

Understanding growing degree days to predict spring phenology under climate change



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Introduction

1. In ecology, we have the fundamental issue of understanding and applying methods to accurately predict shifts in climate and the broader impacts of these shifts.

- (a) Often we use different accumulated degree day models to answer ecological questions, though we do not always understand the intricacies of the model, nor do we investigate what is missing from the model output or even input (i.e., weather data methods).
- (b) These methods can be applied to many ecological questions investigating climate data across global habitats but here we will investigate the effects of climate measurements and site on predicting spring plant phenology.



2. Understanding and predicting plant phenology in temperate deciduous forests is critical as it both shapes community structure and also influences major ecosystem services such as resource and forest management.

- (a) Climate change and urbanization are advancing spring timing—such as budburst and leafout, which are strongly cued by temperature, resulting in longer growing seasons (Chuine *et al.*, 2001) which ultimately impacts these services.
- (b) Temperate forests sequester carbon and help mitigate the negative effects of climate change and— with earlier spring phenology and longer growing seasons—there has been an increase in carbon uptake (Keenan *et al.*, 2014).

- (c) But our understanding of how climate change is impacting this timing of spring is incomplete, especially in urban versus natural forest habitats.
3. Urbanization has led to the formation of urban heat islands, which have been shown to affect plant phenology and lead to earlier spring leafout (Meng *et al.*, 2020).
 - (a) These trends are crucial to understand in order to predict plant development with warming.
 - (b) Tracking heat accumulation is one way to measure and forecast spring budburst, which is often predicted through the growing degree day (GDD) model (Cook *et al.*, 2012; Crimmins & Crimmins, 2019; Phillimore *et al.*, 2013; Schwartz *et al.*, 2006; Vitasse *et al.*, 2011).
 - (c) The GDD model simply sums temperatures above a certain threshold—ideally around 0°C as estimates are proven to be more accurate (Man & Lu, 2010)—and different species often require a different number of GDDs to leaf out.
 - (d) GDDs accumulate at a faster rate when mean temperatures are higher, thus different sites or different climate measurement methods may record different GDD thresholds for budburst.
 - (e) Spring budburst timing can have cascading effects to pollinators (Boggs & Inouye, 2012; Pardee *et al.*, 2017), on carbon dynamics (Richardson *et al.*, 2013) and albedo (Williamson *et al.*, 2016), thus integrating the growing degree day model successfully is essential for predicting the effects of climate change on temperate systems.
 4. Phenology is often measured through satellite, remote sensing or PhenoCam images to detect spring ‘green-up’ (Meng *et al.*, 2020; Liu *et al.*, 2018; Richardson, 2015) but these methods fail to detect the species—or even site-level—nuances in budburst timing (Elmendorf *et al.*, 2019).
 - (a) Intensive, on the ground observations of individual budburst and leafout timing is the most effective way to implement new methods in calculating growing degree days and predicting future phenology.
 - (b) Urban environments additionally provide a natural laboratory for assessing the effects of warming on temperate tree and shrub species as these sites are warming at a faster rate than more rural habitats (Pickett *et al.*, 2011; Grimm *et al.*, 2008).
 5. Arboreta and botanical gardens offer a unique lens to investigate climate change and local adaptation studies by incorporating varying seed sources—or provenance locations—thus they mimic common garden experiments (Primack & Miller-Rushing, 2009).
 - (a) Most arboreta keep diligent acquisition records, providing visitors and scientists information on seed sources and tree age (Dosmann, 2006), whereas in forests, tree cores must be assessed to get as accurate an estimate on tree age and there is no variation in provenance location.

6. As GDD is a predominant indicator of spring phenology, having accurate and consistent weather data is essential for better estimates of budburst or leafout, especially with warming.
 - (a) To facilitate scaling and minimize error due to microclimatic effects, researchers often deploy standalone weather loggers—such as HOBO sensors—which may provide higher resolution weather data (Schwartz *et al.*, 2013; Whiteman *et al.*, 01 Jan. 2000).
 - (b) Though deploying temperature loggers is not always feasible, especially when investigating large spatiotemporal shifts in GDDs.
 - (c) As climate is one of the strongest environmental factors contributing to ecosystem change, it is essential to measure weather data as accurately and efficiently as possible, using methods that are accessible to myriad researchers.
7. Here, we use both simulations and real data to test our hypotheses on modeling GDD accuracy in a warming world and conclude with a series of simulated forecasts to estimate changes in GDD estimates.
 - (a) Our major hypotheses are as follows:
 - (b) Weather stations are less accurate measures of the same weather than hobo loggers.
 - (c) Urban environments require fewer GDDs to budburst than forest habitats.
 - (d) Individuals with provenance latitudes from more northern locations require fewer GDDs to budburst.
 - (e) Weather stations will record warmer temperatures at urban sites and cooler temperatures at forest sites compared to hobo loggers.

Methods

Sites

1. We chose two sites—one urban arboretum and one forest—with overlapping species and climates to compare the number of growing degree days to budburst across species.
 - (a) The urban site is in Boston, MA at the Arnold Arboretum of Harvard University (42°17' N -71°8' W).
 - (b) The Arnold Arboretum is 281 acres and contains 3825 woody plant taxa from North America, Europe and Asia.
 - (c) The forest site is in Petersham, MA at the Harvard Forest (42°31'53.5' N -72°11'24.1' W).
 - (d) The Harvard Forest is 1446 acres and has a range of elevation of 220-410m.

Simulations

1. We simulate test data in order to test our hypotheses and assess the model output results.
 - (a) In order to exhaustively examine all hypotheses, we build our simulation data to address very simple to more complex questions.
 - (b) We first start by examining what the model output would look like if we just make the weather station data less accurate.
 - (c) To do this, we create an effect of method on our GDD threshold value and then increase error on the weather station measurements by increasing the sigma value for our random distribution creation (see Supplemental information on Data Simulation).
 - (d) We then compare model results by running a simulation with increased error on the hobo logger measurements by, again, increasing the sigma value for our random distribution creation on hobo logger observations.
 - (e) Next, we incorporate climate data by again establishing a random distribution around a mean temperature for each site and then add variation to this weather data to create “microclimatic” effects.
 - (f) Using this climate data, we then find the day of budburst when the unique GDD threshold is reached for each individual.
 - (g) For the following hypothesis testing urban effect, we create simulation data that manipulates the GDD threshold for the urban versus rural sites by lowering the GDD threshold for individuals at the more urban locations (e.g., local arboreta).
 - (h) Next, we apply the same “microclimatic effect” as above to test microclimatic variation across the two sites.
 - (i) We repeat these steps for the provenance latitude hypothesis by having individuals from more northern provenances requiring fewer GDDs and then apply the “microclimatic effect”.

Real Data

1. Phenology observations across the Arnold Arboretum were collected by trained citizen scientists from the Tree Spotters National Phenology Network program (USA-NPN, 2016).
 - (a) The Tree Spotter volunteers observed 15 tree and shrub species—ranging from early-budbursting to late-budbursting—and each species had 5 individuals for a total of 75 trees.

- (b) Species included in the study were *Acer saccharum*, *Acer rubrum*, *Aesculus flava*, *Betula nigra*, *Betula alleghaniensis*, *Carya glabra*, *Carya ovata*, *Fagus grandifolia*, *Hamamelis virginiana*, *Populus deltoides*, *Quercus alba*, *Quercus rubra*, *Tilia americana*, *Vaccinium corymbosum*, and *Viburnum nudum* (Figure S2).
 - (c) In September 2018, we placed 15 hobo loggers around the Tree Spotter route to compare hobo logger temperatures to the weather station temperatures recorded.
 - (d) We then used budburst observations for each individual and calculated GDDs until budburst starting from 15 February using both the hobo logger data and then the weather station data.
2. Phenology observations for the Harvard Forest have been collected by Dr John O’Keefe since 1990 (O’Keefe, 2014) along the Prospect Hill Tract.
- (a) Species observed by Dr John O’Keefe include *Acer saccharum*, *Acer rubrum*, *Acer pensylvanicum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Fraxinus americana*, *Hamamelis virginiana*, *Quercus alba* and *Quercus rubra* (Figure S2).
 - (b) The same methods were applied at the Harvard Forest where we placed 15 hobo loggers at regular intervals along the Prospect Hill Tract, calculated GDD estimates from 15 February 2019 until budburst for each individual using hobo logger data and then weather station data.

Forecasting

1. Using simulated data, we tested GDD accuracy across various GDD threshold requirements with warming of 1°C to 10°C.
 - (a) We also evaluate accuracy using different base temperatures for calculating GDD (i.e., 0°C versus 10°C) with variation in sigma around base temperatures (i.e., 0°C and 0.5°C).
 - (b) Accuracy was evaluated as a ratio of observed GDD divided by the expected GDD.

Shiny App

1. To show the above simulations, real data and forecasts in one location we use a Shiny Application.
 - (a) Using the R package ‘shiny’ (Chang *et al.*, 2021), version 1.6.0, we developed a Shiny App that contains five pages: (1) ‘Home’ which has information on the application, (2) ‘Hypothesis Testing’ which runs the simulation data and allows users to manipulate the inputs, (3) ‘Simulation Data for Model Testing’ which runs simulation data to test the model and make sure the model outputs

are accurate, (4) ‘Real Data and Analyze Results’ which uses real data and runs analyses to be used to compare to the ‘Hypothesis Testing’ output and (5) ‘Forecasting GDD with Warming’ which forecasts GDD accuracy under warming.

Data analysis

1. Using Bayesian hierarchical models with the rstan package (Stan Development Team, 2019), version 2.19.2, in R (R Development Core Team, 2017), version 3.3.1, we estimated the effects of urban or provenance effect and method effect and all two-way interactions as predictors on GDDs until budburst.
 - (a) Species were modeled hierarchically as grouping factors, which generates an estimate and posterior distribution of the overall response across the 20 species used in our simulations and 18 species used in our real data.
 - (b) We ran four chains, each with 2 500 warm-up iterations and 3 000 iterations for a total of 2 000 posterior samples for each predictor for each model using weakly informative priors.
 - (c) Increasing priors three-fold did not impact our results.
 - (d) We evaluated our model performance based on \hat{R} values that were close to one and did not include models with divergent transitions in our results.
 - (e) We also evaluated high n_{eff} (3000 for most parameters, but as low as 708 for a couple of parameters in the simulated provenance latitude model).
 - (f) We additionally assessed chain convergence and posterior predictive checks visually (Gelman *et al.*, 2014).

Results

Simulations

1. When we manipulate the simulations to have noisy weather station data, noise is returned as the sigma for the method parameter (Figure 1 a)) and the method parameter is slightly positive ($XX \pm XX$), indicating weather stations require more GDDs until budburst.
 - (a) Though, when we manipulate the simulations to have noisy hobo logger data, the output is nearly identical (Figure 1 b)) but the method parameter is slightly negative ($XX \pm XX$), now indicating hobo loggers require more GDDs until budburst.

- (b) The noise is additionally apparent when visualizing raw data plots, which can detect which method is more noisy (Figure 2).
2. Simulations that manipulate the data to have both methods equally as accurate but also include microclimates at both sites show that the hobo loggers require more GDDs until budburst.
 - (a) When simulating microclimatic effects across the sites, we include greater variation in temperature for the hobo logger data, which is being reflected by the negative slope of the method parameter $(XX \pm XX)$.
 3. We next, using simulations that establish an interaction where the hobo loggers and weather station recorded temperatures differently across the two sites and manipulate the urban parameter, we see that urban sites require fewer GDDs until budburst $(XX \pm XX)$.
 - (a) When we simulate variation in mean temperature across the two methods across the two sites to establish an interaction we see: sigma values for the method effect are large (XX) , though the slope is close to zero $(XX \pm XX)$; individuals at the urban site require fewer GDDs to budburst $(XX \pm XX)$ and there is large sigma (XX) ; and the weather station at the urban site is recording the fewest number of GDDs until budburst $(XX \pm XX)$ though the interaction sigma is close to zero (XX) ; Figure 4 a)).

Real data

1. Individuals at the arboretum (i.e., more urban sites) require fewer GDDs to budburst $(XX \pm XX)$.
 - (a) There is high variation in GDDs between the two methods (XX) though the slope is close to zero $(XX \pm XX)$.
 - (b) There is a large interaction indicating weather station data at the arboretum records the fewest number of GDDs until budburst $(XX \pm XX)$.
 - (c) Using raw data, we see there is higher variation at the arboretum across the two methods and that the arboretum requires fewer GDDs until budburst than the Harvard Forest.

More simulations: provenance latitude model

1. Next, I will dissect the provenance model... well I think. This can also go in the simulations section either before the interaction simulations or after.

Forecasting GDDs

1. The GDD model is most accurate for individuals that have high GDD thresholds and when base temperatures are higher (i.e., 10°C; Figure 6 a)).
 - (a) However, the GDD model becomes less accurate with warming, and accuracy decreases at a faster rate with the higher base temperature (i.e., 10°C) than with the lower base temperature (i.e., 0°C; Figure 6 b)).
 - (b) Under the no warming simulation, using the 10°C base temperature is most consistent across species but with any amount of warming, the 0°C base temperature is more accurate.
 - (c) Additionally, variability in accuracy across GDD thresholds and with warming increases with higher sigmas (Figure 6).


Discussion

Importance of plotting raw data and running simulations

1. Raw data is crucial to plot in order to better interpret model outputs.
 - (a) As we see from the less accurate weather station data example versus the less accurate hobo logger data example, the model outputs are very similar and are even comparable to the microclimate simulation.
 - (b) One way to disentangle which climate measurement method is less accurate is through the use of raw data plots in combination with the model output figures.
 - (c) As is evident from the model outputs, the method which is less accurate requires more GDDs until budburst since GDDs are accumulating at a faster rate with higher temperature variability—and higher temperature days.
 - (d) Using simulations and raw data plots has helped us see through the common pitfalls we make as scientists and conclusions we tend to jump to when interpreting our models.
2. Understanding microclimates versus measurement error is possible, though difficult to detect.
 - (a) By including microclimatic effects at both sites, variation in temperature increases and, thus, the number of days in which the temperature falls below the base GDD threshold is also greater but the days in which temperatures are accumulating, the temperature will likely be greater than what is recorded at the weather station.

- (b) Ultimately, we see that the number of days in which the temperatures falls below the base GDD threshold must be less than the number of days in which temperatures are accumulating at a faster rate than at the weather station since hobo loggers in this simulation require more GDDs until budburst.
- (c) When we compare the microclimate simulation to the inaccurate hobo logger simulation, we see that under the inaccurate hobo logger simulation, hobo loggers may require slightly fewer GDDs until budburst but the effect of method is stronger under the microclimate simulation.
- (d) This is messy but main points: 1) high temperature variability, whether it is due to inaccurate recordings or due to microclimates, results in more days at higher temperatures so the day of budburst records higher GDDs for the method with greater temperature variability. That said, we are seeing inaccurate methods overlap with zero for the method parameter whereas microclimate simulations do not.

The use of simulations to better interpret real data results

1. Real data is hard to interpret, especially as models become more complex through interactions, hierarchy or even non-linearities. 
- (a) By using simulations to manipulate interactions, we can learn how to read our data and interpret our results.
- (b) The Shiny App is meant for users to understand our suggested approach to model testing and interpreting mixed model results as well investigate various, new simulations of interest.

Understanding the real data and the conclusions we can draw

1. Here, I want to reiterate the depth in which we can actually draw conclusions.
 - (a) Our data and our models suggest that individuals at the arboretum require fewer GDDs until budburst than those at the Harvard Forest.
 - (b) We also see that the hobo loggers at both sites record greater variation than the weather station data.
 - (c) But we do not know if this is because the loggers are less accurate measures of the same weather or if the hobo loggers are detecting microclimatic effects across the two sites.

- (d) Based on our simulations, since the method parameter is close to zero, would we presume it is due to less accurate measurements from one of the methods? Probably not because the variation between the methods is comparable across sites. Maybe instead this implies microclimate effects that are in opposite directions between the two sites?
- (e) Finally, we can conclude that the weather station at the arboretum is recording lower temperatures than the hobo loggers, thus data from the weather station at the arboretum is recording the fewest number of GDDs until budburst.

The future of GDD models

1. As we see from our forecasting simulations, regardless of base temperature threshold, GDD models may not be appropriate for the future with warming (Man & Lu, 2010).
 - (a) This is because with warming, GDDs will accumulate at a faster rate, which will reduce accuracy of determining that actual threshold for budburst phenology.
 - (b) Generally higher GDD thresholds means lower a lower GDD observed to GDD expected ratio; this is because being off by a day is a small effect for higher GDD threshold species (and hence greater days) than for lower GDD threshold species, but it really depends on climate variability because high variability means some days you can get accumulate GDDs quickly and that can override the GDD threshold trends.
 - (c) In reality temperature variance likely changes over the spring so this is pretty tricky!
 - (d) In the future, we need to either use a method that is less reliant on accumulated sums—especially if it is a climatological sum—or we must scrutinize results through the use of mixed models and simulated data as we demonstrate here.



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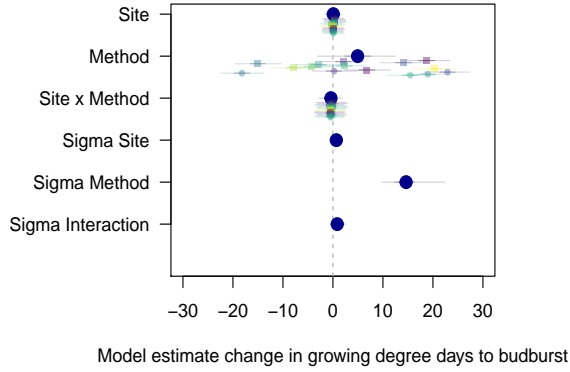
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Tables and Figures

(a)



(b)

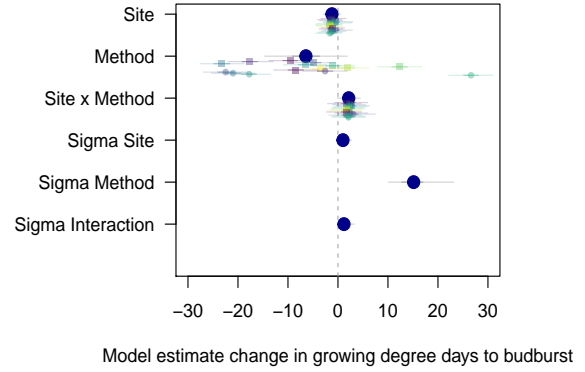
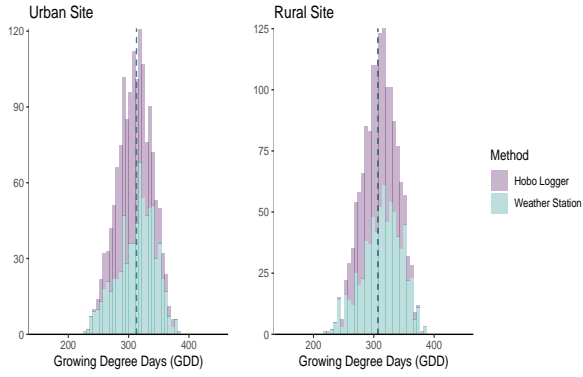


Figure 1: We show effects of site (urban site as ‘1’ or rural site as ‘0’) and climate data method (weather station data as ‘1’ or hobo logger data as ‘0’) on simulated growing degree days (GDDs) until budburst using simulated data (a) with less accurate weather station data and (b) with less accurate hobo logger data. More positive values indicate more GDDs are required for budburst whereas more negative values suggest fewer GDDs are required. Dots and lines show means and 90% uncertainty intervals and thick lines show 50% uncertainty intervals. See Tables S1 and S2 for full model outputs.

(a)



(b)

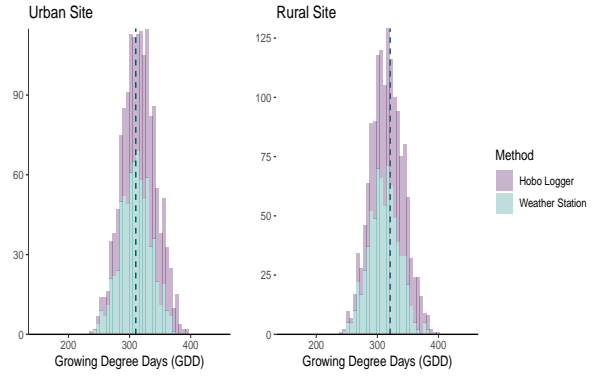
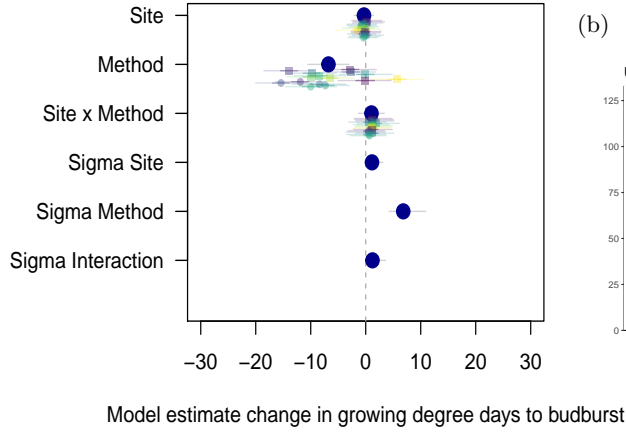


Figure 2: Using simulated data with (a) less accurate weather station data and (b) less accurate hobo logger data, we show histograms of climate data at the urban site and rural site using weather station data and hobo logger data.

(a)



(b)

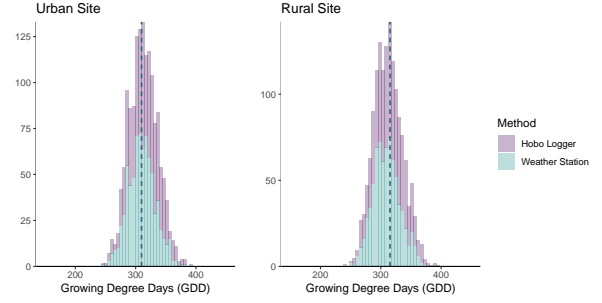


Figure 3: Using simulations data with microclimatic effects at both sites, we show (a) the effects of site (urban site is ‘1’ and rural site is ‘0’) and climate data method (weather station data as ‘1’ or hobo logger data as ‘0’) on simulated growing degree days (GDDs) until budburst using noisy weather station data. More positive values indicate more GDDs are required for budburst whereas more negative values suggest fewer GDDs are required. Dots and thin lines show means and 90% uncertainty intervals and thick lines show 50% uncertainty intervals. See Table S3 for full model output. We also show (b) histograms of GDDs at the urban site and rural site using weather station data and hobo logger data.

(a)

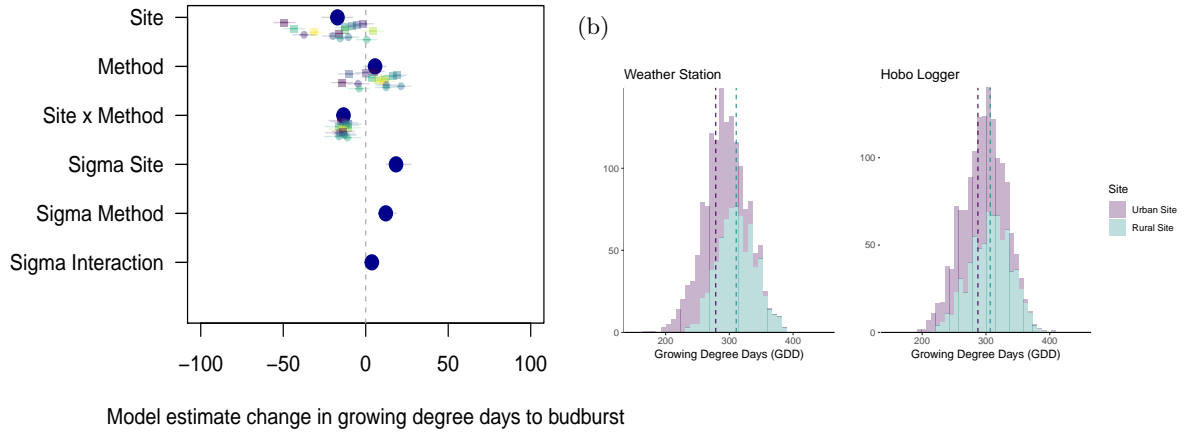
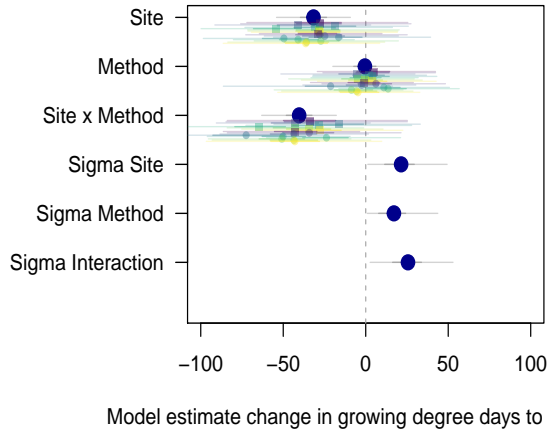


Figure 4: Using simulated data with the urban site hobo loggers recording warmer temperatures and the rural site weather station recording warmer temperatures, we show (a) the effects of site (urban site is ‘1’ and rural site is ‘0’) and climate data method (weather station data as ‘1’ or hobo logger data as ‘0’) on simulated growing degree days (GDDs) until budburst using noisy weather station data. More positive values indicate more GDDs are required for budburst whereas more negative values suggest fewer GDDs are required. Dots and thin lines show means and 90% uncertainty intervals and thick lines show 50% uncertainty intervals. See Table S3 for full model output. We also show (b) histograms of GDDs at the urban site and rural site using weather station data and hobo logger data.

(a)



(b)

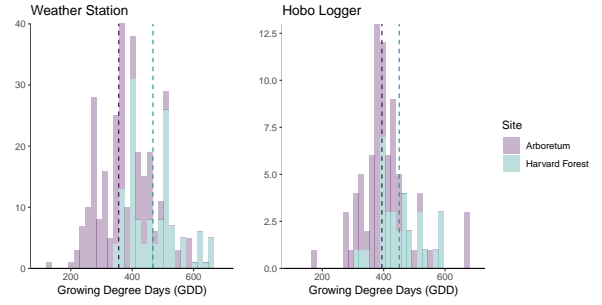
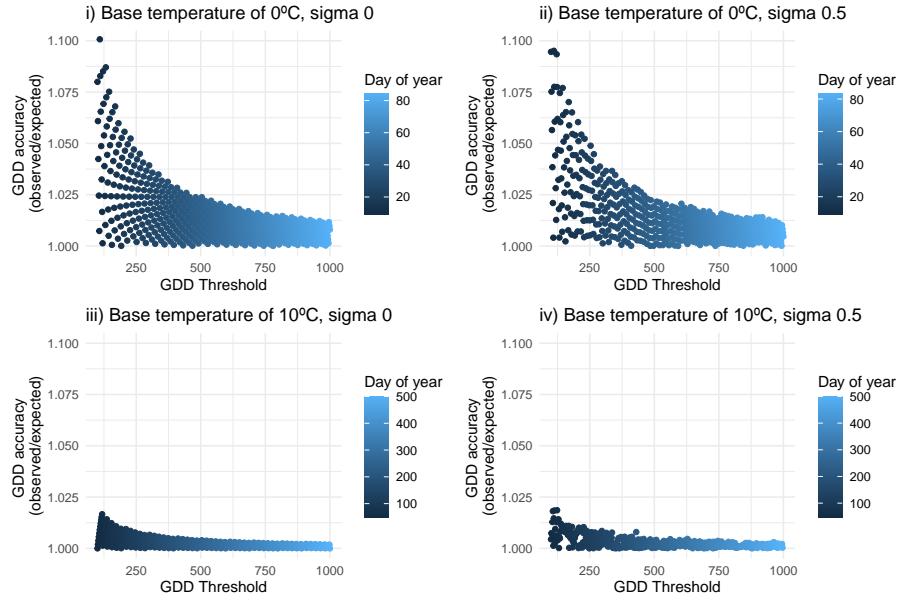


Figure 5: Using real data, we show (a) the effects of site (Arboretum is ‘1’ and Harvard Forest is ‘0’) and climate data method (weather station data as ‘1’ or hobo logger data as ‘0’) on simulated growing degree days (GDDs) until budburst using noisy weather station data. More positive values indicate more GDDs are required for budburst whereas more negative values suggest fewer GDDs are required. Dots and thin lines show means and 90% uncertainty intervals and thick lines show 50% uncertainty intervals. See Table S5 for full model output. We also show (b) histograms of GDDs at the Arboretum and Harvard Forest using weather station data and hobo logger data.

(a)



(b)

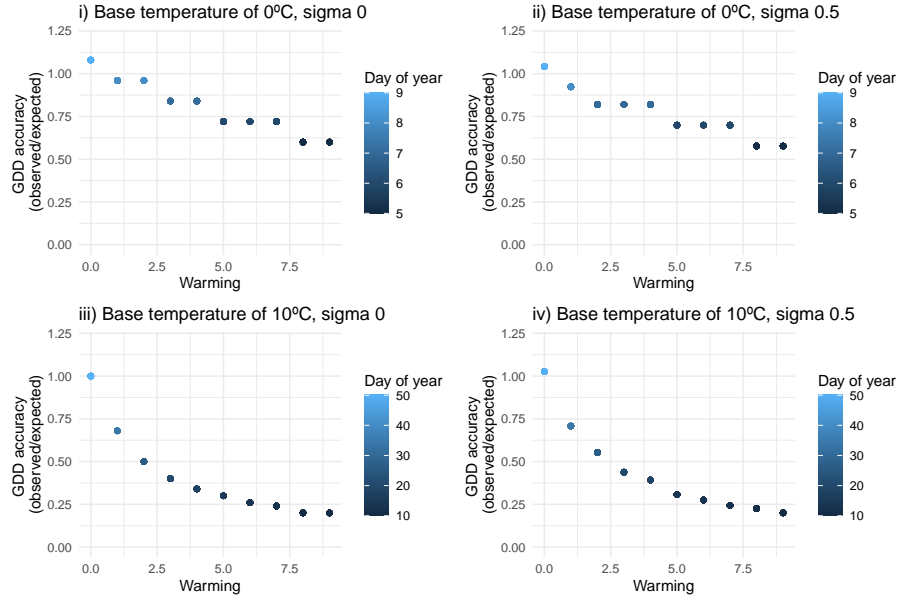


Figure 6: Using simulated data, we show how GDD measurement accuracy changes along (a) varying GDD thresholds and (b) with warming using a base temperature of (i) 0°C and a sigma of 0°C, (ii) 0°C and a sigma of 0.5°C, (iii) 10°C and a sigma of 0°C and (iv) 10°C and a sigma of 0.5°C. GDD accuracy is measured as the observed GDD divided by the expected GDD.