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Detrending phenological time series improves climate–phenology analyses and reveals evidence of plasticity

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Abstract. Time series have played a critical role in documenting how phenology responds to climate change. However, regressing phenological responses against climatic predictors involves the risk of finding potentially spurious climate–phenology relationships simply because both variables also change across years. Detrending by year is a way to address this issue. Additionally, detrending isolates interannual variation in phenology and climate, so that detrended climate–phenology relationships can represent statistical evidence of phenotypic plasticity. Using two flowering phenology time series from Colorado, USA and Greenland, we detrend flowering date and two climate predictors known to be important in these ecosystems: temperature and snowmelt date. In Colorado, all climate–phenology relationships persist after detrending. In Greenland, 75% of the temperature–phenology relationships disappear after detrending (three of four species). At both sites, the relationships that persist after detrending suggest that plasticity is a major component of sensitivity of flowering phenology to climate. Finally, simulations that created different strengths of correlations among year, climate, and phenology provide broader support for our two empirical case studies. This study highlights the utility of detrending to determine whether phenology is related to a climate variable in observational data sets. Applying this as a best practice will increase our understanding of phenological responses to climatic variation and change.

Key words: arctic; climate change; confounded variables; flowering phenology; linear regression; montane; observational data; phenological plasticity; subalpine.

Introduction

Phenological time series provide foundational evidence that changes in the timing of life history events represent a global footprint of climate change (Parmesan 2007, Thackeray et al. 2016). It is common practice to regress the calendar dates of phenological events against interannual climatic variation to elucidate potential abiotic drivers of phenology (e.g., Fitter et al. 1995, Roy and Sparks 2000, Crimmins et al. 2010, Iler et al. 2013*a*). In this paper, abiotic drivers refer to proximate cues or triggers of phenology, as opposed to ultimate ecological factors that shape selection (following Wolkovich et al. 2013). When phenological responses are regressed against abiotic predictors, there is a risk of finding spurious climate–phenology relationships because both variables change across years (Post 2013). In this scenario, in which three variables are all related to one another—phenology, climate, and year—a classic statistical problem of confounding arises: two variables may appear to be related to one another when they are actually related to something else. Detrending variables to check for such confounded relationships with year is considered best practice in time series analysis (Royama 1992). However, detrending is rarely applied to the analysis of phenology time series, which hinders our ability to make the best possible inferences from observational phenology data.

Quantifying relationships between year-detrended climate and phenology variables can additionally serve as statistical evidence for phenotypic plasticity in phenology in

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response to fluctuations in the abiotic environment. Detrending by year decouples interannual variation in phenology and climate from long-term directional change, so that relationships between detrended phenology and climate variables can represent evidence for plasticity (Anderson et al. 2012). This statistical estimation of plasticity is appropriate for scenarios in which an evolutionary response to selection is expected to occur over more than one year (so that rapid selection would not be included in detrended fluctuations in climate and phenology) and will be especially useful for identifying sites and species for future research. Here we apply detrending analyses to two time series of flowering phenology in Colorado and Greenland to highlight its utility for assessing confounded climate drivers and as a statistical test for evidence of plasticity.

Methods

Flowering phenology data

We used two long-term data sets of flowering phenology: one from subalpine meadows at the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA (38°57.5′ N, 106°59.3′ W, 2,900 m above sea level), and the second from Arctic tundra as part of a long-term monitoring program at Zackenberg, Greenland (74°28′ N, 20°34′ W, 35–50 m above sea level). These study sites and observational study protocols are extensively described elsewhere (Iler et al. 2013*a, b*, CaraDonna et al. 2014, Schmidt et al. 2014). In brief, in Colorado, the number of flowers or inflorescences is counted every other day for over 120 plant species across the growing season in 30 2 × 2 m plots (see Inouye 2008 for further details). We limit the analysis of the Colorado data to 28 plots (excluding two plots added in 2004) and to species that are present in at least 20 years (one-half of the total number of possible years), leaving 80 species. Five of the 28 plots were added in the 1980s–1990s; their inclusion does not affect our results and simply contributes more data for analysis. The vast majority of these plant species are long-lived herbaceous perennials. In Greenland, the flowering stage (flower bud, open flower, or senescent flower) is recorded weekly in a series of 25 permanent plots for six common woody and herbaceous perennial species. The sizes of the plots in Greenland vary (1–300 m^2) and are determined by the area required to record the stage of 200 or more inflorescences per plot in each weekly census. We use Colorado data from 1974 to 2013 and exclude 1978 and 1990 when there was no census, and we use Greenland data from 1996 to 2013. Flowering phenology data sets are available online for both Colorado[9] and Greenland.[10]

We use the date of peak flowering to represent flowering phenology because it is a population-level measure of central tendency and is more robust than other measures of phenology to potentially confounding effects (Miller-Rushing et al. 2008, CaraDonna et al. 2014). For the Colorado data set, floral abundance was summed across plots for each species in each year, and we calculated the day on which 50% of flowers were counted for each species to represent peak flowering in that year (see Iler et al. 2013*a, b*). Summing floral abundance across plots allows each plot to contribute to a population-level peak flowering date according to its floral abundance (results do not differ if we average peak flowering date across plots; not shown). For the Greenland data set, we calculated peak flowering date as the midpoint between the day on which 50% of buds had opened (flowering onset) and the day on which 50% of the flowers had senesced (flowering end; see Høye et al. 2007, Iler et al. 2013*a, b*). This calculation was performed for each plot, and the mean of peak flowering date was then calculated across plots for each species in each year (Iler et al. 2013*a, b*). Thus, in both data sets, each year yielded one observation of peak flowering date for each species (one population-level value in Colorado and mean across plots in Greenland). Peak flowering date was calculated differently for each data set because in Colorado floral abundance varies across plots, whereas in Greenland plots differed in size to hold floral abundance relatively constant across plots. Finally, there is no phylogenetic signal for phenological sensitivity to temperature or snowmelt in the Colorado plant community (CaraDonna and Inouye 2015; too few species to test for it in Greenland), so we do not include a phylogenetic analysis here.

Climate data

Our previous work shows that two climate variables are associated with flowering phenology at each site: the timing of spring snowmelt and air temperature in the months preceding flowering (Iler et al. 2013*a*). In Colorado, the timing of snowmelt is defined as the first day of year with bare ground in a permanent ~10 × 10 m plot, and in Greenland the timing of snowmelt is defined as the mean date of bare ground from plots across the landscape (one snowmelt date per year at each site). Following Iler et al. (2013*a*), we use mean monthly air temperature from the month in which daily temperatures warm above freezing at each site (April in Colorado and May in Greenland) through the mean month of flowering for each species. In Colorado, monthly temperature data (mean of daily maximum and minimum temperatures) are from a NOAA weather station in Crested Butte, Colorado, ~9.5 km south of the phenology plots, at 2704 m above sea level. Greenland temperature data come from a weather station on site.

Analysis

Rationale.—The approach we outline here pertains to a scenario in which we observe a temporal shift in a life history event and then want to inquire about potential climatic drivers of that event. Ultimately, we want

[9] https://osf.io/jt4n5/
[10] http://data.g-e-m.dk/

to determine whether the shift in phenology is likely to have occurred in response to changes in climate. To check for potentially confounding effects of year on climate–phenology relationships, we remove the effect of year from both climate and phenology variables by extracting the residuals from independent regressions with year as the predictor. Then we examine the residual covariation between the abiotic environment and phenology. A significant relationship between year-detrended climate and phenology variables (i.e., the residuals) indicates that year is not confounding the original climate–phenology relationship. In contrast, if there is no relationship between year-detrended climate and phenology variables, then the effects of year and climate on phenology cannot be disentangled given the available observational data.

A similar approach is to use year and the climate variable as predictors in a multiple regression with phenology as the response variable. Confirmation that the coefficient for the climate predictor is still significant also serves as a check for potentially confounding effects of year. The climate–phenology slope from multiple regression will be identical to year-detrended climate–phenology slopes (e.g., Freckleton 2002). Although the detrended climate–phenology slopes are identical with either approach, the error estimates and P values will differ slightly because multiple regression includes an additional predictor variable. Detrending is a more accurate estimate of the error for the scenario we present here, but in practice either approach is acceptable as a check for confounding effects of year.

Year-detrended climate variables represent interannual variation in climate that is isolated from directional climate change; this is because detrending statistically removes directional change in climate across years. Similarly, detrended phenology variables represent interannual variation in phenology that is isolated from directional phenological change. Therefore, relationships between year-detrended phenology and climate variables can represent evidence of plasticity (Anderson et al. 2012). Genetic and plastic components of phenology are confounded within observational field data, and we emphasize that field experiments are required to separate these two components. Instead, here we suggest that detrending can be used to reveal statistical evidence of plasticity.

Application.—Year is most likely to have confounding effects when both climate and phenology change significantly through time. We therefore limit our analysis to species in which peak flowering date exhibits evidence of significant change through time: $P \leq 0.05$ in regressions of peak flowering date vs. year (Appendix S1: Table S1). A total of 29 of the 80 species in the Gothic data set and four of the six species in the Zackenberg data set meet these conditions. Temperature and snowmelt date were analyzed as two separate climate variables. In contrast to all other climate variables, change in snowmelt date through time is insignificant in Colorado ($P = 0.14$; Appendix S1: Table S2). However, over a longer timeframe that includes the timing of spring snowmelt from 1935 to 1974 (estimated from the date of springtime peak stream runoff), snowmelt is becoming significantly earlier (Anderson et al. 2012). Its inclusion here is conservative with regard to concern for confounding effects of year, but it allows us to examine evidence for plasticity in response to snowmelt date at both sites.

For each species, we took the residuals from individual simple linear regression models of peak flowering date vs. year and climate vs. year. Flowering date residuals were then regressed against climate residuals, separately for temperature and snowmelt date. We then used two-tailed t tests to compare whether the regular and detrended slopes differed in magnitude.

Our previous work with these two data sets revealed nonlinear flowering responses to climatic variation in seven species in Colorado and one species in Greenland (Iler et al. 2013*a*). We used piecewise regression to analyze residuals from nonlinear climate–phenology relationships (Appendix S2), but other types of regression (e.g., polynomial fits) and other types of detrending may be more appropriate depending on the type of nonlinear relationship (e.g., differencing; Yaffee and McGee 2000). Results from the piecewise regressions are consistent with results from the simple linear regressions, and for simplicity we focus on the linear analysis in the main text.

We checked for temporal autocorrelation in all variables using the Ljung-Box test with 1 yr lag time. Residuals for snowmelt date in Greenland are temporally autocorrelated ($r = -0.57$, $P = 0.018$), as are *Geranium richardsonii* peak flowering date residuals in Colorado ($r = -0.34$, $P = 0.042$). We therefore used an autoregressive linear model to analyze change in Greenland snowmelt date through time and change in flowering date through time for *G. richardsonii*. Using the residuals from the autoregressive model, these relationships were nearly identical to those using residuals from simple linear regression (Appendix S3: Tables S1 and S2), indicating that autocorrelation does not affect our analysis.

Finally, we ran a series of simulations to determine whether our results are more broadly generalizable beyond our two empirical data sets. We created two simulation scenarios: (1) plasticity in response to temperature is the main contributor to observed phenological shifts through time and (2) plasticity in response to temperature + another factor contribute to observed phenological shifts through time (e.g., selection for earlier flowering or response to another climatic cue). In the first scenario, phenology was defined as a linear function of temperature, and the correlation between temperature and phenology was typically stronger than either correlation with year (Appendix S4: Table S1). In scenario 2, phenology was defined as a linear function of year, and the correlation between temperature and phenology was typically weaker than either correlation with year (Appendix S4: Table S1). Therefore, phenological sensitivity to temperature was directly defined in scenario 1,

and the phenology–year and temperature–year relationships indirectly define phenological sensitivity in scenario 2. Temperature was defined as a linear function of year in all simulations.

We assigned slope values to temperature and phenology variables with three different amounts of variation to create different strengths of correlations among year, temperature, and phenology in each scenario. The error around the defined slope was drawn from a normal distribution with assigned mean and standard deviation (greater SD means a larger error term around slope and weaker correlation). Temperature was assigned a mean value of 10°C, with a rate of change of 0.05°C/yr in all simulations. Phenology was assigned a mean value of day 150, with a sensitivity of −6 d/°C for simulations in scenario 1 and a shift of −0.3 d/yr for simulations in scenario 2. (A phenological sensitivity of −6 d/°C is the value necessary to get a −0.3 d/yr advancement in phenology at a rate of temperature increase of 0.05°C/yr). The length of the time series was 40 yr in all simulations. This magnitude of phenological shift and time series length is roughly equal to the mean shift for spring events in the Northern hemisphere and the mean length of data sets used to calculate this mean shift (Parmesan 2007). Because these two values align closely with our Colorado data set, we assigned the rate of temperature increase to correspond with this site (i.e., the slopes are all biologically plausible). Last, we regressed the detrended residuals against one another to evaluate evidence for plasticity. Each scenario and correlation strength combination was run 1000 times (two scenarios, three levels of correlation in each, for a total of six runs of 1000). All analyses were conducted in R (v. 3.2.2; R Core Team 2015).

Results

For all species in Colorado, linear snowmelt–phenology and linear temperature–phenology relationships are still significant after detrending by year (Table 1, Fig. 1; Appendix S5: Tables S1 and S2). The magnitude of the detrended slopes is statistically indistinguishable from the regular slopes for all species, for both snowmelt date and temperature (Table 1; Appendix S5: Tables S1 and S2). In all linear models, peak flowering date becomes earlier as snowmelt becomes earlier and as temperature increases (Fig. 1; Appendix S5: Tables S1 and S2).

In Greenland, all linear phenology–snowmelt relationships persist after detrending (Table 1, Fig. 2a; Appendix S5: Table S1). In contrast, three of the four linear relationships between peak flowering and temperature are no longer significant after detrending (Table 1, Fig. 2b; Appendix S5: Table S2). For the single species in which peak flowering still significantly associates with temperature after detrending (*Silene acaulis*, Caryophyllaceae), the magnitude of the detrended slope is statistically indistinguishable from the regular slope ($t = -0.56$, $P > 0.10$).

The simulations reveal that the *relative* strength of the correlations among the three variables determines whether or not detrending is able to detect plasticity. If phenology is more strongly correlated with temperature than either variable is correlated with year (Fig. 3a–c), then detrending finds evidence of plasticity (Fig. 3d), regardless of whether the variables are strongly or moderately correlated with one another (Appendix S4: Fig. S1, Table S1). Conversely, if phenology is more weakly correlated with temperature than phenology and temperature are correlated with year (Fig. 3e–g), then detrending rarely detects evidence of plasticity (Fig. 3h). Indeed only 4.6–5.6% of runs show such evidence (Appendix S4: Fig. S2, Table S1). This result also holds if either phenology *or* temperature are much more strongly correlated with year relative to the temperature–phenology correlation. See Appendix S4 and Metadata S1 for further information.

Discussion

Although temporal detrending is rarely applied to phenological time series, it is important for assessing whether effects of year and climate can be disentangled in observational data. In Greenland, temperature–phenology relationships disappeared after detrending in three of four species, indicating that the effects of year and climate on phenology cannot be disentangled. Taken in combination with the persistence of snowmelt–phenology

Table 1. Summary of simple linear regression results of regular and year-detrended (residuals) climate and peak flowering date variables from two long-term studies of flowering phenology in Colorado, USA, and Greenland.

Site and climate predictor	Regular slope	Detrended slope	Difference between slopes (%)	*n*	No. differences
Colorado, USA					
Snowmelt date	0.64 ± 0.02 d/1 d_{snow}	0.59 ± 0.02 d/1d_{snow}	7.01 ± 0.53	24	0
Temperature	−6.92 ± 0.17 d/°C	−6.57 ± 0.18 d/°C	5.80 ± 0.73	29	0
Greenland					
Snowmelt date	0.49 ± 0.07 d/1 d_{snow}	0.44 ± 0.08 d/1d_{snow}	13.4 ± 6.00	3	0
Temperature	−4.79 ± 0.33 d/°C	−3.19 ± 0.06 d/°C	39.0 ± 6.69	4	3

Notes: Shown are the across-species slopes (mean ± SE). The units d/1 d_{snow} refers to the number of days that flowering has advanced per 1 day advancement in snowmelt date. The parameter *n* is the number of species used to calculate summaries, and there are fewer species for snowmelt because of nonlinear responses (see Appendix S2). No. differences refers to the number of species in which the detrended slope differed significantly from the regular slope.

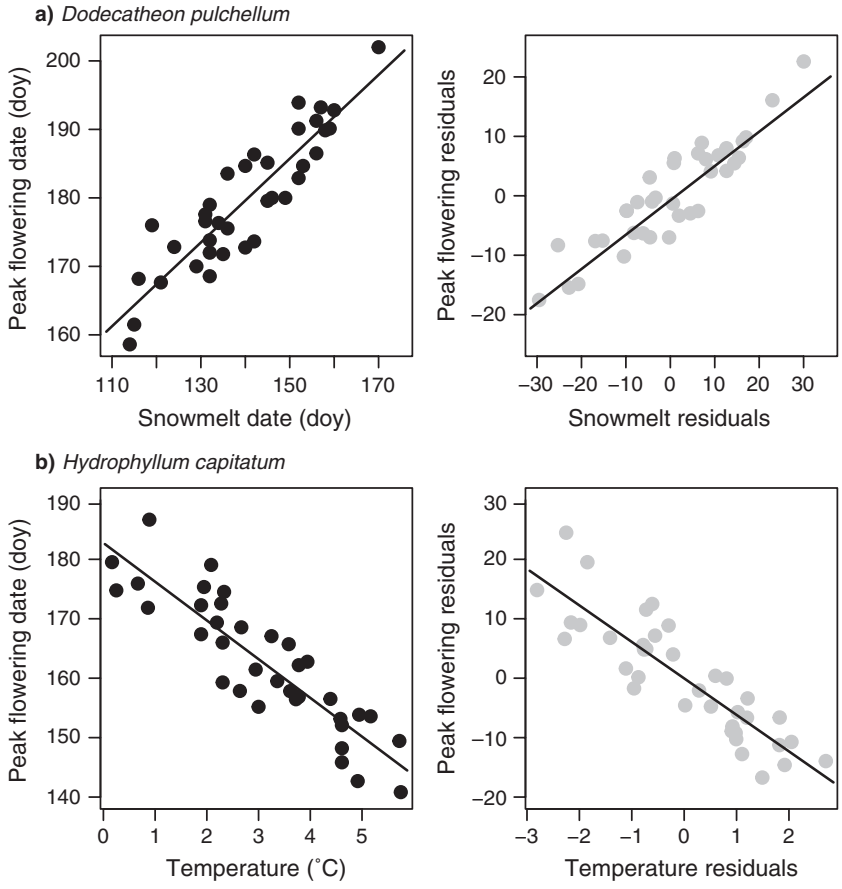


FIG. 1. Regular and residual plots of peak flowering date (day of year, doy) vs. (a) snowmelt and (b) temperature in Gothic, Colorado, USA. Lines of fit are from simple linear regression, and all slopes are significantly different from zero ($P < 0.0001$). Two species are shown, one for each predictor, that exemplify the across-species mean percentage difference between regular and residual slopes. (a) Snowmelt: the residual slope of *Dodecatheon pulchellum* is 6.48% shallower than its regular slope (vs. mean 6.01% difference; $n = 36$). (b) Temperature: the residual slope of *Hydrophyllum capitatum* is 5.62% shallower than its regular slope (vs. mean 5.08% difference, $n = 37$).

relationships following detrending, this result may indicate that the flowering phenology of these three species at the Greenland site is proximately cued by the timing of snowmelt rather than temperature. However, temperature cannot be ruled out as a potential cue based on this result, and experimental research or further data collection is necessary to understand the effect of temperature on flowering dates in these species. These results highlight the utility of detrending for increasing our understanding of phenological responses to climate variability and change using observational data. This will be especially important for habitats in which temperature is unlikely to be the only proximate driver of phenology: the tropics, semiarid and arid habitats, prairies, and high-latitude and high-elevation habitats (Wolkovich et al. 2013).

Observational data sets are most likely to be unable to separate effects of climate from year when climate explains relatively little variation in phenology and when change in climate through time is relatively strong. Indeed, temperature explains approximately one-third of the variation in phenology in Greenland and two-thirds of the variation in phenology in Colorado, averaged across the study species ($R^2 = 0.32$ vs. 0.66, respectively; Iler et al. 2013*a*). The rate of temperature increase is also two times greater in Greenland than in Colorado (Appendix S1: Table S2). Thus, these comparatively weak relationships between temperature and phenology in Greenland disappear after accounting for relatively strong rates of change across years. Our simulations provide more generality to these results. Across a range of correlation values among year, phenology, and climate, the effects of year and climate on phenology cannot typically be separated when year effects are stronger than phenological sensitivity to climate (Fig. 3e–h; Appendix S4). Plasticity may exist in these hypothetical scenarios, but year effects cannot be disentangled from climate effects, analogous to the temperature–phenology results from Greenland. In fact, the simulation runs that fail to detect plasticity when they are expected to (scenario 1) are cases in which correlations with year are indeed stronger than the correlation between phenology and temperature, which occurred by chance in

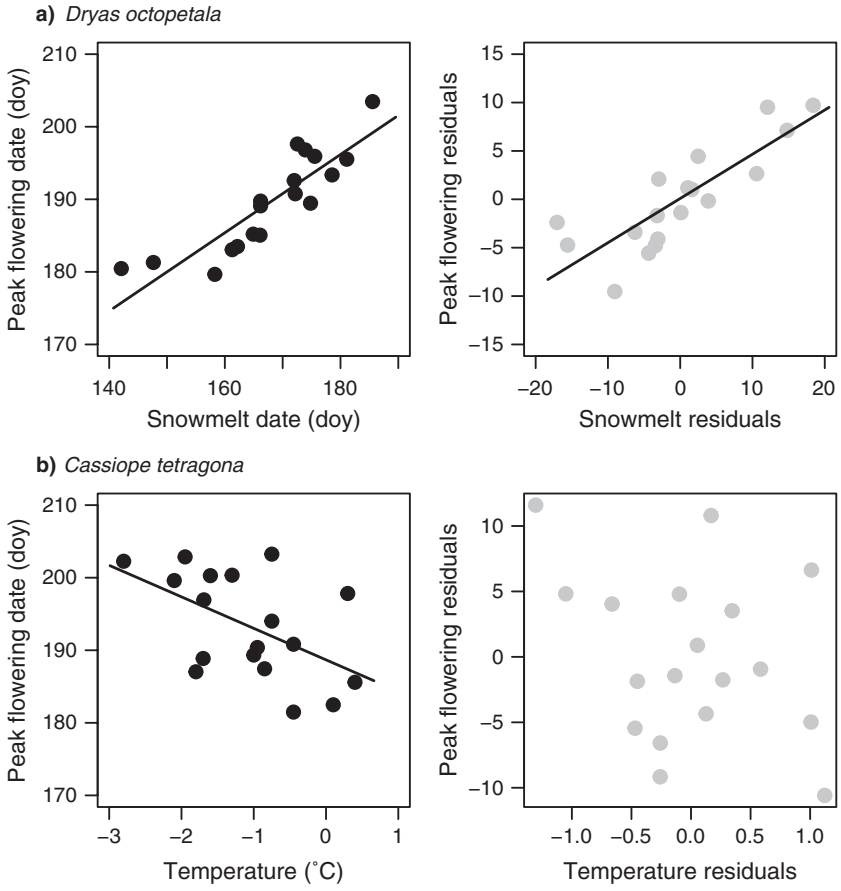


FIG. 2. Regular and residual plots of peak flowering date (day of year, doy) vs. (a) snowmelt and (b) temperature in Zackenberg, Greenland. Lines of fit are from simple linear regression ($n = 18$). Two species are shown, one for each predictor, that exemplify the across-species mean percentage difference between regular and residual slopes. (a) Snowmelt: *Dryas octopetala* residual slope is 15.5% shallower than regular slope (vs. mean 11.8% difference). (b) Temperature: *Cassiope tetragona* residual slope is 31.0% shallower than regular slope (vs. mean 34.0% difference).

a small number of runs because of the amount of variation we assigned (0–0.8% of runs depending on strength of correlation among variables; Appendix S4: Table S1).

Removing effects of year in observational time series of climate and phenology can be used to reveal statistical evidence for plasticity. Our simulations show that if plasticity fully accounts for a phenological shift, there is likely to be some error when detrending by year to estimate the *magnitude* of plasticity (Appendix S4: Table S2), which is why we emphasize detrending as useful for revealing statistical *evidence* for plasticity. Our simulations also show that plasticity can be detected even if change in temperature has been particularly strong and directional, and a plant responds in an almost perfectly plastic way to the change in temperature (plasticity scenario; Fig. 3a–d). The traditional approach for assessing plasticity in a given trait is to employ reciprocal transplants to test whether genotypes are expressed differently in different abiotic environments. Detrending should be especially useful as a screening procedure to select study species likely to exhibit phenological plasticity, which can guide future experiments such as reciprocal transplants or studying the phenology of tagged individuals across multiple years.

Comparisons of the magnitude of regular vs. detrended slopes suggest that the majority of the sensitivity of flowering phenology to snowmelt date may represent plasticity in all 33 plant species (Figs. 1a and 2a; Appendix S5: Tables S1 and S2), including the nonlinear responses (Appendix S2). We previously hypothesized that these nonlinear responses of phenology to climate change may arise if the rate of response to selection for earlier flowering falls behind the rate of climate change (Iler et al. 2013*a*), but the current study suggests instead that these nonlinear responses of phenology to snowmelt date are more likely to reflect limits in plasticity. Plasticity accounting for the majority of phenological sensitivity is consistent with the high degree of variability in the direction and magnitude of snowmelt date over decadal time scales that is mirrored in flowering dates at both sites (Iler et al. 2013*b*), such that we expect plasticity to be adaptive. Furthermore, our results are consistent with

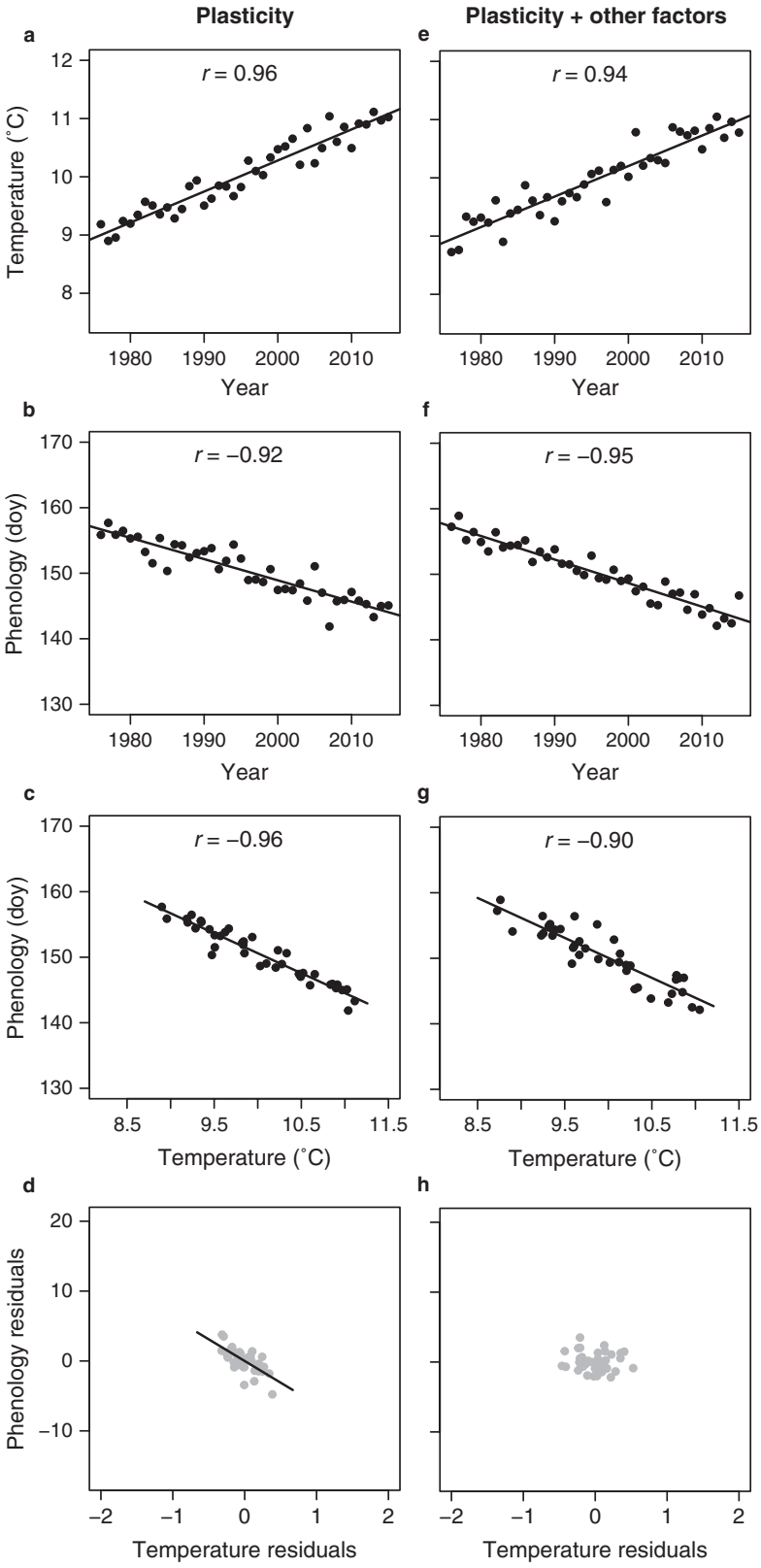


FIG. 3. Examples of simulated temperature and phenology variables from two scenarios: (a–d; scenario 1) mainly plasticity accounts for phenological shifts through time and (e–h; scenario 2) plasticity plus an additional factor accounts for the phenological shift. Pearson correlation coefficients are presented for simulated correlations. Lines of fit are only shown for significant relationships and are from simple linear regression. See Appendix S4 for further examples and *Analysis – Application* for explanation of simulations.

previous work on a single species at the Colorado site that estimates approximately 80% of change through time is plastic, while the remaining 20% represents selection for earlier flowering, despite a high capacity of the study species to rapidly evolve in response to climate change because of its biennial life cycle (Anderson et al. 2012).

Detrending by itself cannot distinguish plasticity from genetic change or from standing genetic variation within the population. We further caution against using detrending to reveal plasticity in species with annual life cycles because each new year in a time series would represent a new generation of individuals. Evolution in response to climate change has likely been minimal over our 18-yr and 40-yr data sets because flowers are counted on many of the same individual plants from one year to the next (A. M. Iler, *unpublished data* for three years and three species), and the plant species in this study are almost all long-lived perennials with time to first flowering probably spanning a minimum of 2–6 years (e.g., Waser and Price 1994; D. W. Inouye, *unpublished data*; J. D. Thomson, *unpublished data*). It is possible that certain genotypes only flower under certain environmental conditions, and we cannot rule out this scenario because individual plants are not tagged. However, flowering phenology is generally a highly plastic trait (reviewed in Levin 2009), and we expect plasticity to be adaptive in both locations as mentioned above. Therefore, plasticity is a more likely explanation for the detrended climate–phenology relationships in this study than different genotypes flowering under different abiotic conditions that vary across years.

We encourage future studies to test routinely for confounding effects of year on climate–phenology relationships in observational time series with the expectation that this will lead to an improved mechanistic understanding of phenological responses to abiotic variation and to climate change. Failing to conduct these tests routinely may hinder our ability to make the best possible inferences from observational phenology data, which is critical given the prominence of phenology as a biological response to climate change.

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