




## RESEARCH ARTICLE

# Earlier reproductive phenology of restored grasslands

Franziska M. Willems<sup>1,2</sup> , Johanna Bantin<sup>3</sup>, Norbert Hölzel<sup>3</sup> , Anna Bucharova<sup>1</sup> 

## Abstract

**Introduction:** Plants introduced to degraded ecosystems during restoration efforts often face novel environmental conditions. Consequently, plant functional traits can differ between restored and reference sites, even within the same species. Studies on such intraspecific variation mainly focused on vegetative traits, while the timing of life-history events, phenology, received less attention so far.

**Objectives:** This study investigates intraspecific and interspecific variation in reproductive phenology (flowering, seed ripening, or seed dispersal) by comparing the timing of phenology events between restored and semi-natural meadows.

**Methods:** We examined the reproductive phenology of 16 flowering plant species across 47 restored meadows and 16 reference, semi-natural meadows within the same region in central Europe.

**Results:** Plant reproductive phenology in restored meadows was, on average, 2 days earlier than in reference meadows. This trend was particularly pronounced among species with early seasonal development.

**Conclusion:** Such phenological shifts highlight how changes in environmental and management conditions may influence plant phenology in the context of restoration. Possible explanations for these shifts include warmer microclimates and different soil properties in restored meadows, as well as differences in management practices, such as earlier mowing. Our findings contribute to a deeper understanding of restoration outcomes and underscore the importance of considering restoration-induced phenological shifts in conservation and management practices.

**Implications for Practice:** Reproductive phenology in plants can vary substantially between restored and semi-natural grasslands, even among populations of the same species within a single region. Such shifts in the timing of flowering and seed production may have far-reaching consequences for ecological interactions, yet their broader impacts remain insufficiently understood. Further research is needed to evaluate how altered phenological patterns influence associated organisms, including pollinators, herbivores, and seed dispersers, as well as overall pollination dynamics and reproductive success. Improving our understanding of ongoing phenological changes will enable practitioners to adjust management timing and site conditions more effectively. This knowledge can help mitigate undesired shifts in restored grasslands or, alternatively, be applied strategically to enhance temporal heterogeneity and support higher biodiversity.

**Key words:** flowering, grasslands, intraspecific variation, management, meadows, phenology, restoration

## Introduction

Ecosystem restoration is crucial to bend the curve of biodiversity decline, recover ecological functionality, and stabilize the Earth's climate (Díaz et al. 2019; IPBES 2019; IPCC 2019). Consequently, the United Nations declared the period between 2021 and 2030 as the “Decade on Ecosystem Restoration” (United Nations General Assembly 2019). Degraded terrestrial ecosystems often lack target vegetation, and their restoration requires the reintroduction of plant diaspores from other sources (Török et al. 2011; Palma & Laurance 2015). However, the establishment and persistence of the vegetation can be challenged by the environment of restored sites.

Environmental conditions at restored sites often differ from the ones at natural sites (Brudvig et al. 2013; Klein-Raufhake et al. 2022). As restored sites are often located on former arable land that has been subject to land consolidation, there are fewer hedges, trees, and other fragmenting elements (Burel & Baudry 1990; Bronstert et al. 1995; Robinson & Sutherland 2002). This can cause differences in microclimate, such as higher temperatures, stronger winds, and less humidity (Kanzler et al. 2019; Jacobs et al. 2022). The soils are affected by post-arable legacies, including enrichment with phosphorus and lack of other essential nutrients such as nitrogen due to

disrupted natural nutrient cycling (Walker et al. 2004; McLachlan 2006; Smits et al. 2008). Land use might also differ because restored areas are sometimes used for other purposes, such as fodder production, timber extraction, agroforestry, or infrastructure installations such as photovoltaic arrays (Dosskey et al. 2012; Bucharova et al. 2024; Zhang et al. 2024).

The environmental differences between restored and natural sites affect plant functional traits, which, in turn, influence ecosystem functions (Pywell et al. 2003; Balazs et al. 2020; Zirbel &

Author contributions: AB, NH conceived the ideas and designed the methodology for this study; JB collected the data; FMW led the data analysis and the writing of the manuscript; AB, JB, NH contributed to the drafts and gave final approval for publication.

<sup>1</sup>Department of Biology, University Marburg, Marburg, Germany

<sup>2</sup>Address correspondence to F. M. Willems, email [franziska.willems@uni-marburg.de](mailto:franziska.willems@uni-marburg.de)

<sup>3</sup>Institute of Landscape Ecology, University Münster, Münster, Germany

© 2026 The Author(s). Restoration Ecology published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.

This is an open access article under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

doi: 10.1111/rec.70298

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.70298/supinfo>

Brudvig 2020). Differences in mean community functional traits in response to the environment are predominantly driven by differences in species composition (Hodgson et al. 2011; Bruelheide et al. 2018). However, evidence is emerging that there are intraspecific differences in functional traits between individuals growing at restored and natural sites (Andrade et al. 2014; Klein-Raufhake et al. 2022; Bucharova et al. 2024). Research typically focused on vegetative functional traits like plant height, leaf traits, or nutrient content in the tissues because there is a well-established link between these traits, the environment, and plant performance (Chaves et al. 2002; Jung et al. 2014). Phenology-related traits received far less attention so far (but see Bucharova et al. 2024).

Phenology, that is, the timing of life-history events such as leaf unfolding, flowering, or seed set, is crucial for plant survival, growth, and reproduction. Plants must synchronize their phenology with suitable environmental conditions and respond to potential changes. Most plants' life cycles are particularly dependent on temperature, daylength, and precipitation (Chmura et al. 2019). However, other factors shape plant phenology, for example, nutrient content in the soil, soil water dynamics, microclimate variation, or land use (Völler et al. 2017; Gómez-Giráldez et al. 2020; Williams et al. 2021). Many of these factors often differ between restored and natural sites, and it is likely that this will affect plant phenology. The difference might be most apparent early in the season, as plants with early phenologies typically react stronger to environmental cues (Chmura et al. 2019).

Reproductive phenology, that is, the timing of flowering, seed ripening, or seed dispersal, is a particularly important life-history trait. Beyond its central role in plant sexual reproduction, it influences population persistence and abundance (Inouye 2008; Willis et al. 2008; Wheeler et al. 2015). Shifts in reproductive timing can have cascading effects across trophic levels by altering interactions with pollinators, seed herbivores, and their predators (Bucharova et al. 2016, 2022). Differences in reproductive phenology between natural and restored meadows may therefore impact large parts of the interacting community (Johansen et al. 2019; Visser & Gienapp 2019; Bucharova et al. 2022). Yet, such differences were rarely documented.

To address this research gap, we recorded the reproductive phenology of 16 flowering species that commonly grow at both restored and ancient, semi-natural floodplain meadows in Germany, central Europe. The seed material for restoration was sourced from the ancient meadows and thus, the population at both types of meadows had the same genetic background at the time of restoration. We hypothesize that (1) the reproductive phenology of plants growing on restored meadows differs from the phenology of their conspecifics on semi-natural meadows, and (2) that these differences are particularly pronounced in species with early seasonal development.

## Methods

### Study System

We studied 47 restored and 17 ancient, semi-natural floodplain meadows in the Upper Rhine Valley, Germany, scattered in an area approximately  $1 \times 3.5$  km ( $49^{\circ}51'N$ ,  $8^{\circ}24'E$ ). For a map

of the study sites, see Figures S1 and S2. In the past, this floodplain has been covered by ancient meadows which were created by humans centuries ago for hay production and stable bedding. The long history of extensive land use of these meadows has led to the establishment of species-rich plant communities, including many specialized species of high conservation value (Donath et al. 2007). A substantial part of these floodplain meadows was converted to arable land in the second half of the twentieth century. Between 2000 and 2007, about 70 ha have been restored back to meadow. The source of diaspores for the restoration was green hay from the remnant semi-natural meadows (Hölzel & Otte 2003; Hölzel et al. 2006). Transfer of green hay is an established restoration method for Central European meadows, which effectively introduces not only high proportions of the target species but also the intraspecific genetic diversity of the donor populations (Hölzel & Otte 2003; Kiehl et al. 2010; Dittberner et al. 2019). Environmental conditions at these restored sites differ from the semi-natural ones. Restored sites included in this study are located on former arable land that was subject to land consolidation, while most of the semi-natural meadows are located along forest edges or hedgerows (Donath et al. 2003). Soils of these restored meadows are affected by agricultural legacies and often contain more phosphorus and potassium (Donath et al. 2007, 2015; Sommer et al. 2023). The land use timing also differs: restored meadows included in this study are typically mown earlier in the year, around mid-June, to preserve the nutritional value of the biomass, which is used as fodder for horses, while the remnants of ancient semi-natural meadows are mown later.

### Data Collection

We carried out the field work during 17 days between May 27 and 12 June 2020. This period was chosen because flowering, seed ripening, and seed dispersal of the observed species typically peak during this time in these meadows. The reproductive phenology of these plant communities is adapted to mowing that has shaped the ecosystem for centuries. Specifically, meadows are mown in summer to produce hay and thus most species flower and set ripe seed before they are mown. The time of field work was set to two and a half weeks prior to the earliest expected mowing date (June 15). No monitoring could take place after this date because at least some meadows were mown.

During the observation period, we repeatedly visited each meadow every three to 4 days. Both semi-natural and restored sites were evenly distributed across observation days (each day covered several semi-natural and several restored meadows) to avoid potential biases. We recorded the current phenology status (see below) for 16 typical grassland species that grow at both ancient and restored sites (Table 1). These 16 species represent all dicot species that achieved any reproductive phenology stage between the start of flowering and seed dispersal (see below) during the field work period and were present at least at three semi-natural and three restored sites. The monitoring was carefully designed to capture within-species variation in reproductive phenology and, in total, summed up to 170 hours of observation.

**Table 1.** List of the 16 species used in the analysis, indicating the number (*n*) of restored (total 47) and semi-natural (total 17) meadows the species was growing on and the phenological status that was recorded as well as the corresponding phenology rank that represents a semiquantitative gradient from early (rank 1) to late development (rank 12).

Species	Restored (n)	Natural (n)	Phenological state	Phenology rank
<i>Arabis nemorensis</i>	4	11	100% Seed ripening	5
<i>Euphorbia esula</i>	11	12	80% Seed ripening	6
<i>Galium album</i>	47	12	5% Seed ripening	9
<i>G. boreale</i>	18	9	50% Flowering	11
<i>G. wirtgenii</i>	49	15	5% Seed ripening	9
<i>Genista tinctoria</i>	16	6	5% Flowering	12
<i>Iris sibirica</i>	5	3	50% Seed ripening	8
<i>Iris. spuria</i>	20	3	80% Seed ripening	6
<i>Leucanthemum vulgare</i>	27	15	70% Seed ripening	7
<i>Lychnis flos-cuculi</i>	16	9	5% Dispersing	4
<i>Medicago lupulina</i>	32	5	20% Dispersing	3
<i>Ranunculus polyanthemus</i>	6	11	70% Seed ripening	7
<i>Securigera varia</i>	21	3	5% Flowering	12
<i>Tragopogon pratensis</i>	39	6	50% Dispersing	1
<i>Trifolium campestre</i>	32	5	30% Dispersing	2
<i>Valeriana pratensis</i>	21	12	70% Flowering	10

### Phenology Status and Rank

The selected 16 species differed in their phenological stages during the study period: while some had just initiated flowering, others were already dispersing seeds. Phenological studies typically focus on a single developmental stage—such as the onset of flowering—and track its timing across populations, species, or years (Tang et al. 2016; Chmura et al. 2019; Primack et al. 2023). Yet, this requires repeated visits over several months, which were logistically impossible in this study because of the global pandemic of the Coronavirus disease 2019 disease. Moreover, many of the meadows included in our study are mown as early as June, necessitating that all data collection be completed before mowing—often before the full reproductive sequence has occurred. As a pragmatic alternative, we defined species-specific phenology status (as explained below) and recorded the day when this status was achieved at each meadow.

Specifically, we recorded the reproductive phenology status that each species reached at each meadow at each visit (flowering, seed ripening, or dispersing seeds), and we estimated how many % of the individuals at a given meadow reached this status on a semicontinuous scale: 5, 20, 30, 50, 70, 80, and 100%. In case we observed more than one phenological stage for a plant species in a meadow—for example, if some individuals were flowering and others had ripening seeds—we estimated the proportion of the more advanced phenological status. For example, when 50% of the individuals on this specific meadow were flowering and 50% had already ripening seeds, we recorded “50% seed ripening.” After the field survey, we inspected the data, and for each species, we identified the phenology status that varied most over the observation period and meadows (Table 1). For example, *Arabis nemorensis*: at the beginning of the observation period, in only a few meadows, 100% of individuals had ripening seeds. At the end of the data collection period, in nearly all meadows, 100% of individuals had ripening seeds. The

phenology status “100% seed ripening” thus best captured the variability among the meadows for this specific species. In other species, this phenology status was different—for example, 5% flowering in *Genista tinctoria* or 70% seed ripening in *Leucanthemum vulgare* (see Table 1). We then noted the day when this species-specific phenology status was achieved at each meadow. This is the value for phenology timing that we used in the analyses. This method was specifically designed to capture within-species variability in reproductive phenology. For an extensive example of the approach, see Supplement S1 and Tables S1 and S2.

In the next step, we ranked all species based on their phenological status as defined in the previous analysis, to differentiate species along a gradient from early to late reproductive development. The species with the most advanced reproductive status during our field survey (*Tragopogon pratensis*, 50% dispersing seeds) was assigned the lowest phenology rank (= 1). In contrast, *G. tinctoria* and *Securigera varia* had only just started reproduction (5% of individuals with open flowers) and were assigned the highest rank (= 12). Other species were in between (Table 1). When the same phenology event was observed for two species, we assigned them the same phenology rank (see Table 1). This phenology rank represents a semiquantitative gradient from early to late reproductive development among the studied species.

### Statistical Analyses

We analyzed the data in two steps. First, to understand whether the timing of reproductive phenology differs between semi-natural and restored meadows, we related the phenology timing to the meadow history (semi-natural vs. restored). Second, to test whether the magnitude of the difference in reproductive phenology between restored and semi-natural meadows varies along the gradient from early to late reproductive development, we

related the species-specific effect sizes from the previous model to the species phenology rank. All analyses were carried out with the R software (R Core Team 2023) using the *rstanarm* package Version 2.32.1 (Goodrich et al. 2024).

In the first step, we tested whether phenology timing differs between restored and natural meadows. We used Bayesian multilevel regression models (also called linear “mixed models”). When phenology timing was the response variable ( $=y$ ) and meadow type was the single predictor (that can take two values  $i$ , “natural” or “restored”) and  $y$  is normally distributed with variance  $\sigma$ , ( $y_i \sim \text{Normal}(\mu, \sigma)$ ) the model can be written as:

$$\mu_i = \beta_{0,\text{species}} + \beta_{1,\text{species}} \text{Meadow type}_i$$

with  $\mu_i$  = predicted phenology timing,  $\beta_0$  = intercept, which is in this case the phenology timing on natural meadows,  $\beta_1$  = the effect of meadow type, that is, the difference in phenology timing on restored meadows. The small  $_{\text{species}}$  annotation implies that we estimated species-specific deviations for the phenology timing on natural meadows (= intercept  $\beta_0$ ) as well as species-specific effects of restoration ( $=\beta_1$ ). This corresponds to using species as a random factor with a random intercept and a random slope for the effect of restoration status. Thereby we estimated how much a species phenology timing differed from the average timing on natural meadows and from the average effect of restoration (i.e. the difference in timing on restored meadows compared to natural meadows). Both  $\beta_{0,\text{species}}$  and  $\beta_{1,\text{species}}$  are assumed to come from a multivariate normal distribution. For a complete model notation see Supplement S2 and for more explanations on this kind of model notation see, e.g. McElreath (2018).

In the second step, we tested whether the species-specific phenology differences between the ancient semi-natural and restored meadows vary along the gradient from early and to later flowering species. To do so we extracted the estimated differences in the phenology timing between semi-natural and restored meadows ( $\beta_{1,\text{species}}$ ) from the model described above for all 16 species. We then related these estimated differences in phenology timing as the response variable ( $=y$ ) to the phenology rank as the single predictor. Given that  $y$  is normally distributed with variance  $\sigma$ , ( $y_i \sim \text{Normal}(\mu, \sigma)$ ) The corresponding model can be written as:

$$\mu_i = \beta_0 + \beta_1 \text{Phenology rank}_i$$

with  $\mu_i$  = predicted average difference in phenology timing and  $\beta_1$  = the effect of phenology rank, that is, an estimate of how much the phenological response (= difference in phenology timing) differs between early and late flowering plants.

We used the *stan\_glm* function with four Markov chain Monte Carlo (MCMC) chains of 2000 iterations in the *rstanarm* package (Stan Development Team 2022; Goodrich et al. 2023) and weakly informative prior distributions (see Table S3) to reduce posterior uncertainty and stabilize the computations (Muth et al. 2018). Because previous information on parameter values (i.e. the effect of restoration status or phenology rank

on phenology timing) was limited, we used weakly informative default priors to avoid imposing strong assumptions on the models. Chain convergence and model fit and convergence was evaluated using the *shinystan* function (Gabry et al. 2022) and by ensuring that all  $\hat{R}$  values were below 1.1. following the procedure described by Muth et al. (2018). Raw data are shown in Figure S3. For graphical and numerical checks of model fit and convergence see Table 1 and Figures S4–S8. We summarized all posterior parameter distributions with their mean and 95% probability intervals (PI), that is, the 2.5 and 97.5% quantile of the posterior, which are the equivalent of the 95% confidence interval in a frequentist context.

## Results

Over all species, the phenology of plants on restored meadows was 2 days advanced in comparison to the plants growing on semi-natural meadows ( $\mu_{\beta_1} = -2.0$ , PI =  $[-2.8, -1.1]$ ) (Table S4; Fig. 1). The species-specific mean differences in phenology timing varied between 2.5 and 1.5 days (with variance  $\sigma^2_{\beta_1} = 0.7$ ) and were credibly different from zero (with 95% probability) for 14 of the 16 species (Tables S4 & S5; Fig. 1). Overall, the estimated difference in phenology timing decreased from early- to late-developing species (Tables S5 & S6; Fig. 2).

## Discussion

Phenology is an important trait that commonly contributes to local adaptation and affects plant interactions with pollinators and seed predators (Elzinga et al. 2007; Bucharova et al. 2022; Trunschke et al. 2024). Here, we show that the reproductive phenology of many species at restored meadows is, on average, 2 days earlier than that of conspecifics at semi-natural meadows in the same region. This trend was more pronounced in species that initiate reproductive development earlier in the season. The mechanisms behind the phenological differences are possibly both phenotypic plasticity and adaptation to the specific conditions at semi-natural and restored meadows (Anderson et al. 2012; Merilä & Hendry 2014; Bucharova et al. 2024). In any case, differences in reproductive phenology between natural and restored meadows could have complex consequences on the interaction biota (Johansen et al. 2019; Visser & Gienapp 2019).

Phenology differences between restored and natural meadows could be a plastic reaction to microclimate, soil conditions, or local plant diversity. Many of the ancient semi-natural meadows are located along forest edges, and they generally contain more trees and hedges compared to the restored meadows, which are usually located on former arable land with little structural diversity. This possibly influences local temperature and humidity, resulting in warmer conditions on restored meadows due to less shading, and consequently, earlier flowering or seed ripening (Tang et al. 2016; Piao et al. 2019; Willems et al. 2022). Earlier reproductive development at restored meadows could also be caused by soil conditions, as soils at these meadows are richer in phosphorus, and higher phosphorus supply advances reproductive phenology (Donath et al. 2007; Nord & Lynch 2008; Petraglia et al. 2014). Lastly, earlier phenology at

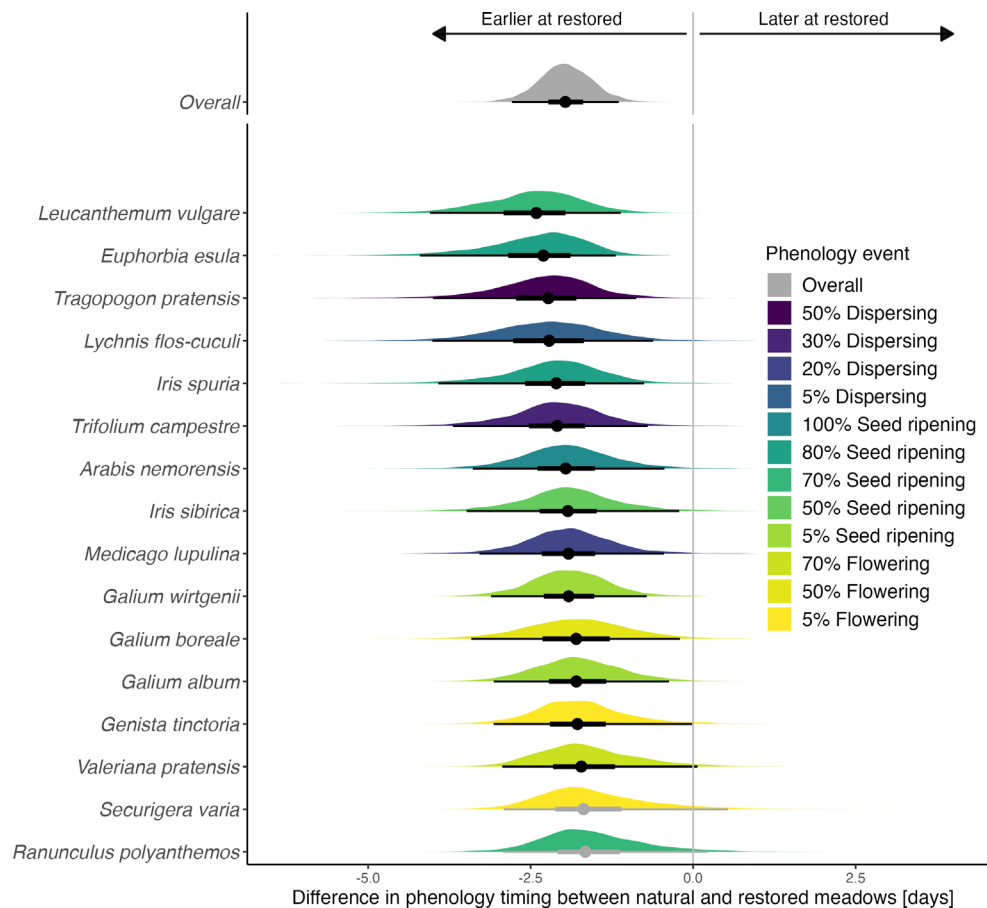


Figure 1. Estimated differences in phenology timing between natural and restored meadows. Negative differences indicate earlier phenology at restored meadows. Shown are posterior predictions, with points indicating the parameter estimates and whiskers their 50% (thick lines) and 95% (thin lines) probability intervals. Intervals credibly different from zero (with 95% probability) are printed in black. The average difference over all species is depicted at the top. Species are ordered by effect size (difference between the meadow types). Colors indicate the recorded phenology event for each species (see Table 1).

restored meadows could be affected by lower diversity of the plant community in comparison with ancient semi-natural meadows (Sommer et al. 2023). Plants growing in less diverse communities have been shown to flower earlier, an effect possibly mediated through changes in microclimate and soil properties (Wolf et al. 2017).

The earlier flowering and seed set at restored meadows could also reflect rapid local adaptation to management practices, specifically mowing regime (Reisch & Poschlod 2009; Völler et al. 2013, 2017). In contrast to late-mown semi-natural meadows, the restored meadows are mown rather early, at the time when many of the grassland species start producing seeds. Consequently, only plants that produce seeds before the vegetation is mown can contribute to the next generation. In species that start seed ripening around the time when the meadows are mown, there should be rather strong selection for earlier flowering. While this process is likely, we cannot provide evidence of rapid adaptation because we observed the plants in the field and we cannot differentiate whether the observed pattern is plastic or a result of selection. However, Bucharova et al. (2024) grew one of the species included in this study, *Galium wirtgenii*, in a

common garden and found evidence for genetic differentiation of flowering time between semi-natural and restored meadows. This differentiation happened over just a few generations because the seed material for restoration was sourced from the studied semi-natural meadows some 20 years ago and thus represented the same genetic pool. Such rapid evolution across just a few generations has been documented also in other study systems (Magnoli 2020; Conrady et al. 2023). Whether it is the case in other species included in this study, for which we detected field differences in phenology, would require a test in a common garden experiment.

The difference in phenology between restored and semi-natural meadows was more pronounced in species that initiate reproductive development earlier in the season. This is in line with previous studies (Fitter & Fitter 2002; Kopp et al. 2020; Freimuth et al. 2022). A reason for this might be that earlier-flowering plants show greater temperature sensitivity, potentially because emerging early helps to avoid competition (Shen et al. 2014; Springate & Kover 2014). In addition, because temperatures fluctuate more strongly early in the year, Menzel et al. (2006) suggest that, for insect-pollinated plants, a

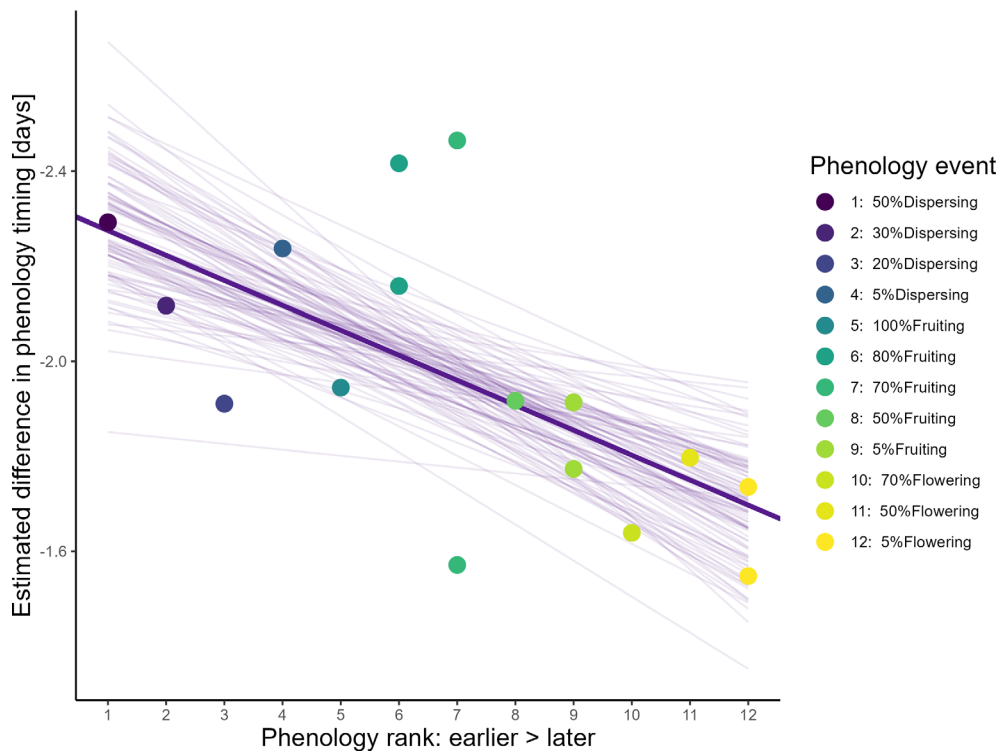


Figure 2. Relationship between the estimated differences in phenology timing (on restored compared to natural meadows) and phenology rank for all 16 species. Overall, the estimated differences in the phenology timing between restored and natural meadows were larger for species that initiate reproductive development earlier in the season. The purple line indicates this trend. Light purple lines are 100 draws of the fitted lines from the posterior distribution.

greater variability in spring phenology could help synchronization with pollinators.

However, in our case, the time elapsed between developmental stages—such as from the onset of flowering to seed maturity—can vary among species. This introduces some uncertainty when making direct comparisons along this gradient of species with comparatively early to late reproductive development. Nonetheless, this variability is unlikely to explain the observed pattern that differences between restored and semi-natural meadows were more pronounced in early-reproducing species, as such a systematic bias would require the duration of reproductive development to consistently co-vary with both phenology rank and meadow type.

Changes in plant reproductive phenology timing may affect interacting species, such as pollinators or seed herbivores. If the timing of phenological events shifts differently for species involved in entangled biotic interactions, this can lead to asynchrony, resulting in mismatches between species and their (food) resources (Schmitz 2013). Disruptions in plant–pollinator interactions can result in reduced quantity and quality of pollination services (Burkle et al. 2013; Forrest 2014; Franco-Cisterna et al. 2020). Furthermore, differences in flowering phenology may also lead to differences in seed-herbivore infestation rates (Bucharova et al. 2016). However, since the phenological differences we observed between restored and semi-natural meadows were rather modest, it is unlikely that they will cause such disruptions in plant–pollinator interactions

or declines in the quantity and quality of pollination services that have been observed elsewhere (Burkle et al. 2013; Forrest 2014; Ramos-Jiliberto et al. 2018). Previous research has even shown that heterogeneous flowering times at the landscape level can even improve floral resources for pollinators in agricultural landscapes (Johansen et al. 2019).

Some of the species included in the study did not reach the seed dispersal stage during the study period. The restored meadows were mown shortly after we finished data collection and thus, these species did not disperse seeds before mowing. The question arises how such species persist at the early mown restored sites. There are several possible mechanisms. In many species, seed ripening accelerates once the plant is cut. Since the cut biomass is typically dried on site for hay production, species with partially ripened seeds at the time of mowing are likely able to produce and disperse at least some viable seeds during the drying process (Martínková & Honěk 2010; Karrer 2016). Other species are able of extensive clonal reproduction (e.g. *G. boreale*), which partially compensates for a lack of generative reproduction (Dale & Elkington 1984). Some species flower and produce seeds when they regrow after being mown—for example, *Securigea varia* (personal observation). The meadows are also occasionally left unmown when the area is flooded during the early vegetation period and too wet for agricultural machinery. This opens a temporal regeneration niche that allows all species to produce seeds (Grubb 1977). For some species (e.g. *Arabis nemorensis*), the seeds can survive

for a long time in the soil and germinate also in the years when no fresh seeds were produced (Burmeier et al. 2011). Nevertheless, some late flowering species that are typical for the semi-natural meadows do not regularly persist at the early mown restored sites, probably because they fail to reproduce (e.g. *Serratula tinctoria*, personal observation). However, these species were not included in our study.

In summary, we have shown that the timing of reproductive development in 16 forb species from restored meadows differs from that of conspecifics growing in temperate semi-natural floodplain meadows. This might be relevant for many other grassland types and adds to mounting evidence that conspecific plants growing at restored and natural sites may significantly differ in functional and life-history traits (Klein-Raufhake et al. 2022; Bucharova et al. 2024).

## Acknowledgments

The data and R-code supporting the findings of this study are openly available in Zenodo. For the data see: <https://doi.org/10.5281/zenodo.16927200>, for coordinates of study sites see: <https://doi.org/10.5281/zenodo.17083835>. For R-code see: <https://doi.org/10.5281/zenodo.17035443>. This is organized via the University of Marburg. They have an agreement with the publisher that covers open access funds. The data that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.16927200>, reference number 16927200. Open Access funding enabled and organized by Projekt DEAL.

## LITERATURE CITED

- Anderson JT, Inouye DW, McKinney AM, Colautti RI, Mitchell-Olds T (2012) Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B: Biological Sciences* 279:3843–3852. <https://doi.org/10.1098/rspb.2012.1051>
- Andrade BO, Overbeck GE, Pilger GE, Hermann J-M, Conradi T, Boldrini II, Kollmann J (2014) Intraspecific trait variation and allocation strategies of calcareous grassland species: results from a restoration experiment. *Basic and Applied Ecology* 15:590–598. <https://doi.org/10.1016/j.baae.2014.08.007>
- Balazs KR, Kramer AT, Munson SM, Talkington N, Still SM, Butterfield BJ (2020) The right trait in the right place at the right time: matching traits to environment improves restoration outcomes. *Ecological Applications* 30: e2110. <https://doi.org/10.1002/eap.2110>
- Bronstert A, Vollmer S, Ihringer J (1995) A review of the impact of land consolidation on runoff production and flooding in Germany. *Physics and Chemistry of the Earth* 20:321–329. [https://doi.org/10.1016/0079-1946\(95\)00044-5](https://doi.org/10.1016/0079-1946(95)00044-5)
- Brudvig LA, Grman E, Habeck CW, Orrock JL, Ledvina JA (2013) Strong legacy of agricultural land use on soils and understory plant communities in long-leaf pine woodlands. *Forest Ecology and Management* 310:944–955. <https://doi.org/10.1016/j.foreco.2013.09.053>
- Bruehlheide H, Dengler J, Purschke O, Lenoir J, Jiménez-Alfaro B, Hennekens SM, et al. (2018) Global trait–environment relationships of plant communities. *Nature Ecology & Evolution* 2:1906–1917. <https://doi.org/10.1038/s41559-018-0699-8>
- Bucharova A, Conrady M, Klein-Raufhake T, Ratka V, Schultz F, Hölzel N (2024) Rapid evolution of flower phenology and clonality in restored populations of multiple grassland species. *Journal of Applied Ecology* 61:836–846. <https://doi.org/10.1111/1365-2664.14600>
- Bucharova A, Frenzel M, Mody K, Parepa M, Durka W, Bossdorf O (2016) Plant ecotype affects interacting organisms across multiple trophic levels. *Basic and Applied Ecology* 17:688–695. <https://doi.org/10.1016/j.baae.2016.09.001>
- Bucharova A, Lampe C, Conrady M, May E, Matheja J, Meyer M, Ott D (2022) Plant provenance affects pollinator network: implications for ecological restoration. *Journal of Applied Ecology* 59:373–383. <https://doi.org/10.1111/1365-2664.13866>
- Burel F, Baudry J (1990) Structural dynamic of a hedgerow network landscape in Brittany France. *Landscape Ecology* 4:197–210. <https://doi.org/10.1007/BF00129828>
- Burkle LA, Marlin JC, Knight TM (2013) Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* 339: 1611–1615. <https://doi.org/10.1126/science.1232728>
- Burmeier S, Eckstein RL, Donath TW, Otte A (2011) Plant pattern development during early post-restoration succession in grasslands—a case study of *Arabis nemorensis*. *Restoration Ecology* 19:648–659. <https://doi.org/10.1111/j.1526-100X.2010.00668.x>
- Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osório ML, Carvalho IF, Faria T, Pinheiro C (2002) How plants cope with water stress in the field. *Photosynthesis and growth*. *Annals of Botany* 89:907–916. <https://doi.org/10.1093/aob/mcf105>
- Chmura HE, Kharouba HM, Ashander J, Ehlman SM, Rivest EB, Yang LH (2019) The mechanisms of phenology: the patterns and processes of phenological shifts. *Ecological Monographs* 89:e01337. <https://doi.org/10.1002/ecm.1337>
- Conrady M, Lampe C, Bossdorf O, Hölzel N, Michalski S, Durka W, Bucharova A (2023) Plants cultivated for ecosystem restoration can evolve toward a domestication syndrome. *Proceedings of the National Academy of Sciences U S A* 120:e2219664120. <https://doi.org/10.1073/pnas.2219664120>
- Dale A, Elkington TT (1984) Distribution of clones of *Galium boreale* L. on Widdybank fell, Teesdale. *New Phytologist* 96:317–330. <https://doi.org/10.1111/j.1469-8137.1984.tb03569.x>
- Díaz S, Settele J, Brondizio ES, Ngo HT, Agard J, Arnett A, et al. (2019) Pervasive human-driven decline of life on earth points to the need for transformative change. *Science* 366:eaax3100. <https://doi.org/10.1126/science.aax3100>
- Dittberner H, Becker C, Jiao W, Schneeberger K, Hölzel N, Tellier A, De Meaux J (2019) Strengths and potential pitfalls of hay transfer for ecological restoration revealed by RAD-seq analysis in floodplain *Arabis* species. *Molecular Ecology* 28:3887–3901. <https://doi.org/10.1111/mec.15194>
- Donath TW, Bissels S, Hölzel N, Otte A (2007) Large scale application of diaspore transfer with plant material in restoration practice—impact of seed and microsite limitation. *Biological Conservation* 138:224–234. <https://doi.org/10.1016/j.biocon.2007.04.020>
- Donath TW, Hölzel N, Otte A (2003) The impact of site conditions and seed dispersal on restoration success in alluvial meadows. *Applied Vegetation Science* 6:13–22. <https://doi.org/10.1111/j.1654-109X.2003.tb00560.x>
- Donath TW, Schmiede R, Otte A (2015) Alluvial grasslands along the northern upper Rhine – nature conservation value vs. agricultural value under non-intensive management. *Agriculture, Ecosystems, & Environment* 200: 102–109. <https://doi.org/10.1016/j.agee.2014.11.004>
- Dosskey MG, Bentrup G, Schoeneberger M (2012) A role for agroforestry in forest restoration in the lower Mississippi Alluvial Valley. *Journal of Forestry* 110:48–55. <https://doi.org/10.5849/jof.10-061>
- Elzinga JA, Atlan A, Biere A, Gigord L, Weis AE, Bemasconi G (2007) Time after time: flowering phenology and biotic interactions. *Trends in Ecology & Evolution* 22:432–439. <https://doi.org/10.1016/j.tree.2007.05.006>
- Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. *Science* 296:1689–1691. <https://doi.org/10.1126/science.1071617>

- Forrest JRK (2014) Plant–pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? *Oikos* 124:4–13. <https://doi.org/10.1111/oik.01386>
- Freimuth J, Bossdorf O, Scheepens JF, Willems FM (2022) Climate warming changes synchrony of plants and pollinators. *Proceedings of the Royal Society B: Biological Sciences* 289:20212142. <https://doi.org/10.1098/rspb.2021.2142>
- Gabry J, Veen D, Stan Development Team, Andrae M, Betancourt M, Carpenter B (2022) shinystan: interactive visual and numerical diagnostics and posterior analysis for Bayesian models (version 2.6.0) [Computer software]. <https://cran.r-project.org/web/packages/shinystan/index.html> (accessed 01 Aug 2025)
- Gómez-Giráldez PJ, Pérez-Palazón MJ, Polo MJ, González-Dugo MP (2020) Monitoring grass phenology and hydrological dynamics of an oak–grass savanna ecosystem using Sentinel-2 and terrestrial photography. *Remote Sensing* 12:600. <https://doi.org/10.3390/rs12040600>
- Goodrich B, Gabry J, Ali I, Brilleman S (2023) rstanarm: Bayesian applied regression modeling via Stan. R package version 2.21.4. <https://mc-stan.org/rstanarm> (accessed 01 Aug 2025)
- Goodrich B, Gabry J, Ali I, Brilleman S (2024) Rstanarm: Bayesian applied regression modeling via Stan. R package version 2.32.1.
- Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52:107–145. <https://doi.org/10.1111/j.1469-185X.1977.tb01347.x>
- Hodgson JG, Montserrat-Martí G, Charles M, Jones G, Wilson P, Shipley B, et al. (2011) Is leaf dry matter content a better predictor of soil fertility than specific leaf area? *Annals of Botany* 108:1337–1345. <https://doi.org/10.1093/aob/mcr225>
- Hölzel N, Bissels S, Donath TW, Handke K, Harnisch M, Otte A (2006) Renaturierung von Stromtalwiesen am hessischen Oberrhein: Ergebnisse eines E+E-Vorhabens des Bundesamtes für Naturschutz. BfN-Schriftenvertrieb im Landwirtschaftsverlag, Münster.
- Hölzel N, Otte A (2003) Restoration of a species-rich flood meadow by topsoil removal and diaspore transfer with plant material. *Applied Vegetation Science* 6:131–140. <https://doi.org/10.1111/j.1654-109X.2003.tb00573.x>
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89:353–362. <https://doi.org/10.1890/06-2128.1>
- IPBES (Intergovernmental Science-policy Platform on Biodiversity and Ecosystem Services) (2019) Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn.
- IPCC (Intergovernmental Panel of Climate Change) (2019) An IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems (SRCCL). World Meteorological Organization. <https://www.ipcc.ch/site/assets/uploads/2019/11/SRCCL-Full-Report-Compiled-191128.pdf> (accessed 01 Aug 2025)
- Jacobs SR, Webber H, Niether W, Grahmann K, Lüttschwager D, Schwartz C, Breuer L, Bellingrath-Kimura SD (2022) Modification of the microclimate and water balance through the integration of trees into temperate cropping systems. *Agricultural and Forest Meteorology* 323:109065. <https://doi.org/10.1016/j.agrformet.2022.109065>
- Johansen L, Westin A, Wehn S, Iuga A, Ivascu CM, Kallioniemi E, Lennartsson T (2019) Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes. *Global Ecology and Conservation* 18:e00619. <https://doi.org/10.1016/j.gecco.2019.e00619>
- Jung V, Albert CH, Violle C, Kunstler G, Loucougaray G, Spiegelberger T (2014) Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology* 102:45–53. <https://doi.org/10.1111/1365-2745.12177>
- Kanzler M, Böhm C, Mirck J, Schmitt D, Veste M (2019) Microclimate effects on evaporation and winter wheat (*Triticum aestivum* L.) yield within a temperate agroforestry system. *Agroforestry Systems* 93:1821–1841. <https://doi.org/10.1007/s10457-018-0289-4>
- Karrer G (2016) Post harvest seed ripening (pot experiment). HALT Ambrosia – final project report and general publication of project findings. Julius-Kühn-Archiv. <https://doi.org/10.5073/jka.2016.455.13>
- Kiehl K, Kirmer A, Donath TW, Rasran L, Hölzel N (2010) Species introduction in restoration projects – evaluation of different techniques for the establishment of semi-natural grasslands in central and northwestern Europe. *Basic and Applied Ecology* 11:285–299. <https://doi.org/10.1016/j.bae.2009.12.004>
- Klein-Raufhake T, Höfner J, Hölzel N, Knorr K-H, Lampei C, Mudrák O, Bucharova A (2022) Nitrogen limitation reduces the performance of target plant species in restored meadows. *Restoration Ecology* 30:e13608. <https://doi.org/10.1111/rec.13608>
- Kopp CW, Neto-Bradley BM, Lipsen LPJ, Sandhar J, Smith S (2020) Herbarium records indicate variation in bloom-time sensitivity to temperature across a geographically diverse region. *International Journal of Biometeorology* 64: 873–880. <https://doi.org/10.1007/s00484-020-01877-1>
- Magnoli SM (2020) Rapid adaptation (or not) in restored plant populations. *Evolutionary Applications* 13:2030–2037. <https://doi.org/10.1111/eva.12959>
- Martínková Z, Honěk A (2010) Effect of desiccation temperature on viability of immature dandelion (*Taraxacum* agg.) seeds dried in mowed inflorescences. *Plant, Soil and Environment* 56:580–583. <https://doi.org/10.17221/81/2010-PSE>
- McElreath R (2018) Statistical rethinking: a Bayesian course with examples in R and Stan. Chapman and Hall/CRC, New York. <https://doi.org/10.1201/9781315372495>
- McLaughlan K (2006) The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. *Ecosystems* 9:1364–1382. <https://doi.org/10.1007/s10021-005-0135-1>
- Menzel A, Sparks TH, Estrella N, Roy DB (2006) Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography* 15:498–504. <https://doi.org/10.1111/j.1466-822X.2006.00247.x>
- Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications* 7:1–14. <https://doi.org/10.1111/eva.12137>
- Muth C, Oravecz Z, Gabry J (2018) User-friendly Bayesian regression modeling: a tutorial with rstanarm and shinystan. *The Quantitative Methods for Psychology* 14:99–119. <https://doi.org/10.20982/tqmp.14.2.p099>
- Nord EA, Lynch JP (2008) Delayed reproduction in *Arabidopsis thaliana* improves fitness in soil with suboptimal phosphorus availability. *Plant, Cell & Environment* 31:1432–1441. <https://doi.org/10.1111/j.1365-3040.2008.01857.x>
- Palma AC, Laurance SGW (2015) A review of the use of direct seeding and seedling plantings in restoration: what do we know and where should we go? *Applied Vegetation Science* 18:561–568. <https://doi.org/10.1111/avsc.12173>
- Petraglia A, Tomaselli M, Mondoni A, Brancaloni L, Carbognani M (2014) Effects of nitrogen and phosphorus supply on growth and flowering phenology of the snowbed forb *Gnaphalium supinum* L. *Flora – Morphology, Distribution, Functional Ecology of Plants* 209:271–278. <https://doi.org/10.1016/j.flora.2014.03.005>
- Piao S, Liu Q, Chen A, Janssens IA, Fu Y, Dai J, Liu L, Lian X, Shen M, Zhu X (2019) Plant phenology and global climate change: current progresses and challenges. *Global Change Biology* 25:1922–1940. <https://doi.org/10.1111/gcb.14619>
- Primack RB, Gallinat AS, Ellwood ER, Crimmins TM, Schwartz MD, Staudinger MD, Miller-Rushing AJ (2023) Ten best practices for effective phenological research. *International Journal of Biometeorology* 67:1509–1522. <https://doi.org/10.1007/s00484-023-02502-7>
- Pywell RF, Bullock JM, Roy DB, Warman L, Walker KJ, Rothery P (2003) Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* 40:65–77. <https://doi.org/10.1046/j.1365-2664.2003.00762.x>
- R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

- Ramos-Jiliberto R, Moisset de Espanés P, Franco-Cisterna M, Petanidou T, Vázquez DP (2018) Phenology determines the robustness of plant-pollinator networks. *Scientific Reports* 8:14873. <https://doi.org/10.1038/s41598-018-33265-6>
- Reisch C, Poschlod P (2009) Land use affects flowering time: seasonal and genetic differentiation in the grassland plant *Scabiosa columbaria*. *Evolutionary Ecology* 23:753–764. <https://doi.org/10.1007/s10682-008-9270-4>
- Robinson RA, Sutherland WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* 39:157–176. <https://doi.org/10.1046/j.1365-2664.2002.00695.x>
- Schmitz OJ (2013) 4.17—terrestrial food webs and vulnerability of the structure and functioning of ecosystems to climate. Pages 213–222. In: Pielke RA (ed) *Climate vulnerability*. Academic Press, Oxford.
- Shen M, Tang Y, Chen J, Yang X, Wang C, Cui X, et al. (2014) Earlier-season vegetation has greater temperature sensitivity of spring phenology in northern hemisphere. Earlier-season vegetation has greater temperature sensitivity of spring phenology in northern hemisphere. *PLoS One* 9:e88178. <https://doi.org/10.1371/journal.pone.0088178>
- Smits NAC, Willems JH, Bobbink R (2008) Long-term after-effects of fertilisation on the restoration of calcareous grasslands. *Applied Vegetation Science* 11:279–286. <https://doi.org/10.3170/2008-7-18417>
- Sommer L, Klinger YP, Donath TW, Kleinebecker T, Harvolk-Schöning S (2023) Long-term success of floodplain meadow restoration on species-poor grassland. *Frontiers in Ecology and Evolution* 10: 1061484. <https://doi.org/10.3389/fevo.2022.1061484>
- Springate DA, Kover PX (2014) Plant responses to elevated temperatures: a field study on phenological sensitivity and fitness responses to simulated climate warming. *Plant responses to elevated temperatures: a field study on phenological sensitivity and fitness responses to simulated climate warming*. *Global Change Biology* 20:456–465. <https://onlinelibrary.wiley.com/doi/10.1111/gcb.12430>
- Stan Development Team (2022) RStan: The R interface to Stan (R package version 2.33) [Computer software]. <http://mc-stan.org/> (accessed 01 Aug 2025)
- Tang J, Körner C, Muraoka H, Piao S, Shen M, Thackeray SJ, Yang X (2016) Emerging opportunities and challenges in phenology: a review. *Ecosphere* 7:e01436. <https://doi.org/10.1002/ecs2.1436>
- Török P, Vida E, Deák B, Lengyel S, Tóthmérész B (2011) Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. *Biodiversity and Conservation* 20:2311–2332. <https://doi.org/10.1007/s10531-011-9992-4>
- Trunschke J, Junker RR, Kudo G, Alexander JM, Richman SK, Till-Bottraud I (2024) Effects of climate change on plant-pollinator interactions and its multitrophic consequences. *Alpine Botany* 134:115–121. <https://doi.org/10.1007/s00035-024-00316-w>
- United Nations General Assembly (2019) Resolution 73/284: United Nations Decade on Ecosystem Restoration (2021–2030), A/RES/73/284. <http://undocs.org/A/RES/73/284> (accessed 01 Aug 2025))
- Visser ME, Gienapp P (2019) Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution* 3:879–885. <https://doi.org/10.1038/s41559-019-0880-8>
- Völler E, Auge H, Bossdorf O, Prati D (2013) Land use causes genetic differentiation of life-history traits in *Bromus hordeaceus*. *Global Change Biology* 19:892–899. <https://doi.org/10.1111/gcb.12087>
- Völler E, Bossdorf O, Prati D, Auge H (2017) Evolutionary responses to land use in eight common grassland plants. *Journal of Ecology* 105:1290–1297. <https://doi.org/10.1111/1365-2745.12746>
- Walker KJ, Stevens PA, Stevens DP, Mountford JO, Manchester SJ, Pywell RF (2004) The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biological Conservation* 119:1–18. <https://doi.org/10.1016/j.biocon.2003.10.020>
- Wheeler HC, Høye TT, Schmidt NM, Svenning J-C, Forchhammer MC (2015) Phenological mismatch with abiotic conditions—implications for flowering in Arctic plants. *Ecology* 96:775–787. <https://doi.org/10.1890/14-0338.1>
- Willems FM, Scheepens JF, Ammer C, Block S, Bucharova A, Schall P, Sehrt M, Bossdorf O (2021) Spring understory herbs flower later in intensively managed forests. *Ecological Applications* 31:e02332. <https://doi.org/10.1002/eap.2332>
- Willems FM, Scheepens JF, Bossdorf O (2022) Forest wildflowers bloom earlier as Europe warms: lessons from herbaria and spatial modelling. *New Phytologist* 235:52–65. <https://doi.org/10.1111/nph.18124>
- Willis CG, Ruhfel B, Primack RB, Miller-Rushing AJ, Davis CC (2008) Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences U S A* 105:17029–17033. <https://doi.org/10.1073/pnas.0806446105>
- Wolf AA, Zavaleta ES, Selmants PC (2017) Flowering phenology shifts in response to biodiversity loss. *Proceedings of the National Academy of Sciences U S A* 114:3463–3468. <https://doi.org/10.1073/pnas.1608357114>
- Zhang B, Zhang R, Li Y, Wang S, Zhang M, Xing F (2024) Deploying photovoltaic arrays in degraded grasslands is a promising win-win strategy for promoting grassland restoration and resolving land use conflicts. *Journal of Environmental Management* 349:119495. <https://doi.org/10.1016/j.jenvman.2023.119495>
- Zirbel CR, Brudvig LA (2020) Trait–environment interactions affect plant establishment success during restoration. *Ecology* 101:e02971. <https://doi.org/10.1002/ecy.2971>

## Supporting Information

The following information may be found in the online version of this article:

- Figure S1:** Overview map of the study sites in the Upper Rhine Valley in Germany.
- Figure S2:** Location of the study sites (except site 57).
- Figure S3:** Raw data of the phenology timing for all 16 species on restored and natural meadows.
- Figure S4.** BARG 2 B: Trace plot for the intercept ( $\beta_0$ , phenology on natural meadows), meadow type ( $\beta_1$ , difference in phenology timing on restored meadows) and sigma.
- Figure S5.** BARG 3 A: Graphical posterior predictive check.
- Figure S6.** BARG 3 A: Observations ( $y$ ) versus average simulated values ( $y_{rep}$ ).
- Figure S7.** BARG 3 A: Distributions of test statistics  $T(y_{rep})$  compared to the value of the statistic computed from the observed data  $T(y)$ .
- Figure S8.** Cohen's  $d$ , indicating a medium effect size estimate for the observed difference in phenology timing between natural and restored meadows.
- Table S1.** Hypothetical example data for *Arabis nemorensis* at three meadows across the sampling period.
- Table S2.** Data on the phenology timing for *Arabis nemorensis* for meadow A, B and C.
- Table S3.** BARG 1 C: Prior distributions of the model.
- Table S4.** BARG 3 B: Posterior summary statistics of the estimated parameters and model diagnostics of the model investigating the effect of meadow restoration status on phenology timing.
- Table S5.** BARG 3 B: Posterior summary statistics of the estimated parameters and model diagnostics of the model.
- Table S6.** BARG 3 B: Species specific estimates for the effect of meadows restoration status on phenology timing.
- Supplement S1.** Detailed description of phenology recording, including an example.
- Supplement S2.** Full model notation.

Coordinating Editor: Valter Amaral

Received: 19 March, 2025; Revised: 4 December, 2025; Accepted: 4 December, 2025