LETTER

REPLY TO ELMENDORF AND ETTINGER:

Photoperiod plays a dominant and irreplaceable role in triggering secondary growth resumption

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In their Letter, Elmendorf and Ettinger (1) question the dominant role of photoperiod in driving secondary growth resumption (hereafter referred to as xylem formation onset) of the Northern Hemisphere conifers, recently reported by Huang et al. (2). Their opinions are grounded on the following three aspects, including 1) the seasonality of the photoperiod, 2) the dependence of the predictor variables (e.g., photoperiod, forcing, and chilling) on the response variable (the date of onset of xylem formation, day of the year [DOY]), and 3) the limited value of the obtained models for interannual forecasting. We think they bring up an interesting issue that deserves further discussion and clarification.

Photoperiod is acknowledged to regulate spring bud swelling while wood formation starts (3, 4). Although photoperiod seasonality occurs at each site, its influence is marginal in our study given that the analysis involved comparisons among sites across the Northern Hemisphere. Our conclusion that photoperiod plays a dominant role was built upon the combination of several coherent pieces of evidence, rather than "the crux of Huang et al. . . ." as they pointed out. First, we clearly stated that model 2, which modeled DOY as a function of the mean annual temperature of the site (MAT), forcing, chilling, and soil moisture, was considered the best model in terms of parsimony

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according to minimum Akaike information criterion and Bayesian information criterion, rather than R^2 as referred to in their Letter. Second, photoperiod interacted with MAT and can explain 61.7% of the variance of MAT alone (2). Therefore, we concluded that secondary growth resumption was driven primarily by MAT and photoperiod or by their interaction, which is challenging to be disentangled without experimental data, we agree. In terms of biological functioning, they play an undoubtedly relevant role in secondary growth resumption, as explained in Huang et al. (2) and Delpierre et al. (5). In contrast, Elmendorf and Ettinger do not provide any biological reason why photoperiod would not control secondary growth resumption, but acknowledge that "on a yearly basis plants may rely on cues beyond average temperature." Finally, following Elmendorf and Ettinger's approach, we found that their models lack biological foundation and their findings are at least questionable or even unrealistic. Therefore, we moderately adapted their code to avoid unrealistic aspects, resulting in more consistent insights than those they reported (Figs. 1 and 2).

According to traditional definitions, several exogenous factors were calculated and retained in the final models after rigorous statistical screening, such as collinearity tests. More importantly, these models are biologically sound and provide perspectives for driving future mechanistically related experimental designs, although we agree that statistical models are imperfect approximations to reality.

The recently developed microsampling technique used in Huang et al. (2) provides high time-resolution (weekly) data of xylogenesis for refining our knowledge on wood formation during the growing season. Therefore, we advocate applying our weekly data-based modeling results into earth system models to better understanding of carbon, water, and energy cycles at intra-annual scale (6), rather than at interannual scale that can be better assessed by dendroecology (7).
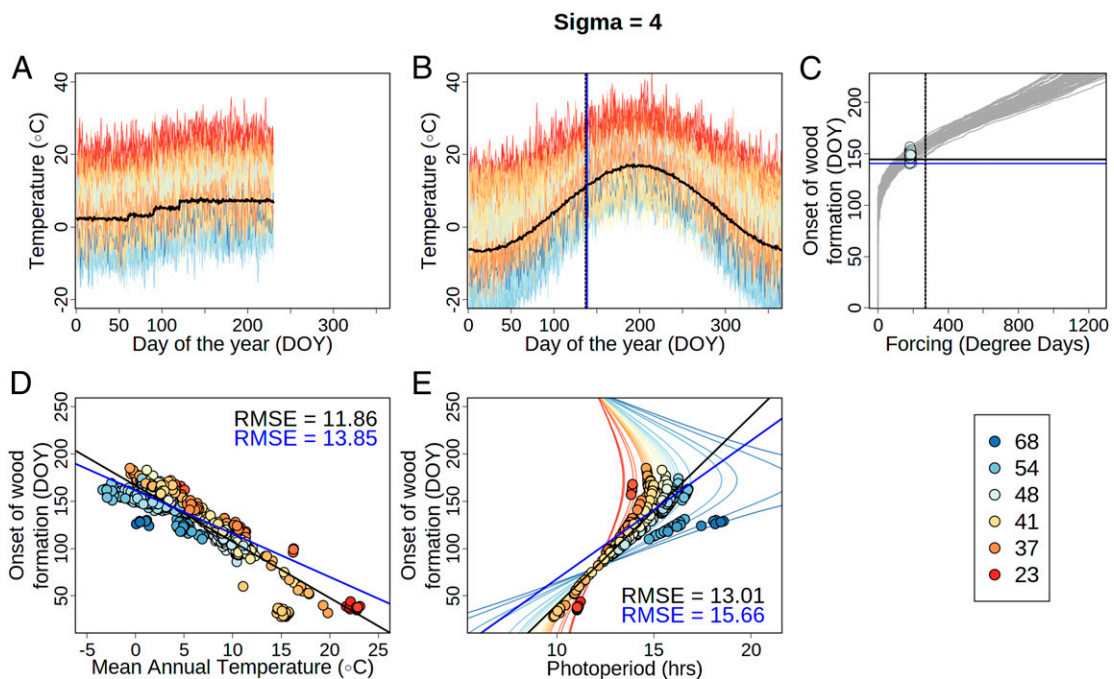
Sigma = 4

Fig. 1. Simulated phenological data [adapted from Elmendorf and Ettinger (1)], produced using mean annual temperature (MAT), latitude, and seasonal temperature variation (estimated for each site as the long-term mean difference between July and January temperatures). (*A*) Simulated time-series of temperature by Elmendorf and Ettinger (sigma = 4), without an evident seasonal trend. Lines are simulated temperature series for each site and year, and the color represents the latitude. The black line represents the mean daily temperature for all sites. (*B*) Simulated time-series of temperature, considering mean annual temperature, temperature seasonality, and with a given level of "noise" (sigma = 4). The detailed equation is as follows: $T_t = MAT - (T_{Jul} - T_{Jan})/2 \times \cos(2 \times \pi/365 \times (t - 15)) + Error$; where T_t is temperature for the DOY of the year (*t*), MAT is mean annual temperature, T_{Jul} (T_{Jan}) is the long-term mean temperature in July (January), and Error is the noise added (sigma = 4). The vertical line in blue (dash in black) gives the mean day of the year (DOY) observed (simulated) of wood formation onset for all studied sites. The black line represents the mean daily temperature for all sites. (*C*) The phenological data were simulated using forcing unit (FU) thresholds described in Huang et al. (2). The gray lines represent seasonal forcing accumulation for the site "SIM" (LAT = 48° N), for the period 2002 to 2014. The horizontal black (blue) line is the mean DOY of onset observed (simulated) for the site "SIM." The dots are simulated dates of wood formation onset at this site. Our simulated data varied forcing units required for onset of wood formation (FU) with latitude, as previously described by Huang et al. (2). (*D*) A linear relationship is found between DOY at the beginning of wood formation (DOY$_{wf}$) and MAT; the root-mean-square error (RMSE) of the simulated temperature and simulated (observed) phenology appears in black (blue). The color dots show dates of wood formation onset, with colors indicating latitude (legend on the *Right* of the panel). (*E*) Linear relationship between DOY$_{wf}$ and photoperiod. Color lines show continuous patterns in photoperiod across the spring. For the observed phenology, the RMSE (in blue) for the photoperiod (*E*) is higher than the RMSE for MAT (*D*), which is held for sigma values in the range 0 to 10. For estimated phenology, the RMSE (in black) for the photoperiod (*E*) is higher than for MAT (*D*); for time-series of simulated temperature with high noise level (sigma > 5) the photoperiod shows a lower RMSE than MAT, but the simulated DOY$_{wf}$ (horizontal black line in *C*) deviates from the observed DOY$_{wf}$ (horizontal blue line in *C*). We found that photoperiod becomes a stronger predictor of phenology for high sigma values (>5), while for lower values of sigma phenology is mainly predicted by MAT alone.
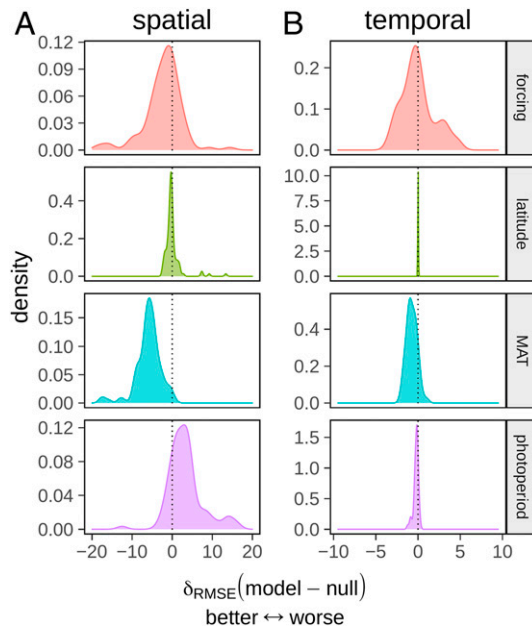
Fig. 2. Predictive performance of the date of wood formation onset (DOY$_{wf}$) based on forcing, latitude, mean annual temperature (MAT), and photoperiod. Linear mixed models were fitted on randomly sampled subsets of the data, in each iteration 25% of sites were dropped (to evaluate the importance of environmental variables across spatial gradients in driving phenology; for each iteration the testing dataset consisted of sites in the latitude range used for training to reduce the bias introduced by the low distribution of sites at low and high latitudes) or a single year (to access the importance of environmental conditions on phenology at the temporal scale; only sites with phenological data over 3 y were considered; for each site 1 y was randomly sampled for testing and the remainder used for training). For latitude and MAT, we modeled the DOY$_{wf}$ directly (e.g., DOY$_{wf}$ ~ MAT + random effects), producing a DOY$_{wf}$ prediction for the evaluation subset. For forcing, chilling, and photoperiod, we used the threshold value of the environmental variable at xylogenesis as the response variable (e.g., FU$_{wf}$ ~ Intercept + random effects), and then used the simulated daily meteorological data with the modeled thresholds to predicted DOY$_{wf}$ (e.g., the first DOY where FU exceeds the predicted FU$_{wf}$ for a given site, species, and year). The predictive performance of each model was defined as the difference in predictive accuracy (root-mean-square error [RMSE] of predicted vs. observed DOY$_{wf}$) in relation to a null model with no environmental drivers for each iteration ($n = 100$). A negative (positive) δ_{RMSE}(model–null) indicates that model with environmental drivers explains more (less) variation than the null model. In the spatial cross-validation (A), the proportion of negative δ_{RMSE}(model–null) is 0.01 for MAT, while MAT presents a proportion of 0.11 negative δ_{RMSE} in the temporal analysis (B). Overall, the predictive performance of the models (A and B) is better than Elmendorf and Ettinger reported. Adapted with permission from ref. 1.

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