Evaluating and modeling variation in site-level maximum carrying capacity of mixed-species forest stands in the Acadian Region of northeastern North America

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ABSTRACT

Currently no universal approach exists to estimate regional site-level maximum carrying capacity in terms of stand density index (SDI_{MAX}) of mixed species stands across contrasting forest ecosystems. Regional research efforts that account for influential stand-level variables and species traits are needed to reliably derive SDI_{MAX} under varying environmental conditions and stand characteristics. This study used regionally comprehensive forest inventory data from various permanent sampling efforts to evaluate the effects of contrasting biotic and abiotic stand- and site-level factors on SDI_{MAX} of multiple-species, structurally heterogeneous stands of the climatically diverse Acadian Forest Region of North America. Specifically, we aimed to i) quantify the stand-level maximum size-density line for an array of forest stands found across the study area, irrespective of stand structure; ii) evaluate the relationship between this stand-specific estimate of SDI_{MAX} and various other stand-level attributes; and, iii) develop a generalized SDI_{MAX} prediction model using SDI_{MAX} estimates from objective i) as well as potential regional drivers of SDI_{MAX} from objective ii). The most influential stand-level factors on SDI_{MAX} were proportion of total stand basal area in hardwood species, basal area weighted mean specific gravity, range in stem diameter, and species diversity. Direct climatic variables were not included in our SDI_{MAX} prediction model due to the limited variation explained, but relationships with elevation and a site quality index based on these climatic variables were. Overall, we conclude that i) variation in SDI_{MAX} appears to be mostly driven by the softwood to hardwood ratio of the mixed species, structurally complex stands evaluated in our study and ii) the general approach offers a viable framework for estimating site maximum carrying capacity at a regional-scale and effectively managing stand density accordingly.

Keywords: New England, Maritime Provinces of Canada, US Forest Inventory & Analysis, maximum size-density relationship, stand density index, spruce-fir, maple-beech-birch, quantile regression, mixedwoods

RÉSUMÉ

Il n'existe actuellement aucune approche universelle de l'évaluation de la capacité maximale de support des sites régionaux reliée à l'indice de densité de peuplement (SDI_{MAX}) des peuplements mélangés retrouvés dans différents écosystèmes forestiers. Des travaux de recherche régionaux qui tiennent compte des variables clés du peuplement et des caractéristiques des espèces, sont requis pour pouvoir calculer de façon fiable le SDI_{MAX} pour des conditions environnementales et des caractéristiques de peuplement variables. Cette étude a utilisé les données globales d'un inventaire forestier régional tirées de différents travaux d'échantillonnage permanent afin d'évaluer les effets des facteurs biotiques et abiotiques divergents des peuplements et du site sur les SDI_{MAX} des peuplements structurellement hétérogènes d'espèces mixtes de la région climatiquement différente de la forêt acadienne de l'Amérique du Nord. Plus précisément, nous avons cherché i) à quantifier le niveau maximum de la taille-densité au niveau du peuplement pour un ensemble de peuplements forestiers retrouvés dans l'aire sous étude, sans égard à la structure du peuplement ; ii) à évaluer la relation entre l'estimé du SDI_{MAX} spécifique au peuplement, ainsi que les autres caractéristiques du peuplement ; et iii) à développer un modèle général de prédiction du SDI_{MAX} au moyen des estimés tirés de l'objectif i), ainsi que les caractéristiques ayant une influence sur le SDI_{MAX} selon l'objectif ii). Les facteurs ayant le plus d'influence sur le SDI_{MAX} au niveau du peuplement ont été identifiés comme étant la proportion des espèces feuillues en termes de la surface terrière du peuplement, la surface terrière de la moyenne pondérée de la masse volumétrique, la distribution des diamètres des tiges et la diversité des espèces. Les variables climatiques à incidence directe n'ont pas été incluses dans notre modèle de prédiction du SDI_{MAX} à cause du peu de variation identifiée, mais les relations selon l'altitude et l'indice de qualité du site reposant sur ces variables climatiques l'ont été. Somme toute, nous concluons que la variation du SDI_{MAX} semble découlée principalement du ratio entre les conifères et les feuillus retrouvés dans ces peuplements mélangés de notre étude qui sont des peuplements dont la structure est complexe, mais l'approche globale offre un cadre de référence fiable lors de l'estimation de la capacité maximale de support à une échelle régionale ainsi que pour l'aménagement efficace de la densité du peuplement.

Mots clés : Nouvelle-Angleterre, provinces maritimes du Canada, inventaire forestier et analyse des forêts américaines, relation taille-densité maximale, indice de densité du peuplement, épinette-sapin, érable-hêtre-bouleau, régression quantile, peuplements mélangés

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Introduction

Forest growth and yield is primarily an outcome of the degree of stand-level competition, site potential, and maximum carrying capacity (Weiskittel *et al.* 2011a). In forestry, the latter is often expressed as the maximum size – density relationship (MSDR also self-thinning line, Zeide 1987, 2010), which is a key forest stand property that governs both stand dynamics and realized productivity (Jack and Long 1996). Fitted as a line to the upper limit of observed size-density data (Kershaw *et al.* 2017), it is usually expressed as a log-log linear relationship of stem density (trees ha⁻¹) as a function of mean tree size (usually quadratic mean stem diameter at breast height (QMD), Weiskittel *et al.* 2011a).

Besides stand density index (SDI), which is an absolute measure that provides the degree of full occupancy in a stand (Andrews *et al.* 2018), maximum stand density index (SDI_{MAX}) is another crucial metric derived from the size-density relationship (Reineke 1933). SDI_{MAX} is the maximum number of trees at a given reference mean tree diameter (commonly 25.4 cm) that can exist in a self-thinning population (*sensu* stand maximum carrying capacity). Relative density (RD, Long 1985), the ratio of SDI and SDI_{MAX}, is highly correlated to certain stand development stages and associated processes of stand dynamics (Jack and Long 1996). RD is thus often used to guide forest management based on so called density management diagrams (DMDs, e.g., Drew and Flewelling 1979; Long 1985; Wilson *et al.* 1999).

The log-log relationship of stem density and mean tree size has been intensively studied for monospecific and mostly even-aged stands with the slope originally assumed to be constant (-1.605) across species and the intercept varying according to the species analyzed (Reineke 1933). While the assumption of a universal slope has been challenged (e.g., Pretzsch and Biber 2005; Weiskittel *et al.* 2009; Charru *et al.* 2012), the proper derivation and representation of the relationship for mixed species stands remains an ongoing and challenging research issue with numerous approaches previously suggested (Puettmann *et al.* 1992; Woodall *et al.* 2005; Ducey and Knapp 2010; Andrews *et al.* 2018; Quiñonez-Barraza and Ramírez-Maldonado 2019). In fact, there appears to be no general consensus whether pure or mixed species stands support higher SDI_{MAX} (Pretzsch and Biber 2016; Kimsey *et al.* 2018).

Moreover, there is increasing evidence that site productivity and/or climatic with soil factors that define it do have a major influence on SDI_{MAX} (e.g., Weiskittel *et al.* 2009;

Condés *et al.* 2017; Ducey *et al.* 2017; Kweon and Comeau 2017; Aquirre *et al.* 2018). However, while there appears to be commonalities in stand and site characteristics in relation to species SDI_{MAX}, currently there is no generalized or universal model that fits across species and ecosystems (Kimsey *et al.* 2018), particularly in areas dominated by mixed species stands. Regional research efforts that take into account influential stand-level variables are therefore needed to reliably derive SDI_{MAX} under varying environmental conditions and stand characteristics (Comeau *et al.* 2010; Zhang *et al.* 2018). Recently, Andrews *et al.* (2018) examined variation in SDI_{MAX} across the Acadian Region and found it primarily related to climatic factors, but used a species-specific approach, which can make it rather difficult to generalize regional trends and patterns across multiple scales.

Regardless of scale, it is rather important to note that the various approaches for estimating SDI_{MAX} can create contrasting levels of observed variation in the value and alter underlying relationships with additional factors considered as important (Salas-Eljatib and Weiskittel 2018). For example, a wide variety of statistical (e.g., quantile regression, stochastic frontier analysis; Zhang *et al.* 2005) and data sources (e.g., tree- vs. stand-level, static vs. dynamic) have been used in past SDI_{MAX} analyses, which all give different MSDRs and degree of variability (Salas-Eljatib and Weiskittel 2018). Generally, linear quantile mixed-effects regression (LQMM; Koenker 2004), introduced for SDI_{MAX} prediction by Andrews *et al.* (2018), has been found to provide the most consistent and robust estimates (Salas-Eljatib and Weiskittel 2018).

Consequently, this study used comprehensive forest inventory data from various regional permanent sampling efforts to evaluate the effects of biotic and abiotic stand- and site-level factors on SDI_{MAX} of mixed and structurally heterogeneous forest stands of the climatically diverse Acadian Forest Region in northeastern North America using the methods of Andrews *et al.* (2018) and an expanded dataset, particularly the inclusion of ecologically unique mature forests (Kuehne *et al.* 2018a, 2018b). Specifically, we aimed to i) quantify the stand-level MSDR for an array of conditions found across the study area irrespective of stand structure; ii) evaluate the relationship between the stand-specific estimate of SDI_{MAX} and various other stand-level attributes; and, iii) develop a generalized SDI_{MAX} prediction model using the estimates from objective i) as well as potential regional drivers from objective ii). Expected findings were that SDI_{MAX} would primarily be driven by species composition followed by structural attributes and climate.

Material and methods

Study area

The Acadian Forest of northeastern Northern America stretches from the northern New England states of the United States of America (USA) to the Maritime Provinces of Canada over diverse elevational and maritime gradients. It is defined as a transitional ecotone between hardwood forests to the south and the boreal forest to the north (Rowe and Halliday 1972). Climate and soil vary immensely in the region and this range has a strong influence on site conditions and forest structure, which also give rise to high regional tree species diversity (Briggs and Lemin 1992; Seymour 1995). Across the region, mean annual precipita-

tion is 110 cm with a range of 72 to 175 cm, while mean growing degree days (sum of temperature > 5 °C) is 1682 with a range of 423 to 3125 days (Andrews *et al.* 2018). Glacial till and alluvium are the principle soil parent materials with soil types ranging from well-drained loams and sandy loams on glacial till ridges to poorly and very poorly drained loams on flat areas (Ferwerda *et al.* 1997).

The majority of the Acadian Forest is dominated by naturally-regenerated, mixed-species stands, while some portions of New Brunswick contain intensively-managed, mostly single-softwood species plantations (Andrews *et al.* 2018). Common forest types in the region include black spruce (*Picea mariana* (Miller) B.S.P), northern white cedar swamps (*Thuja occidentalis* L.), red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* L.) flats, red spruce – balsam fir – red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton) – sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), yellow birch, aspen (*Populus* spp.), paper birch (*Betula papyrifera* Marsh.), white pine (*Pinus strobus* L.) – mixed conifer forest, and red oak (*Quercus rubra* L.) – white pine (Eyre 1980). Other species present include white spruce (*Picea glauca* (Moench) Voss.), Norway spruce (*Picea abies* (L.) Karst.), red pine (*Pinus resinosa* Ait.), Scots pine (*Pinus sylvestris* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), paper birch (*Betula papyrifera* Marsh.), quaking aspen (*Populus tremuloides* Michx.), big-tooth aspen (*Populus grandidentata* Michx.), black cherry (*Prunus serotina* Ehrh.), and white ash (*Fraxinus americana* L.). A comprehensive list of major tree species of the study area is provided in Bose *et al.* (2016).

Data and data preparation

The plot-level individual tree data used in this study was obtained from numerous long-term, fully stem-mapped continuous forest inventory (CFI) plots to ensure representation of the diverse forest conditions throughout the Acadian Region in both the USA and Canada (Table 1, Table S1). In addition to CFI plots from four experimental forests maintained and managed by the State University of New York College of Environmental Science and Forestry (SUNY-ESF) (Weiskittel *et al.* 2016), this data also included the Penobscot Experimental Forest in Maine managed by the US Forest Service (Sendack *et al.* 2003), the US Department of Agriculture (USDA) Forest Service, Forest Inventory and Analysis (FIA) Program in Maine, New Hampshire, New York, and Vermont (Bechtold and Patterson 2005), the Maine Natural Areas Program's Ecological Reserves Network (Kuehne *et al.* 2018a, 2018b), and the Canadian National Forest Inventory Program (Gillis *et al.* 2005) as well as former regional and provincial forest research sampling efforts in New Brunswick, Nova Scotia, and southeastern Quebec. Summary statistics of each dataset are provided in Table S1 and additional detailed information on some of the individual datasets can be found in the Supplementary Materials of Andrews *et al.* (2018).

Based in part on Curtis (2010) and in order to establish a consistent diameter threshold across all datasets, trees <10.2 cm (4 in) diameter at breast height (DBH) were removed from this analysis. Following the approach described in Andrews *et al.* (2018), the individual tree data was summarized at the plot-level by calculating stem density (TPH, # of trees ha⁻¹) and mean tree size, i.e., Reineke's diam-

Table 1. Stand-level summary statistics including standard deviation (SD) for plot observations of the various datasets used in this study by basic forest type, namely hardwoods (HW, N = 25 036), mixedwoods (MW, N = 8925) and softwoods (SW, N = 12 529)

Forest type	Variable ^a	Mean	SD	Min	Max
HW	LON (°)	-72.91	3.13	-79.75	-59.95
	LAT (°)	43.89	1.43	40.72	48.98
	TPH (# ha ⁻¹)	635.64	382.32	79.24	5841.13
	DBH _R (cm)	26.47	7.23	10.58	96.85
	PBAHW (%)	95.88	7.09	75.01	100
	CSI (m)	18.02	3.56	7.20	48.86
MW	LON (°)	-70.94	3.50	-79.66	-59.89
	LAT (°)	44.46	1.43	40.78	48.88
	TPH (# ha ⁻¹)	937.14	485.04	118.97	8123.53
	DBH _R (cm)	24.58	6.50	11.44	70.25
	PBAHW (%)	55	11.64	35	74.99
	CSI (m)	16.26	3.39	6.91	38.76
SW	LON (°)	-69.37	3.52	-79.50	-59.93
	LAT (°)	45.14	1.44	40.79	49.21
	TPH (# ha ⁻¹)	1120.85	517.55	178.45	5992.41
	DBH _R (cm)	22.95	7.21	10.58	75.14
	PBAHW (%)	11.71	11.18	0	35
	CSI (m)	14.67	3.25	5.57	29.57
Overall	LON (°)	-71.58	3.65	-79.75	-59.89
	LAT (°)	44.34	1.53	40.72	49.21
	TPH (# ha ⁻¹)	824.29	491.30	79.24	8123.53
	DBH _R (cm)	25.16	7.25	10.58	96.85
	PBAHW (%)	65.35	37.21	0	100
	CSI (m)	16.78	3.74	5.57	48.86

^aLON – longitude, LAT – latitude, TPH – trees per hectare, DBH_R – Reineke's diameter, PBAHW – proportion of basal area in hardwood species, CSI – climate site index

eter (DBH_R, Zeide 1983) (Table 2). DBH_R was used as an alternative to conventional quadratic mean diameter to account for varying uneven stand structures frequently found in the Acadian Forest Region and is calculated as follows:

$$[1] \quad DBH_R = DBH_{MEAN} * \left(1 + \left(\frac{(b-1)*b}{2} \right) * DBH_{CV} \right)^{\frac{1}{b}}$$

where DBH_{MEAN} is mean DBH, DBH_{CV} is coefficient of variation for DBH and b is Reineke's (1933) slope of 1.6064.

Other plot-level variables computed from ha-based tree distributions derived by applying individual tree expansion factors were median (DBH_{MEDIAN}, cm), maximum (DBH_{MAX}, cm), range in (DBH_{RANGE}, cm), and standard deviation of individual tree DBH (DBH_{SD}, cm), as well as species diversity (SPP_{DIV}, # of species), and Shannon-Weaver index of species diversity (H_{SPP}, Shannon and Weaver 1949, Table 2). Based on the findings of Sterba and Monserud (1993), ha-based diameter distributions were further characterized by calculating dispersion and distribution parameters including the Gini coefficient (GINI, Gini 1921), skewness (SKEW), kurtosis (KURT), as well as the shape (SHAPE) and scale (SCALE) parameters of the three parameter Weibull function with the location parameter set to the previously

Table 2. Summary statistics including standard deviation (SD) for stand-level variables of all analyzed plot observations (N = 46 490)

Variable ^a	Mean	SD	Min	Max
TPH (# ha ⁻¹)	824.29	491.30	79.24	8123.53
DBH _R (cm)	25.16	7.25	10.58	96.85
DBH _{MEAN} (cm)	22.81	6.46	10.54	92.90
DBH _{MEDIAN} (cm)	21.02	7.15	10.20	92.33
DBH _{MAX} (cm)	40.19	12.41	10.67	188.80
DBH _{RANGE} (cm)	26.52	11.97	0.25	178.60
DBH _{SD} (cm)	8.02	3.95	0.13	50.01
GINI	0.18	0.06	0	0.48
SKEW	0.83	0.84	-1.72	7.57
KURT	3.43	2.81	1	69.91
SHAPE	1.83	3.22	0.37	305.77
SCALE	23.38	108.10	0.87	13 020.83
PBAHW (%)	65.35	37.21	0	100
SHADETOL	3.71	0.76	0.98	5.01
SHADETOL _{SD}	0.65	0.40	0	1.97
SG	0.51	0.09	0.30	0.78
SPP _{DIV}	3.53	1.45	1	11
H _{SPP}	0.87	0.42	0	2.08
LON	-71.58	3.65	-79.75	-59.89
LAT	44.34	1.53	40.72	49.21
ELEV (m)	346.61	217.04	0	1313.69
SLOPE (%)	13.15	13.79	0	220
TI	-0.70	13.02	-155.56	140.83
CSI (m)	16.78	3.74	5.57	48.86
MAT (°C)	5.34	1.87	-1.90	11.80
MAP (mm)	1127.87	142.94	777	1812
DD0 (°C)	980.08	311.64	202	2 265
DD5 (°C)	1767.68	309.24	726	3 062
GSDD5 (°C)	1409.28	310.08	509	2 757
GSP (mm)	588.49	58.59	399	883
MTCM (°C)	-9.20	2.70	-18.60	-0.90
MTCMMAP (°C mm ⁻¹)	-0.01	0	-0.02	0
GSPDD5 (mm °C)	1032.39	166.44	537.85	1910.69

^aTPH – trees per hectare, DBH_R – Reineke's diameter, GINI – Gini coefficient of DBH distribution, SHAPE and SCALE – shape and scale parameter of Weibull distribution, PBAHW – proportion of basal area in hardwood species, SHADETOL – shade tolerance, SG – specific gravity, SPP_{DIV} – species diversity, H_{SPP} – Shannon-Weaver index, LON – longitude, LAT – latitude, ELEV – elevation, TI – topographic index, CSI – climate site index, MAT – mean annual temperature, MAP – mean annual precipitation, DD0 and DD5 – annual degree-days < 0°C / > 5°C, GSDD5 – degree-days > 5°C accumulating within the frost free period, GSP – growing season precipitation, MTCM – mean temperature in the coldest month, MTCMMAP – MTCM/MAP, GSPDD5 – GSP*DD5/1000

defined DBH threshold of 10.2 cm (Kershaw *et al.* 2017). Based on the shade tolerance scale by Niinemets and Valldares (2006), we also calculated plot-level, ha-based, and individual tree basal area weighted mean (SHADETOL) and standard deviation of individual tree shade tolerance (SHADETOL_{SD}). Similarly, plot-level, tree basal area weighted mean specific gravity (SG, 12% moisture content volume basis) was quantified based on values from Miles and Smith (2009). Furthermore, the proportion of total stand basal area per ha in hardwood species (PBAHW) was derived (Table 2).

Climate data (1961–1990, Table 2) for each plot were collected from a database maintained by the US Forest Service

Moscow Forest Science Laboratory (<http://charcoal.cnre.vt.edu/climate/>) using plot-specific latitude (LAT), longitude (LON), and elevation (ELEV, m). Climate variables considered here included mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), annual degree-days < 0°C (DD0), annual degree-days > 5°C (DD5), degree-days > 5°C accumulating within the frost free period (GSDD5), growing season (April–September) precipitation (GSP), and mean temperature in the coldest month (MTCM). Based on the results by Andrews *et al.* (2018), some of these climate measures were combined to create interactions potentially useful in quantifying growing conditions of the study area including MTCMAP (MTCM/MAP) and GSPDD5 (GSP*DD5/1000). Missing ELEV, slope (SLOPE, %) and slope aspect (ASPECT, °) values not collected in the field were derived from digital elevation models. A topographic index (TI) modified after Beers *et al.* (1966) and Stage (1976) with greatest values and thus most favorable growing conditions on southerly slopes was calculated as $TI = \cos(ASPECT - 180^\circ) \times SLOPE$ (Table 2). Climate site index (CSI, m) of Weiskittel *et al.* (2011b) was used in place of traditional site index. CSI is a base-age 50 years estimate of site index based on the above mentioned downscaled climate variables and a random forest nonparametric regression model built on field-observed values. The general approach to model and derive CSI has been described in detail previously (Jiang *et al.* 2015). Although not available throughout the entire study area, site productivity was also assessed using the topographic wetness index (TWI) and the biomass growth index (BGI, kg ha⁻¹ yr⁻¹) of Hennigar *et al.* (2016), which includes soil information and is available in Maine as well as New Brunswick at a 20 m resolution. Finally, major forest type group as defined by the USDA Forest Service FIA Program (USDA 2015) and assigned as an indicator variable to each CFI plot was evaluated. Missing forest type group information was derived using plot-level, ha-based, species-specific basal area values and the algorithm provided in Arner *et al.* (2003).

Data analysis

In order to accurately model MSDR, understocked plots were removed from the analysis (Hann 2014). Forest stocking-level was determined for each plot based on basal area stocking diagrams for hard- (≥ 75% of total stand basal area in hardwood species), mixed- (≥ 35–< 75% of total stand basal area in hardwood species), and softwood stands (< 35% of total stand basal area in hardwood species, cf. Solomon *et al.* 1987) of the study area published by Frank and Bjorkbom (1973) and Leak *et al.* (2014), respectively. Plots falling below the B-line of their respective stocking diagram were deemed understocked (Kershaw *et al.* 2017). In addition, plots exhibiting an increase in TPH as well as a decrease in DBH_R in subsequent measurements were also removed. These procedures identified 30 855 or 40% of the total plot-level observations that did not meet the required conditions for the analysis. As a result, a total of 46 490 plots containing 744 372 trees of over 60 identified species were available for this study (Table 1). The top six most frequent species by basal area ha⁻¹ were red and sugar maple, balsam fir, red spruce, eastern hemlock, and American beech, which collectively repre-

sented 58% of total basal area. Trees of unknown species (but recorded as either hard- or softwood) comprised less than 1% of total basal area.

In accordance with the results of Salas-Eljatib and Weiskittel (2018), LQMM with the 'lqmm' package (Geraci 2014) and the programming software R (version 3.3.3, R Core Team 2017) were used to evaluate intercept and slope of the MSDR line based on Reineke's (1933) equation:

$$[2] \quad \ln(TPH) = (b_0 + b_{0i}) + b_1 * \ln(DBH_R)$$

where b_0 and b_1 are fixed effects parameters and b_{0i} is the estimated random effect for plot i .

A quantile of 95% was used as this captured the maximum relationship while removing the effect of highly influential observations (Salas-Eljatib and Weiskittel 2018). The intercept was treated as random yielding an individual intercept value for each plot. This mixed effect implicitly accounts for individual plot-level variance, which includes things such as site quality and the near infinite number of possible additional species compositions present in stands in the Acadian Region (Andrews *et al.* 2018).

From the derived relationship of equation [2] the plot-level maximum stand density index (SDI_{MAX}) for plot i can be calculated as:

$$[3] \quad SDI_{MAX} = \exp((b_0 + b_{0i}) + b_1 * \ln(25.4))$$

where all variables are previously defined above.

Individual SDI_{MAX} values for each plot were further examined to develop a SDI_{MAX} prediction model based on the biotic and abiotic plot-level variables described above. We first used random forest analysis (Breiman 2001) and the R package "randomForest" (Liaw *et al.* 2018) to determine the most influential contributors to SDI_{MAX} . We then used linear mixed effects modeling (Zuur *et al.* 2009) and the R package 'nlme' (Pinheiro *et al.* 2018) with county (administrative subdivision) within state (USA) or province (Canada) treated as random to account for potential local and regional differences not captured in our plot-level explanatory variables. Starting with a null model containing an intercept only, influential SDI_{MAX} drivers were added in a stepwise fashion and retained in the increasingly complex model based on plausibility, statistical significance, and effect on prediction accuracy evaluated based on Akaike's information criterion (AIC) and mean absolute bias (MAB, absolute value of observed – predicted). Variance structures to account for variance heterogeneity (R function "varComb") were incorporated in the final model, while preliminary analysis showed that a spatial correlation structure using plot-level longitude and latitude (R function "corSpher") did not improve model fit (Zuur *et al.* 2009). We further tested for multicollinearity among potential predictor variables using the variance inflation factor (VIF), which was quantified using the "corvif" function in R (Zuur *et al.* 2009). Furthermore, R^2 of the final equation was quantified based on Kvålseth (1985).

Results

Lower plot-level stand density was generally linked with higher mean tree size. TPH varied between 79 and 8124 trees

ha^{-1} with a mean of 824 ± 491 tree ha^{-1} , and DBH_R ranged from 10.6 cm to 96.9 cm with a mean of 25.2 ± 7.3 cm. PBAHW appeared to decrease with increasing longitude (Table 1) exhibiting a mean of $65.4 \pm 37.2\%$. PBAHW was also highly correlated with SG ($r = 0.86$), which varied between 0.30 and 0.78 with a mean of 0.51 ± 0.09 (Table 2).

Maximum size – density relationship (MSDR)

The intercept and slope (fixed effects only) of the LQMM MSDR line estimated for the logarithmic relationship between TPH and DBH_R were 12.0020 (SE = 0.0270) and -1.6388 (SE = 0.0096), respectively (Fig. 1). Plot-level random effects of the intercept varied between -0.6164 and 0.8304 with a mean of 0.0086 ± 0.2168 . The resulting estimated plot-level SDI_{MAX} ranged from 439 to 1866 tree ha^{-1} with a mean of 840 ± 187 trees ha^{-1} , which showed some variation across the contrasting major FIA forest type groups (Table 3).

Influential factors on SDI_{MAX} and prediction model

Based on the variable importance plot derived from the random forest analysis, the three most influential predictor variables were PBAHW, SG, and DBH_{RANGE} (Fig. 2). Other informative explanatory variables included metrics associated with the distribution and dispersion of DBH, shade tolerance, species diversity, and site quality or geographical location, respectively. Irrespective whether direct measures or combined metrics, individual climate variables as well as forest type group indicator variables were the least influential. Where available, TWI and BGI were not more effective than other site quality and location measures for accounting for site potential productivity. Likewise, forest type differences were in part statistically significant (data not shown), but had a limited influence on actual model performance and consequently, were not included in the final model.

Despite being highly correlated, the two predictors PBAHW and SG exhibited VIFs of around 4 when combined into a single SDI_{MAX} prediction model. Further significant and plausible variables which improved model prediction accuracy and thus were included in the model were DBH_{RANGE} , SPP_{DIV}, ELEV, and CSI (Table 4). While increasing DBH_{RANGE} and SPP_{DIV} had a positive effect on SDI_{MAX} , greater PBAHW, SG, and CSI resulted in lower SDI_{MAX} (Table 4). In contrast, ELEV exhibited a unimodal relationship with lowest SDI_{MAX} values at elevations of around 430 m a.s.l. (data not shown). Overall, SDI_{MAX} was most sensitive to SG followed by DBH_{RANGE} and PBAHW (Table 5).

The R^2 of the final model ranged from 0.32 (fixed effects only) to 0.38 (fixed + random effects). MAB of the final prediction model (fixed-effects only) was 116.6 (± 99.8) trees ha^{-1} with slight overprediction and somewhat greater underestimation for lower and greater estimated SDI_{MAX} values, respectively (Fig. 3). No obvious spatial trends in the relative model residuals were present (Fig. 4).

Discussion

Although the MSDR is a well-studied topic in forest sciences, we believe this is one of the very first studies that i) aimed to predict SDI_{MAX} of potentially multiple species stands across a relatively large and highly diverse geographic area and ii) developed an equation using only abiotic and biotic stand-

Fig. 1 Logarithmic relationship between stem density (TPH, # ha⁻¹) and Reinke's diameter (DBH_R, cm) with the linear quantile mixed model estimated maximum size-density relationship (MSDR) depicted as solid line. The general line is not on the boundary of the data envelope due to the use of mixed-effects. Dashed lines represent plot-level upper and lower limit of the MSDR based on maximum and minimum plot-specific random intercepts (plot-level random effects of the general line's intercept), respectively.

level variables after quantifying the underlying plot-level MSDR in an initial separate modeling step. Moreover, this is one of few works that tried to simultaneously address two issues related with the estimation of the MSDR in a single analysis, namely i) difficulty associated with mixed species as well as heterogeneously structured stands and ii) variation in SDI_{MAX} associated with contrasting site factors (cf. Ducey *et al.* 2017). Our findings of the most influential factors on SDI_{MAX} with PBAHW and SG being most critical are mostly in agreement with results of similar previous studies (e.g., Woodall *et al.* 2005; Andrews *et al.* 2018).

Species mixture or composition in mixed stands has been addressed in previous SDI_{MAX} research efforts, but these earlier studies rather quantified percentage of the main species, i.e. stand purity as potential predictor within species-specific SDI_{MAX} equations (Weiskittel *et al.* 2009; Andrews *et al.* 2018; Kimsey *et al.* 2018). In contrast, Solomon and Zhang (2002) derived separate MSDRs for different mixed species stand types. Based on the assumption that i) higher-specific-gravity species can support larger crowns, which in turn ii) requires

Table 3. Number of stand-level observations (N) and summary statistics including standard deviation (SD) of predicted plot-specific maximum stand density index (SDI_{MAX}, # trees ha⁻¹) by major USDA Forest Service, Forest Inventory and Analysis (FIA) forest type group

Forest type group	N	Mean	SD	Min	Max
Aspen-White Birch	2271	817	158.5	439	1485
Elm-Ash-Cottonwood	1325	799	203.1	488	1817
Maple-Beech-Birch	19 868	775	163.1	443	1584
Oak-Hickory	3869	789	175.3	439	1866
Oak-Pine	1812	866	205.8	465	1681
Other	358	910	188.6	503	1509
Spruce-Fir	11 688	909	161.1	483	1757
White-Red-Jack Pine	5299	974	202.1	455	1865
Overall	46 490	840	186.6	439	1866

more growing space per tree and thus iii) potentially results in lower SDI_{MAX}. Woodall *et al.* (2005) used stand-level mean wood specific gravity as a predictor of the maximum stocking potential of mixed species stands, which has been leveraged in several additional follow-up analyses (e.g., Ducey and Knapp 2010; Ducey *et al.* 2017, Bravo-Oviedo *et al.* 2018). Likewise,

Fig. 2 Variable importance derived from the R function "randomForest" (Liaw *et al.* 2018) including indicator variables for major FIA forest type groups (FT). A larger value of the IncNodePurity index indicates a greater importance of the corresponding variable (Kuhn *et al.* 2008).

SG was also among the most influential explanatory variables in this study. Despite being highly correlated with SG, we decided to further include PBAHW in our SDI_{MAX} equation mainly based on the notion that compared with individuals of softwood species, hardwood trees tend to form larger crowns in general (e.g., Russell and Weiskittel 2011). This is of significance as there is evidence that plant phenotypic expressions of crown architecture and shape strongly affect SDI_{MAX} as noted by Kimsey *et al.* (2018).

SPP_{DIV} was another significant variable explaining variation in SDI_{MAX} . Our general results agree with Pretzsch and Biber (2016), who argued that the positive relationship

between species mixing and SDI_{MAX} found in their study likely reflects increased canopy packing including greater canopy stratification and thus overall higher stem density. In addition, Salas-Eljatib and Weiskittel (2018) stated that greater maximum carrying capacities in stands of multiple species as found in their study were a result of the resource-use differentiation among different functional groups. In fact, the positive effect of species diversity on SDI_{MAX} appears to be especially strong for species mixtures with pronounced complementary ecological traits (Pretzsch and Biber 2016). However, adding variation in shade tolerance, which would be such an ecological trait, did not further improve our

Table 4. Maximum stand density index (SDI_{MAX}) linear mixed model parameter estimates and statistics including standard error (SE) fitted with all available plot records (N = 46 490)

Covariate ^a	Value	SE	t-value	p-value
Intercept	475.2079	21.9600	21.6397	<0.0001
PBAHW	-1.5908	0.0366	-43.4114	<0.0001
ln(SG)	-236.9051	7.3652	-32.1654	<0.0001
DBH _{RANGE} ^{1/2}	50.3299	0.6489	77.5658	<0.0001
SPP _{DIV}	13.5202	0.4926	27.4491	<0.0001
ELEV	0.0685	0.0170	4.0364	0.0001
ELEV ^{1/2}	-2.8534	0.6013	-4.7455	<0.0001
CSI ⁻¹	222.7836	84.7455	2.6289	0.0086

^aPBAHW – proportion of basal area in hardwood species, SG – specific gravity, SPP_{DIV} – species diversity, ELEV – elevation, CSI – climate site index

Table 5. Relative change (%) in linear mixed model predicted maximum stand density index (SDI_{MAX}) based on relative change (%) in significant predictors found to be influential on SDI_{MAX} . Overall mean of predicted SDI_{MAX} , i.e. all covariates set to their mean, was 822 trees ha⁻¹. Relative change in SDI_{MAX} was derived by varying the covariate of interest while all others were set to their mean

Covariate ^a	Mean	Relative change			
		-50	-25	+25	+50
PBAHW (%)	65.35	6.3	3.2	-3.2	-6.3
SG	0.51	20	8.3	-6.4	-11.7
DBH _{RANGE} (cm)	26.52	-9.2	-4.2	3.7	7.1
SPP _{DIV}	3.53	-2.9	-1.5	1.5	2.9
ELEV (m)	346.61	0.4	0.1	0	0.1
CSI (m)	16.78	1.6	0.5	-0.3	-0.5

^a PBAHW – proportion of basal area in hardwood species, SG – specific gravity, SPP_{DIV} – species diversity, ELEV – elevation, CSI – climate site index

model. The highly influential variable DBH_{RANGE} likely captured at least part of the associated signal. We believe that similar to SPP_{DIV}, higher DBH_{RANGE} values reflect increasing tree aggregation potential per unit area irrespective whether solely driven by size diversity or in conjunction with species diversity or diversity in ecological traits, respectively (Sterba and Monserud 1993).

Previous studies have also reported significantly positive effects of species shade tolerance on SDI_{MAX} (e.g., Jack and Long 1996; Solomon and Zhang 2000, 2002; Andrews *et al.* 2018). The strong dominance of shade-tolerant species such as spruce, fir, hemlock, beech, and maple in the study area and the available data might have prohibited a similar finding here. In addition, the relationship between SDI_{MAX} and varying levels of species mixture including trees of differing shade tolerances appears to be quite complex as shown by Woodall *et al.* (2005), which might be another reason for the missing relationship in our study. This may also reflect the differences between a species-specific (e.g., Andrews *et al.* 2018) and a more generalized approach like used in our study.

Surprisingly, individual climate metrics and measures that included soils (e.g., BGI) or topographic information (e.g., topographic wetness index) were found to be only slightly influential on SDI_{MAX} when compared to other evaluated stand-level site factors. Consequently, indirect climate measures (ELEV) or measures that reflect a combination of various climate variables (CSI) were included in our SDI_{MAX} equation. The negative relationship of CSI and SDI_{MAX} found here is in agreement with Ducey *et al.* (2017) who found lower carrying capacities for warmer, dryer locales compared to more cool and moist sites. The latter locales in our study area are usually associated with lower PBAHW as hardwood forest types are more common at well-drained, mid-elevation sites in western parts of the Acadian Region. In addition, better sites will often self-thin more intensively and thus tend to have a lower SDI_{MAX} (Weiskittel *et al.* 2009), which might be related to leaf area being higher on better sites.

However, it is worth mentioning that the relationship between site quality and maximum carrying capacity can be positive given different environmental conditions and tree species as compared to our study area (see Rivoire and Le Moguedec 2012). For example, in the Pacific Northwest as well as across the Inland Northwest of Northern America, northerly facing slopes provide greater plant-available soil water throughout the growing season, which in turn supports a greater number of individuals of the prevailing softwood species per unit area (Weiskittel *et al.* 2009; Kimsey *et al.* 2018). Similar findings have been reported for the Iberian Peninsula (Aquirre *et al.* 2018). Again, these differences might also be underscored by differences in the approach in determining SDI_{MAX} (Salas-Eljatib and Weiskittel 2018), particularly a species-specific vs. generalized method like used in this analysis.

In contrast to Kimsey *et al.* (2018) and owing to the lack of appropriate data for the entire study area, individual soil characteristics such as depth to groundwater table or soil drainage could not be further evaluated in our larger study area. However, ELEV also exhibited a significant but unimodal relationship with SDI_{MAX} which also relates to climate and site quality. We believe that increasing SDI_{MAX} values at elevations below 400 m a.s.l. reflect higher soil moisture, i.e., a seasonal high ground water table in combination with limited soil drainage and a stronger exposure to an oceanic climate and thus likely lower PBAHW. In contrast, increasing SDI_{MAX} values at elevations over 400 m reflect exposure and thus overall lower site quality, which also fosters a greater softwood component with individual softwood trees occupying less growing space. Interestingly, more detailed measures of topographic or site productivity such as BGI were not more influential than more simplistic metrics like ELEV or CSI. The relationship between SDI_{MAX} and site productivity thus requires additional evaluation going forward into the future with continual refinement of digital elevation models and derivative products.

Our observed size–density data did not exhibit a curvilinear pattern at its upper limit as described for species-specific datasets evaluated in other SDI_{MAX} studies (e.g., Charru *et al.* 2012). The removal of smaller trees with DBH <10 cm from the analysis in order to establish a consistent size threshold might be a potential explanation. Our

Fig. 3 Maximum stand density index as predicted by abiotic and biotic stand-level variables (SDI_{MAX} predicted, trees ha^{-1}) over linear quantile mixed model estimated maximum stand density index (SDI_{MAX} estimated, trees ha^{-1}) with solid 1:1 line and dashed regression trendline derived with the R function "lowess".

LQMM regression approach with plot-level random effects thus appears to be appropriate for the data analyzed here (Salas-Eljatib and Weiskittel 2018) and is highly recommended for future analyses. The inclusion of these random effects is also important given that the contrasting management history of the vast majority of these plots is relatively unknown and not directly accounted for, particularly given that varying levels of partial harvesting is the primary form of management in this region (e.g., Rice *et al.* 2014, Kuehne *et al.* InPress). In addition, it was assumed that all plots were relatively healthy and free of major natural disturbances especially defoliation caused by spruce budworm (*Choristoneura fumiferana*), which can dramatically alter key long-term stand dynamics (e.g., Chen *et al.* 2017).

Conclusions

Determining SDI_{MAX} is often difficult in mixed-species and/or structurally diverse stands, which are both common in the Acadian Region due to the large number of species present as well as high variation in both climate and topography. Using an extensive regional dataset and methods effective for determining plot-specific SDI_{MAX} , this is one of the first analyses to develop a generalized, trans-species, and regional model for predicting maximum site carrying capacity for this

complex region with relatively robust estimates and findings. The general mean SDI_{MAX} for the region was 840 trees ha^{-1} , but showed significant variation (439–1866 trees ha^{-1}) due to stand structure and site factors. Based on the significance of proportion of total stand basal area in hardwood species and potential effects of other influential stand-level factors of the derived prediction model on hardwood percentage, this variation in SDI_{MAX} appears to be mostly driven by the softwood to hardwood ratio of the structurally heterogeneous stands evaluated here. Overall, the analysis offers a methodology for determining and estimating a regional site-specific estimate of SDI_{MAX} , which should be tested for designing optimal density management regimes as well as evaluated in other regions dominated by mixed-species, structurally diverse stands.

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Fig. 4 Map of study area depicting relative difference (model residuals $\Delta\text{SDI}_{\text{MAX}}$, %) between linear quantile mixed model estimated maximum stand density index (SDI_{MAX} , trees ha^{-1}) and linear mixed model predicted SDI_{MAX} quantified as a percentage of estimated SDI_{MAX} . The map was derived by using inverse distance weighting and the R package “gstat” (Pebesma 2004).

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