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Change in Montane Forests of East-central West Virginia over 250 years

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ABSTRACT

We compared the relative frequencies of witness trees in historical deeds to the relative frequencies of tree species found in the present forests. Changes in relative frequencies of the five dominant tree species were noted in all ecological subsections, although all species found in the past forests are represented in the present. The greatest changes across the study area were a decrease in the representation of white oak and an increase in red maple. The changes in representation by functional groups show a trend toward loss of fire-adapted species of intermediate shade intolerance with associated gains in species of high shade tolerance. Current FIA data on the species composition of trees in the sapling and seedlings size-classes indicate that the trend of reduced of oak species frequency is likely to continue into the near future. This gradual conversion from oak-dominated overstories to maple-dominated understories is a regional trend. Our findings echo a paradox found in the northeastern United States where after 400 years of land use change, forest cover has largely recovered but relative species composition has been transformed. This paradox may add to the difficulty in designing strategies and treatments for ecosystem restoration. However, as we have shown, the changes can be quantified and placed in an ecological context as support for restoration actions.

1. Introduction

Emphasizing the restoration of diverse and resilient ecosystems creates a need for information about historical variability in species composition, disturbance regimes, and forest structure. Historical forest conditions are difficult to assess for much of the eastern United States due to early European settlement and land clearing. While conditions before European settlement may not be appropriate as targets for restoration, the information can still inform goals and strategies by providing reference conditions and an understanding of variability. Qualitative sources, such as traveler's accounts and photographs are useful, however, definitive quantitative information is generally unavailable.

One historical source of information on forest composition is deeds and land grants. In the metes and bounds surveys of the original colonies, surveyors often used trees to describe parcel corners. Trees listed in deeds or land grants (witness, bearing, or line trees) can give an indication of forest conditions at the time of European settlement. A factor important for teasing out ecological meaning from witness trees is that the distribution of tree species across a landscape is not random but rather affected by environmental factors such as climate, soil type, topography, and disturbance regime (Schulte and Mladenoff 2001). Therefore, when surveyors recorded witness, bearing, or line trees from those available to them in the immediate vicinity of a corner, those species or genera reflect a suite of site factors that caused the individual tree to persist and can represent longer time periods than just the year the survey was conducted.

In West Virginia, exploitative logging and destructive fires in the 1900s reshaped the original forests in species composition, structure, and function. In the highest elevations and most remote parts of the state, the timing of this wide-spread disturbance was tied to the development of narrow-gauge railroads, about 1884 (Stephenson 1993) with the headwaters of the Greenbrier River in Pocahontas county reached by rail in 1903 (Lewis 1998). While some trees were not harvested for economic reasons – species, size, or quality – this logging resulted in large areas where forest succession was re-started.

As the forests of West Virginia regrew, harvest began again on both public and private lands. The Monongahela National Forest (MNF), located mainly in the remote, higher elevation, counties of West Virginia, was established in 1920. During the 1940s through the 1960s, timber harvest on the MNF was almost exclusively uneven-aged management (Miller 2014). The perpetuation of mainly shade-tolerant tree species through uneven-aged management was reconsidered and in the 1960s and 1970s the use of clearcut harvesting increased on the MNF.

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In 1986, the first land and resource management plan was created for the MNF, with an emphasis on multiple uses and sustained yields. A new management plan was developed for the MNF in 2006, emphasizing active forest restoration through the creation of a new management prescription for restoration of spruce (*Picea*)-dominated forests and added emphasis on oak (*Quercus*) management through prescribed fire.

Timber harvest on private land in West Virginia is largely diameter-limit harvest—about 62% of timber harvests in one estimate (McGill et al., 2006)—where trees are removed based on size with little regard to the quality of the residual stand. A sampling of logging activities on private lands in West Virginia showed that under diameter-limit harvesting an average of 52% of stand basal area was removed (Luppold and Alderman 2007). The economic nature of this harvest type was evident in these stands in that larger American beech (*Fagus gradifolia*) were not removed even though they met the diameter limit and smaller black cherry (*Prunus serotina*) and sugar maple (*Acer saccharum*) stems were removed (Luppold and Alderman 2007). The resulting stand structure of this harvest practice varies from near clearcut-like conditions if the diameter limit is set low to uneven-aged conditions where shade tolerant species are favored.

As managers on the MNF emphasize forest and ecosystem restoration, an assessment of how the forest has changed in terms of species composition and function is desirable. This information could be used for prioritizing areas for management and giving an ecological context for management actions. Additionally, the comparison of past and present forests is one way to describe the recovery of publicly and privately owned forests from the exploitative logging of the 1900s.

An analysis of witness trees within the proclamation boundary of the MNF (Thomas-Van Gundy and Strager 2012) details the species-site relationships based on deeds from 1752 to 1899. We used an updated version of this dataset to compare the past (1752 to 1899) forest of the eastern mountains of West Virginia to present (2012 to 2018) forest of the area. While centered on the MNF, the witness tree dataset includes private land within the forest proclamation boundary. Since differences were found based on ecological subsection in the historical forests (Thomas-Van Gundy and Strager 2012), the analysis of past and present forests was also made by ecological subsection and study area as a whole. In this analysis, we address the following questions: do the present forests resemble the past forests in terms of tree species composition and functional groups? And if changes are found, do the changes differ based on ecological subsection?

2. Methods

2.1. Study area

The study area, approximately 1,013,793 ha, includes public and private land within the MNF proclamation boundary buffered by 5 km to match the original extent of the witness tree database (Fig. 1). The proclamation boundary of the MNF is the congressionally designated area within which the National Forest can purchase land to add to the national forest system. The MNF makes up about 371,906 ha or 37% of the study area with the rest, 641,887 ha or 63% of the area, in private or other public ownership.

Located in the east-central mountains of West Virginia (Fig. 1), the MNF spans two physiographic sections – the Ridge and Valley and the Allegheny Mountains separated by the Allegheny Front, creating a rain shadow to the east (Cleland et al., 2007). Ecological subsections (Cleland et al., 2007) represented on the MNF include: Ridge and Valley (RV, M221Aa, 137,390 ha), Northern High Allegheny Mountain (NHAM, M221Ba, 215,591 ha), Eastern Allegheny Mountain and Valley (EAMV, M221Bd, 161,518 ha), Western Allegheny Mountain and Valley (WAMV, M221Be, 48,184 ha), Southern High Allegheny Mountain (SHAM, M221Bc, 243,468 ha), Western Allegheny Mountain (WAM, M221Bb, 151,138 ha), and Eastern Coal Fields (ECF, M221Cb, 35,078 ha).

The RV subsection is east of the Allegheny Front with relatively low average annual precipitation (102.3 cm) and potential natural vegetation of about 49% Appalachian oak forest and 41% oak-hickory pine forest. Elevation ranges from 284.7 m to 1,482.5 m with an average of 712.8 m in the study area. The NHAM and SHAM subsections include the higher elevations in the study area with a range of 511.5 m to 1,454.5 m and mean of 1,020.2 m for the NHAM subsection. Potential natural vegetation in this subsection is about 80% northern hardwood forest and 14% northeastern spruce-fir forest with an average annual precipitation of 128.2 cm. The SHAM subsection is similar to NHAM with 138.1 cm of precipitation annually and potential natural vegetation of about 51% northern hardwood forest, 23% mixed mesophytic forest, and 21% northeastern spruce-fir forest; elevation ranges from 446.8 m to 1,478.6 m and an average of 1,043.7 m in the study area; both subsections are in the Allegheny Mountain section. The EAMV (annual average precipitation of 111.0 cm; mean elevation of 824.5 m and a rage of 523.3 to 1,461.8 m) and WAMV (annual average precipitation of 99.7 cm; mean elevation of 731.7 m and a rage of 529.1 m to 1,101.5 m) subsections are in the Allegheny Mountains section but have landforms similar to the Ridge and Valley section. The two subsections differ in potential natural vegetation with EAMV described as about 59% Appalachian oak forest and 41% northern hardwood forest and WAMV as about 86% Appalachian oak forest and 13% northern hardwood forest. The WAM and ECF subsections make up small portions of the study area and both are west of the Allegheny Front with WAM in the Allegheny Mountains section and ECF in the Northern Cumberland Mountains section. Average annual precipitation is 122.2 cm for WAM and 113.7 cm for the ECF subsection; elevations range from 418.2 m to 1,226.8 m (mean of 733.0 m) for WAM and 526.1 m to 956.8 m (mean of 761.0 m) for ECF. The potential natural vegetation for the WAM subsection is described as about 38% mixed mesophytic forest, 35% northern hardwood forest, and 27% Appalachian oak forest. For the ECF subsection, the potential natural vegetation is about 52% mixed mesophytic forest, 28% Appalachian oak forest, and 20% northern hardwood forest. All climate data and potential natural vegetation estimates are from Cleland et al. (2007); elevation data from a digital elevation model of the study area.

The study area is underlain by mainly sedimentary geology of Pennsylvanian, Mississippian, Devonian, Silurian, and Ordovician ages. Lithology includes sandstone, shale, siltstone, coal, and limestone and differing rates of erosion contribute to the variety in soils and topography in the study area. The highest point in the state, Spruce Knob at 1,482 m, is located in the study area. The complex topography and elevational gradient results in a variety of landforms supporting diverse vegetation. Like the larger central Appalachians, the study area experiences the full range of disturbance regimes. Climate-related disturbances include heavy snow and ice, late frosts, and drought (Butler et al., 2015). Human-related fire regimes are also inferred or otherwise documented for the area (Lafon et al., 2017).

2.2. Tree species data

Witness tree data from a previous study (Thomas-Van Gundy and Strager, 2012, 2014) were used to compare past species composition to present species composition. Briefly, old maps of the surveyed polygons made by forest staff in the 1930s were scanned and georeferenced. The copies of the deeds used to create these maps were then used to attribute the survey corners with trees listed in the deed in a GIS. After publication in 2012, while preparing the witness tree dataset for archiving, minor errors in the numbers and species of some corners were found and corrected. This dataset included deeds from 1752 through 1899. Based on past work (Thomas-Van Gundy and Strager 2012) the frequencies for witness trees called “spruce pine” were added to hemlock tallies for this analysis.

At each point (survey corner), the relative frequency of each species

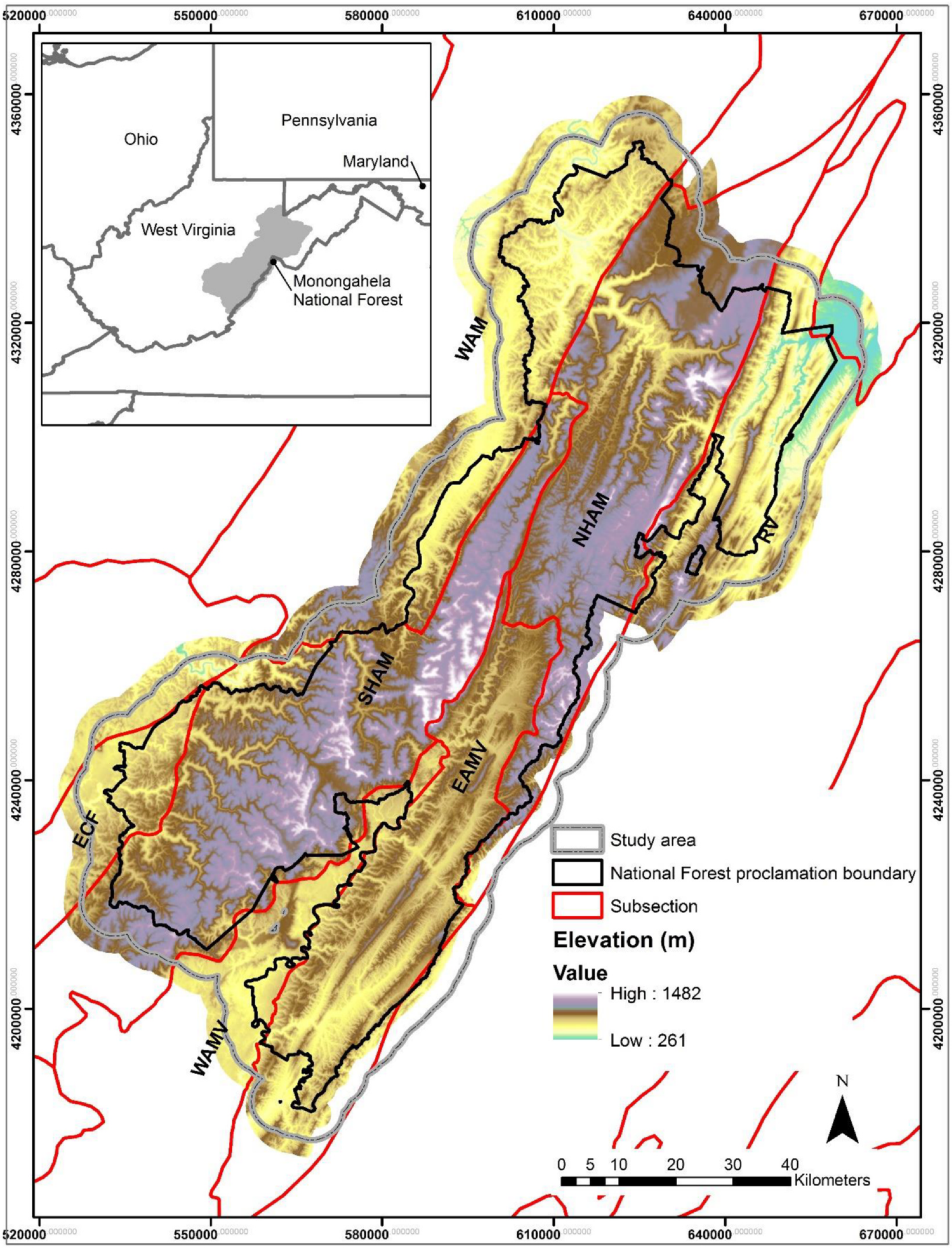

Fig. 1. Location of study area including ecological subsections and elevation. Subsections are: Ridge and Valley (RV), Northern High Allegheny Mountain (NHAM), Eastern Allegheny Mountain and Valley (EAMV), Western Allegheny Mountain and Valley (WAMV), Southern High Allegheny Mountain (SHAM), Western Allegheny Mountain (WAM), and Eastern Coal Fields (ECF).

was calculated by dividing the number of trees of each species or genus by the total number of trees at that corner and multiplying by 100. Species or genus relative frequencies calculated at each point were then averaged by ecological subsection and for the study area as a whole. Corners with no trees were removed from the dataset for this analysis.

The use of witness trees for ecological information has obvious statistical drawbacks given that the past forest cannot be re-sampled, however, the relative description of the original forest we gain from this record is still useful and can be evaluated in an ecological context (Rhemtulla and Mladenoff 2010). Assessments of bias in species and size recorded in Public Land Surveys (PLS) noted bias by an individual surveyor was possible but when analyses included many surveyors, those individual biases were less apparent (Schulte and Mladenoff 2001).

Data for species composition of the current forest (plots sampled in 2012 – 2018) were obtained from USDA Forest Service, Forest Inventory and Analysis (FIA). The FIA sampling design is based on a tessellation of the United States into hexagons of ~2,428 ha with at least one permanent plot established in each hexagon. Tree and site attributes (e.g., species, diameter, aspect, and slope) are measured in plots falling in forest land; in each plot, tree measurements are taken in four 7.3-m fixed-radius subplots and sapling/seedling measurements are taken in four 1.8-m fixed-radius microplots. The buffered MNF proclamation boundary was used to select the FIA plots to be used in the analysis. The plots were grouped by ecological subsection. Raw total numbers of trees, saplings, and seedlings per plot were collected from the FIA Database (USDA 2020) and used to compute mean relative frequencies by species by subsection. Trees are defined as those live individuals greater than 12.7 cm DBH, saplings are defined as live individuals greater than 2.5 cm and less than 12.7 cm DBH, and seedlings are defined as live individuals less than 2.5 cm DBH and greater than 30.5 cm tall (hardwoods) or 15.2 cm tall (softwoods).

Species were also grouped by ecophysiological traits for two characteristics – fire adaptation and shade tolerance (Table 3 gives the species assignments). The fire adaptation classification is based on characteristics such as bark thickness, ability to resprout after repeated fire, and flammability of leaf litter (see Thomas-Van Gundy and Nowacki 2013 for more details). In general, pyrophilic species are those adapted to frequent fire (fire every 0 to 35 years), for example chestnut oak, and pyrophobic species are those not adapted to frequent fire, for example sugar maple. Species or species groups classed as mixed have a response to fire that may vary depending on site factors, age of individual, or fire intensity, for example yellow-poplar. Tree species were placed in five shade tolerance categories (very tolerant, tolerant, intermediate, intolerant, and very intolerant) based on rankings from Lienard and others 2015. These categories are based on the ability of an individual of the species to survive, grow, and compete in shade cast by other trees, acknowledging that this is an aggregate response and that there will be variation due to site, age, and other factors (Lienard et al., 2015). These two characteristics were chosen because they reflect the range of disturbance regimes and species-site associations across environmental gradients in the study area.

2.3. Data analysis

The present and past forest compositions calculated by ecological subsection were used for comparisons by time period and species/genera and between ecological subsections (Tables 1 and 2). Comparisons between the species relative frequencies in the subsections and between past and present time periods were made through table analysis (PROC FREQ; SAS, 2016) using the nonparametric Jonckheere-Terpestra (J-T) test. The relative frequencies of 23 species or species groups (greater than 12.7 cm DBH) species/genera (Tables 1 and 2) by ecological subsection were analyzed. Differences were considered significant at $\alpha = 0.05$. The data sets do not represent two statistical samples given their differences in methods with the witness tree data being an example of an un-designed but random dataset, however they do represent two independent data sets.

We also explored the change over time and space (ecological subsections) through nonmetric multidimensional scaling (NMS) an ordination technique useful for exploring ecological data. The software package PC-ORD version 6.0 (McCune and Medford 2011) was used to perform the NMS. This technique is useful for finding relationships in ecological data particularly when the data are discontinuous or of questionable scales. In calculating the relative distances between data there is no assumption of linear relationships although the use of ranked distances between pairs of observations tends to linearize the relationship. The Sorensen/Bray-Curtis distance measure was used, with random starting coordinates; 250 runs were made with real data, and 500 runs with randomized data were used to determine differences from expected values. Multiple Response Permutation Procedures (MRPP, PC-ORD version 6.0, McCune and Medford 2011) were also used with Bray-Curtis distance to test for homogeneity in the ordination space based on average distance within the groups. Differences were considered significant at $\alpha = 0.05$.

3. Results

3.1. Changes in species composition

The representation of major tree species or genera differed by ecological subsection and through time (Fig. 2). The J-T tests found that

Table 1
Mean relative species frequencies (SE) in past forests of the study area by subsection from deeds dated 1752–1899. Number of corners included in each subsection are also given.

Species	study area (n = 14,333)	RV (n = 1,539)	NHAM (n = 1,675)	EAMV (n = 4,155)	WAMV (n = 714)	SHAM (n = 3,157)	WAM n = (2,812)	ECF (n = 281)
	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)
White oak	19.4 (0.3)	28.3 (1.0)	5.7 (0.5)	32.5 (0.6)	38.2 (1.6)	3.9 (0.3)	17.0 (0.7)	10.7 (1.6)
Sugar maple	10.1 (0.2)	7.0 (0.5)	17.1 (0.8)	4.5 (0.3)	7.3 (0.8)	18.2 (0.6)	7.7 (0.5)	10.1 (1.5)
American beech	8.4 (0.2)	0.8 (0.2)	18.2 (0.8)	1.2 (0.1)	2.9 (0.6)	17.2 (0.5)	9.1 (0.5)	8.3 (1.4)
all pines	6.6 (0.2)	9.3 (0.7)	1.9 (0.3)	13.6 (0.5)	7.1 (0.9)	4.1 (0.3)	1.0 (0.2)	0.0 (0.0)
American chestnut	6.3 (0.2)	4.0 (0.4)	4.0 (0.4)	6.3 (0.3)	6.1 (0.8)	4.7 (0.3)	9.3 (0.5)	18.4 (2.0)
Chestnut oak	5.2 (0.2)	12.3 (0.8)	2.3 (0.3)	6.0 (0.3)	2.2 (0.5)	1.0 (0.2)	7.6 (0.5)	3.0 (0.9)
Red maple	5.0 (0.1)	2.0 (0.3)	6.6 (0.5)	5.6 (0.3)	3.9 (0.6)	4.7 (0.3)	5.0 (0.3)	11.4 (1.4)
Red spruce	2.9 (0.1)	0.8 (0.2)	3.0 (0.3)	1.4 (0.2)	0.4 (0.2)	6.0 (0.4)	3.5 (0.3)	0.0 (0.0)
Birch	4.3 (0.1)	1.1 (0.2)	6.1 (0.5)	1.3 (0.1)	1.8 (0.5)	9.1 (0.4)	4.8 (0.4)	1.8 (0.6)
Hickory	4.1 (0.1)	4.5 (0.4)	1.3 (0.2)	6.1 (0.3)	5.1 (0.7)	1.7 (0.2)	5.3 (0.4)	2.2 (0.6)
Basswood	3.9 (0.1)	3.1 (0.4)	5.9 (0.5)	2.6 (0.2)	1.5 (0.4)	6.9 (0.4)	2.4 (0.3)	4.7 (1.0)
Northern red oak	3.1 (0.1)	4.8 (0.4)	3.4 (0.4)	2.8 (0.2)	2.2 (0.4)	3.1 (0.3)	2.6 (0.3)	2.9 (0.8)
Black oak	2.2 (0.1)	5.6 (0.5)	0.2 (0.1)	2.7 (0.2)	5.0 (0.7)	0.7 (0.1)	1.4 (0.2)	4.0 (1.0)
Yellow-poplar	2.0 (0.1)	1.2 (0.3)	1.3 (0.2)	1.1 (0.1)	1.4 (0.4)	1.1 (0.2)	4.7 (0.3)	10.4 (1.5)
Scarlet oak	2.0 (0.1)	2.0 (0.3)	2.1 (0.3)	1.0 (0.1)	3.8 (0.6)	0.9 (0.1)	4.3 (0.3)	0.5 (0.3)
Ash	1.7 (0.1)	1.7 (0.3)	2.1 (0.3)	0.7 (0.1)	0.7 (0.3)	2.4 (0.2)	2.3 (0.3)	0.5 (0.3)
Hemlock	3.4 (0.1)	1.8 (0.3)	9.0 (0.6)	2.9 (0.2)	0.2 (0.2)	4.8 (0.3)	0.9 (0.2)	3.0 (0.9)
Blackgum	1.2 (0.1)	1.3 (0.2)	0.6 (0.2)	1.1 (0.1)	1.2 (0.4)	0.6 (0.1)	2.1 (0.2)	2.5 (0.8)
Black walnut/ butternut	1.2 (0.1)	2.3 (0.3)	1.1 (0.2)	0.7 (0.1)	1.4 (0.4)	1.4 (0.2)	0.9 (0.2)	0.9 (0.4)
Magnolia	1.1 (0.1)	0.5 (0.2)	2.2 (0.3)	0.1 (0.0)	0.0 (0.0)	1.2 (0.2)	2.4 (0.2)	0.5 (0.4)
Black cherry	1.0 (0.1)	0.2 (0.1)	1.8 (0.3)	0.7 (0.1)	0.6 (0.3)	2.2 (0.2)	0.5 (0.1)	0.2 (0.2)
Black locust	0.8 (0.1)	0.9 (0.2)	0.7 (0.2)	0.7 (0.1)	1.2 (0.3)	1.0 (0.1)	0.9 (0.2)	0.3 (0.2)
Other	4.0 (0.1)	4.4 (0.4)	3.2 (0.3)	4.4 (0.3)	5.6 (0.7)	3.2 (0.2)	4.2 (0.3)	3.5 (0.8)

All pines includes trees listed as pine, yellow pine, or white pine in the witness tree dataset. The category other includes – mulberry, Indian wood (likely Osage orange), witch hazel, hawthorn, sourwood, dogwood, buckeye, striped maple, holly, serviceberry, apple, sycamore, elm, oak-no species, hophornbeam, hornbeam, aspen, willow, cedar, fir, and yew.

Table 2
Mean relative species frequencies (SE) in present forests of the study area by subsection from FIA plots measured from 2012 to 2018. Number of FIA plots included in each subsection are also given.

Species	study area n = 595	RV n = 53	NHAM n = 141	EAMV n = 102	WAMV n = 13	SHAM n = 193	WAM n = 73	ECF n = 20
	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)	mean (SE)
White oak	3.4 (0.4)	3.8 (1.5)	0.7 (0.3)	11.4 (1.5)	16.3 (5.0)	0.1 (0.1)	3.8 (1.0)	3.0 (2.1)
Sugar maple	10.8 (0.7)	12.0 (2.5)	12.4 (1.6)	5.5 (1.2)	5.5 (3.1)	10.6 (1.2)	13.2 (2.0)	18.9 (5.4)
American beech	7.3 (0.5)	0.2 (0.2)	10.5 (1.4)	0.7 (0.3)	1.6(1.6)	11.1 (1.1)	6.7 (1.3)	5.6 (1.9)
all pines	3.1 (0.4)	7.1 (2.3)	0.3 (0.3)	12.5 (1.9)	5.5 (3.6)	0.0 (0.0)	0.8 (0.6)	0.0 (0.0)
American chestnut	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Chestnut oak	6.3 (0.5)	18.8 (2.5)	1.2 (0.4)	17.8 (1.8)	4.0 (1.9)	0.4 (0.2)	8.3 (1.5)	2.3 (1.5)
Red maple	15.7 (0.7)	7.4 (1.6)	20.0 (1.6)	13.2 (1.3)	10.2 (3.8)	16.1 (1.2)	16.6 (1.9)	17.2 (5.6)
Red spruce	5.6 (0.7)	0.4 (0.4)	8.1 (1.8)	0.1 (0.1)	0.0 (0.0)	10.9 (1.4)	0.4 (0.3)	0.0 (0.0)
Birch	11.7 (0.7)	4.2 (1.6)	15.7 (1.6)	3.7 (0.9)	2.8 (1.6)	17.1 (1.2)	7.2 (1.4)	14.2 (4.6)
Hickory	3.2 90.4)	5.0 (1.2)	1.0 (0.3)	8.2 (1.4)	9.0 (4.2)	0.7 (0.2)	3.8 (0.7)	7.1 (4.4)
Basswood	2.4 (0.3)	4.1 (1.6)	1.8 (0.5)	0.5 (0.2)	2.5 (2.1)	3.1 (0.6)	2.7 (0.9)	5.4 (2.5)
Northern red oak	5.1 (0.4)	14.4 (2.1)	4.1 (0.7)	6.2 (0.9)	3.2 (1.5)	2.9 (0.5)	4.9 (0.8)	5.1 (2.2)
Black oak	1.2 (0.2)	2.1 (0.7)	0.3 (0.2)	3.8 (0.6)	4.1 (1.9)	0.0 (0.0)	1.1 (0.5)	0.5 (0.3)
Yellow-poplar	3.0 (0.4)	0.1 (0.1)	0.8 (0.4)	1.9 (0.6)	6.9 (5.3)	2.6 (0.6)	9.4 (2.1)	9.8 (2.4)
Scarlet oak	0.8 (0.1)	1.9 (0.9)	0.0 (0.0)	2.2 (0.4)	2.2 (1.1)	0.2 (0.2)	1.4 (0.5)	0.0 (0.0)
Ash	1.2 (0.2)	1.1 (0.4)	1.3 (0.3)	0.5 (0.2)	2.1 (1.0)	1.6 (0.3)	1.0 (0.4)	0.3 (0.2)
Hemlock	4.8 (0.4)	0.2 (0.1)	6.3 (1.1)	3.7 (0.9)	4.1 (2.3)	6.1 (0.8)	3.8 (1.3)	4.3 (1.7)
Blackgum	0.6 (0.1)	3.2 (1.0)	0.1 (0.1)	0.8 (0.3)	0.0 (0.0)	0.1 (0.0)	0.7 (0.2)	0.2 (0.2)
Black walnut/butternut	0.2 (0.1)	1.1 (0.5)	0.0 (0.0)	0.0 (0.0)	1.4 (1.4)	0.1 (0.1)	0.1 (0.1)	0.0 (0.0)
Magnolia	1.6 (0.2)	0.2 (0.1)	1.5 (0.4)	1.3 (0.4)	0.3 (0.3)	2.3 (0.4)	1.5 (0.5)	0.6 (0.4)
Black cherry	5.1 (0.4)	0.7 (0.2)	9.0 (1.0)	0.5 (0.2)	3.8 (2.1)	6.8 (0.8)	3.2 (1.2)	3.2 (1.7)
Black locust	1.9 (0.3)	7.6 (2.8)	0.3 (0.1)	1.7 (0.5)	3.9 (2.4)	1.8 (0.5)	1.5 (0.5)	0.8 (0.7)
other	5.1 (0.4)	4.7 (1.2)	4.5 (0.7)	3.9 (0.9)	10.3 (3.0)	5.3 (0.8)	7.7 (1.4)	1.4 (0.7)

All pines includes – white, pitch, red, shortleaf, Table Mountain, and Virginia pines. The category other includes – ailanthus, elms, holly, hornbeam, mountain-ass, sycamore, apple, balsam fir, bigtooth aspen, black maple, boxelder, chinkapin oak, hophornbeam, cedar, dogwood, hackberry, hawthorn, mountain maple, Norway spruce, oak (no species), pin cherry, sassafras, serviceberry, sourwood, striped maple, sweet cherry (domesticated), and yellow buckeye.

the differences in species composition were statistically significant between the past and the present forests for all subsections and the study area as a whole (p less than 0.0001 for all subsections other than WAMV where p = 0.003).

White oak (*Q. alba*) was the most frequent tree in the past forest at European settlement and showed the largest drop in relative frequency when compared to the present forest. The greatest change was found in the RV subsection where white oak dropped by 24% (Fig. 2a). The least amount of change in white oak frequency was found in the SHAM subsection at about 4% drop (Fig. 2g).

Past forests in the higher elevation subsections were dominated by American beech, sugar maple, hemlock (*Tsuga canadensis*), red maple (*A. rubrum*), and birch (*Betula* spp.) in the NHAM subsection and sugar maple, American beech, birch, basswood (*Tilia americana*), and red spruce (*P. rubens*) in SHAM (Table 1; Fig. 2f and 2 g). Unlike other subsections and the study area as a whole, white oak was a minor component in the past at 5.7% of witness trees in NHAM and 3.9% in SHAM. Red maple has increased in these subsections and red maple is

Table 3
Functional group assignments and relative change by species and subsection. D - decrease between time periods and I- increase in relative frequency between time periods, and 0 is less than a 0.5% change between time periods.

Species	Functional group		Relative change between past and present							
	Fire adaptation	Shade tolerance	Study area	RV	NHAM	EAMV	WAMV	SHAM	WAM	ECF
White oak	pyrophile	intermediate	**D**	**D**	**D**	**D**	**D**	**D**	**D**	**D**
Sugar maple	pyrophobe	very tolerant	**I**	**I**	**D**	**I**	**D**	**D**	**I**	**I**
American beech	pyrophobe	very tolerant	**D**	**D**	**D**	**D**	**D**	**D**	**D**	**D**
all pines	pyrophile	intolerant	**D**	**D**	**D**	**D**	**0**	**D**	**0**	**0**
American chestnut	pyrophile	intermediate	**D**	**D**	**D**	**D**	**D**	**D**	**D**	**D**
Chestnut oak	pyrophile	intermediate	**I**	**I**	**D**	**I**	**I**	**D**	**I**	**D**
Red maple	pyrophobe	tolerant	**I**	**I**	**I**	**I**	**I**	**I**	**I**	**I**
Red spruce	pyrophobe	very tolerant	**I**	**0**	**I**	**D**	**0**	**I**	**D**	**0**
Birch	mixed	intermediate	**I**	**I**	**I**	**I**	**I**	**I**	**I**	**I**
Hickory	pyrophile	intermediate	**D**	**I**	**0**	**I**	**I**	**D**	**D**	**I**
Basswood	pyrophobe	tolerant	**D**	**I**	**D**	**D**	**I**	**D**	**0**	**I**
Northern red oak	pyrophile	intermediate	**I**	**I**	**I**	**I**	**I**	**0**	**I**	**I**
Black oak	pyrophile	intermediate	**D**	**D**	**0**	**I**	**D**	**D**	**0**	**D**
Yellow-poplar	mixed	intolerant	**I**	**D**	**D**	**I**	**I**	**I**	**I**	**D**
Scarlet oak	pyrophile	very intolerant	**D**	**0**	**D**	**I**	**D**	**D**	**D**	**D**
Ash	pyrophobe	intermediate	**D**	**D**	**D**	**0**	**I**	**D**	**D**	**0**
Hemlock	pyrophobe	very tolerant	**I**	**D**	**D**	**I**	**I**	**I**	**I**	**I**
Blackgum	mixed	tolerant	**D**	**I**	**D**	**0**	**D**	**D**	**D**	**D**
Black walnut/butternut	mixed	intolerant	**D**	**D**	**D**	**D**	**0**	**D**	**D**	**D**
Magnolia	pyrophobe	intermediate	**I**	**0**	**D**	**I**	**I**	**I**	**D**	**0**
Black cherry	pyrophobe	intolerant	**I**	**I**	**I**	**0**	**I**	**I**	**I**	**I**
Black locust	pyrophile	very intolerant	**I**	**I**	**0**	**I**	**I**	**I**	**I**	**I**

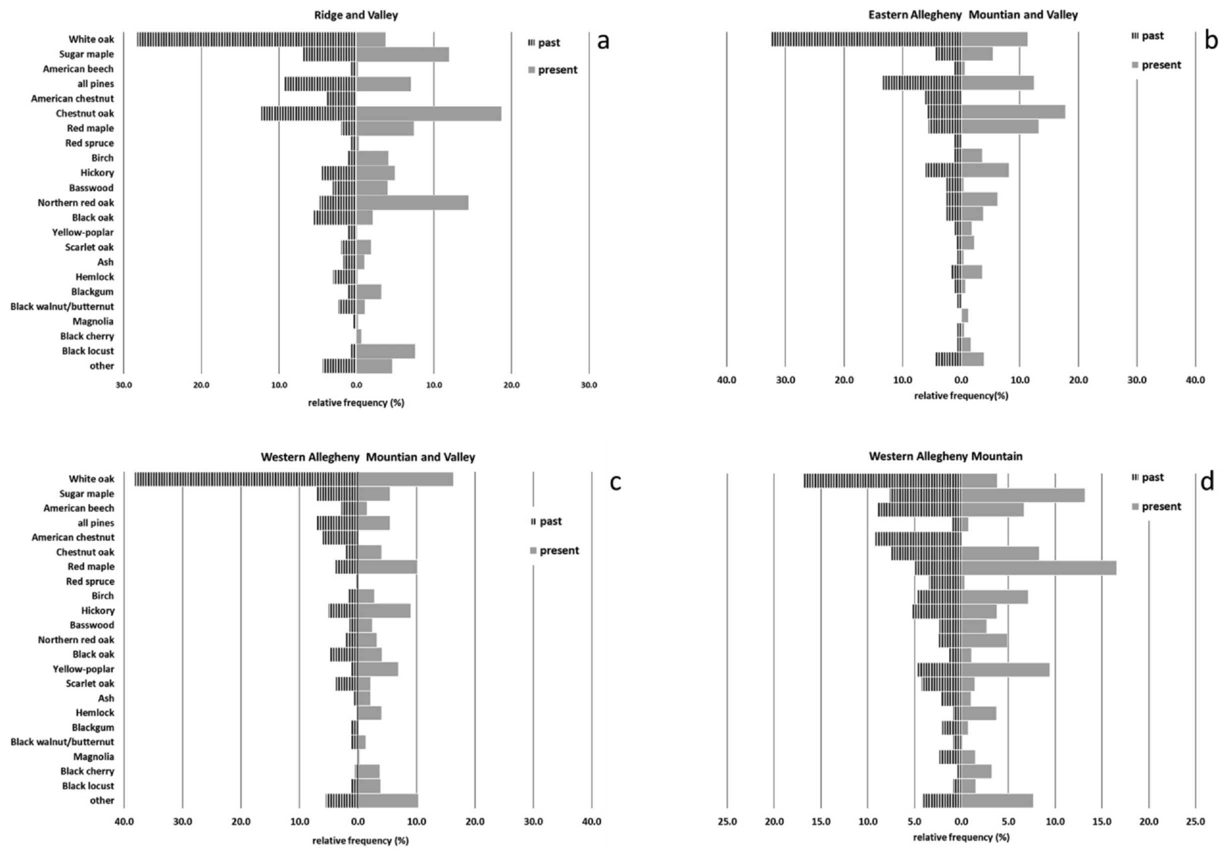

Fig. 2. Mean relative frequencies past and present for the RV (a), EAMV (b), WAMV (c), WAM (d), ECF (e), NHAM (f), and SHAM (g) subsections and the entire study area (h).

now the most frequent species in both subsections (20% in NHAM and 16% in SHAM) with American beech and sugar maple still important contributors to species composition. Interestingly, in both subsections red spruce relative frequencies have increased from the past, by about 5% in both subsections.

In contrast, forests in the generally drier and lower-elevation subsections were dominated by oaks and pines (*Pinus* spp.). White oak made up about 38% of the witness trees in the WAMV subsection, 32% in the EAMV, and 28% in the RV, with chestnut oak (*Q. montana*) (RV) and pines (EAMV) the next most frequent (Table 1; Fig. 2a and 2b). In both the RV and EAMV subsections, decreases in white oak and American chestnut (*Castanea dentata*) appear to have benefited other oak species in the present forests. However in both subsections, red maple has increased in relative frequency, by about 5% in the RV subsection and by about 7% in EAMV, and is now one of the top five ranked species.

3.2. Changes based on functional groups

Changes in species composition based on functional groups shows shifts in relative frequency in nearly all categories (Tables 3 and 4, Fig. 3). Differences in species composition by functional groups were also all statistically significant for all subsections and the study area as a whole based on J-T tests (p less than 0.0001). Across the study area as a whole, there was a reduction of about 50%, in the representation of pyrophilic species including all oak and hickory species.

Forests of the RV, EAMV, and WAMV subsections (approximately 35% of the study area) were dominated in the past by species intermediate in shade tolerance and adapted to fire (Fig. 3a, 3b, and 3c). In contrast, higher elevation forests in the NHAM and SHAM subsections (approximately 45% of the study area) were dominated by species not adapted to fire (Fig. 3f and 3 g). About 50% of the species in the past forests of the NHAM and SHAM subsections were very shade tolerant. In the present forest of these subsections the very tolerant species make up about 37 or 38% respectively.

The greatest decrease (about 24%) in species considered pyrophilic was seen in the WAM subsection and greatest increase in pyrophobic species (about 16%) was found in the ECF subsection. While declines in relative frequencies of fire-adapted species were seen in all subsections (Fig. 3), the least amount of change occurred in the EAMV subsection with a drop of around 8% (Fig. 3b). The percentages of species considered mixed or pyrophobic in fire adaptation increased in all subsections.

The greatest change in shade tolerance representation occurred in the WAM subsection with a 21% decrease for species in the intermediate shade tolerance class (Fig. 3d). This, and the drop in representation by pyrophilic species, is likely due to the decrease in relative frequency of white oak. Representation in the intermediate shade class declined between the two time periods across all subsections and there were increases in the tolerant shade class across all subsections. Since all subsections showed change in all categories between the two time periods, it is difficult to determine an area where the least change occurred, however, in the EAMV subsection, the largest change seen was about a 6% decrease in species in the intermediate class (Fig. 3b).

The current relative frequencies of saplings and seedlings further reinforce many of the changes in species composition of the larger trees (Table 5). The dearth of oak saplings and seedlings is clear given that none of the oaks make up more than 1.3% of total saplings or seedlings in the study area as a whole. Additionally, American beech (27.7% and 20.4%) and red spruce (27.5% and 14.8%), both very shade tolerant, appear poised to continue to have large increases into the tree-size class in the future based on high relative frequencies in the seedling- and sapling-size classes, respectively.

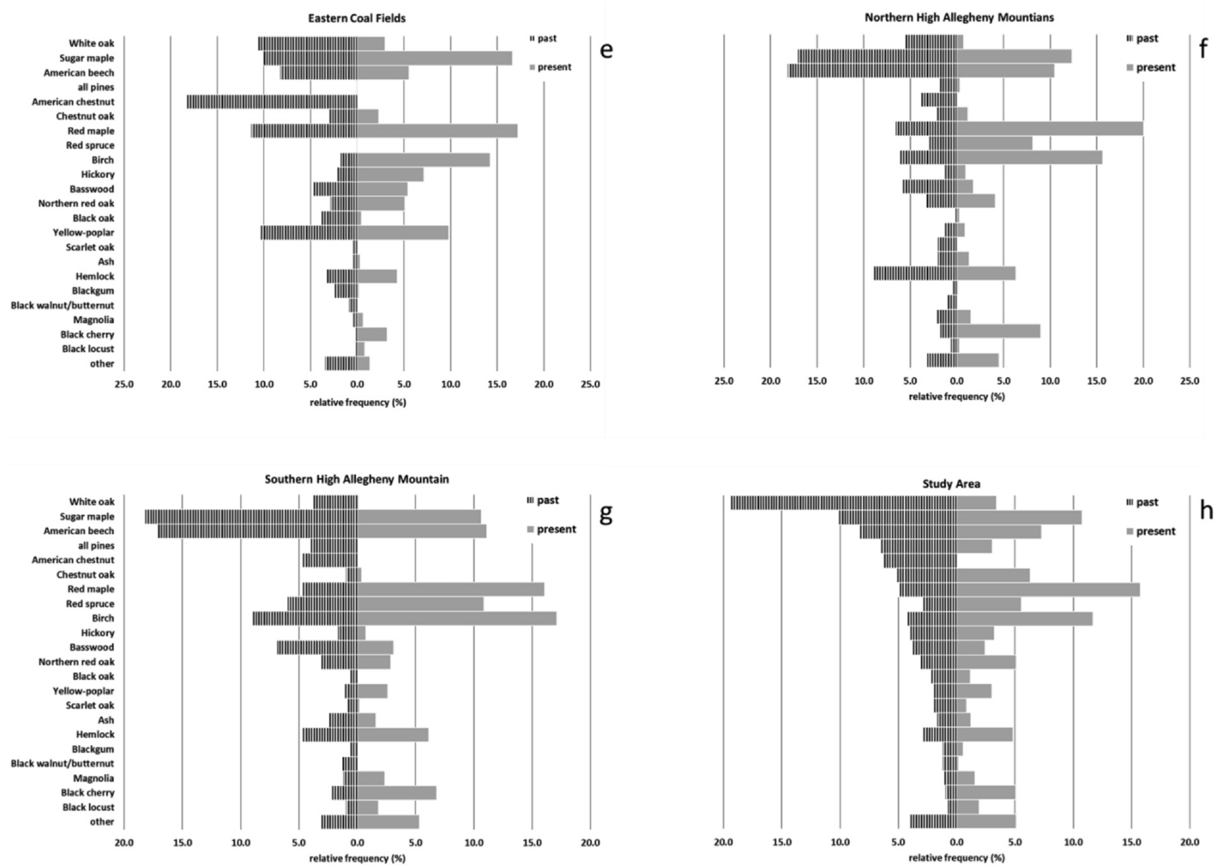

Fig. 2. (*continued*)

3.3. Ordination

A two dimensional model of the species relative frequencies by subsection was determined through NMS with a final stress of 7.83. The two ordination axes cumulatively explain most of the variation ($r^2 = 0.92$) in the data and show the general change between the time periods (Fig. 4). This low level of stress means that there is meaningful structure in the data and that there is little risk of making false inferences (McCune et al., 2002).

A distinct separation of the subsection's species composition between the two time periods is evident in the graphing of the NMS distances (Fig. 4) and confirmed through MRPP with a chance-correct within-group agreement (A) of 0.100 ($p = 0.015$) with the groups defined as the two time periods. An A test value of less than 0 indicates that there is more heterogeneity between groups than expected by chance and that the species compositions between the two time periods are different. The mean distance to the centroids of the species-space for the two time periods has increased slightly over time from 0.39 in the past to 0.40 in the present indicating that while the species compositions of the two time periods are different they both retain a diversity of species.

The groupings of the subsections in ordination "species-space" graphically displays the past and present forest and the changes between them (Fig. 4). In the past forest, the WAMV, EAMV, and RV subsections were tightly grouped along the axis associated with the frequency of pyrophilic species of intermediate shade tolerance. The WAM and ECF subsections were not as closely grouped but were similar with the WAM species composition near the center of the space. The SHAM and HNAM subsections were very similar and mark the other end of the fire-adapted species spectrum. In the present forest, many of these relationships have changed with compositions in the WAMV, EAMV, and RV subsections moving further apart. SHAM and NHAM remain close in ordination space with ECF becoming more similar to these two subsections than in the past.

Table 4
Relative frequencies of species by functional group for the study area by subsection.

Functional group	Study area	Study area	RV	RV	NHAM	NHAM	EAMV	EAMV	WAMV	WAMV	SHAM	SHAM	WAM	WAM	ECF	ECF
	past	pres.	past	pres.	past	pres.	past	pres.	past	pres.	past	pres.	past	pres.	past	pres.
pyrophilic	49.7	25.1	71.7	60.6	21.6	7.8	71.7	63.9	70.9	48.4	21.1	6.2	49.4	25.8	42.0	18.8
mixed	8.7	15.4	5.9	8.6	9.1	16.6	4.2	6.3	5.8	11.2	12.2	19.9	12.5	17.4	15.6	24.2
pyrophobic	37.0	54.4	19.1	26.1	65.9	71.0	18.6	25.9	17.5	30.1	63.6	68.6	33.8	49.1	39.1	55.6
very tolerant	24.3	28.4	11.6	12.7	47.3	37.4	8.9	9.9	10.8	11.1	46.2	38.7	21.2	24.0	21.8	28.8
tolerant	10.1	18.7	6.4	14.7	13.1	21.9	9.3	14.5	6.6	12.7	12.2	19.3	9.5	20.0	18.6	22.8
intermediate	47.4	33.7	62.8	49.5	27.3	25.7	58.5	52.9	61.3	42.0	27.8	25.2	52.7	31.7	44.0	33.2
intolerant	10.8	11.3	13.0	8.9	6.1	10.2	16.1	14.8	10.5	17.7	8.8	9.5	7.1	13.6	11.5	13.0
very intolerant	3.0	2.8	2.2	9.5	3.9	0.3	1.7	4.0	4.4	6.1	3.1	2.0	4.8	3.0	0.7	0.8

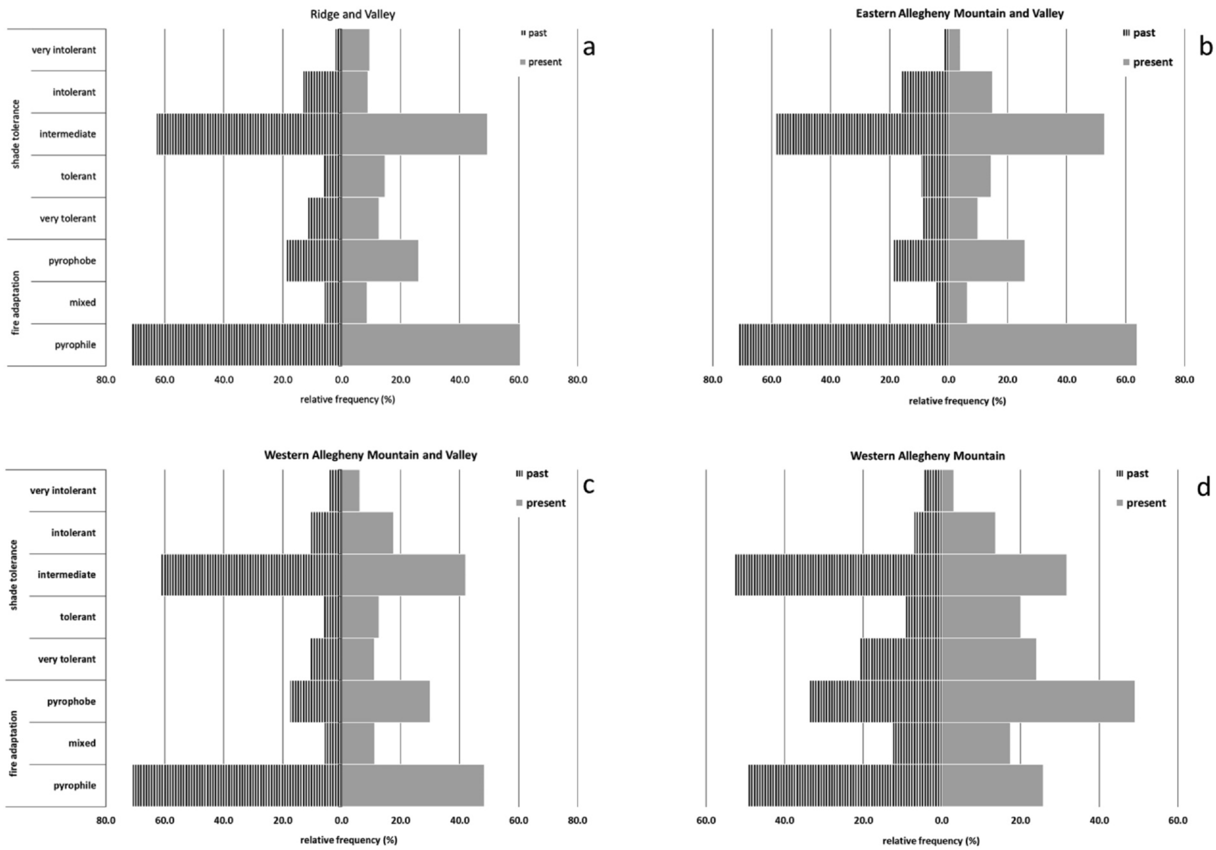

Fig. 3. Mean relative frequencies, past and present, by functional group for the RV (a), EAMV (b), WAMV (c), WAM (d), ECF (e), NHAM (f), and SHAM (g) subsections and the entire study area (h).

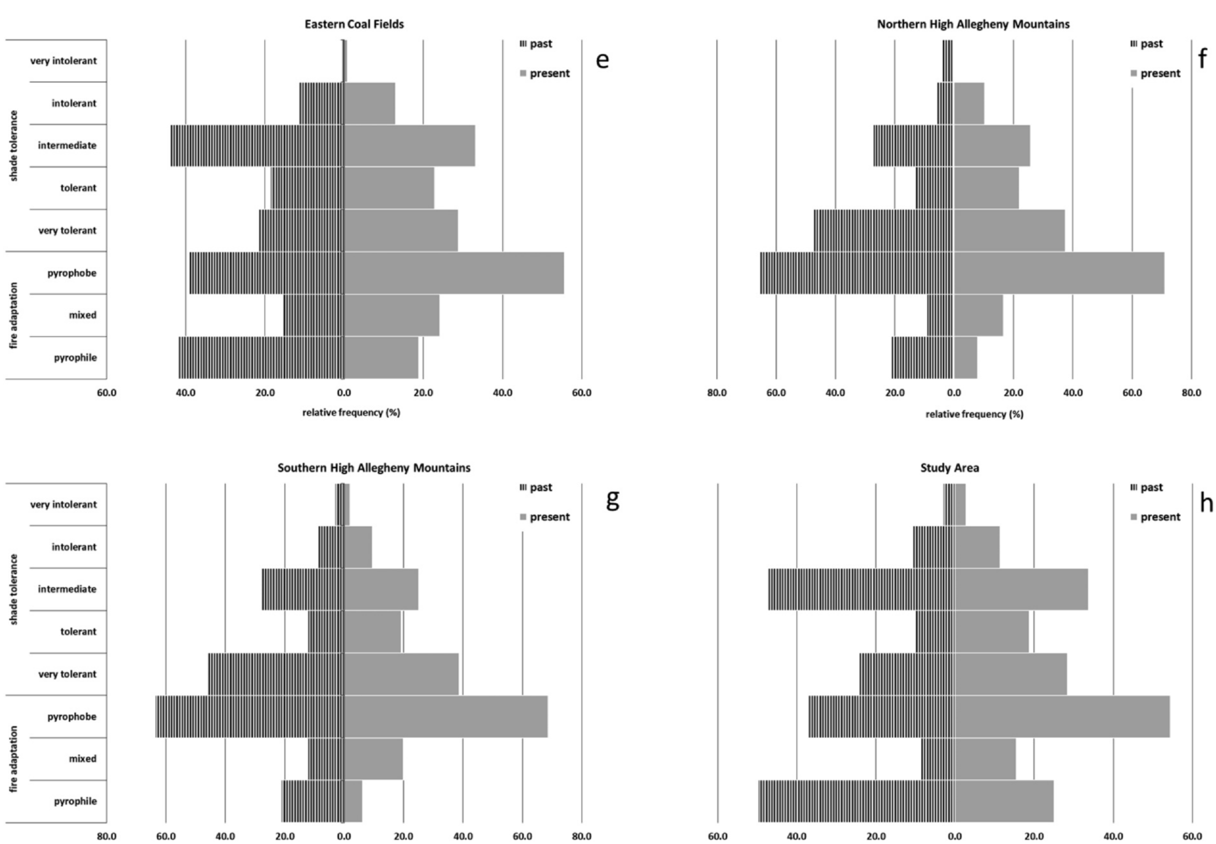

Fig. 3. (*continued*)

Table 5
Mean relative species frequency (%) for sapling and seedlings in present forests within the study area and by subsection based on FIA data.

Species	Study area		RV		NHAM		EAMV		WAMV		SHAM		WAM		ECF	
	sap	seed	sap	seed	sap	seed	sap	seed	sap	seed	sap	seed	sap	seed	sap	seed
White oak	0.4	0.4	0.4	0.0	0.0	0.0	1.6	2.9	3.3	0.0	0.0	0.0	0.3	0.8	2.0	0.3
Sugar maple	9.4	1.8	9.5	0.1	8.3	0.1	4.9	1.4	2.2	0.0	10.4	3.1	11.8	1.0	28.8	3.1
American beech	20.4	27.7	1.8	0.1	38.2	58.4	2.8	7.3	6.6	8.7	20.9	26.5	19.5	28.4	14.0	17.1
American chestnut	0.4	0.0	0.0	0.0	0.5	0.0	1.6	0.1	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.0
Chestnut oak	1.3	0.3	2.3	0.1	0.0	0.0	6.9	1.6	1.1	0.1	0.1	0.0	1.1	1.5	0.0	0.1
Red maple	9.8	6.4	23.9	0.1	5.6	0.1	19.3	12.6	17.4	1.0	5.2	9.2	15.7	5.0	13.0	5.4
All pines	3.2	5.2	3.2	1.0	0.8	0.0	17.5	39.2	13.3	42.4	0.0	0.0	0.0	0.0	0.0	0.0
Birch	6.3	9.8	2.2	0.0	9.1	8.5	0.5	14.6	2.2	0.0	7.1	9.4	6.8	29.1	12.1	10.4
Hickory	2.1	0.1	10.3	0.0	0.7	0.0	7.0	0.1	7.7	0.1	0.2	0.0	0.6	0.3	1.0	0.3
Basswood	0.5	0.0	0.0	0.0	0.7	0.0	0.0	0.0	1.1	0.0	0.7	0.0	0.8	0.0	0.0	0.0
Northern red oak	1.3	1.0	2.2	0.0	0.9	0.2	0.7	4.5	4.4	0.0	0.7	0.4	4.2	3.1	4.0	3.8
Red spruce	14.8	27.5	0.0	0.0	12.9	26.5	1.7	0.0	0.0	0.0	26.9	44.3	1.4	0.3	0.0	0.0
Black oak	0.2	0.1	0.0	0.0	0.0	0.0	0.7	0.7	1.1	0.2	0.0	0.0	0.0	0.1	3.0	1.2
Yellow-poplar	1.6	1.5	0.0	0.0	0.1	0.5	0.9	0.2	0.0	0.0	2.0	0.1	3.7	18.0	4.0	24.3
Scarlet oak	0.2	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ash	0.3	0.4	2.7	0.2	0.1	0.0	0.2	1.1	0.0	0.2	0.1	0.1	0.3	1.9	0.0	5.0
Hemlock	3.7	0.4	0.4	0.3	5.0	0.4	3.8	0.2	6.6	2.3	3.6	0.4	2.8	0.0	2.0	0.0
Blackgum	2.9	0.1	14.9	0.0	0.1	0.0	7.5	0.3	6.5	0.0	0.5	0.0	4.2	0.1	3.0	0.5
Black walnut	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magnolia	1.6	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	3.7	0.1	0.0	0.0	0.0	0.0
Black cherry	2.0	1.1	2.3	0.0	1.1	0.9	0.0	0.1	6.6	0.1	3.0	1.5	2.6	0.1	0.0	12.8
Black locust	1.0	0.1	6.3	0.1	0.5	0.0	0.5	0.2	0.0	0.1	0.8	0.0	1.4	0.2	0.0	0.0
other	16.6	16.2	17.6	98.1	15.4	4.3	20.9	13.0	19.9	44.9	14.1	4.8	22.6	9.9	13.1	15.6

4. Discussion

Given the history of industrial logging in the state, greater gains were expected in the shade intolerant and very intolerant species; however, the greatest changes occurred for species in the intermediate shade tolerance class. Both black cherry (*Prunus serotina*, intolerant) and black locust (*Robinia pseudoacacia*, very intolerant) showed no change or only slight increases in relative frequency across all subsections, but neither species comprised a large percentage of the present or past forest. Yellow-poplar (*Liriodendron tulipifera*), another shade intolerant species expected to increase in the present forest given past disturbances, only reached about 10% relative frequency in the past and present forest in one subsection, the ECF, and has a relative frequency of only about 3% of the present study area as a whole.

About 50% of the species in the past forests of the NHAM and SHAM subsections were very shade tolerant, suggesting disturbances in these subsections were less frequent and lower in intensity than in the drier subsections. Sugar maple, a very shade tolerant species, showed increases in relative frequency in two generally drier subsections, RV and EAMV, but decreases in the high elevation subsections SHAM and NHAM which generally have wetter conditions. This may be a reflection of mesophication (Nowacki and Abrams 2008) on the drier subsections and slow recovery from the exploitative harvesting in the 19th century.

The decrease in relative frequency of white oak is also a regional trend (Abrams 2003). White oak is a very long-lived species (400–450 years; Johnson and Abrams 2009), especially compared to

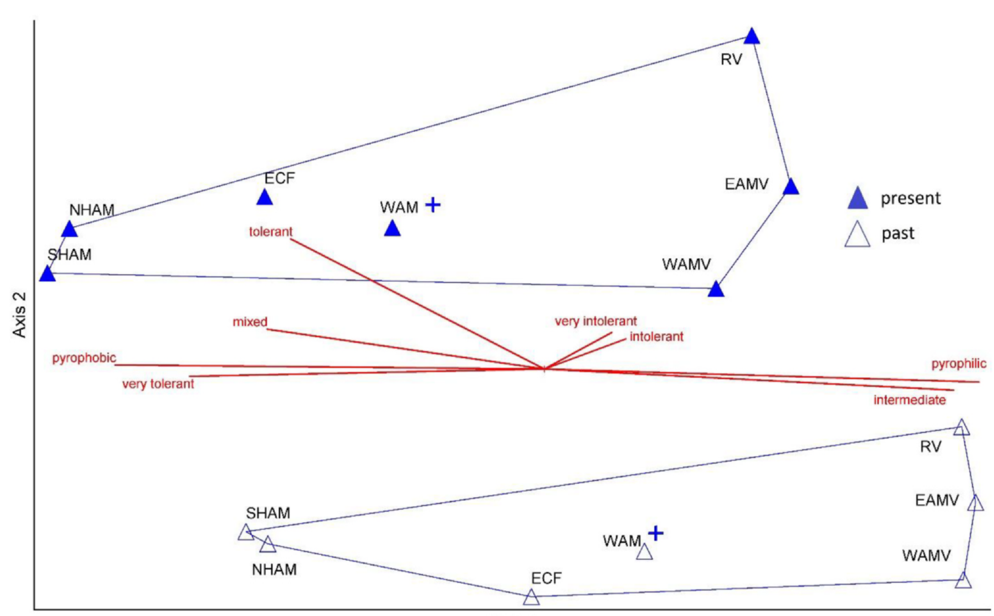

Fig. 4. Results of the NMS ordination displaying species compositions of the subsections, past and present, in relative space. Plus symbols depict centroid of space outlined by the species composition of each subsection by time period.

other oak species in the study area such as Northern red oak (200–250 years; Johnson and Abrams 2009) or black oak (150–200; Johnson and Abrams 2009), and white oak can be competitive on a wide range of sites. These factors likely lead to its dominance in the past forest of the study area, especially in the subsections with more moderate elevations. The role of fire in white-oak recruitment to the overstory in western Maryland, has been documented through dendrochronology (Shumway et al., 2001). However, the post-logging fires during the intensive logging period appear not to have benefitted white oakgiven the decrease in the frequency of white oak documented between past and present forests on our study area. Decreases in other fire-adapted species such as chestnut oak and pines, could be tied to reduced fire frequencies and the subsequent mesophication of these sites as seen across the eastern United States (Nowacki and Abrams 2008).

Reduced fire frequency may also account for the increase in red maple recruitment and coverage found in the study area (about 11%) and the region in general (Fei and Steiner 2007, Nowacki and Abrams 2008). The increase may also be related to various partial harvest management actions that allow red maple, a super-generalist able to function as either a pioneer or late successional species, to outcompete other species (Abrams 1998). Across the eastern forests, red maple was not a major component of the pre-settlement forests, with estimates ranging from 3 to 6% in Ohio and 4% in southern Illinois (Abrams 1998). Competition for site resources resulted in a landscape where red maple gained the advantage on dry and very wet sites and sugar maple dominated mesic sites in pre-European settlement forests (Abrams 1998). This pattern was found in the study area in a more detailed assessment of site-species relationships, where red maple was associated with both well-drained and poorly-drained soils in the early forest (Thomas-Van Gundy and Strager 2012)

Oaks are considered foundational to the forests of the eastern and central United States, with high abundances of oak species, 40 to 70% of total tree composition, documented in pre-European settlement forests (Hanberry and Nowacki 2016). The decrease in representation of oak species and subsequent increase in an unrelated species, red maple, has cascading ecological impacts to forest structure and function (Nowacki and Abrams 2008). This decrease also has implications for wildlife with the reduction in hard mast (McShea et al., 2007) and changes in nutrient cycling with greater soil nitrification occurring under red maples as compared to oaks (Alexander and Arthur 2010) and increased leaf litter decomposition with increased red maple inputs (Alexander and Arthur 2014).

Comparison of the past forest with the present forest is complicated by tree size and the use of common names in deeds for species like hemlock and red spruce. Since no diameter or other size data were given in the witness tree record, we assumed witness trees were at least 12.7 cm in dbh and used this threshold for calculating the relative frequencies for the present forest. Red spruce is expanding in coverage in the study area (Nowacki et al., 2010) and FIA estimates show a 13% increase in red spruce sapling stems from 2000 to 2013 (Morin et al., 2013). The relative frequency of red spruce in the present forest may be higher than in the past because there are greater numbers of smaller red spruce stems in the current forest.

We expected to see a homogenization in the present forest as compared to the past, similar to findings in Minnesota, Wisconsin, and Michigan (Schulte et al., 2007; Hanberry et al., 2012). However our findings echo the paradox found in the northeastern United States where after 400 years of land use change, forest cover has largely recovered but relative species composition has been transformed (Thompson et al., 2013). In east-central West Virginia we find that the relative frequencies of major forest tree species have changed and the relationship between tree species composition and environmental factors, as grouped by ecological subsections, has weakened. The evidence for this is in the dispersion seen in the ordination of species composition by time period (Fig. 4). Others have noted this weakened relationship for forests of the northeast with more detailed comparisons of witness trees and climate variables (Thompson et al., 2013), in this study, ecological subsections are used as proxies for variability in climate and geomorphology across the study area.

While the witness tree data did not include seedlings and saplings, we can use seedling and sapling data from FIA to conceptualize the future forest. American beech is well represented in the seedling-and sapling-size classes (Table 5) but due to continued losses of mature beech to the beech bark disease complex, it is likely that many of these smaller trees may not achieve the high canopy. While hemlock is also very shade tolerant, its low frequency in either the sapling or seedling layer may reflect deer browse pressure. Not reflected in these plot-based frequencies is the future influence of species persistence (such as birch species) in the seed bank until suitable disturbance occurs.

Our finding of “largely unchanged and completely transformed” (Thompson et al., 2013) may add to the difficulty in designing strategies and treatments for ecosystem restoration. These changes are subtle, however they can be quantified and placed in an ecological context as support for restoration actions. For example, these results can be used to support the return of fire as a management tool to reduce red maple frequency and encourage oak species.

5. Conclusions

While substantial changes were seen over a period of approximately 250 years, the same tree species are still in the present-day forests of east-central West Virginia that were found in the past. Changes in relative frequencies of key species have occurred however, including the decrease of white oak and the loss of American chestnut. The regional trend toward dramatic increases in red maple, in both frequency and ranking, is also found in the mountains of east-central West Virginia. The changes in representation by functional groups show a trend toward loss of fire-adapted species of intermediate shade tolerance, lending support for the return of fire as a disturbance to those subsections with the greatest change.

Author Statement

Thomas-Van Gundy, M. conceptualized the study, developed methods, conducted data analysis, and wrote original draft and reviewed and edited final version of paper, Morin, R. developed methods, reviewed and edited the final version of paper.

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.

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References

Abrams, M.D., 1998. The red maple paradox. BioScience 48 (5), 355–364.
Abrams, M.D., 2003. Where has all the white oak gone? BioScience 53 (10), 927–939.
Alexander, H.D., Arthur, M.A., 2010. Implications of a predicted shift from upland oaks to red maple on forestry hydrology and nutrient availability. Canadian Journal of Forest Research 40, 716–726.
Alexander, H.D., Arthur, M.A., 2014. Increasing red maple leaf litter alters decomposition rates and nitrogen cycling in historically oak-dominated forests of the eastern U.S. Ecosystems 17 (8), 1371–1383.

Butler, P.R., Iverson, L., Thompson, F.R., III, Brandt, L., Handler, S., Janowiak, M., Shannon, P.D., and others. 2015. Central Appalachians forest ecosystem vulnerability assessment and synthesis: a report from the Central Appalachians Climate Change Response Framework project. Gen. Tech. Rep. NRS-146. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 310 p.

Cleland, D.T., Freeouf, J.A., Keys, J.E., Nowacki, G.J., Carpenter, C.A., and McNab, W.H. 2007. Ecological Subregions: Sections and Subsections for the conterminous United States. Gen. Tech. Report WO-76D [Map on CD-ROM] (A.M. Sloan, cartographer). Washington, DC: U.S. Department of Agriculture, Forest Service, presentation scale 1:3,500,000; colored.

Fei, S., Steiner, K.C., 2007. Evidence for increasing red maple abundance in the eastern United States. Forest Science 53 (4), 473–477.

Hanberry, B.B., Palik, B.J., He, H.S., 2012. Comparison of historical and current forest surveys for detection of homogenization and mesophication of Minnesota forests. Landscape Ecology 27, 1495–1512.

Hanberry, B.B., Nowacki, G.J., 2016. Oaks were the historical foundation genus of the east-central United States. Quaternary Science Reviews 145, 94–103.

Johnson, S.E., Abrams, M.D., 2009. Age class, longevity and growth rate relationships: protracted growth increases in old trees in the eastern United States. Tree Physiology 29, 1317–1328.

Lafon, C.W., Naito, A.T., Grissino-Mayer, H.D., Horn, S.P. Waldrop, T.A. 2017. Fire history of the Appalachian region: a review and synthesis. Gen. Tech. Rep. SRS-219. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 97 p.

Lewis, R.L., 1998. Transforming the Appalachian countryside: railroads, deforestation, and social change in West Virginia. The University of North Carolina Press, Chapel Hill, NC, pp. 348.

Lienard J., Florescu I., Strigul N. 2015. An appraisal of the classic forest succession paradigm with the shade tolerance index. PLoS One. 10(2):e0117138. Published 2015 Feb 6. doi:10.1371/journal.pone.0117138.

Luppold, W., Alderman, D., 2007. Influence of species on site selection and timber removal: a case study for West Virginia. Northern Journal of Applied Forestry 24 (2), 146–148.

McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR, pp. 300.

McCune, B. and M. J. Mefford. 2011. PC-ORD Multivariate Analysis of Ecological Data, Version 6.0. MjM Software, Gleneden Beach, Oregon, U.S.A.

McGill, D.W., Magill, D.J., Kochenderfer, J., Ford, W.M., Schuler, T. 2006. Information transfer during the timber transaction period in West Virginia, USA. In: Proceedings 7th extension working party symposium, communication strategies for multiple partner involvement in forestry extension, September 2004, Orvieto, Italy. IUFRO working party 6.06.03 extension. 8p.

McShea, W.J., Healy, W.M., Devers, P., Fearer, T., Koch, F.H., Stauffer, D., Waldon, J., 2007. Forestry matters: decline of oaks will impact wildlife in hardwood forests. Journal of Wildlife Management 71 (5), 171–1728.

Miller, G.W., 2014. The Monongahela clearcutting controversy: scientists and land managers develop an alternative practice on the Fernow experimental forest. In: Hayes, D.C., Stout, S.L., Crawford, R.H., Hoover, A.P. (Eds.), USDA Forest Service experimental forests and ranges. Springer, New York, pp. 173–199.

Morin, R.S., G.W. Cook, C.J. Barnett, B.J. Butler, S.J. Crocker, M.A. Hatfield, C.M. Kurtz, T.W. Lister, W.G. Luppold, W.H. McWilliams, P.D. Miles, M.D. Nelson, C.H. Perry, R. J. Piva, J.E. Smith, J.A. Westfall, R.H. Widmann, C.W. Woodall. 2016. West Virginia Forests 2013. Resource Bulletin NRS-105. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 128 p.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. BioScience 58 (2), 123–138.

Nowacki, G., Carr, R., and Van Dyck, M. 2010. The current status of red spruce in the eastern United States: distribution, population trends, and environmental drivers. In Proceedings from the Conference on the Ecology and Management of High Elevation Forests in the Central and Southern Appalachian Mountains. USDA Forest Service Gen Tech Rep NRS-P-64. Northern Research Station, Newtown Square, PA (pp. 140-162).

Rhemtulla, J.M., Mladenoff, D.J., 2010. Relative consistency, not absolute precision, is the strength of the Public Land Survey: response to Bouldin. Ecological Applications 20 (4), 1187–1189.

SAS® Enterprise Guide version 7.13. 2016. SAS Institute Inc., Cary, NC, USA.

Schulte, L.A., Mladenoff, D.J., 2001. The original US public land survey records: Their use and limitations in reconstructing presettlement vegetation. Journal of Forestry 99 (10), 5–10.

Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L.C., Cleland, D.T., 2007. Homogenization of northern US Great lakes forests due to land use. Landscape Ecology 22, 1089–1103.

Shumway, D.L., Abrams, M.D., Ruffner, C.M., 2001. A 400-year history of fire and oak recruitment in an old-growth oak forest in western Maryland, USA Can. J. For. Res. 31, 1437–1443.

Stephenson, S.L. 1993. Upland Forests of West Virginia McClain Printing Co., Parsons, WV.

Thomas-Van Gundy, M.A. and Strager, M.P. 2012. European Settlement-Era Vegetation of the Monongahela National Forest, West Virginia. USDA Forest Service, Northern Research Station, Gen. Tech. Rep. NRS-101. Newtown Square, PA. 39 p.

Thomas-Van Gundy, M.A., Strager, M.P. 2014. Witness trees of the Monongahela National Forest: 1752-1899. Fort Collins, CO: Forest Service Research Data Archive. Updated 15 September 2016. https://doi.org/10.2737/RDS-2014-0022.

Thomas-Van Gundy, M.A., Nowacki, G.J., 2013. The use of witness trees as pyro-indicators for mapping past fire conditions. Forest Ecology and Management 304, 333–344.

Thompson, J.R., Carpenter, D.N., Cogbill, C.V., Foster, D.R., 2013. Four centuries of change in northeastern United States forests. PLOS One 8 (9), e72540.

USDA Forest Service, Forest Inventory and Analysis Database, April 14, 2020, St. Paul, MN: U.S. Department of Agriculture, Forest Service, Northern Research Station. [Available only on internet: https://apps.fs.usda.gov/fia/datamart/datamart.html].