

Phenological patterns of herbaceous Mediterranean plant communities in spring: is there a difference between native and formerly-cultivated grasslands?

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Abstract

Background and aims – Plant phenology, defined as the timing of recurring life events like leaf flushing, flowering, or fruiting, is highly sensitive to environmental factors such as photoperiod, temperature, and moisture. Phenological synchrony between interacting species – such as plants and their pollinators – is of major importance to the structure and functioning of ecosystems. Plant phenology might also be affected by changes in edaphic conditions. However, whether former agricultural activities may shift phenological patterns of plant communities remains poorly understood. In this study, we evaluated the impact of past agricultural practices on herbaceous plant community phenology in the protected Mediterranean xeric grassland of La Crau (France).

Material and methods – We compared (1) species composition, and (2) phenological patterns of annuals, perennials, *Bromus rubens* (annual), and *Lobularia maritima* (perennial), in formerly-cultivated plots – abandoned for 30 years – and intact native grassland plots (steppe), both subjected to itinerant sheep grazing.

Key results and conclusion – Our results suggest that former agricultural activities can affect species composition of Mediterranean xeric grassland communities with differences visible after 30 years of abandonment, but only altered phenological patterns slightly. We suggest that climatic factors and sheep grazing acted as strong habitat filters constraining community assembly at the phenological level.

Keywords

agriculture legacy, Mediterranean dry grassland, plant phenology, phenological patterns, soil disturbance

INTRODUCTION

Plant phenology is defined as the timing of recurring life events (Lieth 1974), and involves reproductive phenomena such as flowering, fruiting, or seed germination, as well as vegetative processes like leaf flushing and shedding (Morellato et al. 2010; Wolkovich and Cleland 2011). Phenology is determined by a balance between intrinsic (e.g. constrained by phylogeny) and extrinsic factors (e.g. temperature, photoperiod; Bisigato et al. 2013).

Biotic pressures, such as seasonal presence of predators, pollinators, and seed dispersers, as well as the presence of sympatric species sharing pollinators or predators may also shape phenological patterns (Rathcke 1983; Fenner 1998). Notably, plant-pollinators interactions may operate as a habitat filter shaping the phenological composition of the community (e.g. the absence of a particular pollinator prevents the establishment of a plant species in a community; Sargent and Ackerly 2008). Flowering time is particularly sensitive to environmental

factors such as temperature, moisture, and photoperiod (Rathcke and Lacey 1985; Price and Waser 1998; Sherry et al. 2007; Bisigato et al. 2013). Phenology has thereby received increased attention over the last decades since it has been considered as the most sensitive and easily observable indicator of terrestrial ecosystem response to current climate change (i.e. advancement of spring events; Peñuelas and Filella 2001; Lavorel and Garnier 2002; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2007; Ding et al. 2013; Guo et al. 2015; Piao et al. 2019).

Shifts in the phenology of interacting species may induce shifts in their synchrony, with cascading consequences for communities, ecosystem dynamics, and ecosystem services (Yang and Rudolf 2010; Morellato et al. 2016; Kharouba et al. 2018). For example, phenological mismatch between the plant species *Corydalis ambigua* Cham. and Schlecht (Papaveraceae) and its pollinator led to a reduction of seed production owing to low pollination service (Kudo and Ida 2013). Other ecosystem services, such as carbon storage can be affected by phenological modifications. For instance, Keenan et al. (2014) showed that carbon uptake by forests might improve due to phenological shifts caused by climate change.

Variations in plant phenology can result from differences in soil structure and chemical composition including nutrient concentrations (Rossiter 1978; Wielgolaski 2001; Petraglia et al. 2014). Such modifications of soil characteristics can arise from agricultural activities. Agriculture is a major component of global changes (Vitousek 1994) and has important impacts on soils and ecosystems that outlast the duration of agricultural activity (Austrheim and Olsson 1999; McLauchlan 2006), notably by altering abiotic (e.g. nutrient content, pH, soil structure, water content) and biotic (e.g. species composition and structure, seed bank) conditions (Hobbs et al. 1988; Römermann et al. 2005). Phosphorus (P), one of the main components of most fertilizers, is a major determinant of plant growth and productivity (Aerts and Chapin 1999; Güsewell 2004). Phosphorus concentration can influence the phenology of annuals, which commonly display delayed flowering and maturity in response to low P (Rossiter 1978; Ma et al. 2002; Nord and Lynch 2008). Soil clay and silt contents, often shifted by agricultural activities, can also affect plant phenology by altering water retention (Wielgolaski 2001; Al Majou et al. 2008). Wielgolaski (2001) found that high clay content may favour high soil moisture, resulting in earlier bud break in *Betula pubescens* Ehrh. In contrast, Mediterranean annual species may shorten their life cycle due to water stress, with low soil moisture resulting in earlier flowering transition (Aronson et al. 1992). However, whether former agricultural activities may shift phenological patterns of re-established plant communities remains unknown.

This study focuses on the impact of former agricultural activities on the phenology of xeric grassland plant communities located in southeastern France, in the Plain of La Crau. La Crau is a protected socio-ecosystem hosting endemic species (e.g. the hedgehog grasshopper

Prionotropis rhodanica Uvarov; Foucart and Lecocq 1998) and unique species-rich plant assemblage (Devaux et al. 1983). The intact steppe vegetation is dominated by perennial species *Brachypodium retusum* (Pers.) P.Beauv. and *Thymus vulgaris* L. which represent approximately 50% of the biomass (Buisson and Dutoit 2006), and hosts a large diversity of annuals (Buisson et al. 2006). The durability of the ecosystem is closely linked with itinerant sheep grazing, which has been the traditional land-use for several centuries (Buisson and Dutoit 2006). We aim to evaluate the phenological patterns of plant communities that grew on different soil type by comparing (1) intact native grasslands, hereafter named steppe, and (2) abandoned fields, hereafter named formerly-cultivated plots. Römermann et al. (2005) reported important changes in the composition of plant communities but also in the physical and chemical soil characteristics of the formerly-cultivated plots; thereby a shift in phenological patterns is expected. At the community level, reproductive strategy (i.e. annuals and perennials) may influence the phenological pattern of the community (Burgheimer et al. 2006; Meng et al. 2016). Annual plants reproduce once and die (i.e. all resources are used for reproduction with none saved for the following season), while perennial plants reproduce repeatedly and cycle through vegetative and reproductive phases. Annual plant phenology may respond faster to environmental variations than that of perennials (i.e. annuals tend to flower earlier in response to climate change; Fitter and Fitter 2002; König et al. 2018), due to their faster generation times and evolution rates (Laroche and Bousquet 1999). The two groups are therefore analyzed separately. Also, because (1) phenological response to environmental variations can be species-specific (Bisigato et al. 2013) and (2) differences in phenology between formerly-cultivated and steppe communities can result from variations in soil conditions but also variations in species composition, we considered phenological patterns of *Bromus rubens* L. and *Lobularia maritima* (L.) Desv., respectively the annual and perennial species recorded in both plot types with the highest occurrence.

MATERIAL AND METHODS

Study area

Located in southeastern France (Bouches-du-Rhône), La Crau is a large plain (11,500 ha) considered as the only Mediterranean pseudo-steppe of France (Fig. 1). This steppe ecosystem is characterized by (1) a dry and windy Mediterranean climate (mean annual temperature 14 °C, mean annual precipitation 500 mm/year, more than 3000 hours of sunshine/year, and very strong winds blowing 334 days/year; Buisson and Dutoit 2004), (2) noticeable geological traits (an extremely flat topography with rounded siliceous stones covering 50% of the soil surface, an average soil depth of 40 cm overlying a 5 to 25

meter thick layer of impermeable conglomerate making the alluvial water table inaccessible to the roots of plants; Colomb and Roux 1978; Devaux et al. 1983; Buisson and Dutoit 2004), and (3) sheep grazing (Buisson and Dutoit 2004, 2006). The primary productivity of the vegetation steppe was assessed at 2.1 tons of Dry Matter/ha/year (Buisson et al. 2004), with a maximal biomass production in spring and autumn.

Since the 1960s, several types of cultivation occurred in some areas of the steppe, resulting in the fragmentation of the formerly homogenous steppe landscape (Buisson and Dutoit 2006). Our study site is located in the Nature Reserve of Peau de Meau (163 ha; Fig. 1), and includes about 25% of remaining steppe and 75% of formerly-cultivated plots. In this study, we focused on three formerly melon-cultivated plots (F1, F2, and F3; Fig. 1) located nearby a remnant patch of steppe (S1, S2, and S3; Fig. 1). Melon cultivation shaped the composition and the structure of the vegetation and the soil: (1) the deep ploughing brought some pieces of conglomerate into the soil and siliceous stones were sometimes removed (Römermann et al. 2004), (2) the plots were watered, fertilized (2500 kg/ha K at the time of ploughing and 250 kg/ha and 5-8-8 N, P, K at the time of setting) and treated against red spiders, aphids, and powdery mildew (Borrey 1965). The fields were cultivated at different time between 1960 and 1984, after which they were grazed by itinerant sheep herds from February to June, like the steppe, at two sheep/ha on average (Buisson and Dutoit 2006).

Edaphic conditions of formerly-cultivated plots are significantly different from the steppe, although

cultivation has been abandoned for many years before their investigation (Römermann et al. 2005; Helm et al. 2019; respectively ca 20 and 30 years). While soil analyses revealed small or no differences in soil nutrient contents between the steppe and formerly-cultivated plots (e.g. potassium, carbon, and organic matter content), the phosphorus content in formerly-cultivated plots could reach up to 4.4 times the content measured in steppe plots. Changes in physical structure of the soil were observed: clay content was higher in the remnant patch of steppe than in formerly-cultivated plots (Römermann et al. 2005).

Field sampling

Sampling was performed at six sites (Fig. 1): three formerly-cultivated plots named F1 (7 ha), F2 (5.2 ha), and F3 (6.7 ha) and three plots on remnant steppe named S1 (1.8 ha), S2 (2.6 ha) and S3 (4.4 ha) close to respective formerly-cultivated plots (see Buisson and Dutoit 2004 for detailed site history and aerial photographs). Such sites are optimal to study the relationships between former land cultivation and plant phenology because the short distance among plots (< 1 km) excludes any difference in climate (i.e. temperature, precipitation, and photoperiod) and soil depth is homogeneous in all plots (Buisson and Dutoit 2004).

We carried out our sampling during the period of the year where the annual species are going through various phenological stages (from vegetative to flower buds, flowers, fruits, and dispersion/senescence), from mid-



Figure 1. Study site. Geographic location and plot location are indicated. Plots S1, S2, and S3 (blue) are located on a remnant patch of steppe. Plots F1, F2 and F3 (pink) are located on formerly-cultivated sites. Maps from Google Earth (data from SOI, NOAA, U.S. Navy, NGA, GEBCO; images Landsat/Copernicus).

April to mid-June 2015 (Bourrelly et al. 1983). We stopped monitoring by mid-June because most plants started to be dry and were poorly identifiable. Every Monday at each of the six site, we randomly placed three 20 × 20 cm quadrats to record (1) the total number of individuals or clumps (i.e. thick group of the same species, probably clones) of each species using the World Flora Online (WFO) Plant List as the reference flora and (2) the number of individuals or clumps of each species in each of the five following phenophases: (a) vegetative state, (b) flower buds: flower buds visible, (c) flowers, (d) fruits: unripe and mature fruits, and (e) dispersal/senescence: seeds already dispersed / senescence of green tissues.

Since sheep grazing occurred at all plots during the experiment, phenological stage was sometimes hard to determine for severely grazed individuals. A sixth category, named 'grazed', was therefore included. As the same sheep flock grazed both types of plots and was not preferentially directed to one or another, we considered that the same grazing pressure was applied on all plots.

Data analyses

Comparison of plant community composition between formerly-cultivated and steppe plots

In order to compare the composition of plant communities, a Correspondence Analysis was run on the total number of individuals for each species (144 quadrats × 80 species) using the function 'dudi.coa' from the package 'ade4' in R v.3.2.0 (R Core Team 2015). Additionally, to examine

whether species richness differed between steppe and formerly-cultivated plots, we used a generalized linear mixed-effects model (GLMM) with negative binomial distribution to account for over-dispersion (Crawley 2007). We considered plot type (steppe or formerly-cultivated) as fixed explanatory variable and site (S1, S2, S3, F1, F2, and F3) as random effect. The analysis was performed using the function 'glmer.nb' from the package 'lme4' in R v.3.6.2 (R Core Team 2019).

Percentage of individuals in each phenophase

For each quadrat, we calculated the percentage of individuals in each phenophase j ($\text{Perc}_{\text{phen}j}$) using the formula:

$$\text{Perc}_{\text{phen}j} = \frac{\sum_{i=1}^k n_{i,j}}{\sum_{i=1}^k \sum_{j=1}^6 n_{i,j}} \times 100$$

where k is the total number of species on each quadrat and $n_{i,j}$ the number of individuals of species i in phenophase j . The formula was used to calculate the percentage of individuals in each phenophase for annuals (60 species), perennials (20 species), *B. rubens* and *L. maritima*.

Comparison of phenological patterns between formerly-cultivated and steppe plots

In order to assess the impact of former agriculture on phenological patterns, we used generalized linear mixed models with beta distribution (with beta family and logit link; Cribari-Neto and Zeileis 2010), to compare the percentage of individuals in each phenophase (i.e. mean $\text{Perc}_{\text{phen}j}$, response variable) at each date between

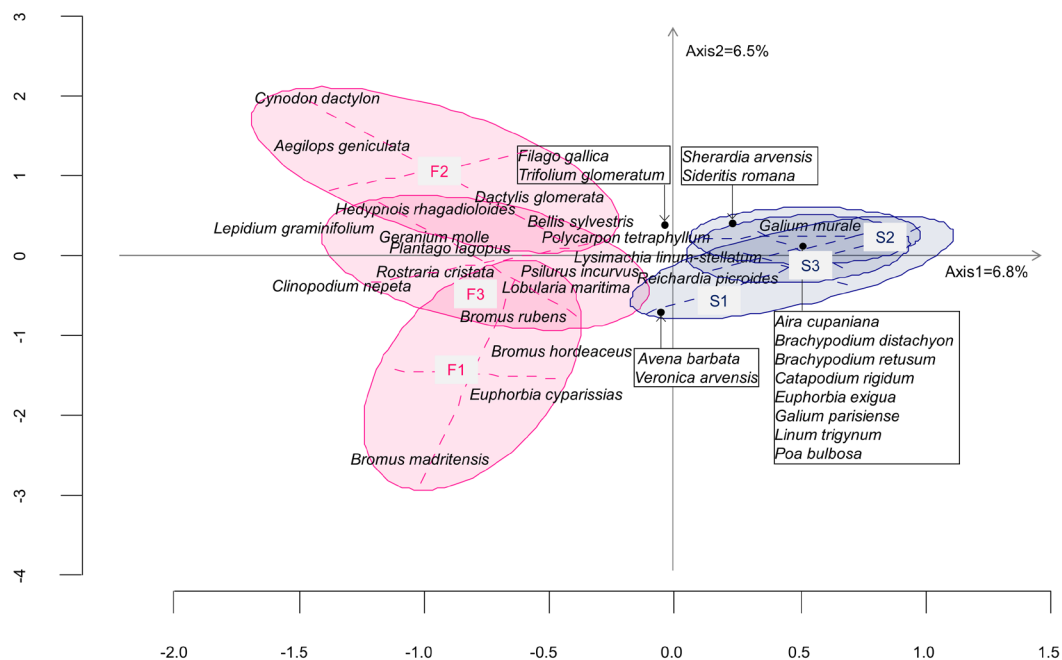


Figure 2. Correspondence analysis (CA) of species composition of the plant communities. S1, S2, and S3 correspond to native steppe plots (blue) and F1, F2, and F3 correspond to formerly-cultivated plots (pink). For each species, the total number of individuals was used for analysis. Species with less than 20 total individuals were not depicted. Final matrix: 144 quadrats × 80 species.

formerly-cultivated plots and steppe plots. We considered plot type (steppe or formerly-cultivated) as fixed explanatory variable and site (S1, S2, S3, F1, F2, and F3) as random effect. This was done for annuals, perennials, *B. rubens*, and *L. maritima*. We constructed 136 models (Supplementary file 1). The analyses were performed with the function 'glmmTMB' from the package 'glmmTMB' in R v.3.6.2 (R Core Team 2019).

RESULTS

Plant community composition

We sampled a total of 18 families, 80 species (60 annuals and 20 perennials), and 3765 individuals (Supplementary file 2). Species richness per quadrat was significantly lower

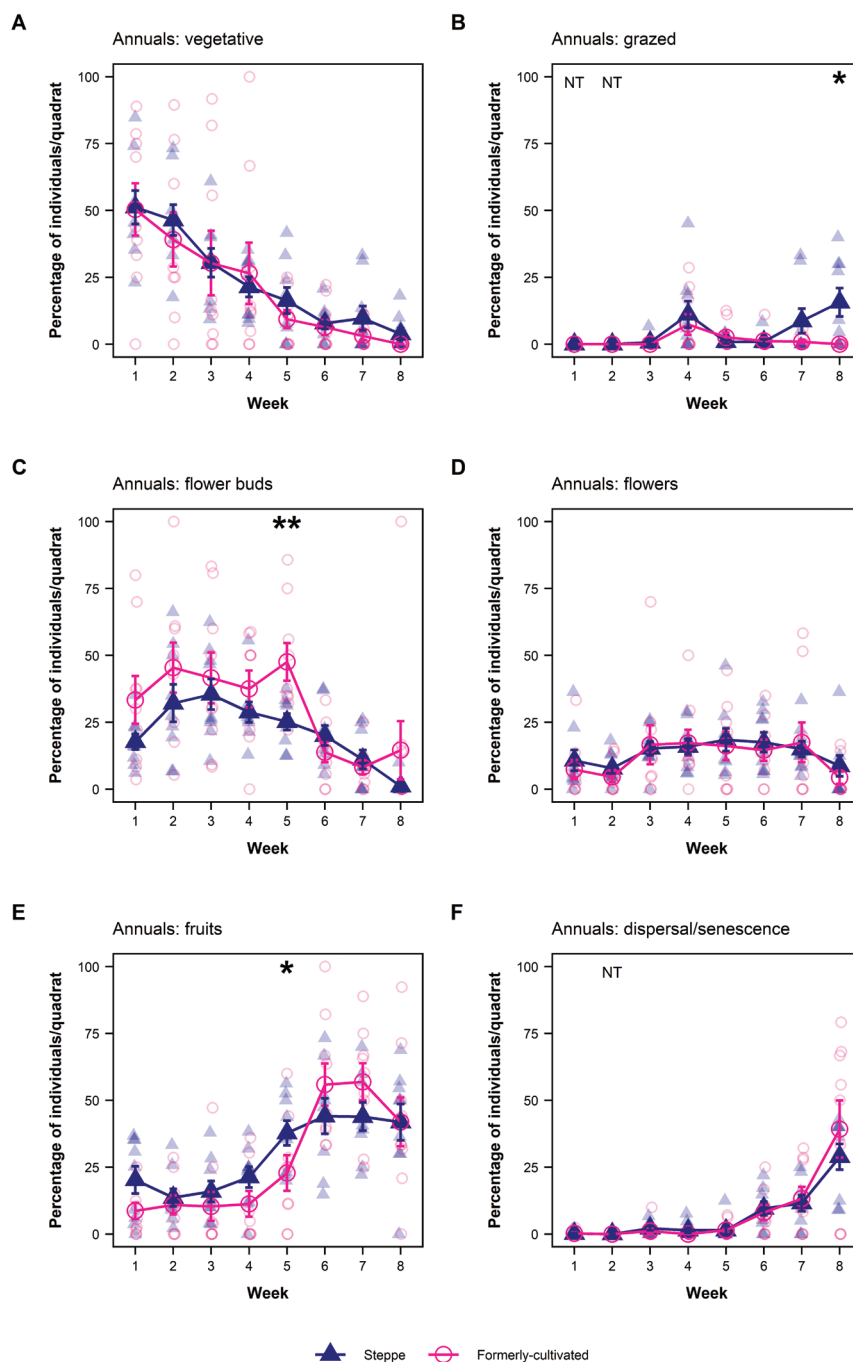


Figure 3. Annual species phenological patterns: percentage of individuals per quadrat over time (weeks) on steppe plots (blue triangles) and formerly-cultivated plots (pink circles). **A.** Vegetative state. **B.** Grazed. **C.** Carrying flower buds. **D.** Carrying flowers. **E.** Carrying fruits. **F.** In dispersal/senescence. Each small, light circle or triangle refers to one measurement (quadrat). Variations in means (\pm SE) are represented by the large, dark circles and triangles linked by segments. Significant differences between percentages of individuals in each phenophase at each date are represented (** $p < 0.01$; * $p < 0.05$). NT indicates that no statistical test was performed.

in formerly-cultivated plots (8.28 ± 0.3 , mean \pm SD) than in steppe plots (12.25 ± 0.9 , mean \pm SD) ($F = 5.681$, $p < 0.01$). Annual individuals represented 69.7% and 68.3% of total individuals in steppe plots and formerly-cultivated plots respectively.

As shown in the Correspondence Analysis (Fig. 2), axis 1 separates the steppe plots on the right (S1, S2, and S3) from cultivated plots (F1, F2, and F3) on the left. Steppe plots are associated with the presence of *Brachypodium*

distachyon (L.) P.Beauv., *B. retusum*, *Euphorbia exigua* L., *Linum trigynum* L., etc., while formerly-cultivated plots are associated with the presence of *Aegilops geniculata* Roth, *Bromus rubens*, *B. madritensis* L., *Clinopodium nepeta* (L.) Kuntze, etc. Axis 2 delineates the three formerly-cultivated plots: plot F1 is associated with the presence of *Bromus hordeaceus* L., *B. madritensis* and *Euphorbia cyparissias* L., plot F2 is associated with the presence of *A. geniculata* and *Cynodon dactylon* (L.) Pers.,

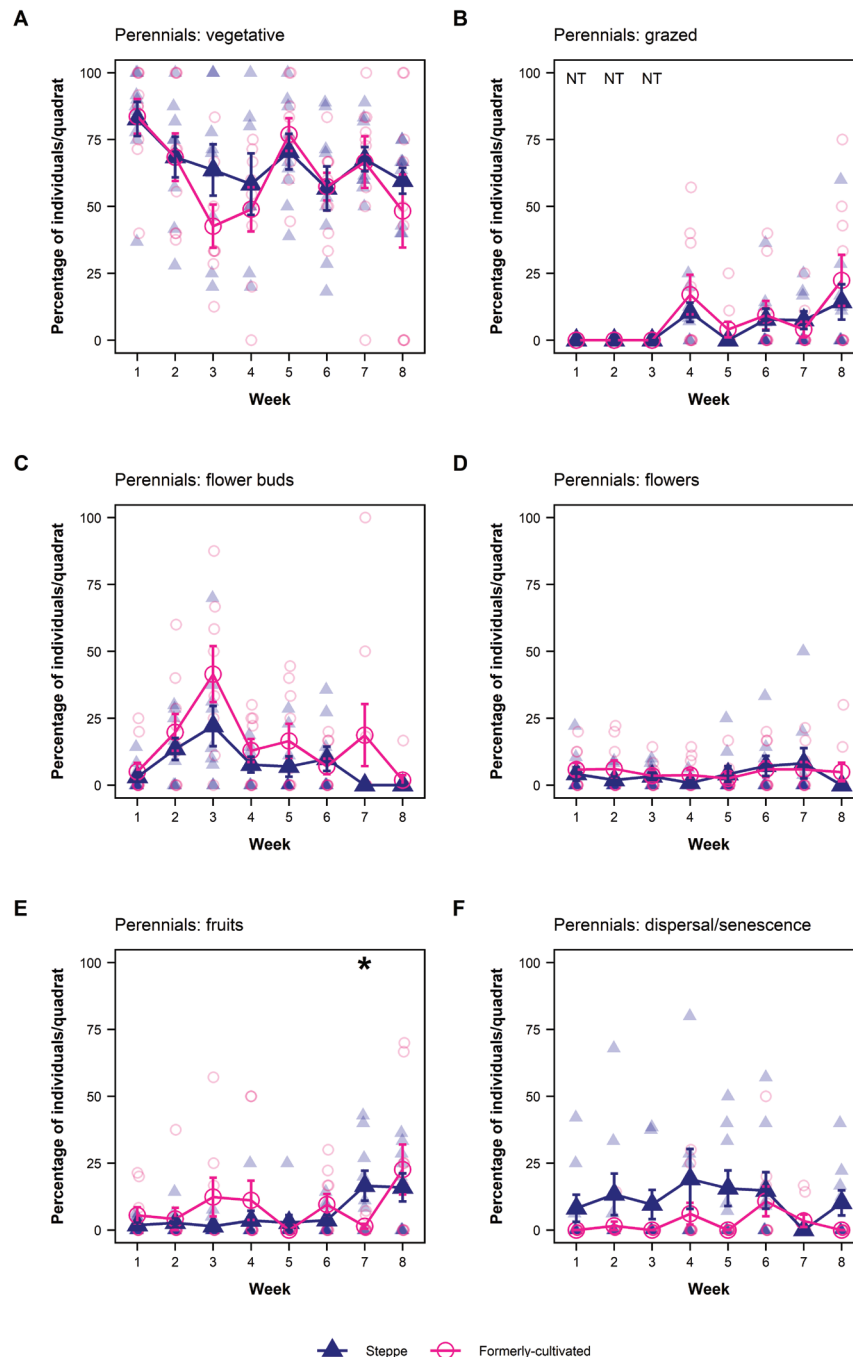


Figure 4. Perennial species phenological patterns: percentage of individuals per quadrat over time (weeks) on steppe plots (blue triangles) and formerly-cultivated plots (pink circles). **A.** Vegetative state. **B.** Grazed. **C.** Carrying flower buds. **D.** Carrying flowers. **E.** Carrying fruits. **F.** In dispersal/senescence. Each small, light circle or triangle refers to one measurement (quadrat). Variations in means (\pm SE) are represented by the large, dark circles and triangles linked by segments. Significant differences between percentages of individuals in each phenophase at each date are represented (* $p < 0.05$). NT indicates that no statistical test was performed.

and plot F3 is associated with the presence of *Lepidium graminifolium* L. and *C. nepeta*.

Phenological patterns

Annuals and perennials

While for both formerly-cultivated plots and steppe plots, the percentage of annuals in vegetative state decreased

over time, the percentage of perennials in that state decreased moderately (Figs 3A, 4A). The percentage of grazed annuals was significantly higher in steppe than in formerly-cultivated plots at week 8 ($z = -2.281$, $p = 0.023$; Supplementary file 1), where it reached its maximal value (16% in steppe plots; Fig. 3B).

The percentage of annuals with flower buds reached 35% at week 3 in steppe plots and 48% at week 5 in formerly-cultivated plots (Fig. 3C). The percentage of

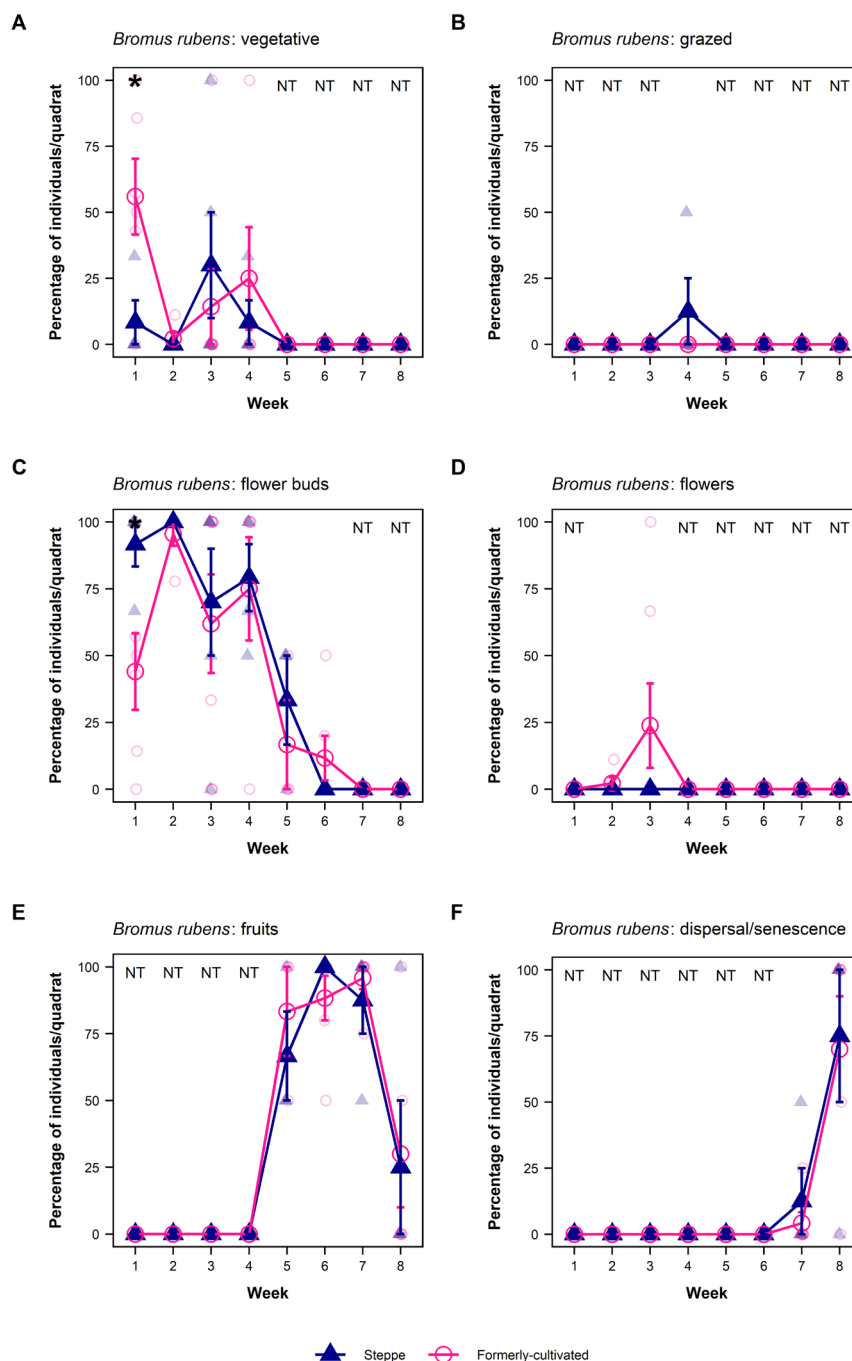


Figure 5. *Bromus rubens* phenological patterns: percentage of individuals per quadrat over time (weeks) on steppe plots (blue triangles) and formerly-cultivated plots (pink circles). **A.** Vegetative state. **B.** Grazed. **C.** Carrying flower buds. **D.** Carrying flowers. **E.** Carrying fruits. **F.** In dispersal/senescence. Each small, light circle or triangle refers to one measurement (quadrat). Variations in means (\pm SE) are represented by the large, dark circles and triangles linked by segments. Significant differences between percentages of individuals in each phenophase at each date are represented (* $p < 0.05$). NT indicates that no statistical test was performed.

annuals with flower buds was significantly higher at week 5 in formerly-cultivated plots than in steppe plots ($z = 2.990$, $p = 0.003$; Supplementary file 1). The percentage of perennials with flower buds reached maximal values at week 3 in steppe plots, with 22% in steppe and 42% in formerly-cultivated plots (Fig. 4C). The percentage of flowering annuals reached 18% at week 5 in steppe plots and was significantly higher than formerly-cultivated

plots ($z = 2.990$, $p = 0.003$; Fig. 3D, Supplementary file 1). The percentage of flowering annuals reached its maximal value (17%) at week 7 in formerly-cultivated plots (Fig. 3D). The percentage of flowering perennials remained quite constant in both plot types, reaching 8% at week 7 in steppe plots and 6% at week 2 in formerly-cultivated plots (Fig. 4D).

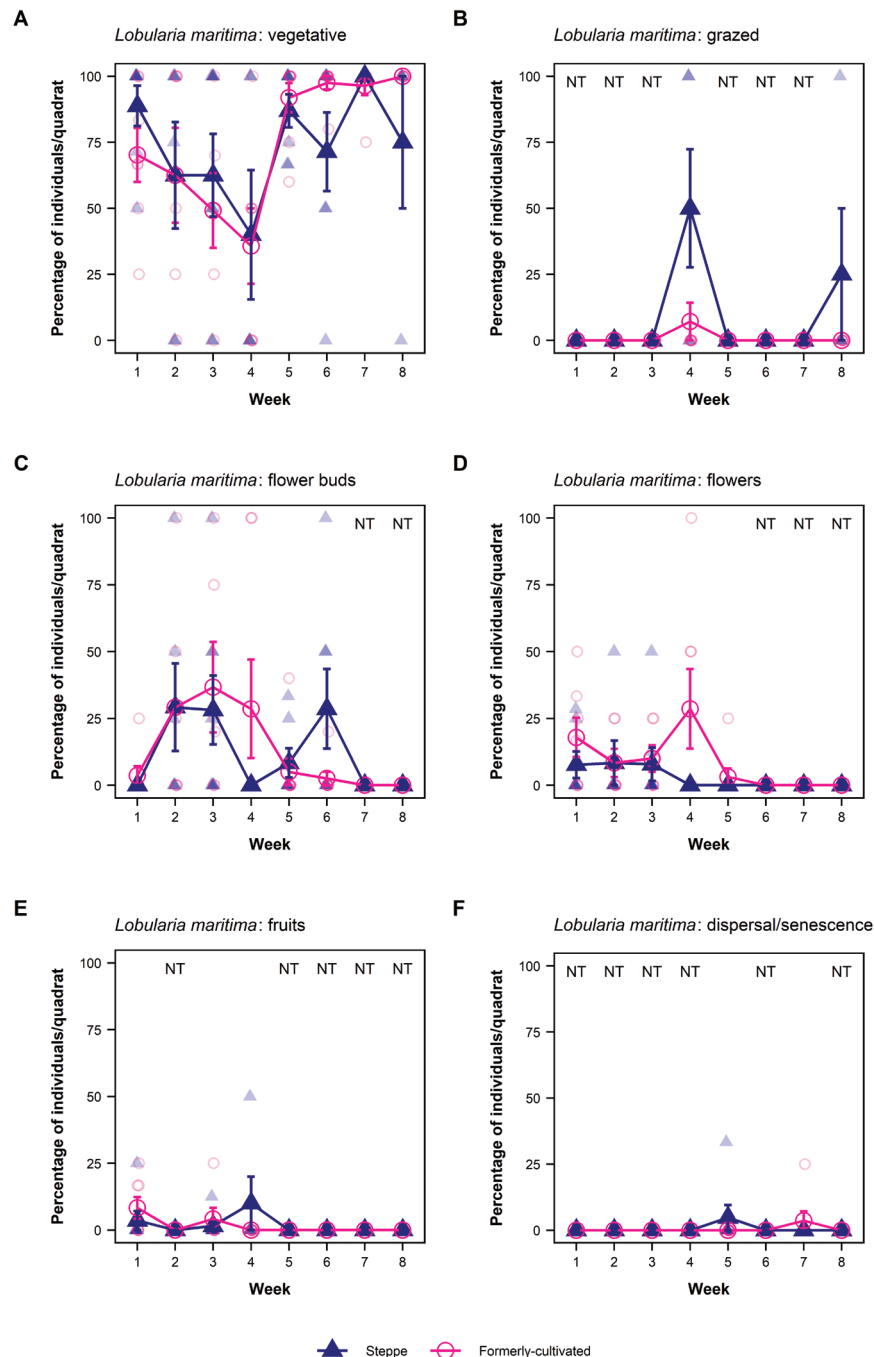


Figure 6. *Lobularia maritima* phenological patterns: percentage of individuals per quadrat over time (weeks) on steppe plots (blue triangles) and formerly-cultivated plots (pink circles). **A.** Vegetative state. **B.** Grazed. **C.** Carrying flower buds. **D.** Carrying flowers. **E.** Carrying fruits. **F.** In dispersal/senescence. Each small, light circle or triangle refers to one measurement (quadrat). Variations in means (\pm SE) are represented by the large, dark circles and triangles linked by segments. NT indicates that no statistical test was performed.

The percentage of fruiting annuals overall increased over time, reaching maximal values at week 6 in steppe plots (44%; Fig. 3E) and at week 7 in formerly-cultivated plots (57%; Fig. 3E). The percentage of fruiting annuals was significantly higher in steppe than in formerly-cultivated plots at week 5 ($z = -2.312$, $p = 0.021$; Supplementary file 1). In both plot types, the percentage of senescing annuals was very low until week 6 ($< 3\%$) and then increased until reaching maximal values at week 8 (29% and 39% in steppe and formerly-cultivated plots, respectively; Fig. 3F).

In steppe plots, the percentage of fruiting perennials was very low until week 6 ($< 4\%$), and reached its maximal value at week 7 (17%; Fig. 4E). In formerly-cultivated plots, the percentage of fruiting perennials reached 12% at week 3 and 23% at week 8 (Fig. 4E). The percentage of senescing perennials was linear over time, reaching its maximal value at week 4 on steppe plots (19%; Fig. 4F) and at week 5 in formerly-cultivated plots (11%; Fig. 4F).

Bromus rubens

For both formerly-cultivated plots and steppe plots, we no longer observed individuals at the vegetative state after week 4 (Fig. 5A). The percentage of individuals in vegetative state was significantly higher in formerly-cultivated than in steppe plots at week 1 ($z = 2.033$, $p = 0.042$; Supplementary file 1). While no grazed individual was observed in formerly-cultivated plots during the study, 15% of individuals were grazed at week 4 in steppe plots (Fig. 5B). In both plot types, the percentage of individuals with flower buds reached maximal values at week 2 (96% and 100% in steppe plots and formerly-cultivated plots, respectively) and we no longer observed individuals with flower buds after week 6 (Fig. 5C). The percentage of individuals with flower buds was significantly higher in steppe than in formerly-cultivated plots at week 1 ($z = -1.986$, $p = 0.047$; Supplementary file 1). While no individual was found flowering in steppe plots, 25% were observed at week 3 in formerly-cultivated plots (Fig. 5D). For both plot types, we did not observe fruiting individuals before week 5, where the percentage of fruiting individuals increased until nearly reaching 100% at week 6 in steppe plots and at week 7 in formerly-cultivated plots (Fig. 5E). The percentage of fruiting individuals then decreased to 25% in both plot types (Fig. 5E). Individuals dispersing seeds/in senescence were observed from week 7 on, and percentages reached 75% at week 8 in both plot types (Fig. 5F).

Lobularia maritima

For both formerly-cultivated plots and steppe plots, the percentage of individuals in vegetative state remained higher than 50% except at week 4, where it decreased to 40% and 36% in steppe and formerly-cultivated plots respectively (Fig. 6A). While the percentage of grazed individuals remained overall very low in formerly-cultivated plots, 50% of individuals were grazed in steppe plots at week 4 and 25% at week 8 (Fig. 6B). While, in

steppe plots, the percentage of individuals with flower buds was the highest (25%) around weeks 2, 3, and 6, a unique peak occurred in formerly-cultivated plots around week 3 (37%; Fig. 6C). While we did not observe flowering individuals in steppe plots, the percentage of flowering individuals reached 25% in formerly-cultivated plots at week 4 (Fig. 6D). Only a few individuals were observed with fruits or in senescence in both plot types (Figs 6E, F).

DISCUSSION

Our study suggests that past cultivation practices can substantially affect the composition of Mediterranean xeric grassland communities with differences visible after 30 years of abandonment, but alter phenological patterns only slightly. Species composition is clearly distinct between steppe and formerly-cultivated communities (Fig. 2, Supplementary file 2), which is consistent with studies carried out in the same area (Römermann et al. 2005; Helm et al. 2019). Steppe communities are dominated by the perennial steppe grass *B. retusum*, while this species is absent from formerly-cultivated plots communities, where meso- to oligotrophic grassland species, such as *A. geniculata*, *B. rubens*, and *Rostraria cristata* (L.) Tzvelev are overabundant (Fig. 2, Supplementary file 2; see Helm et al. 2019 for community composition analysis). The failure of *B. retusum* to re-establish in formerly-cultivated plots is attributed to (1) low seed production (Vidaller et al. 2019a; Buisson et al. 2021), (2) dispersal limitation due to a mainly clonal reproduction in this ecosystem (Dureau and Bonnefon 1998), (3) competition with formerly-cultivated plot species (Coiffait-Gombault et al. 2012; Buisson et al. 2015), (4) the absence of safe sites for rhizomes because stones were removed for cultivation (Caturla et al. 2000; Buisson et al. 2015), and/or (5) grazing pressure in the seedling establishment stage (Vidaller et al. 2019a). Altogether, our results on species composition reflect expected dynamics after soil disturbance in this system.

Despite differences in species composition, our results highlight a convergence in phenological patterns of annuals, perennials, *B. rubens*, and *L. maritima* between plot types (Figs 3–6). Some differences can however be noticed. The reproductive phenology of annuals and *B. rubens* appears slightly in advance in the steppe. The peak of annuals carrying flower buds occurs two weeks earlier (Fig. 3C) and the largest increase of fruiting annuals occurs one week earlier (week 4 to 5 vs week 5 to 6; Fig. 3E) in steppe than in formerly-cultivated plots. Our results also suggest that flower bud formation of the annual grass *B. rubens* started earlier (i.e. 92% vs 44% of individuals with flower buds at week 1; Fig. 5C, Supplementary file 1) and that the fruiting peak occurred one week earlier in steppe plots than in formerly-cultivated plots (Fig. 5D). *Bromus rubens* phenology however displays a high variability within plot types (Fig. 5), implying that one isolated difference should be

interpreted with caution. Repeating the experiment with a larger sample size might be necessary to confirm these results. The phenological advance of annual species in the steppe is unexpected, since the higher clay content, which is likely to preserve soil humidity and lower the P recorded in the steppe soil (Römmermann et al. 2005; Helm et al. 2019), should have delayed reproductive phenology of annuals compared to formerly-cultivated plots (Aronson et al. 1992; Wielgolaski et al. 2001; Nord and Lynch 2008). Indeed, low soil phosphorus decreases root-length but phosphorus accumulation is compensated by a phenological delay (Nord and Lynch 2008). One explanation might be the stone cover, higher in steppe plots than in formerly-cultivated plots from which they were removed for cultivation (Buisson and Dutoit 2004): stones can increase soil temperature and store heat during the day which is released at night (Devaux et al. 1983), thus leading to some phenological advance. At the community level, the occasional differences in the phenology of annuals may also be caused by differences in species composition between plot types (i.e. species-specific differences).

Phenological patterns of perennials appear overall more similar between plot types than annuals (Fig. 4). A high percentage of perennials (Fig. 4A) and of the perennial herb *L. maritima* (Fig. 6A) remained in vegetative state during the 8 weeks of the study. The peak of perennials carrying flowering buds occurring on week 3 is not followed by an increase in flowering individuals the subsequent weeks, which may be explained by flower bud consumption by sheep (Fig. 4B). Grazing may also blur the phenological patterns of *L. maritima* (i.e. consumption of flower buds and flowers resulting in very low proportions of flowering/fruitleaving individuals), especially in steppe plots where no flowering peak occurred (Fig. 6B, D). The highest grazing pressure on annuals and *L. maritima* detected on the steppe plots may be due to the high percent cover of *B. retusum*, which has a low palatability, and thus more grazing on all other species (Meuret et al. 2013).

The distinct phenological patterns between annuals and perennials may be explained by differences in reproductive/survival strategies. In the Mediterranean Basin, summer is the most stressful season for plants with mild to severe drought and high temperatures (Lionello et al. 2006). Most species reach their flowering peak in spring, when temperatures are already warm, but some species also flower in autumn or throughout the year (Picó and Renata 2001), like *L. maritima* (Bourrelly et al. 1983). Annuals flowering in spring must complete their reproductive cycle before periods of high water deficits, and have a short seed maturation period resulting in early dispersal dates (Segrestin et al. 2018). In this sense, we found that most annual species are in a reproductive stage at mid-June (< 4% of annuals in vegetative state at week 8; Fig. 3A). Many perennial species, in contrast, remain in vegetative state over the 8-week study (i.e. min. 57% in steppe plots and 43% in formerly-cultivated plots; Fig.

4A). The high proportion of perennials remaining in vegetative state in spring may be due to perennial species (1) that do not flower every year because of unfavourable environmental conditions, (2) being in a juvenile phase and unable to flower yet, and/or (3) flowering later in the season. For instance, *B. retusum*, the dominant perennial in steppe plots, rarely blooms the first year (Vidaller et al. 2018) and may flower later in the season when subjected to grazing (Vidaller et al. 2019b). The perennial herb *L. maritima*, representing respectively 18% and 29% of perennials in steppe and formerly-cultivated plots, generally flowers for ten months (from September to late June) with the peak of the flowering period in autumn (Bourrelly et al. 1983; Bosch et al. 1997; Picó and Renata 2000). Accordingly, we found that *L. maritima* has a high percentage of individuals in vegetative state during our 8-week spring study (> 50% except at week 4; Fig. 6A).

Overall, phenological patterns of annuals and perennials as well as the annuals/perennials ratio did not differ much between plot types, implying a convergence of annuals/perennials ratio and phenology in communities re-established after disturbance. The convergence of communities at the phenological and reproductive strategy levels suggests that deterministic assembly rules drive community assembly at these levels (i.e. environmental conditions determine the types of available niches and therefore the species that can fill them; Fukami et al. 2005; Helsen et al. 2012). The convergence in high percentage of annuals abundance (close to 70% in both plot types) most likely results from stressful environmental conditions, such as harsh Mediterranean climate (i.e. dry and windy climate with high inter-annual variability tend to favour annuals; Madon and Médail 1997) and recurrent grazing (i.e. grazing favours annuals; Díaz et al. 2007). In addition, in xeric environments, phenological patterns are intimately related to temperature (Rathcke and Lacey 1985), water availability (Abd El-Ghani 1997) but also grazing (Tadey 2020), which could explain the convergence in phenological patterns in our study system.

CONCLUSION

Our results highlight that past cultivation practices can affect the composition of Mediterranean xeric grassland communities with differences visible after 30 years of abandonment, but alters only slightly phenological patterns. We suggest that the harsh Mediterranean climate and sheep grazing most likely acted as strong habitat filters constraining community assembly at the phenological level. We do not exclude that other biotic interactions (e.g. plant-pollinators interaction, inter-specific plant competition for pollinators) may have influenced the phenological composition of the communities established after the disturbance. Quantifying their importance would require further investigation.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, M.C.M. Hess, upon reasonable request.

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REFERENCES

- Abd El-Ghani MM (1997) Phenology of ten common plant species in western Saudi Arabia. *Journal of Arid Environments* 35: 673–683. <https://doi.org/10.1006/jare.1996.0193>
- Aerts R, Chapin FS (1999) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. In: Fitter AH, Raffaelli DG (Eds) *Advances in Ecological Research* vol. 30. Academic Press, San Diego, 1–67. [https://doi.org/10.1016/S0065-2504\(08\)60016-1](https://doi.org/10.1016/S0065-2504(08)60016-1)
- Al Majou H, Bruand A, Muller F, Duval O, Josiere O (2008) Étude des propriétés de rétention en eau des sols argileux. In: Réunion annuelle SSP/AFES. Neuchâtel, Switzerland.
- Aronson J, Kigel J, Shmida A, Klein J (1992) Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. *Oecologia* 89: 17–26. <https://doi.org/10.1007/BF00319010>
- Austrheim G, Olsson EGA (1999) How does continuity in grassland management after ploughing affect plant community patterns? *Plant Ecology* 145: 59–74. <https://doi.org/10.1023/A:1009804509239>
- Bisigato AJ, Campanella MV, Pazos GE (2013) Plant phenology as affected by land degradation in the arid Patagonian Monte, Argentina: a multivariate approach. *Journal of Arid Environments* 91: 79–87. <https://doi.org/10.1016/j.jaridenv.2012.12.003>
- Borrey M (1965) Contribution à la connaissance des petites régions agricoles. La Crau, Ministère de l'Agriculture, Bouches-du-Rhône, France.
- Bosch J, Retana J, Cerdá X (1997) Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia* 109: 583–591. <https://doi.org/10.1007/s004420050120>
- Bourrelly M, Borel L, Devaux JP, Louis-Palluel J, Archiloque A (1983) Dynamique annuelle et production primaire nette de l'écosystème steppique de Crau (Bouches du Rhône). *Biologie-Écologie Méditerranéenne* 10: 55–82.
- Buisson E, Dutoit T (2004) Colonisation by native species of abandoned farmland adjacent to a remnant patch of Mediterranean steppe. *Plant Ecology* 174: 371–384. <https://doi.org/10.1007/BF03543067>
- Buisson E, Dutoit T (2006) Creation of the natural reserve of La Crau: implications for the creation and management of protected areas. *Journal of Environmental Management* 80: 318–326. <https://doi.org/10.1016/j.jenvman.2005.09.013>
- Buisson E, Dutoit T, Wolff A (2004) Bilan de trente années de recherches en écologie dans la steppe de Crau (Bouches-du-Rhône, sud-est de la France). *Ecologia Mediterranea* 30: 7–24. <https://doi.org/10.3406/ecmed.2004.1492>
- Buisson E, Corcket E, Dutoit T (2015) Limiting processes for perennial plant reintroduction to restore dry grasslands. *Restoration Ecology* 23: 947–954. <https://doi.org/10.1111/rec.12255>
- Buisson E, Dutoit T, Torre F, Römermann C, Poschod P (2006) The implications of seed rain and seed bank patterns for plant succession at the edges of abandoned fields in Mediterranean landscapes. *Agriculture, Ecosystems & Environment* 115: 6–14. <https://doi.org/10.1016/j.agee.2005.12.003>
- Buisson E, De Almeida T, Durbecq A, Arruda AJ, Vidaller C, Alignan J, Toma TSP, Hess MCM, Pavon D, Isselin-Nondedeu F, Jaunatre R, Moinardeau C, Young TP, Mesléard F, Dutoit T, Blight O, Bischoff A (2021) Key issues in Northwestern Mediterranean dry grassland restoration. *Restoration Ecology* 29: e13258. <https://doi.org/10.1111/rec.13258>
- Burgheimer J, Wilske B, Maseyk K, Karnieli A, Zaady E, Yakir D, Kesselmeier J (2006) Ground and space spectral measurements for assessing the semi-arid ecosystem phenology related to CO₂ fluxes of biological soil crusts. *Remote Sensing of Environment* 101: 1–12. <https://doi.org/10.1016/j.rse.2005.03.003>
- Caturla RN, Raventós J, Guàrdia R, Vallejo VR (2000) Early post-fire regeneration dynamics of *Brachypodium retusum* Pers. (Beauv.) in old fields of the Valencia region (eastern Spain). *Acta Oecologica* 21: 1–12. [https://doi.org/10.1016/S1146-609X\(00\)00114-4](https://doi.org/10.1016/S1146-609X(00)00114-4)
- Coiffait-Gombault C, Buisson E, Dutoit T (2012) Using a two-phase sowing approach in restoration: sowing foundation species to restore, and subordinate species to evaluate restoration success. *Applied Vegetation Science* 15: 277–289. <https://doi.org/10.1111/j.1654-109X.2012.01182.x>
- Colomb E, Roux RM (1978) La Crau, données nouvelles et interprétations. *Géologie Méditerranéenne* 5: 303–324.
- Crawley MJ (2007) Generalized linear models. In: Crawley MJ (Ed.) *The R book*. John Wiley & Sons, Chichester, 511–526. <https://doi.org/10.1002/9780470515075.ch13>
- Cribari-Neto F, Zeileis A (2010) Beta regression in R. *Journal of Statistical Software* 34: 1–24. <https://doi.org/10.18637/jss.v034.i02>
- Devaux JP, Archiloque A, Borel L, Bourrelly M, Louis-Palluel J (1983) Notice de la carte phyto-écologique de la Crau (Bouches du Rhône). *Biologie-Écologie Méditerranéenne* 10: 5–24.
- Díaz S, Lavorel S, McINTYRE S, Falczuk V, Casanoves E, Milchunas DG, Skarpe C, Rusch G, Sternberg M, Noy-Meir

- I, Landsberg J, Zhang W, Clark H, Campbell BD (2007) Plant trait responses to grazing? A global synthesis. *Global Change Biology* 13: 313–341. <https://doi.org/10.1111/j.1365-2486.2006.01288.x>
- Ding M, Zhang Y, Sun X, Liu L, Wang Z, Bai W (2013) Spatiotemporal variation in alpine grassland phenology in the Qinghai-Tibetan Plateau from 1999 to 2009. *Chinese Science Bulletin* 58: 396–405. <https://doi.org/10.1007/s11434-012-5407-5>
- Dureau R, Bonnefon O (1998) Etude des pratiques de gestion pastorale des coussouls. In: *Patrimoine Nature et Pratiques Pastorales en Crau: Pour Une Gestion Globale de la Plaine*. CEEP Ecomusée de Crau, Saint-Martin-de-Crau, 61–89.
- Fenner M (1998) The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics* 1: 78–91. <https://doi.org/10.1078/1433-8319-00053>
- Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. *Science* 296: 1689–1691. <https://doi.org/10.1126/science.1071617>
- Foucort A, Lecoq M (1998) Major threat to a protected grasshopper, *Prionotropis hystrix rhodanica* (Orthoptera, Pamphagidae, Akicerinae), endemic to southern France. *Journal of Insect Conservation* 2: 187–193. <https://doi.org/10.1023/A:1009691612698>
- Fukami T, Martijn Bezemer T, Mortimer SR, Putten WH (2005) Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters* 8: 1283–1290. <https://doi.org/10.1111/j.1461-0248.2005.00829.x>
- Guo L, Dai J, Wang M, Xu J, Luedeling E (2015) Responses of spring phenology in temperate zone trees to climate warming: a case study of apricot flowering in China. *Agricultural and Forest Meteorology* 201: 1–7. <https://doi.org/10.1016/j.agrformet.2014.10.016>
- Güsewell S (2004) N : P ratios in terrestrial plants: variation and functional significance. *New Phytologist* 164: 243–266. <https://doi.org/10.1111/j.1469-8137.2004.01192.x>
- Helm J, Dutoit T, Saatkamp A, Bucher SF, Leiterer M, Römermann C (2019) Recovery of Mediterranean steppe vegetation after cultivation: legacy effects on plant composition, soil properties and functional traits. Overbeck G (Ed.). *Applied Vegetation Science* 22: 71–84. <https://doi.org/10.1111/avsc.12415>
- Helsen K, Hermy M, Honnay O (2012) Trait but not species convergence during plant community assembly in restored semi-natural grasslands. *Oikos* 121: 2121–2130. <https://doi.org/10.1111/j.1600-0706.2012.20499.x>
- Hobbs RJ, Gulmon SL, Hobbs VJ, Mooney HA (1988) Effects of fertiliser addition and subsequent gopher disturbance on a serpentine annual grassland community. *Oecologia* 75: 291–295. <https://doi.org/10.1007/BF00378612>
- Keenan TF, Gray J, Friedl MA, Toomey M, Bohrer G, Hollinger DY, Munger JW, O’Keefe J, Schmid HP, Wing IS, Yang B, Richardson AD (2014) Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* 4: 598–604. <https://doi.org/10.1038/nclimate2253>
- Kharouba HM, Ehrlén J, Gelman A, Bolmgren K, Allen JM, Travers SE, Wolkovich EM (2018) Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences* 115: 5211–5216. <https://doi.org/10.1073/pnas.1714511115>
- König P, Tautenhahn S, Cornelissen JHC, Kattge J, Bönisch G, Römermann C (2018) Advances in flowering phenology across the Northern Hemisphere are explained by functional traits. *Global Ecology and Biogeography* 27: 310–321. <https://doi.org/10.1111/geb.12696>
- Kudo G, Ida TY (2013) Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* 94: 2311–2320. <https://doi.org/10.1890/12-2003.1>
- Laroche J, Bousquet J (1999) Evolution of the mitochondrial rps3 intron in perennial and annual angiosperms and homology to nad5 intron 1. *Molecular Biology and Evolution* 16: 441–452. <https://doi.org/10.1093/oxfordjournals.molbev.a026126>
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Lieth H (1974) Purposes of a phenology book. In: Lieth H (Ed.) *Phenology and Seasonality Modeling*. Ecological Studies (Analysis and Synthesis). Springer, Berlin Heidelberg, 3–19.
- Lionello P, Malanotte-Rizzoli P, Boscolo R, Alpert P, Artale V, Li L, Luterbacher J, May W, Trigo R, Tsimplis M, Ulbrich U, Xoplaki E (2006) The Mediterranean climate: an overview of the main characteristics and issues. In: Lionello P, Malanotte-Rizzoli P, Boscolo R (Eds) *Developments in Earth and Environmental Sciences*. Elsevier, 1–26. [https://doi.org/10.1016/S1571-9197\(06\)80003-0](https://doi.org/10.1016/S1571-9197(06)80003-0)
- Ma Q, Longnecker N, Atkins C (2002) Varying phosphorus supply and development, growth and seed yield in narrow-leaved lupin. *Plant and Soil* 239: 79–85. <https://doi.org/10.1023/A:1014988219743>
- Madon O, Médail F (1997) The ecological significance of annuals on a Mediterranean grassland (Mt Ventoux, France). *Plant Ecology* 129: 189–199. <https://doi.org/10.1023/A:1009759730000>
- McLauchlan 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>
- Meng F, Cui S, Wang S, Duan J, Jiang L, Zhang Z, Luo C, Wang Q, Zhou Y, Li X, Zhang L, Dorji T, Li Y, Du M, Wang G (2016) Changes in phenological sequences of alpine communities across a natural elevation gradient. *Agricultural and Forest Meteorology* 224: 11–16. <https://doi.org/10.1016/j.agrformet.2016.04.013>
- Meuret M, Gonzalez-Pech P, Agreil C, Wolff A, Minard R (2013). L’intelligence alimentaire des brebis conduites par les bergers au printemps sur la steppe. In: Tatin L, Wolff A, Boutin J, Colliot E, Dutoit T (Eds) *La Crau, Ecologie et Conservation d’une Steppe Méditerranéenne*. Quae Editions, Paris, 176–191.
- Morellato LPC, Camargo MGG, D’Eça Neves FF, Luize BG, Mantovani A, Hudson IL (2010) The influence of sampling method, sample size, and frequency of observations on

- plant phenological patterns and interpretation in tropical forest trees. In: Hudson IL, Keatley MR (Eds), Phenological Research. Springer Netherlands, Dordrecht, 99–121. https://doi.org/10.1007/978-90-481-3335-2_5
- Morellato LPC, Alberton B, Alvarado ST, Borges B, Buisson E, Camargo MGG, Cancian LF, Carstensen DW, Escobar DFE, Leite PTP, Mendoza I, Rocha NMWB, Soares NC, Silva TSF, Staggemeier VG, Streher AS, Vargas BC, Peres CA (2016) Linking plant phenology to conservation biology. *Biological Conservation* 195: 60–72. <https://doi.org/10.1016/j.biocon.2015.12.033>
- 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>
- Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13: 1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42. <https://doi.org/10.1038/nature01286>
- Peñuelas J, Filella I (2001) Responses to a warming world. *Science* 294: 793–795. <https://doi.org/10.1126/science.1066860>
- 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>
- Picó FX, Retana J (2000) Temporal variation in the female components of reproductive success over the extended flowering season of a Mediterranean perennial herb. *Oikos* 89: 485–492. <https://doi.org/10.1034/j.1600-0706.2000.890307.x>
- Picó FX, Retana J (2001) The flowering pattern of the perennial herb *Lobularia maritima*: an unusual case in the Mediterranean basin. *Acta Oecologica* 22: 209–217. [https://doi.org/10.1016/S1146-609X\(01\)01114-6](https://doi.org/10.1016/S1146-609X(01)01114-6)
- Price MV, Waser NM (1998) Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79: 1261–1271. [https://doi.org/10.1890/0012-9658\(1998\)079\[1261:EOEWOP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[1261:EOEWOP]2.0.CO;2)
- R Core Team (2015) R: A language and environment for statistical computing. Version 3.2.0. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/> [accessed 16.06.2015]
- R Core Team (2019) R: A language and environment for statistical computing. Version 3.6.2. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/> [accessed 20.11.2021]
- Rathcke B (1983) Competition and facilitation among plants for pollination. In: *Pollination biology* 305: 329. Academic, New York.
- Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16(1): 179–214. <https://doi.org/10.1146/annurev.es.16.110185.001143>
- Römermann C, Dutoit T, Poschlod P, Buisson E (2005) Influence of former cultivation on the unique Mediterranean steppe of France and consequences for conservation management. *Biological Conservation* 121: 21–33. <https://doi.org/10.1016/j.biocon.2004.04.006>
- Römermann C, Bernhardt M, Dutoit T, Poschlod P, Rolando C (2004) Histoire culturelle de la Crau: potentialités de ré-établissement des espèces caractéristiques du coussous après abandon. *Ecologia Mediterranea* 30: 47–70. <https://doi.org/10.3406/ecmed.2004.1495>
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60. <https://doi.org/10.1038/nature01333>
- Rossiter RC (1978) Phosphorus deficiency and flowering in subterranean clover (*T. subterraneum* L.). *Annals of Botany* 42: 325–329. <https://doi.org/10.1093/oxfordjournals.aob.a085463>
- Sargent RD, Ackerly DD (2008) Plant-pollinator interactions and the assembly of plant communities. *Trends in Ecology & Evolution* 23: 123–130. <https://doi.org/10.1016/j.tree.2007.11.003>
- Segrestin J, Bernard-Verdier M, Violle C, Richarte J, Navas M, Garnier E (2018) When is the best time to flower and disperse? A comparative analysis of plant reproductive phenology in the Mediterranean. Timothy Paine CE (Ed.). *Functional Ecology* 32: 1770–1783. <https://doi.org/10.1111/1365-2435.13098>
- Sherry RA, Zhou X, Gu S, Arnone JA, Schimel DS, Verburg PS, Wallace LL, Luo Y (2007) Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences* 104: 198–202. <https://doi.org/10.1073/pnas.0605642104>
- Tadey M (2020) Reshaping phenology: grazing has stronger effects than climate on flowering and fruiting phenology in desert plants. *Perspectives in Plant Ecology, Evolution and Systematics* 42: 125501. <https://doi.org/10.1016/j.ppees.2019.125501>
- Vidaller C, Dutoit T, Ramone H, Bischoff A (2019a) Factors limiting early establishment of the Mediterranean grassland species *Brachypodium retusum* at disturbed sites. *Basic and Applied Ecology* 37: 10–19. <https://doi.org/10.1016/j.baae.2019.04.003>
- Vidaller C, Dutoit T, Ramone H, Bischoff A (2019b) Fire increases the reproduction of the dominant grass *Brachypodium retusum* and Mediterranean steppe diversity in a combined burning and grazing experiment. Acosta ATR (Ed.). *Applied Vegetation Science* 22: 127–137. <https://doi.org/10.1111/avsc.12418>

- Vidaller C, Dutoit T, Ibrahim Y, Hanslin HM, Bischoff A (2018) Adaptive differentiation among populations of the Mediterranean dry grassland species *Brachypodium retusum*: The role of soil conditions, grazing, and humidity. *American Journal of Botany* 105: 1123–1132. <https://doi.org/10.1002/ajb2.1116>
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology* 75: 1861–1876. <https://doi.org/10.2307/1941591>
- Wielgolaski FE (2001) Phenological modifications in plants by various edaphic factors. *International Journal of Biometeorology* 45: 196–202. <https://doi.org/10.1007/s004840100100>
- Wolkovich EM, Cleland EE (2011) The phenology of plant invasions: a community ecology perspective. *Frontiers in Ecology and the Environment* 9: 287–294. <https://doi.org/10.1890/100033>
- Yang LH, Rudolf VHW (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters* 13: 1–10. <https://doi.org/10.1111/j.1461-0248.2009.01402.x>

SUPPLEMENTARY FILES

Supplementary file 1

Results from generalized linear mixed models (beta distribution) comparing phenological patterns between plot types for annuals, perennials, *Bromus rubens* and *Lobularia maritima*.

Link: <https://doi.org/10.5091/plecevo.86335.supp1>

Supplementary file 2

Total number of individuals per sampled species recorded during the 8 weeks of experiment, in steppe and formerly-cultivated plots.

Link: <https://doi.org/10.5091/plecevo.86335.supp2>