Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming

MAX A. SCHUCHARDT [ID],[1],† BERND J. BERAUER [ID],[1,2] ANDREAS VON HESSBERG,[1] PETER WILFAHRT [ID],[1,3] AND ANKE JENTSCH [ID][1]

[1]*Department of Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, Bayreuth, Germany*
[2]*Department of Plant Ecology, Institute of Landscape and Plant Ecology, University of Hohenheim, Hohenheim, Germany*
[3]*Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota, USA*

Abstract. Warming due to climate change is generally expected to lengthen the growing season in areas of seasonal climate and to advance plant phenology, particularly the onset of leafing and flowering. However, a reduction in aboveground biomass production and reproductive output may occur when warming is accompanied by drought that crosses critical water deficit thresholds. Tracking warmer temperatures has been shown to be species-specific with unknown impacts on community composition and productivity. The variability in species' ability to leverage earlier leaf unfolding and flowering into increased aboveground net primary production (ANPP) or increased investments into reproductive organs has heretofore been poorly explored. We tested whether phenological sensitivity to temperature, as a result of experimental warming, directly translated into increased plant performance, as measured by ANPP and flower abundance. In order to experimentally simulate climate warming, we translocated a total of 45 intact soil–plant communities downslope along an elevational gradient of 900 m within the European Alps from 1260 to 350 m asl and weekly recorded flower abundance and total green cover as well as cumulative biomass production at peak growing season. We found that advanced phenology at lower elevations was related to increased reproductive performance and conditional on whether they experienced drought stress. While a temperature increase of +1K had positive effects on the amount of reproductive organs for species with accelerated phenology, temperature increase going along with drier conditions resulted in plants being unable to sustain early investment in reproduction as measured by flower abundance. This finding highlights that the interaction of two climate change drivers, warming and drought, can push communities' past resistance thresholds. Moreover, we detected biotic competition mechanisms and shifts toward forb-depressed states with graminoids best taking advantage of experimentally altered increased temperature and reduced precipitation. Our results suggest that while species may track warmer future climates, concurrent drought events post a high risk for failure of temperature-driven improvement of reproductive performance and biomass production in the European Alps.

Key words: alpine; Bavarian Alps; climate change; phenological sensitivity; plant community; plant functional type; plant reproduction; translocation experiment; transplant.

† **E-mail:** max.schuchardt@uni-bayreuth.de

INTRODUCTION

Climate change will affect plant community dynamics and functions by unevenly altering species' phenologies (CaraDonna et al. 2014, Alexander and Levine 2019, Giejsztowt et al. 2020). Temperature increase due to climate warming in mountain regions is expected to be two to three times higher than the global average (Appenzeller et al. 2008, Pepin et al. 2015). The potential positive effect of warming in mountain regions on plant growth via longer growing seasons (Gobiet et al. 2014) and increased metabolic rates (Larcher 2003, Körner 2006) can be counterbalanced by late frost events (Inouye 2008, Wipf et al. 2009) or drought effects (Jentsch et al. 2009, Buchner et al. 2015, De Boeck et al. 2016, Berauer et al. 2019). Plant reproductive potential is tightly linked to phenological plant strategies such as the timing and abundance of flower production, making the sensitivity of phenology to climate warming a critical component of future plant community dynamics and ecosystem service provisioning in mountain regions.

Warming is expected to generally advance flowering onset (Menzel and Fabian 1999, Cornelius et al. 2014, Munson and Sher 2015). Long-term monitoring has shown that species that declined in abundance over time showed little or no ability to track warmer local climate and did not advance their flowering phenology (Willis et al. 2008). Changes in flowering phenology are among the earliest observed reactions to changed environmental conditions (Inouye 2008, Box et al. 2019), responding to a variety of abiotic factors (such as photoperiod, above- and below-ground temperatures, soil moisture and snow cover, in other words vernalization cues) and in turn steering biotic interactions (Jentsch et al. 2009, Zhao et al. 2020). Responses to warmer climate have been shown to vary between early- and late-flowering species, with early-flowering species tending to benefit most from increased spring temperatures (Moore and Lauenroth 2017, Arfin Khan et al. 2018). Despite this general trend, late-flowering species can match (Miller-Rushing and Inouye 2009) or exceed (Carbognani et al. 2016) the benefits early-flowering species receive, potentially pointing to deleterious effects of early flowering such as pollinator desynchronization. On a community level, changes in plant phenology can increase a niche overlap of species, decreasing phenological complementarity (Rathke and Lacey 1985). Decreasing phenological complementarity in turn may influence competition between species by increasing overlap in resource acquisition strategies (Nord and Lynch 2009, CaraDonna et al. 2014), plant–pollinator mutualism (Dyer et al. 2021), and trophic synchronization (Hegland et al. 2009, Schmidt et al. 2016) or windows of opportunity for non-native species to establish within the community (Wolkovich and Cleland 2011, Alexander and Levine 2019, Vetter et al. 2019, Giejsztowt et al. 2020).

Warming can also indirectly influence plant phenology by increasing water stress due to amplifying droughts, which will likely increase in abundance due to shifts in precipitation regimes (Gobiet et al. 2014, Spinoni et al. 2018). This is important, as water limitation may suppress both plant growth and reproductive fitness (Engler et al. 2011, Robinson et al. 2013, Leitinger et al. 2015, Dietrich and Smith 2016, Grant et al. 2017). Thus, phenological advancement can make early investments into reproductive organs followed by water stress potentially damaging to an individual. However, phenological responses to drought vary widely, having been shown to advance (Peñuelas et al. 2004, Jentsch et al. 2009, Bernal et al. 2011) or delay plant development (Nagy et al. 2013). Further, phenological response to drought may inert flowering onset, change abundance of flowers (Dunne et al. 2003, Saavedra et al 2003, Abeli et al. 2012, Cornelius et al. 2013) or reduce carbon allocation to reproductive organs (Barnabas et al. 2008, Liu et al. 2012, Zeiter et al. 2016, Kreyling et al. 2017), highlighting species-specific responses (Jentsch et al. 2009). Further, extreme summer conditions such as drought in the temperate zone are known to increase early leaf senescence (Kreyling et al. 2008, Benot et al. 2014, De Boeck et al. 2016), decrease plant vegetative growth, and reduce seed abundance and seed weight (Zeiter et al. 2016), indicating that plant stress reduces plant fitness (Walter et al. 2013). Ultimately, while warming may advance flowering, subsequent drought can interrupt or reverse this pattern as species divest from reproduction.

The effect of warming on the abundance of reproductive organs has shown to be highly species-specific and study system-dependent.

Moreover, it remains unclear whether advanced phenologies of species that are able to track climate change can draw benefits, namely increase in carbon allocation to vegetative biomass or reproductive organs, from these early investments. Increased temperature going along with drought stress can result in drought-induced divestments from reproductive organs (Saavedra et al. 2003, Giménez-Benavides et al. 2007, Abeli et al. 2012, Zeiter et al. 2016). When warming occurs without water stress, the investment into reproductive organs remains unclear. Thus, increasing temperature may reveal underexplored thresholds, where the warming effect on plant growth and reproductive organs changes from positive to negative (Scheffer and Carpenter et al. 2003, Turner et al 2020), which in turn may have strong long-term effects on community reassembly under future climatic conditions.

In this unique study, we explored how experimental warming by downslope translocation of entire plant–soil communities in the German region of the European Alps (Berauer et al. 2019) affected the onset and abundance of flowering in semi-natural grasslands along a temperature–precipitation gradient that ranged from benign to stressful water availability conditions. We additionally explored how different plant functional groups, namely early- vs. late-flowering species, graminoids, forbs, and herbaceous legumes, reacted to this temperature–precipitation change and the relationship to overall aboveground community biomass production. We hypothesize that (1) early-flowering species better track climate change by adjusting flowering onset to the novel climatic conditions as they rely on the higher resource availability of early spring; (2) species that advance their flowering phenology in response to a warmer climate increase their reproductive output as measured by the number of flowers; and (3) carbon allocation toward aboveground net primary production (ANPP) increases with warming.

Methods

Experimental setup

In the summer of 2016, 45 intact plant–soil monoliths were extracted from semi-natural montane grasslands in an extensively managed meadow at 1260 m asl. Monoliths were 30 cm in diameter and 40 cm in depth, representing an area shown to be sufficient to study community responses and interactions in small statured grasslands (Milbau et al. 2007) while maintaining belowground processes. After excavation, monoliths were translocated downslope and reburied flush with the ground at four target sites along an elevational gradient ranging from 1260 m asl (Esterberg; climatic control and recipient site of nine replicates) to 860 m asl (Graswang; +1K) to 600 m asl (Fendt; +3K) to 350 m asl (Bayreuth; +3.5K; for additional details on the study design, see Berauer et al. 2019).

At each climate treatment—including the site of origin—nine replicates were exposed to local climatic conditions. At the lowest climate treatment, an additional set of nine replicates was installed and received an irrigation treatment twice a week starting in spring 2018 (Fig. 5). The irrigation treatment was designed to alleviate communities' water limitation at the lowest elevation climate treatment caused by a sharp decrease in annual precipitation at this experimental site and clear signs of water stress in 2017 (Berauer et al. 2019). The amount of added water was mimicking a subalpine precipitation pattern (in amount and frequency) being calculated as the difference between monitored precipitation at the lowest climate treatment and the long-term monthly average of the subalpine Stubai Valley (1850 m asl, Austria), a higher elevation climate treatment of this project that was not used in this study, corresponding to a mean of 12.35 mm precipitation, twice a week.

The elevational gradient represents an increase of MAT by 3.5K between the highest and lowest experimental site with intermediate steps at +1K and +3K. This experimental setup tests a range of simulated climate change scenarios, with the maximum values representing IPCC Scenario A1B with a mean air temperature rise of 3–4K until 2100 (Körner 2003, IPCC 2007).

Environmental parameters

In spring 2017, a sensor for soil temperature and moisture (EcH2O 5-TM; Decagon Devices, Pullman, WA, USA) was installed horizontally at 5cm depth together with data loggers (EcH2O Em50; Decagon Devices) in one monolith at each climate treatment.

The start of growing season was defined as the first day where daily mean soil temperature was above 5°C for five consecutive days (Table 1; Appendix S1: Fig. S1; Zhang et al. 2011). This temperature threshold describes site-specific energy availability at ground level controlling both biological and biochemical processes (Jentsch and White 2019), which in turn are primarily driving the green-up and onset of flowering of grassland species (Scherrer and Körner 2009, Guo et al. 2018). Moreover, using soil temperature data allowed us to infer site-specific snowmelt regimes, which is especially important at montane sites, where growing season start is often determined by loss of snow cover rather than air temperatures above a certain threshold (Shaver and Kummerow 1992, Oberbauer et al. 2013).

Flowering phenology

Flowering phenology was monitored weekly at each climate treatment along the downslope translocation experiment in 2019, from the beginning of the growing season until peak biomass harvest (for an overview of defined growing season start and peak biomass, see Table 1). We monitored species-specific onset and duration of flowering plus number of flowers or inflorescences. Flowering was defined as the first open flower with visible stamen (Meier 2018). Once multiple individuals of a species in one monolith started flowering, we flagged the first flowering individual to monitor throughout the growing season; the number of flowers was counted from the flagged individual. For all graminoid species, the number of inflorescences was used as the flower unit, so that graminoid species were recorded as flowering once the first anthers were visible (Meier 2018). Due to graminoid's potential vegetative reproduction, all inflorescences of a given species per monolith were counted. We used mean number of flowers (individual-specific over the growing season) for further analysis (Hollister et al. 2005, Cleland et al. 2012). According to Jäger and Rothmaler (2017), we classified species starting to flower before or during May as early-flowering species, whereas species that started flowering after May were classified as late-flowering species. Furthermore, we visually estimated the percent of green cover of each monolith as a proxy for environmental stress (De Boeck et al. 2016, Stampfli et al. 2018, Berauer et al. 2019). Even though monitoring at the control and +3K climate treatment started slightly after local growing season start, we captured initial flowering onset of all present species.

Phenological sensitivity was calculated as the number of days shifted in species-specific flowering onset between the control and warming treatments, per degree warming (Cleland et al. 2012) averaged across all replicates where the species occurred within each respective climate treatment. The control treatment corresponds to the highest experimental site used in this study, which is the site of origin from where all translocated monoliths were excavated. Warming treatments correspond to the experimental sites along the downslope translocation gradient.

$$S_{phen} = \frac{Onset_{warm} - Onset_{ctrl}}{T_{warm} - T_{ctrl}}$$

Table 1. Site names of translocated plant–soil monoliths with elevation, climate treatment intensity, average annual precipitation of years of experimental exposure 2016–2019 (MAP_{exp}), total seasonal precipitation between 15 May and 31 July 2019 ($Precip_{seas}$), average air temperature at 2m unventilated between 2016 and 2019 ($AirTemp_{exp}$), average seasonal air temperature between 15 May and 31 July 2019 ($AirTemp_{seas}$), local growing season ($Start_{GS}$), phenological monitoring ($Start_{mon}$), and peak biomass harvest (PBH).

Locality	Elevation (m asl)	Climate treatment	MAP_{exp} (mm)	$Precip_{seas}$ (mm)	$AirTemp_{exp}$ (°C)	$AirTemp_{seas}$ (°C)	StartGS (DOY)	$Start_{mon}$ (DOY)	PBH (DOY)
Esterberg	1260	ctrl	1797	584	5.6	13.7	121	135	190
Graswang	860	+1K	1349	443	6.8	15.4	87	83	189
Fendt	600	+3K	1015	276	8.8	17	60	76	189
Bayreuth	350	+3.5K	630	114	9.6	18.03	60	62	175

Performance sensitivity was calculated species-specific as the proportional change in number of flowers (averaged across replicates where species occurred within each respective climate treatments) per degree warming. This value indicates if a translocated species is producing more or less flowers compared to the higher elevation climatic control treatment, which is the site of origin.

$$S_{perf} = \frac{(n.\ flowers_{warm} - n.\ flowers_{ctrl})/n.\ flowers_{ctrl}}{T_{warm} - T_{ctrl}}$$

Aboveground biomass and species richness

Aboveground biomass of each monolith was harvested 3cm above the ground at site-specific peak biomass (Table 1). Biomass was sorted to species, dried at 60°C for 48 h, and weighed. Species richness at each climate treatment was calculated as the sum of all flowering species recorded during the phenological monitoring plus all additional non-flowering species found during the biomass harvest (detailed species lists in Appendix S1: Table S3). This approach captured early-flowering species (e.g., *Veronica chamaedrys* L.) that would otherwise be undetected at the peak biomass harvest, as they had already senesced by then.

Statistical analysis

We first tested whether (1) early-flowering species would better track climate change by adjusting flowering onset to the local growing season compared to late-flowering species. For a response variable, we calculated an average flowering onset day for each species in each climate treatment by taking the mean flowering onset day of all monoliths within a climate treatment where a given species was found. We conducted linear mixed-effect models using the nlme package in R (Pinheiro et al. 2021) with mean species-level flowering onset dates as the response variable ($n = 9$ for each climate treatment) and flowering time (two-level factor: early- vs. late-flowering species), climate treatment, and their interaction as explanatory variables. As many species occurred at multiple climate treatments, we used species as a random effect. We examined multiple Tukey-adjusted comparisons to calculate groups with significant differences in flowering onset using the emmeans package (Lenth 2020).

Next, we tested (2) whether performance sensitivity increased with phenological sensitivity. We averaged species-specific onset of flowering and number of flowers across replicates within each climate treatment and calculated sensitivities according to Cleland et al (2012; see section *Flowering phenology* above). Then, we used a linear mixed-effects model to test whether the interaction of phenological sensitivity and flowering onset (levels: early; late) predicted performance sensitivity with species ID as a random effect as species may have occurred at multiple climate treatments. Additionally, we used linear models to test whether phenological sensitivity predicted performance sensitivity for each climate treatment.

We investigated how (3) the production of aboveground plant biomass (ANPP) changed with warming. We used linear models to test whether differences in ANPP were predicted by climate treatments relative to climatic controls and how these differences varied by functional groups. We repeated this process using species richness as a response.

Lastly, we used generalized additive models (GAMs, mgcv package) with treatment as a factor to model and compare the observed green cover vs. days of the year due to non-linearities and potentially important declines in green cover in mid-season. GAMs were fit using restricted maximum likelihood (REML) to identify optimum smoothing parameters and a Gaussian error distribution. We used AIC to verify that our GAM improved the fit relative to a simple linear model. All model residuals were checked for normality and homoscedasticity. All analyses were performed in R Studio version 4.0.3 (R Core Team 2018).

RESULTS

Shifts in onset of flowering

The translocated plant–soil monoliths were able to track experimentally induced climate warming by modulating plant species' flowering onset to local climates ($P < 0.001$; Fig. 1). The mean flowering onset between earliest (lowest = warmest) and latest (highest = coolest) climate treatment differed by 34 d averaged across all species, corresponding to 3.14 d advancement per 100 m elevational change (see Table 2).
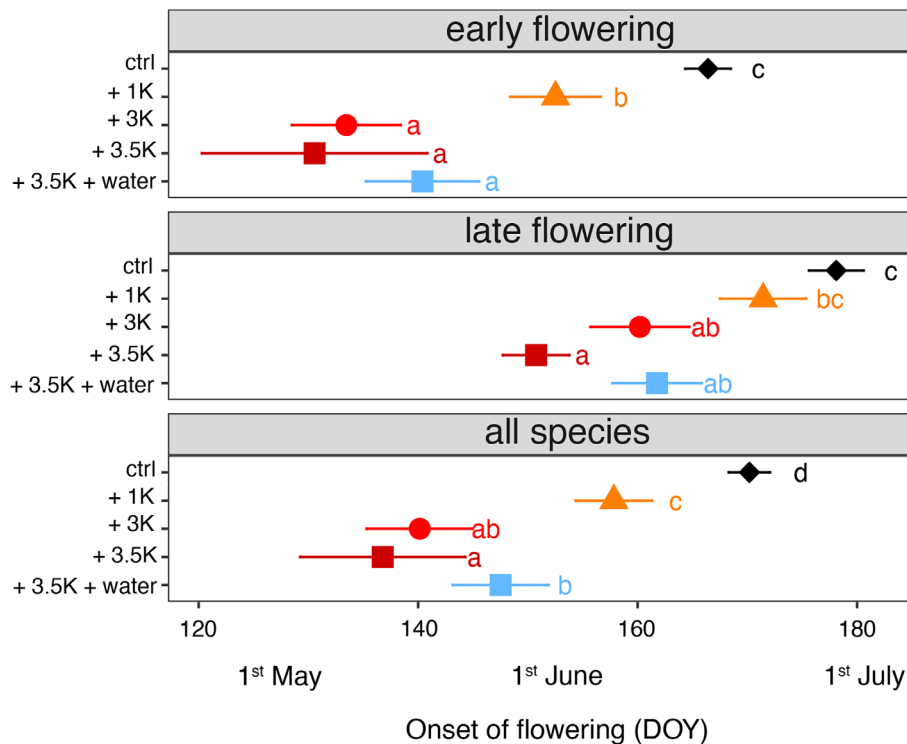
Fig. 1. Flowering onset of translocated plant–soil monoliths along an elevational gradient splits into groups of early- and late-flowering and all present species. Onset of flowering as measure of DOY follows the elevational gradient with earliest flowering onset at lowest elevation. Water addition at the lowest recipient climate treatment led to a shift back in flowering onset, likely indicating drought stress in plant communities without water addition. Letters indicate significant differences between climate treatments. Mean flowering onset between early- and late-flowering species differed marginally, indicating a phenological divergence between these two groups ($P = 0.056$).

Early-flowering species showed a mean advancement of 3.81 d per 100 m elevational change, while late-flowering species showed a mean advancement of 2.3 d per 100 m across all climate treatment (early vs. late: $P = 0.056$). The factors early and late were not confounded with growth form (Appendix S1: Table S3).

Phenological sensitivity and performance

Increased advancement of flowering phenology was correlated with increased investments into reproductive organs, as indicated by a negative relationship between flowering onset advancement and number of flowers produced ($P = 0.007$; Fig. 2). This relationship was consistent for both early- and late-flowering species ($P = 0.912$), indicating that both groups respond similarly to climate warming. The relationship between phenological sensitivity and performance sensitivity did not hold true for all climate treatments (Fig. 3). At the most moderate climate treatment of +1K, the trend was highly significant ($P < 0.001$) and mainly driven by forbs and legumes. The same trend was observed at the strongest climate treatment of +3.5K receiving water addition ($P = 0.039$), although a majority of species in this climate condition produced less flowers relative to the control and the pattern was mainly driven by an important indicator graminoid species *Poa pratensis* (L.) ($P = 0.169$ excluding *P. pratensis*). For the strong climate treatments +3K and +3.5K without watering, this trend was inverted, but non-significant ($P = 0.199$ and $P = 0.068$, respectively). Except for *Plantago lanceolata* (L.) in the +3.5K water addition

Table 2. Mean start of flowering along the elevational gradient with climate treatment intensity, flowering group, number of present species across all nine replicates (N), mean start of flowering, standard deviation (SD), standard error (SE), confidence interval (CI), elevational change, and day shift in mean flowering onset per 100 m elevational change.

Climate treatment	Flowering	N	Start (DOY)	SD	SE	CI	Elevational change (m)	Days per 100 m
Ctrl	Early	21	166.4	9.5	2.1	4.3	0	NA
+1K	Early	23	152.5	19.8	4.1	8.5	400	−3.48
+3K	Early	12	133.5	17.2	5	10.9	660	−4.98
+3.5K	Early	9	130.6	30.8	10.3	23.7	910	−3.93
+3.5K +water	Early	12	140.4	17.9	5.2	11.4	910	−2.86
Mean								−3.81
Ctrl	Late	10	178.1	7.9	2.5	5.6	0	NA
+1K	Late	9	171.4	11.8	3.9	9.1	400	−1.68
+3K	Late	4	160.2	9	4.5	14.3	660	−2.71
+3.5K	Late	4	150.8	6.1	3	9.6	910	−3.0
+3.5K +water	Late	6	161.8	10	4.1	10.5	910	−1.79
Mean								−2.3
Ctrl	All species	31	170.2	10.5	1.9	3.8	0	NA
+1K	All species	32	157.8	19.7	3.5	7.1	400	−3.1
+3K	All species	16	140.1	19.4	4.8	10.3	660	−3.31
+3.5K	All species	13	136.8	27.1	7.5	16.4	910	−3.67
+3.5K +water	All species	18	147.5	18.5	4.4	9.2	910	−2.49
Mean								−3.14

Notes: Note that water addition delayed mean start of flowering for both early- and late-flowering species. Mean onset of flowering between early- and late-flowering species was marginally significant ($P = 0.056$; $F_{77} = 3.738$).

treatment, all monitored species experienced advances in the onset of flowering (Fig. 3).

Productivity and species richness

Community aboveground biomass production (ANPP) did not respond linearly to the experimental climate treatment (Fig. 4A). ANPP increased under modest climate change ($P_{+1K} = 0.025$) fitting findings from previous years (Berauer et al. 2019). Communities under more severe climate change scenarios decreased in ANPP, indicating threshold dynamics after three years of climatic exposure ($P_{+3K} = 0.061$; $P_{+3.5K} < 0.001$; $P_{+3.5K+water} < 0.001$). The significant increase in ANPP at the +1K climate treatment was due to increased biomass production of graminoid species ($P = 0.003$). The increased production of graminoid species is likely at the cost of forb species, which decreased in production under modest warming ($P < 0.001$; Fig. 4B and Appendix S1: Table S1).

Species richness of plant communities declined significantly upon downslope translocation along the elevational gradient (Fig. 4C; Appendix S1: Table S3). While we did not find a significant decline in mean forb richness between the control and +1K climate treatment, forbs declined at +3K ($P < 0.001$), +3.5K ($P < 0.001$), and 3.5K +water ($P < 0.001$). The higher number of recorded forbs at +3.5K compared to +3K and +3.5K with water addition is due to the invasion of new species (i.e., *Senecio vulgaris* (L.), *Pilosella piloselloides* (VILL.) SOJáK) from matrix vegetation. Graminoid species richness declined significantly at +3.5K ($P < 0.001$) and even at +3.5K with water addition ($P = 0.002$). We did not find any significant changes in legume species richness, despite their absence at +3.5K without water addition (Appendix S1: Table S2).

Green tissue as a stress indicator

Our generalized additive model (GAM) analysis indicated that green tissue in the control, +1K, and +3K treatments plateaued and showed no stress from drought effects (ctrl, $F = 22.77$, df = 4.57, $P < 0.001$; +1K, $F = 77.24$, df = 4.60, $P < 0.001$; +3K, $F = 27.17$, df = 4.30, $P < 0.001$). Moreover, green tissue began senescing in the last week of May (DOY = 148) at the most intense climate treatment of +3.5K without water

early flowering

late flowering

phenological sensitivity

performance sensitivity
Δ number of flowers
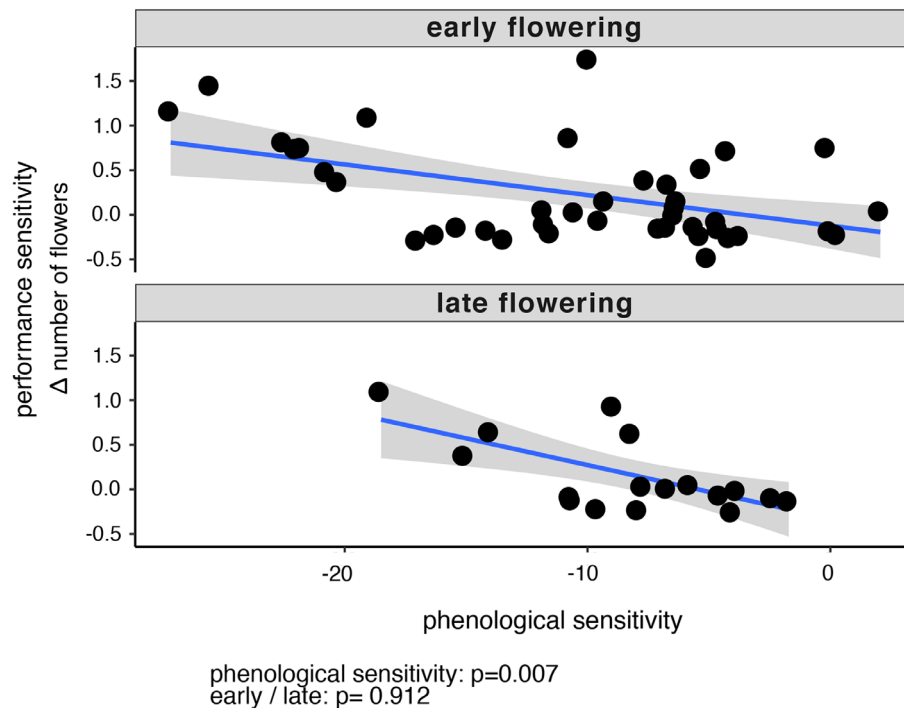
phenological sensitivity: p=0.007
early / late: p= 0.912

Fig. 2. Phenological sensitivity as a significant predictor of flowering performance. Species that tracked experimentally induced climate change by flowering earlier showed positive performance responses. This trend stayed consistent across early- and late-flowering species.

addition (F = 18.35, df = 5.79, P < 0.001; Fig. 5), likely as a result of depleted soil moisture by evapotranspiration. Conversely, no bimodality was observed in the +3.5K with water addition treatment (consistent water supply resulted in a linear increase of green tissue over time). The overall model D^2 was 71%, indicating that the GAM provided a good fit. The GAM indicated that smoothing functions were appropriate for all climate treatments excluding the +3.5K with water addition; model fit using smoothing parameters was better than when using a standard linear model, as evidenced by AIC (AIC_{GAM} = 6056; AIC_{lm} = 6382). Within two weeks from DOY = 142 to DOY = 155, soil moisture was reduced from 40% to 14% at +3K and 20% to 4% at +3.5K, respectively. Soil moisture values stayed low during the critical time of flowering until the harvest date in early July (i.e., soil moisture +3.5K ≤ 15% for 96 d). At the +3.5K climate treatment, monoliths receiving water addition corresponding to a mean of 12.35 mm precipitation twice a week were able

to sustain green tissue. Orographic rainfall in combination with frequent morning dew at the +1K climate treatment continuously provided water to the translocated plant–soil monoliths.

DISCUSSION

As hypothesized, nearly all species in downslope translocated monoliths were able to track climate change by advancing onset of flowering under warmer conditions with early-flowering species seeming to have greater advancement than late-flowering species. Generally, species that were better able to track local climate in flowering phenology were also able to increase their investment into reproductive organs displaying more flowers. However, at climate treatments where precipitation declined with increased temperature, investment into reproductive organs did not increase with advanced flowering dates and even showed a tendency to decline. We found that responses were highly species-specific with the tendency toward
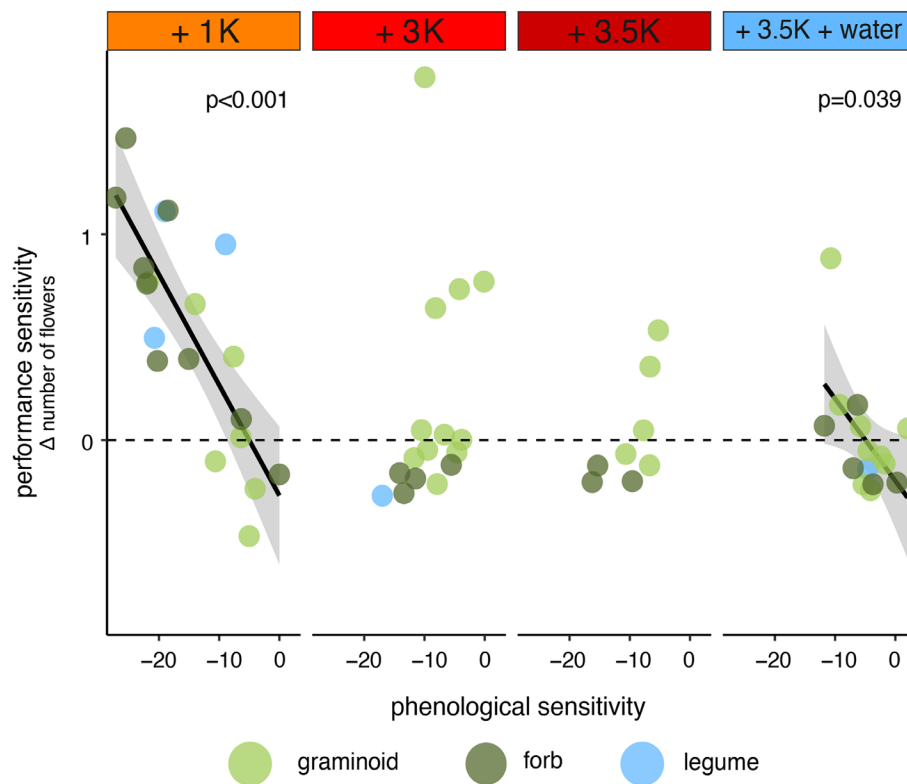
Fig. 3. Relative effect of passive warming on phenological sensitivity and performance sensitivity along the elevational gradient. Climate treatments at the more severe climate treatments of +3K and +3.5K suffering under drought effects reduce investments into reproductive organs. Some graminoid species show increased performance under drought.

increased graminoid reproductive performance at the expense of forb reproductive performance under dry conditions.

Phenological sensitivity predicts flowering performance

As per our hypothesis and in line with previous findings (Jentsch et al. 2009, Cleland et al. 2012), we found that with advancing flowering phenology, the amount of reproductive organs of species increased in general. While others have shown that late-flowering species may delay their flowering phenologies to avoid unfavorable conditions in the middle of summer (Taylor and Garbary 2003, Sherry et al. 2007, Munson and Sher 2015), all species in our study (except one), whether early or late flowering, showed an earlier flowering onset compared to the climatic control, which fits the general observations of

advanced flowering under warming (Menzel and Sparks 2007, Moore and Lauenroth 2017).

Previous studies reported stronger responses to warming in early-flowering species compared to late-flowering species (Miller-Rushing and Inouye 2009, Moore and Lauenroth 2017, Arfin Khan et al. 2018), and we found a similar tendency for early-flowering species to advance flower onset to a greater degree than late-flowering species. We observed a similar, positive relationship between flower onset advancement and reproductive performance, measured as number of flowers per individual, in early- and late-flowering species, but due to the greater advancement potential of some early-flowering species, the greatest increase in investments into reproductive organs was seen in the early-flowering cohort. Graminoids dominated the late-flowering cohort (see Appendix S1:
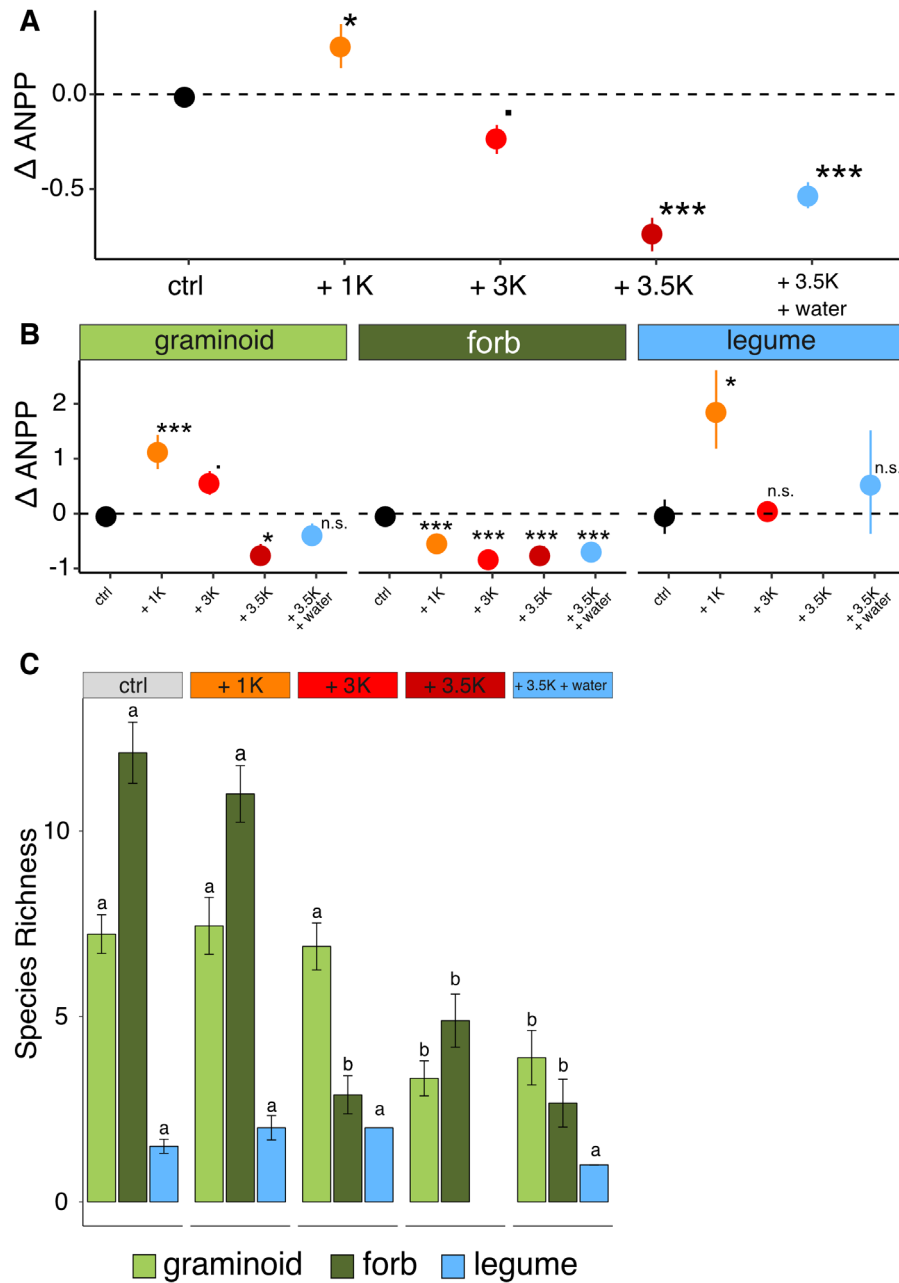
Fig. 4. Aboveground net primary production and species richness along the elevational gradient after three years of passive warming. (A) ANPP of all species present at climate treatments. (B) ANPP of three plant functional groups. Asterisks indicate levels of significance between each recipient climate treatment and the climatic control. (C) Species richness splits into three plant functional groups. For each plant functional group, letters indicate significant changes in species richness due to experimentally altered climate conditions.

Table S3). While most forbs such as *Myosotis sylvatica* ssp. *alpestris* (F.W. Schmidt) and legumes such as *Trifolium pratense* ssp. *pratense* (L.) suffered under water deficiency at the more severe climate treatments (+3K and +3.5K without water addition), certain graminoid species such
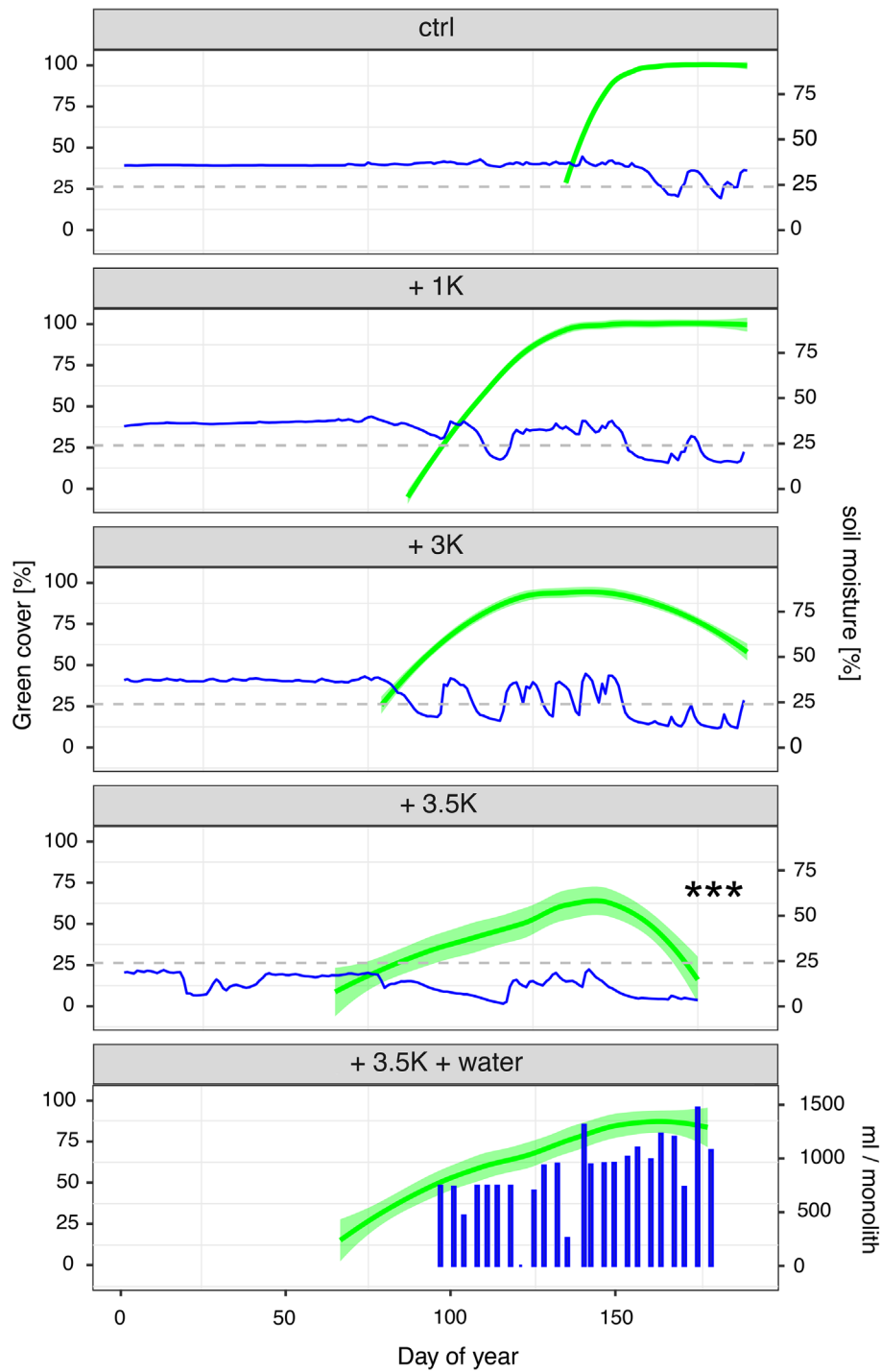
Fig. 5. Green cover of translocated plant communities along the elevational gradient modeled as GAM (solid green line) with 95 confidence interval (green ribbon). Early senescence of plant communities due to soil water depletion indicated as soil moisture at 5 cm (blue lines). Blue bars at the lowest climate treatment indicate biweekly water addition per plant–soil monolith to remove water limitation as soil moisture data were unavailable. Asterisks show significant differences in green cover relative to the control.

as *Elymus repens* (L. Gould) still increased performance compared to the climatic control treatment, potentially masking the signal of forb or legume performance declines in the group of late-flowering species.

Interestingly, the relationship of species-specific phenological sensitivity to climate warming and performance was not consistent along the entire climatic gradient indicating unknown threshold dynamics. Monoliths translocated to a warmer site with sufficient water availability throughout the season produced more flowers with advancing phenologies. This trend was also evident at the warmest site when water was experimentally supplemented, though this pattern was dominated by a single species, *Poa pratensis*. Consequently, the benefit of a species advancing its phenology in warmer environments appears to be dependent on water deficiency. Climate treatments experiencing drought stress even tended to show the reverse trend, with decreased flowering performance with higher climate sensitivity (Saavedra et al. 2003). Under drought conditions, competitive interactions between species of various growth forms have shown to alter species-specific onset and length of flowering period (Jentsch et al. 2009). Likely, this meant that plant communities under stressful, water-limited conditions were not able to sustain this early warming-driven investment in reproduction. Hence, advanced flowering does not necessarily translate into higher reproductive performance and can potentially result in wasted resource investments for a plant (Saavedra et al. 2003), highlighting the need to explore interacting climate change drivers to reveal where critical water deficit thresholds cause species performance to decline (Turner et al 2020).

At the lowest climate treatment receiving biweekly water addition, most present species produced less flowers compared to the climatic control treatment, but still showed a significant negative relationship between phenological sensitivity and flowering performance. Species highly sensitive to warming, thus accelerating their flowering onset, produced more flowers compared to species less sensitive to warming within the same climatic treatment. At +3.5K with water addition, this relationship was driven by *P. pratensis* (L.), a fairly durable and drought-resistant species, which may be an early indicator

for community reassembly (toward graminoid dominance) after three years of climate exposure due to (1) increased investments into reproductive organs and (2) relative dominance in space (40% mean cover in 2019). Plants may shift their resources from reproduction to maintenance (Parsons 1990) or from aboveground to belowground productivity (Barnabas et al. 2008) under stressful conditions (Knapp et al. 2008, da Silveira Pontes et al. 2015). Our watering treatment began in 2018 after observing a sharp decline in community performance in the first year of study after downslope translocation (Berauer et al. 2019). It is likely, then, that even after alleviating water stress, these communities were still recovering from drought conditions, potentially explaining their poor performance relative to the wetter and cooler controls. Moreover, a severe and extended natural drought occurred in Central Europe in the summer of 2018 (Buras et al. 2019), potentially delaying recovery of these communities even with watering as evapotranspirative demand was severe. This finding suggests that plant communities in the +3.5K water addition treatment may be in an intermediate state between recently sufficient water supply and recovering from the 2018 natural drought, thus showing a single species-driven pattern.

Climate-dependent allocation strategies

Biomass production is often reduced under drought conditions, which may decrease overall fitness by reducing fecundity (Shipley and Dion 1992, Tracey and Aarssen 2011, Gellesch et al. 2017, Younginger et al. 2017). In our study, species under modest warming showed higher flower abundances mainly driven by forb and legume forb responses, while the species with the greatest ANPP gains were graminoids, indicating that these two plant functional groups, forbs and graminoids, had complementary allocation strategies under warmer conditions with adequate soil water resource. Under persistent water stress, we found that graminoid species were best able to maintain reproductive and vegetative performance, while forbs and legumes showed a decrease in investment into reproductive organs, a decrease in ANPP, or they even went locally extinct. However, there is a lack of generality regarding graminoid response to

drought; graminoids reduce the number of reproductive shoots relative to forbs and legumes in some systems (Zeiter et al. 2016), while they may recover better from drought in terms of biomass production in others (Grant et al. 2014, Stampfli et al. 2018, Mackie et al. 2019). In temperate grasslands, graminoid species typically develop shallower and more flexible rooting systems compared to forbs or legumes, thus increasing the graminoid's drought sensitivity but also response flexibility (Bardgett et al. 2014, Kübert et al. 2019). Yet, graminoids were shown to react quickly after rewetting events due to their dense mat of roots in upper soil layers (Michalet et al. 2016, Rosbakh et al. 2017) and also respond fast to warming in high latitude grasslands (Klanderud et al. 2015). Capturing small amounts of precipitation after drought periods could lead to the observed positive performance of graminoids with respect to both flower abundance and ANPP.

Declines in species richness

Local declines in species richness likely reflect competitive interactions under decreasing resource levels, finally leading to species loss due to environmental stress, as indicated by decreases in community biomass and green cover. However, this is likely exacerbated by the fact that we observed less investment into reproductive organs under climate change. Moreover, the downslope translocated monoliths were not in their native matrix vegetation, meaning there is less potential for recovery of native species from surrounding seed rain (Stein et al. 2008). This is especially important in alpine and montane plant communities, since they have been shown to lack competitive traits to resist novel species colonization from warmer climate vegetation (Alexander and Levine 2019, Meineri et al. 2020). Investigating actual seed rain in target sites of translocation experiments combined with germination trials of collected seeds is a valuable future avenue of research.

Implications for plant community composition

Almost all species of the translocated plant communities were able to track warmer climate by advancing their flowering onset. Our study highlights the vulnerability of species-rich montane grasslands to future climate changes, mainly due to the inability to withstand drought events under warmer temperatures. Montane plant communities exposed to warmer and drier environments suffered under drought as evidenced by early senescence and decreased plant investments into both reproductive organs and vegetative growth. Decreased number of flowers across many species translates into a decrease in potential seed rain and reproductive success (Liu et al. 2012). This is particularly important since high elevation communities have been shown to be highly susceptible to colonization by either non-native or more competitive graminoid species due to the lack of competitive traits, such as a fast and opportunistic resource acquisition and growth form (Meineri et al. 2020). Furthermore, this study contributes to a growing body of literature (i.e., Klanderud et al. 2015, Rosbakh et al. 2017, Wellstein et al. 2017, Berauer et al. 2019) observing shifts toward graminoid dominated, forb-depressed states in both subalpine and montane semi-natural grassland communities under changing climate. Future plant community dynamics, ecosystem services such as fodder quality (i.e., loss or extirpation of legumes), and biodiversity conservation efforts are highly dependent on species being able to maintain reproductive output under increasingly uncertain temperature and precipitation dynamics.

Literature Cited

Abeli, T., G. Rossi, R. Gentili, M. Gandini, A. Mondoni, and P. Cristofanelli. 2012. Effect of the extreme summer heat waves on isolated populations of two orophitic plants in the north Apennines (Italy). Nordic Journal of Botany 30:109–115.

Alexander, J. M., and J. M. Levine. 2019. Earlier phenology of a nonnative plant increases impacts on native competitors. Proceedings of the National Academy of Sciences of the United States of America 116:6199–6204.

Appenzeller, C., M. Begert, E. Zenklusen, and S. C. Scherrer. 2008. Monitoring climate at Jungfraujoch in the high Swiss Alpine region. Science of the Total Environment 391:262–268.

Arfin Khan, M. A. S., C. Beierkuhnlein, J. Kreyling, S. Backhaus, S. Varga, and A. Jentsch. 2018. Phenological sensitivity of early and late flowering species under seasonal warming and altered precipitation in a seminatural temperate grassland ecosystem. Ecosystems 21:1306–1320.

Bardgett, R. D., L. Mommer, and F. T. De Vries. 2014. Going underground: root traits as drivers of ecosystem processes. Trends in Ecology & Evolution 29:692–699.

Barnabas, B., K. Jäger, and A. Fehér. 2008. The effect of drought and heat stress on reproductive processes in cereals. Plant, Cell & Environment 31:11–38.

Benot, M.-L., P. Saccone, E. Pautrat, R. Vicente, M.-P. Colace, K. Grigulis, J.-C. Clément, and S. Lavorel. 2014. Stronger short-term effects of mowing than extreme summer weather on a subalpine grassland. Ecosystems 17:458–472.

Berauer, B. J., P. A. Wilfahrt, M. A. S. Arfin-Khan, P. Eibes, A. Von Heßberg, J. Ingrisch, M. Schloter, M. A. Schuchardt, and A. Jentsch. 2019. Low resistance of montane and alpine grasslands to abrupt changes in temperature and precipitation regimes. Arctic, Antarctic, and Alpine Research 51:215–231.

Bernal, M., M. Estiarte, and J. Peñuelas. 2011. Drought advances spring growth phenology of the Mediterranean shrub Erica multiflora. Plant Biology 13:252–257.

Box, J. E., et al. 2019. Key indicators of Arctic climate change: 1971–2017. Environmental Research Letters 14:045010.

Buchner, O., M. Stoll, M. Karadar, I. Kranner, and G. Neuner. 2015. Application of heat stress in situ demonstrates a protective role of irradiation on photosynthetic performance in alpine plants: heat stress on alpine plants. Plant, Cell & Environment 38:812–826.

Buras, A., A. Rammig, and C. S. Zang. 2019. Quantifying impacts of the drought 2018 on European ecosystems in comparison to 2003. preprint, Earth System Science/Response to Global Change: Climate Change.

CaraDonna, P. J., A. M. Iler, and D. W. Inouye. 2014. Shifts in flowering phenology reshape a subalpine plant community. Proceedings of the National Academy of Sciences of the United States of America 111:4916–4921.

Carbognani, M., G. Bernareggi, F. Perucco, M. Tomaselli, and A. Petraglia. 2016. Micro-climatic controls and warming effects on flowering time in alpine snowbeds. Oecologia 182:573–585.

Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. Ecology 93:1765–1771.

Cornelius, C., J. Heinichen, M. Drösler, and A. Menzel. 2014. Impacts of temperature and water table manipulation on grassland phenology. Applied Vegetation Science 17:625–635.

Cornelius, C., A. Leingärtner, B. Hoiss, J. Krauss, I. Steffan-Dewenter, and A. Menzel. 2013. Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. Journal of Experimental Botany 64:241–251.

da Silveira Pontes, L., V. Maire, J. Schellberg, and F. Louault. 2015. Grass strategies and grassland community responses to environmental drivers: a review. Agronomy for Sustainable Development 35:1297–1318.

De Boeck, H. J., S. Bassin, M. Verlinden, M. Zeiter, and E. Hiltbrunner. 2016. Simulated heat waves affected alpine grassland only in combination with drought. New Phytologist 209:531–541.

Dietrich, J. D., and M. D. Smith. 2016. The effect of timing of growing season drought on flowering of a dominant C4 grass. Oecologia 181:391–399.

Dunne, J. A., J. Harte, and K. J. Taylor. 2003. Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. Ecological Monographs 73:69–86.

Dyer, A. G., A. Jentsch, M. Burd, J. E. Garcia, J. Giejsztowt, M. G. Gutierrey de Camargo, E. Tjørve, K. M. C. Tjørve, P. S. White, and M. Shrestha. 2021. Fragmentary blue: resolving the rarity paradox in flower colours. Frontiers in Plant Science 11:618203.

Engler, R., et al. 2011. 21st century climate change threatens mountain flora unequally across Europe. Global Change Biology 17:2330–2341.

Gellesch, E., M. A. S. Arfin Khan, A. Jentsch, and C. Beierkuhnlein. 2017. Grassland experiments under climatic extremes: reproductive fitness versus biomass. Environmental and Experimental Botany 144:68–75.

Giejsztowt, J., A. T. Classen, and J. R. Deslippe. 2020. Climate change and invasion may synergistically affect native plant reproduction. Ecology 101:e02913.

Giménez-Benavides, L., A. Escudero, and J. M. Iriondo. 2007. Reproductive limits of a late-

flowering high-mountain Mediterranean plant along an elevational climate gradient. New Phytologist 173:367–382.

Gobiet, A., S. Kotlarski, M. Beniston, G. Heinrich, J. Rajczak, and M. Stoffel. 2014. 21st century climate change in the European Alps—A review. Science of the Total Environment 493:1138–1151.

Grant, K., J. Kreyling, C. Beierkuhnlein, and A. Jentsch. 2017. Importance of seasonality for the response of a mesic temperate grassland to increased precipitation variability and warming. Ecosystems 20:1454–1467.

Grant, K., J. Kreyling, H. Heilmeier, C. Beierkuhnlein, and A. Jentsch. 2014. Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. Ecological Research 29:991–1001.

Guo, L., J. Chen, E. Luedeling, J.-S. He, J. Cheng, Z. Wen, and C. Peng. 2018. Early-spring soil warming partially offsets the enhancement of alpine grassland aboveground productivity induced by warmer growing seasons on the Qinghai-Tibetan Plateau. Plant and Soil 425:177–188.

Hegland, S. J., A. Nielsen, A. Lázaro, A.-L. Bjerknes, and Ø. Totland. 2009. How does climate warming affect plant-pollinator interactions? Ecology Letters 12:184–195.

Hollister, R. D., P. J. Webber, and C. Bay. 2005. Plant response to temperature in Northern Alska: implications for predicting vegetation change. Ecology 86:1562–1570.

Inouye, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362.

IPCC. 2007. Page Climate Change 2007: The Physical Science Basis. Cambridge University Press, Cambridge, UK and New York, New York, USA.

Jäger, E. J., and W. Rothmaler, editors. 2017. Rothmaler - Exkursionsflora von Deutschland. 2: Gefäßpflanzen: Grundband. 21., durchgesehene Auflage. Springer Spektrum, Berlin Heidelberg, Germany.

Jentsch, A., J. Kreyling, J. Boettcher-Treschkow, and C. Beierkuhnlein. 2009. Beyond gradual warming: Extreme weather events alter flower phenology of European grassland and heath species. Global Change Biology 15:837–849.

Jentsch, A., and P. S. White. 2019. A theory of pulse dynamics and disturbance in ecology. Ecology 100: e02734.

Klanderud, K., V. Vandvik, and D. Goldberg. 2015. The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. PLOS ONE 10:e0130205.

Knapp, A. K., et al. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. BioScience 58:811–821.

Körner, C. 2003. Alpine plant life: functional plant ecology of high mountain ecosystems. Second edition. Springer, Berlin, Germany.

Körner, C. 2006. Significance of temperature in plant life. Pages 48–69 in J. I. L. Morison and M. D. Morecroft, editors. Plant growth and climate change. Blackwell Publishing Ltd, Oxford, UK.

Kreyling, J., et al. 2017. Species richness effects on grassland recovery from drought depend on community productivity in a multisite experiment. Ecology Letters 20:1405–1413.

Kreyling, J., M. Wenigmann, C. Beierkuhnlein, and A. Jentsch. 2008. Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition. Ecosystems 11:752–763.

Kübert, A., M. Götz, E. Kuester, A. Piayda, C. Werner, Y. Rothfuss, and M. Dubbert. 2019. Nitrogen loading enhances stress impact of drought on a seminatural temperate grassland. Frontiers in Plant Science 10:1051.

Larcher, W. 2003. Physiological plant ecology: ecophysiology and stress physiology of functional groups. Fourth edition. Springer, Berlin, Germany.

Leitinger, G., R. Ruggenthaler, A. Hammerle, S. Lavorel, U. Schirpke, J.-C. Clement, P. Lamarque, N. Obojes, and U. Tappeiner. 2015. Impact of droughts on water provision in managed alpine grasslands in two climatically different regions of the Alps. Ecohydrology 8:1600–1613.

Lenth, R. 2020. Estimated marginal means, aka least-squares means. R package version 1.5.2-1. https://cran.r-project.org/web/packages/emmeans/index.html

Liu, Y., J. Mu, K. J. Niklas, G. Li, and S. Sun. 2012. Global warming reduces plant reproductive output for temperate multi-inflorescence species on the Tibetan plateau. New Phytologist 195:427–436.

Mackie, K. A., M. Zeiter, J. M. G. Bloor, and A. Stampfli. 2019. Plant functional groups mediate drought resistance and recovery in a multisite grassland experiment. Journal of Ecology 107:937–949.

Meier, U. 2018. Growth stages of mono- and dicotyledonous plants. BBCH Monograph. Open Agrar Repositorium, Quedlinburg, Germany.

Meineri, E., K. Klanderud, J. Guittar, D. E. Goldberg, and V. Vandvik. 2020. Functional traits, not productivity, predict alpine plant community openness to seedling recruitment under climatic warming. Oikos 129:13–23.

Menzel, A., and P. Fabian. 1999. Growing season extended in Europe. Nature 397:659–659.

Menzel, A., and T. Sparks. 2007. Temperature and plant development: phenology and seasonality. Pages 70–95 *in* Plant growth and climate change. John Wiley and Sons, Hoboken, New Jersey, USA.

Michalet, R., C. Schöb, S. Xiao, L. Zhao, T. Chen, L. An, and R. M. Callaway. 2016. Beneficiary feedback effects on alpine cushion benefactors become more negative with increasing cover of graminoids and in dry conditions. Functional Ecology 30:79–87.

Milbau, A., D. Reheul, B. De Cauwer, and I. Nijs. 2007. Factors determining plant–neighbour interactions on different spatial scales in young species-rich grassland communities. Ecological Research 22:242–247.

Miller-Rushing, A. J., and D. W. Inouye. 2009. Variation in the impact of climate change on flowering phenology and abundance: an examination of two pairs of closely related wildflower species. American Journal of Botany 96:1821–1829.

Moore, L. M., and W. K. Lauenroth. 2017. Differential effects of temperature and precipitation on early- vs. late-flowering species. Ecosphere 8:e01819.

Munson, S. M., and A. A. Sher. 2015. Long-term shifts in the phenology of rare and endemic Rocky Mountain plants. American Journal of Botany 102:1268–1276.

Nagy, L., J. Kreyling, E. Gellesch, C. Beierkuhnlein, and A. Jentsch. 2013. Recurring weather extremes alter the flowering phenology of two common temperate shrubs. International Journal of Biometeorology 57:579–588.

Nord, E. A., and J. P. Lynch. 2009. Plant phenology: a critical controller of soil resource acquisition. Journal of Experimental Botany 60:1927–1937.

Oberbauer, S. F., et al. 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment. Philosophical Transactions of the Royal Society B: Biological Sciences 368:20120481–20120481.

Parsons, P. A. 1990. The metabolic cost of multiple environmental stresses: implications for climatic change and conservation. Trends in Ecology & Evolution 5:315–317.

Peñuelas, J., I. Filella, X. Zhang, L. Llorens, R. Ogaya, F. Lloret, P. Comas, M. Estiarte, and J. Terradas. 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. New Phytologist 161:837–846.

Pepin, N., et al. 2015. Elevation-dependent warming in mountain regions of the world. Nature Climate Change 5:424.

Pinheiro J., D. Bates, S. DebRoy, D. Sarkar, R Core Team. 2021. nlme: linear and nonlinear mixed effects models. R package version 3.1-152. https://CRAN.R-project.org/package=nlme

R Core Team. 2018. R version 3.5.2 (code name 'Eggshell Igloo'): a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rathke, B., and E. Lacey. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology, Evolution, and Systematics 16:179–214.

Robinson, T. M. P., K. J. La Pierre, M. A. Vadeboncoeur, K. M. Byrne, M. L. Thomey, and S. E. Colby. 2013. Seasonal, not annual precipitation drives community productivity across ecosystems. Oikos 122:727–738.

Rosbakh, S., A. Leingärtner, B. Hoiss, J. Krauss, I. Steffan-Dewenter, and P. Poschlod. 2017. Contrasting effects of extreme drought and snowmelt patterns on mountain plants along an elevation gradient. Frontiers in Plant Science 8:1478.

Saavedra, F., D. W. Inouye, M. V. Price, and J. Harte. 2003. Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment. Global Change Biology 9:885–894.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology & Evolution 18:648–656.

Scherrer D., and C. Körner. 2009. Infra-red thermometry of alpine landscapes challenges climatic warming projections. Global Change Biology 2602–2613. https://doi.org/10.1111/j.1365-2486.2009.02122.x

Schmidt, N. M., J. B. Mosbacher, P. S. Nielsen, C. Rasmussen, T. T. Høye, and T. Roslin. 2016. An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. Ecography 39:1250–1252.

Shaver, G., and J. Kummerow. 1992. Phenology, resource allocation, and growth of Arctic vascular plants. Pages 193–211 *in* F. Chapin, R. Jefferies, J. Reynolds, G. Shaver, and J. Svoboda, editors. Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, San Diego, California, USA.

Sherry, R. A., X. Zhou, S. Gu, J. A. Arnone, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Luo. 2007. Divergence of reproductive phenology under climate warming. Proceedings of the National Academy of Sciences of the United States of America 104:198–202.

Shipley, B., and J. Dion. 1992. The allometry of seed production in herbaceous angiosperms. American Naturalist 139:467–483.

Spinoni, J., J. V. Vogt, G. Naumann, P. Barbosa, and A. Dosio. 2018. Will drought events become more frequent and severe in Europe? International Journal of Climatology 38:1718–1736.

Stampfli, A., J. M. G. Bloor, M. Fischer, and M. Zeiter. 2018. High land-use intensity exacerbates shifts in grassland vegetation composition after severe experimental drought. Global Change Biology 24:2021–2034.

Stein, C., H. Auge, M. Fischer, W. W. Weisser, and D. Prati. 2008. Dispersal and seed limitation affect diversity and productivity of montane grasslands. Oikos 117:1469–1478.

Taylor, B. R., and D. J. Garbary. 2003. Late flowering plants from Northern Nova Scotia, Canada. Rhodora 105:118–135.

Tracey, A. J., and L. W. Aarssen. 2011. Competition and body size in plants: the between-species trade-off for maximum potential versus minimum reproductive threshold size. Journal of Plant Ecology 4:115–122.

Turner, M. G., et al. 2020. Climate change, ecosystems and abrupt change: science priorities. Philosophical Transactions of the Royal Society B: Biological Sciences 375:20190105.

Vetter, V. M. S., et al. 2019. Invasion windows for a global legume invader are revealed after joint examination of abiotic and biotic filters. Plant Biology 21:832–843.

Walter, J., A. Jentsch, C. Beierkuhnlein, and J. Kreyling. 2013. Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. Environmental and Experimental Botany 94:3–8.

Wellstein, C., P. Poschlod, A. Gohlke, S. Chelli, G. Campetella, S. Rosbakh, R. Canullo, J. Kreyling, A. Jentsch, and C. Beierkuhnlein. 2017. Effects of extreme drought on specific leaf area of grassland species: a meta-analysis of experimental studies in temperate and sub-Mediterranean systems. Global Change Biology 23:2473–2481.

Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. Davis. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. Proceedings of the National Academy of Sciences of the United States of America 105:17029–17033.

Wipf, S., V. Stoeckli, and P. Bebi. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. Climatic Change 94:105–121.

Wolkovich, E. M., and E. E. Cleland. 2011. The phenology of plant invasions: a community ecology perspective. Frontiers in Ecology and the Environment 9:287–294.

Younginger, B. S., D. Sirová, M. B. Cruzan, and D. J. Ballhorn. 2017. Is Biomass a reliable estimate of plant fitness? Applications in Plant Sciences 5:1600094.

Zeiter, M., S. Schärrer, R. Zweifel, D. M. Newbery, and A. Stampfli. 2016. Timing of extreme drought modifies reproductive output in semi-natural grassland. Journal of Vegetation Science 27:238–248.

Zhang, X., L. Alexander, G. C. Hegerl, P. Jones, A. K. Tank, T. C. Peterson, B. Trewin, and F. W. Zwiers. 2011. Indices for monitoring changes in extremes based on daily temperature and precipitation data: indices for monitoring changes in extremes. Wiley Interdisciplinary Reviews: Climate Change 2:851–870.

Zhao, Y., R. L. Antoniou-Kourounioti, G. Calder, C. Dean, and M. Howard. 2020. Temperature-dependent growth contributes to long-term cold sensing. Nature 583:825–829.

DATA AVAILABILITY

Data are available from Zenodo: https://doi.org/10.5281/zenodo.4772698.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3661/full