

BRIEF COMMUNICATION

Climate data and flowering times for 450 species from 1844 deepen the record of phenological change in southern Germany

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PREMISE: State-sponsored weather stations became ubiquitous by the 1880s, yet many old climate data and phenological observations still need to be digitized and made accessible.

METHODS: We here make available flowering times for 450 species of herbs and shrubs gathered in 1844 by Carl Friedrich Philipp von Martius (1794–1868), director of the Munich Botanical Garden. The data formed part of the world's third-oldest phenological monitoring network as we explain in a brief overview of the history of such networks. Using data from one of the world's oldest continuously functioning weather stations, Hohenpeißenberg, we relate temperature to flowering in three species with short flowering times and herbarium collections made since 1844 within the city's perimeter, namely, *Anemone patens*, *A. pulsatilla*, and *Arum maculatum*.

RESULTS: Mean advances in flowering dates were 1.3–2.1 days/decade or 3.2–4.2 days/1°C warming. These advances are in keeping with similar advances in other European herbs during more recent periods.

CONCLUSIONS: Future studies might use the 1844 flowering data made available here as a source of information on the availability of particular flowers for specialized pollinators including insects looking for oviposition sites, such as the *Psychoda* flies that become trapped in *Arum* inflorescences. Another use of Martius's 1844 data would be their incorporation into larger-scale analyses of flowering in southern-central Europe.

KEY WORDS *Anemone*; *Arum*; Carl Friedrich Philipp von Martius; climate change; climate station Hohenpeißenberg; flowering phenology.

As a result of shorter winters and warmer springs, many plants in the Northern Hemisphere are flowering earlier than they did in the past (Fitter and Fitter, 2002; Menzel et al., 2006). In a study of 385 British species with flowering data from 1954 to 2000, nearly all were found to flower earlier in 2000 than in 1954; 10 species, however, flowered significantly later (Fitter and Fitter, 2002). As illustrated by this and other examples, phenological responses to climate change are highly species-specific, and it is therefore important to have empirical data from a broad range of species monitored at multiple locations if we are to understand the mechanisms underlying leaf-out, flowering,

or fruiting times under climate change. Knowledge of plant phenology is also relevant because numerous specialized herbivorous, nectarivorous, or frugivorous insects and other animals that depend on leaves, flowers, or fruits, with higher food chains are affected in turn (Renner and Zohner, 2018). Analyses of phenological time series have shown that study durations of around 20 years are needed for meaningful comparisons of temperature or photoperiod sensitivities among species (Bolmgren et al., 2013). Such long time series are usually only available for economically or horticulturally important species, for example, Japanese cherries, whose flowering

times have been recorded since 850 (Primack et al., 2009) or grapes, whose harvest dates in Burgundy have been recorded since 1370 (Chuine et al., 2004).

Other long-term data on phenology come from phenological garden networks and from stand-alone studies at particular sites that were re-monitored some time later. Examples are the International Phenological Gardens of Europe (IPG), a network founded in 1957 and still in existence today (Kaspar et al., 2014; Humboldt University of Berlin, 2020). The IPG network gathers dates of leaf unfolding, flowering, autumn coloring, and leaf fall for 21 species in 89 gardens (status of 2010). The world's first such garden network functioned from 1750 to 1752 and involved 18 estates distributed over the territory of Sweden (Linnaeus, 1751, 1753; Ihne, 1884; Schnelle, 1955). A second phenological network was maintained from 1781 to 1792 by the Societas Meteorologica Palatina in Mannheim and included several stations across Europe (it is published in the *Ephemerides Societatis Meteorologicae Palatinae* [1784–1795]; <http://opacplus.bsb-muenchen.de/title/342993-3>). A third phenological network was established by the Belgian astronomer, mathematician, and statistician Adolphe Quetelet (1796–1874), a pioneer in the application of quantitative methods in biology. Quetelet's network functioned from 1841 until 1872 and comprised approximately 80 stations throughout Europe (Quetelet, 1842, 1844, 1845, 1849, 1853; Ihne, 1884; Schnelle, 1955). The data appear to have mainly been analyzed by Quetelet's student Ch. Morren who also coined the term phenology (Morren, 1853; Demarée and Chuine, 2007). Two stand-alone legacy data sets both were started in the 1850s. One focused on the phenology of 24 species in the Royal Botanic Garden in Edinburgh that were regularly monitored from 1850 until 1939 (Harper et al., 2004). The other focused on the leaf-out and flowering times of 400 species growing at Walden Pond in Concord, Massachusetts (United States) and was gathered between 1852 and 1860 by Henry David Thoreau (Miller-Rushing and Primack, 2008; Polgar et al., 2014). Thoreau's data have provided important insights into phenological strategies, local extinctions, and plant invasions once they were compared to data from the same site re-monitored from 2004 until 2013 (and continued since).

We recently found unpublished handwritten notes in the Archives of the Bavarian Academy of Science that show that Carl Friedrich Philipp von Martius (1794–1868), director of the Munich Botanical Garden and secretary of the Academy, monitored the phenology of some 450 species in the Botanical Garden and contributed his data to Quetelet's network. Having transcribed Martius's observations, we here make his data available. One way to use the 1844 data would have been to compare them to the same species' modern flowering times at the location where Martius observed them. With the expansion of the city, however, Munich's botanical garden in 1914 was moved to a new location, 5.5 km further west, and none of the old beds and plantings survive today. Many native species included in Martius's data set, however, continue to grow in the city, and, with several years of monitoring, their phenology will become comparable to Martius's 1844 data, similar to Thoreau's legacy data set (Miller-Rushing and Primack, 2008; Polgar et al., 2014).

Here we take an alternative approach for obtaining multiple flowering dates between 1844 and 2020 to link them to climate change and thereby study species responses to shorter winters and warmer and earlier springs. We checked the Munich herbarium for species with >10 fertile collections made between 1844 and 2020 within the city of Munich, focusing on species with short flowering periods to reduce noise, and then linked flowering times to empirical spring air

temperatures for the years 1844 to 2020 from one of the world's oldest continuously functioning observatories, Hohenpeißenberg, close to Munich (Winkler, 2009). State-supported weather stations before the mid-1800s were confined mostly to Europe and the United States, but became ubiquitous by 1880. Today, Hohenpeißenberg is operated by the German Weather Service and its data have been fully digitized. The goals of this study thus were (1) to make Martius's complete 1844 data set available (with modern taxonomic names) and to clarify the role played by Martius and Quetelet in the development of plant phenological monitoring, and (2) to link empirical flowering times to spring air temperatures for the years 1844 to 2020, taking advantage of the Hohenpeißenberg meteorological data.

MATERIALS AND METHODS

Historic research

Coauthor Wesche is the author of a biography of Martius (Wesche, 2020) and familiar with the Martius papers and letters in the Archives of the Bavarian Academy of Sciences. Martius was secretary of the mathematical-natural science section of the Academy from 1841–1868 and, in this function, ran the section's monthly meetings, maintained its records, and engaged in correspondence with members of other academies. We found his handwritten notes on plant phenology in an appendix to the Academy's Archives entitled “Beobachtungen über den periodischen Fortschritt der Vegetation angestellt an 500 Pflanzen während der Monate April, Mai, Juni u. Juli 1844 im königl. botanischen Garten zu München” (“Notes of the periodic development of vegetation based on the monitoring of 500 plants during the months of April, May, June, and July 1844 in the royal botanical garden in Munich”; Martius, 1845). These pages were photographed at high resolution and plant names, observation dates and any notes then entered into an Excel spreadsheet (Microsoft, Redmond, CA, USA). Taxon names were checked and updated as required.

Selecting focal species and determining their temperature sensitivity

Using label data on specimens in the herbarium of Munich (herbarium abbreviation M), we searched for species in Martius's set that had short (i.e., not exceeding 2 weeks) flowering periods and that had been collected at least 10 times between 1844 and 2020 within 28 km from the historic Botanical Garden Munich, with 28 km being essentially the city perimeter (Munich's N to S extension is 20.7 km, its E to W extension 27 km). Unfortunately, most species in Martius's data set have been collected fewer than 10 times within this perimeter (Renner and Rockinger, 2016). Among the few species with sufficient collections and short flowering times are two Ranunculaceae, *Anemone patens* L. and *Anemone pulsatilla* L., that co-occur in the Garchinger Heide, a nature reserve 22 km from the city center where the old botanical garden had been located. This patch of grassland has been a focus of Bavarian botany and conservation since 1854. One other herb, *Arum maculatum* L., likewise has been collected 10 times since 1844, perhaps because its large leaves and inflorescences are conspicuous before most other plants have leafed out.

To determine the temperature sensitivities of these species, we analyzed the effect of spring temperatures on their flowering dates. Information on daily mean air temperatures came from station

data available through the German Meteorological Service (DWD; https://opendata.dwd.de/climate_environment/CDC/observations_germany/climate/daily/kl/recent/), with data for 1844 until 1878 coming from Hohenpeißenberg, from 1879 to 2020 from the city of Munich. The optimal preseason for each species was defined as the period before the mean flowering date (across years) for which the coefficient of determination (R^2) of a linear model between flowering date and air temperature was highest. Preseason temperature refers to the mean temperature for the respective preseason. Tested preseasons ranged from 15 to 90 days (with 15-day steps). Species with earlier mean flowering dates tended to have shorter optimal preseason periods, with flowering dates of *Anemone pulsatilla*, *Anemone patens*, and *Arum maculatum* being best explained (highest R^2) by preseasons of 30, 60, and 90 days, respectively.

RESULTS

Martius's phenological data and his contribution to Quetelet's phenological monitoring network

High-resolution photos of the original pages with Martius's phenology observations are available online as Appendix S1. Appendix S2 provides a list of the 500 plant individuals representing 450 species that he monitored, with their currently accepted scientific names and flowering and fruiting times as recorded in 1844. For each species, Martius noted when it was flowering and later added the dates when that species (likely the same individual) was in fruit. A note at the beginning of his enumeration states that observations were made "10 zu 10 Tagen in jedem Monat" (see Appendix S1, p. 1), that is, every 10 days, which appears to have been the case at least for flowering dates, whereas fruiting times appear to have been recorded three times per month. When a species is recorded as fruiting in "½ August", we took that to mean a date around August 20. For a few species, he also gives the height of each plant, using a format in which an apostrophe must refer to the height in Paris feet or Bavarian feet (e.g., 1½'). A Paris foot would be 32.48 cm, a Bavarian foot 29.178 cm (Meyer-Stoll, 2010, p. 35). The entries for the flowering and fruiting dates are in a different handwriting, suggesting that at least two people were involved, one of them probably M. Gustave Lommler, a name mentioned by Quetelet (1844, p. 22; see below).

According to the protocol of the math.-nat. section meeting of 11 January 1845 (ABAdW, Sitzungsberichte der mathematisch-physikalischen Klasse, Protokolle 1845–1847 [Beilage 61], vol. 1845, Jan. 11, Erste Sitzung, fol. 50–55), Martius on that day presented his phenological observations from the growing season of 1844. The protocol indicates that all data would be sent to Adolphe Quetelet in Brussels to become part of Quetelet's phenological observational network. Between May 1842 and 1867, Martius wrote 38 letters to Quetelet (preserved in the Martius archive in Munich), and Quetelet (1844, 1845) lists Martius's contribution in his "Observations des phénomènes périodiques" in den *Nouveaux mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles*. We could not determine how Martius and Quetelet first got into contact.

Long before his collaboration with Quetelet, however, Martius, then 31 years old, tried to establish a phenological network at the 1827 meeting of the society of German Natural Historians and Physicians for which he served as the local organizer (Isis 21, 5.6, 1828, 431, https://zs.thulb.uni-jena.de/receive/jportal_jportal_ume_00031406).

A report on the meeting in the journal *Flora* (1827, vol. 38, pp. 593–608) states that it was agreed that participants would record and exchange leaf-out dates, flowering times, and fruiting times of widespread species, with the results to be published in the same journal. However, no resulting data seem to have been published.

In later years, Martius wrote two more (unpublished) texts in which he refers to the importance of plant phenology. The first, dating to 1840, was a scientific assessment written for Crown Prince (later King) Maximilian II (1848–1864; BSBM, Martiusiana III, D, 4, 5 Nr. 7 – Büchler and Schumacher, 1990, p. 52), entitled "Denkschrift über die Abfassung einer Pflanzenstatistik von Bayern" or "Memorandum on composing a plant statistics for Bavaria". In this report, Martius mentions the importance of recording periodically repeated plant behavior because he considered an understanding of why trees flower or fruit 4–6 weeks earlier or later at different locations of both theoretical and practical interest. His second text (Martius, 1850) is entitled "Ueber die botanische Erforschung des Königreichs Bayern" ("On the botanical exploration of the kingdom of Bavaria") and states (p. 8) that the length of the annual vegetation period is an important variable to record and that monitoring of periodical plant phenomena, following the "method" of the Belgian astronomer and statistician Adolphe Quetelet, had been ongoing in the Munich Botanical Garden "for several years" (p. 11).

Responsiveness of *Anemone* and *Arum* flowering times to spring temperatures from 1844 to 2020

Using Martius's 1844 flowering records and those documented by herbarium specimens made within the city perimeter between 1844 and 2020 (Appendix S3), along with temperature data from the German Weather Service, we found that the mean advances in flowering date over time (as inferred from linear models) in *Anemone pulsatilla*, *A. patens*, and *Arum maculatum* were, respectively, 2.1, 1.6, and 1.3 days/decade (Fig. 1A). These are average trends over the past 176 years. Figure 1B shows the results when we used a LOESS smoothing function instead of linear regression to account for the nonlinearity of climate warming.

Flowering dates for the three species showed a strong response to spring temperatures, with each 1°C increase in air temperature leading to, respectively, 4.2, 3.2, and 4.2 days earlier flowering (Fig. 1B). The pre-season lengths best explaining the variation in flowering dates were 30, 60, or 90 days, respectively, but the inferred temperature sensitivity remained similar when shorter or longer pre-seasons (30–90 days) were used (temperature sensitivity ranges = −3.1 to −4.6 days/°C for *Anemone pulsatilla*, −2.6 to −3.2 days/°C for *Anemone patens*, and −3.6 to −4.2 for *Arum maculatum*; Fig. 2).

DISCUSSION

Phenological changes in *Anemone* spp. and *Arum maculatum* from 1844 to 2020

Flowering times in *Anemone* and *Arum* over the past 176 years have advanced by 3.2 to 4.2 days per 1°C warming, similar to advances seen in *Anemone nemorosa* and other European herbs during more recent periods (Fitter and Fitter, 2002: 1954–2000; Renner and Zohner, 2018: 1960–2016). Our study combined Martius's observations on living plants, made every 10 days, with label data from

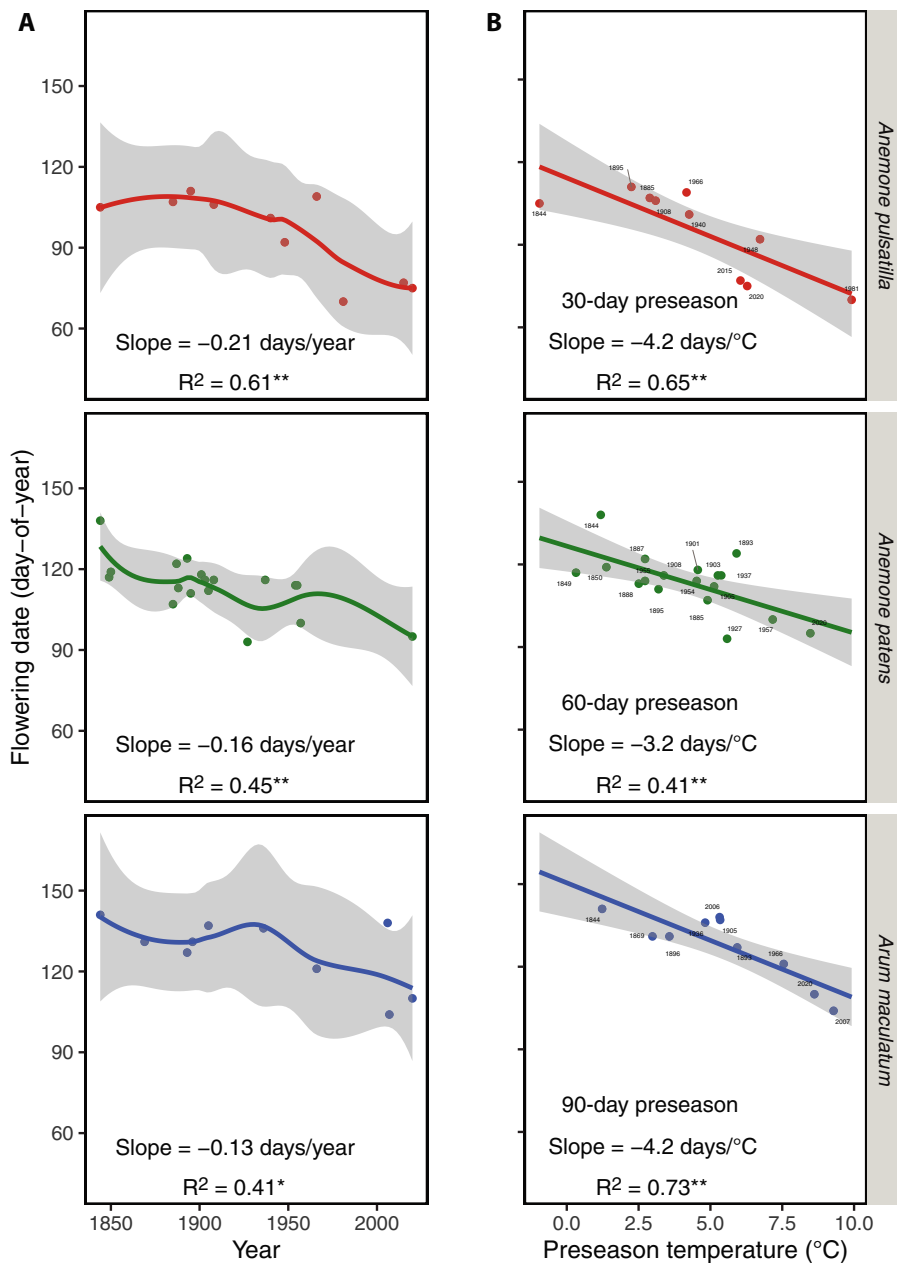


FIGURE 1. The effect of (A) year and (B) preseason temperature on flowering dates for *Anemone pulsatilla*, *Anemone patens*, and *Arum maculatum* in Munich, Germany, between 1844 and 2020. The solid lines represent the best fit using a LOESS smoothing function (A) or ordinary least squares regression (B), shaded areas represent 95% confidence intervals. For each species, preseason temperatures were calculated as the mean of daily temperatures during the period before the mean flowering date that yielded the best correlation with flowering dates (*A. pulsatilla*, 30 days; *A. patens*, 60 days; *A. maculatum*, 90 days; see Fig. 2). Mean flowering dates were day-of-year 95, 114, and 128 for the three species, respectively. Slope and R^2 refer to the slope estimate and coefficient of determination from a linear model between year (A) or preseason temperature (B) and flowering date. ** $P < 0.01$, * $P < 0.05$.

fertile herbarium specimens, which invariably introduced some noise. However, many studies have compared past phenology inferred from herbarium collections with flowering times obtained from field observations and found that both kinds of data yield

essentially the same results (e.g., Borchert; 1996; Primack et al., 2004; Bolmgren and Lönnberg, 2005; Davis et al., 2015; Panchen et al., 2012).

A 6-year-long study (1992–1997) of *A. maculatum* at several locations in England showed that fruit set was lowest in individuals that flowered earlier or later than the majority and interpreted this finding as evidence for stabilizing selection on synchronous flowering (Ollerton and Diaz, 1999). How such synchronous flowering might be affected by climate warming was not discussed. Our results now show that *A. maculatum* has advanced its flowering time to the same extent as other spring-flowering herbs, despite producing just one or few inflorescences per plant with the most fertile period confined to 2 h in the early evening when the spadix warms to 15–25°C above ambient temperatures. The warming enhances the emission of volatile compounds that attract minute flies, which are trapped overnight in female-stage inflorescences and released the next day, loaded with pollen (Bermadinger-Stabentheiner and Stabentheiner, 1995; Gibernau et al., 2004; Wagner et al., 2008). The most common pollinators are *Psychoda phalaenoides* (Linnaeus 1758) and *P. grisescens* (Tonnoir 1922) (Chartier et al., 2013), which each have larger geographic ranges and longer activity periods than *A. maculatum* (Ježek and Barták, 2000). Today's 23-day earlier flowering of *Arum* (compared to 1844) therefore may not have required much shifting in the phenology of the relevant species of *Psychoda*.

Martius's and Quetelet's role in the history of phenological monitoring networks and the significance of legacy data

Martius's 1827 call for phenological observations to be exchanged among a network of collaborators and his own monitoring in the Munich Botanical Garden are among the earliest phenological efforts after Linnaeus (1751) in Sweden and the Societas Meteorologica in Mannheim (1784–1795), and just before the efforts at the Royal Botanic Garden in Edinburgh from 1850 until 1939 (Harper et al., 2004) and at Walden Pond from 1852 until 1860 (Miller-Rushing and Primack, 2008; Polgar et al., 2014). It is their comparison to modern data from the same location that makes legacy data so valuable, and such comparisons become easier once the historic

data have been digitized and tabulated as here done for Martius's observations. One way in which this large data set might be used in future studies would be as a source of information on the availability of particular flowers (with their nectar and pollen) for specialized

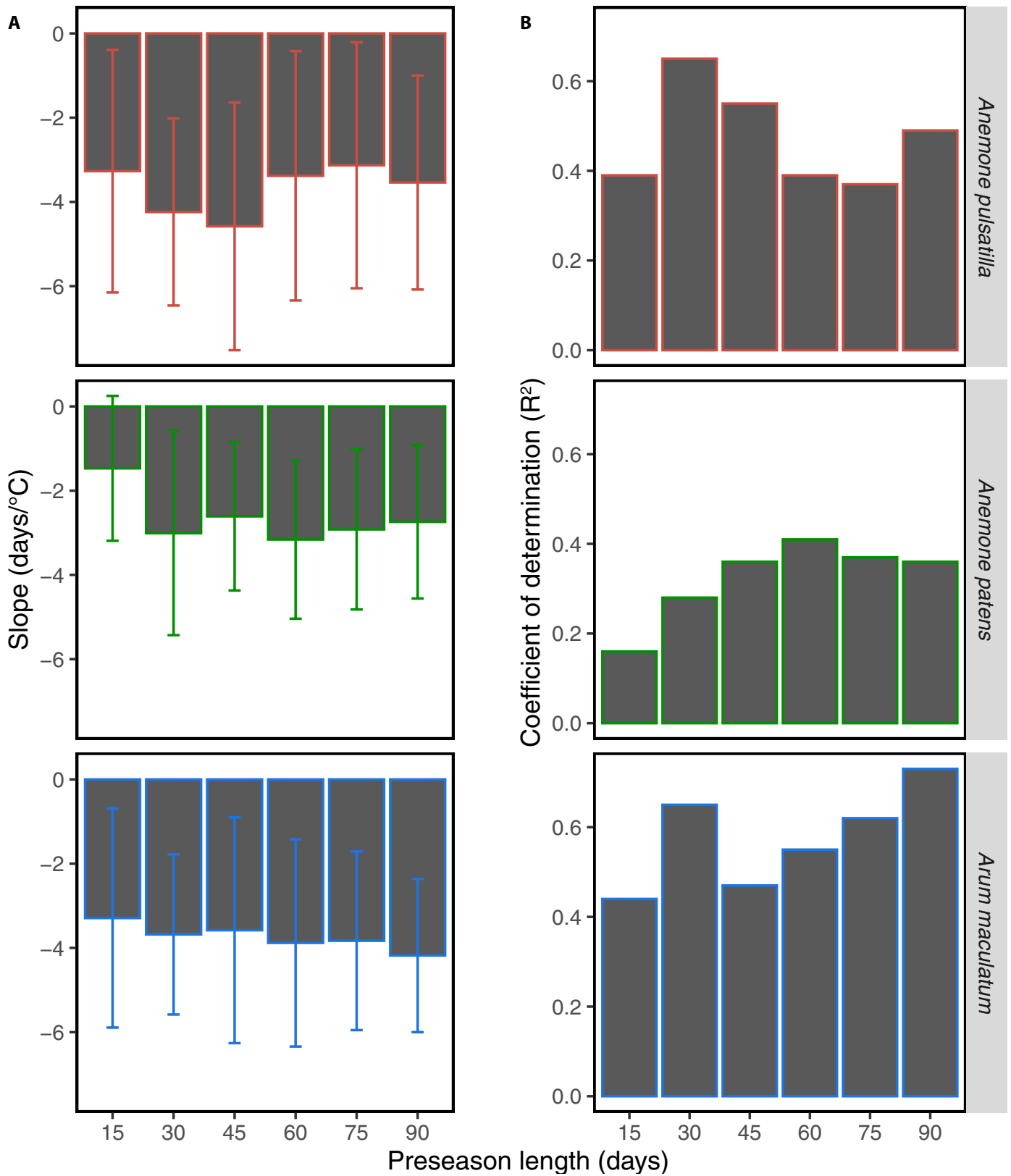


FIGURE 2. The effect of preseason length on (A) model estimates and (B) performance. (A) Slope estimates ± 2 standard errors for the effect of pre-season temperature on flowering dates for *Anemone pulsatilla*, *Anemone patens*, and *Arum maculatum*, using preseasons between 15–90 days. (B) Coefficients of determination (R^2 values) for the effect of preseason temperature on flowering dates.

nectarivorous or pollenivorous insects or insects looking for oviposition sites, such as the *Psychoda* flies that become trapped in *Arum* inflorescences (Gibernau et al., 2004). Another use of Martius's 1844 data would be their incorporation into large-scale analyses of flowering in southern-central Europe, which might allow the inclusion of more specimens from additional herbaria.

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AUTHOR CONTRIBUTIONS

S.S.R. designed and funded the research; M.W. performed historical research; C.M.Z. performed all statistical analyses; all authors co-wrote the paper.

FUNDING STATEMENT

No direct funding was received for this study.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. High-resolution images of the original pages of Martius (1845).

APPENDIX S2. The 500 individuals from 450 species monitored by C. F. P. von Martius, with their currently accepted scientific names and flowering and fruiting times as recorded in 1844.

APPENDIX S3. Specimens of *Anemone pulsatilla*, *Anemone vulgaris*, and *Arum maculatum* in the herbarium of Munich with their locations and flowering dates.

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