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Occurrence, pattern of change, and factors associated with American beech-dominance in stands of the northeastern USA forest

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ABSTRACT

American beech (*Fagus grandifolia* Ehrh) in the understory of tolerant hardwood stands is a major obstacle to improving the quality of forest regeneration in the northeastern USA and southeastern Canada. To better understand patterns of beech occurrence and stand conditions when it is present, we used US Forest Service Forest Inventory and Analysis (USFS-FIA) data from four northeastern USA states (Maine, New Hampshire, New York, and Vermont) across a 16-year period (1999–2015) to: (i) classify stand conditions (i.e., FIA plots) where American beech was present, (ii) identify beech-dominated stand types, (iii) assess the trend of occurrence (percentage of total forest area) of each identified stand type across the study area during the past 16 years, and (iv) evaluate the relationship of each identified stand type with key biotic and abiotic factors. Based on understory, midstory, and overstory characteristics, we identified four stand types where beech was present across the region including: (i) beech-dominated, (ii) commercial hardwood-dominated, (iii) other hardwood-dominated, and (iv) softwood-dominated. Among these four stand types, the beech-dominated stand type currently occupies 27.4% of total northeastern USA forest area and has had a ~5% increase over the past 16 years with an even greater increase (>5%) across the forests of New Hampshire, New York, and Vermont. Our results showed increasing mean annual precipitation and greater overstory basal area were positively correlated with the occurrence probability of the beech-dominated stand type, but negatively correlated with the occurrence probabilities of the other identified stand types. Beech-dominated stands were generally associated with higher elevations, greater mean annual precipitation, warmer temperatures, and larger overstory basal areas. Beech dominance in the understory was associated with overstories dominated by beech, as well as overstories dominated by commercial hardwood species. Therefore, overstory harvesting in stands with beech dominant in the understory (irrespective of overstory composition) will tend to promote beech into the overstory. Our results emphasize the need for greater attention to improving regeneration composition in stands where beech is dominant to increase the long-term productivity and commercial value of northeastern forests of the USA.

1. Introduction

Tolerant hardwood stands, notably those composed of American beech (*Fagus grandifolia* Ehrh), sugar maple (*Acer saccharum*. Marsh.), and yellow birch (*Betula alleghaniensis* Britton) are abundant across the forested landscape of the northeastern USA and southeastern Canada. This is particularly true in Maine (Nelson and Wagner, 2014), New Hampshire (Hane, 2003), Vermont (Hannah, 1999), and New York (Bohn and Nyland, 2003) of USA, as well as Quebec (Duchesne et al., 2005) and New Brunswick (Baral et al., 2016) of Canada. These forests also are the primary source of wood and fiber that supports a large forest products industry in the region (Seymour, 1995).

Beech was a formerly desirable tree species in these forests until beech-bark disease dramatically lowered the commercial value of its wood (Houston, 1975; Nyland et al., 2006; Kasson and Livingston, 2012). The occurrence and impact of beech-bark disease is currently expanding (Lovett et al., 2006), thus exacerbating the problem across eastern North America. Further, interspecific competition from beech suckers can exclude more commercially desirable tree species in these forests, especially sugar maple and yellow birch (Beaudet and Messier, 1998; Nolet et al., 2008).

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In recent years, several studies have reported an increasing dominance of beech relative to commercially desirable species in the understory of hardwood forests in the northeastern USA (e.g., Hannah, 1999; Hane, 2003) and southeastern Canada (e.g., Beaudet et al., 2007; Duchesne and Ouimet, 2009). The dominance of beech in the understory and midstory of tolerant hardwood forests presents a significant forest management challenge, particularly for improving the quality of forest regeneration in the region. A range of factors currently contribute to beech dominance including: (1) greater ability of beech to grow and survive in the deep shade of mature stands relative to other species (Canham, 1988); (2) absence of stand-replacing disturbances and partial harvesting as the general management practice, which creates small overstory openings and favors the extreme shade tolerant beech (Wagner et al., 2010); (3) mortality of overstory beech trees from beech-bark disease also creates small overstory openings, and favors understory beech (Houston, 2001); (4) ability of beech to reproduce vegetatively by root suckering, which are more vigorous than seed-origin stems (Beaudet and Messier, 2008); (5) logging induced root damage promotes the suckering of beech (Nyland et al., 2006); (6) herbivore preference of sugar maple and yellow birch over beech (Nyland et al., 2006; Bose et al., in review-b); (7) beech has shown to be more efficient relative to sugar maple in assimilating carbon under elevated atmospheric CO_2 (Reid and Strain, 1994) and an increased soil acidification (Duchesne and Ouimet, 2009); (8) higher temperature in the growing season (Fang and Lechowicz, 2006) and greater annual precipitation (Bose et al., in review-a) have also favored the beech. Therefore, a more comprehensive understanding of the spatial and temporal changes in beech abundance, and of the compositional and structural characteristics of forest stands that promote beech dominance in the understory are needed to develop effective management strategies for improving the quality of hardwood regeneration across the region.

The classification of forest stands where beech is present, and the characterization of forest stands where beech dominates the understory and midstory, are necessary to develop appropriate management guidelines (Nyland et al., 2006; Wagner et al., 2010). However, a broad-scale, regional analysis to classify stands where beech is present and develop specific silvicultural recommendations has not been investigated to our knowledge.

The overall goals of this study were to identify stand types where beech is dominant and to detect the most important driving factors contributing the occurrence of beech-dominated stands across the northeastern USA. Our specific objectives were to: (i) classify stand conditions where beech is present across the states of Maine, New Hampshire, New York, and Vermont to identify the most challenging stand types (i.e., beech-dominated stand type), (ii) document changes in occurrence (percentage of total forest area) of each identified stand type across the study area for the past ~15 years, and (iii) evaluate the relationship of each identified stand type with key biotic and abiotic factors.

In this context, we tested three hypotheses: (i) the presence and abundance of beech-dominated stands have increased over the past ~15 years (Wagner et al., 2010), with a greater shift in the three other northeastern states than in Maine because the frequency and severity of harvesting activities are higher and the densities of browsers (white-tailed deer (*Odocoileus virginianus*)) are lower in Maine than the three other states, respectively (QDMA, 2016), (ii) biotic factors (e.g., stand basal area) will be superior to abiotic factors (e.g., mean annual temperature) in explaining the occurrence probability of beech-dominated stands. For example, increased overstory basal area may indicate greater canopy closure, and concomitantly favor shade-tolerant beech over other species (Canham, 1988, 1989), and (iii) the occurrence probability of beech-dominated stands will increase with an improved growing condition, which will be indicated by the greater annual precipitation and higher temperature (Saltré et al., 2015; Bose et al., 2016). In addition, higher elevation, which is generally characterized as a less suitable environment for browsing animals, will also favor beech over the other species (Wason and Dovciak, in press).

2. Methods

2.1. Study area

The study area covers all forestland areas of Maine, New Hampshire, Vermont, and New York. The region is located in the northeastern USA (40°56′N–47°43′N, 66°99′W–79°75′W), which has a large topographic variation with an elevational range of 0–1920 m (Seymour, 1995). It consists of a cool yet humid continental climate with a mean annual precipitation of 806–2145 mm and a mean annual temperature of −0.2 to 12.5 °C (averages of 1980–2014). However, both temperature and precipitation have a large spatial variation across the region due to proximity to the coast and changes in topography (Thornton et al., 2014). The growing season is from April to September, but duration of the growing season varies across the region due to a strong elevational gradient (Seymour, 1995). Soils are generally classified as podzols, and soil fertility varies by altitude (Seymour, 1995).

The forest composition in northeastern USA is predominantly mixed with softwood and deciduous species (Seymour, 1995). The combination of a long fire-return interval and the use of partial harvesting as a dominant silvicultural approach have maintained the mixed species composition and promoted dominance of shade-tolerant species in the forested landscape (Seymour, 1995). Trembling aspen (*Populus tremuloides* Michx.), yellow birch, paper birch (*Betula papyrifera* Marsh), and eastern white pine (*Pinus strobus* L.) are the most frequent early successional species. Balsam fir (*Abies balsamea* L.) is the dominant tree species among shade-tolerant softwoods in association with red spruce (*Picea rubens* Sarg.), white spruce (*P. glauca* (Moench) Voss), black spruce (*P. mariana* Mill.), eastern hemlock (*Tsuga canadensis* L.), and eastern white cedar (*Thuja occidentalis* L.). American beech, sugar maple, and red maple (*Acer rubrum* L.) are the dominant shade-tolerant hardwoods (Seymour, 1995; Olson and Wagner, 2011). A total of 57 distinct forest types are generally present in the region with American beech occurring in 44 of them (http://www.fia.fs.fed.us).

2.2. Data

The Forest Inventory and Analysis (*FIA*) database of *USDA* Forest Service (http://www.fia.fs.fed.us) was used for this analysis. *FIA* is a nationwide forest inventory program and uses a consistent sampling protocol across the country. Using satellite imagery, *FIA* defines forestland as areas with at least 10% forest cover with tree species, ≥0.4 ha in size, and ≥36.6 m wide. *FIA* sampling protocol consists of four points arranged in a cluster, where point 1 is the center, with points 2–4 located 36.58 m from point 1 at azimuths of 0, 120, and 240°, respectively. Each point in the cluster is surrounded by a 7.3 m fixed radius subplot, where all trees (≥12.7 cm at diameter at breast height (dbh)) are measured for dbh and species. Each subplot contains one 2.07 m fixed radius microplot where all live saplings (2.5–12.69 cm at dbh) and seedlings (<2.5 cm at dbh) are measured for dbh and species. Softwood and hardwood seedlings must be at least 15.2 and 30.4 cm in height, respectively (Bechtold and Patterson, 2005).

FIA plots from 1999 to 2015 for Maine, New Hampshire, New York, and Vermont were used for this study. Seedling measurements were not conducted between 1983 and 1998, and thus excluded from the final data set. Values of subplots were averaged