

Research article

Plant size and leaf area influence phenological and reproductive responses to warming in semiarid Mediterranean species



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ABSTRACT

Changes in vegetative and reproductive phenology rank among the most obvious plant responses to climate change. These responses vary broadly among species, but it is largely unknown whether they are mediated by functional attributes, such as size or foliar traits. Using a manipulative experiment conducted over two growing seasons, we evaluated the responses in reproductive phenology and output of 14 Mediterranean semiarid species belonging to three functional groups (grasses, nitrogen-fixing legumes and forbs) to a $\sim 3^\circ\text{C}$ increase in temperature, and assessed how leaf and size traits influenced them. Overall, warming advanced flowering and fruiting phenology, extended the duration of flowering and reduced the production of flowers and fruits. The observed reduction in flower and fruit production with warming was likely related to the decrease in soil moisture promoted by this treatment. Phenological responses to warming did not vary among functional groups, albeit forbs had an earlier reproductive phenology than legumes and grasses. Larger species with high leaf area, as well as those with small specific leaf area, had an earlier flowering and a longer flowering duration. The effects of warming on plant size and leaf traits were related to those on reproductive phenology and reproductive output. Species that decreased their leaf area under warming advanced more the onset of flowering, while those that increased their vegetative height produced more flowers. Our results advance our understanding of the phenological responses to warming of Mediterranean semiarid species, and highlight the key role of traits such as plant size and leaf area as determinants of such responses.

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1. Introduction

Ongoing global warming is modifying plant vegetative and reproductive phenology in terrestrial habitats worldwide (Parmesan and Yohe, 2003; Gordo and Sanz, 2010; Körner and Basler, 2010). These changes have multiple consequences for ecosystem structure and functioning, including potential temporal asynchronies between plants and insects, modification in flower quality and seed mass, or reduced survival of plants (Goulden et al., 1996; Walther et al., 2002; Aerts et al., 2004; Williams et al., 2007; Inouye, 2008; Hegland et al., 2009). Vegetative and reproductive phenological responses to warming have been relatively well studied in temperate habitats (Dunne et al., 2003; Parmesan and Yohe, 2003; Sherry et al., 2007; Rollinson and Kaye, 2012), where

temperature is often a limiting factor for plant growth and development (Parmesan, 2007; Liang et al., 2013). In these areas, both observational and experimental studies have shown that warming promotes an earlier and longer flowering season (Dunne et al., 2003; Menzel et al., 2006; Parmesan, 2007; Hovenden et al., 2008; Kardol et al., 2010).

Phenological studies often show a latitudinal variation in their responses, with extended growing seasons and a more advanced flower phenology in warmer compared to milder ecosystems (e.g., Menzel et al., 2006; Gordo and Sanz, 2009). However, few experimental studies have been conducted in arid, semi-arid and dry-subhumid environments (drylands hereafter, *sensu* UNEP, 1992), particularly when compared to the number of studies conducted in temperate ecosystems (Arft et al., 1999; Wolkovich et al., 2012; but see Liancourt et al., 2012). This is a worrying knowledge gap because drylands occupy $\sim 41\%$ of the Earth's surface (Safirel and Adeel, 2005), are a key biome for global plant diversity (White and Nackoney, 2003), and are currently threatened by climate change and desertification (Reynolds et al., 2007; Maestre et al.,

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2012). In addition, the phenological impacts of warming in drylands are likely to differ from those observed in temperate ecosystems. In water-limited environments, warming could advance flowering, but may decrease both the number of flowers/fruits and seed mass (Liancourt et al., 2012) due to reductions in soil moisture (Luo et al., 2001; Peñuelas et al., 2004).

Despite the large body of literature on phenological responses to warming, we do not fully understand why observed responses differ so widely across species (Arft et al., 1999; Peñuelas et al., 2002). To address this variability, such responses have been studied in relation to factors such as soil moisture, vernalization or photoperiod (Partanen et al., 1998; Boss et al., 2004; Turck et al., 2008; Körner and Basler, 2010). Clear connections between flowering time and advances in flowering phenology induced by warming have been found only in some cases (Fitter et al., 1995; Peñuelas and Filella, 2001; Root et al., 2003; but see Liancourt et al., 2012; Whittington, 2012). Plant functional groups, i.e. sets of species that encompass a variety of common functional attributes (Díaz and Cabido, 1997; Gitay and Noble, 1997), allow generalizing how species respond to environmental changes (Wilson, 1999). For example, annual grasses have an earlier flowering time than forbs (Cleland et al., 2006). Sherry et al. (2007) showed that early-flowering species showed an advancement of flowering in response to warming, while late-flowering species did the opposite. However, no previous studies have evaluated whether the same pattern applies to early- or late-flowering functional groups. Changes in the flowering time with warming could modify the coexistence of different species or functional groups within plant communities (i. e. phenological complementarity; Rathcke and Lacey, 1985).

Plant functional traits can shed light on the responses of reproductive phenology to warming, but their influence has received little attention so far (Bolmgren and Cowan, 2008; Miller-Rushing et al., 2008; Richardson et al., 2010). For instance, plant size should correlate with flowering onset (Vile et al., 2006), but its relationship with other reproductive phenological variables is unknown. Thus, a better knowledge about the links between functional traits and phenological responses is needed to enhance our ability to predict plant responses to warming.

To fill current gaps in our understanding about the responses of Mediterranean semiarid species to climate change, we experimentally evaluated the reproductive phenology and reproductive output to warming of 14 Mediterranean semi-arid species belonging to different functional groups. Specifically, we assessed: (1) how warming affects key phenological events, such as flowering (onset, peak, cessation or duration) and fruiting (onset, peak), and reproductive output (number of flowers, fruits or seed mass), (2) whether responses to warming were consistent among the different reproductive phenology and reproductive output variables, and between years with contrasting environmental conditions, (3) the role of functional groups and functional traits on reproductive phenological responses, and how warming modifies them, and (4) whether the magnitude of intraspecific changes in functional traits modulate these responses to warming. We predict that warming would cause an advance of all components of reproductive phenology, an increase in flowering duration and a decrease in the number of flowers, fruits and seed mass (Liancourt et al., 2012). Warming will also result in less water availability compared with the control, and these differences will be especially marked at the end of the growing season (Valencia et al., 2016b). As a consequence, reproductive output might decrease with warming (Liancourt et al., 2012). We also hypothesized that phenological responses to warming will vary among plant functional groups (Cleland et al., 2006), and that these responses will be affected by functional traits such as plant size and leaf area (Vile et al., 2006; Sherry et al., 2007; Bolmgren and Cowan, 2008).

2. Materials and methods

2.1. Study species

We studied 14 species belonging to three broad taxonomical functional groups: grasses (*Cynodon dactylon* [L.] Pers., *Poa pratensis* [L.], *Agropyron cristatum* [L.] Gaertn., *Festuca ovina* [L.]), nitrogen-fixing legumes (*Hedysarum coronarium* [L.], *Dorycnium pentaphyllum* [Scop.], *Anthyllis vulneraria* [L.], *Medicago sativa* [L.], *Bituminaria bituminosa* [L.] C.H. Stirt.) and forbs (*Plantago lanceolata* [L.], *Sanguisorba minor* [Scop.], *Echium boissieri* [Steud.], *Echium plantagineum* [L.], *Asphodelus fistulosus* [L.]; Table S1). We selected these species because they typically coexist in grassland communities, abandoned fields and roadside slopes undergoing secondary succession in semi-arid Mediterranean areas (García-Palacios et al., 2010).

2.1.1. Experimental design

A microcosm experiment was conducted at the Climate Change Outdoor Laboratory, located at the facilities of Rey Juan Carlos University (URJC, Móstoles, Spain: 40°20'37"N, 3°52'00"W, 650 m a.s.l.) between April 1, 2011 and July 31, 2013. Microcosms consisted of plastic pots (depth 38 cm, internal diameter 28 cm) filled with 32 cm of natural soil (sand content: 73.5%, silt content: 18.5%, clay content: 8.0%) and 3 cm of expanded clay for drainage at the base. All the microcosms were initially watered with 500 mL of a soil microbial inoculum to recreate realistic microbial communities, as described in Maestre et al. (2005). All the pots were placed in holes in the ground, and kept under ambient light and rainfall to keep the most natural conditions.

The experiment was designed as a randomized block design, with two treatments: warming (control vs. ~2.9°C annual temperature increase), and functional group (three levels: grasses, nitrogen-fixing legumes and forbs). Microcosms were arranged in four blocks containing a replicate of species per temperature treatment, resulting in 112 microcosms in total. A minimum distance between microcosms of 1 m was established to minimize the risk of sampling non-independent areas.

Seeds for this experiment were obtained from commercial sources (Intersemillas Ltd., Valencia, Spain). In April 2011, we randomly sowed seeds of each species within each microcosm. We planted a monoculture in each microcosm at a density of 160 individuals/m². This density is within the range found in semiarid ecosystems from central Spain (e.g., 131 individuals/m²; Chacón-Labelle et al., 2016). The microcosms were watered with 1 L three times per week during the first six weeks of the experiment, and once a week in July and August 2011, to ensure seed establishment. Weeds were regularly removed during the experiment. The warming treatment was set up on December 05, 2011, once all microcosms had an established population, and the experiment terminated in July 2013. We elevated the temperature in the warming treatment by using open top chambers (OTCs), which have been commonly employed in warming experiments (e.g., Marion et al., 1997; Hollister and Weber, 2000; Escolar et al., 2012; Liancourt et al., 2012). These were hexagonal chambers built of methacrylate plates, with sloping sides of 65–52–42 cm (Fig. S1). Methacrylate has high transmittance in the visible spectrum (92%), very low emission of the infrared wavelength (4%) and high energy transmission (85%; data provided by the supplier, Decorplax Metacrilatos S.L., Madrid, Spain). Chambers were open on their top to allow rainfall and air flow, and were raised 5 cm from the soil surface to achieve adequate air flow and avoid excessive heating. Air temperature and humidity were measured in warming and control plots using automated sensors (HOBO U23 Pro v.2 Temp/RH, Onset Corporation, Bourne, MA, USA). The OTCs employed raised temperature by an average of ~2.9°C compared to control plots during our experiment (Fig.

S2b). This temperature increase was consistent with the predictions of climatic models for the study area, ranging from 2 to 4 °C by the second half of the twenty-first century (RCP 8.5 scenario, Intergovernmental Panel on Climate Change (IPCC, 2013)).

2.1.2. Phenological and plant sampling

Flowering phenology and flower and fruit production in all the plants of each microcosm were scored every two–three days throughout the spring flowering period (from March to early July) of 2012 and 2013. All inflorescences or infructescences were counted in all plants of each microcosm in each census. We focused on the spring flowering because most species only bloomed in this period. From the raw counts we calculated the following phenological variables: dates of onset, peak and cessation of flowering, flowering duration, maximal number of flowers or inflorescences produced at the flowering peak (flower production hereafter), fructification onset and peak, maximal number of fruits or infructescences produced at fructification peak (fruit production hereafter) and seed mass. Flowering onset, peak and cessation were defined as the number of days elapsed between the 1st of March and the first flower, maximal number of flowers and end of blooming, respectively. A few outlier flowers opening very early or very late during the flowering period were excluded from these calculations. Flowering duration was estimated as the difference between flowering onset and cessation. Accordingly, we measured the onset and peak of fructification as the number of days elapsed between the 1st of March and the date when the first fruit and the highest number of fruits were recorded, respectively. Seed mass was estimated by weighing a sample of twenty seeds per microcosm; seeds were collected when plants had ripe fruits at the end of the fructification period of 2013. We did not collect seeds in 2012 to avoid altering the establishment and growth of new plants in the microcosms. Phenological measurements were gathered on twelve species during 2012 (Fig. 1). *Festuca ovina* and *E. boissieri* did not flower in 2012, but did so in 2013. *Poa pratensis* and *H. coronarium* suffered from severe mortality under warming during the summer of 2012, and were dropped from the analysis in 2013.

We visually estimated total cover (TC, cm²) as the area occupied by plants in each microcosm. We also measured the following traits according to standard protocols (Cornelissen et al., 2003): vegetative height (VH, cm), leaf area (LA, cm²), leaf length (LL, cm), leaf width (LW, cm), leaf thickness (LT, mm), specific leaf area (SLA, cm² g⁻¹) and leaf dry matter content (LDMC, g g⁻¹). These traits were selected because they indicate different plant species strategies for acquiring, using and conserving resources, such as light, nutrients and water (Westoby et al., 2002; Wright et al., 2004). Trait measurements were conducted in May 2012 and June 2013 in a randomly chosen individual per microcosm. Additionally, we also measured the number of individuals and the volume (calculated as VH × TC) occupied by each population. Volume was considered as a good proxy of aboveground biomass, as both variables were highly correlated ($r = 0.82$ $P < 0.001$, $n = 92$) at the end of the experiment.

2.2. Statistical analyses

2.2.1. Functional trait classification

As many of the traits measured are correlated among them (Table S2), we reduced our original list of nine traits by means of a principal component analysis (PCA) performed across all species using the mean trait values for each microcosm. This approach is based on selecting one trait for each PCA component as a functional marker representative of each axis of specialization (Garnier et al., 2004). These values were log-transformed prior to PCA analyses. We selected three independent PCA components to identify the main axes of specialization among species, which together explained around 80% of the total variance found in the data (Table

S3). These analyses were carried out separately for each sampling year. The first, second and third PCA components were highly related to plant size (VH, TC and volume), leaf size (LA, LT and LL) and leaf morphology (SLA), respectively, during the two study years (Table S3). To represent each axis of variation, we selected traits strongly correlated with each PCA component that were not strongly correlated ($r < 0.15$) with the remaining traits (Tables S2 and S3). These traits, selected to represent each independent axis in further analyses, were VH, LA and SLA. This procedure has the advantage of considering only independent traits in further analyses, and allows us to identify important traits that reflect independent functional niche axes (Gross et al., 2007; Butterfield and Suding, 2013).

2.2.2. Responses of reproductive phenology and reproductive output to warming

We used General Linear Mixed Models (GLMM) to assess the responses to warming of six phenological variables (onset, peak, duration and cessation of flowering and onset and peak of fructification) and three reproductive output variables (seed mass, flower and fruit production) separately for each year. In all models, warming, functional group and their interaction were considered as fixed factors, whereas block and species, nested within functional group, were considered as random factors. We included VH, LA, SLA and the number of individuals per microcosm as covariates, as well as the interactions between warming and VH, LA, and SLA in our models. Seed mass, flower and fruit production, number of individuals and all the traits were log-transformed prior to GLMM analyses to improve their normality. We used a stepAIC procedure (Grace, 2006) to evaluate the relationships of each factor and covariate with phenological and reproductive variables, and selected the best model based on the Akaike Information Criterion (AIC; Akaike, 1973). When significant responses among functional groups were found, we conducted a Tukey post-hoc analysis to evaluate differences among them.

We quantified the effect of warming on leaf/size traits and phenological variables using the RII index, calculated as $(X_{amb} - X_{war}) / (X_{amb} + X_{war})$, where X_{amb} and X_{war} are the values of each variable in the control and warming treatments, respectively (Armas et al., 2004). This index ranges from -1 to $+1$. Negative values indicate an increase of the variable considered (or a delay in the case of phenological events) under warming, while positive values indicate the opposite. Relationships between changes in leaf and size traits and changes in reproductive phenological responses, as measured with the RII index, were assessed using linear regression.

All statistical analysis were carried out with R (R Development Core Team, 2012), using the packages “lme4” (Bates et al., 2014) and “multcomp” (Hothorn et al., 2008). The raw data used in our analysis are available from figshare (Valencia et al., 2016a).

3. Results

The two years studied had contrasting environmental conditions (Fig. S2a). The first year (2012) was warmer and drier (14.5 °C and 141 mm of mean temperature and precipitation during the growing season, respectively) than the second year (2013; 13.6 °C and 229 mm of mean temperature and precipitation during the growing season, respectively). On average, our warming treatment increased air temperatures by 3.3 °C and 2.6 °C during the growing seasons of 2012 and 2013, respectively.

3.1. Effects of warming on flowering and fruiting phenology

Trends in phenological responses were consistent across years except for the cessation of flowering, where results were highly

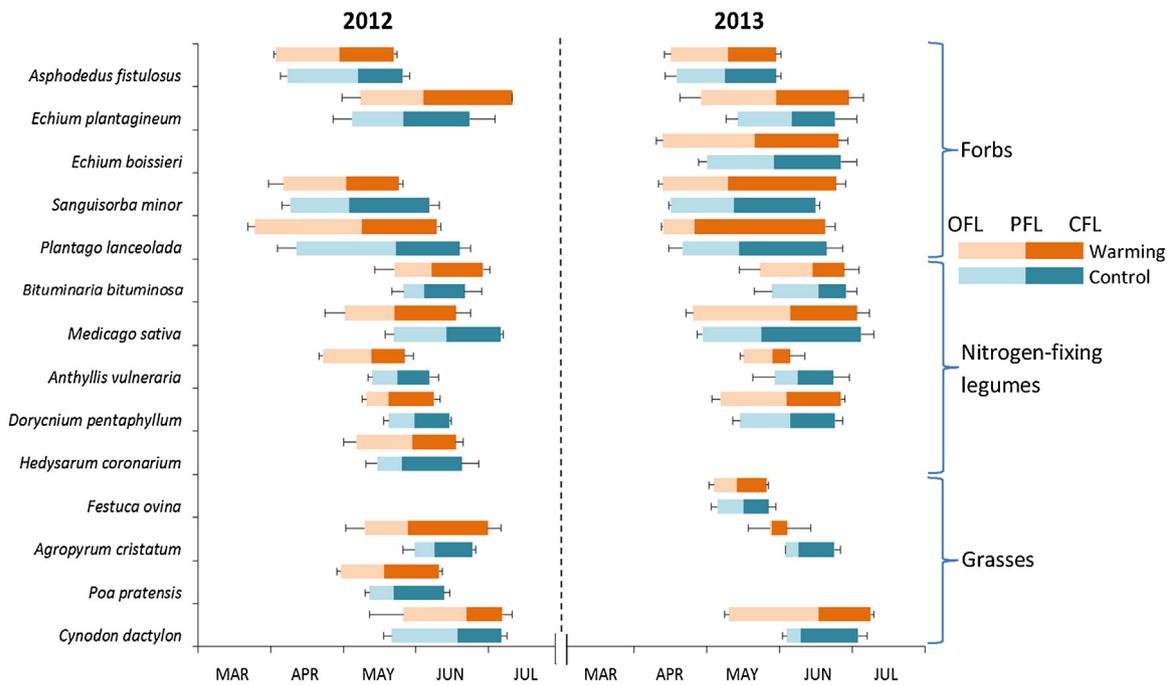


Fig. 1. Flowering phenology of the species studied during the growing seasons of 2012 and 2013. OFL: onset of flowering; PFL: peak of flowering; CFL: cessation of flowering. Data represent means \pm SE at the beginning and end of flowering phenology ($n = 4$ of each species in warming or control).

species-specific (Fig. 1). In both years, the magnitude of the phenological change by warming was higher for the onset of the flowering, compared to the flowering peak or the cessation of flowering (Table 1). In the drier year, warming promoted a significant earlier onset and peak of flowering, and an earlier fruiting onset ($P < 0.05$, Table 1). We also found a marginally significant trend towards a longer duration of flowering with warming ($P = 0.09$, Table 1). In the wetter year, warming led to an earlier flowering and fruiting onset, to an earlier fruiting peak of fruiting, and to a longer flowering duration ($P < 0.05$, Table 1).

Functional group significantly affected flowering variables in both years, and fructification variables in the drier year (Table 1, Fig. 2). The phenology and duration of flowering were earlier and longer in forbs than in grasses and nitrogen-fixing legumes in both years (Fig. 2). The same occurred with fruiting phenology variables, but differences were significant only in the drier year (Table 1, Fig. 2). There were no differences between grasses and nitrogen-fixing legumes in any of the flowering and fruiting variables measured (Fig. 2). The interaction between warming and functional group was not significant for any variable (Table 1).

Leaf and size traits affected flowering and fructification in both years (Table 1). Larger plants had an earlier onset and peak of flowering, and a longer flowering duration in both years (Table 1). Plants with a higher LA had a later date of cessation of flowering in both years, a later peak of flowering and a larger flowering duration in the drier year and an earlier onset of fructification in the wetter year (Table 1). A smaller SLA promoted an earlier onset and peak of flowering, but only in the wetter year. In the drier year, plants with a lower vegetative height in the warming treatment had a significant earlier peak of fructification (warming \times VH interaction; Table 1, Fig. S3a). Plants with a higher LA in the control treatment had a significant longer flowering duration in the wetter year (warming \times LA interaction; Table 1, Fig. S3c).

The analyses of RII values showed that, in the drier year, decreases in LA under warming correlated with an advanced peak of flowering (Fig. S4). In the wetter year, species that decreased

their LA under warming advanced more the onset of flowering than species with the opposite trait response (Fig. S5).

3.2. Effects of warming on reproductive variables

Warming significantly decreased flower and fruit production only in the wetter year ($P < 0.05$, Table 2). Fruit production in forbs was higher than in grasses and legumes in both years (Fig. 2; Table 2). VH was positively correlated with flower and fruit production in both years (Table 2). In the drier year, increases in LA increased flower production (Table 2). Seed mass increased with increases in LA but decreased with increases in SLA (Table 2). Additionally, species that increased VH in response to warming produced more flowers (Fig. S5).

4. Discussion

4.1. Flowering and fruiting responses to warming

In agreement with our hypothesis, warming advanced the onset of flowering, and the onset and peak of fructification; it also increased the duration of flowering throughout the experiment (Table 1). These results qualitatively agree with previous observational and manipulative studies conducted around the world (Fitter and Fitter, 2002; Peñuelas et al., 2002; Matsumoto et al., 2003; Gordo and Sanz, 2009). In our experiment, the onset of flowering was the variable most affected by warming, as some species advanced their flowering up to 20 days in this treatment (Table S4). Previous observational studies have found that warming commonly advances the onset of flowering by three days in northeast North America or four days in England (Fitter et al., 1995; Miller-Rushing et al., 2008; Miller-Rushing and Primack, 2008). However, the large advance observed in the onset of flowering due to warming is comparable to observational studies in Mediterranean ecosystems (Gordo and Sanz, 2009), and to another manipulative study conducted in subarctic areas (Aerts et al., 2004). We suggest that the onset of flowering had a higher response to warming compared to the rest of phenological variables because

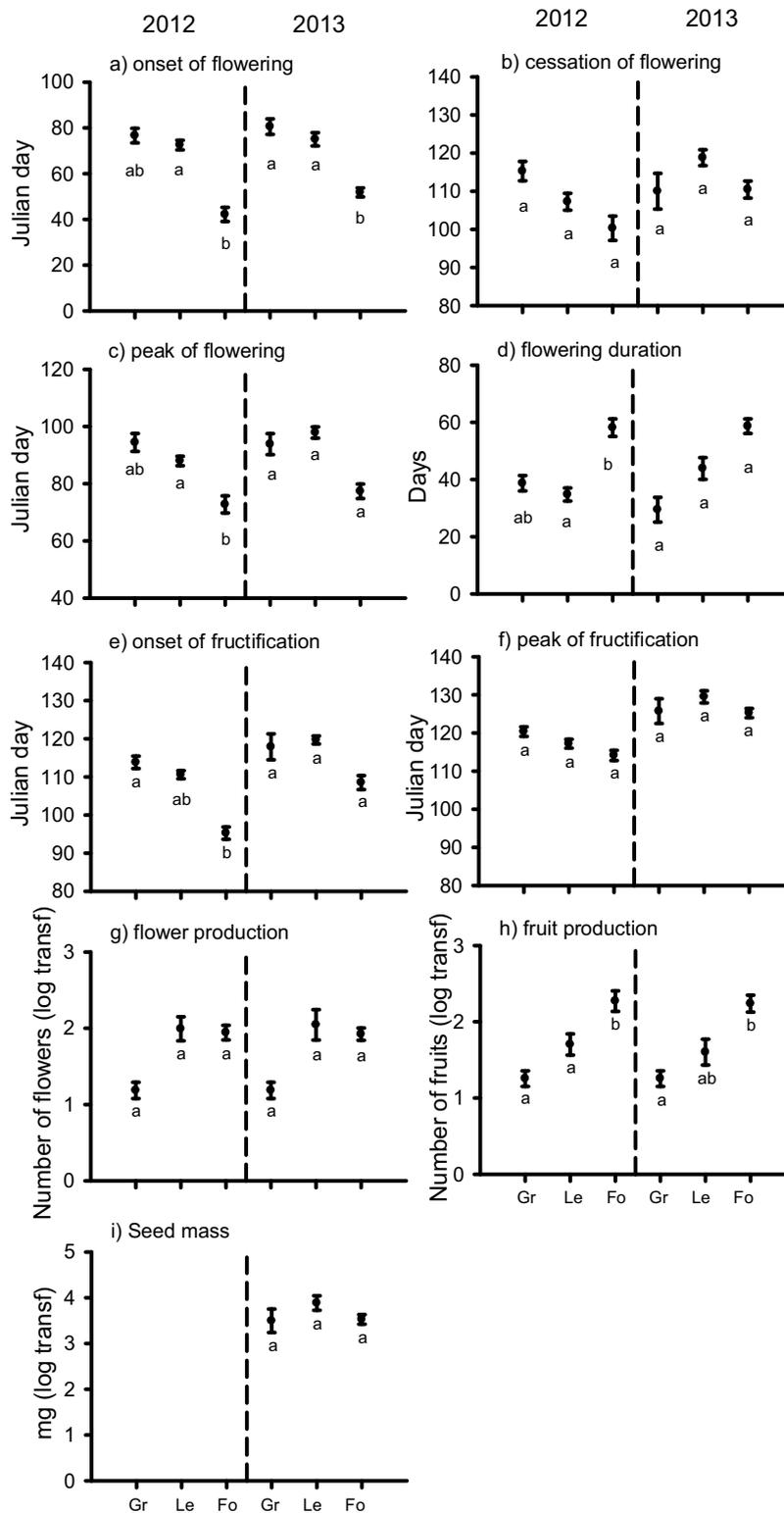


Fig. 2. Phenological and reproductive variables for each functional group. Significant differences among functional groups are indicated by different letters (Tukey post-hoc, $P < 0.05$). Gr: grasses; Le: nitrogen-fixing legumes; Fo: forbs. Data represent means \pm SE ($n = 96$).

it happens during the first stages of the growing season, when temperature, but not water, could be a factor limiting plant development (Fig. S6). Our results increase our knowledge regarding flowering and fruiting responses of semiarid Mediterranean species to warming, and could have important ecological implications. For instance, the large advances in flowering of some species could

promote dramatic ecological asynchronies between neighboring plants (Price and Waser, 1998) or between them and their pollinators or herbivores (Williams et al., 2007), which could lead to changes in the composition or abundance of rural communities (Walther et al., 2002) in drylands.

Table 2

Summary results of the Linear Mixed Models evaluating the effects of warming, functional groups, functional traits and their interactions on the flower production (FLP), fruit production (FRP) and seed mass in 2012 and 2013. VH = vegetative height; LA = leaf area; SLA = specific leaf area; N° ind = number of individuals per microcosm.

| 2012 | | | | | | | | | | |
|-----------------------|------|-------|----------|------------------|-------|----------|------------------|-----------|----------|------------------|
| Treatment | FLP | | | | FRP | | | | | |
| | d.f. | est | χ^2 | P | est | χ^2 | P | | | |
| Warming (W) | 1 | −0.11 | 3.304 | 0.069 | | | | | | |
| Functional group (FG) | 2 | | | | | 13.834 | | | | <0.001 |
| VH | 1 | 0.36 | 48.348 | <0.001 | 0.38 | 17.909 | | | | <0.001 |
| LA | 1 | 0.17 | 7.011 | 0.008 | | | | | | |
| SLA | 1 | | | | | | | | | |
| N° ind | 1 | | | | | | | | | |
| W × FG | 2 | | | | | | | | | |
| W × VH | 1 | | | | | | | | | |
| W × LA | 1 | | | | | | | | | |
| W × SLA | 1 | | | | | | | | | |
| 2013 | | | | | | | | | | |
| Treatment | FLP | | | | FRP | | | Seed mass | | |
| | d.f. | est | χ^2 | P | est | χ^2 | P | est | χ^2 | P |
| Warming (W) | 1 | −0.19 | 5.799 | 0.016 | −0.31 | 8.597 | 0.003 | | | |
| Functional group (FG) | 2 | | 4.709 | 0.095 | | 11.225 | 0.004 | | | |
| VH | 1 | 0.54 | 51.497 | <0.001 | 0.38 | 20.935 | <0.001 | | | |
| LA | 1 | −0.01 | 0.014 | 0.907 | 0.17 | 3.392 | 0.066 | 0.12 | 11.44 | <0.001 |
| SLA | 1 | | | | | | | −0.12 | 5.272 | 0.022 |
| N° ind | 1 | 0.14 | 4.158 | 0.041 | | | | 0.07 | 3.880 | 0.049 |
| W × FG | 2 | | | | | | | | | |
| W × VH | 1 | | | | | | | | | |
| W × LA | 1 | | 2.556 | 0.110 | | 2.660 | 0.103 | | | |
| W × SLA | 1 | | | | | | | | | |

4.2. Reproductive responses to warming

As predicted by our hypothesis, warming reduced flower and fruit production in the studied species. This was probably due to the reduction in soil moisture promoted by warming (Fig. S6). Decreases in soil moisture in this treatment were particularly important at the end of the growing season, where water is scarce and only the largest species could stand these stressful conditions (Tsakalidimi et al., 2012; Villar-Salvador et al., 2013).

The reduction in the reproductive output observed could be also explained by changes in vegetative size under warming (Fig. S5). For instance, these changes could be related with faster plant development throughout the growing season (Springate and Kover, 2013). Another possibility is that reproductive output was indirectly affected by changes in the vegetative and flowering phenology. There are two contrasting scenarios about the relationship between vegetative phenology and flower and fruit production. First, a positive relationship between advances in vegetative phenology and reproductive output could occur if species that advance their leaf phenology under warming also increase their vegetative size, as larger plants usually enhance their fitness (Cleland et al., 2012; Springate and Kover, 2013). Thus, larger vegetative size could occur if increases in the length of the growing period last longer than increases in flowering duration. Second, a negative relationship between advances in vegetative phenology and reproductive output could occur if an earlier onset of flowering involves a reduced allocation of resources to growth, a smaller size, and therefore a reduction of resources available for reproduction (Bolmgren and Cowan, 2008). In the first scenario, we expect that species could accumulate more biomass in these situations (Hollister et al., 2005; Cleland et al., 2012), a response that would lead to more flowers and fruits, and to larger seeds. Previous studies have observed this phenomenon in temperate ecosystems, where warming increased flower and fruit production and seed mass (Hollister and Weber, 2000; Lemmens et al., 2008; Springate and Kover, 2013). In our study, species advanced their flowering but only some species

increased their plant size, being these changes related to changes in flower production (Fig. S5). Further research is required to evaluate how warming responses of vegetative and flowering season length influence plant growth, and how these relationships are related to the reduction in number of flowers and fruits showed in Mediterranean semiarid ecosystems.

4.3. Phenology varies among functional groups

Considering functional groups could potentially help to predict community responses to global change. For example, experiments manipulating variables such as CO₂, N deposition or grazing found differential flowering responses among functional groups (Cleland et al., 2006; Spence et al., 2014). In our case, although reproductive phenology varied consistently among plant functional groups, these differences did not translate into early-flowering functional groups having a significantly higher advancement in their flowering variables with warming than late-flowering functional groups. This contrasts with the results of Sherry et al. (2007), possibly because the species we studied flowered in spring and not across all seasons, as those in that study. Instead, species-specific flowering responses not related to functional groups were found, as in other studies (Hollister and Weber, 2000; Fitter and Fitter, 2002; Liancourt et al., 2012). Our results suggest that functional groups do not seem to provide enough resolution to address plant responses to warming.

4.4. Functional traits affect phenological responses

The axes of specialization represented by size and leaf traits provided different information than that supplied by functional groups (Fig. S7). The selected traits are surrogates of basic functional properties of plants (Westoby et al., 2002). Plant size is a good surrogate for water use efficiency and/or competitive ability (Westoby et al., 2002; Cornelissen et al., 2003). Leaf area is related to light interception and absorption, resource allocation, water uptake strategy and water stress tolerance (Westoby et al., 2002; Gross

et al., 2007). SLA indicates plant relative growth rate and resource capture and utilization (Wright et al., 2004), and is a descriptor of dominant plant strategies (Westoby et al., 2002); for instance higher SLA is related with fast-growing strategy (Freschet et al., 2011). The functional traits measured influenced reproductive phenology and/or reproductive output. Larger species with small LA and SLA had an earlier flowering phenology and longer flowering duration (Table 1). An expanded flowering period could increase the capacity of these species to adapt to warming. In addition, the production of flowers and fruits varied with plant size, while LA and SLA influenced seed mass in opposite directions (Table 2). We speculate that the observed relationships between larger plant size and an earlier flowering can be explained if the stored resources (acquired during previous growing seasons) are more important than resources acquired during the current season, as suggested by Bolmgren and Cowan (2008). Our findings advance our understanding of the responses of reproductive phenology in Mediterranean semiarid species at an interspecific level. Further research is needed to test whether observed responses can be found with other non-herbaceous perennial species (e.g. shrubs or trees; Bolmgren and Cowan, 2008).

The interactions between plant size/leaf area and warming found indicate that these traits influenced the response of the phenological and reproductive variables to warming. The peak of fructification was delayed for plants with higher VH under warming compared to what we found in the control treatment (Fig. S3a). In addition, flowering duration was higher in species with higher leaf area in the control treatment, an effect that vanished under warming (Fig. S3b). We thus believe that the explicit consideration of functional traits can help us to predict which species will be more affected by warming, and hence deserve more attention by future research on this topic. We must note that the functional traits were also modified by warming, as revealed by the RII analyses (Figs. S4 and S5). Thus, warming induced changes in traits that, in turn, could influence the phenological and reproductive responses to warming. For instance, decreases in LA by warming advanced more the onset and peak of flowering (Figs. S4 and S5), so changes in LA were coupled with changes in flowering phenology of the species studied. Furthermore, species that under warming increased their VH had higher flower production compared to those with no change or decreased VH (Fig. S5).

Our findings indicate that increases in size can be a way to mitigate the negative effects of warming on flower and fruit production. Plants could respond to environmental variability by plasticity in functional traits (Sultan et al., 1998). The phenotypic response in our plant traits might be plastic (Bertheaux et al., 2004; Pigliucci, 2005; Nicotra et al., 2010), but we cannot rule out genetic differences. Nevertheless, the plant size/leaf area changes detected were species-specific (Yamori et al., 2009; Gunderson et al., 2010) and essential to withstand changing climate conditions. Morphological and physiological adaptations to mitigate the effects of climatic conditions have been documented (Gianoli and González-Teuber, 2005; García-Verdugo et al., 2009). The degree to which whole plant communities are affected by warming will depend, to a large extent, on the ability of their constituent species to acclimate (*sensu* Smith and Dukes, 2012) to these climatic conditions. Our results highlight the interest of incorporating intraspecific trait variability into models aiming to predict changes in species distributions under different climate change scenarios (Valladares et al., 2014). The ability of species to modify key functional traits (through plastic responses or filtering of genotypes) could be decisive for their future under warming, especially under the more variable climate expected in drylands (Beniston et al., 2007). The study of these parallel changes could anticipate how Mediterranean semiarid species can respond to ongoing climate change.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2016.05.003>.

References

- Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., Van Logtestijn, R.S.P., Callaghan, T.V., 2004. Effects of experimentally imposed climate scenarios on flowering phenology and flower production of subarctic bog species. *Glob. Change Biol.* 10, 1599–1609, <http://dx.doi.org/10.1111/j.1365-2486.2004.00815.x>.
- Akaike, H., 1973. *Information theory and an extension of the maximum likelihood principle*. In: Petrov, B.N., Csaki, F. (Eds.), *Second International Symposium on Information Theory*. Minnesota Studies in the Philosophy of Science: Akademiai Kiado, Budapest.
- Arft, A.M., Walker, M.D., Gurevitch, J.E.A., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R.D., Jónsdóttir, I.S., Laine, K., Lévesque, E., Marion, G.M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., Robinson, C.H., Starr, G., Stenström, A., Stenström, M., Totland, Ø., Turner, P.L., Walker, L.J., Webber, P.J., Welker, J.M., Wookey, P.A., 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecol. Mon.* 69, 491–511, [http://dx.doi.org/10.1890/0012-9615\(1999\)069\[0491:ROTPT\]2.0.CO.2](http://dx.doi.org/10.1890/0012-9615(1999)069[0491:ROTPT]2.0.CO.2).
- Armas, C., Ordiales, R., Pugnaire, F.I., 2004. Measuring plant interactions: a new comparative index. *Ecology* 85, 2682–2686, <http://dx.doi.org/10.1890/03-0650>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. *lme4: Linear Mixed-effects Models Using Eigen and S4*. R Package Version 1., pp. 1–7 (Available from <http://CRAN.R-project.org/package=lme4>).
- Beniston, M., Stephenson, D.B., Christensen, O.B., Ferro, C.A.T., Frei, C., Goyette, S., Halsnaes, K., Holt, T., Jylhä, K., Koffi, B., Palutikof, J., Schöll, R., Semmler, T., Wooh, K., 2007. Future extreme events in European climate: an exploration of regional climate model projections. *Clim. Chan.* 81, 71–95, <http://dx.doi.org/10.1007/s10584-006-9226-z>.
- Bertheaux, D., Reale, D., McAdam, A., Boutin, S., 2004. Keeping pace with fast climate change: can Arctic life count on evolution? *Integr. Comp. Biol.* 44, 140–151, <http://dx.doi.org/10.1093/icb/44.2.140>.
- Bolmgren, K., Cowan, P.D., 2008. Time–size tradeoffs: a phylogenetic comparative study of flowering time, plant height and seed mass in a north-temperate flora. *Oikos* 117, 424–429, <http://dx.doi.org/10.1111/j.2007.0030-1299.16142.x>.
- Boss, P.K., Bastow, R.M., Mylne, J.S., Dean, C., 2004. Multiple pathways in the decision to flower: enabling, promoting, and resetting. *Plant Cell* 16, 18–31 (10.1105/tpc.015958).
- Butterfield, B.J., Suding, K.N., 2013. Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *J. Ecol.* 101, 9–17, <http://dx.doi.org/10.1111/1365-2745.12013>.
- Chacón-Labela, J., Cruz, M., Escudero, A., 2016. Beyond the classical nurse species effect: diversity assembly in a Mediterranean semi-arid dwarf shrubland. *J. Veg. Sci.* 27, 80–88, <http://dx.doi.org/10.1111/jvs.12337>.
- Cleland, E.E., Chiariello, N.R., Loarie, S.R., Mooney, H.A., Field, C.B., 2006. Diverse responses of phenology to global changes in a grassland ecosystem. *Proc. R. Soc. Lond. B.* 103, 13740–13744, <http://dx.doi.org/10.1073/pnas.0600815103>.
- Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E., Wolkovich, E.M., 2012. Phenological tracking enables positive species responses to climate change. *Ecology* 93, 1765–1771, <http://dx.doi.org/10.1890/11-1912.1>.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H., Morgan, H.D., Van Der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335–380, <http://dx.doi.org/10.1071/BT02124>.
- Díaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8, 463–474, <http://dx.doi.org/10.2307/3237198>.
- Dunne, J.A., Harte, J., Taylor, K.J., 2003. Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecol. Mon.* 73, 69–86, [http://dx.doi.org/10.1890/0012-9615\(2003\)073\[0069:SMFPRT\]2.0.CO.2](http://dx.doi.org/10.1890/0012-9615(2003)073[0069:SMFPRT]2.0.CO.2).

- Escobar, C., Martínez, I., Matthew, A.B., Maestre, F.T., 2012. Warming reduces the growth and diversity of biological soil crust in a semi-arid environment: implications for ecosystem structure and function. *Philos. Tran. R. Soc. Lond. B.* 367, 3087–3099, <http://dx.doi.org/10.1098/rstb.2011.0344>.
- Fitter, A.H., Fitter, R.S.R., 2002. Rapid changes in flowering time in British plants. *Science* 296, 1689–1691, <http://dx.doi.org/10.1126/science.1071617>.
- Fitter, A.H., Fitter, R.S.R., Harris, I.T.B., Williamson, M.H., 1995. Relationships between first flowering date and temperature in the flora of a locality in central England. *Funct. Ecol.* 9, 55–60, <http://dx.doi.org/10.2307/2390090>.
- Freschet, G.T., Dias, A.T., Ackerly, D.D., Aerts, R., van Bodegom, P.M., Cornwell, W.K., Dong, M., Kurokawa, H., Liu, G., Onipchenko, V.G., Ordoñez, J.C., Peltzer, D.A., Richardson, S.J., Shidakov, I.I., Soudzilovskaia, N.A., Tao, J., Cornelissen, J.H., 2011. Global to community scale differences in the prevalence of convergent over divergent leaf trait distributions in plant assemblages. *Global Ecol. Biogeogr.* 20, 755–765, <http://dx.doi.org/10.1111/j.1466-8238.2011.00651.x>.
- García-Palacios, P., Soliveres, S., Maestre, F.T., Escudero, A., Castillo-Monroy, A.P., Valladares, F., 2010. Dominant plant species modulate responses to hydroseeding, irrigation and fertilization during the restoration of semiarid motorway slopes. *Ecol. Eng.* 36, 1290–1298, <http://dx.doi.org/10.1016/j.ecoleng.2010.06.005>.
- García-Verdugo, C., Granado-Yela, C., Manrique, E., Rubio de Casas, R., Balaguer, L., 2009. Phenotypic plasticity and integration across the canopy of *Olea europaea* subsp. *guanchica* (Oleaceae) in populations with different wind exposures. *Am. J. Bot.* 96, 1454–1461, <http://dx.doi.org/10.3732/ajb.0800420>.
- Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637, <http://dx.doi.org/10.1890/03-0799>.
- Gianoli, E., González-Teuber, M., 2005. Environmental heterogeneity and population differentiation in plasticity to drought in *Convolvulus chilensis* (Convolvulaceae). *Evol. Ecol.* 19, 603–613, <http://dx.doi.org/10.1007/s10682-005-2220-5>.
- Gitay, H., Noble, I.R., et al., 1997. *What are plant functional types and how should we seek them?* In: Smith, T.M. (Ed.), *Plant Functional Types*. Cambridge University Press, Cambridge, pp. 3–19.
- Gordo, O., Sanz, J.J., 2009. Long-term temporal changes of plant phenology in the Western Mediterranean. *Glob. Change Biol.* 15, 1930–1948, <http://dx.doi.org/10.1111/j.1365-2486.2009.01851.x>.
- Gordo, O., Sanz, J.J., 2010. Impact of climate change on plant phenology in Mediterranean ecosystems. *Glob. Change Biol.* 16, 1082–1106, <http://dx.doi.org/10.1111/j.1365-2486.2009.02084.x>.
- Goulden, M., Munger, J., Fan, S., 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* 271, 1576–1578, <http://dx.doi.org/10.1126/science.271.5255.1576>.
- Grace, J.B., 2006. *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge.
- Gross, N., Suding, K.N., Lavorel, S., 2007. Leaf dry matter content and lateral spread predict response to land use change for six subalpine grassland species. *J. Veg. Sci.* 18, 289–300, <http://dx.doi.org/10.1111/j.1654-1103.2007.tb02540.x>.
- Gunderson, C.A., O'Hara, K.H., Campion, C.M., Walker, A.V., Edwards, N.T., 2010. Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. *Glob. Change Biol.* 16, 2272–2286, <http://dx.doi.org/10.1111/j.1365-2486.2009.02090.x>.
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L., Totland Ø, 2009. How does climate warming affect plant pollinator interactions? *Ecol. Lett.* 12, 184–195, <http://dx.doi.org/10.1111/j.1461-0248.2008.01269.x>.
- Hollister, R.D., Weber, P.J., 2000. Biotic validation of small open-top chambers in a tundra ecosystem. *Glob. Change Biol.* 6, 835–842, <http://dx.doi.org/10.1046/j.1365-2486.2000.00363.x>.
- Hollister, R.D., Webber, P.J., Tweedie, C.E., 2005. The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Glob. Change Biol.* 11, 525–536, <http://dx.doi.org/10.1111/j.1365-2486.2005.00926.x>.
- Hothorn, T., Bretz, F., Westfall, P., 2008. *Simultaneous inference in general parametric models*. *Biom. J.* 50, 346–363.
- Hovenden, M.J., Wills, K.E., Van der Schoor, J.K., Williams, A.L., Newton, P.C.D., 2008. Flowering phenology in a species-rich temperate grassland is sensitive to warming but not elevated CO₂. *New Phytol.* 178, 815–822, <http://dx.doi.org/10.1111/j.1469-8137.2008.02419.x>.
- Inouye, D.W., 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89, 353–362, <http://dx.doi.org/10.1890/06-2128.1>.
- Intergovernmental Panel on Climate Change (IPCC), 2013. *Fifth Assessment Report: Climate Change 2013: The Physical Science Basis*. Cambridge University Press, Cambridge.
- Körner, C., Basler, D., 2010. Phenology under global warming. *Science* 327, 1461–1462, <http://dx.doi.org/10.1126/science.1186473>.
- Kardol, P., Campy, C.E., Souza, L., Norby, R.J., Weltzin, J.F., Classen, A.T., 2010. Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. *Glob. Change Biol.* 16, 2676–2687, <http://dx.doi.org/10.1111/j.1365-2486.2010.02162.x>.
- Lemmens, C., Boeck, H., Zavalloni, C., Nijis, I., Ceulemans, R., 2008. How is phenology of grassland species influenced by climate warming across a range of species richness? *Comm. Ecol.* 9, 33–42, <http://dx.doi.org/10.1556/ComEc.9.2008.5.6>.
- Liancourt, P., Spence, L.A., Boldgiv, B., Lkhagva, A., Helliher, B.R., Casper, B.B., Petraitis, P.S., 2012. Vulnerability of the northern Mongolian steppe to climate change: insights from flower production and phenology. *Ecology* 93, 815–824, <http://dx.doi.org/10.1890/11-1003.1>.
- Liang, J., Xia, J., Liu, L., Wan, S., 2013. Global patterns of the responses of leaf-level photosynthesis and respiration in terrestrial plants to experimental warming. *Plant Ecol.* 6, 437–447, <http://dx.doi.org/10.1093/jpe/rtt003>.
- Luo, Y., Wan, S., Hui, D., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* 413, 622–625, <http://dx.doi.org/10.1038/35098065>.
- Maestre, F.T., Bradford, M.A., Reynolds, J.F., 2005. Soil nutrient heterogeneity interacts with elevated CO₂ and nutrient availability to determine species and assemblage responses in a model grassland community. *New Phytol.* 168, 637–650, <http://dx.doi.org/10.1111/j.1469-8137.2005.01547.x>.
- Maestre, F.T., Salguero-Gómez, R., Quero, J.L., 2012. It's getting hotter in here: determining and projecting the impacts of global change on dryland ecosystems and on the people living in them. *Phil. Tran. R. Soc. Lond. B.* 367, 3062–3075, <http://dx.doi.org/10.1098/rstb.2011.0323>.
- Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H., Lévesque, E., Molau, U., Mølgaard, P., Parsons, A.N., Svoboda, J., Virginia, R.A., 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. *Glob. Change Biol.* 3, 20–32, <http://dx.doi.org/10.1111/j.1365-2486.1997.gcb136.x>.
- Matsumoto, K., Ohta, T., Irasawa, M., Nakamura, T., 2003. Climate change and extension of the *Ginkgo biloba* L. growing season in Japan. *Glob. Change Biol.* 9, 1634–1642, <http://dx.doi.org/10.1046/j.1365-2486.2003.00688.x>.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatcva, K., Mages, F., Mestre, A., Nordli, O., Peñuelas, J., Pirinen, P., Remisova, V., Scheffinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Züst, A., 2006. European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* 12, 1969–1976, <http://dx.doi.org/10.1111/j.1365-2486.2006.01193.x>.
- Miller-Rushing, A.J., Primack, R.B., 2008. Global warming and flowering times in Thoreau's Concord: a community perspective. *Ecology* 89, 332–341, <http://dx.doi.org/10.1890/07-0068.1>.
- Miller-Rushing, A.J., Inouye, D.W., Primack, R.B., 2008. How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *J. Ecol.* 96, 1289–1296, <http://dx.doi.org/10.1111/j.1365-2745.2008.01436.x>.
- Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathiesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F., van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* 15, 684–692, <http://dx.doi.org/10.1016/j.tplants.2010.09.008>.
- Parnesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42, <http://dx.doi.org/10.1038/nature01286>.
- Parnesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Change Biol.* 13, 1860–1872, <http://dx.doi.org/10.1111/j.1365-2486.2007.01404.x>.
- Partanen, J., Koski, V., Hänninen, H., 1998. Effects of photoperiod and temperature on the timing of bud burst in Norway spruce (*Picea abies*). *Tree Phys.* 18, 811–816, <http://dx.doi.org/10.1093/treephys/18.12.811>.
- Peñuelas, J., Filella, I., 2001. Phenology. Responses to a warming world. *Science* 294, 793–795, <http://dx.doi.org/10.1126/science.1066860>.
- Peñuelas, J., Filella, I., Comas, P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Glob. Change Biol.* 8, 531–544, <http://dx.doi.org/10.1046/j.1365-2486.2002.00489.x>.
- Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M., Terradas, J., 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytol.* 161, 837–846, <http://dx.doi.org/10.1111/j.1469-8137.2004.01003.x>.
- Pigliucci, M., 2005. Evolution of phenotypic plasticity: where are we going now? *Trends Ecol. Evol.* 20, 481–486, <http://dx.doi.org/10.1016/j.tree.2005.06.001>.
- Price, M.V., Waser, N.M., 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79, 1261–1271, <http://dx.doi.org/10.2307/176741>.
- R Development Core Team, 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria (Available from) <http://www.R-project.org/>.
- Rathcke, B., Lacey, E.P., 1985. Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.* 16, 179–214, <http://dx.doi.org/10.1146/annurev.es.16.110185.001143>.
- Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernández, R.J., Herrick, J.E., Huber-Sannwald, E., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. *Science* 316, 847–851, <http://dx.doi.org/10.1126/science.1131634>.
- Richardson, A.D., Black, T.A., Ciais, P., Delbart, N., Friedl, M.A., Gobron, N., Hollinger, D.Y.L., Kutsch, W., Longdoz, B., Luuyssaert, S., Migliavacca, M., Munger, J.W., Moors, E., Piao, S., Rebmann, C., Reichstein, M., Saigusa, N., Tomelleri, E., Vargas, R., Varlagin, A., 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Phil. Tran. R. Soc. Lond. B* 365, 3227–3246, <http://dx.doi.org/10.1098/rstb.2010.0102>.
- Rollinson, C.R., Kaye, M.W., 2012. Experimental warming alters spring phenology of certain plant functional groups in an early-successional forest community. *Glob. Change Biol.* 18, 1108–1116, <http://dx.doi.org/10.1111/j.1365-2486.2011.02612.x>.

- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421, 57–60, <http://dx.doi.org/10.1038/nature01333>.
- Safirel, U., Adeel, Z., 2005. *Dryland systems*. In: Hassan, R., Scholes, R., Neville, A. (Eds.), *Ecosystems and Human Well-being: Current State and Trends*, vol. 1. Island Press, Washington, DC, USA, pp. 623–662.
- Sherry, R.A., Zhou, X.H., Gu, S.L., Arnone, J.A., Schimel, D.S., Verburg, P.S., Wallace, L.L., Luo, Y.Q., 2007. Divergence of reproductive phenology under climate warming. *Proc. R. Soc. Lond. B* 104, 198–202, <http://dx.doi.org/10.1073/pnas.0605642104>.
- Smith, N.G., Dukes, J.S., 2012. Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO₂. *Glob. Change Biol.* 19, 45–63, <http://dx.doi.org/10.1111/j.1365-2486.2012.02797.x>.
- Spence, L.A., Liancourt, P., Boldgiv, B., Petraitis, P.S., Casper, B.B., 2014. Climate change and grazing interact to alter flowering patterns in the Mongolian steppe. *Oecologia* 175, 251–260, <http://dx.doi.org/10.1007/s00442-014-2884-z>.
- Springate, D.A., Kover, P.X., 2013. Plant responses to elevated temperatures: a field study on phenological sensitivity and fitness responses to simulated climate warming. *Glob. Change Biol.* 20, 456–465, <http://dx.doi.org/10.1111/gcb.12430>.
- Sultan, S.E., Wilczek, A.M., Bell, D.L., Hand, G., 1998. Physiological response to complex environments in annual *Polygonum* species of contrasting ecological breadth. *Oecologia* 115, 564–578, <http://dx.doi.org/10.1007/s004420050554>.
- Tsakalidimi, M., Ganatsas, P., Jacobs, D.F., 2012. Prediction of planted seedling survival of five Mediterranean species based on initial seedling morphology. *New For.* 44, 327–339, <http://dx.doi.org/10.1007/s11056-012-9339-3>.
- Turck, F., Fornara, F., Coupland, G., 2008. Regulation and identity of florigen: FLOWERING LOCUS T moves center stage. *Annu. Rev. Plant Biol.* 59, 573–594, <http://dx.doi.org/10.1146/annurev.arplant.59.032607.092755>.
- United Nations Environment Programme, 1992. *World Atlas of Desertification*. Edward Arnold, London.
- Valencia, E., Méndez, M., Saavedra, N., Maestre, F.T., 2016a. Data from Plant size and leaf area influence phenological and reproductive responses to warming in semiarid Mediterranean species. *Figshare*, <http://dx.doi.org/10.6084/m9.figshare.3124348.v1>.
- Valencia, E., Quero, J.L., Maestre, F.T., 2016b. Functional leaf and size traits determine the photosynthetic response of ten dryland species to warming. *Plant Ecol.*, <http://dx.doi.org/10.1093/jpe/rtv081>.
- Valladares, F., Matesanz, S., Guilhaumon, F., Araujo, M.B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D.E., Nicotra, A.B., Poorter, H., Zavala, M.A., 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecol. Lett.* 17, 1351–1364, <http://dx.doi.org/10.1111/ele.12348>.
- Vile, D., Shilpley, B., Garnier, E., 2006. A structural equation model to integrate changes in functional strategies during old-field succession. *Ecology* 87, 504–517, <http://dx.doi.org/10.1890/05-0822>.
- Villar-Salvador, P., Peñuelas, J.L., Nicolás-Peragón, J.L., Benito, L.F., Domínguez-Lerena, S., 2013. Is nitrogen fertilization in the nursery a suitable tool for enhancing the performance of Mediterranean oak plantations? *New For.* 44, 733–751, <http://dx.doi.org/10.1007/s11056-013-9374-8>.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.R.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395, <http://dx.doi.org/10.1038/416389a>.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33, 125–159, <http://dx.doi.org/10.1146/annurev.ecolsys.33.010802.150452>.
- White, R.P., Nackoney, J., 2003. *Drylands, People, and Ecosystem Goods and Services: a Web-based Geospatial Analysis*. World Resources Institute, Washington, DC, pp. 2003 www.wri.org/publication/content/8241.
- Whittington, H.R., 2012. *Consequences of Elevated Temperature on Prairie Plants: Legumes, Nitrogen, and Phenology*. Doctoral Dissertation. University of Minnesota.
- Williams, J.W., Jackson, S.T., Kutzbach, J.E., 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proc. R. Soc. Lond. B* 104, 5738–5742, <http://dx.doi.org/10.1073/pnas.0606292104>.
- Wilson, J.B., 1999. Guilds, functional types and ecological groups. *Oikos*, 507–522, <http://dx.doi.org/10.2307/3546655>.
- Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L., Travers, S.E., Pau, S., Regetz, J., Davies, T.J., Kraft, N.J.B., Ault, T.R., Bolmgren, K., Mazer, S.J., McCabe, G.J., McGill, B.J., Parmesan, C., Salamin, N., Schwartz, M.D., Cleland, E.E., 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485, 494–497, <http://dx.doi.org/10.1038/nature11014>.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827, <http://dx.doi.org/10.1038/nature02403>.
- Yamori, W., Noguchi, K., Hikosaka, K., Terashima, I., 2009. Cold-tolerant crop species have greater temperature homeostasis of leaf respiration and photosynthesis than cold-sensitive species. *Plant Cell Physiol.* 50, 203–215, <http://dx.doi.org/10.1093/pcp/pcn189>.