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Long-term forest carbon storage and structural development as influenced by land-use history and reforestation approach

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LONG-TERM FOREST CARBON STORAGE AND STRUCTURAL DEVELOPMENT AS INFLUENCED BY LAND-USE HISTORY AND REFORESTATION APPROACH

A Thesis Presented

by

Andrea R. Urbano

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements for the Degree of Master of Science Specializing in Natural Resources

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ABSTRACT

Temperate forests are an important carbon sink, yet there is uncertainty regarding land-use history effects on biomass accumulation and carbon storage potential in secondary forests. Understanding long-term biomass dynamics is important for managing forests as carbon sinks and for co-benefits such as watershed protection and biodiversity. However there are many unanswered questions regarding these dynamics in northeastern U.S. forests: How have secondary forests of the U.S. Northeast recovered post nineteenth century agricultural abandonment? How has the region’s extensive land-use history influenced long-term structural development and aboveground carbon storage? To answer these questions, we employed a longitudinal study based on twelve years of empirical data (2001-2013) from the Marsh-Billings-Rockefeller (MBR) National Historical Park in Woodstock, VT. MBR Park was the first parcel of land to actively be reforested in the eastern U.S., and as such, its diverse forest mosaic reflects a history of alternate reforestation approaches and varied successional trajectories indicative of secondary forest recovery occurring across the broader northeastern forest landscape. We also used 150 years of documentary data from park management records. This research evaluates the effects of reforestation approaches (planting vs. natural regeneration), management regimes (long-term low-to-intermediate harvest intensities at varied harvest frequencies), and stand development pathways on biomass outcomes. We generated biometrics representative of stand structural complexity, including the $H'$ structural diversity index, and aboveground biomass (live trees, snags, and downed coarse woody debris pools) estimates. Multivariate analyses evaluated the predictive strength of reforestation approach, management history, and site characteristics relative to aboveground carbon pools and stand structural complexity.

Classification and Regression Tree (CART) analysis ranked reforestation approach (plantation or natural regeneration) as the strongest predictor of long-term mean total aboveground carbon storage, while harvest frequency, and stand age were selected as secondary variables. CART ranked forest percent conifer (a metric closely associated with reforestation approach) as the strongest predictor of $H'$ index, while harvest intensity, and harvest frequency were selected as secondary variables. Increases in harvest intensity can significantly reduce aboveground carbon storage. Our results suggest that a variety of long-term recovery pathways converge on high levels of aboveground carbon storage, including both conifer plantations and naturally regenerated hardwood stands, but choice of silvicultural management approach can dramatically alter those trajectories. Importantly, total aboveground biomass (i.e., carbon) co-varied with $H'$ ($r^2 = 0.25$), and thus, our dataset showed a positive relationship between forest carbon storage and structural complexity, supporting the concept of multifunctional forestry emphasizing late-successional habitats.
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CHAPTER 1: LITERATURE REVIEW

1.1. Northeastern United States’ land-use history

The U.S. Northeast’s extensive land-use history offers unprecedented opportunities to explore how land management and change influences ecosystem structure, composition, and function. The northeastern United States (hereafter “the Northeast”) has a particularly interesting land-use history, essential to understanding forest recovery from anthropogenic disturbance and stress.

Beginning with the arrival of the Pilgrims in 1620, European settlers significantly changed the region’s landscape (Cronon 1983, Cogbill 2002). Extensive deforestation due to clearing for homesteads and agricultural uses peaked around 1850, with more than 60% of the entire region’s land cover cleared for agriculture (Harper 1918, Davis 1996). Forests on shallow soils, steep slopes, or low-productivity land were not cleared for agricultural purposes, but were often intensively harvested for timber (Williams 1989, Cogbill 2002). The link between land-use, forests, and the global carbon cycle is made clear by the fact that the regional forest removal at this time caused an increase in global atmospheric CO$_2$ levels (Houghton 2003, Ollinger et al. 2002). In fact, the forest clearing that took place between 1700 and 1935 resulted in a loss of 60% of the total forest carbon stocks, with directly associated carbon emissions peaking at 400-800 Tg C/year around 1900 (Houghton et al. 1999, Birdsey et al. 2006, McKinley et al. 2011). This vast forest clearing also had disastrous consequences for the land and people of the Northeast: mountains were degraded through soil erosion and many lives were taken by severe flooding events, such as the
New England flood of November, 1927 (Davis 1996). By 1891, the Bureau of Forestry, later renamed the U.S. Forest Service, was established to address the loss of forested land cover and to protect vital watersheds (Davis 1996). Nearly all of the Northeast’s forested land had been altered by human activities by the twentieth century.

In the nineteenth and twentieth centuries, industrialization and expansion into the western United States initiated social and economic change for inhabitants of the Northeast. At this time, materials for local production and consumption were increasingly imported, reducing the need for local agriculture and production (Foster & Aber 2004). The Homestead Act of 1862 provided incentive for western migration, with the availability of affordable land beginning in the Ohio Valley and moving further west over time (Shanks 2005). These nation-wide changes triggered competition with northeastern farmers, many of whom only persisted for one or two generations, thereby creating new job and lifestyle opportunities. Thus, western migration resulted in extensive agricultural abandonment and reforestation within the Northeast, yielding an increase in forest CO₂ uptake (Houghton 2003, Ollinger et al. 2002). Forest regrowth in the United States has recovered 40% of the carbon lost to the atmosphere through the deforestation and harvesting that took place prior to 1935 (Birdsey et al. 1993, 2006). Because a significant portion of former forestland is now cropland, pastureland, or developed (Smith et al. 2007), northeastern U.S. forests will not recover all of the forest carbon stocks present prior to European settlement without drastic land-use policy and forest management implications.

The timing, rate, and pattern of land abandonment and reforestation varied
throughout the region. Southern forests in the Northeast recovered first, followed by the forests in New Hampshire and soon after, Vermont (Foster & Aber 2004). Vast areas that were once, during the mid 19th century, mosaics of woodlots scattered throughout open fields and pastures, are now maturing secondary forests that support valuable ecosystem processes and wildlife (Foster & Aber 2004). Today only a small fraction (approximately 0.5%) of primary (i.e., never cleared by humans) forests in the Northeast remain as fragmented patches in old-growth stages of development (i.e., structurally complex and > 150 years of age) (Davis 1996). Prior to European settlement, primary forests dominated the U.S. Northeast landscape. The structural composition and age of primary forests varied throughout the region, and were chiefly governed by natural disturbances (Thompson et al. 2013). The importance of Native American land-use, particularly fire, on presettlement forests is the subject of vigorous debate (Whitney 1994), but likely bared some influence on the structural characteristics of the forested landscape, limiting the amount of forestland deemed “primary” at that time (Cogbill et al. 2002, Thompson et al. 2013). Late-successional species assemblages often characterize the Northeast’s presettlement forests, but a diverse mixture of forestland containing abundant early- and mid-successional species coexisted on the landscape, and was most evident at the local scale (McLachlan 2000).

The causes of the region’s secondary forest recovery are not limited to the cultural and economic influences associated with western colonization. The northeastern U.S.’ forested landscape has also been shaped by natural disturbances, complex successional dynamics, and factors associated with climatic changes. A more
comprehensive understanding of the recovery of U.S. Northeast secondary forests is best approached when considering all these factors.

1.2. Disturbance ecology

Natural disturbances play an important role in structuring the forested landscape. Disturbances range in type, size, frequency, and intensity (White & Pickett 1985, Turner et al. 1998, Lorimer & White 2003). Disturbance regimes on forested landscapes yield varying ecosystem responses (e.g., recovering species composition and changes in carbon storage dynamics) dependent on a multitude of factors, such as post-disturbance abundance and spatial arrangement of biological legacies (live residual trees, dead snags, downed coarse woody debris) (Franklin et al. 2002, Seymour et al. 2002). Understanding the role of different types, scales, and distribution of physical disturbances has become and remains a goal of ecologists, resulting in the scientific field of disturbance ecology.

Natural disturbances have varied effects on a forested landscape. Disturbance regimes in the Northeast are primarily influenced by geographic location, forest type, and local habitat conditions, with disturbance frequency generally decreasing from coastal regions to interior uplands and mountains (Lorimer & White 2003). Northern hardwood forests are most commonly naturally disturbed by wind and ice storms (Jenkins 1995, Lorimer & White 2003), but are increasingly influenced by the widespread impacts of exotic, invasive insects and fungal diseases (Fahey et al. 2005), like the hemlock woolly adelgid (*Adelges tsugae*), and *Nectria* species. Natural disturbances range in intensity from fine-scaled, low-intensity gap forming events to
large-scaled, high intensity stand-replacing disturbances. Return intervals play a key role in subsequent stand development (Seymour et al. 2002).

Evidence convincingly demonstrates that prior to European settlement, northeastern forests were dominated by relatively frequent, intermediate-scaled natural disturbances that produced a diverse mosaic of late-successional species structure and composition. Although natural fire disturbances are uncommon in the Northeast (Lorimer & White 2003), the pre-settlement forested landscape was influenced by Native American-induced fires, which were primarily prescribed along major river corridors (Cogbill 2000) and near settlements and trade routes (Russell 1983). Large scale, stand-replacing events were rare to the region (Seymour et al. 2002); however the Northeast’s widespread deforestation associated with European settlement exemplifies a large, and infrequent anthropogenic disturbance at the landscape scale. By influencing the species composition of residuals, land-use history prior to a large, infrequent disturbance affects early stages of succession (Turner et al. 1998). Because of their size, large and infrequent disturbances encompass a wider range of environmental variation than smaller disturbances and therefore create a range of abiotic conditions (Turner et al. 1998), thereby strongly influencing the mosaic of stand structural and developmental conditions found throughout the U.S. Northeast today.

Secondary forests in the Northeast continue to be characterized by relatively frequent, small-scale disturbances (Payette et al. 1990, Seymour et al. 2002) that are primarily wind driven (Ziegler 2002) and result in canopy gaps. This type of disturbance produces various gap dynamics and biological legacies (Franklin et al.
all of which affect stand development patterns and successional growth.

1.3. Ecological succession

The processes of ecological succession and stand development are inherently influenced by ecological disturbances. Although published definitions of succession vary, it is most commonly viewed as changes in species composition observed after a disturbance in an ecological community. Succession is therefore a process of community development that progresses over time. There is a historical divide between ecologists who emphasize successional patterns of development (Cowles 1889, Clements 1916, Cooper 1926, Elger 1954, Daubenmire 1966, Odum 1969) and ecologists who emphasize successional processes of development (Drury & Nisbet 1973, Connell & Slayter 1977, Oliver 1980, MacMahon 1980, Tilman 1985). Having an understanding of the biological and physical patterns and processes associated with succession aids in the prediction of forest regeneration and thus, can inform land-use management.

Henry David Thoreau’s (1860) observations of succession have been expanded upon by ecologists across the Northeast. Thoreau (1860) was one of the first to acknowledge that the removal of white or pitch pine (often on upland sites) frequently results in the reforestation of hardwoods like maple, oak, birch, chestnut, and ash, that previously grew alongside or in the understory of the pines (Foster & Aber 2004). This observation called attention to the important dynamics of residual trees and spatial aspects of seed bank availability. Observed patterns of forest regrowth were expanded upon in the concepts of sere development (Cowles 1889, Clements 1916) and later
Relay and Initial Floristics (Elger 1954, Oliver & Larson 1996). Traditionally, a Relay Floristics pattern would occur with one species or groups of species invading a disturbed area and eventually being replaced by successive species. This model of succession has been rejected (Elger 1954 and others), as it is not representative of naturally occurring successional dynamics. It is, however, often applied to ecological restoration practices. Initial Floristics is a pattern, thought to be more common in natural systems, in which all species invade at approximately the same time post disturbance, but assert dominance at different times (Oliver and Larson 1996).

Early models of landscape development provided founding concepts of ecological succession. Models like Clementsian Succession (Clements 1916), Relay and Initial Floristics (Elger 1954 and expanded by Oliver & Larson 1996), and Inhibition, Facilitation and Tolerance (Connel & Slayter 1977), are based on characterized stages, linear in progression to an old growth or “climax” stage of development. These models are not fully representative of the regeneration dynamics found in the natural world, as they do not incorporate temporal scales and spatial patterns of development, the role of disturbances, or the developmental importance of biological legacies (Franklin et al. 1997). Applying these complex and multifaceted factors to founding, yet outdated, models is important for sustainable forest ecosystem management and silviculture.

Change is inherent to ecosystems. Thus, the concept of an ecosystem reaching climax stage of development contradicts the dynamism of ecological succession (Hemstrom & Logan 1986, Spies 1997). Instead there are multiple pathways of
succession, often influenced by the structural complexity of a forest following a disturbance. It is possible for structural complexity to arise sooner in successional development than once proposed through conventional successional frameworks. Early onset of structural complexity is possible where canopy closure and competitive exclusion do not occur, as sparse or suppressed tree establishment may actually accelerate the development of certain forms of spatial complexity typically associated with late-successional forests (Donato et al. 2012). Late-successional, complex structural development can be accelerated in northeastern U.S. forests (Keeton 2006), making it possible for early successional canopies to support the equally complex functioning and biodiversity seen in late-successional or old-growth forests (Donato et al. 2012). Non-equilibrium successional models are therefore accepted and explored by many ecologists today. These models represent a shift from deterministic models of succession to ones that incorporate stochastic process inputs (Foster 1992, Mladenoff & Pastor 1993), yielding alternate pathways of succession (Donato et al. 2012).

1.4. Stand development

Ecological succession is a change in species composition over time. This concept differs from stand development, which is defined by structural change. In contrast to ecological succession models, stand development models based on sere stages of development might be viewed as arbitrary, as natural development is not a linear process. Some models are more inclusive of complex processes (e.g., initial disturbances, residual structures, and seed sources) and are therefore more accurate and applicable to forest regrowth dynamics. Franklin et al. (2002), for example, expanded
on Oliver and Larson’s (1996) four stages of stand development (see Appendix A), basing patterns of growth on the severity of the initiating disturbance, the importance of residual structures, and post-disturbance spatial patterning. Quantity and types of biological legacies differ among disturbances, and influence stand development partly by affecting spatial patterns of colonizing seedlings and development rates of horizontal complexity (Franklin et al. 1997). Stages of stand development vary based on the physical and biological processes of the disturbed stand. There are variable rates and pathways of stand development, and as inherent in the continuous nature of development, many processes operate throughout the life of a stand, and not during one developmental stage.

Principles of stand development (Appendix A) often relate biomass accumulation to stand age (Bormann & Liken 1979, Franklin et al. 2002). The size trees attain according to their age is affected by site quality, and the most useful tree size characteristic for site evaluation is thought to be tree height, as diameter growth is more sensitive to stand density (Husch 1963). As site quality increases, trees can grow in height more quickly, yielding a closed canopy. This process expedites time-induced mortality through competition (Spies & Franklin 1991), which results in a lower tree density with larger average diameters. The increase of dominant tree age and density of large trees as stands develop is important, as a strong positive relationship between tree age and density and biomass accumulation has been identified in northeastern US forests (Keeton et al. 2011). Alternate pathways of stand development have been explored and supported (Donato et al. 2012), emphasizing that interspecific competition
can thin out trees soon after a stand-replacing event, precluding overstory canopy closure.

Groundbreaking research conducted at the Hubbard Brook Experimental Forest in New Hampshire predicts peaks in stand development (biomass accumulation) after approximately 170 years (Bormann & Likens 1979). Although this finding was based on empirical observations in younger forests, the stand dynamics identified by Bormann & Likens (1979) were categorized by four stages of development: reorganization, aggregation, transition, and steady state (Appendix A). Studies conducted in primary and old growth forests have provided conflicting results to Bormann & Likens (1979) findings. Some research shows peaks in stand development at 230-260 years of age (Tyrell & Crow 1994), while others found that basal area can continue to increase for up to 400 years of stand age (Ziegler 2000, Keeton et al. 2011). These results were confirmed in a recent study conducted in old-growth Mid-Atlantic forests (McGarvey et al. 2015). It may therefore be possible for northeastern U.S. forests to yield greater biomass accumulation over longer periods of time than previously thought. This consideration, however, conflicts with recent findings at Hubbard Brook that show biomass accumulation slowing earlier than expected, reaching maximum development at 80 years of stand age (Fahey et al. 2005, Siccama et al. 2007).

Although this research indicates biomass accumulation in secondary forests may actually be lower than previously predicted, there are several possible explanations for Fahey et al.’s (2005) findings. It is possible that acid rain deposition and declines in
forest structure caused by pests and diseases altered stand development (as reported in Keeton et al. 2011). The decline in maple (Acer) species, a once-dominant hardwood in Hubbard Brook Experimental Forest, for example, contributed to these dynamics, and may be connected to the study site’s land-use history. The loss of nutrient retention (e.g., Ca) associated with the soil erosion post forest clearing in the 1870s, may have made the recovered system less suitable for long-term biomass development by reducing the species’ growth rates and potential (Juice et al. 2006, Siccama et al. 2007). The varied findings on the relationship between biomass accumulation and stand age in the Northeast are relevant to assessing accumulation dynamics in the region’s current secondary forests. Land-use history and climate change effects, such as changes in resource availability, can alter stand developmental pathways. It is difficult to fit such complex effects into a developmental model; but their consideration is imperative when assessing stand recovery.

1.5. Impacts of climate change on forests

Climate change in the Northeast is altering ecosystem disturbance regimes (Evans & Perschel 2009), with the number of high intensity storms nearly doubling in the past forty years (Frumhoff et al. 2007). Forests are not only impacted by climate change, but they also contribute to climate regulation through carbon sequestration and storage (Evans & Perschel 2009). Terrestrial ecosystems play a vital role in the global carbon cycle by offsetting atmospheric CO$_2$ by storing carbon in above- and belowground biomass. In fact, forests and their associated soils store an estimated 45% of all terrestrial carbon (McGarvey et al. 2015). Forests may prevent carbon emissions
through wood substitution (e.g., wood instead of concrete for construction), biomass substitution (e.g., biomass fuels for energy instead of fossil fuels), wildfire behavior modification (e.g., biomass removal before wildfire emissions), and avoided land-use change (e.g., deforestation) (Woodall et al. 2011). Forests also reduce atmospheric concentrations of carbon through sequestration (e.g., increasing ecosystem carbon storage through standing live tree growth) and carbon storage in wood products (e.g., C stored in lumber and furniture) (Ryan et al. 2010). It has become increasingly important to investigate secondary stand development as disturbance regimes change in the Northeast. Doing so will improve our understanding of if and how northeastern forests’ capacity to store carbon is changing, and thus how to manage for forest carbon.

There is scientific consensus that the Earth’s climate is changing, that humans are the primary cause of the change (Houghton 1996, IPCC 2014), and that Earth has begun to experience the effects (Rustad et al. 2012). Changing climatic conditions will likely impact northeastern forests. Predicting these effects, however, is difficult due to the complex interactions and numerous feedbacks associated with climate change. It is widely supported that mean global temperatures are rising, and are expected to continue to rise with increasing greenhouse gas emissions. Global air temperature has increased by an average of about 0.8°C over the last century (Rustad et al. 2012) with seasonal variation yielding greater temperature increases in the winter (Hayhoe et al. 2007). Anthropogenic atmospheric inputs of greenhouse gases are altering the natural carbon, water, and nitrogen cycles (Aber et al. 2001). These changes, along with the expected changes in precipitation (Easterling et al. 2000, Frumhoff et al. 2007, Rustad et al.
2012) and disturbance regimes (Dale et al. 2001, Hayhoe et al. 2007) are altering forest processes (e.g., net primary production, litter decomposition, and nutrient cycling) (Aber et al. 2001) and productivity (Boisvenue & Running 2006), therefore affecting forest ecosystem carbon dynamics (Scheller et al. 2012).

Although the expected effects of elevated atmospheric CO$_2$ on forested ecosystems vary, it is thought that rates of net photosynthesis and tree growth will increase in the short term (Long et al. 1996). Duke University’s Free Air CO$_2$ Enrichment Experiments (FACE) in North Carolina found a 25% growth increase in loblolly pine under elevated CO$_2$ emissions of 560 ppm (DeLucia et al. 1999, Aber et al. 2001). The later observed decline in these stands’ growth due to soil nitrogen limitation informed the critical importance of understanding nitrogen feedbacks under enriched CO$_2$ conditions (Chapin et al. 2011). Evidence has also shown, however, that long-term exposure to elevated atmospheric CO$_2$ can yield a reduction in photosynthesis rates and carbon uptake (Long et al. 1996, Rey & Jarvic 1998). It is likely that limiting factors, particularly soil nutrients and moisture availability, affect species’ ability to increase growth and photosynthesis rates in the long-term. Water, light, and nutrient (e.g., nitrogen) availability are therefore essential considerations when assessing the long-term effects increased CO$_2$ levels have on photosynthesis rates and carbon uptake.

The Northeast has already experienced a 10mm/decade increase in precipitation (Frumhoff et al. 2007, Hayhoe et al. 2007, Rustad et al. 2012), with more precipitation falling as rain (Huntington et al. 2009). In regions like the Northeast, where climate
change is unlikely to induce severe drought stress, forested ecosystems are more likely to have a longer growing season that could result in increased growth rates, and therefore increased carbon uptake (Aber et al. 2001). This is especially true when soil and nutrient availability are not limiting factors (Nowak et al. 2004). Some model simulations found that increased temperatures and precipitation can either increase or have no effect on forests’ net primary productivity (NPP) through 2050 (White et al. 1999), making it conceivable that more extreme increases in temperature and precipitation can have adverse effects on temperate forests, causing a decline in NPP.

The impacts of climate change on forested ecosystems will vary, not only by region, but also by species, as some species are more resilient and adaptable than others. Many of the FACE experiments exploring the effects of climate change on forests have been conducted in homogeneous stands that do not adequately represent the forest structure and composition found in many large-scale northeastern forests. These findings are therefore limited and not fully applicable to landscape-level responses to CO₂ fertilization.

Other research has more successfully identified the regional changes in tree species productivity. Changes in air temperature, and estimated decreased soil moisture have the potential to influence tree species migration within the Northeast, with maple (Acer), birch (Betula), and beech (Fagus) species shifting northward in their growing region and spruce (Picea) and fir (Abies) species becoming more limited in their range of growth (USGCRP 2009, CCSP 2008). Rustad et al. (2012) performed a more comprehensive simulation model comparing current forest cover to possible forest
cover under low emissions (low fossil-fuel emissions, economic growth in service and information sectors, use of clean and efficient technologies) and high emission (940 ppm atmospheric CO₂ concentrations, rapid economic growth with a global population of nine billion by 2050, efficient energy technologies not employed until late in century) scenarios. Projected forest types in the U.S. Northeast report nearly 100% decline in spruce-fir forests in both emissions scenarios, a dominance of a maple, beech, and birch cover type in the low emissions scenario, and a nearly 100% cover of a oak-hickory forest type in the high emissions scenario (Rustad et al. 2012). This research suggests that northeastern forests are likely to significantly decline in genera and species diversity over time.

Climate change is also altering the frequency, intensity, and duration of natural disturbances. Changes in temperature and precipitation influence disturbance regimes (Turner et al. 1998) and disturbances influence carbon storage dynamics in trees and dead wood (McNulty 2002). As previously mentioned, effects of disturbances are partly mitigated by prior responses to past disturbances. The effects of changing disturbance regimes will therefore vary based on the land-use history of the forested ecosystem, and will play a vital role in stand development (Franklin et al. 2002, Keeton et al. 2007).

Expected changes in disturbance regimes vary around the globe. Modeling scenarios show that the seasonal severity rating of fire hazard, for example, is expected to increase over much of North America (Dale et al. 2001), but regions like the western United States may have greater susceptibility to fire due to the region’s large fuel stocks and greater likelihoods of drought. Northeastern U.S. forests are receiving more
rain and less snow. The region is experiencing increased rainfall intensity and frequency of larger storms, with longer durations of dry periods between storms (Huntington et al. 2009, Rustad et al. 2012). With a 1.0°C air temperature increase in the last century, the average air temperature increase in the Northeast is greater than that of the globe. Regional projections, based on statistically downscaled atmosphere-ocean general circulation models (AOGCMs) suggest an increase in annual air temperature to reach 5.3°C by 2100 (Rustad et al. 2012). Annual precipitation is expected to increase 7-14% by this time, with most change in precipitation occurring in winter (Rustad et al. 2012). The accuracy of these projections is of course dependent on future greenhouse gas emission levels and is therefore susceptible to change. Even though forests in the Northeast are some of the most studied terrestrial ecosystems, responses to climate change are difficult to predict.

Many factors, such as the interacting drivers of change, varying time scales of response, time lags and legacy effects, temporal and spatial heterogeneity, variable species-specific responses, and human influences, are imperative to consider, but nearly impossible to include when estimating northeastern forests’ response to climate change. It is crucial for policy makers, landowners, and all invested stakeholders to take note of the changing forested ecosystem dynamics as influenced by our changing climate.

If climate change significantly alters the ability of northeastern forests to provide their multitude of ecosystem services, upon which humans are reliant, the Northeast is at risk of severe social and economic impacts. It is therefore important to understand carbon sequestration dynamics, one of the greatest ecosystem services
forests provide, so landowners and managers can effectively work to mitigate threats by managing for high-magnitude long-term carbon storage.

1.6. Carbon sequestration in forested ecosystems

Terrestrial ecosystems serve as an important carbon pool within the carbon cycle. Forested ecosystems provide a valuable ecosystem service by storing and sequestering carbon, reducing atmospheric inputs of CO$_2$. In fact, forested ecosystems have been widely acknowledged as a carbon sink, with U.S. terrestrial forests offsetting ten to thirty percent of annual U.S. CO$_2$ emissions (Houghton 2003). Since the time of these findings (1980s), emission levels have risen significantly, and general trends in forest growth suggest a decrease in U.S. forest carbon uptake (Birdsey et al. 2006).

Recent estimates found that the conterminous U.S. annually sequesters between 149 to 330 Tg C, with forests and wood products responsible for a net sequestration up to 91% of this sink (Woodbury et al. 2007). This was not always the case, however, as the emissions associated with the historic clearing of northeastern forests peaked at 400-800 Tg C/year in 1900 (Houghton et al. 1999, Birdsey et al. 2006, McKinley et al. 2011). Indicating the importance of land-use history, northeastern U.S. forests currently serve as a net carbon sink due to the subsequent reforestation that took place after the abandonment of cleared forested land. Land use changes also influence belowground carbon sequestration, as converting cropland or pastureland to timber plantations can yield up to an 18% increase in soil carbon stocks while changing cropland to secondary forest can yield up to a 53% increase in soil carbon stocks (Guo & Gifford 2002).

Aboveground biomass accumulation dynamics have long been studied, but
uncertainty remains regarding secondary forest carbon accumulation dynamics and potential. Birdsey et al. (2006) found general trends in forest growth suggesting a decrease in U.S. forest carbon uptakes. This is likely because northeastern secondary forests are maturing (Lorimer & White 2003), and a reduction in carbon uptake rates has been found in maturing forests (Bormann & Likens 1979, Keeton et al. 2007). Implementing relevant forest management regimes, however, can sequester up to 57% more carbon by reducing harvest frequency and favoring high levels of structural retention (Franklin et al. 1997, Keeton 2006, Nunery & Keeton 2010). Unless otherwise managed for, it is possible that carbon uptake rates will continue to decline as forests age. Even though carbon uptake rates decline with forest maturity, complex forest structure, as often found in primary and mature or old-growth secondary forests, can yield an increase or maintenance in net carbon sequestration (Luyssaert et al. 2008, Nunery & Keeton 2010), with mature forests sequestering the greatest amounts of carbon worldwide (Harmon et al. 1990) (see Glossary of Terms for carbon sequestration, storage, and uptake).

Recent research suggests that stand age is strongly predictive of aboveground biomass in the Northeast, with other variables, including ecoregion and conifer component, accounting for 25-33% of variability (Keeton et al. 2011). While recognizing the possibility for early declines of aboveground biomass as reported by Fahey et al. (2005), Keeton et al. (2011) suggest that aboveground biomass has the potential to accumulate late into succession; with maximum biomass values found in stands with dominate tree ages ranging between 350 and 400 years. These findings are
interesting in the context of Bormann & Likens’ (1979) theoretical findings. Keeton et al.’s (2011) results did not fully support Bormann & Likens (1979) four stages of stand biomass development, as biomass was not found to decline in stands 200-350 years of age, nor was a “steady-state” of biomass development reached in stands 350 years of age. Large tree densities are strongly correlated with tree age and aboveground biomass (Keeton et al. 2011, Stephenson et al. 2014), suggesting a high proportional contribution to total biomass in stands undergoing late-successional development (Brown et al. 1997, Stephenson et al. 2014). Most northeastern secondary forests are between 40 and 140 years of age (Lorimer & White 2003), and have mean aboveground biomass levels of about 107 Mg/ha (Turner et al. 1995, Birdsey & Lewis 2003). Influenced by type and intensity of management (Keeton 2006, Harmon et al. 2009, Nunery & Keeton 2010), aboveground carbon storage in northeastern secondary forests has the potential to double (Rhemtulla et al. 2009, Keeton et al. 2011).

Northeastern secondary forests can continue to sequester more carbon through proper management (see below). Many other factors, however, will influence future trajectories of aboveground biomass accumulation. Rising levels of atmospheric carbon along with other aspects of climate change, like changing disturbance regimes and the spread of exotic pests, further complicate the already complex dynamics of aboveground biomass accumulation. Climate change has the potential to alter successional dynamics, influencing the rate and development of aboveground biomass accumulation (Aber et al. 2001, Bonan 2008, Rustad et al. 2012). Increased levels of CO₂ emissions will not only disrupt the balance of carbon sources and sinks, but will
also affect future carbon storage dynamics of northeastern secondary forests.

1.7. Silviculture

Between 1925 and 1960, U.S. silvicultural practices were based largely on selective harvesting and had too often led to high grading through diameter-limited cutting. Harvest prescriptions often ignored regeneration processes and rarely considered interjecting disturbances (Seymour 2004). The U.S. Forest Service mandated even-aged silvicultural practices, such as clearcutting, on the National Forest System (Boyce & Oliver 1999, Seymour 2004). This production forestry approach simplified natural stand dynamics and encouraged plantation forestry. Although plantation forestry is still used today, there has been a shift in U.S. silvicultural support from production forestry to balanced forestry (Seymour 2004). This shift, emphasizing the need to balance concepts of production forestry with ecological forestry (Seymour & Hunter 1999), was influenced by the reinventing work and advocacy of Oliver (1989) and Franklin (1989) and emerging concepts of biological diversity (Hunter 1990) and disturbance ecology (Oliver & Larson 1996). This work encouraged foresters to increase focus on uneven-aged management.

Silviculture based on natural disturbance regimes and stand development (Oliver & Larson 1996) reinforce the inherent flexibility of management practices. Cohort initiation, for example, varies based on types, intensities and frequencies of disturbance (Oliver & Larson 1996, Seymour et al. 2002). By mimicking the effects of periodic moderate intensity disturbances, as are often apparent in northeastern late-successional forests, foresters can increase species diversity and ecosystem function
and resiliency (Hanson et al. 2012). Low levels of biological legacies, for instance, can be compensated for by permanently reserving trees to live throughout their lifespan or by retaining girdled and felled trees (Hanson & Lorimer 2007, Hanson et al. 2012). Additional ecological forestry alternatives, as demonstrated through structural complexity enhancement (SCE), have been implemented in uneven-aged stands through experimental studies, and promote late-successional, old growth characteristics in northern hardwood-conifer forests (Keeton 2006). Diverse arrays of management regimes are therefore applicable to northeastern U.S. forests.

1.8. Managing forests for carbon storage

Although it is difficult to predict how climate change will affect temperate forests’ ability to sequester carbon, elevated levels of CO₂ have made it increasingly important to manage these forests for carbon storage. Developing carbon markets recognize the important role of forests in the carbon cycle and therefore view sustainable forest management as a vital component of climate change mitigation (Ray et al. 2009b). Thus, informed management is essential to ensure U.S. forests remain a carbon sink.

Research primarily conducted in old growth forests of the U.S. Pacific Northwest suggest that unmanaged forests can sequester greater amounts of carbon than managed forests (Harmon et al. 1990, Harmon & Marks 2002). This research suggests a positive correlation between stand structural complexity and carbon storage. Similarly, many scholars have argued that replacing older forests with younger, less complex forests results in a net release of carbon to the atmosphere (Harmon et al. 1990, Schulze
et al. 2000). This conclusion is supported by research conducted in the Northeast, when accounting for total stocks of carbon is limited to aboveground biomass and wood products (Nunery & Keeton 2010). Although these findings are not indicative of secondary forest dynamics in the Northeast, similar reports within the region exist. Modeling results suggest that unmanaged stands in northern hardwood forests, for example, have been found to sequester about 40 to 115 percent more Mg of carbon per hectare over a 160 year simulation period than found in forests with active management (Nunery & Keeton 2010). This finding deems reserve-based approaches to management valuable when maximizing forest carbon storage.

For nearly two decades, researchers have explored how to promote forest carbon storage through management. Reducing harvesting frequency (Curtis 1997), increasing rotation lengths (Harmon & Marks 2002, Ryan et al. 2010), and encouraging post-harvest structural complexity (Keeton 2006, Franklin et al. 2007, Swanson 2009, Puettmann et al. 2009) have been found to increase stand level carbon storage. Increasing rotation lengths by 20 years in areas of European forests varying from 0.3 to 5.1 M/ha, for example, can achieve the largest eligible carbon sink (as reported in Article 3.4 of the Kyoto Protocol), depending on the forests (Kaipainen et al. 2004). Research conducted in the U.S. upper Great Lakes region found the effectiveness of extended harvest rotations on promoting aboveground carbon storage to depend on stand stocking levels. Increased rotation lengths more effectively maximizes carbon storage in highly stocked stands, but these conditions can result in lower levels of live tree carbon uptake (D’Amato et al. 2011). Thus, maintaining adequate stocking of large
trees (Stephenson et al. 2014), while also allocating growing space for younger trees can promote higher rates of stand-level carbon storage and sequestration (D’Amato et al. 2011). Similarly, a study conducted with U.S. Forest Inventory and Analysis (FIA) data from 30 eastern states (of the U.S.) found stand stocking to be the primary driver of live tree aboveground carbon storage (Woodall et al. 2011). Live aboveground carbon storage also depends on tree species mixtures, as maximum storage decreased by 33% in highly stocked stands when the majority of stocking was in a single species (Woodall et al. 2011). Dead tree biomass did not strongly correlate with levels of stand stocking in this study, and instead was only dependent on interspecific stocking, suggesting increased tree species diversity can result in greater niche occupancy and mortality, and thus expansion of carbon stocks in dead pools (Woodall et al. 2011).

Similar management concepts were recently applied to even- and uneven-aged forests representative of the dominant forest cover found throughout the U.S. Northeast (Nunery & Keeton 2010). The modeling results from Nunery & Keeton (2010) indicate that management intensity strongly affects carbon storage potential. A long-term (25 years) study conducted in a northwestern Pennsylvania Allegheny hardwood stand found plots thinned from below (a relatively low intensity management method) had greater carbon sequestration rates than those thinned from above (Hoover and Stout 2007). These affects, however, can vary based on harvest rotation length (Ryan et al. 2010). Reducing live tree harvest from 100% to 20% in Douglas-fir/western hemlock forests, for example, would increase the average forest carbon stock by 97% for a 25-year harvest interval, but only 30% for a 100-year interval (Harmon 2009). Adjusting
harvest intensities and rotation lengths to mimic the forest’s natural disturbance regimes can effectively enhance stand level carbon storage (Ryan et al. 2010, D’Amato et al. 2011).

Managing forests for greater carbon storage is stand-specific. Certain management prescriptions’ effects on carbon sequestration and storage, for example, are dependent on stand age dynamics. Reducing harvesting frequency more effectively increases carbon sequestration in uneven-aged northeastern U.S. forests than in even-aged stands. Retaining biological legacies also promotes biological diversity by sustaining many organisms and critical ecosystem functions, such as soil stabilization, nutrient retention and recycling, and stand resilience to disturbance (Franklin et al. 2007, Hanson et al. 2012). Both field and simulation studies conducted throughout the U.S. support the superiority of silvicultural prescriptions that maintain a large proportion of mature trees in maintaining or increasing aboveground carbon storage (D’Amato et al. 2011).

The spatial pattern of harvests and the regeneration methods post harvests are also important considerations when managing forests for carbon storage (Swanson et al. 2009). Natural regeneration/recovery can yield a net reduction in landscape-scale carbon storage, while immediate replanting can enhance long-term carbon storage (Swanson et al. 2009). Comparatively, partial harvesting can increase forest carbon storage (Neilson et al. 2006). Employing multi-aged management systems, such as irregular shelterwood and selection systems, can maintain a large proportion of carbon stores in retained mature trees while using thinning to create spatial heterogeneity that
promotes higher sequestration rates in smaller, younger trees (D’Amato et al. 2011). This management approach promotes carbon storage while simultaneously enhancing structural and compositional complexity.

Some forests may not need to be managed (Seymour & Hunter 1999), and instead should develop without intensive human intervention. As mentioned by Harmon et al. (1990) and Nunery & Keeton (2010), this concept is particularly relevant when considering managing forests for carbon sequestration in the U.S. Pacific Northwest. Silvicultural approaches that emulate the frequency and scale of natural disturbances (Seymour et al. 2002, Harmon et al. 2009, Ryan et al. 2010) and increase post-harvest structural retention (Keeton 2006, Franklin et al. 2007, Puettmann et al. 2009, Nunery & Keeton 2010), serve as the most appropriate options in managing for high aboveground biomass in northeastern US forests.

There is an increasing need to manage forests for carbon and other ecological functions, such as biodiversity and hydrologic resilience. Managed forests comprise the majority of the world’s forested landscape (Keeton 2007), harboring the largest proportion of terrestrial biodiversity. The 3.9 billion hectares of remaining forested land worldwide comprise 90% of known terrestrial species and sequester nearly 50% of the carbon in the terrestrial biosphere (Lindenmayer and Franklin 2003, McGarvey et al. 2015). The potential and need to sequester greater quantities of carbon through sustainable management is therefore evident.

Although researchers have identified several techniques to increase forest carbon storage, carbon dynamics will likely become more variable with climate change.
Based on the projected temperature and precipitation changes for the Northeast, it is likely that temperature- and moisture-sensitive processes, like primary productivity and decomposition rates (Harmon et al. 2004), will change (Swanson et al. 2009). These changes, along with shifting disturbance regimes (Dale et al. 2001), will affect forest carbon sequestration dynamics, creating an ongoing need for multifaceted carbon dynamics research in the Northeast.

1.9. Plantation forestry: long-term growth and yield

Plantation forestry plays a key role in meeting the world’s industrial wood product needs (Sedjo 1999). As a result of the industry’s importance, and in effort to accurately predict stand growth and mortality, silviculturalists have long sought simple and effective indices of competition in forested stands. One such index is the Stand Density Index (SDI) (Reineke 1933). The SDI is determined by the number of trees per acre (or hectare) a stand would have at a standard average diameter at breast height (DBH) (Husch 1963), and has become the preferred stocking index for many foresters (Zeide 2005, Shaw 2005). Similarly, the maximum SDI is determined by the maximum number of trees at a given reference diameter that can exist in a self-thinning population (Weiskittel et al. 2009) (see Glossary of Terms).

The self-thinning concept established by Reineke (1933) assumes that a variety of species under self-thinning conditions have the same allometric relationship between size and density. The assumptions associated with Reineke’s (1933) self-thinning concept (as reported in Weiskettel et al. 2009) undermine the accepted carbon management models discussed earlier. Although the assumptions associated with SDI
are considered reasonable approximations (Jack & Long 1996, Weiskettel et al. 2009), a scientific consensus is lacking, and Reineke’s (1933) concepts of self-thinning have therefore been reevaluated (Pretzsch et al. 2005). Contrary to founding concepts of self-thinning, it is likely that each stand has its own self-thinning trajectories (Pittman & Turnblom 2003), that individual stands do not always approach the maximum size-density relationship (Zeide 1987, Weiskettel et al. 2009). More accurate methods may exist to better understand stand density dynamics (Bi 2004, Zhang et al. 2005).

Inferences on stand growth and mortality are traditionally made from the use of tables, equations, and simulation models, collectively referred to as growth and yield models. Growth and yield models provide estimates of stand characteristics like volume, basal area, and number of trees per unit time (Avery & Burkhart 1994), and are therefore helpful forest management tools. Yield tables project expected stand volumes by stand age and site index. The ‘yields’ in growth and yield tables represent the volume of merchantable timber. They are generated based on stocking charts and are species-specific, but expected yields (merchantable timber) can vary within species. Merchantable timber volume of eastern white pine (\textit{Pinus strobus}) stands, for example, vary not only with site quality, but also between uneven- and even-aged stands (Leak et al. 1970) and potentially between naturally regenerated stands and plantations. Due to the quick and uniform establishment of eastern white pine plantations, they often have greater volumes of merchantable timber than those of naturally regenerated white pine stands, but larger volumes of merchantable timber is limited by plant spacing. If white pines are planted too closely to each other, as reported in a four-foot spacing plantation
(Lancaster & Leak 1978), expected merchantable volume could be lower compared to those in naturally regenerated stands. Growth rates of eastern white pine can therefore vary greatly not only with site conditions, but also based on stocking density.

In the Northeast, where harvesting rotations are long (Sendak et al. 2006), interim analyses using justifiable assumptions can provide useful guidance to land managers, but are verifiable only in the long run. Long-term data on growth and merchantable timber volume provide valuable information needed to make stand management decisions. There is now an opportunity to compare projections of eastern white pine growth and volumes of merchantable timber as reported in Frothingham (1914) and Lancaster & Leak (1978) to current stand measurements. The body of existing literature raises questions about the U.S. Northeast’s eastern white pine’s current growth and merchantable timber, and how eastern white pine growth and merchantable timber volume varies between naturally regenerated and planted stands and between even- and uneven-aged stands. Multiple factors are likely to influence stand productivity. Comparing previously projected volumes of merchantable timber to current measurements is the first step in identifying and assessing the role multiple variables play in influencing the region’s current eastern white pine merchantable volume.

Marsh-Billings-Rockefeller National Historical Park (MBR) in Woodstock, VT encompasses both even- and uneven-aged secondary-growth eastern white pine stands (Table 1). MBR provides an exceptional opportunity to reexamine the old growth and yield tables, such as Frothingham’s (1914) and Leak’s (1970), which are often still used
today. Each of MBR’s white pine stands has a site index of 60 and less merchantable volume than projected for white pine stands of similar ages by Frothingham (1914) and Leak et al. (1970), despite their high-magnitude aboveground carbon storage (discussed in Chapter 2). Stand 8 (Table 1), for example, produced fewer cubic meters per hectare of eastern white pine than projected by Leak et al. (1970) for naturally regenerated, even-aged white pine stands of the same age (approximately 60 years). Stand 8 is the only naturally regenerated white pine stand at MBR and produces the least amount of merchantable timber of all the Park’s white pine stands. This stand is comparatively younger in age and smaller in area to other white pine stands in the Park, but its low production is also likely due in part to the interspecies competition for space occurring between the eastern white pines (75% composition) and the hardwood species (25% composition). Comparatively, Stand 18 (Table 1) has a greater white pine species composition, which produces 94% of the stand’s merchantable timber. As of 2003 (prior to recent timber harvests), this even-aged white pine plantation produced less merchantable timber than projected for a white pine stand of the same age by Frothingham (1914).

If Frothingham (1914) and Leak et al. (1970) were accurate in their projections, none of MBR’s white pine stands reached their expected merchantable volumes for their respective ages. There are, of course, limitations to this comparison. To begin with, both Frothingham’s (1914) and Leak et al.’s (1970) projections were based on measurements spanning forests at a much larger spatial scale than what is available at MBR. Although the site indices of their previously published yield tables are similar to
that of MBR’s stands, at this time, the current stocking levels of MBR’s stands are uncertain, and need to be defined for more accurate comparisons. It may also be likely that changes in climate have altered eastern white pine growth and expected volumes of merchantable timber since the publications of Frothingham (1914) and Leak et al. (1970), whose projections did not account for climate change. The growth and merchantable volume of eastern white pine is just one of many informative aspects of recent data collection regarding stand recovery occurring throughout MBR Park, providing insight into the accuracy of earlier concepts of stand density dynamics and self-thinning trajectories.

1.10. Marsh-Billings-Rockefeller National Historical Park: A living laboratory for land-use change effects on carbon dynamics in secondary forests

The Marsh-Billings-Rockefeller National Historical Park, located in Woodstock, Vermont, offers an exceptional opportunity to study the kind of forest recovery, carbon dynamics, and changes in ecosystem service provisioning now occurring across the Northeast. As its name suggests, MBR represents one of the oldest examples of active reforestation in North America. The Park’s land was the birthplace and home of George Perkins Marsh, one of North America's first conservationists, and was later the home of Frederick Billings. Its most recent owners, Laurance S. and Mary F. Rockefeller, restored and preserved the property’s infrastructure and acreage. Primarily because of its long (>140 years) history of scientifically informed forest stewardship, the Park was incorporated into the U.S. National Park system through Congress in 1992.
The Park’s diverse forest mosaic reflects a history of alternate reforestation approaches and varied successional trajectories. Due to farming and harvesting merchantable timber for various forest products, the Woodstock property’s forest cover was significantly reduced by the time of George Perkins Marsh’s birth in 1801. The reduction of Vermont’s and Woodstock’s forest cover continued, and with age, Marsh made connections between deforestation, habitat loss, flooding, and soil erosion, and encouraged Vermont farmers to adjust their harvesting practices.

Locally born, and inspired by Marsh’s publications, Frederick Billings bought the Woodstock property in 1869. Distressed by Vermont’s agricultural practices and forest cover reductions, Billings established a scientifically informed dairy operation and pioneered active reforestation on the steep slopes of Mount Tom. Billings employed progressive forestry methods and planted the only available nursery stock at the time (e.g., European conifers) (MBR Park Records). His eventual creation of carriage roads and trails, paired with his forestry and farming practices ultimately transformed the Woodstock property to be a template for sustainable farming, timber harvesting, and recreation. As the property’s plantation forestry developed, other vacant parcels recovered and naturally regenerated.

Laurance Rockefeller married Billing’s granddaughter, Mary French, and continued to steward the property. The couple remodeled the Billings’ farm and formally opened the Billings Farm and Museum. In 1992, the couple donated the residential property and 555 acres of Mount Tom forestland to the National Park Service. The Park opened its doors to the public in 1998. Most of MBR’s forested
stands are now between 60 and 130 years of age and are undergoing late-successional development. The study area, therefore, is a microcosm of the human-influenced successional dynamics and recovery processes now occurring across the region.
CHAPTER 2: LONG-TERM FOREST STRUCTURAL DEVELOPMENT AND CARBON DYNAMICS AS INFLUENCED BY LAND-USE HISTORY AND REFORESTATION APPROACH

2.1. Introduction

There is an unprecedented opportunity to study the long-term dynamics of secondary forest recovery from land-use change in the northeastern United States. Following widespread forest clearing and subsequent agricultural abandonment in the nineteenth century, the region has reverted to a predominance of forest cover, though cover is again declining in all six New England states (Foster et al. 2011). Northeastern secondary forests are now mostly between 40 and 140 years of age (Lorimer & White 2003), and encompass a wide range of successional and developmental conditions (Foster and Aber 2004). This land-use history and change provides an opportunity to reexamine stand development models based largely on theoretical projections (e.g., Bormann & Likens 1979) and observations spanning a relatively limited range of successional conditions (see reviews in Oliver & Larson 1996). In light of increasing interests in managing forests as carbon sinks (Ruddell et al. 2007, Nunery and Keeton 2010) and for environmental co-benefits, such as watershed protection and biodiversity (Schwenk et al. 2011), understanding long-term biomass (i.e., carbon) accumulation dynamics is essential.

2.1.1. Successional trajectories as influenced by land-use history

Successional dynamics in the northeastern U.S. have been profoundly altered by land-use history, creating multiple potential pathways of compositional development (Foster et al. 1998, McLachlan et al. 2000). Ecosystem recovery pathways are influenced
by complex interactions among edaphic factors and disturbances, both anthropogenic and natural. One such influence is the structural complexity of a forest post disturbance (Franklin et al. 2002). For example, the quantity and types of biological legacies (e.g., live residual trees, dead snags, downed coarse woody debris) differ among disturbances, and influence stand development partly by affecting spatial patterns of colonizing seedlings and development rates of horizontal complexity (Franklin et al. 1997). Retaining biological legacies also promotes biological diversity by sustaining many organisms and critical ecosystem functions, such as soil stabilization, nutrient retention and recycling, and habitat provisioning (Franklin et al. 2007, Hanson et al. 2012).

Prior to European settlement, northeastern forests were acted on by frequent, gap-forming natural disturbances, as well as occasional intermediate intensity wind-throw events (Woods 2004, Hanson et al. 2007), producing a diverse patch mosaic dominated by late-successional structure and composition (Cogbill et al. 2002, Foster and Aber 2004). Large scale, stand-replacing events like hurricanes were relatively rare (Seymour et al. 2002). However, the human-induced deforestation that took place in the U.S. Northeast during and after European settlement fundamentally altered landscape dynamics. Of note are the rate and extent of change in land cover and vegetation, the local extirpation and immigration of flora and fauna, and the major shifts in biogeochemical, hydrologic, and biosphere-atmosphere exchange processes (Foster and Aber 2004). Disturbances of this magnitude encompass sites spanning a wider range of environmental variation than smaller disturbances. Recovery therefore occurs across a diversity of edaphic and climatic conditions (Turner et al. 1998). This, paired with both
variation in regeneration pathway (natural vs. planted) and subsequent management
time, likely strongly influenced the mosaic of forested composition and structural
conditions found throughout the Northeast today (Foster et al. 1998, Thompson et al.
2013).

Our understanding of late-successional dynamics (i.e., structural and
compositional change) in northeastern forests, however, remains incomplete. Despite
recent work on biomass accumulation dynamics in old-growth and primary forests
(Keeton et al. 2011, Gunn et al. 2014, McGarvey et al. 2015) and comparisons of forest
management scenarios (Nunery & Keeton 2010, Woodall et al. 2011, Chen et al. 2015), it
remains uncertain whether the region’s northern hardwood, conifer, and mixed
hardwood-conifer forests are recovering towards a high biomass condition yielding
carbon storage and climate change mitigation benefits. This is partly attributable to
conflicting reports on the relationship between tree growth rates and biomass (i.e.,
carbon) accumulation dynamics. The contention specifically regards aboveground carbon
uptake versus storage (see Glossary of Terms). Since younger trees grow more rapidly
than older trees, accruing biomass at faster rates, it has been argued that intensively (e.g.,
large group selections) managed forests can more efficiently remove atmospheric CO₂
through increased carbon sequestration or uptake. Conversely, carbon stocks (i.e.,
storage) of these younger and more intensively managed forests tend to be less than that
of old-growth (i.e., structurally complex forests >150 years of age) or primary forests
(i.e., never cleared) (Birdsey and Pan 2015, McKinley et al. 2011).

Trends in forest growth suggest a decrease in U.S. forest carbon uptake. This is
likely because northeastern secondary forests are maturing (Lorimer & White 2003), and a reduction in carbon uptake rates has been found in maturing forests (Bormann & Likens 1979). Although carbon uptake rates are slower in older trees, larger trees contribute proportionately greater amounts of carbon to total aboveground storage than younger, smaller trees (Brown et al. 1997). In fact, a recent study reports that continued forest growth is predicted to remain a major driving mechanism for carbon accumulation in the U.S. Northeast (Thompson et al. 2011), as mass growth rates can continuously increase with tree size for most species (Stephenson et al. 2014). Furthermore, a recent global synthesis reports that net primary productivity may be declining at slower rates than previously predicted in late succession, yielding a greater upper limit to carbon storage (Luyssaert et al. 2008, McGarvey et al. 2015).

It is, therefore, unclear if, how, and to what degree the region’s forests are recovering towards a high-biomass, late-successional condition, and furthermore if these two characteristics are tightly or consistently correlated. An important and related question pertains to how over a century of forest management has influenced the pathways of forest structural and compositional development. For instance, there is uncertainty whether the types of partial harvesting systems most typically employed in the Northeast during the 20th century resulted in increased (Neilson et al. 2006, Dyer et al. 2010) or decreased (Bauhus 2009, Nunery & Keeton 2010, Buchholz et al. 2013) biomass accumulation and carbon storage.

This study tests the hypothesis that multiple pathways of recovery and stand development will converge on similar late-successional structural conditions following
reforestation. This is likely in part due to the silvic characteristics of the region’s dominant late-successional species (e.g., eastern hemlock), which include a high degree of shade tolerance and moderate to long (e.g., 200 to 500 year) life spans.

Today, the U.S. Northeast’s forested landscape bears the legacy of altered successional pathways, and thus is not likely analogous to the carbon storage and structural dynamics of pre-European settlement forests (as described in Foster and Aber 2004). While most of the same arboreal taxa persist, current northeastern forests are compositionally distinct from those of the pre-colonial era, with the most significant changes in species relative abundance and distribution observed in areas with historically greater agricultural land-use (Thompson et al. 2013). The abundance of late successional species (e.g. American beech and eastern hemlock) is significantly lower on the modern northeastern landscape, with the primary cause attributable to local and regional deforestation, logging, fire, and more recently, exotic pests (Thompson et al. 2013). When studied at the regional scale, modern forests are more homogenous than pre-colonial forests, and as a result of land-use, reduction in species richness and functional diversity has been observed in both northeastern (Foster et al. 1998, Thompson et al. 2013) and upper Midwestern U.S. forests (Goring et al. in press). Modern forests in the upper Midwestern U.S. have higher stem densities and basal areas, but lower biomass than historical forests (Goring et al. in press). The net reduction in aboveground carbon storage of approximately 158 Mg/ha (Rhemtulla et al. 2009) observed in this region likely results from a shift in allometric scaling associated with changes in species composition (Goring et al. in press). Similarly, total U.S. northeastern forest stocks were
reduced by 60% through forest clearing and conversion between 1700 and 1935. Associated carbon emissions from this land-use change peaked at 400-800 Tg C/year around 1900 (Houghton et al. 1999, Birdsey et al. 2006, McKinley et al. 2011). Despite the region’s forest recovery, its modern secondary forests are reported to store approximately 53 Mg C/ha (Birdsey and Lewis 2003), a net reduction from historic levels. This indicates the potential for continued carbon storage additions.

In this study, we predicted that despite variability in regeneration pathways and disturbance history, stand development will yield structural and compositional characteristics typically associated with late-successional forests, including vertically and horizontally complex canopies dominated by shade tolerant species, high downed CWD volumes, and higher densities of large trees (i.e., ≥ 50 cm DBH) (McGee et al. 1999, Whitman and Hagan 2007), and greater levels of biomass (i.e., carbon storage) relative to younger forests (Keeton et al. 2007, Gunn et al. 2014).

2.1.2. Forest biomass and stand development

The young to mature forests currently dominant in the Northeast have average total (live and dead) biomass levels of approximately 107 Mg/ha (Turner et al. 1995, Birdsey and Lewis 2003). This contrasts with the reported maximum potential aboveground biomass range of 250-450 Mg/ha as they reach old-growth development (Keeton et al. 2011, Gunn et al. 2014), though some papers have reported a lower maximum potential of 216-267 Mg/ha (Hoover et al. 2012). Principles of stand development have traditionally related biomass accumulation to stand age (Odum 1969, Bormann and Likens 1979, Oliver and Larson 1996, Franklin et al. 2002). Research
performed at the Hubbard Brook Experimental Forest in New Hampshire predicts peaks in stand development (i.e., biomass accumulation) after approximately 170 years (Bormann & Likens 1979). This research, however, only used empirical data from young forests and relied on simulation modeling for old-growth forest estimates. Studies using empirical data collected from primary and old growth forests did not match these earlier simulation projections. For example, Tyrell and Crow (1994) found peaks in stand development at 230-260 years of age, while other studies found that basal area can continue to increase for up to 400 years of stand age (Ziegler 2000, Keeton et al. 2011). It may therefore be possible for northeastern U.S. forests to yield greater biomass accumulation over longer periods of time than previously thought. Conversely, secondary forests subject to a range of anthropogenic stresses, such as top soil removal and thus nutrient depletion, may reach peak biomass much earlier and at lower magnitudes than previously predicted (Fahey et al. 2005, Siccama et al. 2007, Bose et al. 2014). The varied findings on the relationship between biomass accumulation and stand age in the Northeast leave open the questions of how biomass accumulation dynamics have and will continue to operate in the region’s secondary forests.

2.1.3. Aboveground carbon storage and structural complexity

This study investigates the relationship between forest age, structural complexity, and biomass accumulation (i.e., carbon storage). Structurally complex forests contribute to biological diversity and ecosystem functioning at landscape scales (Lindenmayer and Franklin 2002, Keeton 2006). As a result of the region’s land-use history and change, the once dominate uneven-aged, old-growth (>150 years) pre-settlement northern hardwood
forests now only occupy about 0.5% of the eastern U.S.’ forested landscape (Davis 1996). This net reduction in aboveground biomass and structural complexity resulted in a decline of forest riparian functions (Keeton et al. 2007), habitat values (Tyrell and Crow 1994, McGee et al. 1999, Dove and Keeton 2015), and carbon storage (Harmon et al. 1990, Houghton et al. 1999, Luyssaert et al. 2008, Burrascano et al. 2013). However, the eastern U.S.’ remaining old-growth forests provide an empirical basis for estimating the long-term carbon storage potential of the region’s recovering secondary forests.

Understanding secondary forest recovery dynamics helps define temporal variations in the global carbon balance, and thus may provide insight into the factors responsible for terrestrial sources and sinks of carbon.

Here, we investigate the influence of (1) different reforestation approaches (i.e. plantation forestry vs. natural recolonization and regeneration) and (2) management history (i.e., long-term low harvest intensities with varying levels of harvest frequencies) on aboveground carbon storage and structural development, and how, if at all, continued management alters these developmental pathways. Our goal is to determine whether secondary forests have the potential to re-achieve the high levels of carbon storage previously reported in chronosequences of primary forests (Keeton et al. 2011, Gunn et al. 2014), or experience the early decline in biomass accumulation observed in some secondary forests (Ryan et al. 1997, Fahey et al. 2005, Siccama et al. 2007, Bose et al. 2014). We hypothesize that multiple pathways of recovery, management, and stand development are converging on similar high biomass conditions, yielding occurring increases in our considered elements of stand structure.
2.1.4. A living laboratory for studying long-term stand development pathways in secondary forests

The Marsh-Billings-Rockefeller National Historical Park, located in Central Vermont, U.S.A., offers an exceptional opportunity to study the kind of forest recovery, carbon dynamics, and changes in ecosystem service provisioning now occurring across the Northeast. Prior to the Park’s establishment in 1992 as a unit of the National Park System, the 260-hectare (643 acres) property’s forestland was cleared for timber products, pastureland, and agriculture. This Park’s land-use history is unique; however, in that it was the first land parcel to be actively reforested and continuously managed within the United States. The Park’s mission today is to interpret this rich history of forest stewardship. In many ways, the Park is a microcosm of the broader northeastern U.S. landscape, reflecting its diversity of plantations (less abundant in the region, mostly originating from plantings by the Civilian Conservation Corps in the 1930s) and naturally regenerated stands (far more abundant in the region, originating primarily from old-field succession).

Both native (e.g., eastern white pine) and non-native (e.g., Norway spruce) conifer plantations were established in Park’s property in the late 1800s. These stands were established with long-term management and natural resource stewardship goals, and as such were fairly consistently maintained through low-intensity thinnings (e.g., from above and below). Most merchantable timber was (and is) extracted for local and regional distribution of saw logs, pulp, and firewood. A significant portion of MBR Park’s land also naturally regenerated or recolonized. These stands were also lightly managed
throughout the 20th century. Pruning and understory thinnings were employed for timber stand improvement, in addition to single tree and small group selection harvests oriented towards the removal of subdominant species. Timber removed from these naturally regenerated stands was (and is) often locally and regionally sold for firewood, saw logs, and biomass chips.

The intensity of MBR Park’s timber harvests increased between 2004 and 2013. Intermediate thinnings, removing approximately one third of stand basal area, were employed in both planted and naturally regenerated stands to meet an array of Park management objectives. Stand improvement thinnings and regeneration harvests, for example, were employed in naturally regenerated stands to promote high quality native northern hardwoods. Biomass was also removed in some of these stands to maintain views along the Park’s carriage road and designated outlooks, an important objective for tourism and visitor recreation. Patch cuts were employed to promote early-successional habitat and associated wildlife populations. Conversion treatments were employed in some plantations to transition them to native species. As a result of MBR Park’s land-use and forest management history, the study site is extremely valuable for assessing northeastern secondary forest recovery dynamics.

2.2. Methodology

2.2.1. Study area

The Marsh-Billings-Rockefeller National Historical Park (MBR Park) lies on the northern edge of Woodstock village in the Ottauquechee Valley of central Vermont (Windsor County), U.S.A. (Figure 1). It is located at the southern limit of the Northern
Appalachian - Boreal Forest ecoregion where it abuts the Lower New England / Northern Piedmont ecoregion (TNC 2001). MBR Park’s terrain ranges from 207 meters (680 ft) to 433 meters (1,421 ft) in elevation. The metamorphic bedrock is of Devonian origin and belongs to the Waits River formation, of which schist, phyllite, and quartzite containing limestone are characteristic (Gawler & Engstrom 2011). Derived from glacial till, the soils are fertile and loamy, ranging in texture from silt loam to loamy fine sand, and of variable stoniness.

Conifer plantations were established beginning in 1882, and as a result of limited nursery stock availability, were comprised primarily of European tree species, such as Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and European larch (*Larix decidua*). Later plantations established between 1905 and 1953 included pure stands of native eastern white pine (*Pinus strobus*) and red pine (*Pinus resinosa*), though these were planted on sites (e.g. loamy upland soils) on which those species were unlikely to have occurred pre-settlement (Cogbill 2000). The plantations today range in age from about 60 to 130 years (Figure 1).

While early stewardship was primarily plantation forestry, the surrounding land naturally regenerated, like most of the Northeast’s landscape, and developed into either pure northern-hardwood, mixed conifer-hardwood, or hemlock-dominated stands over time. The most common northern hardwoods in MBR’s are sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). Drier sites developed with a larger hophormbeam (*Ostrya virginiana*) component. Eastern hemlock (*Tsuga canadensis*) is the most
common conifer present in mixed conifer-hardwood stands, but white pine and balsam fir
(*Abies balsamea*) also comprise minor components in some areas. Stands began to
naturally regenerate in the late 1800s, and thus span a similar age range as the plantations
(Figure 1).

### 2.2.2. Data collection

#### 2.2.2.1. Field Data

We used forest monitoring data from a stratified sample of MBR’s forest stands. A subset of MBR Park’s 50 previously delineated stands (Wiggin 1993) were selected as reference stands by stratifying based on species composition, age, reforestation approach (planted vs. naturally regenerated), and silvicultural management history. Forest cover type classifications followed USDA Forest Service protocol (Brohman et al. 2005) based on percent basal area by species. The largest and/or most representative examples within each stratum were selected. Sixteen reference stands were selected in this way, consisting of eight plantations and eight naturally regenerated stands (Figure 1).

We used inventory data from two measurement periods (2003 and 2013) collected from permanent sampling plots established within each reference stand. The number of plots in a stand was proportionate to the size of the stand, ranging from three to six plots, with the majority of stands containing five plots. Stand 42 was an exception; having only one plot due to its particular dimensions; although statistical sampling was not possible it was selected for limited monitoring due to its unique combination of age and composition. A geographic information system was used to place the plots in a random pattern while ensuring they were well distributed within each stand. Pre-determined plot
centers were located in the field using a Trimble Pro XRS Global Positioning System. A total of 60 monitoring plots were first established in summer 2001, then remeasured in the summers of 2003 and 2013. We used the 2003 dataset to assess long-term stand recovery from 19th century land-use instead of the 2001 dataset because it captured two additional years of forest recovery dynamics with fine-tuned inventory methods.

Each permanent plot consisted of several nested square plots, line transects, and belt transects. Plot design and the corresponding attributes sampled are shown in Figure 2. Nested square plots are 0.1 ha, 0.05 ha, 0.02 ha, and 1 m-squared in size. Canopy closure was measured at the center point of each plot using a spherical densitometer. In the 0.05-ha plot, all live and dead trees greater than 5 cm diameter at breast height (DBH) and greater than 1.37 m tall were permanently tagged, measured, and recorded by species, diameter, height, and decay stage (1-9, snags only). Tree heights and crown depth on each tagged tree are measured using an Impulse 200 laser range finder.

The 0.1-ha plot size was used to record the same information described above for trees over 50 cm DBH (i.e., large trees) and snags over one m tall with upper diameters greater than 10 cm. The 0.02-ha plot was used for tallying saplings (by species) that were greater than 1 m tall but less than 5 cm DBH. Downed CWD (downed logs ≥ 10 cm diameter at intercept; > 1 m length) volume by decay class (1-5) was estimated using a line intercept method (two 31.62 m transects per plot), in which the species of each inventoried log was recorded, following Warren and Olsen (1964) as modified by Shivers and Borders (1996). Tree seedlings (regeneration < 1 m height) were sampled by species within two belt transects that were each 1 m wide and 31.62 m long (Figure 2). Two
dominant canopy trees within each plot were cored at breast height to allow subsequent laboratory determination of tree age and site index.

2.2.2.2. Documentary data

Nearly 150 years of documentary data from Park records were used to assess stand management history spanning the time period of 1880 to 2013. These stand narratives provided the following information: the date of stand establishment, method of establishment (i.e., naturally regenerated or planted), and management history (i.e., harvest frequency and intensity).

The harvest information provided within our documentary data ranged in specificity. Some stand records, for example, provided the quantities and timber product removed, post-harvest remaining basal area, and methods of removal, while other records generally stated, “intermediate thinning” for one or more management year. Most of the harvest information provided for management years between the dates of stand establishment up to the year 2003 met the latter description. The Park’s management history during this time consisted primarily of low intensity treatments, such as understory thinnings and stand improvement cuttings. Silvicultural treatments shifted between the years of 2004 and 2013, with more intensive thinnings employed in some stands, and regeneration harvesting in others to meet an array of Park objectives.

Based on the historical documentation, two ordinal rankings (0-5) and categorical classifications (low vs. high), one for harvest intensity and one for harvest frequency, were assigned to each reference stand in both datasets (2003 and 2013). An ordinal ranking of 0 indicated the stand had no documentation of being harvested, while an
ordinal ranking of 5 indicated the stand had the most intense or frequent harvesting practices detailed in park records. Ordinal frequency rankings were generated based on the number of harvests and the average amount of time (years) between harvests (Table 4). Thus, stands assigned an ordinal ranking of 5 had the greatest number of harvests and least time between harvests observed at MBR Park. Stands with an ordinal ranking of 0-2 were classified with a history of low harvest intensity or frequency and stands assigned an ordinal ranking of 3-5 were classified with a history of high harvest intensity or frequency (Table 4).

The management history predictor variable for our 2003 dataset (spanning date of stand establishment up to 2003) was classified as low intensity (n=12) at nearly equally distributed levels of harvest frequencies (low n=7, high n=9) (Table 2). The number of stands classified with high intensity silvicultural prescriptions doubled (n=8, Table 3) in our 2013 dataset (based on management between the years of 2004 and 2013), thus this dataset was classified with a high intensity management history predictor variable. There was no change in harvest frequency levels between the two datasets.

2.2.3. Statistical analyses

Forest inventory data were input into the Northeast Ecosystem Management Decision Model (NED-2, Twery et al. 2005) to generate a variety of forest-structure metrics, including aboveground live tree biomass estimates based on species group-specific allometric equations developed by Jenkins et al. (2003). Standing dead carbon was quantified according to California Air Resources Board carbon inventory protocol (Bamberger 2013). Each inventoried dead tree height was compared to an allometrically
estimated live tree height to account for the same stem. This allowed us to account for missing biomass due to upper stem breakage (i.e., snaps). Aboveground biomass was adjusted (by thirds) based on the difference between the measured dead and estimated live tree heights. A density reduction factor correlating with dead tree decay stage (Harmon et al. 2011) was then applied to further account for loss of wood density and physical integrity in the remaining dead stem.

We calculated downed CWD biomass (Mg/ha) by multiplying downed log volumes (m$^3$/ha) by their respective species’ specific gravities per decay class (1-5) and adjusting biomass by carbon content per decay class following Harmon et al. (2011). Carbon was calculated by dividing biomass estimates in half. Relative-density calculations followed Curtis (1982). Two plots from Stand 8 containing a few very large (e.g., > 1m DBH), residual open-grown (also called “legacy” or “wolf”) trees were removed from all statistical analyses in both datasets because biomass results were overly skewed by the presence of these three individual trees. Metrics reported in tables include all the plots for comparison purposes.

Departure from normality was tested for all variables using the Shapiro-Wilk test (Zar 1996). Tests of variance (F tests) confirmed equal-variance assumptions. A modified version of Shannon-Wiener diversity index, $H'$, was used to quantify structural complexity following Staudhammer and LeMay (2001). The $H'$ index describes how basal area is apportioned by species and size class for all plots. The index integrates horizontal and vertical aspects of structural complexity, and thus includes living and dead trees. $H'$ considers species evenness and richness, and serves as an appropriate metric for
stand structural characteristics. T-Tests were employed to test the significance of reforestation approach on a suite of forest structural metrics, such as $H'$, quadratic mean diameter (QMD), relative density, and canopy closure. Simple linear regressions were run in JMP Pro 11 software to assess the relationship between forest age, aboveground carbon, and structure ($H'$ index).

Relationships between reforestation approach, site characteristics, and management history (predictor variables) and aboveground carbon and structural complexity (response variables, Table 5) were examined using Classification and Regression Tree (CART) analysis run in S-Plus software (Statistical Sciences 2002). CART is a nonparametric, binary procedure that is ideally suited for analyzing complex ecological data. CART explains variation of a single response variable. It partitions observations in the response variable through a series of splits based on values of the predictor variables (De'ath & Fabricius 2000). Cost-complexity pruning was used to eliminate non-significant nodes. CART was not used to establish definitive thresholds of the predictor variables. Instead, it identified the forest site and management characteristics most strongly associated with aboveground carbon storage and structural complexity outcomes in both long-term and modified post-harvest recovery pathways. Thus, CART’s hierarchy of predictor variables was of primary interest. All statistical tests were considered significant at the 95% level ($\alpha = 0.05$). We ran simple linear regressions to test the significance of individual predictor variables on each carbon outcome (Table 5) following multivariate analyses.

All statistical analyses were conducted twice: once with the 2003 dataset (data
spanning from date of stand establishment to the 2003 inventory) and once with the 2013 dataset. Analyses using the 2003 dataset were employed to examine stand development pathways characterized by long-term recovery from 19th century land-use. Hereafter we will refer to these as the “long-term recovery” pathway. Although the 2013 dataset also represents, in part, the effects of stand development since establishment, it was used to assess more recent changes in stand structure and aboveground carbon storage. Analyses using the 2013 dataset were indicative of altered trajectories of stand development resulting from elevated harvesting activity between 2004 and 2013, which we hereafter refer to as the “contemporary management” pathway. Thus, our 2003 dataset is most indicative of long-term stand recovery dynamics, while our 2013 dataset helps us understand the effects of recent management.

2.3. Results

In our study area, a variety of long-term recovery pathways converged on high levels of aboveground carbon storage, including both conifer plantations and naturally regenerated northern hardwood and mixed wood stands. Choice of silvicultural management approach (harvest intensity and frequency), however, dramatically altered those trajectories. Early declines (e.g. within the timeframe since establishment) in aboveground biomass have not been evident in MBR Park’s now late-successional (i.e. mature) secondary hardwoods and mixed-woods. This also held true for the conifer plantations until the recent increase in harvesting activity. Rather, our data do show positive relationships between forest age, aboveground carbon storage and development of stand structural complexity.
2.3.1. Stand age influences aboveground carbon storage and structural complexity

Total aboveground carbon (i.e., sum of mean live tree C, mean standing dead C, and mean downed CWD C across all decay classes) significantly \( (P = 0.037) \) increased with stand age in the long-term (i.e., \( \leq 130 \) years) recovery pathway. A significant \( (P = 0.009) \) and positive correlation of this nature was also evident in the contemporary management pathway. A consistent positive relationship between stand age and total aboveground carbon was observed in both planted and naturally regenerated stands in both the long-term recovery and contemporary management pathways (Figure 3). This relationship was only significant, however, in the long-term recovery \( (P = 0.030) \) and contemporary management pathway \( (P = 0.009) \) for naturally regenerated (i.e., northern hardwoods and mixed woods) stands, and not in planted stands \( (P = 0.259 \) and \( P = 0.166 \), respectively) (Figure 3). Forest age, although positively related to biomass accumulation in all stands, was therefore more strongly associated with total aboveground carbon storage in naturally regenerated stands compared to planted stands. Although forest age is correlated with aboveground carbon storage in naturally regenerated stands, those stands store, on average, less aboveground carbon than planted stands when controlling for differences in age (Figures 5 and 6). The relationship between stand age and \( H' \) index (Figure 3) was not statistically significant \( (P = 0.292) \) in either the observed long-term secondary forest recovery or contemporary management pathway, but the data do show an indirect association related to the positive correlations both variables showed with carbon storage (see below).
2.3.2. **Structural complexity and aboveground carbon storage**

With one exception, our indicator of structural complexity ($H'$ index) showed a positive relationship with total aboveground carbon in both planted and naturally regenerated stands for both datasets (Figure 4). The exception was long-term plantation development, in which no relationship was observed. As such, the relationship between total aboveground carbon and $H'$ index was only significant in the long-term forest recovery of naturally regenerated stands ($P = 0.004$), and not of planted stands ($P = 0.992$). Despite the observed positive trends (Figure 4), there was no statistically significant relationship between total aboveground carbon and $H'$ index in naturally regenerated ($P = 0.105$) or planted stands ($P = 0.364$) following contemporary management. Though statistically significant when all data was pooled, the regression explained only 25% of the variability in the relationship between these two variables, suggesting a correlation of only moderate strength (Figure 4).

2.3.3. **Forest management influences aboveground carbon storage and structural complexity**

2.3.3.1. **Influence on the recovery of carbon storage**

Classification and Regression Tree analyses suggest that forest management history had the greatest predictive strength for long-term carbon storage in all (live and dead) aboveground biomass pools (Figures 5 and 6). Of the six predictor variables modeled (Table 5), reforestation approach, harvest frequency, and stand age had the greatest predictive strength for long-term total and live aboveground carbon storage (Figure 5). Total and live aboveground carbon outcomes did not significantly differ by
re forestation approach \((P = 0.083)\) in long-term recovery pathway (Table 6). However, re forestation approach showed a strong association in CART results, with naturally regenerated stands storing less aboveground carbon than planted stands (Figure 5). Harvest frequency (0-5 ordinal rankings) and stand age were secondarily predictive of long-term carbon storage in these biomass pools (Figure 5).

The relationship between harvest frequency and long-term total and live aboveground carbon storage pools differ among re forestation approaches (Figure 5). For example, in the long-term recovery pathway, conifer plantations with a history of low harvest frequencies (i.e., \(\leq 2\) ranking) stored greater amounts of total and live carbon than planted stands with a history of high harvest frequencies (i.e., \(\geq 3\) ranking). Planted stands with a low harvest frequency history stored an average of about 60 Mg/ha of total aboveground carbon more than those with a history of high harvest frequencies in the long-term (Figure 5). This was not true for the same carbon pools in naturally regenerated stands, as high harvest frequencies encouraged greater aboveground carbon storage in their long-term recovery. Naturally regenerated stands with a high harvest frequency history stored an average of about 15 Mg/ha of total aboveground carbon more than those with a long-term history of low harvest frequencies.

Older stands stored more carbon in all (i.e., live and dead) aboveground pools (Figure 5 and 6). The greatest total and live carbon storage (208.50 Mg/ha and 195 Mg/ha, respectively) observed in long-term recovery pathway was achieved through a history of plantation forestry at low harvest frequencies (Figure 5A and 5B). The lowest observed long-term total and live carbon storage (77.07 Mg/ha, and 67.24 Mg/ha,
respectively) was achieved through natural regeneration, a history of low harvest frequencies, and in stands less than 93 years of age (Figure 5A and 5B).

Of the six-predictor variables (Table 5) included in our CART analyses, historic harvest intensity had the greatest predictive strength for dead aboveground carbon pools (i.e., snags, downed CWD classes 1-5, downed CWD classes 3-5) recovering over the long-term (Figure 6). Stands subjected to any harvesting, even infrequent, low intensity thinning entries (i.e., intensity ≥ 1), stored less carbon in all dead biomass pools than stands that had no harvesting (n=2) (Figure 6). Percent conifer by basal area and stand age were secondarily associated with partitioned values of dead aboveground carbon pools, but site class (i.e., productivity) was also related to partitioned values of downed CWD carbon pools (Figure 6B and 6C). As with long-term total and live aboveground carbon storage outcomes, older stands stored more carbon in dead biomass pools (Figure 6) than younger stands.

The greatest observed long-term carbon storage (10.78 Mg/ha) in standing dead biomass was achieved in stands with a low intensity (i.e., ≤ 2) harvest history and, dominated by conifers (> 77% of basal area). The least amount of carbon stored in standing dead biomass was observed in stands with a history of high harvest intensities (Figure 6A). The greatest amount of long-term carbon stored in downed CWD pools was observed in stands with little or no harvesting history (Figure 6B and 6C). Downed CWD in decay classes indicative of more advanced decomposition (3-5, see Figure 6C) stored approximately 62% of the total amount of carbon observed in all classes of downed CWD (Figure 6B). The least amount of carbon stored in all classes (1-5) of downed CWD (2.70
Mg/ha) was observed in stands with a harvest history (≥ 1 intensity), that were less productive (site class ≥ 1.25), and equal to or less than approximately 103 years of age (Figure 6B). Similarly, the lowest observed carbon stored in advanced decay classes of downed CWD (1.34 Mg/ha) was achieved in stands with a harvest history (≥ 1 intensity), that were less productive (site class ≥ 1.75) (Figure 6C).

The same subset of variables (Table 5) predictive of long-term recovery also demonstrated predictive strength on forest carbon outcomes following contemporary management. However stand age had the greatest predictive strength for most aboveground carbon pools (all but live tree) in the contemporary management pathway, with reforestation approach, and harvest frequency and intensity rankings being secondarily predictive of all (live and dead) aboveground carbon pools. Site class was additionally associated with downed CWD carbon pools for partitioned values at a subset of the reference stands. Harvest intensity had the greatest predictive strength for live aboveground carbon storage in contemporarily managed stands. Older stands stored significantly (P = 0.009) more carbon in all (live and dead) biomass pools, with the greatest observed total aboveground carbon (183.20 Mg/ha) stored in stands older than 129 years of age following contemporary management. Stands younger than 103 years of age had the least carbon stored in both total and live aboveground carbon pools (85.58 Mg/ha, and 63.15 Mg/ha, respectively). Plantations in the contemporary management pathway following low intensity (i.e., ≤ 2) harvests stored more carbon in live tree biomass than naturally regenerated stands (192.70 Mg/ha and 115.90 Mg/ha, respectively) with the same harvest intensity history. Older (i.e., > 122 years old), more
frequently harvested stands stored, on average, more carbon in standing dead tree pools than those with a less frequent contemporary harvest history.

Although reforestation approach or percent conifer composition demonstrated consistent (though secondary compared to stand age) relationships with aboveground carbon storage post contemporary management, they were most predictive of carbon storage outcomes in long-term recovery. Our results suggest that recent (i.e., 2004-2013) changes in harvest management practices altered long-term biomass development and carbon storage pathways, making stand age and harvest intensity more influential on contemporary aboveground carbon storage.

### 2.3.3.2. Influences on structural complexity development

As seen in long-term aboveground carbon pools, CART analyses also suggest forest management had the greatest predictive strength for long-term recovery of structural complexity as measured by $H'$ index. Of the six-employed predictor variables (Table 5), percent conifer (indicative of reforestation approach) was most predictive of long-term structural complexity (i.e., $H'$ index) (Figure 7). Historic harvest frequency and harvest intensity were secondarily associated with partitioned values of structural complexity outcomes (Figure 7). As of 2003, 10 of the 16 reference stands had less than 78% conifer species composition, eight of which were naturally regenerated. The six reference stands with greater than 78% conifer species composition were planted (Table 2). As such, reforestation approach (i.e., NR vs. PL) significantly influenced percent conifer and hardwood composition of basal area in both long-term recovered (Table 6) and contemporarily managed (Table 7) stands. The strong positive correlation between
percent conifer and long-term and contemporary structural complexity (Figure 7) appears, in our data, to be closely related to reforestation approach.

In fact, when evaluated in a T-Test, structural complexity indices, such as $H'$ ($P = 0.035$), and other metrics of stand structure, such as relative density ($P = 0.001$), were significantly different between reforestation approaches in stands recovering over the long-term (Table 6). Although $H'$ did not significantly differ between planted and naturally regenerated stands following contemporary management (Table 7), plantations and stands with greater percent conifer compositions had greater indices of structural complexity. We can therefore infer that they were more structurally complex despite their length of recovery.

Classification and Regression Tree analyses indicated that historical harvest frequency had the second greatest predictive strength for long-term structural diversity in stands with less than 78% conifer species composition (i.e., naturally regenerated stands) (Figure 7). Naturally regenerated stands that were less frequently (i.e., ranking of ≤ 2) harvested had on average, greater structural complexity ($H' = 0.81$) than those with a history of high harvest frequency ($H' = 0.62$) (Figure 7).

Historical harvest intensity had the second greatest predictive strength for $H'$ in stands comprised of greater than or equal to 78% conifer species (i.e., plantations). Plantations with less intense (i.e., ranking ≤ 2) historic management regimes had on average, less structural complexity ($H' = 1.04$) compared to those with more intensive harvesting histories ($H' = 1.67$) (Figure 7). Managed plantations were, however, more structurally complex (i.e., greater $H'$ indices) than naturally regenerated stands (Figure
The predictor variables (Table 5) demonstrated similar levels of influence on structural complexity outcomes (i.e., $H'$ index) following contemporary management. A notable difference in the CART outcomes was observed in the percent conifer species composition threshold, which decreased to 68% (from 78%). Quadratic mean diameter was the only forest structural variable significantly ($P = 0.015$) different between contemporarily managed naturally regenerated and planted stands (Table 7). The relationship between independent variables of secondary predictor strength, such as harvest frequency and intensity, remained the same in the contemporary management pathway. However, a larger average of $H'$ (1.82) was found for plantations experiencing a recent increase in harvest activities.

### 2.4. Discussion

Our results tell a story of forest recovery spanning over a century of land-use history and change. To previous chronosequence studies on this topic (Dyer et al. 2010, Keeton et al. 2011, Gunn et al. 2014), we add our retrospective analysis of a landscape with a documented management history. The high carbon storage observed in MBR’s mature, planted and naturally regenerated stands supports previous reports that aboveground biomass can accumulate late into stand development in secondary forests (Luyssaert et al. 2008, Keith et al. 2009, Keeton et al. 2011, Gunn et al. 2014, McGarvey et al. 2015), but also suggest the ability to accumulate high levels of biomass earlier than previously reported (Goring et al. in press). While carbon dynamics may differ between primary and secondary forests as hypothesized or reported previously (Siccama et al.
2007, Keeton et al. 2011, Stephenson et al. 2014), our results indicate that secondary forests nevertheless have the potential to re-achieve high levels of carbon storage (Gunn et al. 2014, McGarvey et al. 2015), depending on site-specific variability, disturbances, and degree of anthropogenic stress (Fahey et al. 2005, Seidl et al. 2014).

Our results also suggest forest management practices can both positively and negatively direct or alter pathways of aboveground carbon accumulation and structural complexity development in secondary forests recovering from clearing or disturbance, in this case, 19th century land-use (Pregitzer and Euskirchen 2004, Rhemtulla et al. 2009, Goring et al. in press). This finding is consistent with forward-looking simulation studies (e.g. Harmon & Marks 2002, Nunery & Keeton 2010, Chen et al. 2014), but provides a long-term empirical perspective.

2.4.1. Secondary forest recovery dynamics as influenced by management

Our results suggest the high potential for carbon storage on carefully managed forested landscapes. As of 2003, our 16 reference stands stored an average total aboveground carbon of 153.57 Mg/ha, which is nearly three times the current average reported for secondary forests in the northeastern U.S. (Birdsey & Lewis 2003). This high-magnitude carbon storage reflects the unique context of MBR: namely relatively old stand ages (by comparison with the regional averages), long-term low intensity management, and sizable contributions of biomass in conifer plantations and mixed woods. The recovery that occurred to 2003 suggests the high potential for carbon accumulation on sustainably managed landscapes, particularly where an emphasis is placed on maintaining high stocking, a central requirement of contemporary forest carbon
offset markets (see Russell-Roy et al. 2014 and Kerchner and Keeton 2015). Mean total carbon in aboveground pools decreased to 130.20 Mg/ha in 2013, after a decade of increased harvesting activity, suggesting that carbon accumulation pathways (see Keeton et al. 2011, Thompson et al. 2013) have been altered or redirected, at least over the near term. Previous simulation studies have shown that – even when accounting for the life cycle of carbon transferred to wood products – carbon trajectories altered in this way may take decades or centuries to recover the full net (in-situ plus wood products) carbon storage potential of the no-management or light management pathway (Harmon and Marks 2002, Seidl et al. 2007, Nunery and Keeton 2010). Our finding thus highlights the importance of considering carbon trajectories relative to other important management objectives as were operative at MBR, such as early-successional habitat creation, improved tree regeneration, and commodity production.

MBR Park contains a noteworthy pool of carbon-rich secondary forests. Old white pine stands (e.g., Stands 45 and 42) (Figure 1) are some of the Park’s earliest-established plantations and stored the greatest amount of observed carbon (Table 2 and 3). The carbon stored in these stands’ aboveground biomass pools (live and dead) is nearly equal to the upper threshold of the maximum potential aboveground carbon storage range reported (Keeton et al. 2011) for old-growth northern hardwood-conifer forests (approximately 125-225 Mg/ha). In fact, one of MBR Park’s old white pine stands (Stand 45) surpassed this upper threshold, storing approximately 229 Mg C/ha (Table 3). Despite the high magnitude carbon stored in MBR Park’s eastern white pine plantations, they produced less merchantable timber volume (Table 1) than projected for white pine
stands of similar ages by Frothingham (1914) and Leak et al. (1970) (discussed in Chapter 1). Seymour (2007) found merchantable timber yields and value depend on early manual pruning in eastern white pine old-field monocultures, like those found in MBR Park. Our results indicate that, in some cases, old white pine plantations may develop unusually high levels of carbon storage attributable to both a history of low harvest intensities and frequencies and efficient allocation of canopy growing space achievable through density regulation (Table 2). It is possible that this low-intensity management history limited pruning necessary for greater yields of merchantable timber.

Carbon storage in MBR Park’s eastern white pine plantations was greater than those in non-native plantations (e.g., European larch, Scots pine, and Norway spruce). Furthermore, our results suggest that older plantations store more carbon than younger and naturally regenerated stands. These results should not be misconstrued as an argument favoring conversion of hardwood or other native or endemic forests to conifer plantations. Clearly this would have significant negative biodiversity impacts. Rather it is a recognition that the old plantations, comprising a minor but historically important component of the northeastern landscape are contributing to landscape-scale carbon storage, and that native white pine, in particular, has great potential as one element of holistic forest carbon management.

In notable contrast to some previous studies (Curtis 1997, Balboa-Murias et al. 2006, Nunery and Keeton 2010) naturally regenerated stands stored more carbon when they had a history of slightly more frequent management (Figure 5). This finding is supported by a study that reports frequent low-intensity single tree selection and diameter
limit harvests in Central Appalachian forests to store greater total carbon than when less frequently harvested (Davis et al. 2009). However, our ordinal rankings for the historic management prior to 2003 at MBR encompassed a limited range of harvest intensities - all treatments during this time period were relatively low intensity (e.g., intermediate treatments such as thinnings and stand improvement cuttings). Therefore, while our results do suggest that low intensity treatments in regenerating secondary hardwoods have had a positive effect on carbon development, they are not indicative of a positive effect from more intensive treatments, such as selection system regeneration harvests. This conflicts with prior research on thinnings, which showed some methods, such as thinning from above (Hoover and Stout 2007) and partial harvests (Zhou et al. 2013) having negative effects on aboveground carbon storage.

Moreover, the local effect of harvesting on aboveground carbon storage is highly dependent on initial stand conditions (Harmon et al. 2009). Furthermore, species types (shade tolerant or intolerant) and their compositional development affect the biomass accumulation dynamics of recovering forests (Bauhus et al. 1998, Jacob et al. 2010). The relatively low intensity stand improvement harvests employed in MBR Park’s naturally regenerated stands appears to have been successful at improving stand conditions, including stocking and growth. These results demonstrate that careful, intentional, and scientifically informed stewardship can enhance carbon storage if practiced over the long-term.

In fact, relative to plantations, equally high or greater carbon storage was observed in naturally regenerated stands at MBR. This was even observed in stands with
a limited management history (e.g., Stand 38, Table 2). Mixed woods, particularly stands with native conifers (e.g., Stand 8 and 38, Figure 1), stored the most aboveground carbon observed in MBR Park’s naturally regenerated stands (Table 2 and 3). These notable contributions of carbon storage resulted from the presence of legacy, or old-grown “wolf” trees and were therefore attributed to old-field succession (Egler 1954), and the influential role of biological legacies, and large trees, on stand development (Franklin et al. 2002). Our results indicate limited management intensities in mixed woods encouraged high live and total large tree densities. These outcomes emphasize the importance of stand-specific management, native conifers as a component of mixed-woods, and late-successional biomass accrual on naturally regenerated stands carbon storage potential.

2.4.2. Stand age, biomass, and structure

Principles of stand development often relate biomass accumulation (i.e., carbon storage) to stand age (Bormann & Liken 1979, Oliver & Larson 1996, Franklin et al. 2002). The increase of dominant tree age and density of large trees as stands develop (as seen throughout MBR Park) is important, as a strong positive relationship between tree age, large tree density, and biomass accumulation was identified previously in the northeastern (Keeton et al. 2011), upper Great Lakes (D’Amato et al. 2011) U.S. regions. Our results support these relationships, as older stands at MBR, regardless of reforestation approach, developed significantly more aboveground biomass, with the greatest observed carbon stored in stands with relatively high percent conifer composition (of mostly native species), high large tree densities, and greater indices of structural
complexity (i.e., $H'$ index).

2.4.3. Structural complexity ($H'$ index) increases with total aboveground carbon storage

As the growing body of literature suggests, our results indicated a positive relationship between carbon storage and stand structural complexity (Figure 4). However, our regression analysis suggested that $H'$ index is also strongly influenced by other sources of variability. One of these is clearly the approximately 130 years of natural resource stewardship and management. The lack of relationship observed between total aboveground carbon and structural complexity (i.e., $H'$ index) in the long-term recovery of conifer plantations (n=8) (Figure 4) best demonstrates this dynamic. Aboveground carbon and $H'$ did not correlate in these planted stands. Their long-term history of intermediate harvests likely accelerated growth rates but did not regenerate new cohorts, thus maintaining even-aged structure with low $H'$ index values. Despite the high degree of biomass accrual in plantations (Figure 3), not until advanced regeneration of native, site-endemic, shade-tolerant hardwoods were released by contemporary management practices did multi-cohort structure develop, resulting in higher $H'$ index values (Figure 4). Similarly, the long-term history of stand improvement thinnings and regeneration harvests (e.g., single tree and small group selections) in MBR’s naturally regenerated stands encouraged uneven-aged structural development. The limited management in naturally regenerated stands also promoted high live and total large tree densities. The presence of large trees, and old-grown “wolf” trees are an important aspect of structural complexity, as they possess greater carbon storage potential. Thus, the variability in the
relationship between total aboveground carbon and H’ can be explained, in part, by the stand management employed throughout MBR Park.

2.4.4. Management implications

Our results support a conclusion that reducing harvesting frequency (Curtis 1997), increasing rotation lengths (Harmon & Marks 2002), and encouraging post-harvest structural complexity (Keeton 2006, Franklin et al. 1997, Swanson 2009) increases stand level carbon storage. Reducing harvesting frequency can effectively increase carbon storage in forests with greater percent composition of conifers (especially native species). But our results also showed that carefully planned stand improvement cuttings or low intensity thinnings, as demonstrated by 130 years of scientifically informed forest stewardship at MBR, can actually increase carbon storage in recovering secondary hardwoods, most likely because of improved tree vigor, growth, and stocking.

Only one of our sixteen reference stands had a history completely free of harvests. However, the high-magnitude carbon storage observed in that stand and others with limited management suggest that reserve-based approaches provide an additional and promising option for carbon management. This is particularly relevant to dead aboveground biomass pools, which stored considerably less carbon when stands were subject to management (regardless of intensity level). It is thus important to consider dead wood recruitment and retention in silvicultural practices. This is especially true for secondary forests, in which dead wood is the one of the last carbon pools to develop, especially where timber harvests are present (McGarvey et al. 2015). The pertinence of reserve-based management is also clear when considering MBR’s net reduction in carbon
storage following the recent intensification of harvests. Despite accelerated growth rates in residual trees, it is likely that net carbon storage may be significantly impaired compared to that of unmanaged or less-intensively managed stands based on previous research (Harmon & Marks 2002, Nunery & Keeton 2010, Chen et al. 2015).

Our results reinforce the importance of high post-harvest structural retention, as the retention of biological legacies can significantly affect carbon storage in northeastern forests regardless of stand age (Brown et al. 1997, Nunery & Keeton 2010, D’Amato et al. 2011, McGarvey et al. 2015). While intensive management can increase carbon uptake rates by promoting young tree growth, our results support findings that young forests store significantly less carbon than old forests. Thus, encouraging late-successional and old growth forest structural and compositional dynamics is one forest management approach that can promote aboveground carbon storage (Franklin et al. 2002, Keeton 2006, Rhemtulla et al. 2009, Keeton et al. 2011, McGarvey et al. 2015). It is, however, vital to consider carbon trajectories relative to other important management objectives. If the intent is to integrate carbon storage with other management objectives, like the restoration of native species to exotic conifer plantations, alternative carbon forestry (i.e., post harvest structural retention, extended rotations) practices must be considered with a keen eye on property-scale stocking. Treatments should be scheduled over time and space to carefully minimize net reductions in carbon stocking and potentially emulate the forests’ temporal and spatial natural disturbance regimes.

Although researchers have identified techniques to increase forest carbon storage, carbon dynamics will become more uncertain with climate change. Based on the
projected temperature and precipitation changes for the Northeast (Huntington et al. 2009, Rustad et al. 2012), it is likely that temperature- and moisture-sensitive processes, like primary productivity and decomposition rates (Harmon et al. 2004), will change (Swanson et al. 2009). Climate change also has the potential to alter successional dynamics, influencing the rate and development of aboveground biomass accumulation (Aber et al. 2001). Similarly terrestrial ecosystem’s natural disturbance regimes are shifting (Dale et al. 2001). Although the expected effects of elevated atmospheric CO₂ concentrations on forested ecosystems vary, it is possible for net photosynthesis and tree growth to increase, providing a negative feedback on changing CO₂ concentrations. This negative feedback, however, may be short-lived, as limiting factors (e.g., water and nutrient availability) can affect species’ ability to increase growth and photosynthesis rates in the long-term (Long et al. 1996). These changes, along with the spread of exotic pests and potential alterations of disturbance regimes, will affect forest carbon sequestration dynamics, creating an ongoing need for adaptive planning and management.

Although it is difficult to predict how climate change will affect temperate forests’ ability to store carbon, elevated levels of CO₂ has made it increasingly important to manage these forests for carbon storage, as doing so regulates the climate (Evans & Perschel 2009). Developing carbon markets recognize the important role of forests in the carbon cycle and therefore view sustainable forest management as a vital component of climate change mitigation (Ray et al. 2009b). Thus, informed management is essential to ensure U.S. forests remain a carbon sink.
2.5. Conclusion

Our results add to a growing body of literature showing that late-successional and maturing secondary temperate forests have greater carbon storage potential than previously reported in theoretical projections (e.g., Bormann & Likens 1979) and observations spanning a relatively limited range of successional trajectories (see reviews in Oliver & Larson 1996). Multiple pathways of stand development can occur in secondary forests and are strongly influenced by reforestation approach and subsequent forest management practices. The resulting complex pathways of recovery produce a range of carbon accumulation outcomes. Managing forests for high carbon storage is also likely to provide late-successional habitats important for under-represented elements of biological diversity (Bauhus et al. 2009, McKinley et al. 2011, Lindenmayer et al. 2012, Burrascano et al. 2013). Our results clearly suggest recovering secondary northeastern forests play a vital role in carbon sequestration and thus are helping to mitigate or dampen the future intensity of climate change. This provides a strong impetus for policies and practices that promote and ensure conservation of forest cover and appropriate management practices needed to maximize biomass development and structural diversity.

We now have the opportunity to learn from the Northeast’s unique land-use history. Doing so, however, requires acknowledging that land-use decisions made over a century ago still shape the region’s landscape today. As such, current land-use decisions must be made with both the past and future in mind. The late-successional, high-biomass
recovery of northern hardwood, conifer, and mixed hardwood-conifer stands at MBR Park reflect the resiliency of northeastern U.S. forested ecosystems and their ability to recover through multiple pathways of development. However despite this observed resiliency, U.S. northeastern forests will likely never fully recover the biomass lost during the nineteenth century as a result of regional-scale forest clearing. This is not to suggest inability or limitation of secondary forests to re-achieve high-magnitude carbon storage levels typical of primary or old growth forests. Indeed, our findings demonstrate some recovery pathways yield equally high or greater biomass outcomes. The dynamic nature of long-term forest recovery suggests the need for well-informed, stand-specific management (where management is deemed appropriate), including approaches that provide older and more structurally complex stand development conditions.
LITERATURE CITED


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Frothingham, E.H. 1914. "White pine under forest management."


comparison across decay classes and tree species.


Table 1: Eastern white pine stands and merchantable timber volume at MBR Park. NR = naturally regenerated, PL = plantation. Measurements are derived from 2003 data, yield based on DBH at midpoint.

<table>
<thead>
<tr>
<th>Stand #</th>
<th>Stand area (ha)</th>
<th>Age (years)</th>
<th>Structure</th>
<th>Reforestation approach (NR vs. PL)</th>
<th>White Pine yield cu.m/ha</th>
<th>Total yield cu.m/ha</th>
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</table>
**Table 2. Descriptive information for MBR Park’s 16 reference stands in 2003. NR = naturally regenerated, PL = plantation, RD = relative density. * Two of three of Stand 8’s inventoried plots (plot 23 and 25) contained 1 and 3 wolf trees, respectively, which ultimately skewed analyses. The values reported for Stand 8 therefore excludes data from plot 23 and 25.**

<table>
<thead>
<tr>
<th>Stand #</th>
<th>Stand age (years)</th>
<th>Stand area (ha)</th>
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<th>Reforestation approach</th>
<th>Historical harvest intensity</th>
<th>Historical harvest frequency</th>
<th>Species cover type</th>
<th>Species composition by BA</th>
<th>Total basal area (m²/ha)</th>
<th>Total aboveground carbon (Mg/ha)</th>
<th>$H'$ Index</th>
<th>RD (#/ha)</th>
<th>Big tree density (#/ha)</th>
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</table>

† When all three plots are included in the calculations, Stand 8 has a 26.9% conifer composition of basal area, a total basal area of 62.4 m²/ha, a mean total aboveground carbon of 210.01 Mg/ha, an $H'$ index of 0.49, a RD of 11.98, and total big tree density of 37/ha.
Table 3. Descriptive information of MBR Park’s 16 reference stands in 2013. NR = naturally regenerated, PL = plantation, RD = relative density.

<table>
<thead>
<tr>
<th>Stand #</th>
<th>Stand age (years)</th>
<th>Stand area (ha)</th>
<th>Site class</th>
<th>Reforestation approach</th>
<th>Historical harvest intensity</th>
<th>Historical harvest frequency</th>
<th>Species cover type</th>
<th>Forest cover type</th>
<th>% Conifer (composition by BA)</th>
<th>Total basal area (m²/ha)</th>
<th>Total aboveground carbon (Mg/ha)</th>
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<th>Big tree density (#/ha)</th>
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<td>1</td>
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<td>2.7</td>
<td>1</td>
<td>PL</td>
<td>High</td>
<td>High</td>
<td>Larix decidua-hardwood (European larch-hardwood)</td>
<td>Mixed wood</td>
<td>58.9</td>
<td>32.8</td>
<td>64.00</td>
<td>0.39</td>
<td>5.76</td>
<td>20</td>
</tr>
<tr>
<td>2</td>
<td>126</td>
<td>4.1</td>
<td>1</td>
<td>PL</td>
<td>High</td>
<td>High</td>
<td>Pinus strobus (white pine)</td>
<td>Conifer</td>
<td>95.9</td>
<td>45.7</td>
<td>153.66</td>
<td>1.88</td>
<td>8.54</td>
<td>103</td>
</tr>
<tr>
<td>4</td>
<td>61</td>
<td>6.6</td>
<td>2</td>
<td>PL</td>
<td>High</td>
<td>High</td>
<td>Pinus-hardwoods (pine-hardwoods)</td>
<td>Mixed wood</td>
<td>63.6</td>
<td>18.9</td>
<td>89.32</td>
<td>0.56</td>
<td>3.24</td>
<td>5</td>
</tr>
<tr>
<td>8*</td>
<td>65</td>
<td>3.9</td>
<td>2</td>
<td>NR</td>
<td>Low</td>
<td>High</td>
<td>Pinus-hardwoods (pine-hardwoods)</td>
<td>Mixed wood</td>
<td>26.9</td>
<td>10.0</td>
<td>42.79</td>
<td>0.15</td>
<td>2.03</td>
<td>17</td>
</tr>
<tr>
<td>13</td>
<td>63</td>
<td>1.8</td>
<td>1</td>
<td>PL</td>
<td>Low</td>
<td>High</td>
<td>Picea abies (Norway spruce)</td>
<td>Conifer</td>
<td>100</td>
<td>41.6</td>
<td>113.03</td>
<td>0.29</td>
<td>6.58</td>
<td>20</td>
</tr>
<tr>
<td>17</td>
<td>96</td>
<td>8.5</td>
<td>1</td>
<td>PL</td>
<td>High</td>
<td>High</td>
<td>Pinus resinosa (red pine)</td>
<td>Conifer</td>
<td>83.8</td>
<td>30.7</td>
<td>82.09</td>
<td>1.67</td>
<td>6.48</td>
<td>8</td>
</tr>
<tr>
<td>18</td>
<td>108</td>
<td>9.1</td>
<td>1</td>
<td>PL</td>
<td>High</td>
<td>High</td>
<td>Pinus strobus (white pine)</td>
<td>Conifer</td>
<td>89.5</td>
<td>48.2</td>
<td>144.71</td>
<td>1.90</td>
<td>8.72</td>
<td>100</td>
</tr>
<tr>
<td>21</td>
<td>131</td>
<td>12.6</td>
<td>1</td>
<td>NR</td>
<td>Low</td>
<td>Low</td>
<td>Tsuga-hardwoods (hemlock-hardwoods)</td>
<td>Mixed wood</td>
<td>43.9</td>
<td>40.0</td>
<td>135.69</td>
<td>0.70</td>
<td>7.98</td>
<td>18</td>
</tr>
<tr>
<td>24</td>
<td>93</td>
<td>9.9</td>
<td>1</td>
<td>NR</td>
<td>Low</td>
<td>High</td>
<td>northern hardwoods</td>
<td>Northern hardwood</td>
<td>5.5</td>
<td>21.6</td>
<td>100.68</td>
<td>0.93</td>
<td>4.25</td>
<td>28</td>
</tr>
<tr>
<td>30</td>
<td>113</td>
<td>6.4</td>
<td>1.5</td>
<td>NR</td>
<td>Low</td>
<td>Low</td>
<td>northern hardwoods</td>
<td>Northern hardwood</td>
<td>0</td>
<td>27.1</td>
<td>114.58</td>
<td>1.04</td>
<td>5.32</td>
<td>30</td>
</tr>
<tr>
<td>31</td>
<td>117</td>
<td>6.5</td>
<td>1.5</td>
<td>NR</td>
<td>High</td>
<td>Low</td>
<td>northern hardwoods</td>
<td>Northern hardwood</td>
<td>12.7</td>
<td>36.6</td>
<td>116.06</td>
<td>0.39</td>
<td>8.03</td>
<td>20</td>
</tr>
<tr>
<td>33</td>
<td>131</td>
<td>6</td>
<td>1.5</td>
<td>NR</td>
<td>High</td>
<td>Low</td>
<td>northern hardwoods</td>
<td>Northern hardwood</td>
<td>0</td>
<td>34.4</td>
<td>166.36</td>
<td>0.70</td>
<td>7.01</td>
<td>20</td>
</tr>
<tr>
<td>38</td>
<td>117</td>
<td>3.6</td>
<td>1.5</td>
<td>NR</td>
<td>Low</td>
<td>Low</td>
<td>Tsuga canadensis (eastern hemlock)</td>
<td>Mixed wood</td>
<td>72.5</td>
<td>53.5</td>
<td>183.60</td>
<td>1.03</td>
<td>9.11</td>
<td>77</td>
</tr>
<tr>
<td>39</td>
<td>108</td>
<td>33.7</td>
<td>1.5</td>
<td>NR</td>
<td>Low</td>
<td>Low</td>
<td>Tsuga-hardwoods (hemlock-hardwoods)</td>
<td>Mixed wood</td>
<td>48.1</td>
<td>40.6</td>
<td>136.56</td>
<td>0.65</td>
<td>7.79</td>
<td>33</td>
</tr>
<tr>
<td>42</td>
<td>131</td>
<td>2.1</td>
<td>2</td>
<td>PL</td>
<td>Low</td>
<td>Low</td>
<td>Pinus strobus (white pine), Picea abies (Norway spruce)</td>
<td>Conifer</td>
<td>91.5</td>
<td>62.9</td>
<td>202.06</td>
<td>0.99</td>
<td>10.6</td>
<td>140</td>
</tr>
<tr>
<td>45</td>
<td>131</td>
<td>8.8</td>
<td>1.5</td>
<td>PL</td>
<td>Low</td>
<td>Low</td>
<td>Pinus strobus (white pine)</td>
<td>Conifer</td>
<td>82.6</td>
<td>67.3</td>
<td>228.80</td>
<td>1.35</td>
<td>10.9</td>
<td>90</td>
</tr>
</tbody>
</table>

‡ Although recent harvestings removed the wolf trees inventoried in plot 23 and 25 in 2003, for consistency data from these plots are not included in Stand 8’s values reported below. When all three plots are included in the calculations, Stand 8 has a 44.9% conifer composition of basal area, a total basal area of 31.7 m²/ha, a mean total aboveground carbon of 52.01 Mg/ha, an $H'$ index of 0.17, a RD of 6.53, and a total big tree density of 17/ha.
Table 4. Criteria used to ordinally rank and categorically classify stand management history (i.e., harvest intensity and frequency) at MBR Park. Criteria were derived from MBR Park management records.

<table>
<thead>
<tr>
<th>Categorical classification</th>
<th>Ordinal ranking</th>
<th>Key words from documentary data</th>
<th>Number of harvests</th>
<th>Avg. time between harvests (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>0</td>
<td>no harvest history</td>
<td>0</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>&quot;prunned&quot;</td>
<td>1 - 3</td>
<td>≥61</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>&quot;light thinning&quot;, &quot;thinned&quot;</td>
<td>1 - 3</td>
<td>46 - 60</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>&quot;thinned&quot;</td>
<td>4 - 10</td>
<td>31 - 45</td>
</tr>
<tr>
<td>High</td>
<td>4</td>
<td>&quot;understory completely removed&quot;</td>
<td>11 - 29</td>
<td>16 - 30</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>&quot;dominate species harvested&quot;</td>
<td>≥30</td>
<td>0 - 15</td>
</tr>
</tbody>
</table>
Table 5. Predictor and response variables and variable types employed in statistical analyses. Note that total aboveground carbon is derived from summing the average live, standing dead, and downed CWD (all stages, 1-5).

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>Variable type</th>
<th>Response variable</th>
<th>Variable type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site class</td>
<td>Ordinal</td>
<td>Structure Pools</td>
<td></td>
</tr>
<tr>
<td>Stand age (years)</td>
<td>Continuous ratio scale</td>
<td>H' Index</td>
<td>Continuous ratio scale</td>
</tr>
<tr>
<td>Harvest intensity</td>
<td>Ordinal (0-5), Categorical (low vs. high)</td>
<td>Aboveground Carbon Pools (Mg/ha)</td>
<td></td>
</tr>
<tr>
<td>Harvest frequency</td>
<td>Ordinal (0-5), Categorical (low vs. high)</td>
<td>Total</td>
<td>Continuous ratio scale</td>
</tr>
<tr>
<td>Some variation of:</td>
<td></td>
<td>Standing dead</td>
<td>Continuous ratio scale</td>
</tr>
<tr>
<td>Reforestation approach (NR or PL)</td>
<td>Categorical</td>
<td>Down CWD all stages</td>
<td>Continuous ratio scale</td>
</tr>
<tr>
<td>Cover type</td>
<td>Categorical</td>
<td>Down CWD stages 3-5</td>
<td>Continuous ratio scale</td>
</tr>
<tr>
<td>Percent conifer (by composition BA)</td>
<td>Continuous ratio scale</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note that total aboveground carbon is derived from summing the average live, standing dead, and downed CWD (all stages, 1-5).
Table 6. Descriptive statistics and T-Test results for 2003 forest structural variables grouped by reforestation approach. The boldfaced is used to identify significant P values.

<table>
<thead>
<tr>
<th>Forest structure variable</th>
<th>Natural regeneration</th>
<th>Plantation (PL)</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stocking (live and dead)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal area (m²/ha)</td>
<td>Total 34.72 ± 8.14</td>
<td>55.34 ± 8.14</td>
<td>3.84</td>
<td><strong>0.002</strong></td>
</tr>
<tr>
<td>Aboveground carbon (Mg/ha)</td>
<td>Total 124.39 ± 30.40</td>
<td>161.86 ± 30.40</td>
<td>1.87</td>
<td>0.083</td>
</tr>
<tr>
<td>Big tree density (#/ha)</td>
<td>Total 30.42 ± 33.10</td>
<td>62.52 ± 33.10</td>
<td>1.47</td>
<td>0.163</td>
</tr>
<tr>
<td>Stem density (#/ha)</td>
<td>Total 739.46 ± 231.84</td>
<td>883.66 ± 231.84</td>
<td>0.94</td>
<td>0.362</td>
</tr>
<tr>
<td>Relative density</td>
<td>Total 6.95 ± 1.20</td>
<td>10.41 ± 1.20</td>
<td>4.40</td>
<td><strong>0.001</strong></td>
</tr>
<tr>
<td>Regeneration density (#/ha)</td>
<td>Live 13,629 ± 13,540</td>
<td>20,174 ± 13,540</td>
<td>0.73</td>
<td>0.476</td>
</tr>
<tr>
<td>Composition, by basal area (%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conifer</td>
<td>28.41 ± 15.63</td>
<td>84.38 ± 15.63</td>
<td>5.43</td>
<td><strong>0.0001</strong></td>
</tr>
<tr>
<td>Hardwood</td>
<td>71.59 ± 15.63</td>
<td>15.63 ± 15.63</td>
<td>-5.43</td>
<td><strong>0.0001</strong></td>
</tr>
<tr>
<td>H’ index</td>
<td>0.69 ± 0.31</td>
<td>1.17 ± 0.31</td>
<td>2.34</td>
<td><strong>0.035</strong></td>
</tr>
<tr>
<td>Quadratic mean diameter (cm)</td>
<td>24.589 ± 4.28</td>
<td>29.69 ± 4.28</td>
<td>1.75</td>
<td>0.103</td>
</tr>
<tr>
<td>Canopy closure (m)</td>
<td>85.39 ± 13.54</td>
<td>88.33 ± 13.54</td>
<td>0.33</td>
<td>0.747</td>
</tr>
</tbody>
</table>
Table 7. Descriptive statistics and T-Test results for 2013 forest structural variables grouped by reforestation approach. The boldfaced is used to identify significant P values.

<table>
<thead>
<tr>
<th>Forest structure variable</th>
<th>Values (mean ± 95% CI), by reforestation approach</th>
<th>T-Test results (DF = 14)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Natural regeneration (NR)</td>
<td>Plantation (PL)</td>
</tr>
<tr>
<td>Stocking (live and dead)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Basal area (m²/ha)</td>
<td>Total 32.98 ± 11.27</td>
<td>43.51 ± 11.27</td>
</tr>
<tr>
<td></td>
<td>Aboveground carbon (Mg/ha)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total 124.54 ± 39.02</td>
<td>134.71 ± 39.02</td>
</tr>
<tr>
<td></td>
<td>Big tree density (#/ha)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total 30.23 ± 30.35</td>
<td>60.79 ± 30.35</td>
</tr>
<tr>
<td></td>
<td>Stem density (#/ha)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total 631.11 ± 167.64</td>
<td>502.83 ± 167.64</td>
</tr>
<tr>
<td></td>
<td>Relative density</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total 6.44 ± 1.89</td>
<td>7.96 ± 1.89</td>
</tr>
<tr>
<td></td>
<td>Regeneration density (#/ha)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Live 8,215 ± 5,633</td>
<td>15,644 ± 5,633</td>
</tr>
<tr>
<td>Composition, by basal area (%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conifer</td>
<td>26.20 ± 16.47</td>
<td>83.22 ± 16.47</td>
</tr>
<tr>
<td>Hardwood</td>
<td>73.80 ± 16.27</td>
<td>16.78 ± 16.27</td>
</tr>
<tr>
<td>H' index</td>
<td>0.70 ± 0.39</td>
<td>1.13 ± 0.39</td>
</tr>
<tr>
<td>Quadratic mean diameter (cm)</td>
<td>26.91 ± 3.81</td>
<td>33.85 ± 3.81</td>
</tr>
<tr>
<td>Canopy closure (m)</td>
<td>81.84 ± 17.52</td>
<td>68.21 ± 17.52</td>
</tr>
</tbody>
</table>
Figure 1. Forest reference stands located in MBR National Historical Park. The stands are differentiated by reforestation approach (naturally regenerated vs. planted). Blue circles represent the date (range) of stand establishment, with larger sizes representing older stand ages.
Figure 2. Monitoring plot design and inventory protocol for aboveground biomass pools. Sixty fixed 0.05 ha plots were established throughout 16 reference stands in 2001.
Figure 3. Mean total aboveground carbon (Mg/ha) and $H'$ structural diversity index over time (age), by reforestation approach and year.
<table>
<thead>
<tr>
<th>Year</th>
<th>2003</th>
<th>2013</th>
</tr>
</thead>
</table>

Figure 4. $H'$ structural diversity index over mean total aboveground carbon (Mg/ha), by reforestation approach and year.
Figure 5. CART model, showing statistically significant predictor variables selected, split values, and partitioned mean values (bottom) of the response variable (A. mean total aboveground carbon, B. mean live tree aboveground carbon, n = 16). The figure ranks variables by predictive strength (top to bottom) and in sequential order of importance as the response variable increases (left to right).

Stands with low harvest frequencies received an ordinal classification of ≤ 2. Stands with high harvest frequencies received an ordinal classification of ≥ 3. Stand age is in years. The length of each vertical line is proportional to the amount of deviance explained. Predictor variables were selected from an initial set of 6 variables. Minimum observations required for each split in A. and B. = 2; minimum deviance in A. = 0.01, and in B. = 0.05.
Figure 6. CART model, showing statistically significant predictor variables selected, split values, and partitioned mean values (bottom) of the response variables (A. mean standing dead aboveground carbon, B. mean downed CWD stages 1-5 aboveground carbon, and C. mean downed CWD stages 3-5 aboveground carbon, $n = 16$). Stand age is in years. The figure ranks variables by predictive strength (top to bottom) and in sequential order of importance as the response variable increases (left to right). The length of each vertical line is proportional to the amount of deviance explained. Predictor variables were selected from an initial set of 6 variables. Minimum observations required for each split in each tree = 3; minimum deviance in each tree = 0.05.
Figure 7. CART model, showing statistically significant predictor variables selected, split values, and partitioned mean values (bottom) of the response variable (mean $H'$ structural diversity index, $n = 16$). The figure ranks variables by predictive strength (top to bottom) and in sequential order of importance as $H'$ increases (left to right). Stands with low harvest frequency or intensity received an ordinal classification of $\leq 2$. Stands with high harvest frequency or intensity received an ordinal classification of $\geq 3$. The length of each vertical line is proportional to the amount of deviance explained. Predictor variables were selected from an initial set of 6 variables. Minimum observations required for each split in each tree = 3; minimum deviance in each tree = 0.05.
# APPENDIX A

**Appendix A: Comparison of stand development stages as presented in relevant literature.**

Table modified from Franklin et al. 2002.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Disturbance and legacy creation</td>
<td>Reorganization phase</td>
<td>Ecosystem initiative</td>
<td>Establishment phase</td>
</tr>
<tr>
<td>20</td>
<td>Canopy closure</td>
<td>Aggradation phase</td>
<td>Competitive exclusion</td>
<td>Thinning phase</td>
</tr>
<tr>
<td>80</td>
<td>Transition phase</td>
<td>Understory re-initiation</td>
<td>Mature phase</td>
<td>Understory re-initiation</td>
</tr>
<tr>
<td>150</td>
<td>Botanically diverse</td>
<td>Niche diversification</td>
<td>Transition phase (early)</td>
<td>Steady-state</td>
</tr>
<tr>
<td>300</td>
<td>Old-growth</td>
<td>Transition phase (late)</td>
<td>Horizontal diversification</td>
<td></td>
</tr>
<tr>
<td>800</td>
<td>Shifting-gap phase</td>
<td>Pioneer cohort loss</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1200</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
GLOSSARY OF TERMS

Note that some of the definitions for terms below may vary. They are defined as their meaning is intended for this paper.

BASAL AREA: the total cross-sectional area of all stems in a stand measured at breast height (DBH). It’s used to describe the average amount of an area occupied by tree stems.

\[
\text{Basal area per tree (in square feet per acre): } 0.005454 \times (\text{DBH})^2 \\
\text{Basal area per tree (in square meters per hectare): } 0.00007854 \times (\text{DBH})^2
\]

CARBON SEQUESTRATION: the process of carbon uptake by which CO\(_2\) is removed from the atmosphere to aboveground biomass pools.

CARBON STORAGE: the amount of carbon in aboveground biomass pools at any one time. Indicates carbon stocks.

CARBON UPTAKE: the initial process of carbon sequestration, by which aboveground biomass takes carbon from a source and transfers its’ energy to grow.

DIAMETER AT BREAST HEIGHT (DBH): diameter of a tree (in cm) measured at 1.37 m (4.5 ft) aboveground level, on uphill side of tree.

SITE INDEX: a tool used to determine the relative productivity of a particular location based on the potential for trees to grow in the location. Defined by the height of the dominant and/or codominate tree species at a base age on the site of interest. This is a species-specific measurement.

STAND: a contiguous group of trees considered as a unit. An ecosystem defined by tree species, or a group of trees that occupy a given area and have common structural characteristics (i.e., age, species, size, etc.) that differentiate it from other groups of trees.

STAND DENSITY INDEX (AKA Reineke’s Stand Density Index): a quantitative term that represents the degree of stem crowding within a stand. It’s an expression of relative stand density or stocking of a stand based on the predictable relationship between average tree size (DBH of the average basal area) and trees per unit area.
STOCKING INDEX: assesses the adequacy of a stand to meet a management objective by indicating the number of trees in a stand compared to the desirable number of trees for best growth and management. The A-line in a stocking index diagram represents the upper limit to relative density and the B-line represents the lower limit of crown closure.