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RESEARCH PAPER

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Climate-driven trends in stem wood density of tree species in the eastern United States: Ecological impact and implications for national forest carbon assessments

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Abstract

Aim: For trees, wood density is linked to competing energetic demands and therefore reflects responses to the environment. Climatic trends in wood density are recognized, yet their contribution to regional biogeographical patterns or impact on forest biomass stocks is not understood. This study has the following two objectives: (O1) to characterize wood density–climate trends for coarse (i.e., angiosperm versus gymnosperm) and fine (i.e., within-species) taxonomic units and test a predictive model that incorporates these trends into a model that assumes range-wide wood density is constant; and (O2) to assess the impact of climate-driven intraspecific variation on forest biomass stocks for major tree species.

Location: We use an assemblage of eastern U.S. tree species for assessing climatic trends (O1), and then apply fitted models to forest inventory data spanning the eastern U.S.A. to assess impacts of forest carbon estimation procedures (O2).

Methods: We compared hierarchical models fitted to the full data to characterize wood density/climate gradients and to assess the impact of within-species variation (O1). Then, we compared predictions of biomass stocks from the climate-variable model with those of the static model using the Forest Inventory and Analysis (FIA) database (O2).

Results: We found among- and within-species trends related to temperature and moisture regimes, with differing responses between angiosperms and gymnosperms. Incorporating within-species variation in wood density increases the carbon stock of the study region by an estimated 242 Tg when compared with a species-only model.

Main conclusions: Intraspecific variation in wood density across species ranges suggests that climate influences investment in stem wood within tree species and contributes to biogeographical patterns in wood density in the eastern U.S.A. This variation impacts forest biomass stock assessments, and thus contributes refinements to the U.S. National Greenhouse Gas Inventory. In addition, our work highlights the potential for combining trait data and forest inventory to infer forest ecological processes at broad spatial scales.

KEYWORDS

Bayesian hierarchical models, biomass modelling, climatic variation, forest inventory, stem wood density

1 | INTRODUCTION

Stem wood specific gravity (i.e., the average dry weight of wood per unit green volume, hereafter referred to as ‘wood density’, WD) is a fundamental plant trait that is correlated with many aspects of the life history of woody plants. Wood density is negatively correlated with both mortality rates and growth rates (Kunstler et al., 2016; Woodall, Russell, Walters, D’Amato, Zhu, & Saatchi, 2015) across a broad range of angiosperm and gymnosperm tree species. Various hypotheses for these relationships have been suggested, including that greater wood density confers increased resistance to mechanical breakage (Niklas & Spatz, 2010), greater competitive effects (Kunstler et al., 2016), increased resistance to pests and disease (Chave et al., 2009) and reduced maintenance costs because of reduced trunk surface area (Anten & Schieving, 2010; Larjavaara & Muller-Landau, 2010). Regardless of the underlying mechanism, the relationship between wood density and growth or morality rates implies a trade-off that is ordinated along a wood density gradient (Poorter et al., 2008), and as such, wood density has been described as the central trait of a ‘wood economics spectrum’ that links physiological processes, such as water transport, to the growth and productivity of forested ecosystems across scales (Chave et al., 2009). These relationships make biogeographical patterns in wood density important for understanding broad-scale variation in growth and life history within and among species, with implications for models and management strategies that address future global change scenarios (Swenson et al., 2012).

Beyond these ecological implications, wood density is an important component of live and dead tree biomass estimation procedures and thus impacts the accuracy of national biomass assessments, as well as overall forest carbon stocks developed as part of greenhouse gas inventories. Many nations conduct biomass stock assessments with national forest inventory (NFI) data where tree-scale biomass models are used to make individual predictions based on common forest inventory measurements. In these contexts, volume conversion (VC) approaches are frequently applied, where stem biomass is estimated as the product of stem volume and wood density. VC approaches are used within the U.S. NFI as well as in the inventories of many European nations to ensure consistency between national volume and biomass stock assessments (Neumann et al., 2016; Woodall, Heath, Domke, & Nichols, 2011). Given that allometric relationships between stem diameter/height and tree size (i.e., volume) are relatively static (Enquist & Niklas, 2001), differences in wood density account for much of the variation in biomass model performance across multiple eco-regions and/or forest types (Woodall, Miles, & Vissage, 2005). Understanding geographical variation in wood density has the potential to have a positive impact on the accuracy and precision of forest biomass stock assessments and associated national greenhouse gas inventories (NGHGIs).

The importance of plant traits in governing the distribution of species across geographical and climatic gradients has long been recognized (Schimper, 1898). Several studies have documented general relationships between wood density and climate, as well as other resource gradients, such as soil fertility, across broad spatial extents (Chave, Muller-Landau, Baker, Easdale, & Webb, 2006; Lawton, 1984; Muller-Landau, 2004; Preston, Cornwell, & DeNoyer, 2006; Wiemann & Williamson, 2002). Given the substantial among-species variation in mean wood density (Chave et al., 2006; Swenson & Enquist, 2007), much of this variation is thought to arise from species and/or community sorting along environmental gradients (McGill, Enquist, Weiher, & Westoby, 2006). Dynamics like this have been well documented for the tropics (Chave et al., 2006), where very high diversity necessitates a functional rather than a species-specific approach, but interspecific trends in wood density also influence productivity–climate relationships in Northern Hemisphere forests (Woodall et al., 2015). In temperate regions, such relationships may be driven by trade-offs between competitive ability and resistance to cold and/or drought stress (Kunstler et al., 2016), with overall biogeographical trends influenced by both interspecific variation and broad differences between gymnosperms and angiosperms. For example, the prevalence of gymnosperm species at high latitudes has been attributed to their ability to maintain higher growth rates and therefore invest in fast-growing low-density wood when subject to stresses associated with cold climates (i.e., freeze–thaw dynamics, nutrient limitation) that limit the growth of angiosperms that are more competitive in warmer climates (Hacke, Sperry, Pockman, Davis, & McCulloh, 2001; Sperry & Sullivan, 1992). Wood density also plays a role in drought resistance at broad scales, with greater occurrence of species characterized by denser wood within both taxa in arid environments (Rueda, Godoy, & Hawkins, 2017). These biogeographical patterns have motivated the development of biomass modelling systems that attempt to capture phylogenetic relationships in wood density, either through using it as a covariate (Chave et al., 2014) or through designing allometric models where species are grouped using trait-based relationships (Chojnacky, Heath, & Jenkins, 2013). By integrating ecological information into traditional biometrical frameworks for predicting biomass, such approaches have promise for refining tree size–stem density relationships (Woodall et al., 2005) as well as the verifiability of national forest biomass stocks developed from NFIs.

Despite these advances, substantial uncertainty surrounding forest biomass stock estimates persists (Breidenbach, Antón-Fernández, Petersson, McRoberts, & Astrup, 2014; Chave et al., 2014; Clough, Russell, Domke, & Woodall, 2016; McRoberts & Westfall, 2014), suggesting a need to characterize additional sources of error in predictive models. Considering that species or functional groups are typically assigned an average trait value within NFIs, range-wide variation of wood density within species may represent one such source. Within-species variation in wood density has not been well explored despite a growing literature recognizing the role of intraspecific variability in plant traits, with some studies suggesting that within-species variation may be as great as among-species variation for a host of plant traits (Messier, McGill, & Lechowicz, 2010; Vilá-Cabrera, Martínez-Vilalta, & Retana, 2015). Intraspecific variation, whether arising from differentiation among populations into regional genotypes or from phenotypic plasticity, is increasingly recognized as a potentially important contributor to functional responses within ecosystems at a range of spatial scales (Anderegg, 2015). Wood density is a relatively conservative plant trait (i.e., it exhibits limited intraspecific variation) at the global scale (Siefert et al., 2015), but evidence suggests there may still be some relationship between it and climate. Wood density is believed to contribute to greater drought and freeze–thaw tolerance in many species (Hacke et al., 2001), and chronologies developed based on annual variation in latewood density of individual trees can be used for temperature reconstruction (Briffa et al., 1998; Fritts, 2001). Moisture availability, quantified using aridity indices, has been previously used in other studies assessing the impacts of climatic variation on tree growth and biomass accumulation (i.e., Foster, Finley, D'Amato, Bradford, & Banerjee, 2016) as well as in the development of biometrical models of other plant traits, such as biomass allocation to leaves and roots (Reich et al., 2014). However, the relative contribution of interspecific and intraspecific variation to regional climatic gradients in wood density, along with the impacts of accounting for trends both among and within species on forest biomass estimation procedures, have not been assessed.

This study uses an emerging dataset of wood density observations across forests of the eastern U.S.A. to address the following two broad objectives: (O1) to characterize wood density trends related to temperature and moisture availability for coarse (i.e., angiosperm versus gymnosperm) and fine (i.e., within-species) taxonomic units and test the predictive accuracy of a wood density model that represents these trends; and (O2) to assess the impact of incorporating climate-driven intraspecific variation when quantifying forest biomass stocks for major tree species. To address O1, we proceed with the following hypotheses: (H1) wood density will be positively related to temperature in gymnosperms and negatively related in angiosperms, owing to the better resistance of the former to stressors associated with cold climates (i.e., freeze–thaw, nutrient limitation) and the competitive advantage of the latter in warmer regions (Brodribb, Pittermann, & Coomes, 2012; Richardson et al., 2013; Sperry & Sullivan, 1992); (H2) wood density will be negatively related to moisture availability for both taxa, given the role WD plays in preventing drought-induced cavitation (Brodribb et al., 2012); and (H3) prediction of WD will be improved by accounting for both interspecific variation and intraspecific trends with mean temperature and aridity. Given the role wood density plays in mediating factors related to temperature (i.e., freeze–thaw dynamics), moisture availability (i.e., drought tolerance) and their interaction (i.e., whole-tree carbon allocation), we consider range-wide trends in variables related to both factors: mean annual temperature and an aridity index. To address O2, we assess the impact of incorporating climate-driven trends in WD into the estimation of forest carbon stocks for 10 common tree species of the eastern U.S.A.

2 | METHODS

2.1 | Data

We obtained wood density data from the United States Forest Service (USFS) legacy database (LegacyTreeData, 2016), a large compilation of individual tree attribute data for a range of commercially and ecologically important species within the U.S.A. These data have been compiled for the purposes of designing and validating improved biomass models for U.S. tree species (Radtke et al., 2017; Weiskittel et al., 2015) and are therefore a prime resource for assessing variation in tree traits. We used estimates of 'basic' wood specific gravity, which is defined as a unitless ratio of stem wood over dry weight per unit of green wood volume, divided by the density of water (Williamson & Wiemann, 2010). The dataset used here consisted of 11,842 observations of wood density from 83 species, collected at 505 unique sampling locations (Figure 1; Supporting Information). These data were compiled from 37 different studies across the eastern U.S.A.

Although the legacy data present a robust sample of wood density measurements, they are not uniformly distributed across space and taxonomic units. For example, the data show a geographical bias towards the southeastern U.S.A., with fewer samples in the north. In addition, major genera, such as *Pinus*, *Acer* and *Quercus*, are well represented, whereas less abundant taxa either have few samples or may not be represented at all. We use the full dataset to address our hypotheses related to climatic trends in wood density, but focus on the five gymnosperm and five angiosperm species that are best represented in the legacy data for the purposes of assessing impacts of within-species climate trends on carbon stock assessments (Supporting Information). This subset represents a diverse sample of wide-ranging, ecologically and commercially important tree species of the eastern U.S.A. and therefore presents a reasonable baseline for assessing the importance of climate-driven variation in wood density for improving the accuracy of forest carbon inventories.

To address our hypotheses, we develop models that predict wood density based on two covariates: (a) mean annual temperature (MAT; in degrees Celsius); and (b) an aridity index (AI), given the association these variables have with freeze–thaw cycles and drought. For MAT, we use an interpolated surface drawn from 30-year averages in the WorldClim database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Moisture availability is represented by an aridity index (AI = mean annual precipitation/potential evapotranspiration), from the Consortium for Spatial Information (CGIAR-CSI) Global-PET database (Zomer, Trabucco, Bossio, van Straaten, & Verchot, 2008). In this index, a higher AI corresponds to a wetter climate. These data are derived from WorldClim data and are therefore harmonized with the MAT data used in our study and available at the same scale. In preliminary analyses, we considered a wider suite of climatic variables related to temperature and precipitation extremes and seasonality (Supporting Information), but concluded that observed wood density trends with these variables, examined using graphical checks and summary statistics (R^2), were not significantly different from those observed with MAT and AI (i.e., all temperature and all precipitation variables were generally correlated).

2.2 | O1, H1–H2: Evaluating and comparing climate trends between gymnosperms and angiosperms

To assess differences in the wood density response to climate between gymnosperms and angiosperms, we fitted Bayesian linear regression models to pooled observations for both taxa. These models were

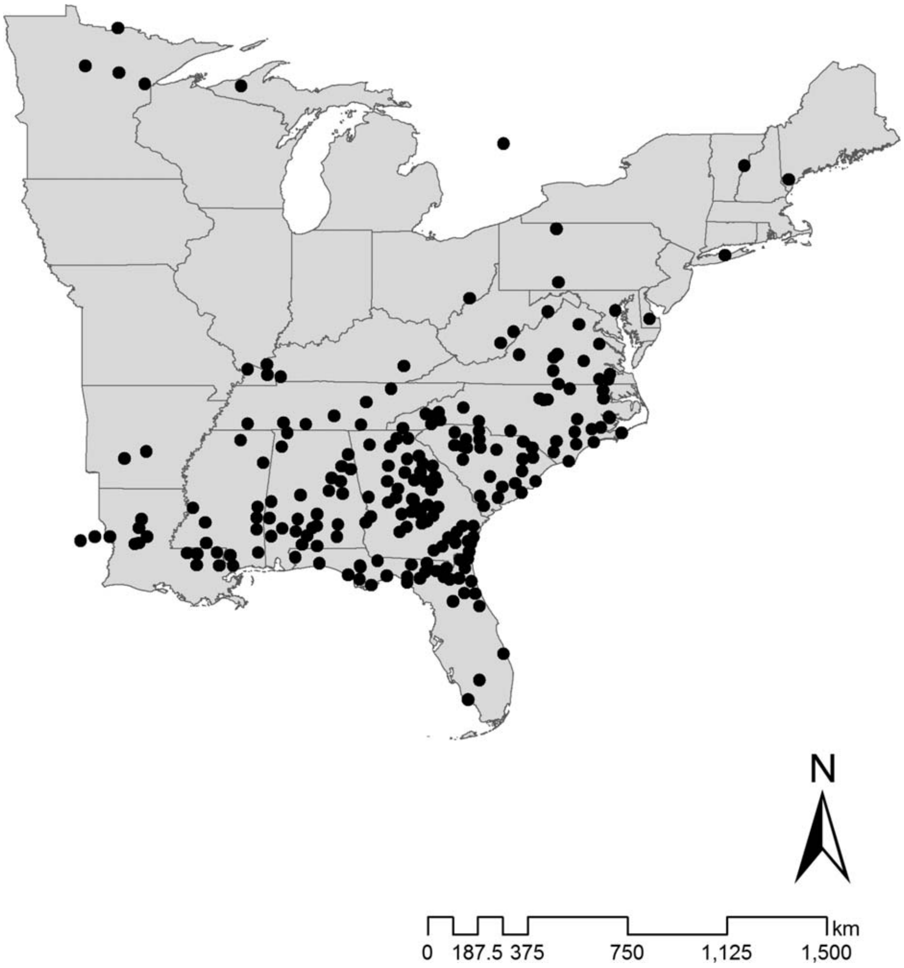

FIGURE 1 Distribution of sampling locations in the legacy wood density database

specified with weakly informative normal priors on the regression coefficients [~*N(0, 5)*] and half-cauchy priors on the data-level variances [~*Cauchy(0, 2.5)*; Gelman, 2006]. Mean trends for both taxa with MAT and AI were assessed graphically, and the degree of difference in climate responses was assessed by examining the degree of overlap of the posterior distributions of the regression coefficients. Separate models were fitted to gymnosperms and angiosperms. Model fitting was performed in Stan called from R using the rstan package (Stan Development Team, 2017a).

2.3 | O1, H3: Impact of among- and within-species climate trends on biogeographical patterns of wood density

To assess the effect of among- and within-species climate trends, we conducted a model comparison between 'pooled' (i.e., fitted to all angiosperm or gymnosperm observations) and 'species-specific' models that incorporate all possible formulations of MAT and AI (no climate trend, MAT only, AI only, MAT + AI, MAT + AI + MAT*AI; Table 1). Given the broad differences and potential climate responses of angiosperm and gymnosperm wood (Hacke et al., 2001), we separately fitted and compared these 10 candidate models to observations of each taxa.

The pooled models are similar to the linear regression models applied to test H1 and H2. The species-specific models fit separate coefficients for all species in the dataset, but allow these to arise from a common underlying hyper-prior distribution (Gelman, Carlin, Stern, & Rubin, 2003). In effect, this approach allows us to extend previously described among-species differences in climate responses to wood density (e.g., Woodall et al., 2015) by also accounting for within-species trends reflected by the fitting legacy data. The model without any climate variables assumes that wood density does not have predictable climate trends and is instead constant across a species' range, which is the same assumption as is made in current forest carbon estimation procedures used by the U.S. Forest Service.

The climate-variable models of wood density are written as:

$$WD_{ij} = \alpha_j + \beta_j \times \mathbf{X}_{ij} + \varepsilon_{ij} \qquad (1)$$

where i indexes 1,. . ., N observations and j indexes 1,. . ., J species, WD_{ij} represents the observed wood density values in the legacy data, $\mathbf{X}_{ij}$ is a design matrix containing measurements of selected climate variables at the sampling locations (i.e., MAT, AI and/or their interaction), β_j is a vector of associated regression coefficients, and ε_{ij} represents a vector of normally distributed 'white noise' error terms. The model parameters α_j and β_j are indexed by species, implying a separate set of

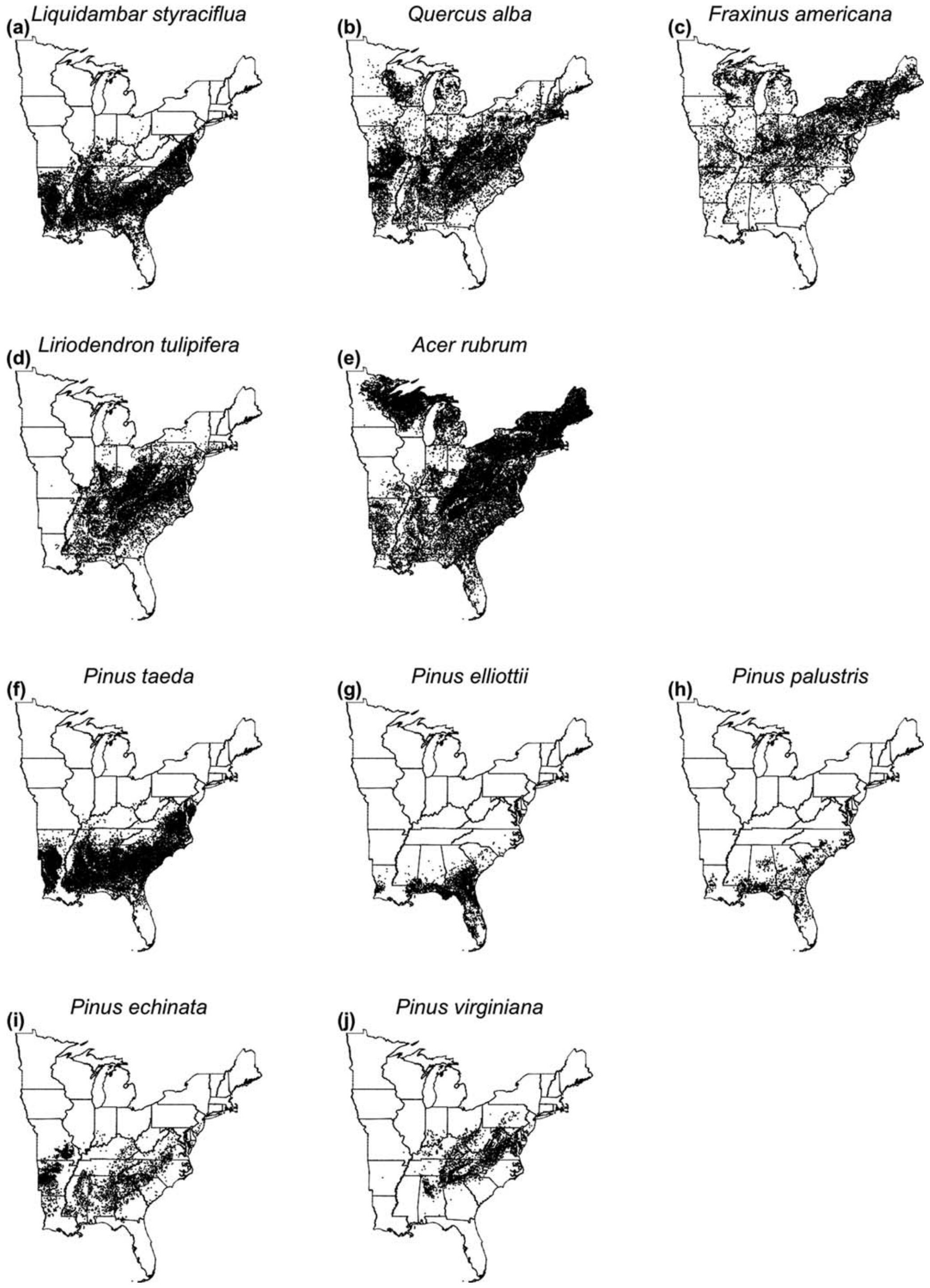

FIGURE 2 Distribution of prediction locations [Forest Inventory and Analysis (FIA) plots] for the most common angiosperm (2a–e) and gymnosperm (2f–j) species in the legacy data

model coefficients for each of the *j* species in the legacy dataset. To accommodate partial pooling among species, these vectors of species-level parameters are modelled with the following prior structure:

$$\alpha_j \sim N(\mu_\alpha,\ \tau_\alpha);\ \ \beta_j \sim N(\mu_\beta, \tau_\beta) \qquad (2)$$

where the location parameters (μ) are given normal hyper-prior distributions, and the scale parameters (τ) are specified with half Cauchy distributions (Gelman, 2006). The 'species-only' model has a similar prior specification to the climate model, but naturally lacks climatic trends:

$$WD_{ij} = \ \alpha_j + \varepsilon_{ij} \qquad (3)$$

where all model terms are as previously defined. This model estimates a species-level intercept from the legacy data but assumes that mean wood

TABLE 1 Overall approximate Bayesian leave-one-out information criteria (LOOIC) scores, model complexity penalties (pLOOIC) and LOOIC standard errors (*SE*) for the climate-variant and static models, fitted to the gymnosperm and angiosperm data

	LOOIC	*SE*	pLOO	ΔLOO	ΔLOO *SE*
Angiosperms					
Universal models					
MAT + AI + MAT*AI	−8,023	74.1	4.5	3,613.6	72.1
MAT + AI	−8,019.8	73.7	3.4	3,615.2	72
MAT	−7,939	71.1	2.5	3,655.6	72.3
AI	−7,979.3	74.1	2.3	3,635.4	71.4
Intercept only	−7,878.9	70.7	1.6	3,685.6	71.6
Species models					
MAT + AI + MAT*AI	−15,250	146	116.6	**	36.3
MAT + AI	−15,131.9	146.6	107.3	117.7	34.4
MAT	−15,043.7	143.7	89.7	205.9	33.2
AI	−14,378.3	148.4	77.5	871.3	11.6
Species intercepts	−14,194	143.4	57.8	1,055.6	32.1
Gymnosperms					
Universal models					
MAT + AI + MAT*AI	−21,246.3	221.2	7.5	1,101.8	58.8
MAT + AI	−20,994.2	219.6	6.3	1,227.8	61.5
MAT	−20,670.5	220.9	5.5	1,389.6	64.3
AI	−19,460.8	205.5	4.5	1,994.5	83.7
Intercept only	−18,865.3	202.1	3.5	2,292.3	85.1
Species models					
MAT + AI + MAT*AI	−23,449	285	36.9	**	32.3
MAT + AI	−23,391	283.9	35.5	57.9	28.1
MAT	−23,078.3	282.8	28.3	370.6	21.3
AI	−23,051.8	280	31.4	397.1	21.8
Species only	−22,583.4	278.9	21.2	865.5	31.3

Note. LOOIC is presented on the deviance scale, so a lower score indicates a better fit. Pointwise differences in LOOIC scores (Δ_{LOOIC}) are relative to the reference species-only model. The best-fitted model for each group is highlighted in bold text. ** indicates the best-fitted model for each taxa.

density for each individual species is constant across climate gradients. As previously indicated, we fitted separate models for angiosperms and gymnosperms. Models were fitted in Stan via the RStan package (Stan Development Team 2017a, 2017b), from four chains (a total of 2,000 Markov chain Monte Carlo simulations, with the initial 2,000 simulations discarded). This sample was sufficient to gain model convergence according to the Gelman–Rubin statistic (Gelman & Rubin, 1992).

We compared the candidate models (Table 1) using Bayesian approximate leave-one-out cross-validation (LOO-CV) and the leave-one-out information criteria (LOOIC; Vehtari, Gelman, & Gabry, 2017). This method is similar to other information criteria, such as Akaike's information criterion (AIC) or the deviance information criterion (DIC), in that it represents a computationally efficient approximation of LOO-CV (Gelman, Hwang, & Vehtari, 2014), but differs in that it uses a log pointwise predictive density (lppd) to evaluate predictive performance based on the full data rather than a plug-in estimate of the predicted mean or median as with AIC and DIC (Gelman et al., 2014; Vehtari et al., 2017). The lppd is represented as:

$$\mathrm{lppd} = \sum_{i=1}^{n} \log \int p(y_i|\theta)\, p_{\mathrm{post}}(\theta|y)\, d\theta \qquad (4)$$

where $\log p(y_i|\theta)$ represents the log predictive density for an individual observation y_i, and $p_{\mathrm{post}}(\theta|y)$ represents the posterior distribution of a fitted model based on the full datset y. The lppd can be expressed on the deviance scale by multiplying by -2, and a penalty for effective number of parameters is applied as with other information criteria (Gelman et al., 2014). Model comparison is then facilitated by comparing the difference in LOOIC (Δ_{LOOIC}) as well as the standard error of this difference (Δ_{SE}) between two fitted models (Vehtari et al., 2017). Posterior estimates of lppd can be obtained from a Stan program with negligible computational cost relative to what is needed to fit the model. We obtained this output for each of our fitted models and computed LOOIC within the 'loo' package for R, following the methods outlined by Vehtari et al. (2017). After ranking all candidate models based on LOOIC, we compared the best-fitted model with the remaining models in order to assess whether they were substantially different (i.e., $\Delta_{\mathrm{LOOIC}} \pm \Delta_{SE}$ does not contain zero).

2.4 | O2: Assessing impact of inter- and intraspecific wood density variation on forest carbon stock assessments

To assess the impact of among- and within-species wood density climate trends on forest carbon (C) stock estimates, we compared predictions of stem wood C from three models for a full cycle of U.S. Forest Service Forest Inventory and Analysis (FIA) data collected between 2009 and 2013 (Figure 2), as follows: (a) a model including both species and climate effects; (b) a 'species-only' model that assumes wood density is constant across climate gradients; and (c) a 'climate-only' model that captures wood density climate trends but ignores interspecific variation among gymnosperms and angiosperms. We confine our analysis to stem wood C because crown and belowground biomass components are predicted directly, rather than using the 'component ratio method' that is currently used in FIA (i.e., volume to biomass conversion using WD; Woodall et al., 2011). The full FIA sample consists of individual tree measurements (e.g., species, stem volume as estimated via U.S. Forest Service procedures) on 70,656 plots distributed across the study region. Before estimating C stocks, we filtered the tree-level data to remove dead trees and seedlings and saplings below 12.7 cm diameter at breast height.

The parameters for the 'species–climate' and 'climate-only' prediction models are the posterior mean estimates derived from fitting to the legacy data, whereas the 'species-only' WD estimates are from Miles and Smith (2009). In the latter case, we prefer using these estimates rather than those from fitting the 'species-only' model to the legacy data because their survey included additional species and they are the WD expansion factors currently used by the USFS. For the 'species–climate' model, when a species represented in the FIA data was not among those in the legacy data, we used average parameter values for angiosperms or gymnosperms instead. The 'climate-only' model also separates prediction of WD into angiosperms and gymnosperms. The climate variables used for prediction (e.g., MAT, AI and their interaction) were determined by model fitting and comparison for the legacy data.

We first calculated stem biomass for individual trees as:

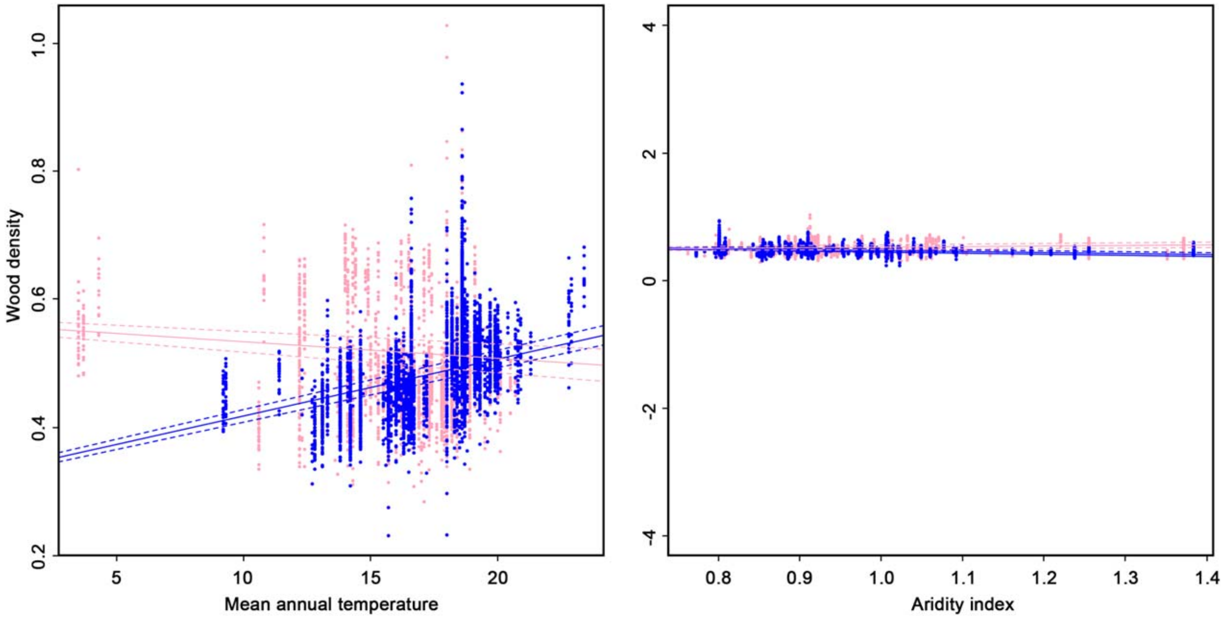

FIGURE 3 Overall relationships between wood density and climate variables for gymnosperms (blue) and angiosperms (red). The continuous lines represent posterior mean trends, whereas the dotted lines represent the upper and lower bounds of the 95% uncertainty interval of the trend line

$$\mathrm{BIO}=\mathrm{VOL}\times\mathrm{WD} \tag{5}$$

where BIO is stem biomass (in kilograms), VOL is stem volume (in cubic metres) previously estimated using standard USFS procedures, and WD is wood density predicted by one of the three models outlined above. After predicting stem biomass at the tree scale, we converted biomass to C via standard U.S. Forest Service conversions ($C = \mathrm{BIO} \times 0.5$), and these were summarized for FIA plots and converted to plot-level stocks (in megagrams per hectare) for comparison of the three C estimation procedures. We examined impacts of incorporating climate and/or species information on the overall stock of the eastern U.S.A. and assessed regional patterns in the degree of difference among plot-level predictions.

3 | RESULTS

3.1 | O1, H1 and H2: Differences in climate relationships between gymnosperms and angiosperms

When data from all species were pooled, we found that posterior mean wood density responses to both MAT and AI were divergent for both gymnosperms and angiosperms, although posterior distributions of the regression coefficients substantially overlapped in the latter case (Figure 3). In the case of MAT, angiosperms showed a slight negative response (posterior mean of slope *c.* −0.003), whereas gymnosperms showed a stronger positive response (posterior mean of slope *c.* 0.008). Regression coefficients for the angiosperm and gymnosperm models were significant (i.e., 0 was outside the 95% uncertainty interval for both taxa) and substantially different (i.e., 95% uncertainty intervals of both slopes and intercepts did not overlap). In the case of AI, the opposite pattern was observed, with gymnosperms showing a slight negative trend (posterior mean slope of *c.* -1.5×10^{-5}) and angiosperms showing a slight positive trend (posterior mean slope of *c.* 8.0×10^{-5}). However, posterior uncertainty of the relationship between wood density and AI was highly uncertain for both taxa, with posterior distributions of the regression coefficients strongly overlapping and including zero. Results of this model comparison present evidence for significant differences in temperature trends between gymnosperms and angiosperms, but do not find that responses to moisture availability exhibit consistent responses at this broad taxonomic scale.

3.2 | O1, H3: Among- and within-species climate trends in wood density

The model comparison analysis indicates that, for both angiosperms and gymnosperms, the species-specific models incorporating both MAT and AI as well as their interaction have the best predictive accuracy (Table 1). In both cases, this model was substantially better than the next best competing model, the species-specific model with MAT and AI but no interaction, when performing a pointwise comparison of differences in predictive performance. Among the universal models, including all climatic information increased the model fit for both angiosperms and gymnosperms, although in the case of angiosperms the improvement was narrow over the other candidate climate models. However, in both taxa the 'intercept-only' species-specific model (i.e., the model accounting for species differences but not climate trends), provided a better fit than any of the universal candidate models.

To provide additional context to the model comparison results and the taxa-level trends, we plotted posterior mean responses to both MAT and AI for the five most common gymnosperm and angiosperm species in the legacy data (Figure 4). The general trend of

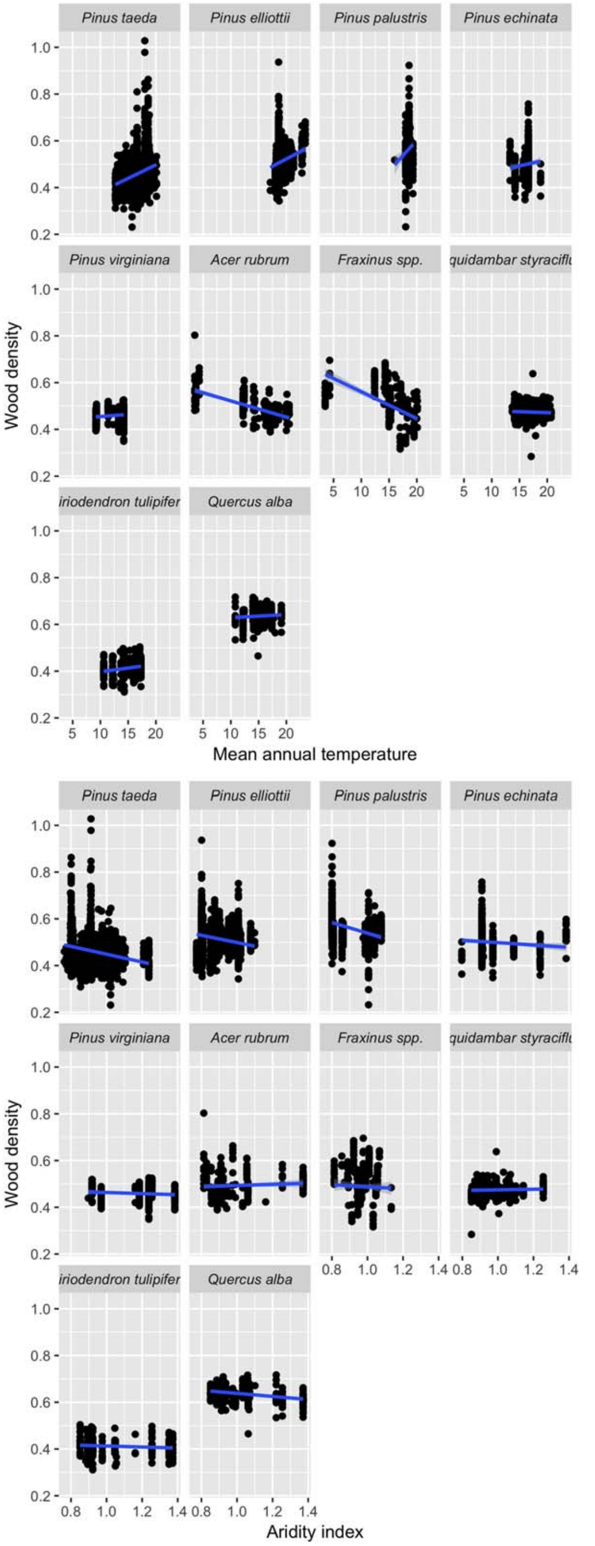

FIGURE 4 Wood density–mean annual temperature and wood density–aridity index relationships for the major species in the legacy database

increasing wood density with increasing MAT and decreasing wood density with increasing AI was observed with all five pine species (Figure 4a–e), although the relationship between wood density and AI for *Pinus virginiana* (Mill.) was weak. Among angiosperms, *Liquidambar styraciflua* (L.; Figure 4h), *Fraxinus* spp. (Figure 4g) and *Acer rubrum* (L.; Figure 4f) agreed with overall negative trends with MAT observed for all angiosperms, while *Quercus alba* (L.; Figure 4j) and *Liriodendron tulipifera* (L.; Figure 4i) showed positive trends. In the case of AI, *Quercus alba* (Figure 4t), *Liriodendron tulipifera* (Figure 4s) and *Fraxinus* spp. (Figure 4q) showed slight negative trends, while the remaining two species showed no trend. These patterns did not agree with the aggregated response of angiosperms to AI, which was slightly positive.

3.3 | O2: Assessing impact on range-wide forest carbon stock assessments

For the sample of eastern U.S. FIA plots that we analysed, the prediction model that incorporated both climate and species information generated the largest average C stocks on FIA plots (31.3 Mg/ha), whereas the model using only climate information produced the smallest biomass stocks on average (25.7 Mg/ha). Incorporating species information without climate gradients also increased biomass stocks relative to the climate-only model, but to a smaller extent when compared with the species–climate model (29.6 Mg/ha). The distribution of predicted forest C stocks of all three models broadly overlap, with each showing a lower 90% quantile bound of *c*. 1.4 Mg/ha and upper bounds ranging from 65.4 Mg/ha (climate only) to 79.8 Mg/ha (climate–species). Plotting predicted C stocks of FIA plots from the climate–species model against the other candidate models exhibited a generally positive bias across all stock sizes when compared with the climate-only model, with a smaller positive bias primarily among larger predicted C stocks when compared with the species-only model (Figure 5).

Assuming a forested land area of 156 million ha for our study region, the total predicted stem C stocks of the climate–species, species-only and climate-only models are 4,886, 4,613 and 4,007 Tg, respectively. These correspond to increases in aboveground forest C stock estimates of 273 Tg over the species-only model and 879 Tg over the climate-only model when incorporating both species and climate information to estimate forest C stocks.

4 | DISCUSSION

Our results demonstrate that variation in temperature and moisture regimes is associated with among- and/or within-species trends in wood density across broad climatic gradients in the eastern U.S.A. These findings contribute to growing literature (e.g., Anderegg, 2015; Siefert et al., 2015) on the plasticity of plant traits across environmental gradients. Our work has clear implications for national forest biomass assessments, as within-species variation in wood density is not typically accounted for when developing stock assessments. Furthermore, by providing a basis for mechanistic studies aimed at understanding the factors driving this intraspecific variation, our findings highlight the potential of wood density as a central trait for interpreting and predicting forest ecological processes across broad spatial extents.

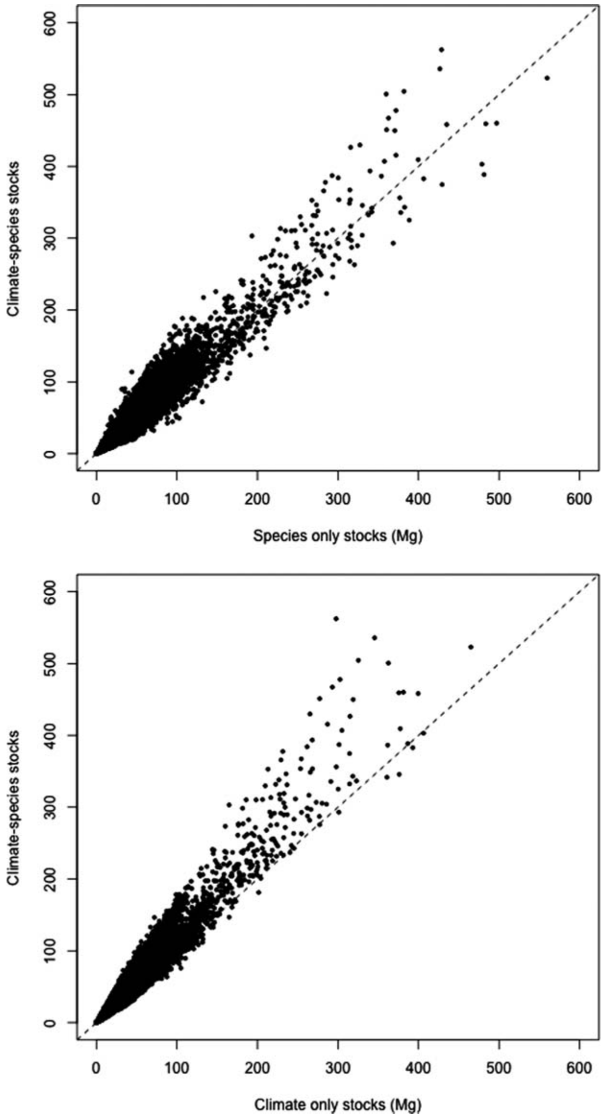

FIGURE 5 Comparison of forest carbon stock predictions, for individual Forest Inventory and Analysis (FIA) plots, from the model incorporating both climate and species information with models using climate only and species only

4.1 | Impact of within- and among-species climate trends on geographical variation in wood density

Our results support our hypothesis regarding varying relationships between wood density and temperature for gymnosperms and angiosperms, but do not confirm our hypothesis regarding relationships with aridity. We suggested that gymnosperms would have a positive relationship between wood density and temperature (i.e., lower density at cooler temperatures), owing to better resistance to freeze–thaw embolism (Brodribb et al., 2012; Sperry & Sullivan, 1992) and/or nutrient limitation in cold environments (Reich et al., 2014; Richardson et al., 2013), whereas angiosperms would display the opposite trend owing to fewer environmental constraints on growth in warmer climates. The patterns we observed aligned with these mechanisms, but the extent to which they are driven by direct impacts of temperature versus other correlated effects was not addressed by our study. For example, the observed lower wood density of many gymnosperm species at colder sites might relate to physiological responses to environment but could also be explained by a need to increase growth rates to compete for light in mixed-species assemblages that are dominated by hardwoods (Carnicer, Barbeta, Sperlich, Coll, & Peñuelas, 2013, Kunstler et al., 2016). The data we analyse include limited observations for boreal conifer species, with much of the gymnosperm data consisting of pine species native to the Atlantic coastal plain of the eastern U.S.A. that intermix with hardwoods at higher latitudes. Despite this biogeographical trend, we found an opposite WD/temperature trend for angiosperm species that supports the hypothesis outlined by Hacke et al. (2001) that better resilience of gymnosperm wood to freeze–thaw stress plays a role in determining biogeographical patterns in wood density.

The lack of a relationship with AI is surprising given the role wood density plays in mitigating impacts of drought. Drought tolerance has been shown to play a significant role in determining the distribution of gymnosperm species within our study region (Rueda et al., 2017). However, none of the sampling locations in the legacy data is hyper-arid, so it is possible that our data did not possess a sufficient range of moisture stress for clear trends to manifest. Alternatively, our results might indicate that other accounted for (temperature) and unaccounted for (e.g., competition, soil fertility gradients) factors are stronger drivers of wood density trends at the regional scale. For example, Reich et al. (2014) found that the impact of aridity on biomass allocation patterns in trees was limited compared with the direct and indirect effects of temperature gradients, whereas Kunstler et al. (2016) have demonstrated globally consistent impacts of competition on biomass storage that may further complicate biogeographical patterns. Additional work is needed to gain a complete understanding of the ecological and physiological mechanisms that underlie the patterns revealed by our study.

Beyond whole-taxa relationships between WD and climate, our model comparison analysis, coupled with graphical analysis of within-species climate trends, confirms our hypothesis that simultaneously accounting for both among- and within-species climate trends will produce the WD model with the best prediction accuracy. These results support findings from other studies that have explored the plastic responses of tree species to environmental gradients, suggesting that intraspecific climate responses contribute to the biogeography of wood density across the eastern U.S.A. Experimental evidence for temperature-driven intraspecific variation in wood density is available for gymnosperms (e.g., *Pinus* species; Kilpeläinen, Gerendiain, Luostarinen, Peltola, & Kellomäki, 2007; Kilpeläinen, Peltola, Ryyppö, & Kellomäki, 2005; Telewski, Swanson, Strain, & Burns, 1999) as well as angiosperms (e.g., *Eucalyptus*; Thomas, Montagu, & Conroy, 2004). Additionally, several studies have documented intra-annual variation in the density of new growth related to climate manipulations (Bouriaud, Leban, Bert, & Deleuze, 2005; Skomarkova et al., 2006), and similar relationships are widely used in dendrochronological studies to reconstruct historical climate records (Briffa et al., 1998). Such experimental evidence, when taken in context with our results and other findings of biogeographical trends of within-species trends in wood density reported in the literature (Richardson et al., 2013; Thomas et al., 2004), indicates that plastic physiological responses are at least in part responsible for driving broad patterns of wood density variation along latitudinal and environmental gradients (Chave et al., 2006; Muller-Landau, 2004; Wiemann & Williamson, 2002; Williamson & Wiemann, 2010). This is significant because it suggests that intraspecific variation, whether related to phenotypic plasticity or to regional variation in genotype (Anderegg, 2015), can contribute to the biogeography of plant traits, rather than broad patterns only arising from species sorting along environmental gradients (Chave et al., 2006; Swenson & Enquist, 2007; Swenson et al., 2012).

4.2 | Practical impacts of wood density–climate trends on forest carbon stock assessments

On average, the prediction model using species and climate information led to a 6% increase in forest C stock estimates for FIA plots when compared with the current approach used by the USFS to expand stem volume into biomass and C estimates (i.e., using standard WD estimates across the full range of individual tree species; Miles and Smith, 2009). Based on a simple expansion of plot-level C stock assessments with estimated total forest land area of the study region, the climate–species model increases the overall forest C stock by *c.* 270 Tg; roughly a third of the overall annual carbon sink from land use, land change and forestry reported within the U.S. NGHGI (787 Tg CO_2 in 2014; United States Environmental Protection Agency 2016). Although the impact on overall forest C stock change can be limited by consistent application of C estimation procedures across a baseline, these results suggest that incorporating climate information can contribute to meeting international C sequestration commitments by reducing the uncertainty associated with forest C estimation approaches. However, our study region represents only a portion of all forested land in the U.S.A., so the extent to which climate information can improve C estimation in forested ecosystems not covered by the legacy data remains unknown. Additional wood density data, particularly from western U.S. species, northern hardwood species and sub-boreal conifers, will enable the impacts of intraspecific climate variation on the national forest biomass stock of the U.S.A. to be assessed fully.

The findings of our work provide a basis for using biogeographical trends in wood density to address broader questions about controls on forest dynamics at the continental scale. We have reported on climate-related trends in within-species variation of wood density and have connected these to physiological mechanisms to interpret divergent trends observed between gymnosperms and angiosperms. However, identifying the mechanism(s) driving these patterns was beyond the scope of our study. Understanding the contribution of climatic adaptation (i.e., plastic responses in wood density to induce resistance to cold and/or drought stress) versus competition (i.e., decreasing wood density resulting from a need to maintain a higher growth rate) is of particular importance (Carnicer et al., 2013; Kunstler et al., 2016). Additionally, the hierarchical modelling framework we propose might be used to describe similar climate trends in other plant traits related to biomass stock distribution. Our results describe relatively small but significant responses of wood density to temperature and corresponding increases in range-wide biomass stocks despite the fact that wood density is a relatively conservative trait across geographical and taxonomic variation (Siefert et al., 2015). Future work should focus on assessing within- and among-species climate trends for more plastic traits, such as leaf traits, which can also impact the accuracy of predictive forest biomass models. Integrating diverse datasets, such as plant trait databases and forest inventory data, within the context of hierarchical models presents significant opportunity for improving prediction and inference of forest dynamics both across space and through time.

5 | CONCLUSIONS

Although interspecific differentiation explains substantial variation in wood density in large assemblages of woody plant species, within-species responses to climate gradients also contribute to overall biogeographical patterns of wood density in forests of the eastern U.S.A. The data from which we draw our inferences are highly variable, but the improved model fit when accounting for within-species wood density temperature and moisture gradients, coupled with the strong patterns in several ecologically important tree species, leads us to suggest that intraspecific variation should be considered as an important explanatory factor of forest growth and biomass distribution across broad spatial extents. The trade-offs we observe between gymnosperm and angiosperm tree species may relate to divergent investments in growth and defense across the temperature gradient, although accounting for underlying mechanisms to observed patterns was beyond the scope of our study. Our results suggest that incorporating a climate-variable model refines biomass stock assessments at a level which has implications for estimating annual stock change estimates at the national scale, and overall estimates at local to regional scales. In addition, understanding the mechanisms that underlie intraspecific variation in wood density will improve our overall understanding of controls on forest growth at the continental scale.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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