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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.

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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

to reduce the variability associated with small-sized subplots within a plot. We considered all *FIA* plots that had at least one individual of American beech irrespective of their size and status (live/dead). It was important to include plots that had only dead beech as we intend to evaluate the effect of time, and hypothesized for an increased beech abundance following the overstory beech mortality. Based on this selection criteria, 49.7% of the total number of *FIA* plots (i.e., 4438 out of 8931) were used in the analysis (Table 1). We characterized the "understory" by seedlings (<2.5 cm at dbh), "midstory" by saplings (2.5–12.7 cm at DBH) and "overstory" by trees (>12.7 cm at dbh). This terminology is maintained throughout the text. For each plot, seedling density, sapling density, live and dead overstory basal area were characterized by four species including American beech, commercial hardwoods, other hardwoods, and softwoods. The commercial hardwood species included northern red oak (*Quercus rubra* L.), paper birch, yellow birch, sugar maple, black ash (*Fraxinus nigra* Marsh.), and white ash (*F. americana* L.). Other hardwood species included all hardwood tree species, except commercial hardwoods and American beech. The softwood species included all softwood species with balsam fir and red spruce being the most dominant.

2.3. Analytical approach

2.3.1. Classification of forest stands where beech was present

Plots were classified/grouped using hierarchical cluster analysis (Kaufman and Rousseeuw, 1990). A total of 16 characteristics that included seedling density, sapling density, live overstory basal area, and dead overstory basal area of four species types (American beech, commercial hardwoods, other hardwoods and softwood) were used to group plots/stands to identify beech-dominated stand type from all plots where beech was present. Classification tree analysis (De'ath and Fabricius, 2000), a commonly used classification method in forestry (e.g., Roynolds and Holsten, 1996; Negrón and Popp, 2004; Clark et al., 2012), was used to indicate which assigned characteristics were responsible for differences among the stand types identified by the hierarchical cluster analysis. Classification tree analysis displays a decision tree illustrating a logical pathway of predicted outcomes (e.g., probability of beech-dominated stand type relative to other stand types) (Negrón and Popp, 2004).

2.3.2. Evaluating the trend of occupation by each stand type across time and states

The occupation percentage (% of total forest area) for each stand type was quantified by the number of plots occupied by a stand type divided by the total number of plots and multiplied by 100. For hypothesis one, the occupation percentage was modeled as a function of state (four levels), year (1999–2015), stand type (four levels), and three-way interactions among the predictors.

2.3.3. Assessing the effects of biotic and abiotic factors

To better understand patterns of stand types across the region, the occurrence probability (presence/absence) of each stand type was assessed as a function of biotic and abiotic factors. Total overstory basal area and conspecific basal area of each stand type were considered as biotic factors, while elevation, mean annual temperature, and total mean annual precipitation were considered as abiotic factors. Stand tree density and dead tree basal area were highly correlated with stand basal area, and therefore not included. Temperature and precipitation data for the period of 1980–2015 were extracted from ~1 km gridded rasters of Daymet Earth Data (https://daymet.ornl.gov/) using available coordinates of sample plots. Although *FIA* plot locations are not reported exactly based on policy and the true plot locations can vary up to 1 km, it was assumed to have limited influence on this analysis as actual elevation was provided by *FIA*.

For hypotheses two and three, we first developed three candidate models based on (1) biotic variables, (2) abiotic variables, and (3) biotic and abiotic variables (Table 3). For the biotic model, we considered additive effects of live stand basal area, conspecific basal area (% of total) of each stand type, stand type (four levels), and two-way interactions among those variables (Table 3). For the abiotic model, we considered the additive effects of elevation, mean annual temperature, mean annual precipitation, stand type (four levels), and various two-way interactions. For the third model (biotic and abiotic), we considered all explanatory variables from the biotic and abiotic models (Table 3).

2.4. Statistical analysis

The statistical programming language R was used to conduct all statistical analysis (R Development Core Team, 2014). The hierarchical clustering was executed using "dist" function and "euclidian" method of R, while the classification tree analysis was performed using the "ctree" function of partykit package of R (Hothorn and Zeileis, 2015).

Effects of explanatory variables on the occurrence probability was assessed by generalized linear mixed-effect models with binomial family using the function glmer in the lme4 package in R (Bates et al., 2015). Plots nested within counties, counties nested within units, units nested within states, and states nested within measurement years were all treated as random factors. Preliminary analysis indicated that an additional error structure to account for plot spatial and temporal autocorrelation did not improve model performance (i.e., the model parsimony by the Akaike Information Criteria) and was not incorporated into the final model. We also assessed potential multicollinearity among explanatory variables in a model using variance inflation factor (*VIF*) with "vif.mer" function of car package in R (Fox and Weisberg, 2011). Elevation, mean annual temperature, and mean annual precipitation were not

Table 1
Attributes of sample plots with history of measurements, and the percentage of plots occupied by American beech in the four states of the northeastern USA.

State	Measurement periods (year)	Total number of sample plots[#]	Remeasurement	Total number of beech plots	Beech plots[a] (% of total)
Maine	1999–2015	3257	Plots were established from 1999 and remeasured in every five years until 2015	1314	40.3
New Hampshire	2002–2015	1098	Plots were established from 2002 and remeasured in every five years until 2015	652	59.4
New York	2002–2015	3604	Plots were established from 2002 and remeasured in every five years until 2015	1801	50.0
Vermont	2003–2015	972	Plots were established from 2003 and remeasured in every five years until 2015	671	69.0
Overall	1999–2015	8931		4438	49.7

[a] Defined as the presence of one or more (live/dead) stems of American beech irrespective of the size. [#]Each sample plot represents the average of four subplots within the sample plot. Total number of sample plots represent the total number of unique plots while incorporating the information of repeated measurements.

Table 2
Descriptive statistics (mean ± SD) of biotic and abiotic characteristics for the four stand types identified in this analysis.

	Stand type-1: Beech dominated		Stand type-2: Commercial hardwood dominated		Stand type-3: Other hardwood dominated		Stand type-4: Softwood dominated	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Biotic characteristics								
Seedling density (stems ha^{-1})								
American beech	2199 ± 2951	0–34,732	1054 ± 1733	0–21,545	1841 ± 2112	0–20,802	1014 ± 1448	0–14,116
Commercial hardwoods	579 ± 1316	0–41,233	5669 ± 7064	0–65,936	3125 ± 2324	0–13,559	1446 ± 2070	0–33,804
Other hardwoods	905 ± 1570	0–34,732	3315 ± 3157	0–28,417	8360 ± 4803	0–41,233	2455 ± 2293	0–15,230
Softwood	675 ± 941	0–10,773	1099 ± 2472	0–23,588	1622 ± 2310	0–20,617	7991 ± 6465	371–72,437
Sapling density (stems ha^{-1})								
American beech	490 ± 622	0–5572	216 ± 349	0–2600	306 ± 455	0–3343	248 ± 430	0–3529
Commercial hardwoods	212 ± 387	0–5944	442 ± 630	0–6129	296 ± 455	0–3529	247 ± 459	0–4458
Other hardwoods	340 ± 523	0–5572	604 ± 806	0–7058	822 ± 1028	0–6315	633 ± 909	0–6872
Softwood	248 ± 470	0–3900	166 ± 386	0–5386	239 ± 482	0–4458	1140 ± 1478	0–13,373
Live overstory basal area (m^2 ha^{-1})								
American beech	3.3 ± 3.9	0.0–37.2	1.3 ± 2.3	0.0–19.8	1.8 ± 2.8	0–17.6	1.3 ± 2.2	0.0–21.7
Commercial hardwoods	8.6 ± 7.2	0.0–80.5	8.0 ± 7.2	0.0–41.9	6.5 ± 6.4	0–32.6	3.9 ± 4.4	0.0–36.9
Other hardwoods	6.2 ± 6.3	0.0–35.8	5.7 ± 6.6	0.0–49.4	4.7 ± 5.7	0–36.8	4.9 ± 4.8	0.0–39.6
Softwood	6.7 ± 8.7	0.0–57.6	5.2 ± 7.7	0.0–50.5	3.9 ± 6.8	0–52.0	10.8 ± 8.9	0.0–51.6
Dead overstory basal area (m^2 ha^{-1})								
American beech	0.7 ± 1.4	0.0–11.7	0.3 ± 1.1	0.0–16.6	0.5 ± 1.3	0–9.0	0.3 ± 0.8	0.0–10.0
Commercial hardwoods	0.8 ± 1.6	0.0–21.9	0.7 ± 1.4	0.0–15.4	0.6 ± 1.4	0–11.3	0.4 ± 1.0	0.0–10.2
Other hardwoods	0.6 ± 1.3	0.0–16.0	0.6 ± 1.3	0.0–15.7	0.7 ± 1.2	0–10.2	0.5 ± 1.0	0.0–11.5
Softwood	0.6 ± 1.5	0.0–25.7	0.6 ± 1.5	0.0–19.3	0.5 ± 1.3	0–15.6	1.5 ± 2.2	0.0–18.3
Abiotic Characteristics								
Elevation (m)	1339 ± 645	0–3799	1267 ± 575	0–3675	1317 ± 582	0–4250	989 ± 592	0–2882
Mean annual temperature (°C)	6.2 ± 1.3	2.0–11.9	5.8 ± 1.6	2.4–11.3	5.3 ± 1.6	1.5–11.3	5.5 ± 1.3	1.6–8.9
Mean annual precipitation (mm)	1292 ± 148	899–1936	1247 ± 131	899–1991	1241 ± 128	916–1893	1248 ± 111	1936–1014

Table 3
Summary of the models included in the analysis. Fit statistics were coefficient of determination (R^2), root mean square error expressed as a percentage (%RMSE). Three candidate models for the response variable *Occurrence probability* were compared by AIC (Akaike's information criterion) and ΔAIC (AIC relative to the most parsimonious model).

Models	AIC	ΔAIC	R^2	%RMSE
Occurrence probability				
Biotic model: Y–BA * ST + BA^2 + CONBA * ST	40842.8	1712.3	0.20	6.6
Abiotic model: Y–ELEV * ST + MAT * ST + MAT^2 + MAP * ST	41460.4	2329.9	0.19	6.4
Combined model: Y–ELEV * ST + MAT * ST + MAT^2 + MAP * ST + BA * ST + BA^2 + CONBA * ST	39130.5	0.0	0.26	6.7
Occupation percentage				
Y–States * Time * ST	–	–	0.94	3.89

Note: ST = stand type (four levels), BA = total stand overstory basal area, CONBA = conspecific basal area (e.g., for stand type-1 (beech dominated), % overstory basal area occupied by beech), ELEV = elevation, MAT = mean annual temperature for the period of 1980–2015, MAT^2 = squared MAT, MAP = mean annual precipitation, States = four states (Maine, New Hampshire, New York and Vermont), and Time = 1999–2015, and * sign indicates interaction between variables.

mutually correlated. The adjusted R^2 of the mixed-effect model was calculated using the function of "r.squaredLR" of muMIn package in R (Bartoń, 2013). The occupation percentage was modeled using the "lm" function of R. We visually verified the assumptions of normality and variance homogeneity of the residuals. Since a large number of sample plots were used in this analysis, 95% confidence intervals with predicted means were reported in all figures.

3. Results

3.1. Structural classification of American beech stands

In stands where beech was present, we identified four stand types based on the hierarchical cluster analysis (Fig. 1 and Table 2). Stand structural and compositional characteristics of the four stand types were:

Stand type-1 (*Beech dominated*): understory and midstory layers were dominated by the beech, but not the overstory layers (live and dead), which were relatively mixed, and dominated by the commercial hardwood species. This stand type had the highest overstory live basal area, but the lowest seedling and sapling density relative to other stand types (Fig. 1 and Table 2).

Stand type-2 (*Commercial hardwood species dominated*): understory and overstory layers were dominated by commercial hardwood species, with relatively mixed midstory and dead overstory layers, where the midstory was dominated by the other hardwood species (Fig. 1 and Table 2).

Stand type-3 (*Other hardwood species dominated*): understory and midstory layers were dominated by the other hardwood species, while the overstory was dominated by the commercial hardwood species. Presence of beech was similar to the commercial hardwood species at the midstory layer of this stand type (Fig. 1 and Table 2).

Stand type-4 (*Softwood dominated*): softwood species dominated all vegetation layers of this stand type. Beech had the lowest seedling and sapling density, as well as the lowest live and dead tree basal area than any other stand types (Fig. 1 and Table 2).

Classification tree analysis showed that overstory basal area (live/dead) was a weak predictor variable in discriminating among stand types (Fig. 2). Sapling density of beech and commercial hardwoods, and seedling density of beech, commercial hardwoods,

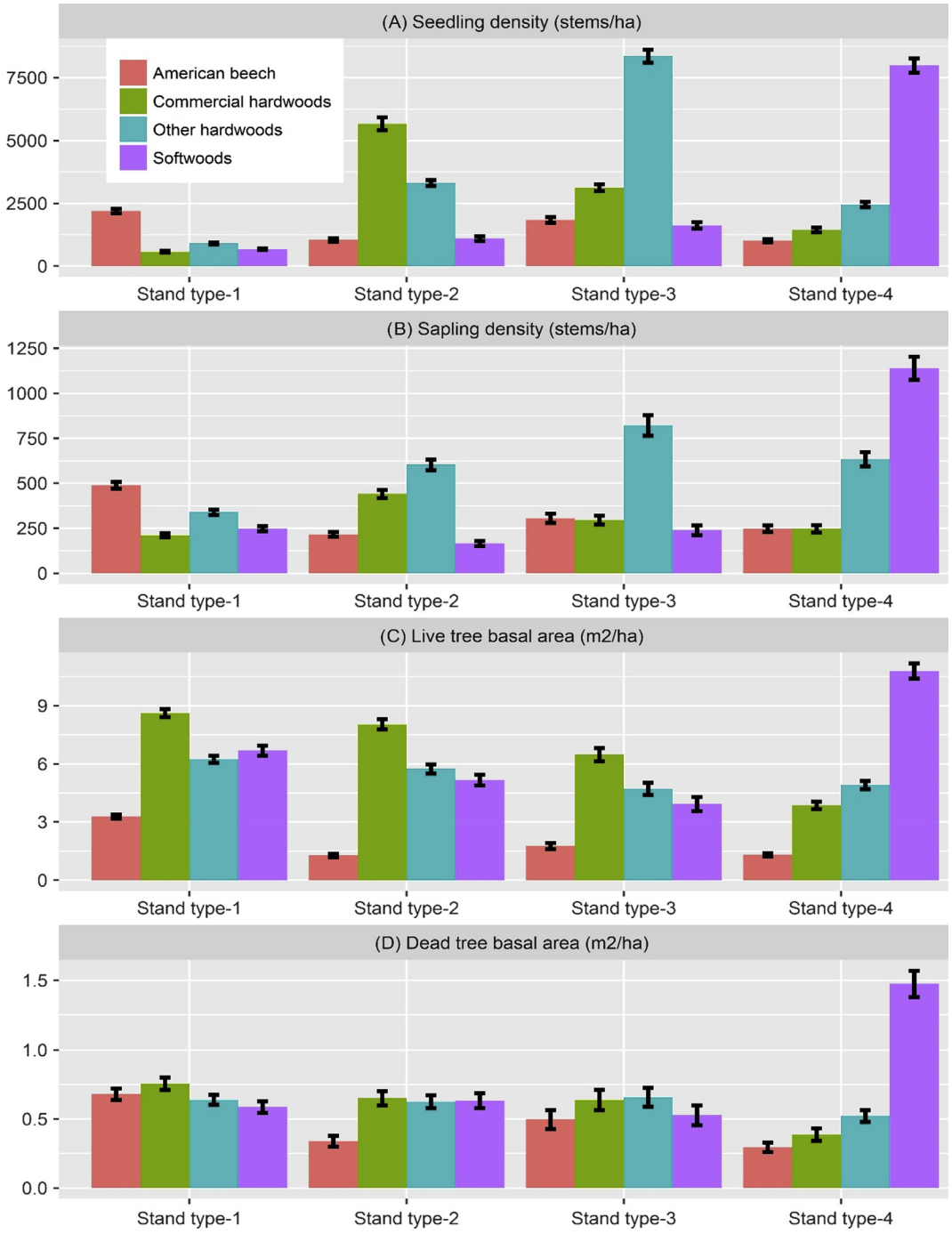


Fig. 1. Structural characteristics of four stand types. Stand type-1: beech dominated, stand type-2: commercial hardwood dominated, stand type-3: other hardwood dominated, and stand type-4: softwood dominated. Error bar represents mean ± 95% CI.

other hardwoods, and softwoods were the most important predictor variables (Fig. 2). For example, classification tree analysis indicated that the probability of stand type-1 (beech-dominated) was 0.60 when the sapling density of beech was >557 stems ha^{-1} (Node 17 of Fig. 2). The probability of stand type-1 (beech-dominated) increased to 0.80 if the sapling density of beech was ≤186 stems ha^{-1}, sapling density of commercial hardwoods was ≤186 stems ha^{-1}, seedling density of softwoods was ≤2972 stems, seedling density of other hardwoods was ≤5015 stems ha^{-1} and seedling density of beech was >1486 stems ha^{-1} (Nodes 1, 2, 3, 4, 5, 6, and 10 of Fig. 2). The overall accuracy of the prediction with 95% CI was 63.7 ± 9% (Table 4).

3.2. Temporal changes in occupation (% of total forest area) for four stand types

The model that evaluated the occupation percentage of the four stand types as a function of the states and time had a $R^2 = 0.91$ (Table 3). Time had a significant positive effect on the occupation percentage of beech-dominated stand type in northeastern USA over the past 16 years (Fig. 3 and Table 5). Overall, the forest area dominated by beech had increased from 22.9 to 27.4% of the total forest area over the past 16 years in northeastern USA (Table 6). Among the four states, Vermont had the highest (11%) and Maine had the lowest (1%) increases in beech-dominated forest areas

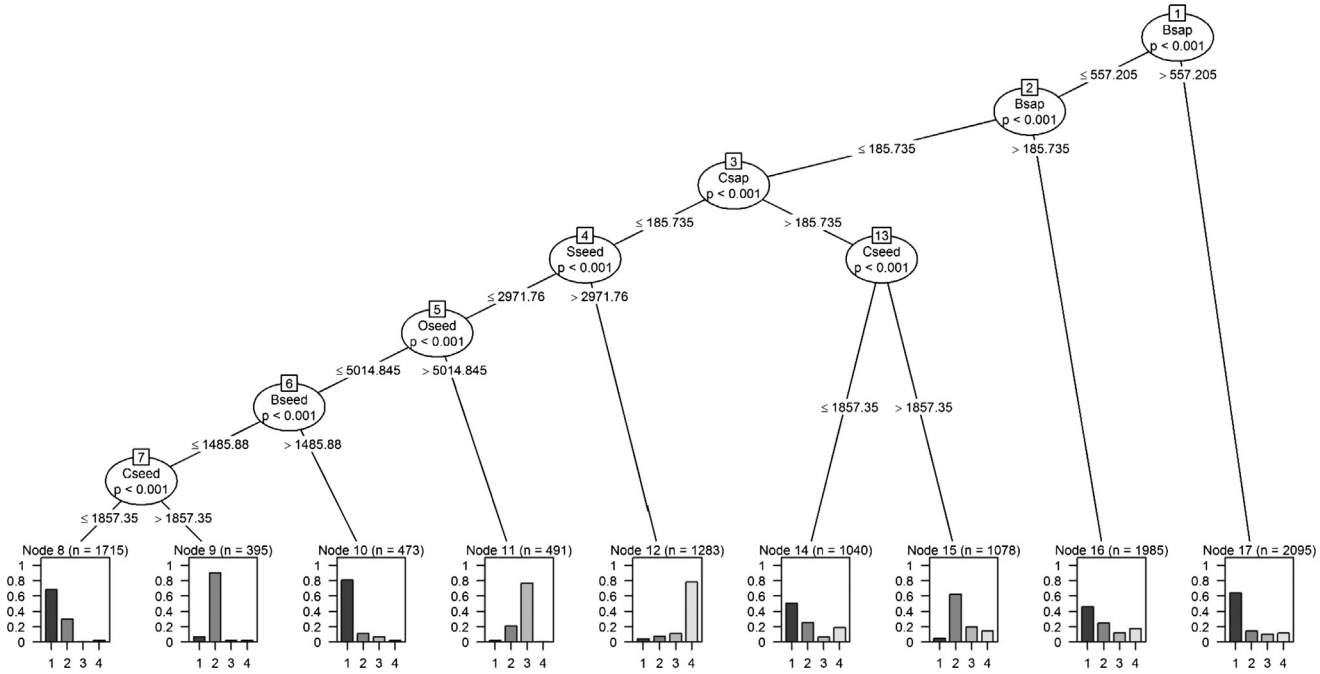


Fig. 2. Pruned decision trees of classification tree analysis. Each split is labeled with its splitting value. Terminal nodes (bar plots) show predicted stand type distribution resulting from classification tree analysis. Variables appearing near the top of the tree are more important than variables invoked lower in the tree. Bsap and Csap represent sapling density of American beech and commercial hardwoods respectively, while Bseed, Cseed, Oseed and Sseed represent seedling density of American beech, commercial hardwoods, other hardwoods and softwoods, respectively. Numbers (1–4) in bar plots represent four stand types described in Fig 1: stand type-1: beech-dominated, stand type-2: commercial hardwood-dominated, stand type-3: other hardwood-dominated, and stand type-4: softwood-dominated, and y-axis of bar plots represent the probabilities of occurrence (%) of four different stand types.

Table 4
Confusion matrix of classification tree analysis with values expressed as a %. The overall accuracy of the prediction with 95% CI was 63.7 ± 9%. Highlighted numbers showed the true positive values (i.e., frequencies of matches between observed and prediction), and other numbers represent the associated errors.

Predicted	Observed			
	Stand type-1: Beech dominated	Stand type-2: Commercial hardwood dominated	Stand type-3: Other hardwood dominated	Stand type-4: Softwood dominated
Stand type-1: Beech dominated	**59.2**	22.0	7.5	11.3
Stand type-2: Commercial hardwood dominated	5.0	**69.7**	14.7	10.6
Stand type-3: Other hardwood dominated	2.0	21.0	**76.6**	0.4
Stand type-4: Softwood dominated	4.0	7.3	10.7	**78.0**

(Fig. 3 and Table 6). Our results showed that when beech was present, only 21% of the forest area was dominated by commercially desirable species (hardwoods and softwoods), and that remained unchanged over the past 16 years (Table 6). In forest areas where beech was present, other hardwoods, which was the aggregation of less commercially desirable hardwood species (excluding beech), currently occupied 4% of the total forest area (Table 6). The softwood-dominated stand type with beech present was more abundant in Maine and New Hampshire than in New York and Vermont (Fig. 3 and Table 6).

The area occupied by beech-dominated stand type increased over the last 16 years in all states, except Maine (Fig. 3A). Commercial hardwood-dominated areas had only increased in Maine, but decreased in three other states (Fig. 3B), while areas dominated by other hardwoods had decreased in all four states, and the areas dominated by softwood dominated stand type had remain unchanged over the last 16 years (Fig. 3C and D).

3.3. Associated abiotic factors of six structural groups

Of the three candidate models of occurrence probability (presence/absence), the model with both biotic and abiotic variables performed best (Table 3) and all parameters were statistically significant (Table 5). Based on this model, increasing elevation had a positive effect on the occurrence probability of the beech-dominated stand type, but a negative effect on the occurrence probability of the softwood-dominated stand type. Commercial hardwood-dominated stand type and other hardwood-dominated stand type had a little influence by the changes of elevation (Fig. 4A). Temperature had a positive effect on the occurrence probability of beech-dominated stand type, but a negative effect on the occurrence probability of softwood-dominated and other hardwood-dominated stand types (Fig. 4B). Unlike increasing elevation and warmer mean annual temperatures, mean annual precipitation had a positive association with the higher occurrence probability of softwood-dominated stand type. However, mean annual precipitation also had a positive association with an increasing occurrence probability of beech-dominated stand type, but negative associations with the occurrence probabilities of commercial hardwood-dominated and other hardwood dominated stand types (Fig. 4C).

Among biotic variables, an increasing conspecific basal area (i.e., stand type-specific overstory basal area) had a positive effect on the occurrence probability of all stand types, but the magnitude

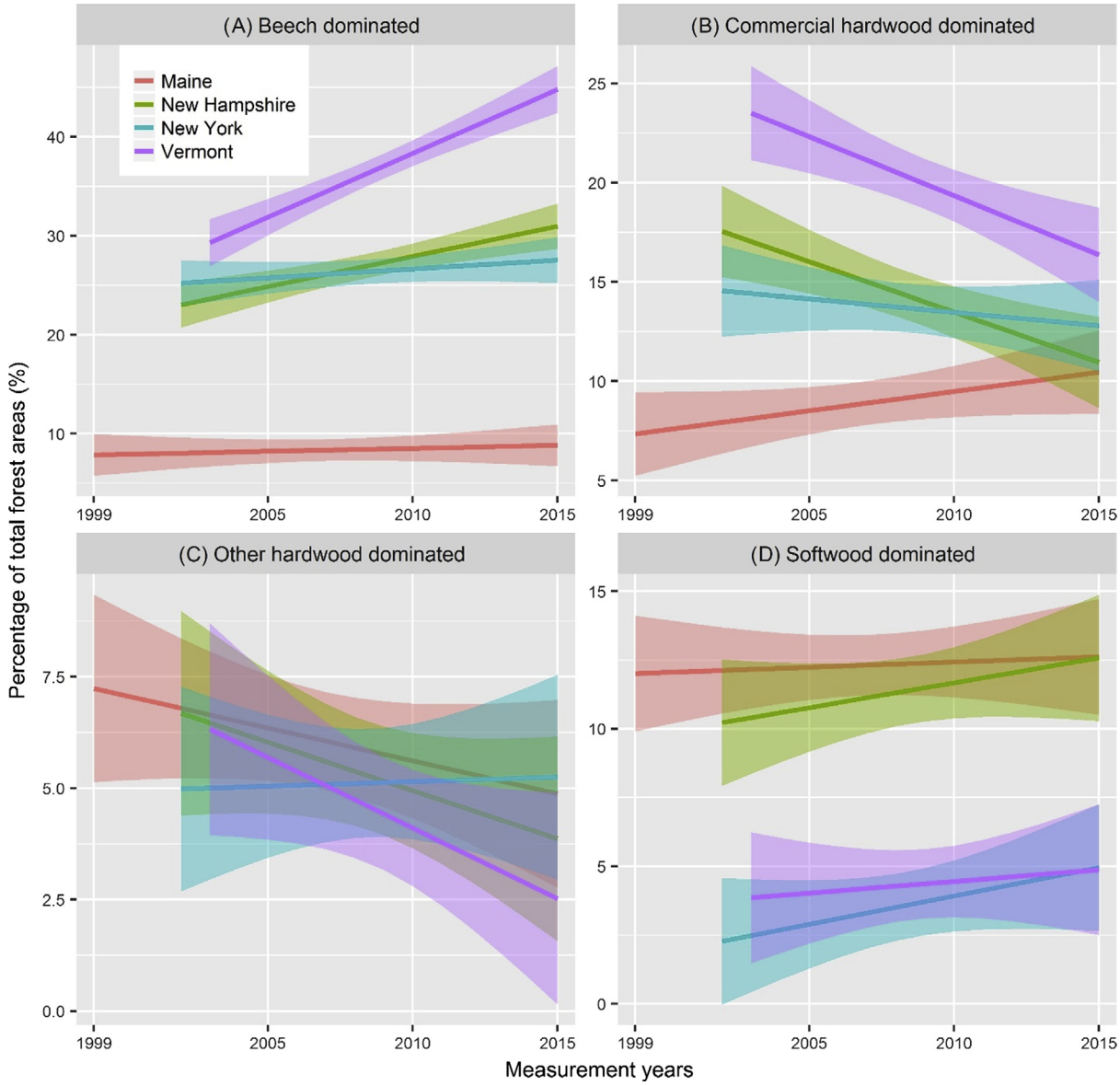


Fig. 3. Predicted changes in occupation (% of total forest area in the region) with 95% confidence intervals for the four stand types over the past 16 years for four northeastern states of USA.

of the effect (i.e., steepness of slope) was greater for beech-dominated stand type than for other stand types (Fig. 4D). An increasing overstory basal area had a positive effect on the occurrence probability of beech-dominated stand type, but a negative effect on the occurrence probabilities of other stand types (Fig. 4E).

4. Discussion

The principle aim of this study was to identify beech-dominated stand types and their associated driving factors (biotic and abiotic) across the forests of the northeastern USA. We were especially interested in identifying whether there were specific stand types where beech was present, their abundance, and whether there were any emerging trends on the landscape over the last two decades.

Overall, we identified four distinct stand types where beech was present (Fig. 1) across nearly half of the northeastern USA forest area. Our results showed 27.4% of total forest understories and midstories of Maine, New Hampshire, New York, and Vermont were currently (2011–2015) dominated by American beech, which represented a ~5% increase over the past 16 years. We also found that the composition of the overstory across our four identified stand types was relatively similar (i.e., mixed and dominated by the commercially desirable hardwood and softwood species) (Fig. 1). Therefore, the dominance of beech in the understory and midstory of forest stands was not dependent on their presence in the overstory (Fig. 1).

Both biotic and abiotic factors were highly influential in discriminating among stand types, with mean annual precipitation and overstory live basal area being the most important abiotic and biotic variables, respectively. Our results indicated that when beech was present, beech-dominated stands were generally associated with higher elevations, greater mean annual precipitation, warmer temperatures, and larger overstory basal area (Fig. 4).

4.1. Temporal changes in abundance of six stand groups

Our results showed that occurrence of the beech-dominated stand type has increased in all states (except Maine) over the past

Table 5
Summary of fixed effects (estimates) with standard error (SE) and p-values of the occurrence probability and occupation percentage models. The top ranked model was used for the occurrence probability.

Occurrence probability				*Occupation percentage*			
	Estimate	SE	Pr > t		Estimate	SE	Pr > t
ST1 *vs* ST2	−0.51	1.52	0.735	ST1 *vs* ST2	9.00	0.36	<0.000
ST1 *vs* ST3	−0.62	1.52	0.683	ST1 *vs* ST3	10.07	0.46	<0.000
ST1 *vs* ST4	4.15	1.52	0.007	ST1 *vs* ST4	7.75	0.42	<0.000
Time	0.06	0.11	0.598	MAT	0.55	0.06	<0.000
Maine *vs* New Hampshire	13.33	1.91	<0.000	MAT^2	−0.006	0.004	0.181
Maine *vs* New York	16.80	1.91	<0.000	MAP	0.002	0.0001	<0.000
Maine *vs* Vermont	16.25	2.12	<0.000	ELEV	0.0005	0.00004	<0.000
Time: ST1 *vs* ST2	0.13	0.16	0.409	CONBA	0.04	0.001	<0.000
Time: ST1 *vs* ST3	−0.21	0.16	0.199	BA	0.07	0.005	<0.000
Time: ST1 *vs* ST4	−0.02	0.16	0.890	BA^2	−0.0004	−0.00009	<0.000
Time: ME *vs* NH	0.55	0.19	0.004	MAT: ST1 *vs* ST2	−0.42	0.03	<0.000
Time: ME *vs* NY	0.11	0.19	0.535	MAT: ST1 *vs* ST3	−0.74	0.03	<0.000
Time: ME *vs* VT	1.23	0.20	<0.000	MAT: ST1 *vs* ST4	−0.98	0.03	<0.000
ST1 of ME *vs* ST2 of NH	−1.61	2.70	0.553	ELEV: ST1 *vs* ST2	−0.0004	0.00006	<0.000
ST1 of ME *vs* ST2 of NY	−9.19	2.70	<0.000	ELEV: ST1 *vs* ST3	−0.0002	0.00008	0.002
ST1 of ME *vs* ST2 of VT	2.29	3.00	0.445	ELEV: ST1 *vs* ST4	−0.002	0.00008	<0.000
ST1 of ME *vs* ST3 of NH	−13.23	2.70	<0.000	MAP: ST1 *vs* ST2	−0.004	0.0002	<0.000
ST1 of ME *vs* ST3 of NY	−19.11	2.70	<0.000	MAP: ST1 *vs* ST3	−0.004	0.0003	<0.000
ST1 of ME *vs* ST3 of VT	−15.90	3.00	<0.000	MAP: ST1 *vs* ST4	−0.0005	0.0003	0.110
ST1 of ME *vs* ST4 of NH	−15.65	2.70	<0.000	CONBA: ST1 *vs* ST2	−0.02	0.002	<0.000
ST1 of ME *vs* ST4 of NY	−27.16	2.70	<0.000	CONBA: ST1 *vs* ST3	−0.03	0.002	<0.000
ST1 of ME *vs* ST4 of VT	−24.74	3.00	<0.000	CONBA: ST1 *vs* ST4	−0.006	0.002	0.002
Time: ST1 of ME *vs* ST2 of NH	−1.25	0.27	<0.000	BA: ST1 *vs* ST2	−0.07	0.003	<0.000
Time: ST1 of ME *vs* ST2 of NY	−0.44	0.27	0.099	BA: ST1 *vs* ST3	−0.09	0.005	<0.000
Time: ST1 of ME *vs* ST2 of VT	−2.02	0.29	<0.000	BA: ST1 *vs* ST4	−0.05	0.004	<0.000
Time: ST1 of ME *vs* ST3 of NH	−0.62	0.27	0.023				
Time: ST1 of ME *vs* ST3 of NY	0.05	0.27	0.856				
Time: ST1 of ME *vs* ST3 of VT	−1.40	0.29	<0.000				
Time: ST1 of ME *vs* ST4 of NH	−0.41	0.27	0.134				
Time: ST1 of ME *vs* ST4 of NY	0.05	0.27	0.856				
Time: ST11 of ME *vs* ST4 of VT	−1.18	0.29	<0.000				

Note: ST1, ST2, ST3, and ST4 represent four stand types described in Table 2, BA = total stand overstory basal area, CONBA = conspecific basal area (e.g., for stand type-1 (beech dominated), % overstory basal area occupied by beech), ELEV = elevation, MAT = mean annual temperature for the period of 1980–2015, MAT^2 = squared MAT, MAP = mean annual precipitation, ME = Maine, NH = New Hampshire, NY = New York and VT = Vermont, and Time = 1999–2015, and ':' indicates an "interaction term".

Table 6
Changes in percentage of forest area occupied by four stand types-where beech was present across each of the four northeastern states and over the past 16 years.

Areas occupied by each stand type (% of total areas)	Maine		New Hampshire		New York		Vermont		Entire region	
	1999–2003	2011–2015	2002–2006	2011–2015	2002–2006	2011–2015	2003–2007	2011–2015	1st period	2nd period
Stand type-1: Beech dominated	8.32	9.04	24.18	29.81	25.82	26.72	33.28	44.01	22.90	27.40
Stand type-2: Commercial hardwood dominated	7.30	9.92	16.81	12.05	13.76	13.63	21.84	16.07	14.92	12.92
Stand type-3: Other hardwood dominated	7.17	5.28	6.14	4.19	4.90	5.09	5.79	3.20	6.00	4.44
Stand type-4: Softwood dominated	11.99	12.20	10.01	11.80	2.68	4.62	3.70	4.78	7.10	8.35
Overall	34.78	36.44	57.14	57.85	47.16	50.06	64.61	68.06	50.92	53.11

16 years. The occurrence of other stand types have either decreased or remained stable, except for the commercial hardwood-dominated stand type in Maine (Fig. 3). This pattern indicated that beech has been expanding into additional forest areas of the northeastern USA. Areas dominated by the beech-dominated stand type were greater in New Hampshire, New York, and Vermont than in Maine, which we initially hypothesized and can likely be attributed to several factors. First, our results show a positive relationship between the occurrence probability of the beech-dominated stand type and warmer temperatures (Fig. 4B). The average temperature in Maine is lower than the three other states. Therefore, the relatively cooler climatic condition of Maine could reduce the occurrence probability of beech-dominated stand type. Second, the harvesting regime in Maine is different than the three other states (New York, New Hampshire, and Vermont). Relative to these three other states, the harvest intensity (% removal) in Maine is greater and the harvesting entries are more frequent based on *FIA* data. These conditions usually create greater and more continuous light availability for understory plants that tend to favor more shade intolerant species than beech. Third, spruce budworm outbreaks are more prominent and frequent in Maine than the three other states. The spruce budworm outbreak cyclically occurs in the spruce-fir forests of Maine in every 60 years (Fraver et al., 2007). Consequently, overstory mortality of balsam fir and spruce species in affected stands often allows the dominance of advanced understory balsam fir and spruce regeneration (MacLean, 1984). Finally, white-tailed deer (*Odocoileus virginianus*), a major browser of sugar maple and yellow birch regeneration, has

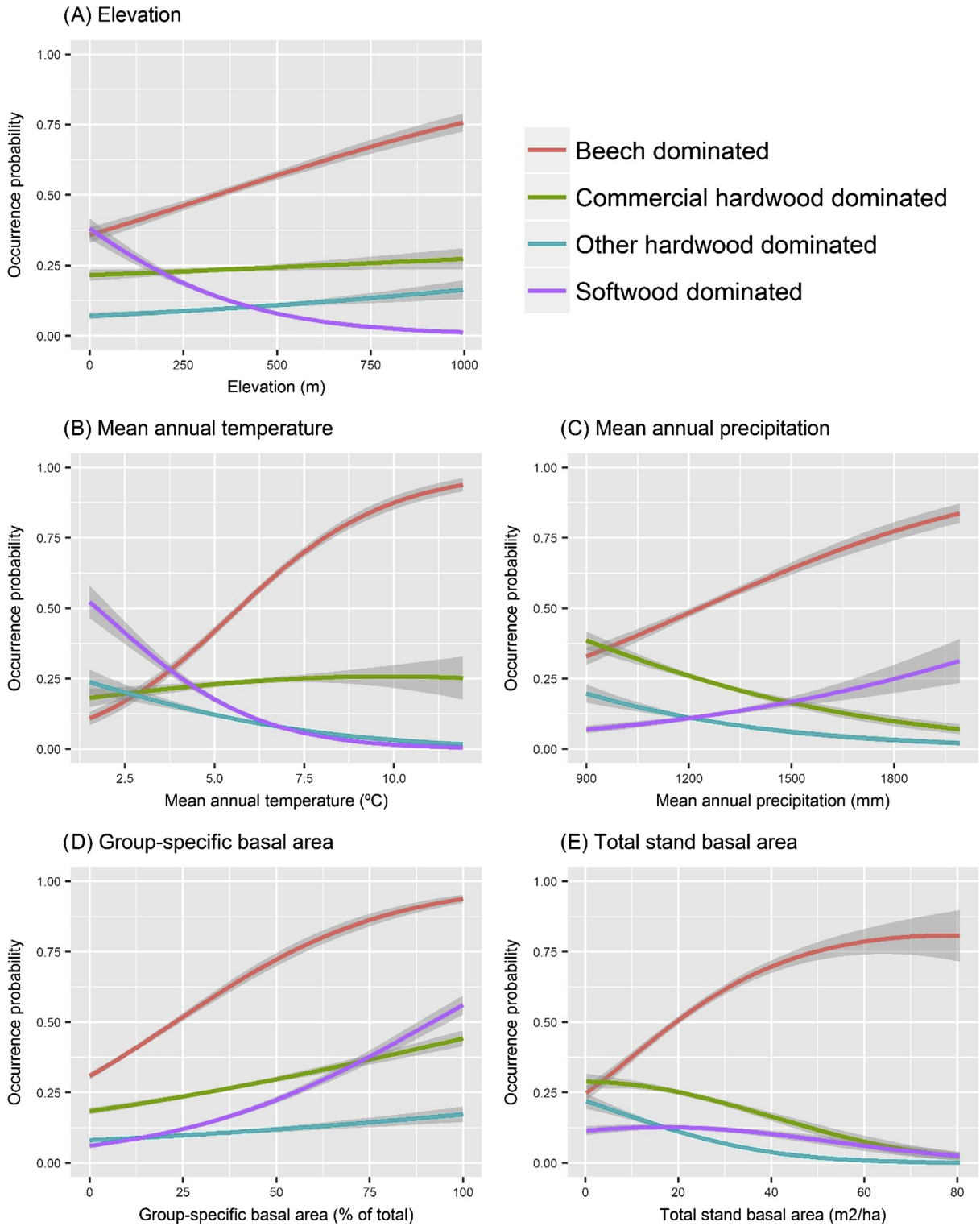


Fig. 4. Predicted occurrence probability with 95% confidence intervals of the four stand types in the four northeastern states by gradients of (A) elevation (m), (B) mean annual temperature for the period of 1980–2015 (°C), (C) total mean annual precipitation for the period of 1980–2015 (mm), (D) conspecific overstory basal area (% of total) of each stand type, and (E) total stand overstory basal area (m^2 ha^{-1}).

much lower densities in Maine than in New York and Vermont (QDMA, 2016), which could reduce the beech dominance and benefit sugar maple and yellow birch seedlings in Maine's forests. Overall, these results highlight a key shift in stand structure and composition across a relatively large area within a relatively short time.

4.2. Factors associated with the four stand types

Our results revealed that incorporating both abiotic and biotic factors into the same model improved model performance (parsimony and fit) for the occurrence probability of four different stand types where beech was present (Table 3). Where beech was

present, the occurrence of the beech-dominated stand type increased linearly with elevation, but the occurrence of softwood-dominated stand type decreased linearly with elevation. A similar result (i.e., beech expansion at higher elevation) has also been reported by Wason and Dovciak (in press) while studying tree species distributions along an elevational gradient on 12 mountains in our study region. They documented beech expansion at higher elevations by the reduction of red spruce. In addition, Seymour (1992) reported three factors including soil drainage, nutrient status, and topographic position to discriminate the occurrence of softwood and hardwood dominated stands in the forests of Maine. The study demonstrated that softwood-dominated stands generally occur on swamps, on shallow glacial tills with impeded drainage, as well as organic or poorly drained mineral soils at low elevations (Seymour, 1992), which is consistent with softwood dominance at lower elevations identified in our study.

Our results also showed a negative relationship between the occurrence of softwood-dominated stand type and temperature, while a positive relationship between the occurrence probability of beech-dominated stand type and temperature was detected (Fig. 4B). Hayhoe et al. (2007) demonstrated climate warming and increased precipitation in the northeast over the past several decades. Warmer climate and higher precipitation generally improve growing conditions, and this improvement may favor beech regeneration when in competition with other species. Our results indicated that precipitation had the strongest positive association with the occurrence of beech-dominated stand type, but was negatively correlated with the occurrence of commercial hardwood-dominated and other hardwood-dominated stand types (Fig. 4C).

Among biotic factors, increasing stand basal area was positively correlated with the occurrence probability of beech-dominated stand type, but was negatively related to the occurrence probabilities of the three other stand types. Higher overstory basal area indicates a denser stand structural condition (McElhinny et al., 2005), which is usually associated with a lower light availability, and is likely benefiting the shade-tolerant American beech over other species (Canham, 1988; Beaudet et al., 1999). An increasing conspecific overstory basal area was strongly correlated with the occurrence probability of beech-dominated stand type relative to the occurrence probabilities of the three other stand types (Fig. 4D). This result may indicate that unlike beech, the other examined stand types, which are primarily dominated by sugar maple, red maple, birch, and softwoods, did not respond linearly to the increased conspecific basal area. Therefore, overstory presence had a greater positive association with seedling/sapling densities of beech than the other species examined. This result may be due: (1) relative to beech, sugar maple, red maple, and birch are more shade intolerant species, hence regeneration growth and survival are more related to understory light availability than the availability of parent trees (Kobe et al., 1995), and (2) browsers (white-tailed deer (*Odocoileus virginianus* Zimmerman) and moose (*Alces alces* L.)) preference for sugar maple, red maple, and birch over beech is independent of their parent tree availability.

5. Management implications

We identified four distinct stand types where beech was present in the northeastern USA (Maine, New Hampshire, New York, and Vermont) using key structural and compositional characteristics. Our findings showed that beech dominance in the understory was associated not only with overstories dominated by beech, but also in stands where the overstory was dominated by other hardwood species. Therefore, overstory harvesting of stands where beech is present in the understory (irrespective of the overstory composition) will likely promote beech into the midstory and overstory over time. This result emphasizes 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.

Further, we documented that an expansion of beech in the understory and midstory of forest stands has been occurring across the region for at least the past 16 years. Increased awareness of this landscape-scale and long-term trends are needed among forest managers of the region. Preventing further expansion of diseased beech (and perhaps reversing this trend) will require a concerted effort to include appropriate silvicultural prescriptions and approaches to harvesting in forest management planning that recognize the need to avoid creating conditions that perpetuate beech in forest understories. These practices include: (1) minimizing harvesting that creates low-light environments for understory regeneration when beech is present (Nyland et al., 2006; Wagner et al., 2010), (2) using herbicides and other vegetation management strategies that can selectively reduce beech abundance while favoring the regeneration and growth of higher-value hardwood species (Nelson and Wagner, 2011), (3) logging primarily during the winter (when the soil is covered by snow) to help minimize root damage and the resulting post-harvest suckering of beech (Jones et al., 1989), and (4) reducing browsing pressure from deer and moose where possible (Nyland et al., 2006; Bose et al., in review-b). In addition, soil scarification in newly created forest gaps (Bédard and DeBlois, 2010), and soil liming in acidic and base-poor soils (Moore et al., 2012), may benefit regeneration of commercially desirable species over beech.

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