Forest Ecology and Management 372 (2016) 175–188

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Quantifying allometric model uncertainty for plot-level live tree biomass stocks with a data-driven, hierarchical framework

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ARTICLE INFO

Article history:
Received 8 January 2016
Received in revised form 31 March 2016
Accepted 1 April 2016
Available online 16 April 2016

Keywords:
Forest biomass
National greenhouse gas inventory
Data assimilation
Bayesian hierarchical models

ABSTRACT

Accurate uncertainty assessments of plot-level live tree biomass stocks are an important precursor to estimating uncertainty in annual national greenhouse gas inventories (NGHGIs) developed from forest inventory data. However, current approaches employed within the United States' NGHGI do not specifically incorporate methods to address error in tree-scale biomass models and as a result may misestimate overall uncertainty surrounding plot-scale assessments. We present a data-driven, hierarchical modeling approach to predict both total aboveground and foliage biomass for inventory plots within the US Forest Service Forest Inventory and Analysis (FIA) program, informed by a large multispecies felled-tree dataset. Our results reveal substantial plot-scale relative uncertainties for total aboveground biomass (11–155% of predicted means) with even larger uncertainties for foliage biomass (27–472%). In addition, we found different distributions of total aboveground and foliage biomass when compared with other generalized biomass models for North America. These results suggest a greater contribution of allometric models to the overall uncertainty of biomass stock estimates than what has been previously reported by the literature. While the relative performance of the hierarchical model is influenced by biases within the fitting data, particularly for woodland and conifer species, our results suggest that poor representation of individual tree model error may lead to unrealistically high confidence in plot-scale estimates of biomass stocks derived from forest inventory data. However, improvements to model design and the quality of felled-tree data for fitting and validation may offer substantial improvements in the accuracy and precision of NGHGIs.

1. Introduction

At the global scale, forest biomass possesses capacity for mitigating anthropogenic emissions of greenhouse gases through growth and related carbon sequestration (Birdsey et al., 2013; Pan et al., 2011). As a result, estimates of live tree forest biomass stocks (hereafter referred to as forest biomass) and associated uncertainty are a key component of national greenhouse gas inventories (NGHGIs) that are used as baselines for assessing overall carbon stock changes among signatory nations of the United Nations' Framework Convention on Climate Change (UNFCCC; Birdsey and Heath, 1995; Woodall et al., 2011). In the United States' (US) NGHGI, as well as those of many European nations, national biomass stocks are calculated from plot-scale estimates which summarize the predictions of tree-scale static allometric models for total aboveground biomass and biomass fractions (e.g., stem, branches, foliage; Domke et al., 2012; Neumann et al., 2016). In addition, general allometric models have also been recommended for calculating forest carbon inventories in tropical regions (Chave et al., 2014). However the overall error of these models as well as the extent to which they contribute to uncertainty (i.e., accuracy and precision) at the plot-level is poorly understood, particularly for highly variable pools such as foliage (Weiskittel et al., 2015). Improving the accuracy and precision of plot-scale total aboveground and component stock assessments can contribute further refinements to the US NGHGI by increasing the utility of forest inventory data for improving national-scale models.

Plot-level estimates of forest biomass used within the US NGHGI are based on the US Forest Service's (USFS) Forest Inventory and Analysis (FIA) data. Currently, these estimates are calculated using the 'component ratio' method (CRM; Woodall et al., 2011; Domke et al., 2012) with uncertainty estimates obtained using a Monte Carlo simulation with constraints on variances around parameters of allometric models for total biomass and components. This approach is supported by recent work which has

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http://dx.doi.org/10.1016/j.foreco.2016.04.001
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applied similar error propagation techniques to assess contributions of model uncertainty to large area estimates of forest attributes, including live tree volume for the US FIA data (McRoberts and Westfall, 2014), and biomass for the Norwegian National Forest Inventory (Breidenbach et al., 2014). Both of these studies found a small contribution of allometric model error to overall uncertainty in stock estimates relative to sampling error in the inventory data, but while this approach allows for probabilistic estimation of biomass stock uncertainty, it requires that assumptions are made about the expected scale of uncertainty. These are typically based on expert opinion and/or results within the literature but are difficult to verify, which contributes to a substantial risk of either overestimating or underestimating variance within predictive models. In contrast, quantifying uncertainty by fitting statistical models allows for the variances of allometric model parameters to be quantified by observed data if an appropriate technique is used. Such an approach facilitates the identification of the largest sources of uncertainty which in turn can enable cost effective improvements to data collection and/or model development with a goal of accurate uncertainty estimates surrounding plot-scale biomass stocks.

Over the last decade, there has been increasing interest in the use of predictive statistical models for estimating forest carbon processes, as well as prediction uncertainty, across large areas (Luo et al., 2011). Such approaches have been used to incorporate data from intensive sampling efforts to inform parameters of carbon process models (Keenan et al., 2012; Weng et al., 2012; Williams et al., 2005) and to predict carbon fluxes and stocks both across space and through time (Scholze et al., 2007; Schwalm et al., 2010; Ziehn et al., 2011). With the goal of data-driven uncertainty estimation and mean prediction of forest biomass stocks, Bayesian hierarchical models present a methodological framework that naturally accounts for uncertainty in both model parameters and predictions of new observations, conditioned upon the observed data the analyst has at hand as well as their prior expectations (Carlin and Louis, 1996; Cressie et al., 2009; Gelman et al., 2003). This feature naturally incorporates model uncertainty into prediction uncertainty and allows for seamless "up-scaling" across individual tree, plot, and population scales. Hierarchical models have been applied to model other forest attributes such as forest growth and biomass at the tree-scale (Green et al., 2000; Zapatas-Cuartas et al., 2012), as well as at larger spatial extents (van Oijen et al., 2013). In addition, several studies have used hierarchical models to predict forest biomass for large areas of the US, using plot-level estimates obtained from FIA data (Datta et al., in press; Finley et al., 2010; Schliep et al., 2015). To our knowledge, hierarchical models have not been applied to leverage felled-tree data to perform robust uncertainty estimation for allometric models and to up-scale these uncertainties to forest inventory plots within the context of NGHGIs.

In this study we employ a data-driven, hierarchical modeling approach that accounts for uncertainty in tree-scale allometric models to estimate total aboveground biomass and foliage biomass stocks for forest inventory plots in the coterminous US. We use a large multispecies database of felled-tree data to inform the model and then generate tree-scale predictions with uncertainty estimation using FIA data. Specific objectives within the US forest study region are to: (1) map the distribution of plot-scale total aboveground and foliage biomass stocks and associated uncertainty bounds; (2) assess the overall contribution of tree-scale predictive models to uncertainty of plot-scale stock estimates; and (3) compare total aboveground and foliage biomass distributions obtained from this data-driven predictive model to those of a widely used set of general biomass models for North America.

2. Methods

2.1. Study region

Our study region consists of forest of the lower 48 contiguous states within the US. This comprises the bulk of the area currently included in the FIA program, spanning four distinct ecoregions and approximately 36 eco-subregions (McNab et al., 2005), with 21 major forest types having been identified across the study area (Ruefenacht et al., 2008). In the northeastern US predominant forest types are oak/hickory and mixed maple/beech, while pine-dominated forests are prevalent in the southeast. In the western US, Douglas-fir forests are the most common, though large areas dominated by pinyon pine, juniper, and other "woodland" species are also present (Oswalt et al., 2014). Using such a large, heterogeneous region enables assessment of model performance across a number of varying forest types, and a range of environmental conditions.

2.2. Data

We employed two datasets for our study: (1) a set of felled-tree biomass data for the major species in North America (hereafter referred to as "legacy data"); and (2) the most recent full cycle (i.e., complete annual inventory) of FIA data collected across our study region from 2009 to 2013. The former is a comprehensive but comparatively sparse sample of destructively sampled biomass data which was used to fit biomass models as a basis for estimating both mean trends and uncertainty bounds in tree and foliage biomass distribution at the national scale. The FIA data, which possess continuous spatial coverage, provides observations of model independent variables (i.e., diameter at breast height [dbh] or species group) to which the fitted model may be applied for predicting total aboveground or foliage biomass at the national scale.

The legacy biomass data is part of an ongoing effort by the USFS and partners to improve resources for calibrating allometric biomass models (Weiskittel et al., 2015). It consists of destructively sampled estimates of total aboveground biomass and biomass components, as well as tree dimensions (e.g., dbh and total height), that have been collated from both historic and contemporary studies throughout North America, converted into common units and harmonized with the FIA data (Weiskittel et al., 2015). We used the portion of the database containing observations of foliage biomass (kg) from trees >1 cm dbh, species, total aboveground biomass (kg), and dbh (cm). We focused on foliage biomass as it is a dynamic, heterogeneous carbon pool that varies substantially across space and time. Additionally, we were interested in assessing a biomass stock we expect to be highly uncertain. Refining the estimation of component NGHGI pools (e.g., foliage) is a current methodological priority of the US NGHGI (Woodall et al., 2011). This sample consists of 5701 observations spanning the 10 species groups used by FIA (99 species in total) gathered from 63 studies and 94 unique sites (Table 1).

We used recent annual FIA inventory data, collected from 2009 to 2013, available for our study region (Fig. 1; for detailed discussion of the inventory program see Bechtold and Patterson, 2005). Beginning around 1998, the FIA program transitioned from a periodic to an annual inventory, in which all plots within each state are sampled over a seven- (eastern US) or ten-year (western US) measurement period, providing a complete inventory for the US across the measurement interval. The sole exception was the state of Nevada, which has not completed an annual inventory yet, but represents a small portion of forest land across the US. The FIA data we used was filtered to remove dead trees and plots that were not measured during our sampling period.

Table 1
Sample size and summary statistics for diameter at breast height (dbh), total aboveground biomass, and foliage biomass for the ten species groups of Jenkins et al. (2003) in the legacy data. Height observations are only available for 3344 of the 5701 trees in the full legacy data.

Jenkins species group	# Trees	dbh (cm)			Total height (m)			Total aboveground biomass (kg)		Foliage biomass (kg)	
		Mean	s.d.	Max	Mean	s.d.	Max	Mean	s.d.	Mean	s.d.
1. Cedar/Larch	67	20.5	9.4	55.6	10.8	4.8	22.9	180.6	187.5	3	5.3
2. Douglas-fir	258	19.72	15.9	96.8	11.8	6.3	31.1	314.3	677.2	12.1	14.5
3. True fir/Hemlock	79	23.9	20	85.1	10.0	5.7	24.6	467.5	962.2	17.2	20.3
4. Pine	969	16.1	11.7	59.9	9.4	5.3	28.3	172.8	295.1	6	8.3
5. Spruce	260	15.6	12.1	71.6	10.1	5.3	25.1	173.3	328.8	18.9	27.8
6. Aspen/alder/cottonwood-willow	326	10.7	9.1	50.8	14.0	7.8	34.6	78.6	166.1	2	3.4
7. Soft maple/birch	517	13.2	10.4	52.4	10.8	6.9	33.6	139.1	266.6	3.5	5.9
8. Mixed hardwood	1797	14.5	11.5	59.7	9.8	5.2	39.7	147.7	265.4	2.8	4.9
9. Hard maple/oak/hickory/beech	1246	19.7	13.7	72.9	11.4	6.3	31.9	367.2	556.4	9.3	13.5
10. Juniper/oak/mesquite	111	23.3	16.3	115.6	6.1	2.3	14.0	295.6	431.2	40.8	35.4

2.3. Model fitting and prediction using FIA data

Producing estimates of plot-level mean biomass stocks (total aboveground and foliage biomass) and accompanying uncertainty intervals occurred in 2 steps: (1) fitting of allometric models to the legacy data within a Bayesian hierarchical framework, with simultaneous generation of tree-scale posterior biomass predictions; and (2) post-processing of tree-level posterior predicted distributions into plot-level posterior predicted distributions. Here, we outline the allometric models and provide a brief overview of the analytical procedure. Further detail on our model design and methodology may be found in Appendix A.

We follow the general approach of Jenkins et al. (2003) by separately predicting total aboveground biomass (BM_{ij}; kg) and a foliage component ratio (FR_{ij}) as:

$$\ln(BM_{ij}) = \alpha_i + \beta_i \ln(\text{dbh}_{ij}) + \varepsilon_{ij}, \tag{1}$$

$$\text{logit}(FR_{ij}) = \gamma_i + \frac{\delta_i}{\text{dbh}_{ij}} + \epsilon_{ij}, \tag{2}$$

and subsequently estimating foliage biomass (kg) as:

$$FOL_{ij} = BM_{ij} * FR_{ij} \tag{3}$$

where dbh_{ij} is observed diameter at breast height (cm), and $\varepsilon_{ij} \sim N(0,\sigma)$ and $\epsilon_{ij} \sim N(0,\tau)$ are data-level variances for the two sub-models. The remaining terms $(\alpha_i, \beta_i, \gamma_i, \delta_i)$ are species group-specific regression coefficients. We used a log-linear model for BM_{ij} and a logistic regression form for FR_{ij} to guarantee that predicted values will be between 0 and 1.0. In (1) and (2), $i = 1, \ldots, 10$, $I = 10$ indexes the I species groups historically used by the USFS within their general biomass models (Jenkins et al., 2003), while j indexes individual trees in the legacy data. We follow this convention and use these same groups within our models, but we depart from Jenkins et al. (2003) in also fitting 10 models using the legacy data for the foliage component ratio, rather than using two (hardwoods and softwoods). In addition to US FIA, models of this general structure are currently employed in many other national forest inventories for estimating aboveground biomass components (Domke et al., 2012; Neumann et al., 2016; Petersson et al., 2012; Woodall et al., 2011; Zianis et al., 2005). In our models dbh is the sole predictor, since it is the only tree dimension that is measured for every tree in the FIA database.

Bayesian inference involves the updating of 'posterior' distributions of model parameters by integrating a likelihood distribution from observed data (i.e., the legacy data) with a second distribution representing prior belief (Gelman et al., 2003). We placed normal prior distributions on the regression coefficients $(\alpha_i, \beta_i, \gamma_i, \delta_i)$ in (1) and (2) and flat, non-informative priors on the data-level variances (σ, τ). In addition, we adopted a hierarchical structure by further placing hyper-prior distributions on the means and variances of the regression coefficients. This hierarchical framework is designed so that $I = 10$ group-level parameters are estimated, but that these arise from common, non-informative hyper-priors on the mean and variance (Gelman et al., 2003). Posterior predictive distributions of total aboveground biomass and foliage ratio were separately derived for individual trees in the FIA data, arising simultaneous to model fitting as a function of the joint posterior of the legacy data and all parameters in either (1) or (2). Posterior predicted foliage biomass was calculated at the tree scale by taking the product of these posterior samples. These tree-scale predictive distributions were aggregated into FIA plot-scale predictive distributions, which were summarized by their mean and 95% uncertainty interval. Model fitting and prediction were conducted via Markov chain Monte Carlo (MCMC) procedures using Stan called from R via the rstan package (Stan Development Team, 2015a, 2015b). In addition to these posterior predictions based on models fitted to the legacy data, we generated mean plot stock estimates with the models of Jenkins et al. (2003) to provide a reference method with which to compare the results of our data-fitted model.

3. Results

3.1. Predicted distributions of total aboveground and foliage biomass

Plot-scale predictions of total aboveground biomass ranged from approximately 0.2 Mg ha^{-1} to approximately 2300 Mg ha^{-1}, with a mean of approximately 125 Mg ha^{-1} and a median of

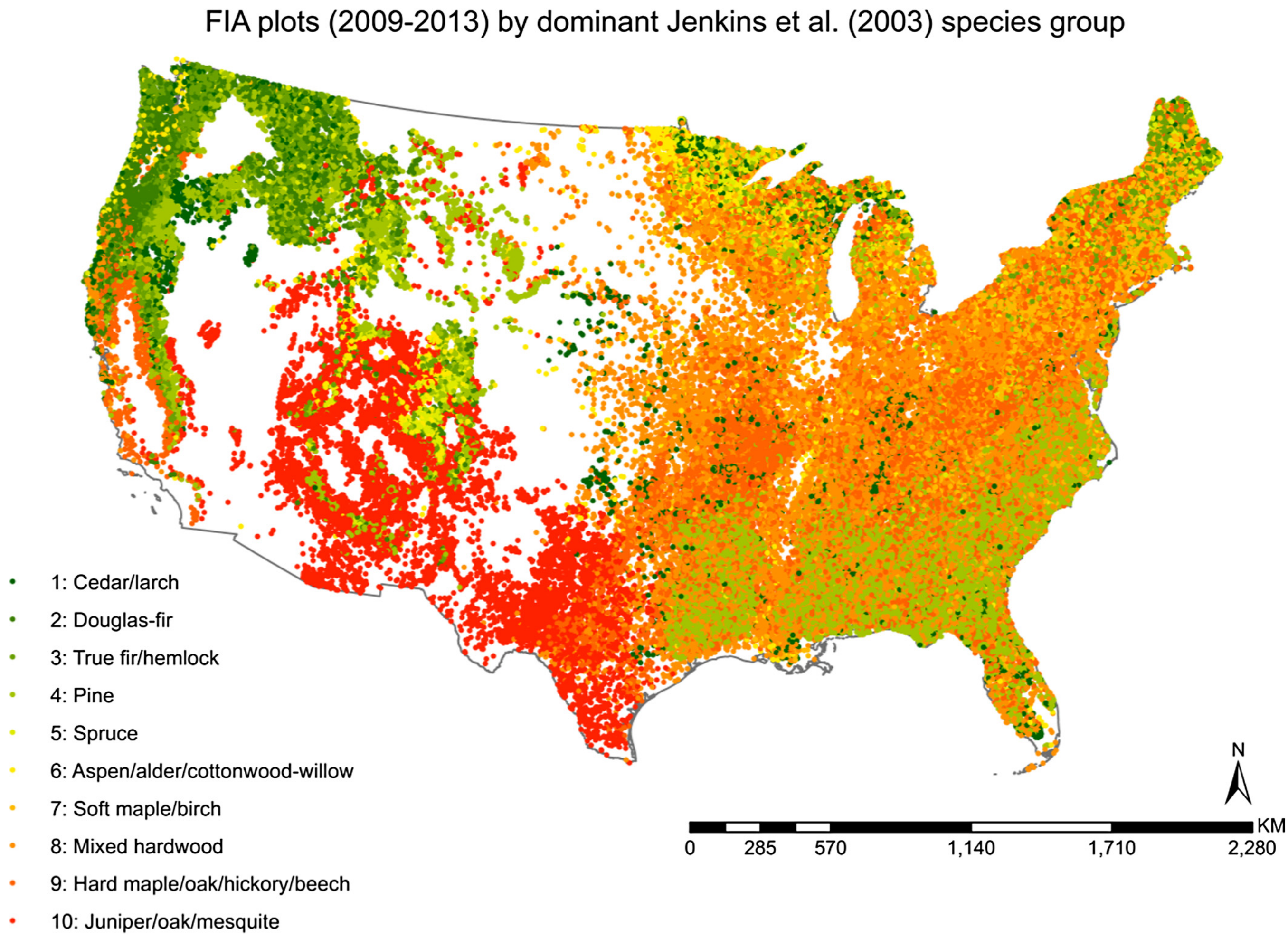


Fig. 1. Distribution of FIA plots, coded by Jenkins et al. (2003) species group.

105 Mg ha^{-1} (Fig. 2). The highest concentrations were in coniferous forests in the Pacific Northwest, extending south along the Pacific coastal range and the Sierra Nevada range. Lowest concentrations were found in scattered forests throughout the Midwest, while moderate biomass stocks were observed in steppe ecosystems of the interior mountain west as well as coniferous dominated forests in the Laurentian mixed forest and Adirondack-New England mixed forest provinces in the northeastern United States. Predicted biomass stocks were notably homogenous across much of the southeastern United States. Plot scale posterior uncertainty intervals ranged from approximately 0.245 to 142,000 Mg ha^{-1} (mean and median 43 Mg ha^{-1} and 33 Mg ha^{-1} respectively), with the largest uncertainty intervals found in regions with the highest mean predicted aboveground biomass.

Predicted foliage biomass from our hierarchical model ranged from approximately 0.02 to 174 Mg ha^{-1} (mean: 7 Mg ha^{-1}; median: 5 Mg ha^{-1}; Fig. 2). Both extremes of this range were identified in forests of the western US. The lowest foliage biomass densities were predicted for dry steppe provinces in California and the Great Plains, as well as prairie parkland ecosystems throughout the Midwest. As with total aboveground biomass, the highest foliage biomass densities were noted in the Pacific Northwest (Cascade mixed forest province and Pacific lowland mixed forest province), as well as in arid, conifer-dominated forests across the intermountain west and the Colorado plateau. In the eastern US, foliage biomass densities were higher in the north, particularly within the Laurentian mixed forest and the Adirondack-New England mixed forest provinces, with somewhat lower densities throughout the coastal plain forests of the southeast. The range of predicted uncertainties was slightly higher than the predicted means, with intervals ranging from approximately 0.064 Mg ha^{-1} to approximately 190 Mg ha^{-1} (mean: 6 Mg ha^{-1}; median: 5 Mg ha^{-1}; Fig. 2). In general, high prediction uncertainty was associated with higher densities of predicted foliage biomass. However, as with total aboveground biomass, average prediction uncertainty was large relative to average mean foliage biomass across most of the study range.

3.2. Relative uncertainty of total aboveground and foliage biomass predictions

Plots of these ratios for total aboveground biomass and foliage biomass (Fig. 3) reveal somewhat divergent trends within these pools. Overall total aboveground biomass predictions were much more certain, with these ratios ranging from 11% to 146%. By contrast, ratios for foliage biomass range from 31% to 450%, suggesting that at best the foliage biomass model was more than twice as uncertain when compared to the total aboveground biomass model. In the worst cases, the range of the uncertainty interval was more than 4.5 times larger than the plot-scale predicted means. Overall, the foliage ratio model had much higher uncertainty than the log-linear model for total aboveground biomass.

The basic distributions of these ratios were similar for both total aboveground and foliage biomass (Fig. 3). High relative

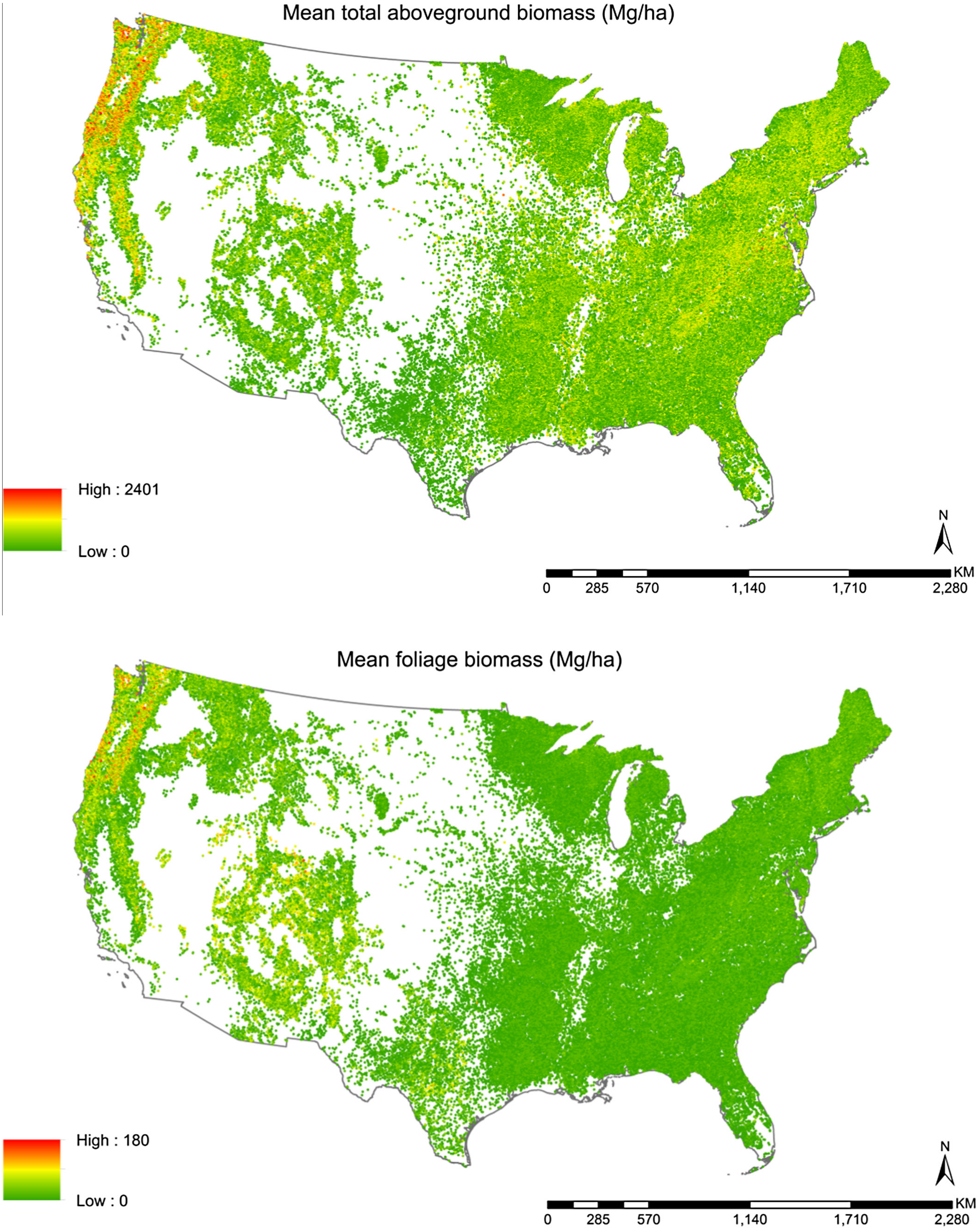
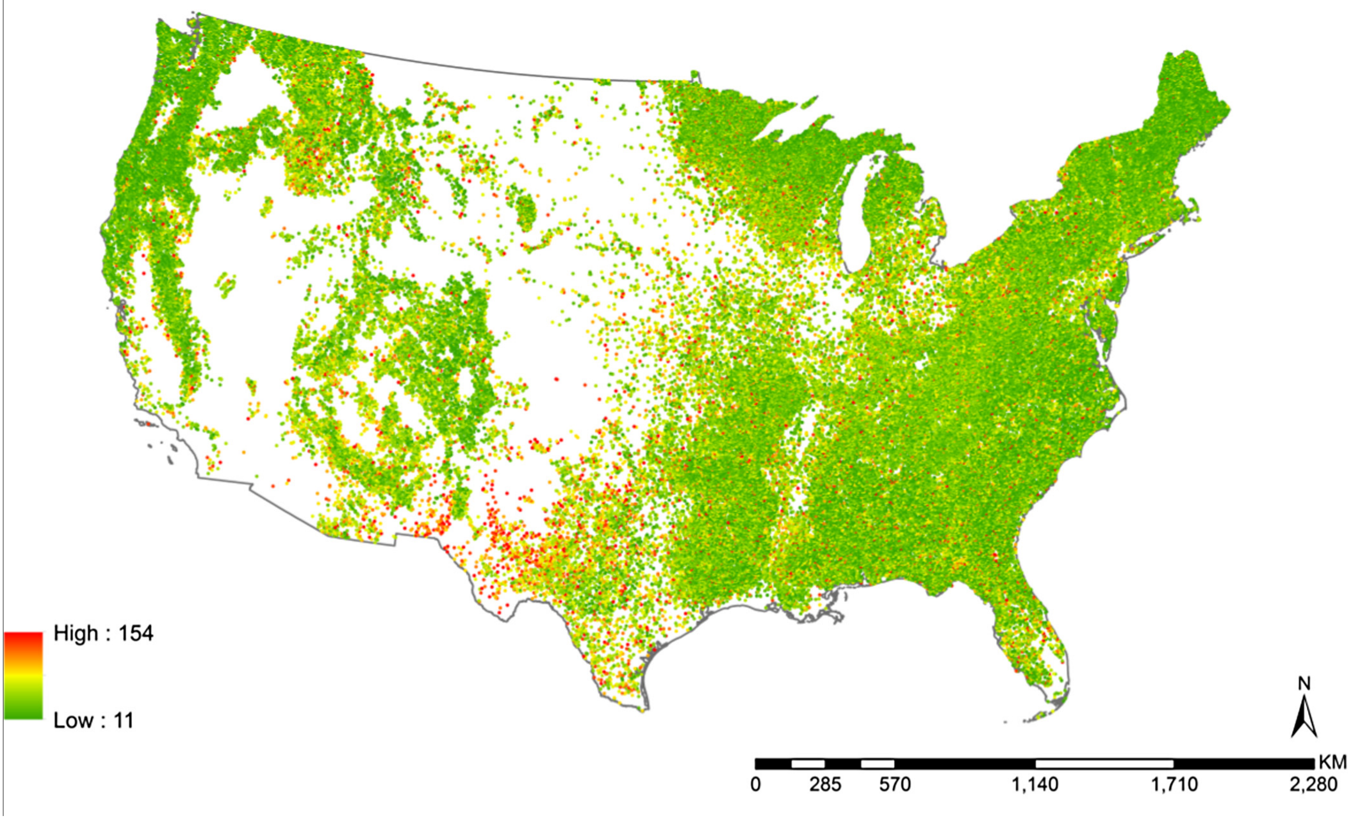


Fig. 2. Plot-scale posterior predicted mean total aboveground biomass (Mg ha^{-1}), and foliage biomass from the hierarchical model.

Relative uncertainty of plot-scale total AGB estimates (%)



Relative uncertainty of plot-scale foliage biomass estimates (%)

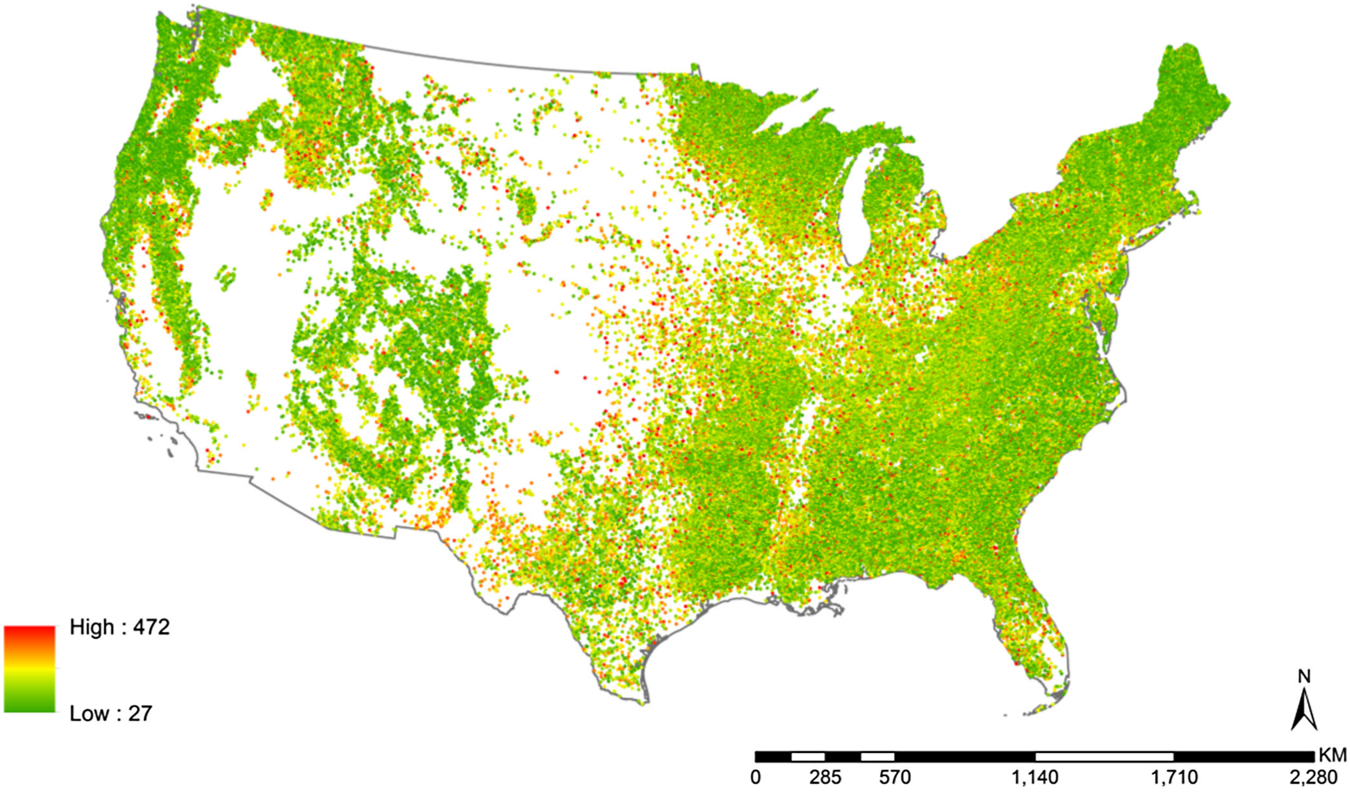


Fig. 3. Plot-scale relative uncertainty (the ratio between the posterior 95% uncertainty interval and the posterior mean) for total aboveground and foliage biomass. Note that the scale for foliage biomass is three times larger than for total aboveground biomass.

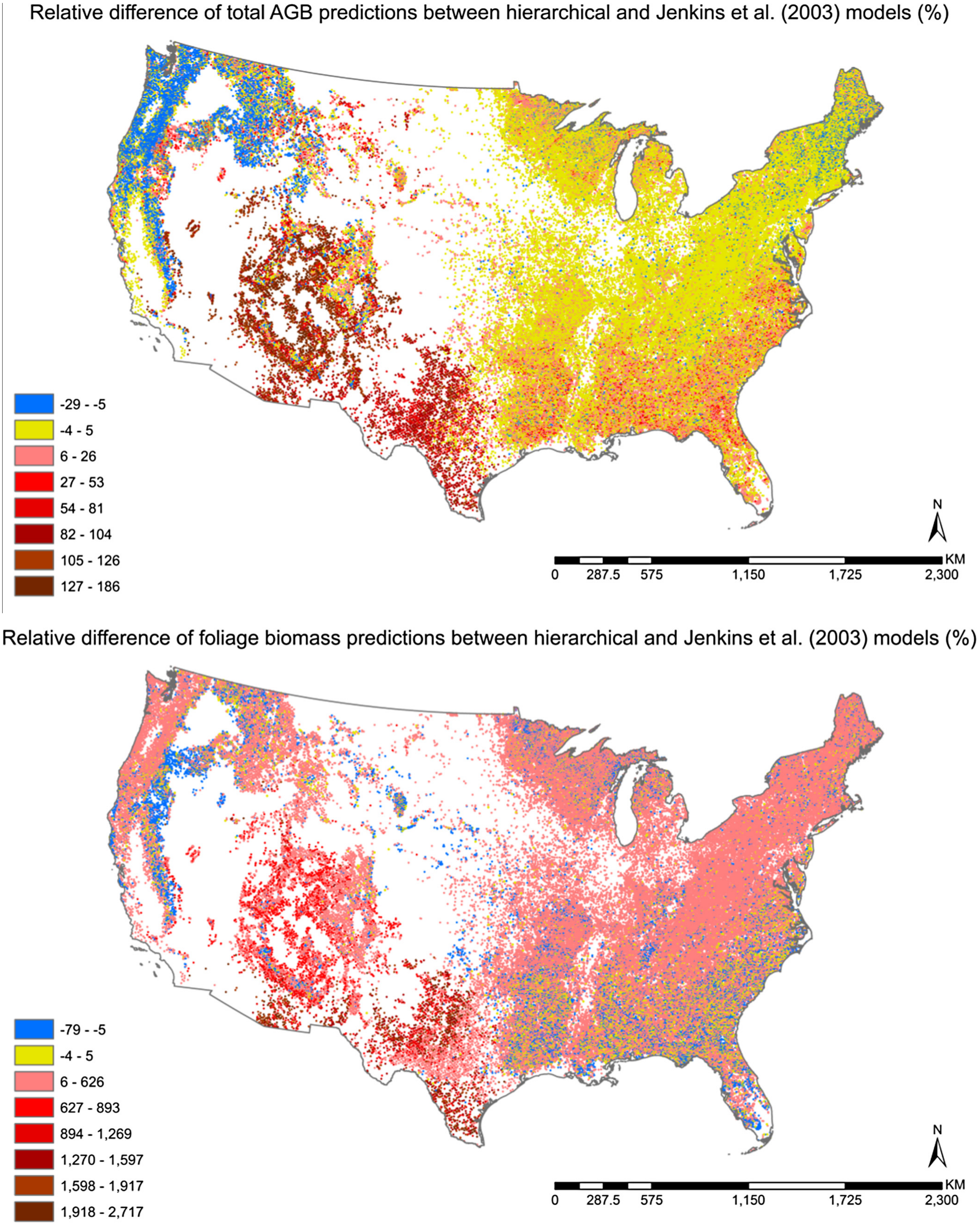


Fig. 4. Relative difference (Mg ha^{-1}) between posterior predictions and the models of Jenkins et al. (2003), for total aboveground and foliage biomass. Plots where predictions of the two methods were within 5% of each other are shown in yellow, while blue indicates lower predicted stocks from the hierarchical model and red indicates higher predicted stocks. Note that the range of differences in foliage biomass is much larger than total aboveground biomass.

uncertainties were particularly notable in the steppe ecosystems of the interior mountain west; particularly within the southern and middle Rocky Mountain steppe provinces. High relative uncertainties in both pools were also common in prairie parkland, desert/semi-desert, and California chaparral ecosystems throughout the western US. In the eastern US there were less consistent patterns, though in general large relative uncertainties are more common in southeastern/central mixed and broadleaf forest provinces when compared to northern forests (i.e., Adirondack-New England, northeastern mixed, and Laurentian mixed forest provinces). The mean relative uncertainty ratio of all plots in the FIA sample was 41% for total aboveground biomass and 117% for foliage biomass.

3.3. Comparison of hierarchical model and Jenkins models

Throughout most forests in the US, the hierarchical model resulted in higher predicted total aboveground (Fig. 4) and foliage (Fig. 4) biomass than the Jenkins models (approximately 11% greater on average for total aboveground biomass, and 9% greater on average for foliage biomass). In both cases, the largest differences were in steppe ecosystems in the intermountain west (~200% greater on average for total aboveground biomass,~800% greater on average for foliage biomass). Beyond that general trend, the differences between approaches were dissimilar for the two pools. For example, the hierarchical model produced larger predictions of foliage biomass in the Cascade mixed forest and throughout the Pacific Northwest, but also generated lower estimates of total aboveground biomass for this same region. A similar pattern was also noted in forest provinces throughout the northern and northeastern US. By contrast, instances where the hierarchical model predicted lower foliage biomass than the Jenkins models were much less common, though this trend is noted along the central range of Oregon and California, in the Everglades province of southern Florida, and in isolated pockets across the coastal plain forests of the southeastern US. While the hierarchical model tended towards larger predictions for both pools, foliage biomass showed pronounced extremes with relative percent differences from −75% to 2493%. By contrast, the range of differences for total aboveground biomass were from −26% to 184%, with the largest differences mainly restricted to the interior mountain west. It is notable that the largest relative differences were found in ecoregions where the hierarchical model was the most uncertain, as evaluated by the relative ratio of the uncertainty interval range and posterior predicted means (Fig. 3).

Comparing means across the 10 species groups confirms that, in general, total aboveground estimates provided by the hierarchical model and the Jenkins models were more similar than those found for foliage biomass (Fig. 5). In the case of total aboveground biomass, the Juniper/oak/mesquite species group was the only group where substantial differences between mean plot-scale estimates from each method were found. These results also demonstrate a trend towards substantially higher foliage biomass predictions within this group. Plots dominated by the Juniper/oak/mesquite group are widespread in steppe ecosystems of the southwestern US and interior mountain west; the regions where we found the largest plot-scale differences between the hierarchical model and Jenkins models for both pools, as well as the largest relative uncertainties. Note, however, that there is substantial variation in estimates of both pools within all species groups.

4. Discussion

The largest plot-scale uncertainties from our analysis represent a substantial increase compared to what is reporting in existing literature (Chave et al., 2004; Djomo et al., 2010; Keller et al., 2001), though uncertainty for most FIA plots was found to be close to the higher end of this range (approximately 1–30% of predicted means). Our results suggest that allometric model error constitutes a large portion of plot-scale uncertainty which varies among species. We found larger relative uncertainties among certain species groups and forest types; most notably the Juniper/oak/mesquite species group within arid forests in the western US. Our analytical approach signifies that differences among species groups arise in large part from variation within the legacy data, which may indicate a higher degree of geographic and/or interspecific variation within this group when compared to others. The legacy data are naturally sparse relative to the FIA sample, meaning that as with most studies using allometric models developed from small felled-tree samples, our predictions are conditioned upon allometric relationships observed at a small number of sites. There is substantial evidence to indicate that stem diameter-biomass relationships vary among taxonomic and/or plant functional groups (Pretzch and Dieler, 2012), and may also be influenced by environmental variables such as temperature regimes (Duncanson et al., 2015; Reich et al., 2014). This may be particularly true for foliage biomass, a highly variable stock that is heavily influenced by stand and landscape level processes (Temesgen et al., 2011). Interestingly, the same forest types in which we observed the highest plot-scale uncertainties were recently found to have the largest discrepancies in predicted biomass stocks for FIA using two different sets of models (Hoover and Smith, 2016), the reference method we used in our work and a set of updated models provided by Chojnacky et al. (2013). These models are based on "pseudodata" generated from many published models and as such are susceptible to similar scaling issues as our legacy data-fitted model when applied to FIA data.

These observations, coupled with the generally larger errors in predicted foliage biomass than total aboveground biomass, argue for several improvements to allometric modeling approaches for quantifying national forest biomass stocks. A natural starting point is the inclusion of additional covariates, such as tree height and crown diameter, within allometric models. Height in particular is strongly related to both total aboveground and foliage biomass (Niklas, 1995; Wirth et al., 2004). Height and crown diameter are only measured for a subset of trees within FIA so predicted estimates of these variables are necessary for projecting total forest carbon stocks, adding another level of uncertainty that must be incorporated into plot-level biomass estimates. However, given the general quality of tree height diameter models (Arabatzis and Burkhart, 1992), as well as the strong relationships between height and biomass, it seems reasonable to expect that even models based on predicted heights may have lower uncertainty. The assumption of constant specific gravity that is implicit in allometric models also substantially contributes to their uncertainty, since both wood and bark density vary across scales (Chave et al., 2004; MacFarlane, 2011). The legacy data contains specific gravity measurements for many tree species, so there is opportunity to develop and compare data-driven models that incorporate uncertainty into biomass expansion factors. Beyond individual tree measurements, climate data (Reich et al., 2014) or plant trait databases (Russell et al., 2014) may also lend further refinements to prediction results, as such variables may influence allometric relationships across a species' geographic range.

In addition to updating models, improving data resources such as the legacy database may contribute further refinements to national forest carbon estimates. Weiskittel et al. (2015) have shown a substantial mismatch in the diameter distribution of the legacy data versus that of a national sample of FIA plots, and when coupled with taxonomic and geographic variation such as we note above, these discrepancies may affect the accuracy and precision of predictive models. For example, our data-fitted model predicted

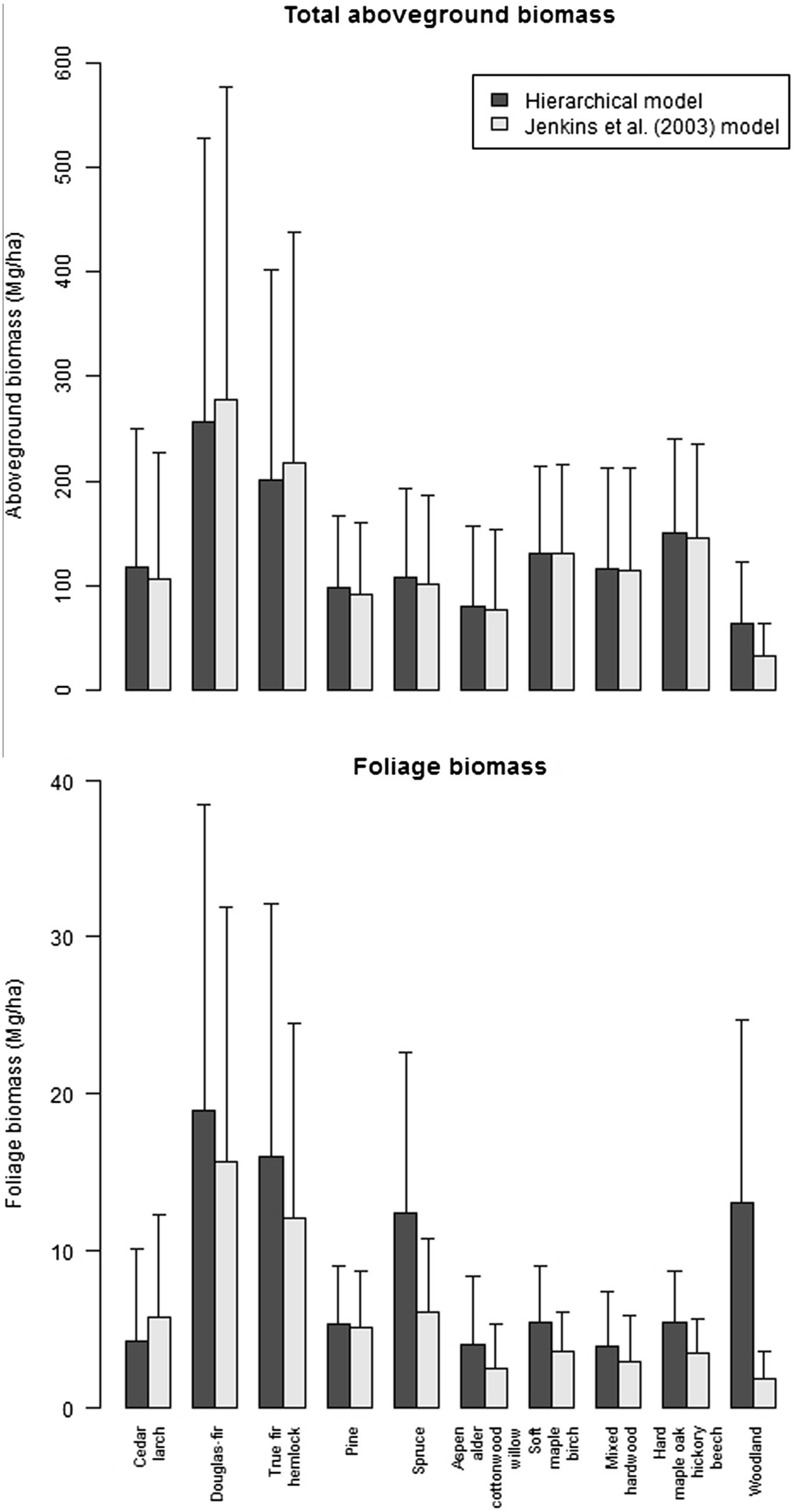


Fig. 5. Comparison of mean plot-scale total aboveground and foliage biomass produced by the hierarchical model and the models of Jenkins et al., for the 10 species groups used in our study. The error bars here represent the standard deviation among the sample of FIA plots within each group.

generally smaller biomass stocks than the Jenkins et al. (2003) models in forest types that are dominated by large trees (i.e., conifer dominated forests in the Pacific Northwest). Efforts are already under way to improve both the spatial and taxonomic coverage of the legacy data (Weiskittel et al., 2015) and to add observations of large individuals for the most common tree species of North

America. In addition, global efforts to collate available biomass data such as the Biomass and Allometry Database (BAAD; Falster et al., 2015) can facilitate the use of data-driven models in other national or international forest carbon inventory efforts. Predictive analyses such as ours can help to guide "gap filling" efforts of existing biomass data by demonstrating where the greatest gains in precision can be made. For example, the large variation we observed in juniper/oak/mesquite indicates additional data from across the range of these species is necessary to accurately estimate uncertainty.

In building our hierarchical model and generating predictions, we make several assumptions that are important for interpreting our results and establishing future improvements to a hierarchical predictive framework. The legacy data consists of multiple datasets, but we chose to pool these data and not attempt to account for random error related to study, in keeping with the reference method used for our comparisons (Chojnacky et al., 2014; Jenkins et al., 2003; Wayson et al., 2014). However, models that incorporate random effects in the fitting and prediction data (Wirth et al., 2004; Wutzler et al., 2008), or spatially varying coefficients (Gelfand et al., 2004), facilitate the reduction of errors arising from these factors. We modeled independent errors for our dependent variables and we assumed that tree-scale errors are additive at the plot-level, though some studies have suggested that models which account for similar growing conditions and/or density dependence can reduce uncertainty in stock projections (Chave et al., 2014; Schliep et al., 2015). However, such sophisticated statistical models are not routinely used by the US or other nations' forest carbon inventories therefore baseline uncertainty assessments using practical methods remain important.

5. Conclusions

It is important that uncertainty estimates accompany the evaluation of forest carbon stock estimates to enable the objective monitoring of terrestrial carbon and associated policies (e.g., United Nations Framework Convention on Climate Change). We evaluated a hierarchical approach to estimate total uncertainty associated with forest biomass stocks. This approach used available data to inform allometric models by generating predictions via simulations from a posterior predictive distribution that seamlessly aggregated errors associated with stock estimates at the tree, plot, and regional scale. Using this framework we have provided evidence that static allometric biomass models risk substantially underestimating the contribution of allometric model error to the overall uncertainty of plot-scale estimates. Our results argue for greater investments to improve the precision of allometric models for worldwide forest carbon inventories by incorporating additional covariates into predictive models (e.g., tree height, climate variables), improving data resources for fitting and validating models, and adopting statistical approaches capable of accounting for the complex error structures needed to develop biomass stocks from tree-scale predictions. The hierarchical framework we employed possesses the flexibility to incorporate such improvements to enhance the US' NGHGI and forest carbon inventories worldwide.

Acknowledgments

We wish to thank the compilers and contributors of the legacy biomass data used in our study, particularly Phil Radtke, Aaron Weiskittel, David Walker, and Jereme Frank. In addition, we thank Johannes Breidenbach, David Bell, Ram Deo, and two anonymous reviewers for commenting on this manuscript. This work is supported by the US Forest Service Northern Research Station and the Minnesota Agricultural Experiment Station.

Appendix A. Detailed statistical and computational methodology

A.1. Statistical model

We used a set of models that separately estimate total aboveground biomass and the fraction of aboveground biomass found within foliage for both fitting to the legacy data and subsequent prediction for FIA data. In order for our plot-scale predictions and uncertainty estimates to be representative of what may be expected when using widely used techniques for forest carbon inventories, we adopt a similar approach. The models for total aboveground biomass (BM_{ij}; kg) and foliage ratio (i.e., observed foliage biomass/observed total aboveground biomass; FR_{ij}) are:

$$\ln(BM_{ij}) = \alpha_i + \beta_i \ln(\mathrm{dbh}_{ij}) + \varepsilon_{ij}, \tag{1}$$

$$\mathrm{logit}(FR_{ij}) = \gamma_i + \frac{\delta_i}{\mathrm{dbh}_{ij}} + \epsilon_{ij}, \tag{2}$$

In these models dbh_{ij} is observed diameter at breast height (cm), and $\varepsilon_{ij} \sim N(0,\sigma)$ and $\epsilon_{ij} \sim N(0,\tau)$ are data-level variances for the two sub-models. The remaining terms $(\alpha_j, \beta_j, \gamma_j, \delta_j)$ are regression coefficients. We used a log-linear model for BM_{ij} and a logistic regression form for FR_{ij} to guarantee that predicted values will be between 0 and 1.0. In (1) and (2), $i = 1, \ldots, 10$, $I = 10$ indexes the I species groups historically used by the USFS within their general biomass models (Jenkins et al., 2003), while j indexes individual observations (tree scale measurements of total aboveground biomass and foliage ratio) in the legacy data. We follow this convention and use these same groups within our models, but we depart from Jenkins et al. (2003) in also fitting 10 models using the legacy data for the foliage component ratio, rather than using two (hardwoods and softwoods). Foliage biomass is indirectly estimated as the product of new predictions of BM_{ij} and FR_{ij}, and this is elaborated upon when we describe our procedure for estimating biomass stocks at the tree scale with the FIA data.

In both (1) and (2), dbh is the sole variable used to predict biomass. While other tree measurements such as total height, wood specific gravity, and crown ratio have been shown to offer substantial improvement in both total aboveground and foliage biomass models (Baldwin, 1989; Chave et al., 2014), these measurements are only available for a subset of the full FIA data. In most large national forest inventories, cost and time constraints prevent detailed measurement of all trees within the sample (Weiskittel et al., 2015). Since our biomass stocks will be estimated from tree-scale predictions, and since we want to be able to conduct full assessment of uncertainty, we chose to limit our models to variables available for every tree within the FIA database. This approach aligns with ongoing USFS efforts to quantify biomass pools using FIA data (Domke et al., 2012; Woodall et al., 2011), which use empirical models that also use dbh as the only predictor variable.

For the purposes of our current work we chose to pool the legacy data for model fitting, despite the fact that observations within these data arise from multiple studies that differ in regional focus, sampling methodologies (particularly for foliage), and the diameter distribution of measured trees. Ignoring random effects related to these factors has an obvious impact on estimates of prediction uncertainty, as errors related to sampling biases within the felled-tree data cannot be separated cannot be separated from the usual "white noise" variation in the dbh and biomass measurements. However, fitting a model to the pooled felled-tree data is analogous to widely used approaches based on biomass "pseudodata" (Chojnacky et al., 2014; Jenkins et al., 2003; Wayson et al., 2014), where allometric models are fitted to simulated data generated from dozens of published biomass models. In fact, many of the studies represented in the legacy database are also included in the database of biomass models compiled by Jenkins et al. (2004). Our goal is to provide baseline plot-level uncertainty assessments that are related to the practical methods used in the United States and many other nations, so we prefer to implement our statistical model in a similar fashion.

A.2. Hierarchical specification

Briefly, our hierarchical model is designed to estimate separate sets of the parameters in (1) and (2) for each of the I species groups, but also assumes exchangeability among these groups. To accomplish this, we first place normal prior distributions on the regression coefficients of each of the I models:

$$\alpha_j \sim N(\mu_\alpha, \varphi_\alpha) \tag{3}$$

$$\beta_j \sim N(\mu_\beta, \varphi_\beta) \tag{4}$$

$$\gamma_j \sim N(\mu_\gamma, \varphi_\gamma) \tag{5}$$

$$\delta_j \sim N(\mu_\delta, \varphi_\delta) \tag{6}$$

In this specification, the coefficient means (μ_x) are completed with normal hyper-prior distributions ($\sim N(0, 25)$) while the coefficient variances (φ_x) are given vague uniform prior distributions ($\sim Unif(0, \infty)$). Note that while J sub-models are fit, each coefficient arises from a common hyper-prior distribution across species groups. This structure provides partial-pooling of the group level variances, stabilizing highly variable groups and/or groups with small sample sizes, while avoiding overly smoothed inference on the relationship between the independent (dbh) and dependent (biomass stocks) variables (Gelman et al., 2003). We utilize such an approach in our study because, while we want to perform inference and prediction on the 10 species groups (Jenkins et al., 2003), legacy samples for groups like cedar/larch, true fir/hemlock, and juniper/oak/mesquite are relatively small (<200 observations). Of course, using this structure implicitly assumes that, while we expect variable allometric scaling among the groups (Chave et al., 2009; Pretzch and Dieler, 2012; MacFarlane, 2015), an underlying basic relationship between dbh and total aboveground biomass/foliage ratio exists (i.e., Enquist and Niklas, 2001). In this way, our model can be thought of as a compromise between fully static (i.e., complete pooling among groups) and fully variable (i.e., no pooling among groups) allometric relationships. Specification of our model is completed by placing a flat uniform prior (i.e., $\sigma \sim Unif(0, \infty)$) on the model variances.We specify all priors and hyper-priors with noninformative prior distributions. In this way we are using Bayes' theorem to take advantage of the hierarchical model structure to allow for partial pooling of variances among allometric model parameters for the different species groups, but not asserting any prior belief about parameter means or variances. In practice this assumption can be relaxed both to improve computational efficiency and to incorporate prior knowledge about model parameters. However, here we are interested in exploring the results of a model that is fully data-driven. For that reason, we default to prior distributions that do not make any assumptions regarding posterior outcomes.

A.3. Prediction

In Bayesian statistics, predicting the response variable when given new observations of the dependent variable(s) is accomplished by taking draws from the posterior predictive distribution (Gelman et al., 2003; Ntzoufras, 2009). In our analysis, we predict individual tree total aboveground biomass and foliage ratio for observations within the FIA database as:

$$p(y_{pred}|y_{legacy}) = \int p(y_{pred}|\theta, y_{legacy})p(\theta|y_{legacy})d\boldsymbol{\theta}, \tag{7}$$

where y_{pred} represents new predictions of total aboveground biomass (BM_{pred}) and foliage ratio (FR_{pred}) given dbh and species group of trees within the FIA database, y_{legacy} represents the observed (legacy) felled-tree data (i.e., total aboveground biomass and foliage ratio), and $\boldsymbol{\theta}$ is all of the posterior estimates of all parameters, as well as their priors and hyper-priors, in (1) and (2) based on fitting to the legacy data. Note that, according to (7), the posterior distributions of the new predicted observations are conditioned upon the posterior distributions of the models fitted to the legacy data. In this way, prediction within the Bayes framework naturally incorporates uncertainty related to the observed felled-tree data and fitting of the allometric models into the new predictions for trees within FIA. For each tree within FIA our approach is to simultaneously predict total biomass and the foliage component ratio, and then multiply these quantities to draw posterior predicted samples of foliage biomass as:

$$FOL_{pred} = BM_{pred} * FR_{pred} \tag{8}$$

A.4. Model implementation

Fitting of our hierarchical model to the legacy data and prediction within FIA were accomplished using Stan, called from R with the RStan package (Stan Development Team, 2015a, 2015b). Stan is a recently developed, open source programming language for conducting Bayesian inference. It has particular advantage over alternative languages, such as BUGS or JAGS, in that it is possible to conduct posterior inference on high dimensional, complex models with only moderate computational resources. Stan accomplishes this by obtaining posteriors with Hamiltonian Monte Carlo, a more efficient algorithm than other commonly used MCMC procedures such as the Gibbs sampler (Carpenter et al., in press). This is particularly advantageous in fitting biomass models to forest inventory data such as we do here, where we are drawing posterior distributions for hundreds of thousands of trees simultaneously.

We drew a total of 500 posterior samples of both total aboveground and foliage biomass from two different Markov chains by thinning every 4th sample from a run of 1000 iterations. This sampling phase followed a "warm up" run of 1000 iterations. During initial tests, this procedure was sufficient to achieve convergence in both model parameters and posterior predicted biomass for a subset of FIA plots. Convergence was assessed both by visual inspection of trace plots and with the Gelman-Rubin diagnostic. This analysis results in an $n \times p$ matrix of posterior predicted total aboveground and foliage biomass for the FIA sample, where n is the number of live trees in the sample of FIA data and p is the 500 posterior simulations.

A.5. Post-processing

Once the matrix of tree-level posterior predicted biomasses was obtained, the next step was to summarize the results into plot-level estimates (Mg ha^{-1}) that preserve the uncertainty represented by our procedure for prediction at the tree-scale. To accomplish this we followed standard procedures used by USFS to project tree-level estimates into areal estimates, applied to columns within the $n \times p$ matrix (i.e., n observations by p posterior predictions). This results in a vector of 500 predicted estimates of total aboveground and foliage biomass for each plot, which can be regarded as a posterior sample of plot-scale biomass when conducting uncertainty estimation. We first applied a ‘trees per hectare’ adjustment to each prediction, to express these as individual contributions to plot-scale areal estimates. After the predicted results were adjusted, they were summed within plots to obtain plot-level predicted biomass. From the resulting vector of plot estimates, we calculated the mean and the 2.5% and 97.5% quantile bounds. This procedure was performed for both posterior predicted total aboveground biomass and foliage biomass.

A.6. Reference method

To compare the results of the hierarchical model to widely-used general biomass models for North America, we also calculated plot-level biomass via the approach outlined by Jenkins et al. (2003; hereafter referred to as the “Jenkins models”). These estimates were similarly obtained at the tree-scale and aggregated into plot-level estimates through the same scaling procedure described above. The difference is that they represent point estimates of biomass since the Jenkins models are parameterized with fixed coefficients. Unlike our model, the Jenkins models do not estimate a foliage ratio for all 10 species groups, but instead simply divide tree species into hardwoods and softwoods.

The Jenkins models were applied to predict total aboveground and foliage biomass for the same set of FIA data used for our hierarchical model. The procedure here was similar: biomass was first estimated at the tree-scale, converted into areal estimates using the same ‘trees per hectare’ adjustment, and then aggregated to produce plot-level estimates of total aboveground and foliage biomass in Mg ha^{-1}. The difference is that the Jenkins models are applied with fixed parameters so this operation is performed upon a single vector of predictions rather than a posterior distribution.

Appendix B. Posterior summaries of the parameters and hyper-parameters of the total aboveground biomass and foliage ratio models (Eqs.(1) and (2)) fitted to the legacy data

	Total aboveground biomass			Foliage ratio		
	Mean	Lower CI	Upper CI	Mean	Lower CI	Upper CI
Regression parameters						
Intercepts						
1. Cedar/Larch	−2.097	−2.542	−1.712	−4.525	−4.800	−4.250
2. Douglas-fir	−2.206	−2.336	−2.081	−2.873	−3.006	−2.720
3. True fir/Hemlock	−2.839	−3.057	−2.627	−2.708	−2.934	−2.493
4. Pine	−1.605	−1.658	−1.546	−3.515	−3.580	−3.448
5. Spruce	−1.816	−1.934	−1.703	−2.136	−2.282	−1.997
6. Aspen/alder/cottonwood-willow	−2.284	−2.374	−2.200	−3.508	−3.651	−3.359
7. Soft maple/birch	−2.041	−2.110	−1.976	−3.719	−3.816	−3.612
8. Mixed hardwood	−2.208	−2.252	−2.167	−4.114	−4.175	−4.058
9. Hard maple/oak/hickory/beech	−1.909	−1.962	−1.848	−3.765	−3.830	−3.706
10. Juniper/oak/mesquite	−0.798	−1.040	−0.532	−1.681	−1.906	−1.492
Slopes						
1. Cedar/Larch	2.322	2.188	2.470	3.556	0.093	6.826
2. Douglas-fir	2.402	2.357	2.447	3.963	2.951	4.953
3. True fir/Hemlock	2.515	2.441	2.593	4.791	3.593	5.968
4. Pine	2.160	2.138	2.181	7.517	7.148	7.926
5. Spruce	2.265	2.222	2.307	2.371	1.708	3.004
6. Aspen/alder/cottonwood-willow	2.413	2.376	2.451	2.673	2.039	3.235
7. Soft maple/birch	2.383	2.355	2.411	3.113	2.669	3.518
8. Mixed hardwood	2.388	2.372	2.405	4.006	3.675	4.354
9. Hard maple/oak/hickory/beech	2.399	2.377	2.418	3.744	3.279	4.162
10. Juniper/oak/mesquite	1.939	1.859	2.016	3.998	2.378	5.795
Data-level variance	0.315	0.309	0.322			
Hyper-parameters						
Total aboveground biomass						
Intercept mean	−1.980	−2.392	−1.594			
Slope mean	2.321	2.178	2.451			
Intercept variance	0.633	0.375	1.038			
Slope variance	0.188	0.112	0.313			
Foliage ratio						
Intercept mean	−3.243	−3.872	−2.567			
Slope mean	4.009	2.784	5.508			
Intercept variance	1.043	0.642	1.728			
Slope variance	1.853	1.056	3.304			

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