Beyond seasonal climate: statistical estimation of phenological responses to weather

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Abstract. Phenological events, such as the timing of flowering or insect emergence, are influenced by a complex combination of climatic and non-climatic factors. Although temperature is generally considered most important, other weather events such as frosts and precipitation events can also influence many species' phenology. Non-climatic variables such as photoperiod and site-specific habitat characteristics can also have important effects on phenology. Forecasting phenological shifts due to climate change requires understanding and quantifying how these multiple factors combine to affect phenology. However, current approaches to analyzing phenological data have a limited ability for quantifying multiple drivers simultaneously. Here, we use a novel statistical approach to estimate the combined effects of multiple variables, including local weather events, on the phenology of several taxa (a tree, an insect, and a fungus). We found that thermal forcing had a significant positive effect on each species, frost events delayed the phenology of the tree and butterfly, and precipitation had a positive effect on fungal fruiting. Using data from sites across latitudinal gradients, we found that these effects are remarkably consistent across sites once latitude and other site effects are accounted for. This consistency suggests an underlying biological response to these variables that is not commonly estimated using data from field observations. This approach's flexibility will be useful for forecasting ongoing phenological responses to changes in climate variability in addition to seasonal trends.

Key words: climate; daily models; frost events; phenology; thermal forcing; weather events.

Introduction

The timing of species' life history events, such as flowering or insect emergence, has important ecological consequences. These phenological events influence individuals' demographic performance (Miller-Rushing et al. 2010), competition among individuals (Yang and Rudolf 2010), trophic interactions (Hegland et al. 2009), and ecosystem processes such as carbon cycling (Leinonen and Kramer 2002). These ecological consequences have made understanding and quantifying phenological responses to climate an important effort in global change biology. However, doing so is complicated by the large geographic, temporal, and taxonomic variation in phenology arising from the complex set of factors that influence phenology (Cleland et al. 2007). Although thermal forcing (commonly quantified as degree days) is understood to be a primary driver of many phenological

events, additional weather events such as frosts and precipitation may also have important effects on phenology, but are less often considered (Jentsch et al. 2009). Non-climatic variables, such as photoperiod, competition with neighbors, resource availability, and other site-specific conditions, can further affect phenology and may alter perceived relationships with climate. The relative importance of these different factors will depend on species' evolutionary histories, but may also vary spatially due to environmental heterogeneity and genetic variability.

Despite broad acknowledgement of these multiple possible effects on phenology, the mechanistic and statistical approaches typically used to model phenology are unable to quantify their combined effects. The "mechanistic" or "process-based" approaches to modeling phenology typically use daily temperature data to parameterize primarily deterministic models describing how both winter chilling and spring forcing trigger phenology (Chuine 2000). The mechanistic description of temperature effects on phenology can be useful for select species when detailed experiments are used to

determine responses to temperature (Harrington et al. 2010) but the physiological response data needed to parameterize these models are unavailable for most species. These models also cannot readily accommodate additional variables (e.g., frosts, precipitation, site effects) nor quantify uncertainty in a manner that is useful for forecasting.

In contrast to these process-based models, statistical approaches can use widely available data from natural populations or common gardens to correlate phenological dates with monthly or seasonal climate (Primack et al. 2009). This approach is able to provide a probabilistic summary of the uncertainty surrounding phenological responses to climate, and can readily incorporate both seasonal climate and other site-specific effects (Ibáñez et al. 2010). However, this approach assumes that monthly or seasonal climate variables are useful proxies for the underlying mechanisms that affect phenology. For example, mean spring temperatures are often able to explain much of the variation in spring events such as bud burst because they are highly correlated with the thermal accumulation thought to be a key mechanistic trigger. The utility of such proxies is likely to vary depending on the climate variable and the organism, and may degrade in the future if patterns of climate means and variability change (Jackson et al. 2009). There is also limited ability to tease apart the relative importance of local weather events such as precipitation or frost events that may serve as proximate mechanisms for triggering phenology.

In this study, we use a novel statistical approach to quantify how multiple proximate mechanisms combine to trigger phenology. The approach is based on survival analysis, a broad class of statistical models used extensively in medical research. Developed to explain which factors influence the amount of time elapsing until an event (e.g., medical applications such as how treatments influence the time until death), these models are well-suited but underutilized for analyzing phenological events (Gienapp et al. 2005, Fieberg and Delgiudice 2008). We extend these previous efforts to analyze phenology using survival analysis by developing models to quantify how local weather events (e.g., recent precipitation and frost events) influence the phenology of several different taxa (a tree, an insect, and a fungus). Furthermore, we use hierarchical models to test whether observed phenological variability among sites arises from different responses to climate or other site-specific characteristics. Using data from multiple sites across latitudinal gradients, we test the hypothesis that species' sensitivities to local weather vary across latitudes. By quantifying in a statistical framework how a combination of daily weather, seasonal climate and non-climatic variables combine to affect phenology, this approach offers unique insights on the biology of phenology and abilities to forecast responses to future climate change.

METHODS

Species and weather data

Three study species were chosen in order to explore how models may be adapted to species with very different life histories. We analyzed the following phenological events: (1) first appearance of an insect, *Pieris rapae* (small white cabbage moth); (2) bud burst of a tree, *Morus bombycis* (mulberry); (3) fruiting dates of an ascomycete fungus, *Helvella macropus*. Species are referred to hereafter by their genus. Data for *Pieris* and *Morus* came from the Japanese Meteorological Agency (JMA), which has been monitoring phenology of dozens of taxa at a network of meteorological stations since 1953. These stations are distributed across a latitudinal and environmental gradient, with sites being generally cooler and drier in northern Japan and ranging to subtropical in the most southern islands (JMA 1985). Plant species were planted in or nearby the meteorological stations in order to monitor their phenology, while natural populations of the animal species were monitored in the vicinity of the station. For this study, we used data from 20 stations distributed across 28°–40° N latitude. For *Pieris* and for *Morus*, 44 years of data were used.

The data on fruiting times of *Helvella* (a summer- and fall-fruiting ascomycete commonly known as an "Elfin saddle") came from herbarium collections at the University of Michigan. These data were collected in nine counties in Michigan, spanning 42°–47° N, from 32 years between 1926 and 1977. Because fruiting bodies are relatively ephemeral and collections are made when specimens are in good condition, collection dates can be used as a reasonable measure of fruiting time (Gange et al. 2007). We used historical climate data (daily temperature and precipitation) from the nearest weather stations in the U.S. historical climate network (USHCN). We return below to further discuss which climatic variables were used to predict the phenology of each species.

Statistical analyses

Survival analysis encompasses a broad class of statistical analyses focused on modeling the time until an event occurs. These models are commonly used in medical research to understand how different treatments influence life span, and have been used in ecology for telemetry data (Fieberg and DelGiudice 2009) and questions about survival rates (Johnson et al. 2004). Despite the natural fit to predicting phenological events, survival analysis has been rarely used for analyzing phenological responses to climate (Gienapp et al. 2005, Fieberg and Delgiudice 2008). As previously used, these methods suffer from the same limitations as standard regression approaches when trying to understand how short-term weather events affect phenology. Namely, when the response variable is the date of an event, defining predictor variables based on that phenological date (e.g., asking whether precipitation events in the

week preceding an event affect phenology) creates an invalid circularity. One approach to using daily weather data to predict phenology is by using penalized signal regression (PSR), which works through a technique to smooth regression coefficients over time (Roberts 2012). Here, we adapted a particular type of daily survival analysis that can estimate how time-dependent covariates (quantities such as precipitation that vary over time) influence the probability of an event occurring. In this case the covariates vary daily, although a similar approach could be useful for covariates that vary over other time scales (e.g., weekly). This type of survival model with time-dependent covariates has also been used in the medical sciences (Sen et al. 2010). Recently, similar daily survival models were used to estimate the effects of forcing and chilling on cherry tree phenology (Terres et al. 2013, Allen et al. 2014). These studies show that, when critical parameters of mechanistic models are known or assumed (in particular, the threshold amount of chilling and the date of transition from chilling to forcing), survival models may offer a useful bridge between mechanistic and statistical models. We further extend previous approaches by using hierarchical models to estimate spatially varying effects of climate and other (typically unknown) site-specific effects.

In order to include time-dependent covariates together with time-independent variables, we specifically use a "counting process" formulation for survival analyses (Andersen and Gill 1982). Specifically, we assume a Poisson process to describe the event history. This amounts to assuming a Poisson distribution for the number of events in a given time interval with a mean that is a function of time and a risk function that depends on the covariates thought to be important for each phenology event. The cumulative mean function $p_{y,d}$ at the dth day in year y can be written generically as

$$p_{y,d} = \mathrm{SF}_d e^{\beta R_{y,d}}$$

where SF_d is the time-varying baseline (SF referring to seasonal forcing) and β is a vector of regression coefficients describing the effects of the risks, R. Thus, to predict the timing of an event, thought to depend on degree days (DD), precipitation, frost events, and winter temperatures, this function becomes:

$$p_{y,d} = \mathrm{SF}_d e^{\beta 1 \mathrm{DD}_{y,d} + \beta 2 \mathrm{precip}_{y,d} + \beta 3 \mathrm{frost}_{y,d} + \beta 4 \mathrm{winterTemp}_{y,d}}.$$

Note that, in this formulation, all covariates are time varying. There is flexibility to tailor this model to the biology of the species of interest. Different covariates can be selected depending on the biology of the organism and regional ecological constraints (e.g., precipitation may be important in arid regions but not mesic ones). Also, variables such as precipitation and frosts can be calculated over different sized moving windows depending on the biology of the organisms.

For the insect, *Pieris*, prior work suggests that a combination of degree days, precipitation, and photo-

period may be important determinants of the timing of emergence in the spring. *Pieris* lays eggs on host plants, progress through five larval instars, and the last instars leave the plant to pupate (Renwick and Radke 1988). In many insects, post-diapause development is controlled by a complex of factors, including temperature, moisture, day length, and biological factors (Tauber and Tauber 1976). Logistic functions have been used to describe insect emergence as a function of degree days (Broatch et al. 2006), but sufficient moisture is also likely to be important (Delahaut 2003). Based on these prior studies, we included cumulative degree days starting 1 January, precipitation in the previous seven days, and the number of frost events in the previous seven days as covariates.

Little is known about the controls of bud burst in *Morus bombycis*, a deciduous tree native to Japan, so we based our choice of models on the broader literature on tree bud burst. In general for temperate trees, a combination of degree days, winter chilling, frost events, precipitation, and photoperiod are thought to be important for bud burst (Hanninen and Tanino 2011). Similarly, relatively little is known about the proximate triggers of fruiting of fungi in nature. However the basic natural history and few previous studies suggest that water availability is quite important for constructing mushroom tissue (Ogaya and Penuelas 2005, Pinna et al. 2010). As a result, for *Helvella* we included cumulative temperature, the amount of precipitation in the previous 10 days, and used a logistic baseline hazard that varied by county, the finest resolution of spatial information associated with the herbarium records. Counties were expected to vary in fruiting timing due to latitude and land use differences.

The form of the baseline function, SF, may also be adjusted according to the biology of the target organism or ecosystem. Here, we modeled the baseline hazard as an increasing function of time that starts at the beginning of the year and ends on the event day each year. This form captures what we refer to as seasonal forcing, which is the increase in probability of the event over time due to changing photoperiod and other unmeasured variables that change over the season. This may be thought of as analogous to an intercept term in a regression that accounts for unexplained differences among sites. Here, because there are many unmeasured variables that may be changing over time at each site, we chose a site-specific baseline function that increases over time. We used a logistic function consisting of three parameters:

$$\mathrm{SF}_d = \frac{p1}{1 + e^{(2.2/p3)(p2-d)}}$$

where $p1$ is the value at which the function asymptotes, $p2$ is the day at which seasonal forcing is halfway to its maximum (the curve's point of inflection), and $p3$ is a measure of how quickly seasonal forcing increases (specifically, $p3$ is the number of days it takes for SF

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to increase from 0.1 to 0.5 of its maximum). This equation has been used for other saturating functions in ecology (Dixon 1976) and has the advantage that parameters have biological interpretations. The existence of the asymptote entails that the event of interest may not be realized for a very long time with a positive probability. The parametric form of SF is in contrast to a common application of the semiparametric version where the form SF is left unspecified. We use the parametric form instead, which is driven by the biology of the process.

These equations describe the basic model for estimating the effects of daily climate on phenology at a given site using observations from different years. An important extension to this model is to allow for spatial variability in phenological responses that results from a combination of environmental and genetic variation. We achieve this by using a hierarchical model structure that allows sites to have unique parameter values, but these values for different sites are drawn from common species-level distributions (Clark 2007). This hierarchical structure is useful for allowing spatial variability in phenological responses and for forecasting likely responses in new areas or under novel conditions (Ibáñez et al. 2010). With this hierarchical structure, incorporating variation among sites, s, the model becomes

$$p_{s,y,d} = \text{SF}_{s,d} e^{\beta 1_s \text{DD}_{s,y,d} + \beta 2_s \text{precip}_{s,y,d} + \beta 3_s \text{frost}_{s,y,d} + \beta 4_s \text{winterTemp}_{s,y,d}}$$

where

$$\text{SF}_{s,d} = \frac{p1_s}{1 + e^{(2.2/p3_s)(p2_s - d)}}.$$

Here, responses to climate and weather variables for each site (parameters $\beta 1_s$, $\beta 2_s$, $\beta 3_s$, $\beta 4_s$) and parameters of the seasonal forcing function (parameters $p1_s$, $p2_s$, $p3_s$) are allowed to vary among sites while also estimating a species' overall responses. Linked through hyper-parameters, estimates for one site were informed by data from other sites. For example, $\beta 1_s \sim$ Normal($\beta 1_{sp}$, σ_{sp}^2), where $\beta 1_{sp}$ is a species-level hyper-parameter representing the mean response for the species to forcing, and σ_{sp}^2 is the estimated variance among sites in these responses. These species-level parameters were given diffuse prior distributions: $\beta 1_{sp} \sim$ Normal(0, 1000). Similarly, the p parameters were given lognormal distributions: $p_s \sim$ LogNormal(p_{sp}, σ_{sp}^2), with p_{sp} assigned normal distributions estimated by the data. This hierarchical structure is critical for making inferences at locations for which we have little or no data and under future climate scenarios. In studies with data from more sites, where spatial autocorrelation of responses and predictors is expected, this approach could be extended to explicitly model the site effects as a spatial process (Latimer et al. 2006, Finley et al. 2009).

Models were fit in a Bayesian framework in order to easily accommodate the hierarchical structure and to facilitate forecasting while still accounting for the different sources of uncertainty, i.e., data, process, and parameters. Because we lacked prior information about what these values should be, we used diffuse prior distributions for all parameters. Models were fit and posterior densities of each parameter were obtained using OpenBUGS 1.4 (Thomas et al. 2006), called using the R2OpenBUGS package (Sturtz et al. 2005) in R version 2.14 (R Development Core Team 2008). BUGS code is provided in the Supplement. Models were run for approximately 50 000 iterations and thinned by 10 in order to reduce autocorrelation of parameter samples. Convergence was assessed visually and by calculating the Gelman-Rubin statistic from three independent chains. Ten thousand pre-convergence burn-in iterations were discarded. Results from these models are inferred from the posterior distributions of model parameters. Two groups of parameters are of particular ecological interest: (1) the baseline functions and (2) the relationships with climate and weather. These two sets of parameters could be used together to build predicted probabilities of the phenological event for a given site and set of climatic conditions. The statistical significance of the covariates was assessed using the posterior distributions of the regression coefficients. Instead of an arbitrary confidence interval, the probability that the posterior density of each site-specific regression coefficient (β's in the models described in *Methods*) were calculated and probabilities greater than 95% were deemed highly likely to be different from zero, greater than 90% were deemed very likely to be different from zero, and greater than 85% were deemed likely to be different from zero.

RESULTS AND DISCUSSION

Although thermal forcing is generally considered the dominant driver of most phenological events, many other factors can influence phenology. The highly variable amount of forcing leading up to events indicates that there are other factors helping to control timing (Fig. 1). Controlled experiments have shown that localized weather events and community context can strongly influence phenology (Jentsch et al. 2009), but measuring these effects from observational field data has not been previously possible, due in part to the complexity of weather preceding events (Fig. 1). The daily survival models used here can help estimate these more proximate effects of weather, while also allowing for spatial variation due to different ecological contexts and/or local adaptation.

Effects of weather on phenology

Relationships between phenology and weather varied among species. For *Morus*, we found positive effects of daily forcing on the probability of bud burst (Fig. 2A), consistent with previous studies showing that bud burst responds to forcing. We also found that frost events decreased the probability of *Morus* budburst at all sites (Fig. 2B). Although it is not well studied, frosts may retard the plant development, thereby slowing endoge-
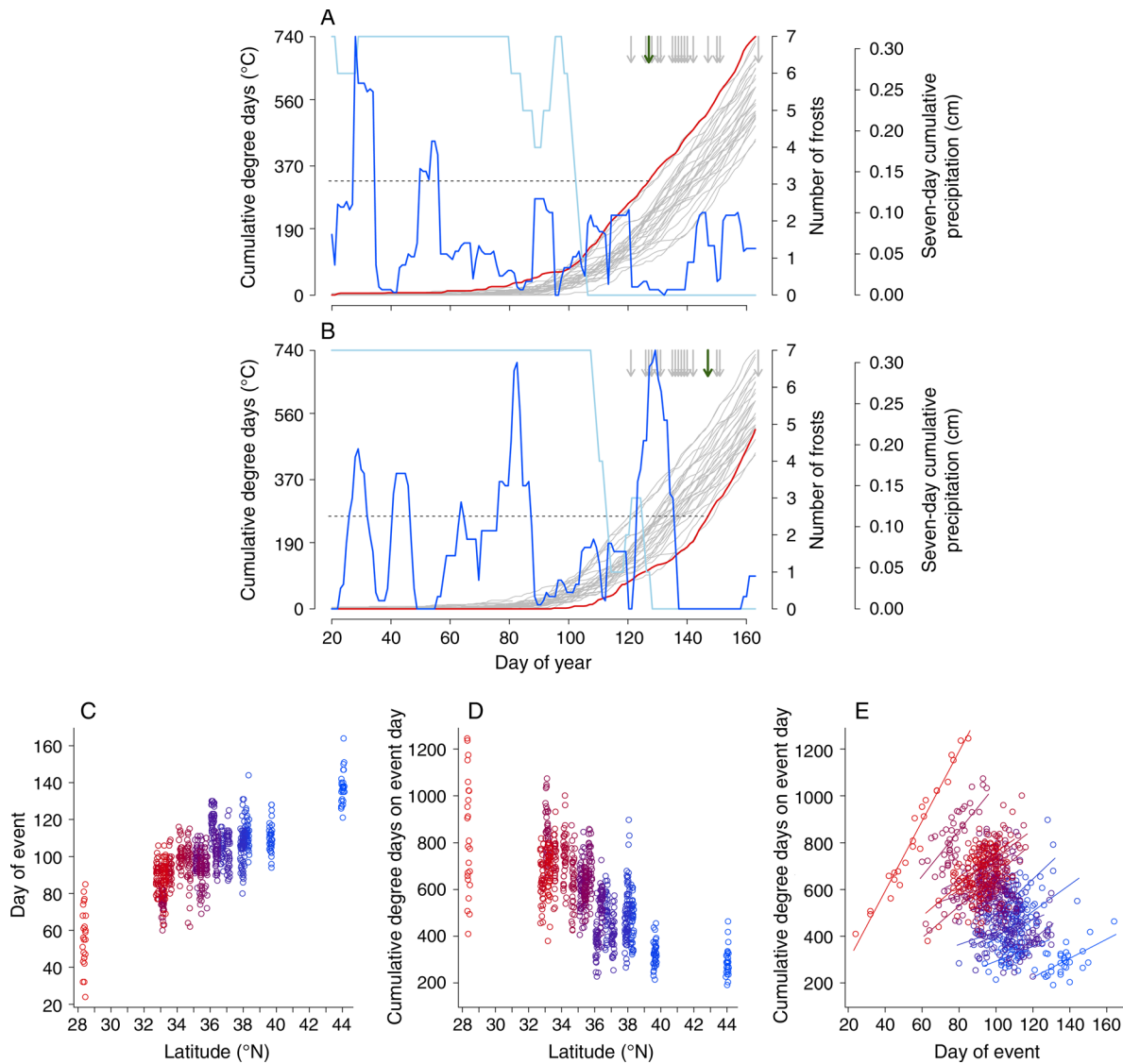
FIG. 1. Climatic and phenological variability at a single site in (A) a warm year and (B) a cool year. The green arrows at the tops of these graphs mark the timing of bud burst of *Morus bombycis* in the example years and the gray arrows mark the timing of bud burst in all other years. The red lines are the cumulative degree days for the example years and gray lines are the degree days in other years. Light blue lines show a moving window of the number of frost events in the previous week, and dark blue lines are precipitation totals in the previous week. For a picture of the within- and among-site variability in the data, (C) all analyzed *Morus* bud burst dates are plotted vs. latitude, (D) the cumulative forcing is plotted vs. latitude, and (E) the relationship between dates of events and forcing is plotted. Colors range from cooler, high-latitude sites (blue) to warmer, lower-latitude sites (red).

nous pathways leading to bud burst and leaf development. This effect of frost is consistent with field observations of delayed foliation in temperate trees following frost events (Augspurger 2009). The effect of recent precipitation events on the probability of *Morus*' bud burst was not significant (Fig. 2C). While it is perhaps not surprising that precipitation was a not a major determinant of bud burst in temperate, mesic Japan, we would expect a stronger role of precipitation for plants in more arid ecosystems (Crimmins et al. 2011, Diez et al. 2012).

For *Pieris*, daily forcing tended to have a positive effect on the probability of emergence, but was not statistically significant (Fig. 2D). By contrast, frost events and recent precipitation had negative effects on emergence probability (Fig. 2E, F). These results are consistent with previous findings of the importance of degree days (Jyoti et al. 2003, Broatch et al. 2006), and moisture (Delahaut 2003) for *Pieris* development, and suggests that frost events may also slow down early spring development. Previous studies of *Pieris* phenology have found earlier appearance with higher mean
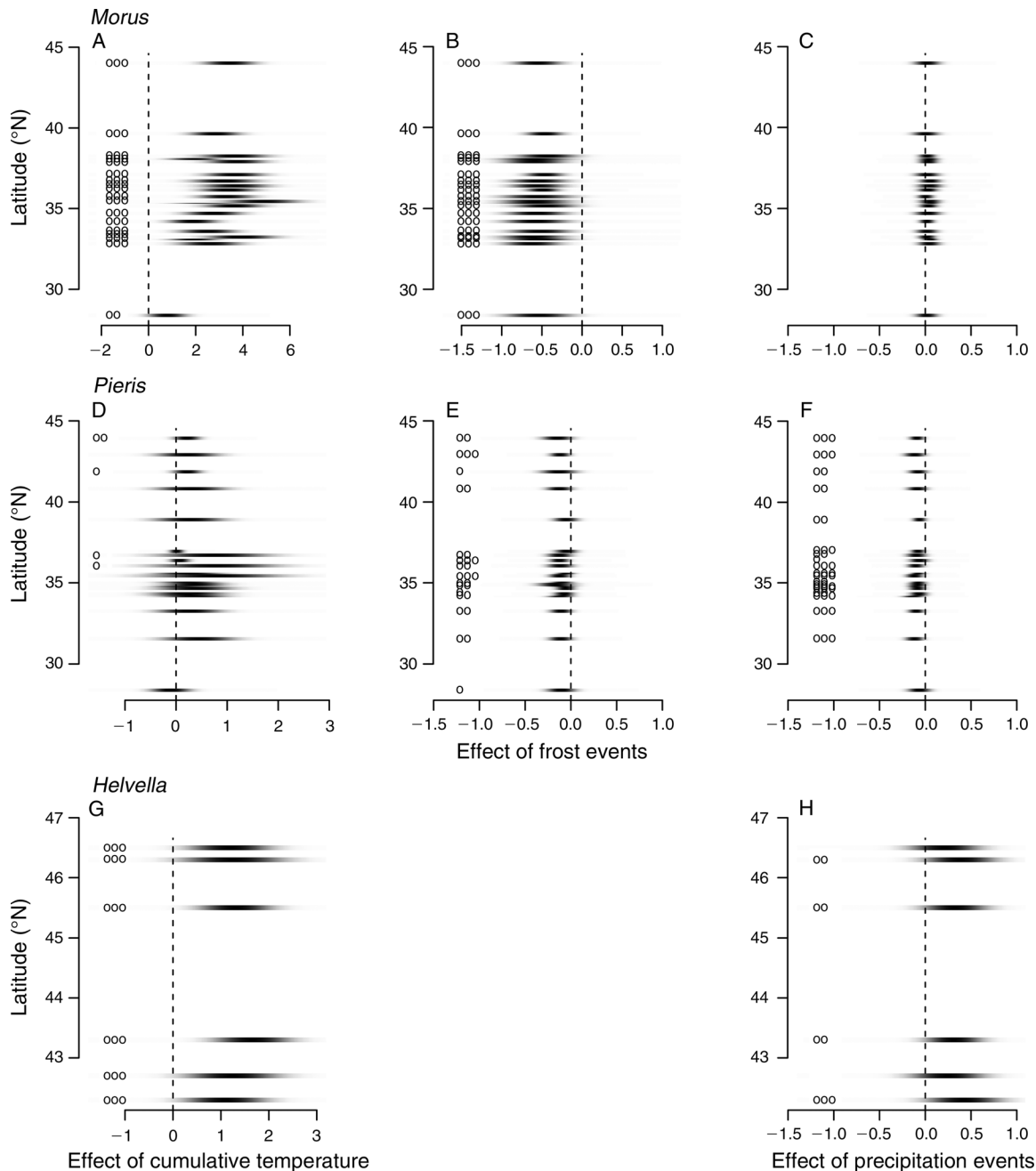
FIG. 2. Effects of climate variables on (A–C) *Morus bombycis* bud burst, (D–F) *Pieris rapae* appearance, and (G, H) *Helvella macropus* fruiting. The posterior densities of site-specific regression coefficients (β in the models described in *Methods*) are plotted as a function of site latitude. Darker portions of these densities represent more likely values of the regression coefficient, and asterisks show three different thresholds of probabilities that the coefficient is different from zero. A single o indicates >85% probability for the effect to be different from zero, oo indicates >90% probability, and ooo indicates >95% probability. There is no frost effect estimated for *Helvella* because it fruits in the late summer.

spring temperatures in Spain, and in dry areas, perhaps related to latitude (Gordo et al. 2010). Primack et al. (2009) found that *Pieris* appeared earlier in years with higher mean winter temperature.

The probability of *Helvella* fruiting was positively affected by daily forcing and precipitation in the preceding 10-day period (Fig. 2G, H). Very little is known about the proximate controls of mushroom production in nature, but these results are consistent with natural history and documented patterns of the importance of water availability for mushroom production (Ogaya and Penuelas 2005, Pinna et al. 2010).

Temperature may affect fungi directly through metabolic activity or indirectly through plant activity, and the phenology of many fungi is likely to be linked to the phenology of associated plants (Dickie et al. 2010). Although the mycorrhizal status of *Helvella macropus* is uncertain, its response to plant phenology may play a role either way. Mycorrhizal species of fungi are likely to be influenced by the seasonal flow of carbon through plant roots, while saprotrophic species may be influenced by litter inputs to the soil or other substrate characteristics. When these additional time-dependent variables can be quantified, they may be added to these models to test their importance relative to precipitation and temperature.

The weather variables tested here are certainly not an exhaustive list of what controls phenology in these organisms, and these daily models could readily incorporate additional climate and weather variables when they are known to affect phenology. However, the mechanisms underlying most phenological events are still not well understood. Studies of a few model organisms suggest that a variety of pathways may be involved in triggering phenological events. For example, detailed study of *Arabidopsis* flowering has uncovered a complex set of environmental signaling pathways affected by temperature and photoperiod, but also endogenous pathways linked to developmental status (Simpson and Dean 2002, Amasino 2010). The interactions between these pathways and the external conditions that affect them are not understood, but it appears likely that any climatic event that affects plant development could influence phenology. The relative importance of different mechanisms is also likely to depend on species' life histories (e.g., early vs. late successional trees; Körner and Basler 2010) and the ecological context (e.g., soils, biotic community, etc.). Distinguishing among potential mechanisms may be best approached through a combination of statistical modeling of observational data and use of controlled experiments. Although statistical models are critical for testing ideas within the complexity of natural systems, they face the difficulty that many variables can co-vary over time and models may become non-identifiable. This problem can be minimized by limiting analysis to a handful of key variables with known biological relevance, as in our study, checking that models converge, and when possible through the use of controlled experiments to determine cause and effect.

Spatial patterns

Spatial variability in phenology complicates predictions of responses to future climate change (Bennie et al. 2009), but also offers opportunities to dissect the mechanisms underlying phenology. These survival analyses explored spatial variability in two ways: first by asking whether species' sensitivities to climatic variables changed across a latitudinal gradient, and second by asking how the site-specific seasonal forcing varied across latitudes. For all species, the effects of covariates showed no significant variation across latitudes (Fig. 2). Despite the high variability of forcing recorded among years and sites (Fig. 1D; and typical of other studies, e.g., Wesołowski and Rowiński [2006]) we found that forcing had a consistent effect for each species across latitudes (Fig. 2). There are mixed expectations for how phenological sensitivity to climate should change across latitudes (Doi and Takahashi 2008). Spring phenology in the temperate zone is thought to be an evolutionary balance between the benefits of longer growing seasons allowed by earlier events, and the risk of being damaged by frosts (Lockhart 1983, Leinonen and Hänninen 2002). Organisms at higher latitudes, with shorter growing seasons, may undergo strong selection to maximize growing season length by responding to photoperiod, but the costs associated with mistimed events should favor high sensitivities to climate. Previous studies reflect these opposing ideas, as Root et al. (2003) found stronger responses to temperature at higher latitudes, while Menzel et al. (2006) found greater responsiveness in warmer countries in Europe. Our findings suggest a different scenario in which species' underlying sensitivities to temperature are comparable across latitudes, with other site-specific variables driving observed differences in phenology among sites (Diez et al. 2012).

In contrast to the consistent climate sensitivities across latitudes, the seasonal forcing curves for each species varied considerably among sites (Fig. 3A), suggesting that there were additional factors underlying site-to-site variation in phenology. Some of this variability could be explained by the parameters describing the seasonal forcing. For *Morus* and *Pieris*, the $p2$ parameter, corresponding to the day of the inflection point, was significantly higher at higher latitudes, suggesting that this function is capturing variation among sites due to photoperiod or other latitudinal trends (Fig. 3C). The parameter $p3$, inversely proportional to the "steepness" of the baseline probability, also tended to be smaller at higher latitudes for *Morus* and *Pieris*. This pattern suggests more rapidly increasing probabilities at higher latitudes, possibly reflecting a smaller window of possible event dates. The asymptote of the baseline hazard, described by the third parameter, $p1$, did not appear to be related to latitude but varied among sites for unknown reasons. The lack of latitudinal patterns for *Helvella* likely reflects the more narrow geographic range of data for this species.

Overall, these models allow a useful dissection of spatial variability in contrast to existing deterministic "process models." Mechanistic process models, such as thermal sum models, assume that the underlying process is constant across space, i.e., spatial stationarity (Pau et al. 2011), which is not helpful for understanding how mechanisms may vary spatially and problematic for making predictions across regions. By allowing for spatial variability, hierarchical daily models could also help
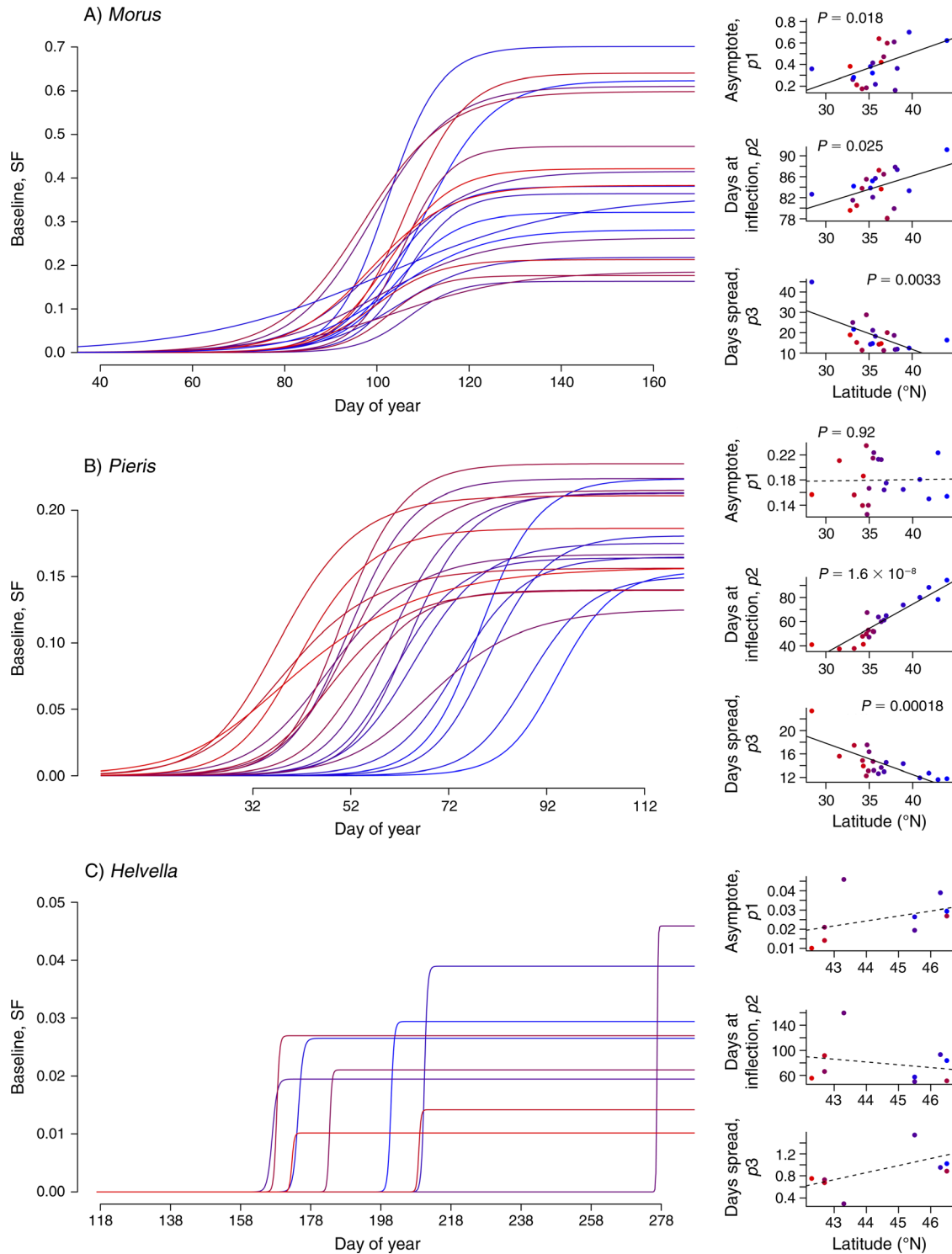
Fig. 3. Seasonal forcing (or "baseline function") curves for (A) *Morus bombycis*, (B) *Pieris rapae*, and (C) *Helvella macropus*. Seasonal forcing curves were estimated for different sites (corresponding to SF in the model described in *Methods*). Colors vary from blue to red reflecting high to low latitudes, respectively. Parameters describing the shape and position of these seasonal forcing curves were related to latitude (on right). Linear regressions are represented with solid lines for significant relationships ($P < 0.05$) and dashed line for nonsignificant relationships.

quantify how phenological responses to climate depend on interactions with other species in the community, as seen in experimental studies (Jentsch et al. 2009).

Conclusions: Why daily models?

Climate trains the boxer, but weather throws the punches.

—Derek Arndt, climatologist, NOAA

Organisms do not respond to mean seasonal climate, but rather daily weather conditions and extreme events (Gutschick and BasssiriRad 2003). When seasonal climate variables serve as effective proxies for the weather that influences phenology, they can be useful for explaining phenological variation. For example, mean spring temperatures can often explain significant variation in spring phenology (e.g., Primack et al. 2009) because they are highly correlated with the accumulated daily forcing that helps trigger many plants' spring phenology. Nonetheless, there are several reasons to develop daily models as a complementary approach to existing mechanistic and statistical methods. First, the correlations between seasonal variables and proximate mechanisms may change over time or across regions, which will cause problems for seasonal analyses. Because both the mean and variance of climate variables are expected to shift with climate change, the correlations between mean climate and extreme values may also change (Jackson et al. 2009).

Second, not all proximate mechanisms have effective seasonal climatic proxies. For example, seasonal precipitation may often be less relevant to organisms' phenology than the specific timing of rainfall events. The fruiting of a fungal species in this study is a good example. Although there is a general seasonality and recurring order to when different species produce fruiting bodies, the specific timing of fruiting may depend in large measure on the specific timing of rain events, rather than whether the season has been wet or dry on average. Therefore, although a summer that is wetter overall is more likely to have earlier rain events and therefore earlier phenology, this is not necessarily the case. Similar dynamics are likely to occur in plant communities that are driven by the timing of rains (Crimmins et al. 2011, Levine et al. 2011).

Third, as downscaled climate projections offering daily climate scenarios become increasingly available, it is important to have a statistically robust framework for estimating and forecasting multiple proximate effects on phenology. By combining the baselines and climate-related risks, daily predictions of events could be made for a given site under predicted weather patterns. Finally, daily models can offer insights on the basic biology of how organisms respond to their environment that seasonal models cannot. Here, we have quantified for the first time how frosts and precipitation may combine with forcing to influence phenology of different organisms. Controlled experiments will remain invaluable way to isolate mechanisms, but daily statistical models can offer complementary insights and make better use of historical data sets and the growing contemporary data sets resulting from citizen science programs and data collection networks.

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SUPPLEMENTAL MATERIAL

Supplement

OpenBUGS computer code for a daily survival model (*Ecological Archives* A024-206-S1).