Comparison of large-scale citizen science data and long-term study data for phenology modeling

Shawn D. Taylor[1], Joan M. Meiners[1], Kristina Riemer[2], Michael C. Orr[3], and Ethan P. White[2,4]

[1]School of Natural Resources and Environment, University of Florida Gainesville, FL, United States

[2]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, United States

[3]Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, P.R. China

[4]Informatics Institute, University of Florida, Gainesville, FL, United States

Corresponding author: Shawn D. Taylor - shawntaylor@weecology.org

Abstract

Large-scale observational data from citizen science efforts are becoming increasingly common in ecology, and researchers often choose between these and data from intensive local-scale studies for their analyses. This choice has trade-offs related to spatial scale, observer variance, and inter-annual variability. Here we explored this issue with phenology by comparing models built using data from the large-scale, citizen science USA National Phenology Network (USA-NPN) effort with models built using data from more intensive studies at Long Term Ecological Research (LTER) sites. We built statistical and process based phenology models for species common to each dataset. From these models we compared parameter estimates, estimates of phenological events, and out-of-sample errors between models derived from both USA-NPN and LTER data. We found that model parameter estimates for the same species were most similar between the two datasets when using simple models, but parameter estimates varied widely as model complexity increased. Despite this, estimates for the date of phenological events and out-of-sample errors were similar, regardless of the model. Predictions for USA-NPN data had the lowest error using models built from the USA-NPN data, while LTER predictions were best made using LTER-derived models, confirming that models perform best when applied at the same scale they were built. This difference in the cross-scale model comparison is likely due to variation in phenological requirements within species. Models using the USA-NPN dataset can integrate parameters over a large spatial scale while those using an LTER dataset can only estimate parameters for a single location. Accordingly, the choice of dataset depends on the research question. Inferences about species-specific phenological requirements are best made with LTER data, and if USA-NPN or similar data are all that is available, then analyses should be limited to simple models. Large-scale predictive modeling is best done with the larger-scale USA-NPN data, which has high spatial representation and a large regional species pool. LTER

datasets, on the other hand, have high site fidelity and thus characterize inter-annual variability extremely well. Future research aimed at forecasting phenology events for particular species over larger scales should develop models which integrate the strengths of both datasets.

Keywords: LTER, USA-NPN, forecasting, budburst, flowering, data integration, scale

Introduction

Plant phenology, the timing of recurring biological events such as flowering, plays an important role in ecological research extending from local to global scales (Cleland et al., 2007; Richardson et al., 2013; Tang et al., 2016). At large scales the timing of spring leaf out and fall senescence influence the carbon budget of earth system models, which has implications for correctly accounting for biosphere-atmosphere feedbacks in long-term climate forecasts (Richardson et al., 2012). At smaller scales, species-specific responses to temperature and precipitation can alter flower communities (Diez et al., 2012; CaraDonna et al., 2014; Theobald et al., 2017) and affect the abundance and richness of both pollinators (Ogilvie and Forrest, 2017; Ogilvie et al., 2017) and organisms at higher trophic levels (Tylianakis et al., 2008). Plant phenology models that are robust at multiple ecological scales, or deemed appropriate for a particular scale, are needed to better understand and forecast the timing of key biological events.

Many plant phenology studies use intensively collected datasets from a single location over a long time-period by a single research group (Cook et al., 2012; Wolkovich et al., 2012; Iler et al., 2013; Roberts et al., 2015). These datasets have regular sampling and large numbers of samples over long periods of time. As a result, the biological and climatic variability at that site is well represented. It is common for phenology models built with observations from a single site to not transfer well to other sites (García-Mozo et al., 2008; Xu and Chen, 2013; Olsson and Jönsson, 2014; Basler, 2016). This lack of transferability can be driven by plasticity in phenology requirements, local adaptation, microclimates, or differences in plant age or population density (Kramer, 1995; Diez et al., 2012). For these reasons, data from a single location are not adequate for larger scale phenology modeling. Accurately forecasting phenology at larger scales will require models

that account for the full range of variation across a species' range (Richardson et al., 2013; Tang et al., 2016; Chuine and Régnière, 2017), which will necessitate the use of data sources beyond traditional single-site studies.

Data from citizen science projects are becoming increasingly important for ecological research (Kelling et al., 2009; Dickinson et al., 2010; Tulloch et al., 2013). Because these data are often collected by large numbers of volunteers, it is possible to gather data at much larger scales than with individual research teams. A relatively new citizen science project started in 2009, Nature's Notebook run by The USA National Phenology Network (USA-NPN), collects phenology observations from volunteers throughout the United States and makes the data openly available (Schwartz et al., 2012). Data from this project have already been used to study variation in oak phenology at a continental scale (Gerst et al., 2017), develop large-scale community phenology models (Melaas et al., 2016), and forecast long-term phenology trends (Jeong et al., 2013). Large-scale datasets from China and Europe have already contributed considerably to phenological research (Xu and Chen, 2013; Olsson and Jönsson, 2014; Basler, 2016; Zhang et al., 2017), and the USA-NPN dataset has the potential to meet these needs for North American plant species and communities. However, the features that allow citizen science projects to collect data at large scales can also introduce spatial biases toward cities and easily-accessible areas, and variation in sampling effort and observer skill (Dickinson et al., 2010). With thousands of participants, the potential for variation among observers in their determination of species identification and dating of phenological events is high. While volunteers have been shown to be accurate at distinguishing different leaf and flower stages for plants (Fuccillo et al., 2015) and can have high agreement on abundance estimates (Feldman et al., 2018), contributions to USA-NPN are sometimes made sporadically across seasons, years,

and locations. This means that the quantity and quality of data at a specific site will typically be more variable for citizen science efforts than for intensive, long-term studies.

In order to accurately model and forecast phenology, it is important to understand how the strengths and weaknesses of intensive local studies and large-scale citizen science projects influence both our inferences about biological processes driving phenology (e.g. warming requirements for a specific plant) and our ability to predict future phenology events (e.g. forecasting when flowering or leaf out occurs). Here, we fit a suite of plant phenology models for the budburst and first-flowering phenophases of 24 plant species to data from both the USA-NPN and a set of intensive long-term studies from the Long Term Ecological Research (LTER) network. We compare the resulting models based on both inference about models and parameters and predictions for unobserved events. We then use this comparison to assess the best methods for both local- and large-scale phenology modeling and to point the way forward for integrating large-scale and local-scale data to determine the best possible models across scales.

Methods

Datasets

The USA National Phenology Network (USA-NPN) protocol uses status-based monitoring, where via a phone app or web based interface observers answer 'yes,' 'no,' or 'unsure' when asked if an individual plant has a specific phenophase present (Denny et al., 2014). Phenophases refer to specific phases in the annual cycle of a plant, such as the presence of emerging leaves, flowers,

fruit, or senescing leaves. Sites in the USA-NPN datasets are located across the U.S. and generally clustered around populated areas (Figure 1). To represent long-term, intensive phenology studies we used four datasets from North America representing three major ecosystem types (Table 1, Figure 1). All four long-term studies are located in the U.S. and are part of the Long Term Ecological Research network (LTER). The Harvard Forest and Hubbard Brook Long Term Experimental Forest are located in the northeastern U.S. and are dominated by deciduous broadleaf species. The H.J. Andrews Experimental Forest is a coniferous forest in the coastal range of the western U.S. The Jornada Experimental Range is in the Chihuahua desert of the southwestern U.S.

We downloaded all USA-NPN observations from 2009, when collections began, to 2016 for the following phenophases: Breaking Leaf Buds, Breaking Needle Buds, Emerging Needles, and Open Flowers (USA National Phenology Network, 2017). The first three phenophases apply to the 'leaf out' phase for deciduous broadleafs, evergreen conifers, and pines, respectively. The 'Open Flowers' phenophase refers to fully-open flowers and applies to all angiosperms. Hereafter, we will refer to these as either 'Flowers' for the Open Flower phenophase, or 'Budburst' for all other phenophases. We subset the USA-NPN observations similar to methods outlined in Crimmins et al. (2017). First, 'yes' observations for individual plants were kept only if they were preceded by a 'no' observation within 30 days. Observations for 'Budburst' that were past day of year (DOY) 172, and for 'Flowers' that were past DOY 213 were dropped to minimize any influence from outliers. We inferred the observed DOY of each phenophase as the midpoint between each 'yes' observation and the preceding 'no' observation. Finally, only species that had greater than 30 total observations were kept. Crimmins et al. (2017) only kept observations that were preceded by a 'no' within 15 days, and also grouped multiple individuals at single sites to a single observation. We

used 30 days to allow for a greater number of species to be compared. We tested the sensitivity of this choice by also performing the analysis using a 15 day cutoff. We chose not to group multiple individuals at a single site to better incorporate intra-site variability.

In the LTER datasets observation metrics varied widely due to different protocols. To match the USA-NPN data we converted all metrics to binary 'yes' and 'no' observations for each phenophase (see Appendix S1 for details). Three of the LTER datasets (Hubbard Brook, Harvard Forest, and H.J. Andrews) had a sampling frequency of 3-7 days during the growing season. The Jornada dataset had a sampling frequency of 30 days. As with the USA-NPN data, we inferred the date for each phenophase as the midpoint between the first 'yes' observation and most recent 'no' observation, and only kept species and phenophase combinations which had at least 30 total observations. After data processing there were 38 species and phenophase combinations (with 24 unique species) common to both the USA-NPN and LTER datasets to use in the analysis (Table 1 & Appendix S2: Table S1). Using a 15 day cutoff in the USA-NPN dataset resulted in 35 unique combinations with 23 species.

Models

It is common to fit multiple plant phenology models to find the one that best represents a specific species and phenophase (Chuine et al., 2013). For each of the 38 species and phenophase combinations in the five datasets (USA-NPN and four LTER datasets), we fit eight phenology models (Table 2). The *Naive model* uses the mean DOY from prior observations as the estimated DOY. The *Linear model* uses a regression with the mean spring (Jan. 1 - March 31) temperature as the independent variable and DOY as the response variable. For the six remaining models, the general

147 form is based on the idea that a phenological event will occur once sufficient thermal forcing units,
148 F^*, accumulate from a particular start day of the year (t_1). Forcing units are a transformation of
149 the daily mean temperature and are calculated differently for each model (Table 2). The start day
150 can either be estimated or fixed. For the *Growing Degree Day (GDD)* model, forcing units are
151 the total degrees above the threshold T_{base} (Réaumur, 1735; Wang, 1960; Hunter and Lechowicz,
152 1992). The *Fixed GDD model* uses the same form but has fixed values for start day (t_1 = Jan 1)
153 and temperature threshold (T_{base} = 0°C). The *Alternating model* has a variable number of required
154 forcing units defined as a function of the total number of days below 0°C since Jan. 1 (number of
155 chill days - *NCD*). The *Uniforc model* is like the *GDD model* but with the forcing units transformed
156 via a sigmoid function (Chuine, 2000).

157 We also fit two models that attempt to capture spatial variation in phenological requirements. The
158 first spatial model, *M1*, is an extension of the *GDD model* which adds a correction in the required
159 forcing using the photoperiod (L) (Blümel and Chmielewski, 2012). The second, the *Macroscale*
160 *Species-specific Budburst model (MSB)*, uses the mean spring temperature as a linear correction
161 on the total forcing required in the *Alternating model* (Jeong et al., 2013). Since there is little to
162 no spatial variation in the LTER datasets, we fit the two spatial models to data from the USA-NPN
163 only. We compared the resulting parameters, estimates, and errors for the USA-NPN derived *M1*
164 and *MSB* models to their non-spatial analogs (the *GDD* and *Alternating models*, respectively) for
165 each species and phenophase in the LTER data.

166 We extracted corresponding daily mean temperature for all USA-NPN and LTER observations
167 from the gridded PRISM dataset using the latitude and longitude of the site associated with each
168 observation (PRISM Climate Group, 2004). We parameterized all models using differential evo-

lution to minimize the root mean square error (RMSE) of the estimated DOY of the phenological event. Differential evolution is a global optimization algorithm which uses a population of randomly initialized models to find the set of parameters that minimize the RMSE (Storn and Price, 1997). Confidence intervals for parameters were obtained by bootstrapping, in which individual models were re-fit 250 times using a random sample, with replacement, of the data. We made predictions by taking the mean DOY estimated from the 250 bootstrapped iterations. A random subset consisting of 20% of observations from each species and phenophase combination was held out from model fitting for later evaluation.

Analysis

As described above, we fit two sets of models for each species and phenophase: one set of models parameterized using only USA-NPN data, and one set parameterized using only LTER data (with the exception of the *M1* and *MSB* models, see above). We performed three primary analyses from these model outputs by comparing: 1) the model parameters, 2) estimates from the models, and 3) out-of-sample errors from each model.

To compare the inferences about process made by the two datasets, we compared the distribution of each parameter between LTER and USA-NPN derived models for each species and phenophase combination. Using the mean value of each bootstrapped parameter, we also calculated the coefficient of determination (R^2) between LTER and USA-NPN derived models among the 38 species-phenophases. In three cases where a species phenophase combination occurred in two LTER sites (Budburst for *Acer saccharum*, *Betula alleghaniensis*, and *Fagus grandifolia* in the Harvard and Hubbard Brook datasets) they were compared separately to the USA-NPN data.

Next we compared the estimates of phenological events between models. Models with different parameter values, and even entirely different structures, can produce similar estimates for the date of phenological events (Basler, 2016). Therefore, to compare the predictions and potential forecasts for models fit to the different datasets, we compared the estimated DOY predicted by the LTER and USA-NPN derived models for all held out observations. For each of the eight models, we calculated the coefficient of determination (R^2) between LTER and USA-NPN derived estimates for estimates made at the four LTER sites and across all USA-NPN sites.

Finally, we directly evaluated performance using out-of-sample errors from the four combinations of models and observed data: A) LTER-derived models predicting LTER observations, B) USA-NPN derived models predicting LTER observations, C) LTER-derived models predicting USA-NPN observations, and D) USA-NPN derived models predicting USA-NPN observations. Using the RMSE values from held out observations, we compared the performance of LTER and USA-NPN derived models on different data types in two different ways. First, we focused on local-scale prediction by calculating the difference in the RMSE of LTER and USA-NPN derived models solely with LTER observations. Secondly, to focus on large-scale prediction we calculated the difference in RMSE using solely USA-NPN data. These differences were calculated for each of the model types and 38 species-phenophase combinations. Negative values indicate that LTER-derived models perform better, while positive values indicate that the USA-NPN derived model performed better. We used a t-test to test the difference from zero in these values. In the three cases where the same species and phenophase combination occurred in two LTER sites, we made the LTER-LTER comparison within each site, not across sites, to focus on local scale prediction when LTER data are available. Absolute RMSE values as well as Pearson correlation coefficients

are provided in the supplement for specific species (Appendix S2: Figure S5-S7) and with all observations aggregated together (Appendix S2: Table S2).

We performed all analysis using both the R and Python programming languages (R Core Team, 2017; Python Software Foundation, 2018). Primary R packages used in the analysis included dplyr (Wickham et al., 2017), tidyr (Wickham and Henry, 2018), ggplot2 (Wickham, 2016), lubridate (Grolemund and Wickham, 2011), prism (Hart and Bell, 2015), raster (Hijmans, 2017), and sp (Pebesma and Bivand, 2005). Primary Python packages included SciPy (Jones et al., 2001), NumPy (Oliphant, 2006), Pandas (McKinney, 2010), and MPI for Python (Dalcin et al., 2011). Code to fully reproduce this analysis is available on GitHub (https://github.com/sdtaylor/phenology_dataset_study) and archived on Zenodo (https://doi.org/10.5281/zenodo.1256705)

Results

Throughout the analysis there were no qualitative differences between a 30-day or 15-day threshold between the first 'yes' and most recent 'no' observation in the USA-NPN dataset. Results presented here reflect the 30 day cutoff; see the supplementary figures S2-S4 in Appendix S2 for matching figures using a 15 day cutoff.

The best matches between parameter estimates based on USA-NPN and LTER data were the *Fixed GDD model* (R^2 = 0.49) and the *Linear model* (R^2 = 0.39 for β_1 and -0.05 for β_2). The parameters for all other models had R^2 values <0 indicating that the relationship was worse than no relationship between the parameters (but with matching mean parameter values across the two sets of models) (Figure 2). The *Naive model* showed a distinct late bias in mean DOY estimates for

phenological events, likely resulting from the LTER datasets being mostly in the northern United States compared to the site locations of the USA-NPN dataset (Figure 2). The large outlier for the *Fixed GDD model* is *Larrea tridentata*; this species' flower phenology is largely driven by precipitation, which is not considered in the Fixed GDD model (Beatley, 1974). While the *Fixed GDD* and *Linear* models showed reasonable correspondence between parameter estimates, all parameters for individual species and phenophase combinations had different distributions between USA-NPN and LTER-derived models (Appendix S2: Figure S10-S11).

When comparing estimates of phenological events between the two sets of models, many USA-NPN and LTER models produced similar estimates (Figure 3). The *Fixed GDD model* had the highest correlation between the two model sets at USA-NPN sites ($R^2 = 0.82$), while the *GDD*, *M1*, and *Uniforc* models had the highest correlation at LTER sites ($R^2 = 0.51$, 0.52, and 0.51, respectively). Comparing models with spatial corrections to the non-spatial alternatives, the *MSB* (an extension of the *Alternating model* with a spatial correction based on mean spring temperature, see Table 2 and Methods) improved the correlation between the two datasets over the *Alternating model*. The *MSB model* improved the R^2 from 0.36 to 0.45 at LTER sites, and from -0.23 to -0.15 at USA-NPN sites. The *M1 model* (an extension of the *GDD model* with a spatial correction based on day length) improved the correlation over the *GDD model* only slightly at LTER sites (from 0.51 to 0.52) and did not improve the correlation at USA-NPN sites.

When comparing the predictive performance using out-of-sample errors, USA-NPN derived models made more accurate predictions for held-out USA-NPN observations, and LTER-derived models performed better on held-out LTER observations (all $p < 0.001$, Figure 4). The *Naive* and *Linear* models had the largest differences between the two model sets, while the *Fixed GDD model*

had relatively similar errors when evaluated on both USA-NPN and LTER held-out observations. Although the *Fixed GDD model* had the highest agreement in accuracy between USA-NPN and LTER-derived models, it was not the best performing model overall. The *GDD* and *Uniforc* models made the best out of sample predictions, having the lowest RMSE and Pearson coefficient when aggregating all observations together (Appendix S2: Table S2). One exception was that the Fixed GDD model had a slightly higher Pearson value when using LTER-derived models to make predictions for USA-NPN data. The best model for specific species and phenophases varied, but was commonly the *Uniforc* or *GDD* models (Appendix S2: Figs. S5-S6).

Discussion

Data used to build phenology models typically fall into two categories: intensive long-term data with long time-series at a small number of locations (e.g., LTER data in this study), and large-scale data with less intensive sampling at hundreds of locations (e.g., USA-NPN data) (Table 3). This data scenario–a small amount of intensive data and a large amount of less intensive data–is common in many areas of science and makes it necessary to understand how to choose between, or combine, data sources (Hanks et al., 2011). We explored this issue for phenology modeling in relation to making predictions and inferring process from models. For inference we found that models based on different data sources resulted in different parameter estimates for all but the simplest models. For prediction we found that models fit to different data sources tended to make similar predictions, but that models better predicted out-of-sample data from the data type to which they were fit. These results are consistent with other research showing that phenology model

performance decreases when transferring single-site models to other locations (García-Mozo et al., 2008; Xu and Chen, 2013; Basler, 2016), and with the call for models that better incorporate spatial variation in phenology requirements (Richardson et al., 2013; Chuine and Régnière, 2017). Understanding and making predictions for the phenology of a single location is best served by intensive local-scale data, when available, but large-scale datasets work better for extrapolating phenology predictions across a species range. Thus, the best choice of both data and models depends on the desired research goals.

In this study, parameter estimates differed widely within the same phenology model when fit to the two different types of data, except for the simplest process-oriented model: the *Fixed GDD* (Figure 2). These differences may be caused by a variety of factors that have different implications for interpreting process-oriented models and their parameters. First, the differences could result from limitations in the sampling of the USA-NPN dataset, such as irregular sampling of the same location within or between seasons, leading to less accurate parameter estimates. If this is the case, it would suggest that using LTER data is ideal for making inferences about plant physiology, and that focusing on the *Fixed GDD model* is best for making inferences when USA-NPN data are all that is available. Second, spatial variation (e.g. from local adaptation, acclimation, microclimates, or plant age) in phenology requirements and drivers could contribute to these differences (Diez et al., 2012; Zhang et al., 2017). Models built using USA-NPN data integrate over that spatial variation, while models built using LTER data only estimate the phenological requirements for a specific site. In this case, USA-NPN data would provide a better estimate of the general phenological requirements of a species, but LTER data would provide a more accurate understanding for a single site. The best solution to this issue would be the development of models that accurately incorporate

spatial variation, such as including genetic variation between different populations (Chuine and Régnière, 2017), although localized models could also be generated when large-scale predictions are unnecessary. Third, these differences could result from issues with model identifiability: since different parameter values can yield nearly identical estimates of phenological events, parameter estimates can differ between datasets even when the underlying processes generating the data are the same. Information about which of these issues may be causing the differences between datasets can be explored using the analyses in the current study, as will be explained below.

Despite substantial differences in parameter estimates, LTER and USA-NPN derived models produced similar estimates for phenological events in most cases (Figure 3). This greater correspondence between predictions than parameters suggests that more complex models may have identifiability issues. For example, two *GDD* models with parameters of t_1=1, F=10, T_{base}=0 and t_1=5, F=5, T_{base}=0 produce nearly identical estimates in many scenarios. This possibility is supported by the fact that the highest correlation between parameter estimates is seen in models with only 1 or 2 parameters. In addition, bootstrap results for more complex models suggest a high degree of variability in parameter estimates and potentially multiple local optima in fits to both USA-NPN and LTER data (Appendix S2: Figure S10-S11). Finally, parameter estimates of more complex models are also not consistent among models for the same species when comparing multiple LTER datasets (Appendix S2: Figure S8-S9). These results are consistent with research showing that models failed to estimate the starting day of warming accumulation solely from budbreak time-series, thus producing parameter estimates that were not biologically realistic (Chuine et al., 2016). Basler (2016) suggests that the key component in phenology models is the thermal forcing, with additional parameters being sensitive to over-fitting. Here, our simplest model, the

Fixed GDD model which uses only a warming component, had the highest correlation among parameters between LTER and USA-NPN datasets. In combination with the aforementioned studies, our results indicate that caution is warranted in interpreting parameter estimates from complex phenology models regardless of the data source used for fitting the models.

While more complex phenology models appear to have identifiability issues, there is also evidence that they capture useful information, beyond the *Fixed GDD model*, based on their ability to make out-of-sample predictions. Based on the RMSE, the *GDD* and *Uniforc* models produce the best out-of-sample predictions for the majority of species and phenophases at both USA-NPN and LTER datasets (Appendix S2: Figure S5 & S6). This demonstrates that the more complex models are capturing additional information about phenology, and that some of the differences between datasets result from differences in either the scales or the sampling of the data. Spatial variation in phenological requirements is known to exist in plants (Zhang et al., 2017). In combination with our results showing observed differences in parameter estimates between LTER sites (Appendix S2: Figure S8-S9), this suggests that variation in phenological requirements across the range is likely important. However, the models that attempted to address this by incorporating spatial variation did not yield improvements over their base models in our analyses. Specifically, correspondence between parameter estimates (Figure 2), estimates of phenological events (Figure 3), and out-of-sample error rates (Figure 4) for the *MSB* and *M1* models were essentially the same as the *Alternating* and *GDD* models, respectively. This lack of improvement from incorporating spatial variation could be caused either by models not adequately capturing the process driving the spatial variation, the USA-NPN dataset having biases from variation in sampling effort and/or spatial auto-correlation, or some combination of these factors. Basler (2016) used the *M1* model to predict

budburst for six species across Europe and found it was generally among the best models in terms of RMSE, albeit never by more than a single day. Their result was strengthened by having a 40-year time-series across a large region. Chuine and Régnière (2017) listed the incorporation of spatial variation in warming requirements in models as a primary issue in future phenology research. Large-scale phenology datasets, like USA-NPN, will be key in addressing this and other phenological research needs.

In addition to exploring differences between phenology datasets, our analyses provide guidance on which models to use when making predictions at a local scale using models built from large-scale data, or vice versa. Among the eight models tested, the *Uniforc* and *GDD* models performed the best overall in the cross dataset comparison in terms of Pearson correlation and RMSE (Appendix S2: Figure S5-S6, Table S2). The *GDD* model has one less parameter than the *Uniforc* model, thus the *GDD* model is a suitable choice for making predictions when there is little to no information at the location of interest (e.g. making phenology forecasts at a new location distant from any observed data). This guidance can vary between species, though, and model testing should still be performed when suitable data are available.

In conclusion, our results suggest that both LTER and USA-NPN data provide valuable information on plant phenology. Models built using both data sources yield effective predictions for phenological events, but parameter estimates from the two data sources differ and models from each source best predict that data source's phenology events. The primary difference in the datasets is spatial scale, but due to trade-offs in data collection efforts, the larger scale USA-NPN data have shorter time-series, less site fidelity and other differences from the intensively collected LTER data (Table 3). These differences can be strengths or potential limitations. Observers sampling opportunisti-

cally allows the USA-NPN dataset to have a large spatial scale, but also leads to low site fidelity, which limits the ability to measure long-term trends at local scales (Gerst et al., 2016). Tracking long-term trends is the major strength of LTER data, but having a relatively small species pool limits their use in species-level predictive modeling. Due to these differences, the best data source for making predictions depends on the scale at which the predictions are being made. Identifying the most effective data sources for different types and scales of analysis is a useful first step, but the ultimate solution to working with diverse data types is to focus on integrating all types of data into analyses and forecasts (Hanks et al., 2011; Melaas et al., 2016). Our results suggest that methods that can learn from the intensive information available in LTER data in regions where they are available, and simultaneously use large-scale data to capture spatial variation in phenological requirements will help improve our ability to understand and predict phenology. Data integration efforts should also leverage data from remote sensing sources such as the PHENOCAM network or satellite imagery, which have both a large spatial extent and high temporal resolution (Peng et al., 2017; Richardson et al., 2018a,b). Data integration provides the potential to use data from many sources to produce the best opportunity for accurate inference about, and forecasting of, the timing of biological events.

Acknowledgments

This research was supported by the Gordon and Betty Moore Foundation's Data-Driven Discovery Initiative through Grant GBMF4563 to E.P. White. J.M. Meiners was supported by the University of Florida Biodiversity Institute Graduate Research Fellowship. We thank the developers and

providers of the data that made this research possible including: the USA National Phenology Network and the many participants who contribute to its Nature's Notebook program; the H.J. Andrews Experimental Forest research program, funded by the National Science Foundation's (NSF) LTER Program (DEB-1440409), US Forest Service Pacific Northwest Research Station, and Oregon State University; the Jornada Basin LTER project (NSF Grant DEB-1235828); the Hubbard Brook Experimental Forest, which is operated and maintained by the USDA Forest Service, Northern Research Station, Newtown Square, PA.; the Harvard Forest LTER; and the PRISM Climate Group at Oregon State University.

References

Bailey, A. (2018). Hubbard brook experimental forest (us forest service): Routine seasonal phenology measurements, 1989 - present. environmental data initiative. https://doi.org/10.6073/pasta/765084e2b4a5ec389403238c58784572.

Basler, D. (2016). Evaluating phenological models for the prediction of leaf-out dates in six temperate tree species across central europe. *Agricultural and Forest Meteorology*, 217:10–21.

Beatley, J. C. (1974). Effects of rainfall and temperature on the distribution and behavior of larrea tridentata (creosote-bush) in the mojave desert of nevada. *Ecology*, 55(2):245–261.

Blümel, K. and Chmielewski, F. M. (2012). Shortcomings of classical phenological forcing models and a way to overcome them. *Agricultural and Forest Meteorology*, 164:10–19.

Cannell, M. G. R. and Smith, R. I. (1983). Thermal time, chill days and prediction of budburst in picea sitchensis. *The Journal of Applied Ecology*, 20(3):951.

CaraDonna, P. J., Iler, A. M., and Inouye, D. W. (2014). Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences*, 111(13):4916–4921.

Chuine, I. (2000). A unified model for budburst of trees. *Journal of Theoretical Biology*, 207(3):337–347.

Chuine, I., Bonhomme, M., Legave, J. M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A., and Améglio, T. (2016). Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. *Global Change Biology*, 22(10):3444–3460.

Chuine, I., de Cortazar-Atauri, I. G., Kramer, K., and Hänninen, H. (2013). Plant development models. In Schwartz, M. D., editor, *Phenology: An Integrative Environmental Science*, pages 275–293. Springer Netherlands, Dordrecht.

Chuine, I. and Régnière, J. (2017). Process-Based Models of Phenology for Plants and Animals. *Annual Review of Ecology, Evolution, and Systematics*, 48(1):159–182.

Cleland, E., Chuine, I., Menzel, A., Mooney, H., and Schwartz, M. (2007). Shifting plant phenology in response to global change. *Trends in Ecology Evolution*, 22(7):357–365.

Cook, B. I., Wolkovich, E. M., and Parmesan, C. (2012). Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences*, 109(23):9000–9005.

Crimmins, T. M., Crimmins, M. A., Gerst, K. L., Rosemartin, A. H., and Weltzin, J. F. (2017).

Usa national phenology network's volunteer-contributed observations yield predictive models of phenological transitions. *PLOS ONE*, 12(8):e0182919.

Dalcin, L. D., Paz, R. R., Kler, P. A., and Cosimo, A. (2011). Parallel distributed computing using python. *Advances in Water Resources*, 34(9):1124–1139.

Denny, E. G., Gerst, K. L., Miller-Rushing, A. J., Tierney, G. L., Crimmins, T. M., Enquist, C. A. F., Guertin, P., Rosemartin, A. H., Schwartz, M. D., Thomas, K. A., and Weltzin, J. F. (2014). Standardized phenology monitoring methods to track plant and animal activity for science and resource management applications. *International Journal of Biometeorology*, 58(4):591–601.

Dickinson, J., Zuckerberg, B., and Bonter, D. (2010). Citizen science as an ecological research tool: Challenges and benefits. *Annual Review of Ecology, Evolution and Systematics*, 41(1):149–172.

Diez, J. M., Ibáñez, I., Miller-Rushing, A. J., Mazer, S. J., Crimmins, T. M., Crimmins, M. A., Bertelsen, C. D., and Inouye, D. W. (2012). Forecasting phenology: from species variability to community patterns. *Ecology Letters*, 15(6):545–553.

Feldman, R. E., Žemaitė, I., and Miller-Rushing, A. J. (2018). How training citizen scientists affects the accuracy and precision of phenological data. *International Journal of Biometeorology*, 62(8):1421–1435.

Fuccillo, K. K., Crimmins, T. M., de Rivera, C. E., and Elder, T. S. (2015). Assessing accuracy in citizen science-based plant phenology monitoring. *International Journal of Biometeorology*, 59(7):917–926.

García-Mozo, H., Chuine, I., Aira, M., Belmonte, J., Bermejo, D., Díaz de la Guardia, C., Elvira,

443 B., Gutiérrez, M., Rodríguez-Rajo, J., Ruiz, L., Trigo, M., Tormo, R., Valencia, R., and Galán,
444 C. (2008). Regional phenological models for forecasting the start and peak of the quercus pollen
445 season in spain. *Agricultural and Forest Meteorology*, 148(3):372–380.

446 Gerst, K. L., Kellermann, J. L., Enquist, C. A. F., Rosemartin, A. H., and Denny, E. G. (2016).
447 Estimating the onset of spring from a complex phenology database: trade-offs across geographic
448 scales. *International Journal of Biometeorology*, 60(3):391–400.

449 Gerst, K. L., Rossington, N. L., and Mazer, S. J. (2017). Phenological responsiveness to climate
450 differs among four species of quercus in north america. *Journal of Ecology*, 38(1):42–49.

451 Grolemund, G. and Wickham, H. (2011). Dates and times made easy with lubridate. *Journal of*
452 *Statistical Software*, 40(3):1–25.

453 Hanks, E. M., Hooten, M. B., and Baker, F. A. (2011). Reconciling multiple data sources to
454 improve accuracy of large-scale prediction of forest disease incidence. *Ecological Applications*,
455 21(4):1173–1188.

456 Hart, E. M. and Bell, K. (2015). prism: Download data from the oregon prism project.
457 http://github.com/ropensci/prism.

458 Hijmans, R. J. (2017). raster: Geographic data analysis and modeling. r package version 2.6-7.
459 https://CRAN.R-project.org/package=raster.

460 Hunter, A. F. and Lechowicz, M. J. (1992). Predicting the Timing of Budburst in Temperate Trees.
461 *The Journal of Applied Ecology*, 29(3):597.

462 Iler, A. M., Høye, T. T., Inouye, D. W., and Schmidt, N. M. (2013). Nonlinear flowering re-

sponses to climate: are species approaching their limits of phenological change? *Philosophical Transactions of the Royal Society of London*, 368(1624):20120489.

Jeong, S.-J., Medvigy, D., Shevliakova, E., and Malyshev, S. (2013). Predicting changes in temperate forest budburst using continental-scale observations and models. *Geophysical Research Letters*, 40(2):359–364.

Jones, E., Oliphant, T., Peterson, P., and Others (2001). Scipy: Open source scientific tools for python. http://www.scipy.org/.

Kelling, S., Hochachka, W. M., Fink, D., Riedewald, M., Caruana, R., Ballard, G., and Hooker, G. (2009). Data-intensive science: A new paradigm for biodiversity studies. *BioScience*, 59(7):613–620.

Kramer, K. (1995). Phenotypic plasticity of the phenology of seven european tree species in relation to climatic warming. *Plant, Cell and Environment*, 18(2):93–104.

McKinney, W. (2010). Data structures for statistical computing in python. In *Proceedings of the 9th Python in Science Conference*, pages 51–56.

Melaas, E. K., Friedl, M. A., and Richardson, A. D. (2016). Multiscale modeling of spring phenology across deciduous forests in the eastern united states. *Global Change Biology*, 22(2):792–805.

Ogilvie, J. E. and Forrest, J. R. (2017). Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science*, 21:75–82.

Ogilvie, J. E., Griffin, S. R., Gezon, Z. J., Inouye, B. D., Underwood, N., Inouye, D. W., and Irwin,

484 R. E. (2017). Interannual bumble bee abundance is driven by indirect climate effects on floral
485 resource phenology. *Ecology Letters*, 20(12):1507–1515.

486 O'Keefe, J. (2015). Phenology of woody species at harvard forest since 1990. harvard forest data
487 archive: Hf003.

488 Oliphant, T. (2006). A guide to numpy. USA: Trelgol Publishing.

489 Olsson, C. and Jönsson, A. M. (2014). Process-based models not always better than empirical
490 models for simulating budburst of norway spruce and birch in europe. *Global Change Biology*,
491 20(11):3492–3507.

492 Pebesma, E. J. and Bivand, R. S. (2005). Classes and methods for spatial data in R. *R News*,
493 5(2):9–13.

494 Peng, D., Wu, C., Li, C., Zhang, X., Liu, Z., Ye, H., Luo, S., Liu, X., Hu, Y., and Fang, B. (2017).
495 Spring green-up phenology products derived from MODIS NDVI and EVI: Intercomparison,
496 interpretation and validation using National Phenology Network and AmeriFlux observations.
497 *Ecological Indicators*, 77:323–336.

498 PRISM Climate Group (2004). Oregon state university. http://prism.oregonstate.edu.

499 Python Software Foundation (2018). Python Language Reference Manual, version 3.6.
500 http://www.python.org.

501 R Core Team (2017). R: a language and environment for statistical computing.

502 Réaumur, R. (1735). Observations du thermomètres, faites a Paris pendant l'année 1735, com-

parées avec celles qui ont été faites sous la ligne, a l'isle de France, a Alger et quelques unes de nos isles de l'Amérique. *Mem Paris Acad Sci*, 1735(545).

Richardson, A. D., Anderson, R. S., Arain, M. A., Barr, A. G., Bohrer, G., Chen, G., Chen, J. M., Ciais, P., Davis, K. J., Desai, A. R., Dietze, M. C., Dragoni, D., Garrity, S. R., Gough, C. M., Grant, R., Hollinger, D. Y., Margolis, H. A., McCaughey, H., Migliavacca, M., Monson, R. K., Munger, J. W., Poulter, B., Raczka, B. M., Ricciuto, D. M., Sahoo, A. K., Schaefer, K., Tian, H., Vargas, R., Verbeeck, H., Xiao, J., and Xue, Y. (2012). Terrestrial biosphere models need better representation of vegetation phenology: results from the north american carbon program site synthesis. *Global Change Biology*, 18(2):566–584.

Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Chen, M., Gray, J. M., Johnston, M. R., Keenan, T. F., Klosterman, S. T., Kosmala, M., Melaas, E. K., Friedl, M. A., and Frolking, S. (2018a). Tracking vegetation phenology across diverse north american biomes using phenocam imagery. *Scientific Data*, 5:180028.

Richardson, A. D., Hufkens, K., Milliman, T., and Frolking, S. (2018b). Intercomparison of phenological transition dates derived from the PhenoCam Dataset V1.0 and MODIS satellite remote sensing. *Scientific Reports*, 8(1):5679.

Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., and Toomey, M. (2013). Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169:156–173.

Roberts, A. M. I., Tansey, C., Smithers, R. J., and Phillimore, A. B. (2015). Predicting a change in the order of spring phenology in temperate forests. *Global Change Biology*, 21(7):2603–2611.

Schulze, M. D. (2017). Vegetative phenology observations at the andrews experimental forest, 2009 - present. long-term ecological research. forest science data bank. corvallis, or. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TV075.

Schwartz, M. D., Betancourt, J. L., and Weltzin, J. F. (2012). From caprio's lilacs to the usa national phenology network. *Frontiers in Ecology and the Environment*, 10(6):324–327.

Storn, R. and Price, K. (1997). Differential evolution – a simple and efficient heuristic for global optimization over continuous spaces. *Journal of Global Optimization*, 11(4):341–359.

Tang, J., Körner, C., Muraoka, H., Piao, S., Shen, M., Thackeray, S. J., and Yang, X. (2016). Emerging opportunities and challenges in phenology: a review. *Ecosphere*, 7(8):e01436.

Theobald, E. J., Breckheimer, I., and HilleRisLambers, J. (2017). Climate drives phenological reassembly of a mountain wildflower meadow community. *Ecology*, 98(11):2799–2812.

Tulloch, A. I. T., Possingham, H. P., Joseph, L. N., Szabo, J., and Martin, T. G. (2013). Realising the full potential of citizen science monitoring programs. *Biological Conservation*, 165:128–138.

Tylianakis, J. M., Didham, R. K., Bascompte, J., and Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, 11(12):1351–1363.

USA National Phenology Network (2017). Plant and animal phenology data. data type: Status and intensity. 01/01/2009-04/31/2017 for region: 49.9375, -66.4791667 (ur); 24.0625, -125.0208333 (ll). USA-NPN, Tucson, Arizona, USA. Data set accessed 04/20/2017 at http://doi.org/10.5066/F78S4N1V.

Wang, J. Y. (1960). A Critique of the Heat Unit Approach to Plant Response Studies. *Ecology*, 41(4):785–790.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

Wickham, H., Francois, R., Henry, L., and Müller, K. (2017). dplyr: A grammar of data manipulation.

Wickham, H. and Henry, L. (2018). *tidyr: Easily Tidy Data with 'spread()' and 'gather()' Functions*.

Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., Pau, S., Regetz, J., Davies, T. J., Kraft, N. J. B., Ault, T. R., Bolmgren, K., Mazer, S. J., McCabe, G. J., McGill, B. J., Parmesan, C., Salamin, N., Schwartz, M. D., and Cleland, E. E. (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature*, 485(7399):494–497.

Xu, L. and Chen, X. (2013). Regional unified model-based leaf unfolding prediction from 1960 to 2009 across northern china. *Global Change Biology*, 19(4):1275–1284.

Zhang, H., Liu, S., Regnier, P., and Yuan, W. (2017). New insights on plant phenological response to temperature revealed from long-term widespread observations in china. *Global Change Biology*, 12(10):3218–3221.

Dataset Name	Habitat	Phenological Event (Num. Species)	Reference
Harvard Forest	N.E. Deciduous Forest	Budburst (17) Flowering (7)	(O'Keefe, 2015)
Jornada Experimental Range	Chihuahuan Desert	Flowering (2)	
H.J. Andrews Experimental Forest	N.W. Wet Coniferous Forest	Budburst (5) Flowering (4)	(Schulze, 2017)
Hubbard Brook	N.E. Deciduous Forest	Budburst (3)	(Bailey, 2018)

Table 1: LTER datasets used in the analysis

Name	DOY Estimator	Forcing Equations	Total Parameters	Reference
Naive	$\overline{DOY}$	-	1	-
Linear	$DOY = \beta_1 + \beta_2 T_{mean}$	-	2	-
GDD	$\sum_{t=t_1}^{DOY} R_f(T_i) \geq F^*$	$R_f(T_i) = max(T_i - T_{base}, 0)$	3	(Réaumur, 1735; Wang, 1960; Hunter and Lechowicz, 1992)
Fixed GDD	$\sum_{t=1}^{DOY} R_f(T_i) \geq F^*$	$R_f(T_i) = max(T_i, 0)$	1	(Réaumur, 1735; Wang, 1960; Hunter and Lechowicz, 1992)
Alternating	$\sum_{t=1}^{DOY} R_f(T_i) \geq a + be^{cNCD(t)}$	$R_f(T_i) = max(T_i - 5, 0)$	3	(Cannell and Smith, 1983)
Uniforc	$\sum_{t=t_1}^{DOY} R_f(T_i) \geq F^*$	$R_f(T_i) = \frac{1}{1+e^{b(T_i - c)}}$	4	(Chuine, 2000)
M1	$\sum_{t=t_1}^{DOY} R_f(T_i) \geq (\frac{L_i}{24})^k F^*$	$R_f(T_i) = max(T_i - T_{base}, 5)$	4	(Blümel and Chmielewski, 2012)
MSB	$\sum_{t=1}^{DOY} R_f(T_i) \geq a + be^{cNCD_i} + dT_{mean}$	$R_f(T_i) = max(T_i - 5, 0)$	4	(Jeong et al., 2013)

Table 2: Phenology models used in the analysis. For all models, except the Naive and Linear models, the daily mean temperature T_i is first transformed via the specified forcing equation. The cumulative sum of forcing is then calculated from a specific start date (either $DOY = 1$ or using the fitted parameter t_1). The phenological event is estimated as the DOY in which cumulative forcing is greater than or equal to the specified total required forcing (either F^* or the specified equation). Parameters for each model are as follows: For the Naive model $\overline{DOY}$ is the mean day of year (ie. the Julian date) of a phenological event; for the Linear model β_1 and β_2 are the intercept and slope, respectively and T_{mean} is the average daily temperature between January 1 and March 31; for the GDD model F^* is the total accumulated forcing required, t_1 is the start date of forcing accumulation, and T_{base} is the threshold daily mean temperature above which forcing accumulates; for the Fixed GDD model F^* is the total accumulated forcing required; for the Alternating model NCD is the number of chill days (daily mean temperature below 0°C) from $DOY = 0$ to the DOY of the phenological event, a, b, and c are the three fitted model coefficients; for the Uniforc model, is F^* is the total accumulated forcing required, t_1 is the start date of forcing accumulation, and b and c are two additional fitted parameters which define the sigmoid function; the M1 model is the same as the GDD model, but with the additional fitted parameter k that adjusts the total forcing accumulation according to day length; the MSB model is the same as the Alternating model, but with the additional fitted parameter d to correct the model according to mean spring temperature.

	LTER	USA-NPN
Time-series length	**High**	**Low**
Spatial extent	Low	**High**
Local species representation	High	Low
Regional/Continental species representation	Low	**High**
Number of observers	**Low**	**High**
Site fidelity	High	Low

Table 3: Attributes of the two datasets used in this study. Bold text indicates an attribute is expected to increase over time.

Figure 1: Locations of U.S.A. National Phenology Network sites used (black points) and Long Term Ecological Research sites (labeled circles), with greyscale showing elevation.

582 **Figure 2**: Comparisons of parameter estimates between USA-NPN and LTER derived models. Each point represents a parameter value for a
583 specific species and phenophase, and is the mean value from 250 bootstrap iterations. The black line is the 1:1 line. The R^2 is the coefficient
584 of determination, which can be negative if the relationship between the two parameter sets is worse than no relationship but with the same mean
585 values.

Figure 3: Comparison of predicted day of year (DOY) of all phenological events between USA-NPN and LTER-derived models. Top panels show comparisons at LTER sites and bottom panels show comparisons at USA-NPN sites. Each point is an estimate for a single held-out observation. Colors indicate observations for a single species and phenophase combination.

589 **Figure 4**: Differences in prediction error between USA-NPN and LTER-derived models. Density plots for comparisons of predictions on LTER data
590 (top row) and USA-NPN data (bottom row). Each plot represents the difference between the RMSE for LTER-derived model and the USA-NPN
591 derived model, meaning that values less than zero indicate more accurate prediction by LTER-derived models and values greater than zero indicate
592 more accurate prediction by NPN-derived models. p <0.001 for all t-tests. Differences are calculated pairwise for the 38 species/phenophase
593 comparisons.

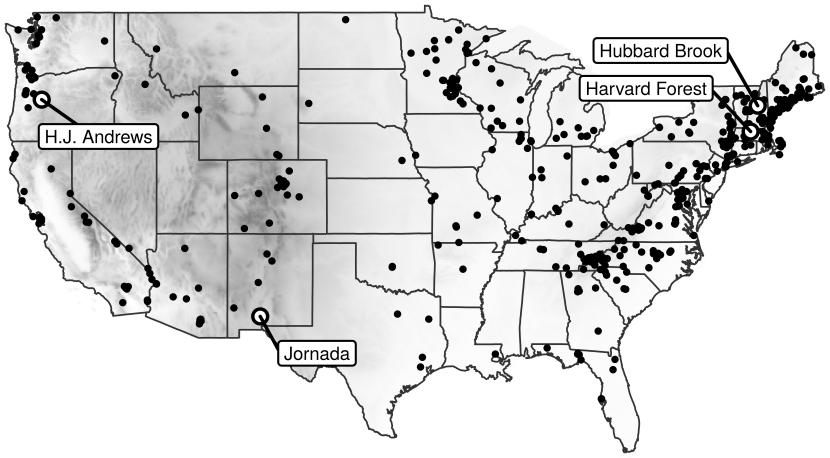

Figure 1: .

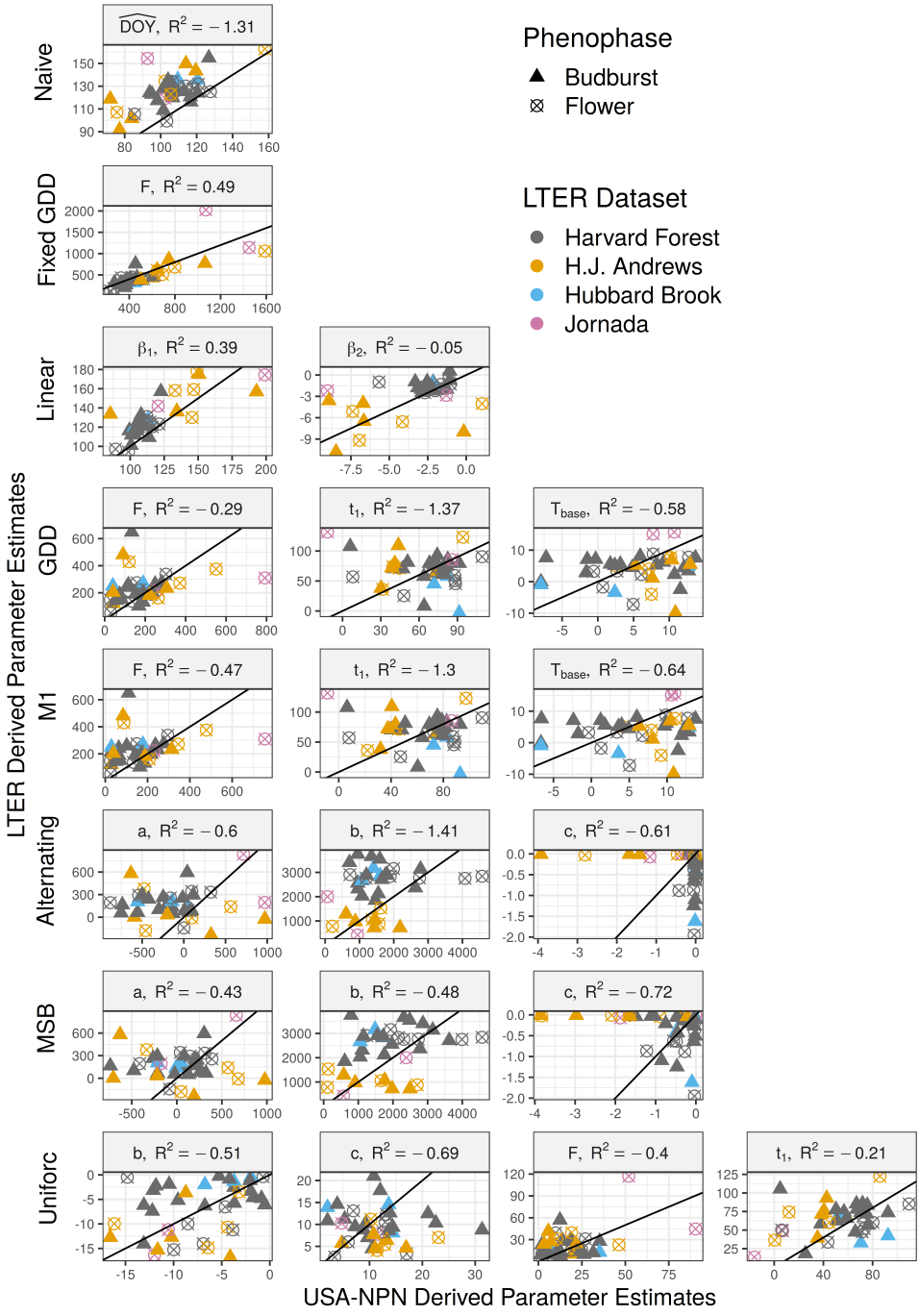
Phenophase
Budburst
Flower
LTER Dataset
Harvard Forest
H.J. Andrews
Hubbard Brook
Jornada
LTER Derived Parameter Estimates
USA-NPN Derived Parameter Estimates
Naive
Fixed GDD
Linear
GDD
M1
Alternating
MSB
Uniforc
DOY, R2 = −1.31
F, R2 = 0.49
β1, R2 = 0.39
β2, R2 = −0.05
F, R2 = −0.29
t1, R2 = −1.37
Tbase, R2 = −0.58
F, R2 = −0.47
t1, R2 = −1.3
Tbase, R2 = −0.64
a, R2 = −0.6
b, R2 = −1.41
c, R2 = −0.61
a, R2 = −0.43
b, R2 = −0.48
c, R2 = −0.72
b, R2 = −0.51
c, R2 = −0.69
F, R2 = −0.4
t1, R2 = −0.21

Figure 2: .

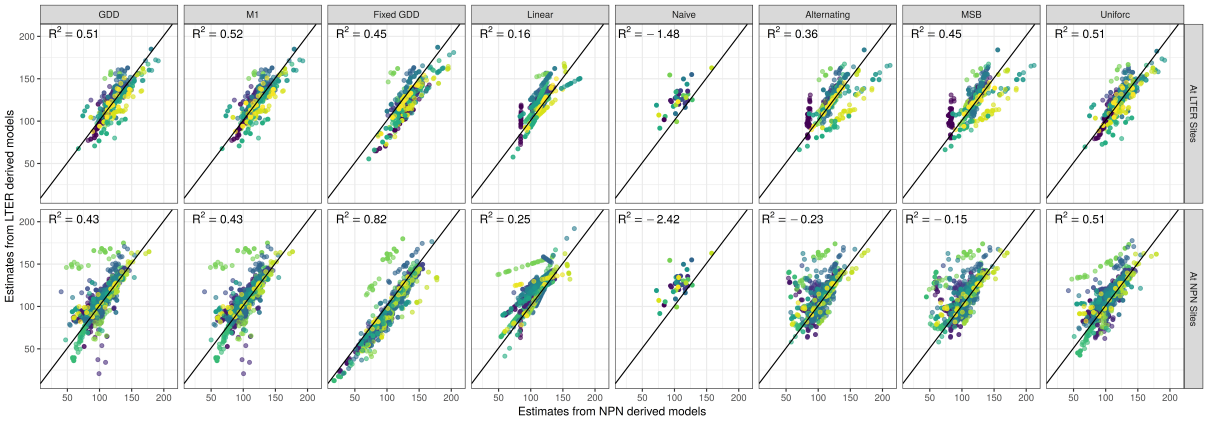
GDD
M1
Fixed GDD
Linear
Naive
Alternating
MSB
Uniforc
At LTER Sites
At NPN Sites
$R^2 = 0.51$
$R^2 = 0.52$
$R^2 = 0.45$
$R^2 = 0.16$
$R^2 = -1.48$
$R^2 = 0.36$
$R^2 = 0.45$
$R^2 = 0.51$
$R^2 = 0.43$
$R^2 = 0.43$
$R^2 = 0.82$
$R^2 = 0.25$
$R^2 = -2.42$
$R^2 = -0.23$
$R^2 = -0.15$
$R^2 = 0.51$
Estimates from LTER derived models
Estimates from NPN derived models
50
100
150
200

Figure 3: .

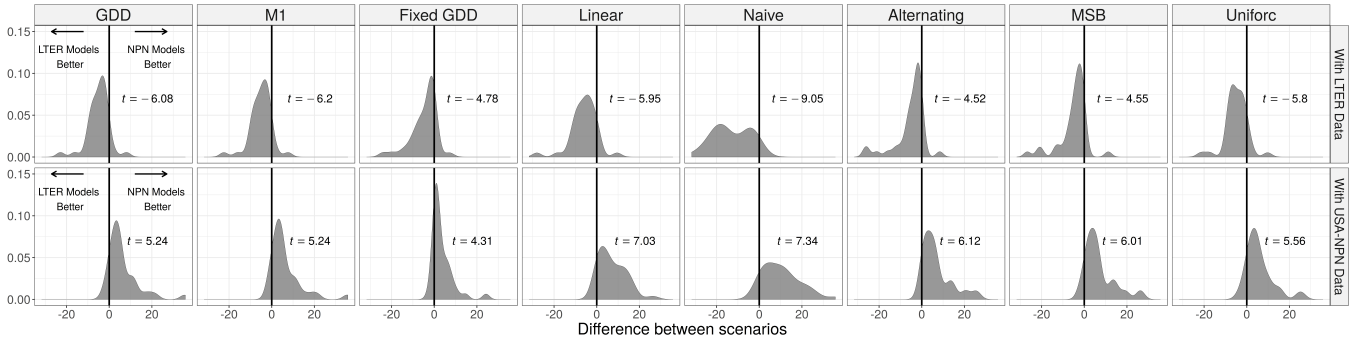
GDD
M1
Fixed GDD
Linear
Naive
Alternating
MSB
Uniforc
LTER Models Better
NPN Models Better
t = −6.08
t = −6.2
t = −4.78
t = −5.95
t = −9.05
t = −4.52
t = −4.55
t = −5.8
t = 5.24
t = 5.24
t = 4.31
t = 7.03
t = 7.34
t = 6.12
t = 6.01
t = 5.56
With LTER Data
With USA-NPN Data
0.15
0.10
0.05
0.00
-20
0
20
Difference between scenarios

Figure 4: .