

Understanding growing degree days to predict spring phenology in a warming world

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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 mixed models to answer ecological questions, though we do not always understand the intricacies of the model output, nor do we investigate what is missing from the model output.
 - (b) Here, we work to understand mixed models using simulation data and test myriad hypotheses through these simulations.
 - (c) 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 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 leafout, 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 leafout.
 - (e) Spring leafout 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 leafout 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.
7. Here, we use both simulations, models 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 leafout than forest habitats.
 - (d) Individuals with provenance latitudes from more northern locations require fewer GDDs to leafout.
 - (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 leafout 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) Next, we incorporate climate data by again establishing a random distribution around a mean temperature for each site and then add noise to this weather data to create “microclimatic” effects.
 - (e) Using this climate data, we then find the day of budburst when the unique GDD threshold is reached for each individual.
 - (f) For the following hypothesis testing urban effect, we create simulation data that manipulates the GDD threshold for the urban versus forest sites by lowering the GDD threshold for individuals at the arboretum.
 - (g) Next, we apply the same “microclimatic effect” as above to test microclimatic variation across the two sites.
 - (h) 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 1).

- (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 1).
 - (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., -5°C, 0°C, 5°C and 10°C).

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.
 - (b) The Shiny App is meant for users to understand our suggested approach to model testing and interpreting mixed model results.

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 leafout.
 - (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 4 000 sampling iterations for a total of 6 000 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} (4000 for most parameters, but as low as 1400 for a couple of parameters in the shoot apical meristem model).
 - (f) We additionally assessed chain convergence and posterior predictive checks visually (Gelman *et al.*, 2014).

Results

1. Urban environments require fewer GDDs to leafout than forest habitats.
2. Individuals with provenance latitudes from more northern locations require fewer GDDs to leafout.
3. Hobo loggers are less accurate measures of the same weather as weather stations.
4. Hobo loggers better capture urban or provenance effects.
5. Shiny App
6. Real data

Discussion

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 leafout phenology.
 - (b) 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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Tables and Figures

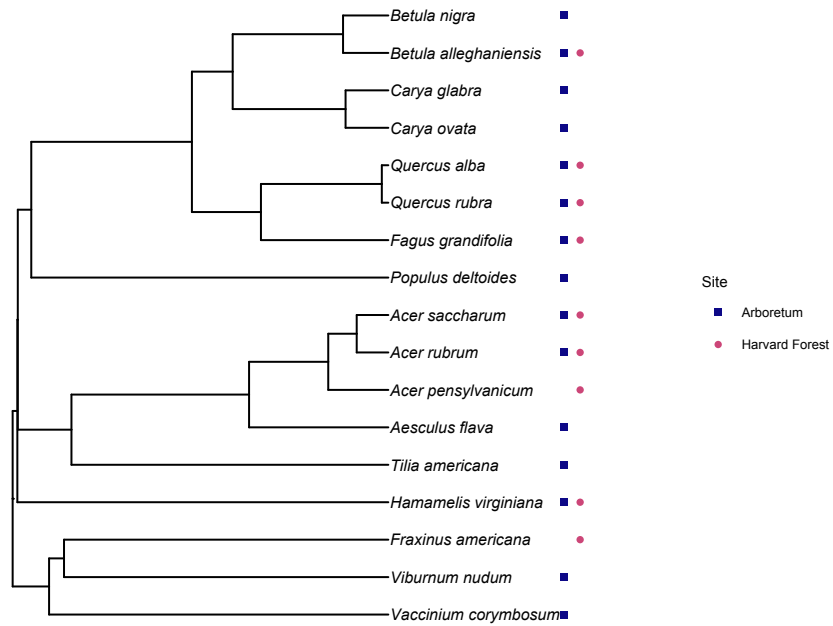


Figure 1: Phylogeny indicating species across the two sites

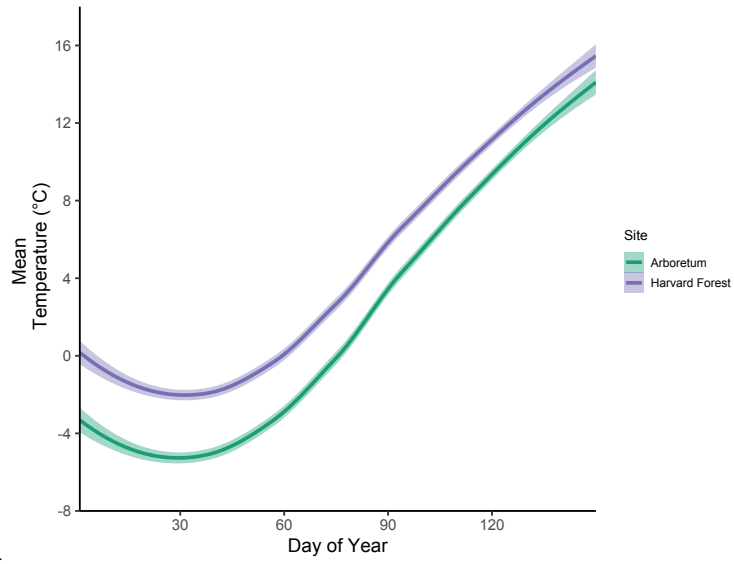


Figure 2: Smoothing spline of mean temperature with 90% credible interval across the two sites.

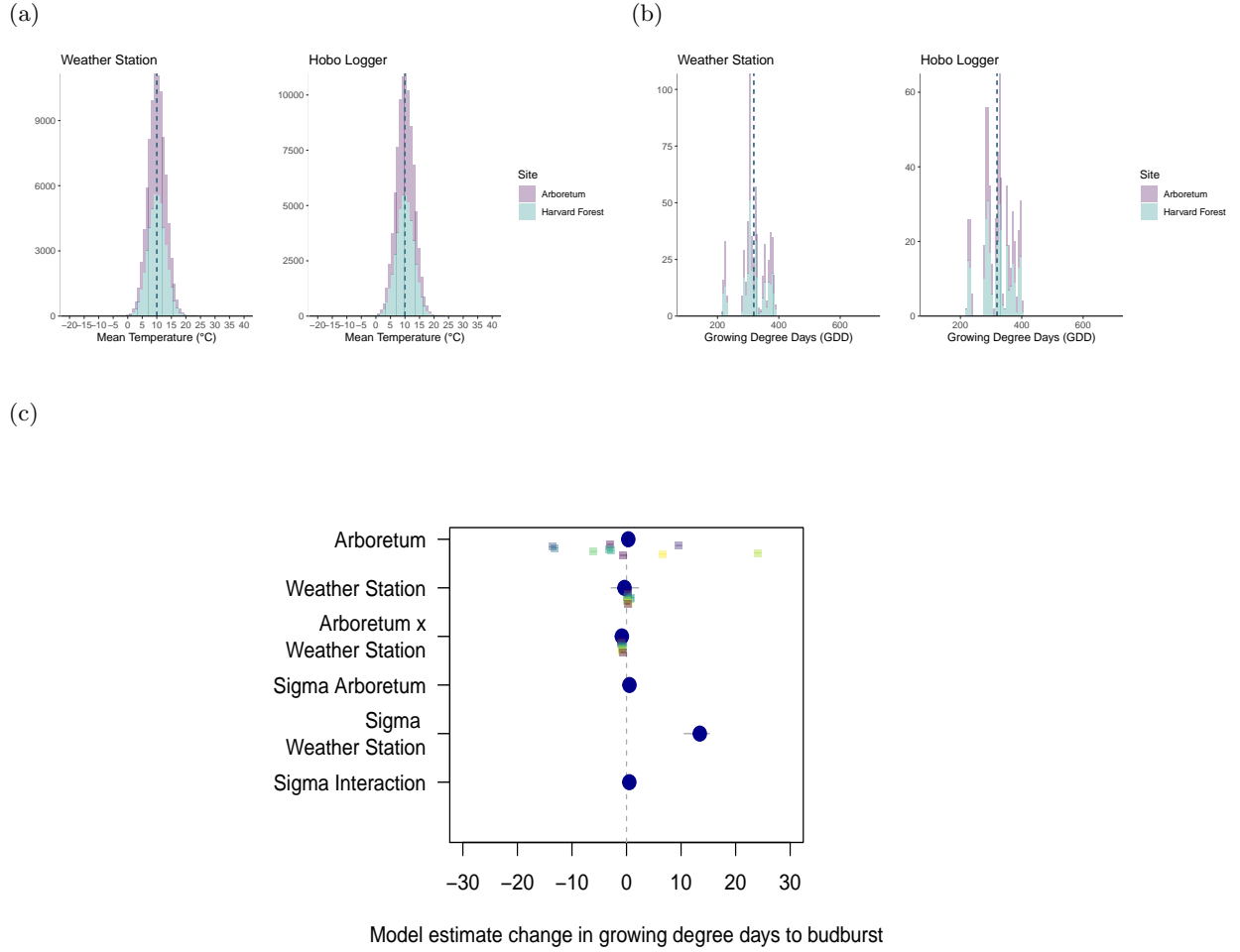


Figure 3: Using simulated data with less accurate weather station data, we show (a) histograms of climate data at the Arboretum and Harvard Forest using weather station data and hobo logger data. (b) Histograms of GDDs at the Arboretum and Harvard Forest using weather station data and hobo logger data. (c) Effects of site (Arboretum as ‘1’ or Harvard Forest 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 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 lines show means and 50% uncertainty intervals. See Table XX for full model output.

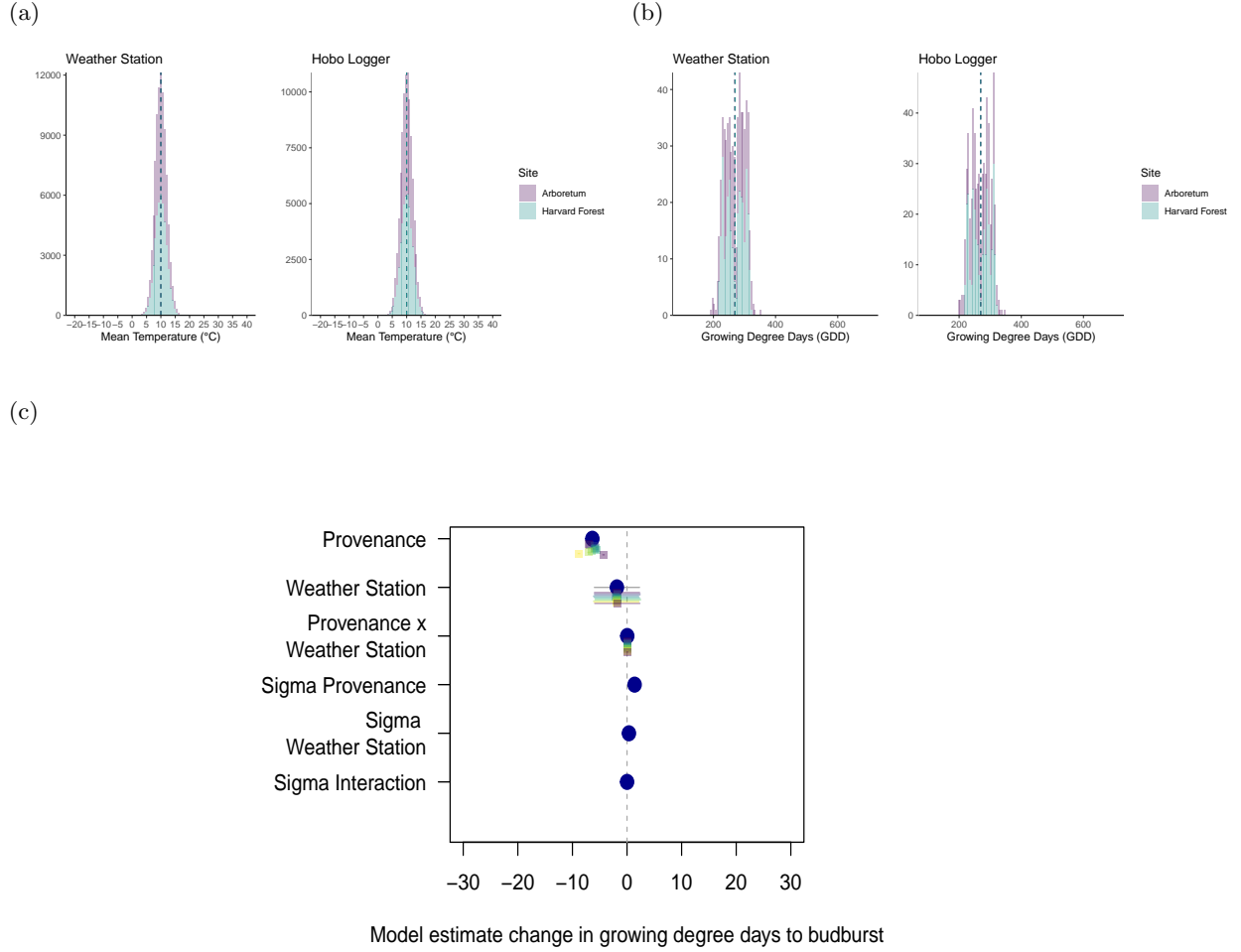


Figure 4: Using simulated data to test provenance latitude, we show (a) histograms of climate data at the Arboretum and Harvard Forest using weather station data and hobo logger data. (b) Histograms of GDDs at the Arboretum and Harvard Forest using weather station data and hobo logger data. (c) Effects of provenance latitude 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 lines show means and 50% uncertainty intervals. See Table XX for full model output.

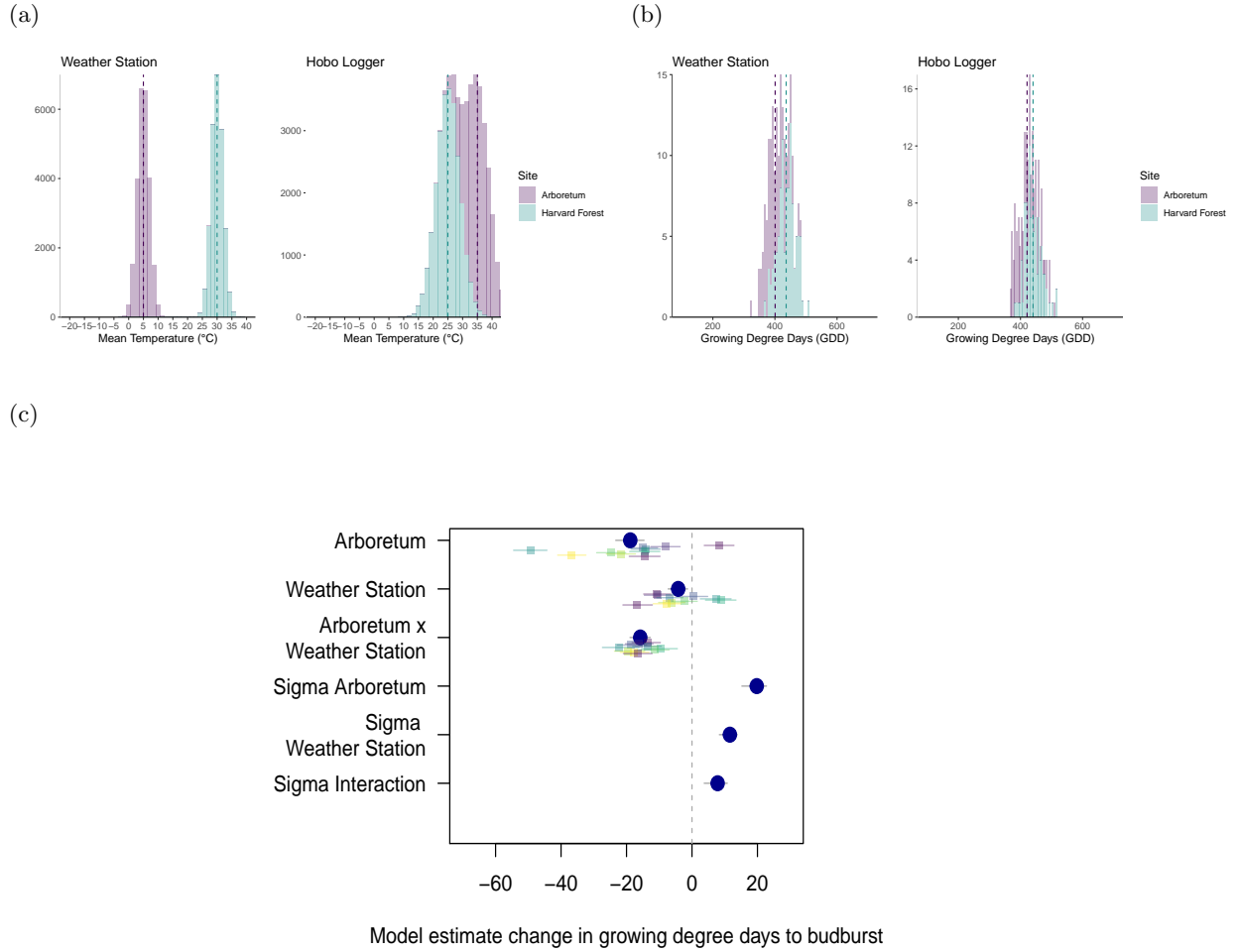


Figure 5: Using simulated data with the Arboretum hobo loggers recording warmer temperatures and the Harvard Forest weather station recording warmer temperatures, we show (a) histograms of climate data at the Arboretum and Harvard Forest using weather station data and hobo logger data. (b) Histograms of GDDs at the Arboretum and Harvard Forest using weather station data and hobo logger data. (c) 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 lines show means and 50% uncertainty intervals. See Table XX for full model output.

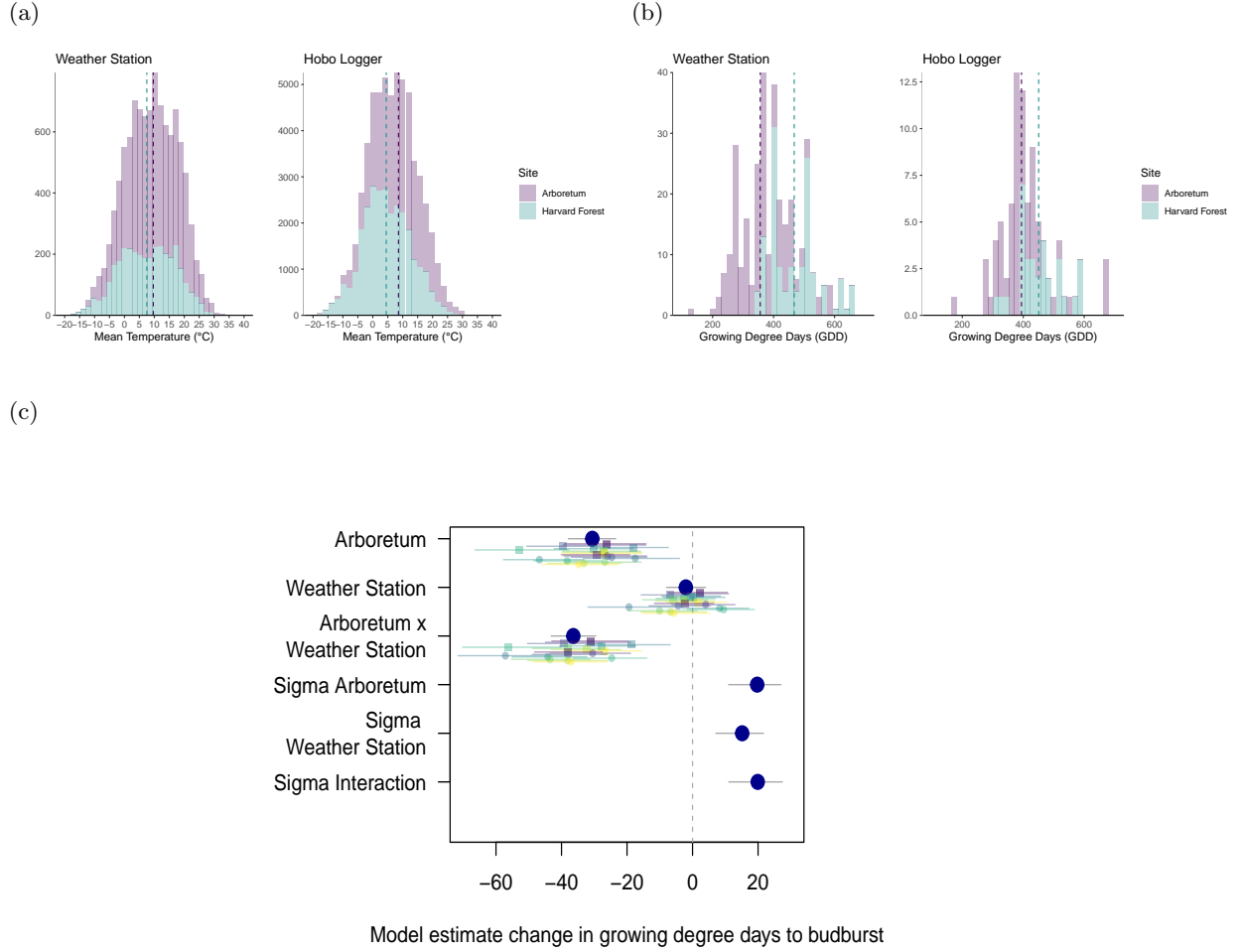


Figure 6: Using real data, we show (a) histograms of climate data at the Arboretum and Harvard Forest using weather station data and hobo logger data. (b) Histograms of GDDs at the Arboretum and Harvard Forest using weather station data and hobo logger data. (c) Effects of site (Arboretum is ‘1’ and 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 lines show means and 50% uncertainty intervals. See Table XX for full model output.