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The demographics and regeneration dynamic of hickory in second-growth temperate forest

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ABSTRACT

Hickory (*Carya* spp.) is an economically and ecologically important genus to the eastern deciduous forest of North America. Yet, much of our knowledge about the genus comes from observational and anecdotal studies that examine the genus as a whole, or from research that examines only one species, in only one part of its range. Here, we use data sets from three different spatial scales to determine the demographics and regeneration patterns of the four most abundant hickory species in the Northeastern United States. These species were the shagbark (*C. ovata*), pignut (*C. glabra*), mockernut (*C. tomentosa*), and bitternut (*C. cordiformis*) hickories. We examine trends in hickory demographics, age class and structure at the regional scale (New England and New York), the landscape scale (a 3000 ha forest in northwestern Connecticut) and at the stand scale (0.25–5 ha). Our analysis at all three scales show that individual hickory species are site specific with clumped distribution patterns associated with climate and geology at regional scales; and with soil moisture and fertility at landscape scales. Although hickory represents a fairly small percent of the total basal area (2.5%) across a forest landscape, upland oak-hickory stands can have a much higher basal area of hickory (49%), especially in the larger height and diameter classes. Additionally, dendrochronological results show that hickory trees in mature, second growth forests originated or were released over a half-century long period of stand development; but patterns in seedling recruitment in the understory is continuous and builds up as advance regeneration over decades, with some surviving in a suppressed state for over forty years. This contrasts with oak where recruitment of regeneration is strongly pulsed in association with mast years.

1. Introduction

The genus *Carya* (Juglandaceae, walnut family) represents a diverse group of nineteen tree species (USDA, 2017) of which twelve are found across eastern North America, with the remaining species in northeastern China. Their range extends from Florida and Texas north towards the Great Lakes and into central New England (Burns, 1983; Braun, 1964). In the Northeastern United States, four main hickory species are abundant; shagbark (*C. ovata* (Mill.) K. Koch), pignut (*C. glabra* (Mill.) Sweet), mockernut (*C. tomentosa* (Poir.) Nutt.), and bitternut (*C. cordiformis* (Wangenh.) K. Koch). These species comprise a late successional component of the oak-hickory association, a forest type that ranges across the whole of eastern North America (Braun, 1964). The genus *Carya* is both ecologically and economically important; providing wildlife habitat and forage for many birds and mammals (Lewis, 1982; MacDaniels, 1952; Martin et al., 1961; McCarthy, 1994; Sork, 1983a, 1983b) and producing strong, high quality wood (Boisen and Newlin, 1910; Burns and Honkala, 1990; Phillips, 1973).

A number of observational and anecdotal studies have been conducted to determine the general autecology of these species. Hickory as a group are fairly shade tolerant, have the ability to withstand moderate fires, can vigorously stump-sprout and have the tendency to produce a very high number of seeds during mast years (Boisen and Newlin, 1910; Burns and Honkala, 1990; Hawley and Hawes, 1918; Nelson, 1965), though certain traits are often more strongly expressed by one species over another. In the first classic study by Boisen and Newlin (1910) hickory are considered to be “exacting in their soil requirements”, but these preferences vary significantly between species. While such observational studies provide a useful foundation about the ecology of the genus, there has been very little empirical evidence provided to support these observations.

While demographic information is known about hickory species in specific forest regions (Christensen, 1977; Fredericksen et al., 1998; McCarthy and Wistendahl, 1988; Cowden et al., 2014; Holzmueller et al., 2014), to date there has not been regional or landscape scale

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analysis of this important genus. Prior studies of hickory either focused exclusively on a single species of hickory, making it difficult to compare and contrast generalizations and differences across the genus (e.g. Monk, 1981; Sork, 1983a; Lewis, 1982; Robison and McCarthy, 1999); or combined hickory species together as a genus (*Carya* spp.), or as part of the larger oak-hickory complex ignoring species-specific differences (Holzmueller et al., 2014; Hutchinson et al., 2012; Jackson et al., 2006; Rebertus and Meier, 2001; Cowden et al., 2014).

Temporal shifts in hickory demographics are not well understood, but recruitment in oak-hickory forests has implication for future demographic patterns (McCarthy and Wistendahl, 1988; Robison and McCarthy, 1999). Undisturbed second-growth oak-hickory forests have undergone successional shifts in species composition (Christensen, 1977); with canopy trees of oak and hickory being replaced by more shade tolerant sugar maple (*Acer saccharum* (Marshall)) and beech (*Fagus grandifolia* (Ehrh.)) (McCarthy and Wistendahl, 1988; Oliver and Larson, 1996; Shotola et al., 1992). While all these studies indicate that hickory species face many barriers before successful establishment and over successional time, there has been no research that examines their post-establishment inter- and intra-specific pattern in population demographic and structure (McCarthy, 1994; Barnett, 1977; Lewis, 1982; Sork, 1983a, 1983b). Additionally, there has been no research into how these patterns vary at the stand, landscape, or regional scale. Better understanding of species-specific trends and their relation to scale is critical in determining the role of hickory in future forests, and providing insight into future stand dynamics under uncertain changes in a climate that is predicted to be warmer and wetter (Rustad et al., 2012).

In this study, we examine the population structure and demographics of the genus *Carya* in northeastern North America across a variety of scales. These data provide critical insight into the understanding of hickory stand dynamics within the widespread oak-hickory forest type of the eastern deciduous forest of North America. Our specific objectives are to (1) to document regional demographic information of hickory in relation to climate, geology, and physiography; and (2) examine and document the regeneration patterns, age class, and structural composition of hickory within oak-hickory stands. Because ecological phenomena occur at different spatial scales (Levin, 1992; Wiens, 1989), we used datasets at three scales; the regional scale of the northeastern United States (the six New England states plus New York), the landscape scale (a 3000 ha forest in Connecticut), and the stand scale (0.25–5 Ha).

2. Methods

2.1. Forest description of study region

Most hickory occurs in the oak-hickory forest type (Westveld, 1956; Barbour and Billings, 2000); a forest type that spans the core heart of eastern North America from southern New England west to Iowa and south to Oklahoma and across to the northern portions of the Gulf states. The core species of oak in this range include red (*Quercus rubra* L.), black (*Q. velutina* Lam.,), scarlet (*Q. coccinea* Muenchh.,), white (*Quercus alba* L.), and chestnut (*Q. Montana* Willd.); while the hickories comprise shagbark, pignut, mockernut, and bitternut (Barbour and Billings, 2000).

In the northeastern United States the oak-hickory forest type is described as having a large component of either red oak or white oak with varying amounts of hickory, and is commonly found on ridgetop sites (Braun, 1964; Greller, 1988). In New England and New York, before European colonial settlement, oak-hickory forests were comparable in composition to the forests of today (Oswald and Foster, 2011), with hickory being identified as early as the 1600s (Wood, 1634) and recorded as witness trees in Connecticut in the early 1700s (Marshall, 2011). These historic oak-hickory forests were likely maintained by Native Americans through the use of frequent low-intensity fires (Cutter and Guyette, 1994; Holzmueller et al., 2009; Patterson and Sassman, 1988, Mann, 2006), but many of the current oak-hickory forests are potentially the result of release events caused by white pine timber harvests in the early 20th century and the hurricane of 1938 (Foster, 1992); as well as repeatedly grazed and cutover upland forests that once had chestnut.

We used U.S. Forest Service forest inventory data for seven northeastern states (New York and the six New England states) to both define and conduct the regional analyses of the oak-hickory forest type. For the landscape and stand scale analysis, we conducted observational surveys at the Yale-Myers Forest, a 3213-hectare research and demonstration forest located in northeastern Connecticut (41°58′N, 72°80′W). Yale-Myers Forest is within the core distribution of oak-hickory for the region according to the U.S. Forest service data. The forest history of this landscape is also typical for the region. Originally the use of fire promoted the fire-tolerant oak and hickory by Native Americans. These trees produced mast nuts that were an important source of food for Native Americans and their game; and the grass groundstory promoted by fire was a source of forage for game, and created openness for movement and hunting (Cronon, 2011). After European colonization forests were cleared and intense agrarian land use in the 1700s and 1800s was followed by farm abandonment and recruitment of old-field white pine (Foster, 1992). The mature pine was subsequently timbered in the 1900s thereby releasing and establishing second-growth oak-hickory forests (Meyer and Plusnin, 1945). Though defined as oak-hickory, the tree species composition of Yale-Myers Forest is diverse and spatially heterogeneous including white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* L.), oak (*Quercus* spp.), hickory (*Carya* spp.), maple (*Acer* spp.), and birch (*Betula* spp.). Natural disturbances include wind and ice-storms, fire (mostly of human origin), and insect and pathogen outbreaks (Bormann and Likens, 1994; Siccama et al., 1976), with many stands in the forest regenerating after the hurricane of the 1938 (Meyer and Plusnin, 1945).

The topography of this landscape is reflective of its underlying geology, containing ridges and valleys that range in elevation between 170 m and 300 m above sea level. Slopes rarely exceed 40%. The soils are inceptisols derived largely from glacial tills of moderate to well-drained stony loams that overly metamorphic schist-gneiss bedrock (NRCS, 2009). Changes in slope, aspect, and depth to bedrock create a heterogeneous landscape that spans drainage from poorly-drained hydric to excessively well-drained xeric soils. This heterogeneous landscape provides a perfect template to investigate hickory demographics in relation to site within one regional geology — in this case the eastern metamorphic uplands of Connecticut. The climate in the region is cool temperate with mean temperatures of 21.2 °C and 4.1 °C for July (summer) and January (winter), respectively. Precipitation is distributed evenly throughout the year, with an annual mean of 110 cm (NOAA, 2017).

2.2. Sampling design

2.2.1. Distribution and demographic characteristics across the northeast region

To determine regional trends in the distribution of hickory species across the northeastern United States, we used Phase 2 plot data collected through the U. S. Forest Service Forest Inventory and Analysis (FIA) program (FIA National Field Guide, 2016). Data from all six New England states and New York were included in this analysis. We supplemented these data by intersecting the locations of each FIA plot with the corresponding Geographic Information System (GIS) map data from the United States Department of Agriculture Plant Hardiness Zones (USDA, 2012), United States Geological Survey (USGS) bedrock materials (Schruben et al., 1994), and USGS surficial materials (Nicholson et al., 2006; Dicken et al., 2005).

2.2.2. Demographics and size class distributions across a Connecticut landscape

We used data from 420 plots across the Yale Myers Forest to determine the factors that correlate with the presence of hickory across a landscape and its proportional representation within the forest. We collected this data in the summers of 2013 and 2014 from 21 paired transects, each containing 10 sampling points (420 plots total). Each transect starts at a random location along a road or trail, and has a paired transect that starts 50 m to the west. The transects run north–-south, with sampling points spaced 20 m apart. Each sampling point comprises an overstory variable radius sampling point (Basal Area Factor 2.3 m^2 Ha^{-1}) where we measured all trees > 5 cm diameter at breast height (DBH), and an understory, circular, 50 m^2 fixed area plot where we recorded all regeneration < 5 cm DBH. In 2013, we completed the overstory inventory in all 420 variable radius plots using an angle gauge, and recorded the species and DBH of each "in" tree. In the summer of 2014, we revisited each sampling point to collect environmental data using the methods described in Duguid (2017). These data included mean ambient soil temperature and volumetric water content (VWC) in the spring, summer, and fall; pH; gravimetric moisture; nitrogen and carbon content; organic matter; slope; and aspect.

2.2.3. Distribution, size and age class relations within hickory stands

To examine the size and age class distributions within hickory-dominated second-growth stands, we established quarter-hectare (50 m × 50 m) plots across four ridge-tops where hickory comprised at least one third of the total basal area (Table 1). One of the four plots measured 40 m × 62.5 m to accommodate the topography, shape, and tree distribution within the stand. All four sites were in a similar stage of stand development and share the land-use history previously described that can be considered widespread across the region. These stands were originally brush meadows (unimproved open grazing lands) maintained by groundstory fires, and later reverted to old-field pine in the 1850s with the collapse of the wool market. The pine stands that arose were cutover in the 1900s for boxwood releasing the second-growth hardwoods of today.

Soils at these sites consist of well-drained glacial till, shallow to bedrock (USDA, 1975) in the Hollis, Chatfield, and Charlton series (NRCS, 2009). Overstory vegetation is dominated by second growth hickory and oak, with occasional birch, maple, and hemlock. The understory, reflecting the dry site, is largely dominated by sedges (*Carex pensylvanica* Lam.) with some lowbush blueberry (*Vaccinium angustifolium* Aiton.) and occasional forbs. At each plot, we established a 10 m × 10 m grid over the entire quarter-hectare and recorded the relative spatial location of all woody plants > 1.5 m in height. We identified each individual by species, measured DBH, measured height using a rangefinder (Nikon Forestry Pro laser), and determined crown area by measuring the length of crown spread in each cardinal direction to the nearest 0.1 m. We documented whether the individual was an adult/small tree (dbh ≥ 5 cm) or a sapling (dbh < 5 cm and height > 1.5 m). In each plot, we also recorded the spatial location of all hickory seedlings (height < 1.5 m), identified each seedling to species when possible (if uncertain, we recorded the genus), and measured height. At the Morse Ridge plot, we made an adjustment to this method as there was a prohibitively large number of seedlings. There, we established a systematic grid and randomly selected 25 3.33 m × 3.33 m subplots covering 278 m^2 (~11%) of the ¼ ha area. For each plot, we collected the same data regarding seedling species, height, and spatial location. We collected this data in the summer of 2016.

To determine tree age since release, and the trees to be cored, we grouped all adult individuals into five diameter classes (5–15 cm, 15–25 cm, 25–35 cm, 35–45 cm, and 45 + cm), and all saplings into 2 diameter classes (< 2.5 cm and 2.5–5 cm). We random selected 25% of trees in each of these diameters for collection of one increment core at a height of 1.3 m. We mounted the cores using standard dendrochronological methods (Speer, 2010), sanding them with progressively finer sandpaper up to 600-grit. We then scanned each core at 1200DPI (dots per inch) using a high-resolution scanner (Epson Expression 1640XL), and imported each scan into the Coorecorder software program from Cybis Dendrochronology (Larsson and Larsson, 2016) where we counted annual rings and measured ring-widths.

Lastly, we collected a random 10% subsample of seedlings and stored them in a freezer until they could be processed. We began by cutting a 2–3 cm segment of each sample, such that one of the cuts was made 0.5 cm above the root collar. We then immersed each segment in boiling water for 15 s, and used a sliding microtome to obtain five cross sectional samples from the edge closest to the root collar. We varied the thickness of each cross section from 2 to 5 μm, and stained all of the samples using an Astrablue/safranin mixture (Van der Werf et al., 2007) for fifteen minutes. We then rinsed each sample with deionized water, prepared temporary microscope slides, and took digital images of the samples at 5× to 50× magnification using a Canon EOS 6D mounted to a compound light microscope (Olympus BX60). We used FIJI image analysis software (Schindelin et al., 2012) to stitch together multiple images of the same sample, and to calibrate scale based on images taken of a stage-micrometer. We then counted the annual rings along a minimum of three radial sections to avoid false or missing rings and obtained an estimate for age since germination.

2.3. Data analysis

2.3.1. Distribution and demographic characteristics across the northeast region

Using the genus-level stem density estimates of hickory from the FIA plot data for New York and New England, we created a kernel-smoothed density raster map (Wand and Jones, 1994) of the region (see S.1 in supplemental information). This was done using the "spatstat" package in R (Baddeley et al., 2015). We then tested for spatial randomness and spatial autocorrelation with Moran's I using the "ape" package (Paradis et al., 2004) and by creating variograms using the "geoR" package (Ribeiro and Diggle, 2016). Next, we compared the genus distribution map to the individual species of hickory using raster data from the USFS (Fig. 1) (Wilson et al., 2013).

Table 1
Summary of the site characteristics for the four ¼ hectare plots used in the stand-scale analysis within the Yale-Myers Research and Demonstration Forest, CT.

Site	Boston Hollow	Morse Ridge	Nagy Road	Turkey Hill
Coordinates	41.939, −72.159	41.954, −72.131	41.943, −72.171	41.928, −72.160
Elevation (m)	265	260	290	255
Slope (°)	17°	6°, undulating	5°	11°, undulating
Aspect (°)	130°	110°	90°	190°
Soil Series	Charlton/Chatfield complex	Charlton/Chatfield complex	Charlton/Chatfield complex	Hollis/Chatfield and Charlton/Chatfield complexes
Drainage Class	Well drained	Well drained	Well drained	Somewhat excessively drained
Total BA/hickory BA (m^2/ha)	26.56/16.29	32.64/17.79	30.67/10.91	24.47/9.88
All stems/hickory stems (#/ha)	524/352	472/204	608/344	632/176
Mean tree height (m)	15.18	18.79	13.48	13.59

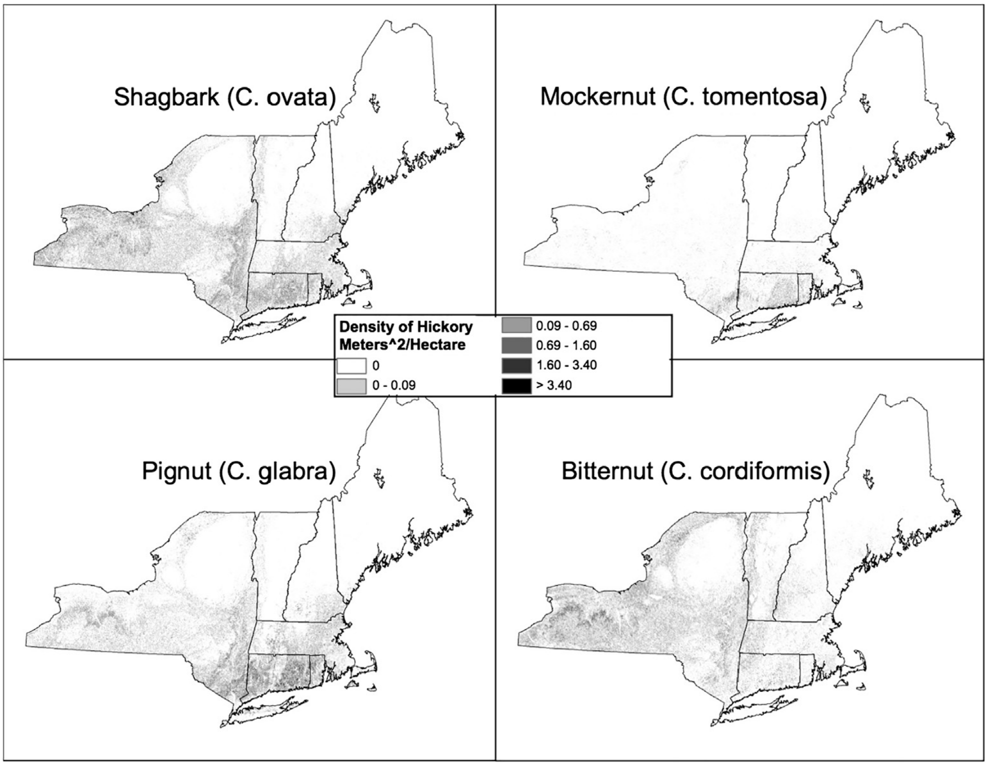

Fig. 1. Species distribution maps created using raster data obtained from the USFS. Basal area categories were broken up using quantiles to better illustrate the abundance of hickory in regions where it may be scarce, but present. There are clear patterns in the distribution of each species of hickory based on geology and climate, as well as variances across the genus.

To determine the factors that significantly influenced the establishment of hickory at the regional scale, we created four different species-specific generalized linear models (GLM) using the "stats" package (R Core Team, 2014). For each GLM, our response variable was the basal area of one species of hickory in the FIA plots that had a basal area greater than zero. Our predictors were elevation, slope, aspect and physiographic code (associated with the FIA plot) as well as plant hardiness zone, surficial soil material, and bedrock age (obtained from the data intersection described earlier). Aspect was transformed using the formula $A' = \frac{180 - |\,aspect - 180|}{\frac{180}{\pi}}$, to account for the fact that degrees close to 0 and 360 were more similar than dissimilar. We used GLMs with Gamma errors and a log link, as each species' basal area did not have a normal distribution, but was always a positive value and positively skewed.

2.3.2. Demographics and size class distributions across a Connecticut landscape

Using landscape data collected at the Yale-Myers forest, we examined the abundance of hickory using both individual counts and total basal area. We compared these results to oak found in the same plots in an attempt to quantify the abundance of hickory in this oak-hickory forest. To determine the factors that most closely correlate with the presence of hickory at the landscape scale, we performed a zero-inflated Poisson regression (ZIP regression), using the "pscl" package (Jackman, 2015; Zeileis et al., 2008). ZIP regressions are two-component mixture models that contain a count component and a zero-inflated component that allows for accurate analysis of count data with many zeros (Lambert, 1992). To eliminate any correlation within environmental variables, we utilized principle components analysis (PCA) for variable reduction with log transformations of volumetric water content, gravimetric water, and slope. We determined there to be 4 principle components by creating a scree plot (Cattell, 1966) and by counting the number of principle components (PCs) with eigenvalues greater than one (Guttman 1954, and Kaiser 1960). Using bi-plots (Gabriel, 1971) and the loadings associated with each variable, we were able to interpret what each principle component signified. Our interpretations of the loadings indicate that PC1 was related to dry soils and low soil nutrients (nitrogen, carbon, and organic matter), PC2 related to low soil temperature and low pH values (acidic soils), PC3 related to high soil nutrients, but with smaller loadings than PC1, and PC4 related to high seasonal variation in mean soil temperature. We constructed our models using the count of the number of hickory in each plot as the dependent variable, the first four principle components as independent factors (count component), and used a blocking factor based on location (pairs of transects) as the zero-inflated component. We then compared this with an analogous Poisson regression and preformed a Vuong closeness test (Vuong, 1989) and determined that the ZIP model was superior to the regression.

2.3.3. Distribution, size and age class relations within hickory stands

At the stand-scale, we compared the diameter, height, and age distributions among the dominant tree species: this includes adult hickories, oaks, black birches (*Betula lenta* L.), and red maples (*Acer rubrum* L.). We did this by calculating and comparing the mean, standard deviation, skewness, and kurtosis of each species using the "moments" package (Komsta and Novomestky, 2015). We also used Analysis of Variance (ANOVA) with Tukey honest significant difference (HSD) post hoc test to test for significant differences between the mean diameters, heights, and ages of different species.

We analyzed the spatial distribution and relationship between seedling and adult hickories in three of the four stands; eliminating the site with the altered sampling methodology. First, we used the density mapping function in the "spatstat" package to examine the spatial distribution of the different species of hickory seedlings and adults across the three plots. We then used the G-cross function in "spatstat" to examine the spatial relationships between different seedling species, and between seedlings and adults to test for predictable associations, negative density dependence or randomness. We also tested for spatial randomness of adults and seedlings using the K estimation function and Clark Evans test, both in "spatstat". All statistics were carried out using R 2.11.1 (R Development Core Team, Geneva, Switzerland, 2014).

Table 2
Significant (p < 0.1) predictors of abundant hickory obtained from GLM output. Cells in bold indicate a p-value less than 0.1. Blank cells indicate that, for a given species, there was not enough data to complete the analysis, or that no plots fell into that category. There was not enough data to complete the analysis for *Carya tomentosa*. Other categorical variables were included in the model, but omitted from this table because they were not significant for any species, or the genus as a whole.

Predictor	Predictor category	All Carya		Carya cordiformis		Carya glabra		Carya ovata	
		P-Value	Estimate	P-Value	Estimate	P-Value	Estimate	P-Value	Estimate
Elevation	N/A	0.986	0.000	0.836	0.000	0.184	0.000	0.501	0.000
Slope	N/A	0.467	0.004	0.303	0.009	0.102	−0.018	0.205	−0.010
Aspect	N/A	0.538	−0.021	0.272	−0.068	**0.001**	−0.207	0.527	0.032
Plant Hardiness Zone	4b	0.246	−0.949	0.103	−1.527				
	5a	0.202	−1.071	0.138	−1.510	**0.012**	−3.090	0.315	−1.203
	5b	0.155	−1.199	**0.083**	−1.792	**0.021**	−2.612	0.389	−1.070
	6a	0.378	−0.755	0.377	−0.946	**0.069**	−2.145	0.298	−1.318
	6b	0.305	−0.962	0.158	−2.171	0.853	−0.284	0.902	−0.166
	7a	0.620	0.878			0.653	−0.629		
Physiographic Class	21 (flatwoods)	0.749	0.346	0.138	1.803	0.142	1.415	**0.082**	−1.866
	22 (rolling uplands)	0.962	−0.050	0.296	1.223	**0.077**	1.800	**0.051**	−1.949
	25 (broad floodplains/bottomlands)	0.434	0.961	**0.082**	2.353	0.349	−1.249	**0.006**	−3.419
	31 (swamp/bog)	0.852	−0.219	0.215	1.680			**0.001**	−4.204
	32 (small drains)	0.949	−0.099			**0.090**	2.500		
Surficial Rock Type	Dolostone (dolomite)	0.812	−0.351	**0.089**	−3.552			0.751	0.609
	Granitic gneiss	0.884	−0.147	**0.015**	−5.536	0.598	0.853	0.774	0.384
	Granofels	0.780	0.319			0.686	0.590	**0.097**	3.616
	Graywacke	0.712	−0.397	0.136	−2.634	**0.100**	1.912	0.326	1.879
	Limestone	0.538	−0.661	**0.051**	−3.251			0.468	1.588
	Marble	0.195	1.746	**0.047**	−4.986				
	Metavolcanic rock	0.845	−0.310	**0.031**	−4.132			0.139	2.559
	Paragneiss	**0.043**	3.314	0.155	-3.276				
	Phyllite	0.978	0.031	**0.088**	−3.174	0.124	2.397	0.519	1.238
	Quartzite	0.991	−0.017	**0.010**	−7.622			0.159	2.300
	Sandstone	0.338	−1.056	**0.039**	−3.539	0.772	0.310	0.830	0.305
	Schist	0.878	0.156	**0.015**	−4.911	0.266	1.495	0.150	3.313
	Shale	0.471	−0.754	**0.058**	−3.109	0.728	0.325	0.850	0.316
Bedrock	106 D2 Middle Devonian	0.145	1.373	0.958	0.020	**0.043**	0.852	**0.038**	2.525
	108 D2c Middle Devonian continental	0.187	1.318	0.263	0.886	0.754	0.183	**0.047**	2.582
	118 S2 Middle Silurian (Niagaran)	0.361	1.011	0.844	0.165			**0.021**	3.818
	123 O3 Upper Ordovician (Cincinnatian)	0.264	0.958	0.540	0.386	**0.046**	−2.137	0.279	1.199
	125 O2 Middle Ordovician (Mohawkian)	0.735	−0.316	**0.029**	−1.465	**0.057**	−1.472	0.787	−0.371
	133 OC Lower Ordovician and Cambrian carbonate rocks	0.641	−0.613	0.126	3.225	**0.096**	−2.048		
	135 Ce Cambrian eugeosynclinal	0.811	−0.231	**0.005**	−2.264	0.478	−0.572	0.464	0.915
	139 Z Z sedimentary rocks	**0.056**	−3.467			**0.065**	−3.666		
	143 Y Y sedimentary rocks	**0.025**	−3.808	0.612	−1.033				
	147 Ym Paragneiss and schist	**0.079**	−2.145	0.919	0.219	0.461	−0.845		
	153 Ygn Orthogneiss	**0.060**	−3.775						

3. Results

3.1. Distribution and demographic characteristics across the northeast region

Results from kernel smoothing indicate clumping of hickory populations at the regional scale (Supplemental information S1). We found evidence of spatial autocorrelation with a small positive value (0.0272) for Moran's I with a significance value of < 0.001 that shows hickory distributions are clustered at regional scales.

At the genus level, results from the GLMs (Table 2) indicate that few of the variables incorporated into the model were significant predictors of abundant hickory, apart from four different types of bedrock (paragneiss and schist (p = 0.079), orthogneiss (p = 0.060), and two types of sedimentary rock (p = 0.056, p = 0.025)); as well as surficial material composed of paragneiss (p = 0.043). However, at the species level the GLM results were dramatically different for each individual species.

Shagbark hickory had the greatest number of variables associated with the physiographic class (flatwoods (p = 0.08), rolling uplands (p = 0.051); and more strongly with broad floodplains/bottomlands (p = 0.006), and swamps/bogs (p = 0.001). Surficial materials composed of granofels were also associated with shagbark hickory (p = 0.09) that were largely linked to the Devonian and Silurian geology of the northern Allegheny plateau of southeastern New York.

Pignut hickory had the greatest number of significant plant hardiness zones (5a (p = 0.01), 5b (p = 0.02), and 6a (p = 0.07) and was also strongly associated with southern aspect (p = 0.001). Physiographic regions of rolling uplands (p = 0.07) and small drains (p = 0.09) were also associated with high densities of pignut hickory. Like shagbark it was associated, but more weakly so, with the Silurian/Devonian geology of the Allegheny. However, it was noticeably negatively associated with the Connecticut River Valley and the Ordovician igneous/volcanic slopes on either side.

Bitternut hickory had the greatest number of significant surficial material categories all of which were negative associations (10 at p > 0.10), and none of which were associated with clay-based soils. Like pignut hickory it was also not associated with the Ordovician slopes of the Connecticut River Valley or the Cambrian region that make up the slopes of the Hudson River. Bitternut hickory was also associated with broad floodplains/bottomlands (p = 0.08), and plant hardiness zone 5b (p = 0.08). Elevation and slope were not significant predictors for any species of hickory. There was not enough data to complete the analysis for mockernut hickory.

Table 3
Summarized statistics for hickory, oak, red maple, and black birch and total number of stems (all trees and species) across 420 plots within the Yale-Myers Research and Demonstration Forest, CT. Significant differences ($p < 0.05$) in mean DBH, found using Tukey post hoc tests, are noted. Some species with small numbers of individuals were omitted from the table for clarity. Letters denote differences ($a < b < c$).

	Number of individuals	Mean DBH (cm)	DBH standard deviation	DBH skewness	DBH Kurtosis	Sum of basal area (m^2)
Carya cordiformis	1	42.67	NA	NA	NA	0.14
Carya glabra	21	24.76[b,c]	12.142	1.024	3.313	1.24
Carya ovata	91	33.07[a,b,c]	12.262	−0.012	2.666	8.88
Carya tomentosa	66	30.82[a,b,c]	9.582	0.088	3.017	5.39
Quercus alba	234	36.80[a,b,c]	14.162	1.236	7.806	28.56
Quercus rubra	973	46.67[a]	14.226	−0.023	3.411	181.89
Quercus velutina	149	41.31[a,b]	12.068	−0.206	3.532	21.67
Acer rubrum	498	27.84[b,c]	11.974	0.483	3.282	35.90
Betula lenta	386	22.34[c]	13.243	0.705	4.987	20.43
Total (all stems combined)	3657	37.63	17.007	0.335	3.209	644.55

3.2. Landscape scale demographic and size class distribution

Data from the 420 plots at Yale-Myers Forest reveal that hickory was found in only 24.6% of the plots and represented 2.4% of the total basal area. Across the forest, the ratio of hickory to oak is 1.3–10. Similarly, hickory represents only 6.7% of the basal area of oak. When only evaluating the plots with hickory, the ratio of hickory to oak is 0.55:1; while hickory comprises 24.9% of the basal area of oak and 9.6% of the total basal area as compared to oak which represents 38.7%. An analysis using only the plots with hickory demonstrates that each species has different diameter distributions (Table 3). Mean stem diameters showed the red oaks (*Q. rubra* and *Q. velutina*) to be significantly larger than the red maple, black birch and pignut hickory, with the white oak and other hickory to be intermediate in size. Interestingly, pignut hickory and white oak both exhibit strong positive skewness to the right in their diameter distributions, meaning that they have many more small trees but also a few wide ranging larger ones. The red oaks and shagbark hickory are slightly negatively skewed to the left meaning the opposite, that there are a few smaller individuals but the majority of the trees are large; whereas black birch and red maple are close to normal in distribution (Table 3). All species showed some degree of kurtosis, but both red and white oak and black birch exhibited the greatest compared to hickory and red maple. The average basal area across the whole forest is 20 m^2 Ha^{-1} with only a very small proportion representing hickory as a genus. Basal area was represented largely by pine (*Pinus strobus* L.,), eastern hemlock (*Tsuga canadensis* (L.) Carriere), and the genus (*Quercus*). Only one bitternut hickory was observed in all 420 plots, so comparisons could not be drawn with this species.

ZIP regression showed that the first three principle components were significant. PC1 ($p = 0.02$; $B = -0.12$) relates to low volumetric water content, gravimetric water, and nutrient levels, indicating that the number of hickory increases as soil moisture and nutrients decrease; suggesting that hickory as a genus are found on drier more infertile soils. PC2 ($p = 0.04$; $B = -0.14$) relates to low temperature and low pH, and indicates that the number of hickory decrease as soil temperature and pH increase; suggesting that hickory are found on colder and more acidic soils. PC3 ($p = 0.04$; $B = -0.15$) relates to high nutrient levels, and indicates that the number of hickory increase as soil nutrients decrease, supporting the trends in PC1. We did not find spatial location within the forest (paired transect) to be a significant predictor (the smallest p value was 0.6) meaning that a plot's presence along any given transect does not increase the likelihood of finding hickory within that plot.

3.3. Stand scale: Adult distribution, size and age class relations

Data obtained from the four stand-scale plots were used to construct histograms for diameter, age, and height distributions of the adult trees (Fig. 2a–c), to calculate the mean and standard deviations, and test for skewness and kurtosis within these distributions (Table 4). The diameter and height data show similar trends, in that the three observed species of hickory are present in nearly every diameter and height class, and as a genus, have a somewhat normal distribution for both measurements. Unlike the differences observed at the landscape scale, the three species of hickory in the stand-scale plots had almost identical mean diameters of 23 cm, and very similar mean heights of around 17 m. These measurements are similar to the oaks, with only red oak having a statistically different (larger) diameter, and chestnut oak having a statistically different (smaller) height than all three species of hickory. Other species found in the understory of the plot, namely black birch, red maple, and hophornbeam (as defined by other in Fig. 2), also had smaller heights and diameters. The diameter and height distributions for all species, including hickory, were not highly skewed (either < 0.5 or > -0.5) with the exception of black birch which was positively skewed for both. The diameter distributions for the three species of hickory exhibited negative kurtosis across their ranges of height (-2.12, -2.12, and -2.70 for pignut, shagbark, and mockernut, respectively).

Age distributions, however, show much different trends as compared to diameter and height distributions for hickory. Though hickory as a genus has wide ranging diameter and height classes they all represent older age classes of 70–160 years since release. The mean ages for each species of hickory ranged from 110 for pignut hickory, to 125 for mockernut hickory, to 136 for shagbark hickory. Black birch was the only species in the plots that was younger in age, when compared to hickory as a genus. Pignut hickory had the most skewed age distribution (skewness = -1.2) while the other two hickory species were not skewed (either < 0.5 or > -0.5), and no individual species exhibited any significant kurtosis. An analysis of hickory distribution patterns using the Clark-Evans test (where $R < 1$ suggests clustering) indicate a small degree of clumping of adult hickory within each plot with R values of 0.88, 0.92, 0.91, 0.88 ($p < 0.015$ for all plots).

3.4. Stand scale: Juvenile distribution, size and age class relations

Hickory seedling ages follow a different pattern than their adult counterparts (Fig. 3a), with a negative exponential distribution ($p = 0.008$) as described by Monk (1981) for mockernut hickory. Our observed distribution had a median age of 7 years and a mean age of 10 years, with a standard deviation of 8.9. The distribution was positively skewed (1.81), and extremely leptokurtic with a kurtosis value of 5.97. The oldest hickory seedling we observed was 42 years of age (Fig. 4), with 20 of the 63 measured seedlings being greater than a decade in age. This distribution is similar to the seedlings height distribution (Fig. 3b), which had a mean of 0.13 m and a standard deviation of 0.092. The trend also represents a negative exponential decline, but is much more positively skewed (skewness = 7.03) than the seedling age class distribution.

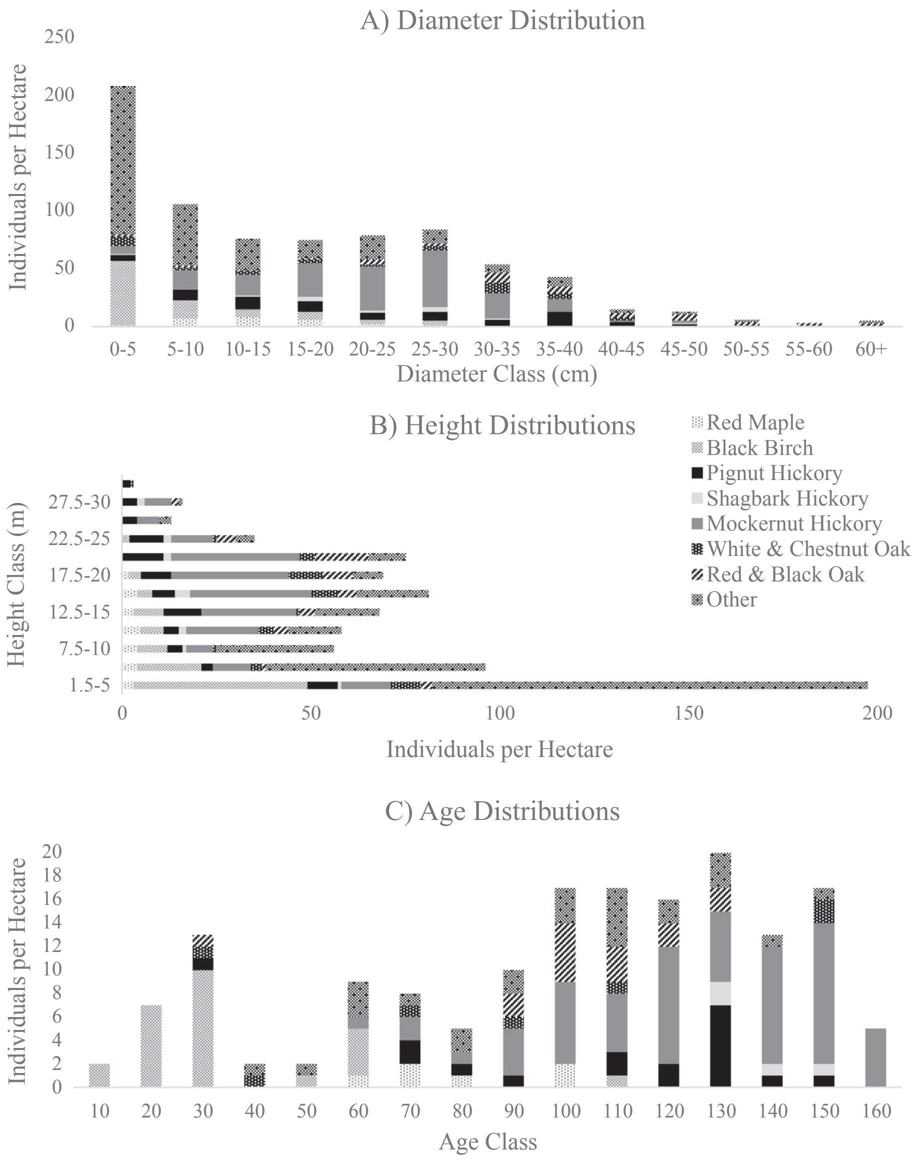

Fig. 2. (A) Diameter, (B) height, and (C) age distributions for the four, quarter-hectare, stand-level plots within the Yale-Myers Research and Demonstration Forest, CT. Hickory tend to comprise the intermediate height and diameter classes, but are far more common in the older age classes. “Other” species include hemlock, white pine, white ash, sugar maple, black cherry, hop hornbeam, and paper birch.

Table 4
Summarized statistics for hickory, oak, red maple, and black birch across four, quarter-hectare stand-level plots within the Yale-Myers Research and Demonstration Forest, CT. Significant differences ($p < 0.05$) between mean DBH, height, and age, found using Tukey post hoc tests, are noted. Some species with small numbers of individuals were omitted from the table for clarity. Letters denote differences ($a < b < c$).

		Acer rubrum	*Betula lenta*	*Carya glabra*	*Carya ovta*	*Carya tomentosa*	*Quercus alba*	*Quercus prinus*	*Quercus rubra*	*Quercus velutina*
	Number of Individuals	25	94	73	14	195	26	13	40	6
Diameter	Mean	13.13^{b,c}	6.81^{c}	23.02^{a,b,c}	22.87^{a,b,c}	22.42^{a,b,c}	26.82^{a,b}	15.42^{a,b,c}	37.28^{a}	34.10^{a,b}
	Standard Deviation	5.66	6.88	12.79	10.85	9.49	13.43	12.20	16.09	18.37
	Skewness	0.47	1.52	0.10	0.43	−0.04	−0.72	0.47	−0.24	−0.44
	Kurtosis	2.73	4.28	1.78	3.64	2.95	2.28	2.01	3.01	2.12
Height	Mean	10.83^{b}	7.14^{b}	16.92^{a,b}	17.53^{a,b}	16.22^{a,b}	15.51^{a,b}	9.36^{a,b,c}	17.69^{a,b}	17.40^{a}
	Standard Deviation	4.42	5.14	7.74	7.29	6.19	6.83	6.31	5.99	7.161
	Skewness	0.01	1.32	−0.19	−0.12	−0.32	−0.17	0.15	−1.01	−0.72
	Kurtosis	1.86	4.12	2.12	2.12	2.70	3.06	1.48	4.21	2.04
Age	Mean	78.50^{b,c}	32.92^{c}	109.89^{a,b}	136.0^{a}	124.71^{a,b}	106.67^{a,b,c}	76.25^{a,b,c}	103.07^{a,b}	103.0
	Standard Deviation	15.42	21.76	31.53	7.53	24.86	70.74	31.32	25.58	NA
	Skewness	0.29	1.78	−1.21	0.16	−0.60	−0.71	−0.22	−1.96	NA
	Kurtosis	1.55	6.15	3.52	1.52	2.55	1.50	1.56	7.07	NA

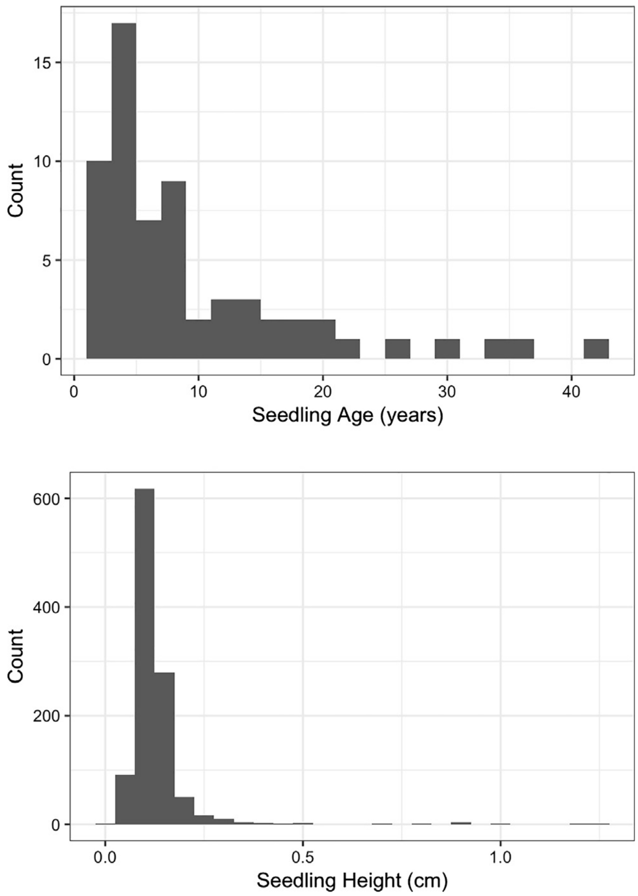

Fig. 3. (a) Age distributions from a subsample of seedlings selected randomly (n = 64) from the three ¼ hectare plots where all regeneration was measured; (b) heights of all seedling measurements in the three ¼ hectare plots where all regeneration was measured. Distributions have a similar trend to age, but are much more confined around smaller height classes as compared to age classes.

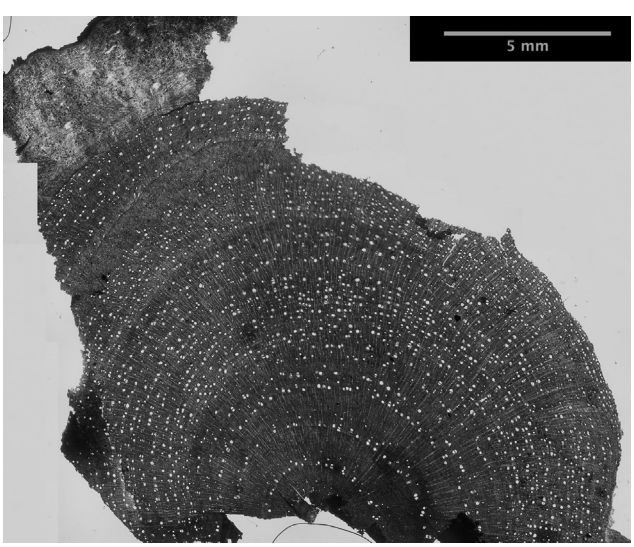

Fig. 4. A cross section taken at the root collar of the oldest observed hickory seedlings shows an age of 42 years. This indicates that hickory has the capacity to linger in the understory for decades, awaiting release.

The number of hickory seedlings per hectare ranged dramatically from 684 in both the Boston Hollow and Nagy Road plots, to 1452 at Turkey Hill, up to 13,860 at Morse Ridge. The results of the spatial analysis indicate that hickory seedlings decrease in density with proximity to canopy trees, possibly exhibiting negative density dependence. Density maps, G-cross plots, and enveloped G-cross plots for all three stands show that more hickory seedlings are found at distances further away from their adult counterparts (Supplemental Information S 2a). These seedlings also tend to cluster within the stand, as confirmed by a Clark-Evans test. This test yielded significant ($p < 0.0001$) R values of 0.89, 0.83, and 0.79 for each plot (where $R < 1$ is evidence of clustering). These R values are also lower than those for adult hickory, indicating that seedlings are more clustered than adults within the plots. There is also some evidence that within these stands, pignut and mockernut hickory seedlings "avoid" growing near one another (Supplemental Information S 2b), but this trend was not observed across all three stands. Due to the scarceness of shagbark hickory seedlings and the absence of bitternut hickory, we could not test the spatial relationships between these species.

4. Discussion

4.1. Geographic distribution of hickory at regional and landscape scales

By combining the results of our GLM (Table 2) with the USFS species distribution raster files (Fig. 1), we are able to examine the factors that might be influencing the distribution of each species of hickory at the regional scale. There are clear relationships between the abundance of hickory and the surficial and bedrock materials across the northeastern United Sates, a trend that has been observed for other tree and understory species (Holzinger et al., 2008; Pausas and Carreras, 1995). It is important to note that, when examining the results of the GLM, the significant predictors for individual species were often different from the results obtained when all of the species were pooled together, especially in regards to bedrock and surficial material. For example, the results of GLM for pignut hickory indicate that the species associates with greywacke surficial material (commonly found in the region of southern New York near Hudson River), yet this material was not a significant predictor for the entire genus. These results substantiate the observations made by Boisen and Newlin in 1910 regarding the unique site requirements for each species of hickory.

Site characteristics aside from bedrock and surficial material are also important predictors of individual hickory species at the regional scale, even though these results were not significant at the genus-level. Bitternut hickory, usually thought to compete well on mesic and hydric sites (Burns and Honkala, 1990; Gupton, 1977), had a positive coefficient for areas classified as floodplains and bottomlands. Pignut hickory had negative coefficients for most of the colder plant-hardiness zones that were included in the analysis, and had a strong preference for south-facing aspects (similar to McCarthy and Wistendahl, 1988), indicating that climate and temperature is an important factor that impacts hickory species' preferred sites.

At the landscape scale, the results of our ZIP regression for the Yale-Myers Forest, CT, show that dry, acidic, and nutrient-poor sites favor the establishment of hickory. While there were not enough individual hickories of each of the four species in our study to run species-specific analyses, our findings are consistent with many of the descriptive studies that characterize the preferred sites for hickory elsewhere (Boisen and Newlin, 1910; Monk, 1981; Phillips, 1973). In forests classified as oak-hickory, hickory is much less abundant than oak, with only 13% of the number of individuals, and 6.7% of the basal area of oak. These ratios are much lower than the composition of oak-hickory forests in more southern regions of the United States. In North Carolina, Christensen (1977) documented there being between 30% and 60% of the number of individuals and 8–10% of the basal area of oak at different stages in succession, while Shotola et al. (1992) found the basal area of hickory in southwestern Illinois to be as much as 48–64% that of oak at various stages in succession. The combination of a hotter, drier more continental climate may promote hickory's greater dominance in basal area - as in the western parts of its range. The climate of northeastern United States is wetter, with a greater maritime influence of the Atlantic Ocean.

4.2. Spatial distribution of hickory at stand scales

Our results demonstrate that there are environmental factors influencing the spatial distribution of these species at smaller scales. At the stand scale, there is evidence of negative density dependence and clustering for both adult and seedling hickories. This may be related to the activity of rodents which are important predators of hickory nuts. Grey squirrels (*Sciurus carolinensis*) prefer hickory nuts over acorns due to their low tannin and high fat and protein levels (Lewis, 1982, Smallwood and Peters, 1986), and have been shown to consume 90–95% of the fallen hickory nuts in a given area (Barnett, 1977; McCarthy, 1994). Because rodents are territorial (Hungerford, and Wilder, 1941) and need to limit predation risk (Lima and Valone, 1986), they may inadvertently create areas with high and low seed predation, causing clusters of hickory seedlings to germinate. However, at the landscape scale, our ZIP regression indicated that location was not a significant predictor of abundant hickory, meaning that seed dispersal and predation were not driving the establishment of hickory trees across a forest but that soil moisture (drier) and fertility (poorer) were important defining factors in distribution.

4.3. Structural and age class composition of hickory stands

The height and diameter distribution of hickory in the four spatial plots shows individuals are present in nearly every height and diameter class (Fig. 2a and b). This pattern is contrary to other species in these stands, which are heavily skewed towards smaller size classes (e.g. early-successional black birch) or large size classes (e.g. mid-successional oak). However, although hickory has not been recruiting in any large quantities for the past 60–70 years, the hickory that comprises the current stands originated over a long, protracted recruitment period that lasted as long as half a century. This pattern is different to that observed in oak within our study sites, which established more discretely as a single even-aged cohort. Our study confirms many other studies that report that the majority of canopy oaks in second growth forests are of a single cohort (Allison et al., 2003; Larsen and Johnson, 1998; Liptzin and Ashton, 1999; Smith and Ashton, 2010). We show that, due to the extended recruitment period, a higher proportion of hickory enter an intermediate or suppressed canopy position and stay there for decades before ever reaching the canopy. Nixon et al. (1983) showed that these suppressed hickories do respond to release events, indicating that small canopy gaps above suppressed hickory may allow these trees to assume a co-dominant canopy position.

Hickory seedlings, however, exhibit constant recruitment within stands. Although there is a negative exponential decline in seedlings over time, more than half of the individuals we sampled were greater than five years old, and one third of the individuals were > 10 years old. This trend is different from observations on oak recruitment made in the same stands as this study that show a distinctly more periodic recruitment, based on the confluence of mast years and environmental conditions that favor germination (Frey et al., 2007). However, for both oak and hickory, though their patterns of recruitment are different, advance regeneration of both species show no signs of progressive growth upwards but largely stay suppressed in the forest understory. In the case of hickory, the oldest seedlings measured in our study were over forty years and less than half a meter in height. Studies in other regions have found that, when canopy gaps are created by logging or windstorms, advance hickory regeneration can be successfully released (Cowden et al., 2014; Rebertus and Meier, 2001).

5. Management implications

Compared to oak, hickory regeneration builds up over decades (constant recruitment) and has a more protracted period of release to form new second-growth stands. This can mean that securing regeneration, once present, can more dependably lead to its presence in new forests. Adult trees are found in a variety of different diameter and height classes, suggesting hickory can respond well to thinning and is more tolerant of competition and shade from taller trees.

Our study also demonstrates that hickory only represents a small proportion of the basal area in oak-hickory forests of the northeastern United States; and its distribution within the region is clumped – associated with drier more infertile soils of the uplands. This implies managing forests for hickory need to be site specific.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.03.027.

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