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Seeing past the green: Structure, composition, and biomass differences in high graded and silviculture-managed forests of similar stand density



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ABSTRACT

Forests of the eastern United States (US) mostly comprise a mix of stands managed following silvicultural principles and stands managed with exploitative timber harvesting practices. These stands can have similar stand densities (e.g., basal area per hectare) but vary vastly in structure, composition, and biomass and carbon storage. High grading, a prevalent exploitative timber harvesting practice in the eastern US, is of particular concern because it can negatively affect future forest health and productivity. This study quantifies differences in forest structure, composition, and biomass and carbon storage between high graded stands and stands that received a seed/establishment cut of a uniform shelterwood regeneration sequence treatment, which is a comparable and well-established silvicultural method used to regenerate mixed-oak forests. It focuses on mixed-oak forests (mixed-Quercus), where the effects of high grading have been understudied, and uses a sample with broader spatial coverage than previous studies. The sample comprised nine stands that were known to have been high graded 8-15 years ago and nine stands that received the seed/establishment cut of a uniform shelterwood regeneration sequence. Stand were systematically sampled using fixed-area plots. Field measurements were collected and used to calculate metrics describing forest structure and function. The structure of high graded stands was characterized by a higher proportion of trees with poor health and/or form compared to shelterwood stands, with 18.3 % less acceptable growing stock and trees with lower crown compaction. Diameter distributions of high graded stands were characterized by numerous small trees and few large-diameter trees. Spatial variability of overstory trees was contingent on the tree size range evaluated, with a larger variability of sawtimber-sized trees (trees \geq 29.2 cm in diameter at breast height) in high graded stands. High graded stands also had 2.2 times fewer oak trees (Quercus spp.) in the overstory canopy, 17,897 fewer seedlings per hectare (ha), and 45 Mg/ha less biomass than shelterwood stands. These results indicate that high grading generally degrades mixed-oak forests and impairs their long-term capacity to supply vital ecosystem services such as habitat for specific wildlife species, carbon storage, and high-quality wood products.

1. Introduction

Forests in the eastern United States (US) cover millions of hectares of land (Butler et al. 2016). Much of these forests comprise a mix of stands managed following silvicultural principles and stands that have received non-silvicultural harvests (e.g., Belair and Ducey 2018). These stands can have similar stand densities (e.g., basal area per hectare) but vary vastly in structure, composition, and biomass and carbon storage. The structural and functional differences arising from high grading, one of the most common exploitative timber harvesting methods in the eastern US (Fajvan et al. 1998, Nyland 2000, McGill et al. 2006, Metcalf et al. 2012, Belair and Ducey 2018), can be of particular concern because high grading (including diameter-limit cutting and select/selective cutting) can hamper the future health and productivity of forests and their ability to provision ecosystem services such as habitat for wildlife species, carbon storage (e.g., Powers et al. 2011, Puhlick et al. 2020), and valuable wood products (e.g., Bohn et al. 2011, Rogers et al. 2018).

In contrast to well-established silvicultural practices – such as shelterwood or selection systems – that control for species composition, spacing, and tree health and form, high grading only removes the largest and most economically valuable stems with no consideration for future forest health or productivity. Even though both, silvicultural practices

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and high grading, alter forest structure and composition, the effects of high grading can hamper forest sustainability and limit management alternatives for the future stand. For example, reduced tree health and/ or form, a common outcome of high grading, is typically linked to reduced timber quality (e.g., tree grade and non-salable wood volume; Fajvan et al. 2002, Kenefic et al. 2005, Ward et al. 2005, Brown et al. 2018) and/or an increased risk of mortality/vulnerability to stressors such as insect defoliation (Manion 1991, Cherubini et al. 2002, Marcais and Bréda 2006). Wood volume growth following high grading is also generally more irregular/unpredictable over multiple harvest cycles compared to stands managed following silvicultural practices (Nyland 2005, Ward et al. 2005, Bohn et al. 2011, Rogers et al. 2018). The latter (e.g., selection system) generally produces lower initial volumes, but provides more regular and consistent future volume yields (Nyland 2005, Ward et al. 2005, Bohn et al. 2011, Rogers et al. 2018; although see Schuler 2004, Schuler et al. 2017 for an exception). The more irregular spatial arrangements of residual overstory trees in high graded stands compared to unmanaged stands and/or stands managed with silviculture (Grushecky and Fajvan 1999, Bohn 2005, Saunders and Wagner 2008) affect the spatial distribution and management of tree regeneration (Deluca et al. 2009). Additionally, visual analysis of stands' diameter distributions indicate that high grading generally reduces the number of large-diameter trees and truncates diameter distributions (Kenefic et al. 2005, Schuler et al. 2017, Rogers et al. 2018), thereby limiting management options for the future stand.

High grading can lead to shifts in species composition for certain forest types by focusing growth on a handful of species of lower economic value. Shifts in species composition may be most pronounced in mixed-oak (mixed-Quercus) forests because the canopy layers are commonly vertically stratified based on shade tolerance with less shadetolerant species (e.g., oak [Quercus spp.]) occupying the upper canopy layers and more shade-tolerant species (e.g., maple [Acer spp.], birch [Betula spp.]) occupying lower canopy layers (Oliver 1978, 1980). While many eastern mixed-oak forests are transitioning to more mesic and shade-tolerant species (Nowacki and Abrams 2008) for a variety of reasons such as lack of fire disturbances, impacts from white-tailed deer (Odocoileus virginianus), and invasive pests and pathogens (e.g., review by Dey 2014), high grading makes no attempt to actively resist these shifts through silviculture and has been observed to accelerate these conversions (Heiligmann and Ward 1993, Ward et al. 2005). Despite the potential consequences of high grading on accelerating the loss of mixed-oak forests, studies of compositional differences between mixedoak stands that were high graded versus managed with silviculture are few and based on small samples of limited geographic extent.

High grading is also expected to negatively affect carbon storage by impacting tree health (Fajvan et al. 2002, Rogers et al. 2018), focusing growth on lower-vigor trees that may exhibit poorer growth responses following release compared to more vigorous individuals (e.g., Ward 2002, Devine and Harrington 2006, Baral et al. 2016), and by changing species composition. Empirical studies indicate that repeated high grading resulted in lower carbon stock accumulation rates and/or total carbon stocks than unmanaged stands and/or stands managed with uneven-aged silviculture (Hoover and Stout 2007, Powers et al. 2011, Puhlick et al. 2020; although see Davis et al. 2009 for an exception). However, the effects of high grading on carbon storage compared to even-aged silviculture (e.g., uniform shelterwood system) remain less conclusive among the existing studies (Powers et al. 2011, Puhlick et al. 2020) and remain unevaluated for mixed-oak forests.

Past studies have primarily assessed the impacts of high grading on forest structure, forest composition, and carbon storage across a range of forest types in the northeastern and northcentral US. However, past evaluations of tree health, spatial variability, diameter distributions, and carbon storage have solely been focused on Allegheny hardwood, northern hardwood/conifer, or mesophytic hardwood forest types and most of these studies used small sample sizes of reduced inferential scope (i.e., one to 3 spatially close study sites) wherein tree harvesting treatments were experimentally controlled (e.g., Grushecky and Fajvan 1999, Kenefic et al. 2005, Powers et al. 2011, Rogers et al. 2018).

Using a sample that provides broader inferential scope, our general goal is to see past the green and uncover differences in forest structure, composition, and biomass between high graded stands and stands managed following a specific silvicultural practice that can hide under a similar metric of stand density. We used stand density as a standardizing dimension because of its confounding and important effect on forest structure. Our specific objectives are to quantify differences in (1) forest structure through tree health and form, stand diameter distributions, and spatial variability of overstory trees, (2) overstory and regeneration composition, and (3) aboveground overstory live-tree biomass, between 9 high graded mixed-oak stands and 9 mixed-oak stands that received the seed/establishment cut of a uniform shelterwood regeneration sequence. The latter is a comparable, well-established silvicultural treatment that is most commonly used to regenerate mixed-oak forests in the eastern US (e.g., Loftis 1990, Brose et al. 2008). The seed/establishment cut also serves as a good comparison to high grading because both are partial harvests that leave similar amounts of total residual basal area per unit area. We built upon past studies by utilizing a larger sample to increase the scope of inference, evaluating a comprehensive set of metrics, and focusing on mixed-oak forests.

2. Methods

2.1. Description and selection of study sites

The study area is the mixed-oak forests of the central and northeastern regions of Pennsylvania. We selected 9 stands that were reported by the current landowner or forest manager to have been high graded 8 to 15 years ago, and 9 stands that were reported by the Pennsylvania Department of Conservation and Natural Resources Bureau of Forestry (BoF) or Pennsylvania Game Commission (PCG) to have received the seed/establishment cut ("first removal cut" in accordance with terminology used by Brose et al. 2008 for oak stands) of a uniform shelterwood regeneration sequence 4 to 10 years ago (hereafter "shelterwood stands"/"shelterwood treatment"). Of those stands, 6 high graded and 6 shelterwood stands were in the central region while 3 high graded and 3 shelterwood stands were in the northeastern region. All of the shelterwood stands were mixed-oak, while the high graded stands were either currently mixed-oak stands or surmised to have been mixed-oak prior to the most recent high grade timber harvest. To surmise the preharvest forest type of the high graded stands, we assessed the species of stumps, asked the landowner or forest manager about their recollection of preharvest species composition, and assessed the species composition of adjacent unharvested forests of similar topographic position and aspect. We restricted the selection of the high graded stands to those with areas of at least 4.05 ha and those with total basal areas (BA) of roughly 12.6 to 27.5 m²/ha for all living stems > 12.7 cm in diameter at breast height (DBH, measured at 1.37 m from the ground) at the time of this study's measurements to exclude very intensively (e.g., approaching commercial clearcuts) and very lightly high graded stands. Given the focus on forests of similar stand density, we selected shelterwood stands that fell within the same stand area and BA range as the high graded stands at the time of this study's measurement. All of the high graded stands received no management since the most recent high grade timber harvest. Seven of the 9 shelterwood stands received no herbicide or deer fence treatment, while one shelterwood stand received an herbicide treatment, and one shelterwood stand received an herbicide and deer fence treatment. We avoided stands that received a salvage timber harvest due to mortality from Lymantria dispar. We obtained site index from the United States Forest Inventory and Analysis database (USDA Forest Service 2020) for the majority of the stands. When site index for northern red oak was not available in a stand, we converted the available site index for another species to northern red oak at base age of 50 years using published conversion equations (Doolittle 1958, Carmean and Hahn

1983). Summary statistics and locations of the stands in the sample are presented in Table 1 and Fig. 1, respectively.

2.2. Field data collection

We collected data on the overstory trees and tree regeneration using nested, circular fixed-area plots that were systematically located throughout the stands using ArcGIS 10.6 (ESRI 2017). We allocated the number of regeneration plots at a rate of 20 plots for the first 4.05 ha and then 2 additional plots for every additional 2.02 ha over 4.05 ha, while we allocated the number of overstory plots at half the rate of the regeneration plots (Brose et al. 2008). To inventory the 9 high graded stands, we used an average of 14 (range: 11 to 17) overstory and 28 (range: 22 to 34) regeneration plots, while we used an average of 14 (range: 12 to 19) overstory and 29 (range: 25 to 38) regeneration plots to inventory the 9 shelterwood stands. Supplementary Material S1 includes all species recorded in the overstory and regeneration plots.

2.3. Overstory tree inventory

We measured all living trees ≥ 12.7 cm in DBH in 405 m² circular fixed-area plots in each stand. In each plot, we recorded tree species, DBH, and tree quality. We assessed tree quality by classifying each tree as acceptable growing stock (AGS) or unacceptable growing stock (UGS). A tree qualifies as AGS if it is healthy enough to live for another 15 years and is of good form (e.g., straight stem) such that it currently can (or will in the future) produce salable wood products (i.e., at least one 2.4 m log meeting minimum requirements for sawtimber; Brose et al. 2008). However, in contrast to Brose et al. (2008), a tree did not need to be considered a "desirable" species to qualify as AGS except for (1) striped maple (*Acer pensylvanicum*), and (2) any non-native tree species (e.g., tree of heaven, *Ailanthus altissima*), which we automatically considered UGS regardless of health and form.

We identified the most dominant tree in each plot using the 4-category tree crown class system commonly used in even-aged stands in North America (Nyland, 2016) and measured uncompacted crown length and estimated compacted crown length to the nearest foot. Uncompacted crown length represents the distance from the top of the living crown to the crown base after which no more live branches (\geq 2.54 cm in diameter) attach to the stem. In most cases, there is a clear crown base. However, in cases where lower live branches were spaced, we identified the crown base as the height from the ground after which all live branches were no farther apart than 1.52 m (Schomaker et al. 2007, see diagram in Supplementary Material S2). To estimate the compacted crown length, we visually transferred lower branches to fill in gaps in the crown that lacked living branches until an even crown without gaps/holes was achieved. We avoided compacting the branches tighter than the natural branch spacing of the species in question (USDA Forest Service 2018; Supplementary Material S2).

2.4. Tree regeneration inventory

We recorded all tree seedlings ≥ 5.1 cm tall and < 2.54 cm in DBH by species using 10.5 m² circular fixed-area plots. For seedling stump sprouts, we recorded the tallest stem in the sprouting cluster.

2.5. Metrics used to characterize the residual forests

Metrics used to compare the effects of high grading and shelterwood treatments on residual forest structure, composition, and function are summarized in Table 2. We used several metrics to assess forest structure at the stand level: (1) Proportion of acceptable growing stock (PropAGS), which is a metric commonly used in forestry to quantify timber resources that also provides a good indication of overall health and form of the overstory trees in the forest; (2) Average crown compaction of trees in the stand, which provides an indication of average tree health and form in the stand because crown compaction could be indicative of the level of epicormic branching since epicormic branches are often scattered along tree boles, thus resulting in gaps/holes in the live crown; (3) Within-stand spatial variability using the coefficient of variation (CV) of plot-level estimates of total and sawtimber BA and Global Moran's I (explained in Statistical analyses section, Moran 1950, Cliff and Ord 1981), which is important because it influences the capacity of forests to evenly regenerate a stand by altering the distribution of light and growing space, tree seed sources, and vegetation that interferes with tree regeneration; (4) Stand diameter distribution using the ratio of median to mean tree DBH (DRatio), the quadratic mean diameter (QMD), and by modeling the stand diameter distributions with a Weibull probability density function. Diameter distributions influence future forest trajectories and potential silvicultural treatment options, and quantifying differences arising from high grading can aid in understanding its longterm effects on forests.

To evaluate forest composition, we assessed the overstory and understory tree communities as both affect ecosystem function, wildlife habitat quality, carbon storage, silvicultural treatment options, and economic value of forests. We also evaluated a metric reflecting forest function, biomass (and thus carbon storage) in the overstory layer (trees with DBH \geq 12.7 cm), which is an important ecosystem service in forests, especially when evaluating forests for their climate change mitigation potential. To estimate tree biomass, we used allometric equations from Chojnacky et al. (2014, see Supplementary Material S1).

2.6. Statistical analyses

To evaluate whether the selected metrics differed between stands that received either the high grading and shelterwood treatment (hereafter "HarvestType"), we fit models that included HarvestType, site index (hereafter "SiteIndex"), geographic region of Pennsylvania (central or northeastern, Fig. 1) in which stand is located (hereafter "Region"), and BA when appropriate, as well as interactions between these predictor variables to ensure other potentially explanatory variables were accounted for and not obscuring the effects of HarvestType. We coded the type of timber harvest treatment (high grading or shelterwood) and Region (central or northeastern) using sum-to-zero contrasts and present Type III sums of squares (car package, Fox and Weisberg 2019). We conducted all analyses using an alpha level of 0.05 and used R version 4.0.2 (R Core Team 2020).

For metrics bounded between zero and one we used beta regression models (betareg R package, Cribari-Neto and Zeileis 2010), while for the other metrics we used linear regression, and transformed variables when necessary to meet regression assumptions (Table 3). We fit models with

Table 1

Descriptive summary (mean and standard deviation in parentheses) of stands area, topography, and overstory (stems \geq 12.7 cm) characteristics at time of measurement for the 18 study stands. (HG = high graded stand, SW = shelterwood stand).

	Area (ha)	Site index ¹ (m)	Elevation ² (m)	Percent slope ²	Basal area (m ² /ha)		Trees per hectare	
					Oaks	Non-oaks	Oaks	Non-oaks
HG	10.8 (3.9)	19.1 (2.2)	380 (102)	51.3 (32.0)	7.3 (4.4)	12.0 (4.7)	109.5 (75.4)	268.9 (89.0)
SW	12.1 (4.7)	18.8 (2.3)	455 (67)	56.5 (14.9)	15.4 (5.0)	4.0 (5.1)	83.1 (36.5)	61.2 (63.4)

¹ Site index for northern red oak (*Quercus rubra*) at base age of 50 years (from USDA Forest Service 2020).

² Values calculated using data from PAMAP (2008) and USGS (2016).



Fig. 1. Geographic location of high graded ("HG", blue squares) and shelterwood ("SW", green circles) stands. Locations have been slightly shifted in random directions to preserve landowner privacy. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Summary of metrics used to characterize high graded and shelterwood stands. Metrics describing the overstory include all stems \geq 12.7 cm in DBH unless otherwise specified.

Characteristic	Metric	Description		
Forest structure				
Tree health and/or form	PropAGS	Proportion of total BA classified as acceptable growing stock (AGS)		
	Crown compaction	Ratio of the compacted to uncompacted live crown lengths of the most dominant tree in a plot, averaged across plots to obtain an average stand- level value		
Spatial variability	CV total BA	Coefficient of variation (CV) of plot- level BA estimates for all stems		
	CV sawtimber BA	CV of plot-level BA estimates for sawtimber-sized trees (stems \geq 29.2 cm in DBH)		
	Moran's I	Global Moran's I statistic for plot-level BA estimates of (1) all stems ("total"), and (2) sawtimber-sized trees (stems \geq 29.2 cm in DBH)		
Diameter distribution	DRatio	Ratio of the median to mean tree DBH		
	Diameter	Shape and scale parameters from fitted		
	distribution	Weibull distribution. Only applicable		
	parameters	for unimodal fits.		
	QMD	Quadratic mean diameter		
Forest composition				
Overstory composition		Percent of total BA by species group		
Regeneration		Density (per hectare) of tree seedlings		
composition		\geq 5.1 cm tall and $<$ 2.54 cm in DBH by		
<i>F</i>		species group and all species combined		
Forest function				
Biomass		Total live-tree aboveground biomass in the overstory layer (in Mg/ha)		

Table 3

Summary of statistical analyses and variables included in the model selection process.

Metric	Evaluated variables ¹	Analysis type	Covariates ¹				
Forest structure							
PropAGS	HarvestType	beta regression	Region, SiteInde				
Crown compaction	HarvestType	beta regression	Region, SiteIndex				
CV total BA	HarvestType	linear regression	Region, SiteIndex				
CV sawtimber BA	HarvestType	linear regression	Region, SiteIndex				
DRatio	HarvestType	Mann-Whitney					
		U test					
QMD	HarvestType	linear regression	Region, SiteIndez				
	Forest com	position					
Overstory composition	HarvestType	beta regression	Region, SiteIndez				
Regeneration	HarvestType	linear regression	BA, Region,				
composition	inii (cotri jpc	inical regression	SiteIndex				
	Forest fu	nction					
Biomass	BA, HarvestType	linear regression	Region, SiteInde				

¹ "BA" = BA for stems \geq 12.7 cm in DBH.

HarvestType and covariates (i.e., Region, SiteIndex, and BA) and then evaluated the need for the covariates using the Akaike Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson 2002) with the MuMIn R package (Barton 2020). When models were within two AICc units of each other, we followed the parsimony principle and chose the model with fewer model parameters (Burnham and Anderson 2002).

To evaluate CV total BA, we excluded one stand from the analysis because it was identified as an extreme and influential value by analysis of residuals. To calculate Global Moran's I (hereafter "Moran's I") and conduct hypothesis testing we used the spdep R package (Bivand et al. 2013, Bivand and Wong 2018). Moran's I evaluates whether the spatial

distribution of values (e.g., BA) in a defined geographic extent (e.g., forest stand) are random (i.e., not spatially autocorrelated), or follow non-random spatial patterns (i.e., are positively or negatively spatially autocorrelated; see Moran 1950, Cliff and Ord 1981). For the spatial weights matrix, we used the four nearest neighbors and weighted each neighbor using inverse distance weighting. We evaluated the null hypothesis of spatial randomness by (1) computing an analytical p-value based on the standard deviate under the assumption of randomization (spdep::moran.test), and (2) computing a pseudo p-value using a permutation test for Moran's I statistic with 9999 simulations (spdep::moran.mc).

To model the diameter distribution of each stand, we fit a truncated Weibull distribution with (1) one mode ("unimodal"), and (2) two modes ("bimodal") to the vector of diameters for each stand using the ltmix R package (Blostein and Miljkovic 2019). We specified 12.7 cm as the truncation diameter. We compared the AIC values between the unimodal and bimodal fits to determine which one best described the diameter distribution of each stand. However, we found that this method had the tendency to favor the more complex bimodal fit and so we supplemented with visual selection for 8 of the 18 stands. To accomplish this, we plotted the fitted unimodal and bimodal Weibull probability density functions (PDF) and the histogram of diameters for each stand and evaluated whether the AIC values were leading to a selection of a more complex model due to a small change in a diameter class. We recorded whether the fit was unimodal or bimodal, and, if unimodal, we extracted the shape and scale parameters that describe the Weibull PDF. Nine high graded stands and 5 shelterwood stands fit with a unimodal Weibull. Given the small sample size of unimodal fits (n = 9and 5), we used non-parametric models to evaluate the effect of HarvestType on the diameter distributions' shape and scale parameters. We conducted a permutation test on the difference in medians using all possible permutations.

To evaluate overstory and species composition, we grouped overstory and seedling regeneration species into 4 species groups: (1) red maple (Acer rubrum), (2) birch, (3) oak, and 4) Other, and fit individual beta regression models suitable for modeling proportions for each species group (Table 3). The model for birch was the only model that included a variable dispersion parameter for HarvestType. We replaced proportions of zero with the smallest non-zero proportion in the entire dataset as proposed by Warton and Hui (2011). For the regeneration composition, we calculated seedlings per hectare by stand and fit individual linear models for each species group and all species combined (Table 3). We excluded the two shelterwood stands that received an herbicide and/or deer fence treatment from this analysis to avoid factors that could confound the effects of HarvestType on regeneration composition. Models for red maple, oak, and all species combined used the untransformed response, while models for birch and Other were fit using a square root and a natural log transformation on the response, respectively.

3. Results

3.1. Forest structure

The final PropAGS model included HarvestType and Region. When averaged over Region, high graded stands had a 18.3 % (standard error [SE] = 3.6) lower PropAGS than the shelterwood stands (z = -5.00, P < 0.0001; Fig. 2). PropAGS was significantly higher in the northeastern compared to the central Pennsylvania region (z = -3.34, P = 0.0008). Additionally, the difference in mean crown compaction was small (0.075, SE = 0.017), but significantly lower in the high graded compared to the shelterwood stands (Table 4; z = -4.34, P < 0.0001, Supplementary Material S3).

Within-stand variability of BA differed between HarvestTypes (Table 4). CV total BA was significantly lower (0.085 CV units, SE = 0.038) in the high graded compared to the shelterwood stands (F = 5.10,



Fig. 2. Boxplot of PropAGS by HarvestType and Region. Triangles represent model-estimated marginal means for high graded (blue) and shelterwood stands (green) ("HG-CEN" = high graded stands in central region, "HG-NE" = high graded stands in northeastern region, "SW-CEN" = shelterwood stands in central region, "SW-NE" = shelterwood stands in northeastern region). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Summary of final models and predicted means with their 95% confidence interval by HarvestType for crown compaction, CV total BA, and CV sawtimber BA.

	High graded stands		Shelterwood stands			
Metric	Mean ¹	95 % CI	Mean ¹	95 % CI	Model	
Crown	0.878b	(0.848,	0.953	(0.934,	HarvestType	
compaction		0.909)	а	0.972)		
CV total BA	0.291b	(0.233,	0.376	(0.321,	HarvestType	
		0.349)	а	0.431)		
CV sawtimber	0.555	(0.480,	0.420b	(0.346,	HarvestType +	
BA	а	0.629)		0.495)	SiteIndex	

¹ Means in the same row with different letters indicate significant differences at alpha of 0.05.

P = 0.0393). In contrast, the CV sawtimber BA was 0.135 CV units (SE = 0.049) larger in the high graded than the shelterwood stands (F = 7.39, P = 0.0158, Supplementary Material S3). For Moran's I analyses, the standard normal deviate and permutation distribution methods suggested the same random spatial patterns in 17 of the 18 stands for total BA and in all the stands for sawtimber BA (Supplementary Material S3).

Average tree size and the shape of the diameter distributions differed between the HarvestTypes (Fig. 3, model summaries are presented in Supplementary Material S3). Mean tree diameter as reflected by the QMD was, on average, 19.0 cm (SE = 1.7) smaller in the high graded (mean = 25.3 cm, SE = 1.2) compared to the shelterwood (mean = 44.3, SE = 1.2) stands (F = 120.81, P < 0.0001; Fig. 3a). Diameter distribution shape differed between HarvestTypes based on (1) the number of modes (one or 2), and (2) the skew of the unimodal distribution fits. Four shelterwood stands and none of the high graded stands were bimodal, while the rest were unimodal but with a difference in the skew between shelterwood and high graded stands. To illustrate the 3 types of diameter distributions found among the 18 stands, i.e., unimodal high graded, unimodal shelterwood, and bimodal shelterwood stands, we present the



Fig. 3. a) Boxplot of QMD (cm) by HarvestType and Region. Triangles represent estimated marginal means for high graded (blue) and shelterwood stands (green) ("HG-CEN" = high graded stands in central region, "HG-NE" = high graded stands in northeastern region, "SW-CEN" = shelterwood stands in central region, "SW-NE" = shelterwood stands in northeastern region). b) Boxplot of DRatio by HarvestType. c) Tree diameter distributions for 3 stands illustrating the 3 diameter distribution types found for among stands: unimodal high graded stands (solid blue line), unimodal shelterwood stands (solid green line), and bimodal shelterwood stands (dot-dash green line). (HG = high graded stand, SW = shelterwood stand). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

distribution of a representative stand for each distribution type in Fig. 3c. In a truncated Weibull, the shape parameter qualitatively describes the shape of the distribution above the truncation value, with smaller shape values reflecting progressively greater positive skew. The scale parameter provides a rough indication of tree size with larger shape values relating to more trees in the larger diameter classes. The shape parameter was significantly smaller in the high graded stands (P = 0.0240), which suggests that the distributions for the high graded stands (Fig. 3c). The scale parameter was significantly smaller in the high graded stands (Fig. 3c). The scale parameter was significantly smaller in the high graded stands (P = 0.0200), which indicates greater proportions of large-diameter trees in the shelterwood stands. Results from the DRatio analyses also point to differences in diameter distribution shapes. The DRatio reflects general trends in distribution shape with values below one indicating that the median is smaller than the mean, and thus, a

positive skew. The median DRatio was significantly lower (0.07 units) in the high graded compared to the shelterwood stands (Fig. 3b; U = 16.5, P = 0.0327).

3.2. Forest composition

Overstory composition differed between the HarvestTypes (model summaries presented in Supplementary Material S3). The shelterwood stands contained 2.2 times more oak (z = -4.71, P < 0.0001), 6 times less red maple (z = 4.44, P < 0.0001), 10.1 times less birch (z = 3.82, P = 0.0001), and 2 times less Other species (z = 2.98, P = 0.0029) than the high graded stands (Fig. 4a, 4b). In terms of regeneration composition, the shelterwood stands, on average, contained 6,329 (SE = 4,764) more red maple seedlings/ha (1.5 times more) than the high graded stands, but this difference was not significant (Fig. 4c, 4d; F = 1.74, P = 0.2097).



Fig. 4. a) Difference in the percent of total overstory BA between shelterwood and high graded stands by species group. b) Boxplot of BA of stems \geq 12.7 cm in DBH by HarvestType. c) Difference in seedling density (seedlings/ha) between shelterwood and high graded stands by species group. d) Boxplot of total seedlings per hectare by HarvestType. Stars on bars indicate significant differences according to the models used in each evaluation (* P < 0.05, ** P < 0.01, *** P < 0.0001). (ACRU = red maple, BETUL = birch, QUERC = oak, and Other = All other species; HG = high graded stand, SW = shelterwood stand). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Birch was the only species group that was statistically different between the HarvestTypes with 9,689 (SE = 3,348) more seedlings/ha (4.1 times more) in the shelterwood stands (Fig. 4c, 4d; F = 11.74, P = 0.0041). When all species are combined, the shelterwood stands contained 17,897 (SE = 7,710) more seedlings per hectare than the high graded stands (1.6 times more; Fig. 4d; F = 5.39, P = 0.0359).

3.3. Forest function

The final model for biomass included BA and HarvestType (Supplementary Material S3). Biomass was positively related to BA (F = 347.87, P < 0.0001) and the high graded stands contained 45.0 (SE = 4.3) Mg/ ha less biomass than the shelterwood stands (Fig. 5; F = 111.55, P < 0.0001). Using a conversion factor of 0.47 (IPCC 2006), this is a difference of 21.2 Mg/ha in carbon stored. Tree DBH and species influence the amount of biomass stored in trees (Chojnacky et al. 2014) and Fig. 5 indicates that tree DBH accounted for a considerable portion of the differences in biomass per hectare between HarvestTypes. For a given

BA, shelterwood stands had larger QMDs. Given the exponential relationship between tree DBH and tree aboveground biomass (Chojnacky et al. 2014), the fewer but larger trees in the shelterwood stands result in higher biomass per unit area.

4. Discussion

High grading is one of the most common methods of harvesting timber in the eastern US (e.g., Fajvan et al. 1998, McGill et al. 2006, Metcalf et al. 2012). While the effects of high grading have been studied in the eastern US, conclusions are based on small samples of limited inferential scope. Here we provide estimates of residual forest characteristics resulting from high grading versus a comparable, wellestablished silvicultural practice when stands have similar density (as measured by BA), with a focus on mixed-oak forests and a sample that is intended to be more representative of broad-scale harvesting patterns.



Fig. 5. Biomass (Mg/ha) versus BA of stems \geq 12.7 cm in DBH (m²/ha) by HarvestType. Dot size reflects the QMD (cm) for the stand. (HG = high graded stand, SW = shelterwood stand).

4.1. Forest structure

The crown compaction and PropAGS metrics indicate that tree vigor and/or form is worse in high graded stands. Although timber quality has been assessed in terms of tree grade and non-salable wood volume (e.g., see Hanks 1976) in other studies (e.g., Kenefic et al. 2005, Brown et al. 2018), no studies have directly evaluated tree vigor and quality in mixed-oak forests. The crown compaction metric is intended to provide an indication of the level of epicormic branching. Assessments of epicormic branching are important because these branches can affect timber quality especially for hardwoods (e.g., Rast et al. 1973, Meadows and Burkhardt 2001) and can signal that a tree is stressed and/or less vigorous (review by Meier et al. 2012, Meier and Saunders 2013). The lower crown compaction values in the high graded stands thus suggest that there was a higher incidence of epicormic branching on trees' stems. The lower PropAGS in the high graded stands indicates that this practice adversely impacts tree vigor and/or form across multiple forest types of the eastern US (e.g., Fajvan et al. 2002, Kenefic et al. 2005, Brown et al. 2018). The important consequences of poorer tree vigor and/or form in high graded stands are a weakened capacity of forests to store carbon due to reduced growth rates and/or reduced tree survival rates (e.g., Powers et al. 2011, Baral et al. 2016, Puhlick et al. 2020), reductions in salable wood volume yield and/or wood product value (Castle et al. 2017, 2018), and a limited and sometimes more costly array of forest management options.

We found that the spatial distribution of BA was predominately random in the HarvestTypes based on Moran's I, indicating that high and low BA values were randomly located across the stands in both HarvestTypes. However, the within-stand variability of BA (i.e., CV sawtimber BA and CV total BA) differed between the HarvestTypes and was contingent on the metric evaluated (i.e., CV sawtimber BA or CV total BA). Overall, the CV sawtimber BA was higher across Harvest-Types. While the prevailing anecdotal understanding is that high grading increases variability in the overstory and regeneration layers compared to silvicultural treatments (e.g., Trimble 1971), few studies have quantified spatial variability in high graded stands (Grushecky and Fajvan 1999, Bohn 2005, Saunders and Wagner 2008) and none in mixed-oak forests. The CV sawtimber BA was larger in the high graded stands, indicating areas of very dissimilar values, and this aligns with reports by Bohn (2005). The CV sawtimber BA values reported here for high graded stands also align with reported values for northern hardwood stands that received a high grade timber harvest 10-25 years prior to measurement (0.4 to 0.6, Bohn 2005). However, the lower CV total BA in the high graded stands reported here run somewhat contrary to previous reports (Grushecky and Fajvan 1999, Saunders and Wagner 2008). The slightly lower CV total BA (0.085 CV units) in the high graded stands likely reflects differences in the treatment objectives and trees selected for removal. While in a shelterwood treatment large and small trees are strategically removed to promote advance reproduction, in a high grade timber harvest only trees of economic value are removed, leaving behind numerous small trees. Therefore, there likely are larger gaps between canopy trees in shelterwood stands. Higher CV sawtimber BA in high graded stands could impact tree regeneration because seed trees and understory conditions suitable for seedling establishment and development (e.g., sufficient light) may not spatially overlap.

The diameter distribution parameters, DRatio, and QMD metrics provided a quantitative comparison of diameter distributions between HarvestTypes. The benefit of this quantitative approach compared to the qualitative approach that has been previously used (Kenefic et al. 2005, Schuler et al. 2017, Rogers et al. 2018) is that it provides a framework in which continuous numeric values are used to describe multiple elements of diameter distributions (e.g., shape, data spread, and central tendency), which can subsequently be statistically compared between HarvestTypes. Diameter distributions in the high graded stands were characterized by an abundance of small-diameter trees and a limited number of large-diameter trees and resemble a reverse J-shaped distribution characteristic of uneven-aged stands managed with selection system silviculture. However, unlike stands managed with uneven-aged silviculture where there is a correlation between tree size and age (Kenefic and Nyland 1999), the small trees in high graded stands are not necessarily younger than the overstory trees. Consequently, silvicultural treatment options may be more restricted and novel options (e.g., Lussier and Meek 2014) may be more complex and incur larger financial investments. Additionally, this loss of large-diameter trees could negatively impact insectivorous birds through a reduction in insect prey abundance. Some data indicate that small-diameter trees (e.g., oak, hickory [Carya spp.]) tend to have fewer bark microhabitats such as fissures (MacFarlane and Luo 2009, Michel et al. 2011), and thus, may support fewer bark-dwelling insects. This loss could also impact species - such as the cerulean warbler (Setophaga cerulea) and fisher (Martes pennanti) - that preferentially use large-diameter trees for nesting (cerulean warbler; Bakermans and Rodewald 2009, Newell and Rodewald 2011, Boves et al. 2013) and as resting structures (fisher; Gess et al. 2013). The availability of food for wildlife may also be reduced because small-diameter oak trees produce fewer acorns than large-diameter oak trees (Goodrum et al. 1971).

4.2. Forest composition

The lack of control over residual forest conditions typical of high

grading may jeopardize the conservation of mixed-oak forests in the eastern US. Results indicate that oak species are less abundant in the overstory, suggesting that high grading may accelerate the conversion of mixed-oak forests to forests dominated by mesic hardwood species (e.g., maple and birch). The transition to mesic hardwood forest types is, however, not solely driven by high grading and is naturally occurring in numerous mixed-oak forests of the eastern US especially, in Pennsylvania and adjoining states (Fei and Steiner 2007, Nowacki and Abrams 2008, Fei et al. 2011). These transitions to mesic hardwood types are likely caused by numerous factors such as browse impacts from ungulates, stresses from pests and pathogens, and changing disturbance regimes (e.g., review by Dey 2014). High grading, unlike certain silvicultural methods (e.g., shelterwood system), makes no attempt to mitigate these conversions through the retention of oak seed trees or through the creation of conditions that promote the growth and establishment of oak. The loss of oak in forests of the eastern US signifies a loss in an ecologically and economically invaluable genus that supports countless wildlife species and provides high-value wood products (e.g., McShea and Healy 2002, Luppold and Pugh 2016).

Results indicate that high grading is somewhat less consistent and effective at regenerating any tree species. Though the average density of seedlings in the high graded stands was moderately high (31,534 seedlings/ha), the high graded stands still contained considerably fewer seedlings (17,897 seedlings/ha) and displayed a larger variation in total seedling densities between stands (i.e., 0.153 CV units higher) than the shelterwood stands. This could indicate that the shelterwood treatment more reliably created optimal understory light conditions that facilitated the recruitment of various tree species, especially red maple and birch. The low abundance of oak regeneration across HarvestTypes highlights the challenges associated with regenerating oak in general (e. g., review by Dey 2014) and may indicate that treatments in addition to tree harvesting (e.g., prescribed fire, ungulate exclusion fencing) may be necessary to regenerate oak in certain situations. However, because of the much lower quantity of overstory oak trees that can serve as a seed source in the high graded compared to the shelterwood stands (Table 1, Fig. 4a), it may be more difficult and/or costly to regenerate a mixed-oak stand in the high graded stands (e.g., Curtze et al. 2022).

4.3. Forest function

We use forest biomass as a metric that partly reflects forest function and provides an estimate of differences in biomass, and thus carbon stocks, accumulated in live overstory trees in forests of similar stand density and dissimilar management. High grading has the potential to reduce biomass, carbon storage, and wood volume growth in forests. This occurs via 3 not mutually exclusive mechanisms: (1) removal of the largest trees that typically store the most biomass, (2) altered species composition, and (3) possibly reduced growth rates of residual trees due to lower vigor. The removal of large-diameter trees greatly reduced biomass because biomass has an exponential relationship with DBH (Chojnacky et al. 2014). Although the dominant/codominant trees in the high graded stands were, on average, 24.1 years (SE = 7.8) younger than the trees in the shelterwood stands (Supplementary Material S4), this difference in age likely does not fully account for the 19 cm difference in QMD between HarvestTypes since many northeastern hardwood tree species grow around 0.25 to 0.50 cm in diameter every year (Teck and Hilt 1991). Altered species composition can lead to differences in biomass because for a given DBH, species can have different amounts of biomass. For example, one 40 cm DBH (i.e., mean QMD in the shelterwood stands) red maple stem is estimated to contain $\sim 170 \text{ kg}$ less biomass than one 40 cm oak stem (Chojnacky et al. 2014). Given that the shelterwood stands contained, on average, 44.3 % more oak and 24.2 % less red maple than the high graded stands (Fig. 4a), compositional differences between the HarvestTypes likely also contributed to the higher biomass per unit BA in the shelterwood compared to the high graded stands.

Retaining less vigorous trees in a stand has the potential to reduce future carbon storage and volume growth rates (Schlesinger 1978, Ward 2002, Devine and Harrington 2006, Baral et al. 2016). This is because trees that have been suppressed for a long period, are initially in lower crown positions, and/or are from shade-intolerant species may be less likely to respond to the release from competition that occurs after harvest (Schlesinger 1978, Ward 2002, Devine and Harrington 2006, Baral et al. 2016). Thus, a potential consequence of removing the largest and most vigorously growing trees during a high grade timber harvest is that the future growth rates of the residual trees, especially the less shadetolerant individuals, may not realize the full growth potential afforded by the growing site.

5. Conclusions

In summary, the purpose of this study was to quantify differences in residual forest characteristics of high graded mixed-oak stands versus mixed-oak stands that received a comparable, well-established silvicultural treatment. We used new metrics to either assess attributes of forest structure that haven't been previously studied in mixed-oak forests (e.g., tree crown compaction) or to quantitatively describe diameter distributions. We found that the high graded stands contained higher relative abundances of unhealthy and/or poorly formed trees, fewer large-diameter trees, lower proportions of oak in the overstory canopy, less total tree regeneration per hectare, and much less aboveground livetree biomass per hectare (and therefore carbon stocks) than the shelterwood stands. These characteristics compromise forest health and productivity, hamper the ability of forests to provision ecosystem services such as habitat for specific wildlife species, carbon storage, and valuable wood products, and restrict silvicultural treatment options. Given the prevalence of high grading in the eastern US (e.g., Fajvan et al. 1998, McGill et al. 2006, Metcalf et al. 2012), the sustainability of forests of the eastern US depends on the implementation and expansion of forestry practices based on silvicultural principles and that consider the future forest when determining which trees to harvest rather than solely removing trees based on tree diameter and economic value. Results from this study have the potential to support and enhance forest conservation efforts on private lands through programs such as the US Department of Agriculture Natural Resources Conservation Service's Environmental Quality Incentives Program, Regional Conservation Partnership Program, and Working Lands for Wildlife. Future research should emphasize the identification of management practices and the development of decision support tools for the rehabilitation of high graded stands.

CRediT authorship contribution statement

Alexander C. Curtze: Conceptualization, Methodology, Formal analysis, Writing – original draft. Allyson B. Muth: Conceptualization, Writing – review & editing, Resources. Jeffery L. Larkin: Conceptualization, Writing – review & editing, Resources, Funding acquisition. Laura P. Leites: Conceptualization, Methodology, Formal analysis, Writing – original draft, Funding acquisition.

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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Appendix A. Supplementary material

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