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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.

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; Kjøhl 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

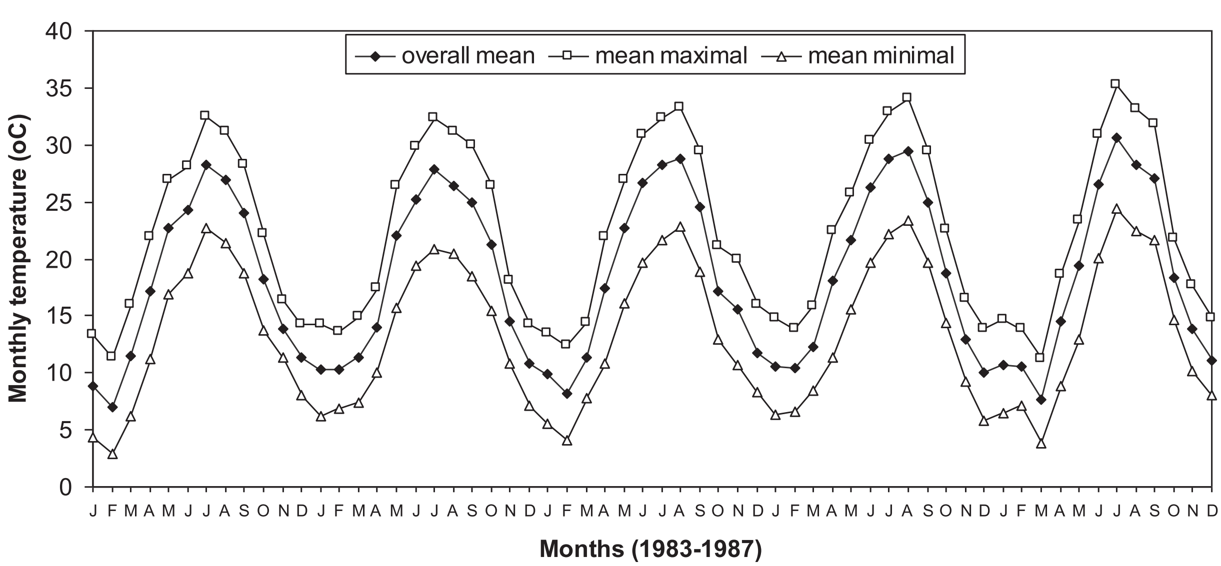

Fig. 1. Monthly temperature data (overall mean, mean daily maximal and minimal) of the study site over the entire study period. The data (for the period 1958–2003) are from the nearby Eleusis National Meteorological Station.