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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).