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Phenological tracking enables positive species responses to climate change

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Abstract. Earlier spring phenology observed in many plant species in recent decades provides compelling evidence that species are already responding to the rising global temperatures associated with anthropogenic climate change. There is great variability among species, however, in their phenological sensitivity to temperature. Species that do not phenologically "track" climate change may be at a disadvantage if their growth becomes limited by missed interactions with mutualists, or a shorter growing season relative to earlier-active competitors. Here, we set out to test the hypothesis that phenological sensitivity could be used to predict species performance in a warming climate, by synthesizing results across terrestrial warming experiments. We assembled data for 57 species across 24 studies where flowering or vegetative phenology was matched with a measure of species performance. Performance metrics included biomass, percent cover, number of flowers, or individual growth. We found that species that advanced their phenology with warming also increased their performance, whereas those that did not advance tended to decline in performance with warming. This indicates that species that cannot phenologically "track" climate may be at increased risk with future climate change, and it suggests that phenological monitoring may provide an important tool for setting future conservation priorities.

Key words: climate change; conservation; meta-analysis; phenology; synthesis; temperature sensitivity; tracking climate; warming experiment.

INTRODUCTION

With the predicted 2–7°C rise in global average temperatures over the next century (Meehl et al. 2007), land managers are challenged with setting conservation priorities in order to minimize biodiversity loss, given a limited pool of resources. Simple indicators are therefore needed to predict how species are likely to respond to climate change. Some of the best evidence that species are already responding to climate change comes from earlier spring phenology (i.e., timing of seasonal events

such as flowering or leaf emergence) observed around the globe in recent decades (Walther et al. 2002, Root et al. 2003, Parmesan 2006). Phenological sensitivity, defined as the shift in phenological event date per degree of temperature change, is a commonly used metric that can be compared across studies. For instance, out of 542 species observed in Europe from 1971 to 2000, 78% displayed earlier phenology (30% significantly) in the more recent, warmer years (Menzel et al. 2006). There was, however, large variation in phenological sensitivity among species, and 22% of species exhibited delayed spring phenology (3% significantly). Variation in phenological sensitivity reflects individual species' ability to "track" climate change, and could be a promising indicator to predict which species will persist and which will decline in response to future

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climate changes. Accordingly, phenology was incorporated as an indicator of both sensitivity and adaptive capacity to future climate change in a recent wildlife vulnerability assessment (Glick et al. 2011).

The timing of seasonal events such as leafing and flowering can be critical for maintaining rates of survival and reproduction of plant populations, due to short growing seasons, narrow windows for interactions with pollinators or dispersers, or to avoid interspecific competition with other plant species by maintaining complementary phenology (Rathcke and Lacey 1985). Especially for species from temperate climates, rising air or soil temperature is one of the dominant cues indicating the onset of the growing season (Lieth 1974), so it is logical to hypothesize that species would need to accelerate their phenology in a warming climate in order to maintain their performance (i.e., population size and reproductive output). Unfortunately, although the synthesis of long-term phenological observations provides convincing evidence that species are responding to environmental changes, they are seldom associated with data on shifting species abundance over time, with a few notable exceptions. In a study of spring migration timing of 100 European birds, species with stable populations showed advancement in migration timing, while species with declining abundance did not advance (Møller et al. 2008). A 32-year data set of yellow bellied-marmots showed a similar pattern for mammals: earlier emergence from hibernation was associated with increased population size (Ozgul et al. 2010). Observations of shifting plant phenology show a similar trend. A study comparing recent observations of plant species phenology to those made ~150 years ago found that species that declined in abundance did not flower earlier (Willis et al. 2008). Similarly, a study of 347 species in the British Isles showed that species with stronger phenological advance with climate change also had greater local increases in abundance and spatial expansion of their range limits (Hulme 2011).

These studies provide strong evidence that phenological sensitivity to shifting environmental conditions is a good indicator of species performance, but the findings are limited to localized regions and need to be interpreted with the awareness that many factors, in addition to temperature, have changed over time. Here, we set out to test the generality of these findings for plant species by synthesizing data from terrestrial warming experiments, which frequently monitor both species phenology and abundance responses to warming, and ideally have greater control over the environmental parameter of interest (temperature) while holding other factors constant. Specifically, we tested the hypothesis that species that track climate by flowering or leafing earlier with warming temperatures will maintain or even increase their performance relative to species with unresponsive or delayed phenology.

METHODS

Data compilation

To test the hypothesis that phenological sensitivity to temperature predicts species performance responses to warming, we compiled data from terrestrial warming experiments (see Plate 1). We searched for experimental warming studies in Google Scholar using the search string "Web of Science (ISI) for Topic = (warm* OR temperature*) AND Topic = (plant*AND phenolog*) AND Topic = (experiment* OR manip*)" to identify studies in peer-reviewed journals prior to December 2010. To be selected, a study needed replicated experimental units for warming and ambient controls, where the warming treatment extended throughout the growing season, and species-level phenology that could be extracted in units of days shift per degree temperature change. Pot experiments were excluded to focus on field experiments where plants experienced realistic soil water conditions, and only non-crop species were included in the database. Data were extracted directly from text and tables, or from figures using Engauge software (*available online*).[10] When factors other than temperature were manipulated, we only include data when the other factors were kept at ambient levels. If a publication indicated that phenology data were collected but not presented, we contacted the authors to ask for data for all species for which data were collected to avoid publication bias against nonsignificant results (Jennions and Møller 2002). Mean values for treatment and control were extracted, along with the number of experimental units and standard error of the mean when possible. Multiple years of data were entered if available, and mean values for phenology and performance were averaged across years. For each study, we recorded the amount of warming achieved and the medium in which the effect was measured (air, soil, vegetation surface), the method of warming (overhead infrared heaters, passive warming chambers, and nighttime warming), latitude, longitude, elevation, experimental duration, and biome type for each study (Appendix B: Table B1).

If multiple publications resulted from one experiment, all data fell under the same study ID. When multiple phenological events were recorded in a given study, we prioritized first flowering date because it was the most common metric. If only vegetative phenology was recorded, then we prioritized first leaf or bud date. Phenological events in the database included flowering, budburst, leaf expansion, and seed set, and metrics included the first, mean, median, or mode day of each event (Table 1). For each phenology study, we searched for matching performance data that reflected species fitness responses. We prioritized population-level metrics (e.g., percent cover, plot biomass) over proxies for reproductive fitness at the individual level (seed number, number of flowers, seed mass). If these preferred metrics

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[10] http://digitizer.sourceforge.net/

TABLE 1. Frequency of phenology and performance metrics utilized in this synthetic analysis.

Measurement	Reproductive or fitness traits		Vegetative traits	
	Metric	No. studies	Metric	No. studies
Phenology	first flowering date	13	budburst or first leaf date	9
	median flowering date	1		
	mode flowering date	1		
Performance	seed number	3	biomass	7
	seed mass	1	percent cover	2
	flower number	4	individual growth	8

were not available, we used data for growth responses of individuals (shoot elongation or diameter at breast height). Ecophysiological measures of performance such as photosynthetic rates and rates of leaf expansion were not included. If performance and phenology data were presented in separate publications, they were included in the database only if the mean values could be paired by experiment, species, and year of observation.

The resulting database included paired phenological and performance responses for 57 species across 24 terrestrial warming experiments (see Appendices A and B for detailed methods and table of experiments). Few warming experiments have been conducted in arid or semiarid ecosystems, and this bias is reflected in our data set. Although species were predominantly found at only one site, a few species occurred in multiple studies for a total of 65 paired phenology–performance comparisons (51 species occurred in only one study, 5 species occurred in two studies, 1 species occurred in three studies).

Calculating sensitivity

Species responses to warming within each study were transformed to sensitivities because of variation among studies in the magnitude of experimental warming (+0.4°C to +5°C). Phenological and performance sensitivities were calculated in slightly different ways. Phenological sensitivity (phen) was calculated as the days shift in phenological event (E) between the control (cont) and warming (warm) treatments, per degree warming. If T is temperature (°C) and S is sensitivity, then

$$S_{phen} = (E_{warm} - E_{cont})/(T_{warm} - T_{cont}).$$

Performance data (perf) were often collected in different units (e.g., percent cover vs. grams biomass), so sensitivities were calculated as proportional change in performance per degree of warming. If P is performance, then

$$S_{perf} = \frac{(P_{warm} - P_{cont})/P_{cont}}{(T_{warm} - T_{cont})}.$$

Statistical analysis

Data analysis was performed in R 2.12 (R Development Core Team 2011). To test the hypothesis that

species will have positive performance responses when they phenologically track climate change (high positive phenological sensitivity to warming), we performed a linear mixed-model analysis (function "lme," R package "nlme") in which performance sensitivity was predicted by phenological sensitivity and each datum represented the response of one species in one experiment, averaged across all years of observation. To ask whether the type of phenology metric, either flowering or vegetative, influenced the slope of the relationship between performance and phenology, "PhenType" was included in the model as a fixed effect, and the interaction between phenology type and phenological sensitivity was assessed. Studies varied in their methodologies and in the number of species monitored; to account for this, "StudyID" was included as a random effect in the model. Our mixed-model framework accounts for the nonindependence of multiple species sampled at the same site. It does not consider evolutionary relatedness of species; however, results from models considering taxonomic structure were similar to those presented here (see Appendix B). We report a pseudo R^2 value (the squared correlation between the fitted and observed values) as an estimate of the amount of variance explained by each mixed model, but these values are not meant to compare fit across models because it remains unclear how random effects should contribute to pseudo R^2 calculations when comparing multiple mixed models.

We had limited opportunity for local-scale analysis because there tended to be few species monitored in each experiment (the maximum number was 9 species in one experiment; in 10 out of 24 experiments, only 1 species was monitored for both phenology and performance). For experiments with 7 or more species, we additionally performed site-level linear model analyses on the relationship between phenological and performance sensitivities. PhenType was not included in these site specific models because we did not include multiple metrics for a study in our database.

RESULTS

There were two extreme values for phenological sensitivity (−18.1, +27.5 days/°C), that were more than 10 units lower or higher than the next greatest sensitivity in the data set. Both of these extreme values came from experiments where the reported magnitude of experi-
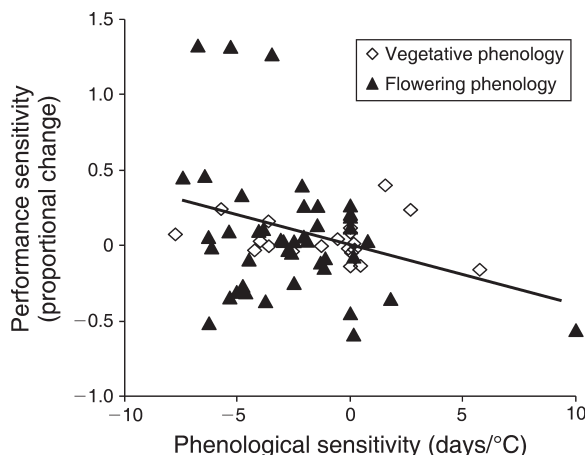
FIG. 1. Relationship between phenological sensitivity and performance for species in terrestrial warming experiments. Phenological sensitivity is expressed as the number of days earlier (−) or later (+) that the vegetative or flowering event occurred under experimental warming as compared with controls, divided by the amount of warming in °C. Performance sensitivity is expressed as a proportional shift, with 0 indicating no change, −1 indicating a 100% decline, and 1 indicating 100% increase in performance. Each datum represents one species in one experiment. The trend line represents the mixed-model fit across both vegetative and flowering phenology as predictors of species performance, because neither phenology type nor the interaction between phenology type and phenological sensitivity was a significant predictor of performance. For species identities, see Appendix A: Fig. A1.

mental warming was less than 1°C. Phenological sensitivity was calculated in units of days/°C, so an event date shifted by only a few days could result in a very large sensitivity if the amount of reported warming was small. Given the challenge of accurately measuring small temperature changes under field conditions, any error in this measurement could easily contribute to large outliers in sensitivity. These two outliers were subsequently excluded from the analysis, although their exclusion did not qualitatively change the results (see Appendix A for analysis including outliers).

Across all studies, we found that phenological sensitivity was a significant predictor of performance under warmed conditions ($F_{1,37} = 6.5$, $P = 0.015$; Fig. 1), where species that had accelerated phenology also tended to have higher performance under warmed conditions. This relationship had relatively low predictive power, however (pseudo $R^2 = 0.23$). The slope of this relationship did not depend on whether flowering or vegetative phenology was recorded (no significant interaction between phenological sensitivity and phenology type). The relationship between phenological and performance sensitivities remained significant regardless of whether we included or omitted extreme values in performance sensitivity (values greater than 1), and results considering taxonomic structure were similar to the ones presented here (see Appendix B). Further, phenological sensitivity remained a significant predictor

of performance when restricting the data set to exclude species that occurred in more than one experiment ($F_{1,28} = 4.35$, $P = 0.046$, pseudo $R^2 = 0.30$; for labels linking species identities, see Appendix A: Fig. A1).

In the Jasper Ridge Global Change Experiment (Zavaleta et al. 2003, Cleland et al. 2006), in which the greatest number of species was monitored for both phenology and performance ($N = 9$ species), the species that had the greatest acceleration of flowering phenology also had the greatest increase in abundance ($P = 0.02$, adjusted $R^2 = 0.45$; Fig. 2A). The relationship was marginally significant ($P = 0.09$, adjusted $R^2 = 0.34$; Fig. 2B) in a warmed subalpine meadow community located near the Rocky Mountain Biological Laboratory in Gothic, Colorado, USA (de Valpine and Harte 2001, Dunne et al. 2003). In contrast, there was no significant relationship between timing of budburst and growth responses (measured as change in diameter at breast height for individual trees) for species in the Harvard Forest warming experiment (Appendix A: Fig. A2).

DISCUSSION

Results of this analysis indicate that species that "track" climate change by flowering or leafing earlier in the growing season are likely to fare better with future
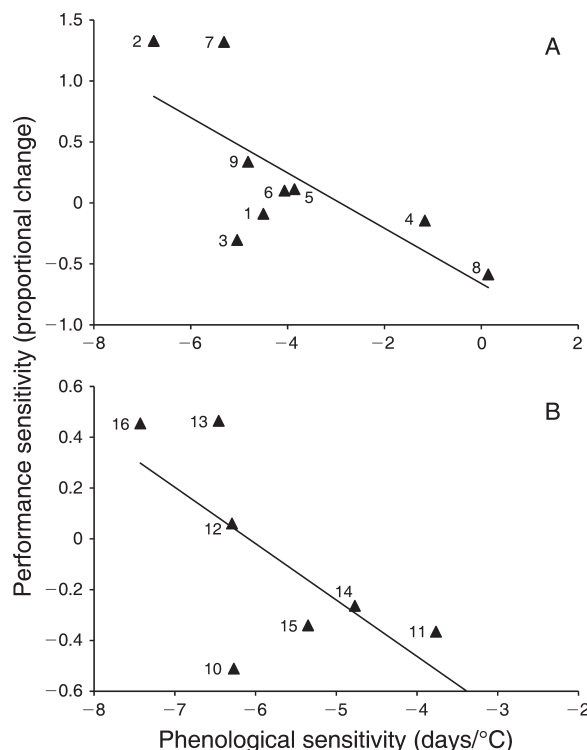

FIG. 2. The relationship between phenological sensitivity and performance for species in (A) the Jasper Ridge Global Change Experiment and (B) the Rocky Mountain Biological Laboratory Warming Meadow. Numbered labels next to each datum correspond to species listed in Appendix B: Table B1. Performance sensitivity and phenological sensitivity are measured as described in Fig. 1.

PLATE 1. A currently running open-top warming experiment in the White Mountains, California, USA. Photo credit: Christopher Kopp.

climate change than species without plastic phenological responses, or those that respond by flowering later. In long-term observational data sets, the majority of species respond to warmer spring temperatures with earlier flowering (Parmesan and Yohe 2003, Root et al. 2003, Menzel et al. 2006, Wolkovich et al. 2012). Across many studies, however, there is a small but consistent proportion of species that show the opposite pattern: delayed phenology in recent years despite warming trends (i.e., Fitter and Fitter 2002, Menzel et al. 2006). Although the present analysis suggests that there are negative fitness consequences to having delayed phenology with warming, a delayed response could be beneficial for species that become active later in the growing season, as opposed to the early-season species that often are the most sensitive to warming (Menzel et al. 2006, Miller-Rushing and Primack 2008). For instance, in both a warming experiment (Sherry et al. 2007) and in warmer years in an alpine meadow (Aldridge et al. 2011), early-season species showed accelerated phenology, whereas late-season species were delayed, potentially allowing both groups to avoid flowering during the middle of summer when daytime

high temperatures can exceed the physiological thresholds for these species. Alternatively, for species that rely on chilling requirements to break dormancy in the spring, warming could delay spring phenology (Körner and Basler 2010, Yu et al. 2010), leading to suboptimal performance as a result of novel interactions among cues. Finally, it is important to note that the data analyzed in this study came from warming experiments located primarily in mesic systems. In both arid and seasonally dry tropical ecosystems, soil moisture availability, rather than temperature, is likely to be a critical cue related to the onset of growth (Augspurger 1981, Peñuelas et al. 2004). Hence, the correlation between acceleration of phenology with warming and plant performance may be limited to systems where temperature, rather than moisture, cues the onset of growth and development.

Despite the statistical significance of the relationship, the proportion of variation in performance explained by phenological sensitivity was relatively low. Some of this variation is probably due to differences in the way that experiments were conducted or in the metrics used to measure both phenology and performance. In addition, numerous other factors may have influenced species performance under warmer conditions, such as trophic interactions with competitors, herbivores, pathogens, or symbionts (reviewed in Van der Putten et al. 2010), or non-trophic interactions such as plant–pollinator mutualisms (Hegland et al. 2009). Evolutionary relationships among the species in our data set also may have influenced the relationship between phenological sensitivity and performance. Prior research has found phylogenetic conservatism in patterns of both phenological sensitivity and abundance responses over periods of warming climate (Davis et al. 2010). The one major study that considered evolutionary distance between species when relating phenological sensitivity and abundance response over time to warming found that the relationship was robust to the inclusion of phylogenetic relatedness (Willis et al. 2008). This suggests that this phenological tracking–performance relationship was not purely driven by phylogenetic artifacts.

Further testing of the generality of the relationship between phenological sensitivity and performance under climate change will require observations of more species across a wider array of communities and environmental conditions (Pau et al. 2011). One approach to increasing this pool of observations is to engage citizen scientists. There are opportunities for individuals of various ages and skill levels to contribute observations of plant and animal phenology, including The USA National Phenology Network's plant and animal phenology observation program, *Nature's Notebook*, and Project BudBurst (both *available online*).[11,12] These efforts could provide an important starting point for regional

[11] www.usanpn.org
[12] www.budburst.org

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conservation organizations wishing to identify species that do not phenologically track interannual climate variation; such species may be at risk for declines in the face of future climate change.

There is also a growing emphasis on phenological monitoring among land-management organizations as a way to measure the potential adaptive capacity for species to climate change (Glick et al. 2011). However, in order for individual management units to justify the effort and expense of phenological monitoring, the relationship between phenological sensitivity and performance needs to be evident on the local scale. Prior observations of phenology in relation to shifting climate over time suggest that this relationship can be predictive at local or regional scales for populations of both animals (Møller et al. 2008, Ozgul et al. 2010) and plants (Willis et al. 2008, Hulme 2011). We also found that phenological sensitivity predicted performance responses in two studies that measured population-level processes in seven or more focal plant species (measuring performance as abundance or biomass accumulation at the population level). In contrast, there was no significant relationship between timing of budburst and individual growth responses for trees in the Harvard Forest warming experiment; this suggests either that longer-lived species may integrate phenological responses to climate change over longer timescales (Farnsworth et al. 1995), or that individual-level performance is unlikely to be predicted simply on the basis of phenological tracking. Although preliminary, these findings suggest that land managers should design monitoring schemes to ensure that both phenology and performance are measured at the scale of whole populations, rather than focusing on individuals, and that monitoring should continue for a period long enough to capture the responses of long-lived species.

Ultimately, species performance in a changing climate will be related not only to phenological sensitivity, but also to a host of other responses associated with physiology, demography, and interspecific interactions (Suttle et al. 2007, Tylianakis et al. 2008). Particularly for plants, where individuals interact in small neighborhoods, responses to shifting climate are likely to depend on the relative responses of competitors, including potential invasive species (Dukes 2011). Invasive species may benefit from having phenology that is distinctive or more sensitive to climate fluctuations (Wolkovich and Cleland 2011), which could influence the performance responses of native species. Of the few studies on this topic, results are divergent; one study found that invasive species had both greater phenological sensitivity to rising temperatures and greater increases in abundance over time (Willis et al. 2010), whereas another study found that increases in invasive species abundance were not explained by phenologcal sensitivity, but were probably driven by other extrinsic factors instead (Hulme 2011). In the current analysis, we were unable to compare the phenology and performance responses of co-occurring native and invasive species due to low replication of species within studies, suggesting that this is an important avenue for future research.

In conclusion, we found that phenological sensitivity was a significant predictor of species performance under experimental warming. These results provide important justification for current and proposed phenological monitoring efforts, and suggest that phenological sensitivity may be useful as an indicator for identifying species at particular risk for declines with future climate change.

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Supplemental Material

Appendix A

Full model output for statistical analyses (including and excluding outliers) and figures showing the relationship between phenological sensitivity and performance for flowering and vegetative phenology and proportional increase in dbh for species in the Harvard Forest Warming Experiment (*Ecological Archives* E093-154-A1).

Appendix B

A table of scientific names, phenology and performance response types used, data sources, and additional details including full citations for all studies included in the analysis (*Ecological Archives* E093-154-A2).