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

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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 potential 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 National Phenology Network (NPN) effort with models built using data from more intensive studies at Long Term Ecological Research (LTER) sites. We built 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 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 chosen. Predictions for NPN data had the lowest error when using models built from the 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. Accordingly, the choice of dataset depends on the research question. Inferences about species-specific phenological requirements are best made with LTER data, and if 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 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.

37 Keywords: LTER, NPN, forecasting, budburst, flowering, data integration, scale

38 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, uncertainty in 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; 51 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 is 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 is becoming increasingly important for ecological research (Kelling et al., 2009; Dickinson et al., 2010; Tulloch et al., 2013). Because this data is 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, The National Phenology Network (NPN), collects phenology observations from volunteers throughout North America and makes the data openly available (Schwartz et al., 2012). Data from this project has 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 71 contributed considerably to phenological research (Xu and Chen, 2013; Olsson and Jönsson, 2014; Basler, 2016; Zhang et al., 2017), and the 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-75 accessible areas, and variation in sampling effort and observer skill (Dickinson et al., 2010). With hundreds of participants across North America, 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), observations are sometimes made sporadically across seasons, years, and locations. This means that the quanity 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 and our ability to predict future phenology events. 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 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

94 Datasets

The National Phenology Network 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 NPN datasets are located across the U.S. and generally clustered around populated areas (Fig. 1). To represent long-term, intensive phenology studies we used four datasets from North

America representing three major ecosystem types (Table 1, Fig. 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 NPN observations from 2009, when collections began, to 2016 for the fol-107 lowing phenophases: Breaking Leaf Buds, Breaking Needle Buds, Emerging Needles, and Open 108 Flowers. The first three phenophases apply to the 'leaf out' phase for deciduous broadleafs, ev-109 ergreen conifers, and pines, respectively. The 'Open Flowers' phenophase refers to fully-open 110 flowers and applies to all angiosperms. Hereafter, we will refer to these as either 'Flowers' for the 111 Open Flower phenophase, or 'Budburst' for all other phenophases. We subset the NPN observa-112 tions similar to methods outlined in Crimmins et al. (2017). First, 'yes' observations for individual 113 plants were kept only if they were preceded by a 'no' observation within 30 days. Observations 114 for 'Budburst' that were past day of year (DOY) 172, and for 'Flowers' that were past DOY 213 115 were dropped to minimize any influence from outliers. We inferred the observed DOY of each 116 phenophase as the midpoint between each 'yes' observation and the preceding 'no' observation. 117 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 119 individuals at single sites to a single observation. We used 30 days to allow for a greater number of species to be compared. 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
NPN data we converted all metrics to binary 'yes' and 'no' observations for each phenophase
(see supplementary methods). As with the 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 phenophases 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 NPN and LTER datasets to use in the analysis (Table 1 & S1).

130 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 combina-132 tions in the five datasets (NPN and four LTER datasets), we fit eight phenology models (Table 2). 133 The *Naive model* uses the mean DOY from prior observations as the estimated DOY. The *Linear* 134 model uses a regression with the mean spring (Jan. 1 - March 31) temperature as the independent 135 variable and DOY as the response variable. For the six remaining models, the general form is based 136 on the idea that a phenological event will occur once sufficient thermal forcing units, F^* , accumu-137 late from a particular start day of the year (t_1) . Forcing units are a transformation of the daily mean 138 temperature. The start day can either be estimated or fixed. For the *Growing Degree Day (GDD)* 139 model, forcing units are the total degrees above the threshold T. The Fixed GDD model uses the 140 same form but has fixed values for start day $(t_1 = \text{Jan 1})$ and temperature threshold $(T = 0^{\circ}\text{C})$. The Alternating model has a variable number of required forcing units defined as a function of the total number of days below 0°C since Jan. 1 (NCD). The Uniforc model is like the GDD model but with the forcing units transformed via a sigmoid function (Chuine, 2000). These models are some
of the most commonly used in phenology research and serve as a suitable baseline for comparing
the NPN and LTER datasets.

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

We extracted corresponding daily mean temperature for all NPN and LTER observations from 156 the gridded PRISM dataset (PRISM Climate Group, 2004). We parameterized all models using 157 differential evolution to minimize the root mean square error (RMSE) of the estimated DOY of 158 the phenological event. Differential evolution is a global optimization algorithm which uses a 159 population of randomly initialized models to find the set of parameters that minimize the RMSE 160 (Storn and Price, 1997). Confidence intervals for parameters were obtained by bootstrapping, 161 in which individual models were re-fit 250 times using a random sample, with replacement, of 162 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.

166 Analysis

As described above, we fit two sets of models for each species and phenophase: one set of models parameterized using only NPN data, and one set parameterized using only LTER data (with the ex-168 ception of the M1 and MSB models, see above). To compare the inferences about process made by 169 the two datasets, we compared the distribution of each parameter between LTER and NPN-derived 170 models for each species and phenophase combination. Using the mean value of each bootstrapped 171 parameter, we also calculated the coefficient of determination (R^2) between LTER and NPN-172 derived models among the 38 species-phenophases. In three cases where a species phenophase 173 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 NPN data.

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 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 NPN-derived estimates for estimates made at the four LTER sites and across all NPN sites.

We also directly evaluated model performance using four combinations of models and observed data: A) LTER-derived models predicting LTER observations, B) NPN-derived models predicting LTER observations, C) LTER-derived models predicting NPN observations, and D) NPN-derived models predicting NPN observations, Within each of these scenarios, we calculated the RMSE of

the held-out observations for each species, phenophase, and model type. Using the RMSE values, we calculated two different metrics to compare the performance of LTER and NPN-derived models 188 on different data types. The first metric focuses on local-scale prediction by comparing the fits of LTER and NPN-derived models on LTER observations: $RMSE_A - RMSE_B$. The second metric focuses on large-scale prediction by comparing the fits of LTER and NPN-derived models on the 191 NPN data: $RMSE_C - RMSE_D$. These metrics were calculated for each of the model types and 38 192 species-phenophase combinations. Negative values indicate that LTER-derived models perform 193 better, while positive values indicate that the NPN-derived model performed better. In the three 194 cases where the same species and phenophase combination occurred in two LTER sites, we made 195 the LTER-LTER comparison (scenario A) within each site, not across sites, to focus on local scale 196 prediction when LTER data is available. Absolute RMSE values are provided in the supplement 197 (Fig. S1-S3). 198

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)

207 Results

The best matches between parameter estimates based on NPN and LTER data were the Fixed GDD 208 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 209 all other models had R^2 values <0 indicating that the relationship was worse than no relationship 210 between the parameters (but with matching mean parameter values across the two sets of models) 211 (Fig. 2). The *Naive model* showed a distinct late bias in mean DOY estimates for phenological 212 events, likely resulting from the LTER datasets being mostly in the northern United States com-213 pared to the site locations of the NPN dataset (Fig. 2). The large outlier for the Fixed GDD model 214 is Larrea tridentata; this species' flower phenology is largely driven by precipitation, which is 215 not considered in the Fixed GDD model (Beatley, 1974). While the Fixed GDD and Linear mod-216 els showed reasonable correspondence between parameter estimates, all parameters for individual 217 species and phenophase combinations had different distributions between NPN and LTER-derived 218 models (Fig. S6-S7). 219 When comparing estimates of phenological events between the two sets of models, many NPN 220 and LTER models produced similar estimates (Fig. 3). The Fixed GDD model had the highest 221 correlation between the two models sets at NPN sites ($R^2 = 0.82$), while the GDD, M1, and Uni-222 forc models had the highest correlation at LTER sites ($R^2 = 0.51$, 0.52, and 0.51, respectively). 223 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 2 225 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 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 NPN sites.

When comparing the prediction accuracy on held-out data, NPN-derived models made more ac-231 curate predictions for held-out NPN observations, and LTER-derived models performed better on held-out LTER observations (Fig. 4). The *Naive* and *Linear* models had the largest differences be-233 tween the two model sets, while the *Fixed GDD model* had relatively similar errors when evaluated on both NPN and LTER held-out observations. Although the Fixed GDD model had the highest 235 agreement in accuracy between NPN and LTER-derived models, it was not the best performing 236 model overall. The GDD and Uniforc models commonly made the best predictions, having the 237 lowest RMSE in 23% and 40% of cases among NPN-derived models, and 42% and 32% of cases 238 among LTER-derived models, respectively (Fig. S1 & S2). 230

Discussion

Data used to build phenology models typically falls 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., 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 de-251 creases 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 253 phenology requirements (Richardson et al., 2013; Chuine and Régnière, 2017). Understanding and 254 making predictions for the phenology of a single location is best served by intensive local-scale 255 data, when available, but large-scale datasets work better for extrapolating phenology predictions 256 across a species range. Thus, the best choice of both data and models depends on the desired 257 research goals. 258

In this study, parameter estimates differed widely within the same phenology model when fit to 259 the two different types of data, except for the simplest process-oriented model: the Fixed GDD 260 (Fig. 2). These differences may be caused by a variety of factors that have different implications 261 for interpreting process-oriented models and their parameters. First, the differences could result 262 from limitations in the sampling of the NPN dataset, leading to less accurate parameter estimates. 263 If this is the case, it would suggest that using LTER data is ideal for making inferences about 264 plant physiology, and that focusing on the Fixed GDD model is best for making inferences when 265 NPN data is all that is available. Second, spatial variation in phenology requirements could drive 266 these differences, because NPN data integrates over that spatial variation, while LTER data only 267 estimates the phenological requirements for a specific site. In this case, NPN data would provide 268 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). 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 these analyses, as will be explained below.

Despite substantial differences in parameter estimates, LTER and NPN-derived models produced similar estimates for phenological events in most cases (Fig. 3). This greater correspondence 279 between predictions than parameters suggests that more complex models may have identifiability 280 issues. For example, two GDD models with parameters of $t_1=1$, F=10, $T^*=0$ and $t_1=5$, F=5, $T^*=0$ 281 produce nearly identical estimates in many scenarios. This possibility is supported by the fact that 282 the highest correlation between parameter estimates is seen in models with only 1 or 2 parame-283 ters. In addition, bootstrap results for more complex models suggest a high degree of variability 284 in parameter estimates and potentially multiple local optima in fits to both NPN and LTER data 285 (Fig. S6-S7). Finally, parameter estimates of more complex models are also not consistent among 286 models for the same species when comparing multiple LTER datasets (Fig. S4-S5). These results 287 are consistent with research showing that models estimating the starting day of warming accumu-288 lation from budbreak time-series failed to accurately infer the internal phenology described in the 289 models (Chuine et al., 2016). Basler (2016) suggests that the key component in phenology models 290 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 ²⁹³ among parameters between LTER and NPN datasets. In combination with this previous research,
²⁹⁴ our results warrant caution in interpreting parameter estimates from complex phenology models
²⁹⁵ 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 297 out-of-sample predictions. Based on the RMSE, the GDD and Uniforc models produce the best 298 out-of-sample predictions for the majority of species and phenophases at both NPN and LTER 290 datasets (Fig. S1 & S2). This demonstrates that the more complex models are capturing additional 300 information about phenology, and that some of the differences between datasets result from differ-301 ences in either the scales or the sampling of the data. Spatial variation in phenological requirements 302 is known to exist in plants (Zhang et al., 2017). In combination with our results showing observed 303 differences in parameter estimates between LTER sites (Fig. S4-S5), this suggests that variation 304 in phenological requirements across the the range is likely important. However, the models that 305 attempted to address this by incorporating spatial variation did not yield improvements over their 306 base models in our analyses. Specifically, correspondence between parameter estimates (Fig. 2), 307 estimates of phenological events (Fig. 3), and out-of-sample error rates (Fig. 4) for the MSB 308 and M1 models were essentially the same as the Alternating and GDD models, respectively. This 309 lack of improvement from incorporating spatial variation could be caused either by models not 310 adequately capturing the process driving the spatial variation, the NPN dataset having biases from 311 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 NPN, will be key in addressing this and other phenological research needs.

In conclusion, our results suggest that both LTER and NPN data provide valuable information on plant phenology. Models built using both data sources yield effective predictions for phenological 320 events, but parameter estimates from the two data sources differ and models from each source best 321 predict that data source's phenology events. The primary difference in the datasets is spatial scale, 322 but due to trade-offs in data collection efforts, the larger scale NPN data has shorter time-series, 323 less site fidelity and other differences from the intensively collected LTER data (Table 3). These 324 differences can be strengths or potential limitations. Observers sampling opportunistically allows 325 the NPN dataset to have a large spatial scale, but also leads to low site fidelity which limits the 326 ability to measure long-term trends at local scales (Gerst et al., 2016). Tracking long-term trends is 327 the major strength of LTER data, but having a relatively small species pool limits its use in species-328 level predictive modeling. Due to these differences, the best data source for making predictions 329 depends on the scale at which the predictions are being made. Identifying the most effective data 330 sources for different types and scales of analysis is a useful first step, but the ultimate solution 331 to working with diverse data types is to focus on integrating all types of data into analyses and 332 forecasts (Hanks et al., 2011; Melaas et al., 2016). Our results suggest that methods that can 333 learn from the intensive information available in LTER data in regions where it is 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 (Richardson et al., 2018). 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.

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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.

- ³⁷⁶ Chuine, I. and Régnière, J. (2017). Process-based models of phenology for plants and animals.
- 377 Annu. Rev. Ecol. Evol. Syst, 48:159–82.
- ³⁷⁸ Cleland, E., Chuine, I., Menzel, A., Mooney, H., and Schwartz, M. (2007). Shifting plant phenol-
- ogy 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*
- 382 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).
- 390 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–
- 394 172.
- 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.
- 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,
- B., Gutiérrez, M., Rodríguez-Rajo, J., Ruiz, L., Trigo, M., Tormo, R., Valencia, R., and Galán,
- 403 C. (2008). Regional phenological models for forecasting the start and peak of the quercus pollen
- season in spain. Agricultural and Forest Meteorology, 148(3):372–380.
- Gerst, K. L., Kellermann, J. L., Enquist, C. A. F., Rosemartin, A. H., and Denny, E. G. (2016).
- Estimating the onset of spring from a complex phenology database: trade-offs across geographic
- scales. *International Journal of Biometeorology*, 60(3):391–400.
- Gerst, K. L., Rossington, N. L., and Mazer, S. J. (2017). Phenological responsiveness to climate
- differs among four species of quercus in north america. *Journal of Ecology*, 38(1):42–49.
- 410 Grolemund, G. and Wickham, H. (2011). Dates and times made easy with lubridate. Journal of
- Statistical Software, 40(3):1–25.
- Hanks, E. M., Hooten, M. B., and Baker, F. A. (2011). Reconciling multiple data sources to
- improve accuracy of large-scale prediction of forest disease incidence. *Ecological Applications*,
- 21(4):1173–1188.
- Hart, E. M. and Bell, K. (2015). prism: Download data from the oregon prism project.
- http://github.com/ropensci/prism.

- 417 Hijmans, R. J. (2017). raster: Geographic data analysis and modeling. r package version 2.6-7.
- https://CRAN.R-project.org/package=raster.
- 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 tem-
- perate 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.
- 430 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.
- 432 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 phenol-
- ogy across deciduous forests in the eastern united states. Global Change Biology, 22(2):792–
- 436 805.
- 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–
- 439 82.
- Ogilvie, J. E., Griffin, S. R., Gezon, Z. J., Inouye, B. D., Underwood, N., Inouye, D. W., and Irwin,
- R. E. (2017). Interannual bumble bee abundance is driven by indirect climate effects on floral
- resource phenology. *Ecology Letters*, 20(12):1507–1515.
- O'Keefe, J. (2015). Phenology of woody species at harvard forest since 1990. harvard forest data
- archive: Hf003.
- Oliphant, T. (2006). A guide to numpy. USA: Trelgol Publishing.
- Olsson, C. and Jönsson, A. M. (2014). Process-based models not always better than empirical
- models for simulating budburst of norway spruce and birch in europe. Global Change Biology,
- 448 20(11):3492–3507.
- Pebesma, E. J. and Bivand, R. S. (2005). Classes and methods for spatial data in R. R News,
- 450 5(2):9–13.
- PRISM Climate Group (2004). Oregon state university. http://prism.oregonstate.edu.
- Python Software Foundation (2018). Python Language Reference Manual, version 3.6.
- http://www.python.org.
- R Core Team (2017). R: a language and environment for statistical computing.
- 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. (2018). Tracking vegetation phenology across diverse north american biomes using phenocam
- imagery. Scientific Data, 5:180028.
- ⁴⁶⁶ 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 for-
- est, 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.
- 476 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–
- 484 138.
- 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.
- 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 manipu-
- lation.
- Wickham, H. and Henry, L. (2018). tidyr: Easily Tidy Data with 'spread()' and 'gather()' Func-
- 491 tions.
- 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.
- 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.

- ⁴⁹⁹ 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 Biol-
- *ogy*, 12(10):3218–3221.

Dataset Name	Habitat	Phenological Event (Num. Species) Reference	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)	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	Reference
			Parameters	ıs
Naive	\overline{DOY}	ı	1	1
Fixed GDD	$\sum_{t=0}^{DOY} R_f(T_i) \geq F^*$	$R_f(T_i) = min(T_i,0)$	1	1
Linear	$DOY = eta_1 + eta_2 T_{mean}$	ı	2	1
GDD	$\sum_{I=t_1}^{DOY} R_f(T_i) \geq F^*$	$R_f(T_i) = max(T_i - T^*, 0)$	3	1
M1	$\sum_{l=t_1}^{DOY} R_f(T_l) \geq (rac{L_i}{24})^k F^*$	$R_f(T_i) = max(T_i - T^*, 5)$	4	(Blümel and Chmielewski, 2012)
Alternating	$\sum_{t=0}^{DOY} R_f(T_i) \geq a + b e^{cNCD(t)}$	$R_f(T_i) = max(T_i - 5, 0)$	8	(Cannell and Smith, 1983)
MSB	$\sum_{i=0}^{DOY} R_f(T_i) \ge a + be^{cNCD_i} + dT_{mean}$	$R_f(T_i) = max(T_i - 5, 0)$	4	(Jeong et al., 2013)
Uniforc	$\sum_{l=t_1}^{DOY} R_f(T_l) \geq F^*$	$R_f(T_i) = rac{1}{1+e^{b(T_i-c)}}$	4	(Chuine, 2000)

 Table 2: Phenology models used in the analysis

		<u>LTER</u>	<u>NPN</u>
	Time-series length	High	Low
	Spatial extent	Low	High
506	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 National Phenology Network sites used (black points) and Long Term

Ecological Research sites (labeled circles), with greyscale showing elevation.

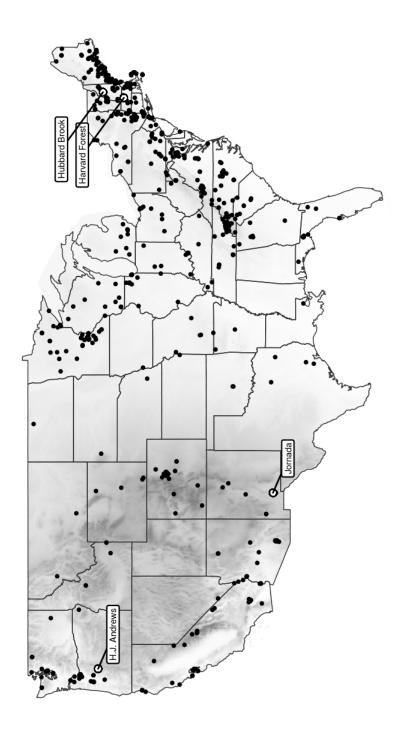


Figure 1: .

Figure 2: Comparisons of parameter estimates between NPN and LTER derived models. Each point represents a parameter value for a 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 of determination, which can be negative if the relationship between the two parameter sets is worse than no relationship but with the same mean values.

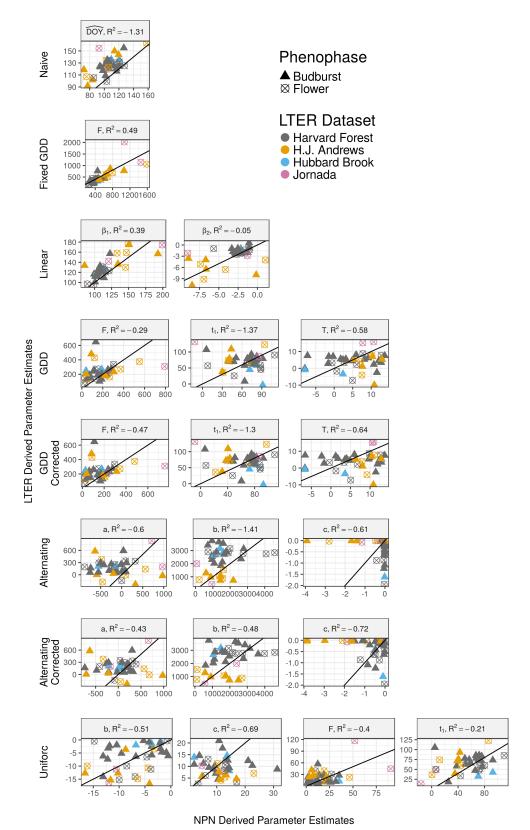


Figure 2: .

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

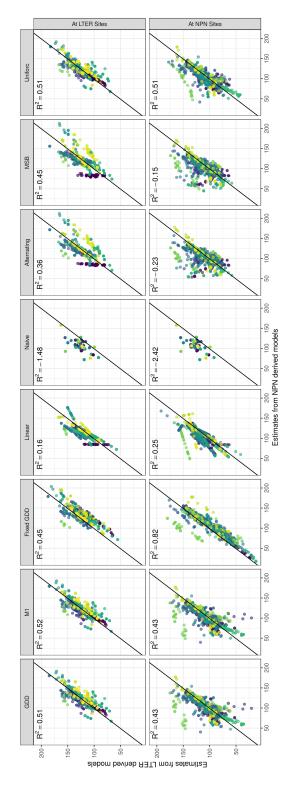


Figure 3: .

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

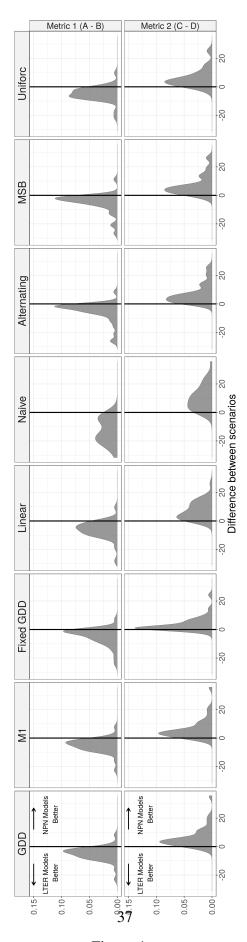


Figure 4: .