Variation in the maximum stand density index and its linkage to climate in mixed species forests of the North American Acadian Region

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ABSTRACT

Maximum stand density index (SDImax) is an important factor controlling stand dynamics that varies by species and region, but less is understood how it differs within a region for a given species. In this analysis, linear quantile mixed modeling (LQMM) and an extensive network of permanent plots were utilized to examine regional variation in the SDImax of 15 species (7 softwoods and 8 hardwoods) across the complex forests of the Acadian Region in North America. Observed plot-level SDImax was then linked to various stand, plant trait, site, and climatic factors and the spatial patterns throughout the region examined. Results indicated high variability of SDImax for a given species with northern hardwood species like yellow birch (*Betula alleghaniensis* Britt.), sugar maple (*Acer saccharum* Marsh.), and American beech (*Fagus grandifolia* Ehrh.) having the lowest values (555 – 627), while softwood species such as northern white cedar (*Thuja occidentalis* L.; 1014), eastern hemlock (*Tsuga canadensis* (L.) Carr.; 1026), and white pine (*Pinus strobus* L.; 967) had the highest values. Compared to the other stand and site factors examined, climate showed the strongest relationship with SDImax with R^2 ranging from 82 to 98%. Of the climatic variables examined, those representing growing season length and the timing of precipitation were most influential. For the majority of the species examined, reductions in SDImax were forecasted due to changing climatic conditions. Across species, mean SDImax was found to linearly decline with wood specific gravity and increase with leaf longevity, but showed limited relationships with other species-level functional traits. Overall, the analysis highlights the strong variability of SDImax within and between species as well as the important role that climate has on this attribute within a region.

1. Introduction

Maximum stand density index (SDImax) is a dynamic attribute that can be used to assess full site occupancy based upon species composition (Zeide, 2005). The importance of this concept has long been recognized by ecologists (Yoda et al., 1963; Fowler, 1981) and foresters (Reineke, 1933; Drew and Flewelling, 1977) alike, and can be viewed as the potential carrying capacity for a particular site and species. Integral to the utilization of the maximum stand density relations in forest planning is the concept of the stand density index (SDI), which is an absolute measure that provides the degree of full occupancy in a stand. SDI is particularly useful when combined with SDImax to estimate relative density (RD) because the latter is highly correlated to certain stand developmental stages and can be used to construct density management diagrams (DMDs; Jack and Long, 1996), as well as constrain the predictions of growth and yield models (e.g. Yang and Titus, 2002), which aid forest managers to better predict and manage stand

dynamics. These tools are not only important for traditional forestry operations, but can also be applied to management plans that hasten restoration (Churchill et al., 2013) or account for carbon in forest stands (Woodall et al. 2011).

The theoretical concept of the SDImax relationship is well established in a number of concrete mathematical equations (Drew and Flewelling, 1977; Reineke, 1933; Zeide, 1987). Although the details can vary, the core components of this theory are a log-log linear relationship between a size and density variables where: (1) the slope of the line represents the thinning rate, otherwise known as the self-thinning line, and was originally conceived as constant for all species and (2) the intercept varies between species, but is consistent for a particular species. Therefore, the intercept implicitly accounts for site level variation, including species composition and physical site properties. While these equations have proven to be suitable for even-aged, single-species stands, their adaptation to stands with diverse stand structure and composition is not always clear.

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Various studies have explored SDImax estimates in mixed species stands and are typically in one of three categories, namely: (1) an empirical static relationship developed for a stand composed of a particular species-composition (e.g. Solomon and Zhang, 2000, 2002; Sturtevant et al., 1998; Williams, 2003; Wilson et al., 1999; Yang and Titus, 2002); (2) a dynamic SDImax surface that varies with species composition, but the range in species composition is limited (Puettmann et al., 1992; Rivoire and Le Moguedec, 2012; Stout and Nyland, 1986; Swift et al., 2007); or (3) allometric relationships that are developed between stand level SDImax and another functional trait variable, such as specific gravity (Ducey et al. 2017; Ducey and Knapp, 2010; Woodall et al., 2005), shade tolerance (Ducey et al. 2017), or growing area requirements (Pretzsch and Schütze, 2016; Pretzsch et al., 2015). Many of these approaches have been successful in estimating and predicting SDImax in a given study area, but often rely on relatively complicated model forms and may fail to extrapolate to unique conditions, particularly those in the future.

While it is widely recognized that species composition influences SDImax (e.g. Ducey and Knapp, 2010; Woodall et al., 2005), the effect of site-specific properties has been widely debated. Early studies argued that SDImax was achieved independent of site quality, age, and management and that these factors would only affect the time it takes for a stand to reach the maximum (Jack and Long, 1996; Reineke, 1933). Numerous additional studies have focused on testing this theory and have proven the effect of stand-level differences on obtainable SDImax, including site nutrient quality (Morris and Myerscough, 1991), age (Zeide, 2005), site index (Weiskittel et al., 2009), stand origin (Weiskittel et al., 2009), and soil fertility (Bi, 2004). This debate, however, is rooted in a general misinterpretation of the original meaning of maximum stand density theory. The original concept of maximum stand density was in regards to the species boundary line, or the maximum possible combination of size and density for a particular species across the landscape, regardless of site age and quality (Hamilton et al., 1995). This is an important distinction because it recognizes that for a given species composition, site-level SDImax will indeed vary across the landscape dependent upon site conditions. Therefore, a potentially better approach to determining the actual SDImax for a species or combination of species would be to perform the analysis at a regional-level, so that a variety of site level effects can be evaluated, and the optimal conditions contributing towards a species' SDImax recognized.

In particular, climate deserves attention in regards to its influence on SDImax. Climate is a known predictor of site quality (e.g. Hennigar et al. 2017) and can explain forest composition differences (Tang and Beckage, 2010). In addition, it is widely accepted that climate is currently changing and forest communities are already experiencing shifts in habitat ranges as climate warms. Numerous studies have focused on this change in species' or forest communities' distributions with more recent work focused on shifts in relative importance of species (e.g. Iverson et al. 2011), which is critical for quantifying potential changes to forests in a way that is practical for land managers. However, assessing the relationship directly between climate and the regional SDImax could provide more utility to land managers, as the functionality of this metric within a forest management framework is clear, and individual sites can be assessed for positive and negative impacts of climate. Recently, Ducey et al. (2017) examined the influence of climate and species functional traits on SDImax in the US Lake States and found that both were highly influential in determining the maximum stocking for a given species. Likewise, Condés et al. (2017) examined the influence of climate on the maximum size-density relationship for Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) stands and found it to be influential, but the effects varied by species. Both of these recent works highlight the high regional variability of SDImax and the need to better understand its relationship with climate, particularly across a broader range of species with varying ecological attributes.

Regardless of the influence of climate, it is clear that an adaptable method for estimating both site and regional SDImax for diverse multiage and multi-species stands would be useful to foresters planning for management activities in both the near and distant future. A relatively new and novel statistical method, linear quantile mixed models (LQMM; Koenker, 2004), shows potential promise for describing SDImax relationships in these type of stands. Quantile regression has been applied successfully in previous SDImax analyses (e.g. Zhang et al., 2005) for primarily single species stands. With the multi-level component of LQMM, hierarchical structure can be accounted for in the analysis and SDImax estimates generated for individual stands, while taking into account the overall maximum relationship between size-density across the landscape. These individual estimates can not only implicitly take into account site-level factors such as site quality, but also can account for the near infinite variation in species composition that may influence overall SDImax. Additionally, by linking site-specific estimates with both physical and endogenous site properties through machine learning analyses, the importance of particular factors can be assessed, and potential changes to SDImax under different climate scenarios be evaluated.

The overall goal of this study was to evaluate species and regional variation in SDImax in mixed composition and multi-cohort forests of the Acadian Region of the US and Canada. Specifically, a novel modelling approach of LQMM was tested for its effectiveness in estimating SDImax in forests with a number of commercially-important hardwood and softwood species. Furthermore, the influence of both physical and endogenous site properties, as well as plant traits, were assessed for their role in influencing SDImax for a given species, and across species. Lastly, both current and future spatial trends in species-specific SDImax distributions were evaluated across the region in order to better understand regional landscape patterns.

2. Methods

2.1. Study area

The Acadian Forest of Northeastern North America was chosen as the study area to evaluate our methods. This Forest stretches from the northern New England states of the United States (US) to the Maritime Provinces of Canada over diverse elevational and maritime gradients and is defined as a transitional ecotone between hardwood forests to the south and the boreal forest to the north. The region has a long history of forestry activity (Loo and Ives, 2003) and most forests have a legacy of land use. Climate (Fig. 1, gray background) and soil vary immensely in this region and this range gives rise to high regional tree species diversity (Barton et al., 2012). Across the region, mean annual precipitation 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. Glacial till is the principle soil parent material 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 between low-profile ridges.

The majority of the Acadian Forest is dominated by naturally-regenerated, mixed-species stands that display either even- or uneven-aged stand structures, while some portions of New Brunswick contain intensively-managed, single-species plantations. Over 60 species dominate the region, and common softwood species include balsam fir (*Abies balsamea* (L.)), red spruce (*Picea rubens* (Sarg.)), white spruce (*Picea glauca* (Moench) Voss.), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), black spruce (*Picea mariana* (Mill.) B.S.P), and northern white-cedar (*Thuja occidentalis* L.). Common hardwoods include red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), gray birch (*Betula populifolia* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), bigtooth aspen (*Populus grandidentata* Michx), American beech (*Fagus grandifolia* Ehrh.), northern red oak (*Quercus rubra* L.), and sugar maple (*Acer saccharum* Marsh.).