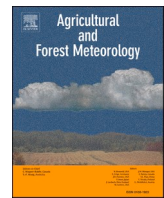


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Spring phenological variability promoted by topography and vegetation assembly processes in a temperate forest landscape

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ABSTRACT

Plant phenological processes significantly impact ecosystem function and services across multiple ecological scales and are widely viewed to be among the most sensitive indicators of global environmental change. Remote sensing has crucially expanded our understanding of phenological variability. Yet, we continue to lack a complete mechanistic understanding of phenology and its variability and drivers, which is important to the development of predictive models, especially under continued environmental change. We combined field inventories and Land Surface Phenology (LSP) approaches, using 36 years of Landsat phenological observations, to characterize the degree to which long-term spring greenup patterns are shaped by topography, vegetation, and topographically structured vegetation assembly processes within a dissected forest landscape in southeastern Ohio. We found temporal and spatial variability among the field samples where greenup patterns displayed rapid change (18 total days) over relatively short distances (<1 km). Slope position explained the most variation (35%), where the bases of hills displayed the latest timing in spring greenup. However, we found that differences in terrain aspect and slope influenced canopy diversity, height, and composition of forest stands, influencing plant community processes that support heterogeneity in spring leaf-out timing. Understanding how forest phenology is shaped by direct and often complex interacting processes that influence the distribution of species assemblages supports new insight into phenological variability and, importantly, the management of forest ecosystems facing continued environmental change.

1. Introduction

Vegetation phenology significantly influences diverse ecosystem processes across multiple ecological scales, from local organismal interactions (Halupka and Halupka, 2017; Heberling et al., 2019; Royo and Stanovick, 2019; Singer and Parmesan, 2010; Visser et al., 2004) to global biogeochemical cycles (Morissette et al., 2009; Richardson et al., 2013). Vegetation phenology is also among the most sensitive indicators of global environmental change, supporting improved understanding of climate change impacts on terrestrial ecosystems (Fitter and Fitter, 2002; Morissette et al., 2009; Root et al., 2003). As a result, vegetation phenology is increasingly studied, particularly in light of advancing remote sensing technologies that repetitively resolve phenological patterns, aka, Land Surface Phenology (LSP), across multiple spatial and

temporal scales (Cleland et al., 2007; Morissette et al., 2009; Nagai et al., 2016). However, despite increased research capacity, we continue to lack adequate mechanistic understandings of vegetation phenology and its variability and drivers (Chmura et al., 2019), limiting the development of predictive models in the face of continued environmental change (Basler, 2016; Richardson et al., 2013).

The timing of spring leaf development among temperate forest ecosystems has been shown to be particularly sensitive to temperature (Linkosalo et al., 2006; Polgar et al., 2014; Polgar and Primack, 2011; Vitasse et al., 2009). At large spatial scales, phenological patterns remain largely consistent with climatic variation across broad latitudinal and elevational gradients (Fitzjarrald et al., 2001; Hopkins, 1918). However, spatial patterns often reveal significant fine-scale variation as well (Elmore et al., 2012; Fisher et al., 2006; Liang et al.,

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2011; Melaas et al., 2013). Thus, phenological patterns likely also incorporate a variety of possibly interacting local processes (Chmura et al., 2019). For example, local topography influences microclimatic variation, such as processes contributing to cold air drainage into small valleys, which has been shown to delay phenological timing of forest vegetation in comparison to surrounding uplands (Fisher et al., 2006; Schuster et al., 2014). Individual tree species, which also frequently sort according to local topography (Desta et al., 2004; Hix, 1988; Hix and Pearcy, 1997; Martin et al., 2011), can display large interspecific variation in phenological timing as well (Delpierre et al., 2017; Denéchére et al., 2019; Lechowicz, 1984; Murray et al., 1989; Richardson et al., 2006). There also exists some variability in leaf phenology that can be explained by differences in tree height (Osada and Hiura, 2019; Seiwa, 1999), likely serving as a proxy for both individual tree response to site conditions (Bassow and Bazzaz, 1998) as well as differences between juvenile and adult age classes (Augspurger and Bartlett, 2003; de Souza and da Costa, 2020). Because spatial variability likely incorporates a greater range of direct and indirect processes at more local scales, as opposed to more direct climatic forcing across large regions, models at these scales should account for the combined effects of local topography on the composition of forest vegetation and how these factors interact to influence phenological behavior.

Significant efforts have identified the dual importance of topography and forest stand characteristics in explaining variation in LSP behavior (Isaacson et al., 2012; Kraus et al., 2016; Liang et al., 2011; Misra et al., 2018; Reaves et al., 2018; Xie et al., 2015). However, few studies have interpreted spatial variation in light of interactions between topography and forest vegetation composition (Reaves et al., 2018; Xie et al., 2015). First, many LSP studies continue to incorporate generalized models of broad forest types in lieu of detailed species-level information resolving the ecophysiological variation of forest stands (Isaacson et al., 2012; Xie et al., 2015). Second, modeling efforts should also ideally employ statistical procedures that account for the often causative and correlative factors among spatial drivers (Bassow and Bazzaz, 1998; Schemske and Horvitz, 1988). For example, oak (*Quercus* spp.) dominated forests among dissected landscapes of the Central Hardwood Region of the United States often display strong topographically-mediated vegetation gradients that underlie variation in the fundamental ecological strategies of component tree species (Fralish, 2003). Here, drought-tolerant oaks dominate drier site conditions on southwest-facing hillslopes and ridgetops and transition to mixed mesophytic species assemblages, adapted to withstand increased competition, on opposing mesic northeast-facing hillslopes and bottomlands (Adams et al., 2019; Desta et al., 2004; Martin et al., 2011). Understanding how these environmental and organismal processes (and interactions) contribute to phenological patterns could help improve forest management practices in supporting plant diversity in light-structured environments (Heberling et al., 2019; Royo and Stanovick, 2019), especially in predicting the potential consequences of anticipated environmental change (Iverson et al., 2019b; McEwan et al., 2011).

We designed a study to determine how variation in the timing of spring greenup is explained by topography and vegetation assembly processes across a topographically complex and diverse forest landscape in southeastern Ohio, USA. We used LSP methods, combining multi-temporal Landsat observations from the years 1984 to 2020 (including an 8-day temporal resolution for a given sensor among overlapping scenes), to retrieve long-term average dates of spring greenup across a series of field inventories. Phenological curves fitted to multidecadal Landsat observations were used to resolve long-term climatological average spring greenup dates, insensitive to annual climate anomalies (Fisher et al., 2006; Melaas et al., 2013) and at spatial resolutions (30 m) complementary to local management activities (Adams et al., 2019; Iverson et al., 2017). Field inventories elucidated variation in tree species richness and community mean wood density (WD), the ratio of oven-dry mass to total green volume. We used WD to collectively represent variation in assemblage and functional composition of

individual tree stands (Chave et al., 2009; Stahl et al., 2013). Finally, data from digital elevation models and LiDAR were used to quantify key topographic variables (elevation, slope percent, and aspect) and mean vertical canopy height.

Our layered approach used regression modeling and variance partitioning procedures to determine the extent to which site-to-site variation in spring greenup is explained by topography, vegetation, and topographically-structured vegetation assembly processes. Next, we incorporated path analysis to precisely determine how topographic features influence phenological variation by mediating changes in forest stand vegetation. Finally, we isolated the relative importance of individual species in explaining forest stand phenological variation, based on relative dominance profiles and contributions towards community-level functional composition. Together, we illustrate how spring leaf phenology is shaped by direct and often complex interacting processes across tightly integrated forest ecosystems.

2. Methods

2.1. Study area

We targeted neighboring forest sites (Vinton Furnace State Experimental Forest and Zaleski State Forest) within a “sidelap” region (overlapping zones between Landsat scenes P19/R33 and P18/R33, which improves the temporal frequency from 16 to 8 days for a single instrument and earlier depending on whether more than one instrument is operating at a time and at 30 m resolution) in the Western Hocking Plateau ecological subsection of southeastern Ohio for this study (Bailey et al., 1994) (Fig. 1). The study area features a dissected terrain corresponding to a repeated ridge and valley pattern composed of sharp ridges, slopes, and narrow valley bottomlands. Local relief (~100 m) is roughly equivalent to the total elevation range across the study area, 182–336 m above sea level (m.a.s.l.). Thus, elevation largely reflects topographic position relative to valley bottomlands. Deciduous hardwood forests, composed of ~70 tree species regenerating post-clearcutting in the early 20th century, dominate the landscape (Iverson et al., 2019a; Stout, 1933). Species composition and structure is largely influenced by slope position and aspect (Fralish, 2003). Here, mature forest canopies are primarily dominated by oak species along dry southwesterly aspects while mesic assemblages, including *Acer saccharum*, *Liriodendron tulipifera*, and *Fagus grandifolia*, characterize moist northeastern hillslopes and valleys. Annual precipitation and temperature averages 106.4 cm and 11.6 °C, respectively (Iverson et al., 2019a).

2.2. Field data

Circular plots, 11.3 m radius (0.04 ha in size), were established in 2015–2016 by arranging arrays of two or three plots (each ≥ 25 m apart) across each study forest (<400 m from roads and trails and >150 m apart) according to a generalized tessellation stratified sampling design (Adams et al., 2019). We measured and identified all stems with a diameter ≥ 8 cm within each plot. Among the field data used in this study, all stems were identified to species except for *Carya* spp. and *Crataegus* spp. We used the plot data to quantify two vegetation variables: tree species richness and the community-weighted mean WD (g cm^{-3}). Community mean WD was used to reflect variation in both plot-level species mix as well as functional trait composition. Given the tendency for species with greater WD, especially oak species, to display relatively later leaf-out timing (Lechowicz, 1984; Samtani et al., 2015; Xie et al., 2015), we expected a positive correlation with spring greenup timing. Plot-level WD was quantified according to the relative basal area (BA, $\text{m}^2 \text{ha}^{-1}$) and mean WD values (Chave et al., 2009) of each tree species as follows: $\sum BA_{ij} \times WD_i$, where BA_{ij} is the relative BA of species i in plot j and WD_i is its mean WD. For stems recorded to genus or where species-level WD estimates were unavailable, we used genus-level mean WD values (see Fig. 2 for a summary of the field data). The field data

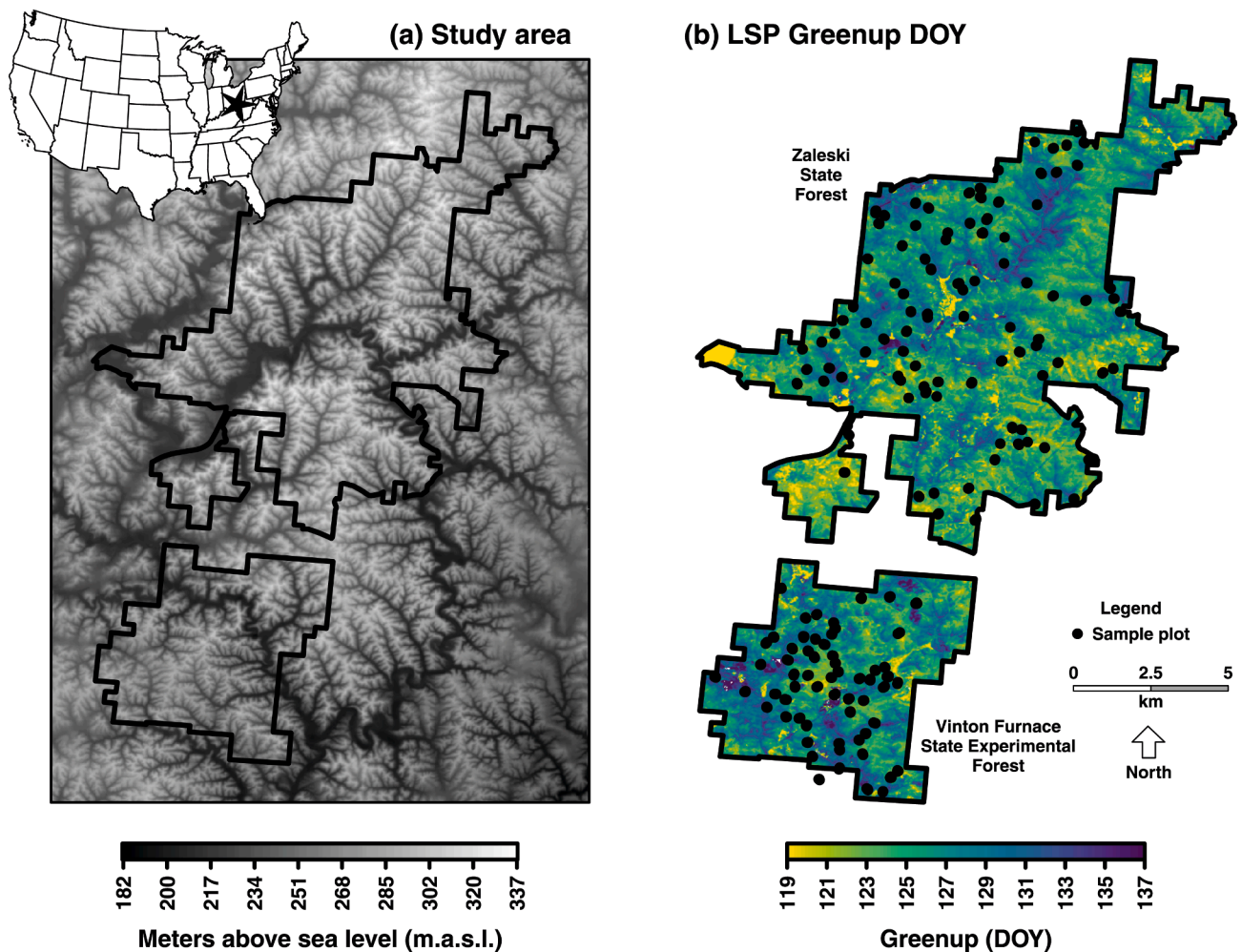


Fig. 1. The study area displaying variation in elevation (a) and Land Surface Phenology (LSP) derived spring greenup dates (b). Panel (a) displays a digital elevation model and the location of the study area within southeastern Ohio (inset map). Emerging from the study forests is an unvalidated spring phenology map for the reference period 1984–2020 (b), provided here to aid interpretation of the statistical analyses. Displayed on it are the locations of $n = 373$ vegetation plots used in this study.

were combined with spatial data on topography and vertical canopy height derived from a digital elevation model (DEM) and LiDAR data, respectively. A final sample of $n = 373$ total plots, including $n = 6,913$ measured stems of $n = 48$ tree species, were considered in this study (see Quality Control section).

2.3. Spatial data

From a 10 m digital elevation model (DEM), derived from USGS 7.5 min quadrangle contours (Ohio Environmental Agency Division of Emergency and Remedial Response), we derived spatial grids of elevation (m), slope ($^{\circ}$), and transformed aspect, relating to site productivity according to $[\cosine(\text{azimuth} - 45)] + 1$ (Beers et al., 1966). Transformed aspect converted raw aspect measurements in azimuth degrees to a metric distinguishing less productive, southwest facing slopes ($225^{\circ} = 0$) from more productive, mesic northeast slopes ($45^{\circ} = 2$) to avoid problems with treating a circular statistic as linear. Vertical canopy height (m) was quantified via LiDAR data provided by the Ohio Geographic Reference Information Program, collected during spring 2007 (<http://ogrip.oit.ohio.gov/Home.aspx>; accessed 13 October 2014). The LiDAR data, including filtered ground and vegetation height returns, had an average spacing and density of 1.27 m and 0.27 returns m^{-2} , respectively. We developed a 5 m resolution canopy height model (CHM) using conventional procedures: separate bare ground and

top-of-surface models were quantified using bilinear interpolation and mean ground and maximum vegetation heights, respectively; after which bare ground heights were subtracted from surface heights to provide a CHM according to top of canopy heights across the study area. Spatial data on topography and canopy height were projected to the same Universal Transverse Mercator Zone (UTM Zone 17N), aggregated, using mean values to align with the native Landsat resolution (30 m), and extracted for the vegetation plots using the pixel values intersecting plot center of the field data.

2.4. Landsat data

We prepared a large Landsat time series, using all-available Landsat data for the study area, beginning in 1984, within the Google Earth Engine (GEE) cloud-computing platform (Gorelick et al., 2017). We assembled observations from closely related Thematic Mapper (TM), Enhanced Thematic Mapper Plus (ETM+), and Operational Land Imager (OLI) instruments onboard Landsat 5, 7, and 8, respectively, and exploited improved data density provided by overlapping Landsat scenes, P19/R33 and P18/R33, within the sidelay region comprising the study area. We used Level 2 (Landsat Science Products) images processed to surface reflectance according to USGS Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS) and Landsat Surface Reflectance Code (LaSRC) (Holden and Woodcock, 2016; Roy et al.,

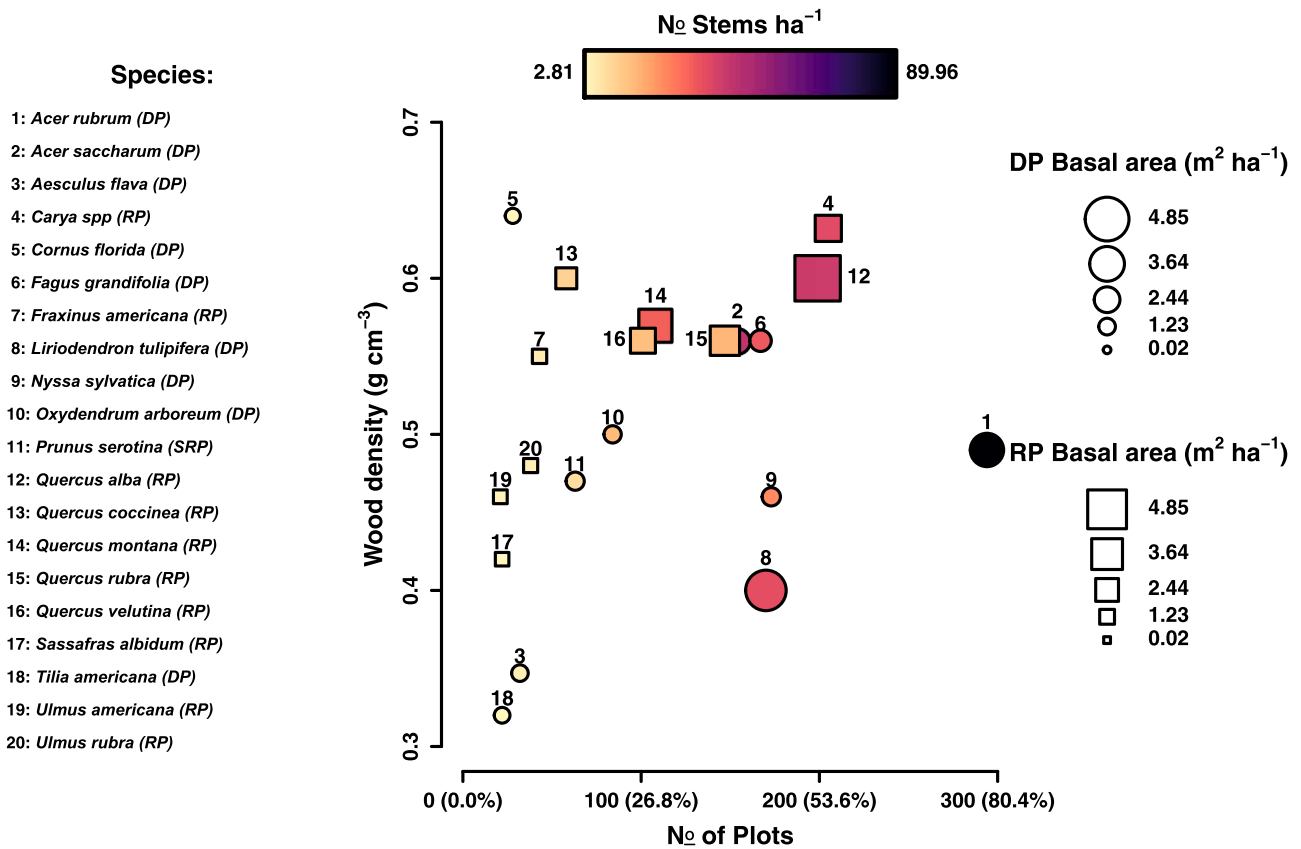


Fig. 2. Variation in the frequency of occurrence (N_0 plots), mean basal area (BA, $m^2 ha^{-1}$), and mean stem density (N^0 stems ha^{-1}) relative to the wood density (WD, $g cm^{-3}$) and stem anatomy (DP = diffuse porous; RP = ring porous; SRP = semi-ring porous) of the top 20 tree species used in this study. Note SRP is combined with RP in the legend.

2016; Vermote et al., 2016). All-available data were filtered within GEE to include images with geometric $RMSE < 10$ m, suitable for time series analysis (Young et al., 2017), and image quality = 9 (indicating no errors were detected during internal Landsat processing). Clouds and cloud shadows were masked according to provided pixel quality attributes (pixel_qa band) generated by the CFMASK algorithm (Zhu and Woodcock, 2012). We harmonized TM and ETM+ surface reflectance to OLI surface reflectance to account for slight differences in spectral characteristics among the instruments (Roy et al., 2016). In addition, we normalized surface reflectance values using the Modified Sun-Canopy-Sensor Topographic Correction method (SCS+C), described in Soenen et al. (2005), and the ALOS (Advanced Land Observing Satellite) Global Surface Model (Tadono et al., 2014) to correct for topographic shadows. We used the enhanced vegetation index (EVI), a proxy for photosynthetic activity, for deriving LSP (Huete et al., 2002): $EVI = \frac{2.5 \times (\rho_{NIR} - \rho_R)}{(\rho_{NIR} + 6 \times \rho_R - 7.5 \times \rho_B + 1)}$, where ρ_{NIR} , ρ_R , and ρ_B , correspond to spectral values in the near-infrared, red, and blue wavelengths, respectively. All resulting EVI images were clipped to the study area and downloaded locally for further analysis in the R statistical environment (<https://cran.r-project.org/>). We calculated the percentage of clear observations within the clipped region and considered only images with cloud cover $< 90\%$, resulting in a final Landsat time series comprising 1105 images inclusive from dates 27-March-1984 to 4-April-2020.

2.5. Land surface phenology

The time series was organized by day of year (DOY) and LSP was quantified using the "greendown" model developed by Elmore et al. (2012):

$$f_{evi}(t, m) = m_1 + (m_2 - m_7 t) \left(\frac{1}{1 + e^{\frac{m_3 - t}{m_4}}} - \frac{1}{1 + e^{\frac{m_5 - t}{m_6}}} \right),$$

where t is the image DOY and parameters $m_1 - m_7$ control the shape of the curve. The model is specifically tuned to account for gradual declines in greenness between spring and autumn curves (m_7), commonly observed among broadleaf deciduous forests. This additional parameter improves the quantification of LSP (Elmore et al., 2012; Reaves et al., 2018). We used the Levenberg-Marquardt algorithm to optimize the nonlinear model-fitting procedure (Levenberg, 1944). The timing of spring greenup was estimated according to model coefficient m_3 , which includes the DOY of maximum change rate (inflection point) in the spring curve.

2.6. Quality control

We established quality control checks to reduce extraneous factors in the time series unrelated to long-term phenological timing. Specifically, we removed spurious EVI outliers ($EVI \leq Q_1 - (1.5 \cdot IQR)$; $EVI \geq Q_3 + (1.5 \cdot IQR)$) emanating from sensor error or residual cloud effects before fitting the greendown model. The greendown model was fitted to the entire time series using these criteria to provide an unvalidated map of spring greenup dates across the study area, presented in Fig 1b, to assist interpretation of the statistical analyses. All field data, however, were subjected to additional scrutiny to ensure only vegetation plots that did not experience disturbance (most notably forest management) over the study period were used in the statistical analysis. Here, we developed a semi-automated approach to remove vegetation plots with detected disturbances in the time series. We extracted the unique time series for each plot using the pixel values intersecting plot center. Inspecting each individual plot's time series, we used recent 1 m orthophotos (year

2015, National Agriculture Imagery Program) to identify vegetation plots showing signs of harvesting over the previous decade. Orthophoto interpretation was assisted with the Bayesian Estimator of Abrupt Change, Seasonal change, and Trend (BEAST) algorithm to identify earlier and often subtle disturbances in each time series not otherwise apparent in the imagery (Zhao et al., 2019). Specifically, the probability of a trend changepoint was averaged over a moving window of 20 timesteps comprised of a bi-weekly average of EVI values to provide a regular sampling scheme required by BEAST (see Zhao et al. 2019 for further details). We flagged locations where the probability of change was >0.10 (i.e., a value we determined to be low enough to not miss potential disturbances) and inspected the trend sign to determine whether the potential change was a disturbance- or recovery-type changepoint. We considered large disturbances to include patterns displaying negative (disturbance) followed by positive (recovery) trends in greenness. In combination, both procedures allowed us to identify recent harvests and those that occurred at earlier periods over the 36-year study period. Subsequently, we removed plots experiencing a significant disturbance followed by recovery ($n = 205$). Finally, several additional criteria were applied to remove specific plot outliers, including plots with increasing greenness between spring and autumn ($n = 3$), poor fit model fit ($r \leq 0.90$) between observed versus fitted EVI values in the greendown model ($n = 2$), ≤ 10 m in canopy height ($n = 3$), and containing $\geq 25\%$ coniferous stems ($n = 11$), to arrive at a final sample of $n = 373$ plots for analysis.

2.7. Landscape controls over spring phenology

We contrasted three approaches to characterize how local topography and vegetation characteristics influences spring phenology across dissected landscapes. Our initial approach involved calibrating a simple ordinary least squares regression model to the remotely sensed spring phenology dates. Preliminary inspection of the variables, as well as visual relationships observed in Fig 1b, determined a nonlinear effect of elevation on spring greenup, with clear differences on lower hillslopes and ridgetops relative to valley bottomlands and mid-to-upper hillslopes. Therefore, elevation included a cubic function in the model. The model form was the following:

$$\begin{aligned} \text{Spring onset}_{DOY} \sim & b_0 + b_1^* \text{Elevation} + b_2^* \text{Elevation}^2 + b_3^* \text{Elevation}^3 \\ & + b_4^* \text{Slope} + b_5^* \text{Transformed aspect} + b_6^* \text{Species richness} \\ & + b_7^* \text{Wood density} + b_8^* \text{Canopy height} + \epsilon_r \end{aligned}$$

Support for a nonlinear effect was reinforced according to the difference in model fit between this model and a simpler model incorporating a linear effect ($\Delta\text{AIC} = 76.8$).

We then used variance partitioning to isolate the roles of topography and vegetation characteristics into individual and combined components, and to determine how these data are correlated with variation in spring phenology (Borcard et al., 1992). We used the *varpart* function in the *vegan* R package for this analysis (Oksanen et al., 2018). We assigned slope and transformed aspect variables into a Slope/Aspect group and species richness, community mean WD, and canopy height variables into a Vegetation group. Elevation terms were organized into a separate Elevation group, as we expected elevation to influence vegetation characteristics separately from that of Slope/Aspect variables.

Our second approach incorporated path analysis to test how relationships between topographic conditions and vegetation characteristics influence spring phenological variation. Topographic variables were treated as exogenous variables, while vegetation characteristics and spring phenology dates were treated as endogenous variables (Grace et al., 2010). These models included direct and indirect pathways connecting topographic variables directly to spring LSP greenup dates as well as through vegetation variables to characterize how spring phenology is mediated through changes in the diversity, functional

composition, and structure of forest stands, and how these variables are, in turn, influenced by variation in local topography. We included covariance terms linking vegetation characteristics as these conditions typically covary along topographic gradients in predictable ways across the study area (Adams and Matthews, 2019). We standardized all variables to units SD relative to mean values (i.e., z-scores) to aid in model convergence (Rosseele, 2012). We calculated all individual standardized path coefficients and *P*-values and used stepwise removal of insignificant paths ($P > 0.05$), using AIC, to arrive at the final model. A Chi-squared test was used to determine model fit, where $P > 0.05$ indicates acceptable fit of the model to the data (Grace et al., 2010). We used the *lavaan* R package to fit the path models (Rosseele, 2012).

2.8. Species controls over spring phenology

Our final analysis examined the relative importance of individual tree species on spring phenological timing. To do this, we developed a statistical leave-one-species-out approach, in which we re-calibrated a series of models, each time withholding a specific tree species from the calculation of community mean WD. For each species, we left one plot out at a time and recalculated the AIC value of the regression model, as well as the beta coefficient of WD (b_7^* Wood density), to obtain a distribution of the influence of individual tree species on model parameters. The relative change in model fit and coefficient estimates of WD were used to determine how much the relationship and model depends on specific tree species. For comparison, the permutation procedure was also repeated without altering the original WD values to generate a distribution of model parameters with all species included. We expected variation in parameters to reflect interactions between species biology and relative dominance. For example, we expected relatively dominant species with greater differences in average leaf-out timing relative to other species to influence the magnitude more greatly in model performance change.

3. Results

LSP revealed high spatial and temporal variability in long-term climatological average phenology dates across the study area (Fig. 1b) and field data. The timing of spring greenup occurred over an ~ 18 -day window, ranging from day 119 (April 30th) to day 137 (May 17th). The simple regression model, including topography, tree species richness, community-mean WD, and canopy height terms, explained nearly 52% of the variation in greenup across the field data. Although slope was the only insignificant variable at $P < 0.05$, we retained this variable to better understand how this information interacts with other stand features to influence vegetation phenology. Parameter estimates the regression model are displayed in Table 1.

Spatially, large temporal gradients in greenup occurred over relatively short distances and closely tracked changes in local elevation (i.e., relief). Specifically, the timing of spring greenup largely varied according to different segments of the slope in this dissected landscape. For

Table 1

Parameter estimates of the simple regression model explaining spatial variability in long-term annual spring greenup dates according to Land Surface Phenology image analysis.

Variable	β	\pm SE	<i>P</i>
Intercept	-766.40	96.90	<0.001
Elevation	10.51	1.13	<0.001
Elevation ²	-0.04	0.00	<0.001
Elevation ³	5.21 e^{-5}	4.35 e^{-3}	<0.001
Slope	0.02	0.02	0.52
Transformed aspect	-0.66	0.18	<0.001
Species richness	0.14	0.06	0.03
Wood density	12.42	2.63	<0.001
Canopy height	-0.16	0.03	<0.001

example, for the first 25 m of elevation increase (204–229 m.a.s.l. on our study site), reflecting upslope relief from valley bottomlands, spring greenup occurred later at a pace of about 2.7 days 10 m⁻¹. From 25 to 75 m above valley bottomlands (229–279 m.a.s.l), however, greenup entered a downward trend with increasing elevation, occurring earlier by -1.4 days 10 m⁻¹. Finally, from 75 to 132 m above valley bottoms (279–336 m.a.s.l.), largely reflecting relief along upper hillslopes and ridgetops, the regression again displayed a positive trend of 0.7 days 10 m⁻¹. In addition, the regression model revealed that spring greenup occurred later on southwestern aspects with comparatively lower canopy heights; these aspects also had greater species richness and community mean WD (Fig 3).

Variance partitioning revealed that elevation was the single best predictor of spring phenology at 38%, followed by vegetation (13%) and slope/aspect features (9%, Fig. 4). Elevation also explained the greatest

amount of residual variation (35%) after controlling for vegetation and slope/aspect, whereas vegetation and slope/aspect features accounted for only 8 and 2% of the unique variation, respectively. Nearly 30% of the total variation explained by vegetation can also be attributed to variation in slope and aspect, reflecting the influence of slope and aspect on vegetation composition across the study area. Similarly, elevation and slope/aspect also overlapped in explained variance, considering how variation in elevation shapes variation in slope and aspect. Collectively, though, all three factors share relatively little common variance (0.5%), suggesting that variation in the timing of spring greenup manifests out of two key relationships in the data: (1) the strong influence of elevation and its likely influence on microclimatic variation (Fisher et al., 2006); and (2) the influence of slope and aspect on forest vegetation composition (Hix and Pearcy, 1997).

Path analysis supported an improved understanding of the

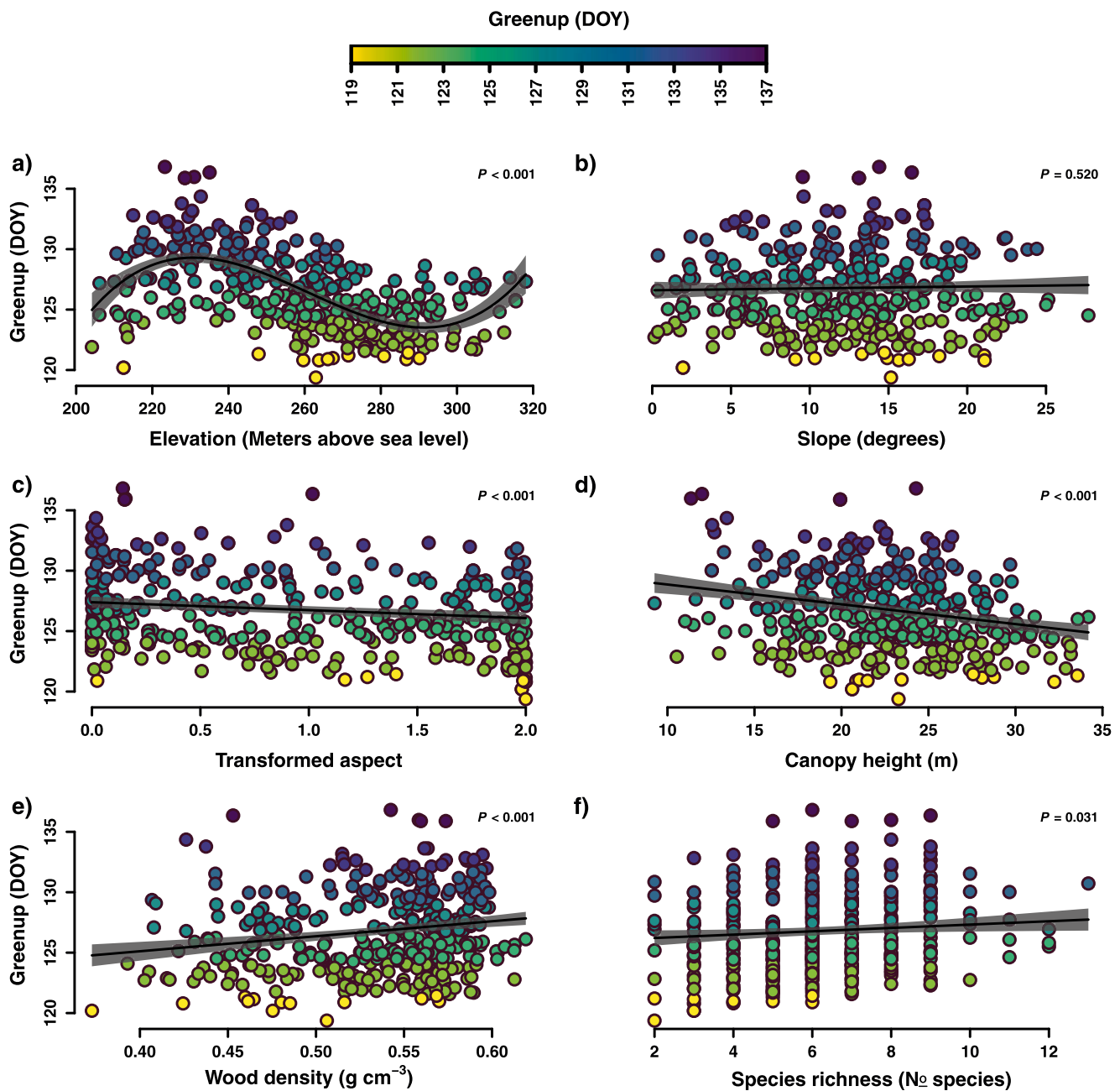


Fig. 3. Variation in predictor variables, (a) elevation, (b) slope percent, (c) transformed aspect, (d) canopy height, (e) community mean wood density, and (f) tree species richness, relative to long-term annual spring greenup dates estimated according to Land Surface Phenology image analysis. Break points and slopes in the relationship between elevation and greenup (a) were identified using segmented regression.

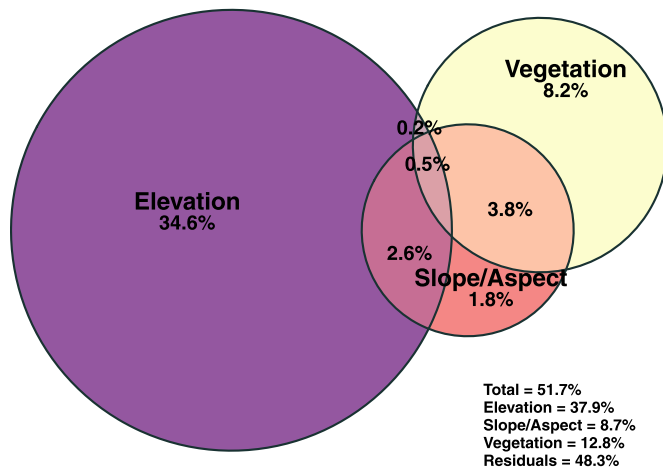


Fig. 4. A Euler diagram displaying the fractions of explained variation in spring phenology according to the pure, shared, and total contributions of each feature set. The size of each shape and overlap section corresponds the amount of pure and shared explained variation, respectively. Total variation of each feature set is provided in the legend in the lower left corner.

underlying processes regulating vegetation phenology across the study area (Fig. 5). The model fit the data well ($\chi^2 = 1.52, P = 0.82$). The model included direct pathways from elevation and transformed aspect to spring greenup dates. However, slope included only indirect pathways through community mean WD and tree species richness, consistent with its weak relationship in the regression model; yet underscoring the fundamental importance of slope on vegetation features influencing phenological patterns. Overall, topographic variables explained 2%, 13%, and 5% of the variation in vertical canopy height, WD, and tree species richness, respectively. In particular, the path model revealed strong influences of slope and transformed aspect on compositional and structural elements of the vegetation, consistent with variance partitioning results: community mean WD peaked on southwestern aspects, while canopy height peaked on northeastern aspects. Community mean

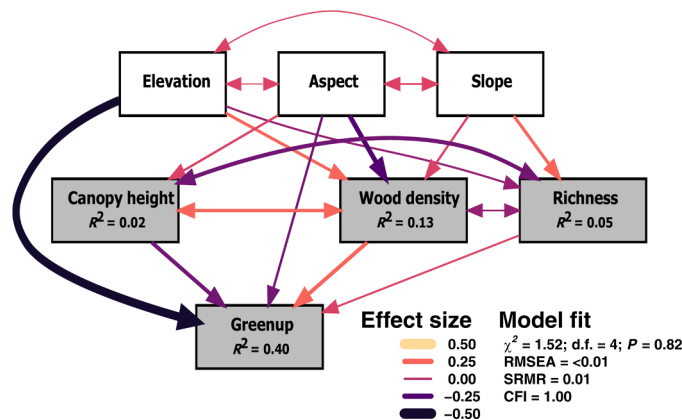


Fig.5. Path analysis model relating spring greenup dates to canopy height (m), community mean wood density (g cm^{-3}), species richness, elevation (m), transformed aspect, and slope ($^\circ$). Exogeneous variables were three topography variables indicated by white boxes, while endogenous variables are indicated by gray boxes. Explained variation (R^2) is listed for each endogenous variable. All pathways were significant at $P < 0.05$. The value of each standardized path coefficient corresponds to the width of each arrow (proportional to effect sizes reported in the legend), where positive to negative relationships reflect a color gradient from light tan to black, respectively. Covariance terms are denoted by bi-directional arrows. All summary fit statistics indicated good agreement between the model and the data, including the root mean square error of approximation (RMSEA), standardized root mean square residual (SRMR), and the comparative fit index (CFI).

WD, together with tree species richness, was also linked to elevation and slope, and collectively, indicated that WD peaked on upper hillslopes, while richness peaked on lower hillslopes.

The path model also helped to expose the emergent properties of vegetation features that help to contextualize landscape variation in vegetation phenology. We found a negative relationship between canopy height and species richness, where field plots with taller canopies generally contained a fewer number of tree species with relatively earlier greenup dates. Despite finding canopy height and WD to peak along dissimilar aspects (i.e., northeastern vs. southwestern slopes), we also found a positive relationship between these features, according to standardized path coefficients. This association likely emerges out of the relationship between stand-level BA and canopy height, where field plots dominated by taller trees also display an increasing density of trees with relatively larger stem diameters, regardless of species-level WD. In fact, plot-level mean canopy height generally showed some correlation with BA ($r = 0.35, P < 0.001$), while plot-level mean WD did not ($r = 0.05, P = 0.28$). Thus, plot-level WD primarily reflected a unique compositional signal.

Lastly, we tested the relative importance of individual species. Our species permutation procedure demonstrated changes in model fit (i.e., ΔAIC) and parameter estimates (i.e., b_7^* Wood density) according to the removal of species from mean WD calculations (Fig. 6). Once removed from plot-level mean WD estimates, two species, *Acer saccharum* and *Quercus montana*, displayed significant improvements in model fit based on non-overlapping median ($\pm 95\%$ C.I.) ΔAIC values $> \Delta\text{AIC} = 2$. In contrast, four taxa, *Aesculus flava*, *Carya* spp., *Quercus alba*, and *Q. rubra*, showed significantly worse model fit statistics once removed from the computation of plot-level mean WD. Removing one species in particular, *Quercus alba*, caused the largest change in model fit ($\Delta\text{AIC} = 16.74 \pm 0.11$) and underestimates in mean WD ($\pm 95\%$ C.I.) parameters (i.e., $\Delta b_7^* \text{Wood density} = -5.98 \pm 0.02$).

4. Discussion

4.1. Landscape controls over spring phenology

This study combined LSP techniques and field inventories to examine the relationships of topography and vegetation characteristics on phenological patterns at landscape scales. Our analyses reiterated the dual importance of local topography and vegetation characteristics on the timing of spring greenup, following prior studies over a variety of forest types (Klosterman et al., 2018; Liang et al., 2011; Misra et al., 2018; Xie et al., 2015). However, our analyses extended the results of previous studies by examining the often causative and correlative factors among phenological drivers of spring greenup timing. The variance partitioning and path analyses emphasized how topography shapes the composition and height relationships of forest vegetation and how these interactions influence phenological variability. While these relationships might be expected, phenological variation is rarely interpreted in this way (Reaves et al., 2018). Our approach thus supports an improved ecophysiological understanding of the spatial variability in spring phenology of temperate forestlands.

There exists a critical need in disentangling the environmental and organismal processes that drive spatial variation in vegetation phenology (Chmura et al., 2019) and our analyses provide direct evidence of how these two components shape the timing of spring greenup at landscape scales. First, elevation emerged as a dominant driver of spring greenup, explaining $\sim 35\%$ of the unique variation in the regression model. The importance of elevation has been reported in numerous studies across eastern deciduous forests, whereby local relief is thought to support phenologically relevant microclimates (Elmore et al., 2012; Fisher et al., 2006; Melaas et al., 2013). The relationships observed in this study were also nonlinear, efficiently summarizing variation along different segments of the slope (i.e., relief relative to valley bottomlands). For example, canopy development occurred later

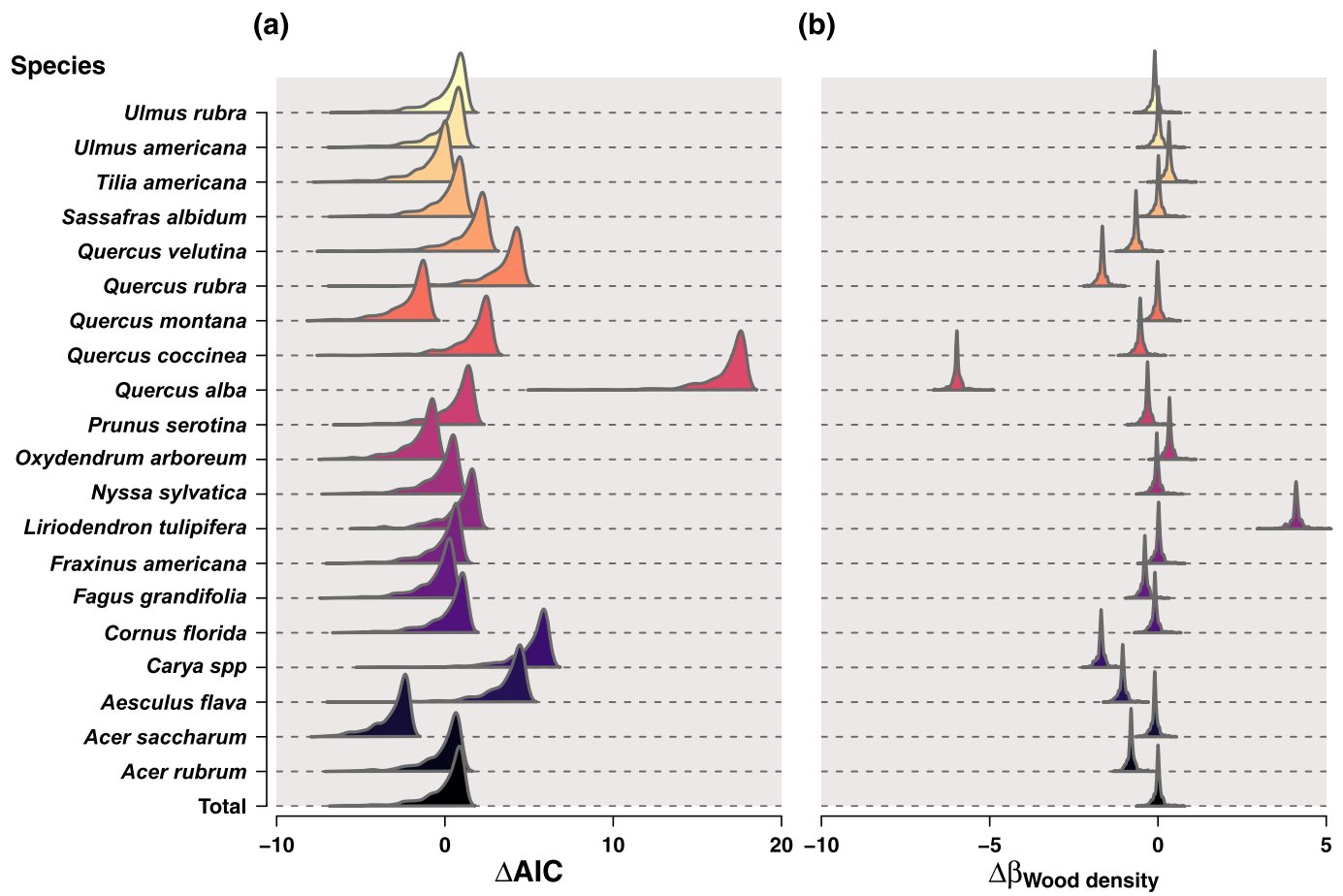


Fig. 6. Variation in model fit statistics (a) and community mean wood density parameters (b) following the removal of individual tree species from wood density estimates.

at the base of hills and ridgetops, and earlier within valley bottomlands and mid- to upper-hillslopes across an ~18-day temporal window among the field data. Future work should directly examine potential microclimatic differences among these slope segments to improve our understanding of elevation controls on vegetation phenology. Ultimately, the potential presence of persistent microclimates in a region with minimal elevational relief demonstrates the inherent influence of a dissected landscape and should be examined further in future work.

Second, slope and aspect also explained some of the phenological variability observed in this study, albeit less than elevation (~2% of the unique variation in the regression model). In particular, the path model revealed direct pathways between aspect and spring phenology, suggesting that this feature alone was primarily responsible for the direct relationships observed among slope and aspect. As a topographic feature, aspect directly influences the amount of solar radiation experienced across the landscape, and, as such, has an influence on energy exchange, soil moisture and nutrients, as well as microclimate variation, particularly air temperature (Desta et al., 2004; Hix and Pearcy, 1997; Iverson et al., 1997). These factors in turn interact to influence site productivity, growth (Radcliffe et al., 2020), and photosynthetic capacity (Bassow and Bazzaz, 1998) of forest vegetation, which might directly influence phenological variation of the vegetation as well.

Third, our results demonstrated the importance of vegetation components, particularly tree species composition, on spring phenology, explaining ~8% of the phenological variability in the regression model. Species distributions are considered first-order factors governing the timing of green-leaf development across forest landscapes and regions (Klosterman et al., 2018; Polgar and Primack, 2011). As an important species-level variable, stem anatomy, specifically whether a tree species

displays diffuse- versus ring-porous vessel elements, contributes to differences in leaf-out timing among individual tree species (Lechowicz, 1984; Sanz-Pérez et al., 2009). Specifically, the smaller vessels of diffuse-porous species reduces sensitivity to winter chilling, supporting earlier leaf-out relative to ring-porous species which often must compensate by producing new spring vessels (Barbaroux and Bréda, 2002; Wang et al., 1992). Such relationships illustrate the coordination of certain stem and leaf traits among woody plants, whereby fundamental biophysical attributes are interconnected to meet the demands of a range of ecological strategies (Chave et al., 2009; Lima and Rodal, 2010; MacFarlane, 2020; Stahl et al., 2013).

We used community mean WD to reflect ecophysiological differences, particularly porosity, among component tree species, which provided a clear compositional signal relevant in explaining the timing of spring greenup in LSP. Community mean WD has also been related to plant phenology within a tropical forest (Lima and Rodal, 2010), but its application in temperate phenological studies has not yet been thoroughly examined. There are examples of species with delayed leaf-out timing also exhibiting greater WD, e.g., oak species (Samtani et al., 2015). When averaged among all species within a field plot, we found a strong negative correlation between community mean WD and spring greenup. Indeed, the detection of delayed greenup patterns within LSP pixels has been related to greater oak species volume in another study (Xie et al., 2015). Our findings provide new insights into the ways we can incorporate ecophysiological information into plant community studies and suggest similar consideration in other studies.

Variation in forest vegetation effects did not emerge in isolation of local topography, however. Thus, our study also demonstrates how topography influences vegetation characteristics to shape phenological

variability at landscape scales. Understanding how phenological variation manifests at landscape extents required more nuanced approaches that allowed for the inclusion of vegetation assembly processes that influence species distributions across dissected landscapes. The novelty in this study lies in the explicit consideration of these processes through variance partitioning and path analysis procedures. Indeed, the behavior of phenological attributes in response to local topography has been interpreted in light of species distributions in other studies (Reaves et al., 2018; Xie et al., 2015). However, the interpretation of these processes remains severely limited in the literature (Isaacson et al., 2012). Our southeastern Ohio study area provided an exceptional case study, in which decades of ecological and silvicultural studies have documented species assemblage variation as related to topographic position and aspect (Adams et al., 2019; Hix and Pearcy, 1997; Iverson et al., 2017, 1997; Martin et al., 2011; Palus et al., 2018).

Nearly 30% of the total variation in the timing of greenup explained by forest height relationships, diversity, and functional composition of the vegetation was also explained by slope and aspect. This is because these factors, particularly aspect relative to north, strongly contributes to the establishment of species turnover in these landscapes. Species with life histories geared towards survival, greater WD, and tolerance of xeric site conditions dominate southwest-facing hillslopes (i.e., *Quercus* spp. and *Carya* spp.), while species facing fierce competition, exhibiting greater shade tolerance and faster growth (i.e., *Acer saccharum* and *Liriodendron tulipifera*), dominate the more productive northeast-facing hillslopes (Stahl et al., 2013).

These relationships were reiterated in the path analysis and explains the strong negative correlation between transformed aspect and community mean WD. The model also revealed a positive correlation between canopy height and transformed aspect, indicating that the tallest canopies were typically associated with northeastern exposures and earlier greenup patterns. While the final path model did not include a direct pathway from slope to greenup timing, it included indirect pathways through community mean WD and tree species richness, reinforcing the importance of slope on community assembly processes. The path model also indicated that WD peaked on upper hillslopes, while richness peaked on lower hillslopes. Thus, while local elevation displayed the single greatest direct effect on phenological variability, it also contributed to variation in vegetation features that correlate with phenological variation. The remaining unexplained variance also indicates that there may be other independent factors that influence to phenological variability. In particular, future studies should more directly incorporate microclimatic (air temperature, humidity) and soils variables to better account for the possible mechanisms regulating spring phenology and examine their interactions with topography and vegetation characteristics (Desta et al., 2004).

4.2. Species controls over spring phenology

Another key result in this study was the identification of species-level effects on spring phenological patterns among mixed-species stands. White oak (*Quercus alba*) emerged as a particularly important species in our permutation analysis. This species, along with other oaks, tend to leaf-out later than conspecific mesophytic species, such as *Acer saccharum*, by about a week (Lechowicz, 1984). As a result, we observed a diminished parameter effect of community mean WD when white oak was excluded from the analysis, suggesting that this species contributed significantly towards the negative relationship in spring greenup patterns relative to community mean WD. In addition to species biology (i.e., variation in leaf-out timing), there are two additional, potentially interacting, factors that could help explain the relative importance of white oak: (1) species relative dominance, and (2) species distribution along the phenological gradient. For example, while only present in just over half of the forest plots considered, white oak was generally the most dominant species where it did occur, according to BA measurements presented in Fig. 2. Second, white oak has been shown to reach peak

dominance along ridgetops and at the base of southwestern hillslopes in portions of the study area (Adams et al., 2019), locations also displaying the latest greenup patterns.

Oaks are considered foundational species in eastern forests (Ellison et al., 2005; Hanberry and Nowacki, 2016) and their regeneration ecology has been the subject of considerable scientific study for decades (Brose et al., 2013; Carvell and Tryon, 1961). However, exploiting the phenological characteristics of these species has yet to be explored as an explicit research objective in this and other similar landscapes. These results inspire further investigation, particularly towards identifying whether species such as white oak help to regulate phenological interactions and whether there are unique factors that contribute to the phenological variability of this species (Cole and Sheldon, 2017; Heberling et al., 2019). Collectively, these results underscore continued research on the effect of phenological variation on key species interactions that influence the stability of entire ecosystems (Polgar and Primack, 2011).

4.3. Limitations

There are of course limitations in interpreting phenological variation from LSP methods. A key discrepancy between ground-based approaches and those based on coarse spatial resolution remote sensing data is the type of information actually being measured (Berra et al., 2019; Bolton et al., 2020; Fisher and Mustard, 2007; Klosterman et al., 2018). Ground-based observations are typically taken at the scale of individual tree canopies, while coarse spatial resolution images record variation at the ecosystem level. Between these scales, within medium resolution Landsat data, is where remote sensing analysts have demonstrated great success in resolving ecological processes and addressing questions on the spatial drivers of landscape phenology (Elmore et al., 2012; Fisher et al., 2006; Melaas et al., 2013; Reaves et al., 2018). In the future, finer-scale satellite data (e.g., 10 m Sentinel-2 data, accumulating via the HiForm project (hiform.org)), along with enhanced processing capabilities, will allow refinement to these interpretations. However, discussing the complexities in LSP and agreement with ground-based phenology is beyond the scope of this study. Instead, we simply used supported methods in the literature to derive LSP across our study area and examined the variability in the timing of spring greenup relative to topographic and stand-level characteristics.

5. Conclusion

LSP revealed spatial and temporal variation in the phenological timing of forests across the dissected study area. This variation was attributed directly to variation in topography and vegetation features, including vertical canopy height, diversity, and species and functional composition. Elevation, related to relief above valley bottomlands, explained particularly large portions of this variance. However, this relationship was nonlinear, and implied varying rates of canopy development across different slope segments. Additionally, complex relationships between topography and vegetation features emerged out of plant community processes that influence the distribution of species assemblages. To fully appreciate these complexities, more nuanced approaches were required to help unravel the combined effects of topography on vegetation patterns and how these interactions ultimately influence variation in spring phenology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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