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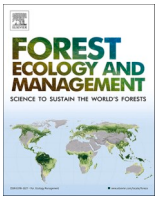

Adaptation and mitigation capacity of wildland forests in the northeastern United States

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ABSTRACT

Managing forests to mitigate climate change and increase their capacity to adapt to future climate-related disturbances and conditions typically involves protecting and enhancing forest carbon stocks and sequestration capacity while promoting structural diversity. While the focus has been on comparing active management approaches for meeting these objectives, there are few empirical assessments of passive management. Here we used quasi-experimental methods to compare carbon and structural complexity within "wildlands," where harvesting and other land uses are prohibited, to environmentally comparable forests without protection from timber harvesting. Using USDA Forest Inventory and Analysis (FIA) plots from the Adirondack-New England region of the Northeastern U.S., we compared aboveground carbon, total forest basal area increment (our proxy for carbon sequestration), and six forest-level structural variables in forests. To help explain observed differences, we examined (1) the recent history of harvesting within unprotected forests, (2) stand age in wildland and unprotected forests, and (3) the carbon and structural attributes of protected and unprotected plots at the initiation of wildlands protection. Aboveground carbon was 20% higher in wildlands overall ($P < 0.0001$), with differences greatest in wildlands of New York (+32%; $P = 0.0001$) and in Maine (+34%; $P = 0.01$) where recent harvesting intensity and differences in stand age between protection categories were highest. Basal area increment did not differ between protected areas at the regional and sub-regional scale, but was 37% higher in wildlands ($P = 0.03$) than in recently harvested areas. Structural complexity was generally higher in wildlands, with four structural variables – large live (>60 cm DBH) and large dead (>45 cm DBH) tree density, maximum tree height, and diversity of diameter size classes) – greater in wildlands than in unprotected forests. Two variables (adult tree species richness and standard deviation of tree height) did not differ between protection categories. Both carbon and structural differences were amplified by recent harvesting in unprotected plots. For the subset of plots that allowed for comparison, wildlands did not differ in carbon and structural attributes from unprotected plots at the onset of wildlands protection, suggesting that subsequent management rather than initial differences was the driver of carbon and structural differences between protection categories. Our results highlight the adaptation and mitigation benefits of allowing natural processes to predominate in strictly protected areas.

1. Introduction

Managing forests for mitigation and adaptation in response to climate change is a major priority for forest managers (D'Amato et al. 2011; Swanston et al. 2016). Mitigation in forests refers to increasing the amount of carbon stored and sequestered to reduce carbon dioxide concentrations in the atmosphere (D'Amato et al. 2011). Adaptation refers to managing forests for structural, species, and functional diversity to increase resistance or resilience to stress and disturbances (i.e., insect outbreaks, drought, fire, and windstorms) that are becoming more frequent and intense with climate change (D'Amato et al. 2011; Ontl et al. 2020).

Forests that are protected by legal or administrative mechanisms from active management in order to allow forests to develop through

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natural processes (i.e., wilderness areas, strict nature preserves, forever wild easements, and many national parks ["wildlands"]; Foster et al. 2023) have become increasingly recognized as potential contributors to climate mitigation strategies which attempt to maximize carbon storage and retain forest complexity (Foster et al. 2010; Moomaw et al. 2019; Mackey et al. 2020). Nonetheless, wildlands are often overlooked as natural climate solutions for mitigation (e.g., Griscom et al. 2017; Fargione et al. 2018; Dugan et al. 2021, but see Meyer et al. 2022) and are frequently excluded from climate adaptation literature (e.g., Brandt et al. 2017; Janowiak et al. 2018; Swanston et al. 2018). Contemporary definitions of forest health and resilience focus on the capacity of forests to provide the full range of ecosystem services to humans (Millar and Stephenson 2015). Wildlands, by definition, do not provide wood products, which likely explains their exclusion from much of the climate adaptation literature. However, independent of their ability to provide the full range of human services, there is reason to believe that wildlands may be more resilient (i.e., better able to withstand perturbations) than forests that are actively managed because of their greater structural complexity and tree species diversity (e.g., Forzieri et al. 2022; Potterf et al., 2023).

Wildland protection promotes compositional and structural development toward mature and old growth forest characteristics (Albrich et al. 2021). Old forests are well known to harbor complex structures that are less prominently found in second growth and actively managed forests (McGee et al. 1999, Franklin et al. 2002; Keeton et al. 2011). Older unharvested forests also store high levels of carbon relative to recently harvested forests, including those managed with increased rotation times and greater structural retentions (Harmon et al. 1990; Nunery and Keeton 2010). Indeed, forest management has a profound effect on carbon stores across the United States and the globe, reducing potential carbon stores by about 36% (Harris et al. 2016; Erb et al. 2018). Nonetheless, timber harvesting is often excluded as a driver of forest change in assessments of forest ecosystem climate vulnerability (e.g., Janowiak et al. 2018) even though it is the predominant disturbance process in these same landscapes (Thompson et al. 2017; Brown et al. 2018).

An unresolved aspect of managing for adaptation and mitigation in forests is to what extent there are synergies and/or tradeoffs between carbon storage and structural complexity. Some studies have reported a positive correlation between structural complexity and carbon sequestration and storage because structurally complex forests absorb more light and use it more efficiently (Gough et al. 2019), or because niche complementarity is believed to increase photosynthesis and nutrient cycling rates (Thom and Keeton 2019). Other studies have reported tradeoffs between forest structural complexity and carbon storage (D'Amato et al. 2011). Additionally, some authors have reported tradeoffs between carbon storage and rates of carbon sequestration (Nunery and Keeton 2010; D'Amato et al. 2011; Patton et al. 2022), while still others report that carbon storage and sequestration are higher in wildlands than in managed forests (Brown et al. 2018). Thus, the extent to which tradeoffs exist between adaptation and mitigation capacity and carbon storage and carbon sequestration in wildlands remains unclear.

Several interrelated factors likely determine the degree to which the structural complexity, carbon storage, and sequestration in wildlands may diverge from nearby forests that are not protected from harvesting and other active management (hereafter "unprotected"). One is the amount of time since a wildland forest was protected and therefore last potentially managed (Paillet et al. 2010; Atrena et al. 2020). A second factor is the frequency and intensity of harvesting in unprotected forests (Duveneck and Thompson 2019). A third factor is the difference in average age or developmental stage between wildland and unprotected areas, as carbon storage and structural complexity generally increase with age (e.g., Franklin et al. 2002; Keeton et al. 2011; Miller et al. 2016).

In the northeastern United States, most forests are relatively young (<100 years old on average) compared to their pre-colonial counterparts and are recovering from land clearance, fire, and logging in the 19th and 20th centuries (Foster et al. 2005; Thompson et al. 2013). Thus, at the time of wildland designation, many protected forests likely have a similar age and management history to nearby unprotected forests (Miller et al. 2016), particularly in larger preserves (e.g., federal wilderness areas and large state preserves in New York and Maine). However, it's possible that some wildlands were and continue to be selected in part because of their old age characteristics, particularly in some smaller forever wild preserves.

Here we ask the following: (1) To what extent are wildland forests in the Northeastern United States distinct from environmentally similar but unprotected forests in terms of mitigation (carbon storage and sequestration) and adaptation capacity (structural complexity)? (2) How has recent vs. non-recent harvesting activity in unprotected forests influenced these differences? (3) Are there tradeoffs in adaptation and mitigation capacity or tradeoffs between carbon storage and sequestration? (4) To what extent are initial differences in forest characteristics at the time of wildland designation vs. subsequent differences in exposure to harvesting and management following wildland protection, the more important driver of change between protection categories?

2. Materials and methods

2.1. Study area and experimental design

Our study area included the Adirondack-New England forest region, which spans two level II ecoregions and comprises much of the boreal-temperate ecotone of eastern North America. These ecoregions include the Atlantic Highlands of the Adirondacks, Catskills, and New England Mountain ranges and the Mixed Wood Plains of southern New England and coastal Maine (US EPA 2021; Fig. 1). The forests include greater elements of boreal spruce (*Picea* spp.)-balsam fir (*Abies balsamea*) along with northern hardwoods in the Atlantic Highlands and temperate broadleaf beech (*Fagus grandifolia*), birch (*Betula* spp.), maple (*Acer* spp.), and oaks (*Quercus* spp.) in the Mixed Wood Plains.

We defined the region's wildlands as lands secured, either legally or administratively, with the intent to be shaped by natural processes and free from active management, including timber harvesting (Foster et al. 2023); the land use restrictions in these areas correspond roughly to the IUCN protected area categories of 1a and 1b (strictly protected areas and wilderness areas; Dudley et al., 2013), and include some of the more strictly managed categories 2 and 3 (national parks and natural monuments). Wildlands in the northeastern U.S. are dominated by large public conservation lands including the Adirondack Forest Preserve, NY (~1,000,000 ha), the Catskill Forest Preserve, NY (116,000 ha), Baxter State Park, ME (85,000 ha), White Mountain National Forest Wilderness areas, NH (60,000 ha), Green Mountain National Forest Wilderness Areas, VT (40,000 ha), and Katahdin Woods National Monument, ME (35,000 ha). In New York we included only the state-owned Adirondack and Catskill Forest Preserves because of limited data availability from privately owned wildlands. For the six states in New England (Maine, New Hampshire, Vermont, Massachusetts, Connecticut, and Rhode Island), we included the many smaller public and private wildlands parcels conserved by federal, state and municipal agencies and by conservation organizations as recently documented by Foster et al. (2023). Parcels included those at least 4 ha in size and ranged in duration of protection from at least 1 year to > 120 years. In the region, the New York preserves make up 69% of wildland area, followed in size by Maine (17%), New Hampshire and Vermont (11% combined), and the three southern New England states (3% combined). In terms of total forest area, the Adirondack and Catskill (New York) regions comprised 19% of the study region, Maine 45% of the region, New Hampshire and Vermont 24%, and the southern New England states 13%. We obtained data on time since protection of the wildland (i.e., date of protection) for two-thirds of the New England plots (Foster et al. 2023), but only 20% of

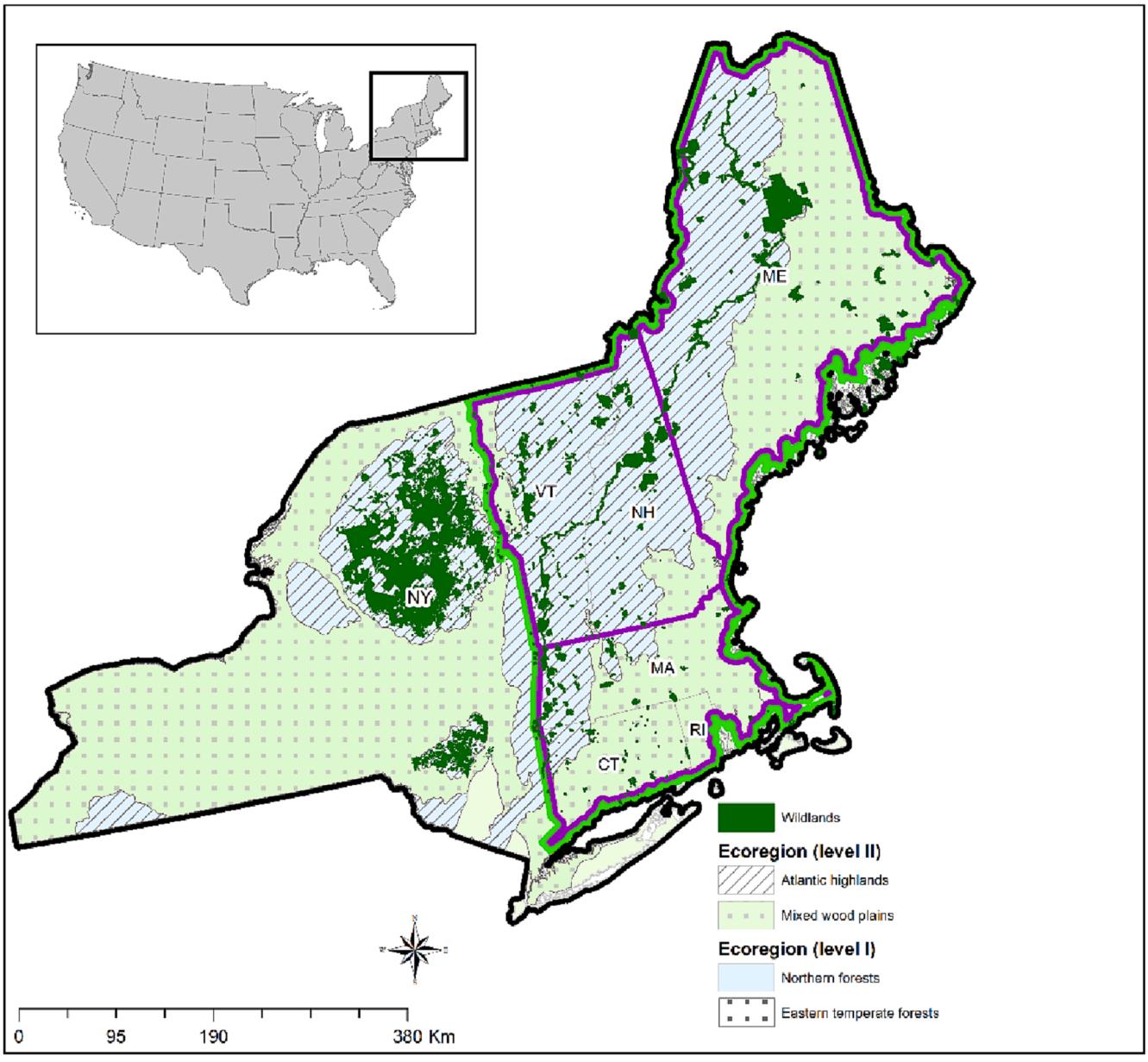

Fig. 1. Study area map of the Adirondack-New England region in the Northeastern United States with strictly protected wildlands shown. The purple line delineates the boundaries of the four socioecological sub-regions used in the analysis. Note that all known wildlands are included in New England, while only the Adirondack and Catskill Forest Preserves are included in New York.

the New York plots (NY DEC; Table 1). Timber harvesting is the leading forest disturbance and cause of adult tree mortality in the northeastern United States and generally increases in intensity from south to North, with the highest levels of cutting in Maine (Thompson et al. 2017).

We used forest inventory data from the USDA's Forest Service Inventory and Analysis (FIA) program (2013–2019) to compare carbon and structural attributes of wildlands to lands in which timber harvesting was permitted and/or conservation of nature was not the first priority (unprotected; Dudley et al., 2013; USGS, 2021). Unprotected forests excluded any Gap 1 or Gap 2 lands (those which are managed primarily for a "natural" state) that did not occur in our wildlands data layer and included USGS Gap 3 lands (subject to timber harvesting) and Gap 4 lands (without any known protection from development; USGS, 2021).

The FIA is a stratified design of permanent, fixed-area (675 m^2) forest plots across the conterminous United States, with the plots arranged as a spatially representative sample with a plot per every 24 km^2 (Bechtold and Patterson, 2005). The FIA includes records of trees, seedlings, and environmental conditions, established circa 2000 and remeasured in our study area every 5–7 years. The primary measurements of the diameter, species, and height of live and standing dead adult trees (≥12.7 cm DBH) are taken within four fixed points, i.e., subplots, arranged around the plot center. Details on the plot condition, including physiographic variables (i.e. slope and elevation), are recorded within the four subplots as well. Saplings (2.5–12,6 cm DBH) are measured in smaller subsections, microplots (2.07 m radius), nested within each subplot. Though the true coordinates of FIA plots are not publicly available, an agreement between the USFS and the Harvard Forest allowed us access to the unfuzzed plot locations.

Wildlands are not randomly distributed across the landscape. To

Table 1
Tree harvesting intensity (means and standard errors) in unprotected plots and duration of wildland protection by region and sub-region in the Northeastern US.

	Unprotected				Wildlands		
	n	Mean basal area removed since 1999 (m^2/ha)	Mean density of trees removed since 1999 (no./ha)	% of plots recently harvested since 1999	n	Mean time since protection	% of plots with data on time since protection
CT-MA-RI[a]	9	0	0	0	9	15.2 (6.4)	67
Maine	38	2.0 (0.92)	42.7 (18.1)	18.4	38	26.0 (5.3)	71
New Hampshire-Vermont	69	0	0	0	69	25.9 (2.4)	65
New York[b]	88	1.27 (0.38)	18.6 (5.6)	14.8	88	80.1 (11.2)	20
All[c]	207	0.91 (0.24)	15.7 (4.2)	9.7	207	34.8 (3.5)	47
Recently harvested since 1999	20	9.4 (1.5)	162.9 (26.6)	100	0	NA	NA

[a] Connecticut, Massachusetts, & Rhode Island combined.
[b] Adirondack & Catskill Forest Preserves.
[c] Combined New York and New England. Includes three pair of plots that crossed sub-regional boundaries and were not included in the New York, CT-MA-RI, and New Hampshire-Vermont comparisons.

control for potential selection bias, such as systematic differences in environmental conditions between wildlands and unprotected forests, we used covariate pre-matching, a causal inference approach that creates a quasi-experimental design (e.g., Butsic et al. 2017, Morreale et al. 2021). Matching mimics an experimental design where the control plots (unprotected forest) are selected based on similarity across potential confounding variables to the treatment (wildland forest) plots. We matched FIA plots located within wildlands to environmentally similar FIA plots in unprotected forest. We selected: elevation (FIA), slope (FIA), latitude (FIA), longitude (FIA), light, water, temperature, nitrogen deposition 2018 (sensu Morreale et al. 2021; Nemani et al., 2003), and USDA ecological subsection (Miller et al. 2016) as our matching covariates in order to account for the most likely sources of confounding influence on forest structure. Ecological subsections are "areas of similar surficial geology, lithology, geomorphic process, soil groups, subregional climate, and potential natural communities" (O'Connell et al., 2017), while latitude and longitude further controlled for geographical variation. To reduce the potential for edge effects on forest growth (Morreale et al. 2021), we excluded plots < 91 m from a road and used only completely forested plots (i.e., all four subplots classified as forest). Matching was performed in R with the Matchit package (Ho et al. 2011), with ecological subsection matched exactly and all other variables matched using nearest-neighbor covariate matching determined by Mahalnobis distance with calipers of 0.25 for continuous variables except slope and elevation which had calipers of 0.3 (Lunt 2014). Calipers are the standard deviations of the propensity score within which to draw control units (default = 0). To ensure the effect we saw was not an outcome of the matching order, we randomly ordered the rows of the database and ran matchit 1000 times. The best ordering of matches yielded 414 FIA plots in total, with 207 in wildland forests and paired unprotected controls distributed across the Adirondack-New England region (Table 1). Twenty of the 207 (9.7%) unprotected plots were recently harvested, defined as those plots exhibiting evidence of signs of tree cutting and removal since the year 1999, based on the STATUSCD in the TREE table (Table 1). Recently harvested plots only occurred in New York (13 of the 88 unprotected plot; 14.8%) and in Maine (7 of 38 plots – 18.4%).

2.2. Carbon

We estimated aboveground carbon storage on each FIA plot to assess differences in carbon storage between wildlands and unprotected forests. Aboveground carbon storage values (AGC) were obtained from the FIA database, which estimates carbon (pounds) in the aboveground portion, excluding foliage, of live trees with a diameter ≥ 2.5 cm, and dead trees with a diameter > 12.7 cm DBH. AGC was converted to megagrams/hectare (Mg/ha). As a proxy for carbon sequestration, we used total forest basal area increment (BAI; Reinmann et al. 2020; Morreale et al. 2021). BAI was calculated for each tree (live stems ≥ 2.5 cm DBH) as the difference in radial growth of trees between the most recent and previous measurements, and then annualized based on the remeasurement period. Individual tree BAI was then summed across the plot and converted to total forest BAI (m^2 ha^{-1} yr^{-1}).

2.3. Structural complexity

Forest adaptation generally involves managing for structural, functional, and compositional diversity (D'Amato et al. 2011). Because structural complexity has been shown to be a strong proxy of functional complexity (Franklin et al. 2002; Thom et al. 2021), we assumed that examining structural features would adequately account for functional diversity. Structural complexity refers to the heterogeneity in the vertical and horizontal distribution of biomass within a forest system (D'Amato et al. 2011). We focused on structural complexity at the stand scale and included six structural features: 1. Large live tree (no. stems/ha > 60 cm DBH) density (Keeton 2006; D'Amato et al. 2011); 2. Tree diameter size class diversity (D'Amato et al. 2011), which was calculated as the relative basal area of 5 cm DBH classes (2.5–7.5, 7.6–12.6… 58.5–63.5, >63.5) using the Shannon Diversity Index (Buongiorno et al. 2000; Lexerød and Eid, 2006); 3. Maximum tree height (Gough et al. 2020); 4. Standard deviation of mean tree height (McElhinny et al. 2005; Keeton 2006); 5. Large dead tree density (no. stems/ha > 45 cm DBH; Keeton 2006); 6. Adult (>12.7 cm DBH) tree species richness (no. species/plot; McElhinny et al. 2005).

One known limitation of FIA data is varying quality between attribute measurements: tree diameter is highly accurate but individual height can be difficult to measure in the field, and tree ages are estimated attributes (Gormanson et al., 2018). Here we leverage multiple metrics of structural complexity to provide robustness against possible uncertainties associated with any single metric. The diameter of all adult live and dead trees (>12.7 cm DBH) were measured within FIA subplots, and sapling (2.5–12.6 cm DBH) counts were conducted in the four nested microplots (Gormanson et al., 2018). Adult tree measurements were summed to the plot level, and adult stem density, in stems ha^{-1} was calculated for each plot.

We also examined age class distribution and diversity as a proxy for successional stage diversity using 20-year stand age classes from 0 to 180 years and the Shannon Diversity Index to calculate age class diversity. Stand age is estimated on an FIA plot by coring 2–3 dominant canopy trees, counting tree rings to determine individual tree age, and then calculating a weighted average age. As our study area typically contains uneven-aged forests, we used stand age as a loose proxy for time of establishment. We were unable to examine other important structural features such as coarse woody debris because of limited replication of plots in the FIA that measure this variable. We conducted two sample t-tests on the matched dataset to compare all structural and

carbon variables between wildlands and matched unprotected plots, and we compared attributes at two spatial scales: regional – Northeastern US (all plots) and sub-regional (New York, Maine, New Hampshire-Vermont, and Connecticut-Massachusetts-Rhode Island). The subregional analyses allowed for greater understanding of the variation in carbon and structural features in wildlands with different times since protection and unprotected plots with different management intensities, as well as the variation in carbon and structural features that span the study region, independent of wildland protection. We combined Vermont and New Hampshire into one subregion because they have similar (recent) harvest intensities that are much lower than Maine and considerably higher than southern New England (USDA FIA, 2023). We also combined the three southern New England states into a single category because of limited sample size and a similar age since protection of wildlands (Foster et al. 2023). Additionally, we compared the small subset of recently harvested plots (harvested since 1999) to their matched wildlands, as well as unprotected plots with no sign of recent harvesting to their matched wildlands, in order to better understand the effects of recent and non-recent harvesting on carbon and structural attributes. We transformed all non-percentage data prior to analysis using square root transformations (Gotelli and Ellison 2014). All data were analyzed using the R statistical computing language (R Statistical Computing 2021).

To understand whether any observed differences between wildlands and unprotected site were a result of a selection effect (e.g., the sites were different at the time of protection) or due to the protection itself, we compared forest conditions at the time of protection. Unfortunately, limitations in the temporal scope of the FIA data precluded a detailed characterization of the effects of duration of protection on wildlands structure and carbon dynamics. However, by combining the full temporal extent of modern FIA measurements, circa 1999, with information on the year of protection, we performed additional analyses of forest carbon and structural characteristics at the onset of wildland protection. We identified 48 wildland plots (and their paired unprotected plots)

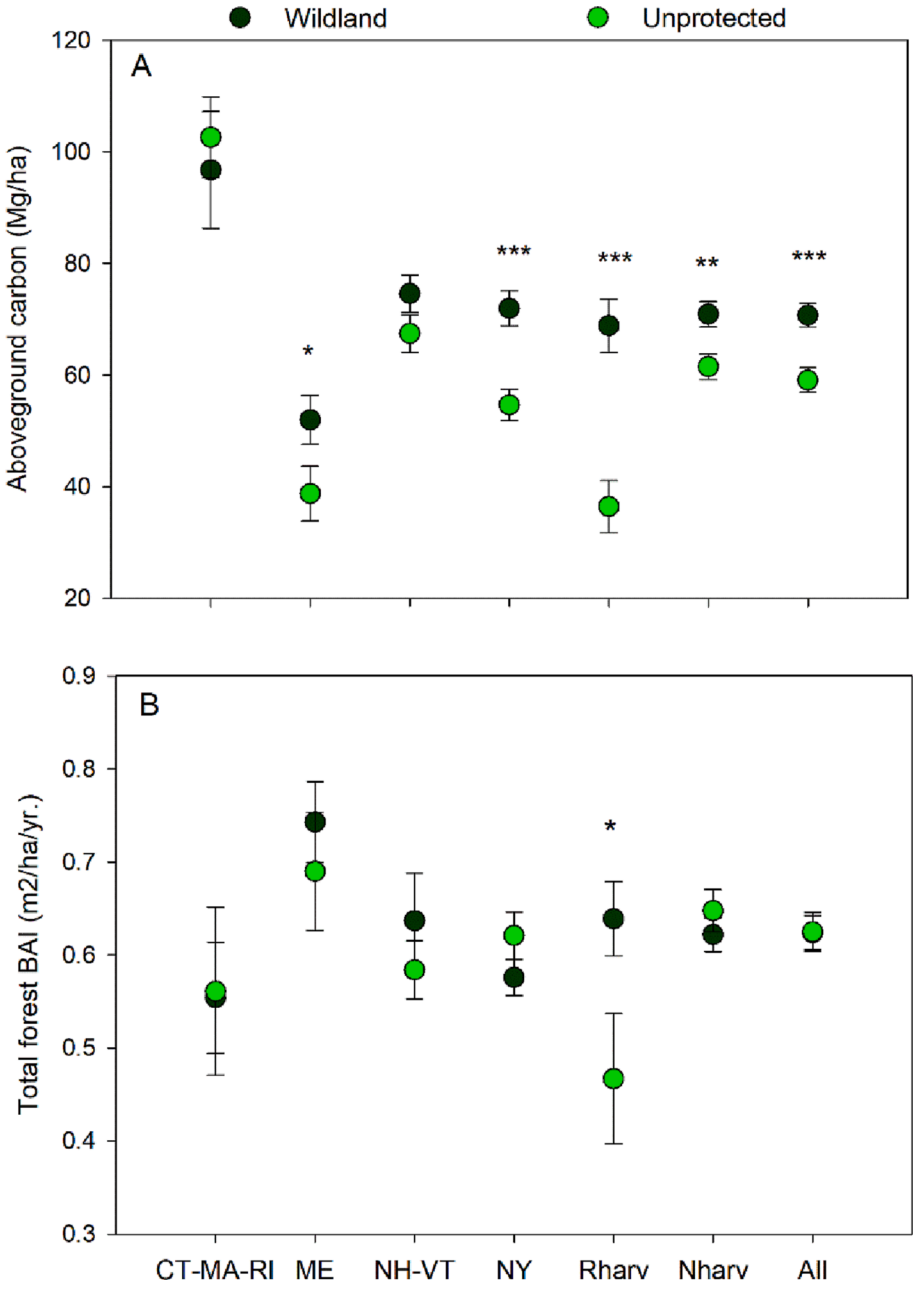

Fig. 2. Mitigation in wildlands and unprotected forests by region, sub-region, and recent harvest status. (A) Aboveground carbon storage and (B) total forest basal area increment (BAI). CT-MA-RI = combined Connecticut, Massachusetts, and Rhode Island; n = 9), ME = Maine (n = 38), NH-VT = combined New Hampshire and Vermont (n = 69); NY = New York (n = 88); ALL = entire region (n = 207). Rharv = unprotected plots with signs of recent tree harvesting since 1999 compared to matched wildlands (n = 20). Nharv = unprotected plots with no sign of recent harvesting compared to matched wildlands (n = 187). *P < 0.05, **P < 0.01, ***P < 0.001. Bars = mean ± SE.

with a year of initial protection that had a corresponding FIA measurement (within 5 years of protection date). We used two-sample t-tests on the subsetted dataset to assess whether there were differences in forest structure when wildland protections began.

3. Results

3.1. Mitigation

3.1.1. Aboveground carbon

Overall, wildlands (70.7 Mg/ha; SE = 2.1) had 20% greater AGC storage than unprotected forests (59.1 Mg/ha; SE = 2.2; P < 0.0001; Fig. 2a). AGC was 34% higher in Maine wildlands (P = 0.012), 32% higher in New York wildlands (P = 0.0001), but did not differ between protection categories in New Hampshire-Vermont (P = 0.10) or Connecticut-Massachusetts-Rhode Island combined (P = 0.53). Compared to recently harvested forests, wildlands stored 89% greater AGC (P < 0.0001), and compared to non-recently harvested plots, wildlands stored 15% greater AGC (P = 0.002; Fig. 2a).

3.1.2. Total forest basal area increment

Total forest BAI did not differ between wildlands (0.624 m^2/ha/yr.) and unprotected forests at the regional (0.625 m^2/ha/yr.; P = 0.97) or at the sub-regional scale (P > 0.16; Fig. 2b). However, BAI was 37% higher in wildlands (0.64 m^2/ha/yr.; SE = 0.07) compared to recently harvested forests (0.37 m^2/ha/yr.; SE = 0.04; P = 0.03; Fig. 2b).

3.2. Structural complexity (Adaptation)

3.2.1. Tree diameter

Density of large live trees (>60 cm DBH) was 84% higher in Northeastern wildlands compared to unprotected forests (P = 0.01; Fig. 3a). In New York, wildlands had over twice the number of large trees as unprotected plots (P = 0.029); and large trees were 8 times more abundant in wildlands compared to recently harvested forests (P = 0.03). Compared to unprotected plots without recent harvest, wildlands had marginally higher densities of large trees (P = 0.053; Fig. 3a). Large tree densities did not differ between protection categories in New Hampshire-Vermont (P = 0.26) or in Maine (P = 0.65); in CT-MA-RI, large trees only occurred in wildland plots (P = 0.06; Fig. 3a). Diversity of tree diameter classes was greater in wildlands than in unprotected plots at the regional scale (P < 0.0001) and in all subregions (P < 0.05) and harvesting classes (P < 0.001), except for CT-MA-RI (P = 0.24; Fig. 3b).

3.2.2. Tree height

Maximum tree height in wildlands was, on average, 1.1 m taller across the Northeast (P = 0.01) and 2.5 m taller in Maine (P = 0.014) compared to unprotected plots (Fig. 4). Maximum tree heights did not differ across New York (P = 0.06) or other sub-regions. Maximum tree height was taller in wildlands than in both recently harvested (P = 0.036) and non-recently harvested unprotected areas (P = 0.046; Fig. 4). Standard deviation of mean tree height did not differ between wildlands and unprotected plots at any spatial scale or relative to harvesting status of unprotected plots (P > 0.10).

3.2.3. Standing deadwood

Densities of large dead trees (>45 cm DBH) were 3.7 times higher in wildlands overall and 7.8 times higher in New York wildlands compared to unprotected forests (P < 0.0001; Fig. 5). Large dead trees did not occur in any recently harvested plots. Large dead trees did not differ between protection categories in the New England sub-regions, although in CT-MA-RI they only occurred in unprotected plots (Fig. 5).

3.2.4. Tree species richness

Adult tree species (>12.7 cm dia.) richness was similar between protection categories at all spatial scales and was virtually identical between wildland (5.2 species/plot; SE = 0.12 and unprotected (5.3 species/plot; SE = 0.13) forests overall (Fig. 6). However, species richness was higher in wildlands (5.65 species; SE = 0.36) than in recently harvested unprotected plots (4.6 species; SE = 0.38; P = 0.048; Fig. 6).

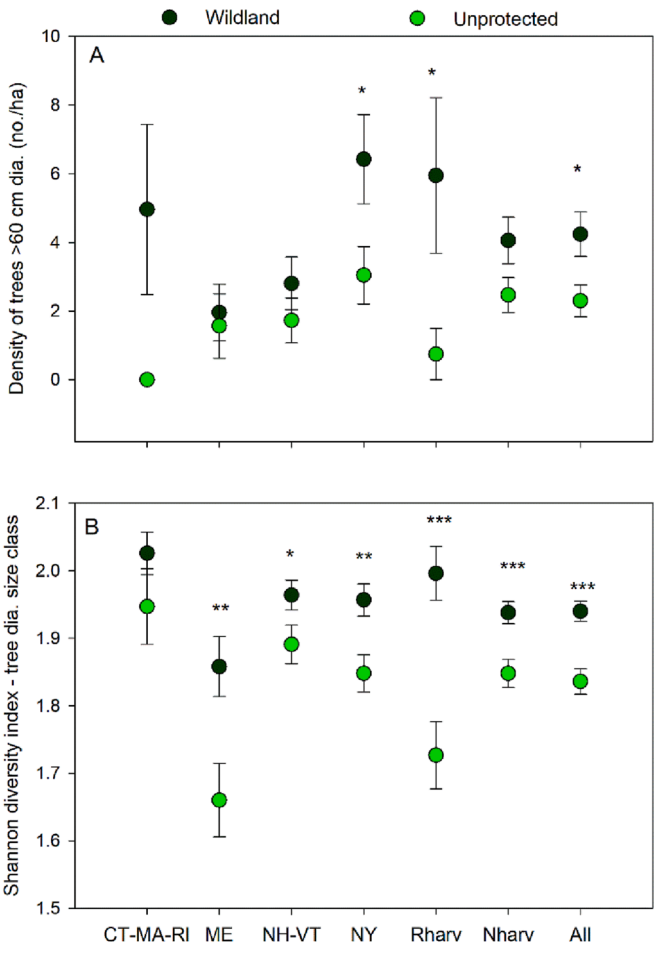

Fig. 3. Tree diameter in wildland and unprotected plots by region, sub-region, and recent harvest status. (A) Density of large trees (>60 cm dia.) and (B) Shannon Diversity of tree dia. size classes (relative basal area of 5 cm dia. classes – 2.5 cm-63.5 cm DBH). See Fig. 2 caption for abbreviation key and sample sizes. *P < 0.05, **P < 0.01, ***P < 0.001. Bars = mean ± SE.

3.2.5. Forest conditions at the time of protection

We compared forest carbon and structural characteristics between wildlands and unprotected forest plots at the initiation of wildlands protection (Fig. 7). We found no significant differences in forest carbon, number of large live or dead trees, tree height, or tree species richness (P > 0.45 for all attributes).

3.2.6. Stand age

Stand age ranged from 13 to 172 years in wildlands and 3 to 161 years in unprotected forests. Wildlands were, on average, 10.7 years older than unprotected forest (P < 0.0001), with wildlands in Maine (+15.4 years) and New York (+11.1 years) having above average difference in age (Table 2). Difference in stand age between wildlands and unprotected plots was much smaller in CT-MA-RI plots (1.3 years) than other sub-regions and the regional average. Recently harvested forests were over 20 years younger than paired wildland plots (Table 2).

Wildlands (34.3%) and unprotected forests (30.9%) occurred most frequently in the 80–99 age class (Fig. 8a). Wildlands had a higher frequency of forests 120–180 years of age (6.3%) compared to unprotected

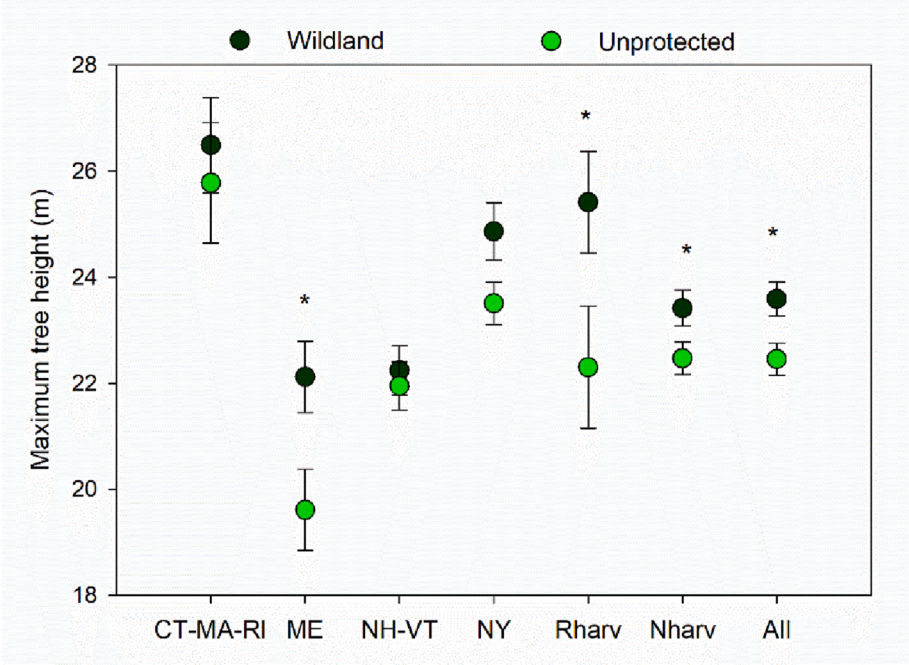

Fig. 4. Maximum tree height in wildland and unprotected plots by region, sub-region, and harvest status. See Fig. 2 caption for abbreviation key and sample sizes. *P < 0.05, **P < 0.01, ***P < 0.001. Bars = mean ± SE.

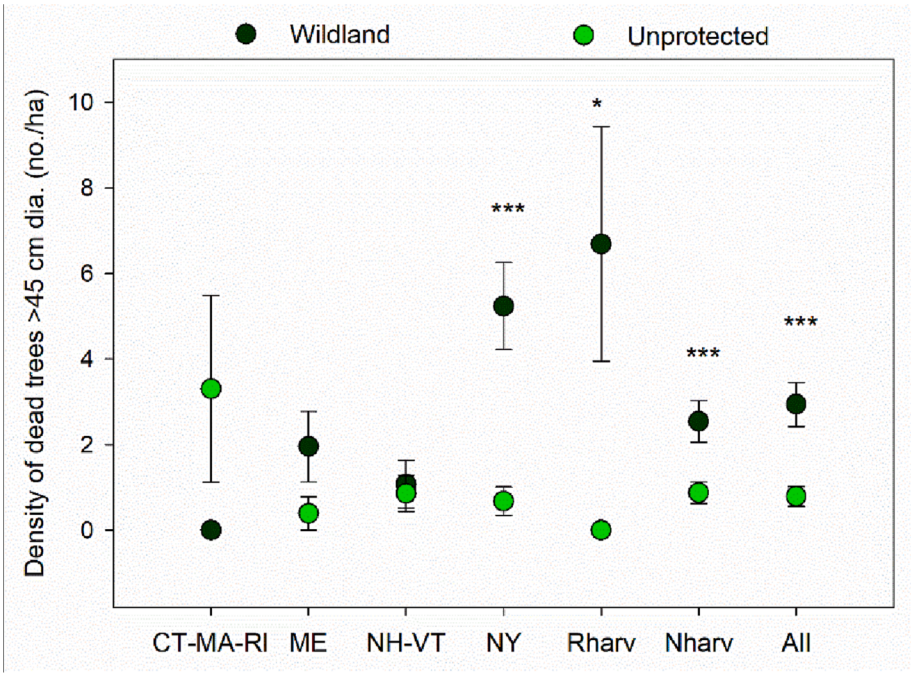

Fig. 5. Large (>45 cm DBH) dead tree density by region, sub-region, and recent harvest status in wildland and unprotected plots. See Fig. 2 caption for abbreviation key and sample sizes. *P < 0.05, **P < 0.01, ***P < 0.001. Bars = mean ± SE.

forest (3.4%). Unprotected forests had over twice the frequency in the 20–59 year age range (22.7%) compared to wildlands (11.1%) and the same frequency in the youngest age class (0–19 years; 1%; Fig. 8a). Stand age class diversity was greater in CT-MA-RI and Maine wildlands and lower in New Hampshire-Vermont and New York wildlands than in unprotected areas; age class diversity was highest in Maine wildlands. Across the Northeastern region, age class diversity was similar between protection categories (Fig. 8b).

4. Discussion

In an era of rapidly changing climate and accompanying forest disturbances and tree decline (Cohen et al. 2016), strict wildland protection is frequently discounted as a strategy to provide sustained adaptation and mitigation benefits into the future across forested landscapes (Prichard et al., 2021; Swanston et al. 2016; Mackey et al. 2020). Our results suggest that wildland forests have greater carbon storage, similar carbon sequestration (i.e., forest growth) rates, and generally higher stand-level

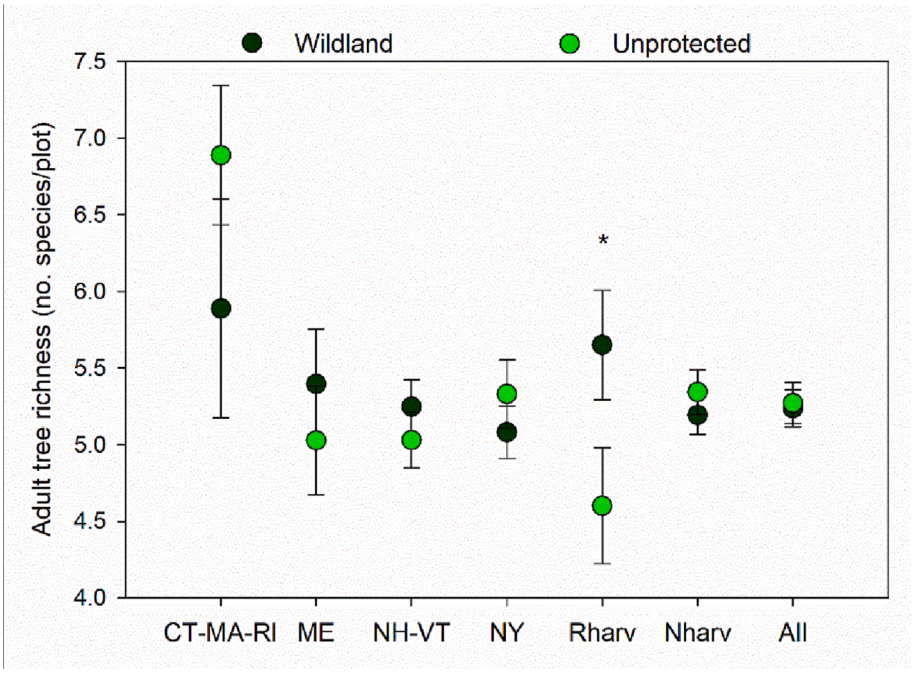

Fig. 6. Adult tree (>12.7 cm DBH) species richness by region, sub-region, and recent harvest status in wildland and unprotected plots. See Fig. 2 caption for abbreviation key and sample sizes. *P < 0.05, **P < 0.01, ***P < 0.001. Bars = mean ± SE.

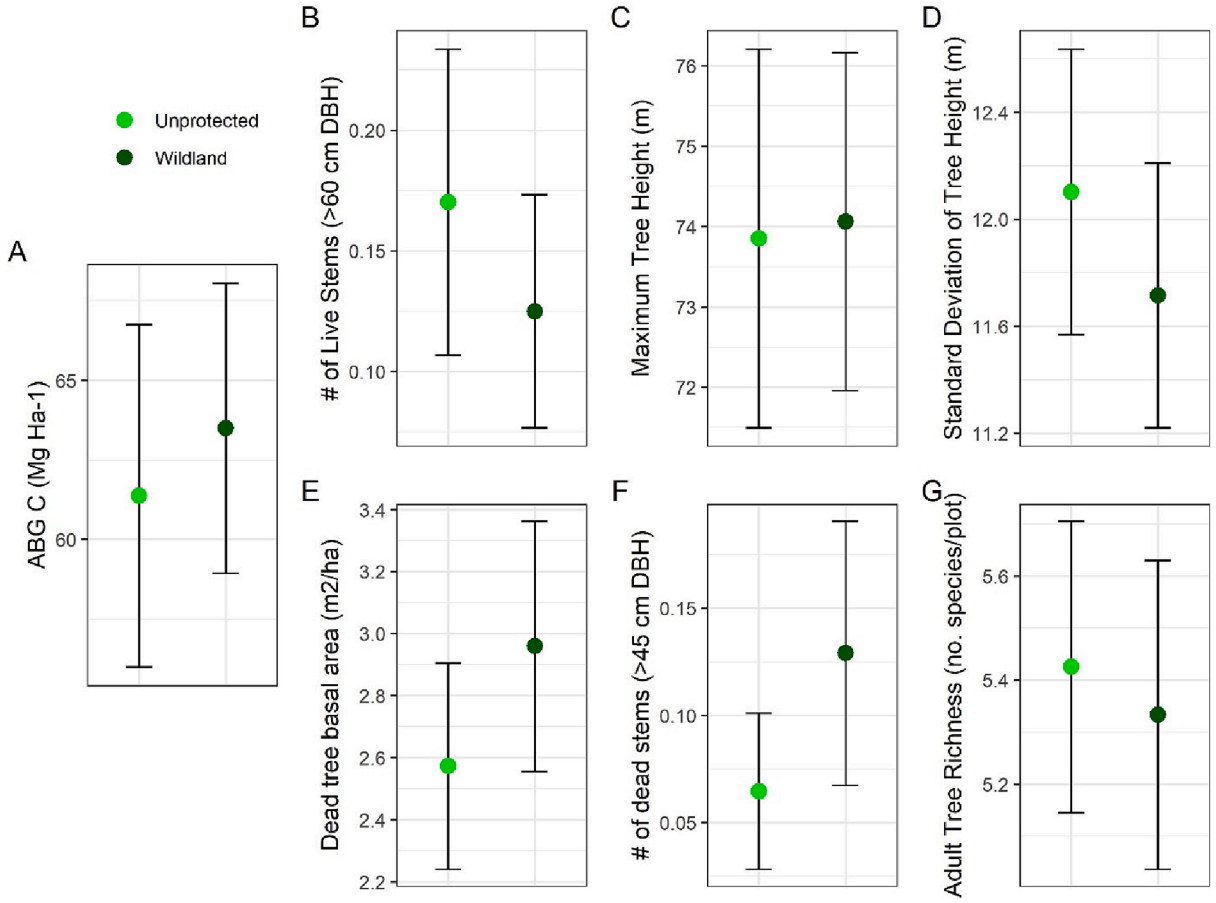

Fig. 7. Comparison of aboveground carbon storage (A) and forest structural characteristics (B-G) between unprotected plots (n = 48) and wildland plots (n = 48) at the time of protection. Bars = mean ± SE.

Table 2
Stand age (standard errors in parentheses) of wildland and unprotected forests by region, sub-region, and recent harvesting history.

	n	Mean stand age wildland	Mean stand age unprotected	Difference in mean stand age
CT-MA-RI[a]	9	89.4 (3.2)	88.1 (4.0)	1.3
Maine	38	86.5 (5.4)	71.1 (5.0)	15.4*
New Hampshire-Vermont	69	81.5 (2.0)	73.1 (2.7)	8.4**
New York[b]	88	88.5 (2.9)	77.4 (2.7)	11.1**
All[c]	207	86.1 (1.7)	75.4 (1.8)	10.7***
Recently harvested (since 1999)	20	97.2 (5.9)	74.8 (6.1)	22.4*
Not recently harvested	187	84.9	75.5	9.4***

[a] Connecticut, Massachusetts, & Rhode Island combined.
[b] Adirondack & Catskill Forest Preserves.
[c] Combined New York and New England. Includes three pairs of plots that crossed sub-regional boundaries and were not included in the New York, CT-MA-RI, and New Hampshire-Vermont comparisons.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

structural complexity relative to unprotected forests (Question 1). Therefore forest condition in areas with different levels of protection warrants greater recognition when assessing the vulnerability or adaptation capacity of a region's forestlands (Mackey et al., 2020).

4.1. Aboveground carbon

Aboveground carbon storage was 20% higher in wildland forests than in environmentally similar unprotected forests across the Northeastern US. Intensity of harvest in unprotected forests likely played an important role in these differences, as the greatest difference in AGC in wildlands occurred relative to recently harvested areas (+89%), as well as in New York (+32%) and in Maine (+34%), where harvesting occurred at a relatively high intensity (Question 2). Our regional sample likely underestimated recent harvest intensity – and therefore differences in carbon storage in wildlands and unprotected forests – as the proportion of plots in our sample with recent harvesting (9.7%) was notably lower than in all FIA plots in the study area (13.4%). Our results underestimated recent harvest intensity in Maine (18.4% of plots this study vs. 22.1% all FIA plots), overestimated recent harvesting in New York (14.8% of plots this study vs. 12.6% all FIA plots) and substantially underestimated recent harvest intensity in New Hampshire-Vermont (0% this study vs. 10.7% all FIA) and Connecticut-Massachusetts-Rhode Island (0% this study vs. 6.9% all FIA; USDA Forest Service 2023). Despite the importance of recent timber harvesting in determining differences in AGC, our results also revealed lasting and significant differences in carbon storage between wildlands and unprotected forests in which no harvesting occurred since 1999. This points to the legacy of older harvests differentiating wildlands from unprotected forests (Question 2).

Difference in AGC between wildlands and unprotected forests generally increased with increasing difference in forest age between protection categories, which was highest in Maine, New York, and in recently harvested areas. In CT-MA-RI, where wildlands and unprotected forests had almost no difference in average forest age (1.3 years), and where the small sample size did not include any recent harvesting, there was little difference in AGC. CT-MA-RI forests were notable for having the highest AGC in the region, which likely reflects a relatively old stand age, a longer growing season, and a high component of oaks, which generally have higher biomass than other northern species (cf. Keeton et al. 2011; Finzi et al. 2020). Overall, our results are consistent with studies that reported higher AGC in old and unmanaged forests relative to young and actively managed forests (Harmon et al. 1990; Nunery and Keeton 2010).

4.2. Total forest BAI

In contrast to AGC, total forest BAI did not differ between wildlands and unprotected forests at any spatial scale, revealing no apparent tradeoffs between carbon storage and sequestration rate in our study area (Question 3). This finding is, in some respects, not surprising given the sites were matched on the primary environmental controls of growth. However, wildlands had 37% higher total forest BAI compared to recently harvested (and younger) forests. This result runs counter to age-related declines in carbon sequestration that others have reported (e.g., Ryan et al. 1997; Pregitzer and Euskirchen 2004, Bradford and Kastendick 2010; D'Amato et al. 2011). One possible explanation for our results is that stem density was higher in wildlands than in recently harvested forests in our study area. In contrast, stem density is often higher in younger forests with greater sequestration rates (e.g., Ryan and Waring 1992). Hence, even though individual trees often had greater BAIs in recently harvested areas in our study, the summed BAIs of a smaller density of stems in these stands did not exceed the summed BAIs of a greater density of stems in wildlands. Our findings call into question mitigation strategies that aim to increase stand-level or regional scale carbon sequestration rates through forest management. Not only are sequestration rates unlikely to increase in managed forests relative to wildland forests in the northeastern US (cf. Brown et al. 2018; Canham 2021), they will likely decline for 15–20 years compared to surrounding intact forests. Moreover, the re-growing forest will generally not equal the carbon lost from a harvested mature stand (and the foregone carbon the stand would have sequestered) for many decades to over a century (Harmon et al. 1990; Keeton et al. 2011).

4.3. Structural complexity differences and drivers

Wildland forests generally showed greater structural complexity than unprotected forests, as four structural variables (no. of large live and dead trees, maximum tree height, and diversity of diameter size classes) were greater in wildlands overall, while two variables (standard deviation of tree height and adult tree richness) did not differ between wildlands and unprotected forests. This consistent trend across multiple metrics of structural complexity, especially in those associated with high-quality FIA DBH measurements, provides strong support of a treatment effect in wildland forests that also corroborates other recent studies (Zlonis and Niemi 2014; Miller et al. 2016). With respect to Question 2, recent harvesting history of unprotected forests amplified differences in the structural variables. Still, structural differences in the four tree layer variables generally remained greater in wildlands than in unprotected plots without recent harvesting ($P \leq 0.05$), suggesting both recent and long-term legacy effects of harvesting on these variables, particularly in the northern parts of the region (Belair and Ducey, 2018; Gunn et al. 2019).

Overall, related to Question 3, our results showed a positive relationship between structural complexity and AGC and an absence of a negative relationship between structure and carbon sequestration (BAI). Our results are therefore generally in accord with those reported by Thom and Keeton (2019) and Gough et al. (2019).

In CT-MA-RI, where mean stand age was quite similar between protection categories (89 vs. 88 years) and average time since protection as wildlands relatively short (15 years), none of the structural variables differed significantly between protection categories. However, a small sample size ($n = 9$) in this sub-region, which underrepresented recent harvest activity, also likely contributed to the high variability and low power in detecting differences in forest conditions.

Attributing increases in structural complexity and carbon storage in wildlands to the treatment effects of protection requires disentangling of biases in selection. Areas that are chosen for wildlands protection may

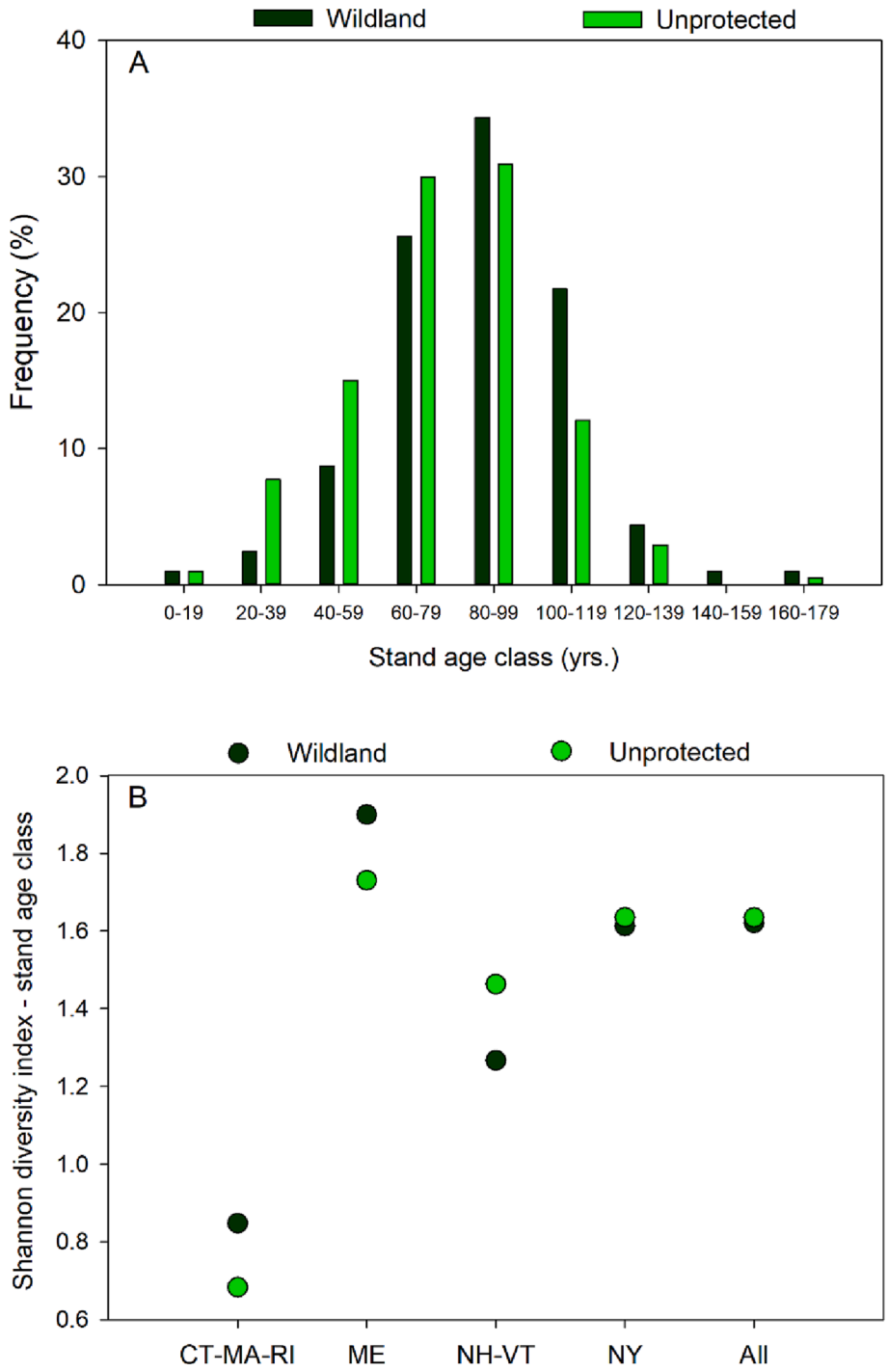

Fig. 8. Stand age distribution in (A) 20-year age classes across all plots (n = 207) in the northeastern US and (B) Shannon Diversity index of 20-year age classes by region and sub-region in wildland and unprotected plots. See Fig. 2 caption for abbreviation key and sample sizes.

be selected, in part, due to nonrandom differences in the underlying environment or attributes of the forest itself. With a quasi-experimental design, we were able to control for variation in the underlying environment, ensuring that our results were not driven by differences in site potential. Our analysis of recently protected plots with a corresponding FIA measurement allowed us to investigate selection bias driven by differences in forest structure (Question 4). We found no differences at the time of protection in either aboveground carbon or structural diversity between wildlands and unprotected forests. This further supports our conclusions that increases in forest carbon and structural diversity are attributable to wildlands protection and not by differences in the site or initial forest. However, because we could only compare conditions at the time of protection for sites protected after the year 2000, we cannot rule out that the older wildlands in our sample, did not have an initial selection bias for greater carbon and structural complexity.

4.4. *Stand age class distribution and species diversity*

Despite the legacy of management in unprotected areas, we detected virtually no difference in age class diversity between wildlands and unprotected forests at a regional scale. Wildlands were more homogenous (i.e., a higher frequency of plots) at their median age class;

however, wildlands had four times the frequency of plots in the oldest age classes (140–180 years) and the same frequency of plots (~1%) in the youngest age class (0–19 years) as unprotected forests.

Structural complexity, including age class diversity, is directly related to biodiversity, due to the greater numbers of habitat niches and resources in the varying sizes of live and dead biomass and varying successional stages (McElhinny et al. 2005). Older forests with more deadwood generally result in a greater diversity of lichens and fungi compared to younger and less complex forests (Hilmers et al., 2018; Atrena et al. 2020). Vertebrate and invertebrate animal diversity generally exhibit a U-shaped pattern with stand age, but eventually reach their highest levels of species richness in older, more complex forests (DeGraaf et al. 2006; Hilmers et al., 2018). Understory vascular plant diversity, on the other hand, may increase or decrease in older forests with greater complexity (Hilmers et al., 2018; Thom et al. 2019), although recently managed forests in the Northeastern U.S. often have higher understory plant diversity than unmanaged controls (Smith et al. 2008; Ellison et al. 2015).

Although previous studies in wilderness areas and national parks in the eastern US reported higher adult tree species richness in protected than in unprotected areas (Zlonis and Niemi 2014; Miller et al. 2018), we detected no difference in tree species richness overall. However, we did find tree richness to be higher in wildlands compared to recently harvested areas. Our results suggest that adult tree richness in unprotected areas has not declined with a legacy of timber management, although richness does temporarily decline for 15–20 years after harvesting. At the same time we found no evidence that eliminating harvesting and management leads to a decline in adult tree richness, because of a reduction in canopy disturbance, as some authors have reported.

5. Conclusions

Our results showed strong divergence in carbon storage and many aspects of structural complexity in wildlands relative to forests open to harvesting in similar environmental conditions across the Adirondack-New England region. These patterns developed despite < 10% of unprotected plots in our sample being harvested since 1999, which underestimated regional harvesting activity, and wildlands being only 11 years older on average than unprotected forests. Thus, unprotected forests that appear intact and relatively undisturbed are, on average, less carbon dense and structurally simpler than nearby wildland forests. Protection status (and resulting forest condition), in other words, is a critical factor when considering the climate adaptation and mitigation capacity of forests.

Additionally, we detected few tradeoffs between mitigation and adaptation capacity in wildlands or between the benefits of carbon storage and carbon sequestration in wildland forests. Our results suggest the need for forest managers and conservation biologists to reexamine the rush to incorporate more management for climate adaptation and mitigation in northern temperate forests that are not specifically being managed for wood products and to consider instead the multiple benefits of stricter protection and allowing natural processes to do more.

CRediT authorship contribution statement

Edward K. Faison: Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Investigation. **Danelle Laflower:** Methodology, Software, Validation, Formal analysis, Visualization, Data curation, Investigation, Writing – review & editing. **Luca L. Morreale:** Methodology, Software, Visualization, Validation, Formal analysis, Data curation, Writing – review & editing. **David R. Foster:** Resources, Investigation, Writing – review & editing. **Brian Hall:** Visualization, Resources, Data curation, Writing – review & editing. **Emily Johnson:** Resources, Data curation, Investigation. **Jonathan R. Thompson:** Funding acquisition, Supervision, Project administration, Writing – review & editing, Resources, Conceptualization, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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