Forest Ecology and Management 386 (2017) 51–61

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Climate and species functional traits influence maximum live tree stocking in the Lake States, USA

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ARTICLE INFO

Article history:
Received 22 August 2016
Received in revised form 7 December 2016
Accepted 9 December 2016

Keywords:
Competition
Stand density management
Relative density
Stocking
Functional traits
Climate change

ABSTRACT

Quantifying the density of live trees in forest stands and partitioning it between species or other stand components is critical for predicting forest dynamics and responses to management, as well as understanding the impacts of stand composition and structure on productivity. As plant traits such as shade tolerance have been proven to refine understanding of plant community dynamics, we extended a previous model relating maximum stand density to wood specific gravity to incorporate shade tolerance as an additional functional trait. Additionally, we included climatic variables that might influence ecological dynamics and modulate species-specific traits, across a region and also potentially over time under climate change scenarios. We used data from the USDA Forest Service, Forest Inventory and Analysis program for three states in the northern United States (Minnesota, Wisconsin, and Michigan) that reflect strong gradients in climate and species composition, to fit a maximum density model by quantile regression. The resulting strictly additive density measure conforms well to both existing silvicultural guidance and to observed densities of monocultures that lack such guidance. Wood specific gravity appears to interact with precipitation, while shade tolerance interacts with temperature, in driving maximum density relationships. Our proposed maximum stand density model is not only parsimonious for field application in management situations, but also empowers the evaluation of the effects of future climate and tree range scenarios on forest management guidelines.

1. Introduction

The assessment of stand density is a critical task for silvicultural diagnosis and prescription, and for strategic-scale assessments of forest characteristics (Long, 1985; Woodall et al., 2005). Stand density is a driving factor in trajectories of stand volume and carbon sequestration due to ordinary stand dynamics (Oliver and Larson, 1996; Pretzsch, 2009), and is a key predictor of wood quality (e.g. Mason, 2012; Groot and Luther, 2015). It can also indicate predisposition to catastrophic changes due to disturbances such as fire (Woodall et al., 2006), wind (Castedo-Dorado et al., 2009; Lindroth et al., 2009; Pretzsch et al., 2015), and insects (Kurz et al., 2008; Zhang et al., 2013), and can modulate forest responses to climatic stress (Trouvé et al., 2014). The archetypal approach to stand density assessment is that of Reineke (1933), while other approaches have built on those of Hart (1928) and Yoda et al. (1963). All of these approaches combine some measure of tree size (diameter, height, or biomass) with an absolute density of trees to establish reference density levels. The original approaches, (e.g., Reineke, 1933) along with most succeeding applications (e.g., Long, 1985), have been designed for single-cohort monocultures.

In many forested regions, mixed-species forests are the rule rather than the exception, while in others (e.g., Europe) they are expanding in prevalence and associated management interest (Bravo-Oviedo et al., 2014; del Río et al., 2016). In regions with relatively complex forests, individual species may be rare, but collectively rare species may be present in a large fraction of stands. Misguided approaches to quantifying total density and its partition among tree species and size classes can lead to erroneous management decisions and ecological inferences (Sterba et al., 2014). However, direct attention to the problem of describing stand density in complex mixed-species, multi-cohort forests in a fashion that accounts for variation in species composition has been limited. Stout and Nyland (1986) and Stout et al. (1987) adapted an early

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http://dx.doi.org/10.1016/j.foreco.2016.12.007
0378-1127/© 2016 Published by Elsevier B.V.

approach by Chisman and Schumacher (1940) by using broad species groups to develop multi-species stocking indices in the Allegheny region of Pennsylvania. These approaches were highly dependent on observing maximum size density relationships across a population of trees (i.e., a region) which can overlook rare or non-commercial tree species. In contrast, Woodall et al. (2005, 2006), building on work by Dean and Baldwin (1996), proposed an approach where only the average wood specific gravity within a stand was needed to estimate the maximum size/density relationship for any particular combination of tree species. Such national-scale stocking indices enables large-scale evaluation of stand dynamics such as dead wood (Woodall and Westfall 2009) and live tree biomass accretion (Woodall et al. 2015). Ducey and Knapp (2010) further extended Woodall's approach (2005) to develop an additive version of Reineke's (1933) stand density index, similar to the form outlined by Curtis (1971), accounting for interspecific variation using specific gravity as a predictive functional trait. The incorporation of species-specific functional traits in the assessment of stand density paves the way to a more mechanistic explanation of site occupancy in complex forests. However, a single-trait approach, like specific gravity, reduces the maximum density that a stand can support to species tolerance to bending stress (Dean and Baldwin, 1996). In mixed-species forests tolerance to low light intensity could be more influential in size-density relationships than mechanical properties because of the key role of shade tolerance in shaping plant communities (Valladares and Niinemets, 2008). Another approach to capture the interspecific variation in maximum density is that presented by Rivoire and Le Moguedec (2012) based on resource availability for some European mixtures; however, calibration of their approach requires information on monocultures of each species, which is often unavailable for complex mixtures.

Another potential challenge for modeling stand density in complex mixtures is the influence of climate and other environmental factors. Although Reineke (1933) suggested that maximum stand density for a given species might be insensitive to site quality, recent work suggests otherwise. For example, Bi et al. (2000) working in radiata pine (*Pinus radiata*) and Pittman and Turnblom (2003) in Douglas-fir (*Pseudotsuga menziesii*) found that site index influenced maximum species density and individual-stand self-thinning trajectories. Weiskittel et al. (2009) found that stand origin, purity, and site index influenced the maximum density boundary for Douglas-fir and western hemlock (*Tsuga heterophylla*). In addition, they found that soil and climatic variables related to dryness also influenced the boundary for red alder (*Alnus rubra*). At a broad scale, Comeau et al. (2010) suggest climate as a factor driving differences in maximum density for Douglas-fir and Sitka spruce (*Picea sitchensis*) between Canada and the U.K. In mixed-species forests, Reyes-Hernández et al. (2013) identify both species composition and site factors as important drivers of density relationships. In addition, variation of specific wood gravity with site conditions (e.g. temperature and precipitation) has been observed across spatial gradients (Wiemann and Williamson, 2002; Antony et al., 2010) whereas shade tolerance is known to be modulated by climate and soil moisture conditions (Carter and Klinka, 1992; Niinemets and Valladares, 2006). If species composition responds to some of the same environmental drivers as stand density, then the influences of species identity and associated functional traits could be confounded with those of environmental factors that are not incorporated into the analysis. However, the interplay between species specific characteristics (i.e. functional traits) and climate to predict stand density is unexplored.

The overarching goal of this study is the exploration of the relationship between climatic factors, species functional traits (specific gravity and shade tolerance), and stand density for three of the Lake States (Minnesota, Wisconsin, and Michigan) in the north-central United States. The study region features complex species mixtures as well as some monocultures, along with strong climatic and ecological gradients from prairie and open woodland on the western edge, to boreal forest on the north, and mixed hardwoods on the south. Historically, the region has been viewed as a "tension zone" characterized by climatically-driven transitions (Curtis, 1959), and thus serves as a challenging but appropriate test for efforts to incorporate climate into density assessment.

It is hoped that accomplishing this overarching goal could provide a means to update the national-scale stand density approach of Woodall et al. (2005) while adhering to the aspirational goals for a regional or national density measure postulated by Ducey and Knapp (2010):

- The density measure must accommodate a wide range of diameter distributions and species compositions.
- It must be able to incorporate rare species, and species that appear too rarely (if ever) as monocultures to allow separate modeling of their maximum density relationships.
- Where possible, the density measure should be consistent with accepted empirical relationships developed from common monocultures in the region.
- The density measure should be spatially consistent, and avoid arbitrary modifications following artificial boundaries (such as political subdivisions).
- The density measure should have a reasonably simple mathematical form, preferably one that simplifies evaluation of sampling error when used in practice (Ducey and Larson, 1997, 2003).

Addressing species composition, along with climate or other types of environmental variability, could conflict with the overarching goals of simplicity and transparency outlined above. The biology and ecology of species interactions can be complex, even in mixtures containing a small number of species (Forrester, 2014; Pretzsch, 2014). Attempts to quantify a stand's full complexity could render associated stand density measures impractical for broad assessments and/or stand management exercises. Hence, the specific objectives of our study are:

1. To outline a mathematical approach for incorporating multiple species functional traits, including shade tolerance as key functional trait in shaping forest structure and dynamics (Valladares and Niinemets, 2008), and potentially in interaction with climate or other environmental variables, into the mixed-species density model of Ducey and Knapp (2010);
2. To fit the resulting model to inventory data to our study region, evaluating whether common climate variables and functional traits other than specific gravity improve the statistical performance of the model; and
3. To assess the ecological and management implications and limitations of the model.

2. Materials and methods

2.1. Theory

Reineke's (1933) original stand density index (SDI) for single-cohort monocultures relies on an empirical relationship between number of trees per unit area (N) and the quadratic mean diameter (QMD, typically cm but inches in Reineke, 1933) of normally-stocked stands:

$$\log_{10}\mathrm{N} = -1.605\log_{10}\mathrm{QMD} + \mathrm{k} \quad (1)$$

where k is a constant varying with species. This in turn implies that at maximum stocking

$$N \times QMD^{1.605} = 10^k \tag{2}$$

The corresponding density index is

$$SDI = N(QMD/25.4)^{1.605} \tag{3}$$

where the quantity 25.4 is used to normalize SDI to a convenient reference diameter (cm). Comparison of the value of SDI calculated using Eq. (3) using observed values of N and QMD for a stand, with the density of a normally-stocked stand implied by Eq. (1) or (2) (i.e., the maximum SDI for that species), allows assessment of the density of a given stand relative to reference conditions. Reineke's basic formulation has been widely used for even-aged single species stands (Shaw, 2000; Woodall et al., 2005; Shaw, 2006). Density measures related to SDI often have exponents near 1.6, but may show slight deviations. For example, Pretzsch and Biber (2005), Río and Sterba (2009), and Condés et al. (2013) found variations between species in their studies, with exponents often different from the nominal value of 1.6. However, Reineke's original (1933) exponent, fitted by hand, appears approximately correct in many situations.

Curtis (1970, 1971) developed a power-law density measure for Douglas-fir stands that was closely related to SDI. This measure was reformulated by Long and Daniel (1990), who (along with Long, 1985; Shaw, 2000) suggested its use in multicohort stands:

$$ASDI = \sum_i N_i \left(\frac{DBH_i}{25}\right)^{1.6} \tag{4}$$

where ASDI is the additive formulation of SDI, N_i is the number of trees per hectare in the *i*th diameter class, and DBH_i is the diameter of the class. As formulated, Eq. (4) would require a maximum value for comparison for individual species and for species mixtures Several studies have explored the behavior and predictions of either the original SDI (Eq. (3)), ASDI (Eq. (4)), or related density measures based on the self-thinning line of Yoda et al. (1963) in relatively simple mixtures of 2–3 species (Puettmann et al., 1992; Poage et al., 2007; de Montigny and Nigh, 2007; Penner, 2008; Weiskittel et al., 2009; Condés et al., 2013; Dirnberger and Sterba, 2014; Sterba et al., 2014). However, establishing an appropriate maximum for mixtures has not proven trivial, even in simple cases.

Woodall et al. (2005), building on mechanistic work by Dean and Baldwin (1996), recognized that wood specific gravity might be used as a functional trait to predict maximum SDI:

$$SDI_{max} = a_0 + a_1\overline{SG} \tag{5}$$

where SDI_{max} is the maximum value of ASDI for a given mixture, a_0 and a_1 are empirical coefficients and $\overline{SG}$ is the mean specific gravity of trees in the stand. The coefficient a_1 should be negative, as (all else being equal) the stems of trees with denser, stronger wood can support a greater canopy mass, and hence occupy a given area more fully. The resulting density measure,

$$WD = \frac{ASDI}{a_0 + a_1\overline{SG}} \tag{6}$$

is straightforward to calculate once the two coefficients have been estimated, but the resulting equation form (with $\overline{SG}$ in the denominator) introduces a nonlinearity that makes computation of sampling standard errors slightly challenging (Ducey and Larson, 1999).

Chisman and Schumacher (1940) developed an alternative formulation, designed to be fit via multiple regression procedures. They modeled the growing space requirement of an individual tree (A_i) at normal stocking as a quadratic equation in DBH,

$$A_i = c_0 + c_1 DBH_i + c_2 DBH_i^2 \tag{7}$$

where c_0, c_1 and c_2 are coefficients. The tree area ratio, or TAR, represents the growing space requirement of the trees in the stand:

$$TAR = c_0 N + c_1 \sum_i N_i DBH_i + c_2 \sum_i N_i DBH_i^2 \tag{8}$$

where the summation is over all diameter classes. If data from many normally-stocked stands are available, and TAR is set to 1 for all such stands, the parameters can be estimated using ordinary multiple regression. Then, calculation of TAR using observed data for other stands in Eq. (8) provides the density of those stands as a fraction of normal stocking. Stout et al. (1987) generalized this approach to a mixed-species situation. In principle, a separate set of the coefficients c_0, c_1 and c_2 could be estimated for each species in a region, but in practice the number of parameters could be very large and estimation for rare species would be problematic. Therefore, Stout et al. (1987) used a small number of species groups.

Ducey and Knapp (2010) modified the exponential formulation of Curtis (1971), and followed the lead of Woodall et al. (2005) in using specific gravity to model the influence of individual species:

$$A_i = (b_0 + b_1 SG_i)(DBH_i/25)^{1.6} \tag{9}$$

Using a functional trait, instead of individual species identities, allows for a much more parsimonious model and one that can be applied to rare species as well as common ones, provided the functional trait values are known. Summing over all components in the stand (i.e., combinations of diameter and species) gives a relative density measure akin to TAR,

$$\begin{aligned} RD &= \sum_i N_i (b_0 + b_1 SG_i)(DBH_i/25)^{1.6} \\ &= b_0 \sum_i N_i (DBH_i/25)^{1.6} + b_1 \sum_i SG_i N_i (DBH_i/25)^{1.6} \\ &= b_0 \sum_i ASDI_i + b_1 \sum_i SG_i ASDI_i \end{aligned} \tag{10}$$

which can be seen as comprised of two elements. The first element is just coefficient b_0 multiplied by the ASDI of the stand, while the second element is coefficient b_1 multiplied by the sum of the ASDIs of each component, weighted by specific gravity. RD requires only two coefficients to be estimated, no matter how many species are modeled, and by its construction it is additive, simplifying error analysis (Ducey and Larson, 1997). To avoid the problem of preselecting stands representing a normal stocking condition, Ducey and Knapp fit Eq. (10) using quantile regression rather than ordinary least squares.

As written, Eqs. (9) and (10) cannot contend with multiple functional traits (for example, incorporating shade tolerance as well as specific gravity), nor do they allow for the potential influence of climate or other environmental variables on density relationships. First, suppose that we wish to extend the model to incorporate a set of functional traits varying over the components T_{ij}, $j = 1 \ldots J$ rather than only a single trait (SG). A natural reformulation of Eq. (9) would be

$$A_i = \left(b_0 + \sum_{j=1}^{J} b_j T_{ij}\right)(DBH_i/25)^{1.6} \tag{11}$$

Now, suppose that a set of environmental variables X_k, $k = 1 \ldots K$ has the potential to influence the growing space requirement of an individual tree, either alone or in interaction with one or more of the functional traits. Let

$$b_0 = c_{00} + c_{01}X_1 + c_{02}X_2 + \cdots + c_{0K}X_K = c_{00} + \sum_k c_{0k}X_k$$

$$b_j = c_{j0} + c_{j1}X_1 + c_{j2}X_2 + \cdots + c_{jK}X_K = c_{j0} + \sum_k c_{jk}X_k$$

Then, substituting in Eq. (11) to obtain individual tree growing space, and substituting in turn to develop an expression for relative density, we obtain

$$\mathrm{RD} = \sum_i \left\{ c_{00}\mathrm{ASDI}_i + \left(\sum_k c_{0k}X_k\mathrm{ASDI}_i\right) + \sum_j T_{ij}\left[c_{j0}\mathrm{ASDI}_i + \left(\sum_k c_{jk}X_k\mathrm{ASDI}_i\right)\right]\right\} \tag{12}$$

To simplify the notation somewhat, let $T_0 = 1$ and $X_0 = 1$. Then we may rewrite Eq. (12) as

$$\mathrm{RD} = \sum_i \sum_{j=0}^{J} \sum_{k=0}^{K} c_{jk}T_{ij}X_k\mathrm{ASDI}_i = \sum_{j=0}^{J}\sum_{k=0}^{K} c_{jk}X_k\left(\sum_i T_{ij}\mathrm{ASDI}_i\right) \tag{13}$$

In principle, there are as many as (J + 1)(K + 1) free coefficients to be estimated, but not all interactions may enter into the model; thus, the number may be fewer.

For a given species with traits T_{ij}, growing under environmental conditions specified by variables X_k, and given a set of coefficients c_{jk}, Eq. (13) implies a maximum ASDI for that species growing in a hypothetical monoculture:

$$\mathrm{ASDI}_{\max,i} = \frac{1}{\sum_{j=0}^{J}\sum_{k=0}^{K} c_{jk}T_{ij}X_k} \tag{14}$$

For species that do grow as monocultures, $\mathrm{ASDI}_{\max,i}$ can be compared with reference values observed in monoculture conditions (i.e., reference literature). For those that do not, $\mathrm{ASDI}_{\max,i}$ may still be useful for visualizing sensitivity to environmental conditions, and for comparing growing space requirements among species with different traits.

If it were possible to pre-screen stands or plots so that only those in the reference condition (i.e. maximum or normal stocking) could be included, then it should be possible to follow the lead of Chisman and Schumacher (1940), set RD = 1 for all plots, and fit the c_{jk} using ordinary least squares. However, for regional analyses using large datasets, prescreening is not possible. In that situation, frontier-fitting methods, such as stochastic frontier analysis (Bi, 2004; Zhang et al., 2005; de Montigny and Nigh, 2007; Weiskittel et al., 2009) or quantile regression (Koenker and Bassett, 1978; Scharf et al., 1998; Cade and Noon, 2003; Zhang et al., 2005; Ducey and Knapp, 2010) could also be used. We employ the latter in this study.

2.2. Data

We used data collected by the USDA Forest Service, Forest Inventory and Analysis (FIA) program for the states of Minnesota, Wisconsin, and Michigan. The data were downloaded from the FIA website http://www.fia.fs.fed.us/ [accessed on 14 December 2013], and the plot data from the last full inventory cycle for which data quality control and screening were complete (measurement years 2008–2012) were used. The raw tree data include all measured trees with DBH > 2.5 cm, measured using a nested set of subplots with plot clusters located systematically on all forested lands in the study region. We included only live trees in our analysis. For full details on the FIA program, its associated designs, and estimators see Bechtold and Patterson (2005).

The FIA database includes species identification, diameter at breast height, and a tree expansion factor (i.e., the reciprocal of plot area for the appropriate nested subplot). We used wood specific gravities based on those in Miles and Smith (2009), with additional species from the FIA database. We used specific gravity based on green volume and dry weight for model fitting. The database for this region included species ranging from a low of 0.29 (*Thuja occidentalis*) to a high of 0.84 (*Carpinus caroliniana*). Although wood specific gravity values have been proven to have both intra-specific and individual tree (i.e., within bole) variation, we adopted a uniform specific gravity for each species as empirical information for such variation across our study region is absent. We used shade tolerance rankings from Niinemets and Valladares (2006) defined by the capacity of growth in the shade. For a small number of species, shade tolerance rankings were unavailable; we substituted shade tolerance values for ecologically-similar congenerics or closely related species where necessary. Shade-tolerance values ranged from 0.98 (*Larix laricina*) to 5.01 (*Abies balsamea*).

We used downscaled daily climate data from the PRISM Climate Group at Oregon State University (www.prism.oregonstate.edu). The PRISM AN81d dataset provides daily precipitation, minimum, and maximum temperature at a resolution of 30 s of latitude and longitude (approximately 4 km). We used data for calendar years 1981 through 2012 to calculate a series of climate variables (Table 1). The FIA database includes latitude and longitude for each plot, with a random dithering applied to maintain individual landowner confidentiality. This dithering is typically on the order of only a few kilometers, and would be too small under ordinary circumstances to displace a plot by more than one pixel within the PRISM data. We used the published coordinates to extract all of the calculated climate variables for each plot location in the data.

We treated individual FIA plots as observations, aggregating across subplots within a cluster, and omitting plots that included a non-forest condition or that spanned multiple conditions (i.e. combinations of forest type, size class, or ownership). This exclusion mitigates the potential problem of aggregating dissimilar subplots, though it is still possible for a stand boundary or nonforest edge to fall near the perimeter of a subplot but outside the measured area. We treated each live tree on each plot as a stand component, and calculated ASDI_i following Eq. (4). We then multiplied ASDI_i by the specific gravity of the tree, and by the shade tolerance ranking of the tree to obtain T_{i1} ASDI_i, and T_{i2} ASDI_i, respectively. Each of the climate variables was treated as an environmental variable (X_k), and a matrix of T_{ij} V_k ASDI_i values was computed (e.g. Eq. (13)), with one row per plot. This data matrix provided the basic input for subsequent analysis.

2.3. Statistical analysis

We followed Ducey and Knapp (2010) in estimating parameters using quantile regression (Koenker and Bassett, 1978; Koenker, 2005). The use of quantile regression to estimate density relationships does not require the subjective selection of a subset of the data based on predefined criteria, such as prescreening to ensure all plots are at normal or maximum stocking (Zhang et al., 2005). Quantile regression is also insensitive to the presence of extreme outliers (Scharf et al., 1998), which is helpful in dealing with very large data sets where occasional errors or anomalies may occur. For further discussion on the application of quantile regression in ecological settings, see Cade and Noon (2003).

The quantile τ represents a free parameter in quantile regression. For example, in simple quantile regression (i.e. with only one independent variable), if $\tau = 0.5$ then the regression line predicts the conditional median of the data. If $\tau = 0.9$ then 90% of the data are expected to fall below the line, while 10% fall above it; if $\tau = 0.95$ then 95% of the data fall below the line and 5% above it, and so on. Ducey and Knapp (2010) chose the quantile so that their density measure would conform to existing guidance from a series of silvicultural guides that used Reineke-style density measures for single species or well-defined simple mixtures. We chose to follow that approach; however, the menu of such guides for the Lake States is somewhat limited. We selected the density management guidance of Benzie (1977b) for *Pinus resinosa* as a benchmark. *Pinus resinosa* has been widely used as a plantation species in the Lake States, its dynamics have been well-studied, and the stocking diagram of Benzie (1977b) has been broadly adopted in the region.

Table 1
Climate variables computed from PRISM daily data at 30 s resolution.

Variable	Description	Units	Minimum	Mean	Maximum
AnnMaxTemp	Annual maximum temperature, averaged over years 1981–2012	C	27.04	33.20	36.41
AnnMinTemp	Annual minimum temperature, averaged over years 1981–2012	C	-38.91	-30.93	-18.93
AnnPPTSum	Total annual precipitation, averaged over years 1981–2012	mm (×100)	4.38	7.11	9.92
AnnTempMean	Mean annual temperature, averaged over years 1981–2012	C	2.02	5.53	10.14
GSLength	Growing season length (continuous frost-free days), averaged over years 1981–2012	days	152.8	216.8	250.6
GSPPTSum	Total growing season precipitation, averaged over years 1981–2012	mm (×100)	0.65	2.42	4.17
GSPPTMean	Mean daily precipitation during the growing season, averaged over years 1981–2012	mm (x100)	0.0029	0.0108	0.0178
GSTempSum	Total growing season degree-days above 0, averaged over years 1981–2012	days C	447.8	1485.3	2673.0
GSTempMean	Mean daily temperature during the growing season, averaged over years 1981–2012	C	1.88	6.58	10.40

That stocking guide indicates that 865 trees of 25 cm DBH would provide normal stocking for the species. We fit a series of quantile regression models with τ ranging from 0.500 to 0.995, using the simple Ducey and Knapp (2010) model (i.e. with no environmental variables, and using only specific gravity as a functional trait), and selected the τ that resulted in an implied maximum SDI closest to 865 for *Pinus resinosa*. This quantile was then used in all subsequent modeling.

Having selected a quantile, we then proceeded to evaluate shade tolerance as an additional trait, and the climate variables as potential environmental modifiers. We began with the basic Ducey and Knapp (2010) model, and evaluated additional more complex models in a forward, stepwise fashion. We used Schwarz's Bayesian Information Criterion (BIC; Schwarz, 1978) to assess whether adding a term to the model improved model fit. BIC is related to the more popular Akaike Information Criterion (Akaike, 1974; Burnham and Anderson, 2002), in that it includes both the likelihood as a measure of goodness-of-fit as well as a model complexity penalty:

$$\mathrm{BIC} = -2\ln(\mathrm{L}) + \mathrm{k}\ln(\mathrm{n}) \tag{15}$$

where L is the log-likelihood of the data given the model, k is the number of parameters in the model, and n is the number of observations. Lower values of BIC indicate improvements in the model with increasing complexity, while higher values indicate overfitting. BIC typically selects models that are more parsimonious than AIC; Claeskens and Hjort (2008) summarize the theoretical underpinnings and differences between AIC and BIC. The use of BIC (or AIC) with quantile regression involves the use of a pseudo-likelihood based on an asymmetric, double-exponential distribution for the residuals; however, model selection for quantile regression appears to be quite robust to departures from that distributional assumption (e.g. Machado, 1993; Cade et al., 2005).

Once a final model was selected, we used data visualization to better understand its behavior across species and across the study region. We mapped $\mathrm{ASDI}_{\mathrm{max}}$ for selected species using the PRISM climate data, focusing on species that represented extreme combinations of functional traits (i.e., those on the convex hull of the cloud of species, when plotted in the specific gravity-shade tolerance plane). To assess the predictive capacity of the model for those species that do occur as monocultures, we constructed a set of Reineke-style charts. There is no single, uniform definition for what constitutes a single-species vs. a mixed-species stand (Bravo-Oviedo et al., 2014); we followed Toumey and Korstian (1947) in using a basal area threshold, under which a plot was considered "single species" if 90% or more of the basal area on the plot was composed of a single species. For all species represented as monocultures on at least 75 plots, we constructed log-log plots of trees/ha vs. stand quadratic mean diameter, and overlaid the mean, minimum, and maximum lines implied by a single-component stand of that species under the actual range of environmental variables for the monoculture plots.

3. Results

In total, 12,446 plots were available for analysis, containing 355,365 trees of 101 species. These top 12 most abundant species by basal area collectively represented 67.9% of the total basal area and 66.8% of the total number of trees (Table 2).

The implied $\mathrm{ASDI}_{\mathrm{max}}$ for *Pinus resinosa* with changing quantile was compared to the standard guidance from Benzie (1977b) (Fig. 1). The closest match occurred at $\tau = 0.90$ which was the quantile was used in all subsequent modeling.

Forward selection using BIC, and starting from the Ducey and Knapp (2010) model that included only specific gravity and no climate variables, led to the inclusion of shade tolerance and three climate variables, along with some interactions for a total of 7 parameters. The model can be written in equation form as (parameter estimates and associated standard errors in Table 3):

$$\begin{aligned}\mathrm{RD} = {} & (c_{00} + c_{01}\mathrm{GsPPTMean})\sum_i \mathrm{ASDI}_i + (c_{10} \\ & + c_{11}\mathrm{GsPPTMean})\sum_i \mathrm{S\ G}_i\mathrm{ASDI}_i + (c_{20} + c_{22}\mathrm{GsLength} \\ & + c_{23}\mathrm{AnnMinTemp})\sum_i \mathrm{S\ T}_i\mathrm{ASDI}_i\end{aligned} \tag{16}$$

The implications of Eq. (15) can be visualized by mapping the implied values of $\mathrm{ASDI}_{\mathrm{max}}$ for species that differ in their functional traits (Fig. 2). In general, the species with the lowest specific gravities can support the highest densities, regardless of shade tolerance (e.g. *Thuja occidentalis*, SG = 0.29, ST = 3.45; *Populus balsamifera*, SG = 0.31, ST = 1.27; and *Abies balsamea*, SG = 0.33, ST = 5.01), while high specific gravity is associated with low maximum density (e.g. *Cornus florida*, SG = 0.64, ST = 4.87; *Amelanchier arborea*, SG = 0.66, ST = 4.33; *Maclura pomifera*, SG = 0.76, ST = 1.45). All species show a gradient of lower to higher maximum density from the relatively dry prairie margin on the western portion of the study area, to the cooler and wetter northern and eastern portions of the region. However, the pattern of sensitivity is somewhat different between shade-tolerant and shade-intolerant species, reflecting the interaction of shade tolerance with climate variables reflecting overall warmth or coolness in Eq. (15).

Only 6 species were represented as monocultures or near-monocultures on more than 75 plots in the region. Reineke-style charts for these species exhibit a small number of plots above the density line, consistent with the use of the 0.9 quantile (10% of plots are expected to fall above the fitted line) (Fig. 3). Visually, the fits are nearly all similar to that for *Pinus resinosa*, the only species used in quantile selection. The main exception is *Acer saccharum*, which shows a slightly larger portion of plots at or above the fitted line.

Table 2
Abundance and functional traits of the 12 most common species by basal area in the Lake States.

Species	Basal area, % of total	Trees, % of total	Specific gravity (green volume, dry weight)	Shade tolerance
Populus tremuloides	11.1	16.4	0.35	1.21
Acer saccharum	9.8	7.2	0.56	4.76
Acer rubrum	9.1	8.7	0.49	3.44
Thuja occidentalis	6.6	4.3	0.29	3.45
Pinus resinosa	5.0	1.8	0.41	1.89
Quercus rubra	4.8	1.5	0.56	2.75
Abies balsamea	4.5	11.1	0.33	5.01
Tilia americana	3.8	2.0	0.32	3.98
Fraxinus nigra	3.5	4.5	0.45	2.96
Picea mariana	3.3	6.3	0.38	4.08
Betula papyrifera	3.3	3.2	0.48	1.54
Pinus strobus	3.2	1.8	0.34	3.21

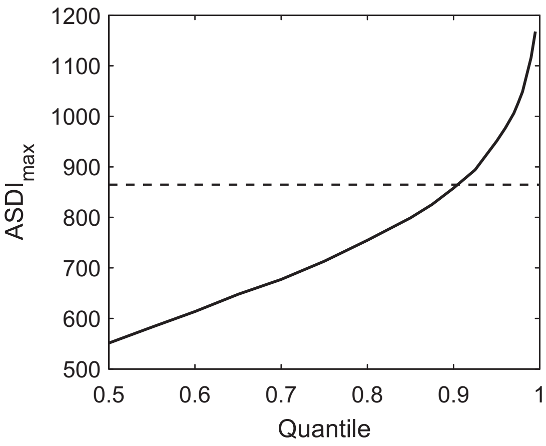

Fig. 1. Change in $\mathrm{ASDI}_{\max}$ for *Pinus resinosa*, as a function of the quantile τ used to fit the basic Ducey and Knapp (2010) density model (solid line). The reference value from Benzie (1977b) is also shown (dashed line).

4. Discussion

Plant traits (structural and functional among others) determine how species are adapted to environmental stressors (Kattge et al., 2011) and they have been recently used to model species response to global change in terms of tree growth (Ratcliff et al., 2016) or species distribution based on specific wood density (Swenson et al., 2010) or drought tolerance (Liénard et al., 2016). In forestry, Woodall et al. (2005) were the first to use a structural trait (specific wood gravity) to explain the maximum density that a stand can support based on the mechanical properties of stems (Dean and Baldwin, 1996) and the species-specific tolerance to bending stress. Based on this, Ducey and Knapp (2010) built a specific relative density applicable to mixed-species forests. Here we expand the Ducey and Knapp's (2010) model to include tolerance to shade, a major driver of forest dynamics in the study area, as well as the interplay of species-specific traits with climate.

The model formulation in Eq. (13), coupled with conservative model selection criteria, leads to an overall density model that met several of the aspirational goals outlined by Ducey and Knapp (2010). It can accommodate a wide range of diameter distributions and species compositions, including (in principle) novel or rare species, so long as a value of wood specific gravity and shade tolerance index can be identified. To be included in the model our approach does not require species to be present as monocultures in the data. Additionally, it uses broad geospatial data rather than arbitrary political or ecological regions to address spatial heterogeneity in maximum stocking. By construction, it is strictly additive – total stand density is the sum of individual tree contributions – so parsing the contributions of different species or diameter classes, and estimating sampling errors, is straightforward (Ducey and Larson, 1997, 2003). This latter advantage is shared by the formulation of Rivoire and Le Moguedec (2012), but their species-specific approach – while likely advantageous in situations where most or all of the species occur frequently enough as monocultures to be modeled individually – would be challenging in a diverse region with many rare species. Despite a relatively large sample size, the number of climate variables (three) and species functional traits (two) incorporated in the model is manageable.

Assessing consistency with accepted empirical relationships presents some challenges. Exact agreement with previously published studies should not be expected. The implied maximum density for a given species varies geographically depending on climate, but the precise geographic distribution of study plots on which older silvicultural guidance was based is rarely available. Additionally, it cannot be assumed that the distribution of a particular species within the current regional FIA data, matches that considered by the authors of previous studies. Indeed, McGill et al. (1999) suggest that the Lake States region lacks adequate within-region guidance on stand density management, often forcing a reliance on guidelines from nearby regions with slightly different climate, soils, and species composition. Nonetheless, there is broad qualitative and quantitative agreement between our model and the guidance from several published studies. For example, McGill et al. (1999) present stocking guidance for *Quercus rubra* in Wisconsin,

Table 3
Parameter estimates and associated standard errors for the full density model (Eq. (15)).

Symbol	Functional trait	Climate variable	Estimate	Standard error
c_{00}	–	–	−0.00042	0.00017
c_{01}	–	GsPPTMean	0.07682	0.01698
c_{10}	Specific gravity	–	0.00389	0.00039
c_{11}	Specific gravity	GsPPTMean	−0.11365	0.03755
c_{20}	Shade tolerance	–	0.00011	0.00004
c_{22}	Shade tolerance	GsLength	$-1.197 * 10^{-6}$	$0.157 * 10^{-6}$
c_{23}	Shade tolerance	AnnMinTemp	$-1.824 * 10^{-6}$	$0.452 * 10^{-6}$

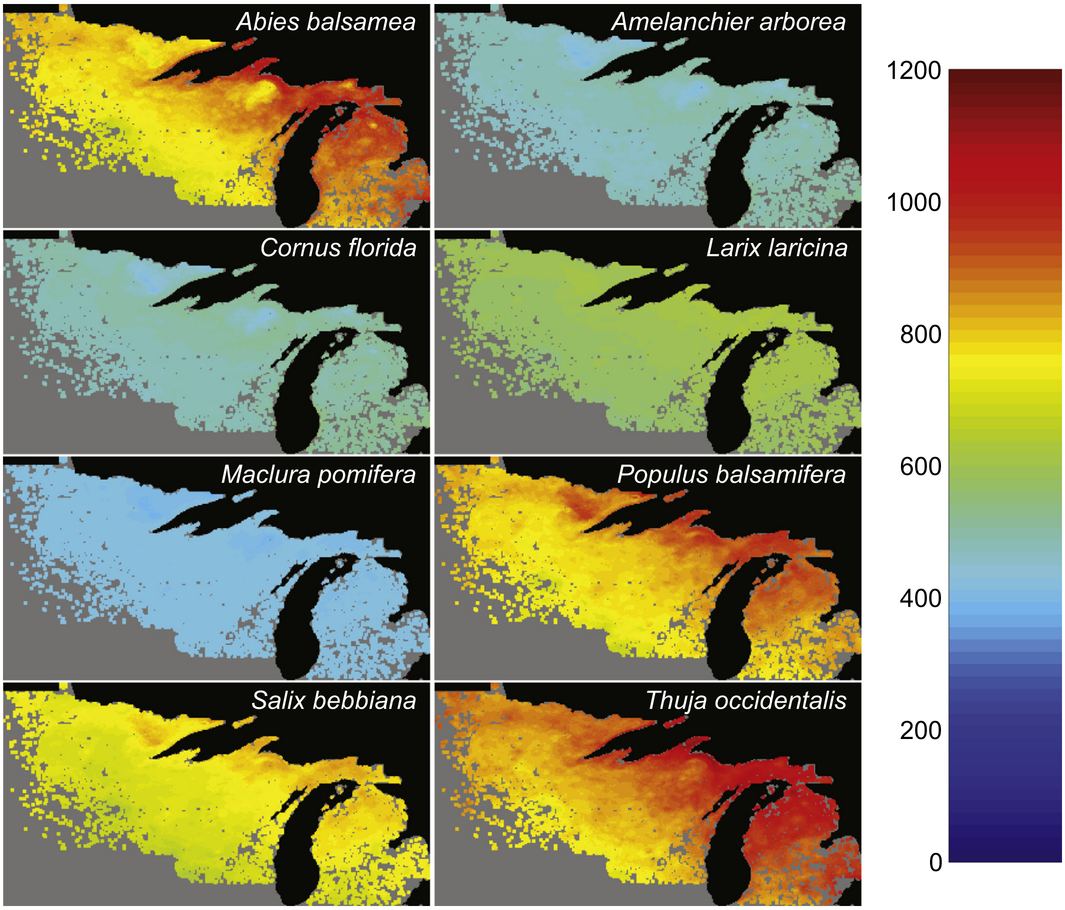

Fig. 2. Spatial pattern of $ASDI_{max}$ for eight species with divergent functional traits.

corresponding to a maximum ASDI of approximately 595. Substituting the species traits of *Quercus rubra*, and the mean regional climate values from Table 1, into Eq. (14) yields a maximum ASDI for *Q. rubra* of 647, a discrepancy of just over 8%. McGill et al. (1999) motivated their work on the observation that *Quercus rubra* stands in the Lake States are known to achieve higher stocking levels than the widely-used stocking guide of Gingrich (1967), which implies a maximum ASDI of 526. Not only was the Gingrich (1967) stocking guide developed outside the region (to the south), the species mix reflected a more drought-tolerant mix of *Q. alba, Q. velutina, Q. prinus,* and *Q. coccinea* with relatively little *Q. rubra.* Substituting the mean properties of that species mix, into mean regional climate variables, yields a maximum ASDI of 615, suggesting that much of the difference between the stocking levels of Gingrich (1967) and McGill et al. (1999) is attributable to climate or other regional differences, with a small but important contribution of species traits. At one end of the spectrum, the highest reported maximum density for a species in the Lake States is that of Saunders and Puettmann (2000) for *Picea glauca*, at approximately 1110; substitution of mean climate in our model gives a maximum ASDI of 1203, or an 8% difference. Our model predicts similar maximum ASDI for *Pinus banksiana* and *Pinus resinosa* at the mean regional climate (753 and 784, respectively), even though published guidance differs somewhat for the two species (865 for *P. resinosa* and 680 for *P. banksiana*; Benzie, 1977a,b). Indeed, the model in this study was calibrated for agreement with *P. resinosa* guidance, and the discrepancy thus reflects differences between the maximum ASDI of that species at a regional mean climate, and its maximum ASDI in its realized niche. The discrepancy for *P. banksiana* may partly reflect differences between the mean climate and its realized niche, and partly the tendency for *P. banksiana* to be found on droughty, nutrient-limited sites: soil and site factors are not incorporated in our model. Nonetheless, both species reveal discrepancies of less than 10%. Tubbs (1977) gives density recommendations for northern hardwood forests. Given the wide range of species composition no meaningful quantitative comparisons can be made. However, Tubbs (1977) does assert that maximum stocking increases substantially with an increase in the proportion of either *Tilia americana* or *Tsuga canadensis*. Both are relatively light-wooded and shade-tolerant, and would be associated with high maximum ASDI in our model. The most obvious discrepancy with published guidance is for *Ulmus-Fraxinus-Populus* forests, for which Myers and Buchman (1984) imply a maximum ASDI of 618. Substituting the mean regional climate gives a maximum ASDI with our model of 755, or 22% higher. However, the *Ulmus-Fraxinus-Populus* type is most closely associated with riparian forests on the western, prairie margin of our study region, where maximum ASDI is lower regardless of species traits (e.g. Fig. 2). Thus, a substantial discrepancy in comparison with the mean regional climate is to be expected.

Broadly speaking, our study's model captures an intuitive gradient in maximum density from low levels at the prairie margins and in the relatively warmer, drier forests on the southern edge of the study area, to higher levels in the colder and wetter forests to the north and east. However, the exact relationships depend on an interaction between species traits and climate. The positive relationship between specific gravity and site occupancy of individual trees, and the consequent negative relationship between specific gravity and maximum ASDI, as observed by Dean and Baldwin (1996), Woodall et al. (2005), and Ducey and Knapp (2010), could

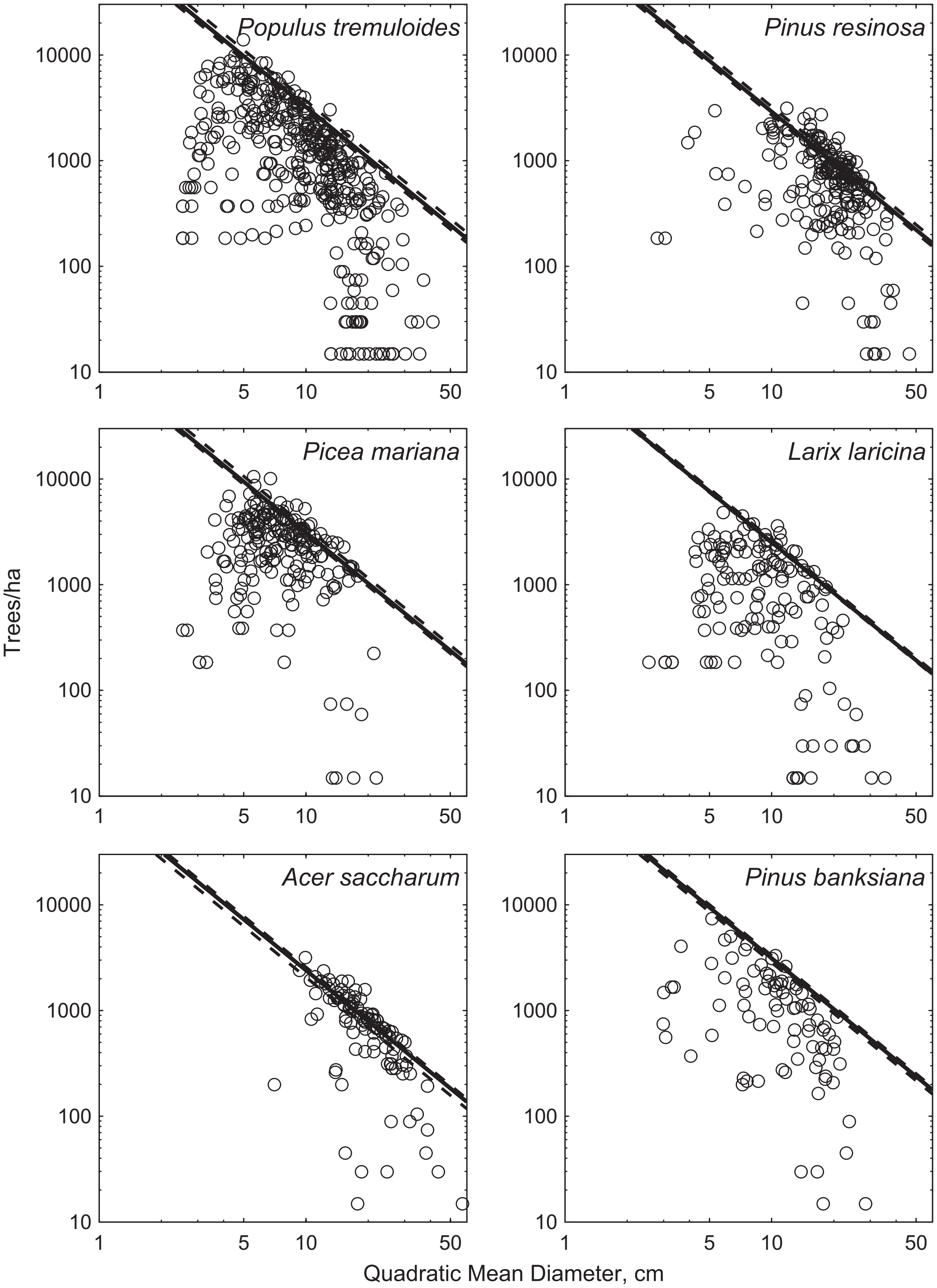

Fig. 3. Reineke-style charts for species occurring as monocultures in the study region. Individual monoculture plots are shown as circles; the maximum density line for the species at the mean climate of the monoculture plots is shown as a solid line; and the range of maximum densities given the range of climate in the monoculture plots is shown with a pair of dashed lines.

be modulated by growing season precipitation in accordance to intra-specific variation of specific gravity with summer precipitation, temperature and growing season length found in *Pinus taeda* stands (Antony et al., 2010). On the other hand, cooler temperatures (as captured by minimum annual temperature and shorter growing season length) are associated with the ability to sustain higher densities of shade-tolerant species. It is unclear whether this capacity to sustain shade-tolerants at high density relates to reductions in maintenance respiration costs, differences in evapotranspirative demand, more even moisture availability through the growing season (e.g. through shifts in the proportion of annual precipitation falling as snow), or some other underlying mechanism. Whether these associations reflect underlying mechanisms, or are purely correlative, remains to be seen; comparison with other regions may prove fruitful.

A strictly additive density model presents advantages for computing sampling variances (Ducey and Larson, 1997, 2003), but it also creates constraints on the kinds of biological interactions that can be captured faithfully (Ducey and Knapp, 2010). For example, facilitation or mutualism, resource use complementarity, or allelopathic interactions cannot be captured in a strictly additive model such as the one presented here, because the growing space requirement (or density contribution) of an individual tree does not depend on the species identity or functional traits of its neighbors. However, a strictly additive model can serve as a useful baseline or null model against which to test for over- or under-yielding of species mixtures (e.g. Condés et al., 2013; Forrester et al., 2013; Huber et al., 2014; Drössler et al., 2015; Toïgo et al., 2015). The assessment of such effects can be sensitive to the method of partitioning stand density among species (Dirnberger and Sterba, 2014; Sterba et al., 2014). Thus, development of appropriate baselines may be critical given the emerging interest in understanding the impact of species mixture and its interaction with environmental effects and stand development in modulating total forest ecosystem production (Forrester et al., 2013; Forrester, 2014; Chaturvedi and Raghubanshi, 2015; Laganière et al., 2015).

The comparison of maximum ASDIs estimated from our model versus published silvicultural guidance raises important questions, especially in relation to the possibility of extending such an analysis to broader geographic areas. The alignment of our results with existing silvicultural guidance is reassuring. However, one can imagine situations where divergence would be expected or even desirable. For example, if maximum densities are very sensitive to climate, one should not necessarily expect that a climate-sensitive model will agree, on average or in its location-specific predictions, with guidance derived from an intensively-studied but purposively designed growth and yield study. Changing guidance is a potential source of confusion, especially when existing sources enjoy a long tradition of use. On the other hand, contemporary, systematic inventories across the entire population of interest (such as those in many national forest inventories) compiled in a georeferenced database could allow incorporating the inherent species complexity found in many forests (via functional traits), varying climatic conditions (via temperature and precipitation), and significant interactions into dynamic live tree stocking indices. Given contemporary advances in portable, handheld, spatially-aware computing power represented by devices such as the “smart phone,” the ability to incorporate such information in management may not be as restrictive as it once was.

Even when a quantile of 0.90 was used to estimate maximum ASDI in this study, it was found that published maximum ASDI values were most often below those estimated by the models produced in this study. Perhaps the use of a systematic inventory to sample the population of interest will capture the true maximum stocking potential of the population in contrast to past attempts with limited data and/or restriction to portions of species’ ranges. Hence, the selection of quantiles, such as 0.90 (as used in this study) may be somewhat arbitrary and reactive to maximum ASDI values derived from literature that used a diversity of methods and sampling efforts/strategies. We can suggest one potential path forward. The selection of quantiles for fitting our study’s maximum ASDI models might be based on maximum ASDI’s from the literature in the cases where common tree species are managed in monocultures with associated supply chains (landowners to forests to the wood products industry) having fully assimilated such guidance into their work streams for many decades. In the cases of stand density evaluations across entire regions (Woodall et al., 2006, 2015) or in highly diverse forests it may be more objective to allow maximum ASDI model fits to express the maximums (i.e., quantile = 0.99; Woodall et al., 2006) found in the data which can be hypothesized as the true expression of the maximum stocking for any individual tree species.

5. Conclusions

A relatively parsimonious maximum live tree stocking model was developed that is additive across stand components (such as tree size) and dependent on tree species functional traits (shade tolerance and specific gravity) and climate (temperature and precipitation). Such a model produces dynamic estimates of maximum tree stocking in situations where traditional stocking guides are not available: mixed species forests (especially those containing uncommon species) and species whose ranges traverse strong climatic gradients (i.e., using a species stocking guide in a climate divergent from the one where it was developed). Although the model presented here is a simplification of mixed-species stand complexity, we believe it is appropriate for model-assisted description, diagnosis, and prescription in operational silviculture, as well as for more strategic-level assessments of forest conditions). As such, it can be refined through alternative methods of describing species traits or environmental variation. Finally, our study’s maximum tree stocking model may present a path forward for development of future forest stocking metrics in the face of climate change and tree range shift scenarios. Under these future scenarios, we would surmise that tree stocking indices might need to be as dynamic as the changing climate and novel tree species mixtures that foresters may face.

Acknowledgments

This work was supported under Joint Research Venture 12-JV-11242305038 between the U.S.D.A. Forest Service and the University of New Hampshire. AB-O was granted with a Short Term Scientific Mission at UNH supported by COST (European Cooperation in Science and Technology) Action FP1206. Rich Maclean, Felicia Morrissette, and Ethan Belair assisted with data assimilation and supporting analysis.

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