



Original article

Variable flowering phenology and pollinator use in a community suggest future phenological mismatch



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ABSTRACT

Recent anthropogenic climate change is strongly associated with average shifts toward earlier seasonal timing of activity (phenology) in temperate-zone species. Shifts in phenology have the potential to alter ecological interactions, to the detriment of one or more interacting species. Recent models predict that detrimental phenological mismatch may increasingly occur between plants and their pollinators. One way to test this prediction is to examine data from ecological communities that experience large annual weather fluctuations. Taking this approach, we analyzed interactions over a four-year period among 132 plant species and 665 pollinating insect species within a Mediterranean community. For each plant species we recorded onset and duration of flowering and number of pollinator species. Flowering onset varied among years, and a year of earlier flowering of a species tended to be a year of fewer species pollinating its flowers. This relationship was attributable principally to early-flowering species, suggesting that shifts toward earlier phenology driven by climate change may reduce pollination services due to phenological mismatch. Earlier flowering onset of a species also was associated with prolonged flowering duration, but it is not certain that this will counterbalance any negative effects of lower pollinator species richness on plant reproductive success. Among plants with different life histories, annuals were more severely affected by flowering–pollinator mismatches than perennials. Specialized plant species (those attracting a smaller number of pollinator species) did not experience disproportionate interannual fluctuations in phenology. Thus they do not appear to be faced with disproportionate fluctuations in pollinator species richness, contrary to the expectation that specialists are at greatest risk of losing mutualistic interactions because of climate change.

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1. Introduction

Anthropogenic change in Earth's climate is affecting many aspects of ecological systems (Traill et al., 2010), including the seasonal timing (phenology) of biological events. One important example is a substantial shift over recent decades in the phenology of reproduction of flowering plants in temperate regions (Liu et al., 2010; Kjøl et al., 2011; McEwan et al., 2011; Molnár et al., 2012). Although this phenological shift on average is toward earlier spring flowering, the exact response varies across plant species (CaraDonna et al., 2014). Because most species of flowering plants

rely on insects and other animals for pollination (Ollerton et al., 2011), and because climate change does not necessarily shift phenology of plants and pollinators in exactly the same way (Schweiger et al., 2008), there is the potential for a growing phenological mismatch between the mutualistic partners. This potential has been explored with theoretical approaches (e.g. Memmott et al., 2007; Tylianakis et al., 2008; Hegland et al., 2009; Schweiger et al., 2010), and with experiments and meta-analyses (e.g. Memmott et al., 2010; Forrest and Thomson, 2011; Rafferty and Ives, 2011, 2012; Bartomeus et al., 2013) and observations (e.g. Wall et al., 2003; Kudo et al., 2004; Thomson, 2010; McKinney et al., 2012) using single species or small sets of species. Many such studies (although not all of them) conclude that phenological mismatch is likely to increasingly disrupt pollination and plant reproduction.

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To augment empirical studies of small numbers of species it will be valuable to explore phenological shifts and pollination service at the larger scale of ecological communities. All species are embedded in communities and interact with other community members directly or indirectly, so that a change in phenology of one species has the potential to cause cascading changes that would not be revealed by examining smaller subsets of species (Lázaro et al., 2008; Miller-Rushing et al., 2010; Woodward et al., 2010). How should community-level studies be designed? To date it has been impractical to mimic elements of expected climate change on a spatial scale that captures the mobility of animal pollinators, as would be necessary in order to manipulate plants and pollinators simultaneously. Long-term data on unmanipulated plant and pollinator communities also might reveal how interactions change with climate change, but no such data are available to our knowledge.

A further possibility is to explore how natural variation in weather affects flowering phenology and pollinator availability, reasoning that natural extremes capture elements of directional anthropogenic change, e.g. that years of warmer temperatures will shed light on ongoing increase in mean temperature. Here we take this approach, using four years of data from a Greek community in which Petanidou et al. (1995c) found that timing of flowering of all species was influenced by temperature surplus in the month immediately preceding the flowering onset of each of the species.

We ask how interannual variation in the date of flowering onset of individual plant species caused by variation in weather conditions relates to variation in the number of pollinator species visiting the flowers of that species. Our rationale for exploring this relationship is the possibility (discussed below) that pollination success increases with pollinator species richness and that phenological mismatch contributes to lower species richness in years of earlier flowering. We also relate date of a species' flowering onset to overall duration of its flowering season, another aspect of its phenology. We then examine several traits of plants that might affect how strongly species richness of their pollinators varies with weather variation. First, the season of flowering might influence which environmental cues affect a species' phenology, so we compare responses to weather variation by early- vs. late-flowering species. Second, a plant producing many flowers might be capable of substantial plasticity in aspects of its phenology, so we examine

whether variation in phenology and pollinator species richness depend on flower number. The hypothesis behind this is that populations with many flowers per individual plant may be prone to more staggered flowering vs. those with few flowers per plant. Third, annuals may be more dependent on pollinators for their persistence in a community than are perennials, so we examine whether variation in phenology and pollinator species richness depend on life history. Fourth, we explore whether plants whose flowers attract relatively few pollinator species vary especially strongly across years in their flowering phenology. Such pollination specialists are often considered to be especially vulnerable to disruption of pollination services. We examine whether the flowering phenology of such plant species fluctuated more strongly than that of generalist plants.

2. Materials and methods

2.1. Study site

We studied pollination in a “phrygana”, a low scrub community dominated by insect-pollinated woody shrubs and annual plants, within the “I. & A. Diomedes Botanical Garden” of the University of Athens, a nature reserve at Daphni, ca. 10 km west of Athens, Greece. The site is described further in Petanidou and Ellis (1993) and Petanidou et al. (1995c, 2008). The climate is Mediterranean with dry, hot summers and relatively cool, wet winters. Long-term mean annual rainfall is 372.2 mm, and mean annual temperature is 18.3°C (1958–2003 data from Eleusis National Meteorological Station). The severity of a given winter or summer, however, is unpredictable. In particular, winters vary from relatively dry and warm to much wetter and cooler, which influences the onset of spring-like conditions and therefore the timing of flowering of plant species. Fig. 1 summarizes data on temperature variation during our study; more detailed data are available in Petanidou et al. (1995c).

2.2. Census design and data taken

From April 1983 until May 1987 we monitored all possible interactions between plants and pollinators in the Daphni community. Every 10 days (from February through June; and from

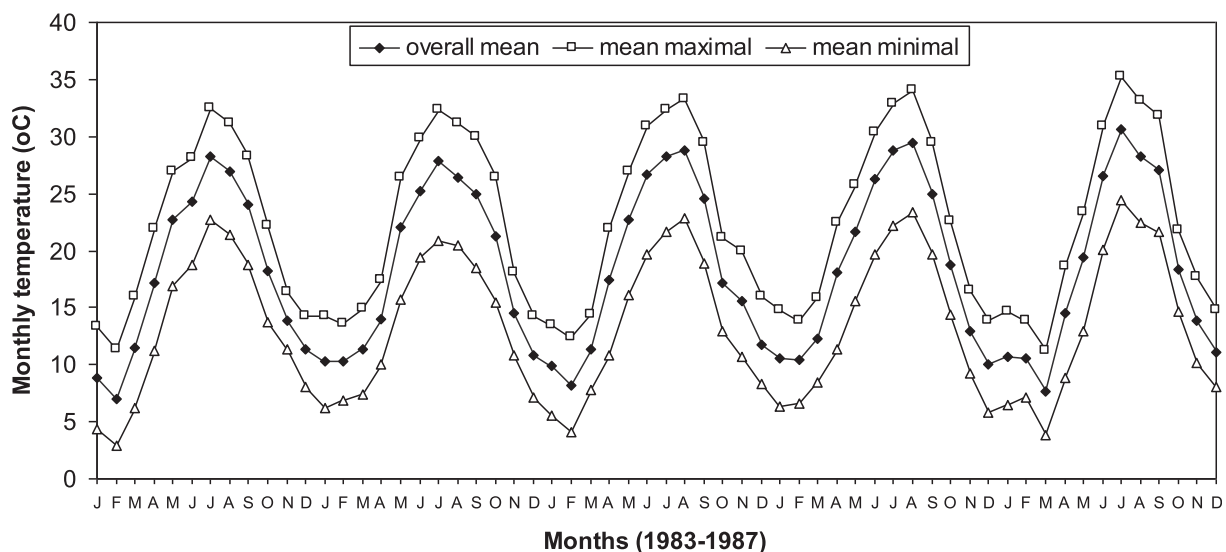


Fig. 1. Monthly temperature data (overall mean, mean daily maximal and minimal) of the study site over the entire study period. The data (for the period 1958–2003) are from the nearby Eleusis National Meteorological Station.

September to November) or 20 days (remaining months), we recorded flowering phenology by counting flowers within 2–6 plots set up haphazardly for each insect-pollinated plant species. Plots ranged in size from 1 m² to 20 m² depending on the species. Plots were selected to be spread as widely as possible across the entire study site, and we used the same plots throughout a given season. Censuses were made at various times of day so as to capture the time of maximal opening of the flowers of each species (e.g. from 0600 for *Verbascum undulatum* to 2100 for *Capparis spinosa*). In each census we counted the total number of flowers or functional reproductive units (e.g. flower heads in Asteraceae and Umbelliferae) over all plots for each species.

We scored onset of flowering for a species as the date on which we first observed >2% of the maximum number of flowers of that species counted across all plots in that year; cessation of flowering as the subsequent date on which we first counted <2%; and duration of flowering as the period between onset and cessation. For at least two out of every 20 days throughout the flowering duration of each plant species we recorded the total number of pollinator species that interacted with its flowers, operationally defined as insect visitors that contacted floral reproductive organs. Sampling effort did not vary substantially between years (28–30 surveys per year). In total we accumulated 5000 h of diurnal observations and collected >18,000 specimens of pollinators. Both plants and insects were identified to species by specialists listed in Petanidou et al. (1995c: plants) and Petanidou (1991b: insects). The community was found to comprise 665 pollinator species visiting 132 plant species (see Petanidou, 1991a,b for complete lists and Petanidou and Ellis, 1993; Petanidou et al., 1995c, 2008 for summaries). The pollinators were mostly bees, followed by flies (muscoïd and hoverflies), beetles, wasps, butterflies, and true bugs (Heteroptera).

We used the number of pollinator species visiting a plant species (i.e. pollinator species richness) as a proxy for the success of that species in obtaining pollination. Although pollination success is certainly also affected by the rate with which each pollinator visits flowers (e.g. Vázquez et al., 2005), we do not have such data for our system. Using species richness as a proxy is justified here because of the dominance of solitary bees, whose population densities and rates of flower visitation are relatively low and

uniform. Although social insects like bumble bees often achieve high population densities, these insects were rare at the study site. We observed only two species of bumble bees and these were not frequent flower visitors (Petanidou, 1991a; Petanidou and Ellis, 1993). Honey bee presence was similarly low throughout the study period (0–3 hives/Km², one of the lowest in Greece; T. Petanidou unpublished data). Moreover, there is evidence (Petanidou and Ellis, 1996) that our system is dominated for long periods by families of solitary bees (e.g. Andrenidae and Anthophoridae, which are common in early spring) rather than families exhibiting higher levels of sociality and higher density (e.g. Halictidae, with a limited presence until mid April).

2.3. Data analysis

We first expressed phenology in terms of Julian dates (1 for January 1st through 365 for December 31st), and then calculated the mean Julian date of flowering onset for each species across all years for which we had records at the site. We next calculated the year-by-year deviation for each species from its mean value (i.e. yearly value minus the mean value, so for species that were sampled for 4 years we have 4 measurements of deviation from the mean), with a positive deviation indicating later onset than the mean. Comparable calculations were made for flowering duration, with positive values indicating flowering that lasted longer than the mean, and for the number of different pollinator species visiting a plant species, with positive values indicating pollinator species richness greater than the mean for that species. For all three variables, the distribution of values was symmetrical and unimodal with mean and median not significantly different than zero.

To explore how species-specific deviations in date of flowering onset, flowering duration, and pollinator species richness are interrelated, we used Type II linear regressions, as is appropriate when all variables include measurement error. These analyses used the lmodel2 package in R version 2.14.1 (R Development Core Team, 2012) which is a realization of the methods of Legendre and Legendre (1998). Since we primarily wished to look for significant relationships in pairwise correlations between the three deviation

Table 1
Relationships between the magnitude of annual deviation in onset of flowering of plant species from their mean onset, the deviation in the number of pollinator species visiting the plant in that year, and the deviation in flowering duration of the species (for more details see Fig. 2). These relationships are shown for all species and for subsets, i.e. few- vs. many-flowered plant species, and species with different life histories in the community. N is the number of plant species recorded in at least 3 years (in the grouping “All species in the community”) or at least 2 years (all remaining groupings); n is the number of years for which paired data are available for both plants and pollinating insects.

Variables tested	r	r ²	P-permutations
All species in the community (N = 46, n = 154)			
Onset of flowering vs. pollinator richness	0.318	0.101	0.001
Flowering duration vs. pollinator richness	−0.215	0.046	0.005
Onset of flowering vs. flowering duration	−0.537	0.288	0.001
Few-flowered species (N = 12, n = 18)			
Onset of flowering vs. pollinator richness	0.641	0.411	0.004
Flowering duration vs. pollinator richness	−0.666	0.443	0.005
Onset of flowering vs. flowering duration	−0.716	0.513	0.001
Many-flowered species (N = 120, n = 259)			
Onset of flowering vs. pollinator richness	0.244	0.060	0.001
Flowering duration vs. pollinator richness	−0.113	0.013	0.040
Onset of flowering vs. flowering duration	−0.525	0.275	0.001
Annuals (N = 51, n = 107)			
Onset of flowering vs. pollinator richness	0.340	0.116	0.001
Flowering duration vs. pollinator richness	−0.253	0.064	0.002
Onset of flowering vs. flowering duration	−0.599	0.359	0.001
Perennials (N = 81, n = 170)			
Onset of flowering vs. pollinator richness	0.208	0.043	0.005
Flowering duration vs. pollinator richness	−0.038	0.001	0.321
Onset of flowering vs. flowering duration	−0.490	0.240	0.001

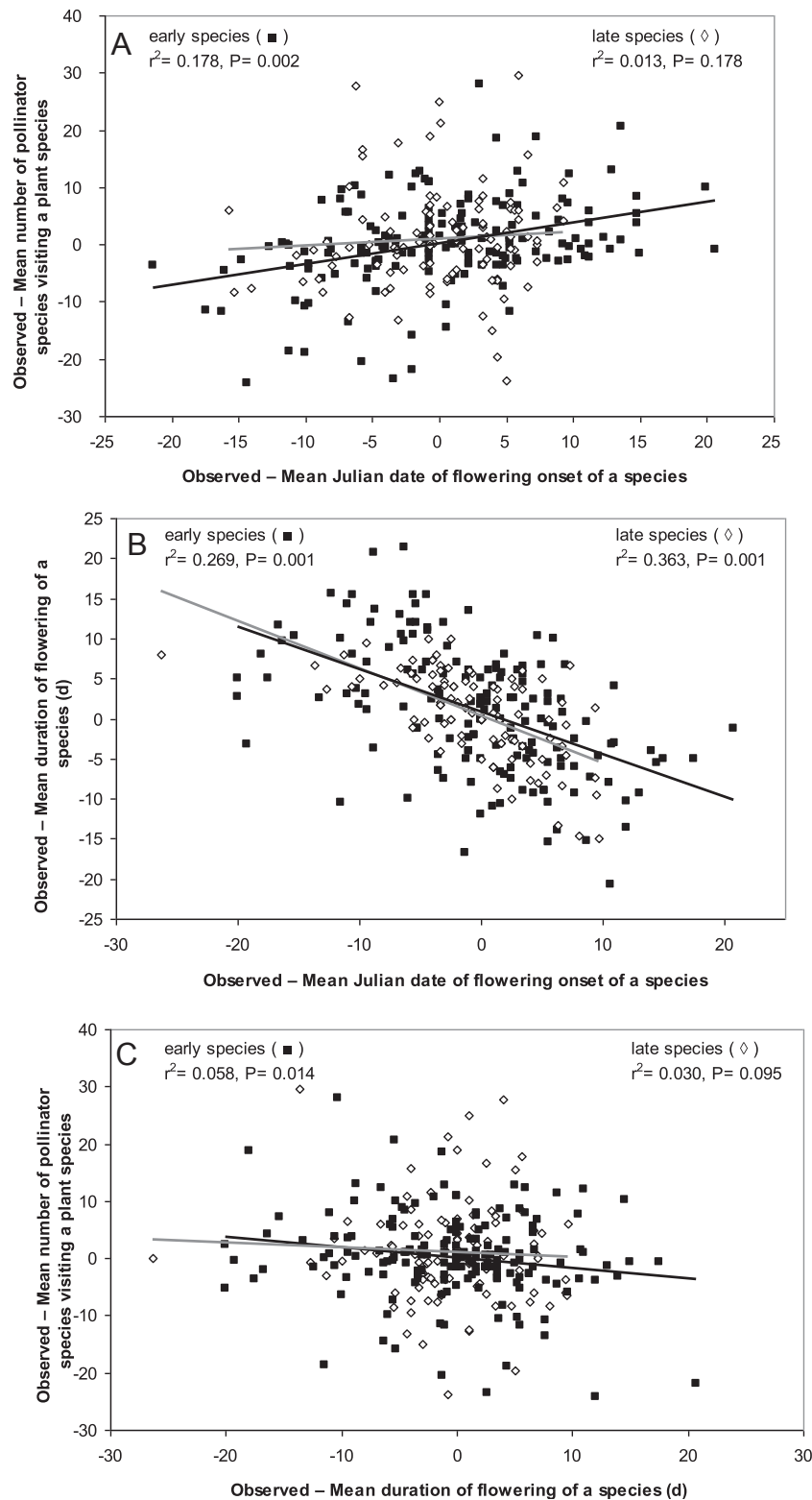


Fig. 2. Relationships between (A) the magnitude of annual deviation in onset of flowering of plant species from their mean onset and of deviation in the number of pollinator species visiting the plant in that year, where positive deviations indicate respectively later than average onset and greater than average pollinator species richness (the OLS estimated slope of the relationship for the early flowering species is 0.36, and for the late flowering species is 0.12); (B) the magnitude of annual deviation in onset of flowering and of deviation in flowering duration of the species, where positive deviations indicate respectively later onset and longer than average duration (the OLS estimated slope of the relationship for the early flowering species is -0.53 , and for the late flowering species is -0.59); and (C) the magnitude of deviation in flowering duration and of deviation in the number of pollinator species, where positive deviations indicate respectively longer duration and greater pollinator species richness (the OLS estimated slope of the relationship for the early flowering species is -0.18 , and for the late flowering species is -0.08). Early and late flowering species are analyzed separately with their best-fit relationships shown respectively as black and grey lines and with statistical relationships indicated.

variables, we calculated both ordinary least squares (OLS) and major axis (MA) regressions. The statistical significance in all cases was similar and led to the same inference for both methods, so we report only one value. To estimate the statistical significance of correlations we used permutation tests with 999 permutations performed in the *lmodel2* package (Legendre and Legendre, 1998). The significance of the model was tested by permutation, so as to be valid even if the distributional assumptions of parametric testing are not satisfied. Another issue in regression analysis is the effect size of each regression. Cohen (1988) proposed using the correlation coefficient (r) as a measure of the effect size, with absolute values greater than 0.5 signifying large effect size, absolute values between 0.3 and 0.5 medium, and absolute values between 0.1 and 0.3 small effect size; absolute values less than 0.1 are considered trivial. In Cohen's (1988) terminology, a small effect size is a real effect but which can only be observed through careful study; while a large effect size is an effect which is big enough, and/or consistent enough, to observe with ease.

To explore whether the season of flowering affects interannual variation in flowering phenology we classified plant species as “early” (onset of flowering between 1st January and 30th April) and “late” (onset after this date). To explore whether flower number had an effect we classified species as few-flowered (<10 flowers or reproductive units per plant) or many-flowered (>10). All few-flowered species were geophytes (plants with underground persistent tubers or bulbs) with relatively large flowers compared to many-flowered species having mostly small flowers. To explore whether life history had an effect we classified species as annuals (plants that survive harsh seasons as seeds), and perennials (including herbaceous and woody perennials, as well as geophytes). All the above assignments follow Petanidou et al. (1995c). We also investigated whether the apparent degree of pollinator specialization of a plant species, indicated by its mean pollinator species richness, was related to the magnitude of year-to-year fluctuations in flowering onset, flowering duration, or available pollinator species richness. For this we ran Type II linear regressions where each plant species was considered as a single data point, and quantified year-to-year fluctuations as the standard deviations of all yearly values for each species. Analyses of pollinator specialization were run with early, late, and total plant species, using only those species for which we had data for at least three of the four study years. In contrast, we used data from all plant species to examine effects of flower number and life history, since sample sizes otherwise would have been too small to allow meaningful conclusions.

3. Results

3.1. Overall patterns in the data

Among the 132 study plant species in the community, 18 were recorded flowering only in one year of the study and were visited by 170 pollinator species; 38 were recorded in two years and were visited by 272 pollinator species; 56 were recorded in three years and were visited by 477 pollinator species; and 20 were recorded in four years and were visited by 380 pollinator species. Simultaneous data on flowering phenology and pollinator visitation are available for 46 of the 76 species recorded in ≥ 3 years.

Considering only years and plant species for which we obtained simultaneous information on flowering phenology and pollinator species richness leaves us with 278 records. The mean Julian date of flowering onset for this subset of the data was 112.1 (i.e. 21 April) ± 65.7 (SD) days. Similarly, the mean flowering duration was 55.7 ± 25.0 days, while the mean number of pollinator species visiting a plant was 13.8 ± 14.3 . The average annual deviation in

onset of flowering across the 278 records was 0.86 ± 6.81 days whereas that for deviation in flowering duration was -0.39 ± 6.66 days and that for deviation in pollinator species richness was 0.54 ± 8.08 .

3.2. Early- vs. late-flowering species

Across all 76 plant species for which 3 years of data are available, years in which a given species began flowering before its mean date of onset of flowering tended to be years in which fewer insect species visited its flowers ($P < 0.001$, $r^2 = 0.101$; Table 1), and this effect size is considered medium. The slope of the linear model indicates that for each day of deviation towards earlier flowering, a plant species on average lost 0.31 species of pollinators. If we limit the analysis only to early species (i.e. that began flowering within January–April), before peak pollinator activity, the relationship becomes stronger ($r^2 = 0.178$; Fig. 2A), whereas there is no relationship if only late species are considered ($P > 0.05$; Fig. 2A). Years of earlier-than-average flowering also tended to be those in which a species flowered for a longer-than-average duration ($P < 0.001$, $r^2 = 0.288$), a tendency found in both early- and late-flowering species (Fig. 2B). Finally, given that the magnitude of annual phenological shifts was related significantly to changes both in pollinator species richness and flowering duration, the relationship between deviation of flowering duration and of pollinator species richness is also significant ($P = 0.005$, $r^2 = 0.046$; Table 1), with longer-than-average duration being associated with lower-than-average pollinator species richness. This relation is also attributable to early-rather than late-flowering species (Fig. 2C). As expected, early-flowering species exhibited stronger phenological shifts in the date of flowering onset than late-flowering species (Fig. 3).

3.3. Differences based on ecological traits

Few-flowered and many-flowered species contributed to the three trends just described, exhibiting qualitatively-similar relationships among deviations in onset of flowering, flowering duration, and pollinator species richness (Table 1). Deviation in the onset of flowering was related to that in flowering duration for both classifications of life history, but only annuals exhibited a strong relationship between these and deviation in pollinator species richness (Table 1). In the perennial plants we did not detect a relationship between deviation in flowering duration and in pollinator species richness ($P = 0.321$).

We detected no relationship between apparent specialization (mean across all yearly values of the pollinator species richness for a given plant species) and the standard deviations either in onset of flowering ($P = 0.447$), or in flowering duration ($P = 0.827$). When apparent specialization was quantified as the minimum number (rather than the mean number) of pollinators observed visiting a given plant species in any of the study years, we again detected no relationship with standard deviations of flowering onset ($P = 0.218$) or flowering duration ($P = 0.839$).

4. Discussion

4.1. What are the drivers of flowering phenology vs. pollinator activity mismatches?

Based on observed variation among plant and pollinator species in phenological response to the past few decades of climate change, several authors have predicted an increasing phenological mismatch between these mutualistic partners. Our analysis of annual variation in phenology and in insect species richness within

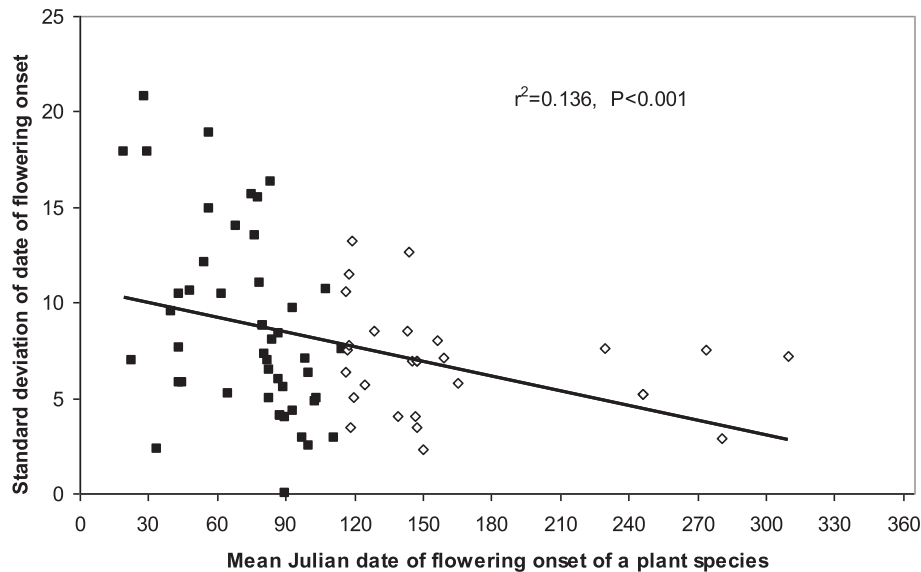


Fig. 3. Relationship between the mean Julian date of onset of flowering of a species and the magnitude of interannual shifts in onset, expressed in units of standard deviation. Each point represents a single plant species (early species shown as squares, late species as diamonds). The overall linear fit is significant ($r^2 = 0.136$, $P < 0.001$) and negative (the OLS estimated slope of the relationship is -0.026).

a single community is consistent with this prediction: earlier flowering of a species in a given year was associated with a lower number of pollinator species than anticipated by the medium-term average, a pattern that might reflect temporal mismatch. Statistically, the effect size of this association is medium. Because this finding applied to early-flowering species and not to those flowering later in the season, we conclude that plants may respond differently than insects to weather vicissitudes early in the year whereas there is no detectable difference in their response as the Mediterranean summer begins.

All ecological groups tested (Table 1) showed significant variation in the onset and the duration of flowering, a finding in agreement with Petanidou et al. (1995c). This variation, however, was at best only loosely related to lower pollinator species richness in perennials, whereas the relationship was stronger and highly significant for annuals. This is probably the result of the annuals tending to flower earlier than perennials and to go to seed before the onset of the hot dry summer, and of their shifting more strongly toward earlier flowering onset in years of warmer winters than do the perennials (see Petanidou et al., 1995c; Fitter and Fitter, 2002). As a result annuals are more likely to experience a period during which pollinator activity is constrained by cool temperatures. Thus the annuals largely represent the early-flowering species discussed above.

We can think of three possible explanations for the association between earlier flowering and reduced pollinator species richness. First, the onset of flight activity of most pollinators may fluctuate less across years than the onset of flowering, so that years of warmest winters might expose the earliest-flowering species to fewer insect species. Second, pollinators may fly for shorter periods in years of earliest flowering, again reducing phenological overlap with flowers. Third, years of warmer winters may correspond to those of smaller pollinator populations, which we might have recorded as years of lower species richness simply because of missing rarer species in our sampling. All these mechanisms are plausible given the unpredictability of the Mediterranean climate (Petanidou et al., 1995b) and the fact that the association between flowering and pollinator richness is driven entirely by early plant species. Most rain at our site falls at the end of winter and beginning of spring, when early plants are in flower. Most pollinators are

native wild bees, whose activity and diversity is highest in warm and dry situations (O'Toole and Raw, 1991; Petanidou and Ellis, 1993, 1996; Michener, 2000; Petanidou and Lamborn, 2005; Nielsen et al., 2011) and whose activity has been shown elsewhere to be negatively correlated with precipitation (e.g. Devoto et al., 2009; González et al., 2009). In Mediterranean systems the advancement of plant flowering towards winter is induced by a higher-than-average temperature of the previous month (Petanidou et al., 1995c), while at the same time earlier bee activity is likely to be suppressed because precipitation retards larval development and flight of resulting adults (Eickwort and Ginsberg, 1980; but see Fründ et al., 2013, who showed that in continental Europe different bee species respond differently to winter temperature increase with some species benefiting compared to others).

These considerations suggest that phenological shifts of plants toward earlier flowering under anthropogenic climate warming may expose early-flowering species to lower pollination service, either because the plants leave the insects “behind” or because of lower pollinator population sizes. The former possibility seems to be at odds with two recent studies from North America—but only at first glance. Iler et al. (2013) presented evidence for persistent synchrony between hoverfly activity and flowering phenology over the past several decades. However, this result applies to a montane site with a short summer growing season of 3–4 months, whereas our phrygana supports flowering throughout the year with peaks in spring and autumn (Petanidou et al., 1995c). Furthermore, hoverflies are more numerous and active in colder climates whereas they fare poorly in the hotter and drier Mediterranean (Petanidou and Ellis, 1993; Petanidou et al., 2011). This means that hoverflies are expected to respond more readily to climate change and be active in colder periods as compared to more heat-loving bees. Similarly, Bartomeus et al. (2011) argued that “bee emergence is keeping pace with shifts in host–plant flowering, at least among the generalist species”, but this was based on data for only 10 bee species gleaned from museum collections representing different geographic regions and on “best available data” for plants taken from literature, a very coarse-grained approach. Bartomeus et al. (2013) “found extensive synchrony between bee activity and apple peak bloom due to complementarity among bee species’ activity periods”, but

this was based mainly on historical data from field (apple flowering) and museum collections (bees). In contrast, our study represents the actual interacting plants and pollinators living at a single site and experiencing the same climatic and other environmental conditions; moreover, all interactions were recorded in nature and not assumed based on whether the species co-occurred in time.

What can we say about pollination services for plant species that flower early in our system? Because the population densities of most pollinator species are similarly low, as described earlier, and keeping in mind the overwhelming difficulty of measuring per-visit effectiveness of 665 pollinator species for 132 plant species, we have taken pollinator species richness as a proxy for pollination services. Indeed, there is evidence that plant reproductive output declines as pollinator species richness does (Biesmeijer et al., 2006). On the other hand, we documented a positive association between earliness of flowering and the duration of flowering (as reported by Dunne et al. (2003) for the same montane system studied by Iler et al. (2013), although Price and Waser (1998) and Forrest et al. (2010) found no such association for that system). An extended flowering duration might occur because of longer life span of individual flowers, or extended production of new flowers, or staggered flowering of different individuals within the same plant population, and all of these might conceivably be adaptive plastic responses under weather or pollinator limitation scenarios (Petanidou et al., 1995c; Clark and Husband, 2007; Willmer et al., 2009). Longer flowering might counterbalance any loss of pollination services from reduced pollinator richness, but we note that female fecundity tends to decline through the season within a plant community, probably due to nutrient limitation (Petanidou et al., 1995a). Thus a longer season might yield no benefit to counterbalance an early reduction in pollination services. Autogamy might ameliorate this situation, as in some Hungarian orchids that have shifted their flowering onset earlier in the season (Molnár et al., 2012), but a capacity for self-pollination and self-fertilization is far from universal.

4.2. Are Mediterranean communities more at risk than others?

An important functional trait that has been thought to increase extinction risk from failure of pollination is the degree to which a plant species is specialized in use of pollinators, or vice versa (e.g. for bees and hoverflies see Biesmeijer et al., 2006). However, we detected no significant relationships between apparent pollinator specialization of plants and year-to-year changes either in flowering onset or duration. This implies that pollinator specialist plant species did not experience disproportionate fluctuations in their phenology due to weather vicissitudes (and possibly future climate change) compared to pollinator generalists. In other words, our system retains some stability as to the number of pollinator species servicing each plant species, notwithstanding the year-to-year changes in weather – a feature that fits well with the temporal stability in topology of the plant–pollinator network in this system (Petanidou et al., 2008). This conclusion of relative stability is further supported by the finding that among five different biomes studied, the Mediterranean communities (among them the phrygana studied here) had the highest residual connectance (Olesen and Jordano, 2002), meaning that their plant–pollinator network was most tightly connected. Following Dunne et al. (2002) this implies that Mediterranean community networks are less prone to biodiversity loss than alpine, arctic, temperate, or tropical systems.

In order to extend our results to future anthropogenic climate change, we have admittedly made a number of critical assumptions. The most central one is that continued advancement of mean flowering onset will increasingly expose plant species to reduced pollinator services, either because of phenological mismatches

with pollinators or because of reduced pollinator populations. The possibility of phenological mismatch seems especially real for ecosystems (such as Mediterranean ecosystems) that are poor in insect species known to be active early in the season (such as bumble bees). What is the ultimate likely outcome if pollination services decline by either mechanism? If the earliest flowers increasingly receive no visits, pollination-mediated selection against earlier flowering may act on any available heritable variation in cues that trigger flowering onset, and phenology may cease to advance. Drawing parallels between our results and climate change does assume, of course, that patterns of interannual weather variation when our data were collected can be used as a proxy for critical elements of future change – an assumption also made in recent experimental studies of phenological mismatch (Rafferty and Ives, 2011, 2012). In spite of this caveat, and the limitation that patterns in a Mediterranean community may not resemble those in other ecosystems (especially tropical ones), we contend that a search for statistical association between interannual weather variation and aspects of pollination adds to our power to foresee effects of climate change on pollination, especially in the absence of experiments of sufficient spatial and temporal extent to capture dynamics within entire ecological communities.

Author contributions

TP, ASK, JDP and SPS originally conceived the idea. TP conducted fieldwork and collected the data. ASK and ADM performed statistical analyses. TP, ASK, NMW and SPS wrote the manuscript.

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