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ARTICLE

A vegetative index of stand productivity based on tree inventory for predicting oak site index in the Central Hardwood Region

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Abstract: Models for prediction of site index (SI) typically include only abiotic causal variables (e.g., soil) and lack biotic response variables (e.g., vegetation), which could exhibit greater sensitivity to important environmental factors affecting tree height growth. Our study objective was to evaluate Whittaker's moisture condition index (MCI) (R.H. Whittaker. 1956. Ecol. Monogr. **26**: 1–80) as a potential biotic variable for inclusion with conventional abiotic variables in oak (*Quercus* L.) SI prediction models. The MCI is the sum of relative abundances of inventoried plot tree species weighted by their moisture affinity classification. We compared regression parameters of conventional base models including only abiotic variables with exploratory models configured with abiotic variables and MCI for explaining variation of SI. The best abiotic model included only aspect. When MCI was included in the abiotic model, aspect became insignificant, resulting in a single-variable biotic model that accounted for increased SI variation. The MCI biotic model remained significant when tested with independent data from a distant location. The MCI is easily calculated using plot inventory data, and with further evaluation, it may be confirmed as a useful biotic variable in combination with abiotic soil and topographic variables for prediction of oak SI.

Key words: moisture affinity, moisture condition index, productivity, *Quercus*, site index.

Résumé : Les modèles de prévision de l'indice de qualité de station (IQS) n'incluent généralement que des variables causales abiotiques (p. ex. le sol) et ne comportent pas de variables réponses biotiques (p. ex. la végétation) qui pourraient présenter une plus grande sensibilité aux facteurs environnementaux importants qui affectent la croissance en hauteur des arbres. L'objectif de notre étude était d'évaluer l'indice des conditions d'humidité (ICH) de Whittaker (R.H. Whittaker. 1956. Ecol. Monogr. **26**: 1–80) comme variable biotique potentielle à inclure avec les variables abiotiques conventionnelles dans les modèles de prévision de l'IQS du chêne (*Quercus* L.). L'ICH est la somme de l'abondance relative des espèces d'arbres dans les placettes inventoriées, pondérées par leur classe d'affinité à l'humidité. Nous avons comparé les paramètres de régression des modèles de base conventionnels comprenant uniquement des variables abiotiques à ceux de modèles exploratoires incluant des variables abiotiques et l'ICH pour expliquer la variation de l'IQS. Le meilleur modèle abiotique ne comprend que l'exposition de la station. Lorsque l'ICH est inclus dans le modèle abiotique, l'exposition de la station devient non significative, ce qui produit un modèle biotique à une seule variable qui explique davantage de variation de l'IQS. Le modèle biotique incluant l'ICH reste significatif lorsqu'il est testé avec des données indépendantes provenant d'un emplacement éloigné. Puisque l'ICH est facilement calculé à l'aide de données d'inventaire de placettes, une évaluation plus approfondie pourrait permettre de le considérer comme une variable biotique utile en la combinant avec des variables abiotiques du sol et de la topographie pour prévoir l'IQS du chêne. [Traduit par la Rédaction]

Mots-clés : affinité à l'humidité, indice des conditions d'humidité, productivité, *Quercus*, indice de qualité de station.

Introduction

Assessment of forest productivity (the rate of biomass generation per unit area) is essential for evaluating economics of silvicultural treatments, assessing current and future sustainability, and predicting likely ecological responses to management activities such as those associated with wildlife habitat (Bontemps and Bouriaud 2014). Forest productivity may be quantified by direct measurement of annual biomass production, a method more often used for agricultural crops than for longer maturing stands of trees (Schoenholtz et al. 2000). Indirect methods are usually used to estimate forest productivity by measuring highly correlated variables such as leaf area index (Jose and Gillespie 1997; Bolstad et al. 2001) or assessing site quality. Site quality is the inherent capability of a stand to produce biomass as a function of available water and nutrients associated with climate, soil, and topography (Schoenholtz et al. 2000) and may be considered equivalent to productivity (Assmann 1970, as referenced by Bontemps and Bouriaud 2014). A biotic expression of site quality is site index (SI) defined as the mean total height of dominant and codominant trees in an even-aged stand at a reference age for a specified species (Bontemps et al. 2012). For nearly 100 years, SI has been the primary method used by foresters globally for indirectly assessing forest site productivity (Skovsgaard and Vanclay 2008; Moreno-Fernandez et al. 2018), although its continued relevancy is questionable because climate changes could affect growth rates of certain species (Bontemps and Bouriaud 2014). Unbiased field estimation of SI can be problematic, however, because one or more of the underlying principles of the method are not followed in practice, particularly sample tree selection (Beck and Trousdell 1973). Carmean and Lenthall (1989) stated that SI sample trees should consist of preferred management species that are either domi-

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nant or codominant crown class, undamaged, unsuppressed, near the reference age, and selected from well-stocked, even-aged stands. Lamson (1980) suggested that measuring too few sample trees is the primary source of error when using SI to assess forest site quality.

Suitable sample trees for SI estimation are often lacking in the mixed forests dominated by oak (*Quercus* L.) and hickory (*Carya* Nutt.) in the Central Hardwood Region (CHR) of the United States. Stands in these forests are typically uneven aged, resulting from the development of tree seedlings in canopy gaps (Ruffner and Abrams 1998; Rentch et al. 2003) and opportunistic harvesting of commercial species by landowners (Birch 1997). Also, dominant trees in unmanaged mixed hardwood stands are often much older than an SI reference age (usually 50 years) and are more likely to exhibit damage from severe weather disturbances such as limb breakage from ice storms (Turcotte et al. 2012). Indirect prediction of SI based on models formulated with geocentric (earth-based) and phytocentric (vegetation-based) variables is typically used in stands lacking suitable sample trees (Skovsgaard and Vanclay 2008). Models for predicting SI as a function of quantifiable abiotic variables of soil and topography were developed for many CHR commercial species during the period of 1950–1980. In a review of forest site quality evaluation methods, Carmean (1975) reported that abiotic variables associated with the quantity of soil water available during the growing season (e.g., soil texture and solum thickness) and topographic variables related to solar radiation received and ambient soil moisture (e.g., aspect and slope position) typically account for 50% or more of SI variability. Notably lacking from nearly all SI models are vegetative variables, which Fralish et al. (1978) suggested should logically be an equal or superior indicator of site quality compared with abiotic soil and topographic variables.

Daubenmire (1976) reported mixed, generally poor results on the value of vegetation for assessing productivity in hardwood forests of the eastern United States. Reasons for the poor results include multispecies complexity of communities and insufficient time for stand recovery following frequent, successive disturbances from harvesting and weather. A few successful uses of vegetation for SI estimation in North American forests include MacLean and Bolsinger (1973) in western conifers, Hodgkins (1960) in longleaf pine (*Pinus palustris* Mill.), Wiant et al. (1975) and Fountain (1977) in mixed oak stands, and Corns and Pluth (1984) in conifer stands of Alberta, Canada. Seynave et al. (2005) suggested that understory vegetation may be a better indicator of nutrient status than soil chemical properties. Species richness, or the number of occurring plant species, has been studied extensively in relation to site productivity, but results have been variable and often negative at landscape or vegetative community scales (Waide et al. 1999). Richness is more often used as a measure of ecosystem function and resiliency (Walker et al. 1999).

A biotic variable long overlooked for inclusion in SI prediction models is moisture condition index (MCI), developed by Whittaker (1956, 1966) for assessing forest productivity in relation to moisture gradients. The MCI is a measure of soil water relations of a site as manifested by the total occurring tree community, where each species is an expression of long-term moisture relations and other site factors. McNab (2017) found that MCI was an important variable in a model predicting the occurrence of American chestnut (*Castanea dentata* (Marsh.) Borkh.) in western North Carolina, United States.

The primary purpose of our study was to evaluate the significance of Whittaker's MCI as an explanatory biotic variable in combination with conventional abiotic variables in prediction models for oak SI. We asked the following questions.

(*i*) Are tree species on our study sites individually associated with SI?

(*ii*) If SI is predicted, does MCI account for significant variation when included with conventional abiotic variables in models?

(*iii*) If MCI is a significant variable in an SI model developed for the study area, does it remain significant if that model is evaluated with independent data from a widely separated test area?

Methods

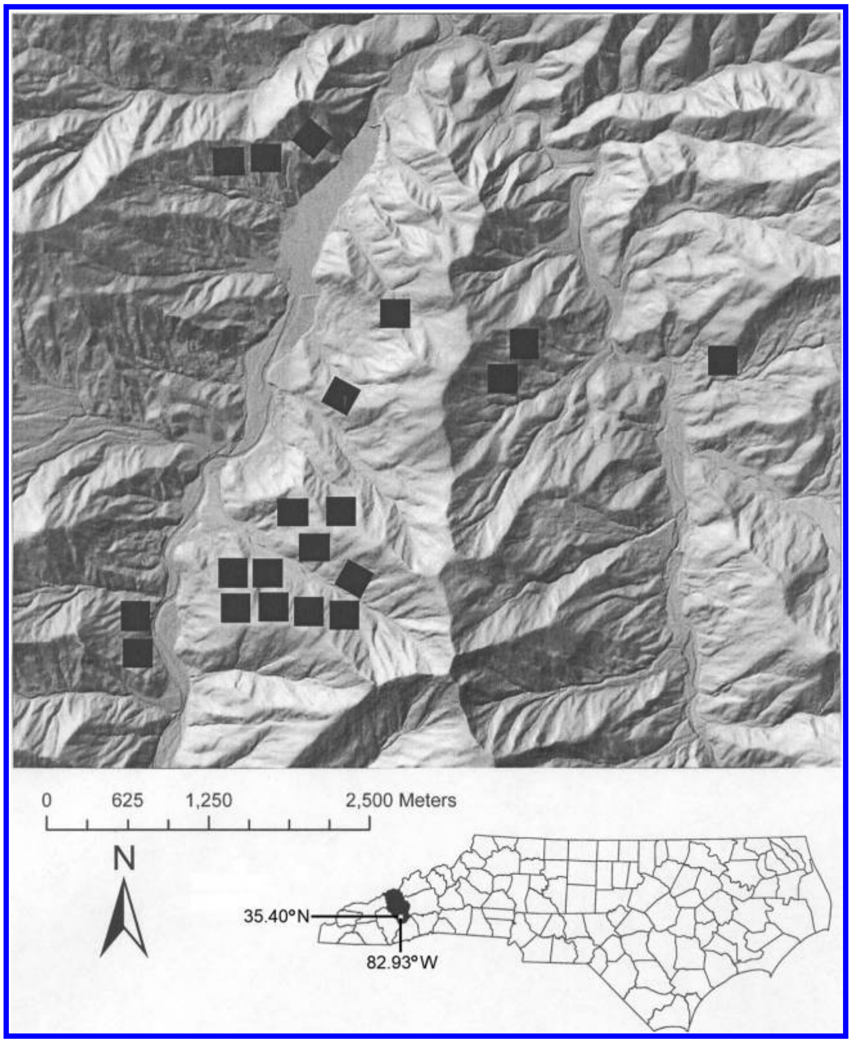
Study area

Our study area was the 1333 ha Cold Mountain Game Lands (CMGL) in the Pigeon River watershed (35.40°N, 82.93°W) on the western slope of the Great Balsam Mountains in Haywood County, North Carolina (Fig. 1). The CMGL lies in two climatic zones of the southern Appalachian Mountains physiographic province: a cool zone above ~1350 m elevation and a warm zone extending down to ~900 m. We conducted our study in the warm zone, characterized by a humid climate with short, mild winters. Mean daily temperatures range from 3 °C in January to 24 °C in July. Annual precipitation is approximately 1300 mm and is evenly distributed seasonally, though a brief period of low soil moisture may occur occasionally during the late growing season. Geologic formations are gneisses and schists of Precambrian age that have weathered to form a complex, highly dissected land surface consisting of secondary and tertiary ridges and associated valleys extending from the primary Great Balsams.

Soils in the CMGL are classified in two taxonomic orders: Inceptisols and Ultisols (Allison and Hale 1997). Inceptisols, which lack an appreciable accumulation of clay in the B horizon, typically occur in colluvium in coves and on steep slopes and are mapped as two series: Edneyville, a coarse-loamy Typic Dystrudepts, and Plott, a fine-loamy Typic Humudepts. Ultisols occur in residuum on ridge summits and gentle side slopes and are mapped as three series: Evard, a fine-loamy Typic Hapludults, Saunook, a fine-loamy Humic Hapludults, and Trimont, a fine-loamy Humic Hapludults. Inceptisols typically occur at elevations above 1100 m, and Ultisols usually occur at lower elevations (Soil Survey Staff 2019). Parent material of all soils is felsic to mafic high-grade metamorphic or igneous rocks, including granite and hornblende gneiss. Fertility is typically low throughout the CMGL but tends to be higher in valleys and lower slopes where soil organic matter accumulates and consistent mesic conditions increase biological activity and nutrient cycling. Small lenses of amphibolite-bearing rocks occur throughout the CMGL that form local, unmapped inclusions of soil with higher pH and fertility. Forest productivity within an elevation zone is better associated with moisture gradients than soil fertility and ranges from lowest on ridges and upper slopes to highest in coves and on lower slopes (Bolstad et al. 2001). Variations in local soil moisture regimes result from complex interactions among soil properties and topographic variables of aspect (as a surrogate variable for solar radiation received), elevation, slope gradient, and slope position (Whittaker 1956).

Forest community types of the CMGL warm zone are predominantly mixtures of upland oaks forming three communities distributed primarily in relation to soil moisture gradients associated with landforms: (*i*) *Quercus montana*, which occupies ridgetops and dry slopes with an oak canopy dominated by *Quercus montana* (Willd.) and *Quercus coccinea* Münchh.; (*ii*) montane *Quercus–Carya*, which occupies dry-mesic slopes with a canopy dominated by a diverse mixture of species, including *Quercus alba* L., *Quercus rubra* L., *Carya tomentosa* (Lam. ex Poir.) Nutt., *Carya glabra* (Mill.) Sweet, *Quercus velutina* Lam., and *Liriodendron tulipifera* L.; and (*iii*) acidic cove, which occupies mesic slopes and valleys with a canopy dominated by *Liriodendron tulipifera* and a mixture of *Quercus rubra*, *Betula lenta* L., and *Tsuga canadensis* (L.) Carrière (Schafale and Weakley 1990). Shade-tolerant midstory arborescent species include *Acer rubrum* L., *Oxydendrum arboreum* (L.) DC., *Cornus florida* L., and *Nyssa sylvatica* Marshall. Species of all communities may occur as individuals throughout the study area. Mature, un-

Fig. 1. Location of the twenty 5.1 ha stand treatment units displayed to approximate scale on midslope positions in the mountainous terrain of the Cold Mountain Game Lands (CMGL), Haywood County, North Carolina. In the small map of North Carolina counties, Haywood County is shaded, and the white, closed circle shows the location of the study area, with its centrally designated latitude and longitude in degrees. (T. Roof, U.S. Department of Agriculture, Forest Service, using ArcMap (Esri, Redlands, Calif., USA), created the topographic base image from U.S. Geological Survey digital elevation data and overlay of treatment unit locations from on-site boundary traverses.)



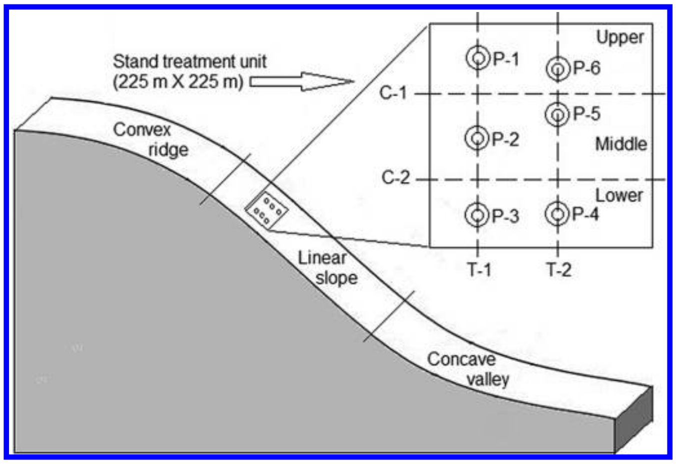
managed stands are typically uneven aged because seedlings of many tree species can become established in the understory as advance regeneration and ascend into the overstory following canopy disturbances (Rentch et al. 2003).

Study design and field sample plots

Twenty stands, relatively undisturbed during the past 20 years, were selected throughout CMGL (Fig. 1) for installation of a parent study on the effects of silvicultural treatments on regeneration (described by Greenberg et al. 2012). Stands suitable for the study's completely randomized design were mature (>70 years), predominantly closed canopied, and oak dominated or consisting of mixed-oak species composition. The stands were located without regard to soil, topography, or other environmental conditions, but the study was restricted to stands occupied by the montane oak–hickory forest type typical of dry-mesic slopes and partly sheltered ridges. These areas are typically difficult to regenerate with a desirable mixed-species composition where *Liriodendron tulipifera* will likely be a strong competitor (Loftis 1990).

Stands occurred primarily at midslope positions, between upper slopes of convex ridge crests and lower slopes along concave stream drainages (Fig. 2). Midslope topography in each treatment unit was relatively planar but occasionally included minor concave-to-convex land surface and soil variations typical of dissected mountain slopes. Site quality among stands was relatively homogeneous at the landscape scale of midslope positions but varied within stands in relation to sample location in ecotones with adjacent lower and upper slope positions. In each stand, we established a 5.1 ha (225 m × 225 m) silvicultural treatment unit, oriented parallel with upper and lower slope contours. The upper-slope boundary of each treatment unit formed a 225 m baseline (along a contour) that allowed for potential location of 10 cross-contour transects for sample plot establishment. Two transects were randomly selected for vegetation sampling. Each transect, which delineated a short elevation gradient of approximately 20 m (depending on gradient), was subdivided into three equal segments that represented relative upper, middle, and lower slope subpositions within the larger midslope topographic position. We established a permanent sample plot in the three segments on each transect for a total of six per stand (a total of 120 sample sites). The location of sample plots along transects was adjusted as needed to avoid minor unsuitable site conditions such as a rock outcrop, road, or a recently formed canopy gap. Sample plots were referenced by Global Positioning System (GPS) coordinates. We established a 0.05 ha circular main plot and a concentric nested

Fig. 2. Field layout of a typical 5.1 ha (225 m × 225 m) stand treatment unit and six sample plots on midslope positions between the upper ridge and lower valley hillslope components of mountainous topography. The two horizontal dashed lines in the unit represent contours (C-1 and C-2) of uniform elevations that delineate three slope positions (upper, middle, and lower) in each unit. The two vertical dashed lines in the treatment unit indicate two randomly located transects (T-1 and T-2) for placement of three systematically spaced 0.05 ha circular sample plots (P-1–P-6) and nested 0.01 ha subsample plot. Sample locations were occasionally adjusted along transects within a slope position to avoid rock outcrops or canopy gaps, as illustrated by plots P-5 and P-6.



0.01 ha subplot at each sample site. Predominantly, overstory trees (≥25 cm diameter at breast height (DBH; breast height = 1.30 m)) were inventoried by species on main plots, and midstory trees (5 cm ≤ DBH < 25 cm) were inventoried on subplots.

Site index estimation

Site index for each sample site was determined as a measure of site quality to account for variation of regeneration response to silvicultural treatments. One tree per plot that was within the 0.05 ha plot boundary, had a dominant or codominant crown position, and showed no evidence of recent crown damage was sampled for SI. *Quercus rubra* was the preferred SI species, followed by any oak species and lastly, *Liriodendron tulipifera*. Total height was measured to the nearest 0.5 m using a Haglöf Vertex hypsometer (Haglöf Sweden, Långsele, Sweden). Age was determined from one increment core extracted at breast height on the upper-slope side of the tree. Cores were returned to the laboratory and prepared using standard mounting and smoothing procedures to facilitate counting of annual rings using a binocular microscope. A transparent template of concentric circles was used to estimate missing rings on cores not intersecting the pith. Oak SI (base age 50 years) was estimated from height–age relationships developed by Olson (1959) for upland oak stands in the southern Appalachians. Carmean et al. (1989) quantified Olson's (1959) plotted height–age curves with a nonlinear model, which we used for direct approximation of SI from measured tree age and height rather than interpolating from the set of plotted curves. *Liriodendron tulipifera* SI (base age 50 years) was estimated from curves prepared by Beck (1962) for the southern Appalachians and then converted to an equivalent value for oak using the relationship developed by Doolittle (1958). Although other measures of productivity could have been more appropriate in these stands of multiple species and ages (Huang and Titus 1993), we used SI because it has been demonstrated by Rauscher et al. (2000) as an acceptable measure of site quality in growth and yield models for upland hardwood stands of the southern Appalachian Mountains area of the CHR.

Abiotic soil and topographic variables

Soil series were determined from GPS coordinates of each sample plot overlaid on 1:12 000 scale maps (Allison and Hale 1997). Following methods used by Elliott et al. (1999), we used published maximum values of A horizon thickness, solum thickness, available water content, clay content, and organic matter content (Soil Survey Staff 2019) of each series to account for effects of the soil moisture regime on SI at each plot.

For each site, we quantified conventional topographic characteristics that have long been used as independent variables in geocentric studies for SI prediction (Carmean 1975): elevation, estimated to the nearest 10 m from 1:24 000 digital elevation models of topographic maps at the GPS plot locations; aspect, measured as the horizontal angle from north in degrees azimuth; and gradient (slope steepness), quantified as a percentage. At each plot, we also measured topographic variables associated with SI of *Liriodendron tulipifera* on upland hardwood sites in the CHR (McNab 1989, 1993): landform index, which quantifies site location in relation to macrophysiography (e.g., valley, slope, or ridge), and terrain shape index, which quantifies land surface shape (e.g., concave, planar, or convex) of the site. The three plots along each transect were classified by position (upper, middle, or lower) relative to their location in the 5.1 ha treatment unit to account for gravitational soil moisture differences (Fig. 2). Azimuth was transformed (hereafter "Taz") using the cosine relationship of Beers et al. (1966), resulting in values between 0 and 2 for sites receiving maximum (225° azimuth) and minimum (45° azimuth) potential solar radiation, respectively, in the Northern Hemisphere.

Biotic vegetative variables

Species richness was determined as the total count of tree species occurring on each sample plot without regard to their abundance. We estimated MCI following methods reported by Whittaker (1956, p. 6; 1966, p. 116). Each tree species occurring in the 120 sample plots was assigned to a moisture affinity class defined by Whittaker (1956) as mesic, submesic, subxeric, or xeric. The number of stems in each moisture class was multiplied by a weight for each affinity class: 0 for mesics, 1 for submesics, 2 for subxerics, and 3 for xerics. The total of weighted stem numbers on each plot was divided by the total number of stems:

$$\mathrm{MCI} = \Sigma[(\mathrm{weight}_i \times \mathrm{number}_i + \ldots + \mathrm{weight}_j \times \mathrm{number}_j)/\Sigma\mathrm{number}_{i\ldots j}]$$

where MCI is Whittaker's moisture condition index, $\mathrm{weight}_{i\ldots j}$ is the moisture affinity classification of each arborescent species present, and $\mathrm{number}_{i\ldots j}$ is the count (abundance) of all stems with DBH ≥ 5 cm of each arborescent species present on the main plot and subplot at each sample site. Although our primary interest in evaluating MCI was to follow Whittaker's (1956) method based on species abundance, we also explored presence–absence and basal area as measures of species occurrence and dominance, respectively, on sample sites. Although less well known than basal area for quantifying occurrence and dominance of species, the binary measure presence–absence is an effective and efficient binary variable for relating vegetation with environment (Strahler 1978). Species basal area was suggested by Whittaker (1966) as an alternate but more complex weighting factor compared with abundance. Hereafter, calculation of MCI based on species abundance, presence–absence, or basal area will be referred to as MCIa, MCIpa, or MCIba, respectively. We use MCIx to indicate the generic form of MCI without reference to a specific method of calculation based on abundance, presence–absence, or basal area.

Data analysis

Correlation and regression were the primary methods used to determine the relationship of SI with abiotic and biotic site variables. Univariate normality was evaluated with the Shapiro–Wilk test. Differences of SI among sample tree species were evaluated by one-way analysis of variance (ANOVA) and the Welch test, assuming unequal variances for separation of means. We used logistic regression to determine the relationship of frequently occurring inventoried tree species ($n \geq 10$ sample sites) with SI and tested the relationship with the Wald statistic. Histogram plots were used for insight of unexpected trends of certain tree species with SI. Kendall's rank correlation (τ) was used to examine associations of abiotic and biotic variables with SI and evidence of collinearity between selected variables. We tested variation of SI in response to soil order and soil series using two-way ANOVA with an interaction term (stand × soil order or soil series). We used one-way ANOVA and Tukey's honestly significant difference (HSD) test for post hoc comparisons of SI with the relative slope positions of the three sample plots of each transect.

Our study design required the development of two to four multiple regression SI models depending on significance of the three MCIx variables. To evaluate the potential value of MCIx as an explanatory variable, we developed one (base) model using only significant conventional abiotic variables of soil and topography. Because we were interested in the relative performance of the three methods used for calculating MCIx, separate prediction models were developed that included MCIa, MCIpa, or MCIba as an independent variable in combination with the other significant abiotic variables of the base model. Categories of soil and slope position significantly associated with SI were included in the regression analysis as binary indicator variables. We used stepwise multiple linear regression to model SI with initial formulations consisting of variables significantly correlated with SI. Collinearity was minimized by excluding one of a pair of correlated significant independent variables. Successive, more parsimonious models were developed by manually omitting variables with $p > 0.05$. We used the Bonferroni test to identify potential outlier observations. Competing final SI models were evaluated using the conventional measures of multivariate coefficient of determination (R^2), root mean square error (RMSE), and the Akaike information criterion (AIC). Pairs of competing final models were judged to be similar if the difference of AIC was <2. We assessed fit of models with SI by scatter plotting residuals. We validated parameters of final prediction models (i.e., standard errors of regression coefficients) developed with the CMGL data by bootstrapping with 999 iterations. The 10-fold method of cross-validation was used to evaluate potential performance (quantified by RMSE) of best models to estimate accuracy for field applications. Each of the 12 iterations of the 10-fold process followed the method used for the initial model selection without a priori knowledge of significant variable components of an optimum formulation.

We tested the best models with an independent data set from the 1800 ha Bent Creek Experimental Forest (BCEF) (35.500°N, 82.625°W) located 21 km northeast of CMGL with similar soils, forest communities, and annual precipitation but with somewhat subdued topography associated with lower mean elevation (~800 m). Almost all BCEF sites with similar canopy species composition (particularly *Quercus rubra*) were cleared and cultivated during the mid to late 1800s and abandoned around 1900, followed by old-field succession to stands dominated by *Liriodendron tulipifera*. The BCEF test data set included thirty-four 0.10 ha plots established in the early 1950s on mesic and dry-mesic sites dominated by nearly pure, even-aged stands of *Liriodendron tulipifera* used for modeling growth and yield (McGee and Della-Bianca 1967). Site index had been estimated from five or more trees on each BCEF plot, with oak SI averaging 26.3 m (standard error = 0.29 m) and ranging from 21.9 to 29.3 m, which matched the mean SI for CMGL (26.3 m). Species typically associated with higher elevations (*Acer saccharum* Marsh. and *Acer pensylvanicum* L.) at CMGL do not occur in BCEF, where topography resulted in many sample plots being located on lower slopes or in shallow coves. Abiotic soil and topographic variables quantified at CMGL were available for the BCEF sites, which allowed testing of the best conventional abiotic model. However, species composition of stems with DBH ≥ 1 cm (see McNab and Loftis 2013) was the only biotic variable available for all trees in the BCEF plots, which restricted testing of the CMGL formulation to the MCIpa form. We used two-sample Student's *t* tests to compare SI measured at BCEF with predictions based on (*i*) the best CMGL abiotic conventional (base) model and (*ii*) the best CMGL model including MCIpa if the biotic variable was significant.

For all statistical tests and modeling, we used software packages in R version 3.5.1 (R Development Core Team 2011). We used R Commander version 2.5-3 to execute the various R statistical packages (Fox 2019). Statistically significant relationships were determined using a critical value of $\alpha = 0.05$.

Results

Site index samples

Five oak species accounted for 100 (83%) of the 120 trees sampled for SI; 19 sample trees were *Liriodendron tulipifera*, and one was *Fraxinus americana* L. (Table 1). We treated *Fraxinus americana* as *Liriodendron tulipifera* because a suitable SI model was not available for it, both species can co-occur on mesic sites in the southern Appalachians (Beck and Della-Bianca 1981), and both have similar rates of height growth as overstory stand components (W.H. McNab, personal observation). Fifty-one (51%) of the oak trees sampled for SI were *Quercus rubra*. Suitable SI trees were not present on nine (16%) sample sites; for these sites, a sample tree was selected beyond the main plot boundary. Sample tree ages ranged from 48 to 105 years (mean of 74.8 years). Total heights ranged from 18.9 to 39.6 m (mean of 30.6 m).

Mean SI for the entire study area was 26.3 m (Table 1) and ranged from 15.5 to 34.4 m. Mean SI among species ranged from 23.5 m for *Quercus montana* to 27.5 m for *Quercus rubra*. The pith was not intersected in cores from 44 (37%) of the sample trees. Cores from 55 (46%) of the sample trees, mostly oaks, showed evidence of previous suppression, typically occurring during juvenile ages. Overall, we estimated that tree age was within ±2 years for 82% of the sample trees and within ±5 years for 16% of the sample trees. Mean oak SI based on *Liriodendron tulipifera* was not different ($p = 0.728$) from sites where an oak was sampled. There was no difference ($p = 0.126$) in SI among the six species of trees.

Tree species and biotic variables

Thirty-five tree species were inventoried on the 120 sample plots in CMGL (Table 2). The greatest number of species ($n = 15$; 43%) was in the mesic moisture affinity class, followed by 10 species (28%) in the submesic class and eight species (23%) in the subxeric class. *Acer rubrum* was the species of greatest occurrence (present on 67.5% of plots) and density (115.0 stems·ha^{-1}). Nearly one-third (31.2%) of the total tree stems inventoried (640.3 stems·ha^{-1}) consisted of five oak (17.8%) and four hickory (13.4%) species. Species classified as submesic accounted for nearly half (49.2%) of stems inventoried.

The mesic and submesic classes each had eight frequently occurring species (present on ≥10 plots) (Table 3). Six species occurred frequently in the subxeric class, and only one species, *Quercus coccinea*, occurred frequently in the xeric class. Mean SI was greatest (28.2 m) for plots occupied by mesic species and least (24.4 m) for plots occupied by xeric species. We found significant relationships with SI for six mesic species (75%), four submesic species (50%), and four subxeric species (67%) (Table 3). Positive relationships with SI (i.e., probability of occurrence increased with greater SI) were found for the eight mesic species; trends for

Table 1. Mean number, size, and age (with standard errors (SE) in parentheses) of trees sampled for estimated oak site index (SI) by species on 120 plots established in the Cold Mountain Game Lands (CMGL) study area, Haywood County, and 34 plots established in the Bent Creek Experimental Forest (BCEF) test area, Buncombe County, North Carolina.

Species	*n*	DBH (cm)	Height (m)	Age (years)	SI (m)
CMGL					
Liriodendron tulipifera	20	53.4 (2.89)	33.5 (1.03)c	71.9 (2.09)a	25.9 (0.56)a
Quercus coccinea	21	46.0 (2.25)	29.1 (1.07)ab	73.5 (2.62)a	25.2 (0.88)a
Quercus montana	7	42.6 (4.31)	25.3 (2.16)a	84.7 (5.96)a	23.5 (2.07)a
Quercus rubra	51	51.7 (2.12)	31.4 (0.68)bc	74.5 (1.60)a	27.5 (0.57)b
Quercus spp.	15	40.5 (2.26)	28.2 (1.09)ab	75.5 (3.07)a	24.6 (0.95)a
Quercus velutina	6	50.5 (5.22)	30.7 (1.23)ac	79.2 (5.92)a	26.6 (0.98)a
Total or mean	120	49.1 (1.24)	30.6 (0.46)	74.8 (1.08)	26.3 (0.36)
BCEF					
Liriodendron tulipifera	34	42.1 (1.06)	31.4 (0.62)	56.7 (1.51)	26.3 (0.29)

Note: The category *Quercus* spp. includes oak sample trees for which species could not be confidently identified. For the CMGL plots, values of mean height, age, and SI followed by the same letter are not different at the $p = 0.05$ level of probability. Site index for *Liriodendron tulipifera* was calculated using a formulation of Carmean et al. (1989) for the SI model developed by Beck (1962) (with height in feet and age in years): $\mathrm{SI} = 0.7609 \times \mathrm{height}^{1.0097} \times \{[1 - \exp(-0.0346 \times \mathrm{age})]^{(-1.4002\mathrm{height}^{-0.0402})}\}$. Site index for *Quercus* spp. was calculated using a formulation of Carmean et al. (1989) for the SI model developed by Olson (1959) (with height in feet and age in years): $\mathrm{SI} = 0.7709 \times \mathrm{height}^{1.0063} \times \{[1 - \exp(-0.0856 \times \mathrm{age})]^{(-1.5038 \times \mathrm{height}^{-0.0419})}\}$. Mean SI for *Liriodendron tulipifera* in the test area was 100.3 feet before conversion to oak SI using the relationship oak SI (in feet) = 27.642 + 0.586 × (*Liriodendron tulipifera* SI) (Doolittle (1958). DBH, diameter at breast height.

six selected species are shown in Fig. 3A. We generally found negative relationships with SI for submesic, subxeric, and xeric species (Figs. 3B, 3C, and 3D, respectively), but *Quercus rubra*, *Quercus velutina*, and *Robinia pseudoacacia* L. had positive trends.

Richness averaged 6.6 tree species across the 120 sample plots. The minimum number of species was three, which occurred on three plots; the maximum number of species was 10, which also occurred on three plots. Site index was not associated with richness ($r = 0.007$, $p = 0.939$). Because of its lack of a significant relationship with SI, richness was omitted from further evaluation.

Abiotic soil and topographic variables

Sixty-seven (56%) of the sample plots were established in soils classified as Inceptisols consisting of two series, and 53 plots occurred in three series classified as Ultisols (Table 4). The difference between the minimum and maximum values of estimated SI among series varied from 11.5 m for Saunook to 15.4 m for Evard. Analysis of variance indicated a significant difference ($p < 0.01$) of mean SI among the five series. Separation of means using Tukey's HSD test revealed a significant difference only among series with the highest (Plott, 27.8 m) and lowest (Evard, 24.4 m) values of mean SI, confirmed by rank correlation analysis. However, Plott, Evard, and Trimont were strongly correlated ($p < 0.0017$) with Taz. Mean SI was higher for Inceptisols (27.1 m) than Ultisols (25.3 m) ($p < 0.014$). Mean oak SI of soil orders was weakly correlated ($p = 0.023$) with Taz.

Maximum values of all physical soil properties except clay content were consistently greater for Ultisols (Table 4). We found that SI was correlated with the maximum value of all physical soil properties ($p < 0.05$) except clay content ($p = 0.50$; data not shown). Significant correlations ($p < 0.05$) were also present among all physical soil properties (i.e., A horizon thickness and available water content were correlated; data not shown).

Site index correlations and prediction models

Rank correlation analysis identified many site variables individually associated with SI, which were potential candidates for a regression model with consideration of collinearity with other variables (Table 5). Mean values of MCIa, MCIpa, and MCIba were 0.9, 1.0, and 1.0, ranging from 0 to 2.1, 0 to 2.0, and 0 to 2.1, respectively. Oak SI was significantly correlated ($p < 0.001$) with all formulations of MCIx, only Taz among the topographic variables, and all soil variables except for clay content. As an indication of possible collinearity among the abiotic and biotic variables in the regression analysis, we found strong correlations ($p < 0.001$; data not provided) between Taz and MCIx and a weaker correlation ($p = 0.030$) between slope gradient and MCIpa.

Our Bonferroni test for potential outliers revealed that none of the 120 samples qualified for exclusion. Multiple linear regression analysis indicated that Taz was the only abiotic explanatory variable that accounted for significant SI variation (Table 6). The base Taz model for SI was significant ($p = 0.001$) but had a low adjusted R^2 value of 0.076. However, Taz became nonsignificant ($p > 0.05$) when the three formulations of MCIx were included separately in the base (Taz) model to determine if a biotic variable accounted for additional SI variation. This resulted in three models for SI prediction with a single explanatory variable: MCIa, MCIpa, or MCIba. All three MCIx models were significant ($p < 0.001$) and resulted in adjusted R^2 values ranging from 0.158 to 0.206. The biotic model based on MCIa was best among the MCIx models in terms of AIC, R^2, and RMSE (Table 6). The 10-fold cross-validation produced mean RMSE values similar to the residuals for all models. Bootstrap distributions of the 95% confidence intervals for the regression intercepts and coefficients for the base Taz model and three biotic MCIx models indicated significant values and normal distributions. Confidence limits of SI predictions were wider for the Taz model than for the three MCIx models, which were similar to one another (Fig. 4). We found no evidence that residuals for the four models were correlated with excluded variables. Overall, errors were similar among the abiotic and biotic models, with RMSE marginally higher (6.3%) for Taz than the mean for MCIx.

Tests of prediction models

Results of the two SI prediction model tests at BCEF (base Taz and MCIpa) developed with field data from CMGL are provided in Fig. 5. Confidence limits for prediction models and SI predictions were similar for the Taz model (Fig. 5A) and MCIpa model (Fig. 5B). Two-sample *t* tests revealed no significant difference ($p = 0.163$) between observed oak SI on the BCEF plots and oak SI predicted using the Taz model developed with CMGL data. In a similar *t* test using the MCIpa model, we found no significant difference ($p = 0.193$) between predicted and observed oak SI. Residuals were randomly

Table 2. Scientific and common names of tree species with DBH ≥ 5 cm grouped by moisture affinity class in sample plots in CMGL.

Scientific name	Common name	Occurrence (%)	Density (stems·ha^{-1})	BA (m^2·ha^{-1})	QMD (cm)
Mesic affinity class					
Liriodendron tulipifera L.	Yellow-poplar	37.5	38.33	4.940	40.5
Acer saccharum Marsh.	Sugar maple	27.5	55.00	0.758	13.2
Prunus serotina Ehrh.	Black cherry	20.0	14.83	1.926	40.7
Carya cordiformis (Wangenh.) K. Koch	Bitternut hickory	17.5	10.33	0.564	26.4
Fraxinus americana L.	White ash	17.5	9.83	0.025	28.7
Tilia heterophylla Vent.	White basswood	17.5	16.00	0.822	25.6
Magnolia acuminata (L.) L.	Cucumber magnolia	14.2	6.67	0.354	26.0
Halesia tetraptera L.	Carolina silverbell	10.0	16.50	0.261	14.2
Ostrya virginiana (Mill.) K. Koch	Hophornbeam	4.2	9.33	0.078	10.3
Fagus grandifolia Ehrh.	American beech	3.3	3.33	0.025	9.7
Tsuga canadensis (L.) Carrière	Eastern hemlock	2.5	5.83	0.052	10.6
Aesculus octandra Marshall	Yellow buckeye	0.8	1.00	0.037	21.6
Carpinus caroliniana Walter	American hornbeam	0.8	0.83	0.006	9.2
Cornus alternifolia L. f.	Alternate-leaf dogwood	0.8	0.83	0.002	6.1
Magnolia fraseri Walter	Fraser magnolia	0.8	0.33	0.031	34.4
Submesic affinity class					
Acer rubrum L.	Red maple	67.5	115.00	3.481	19.6
Quercus rubra L.	Northern red oak	59.2	45.00	6.182	41.8
Carya ovata (Mill.) K. Koch.	Shagbark hickory	44.2	33.17	2.454	30.1
Carya glabra (Mill.) Sweet	Pignut hickory	35.8	24.17	1.238	25.5
Carya tomentosa (Lam. ex Poir.) Nutt.	Mockernut hickory	25.0	17.83	0.652	21.6
Cornus florida L.	Flowering dogwood	23.3	44.17	0.197	7.5
Betula lenta L.	Sweet birch	17.5	15.33	0.846	26.5
Acer pensylvanicum L.	Striped maple	10.0	18.33	0.070	7.0
Juglans nigra L.	Black walnut	1.7	1.33	0.049	21.6
Amelanchier arborea (F. Michx.) Fernald	Serviceberry	0.8	0.83	0.003	6.2
Subxeric affinity class					
Quercus montana Willd.	Chestnut oak	46.7	35.50	3.349	34.6
Robinia pseudoacacia L.	Black locust	42.5	16.33	1.425	33.3
Quercus velutina Lam.	Black oak	30.8	17.00	1.942	38.1
Oxydendrum arboreum (L.) DC.	Sourwood	26.7	35.17	0.729	16.2
Quercus alba L.	White oak	17.5	5.50	0.593	37.1
Nyssa sylvatica Marshall	Blackgum	10.0	12.83	0.226	15.0
Sassafras albidum (Nutt.) Nees	Sassafras	3.3	1.33	0.076	27.0
Pinus strobus L.	Eastern white pine	1.7	3.33	0.020	8.8
Quercus spp.	Undetermined	0.8	0.83	0.017	36.0
Xeric affinity class					
Quercus coccinea Münchh.	Scarlet oak	16.7	8.83	0.852	35.0
Pinus virginiana Mill.	Virginia pine	0.8	0.17	0.010	27.5

Note: Occurrence refers to the occurrence in 120 plots. BA, basal area; QMD, quadratic mean diameter at breast height.

distributed in bands of uniform width around the *x* axis for both models (data not shown). At BCEF, RMSE was 2.08 m for the Taz model and 1.65 m for the MCIpa model, lower than the values at CMGL (3.79 and 3.56 m, respectively). Values of RMSE for the Taz and MCIpa models had a small difference of 5.6% at CMGL and a large difference of 26.1% at BCEF, which prompted an unanticipated question: Do SI model parameters differ between the study and test areas, suggesting an unstable association of SI with environmental relationships at landscape scales?

Because the effect of aspect on SI should be consistent within subregions of similar climate, geology, soils, and landforms, we made an unplanned analysis to investigate the strength of the relationship of Taz and MCIpa beyond the CMGL study area. We used the two model formulations developed at CMGL (i.e., SI as a function of Taz and MCIpa) and derived new coefficients using azimuth and vegetation inventory data from the 34 BCEF test plots. A model developed using Taz data from BCEF to predict SI explained almost no variation (adjusted $R^2 > 0.01$) and was not significant ($p = 0.36$). We also used MCIpa data from BCEF and derived a significant model ($p = 0.03$) with an adjusted R^2 value of 0.11. We used analysis of covariance (ANCOVA) to compare coefficients of the CMGL and BCEF regression models and found nonsignificant differences ($p = 0.07$) between the two Taz models and nonsignificant differences ($p = 0.99$) between the CMGL and BCEF model parameters for MCIpa. Comparison of SI estimated using Taz for the CMGL and BCEF models showed marginal agreement (i.e., nearly horizontal trend) with the 1:1 diagonal line of exact correspondence (Fig. 6). In contrast, SI predictions based on MCIpa were in close agreement for the CMGL and BCEF models as shown by the nearly parallel relationship of the regression trend line with the diagonal. Trend line lengths in Fig. 6 represent the SI range predicted by minimum and maximum values of Taz and MCIpa measured at CMGL and BCEF. For example, measured minimum and maximum plot Taz values were similar for the CMGL study area (0.0 and 2.00, respectively) and the BCEF test area (0.1 and 2.00, respectively) (Table 5). However, predicted minimum and maximum SI values based on the two Taz models were not similar: CMGL (24.5 and 27.7 m) and BCEF (26.2 and 26.8 m) (Fig. 6). For MCIpa, in comparison, predicted SI values were similar for the CMGL study area (19.2 and 30.0 m) and the BCEF test area (20.2 and 30.1 m) (Fig. 6). The Taz model for CMGL was significant ($p = 0.001$, $R^2 = 0.076$; Table 6), but a model for BCEF was not significant ($p = 0.365$, $R^2 = 0.005$), which partly explains the horizontal trend.

Table 3. Logistic regression parameters for estimating the probability of occurrence in response to oak SI of common (present on ≥10 sample sites) species with DBH ≥ 5 cm classified by soil moisture affinity class in CMGL.

Species	Oak SI (m)	α (SE)	β (SE)	Z	p	OR
Mesic affinity class						
Liriodendron tulipifera	27.1 (0.55)	−2.741 (1.328)	0.084 (0.049)	1.707	0.088	1.088
Acer saccharum	28.3 (0.50)	−6.263 (1.695)	0.196 (0.061)	3.220	0.001	1.217
Prunus serotina	29.0 (0.67)	−8.527 (2.136)	0.261 (0.075)	3.475	<0.001	1.300
Carya cordiformis	28.4 (0.55)	−6.326 (1.968)	0.176 (0.070)	2.517	0.018	1.192
Fraxinus americana	28.5 (0.64)	−6.822 (2.023)	0.194 (0.072)	2.706	0.007	1.214
Tilia heterophylla	28.6 (0.68)	−7.282 (2.077)	0.210 (0.073)	2.869	0.004	1.234
Magnolia acuminata	27.6 (0.96)	−4.476 (1.935)	0.100 (0.070)	1.422	0.155	1.105
Halesia tetraptera	28.5 (0.88)	−7.076 (0.088)	0.178 (0.089)	2.010	0.044	1.195
Submesic affinity class						
Acer rubrum	25.8 (0.44)	3.589 (1.417)	−0.108 (0.052)	2.060	0.039	0.898
Quercus rubra	26.7 (0.45)	−1.442 (1.257)	0.069 (0.047)	1.454	0.146	1.072
Carya ovata	25.4 (0.52)	2.582 (1.282)	−0.108 (0.048)	2.215	0.027	0.898
Carya glabra	25.8 (0.68)	0.779 (1.273)	−0.052 (0.048)	1.077	0.282	0.949
Carya tomentosa	24.4 (0.77)	3.092 (1.464)	−0.163 (0.058)	2.834	0.005	0.849
Cornus florida	25.0 (0.73)	1.682 (1.440)	−0.111 (0.096)	1.984	0.047	0.895
Betula lenta	25.9 (0.88)	−0.849 (1.588)	−0.027 (0.060)	0.445	0.656	0.974
Acer pensylvanicum	26.4 (1.17)	−2.482 (2.056)	0.011 (0.077)	0.141	0.888	1.010
Subxeric affinity class						
Quercus velutina	26.5 (0.68)	−1.441 (1.339)	0.024 (0.050)	0.480	0.632	1.024
Oxydendrum arboreum	24.5 (0.68)	3.107 (1.438)	−0.160 (0.056)	2.841	0.004	0.852
Robinia pseudoacacia	27.1 (0.56)	−2.708 (1.300)	0.091 (0.048)	1.878	0.060	1.095
Quercus montana	25.1 (0.56)	3.871 (1.342)	−0.153 (0.051)	3.011	0.003	0.853
Quercus alba	24.3 (0.95)	2.495 (1.614)	−0.159 (0.064)	2.463	0.014	0.853
Nyssa sylvatica	24.0 (1.28)	1.973 (1.981)	−0.165 (0.081)	2.050	0.040	0.848
Xeric affinity class						
Quercus coccinea	24.4 (0.86)	2.144 (1.630)	−0.147 (0.065)	2.267	0.023	0.864

Note: Species in boldface type denote response curves shown in Fig. 3. Values in parentheses are SEs. α and β, logistic regression coefficients; *Z*, ratio of β/β(SE); *p*, probability of (>|*Z*|); OR, odds ratio.

Discussion

The purpose of our study was to determine if MCIx, a tree species-based vegetative index developed by Whittaker (1966) to quantify site moisture gradients and correlated with forest productivity, would account for significant oak SI variation in combination with conventional abiotic variables. In our study area, we found that only one of 10 abiotic soil and topographic variables, Taz, was significant ($p = 0.001$) in a multiple regression model, but it explained little SI variation ($R^2 = 0.076$). When MCIx was included in the base model of abiotic variables, it was significant ($p < 0.0001$), R^2 increased (0.208), and Taz became nonsignificant ($p = 0.238$). Results differed from those of nearly all other North American studies of biotic variables associated with SI. Except for occasional research success of including groups of understory plants in SI models, such as reported by Wang (1995) for white spruce (*Picea glauca* (Moench) Voss), no vegetative variables have been identified as widely useful and achieved operational application. We believe that ours is the first evaluation of Whittaker's (1966) MCI as a potentially practical and relevant biotic variable for inclusion in oak SI prediction models. Because MCI is a continuous measure, it is potentially more precise as an SI predictor variable compared with nominal variables. For example, Ike and Huppuch (1968) adjusted SI predictions by fixed amounts based on the presence or absence of certain site conditions. The MCI is similar in application to the continuous measure of species indicating nitrogen-poor or -rich site conditions that Wang (1995) used in models for prediction of *Picea glauca* SI. As Wang (1995), Seynave et al. (2005), and others have reported, including biotic variables in prediction models can account for SI variation not explained by conventional abiotic environmental variables associated with soil and topography.

Species associated with site index

In the southern Appalachian region of relatively high, uniformly distributed annual precipitation, aspect is influential but less important than slope position as a factor affecting soil moisture regimes (Yeakley et al. 1998). Carmean (1975) reported that slope position typically accounts for significant SI variation in hilly terrain in the CHR. It was not significant in our study area probably because nearly all sample stands were located on side slopes between ridgetops and valley floors, which resulted in similar slope positions.

Growing season moisture availability is an important factor affecting tree species distributions and site productivity in the southern Appalachians (Bolstad et al. 2001) and elsewhere in North America (Adams and Anderson 1980; Fralish et al. 1978; Wang 1995). In the same geographic region as our study, Whittaker (1966) reported a modal occurrence of many tree species with perceived classes of site moisture regimes. In agreement with Whittaker's (1966) moisture affinity classification, we found a significant relationship with site quality for 15 of 23 tree species occurring on ≥10 sample sites (Table 3). Trends of species occurrence with SI were generally consistent within a moisture affinity class (Fig. 3); however, the response curves for *Quercus rubra*, *Quercus velutina*, and *Robinia pseudoacacia* were inconsistent with those of other species in their respective affinity classes, and their trend lines appeared to be better aligned with species in the mesic class (Fig. 3). We adjusted their MCIx values to those of mesic species (affinity class = 0) and reanalyzed the field data but found little difference in results. Except for field data artifacts, we have no satisfactory explanation for this aberrant behavior. *Quercus rubra* occurs across a range of sites in the southern Appalachians but mostly at higher elevations on moist cove sites of higher quality (Loftis 1990). We assigned *Quercus velutina* to the subxeric class because it typically occurs on sites that are less mesic than those

Fig. 3. Probability of occurrence of selected tree species in relation to oak site index (SI) in CMGL. Species are grouped in panels by soil moisture affinity class: (A) mesic species, (B) submesic species, (C) subxeric species, and (D) xeric species, following assignments by Whittaker (1956). See Table 2 for complete species scientific and common names and Table 3 for model formulations. Trend lines for some species are omitted for clarity of display.

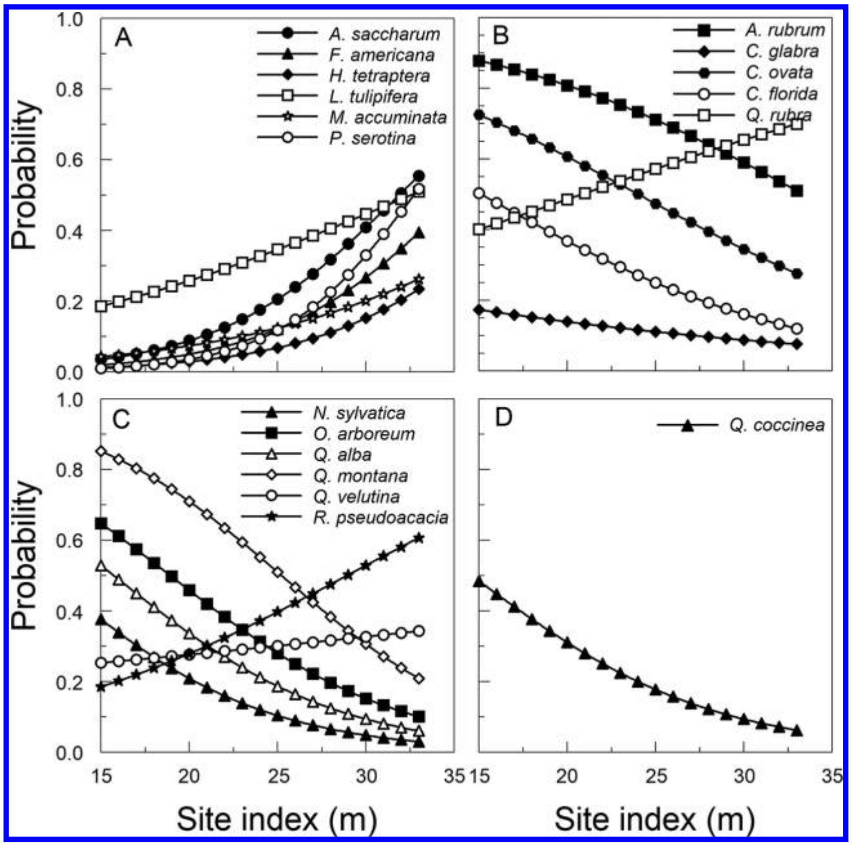


Table 4. Mapped soil series (grouped by soil order) occurring on 120 sample plots in the CMGL.

Series	No. of plots	SI (m)	A horizon thickness (cm)	Solum thickness (cm)	OM content (%)	Clay content (%)	AWC (cm·cm^{-1})
Inceptisols							
Edneyville	29	26.1 (19.7–34.4)ab	3–25	51–140	3–8	5–20	0.20–0.41
Plott	38	27.8 (20.2–33.2)a	5–18	51–102	1–8	5–20	0.20–0.41
Total or mean	67	27.1 A					
Ultisols							
Evard	34	24.4 (15.5–30.9)b	25–51	76–152	5–15	2–20	0.13–0.71
Saunook	9	27.4 (22.6–34.1)ab	15–38	102–152	3–10	7–35	0.18–0.51
Trimont	10	26.5 (21.2–32.9)ab	18–41	69–152	3–9	8–35	0.25–0.51
Total or mean	53	25.3 B					

Note: Values for A horizon thickness, Solum thickness, OM content, Clay content, and AWC show the range of maximum tabular values. Oak SI values of soil series followed by the same lowercase letter and soil orders followed by the same uppercase letter are not different at the $p = 0.05$ level of probability. OM, organic matter; AWC, available water content.

of *Quercus rubra*. *Robinia pseudoacacia* is a leguminous, shade-intolerant species and a minor component of mature stands, typically regenerates by root sprouts after canopy and soil disturbance, and could be a generalist species like *Acer rubrum*.

The lack of correlation of species richness with SI ($r = 0.007$) was not surprising and agrees with results from other ecological studies of productivity. In a meta-analysis, Waide et al. (1999) reported better relationships of terrestrial species richness with productivity at continental and regional scales than at landscape and local scales. A study of plant diversity by Walker et al. (1999) reported that although species richness can be associated with site productivity, it is perhaps better correlated with ecosystem function and resilience to disturbance. In our landscape-scale study, for example, the two biotic variables of richness and MCIpa were similar in that both were counts of the 35 species that were present on each of the 120 sample plots. However, interpretation of the two biotic variables can differ. Species used in calculation of MCIpa are weighted by their moisture affinity class, which allows an ecological interpretation of their occurrences as being related to different moisture regimes and associated productivities.

Site variables correlated with site index

We found little evidence that oak SI differed among mapped soil series, which agrees with other CHR studies. Although SI variation was associated with the five series in our study area, a meaningful difference was present only between the series with

Table 5. Mean (with SE in parentheses), minimum, and maximum values of independent abiotic and biotic variables quantified on 120 sample plots in CMGL and 34 sample plots in BCEF.

Independent variable	Mean	Min–max	τ	p
CMGL				
Abiotic – soil				
A horizon (cm)	33.5 (1.25)	3–51	0.253	0.0002
Solum depth (cm)	134.9 (1.98)	51–152	0.257	0.0003
Organic matter (%)	10.4 (0.29)	1–15	0.247	0.0005
Clay content (%)	23.4 (0.50)	5–35	0.047	0.5340
AWC (cm·cm^{-1})	0.52 (0.01)	0.13–0.71	0.257	0.0002
Abiotic – topographic				
Elevation (m)	1091.6 (6.70)	938–1251	0.046	0.4596
Gradient (%)	47.5 (1.07)	17.5–70.5	0.016	0.7994
Landform index	26.8 (0.49)	13.4–42.0	0.015	0.8029
Terrain shape index	1.8 (0.51)	–12.8–16.4	0.118	0.1180
Taz	1.1 (0.06)	0–2.0	0.257	0.0003
Biotic – vegetative				
MCIa	0.9 (0.04)	0–2.1	–0.311	<0.0001
MCIpa	1.0 (0.04)	0–2.0	–0.294	<0.0001
MCIba	1.0 (0.05)	0–2.1	–0.268	<0.0001
BCEF				
Abiotic – topographic				
Elevation (m)	812.9 (13.36)	671–976	NA	NA
Gradient (%)	30.4 (2.60)	2.0–62.0	NA	NA
Landform index	23.3 (0.90)	9.8–30.6	NA	NA
Terrain shape index	3.3 (0.90)	–8.0–15.6	NA	NA
Taz	1.4 (0.09)	0.1–2.0	NA	NA
Biotic – vegetative				
MCIpa	1.1 (0.03)	0.8–1.5	NA	NA

Note: Min–max represents the minimum and maximum values of soil, topographic, and moisture condition index (MCIx) variables quantified on sample plots. τ, Kendall's rank correlation; p, probability level of Kendall's τ; Taz, transformed azimuth (Beers et al. 1966); MCIa, moisture condition index based on species abundance; MCIpa, moisture condition index based on species presence–absence; MCIba, moisture condition index based on species basal area; NA, not applicable.

Table 6. Parameters and properties of models formulated with significant conventional abiotic variables (Taz) or three biotic exploratory variables (MCIx) for estimation of oak SI in CMGL.

	Abiotic base model	Biotic models (MCIx)		
Item	Taz	MCIa	MCIpa	MCIba
No. of samples (n)	120	120	120	120
α (SE)	24.502 (0.644)	29.619 (0.675)	29.998 (0.816)	29.408 (0.729)
β (SE)	1.615 (0.491)	–3.720 (0.660)	–3.596 (0.721)	–2.978 (0.617)
AIC	666.729	648.647	654.318	655.657
p value	0.001	<0.001	<0.001	<0.001
Adjusted R^2	0.076	0.206	0.167	0.158
RMSE model (m)	3.796	3.521	3.563	3.625
RMSE 10-fold (m)	3.822	3.535	3.620	3.639
Bootstrap α CI	23.394, 25.662	28.427, 30.778	28.680, 31.352	27.958, 30.662
Bootstrap β CI	0.710, 2.436	–4.926, –2.478	–4.911, –2.282	–4.110, –1.740

Note: α and β, regression intercept and slope parameters; AIC, Akaike information criterion; R^2, multivariate coefficient of determination; RMSE, root mean square error; CI, confidence interval (lower and upper values).

the highest (Plott, 27.8 m) and lowest (Evard, 24.4 m) means (Table 4). None of the soil series accounted for significant SI variation in the regression analysis. Similarly, mean oak SI differed by soil order, but order was not significant in regression models. Our findings that mapped soil series alone do not provide precise SI estimates agree with the findings of Carmean (1967), Van Lear and Hosner (1967), and Ike and Huppuch (1968). We found that properties of soil series likely associated with water availability, including A horizon and solum thickness, were significant factors associated with SI (Table 4), which agrees with findings from soil-site studies reviewed by Carmean (1975). Fralish (1994) found that plot soil properties accounted for 60% of SI variation for upland oaks. Carmean (1975) reported that soil properties are often associated with topographic variables. Because detailed soil properties were not available for plots and four soil series in our study area were associated with aspect (e.g., Edneyville was mapped on south- and west-facing side slopes; Soil Survey Staff 2019), aspect likely accounted for small but significant effects of soil properties in the models. On-site soil data would have been a superior evaluation of soil properties affecting SI.

Our study stands were on topographically uniform midslope sites that varied primarily by aspect, which typically accounts for small SI variation not associated with soil variables such as temperature and evapotranspiration (Hartung and Lloyd 1969; Fralish 1994). In agreement with our results, aspect has been reported as an important influence on site quality in numerous upland hardwood soil-site studies (Carmean 1967). We found, however, that Taz was weakly correlated with all topographic variables except slope gradient and strongly correlated with all soil properties except clay content, likely allowing Taz to supplant soil variables

Fig. 4. Oak SI predicted as a function of (A) transformed azimuth (Taz) and (B–D) three formulations of site moisture condition index (MCI) calculated as a weighted mean of tree species with DBH ≥ 5 cm based on (B) abundance (MCIa), (C) presence–absence (MCIpa), and (D) basal area (MCIba) on sample plots in CMGL. Dashed lines in each panel represent confidence limits of predictions. Terms above the *x* axes are environmental conditions represented by the units of measure.

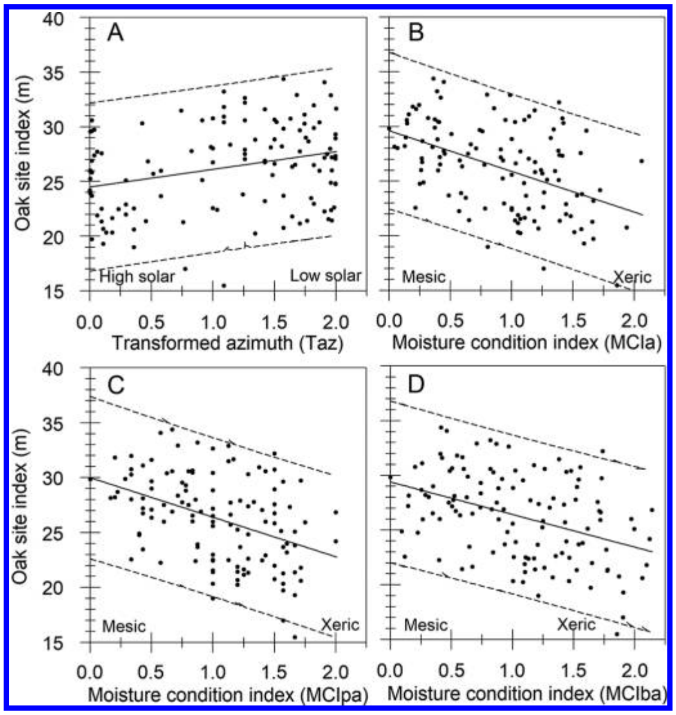


Fig. 5. Measured oak SI in relation to (A) Taz and (B) MCIpa for 34 sample plots (closed circles) at the Bent Creek Experimental Forest (BCEF), Buncombe County, North Carolina. Overlaid on the BCEF field data in each panel are two SI prediction models fitted using (*i*) the model formulations for (A) Taz and (B) MCIpa developed at CMGL (thick solid line) and (*ii*) a prediction model fitted to the BCEF field data (thin solid line) with 95% confidence limits of the model (two narrowly separated dashed lines) and 95% confidence limits of SI predictions (two widely separated dotted lines). Terms above the *x* axes are environmental conditions represented by the units of measure.

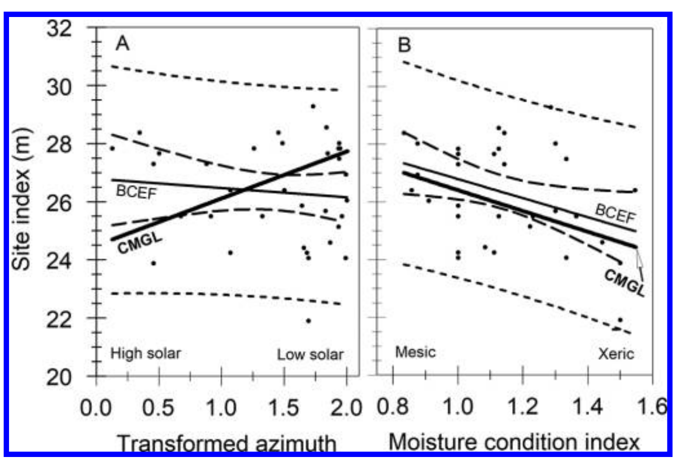
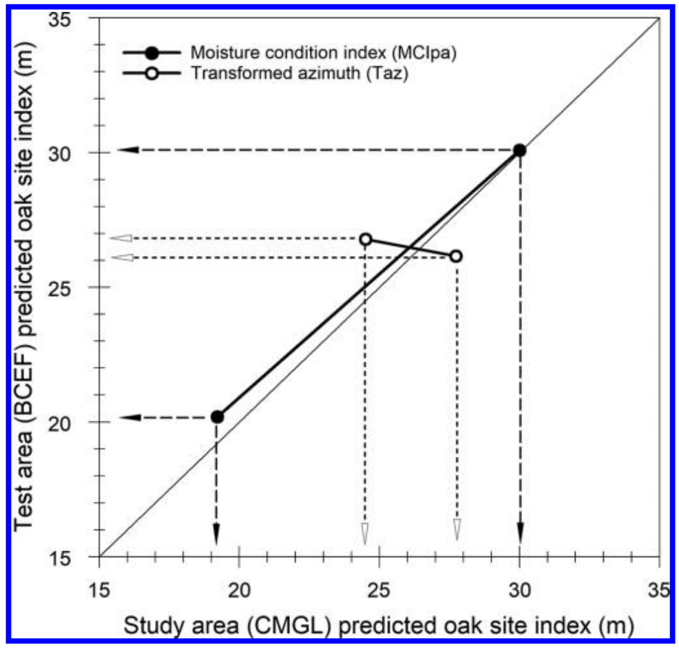


Fig. 6. Comparison of predicted oak SI for model formulations of Taz and MCIpa developed using data from CMGL and BCEF. Each pair of plotting symbols connected with a trend line represents predicted SI for the minimum and maximum measured values of Taz and MCIpa, which were similar at both areas (Table 5). The thin diagonal line represents identical SI predictions for the CMGL and BCEF models based on Taz and MCIpa.



and slope gradient in the base regression as a factor significantly affecting SI.

Our results demonstrated that the MCIx biotic variables were correlated with oak SI and were significant biotic explanatory variables in prediction models. Our study may be unique; we found no reports of other tree inventories of sample sites used to explain variation of oak SI. A nearly comparable study by Fralish et al. (1978) in the hilly landscape of southern Illinois, United States, revealed association of tree species with available soil water and site productivity (measured by basal area) with an index of plot tree species composition. Importantly, Fralish et al. (1978) suggested that SI would likely also have been associated with their species composition index, but they did not test that relationship. Except for the study by Fountain (1977), in which total plot basal area of oaks was correlated with SI, we found no comparable reports of other research in the CHR. In southern France, Berges et al. (2006) reported that a weighted index of six Ellenberg values for species in the understory shrub community was equivalent to topographic variables in models for predicting SI of sessile oak (*Quercus petraea* (Matt.) Liebl.). Weighted means of species composition have long been used for ecological studies of wetland delineation (Wentworth et al. 1988; Carter et al. 1988); however, ours was among the first to show the potential value of including a tree species moisture affinity index as an independent variable in models for SI prediction.

In undulating topography, site-quality studies typically find that slope position is a significant variable affecting soil moisture (Carmean 1975). A strength of our study was the uniform topography of midslope sample sites, which probably contributed to the lack of significance of all conventional abiotic variables except aspect (quantified as Taz). Under these relatively homogeneous environmental conditions, however, MCIx biotic variables were highly significant in prediction models, suggesting that tree species composition was sensitive to environmental conditions not manifested by soil and topographic variables evaluated for association with SI.

Restriction of sample sites to the midslope topographic position may also be a weakness because our scope was limited to approximately one-third of the mountainous landscape, thus excluding moist valleys and dry ridges with likely higher and lower SI values, respectively. Data from those slope positions could have affected the SI trend line of our regression analysis, as reported for oaks in Ohio (Carmean 1965) and Georgia (Ike and Huppuch 1968), United States. Although our samples included individuals of species more often occurring in mesic valleys (*Liriodendron tulipifera*) and on xeric ridges (*Quercus coccinea*), these species were also present as minor components of stands in the ecotone of the midslope position. However, generally uniform environmental conditions and species compositions of the sample sites revealed a strong association of the biotic variables with SI and a weak association of abiotic variables with SI, as measured by R^2. Typically, field sampling for forest site-quality studies extends over the range of landscape variability (mesic to xeric sites) rather than a subset of only dry-mesic conditions (as in our study) and is limited to carefully selected sites: stands with uniform species composition and one age class of trees (Carmean 1965; Ike and Huppuch 1968; Fralish 1994). We suggest that the relatively low R^2 and high SE values of models in our study using data from random sites resulted partially from sample trees that were suitable for our purpose of evaluating MCIx but less suitable for the derivation of high-quality SI prediction models. In support of the notion that sample tree quality affects prediction accuracy, the lower RMSE of MCIpa models for BCEF (1.65 m) compared with that of CMGL (3.56 m) could have resulted from the higher quality of the BCEF sites, stands, and sample trees, which were used for research purposes in the development of growth and yield models (McGee and Della-Bianca 1967). Recognizing limitations of the sample trees in our study, however, the significant relationship ($p < 0.0001$) of SI models that included MCIx suggests the need for further evaluation of this biotic variable in combination with abiotic variables from better controlled site and stand conditions.

Our findings were likely influenced by several minor limitations of the available field data from the parent silviculture study. Probably most influential was the estimation of site quality from a single sample tree, which likely increased variation of our dependent variable, SI, in relation to site variables measured at each sample site. Lamson (1980) found that five trees should generally be sampled for SI evaluation to achieve a half-width 95% confidence interval of 5 feet (1.52 m) for red (*Quercus rubra*) and white (*Quercus alba*) oaks aged 70 years in even-aged stands in West Virginia, United States. Our primary interest was the SI of *Quercus rubra*, but in its absence, we sampled *Liriodendron tulipifera* and converted its SI to that for upland oaks, thereby introducing an unknown data error from Doolittle's (1958) species conversion equation. Doolittle (1958) reported a large standard error (2.1 m) associated with his model to convert SI from *Liriodendron tulipifera* to *Quercus*, but it was applied to a relatively small proportion (17%) of our samples. Also, we used a single SI relationship of height and age for four oak species, which averaged about 75 years of age. However, Lamson (1980) reported little SI difference between red and white oak species at stands aged 70 years and older. Also, most (85%) of our sample trees were older than 60 years and were more likely to have had undetected crown damage from ice storms. Lack of on-site soil properties for use as quantified variables was likely the primary reason that our significant abiotic model based on Taz accounted for only 7.6% of SI variation, and the best biotic model (MCIa) was only marginally better, explaining a relatively small 20.6%. We suggest, however, that the small number of SI sample trees and lack of detailed soil properties were not major impediments to achieving our primary study objectives, which were to evaluate MCIx as potential explanatory variables and not to derive accurate SI prediction models based on MCIx.

A potential minor problem with evaluation and application of MCIx elsewhere is the need for knowledge of species–moisture relationships. We used Whittaker's (1956) moisture affinity classification derived in the same ecoregion as our study area, which generally agreed with our own long-term field observations. Based on personal knowledge, we provided moisture affinity assignments for three locally occurring species in the CMGL study area (Table 2) not referenced by Whittaker (1956). Different species in other ecoregions will require published sources of information or expert opinion for initial moisture classification assignments. Initial classification of new species can be adjusted with field observations of their common occurrence with associates.

We found satisfactory but contradictory results from evaluating performance of models developed in the CMGL study area and tested with independent data from a widely separated area (BCEF). Trend line slopes differed between the CMGL and BCEF areas for the abiotic Taz models (Fig. 5A) but were similar for the study and test biotic MCIpa models (Fig. 5B), suggesting that the effect of aspect on SI may vary among mountainous areas with apparently similar local climates. The effect of soil A horizon thickness on oak SI can also vary between two locations with similar climates (Ike and Huppuch 1968). However, the relationship of SI with MCIpa was consistent between CMGL and BCEF, suggesting that the response of tree species to soil moisture may be more consistent than abiotic variables across landscapes with similar annual precipitation; this is also noteworthy because the heavily disturbed land-use history at BCEF suggests that species occurrences indicate similar site moisture regimes, although slope positions may differ. Slope positions at CMGL were side slopes, between ridge and cove, but positions at BCEF were lower slopes and shallow coves. Because the purpose of our test was to assess performance of MCIpa (not Taz) at a location with site attributes potentially different from the study area, our evaluation results could be deemed successful and suggest that Whittaker's (1966) index of soil moisture regimes could have wider application as an easy and meaningful biotic variable in other SI models.

Shrubs were not included in our study, although Whittaker (1956) included shrub species in his study area as vegetative components of MCI. Shrub and midcanopy species have been evaluated as potential biotic variables in many studies (Daubenmire 1976; Fralish et al. 1978) and offer a possible refinement of MCIx values derived from a plot inventory including only trees. For example, in a similar site-quality study in BCEF, McNab (2010) reported that the presence or absence of two conspicuous fertility- and moisture-sensitive shrubs (mesophytic *Lindera benzoin* (L.) Blume and xerophytic *Kalmia latifolia* L.) respectively increased and decreased predicted SI.

Site index prediction using a model formulated with environmental variables correlated with a site's soil moisture regime may be the only viable alternative for assessing forest productivity when suitable trees are not available on site for sampling. Identification of a biotic variable to supplement conventional abiotic soil and topographic variables has been an objective of many CHR forest-productivity studies for over 50 years. Except for marginal, local success with herbaceous and shrub indicator species, a suitable biotic variable has not been adopted for operational application. Our study revealed that a vegetative index based on occurring tree species weighted by moisture affinities was a significant biotic explanatory variable for predicting oak SI on a subset of sites in the southern Appalachians of the CHR. However, our study was conducted only on topographic sites of relatively uniform dry-mesic environmental conditions. The relatively uniform sample sites of our study provided a rigorous evaluation of estimated SI precision in relation to vegetation (MCI) on middle slopes in the CMGL, but we did not include mesic and xeric sites present at lower and higher positions. Additional research across the full moisture gradient of mountainous topography is needed before Whittaker's (1966) index can be considered a potentially useful biotic variable for SI prediction elsewhere, particularly where species diversity is less than in our study area. A limitation of the MCI variable is the requirement of empirical or expert knowledge of tree species affinities in relation to moisture gradients. Regardless, advantages of MCIx include simplicity of application using plot inventory data, adaptability to local variation of species occurrence in relation to soil moisture regimes, direct connection between observable (species) and quantifiable (SI) components of site quality, and ease of transfer to practitioners. Our evaluation of MCIpa using data from two locations suggests that the relationship of tree species with SI may be relatively stable across landscapes with similar climates, somewhat different topography, and greatly different past land uses. Although limitations of data from our study site (only middle slopes) and sample trees (mixed SI species) may imply circular logic for developing accurate models, the purpose of our study was to evaluate the potential value of MCIx as biotic variables in SI models, not to derive SI prediction models for application elsewhere.

Conflict of interest statement

The authors declare they have no conflicts of interest.

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