indicators, warming leads to more plant growth but also more idiosyncratic species-specific responses, for example, to either decreases or increases in reproductive performance (Aldridge et al., 2011; Carlson et al., 2017; Li et al., 2016; Liu et al., 2012). Additionally, while climate warming might generally improve conditions for plant growth, it is often associated with lower snow cover protection and more frequent exposure to freezing events due to early snowmelt which may limit some species (Choler, 2015). In contrast to time-related indicators, we expect performance-related indicators to be more limited by physiological constraints, to be less plastic and thus, be much slower in adjusting (Baptist et al., 2010).

Hitherto, warming studies have mainly focussed on a single type of indicator (Aldridge et al., 2011; Li et al., 2016; Meng et al., 2019; Wang, Meng, et al., 2014; Wang, Ottlé, et al., 2014) (but see counter examples: Wang et al., 2020; Wang, Wang, et al., 2014) and quantified phenological changes as a response to warming (i.e. the warming effect; Piao et al., 2019; Shen et al., 2015; Wolkovich et al., 2012) but rarely measured acclimation lags (Ryo et al., 2019). Measuring

**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)

			Level	
Indicators			Community-level	Species-level
Phenology	Time related	Days after maximum plant growth	g	
		Days before maximum 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

acclimation lags is a challenge as it requires to identify the adjusted community state after complete acclimation (Visser & Both, 2005).

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

To measure acclimation lags we assume that plants in control plots are in equilibrium with climatic conditions. To justify this assumption despite ongoing climate change, we argue that (a) the historical climate warming is a slow- and long-term phenomenon compared to the experimental manipulation and thus negligible in comparison (Table S3), and (b) the ongoing climate change has not induced yet a trend of longer growing seasons even though this is an expected phenomenon (Jacob et al., 2014; Wang et al., 2021). Moreover,

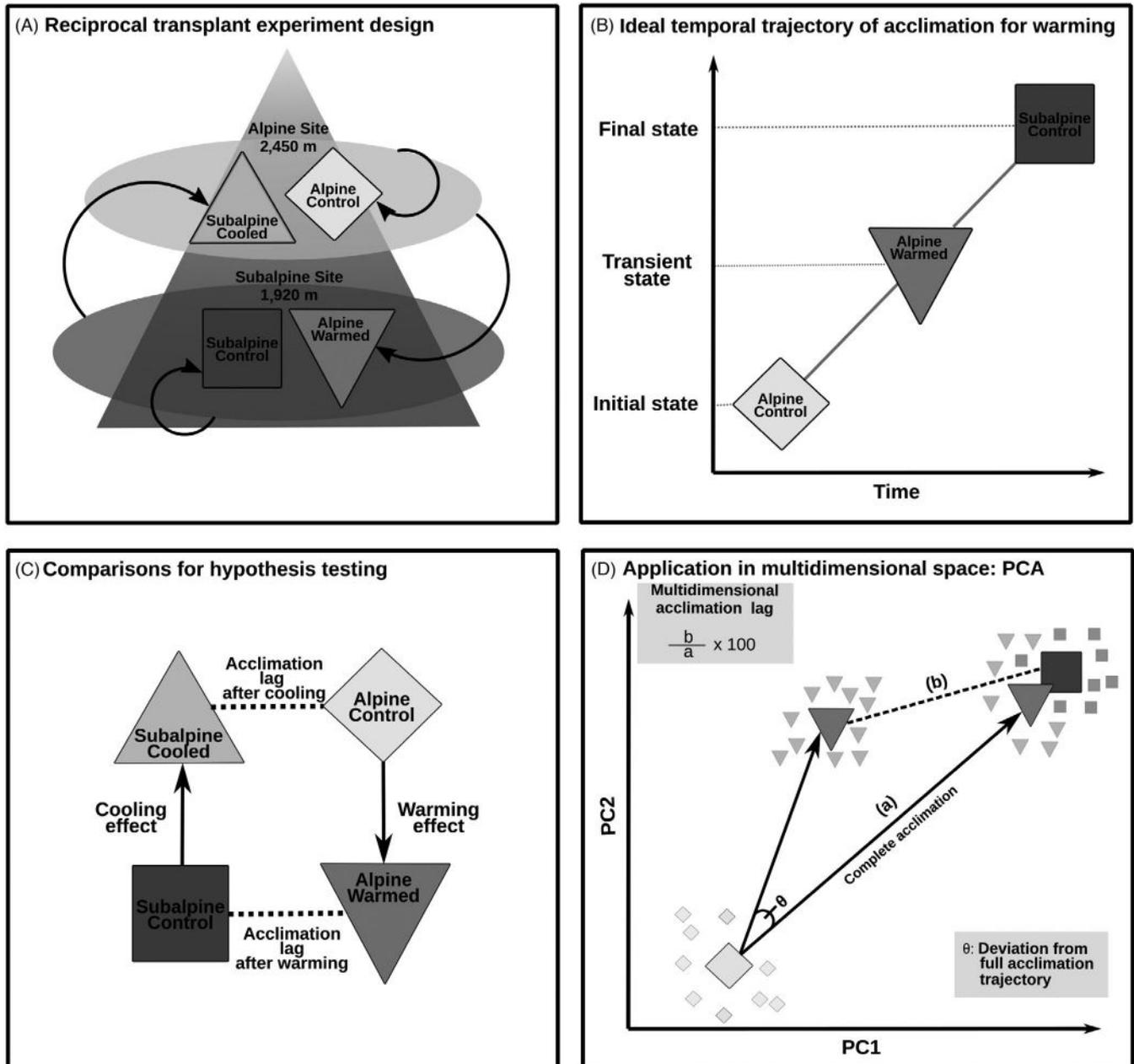
results would only be more extreme if we had transplanted communities from long-term climate equilibrium. Acclimation lags can then be measured by comparing where the state of AlpineWarmed plots (or SubalpineCooled plots) is relative to the shortest trajectory of acclimation which we define here as the shortest distance between states of AlpineControl and SubalpineControl plots (Figure 1B,D). We suggest two measurements (Figure 1D): Acclimation lags can be big either because little acclimation has been achieved yet and the still to cover distance is much larger than the distance already covered (deficient acclimation) and/or because transient adjustments deviate in direction from the shortest trajectory to complete acclimation (deviating acclimation). Theoretically, we expect that in the very long-term lags will close and compared plots will be indistinguishable.

Combining a species to community scale approach, a multi index approach for phenology and our conceptual framework, we asked whether: (a) mountain grassland phenology completely acclimated in timing and performance over 3 years of warming; (b) the lag in acclimation was due to deficient and/or divergent warming effects and (c) the transient responses to warming and cooling were symmetric.

## 2 | MATERIALS AND METHODS

### 2.1 | Experimental design

The experiment was implemented close to the Col du Lautaret (45°02'04"N 06°24'18"E) in the French Alps in September



**FIGURE 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

2016 (Figure 1A). The transplantation sites are the subalpine site 'Lautaret' (45°04'00"N 06°41'90"E) at 1,920 m altitude and the alpine site 'Galibier' (45°05'44"N 06°40'06"E) at 2,450 m altitude. Sites are close to each other (~2 km airline distance), have a similar orientation (south-east at alpine and south-south-west at subalpine site), bedrock (base-riched flysch) and soil (dystric cambisols). During the observation period (autumn

2016–autumn 2019), average annual soil temperature at the subalpine site was 3.2°C warmer than at the alpine site (and days with similar temperatures at the two sites were very rare), average July soil temperature was 3.1°C warmer and snow-free season was 58.7 days longer (Table S1; Figure 2A). At the subalpine site, plant communities were mainly dominated by the graminoids *Patzkea paniculata*, *Carex sempervirens* and *Festuca*

*nigrescens*, and the forbs *Centaurea uniflora*, *Helianthemum nummularium* and *Meum athamanticum* (Figure S13). At the alpine site, plant communities were mainly dominated by the graminoids *Carex sempervirens*, *Festuca nigrescens* and *Poa alpina*, and the forbs *Potentilla aurea*, *Trifolium alpinum* and *Geum montanum* (Figure S13). Overall, the dominant graminoid species in AlpineControl and SubalpineControl plots makeup to 22.5% and 26.5% of relative abundance respectively. All plant communities were dominated by perennial species.

In 2016, to simulate the effect of warming on alpine grasslands, we transplanted 10 replicates 4 m<sup>2</sup> blocks of vegetation with at least 20 cm of their intact below-ground parts and the surrounding soils from the alpine to the subalpine site (AlpineWarmed plots in the following). For transport, each block was cut in 4 × 1 m<sup>2</sup> sub-blocks that were re-assembled in their original composition when re-planted. To simulate the effect of cooling on subalpine communities, 10 intact 4 m<sup>2</sup> blocks of vegetation and soils were transplanted from the subalpine to the alpine site (SubalpineCooled plots). To control for the transplantation stress, we also horizontally transplanted 10 intact 1 m<sup>2</sup> blocks at both the subalpine and the alpine sites (SubalpineControl plots and AlpineControl plots respectively). Around the turfs we placed water permeable root barriers to avoid root ingrowth from the natural vegetation around the plots. At both sites, cattle and sheep were kept out by electric fences.

## 2.2 | Defining the growing season

We considered the start and end of phenological events always relative to the start of the growing season and the end of the growing season respectively (Table S1). This choice assures that (a) plots in different sites and years are comparable and (b) we compare the direct phenological response rather than the differences in calendar dates (Johansson et al., 2013). We defined the start (end) of the growing season as the first date when the normalized difference vegetation index (NDVI) based on Moderate Resolution Imaging Spectroradiometer (MODIS) remote-sensed data was above (below) 0.1 and the locally measured daily soil temperature was above (below) 1°C (Choler, 2015, 2018; Figure 2). For the remote-sensing data (RS-based NDVI), we downloaded the MOD09Q1 surface reflectance products corresponding to tile h18.v4 (40–50°N, 0–15.6°E) from the Land Processes Distributed Active Archive Center (LP DAAC). We used surface reflectance in the red and near-infrared to calculate the 250-m-resolution NDVI 8-day times series corresponding to the two sites. The RS-based NDVI time-series data were BISE (Best Index Slope Extraction) corrected, gap-filled with cubic spline interpolation and smoothed using the Savitzky–Golay filter (Choler, 2015). For the local soil temperature measurements, we equipped the two sites with standalone soil temperature data loggers (Hobo pendant UA; Onset Computer Corporation) buried at 5 cm below-ground. We smoothed daily soil temperature time series with cubic spline interpolation.

## 2.3 | On site measurements and phenological indicators

### 2.3.1 | Community-level

We tracked the phenology at community level using NDVI as a measurement of greening and a proxy for photosynthetic activity and plant growth (Myneni & Williams, 1994; Figure 2C). We measured NDVI in each treatment sub-block (10 × 4 × 1 m<sup>2</sup> sub-blocks for AlpineWarmed and for SubalpineCooled) and in each control block (10 × 1 m<sup>2</sup> blocks for AlpineControl and SubalpineControl) with three measurement repetitions once (twice at maximum growth) per week during the growing seasons of the years 2017, 2018 and 2019. We took the measurements with a Decagon ProCheck spectral reflectance sensor for NDVI with 630 nm (red) and 800 nm (near-infrared) spectral irradiance. The measurements were taken at clear sky from 9 a.m. to 4 p.m. during on the same day for both sites. We derived indicators from the NDVI curves over the growing season independently for each year, treatment sub-blocks, control blocks and replicates. We gap-filled the time series (i.e. the other days of the week) using cubic smoothing spline interpolation and smoothed using Savitzky–Golay filter (Choler, 2015).

Based on these time series, we calculated several indicators. These indicators were based on the definition of seasons within the whole growing season: (a) early season as the period starting from the onset of the growing season to the last day when the NDVI values were below the 90% of the maximum NDVI, (b) mid season as the period when the NDVI values stayed above 90% of the maximum NDVI and (c) late season as the period between the first day where NDVI values dropped below 90% of the maximum NDVI until the offset of the growing season. A threshold choice of 80% of maximum NDVI was also tested and it did not affect the results (unpublished). While the start and end of growing seasons were identified with MODIS remote-sensed data, we were able capture the unique phenological dynamics in plant growth of each plot repetition by (a) starting NDVI measurements right after the snow melt when the field site was accessible, (b) identifying the maximum NDVI based on field measurements for each plot.

We calculated time-related indicators as (Table 1): (a) the days from the start of the growing season until 90% of the maximum plant growth (greening days), (b) greening speed as the rate of increase in the NDVI values (i.e. from 0.1 of onset value to 90% of maximum NDVI value) during early season (Equation 2), (c) ratio of mid-season days to growing season days, (d) days after 90% of the maximum plant growth until the end of the growing season (browning days) and (e) browning speed as the rate of decrease in the NDVI values (from 90% of maximum NDVI value to 0.1 of offset value) during late season (Equation 1).

$$\text{Greening speed} = \left| \frac{0.9 \times \max \text{NDVI} - 0.1}{\text{Greening days}} \right|, \quad (1)$$

$$\text{Browning speed} = \left| \frac{0.1 - 0.9 \times \max \text{NDVI}}{\text{Browning days}} \right|. \quad (2)$$

We calculated performance-related indicators as proxies for biomass production and plant growth as the areas under NDVI curves for each season (Table 1): (a) early plant growth, (b) mid-season plant growth, (c) late plant growth and (d) annual (i.e. whole growing season) plant growth.

### 2.3.2 | Species-level

We tracked the phenology of focal dominant species (Table S2) in one sub-block of each treatment block ( $20 \times 1 \text{ m}^2$  sub-blocks in total) and in each control block ( $20 \times 1 \text{ m}^2$  blocks in total) every week during the growing seasons of 2017, 2018 and 2019. The selected dominant species for the blocks with subalpine origin (SubalpineControl and SubalpineCooled) were *Patzkea paniculata*, *Carex sempervirens*, *Festuca nigrescens*, *Centaurea uniflora*, *Helianthemum nummularium* and *Meum athamanticum*. The selected species for the blocks with alpine origin (AlpineWarmed and AlpineControl) were *Carex sempervirens*, *Festuca nigrescens*, *Poa alpina*, *Potentilla aurea*, *Trifolium alpinum* and *Geum montanum*. We focus here on the flowering, fruiting and dissemination phases as they reflect both early- and late-season plant growth and reproduction phenologies. For each treatment sub-block and control block and each species, we determined the phenophases of 10 randomly selected individuals (or the maximum number of individuals available when <10, see Table S2 for percentage of observations when <10 individuals were observed). During the peak of the growing season, we increased the frequency of NDVI and phenology measurements to two times a week.

To reduce observation bias, we determined the start of the phenophase for a species as the average of (a) the last date when no individuals of the given species in the given phenophase were observed and (b) the first date when the individuals of the given species in the given phenophase were observed (vice versa for the end of phenophase; Li et al., 2016). In case this averaging is not possible for the fact that the start or end of a phenophase were exactly the start or the end of the observation period on the field, the latter dates were taken.

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

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

## 2.4 | Statistical analyses

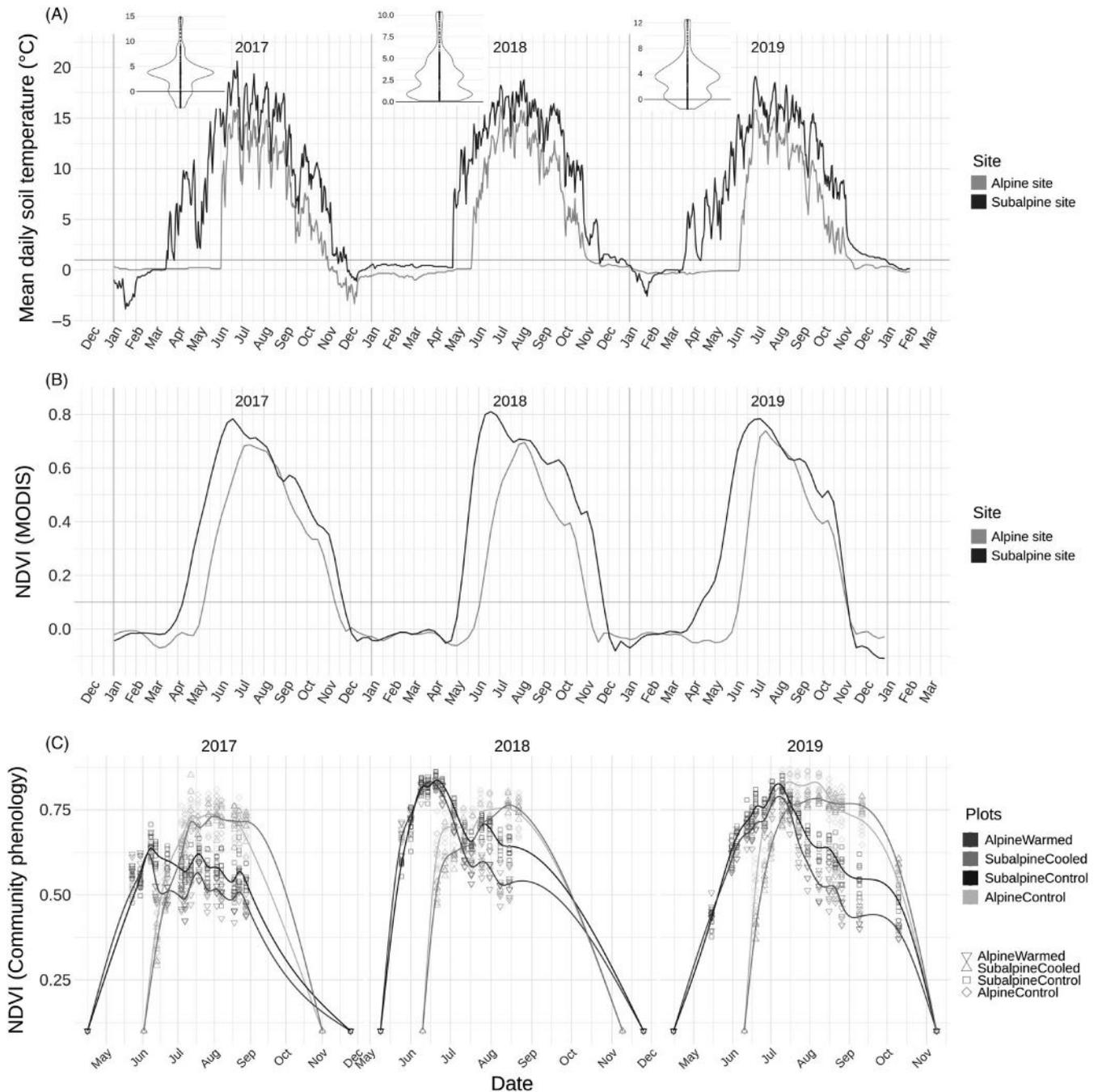
For our sets of phenological indicators (community- vs. species-level and time vs. performance related), we analysed four different treatment effects (Figure 1C): (a) a warming effect by comparing

AlpineWarmed to AlpineControl plots, (b) a cooling effect by comparing SubalpineCooled to SubalpineControl plots, (c) an acclimation lag after warming by comparing SubalpineControl to AlpineWarmed plots and (d) an acclimation lag after cooling by comparing AlpineControl to SubalpineCooled plots. We conducted all the statistical analyses on R (R Core Team, 2017).

First, we tested the different treatment effects for each phenology indicator independently using linear mixed effects models (NLME R package). At the community level, we took the median of the measurement repetitions to avoid including measurement errors due to the handheld NDVI sensor. We considered treatment (custom contrast setting of above-explained comparisons, Figure 1C) and year as fixed effects and subplot identity nested in plot identity as random effect. At the species level, we accounted for treatment, year and functional group (forbs or graminoids) as fixed effects and block and species identity as random effects. As we conducted multiple tests, we adjusted the *p*-values with multivariate *t*-distribution adjustment within the EMMEANS package in R (Lenth, 2016). Here, we discuss the common responses of forbs and graminoids, and report the species-specific responses in the Appendix (Figure S1).

Second, in order to summarize results for timing- versus performance-related phenological indicators, we performed six different principal component analyses (PCAs) for time-related versus performance-related indicators for communities, forbs and graminoids. We visualized the first two components of each PCA in the Appendix (Figures S4–S6). For further analyses we determined the number of significant principal components (PCs) with Horn's parallel analysis in the R package PARAN (Dinno, 2018; Franklin et al., 1995; Figure S12). As a result, we retained the first two PCs. For community-level PCAs two PCs were necessary to well capture the variation, and for species-level PCAs one PC was sufficient. Then calculated (a) the multidimensional acclimation lag (here 'multidimensional' refers to the multiple indicators and the one or two PC axes describing their variation) as the percentage of the remaining acclimation relative to the complete acclimation (Figure 1D), (b) the deviation from the shortest acclimation trajectory as the angle between the shortest acclimation trajectory and the warming effect (Figure 1D) with the shortest acclimation trajectory being the Euclidean distance between AlpineControl and SubalpineControl plots. In the case of two significant PCs (i.e. community level), we calculated the Euclidean distances with the *dist* function within the STATS package and the angles with the *Angle* function within the LEARNGEOM package in R (Briz-Redón & Serrano-Aroca, 2018). In the case of a single significant PC (i.e. species level), angles were set either to  $0^\circ$  (i.e. on the acclimation trajectory) or to  $180^\circ$  (opposite direction of the acclimation trajectory).

For interpretation, we speak of 'acclimation lag' or 'deficient warming effect' if we found a significant difference between SubalpineControl and AlpineWarmed or AlpineControl and SubalpineCooled and of 'complete acclimation' otherwise. We speak of a divergent warming or cooling effect if the observed trajectory deviates from the shortest trajectory of complete acclimation. Importantly, acclimation lags can be much higher than 100% when



**FIGURE 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 Section 2 for details)

the distance to the optimally adapted community is not narrowing down over time but is instead increasing during the transient dynamics. This can either happen when the adjustment response goes in the ‘wrong’ direction or when the adjustment response goes in the ‘right’ direction but then overshoots largely. We consider that the acclimation lags in warming and cooling are symmetrical when they have almost the same (i.e. maximum 10% difference) multidimensional acclimation lag.

### 3 | RESULTS

#### 3.1 | Was phenology completely acclimated after 3 years of warming?

In a first step, we summarized results for the six sets of indicators (Table 1, combinations of community, forbs, graminoids with time related and performance related) and depending on whether at least

one indicator per set showed a significant acclimation lag, we give further details in upcoming sections.

After 3 years of warming, the phenology of communities and focal species did not completely acclimate, with the exception of graminoids (Figure 3). For time-related indicators (Figure 3A), we observed complete acclimation to warming in most cases, especially during early-season and flowering. However, late-season phenology (i.e. days after maximum plant growth) for communities and fruiting phenophase for forbs showed a significant acclimation lag.

For performance-related indicators (Figure 3B), we observed significant acclimation lags under warming except for the graminoids. Both annual and mid-season plant growth for communities and flowering phenophase (i.e. both flowering length and max % flowering) for forbs failed to reach complete acclimation.

### 3.2 | Was the warming effect on phenology deficient and/or divergent?

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

For time-related indicators, the community-level acclimation lag was relatively small, 10%, and deviated only slightly from the shortest trajectory, 5° (Figure 4). With warming and longer season length (Figure 2; Table S1), alpine community plant growth in the early season slowed down and communities took longer to reach their maximum plant growth (compared to AlpineControl). In late season, communities decreased browning speed and increased browning days (i.e. days after maximum plant growth) but failed to acclimate to the complete use of the late-season which constitutes the major part of the acclimation lag. Interestingly, plant communities could only acclimate their greening speed to longer season length in the third year but failed to do so in the first 2 years after transplantation (Figure S6a). At the species level, forbs did not only fail to close the acclimation lag due to the absence of any warming effect (Figures 3a and 4), but they even increased the lag by responding in the 'wrong' direction (i.e. 180° away from the shortest trajectory to complete acclimation. Specifically, fruiting for the AlpineWarmed species started earlier than for the SubalpineControls in all 3 years after the transplantation.

For performance-related indicators, the community-level acclimation lag was relatively large, 26%, but deviated only moderately from the shortest trajectory, 15° (Figure 4). Thus, even if communities could increase their performance during early and late season, their underperformance in the most important mid season resulted

in an important acclimation lag (Figure 3). In addition, this acclimation lag tended to increase over years (Figure S7a). Forbs showed an even bigger acclimation lag (685%) because they responded in the 'right' direction but exceeded far beyond the acclimation state. Notably, such large lags occur because the original distance between the phenology of alpine and subalpine plants was small and the response is measured relative to this original distance (Figure 4). This was especially the case for reproduction in the indispensable flowering stage (length of flowering period and number of individuals reaching this phenophase; Figure 3).

### 3.3 | Were acclimation lags in warming and cooling symmetric?

Acclimation lags in warming and cooling were not always symmetric. However, the strongest acclimation lags caused by warming (i.e. performance-related indicators for communities and forbs and time-related indicators for forbs) were symmetric for cooling (Figure 4; Figures S4 and S5).

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

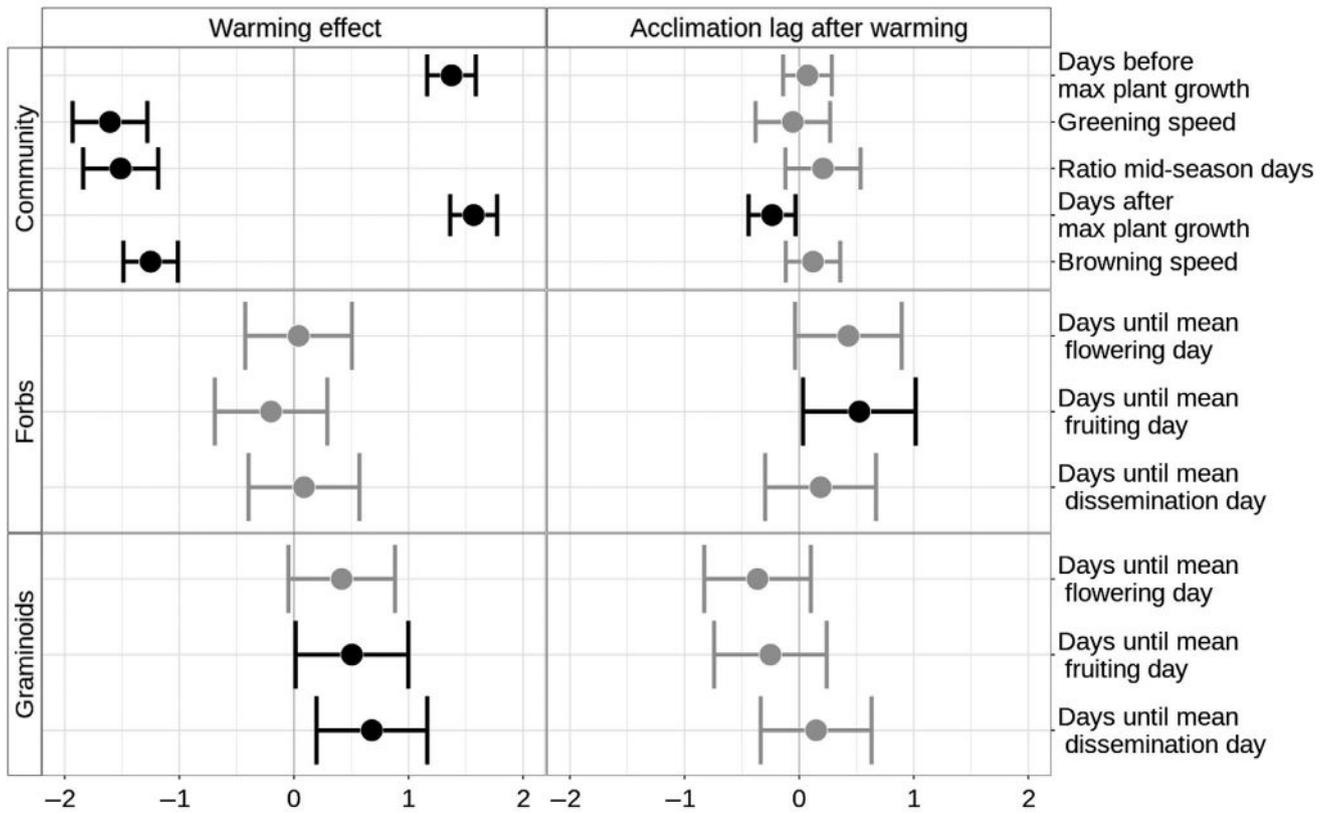
For performance-related indicators, at the community level, acclimation lags and deviations from shortest trajectories were comparable to warming and cooling (Figure 4; Figure S5a). After cooling, annual and mid-season plant growth could acclimate completely but early- and late-season plant growth failed to acclimate (Figure S3b). Forbs suffered even more from cooling than from warming and this was true for lag size and deviation from shortest trajectories. This trend holds for graminoids even though their acclimation lags were not significant.

## 4 | DISCUSSION

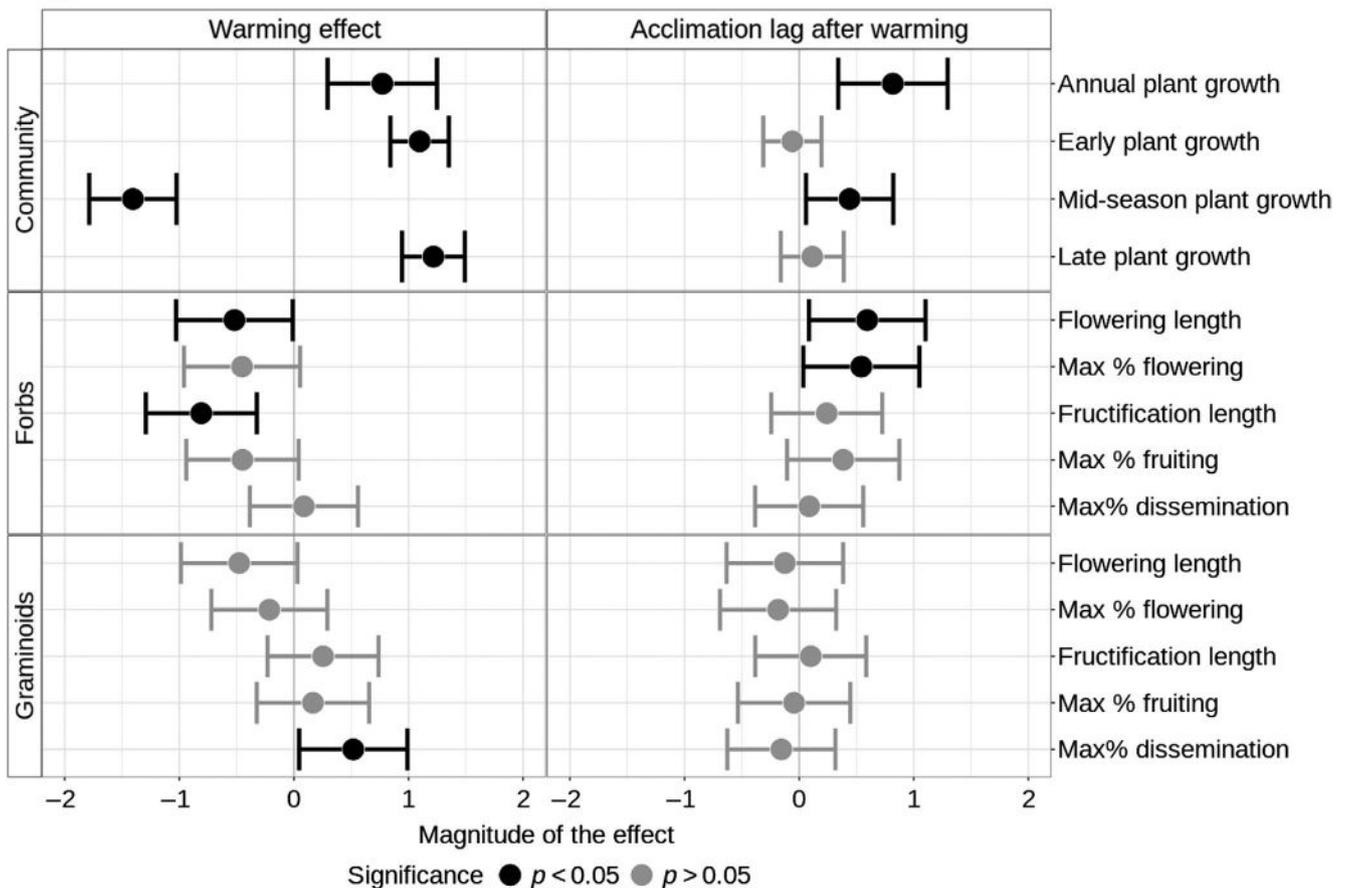
The phenology of mountain grasslands is known to strongly respond to climate change but so far little was known about remaining acclimation lags. Here, we built on our conceptual framework and a reciprocal transplant experiment to unravel whether phenological responses to warming and cooling follow the shortest trajectories to complete acclimation and how big remaining lags to complete acclimation are. We found that important aspects of phenology did not acclimate after 3 years of warming. This suggests that the projected climate warming is exceeding the limits of phenological plasticity of the here studied

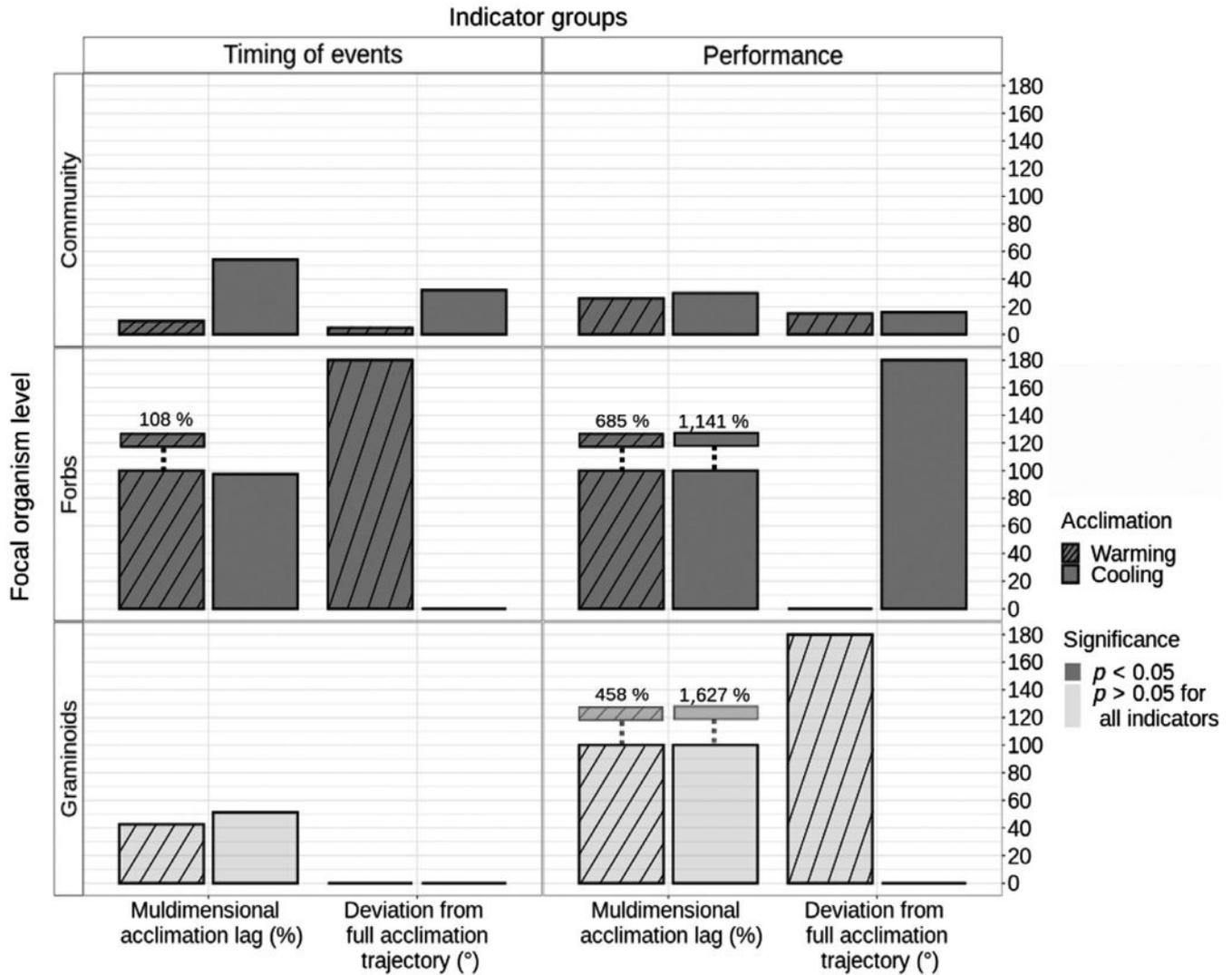
**FIGURE 3** Standardized effect sizes as the magnitude of warming effect and acclimation lag after warming at each focal organism level (community-level, species-level forbs and graminoids) for (A) timing of events and (B) performance related phenological indicators. Significant results are shown in 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

## (A) Timing of events



## (B) Performance





**FIGURE 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)

grasslands. This was especially true for indicators that are key for demographic performance and thus success. Forbs and overall community phenology were most affected, while graminoids coped overall well with climate changes. Importantly, even though we observed strong warming effects, they were not strong enough to lead to complete acclimation and we also found that transient dynamics largely deviated from the shortest trajectory to acclimation, especially for forbs. Finally, the symmetry between acclimation lags under warming and cooling underlines that important phenological processes adjust too slowly. This might indicate that the functioning of mountain grasslands under the threat of climate change can be reversible in the short term.

#### 4.1 | Timing of phenological events

Earlier works found that climate warming led to earlier phenology (experimental warming: Meng et al., 2018, 2019; review on existing

studies: Parmesan & Hanley, 2015; review on alpine ecosystem: Winkler et al., 2019) and faster plant growth (Wang et al., 2020). In apparent contradiction, our climate warming experiment promoted later phenology (i.e. later maximal plant growth, later starts of fruiting and dissemination periods of graminoids) and slower early-season increase in growth (i.e. slower greening speed). These warming effects allowed complete acclimation of the early- and mid-season timing of phenology to subalpine conditions for graminoids and communities. One major reason for this difference with other studies is that we used the growing season start and not calendar days as a reference (Johansson et al., 2013). Our main arguments for this choice are that the snow-free growing season is a major driver of alpine ecosystems (Choler, 2015), that plants physiologically respond to the first frost free days and that thus the comparison among study sites is ecologically less meaningful when it is based on calendar days. Another reason for our results is that with our in situ transplant experiment, we did not only manipulate temperature but

also the expected accompanying changes in snow cover and growing season length (Choler, 2015). In fact, once we calculated the warming effect on greening days based on calendar days, we found an advancement too (i.e. 24.85, with  $p < 0.001$  according to two sample  $t$  test) but this reflects mainly the advancement of snow melt.

Our results are consistent with apparent strategies of alpine communities: alpine conditions force plants to squeeze life cycles in shorter growing seasons (Körner, 1999) and induce faster plant growth right after the snow melt that is later in the year and thus, plants experience higher air temperatures directly after the snowmelt (Jonas et al., 2008). Yet, with warming and longer growing seasons (just as in subalpine conditions), snowmelt is earlier, the protective effect of snow cover is lost and thus, lower air temperatures are accompanied by potential spring freezing events that together slow down plant growth in the early season and can kill flower buds and leaves of frost-sensitive species (Choler, 2018; Inouye, 2000, 2008). For the end of the growing season, we found in concordance with Wang et al. (2020) that plant communities could not sustain the high mid-season plant growth rates. Potential explanations are warming-associated increases in drought stress (Wang et al., 2020) (i.e. even though the airborne estimated water balance of precipitation and evapotranspiration is comparable between sites, *unpublished results*) or inherent allocation trade-offs (Johansson et al., 2013).

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

## 4.2 | Phenological indicators linked to performance

In our experiment, the warming of grasslands increased yearly plant community growth (i.e. photosynthetic activity approximated by NDVI curves) which is consistent with several earlier studies (Cao et al., 2015; Carlson et al., 2017; Wang et al., 2012; Yang et al., 2019) but in contradiction to Wang et al. (2020). Our observed yearly increase was due to increased early and late plant growth, despite reduced mid-season plant growth. While our early-season results coincide with those of Wang et al. (2020), they differ for the mid and late season (i.e. no change and decrease). Reasons might be the fact that they (a) could only record for 2°C of warming and (b) defined early and late seasons on the basis of months rather than considering yearly differences in seasonal dynamics (i.e. interannual differences in start and end of growing season). Here, we suggest that (a) when 3°C is exceeded, a negative warming effect can be imposed on mid-season community performance and (b) it is important to consider interannual differences in identifying the seasons and warming effects on them.

Interestingly, in our experiment these strong warming effects were mostly due to short-term responses of the communities, such as phenotypic plasticity, and not due to compositional changes of plant communities. As most species in our observed grasslands were perennials, limited species turnover took place in the first 3 years after transplantation (Figure S8).

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

The community-wide warming effects on growth do not necessarily translate into increased reproductive performance at the species-level (Doak & Morris, 2010). Earlier studies found idiosyncratic warming effects on reproductive performance at the species level. Some found an increase (Iler et al., 2019; Kudernatsch et al., 2008; Li et al., 2016), no change at all (Dorji et al., 2020) or a decrease (Aldridge et al., 2011; Gugger et al., 2015; Liu et al., 2012) depending on species and ecosystem and others identified species-specific responses (Wang, Wang, et al., 2014; Winkler et al., 2019). In our study, we could relate the species-specific responses to growth forms with forbs failing to acclimate to warmer conditions (i.e. shorter flowering period, fewer individuals flowering) but alpine graminoids performing as well as subalpine graminoids in warmer, subalpine climate. This is in line with independent Ellenberg indicator values (i.e. categorical values indicating the species' abiotic niche; (Bartelheimer & Poschlod, 2016) suggesting that the dominant forbs in our study system are much less tolerant to variation in temperature (and moisture) than the dominant graminoids (Figure S9). Specifically, we argue that problems of forbs to acclimate could be linked to: (a) disrupted vernalization (i.e. flower bud formation depends on low temperatures, especially during winter; (Liu et al., 2012), (b) more allocation of resources to somatic growth than to reproduction (Johansson et al., 2013; Liu et al., 2012), (c) shading created by graminoids that have the potential to grow taller than forbs.

The observed acclimation lag of forbs in flowering performance is prone to cascade to the other trophic levels, specifically to associated pollinators (Gezon et al., 2016) and thus to further disrupt functioning of warmed alpine communities. In addition, responses specific to growth form may also cause a community composition shift in favour of graminoids. This is in line with a recent global review on the ecological flexibility of graminoids in their climate and habitat range, their success in establishment and dispersal and ecological competitiveness due to their functional and physiological traits (Linder et al., 2018). Yet, such shift in communities also risks the well-being of the whole multitrophic network and ecosystem functioning through further reduction of pollination services (Burkle et al., 2013; Gezon et al., 2016). In our study site, we already found indications of a significant acclimation lag in pollinator diversity after 3 years of warming (Figure S10).

The short-term community-level and growth form-specific results point to expected long-term responses of mountain grasslands (Pironon et al., 2017), including range shifts and restructuring of communities.

With warming, we know that some plant communities will be able to track their climatic niche and some will not, either due to migration failures or the absence of niche space on mountain tops (Alexander et al., 2015, 2016; Matteodo et al., 2013). In a scenario where subalpine plant communities can track their climate but alpine communities remain within their current niche, alpine species may not be able to increase their demographic performance either in plant growth or in reproduction fast enough and will thus be outcompeted by the subalpine species (Alexander et al., 2015, 2016). The increase in community plant growth and the competitive exclusion of slower-growing alpine species will also change plant–soil feedbacks. According to the ‘fast–slow’ plant economics spectrum, faster growth is associated with more exploitative plant traits (and thus, functional strategies), especially under favourable environmental conditions (Martinez-Almoyna et al., 2020; Reich, 2014). Such an above-ground functional strategy shift towards the faster part of the economic spectrum will affect the micro-organisms involved in plant litter composition (e.g. higher bacteria:fungi ratio), will change their ecosystem functions (e.g. faster nutrient cycling) and will then feedback to the plant communities, potentially further accelerating changes (Bardgett & Wardle, 2010).

### 4.3 | Divergent warming effects

It has been recently highlighted that perturbations to an ecosystem's steady state can trigger transient responses of ecological relevance (Mari et al., 2017). The question is not only how long it will take until the new steady state is reached but also how strongly responses are initially amplified before decaying towards a final state. Here we demonstrate that warming effects, especially on the phenology of alpine forbs, can be not only divergent (Ryo et al., 2019) but can lead phenology far away from any acclimation. In line with a previous long-term study (Wu et al., 2012), we found a similar but weaker response at the community level. Overall, determining the divergent responses can inform us on the long-term trajectory of the warming effect, and can serve as an early warning signal for negative impacts on ecosystem functioning (Scheffer et al., 2009). For example, fine scale NDVI measurements on communities are relatively easy to implement and according to our results, monitoring only for community productivity can serve for early detecting shifts in communities and ecosystem functioning.

### 4.4 | Symmetry between acclimation lag after warming and cooling

We found most of the acclimation lags after warming and cooling to be symmetric, indicating some plasticity in phenological responses to climate change that is, however, not sufficient for short-term acclimation to realistic warming scenarios. We conclude that slow phenological acclimation to new thermal conditions is a general phenomenon for mountain plant communities. Notably, for some phenological indicators (i.e. timing of community growth and flowering performance of forbs), the acclimation lag after cooling was

significantly wider than for warming. It has been suggested earlier that for mountain grasslands, physiological limits at the cold thermal range edge are much more pronounced than at the warm edge (Pellissier et al., 2013). In addition, it has been shown that a major driver of the warm edge is competition (Alexander et al., 2015), which has not yet started to act at its full force in our experiment. However, decrease in flowering performance both with warming and cooling indicates that flowering phenology is highly sensitive at both ends of the thermal limits (Li et al., 2016; Wang, Meng, et al., 2014).

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

## 5 | CONCLUSIONS

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

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### CONFLICT OF INTEREST

The authors do not have any conflicts of interest to declare.

## AUTHORS' CONTRIBUTIONS

B.B., W.T. and T.M. conceived the ideas and designed the methodology and led the writing of the manuscript; P.C. substantially helped with the interpretation of the results and design of the conceptual framework; A.S. and T.M. organized the fieldwork; M.-P.C., J.R., A.S. and T.M. established the protocol; J.R. managed the database; B.B., R.D.V., J.R. and M.-P.C. collected the data; B.B. analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.3r2280ggb> (Bektaş et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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