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The long-term case for partial-cutting over clear-cutting in the southern Appalachians USA

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Abstract

Prior to the 1950s, common partial harvesting operations in the southern Appalachians USA involved the removal of logs by ground-skidding and the construction of steep access roads and skid trails along stream channels. Little is known about how these historical practices affected long-term vegetation changes. An experimental watershed in the Coweeta Hydrologic Laboratory was partially harvested in the years 1942–1952 according to these exploitive practices. We compared the partial-cut watershed to a clear-cut watershed and an untreated, reference watershed. Using long-term vegetation surveys, we analyzed patterns in aboveground biomass accumulation, species composition and diversity (Shannon's index H′ and species richness) among watersheds. Contrary to our expectations, the partial-cut watershed recovered to reference levels of aboveground biomass and their species composition was similar over time. The clear-cut watershed had greater abundance of tulip poplar (*Liriodendron tulipifera*) and black locust (*Robinia pseudoacacia*) than the other two watersheds. The partial-cut watershed increased in diversity over time, but it remained less diverse than the reference watershed; whereas, the clear-cut watershed had lower diversity than the other two watersheds, and its diversity did not change over time. Distributions of functional groups based on water use and nutrient acquisition traits, and shade tolerance were similar between the partial-cut and the reference watersheds, but differed from the clear-cut watershed. By the 2010s, partial-cut and reference watersheds had similar proportions of diffuse-porous (32% and 33%) and ring-porous (48% and 42%) basal area, while the clear-cut watershed had more diffuse-porous (43%) and less ring-porous (36%) species than the partial-cut or reference watersheds. Tree species associated with arbuscular mycorrhiza were more abundant in the clear-cut watershed than the partial-cut or reference watersheds. Overall, the partial-cut watershed, even with the extreme soil disturbance, did not alter long-term species composition and diversity as dramatically as the clear-cut watershed. These results could help forest managers, conservationists, and hydrologists understand the long-term effects of partial-cutting versus clear-cutting.

Keywords Coweeta Hydrologic Laboratory · Tree diversity · Forest composition · Deciduous · Logging · Partial harvest · Functional traits

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11056-019-09731-y) contains supplementary material, which is available to authorized users.

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Introduction

In the southern Appalachians USA, forests are highly productive and have thus been logged for more than 200 years; however, logging practices have changed markedly over time. From the late 1800s to the early 1900s, widespread, intensive logging was common in the region (Brose et al. 2001; Elliott and Swank 2008; Dey et al. 2019) with millions of cubic meters of timber removed (Douglass and Hoover 1988; Yarnell 1998). Logging in the southern Appalachians continued throughout the 1900s, and up to the 1950s, typical harvesting operations removed logs by ground-skidding with horse or mule teams (Yarnell 1998). Steep access roads and skid trails were placed along the path of least resistance adjacent to stream channels (Lieberman and Hoover 1948). Prior to the 1950s, most harvesting did not follow any particular silvicultural method, rather the largest trees with the greatest commercial value were cut (often referred to as high-grading or diameter-limit, Kenefic and Nyland 2006). From the 1960s to the 1980s, clear-cutting (a regeneration method within the even-aged silvicultural system) was promoted as the most effective and efficient form of timber management in this region (Roach and Gingrich 1968; Smith et al. 1989). Current silvicultural recommendations for forest management readily prescribe two-age regeneration harvests (also referred to as shelterwood with reserves or deferment cut) (https://www.fs.usda.gov/main/nfsnc/landmanagement/planning). A two-age harvest was designed to leave a low residual basal area of 2.3–6.9 m^2 ha^{-1} (Miller et al. 1995) and be more aesthetically pleasing than clear-cutting because a few individual stems (30–40 trees ha^{-1}) are retained to persist in the stand through the next rotation, creating two distinct age classes (Smith et al. 1989). In practice, the residual basal area after two-age harvests were often at the low end, leaving less than 10% of the original forest stand (Miller et al. 1995; Keyser and Loftis 2015; Elliott and Vose 2016). Other partial-harvesting practices such as shelterwood, group and single tree selection are used to a lesser extent in the southern Appalachians on National Forest lands (https://www.fs.usda.gov/main/nfsnc/landmanagement/planning). However, most of the forested lands in the eastern USA are privately owned (ca. 90%), and while private owners follow state Best Management Practices (BMPs) (Ice et al. 2010), their harvest techniques and timber extraction methods were not well documented (Smith et al. 2009).

Numerous research studies in the eastern USA have examined the effects of various levels of partial-harvest (used interchangeable with partial-cut) on tree growth and diversity (e.g., McGee et al. 1999; Schuler and Gillespie 2000; Schuler 2004; Jones et al. 2009; D'Amato et al. 2011; Keyser and Loftis 2013; see review Nolet et al. 2018); however, few have examined the long-term effects on tree species composition and diversity due to the exploitive logging practices of the 1940s. Partial-cuts of the 1900–1950s likely affected growth recovery rates and long-term species composition, with lasting legacy effects on ecosystem processes. This type of log extraction with deeply furrowed skid trails (Hoover 1945) disrupts soil physical properties (Aust et al. 1998), severs root systems and reduces mycorrhizal colonization (Jasper et al. 1991), displaces buried seeds (Pinard et al. 2000), and removes nutrient rich soil O-horizons (Yanai et al. 2003; Mushinski et al. 2018); all of which could hinder forest vegetation recovery. Partial-cuts also alter light penetration onto the forest floor (e.g., Grayson et al. 2012; Elliott and Vose 2016), which could subsequently affect species composition. For example, northern red oak (*Quercus rubra* L.) grows faster at low light than does tulip poplar (*Liriodendron tulipifera* L.) (Kolb et al. 1990); and northern red oak seedling growth and photosynthetic rates respond more strongly to modest increases in light (up to 20% light) than red maple (*Acer rubrum* L.) seedlings (Kobe et al. 1995; Parker and Dey 2008). Northern red oak and chestnut oak (*Quercus montana* Willd.) maintain higher growth rates at low light than do black oak (*Quercus velutina* Lam.) and white oak (*Quercus alba* L.) (Gottschalk 1994; Rebbeck et al. 2011; Brose and Rebbeck 2017).

Changes in species composition could have cascading effects on ecosystem services such as hydrology and water yield (Buttle et al. 2018), biogeochemical cycling, productivity and future commercial timber value (Perera et al. 2018). The amount of water used by trees varies based on their xylem anatomy type (Ford et al. 2011), so changes in species composition can potentially alter water use and subsequently water yield (Swank et al. 2014; Brantley et al. 2015; Elliott et al. 2017; Jackson et al. 2018). Ring-porous oak (*Quercus*) species, for example, have large diameter xylem conduits that can embolize in freeze-thaw and drought events, resulting in narrow functional sapwood area and relatively low water use compared to other species after such events. On the other hand, species with deep functional sapwood and narrower vessel element diameters, i.e., diffuse-porous, often show greater, and more seasonally-uniform, water use compared to ring-porous species (Taneda and Sperry 2008). Land management practices that shift forest species composition from dominance by the former to the latter functional sapwood type can reduce water yield by as much as 16% (Elliott et al. 2017). Trees also have differences in their nutrient acquisition traits including their mycorrhizal associations and nitrogen fixation that have the potential to alter nutrient cycling (Phillips et al. 2013; Mushinski et al. 2018; Zhu et al. 2018), forest productivity and population dynamics (Bennett et al. 2017).

Two experimental watersheds in the Coweeta Basin, in western North Carolina USA, carried out two management practices: one was a partial-cut watershed in years 1942–1952 to simulate the traditional harvesting practices of the 1940s, where log extraction resulted in extensive soil erosion and sediment movement; the other was a clear-cut watershed using a cable and yarding system that sought to minimize soil disturbance and skidding trails. The former watershed treatment came well before the 1972 Clean Water Act (CWA); and helped inform and ensure the eventual adoption of BMPs by southern states (Aust and Blinn 2004; Sun et al. 2004; Ice et al. 2010; Anderson and Lockaby 2011). These BMPs included strategic road designs (e.g., broad-base dip, road crossings perpendicular to streams) and minimized skid trails and sediment delivery to streams (Anderson and Lockaby 2011). The latter watershed treatment was executed after the CWA and incorporated BMPs, but came during a time of extensive clearing of forest land in the southern USA. Long-term vegetation dynamics of the clear-cut watershed have been reported on (Elliott et al. 1997; Boring et al. 2014); however, no vegetation dynamics data have been published for the partial-cut watershed.

We provide a case study using three watersheds in the Coweeta Hydrologic Laboratory to evaluate the long-term effect of partial harvesting with exploitive logging practices on vegetation dynamics. Our objectives were to (1) determine the changes in forest aboveground biomass, composition and diversity in the partial-cut watershed over time, (2) compare these changes to a clear-cut watershed and a mature, reference watershed, and (3) discuss the implications of species compositional changes on hydrology and biogeochemistry based on species-specific functional traits of water use, nutrient acquisition and shade tolerance. We expected that the partial-cut watershed with extensive soil disturbance and erosion would delay or impede forest recovery and shift species composition compared to the reference watershed. We used long-term survey data, first collected in 1934, from these three watersheds within the Coweeta Basin.

Materials and methods

Study area

Coweeta Hydrologic Laboratory is a 2185 ha experimental forest of the Southern Research Station, USDA Forest Service. Coweeta is located in the Nantahala National Forest, western North Carolina, in the Blue Ridge Physiographic Province of the southern Appalachian Mountains (latitude 35°03′N, longitude 83°25′W). Elevations range from 675 to 1592 m and slopes range from 30 to 100%. Mean annual temperature is 12.6 °C and mean annual precipitation is 180 cm (Swift et al. 1988). Soils are deep sandy loams underlain by folded schist and gneiss (Thomas 1996). Vegetation is southern mixed deciduous forests with overstory codominance by oaks, maples (*Acer*), hickories (*Carya*) and tulip poplar and an evergreen understory of rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.) (Day et al. 1988; Elliott and Swank 2008). Three watersheds within the Coweeta Basin were examined in this study; partial-cut (watershed 10), clear-cut (watershed 7), and reference (watershed 14) (Table 1, Fig. 1). The partial-cut and clear-cut watersheds are south-facing and the reference watershed is north-facing.

Disturbance history

Prior to establishment of the Coweeta Hydrologic Laboratory, the Coweeta Basin was disturbed by burning and grazing by the Cherokee Indian Nation and European settlers (Douglass and Hoover 1988). Additional disturbances afterwards included Dogwood anthracnose caused by *Discula destructiva* Redlin affecting flowering dogwood (*Cornus florida* L.) (Chellemi and Britton 1992), a major drought from 1985 to 1988 (Swift et al. 1989), the southern pine beetle (*Dendroctonus frontalis* Zimmerman) attack on pitch pine (*Pinus rigida* Miller) on dry ridges (Smith 1991), large blowdowns caused by hurricanes (Greenberg and McNab 1998; Elliott et al. 2002), landslides (Hales et al. 2009), and hemlock woolly adelgid (*Adelges tsugae* Annand) infestation along riparian corridors, first reported in Coweeta in 2003 (Elliott and Vose 2011; Ford et al. 2012; Fraterrigo et al. 2018). The most dramatic disturbances, however, were widespread logging and the chestnut blight fungus (*Cryphonectria parasitica* (Murr.) Barr) in the early 1900s. The J.A. Porter Logging Company held the rights for timber over 38 cm diameter and performed selective logging (also referred to as diameter-limit harvests). When the Forest Service took over administration of the Coweeta Basin in 1923, 19,000 m^3 of timber had been removed (Douglass and Hoover 1988). Chestnut blight, common across the region, was first reported in Coweeta in 1926. American chestnut (*Castanea dentata* (Marsh.) Borkh.) was the most abundant species in the Coweeta Basin based on the 1934 survey, contributing 22% of the total density

Table 1 Description of three watersheds compared in this study. Treatment, time since last cut, watershed size, elevation range, aspect, and number of sample plots

Treatment	Last cut (years ago)	Size (ha)	Elevation range (m)	Aspect	Sample plots
Reference	89	61	707–992	NW	31
Partial-cut	62	86	742–1159	SSE	43
Clear-cut	31	59	722–1077	S	24

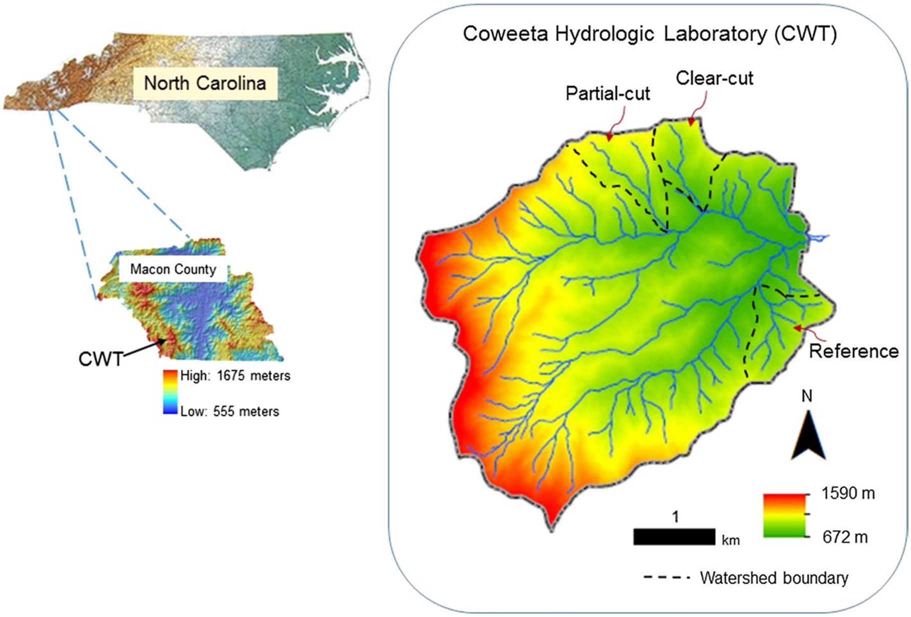

Fig. 1 Map of the locations of three watersheds (reference, partial-cut, and clear-cut) within the Coweeta Hydrologic Laboratory (latitude 35°03′N, longitude 83°25′W), western North Carolina, USA. Long-term permanent plots are arrayed along north–south transects (330°) at 200 m intervals

and 36% of the total basal area (Elliott and Swank 2008). By 1940, virtually all American chestnut trees were killed (Douglass and Hoover 1988).

Most of the Coweeta Basin was logged between 1919 and 1923 with about 20% of the basal area removed. Lower elevations such as the partial-cut, clear-cut and reference watersheds were the first to be logged (Douglass and Hoover 1988; Elliott and Swank 2008). At the time of the 1st survey in 1934, it had only been a few years since logging before the chestnut blight pandemic eliminated virtually all American chestnut trees. Since American chestnut and oak species were the preferred commercial trees (Ashe 1911) at the time of the 1880–1920s logging period, it is likely these were the species that were selectively cut from the Coweeta Basin as well. Thus, in 1934, the forest was in a recently disturbed condition and was recovering from logging and loss of American chestnut.

While the reference watershed was affected by these early disturbances, it has remained an unmanaged watershed since 1923 with no observed hurricane or landslide disturbances. The partial-cut and clear-cut watersheds were subjected to additional management treatments by researchers at Coweeta Hydrologic Laboratory. Logging occurred from 1942 to 1952 in the partial-cut watershed; most of the logging occurred between 1942 and 1947 with only a small portion in the upper NE corner cut after that (plots used in this study were cut before 1952; hereafter, 1952), according to the typical local logging practices of the time (Lieberman and Hoover 1948) before BMPs (Sun et al. 2004). “Because of the steep slopes, main skidding roads or trails are generally built paralleling the stream course and are roughly leveled off for a width of 4–6 feet. Logs are pulled from the stump into the road, where they are fastened together by grabs and skidded to the landing. The dragging of the logs creates a channel which concentrates runoff from the road surface into a stream that develops considerable erosive force” (Hoover 1945, p 765). Over a three month period, Jun–Aug 1942, an estimated sediment loss of 306 m^3 ha^{-1} was attributed to access roads and skid trails (Lieberman and Hoover 1948; Hoover 1952). Horse and mule teams were used to drag logs (Fig. 2a), and the log bundles created wide and deep skid trails (Fig. 2b) across the watershed. Harvesting removed 471 m^3 of timber and 30% of the total basal area (Douglass and Hoover 1988).

The clear-cut watershed was harvested over a six-month period in 1977, primarily using high-lead yarding systems. Using this system, logs were suspended completely above the ground (Fig. 2c). Tractor skidding was used on about 9 ha (lower elevation of the watershed) where slopes were less than 20%. All stems $\geq$ 2.5 cm at diameter at breast height (dbh, 1.37 m height) were cut and logging debris was left in place with no further site preparation (Elliott et al. 1997; Swank and Webster 2014). The total timber sale volume was about 2300 m^3 and this was distributed over 41 ha; 16 ha on upper slopes and ridges were cut but left on the ground due to insufficient volumes of marketable timber. Road construction activities incorporated BMPs to reduce erosion and sediment movement (Swift 1988; Swift and Burns 1999), and roads were constructed perpendicular to streams (Fig. 2d).

Vegetation surveys

Permanent plots were used to examine changes in vegetation patterns in all three watersheds. Permanent 0.08 ha (20-m × 40-m) plots were established in 1934 along 13 parallel,

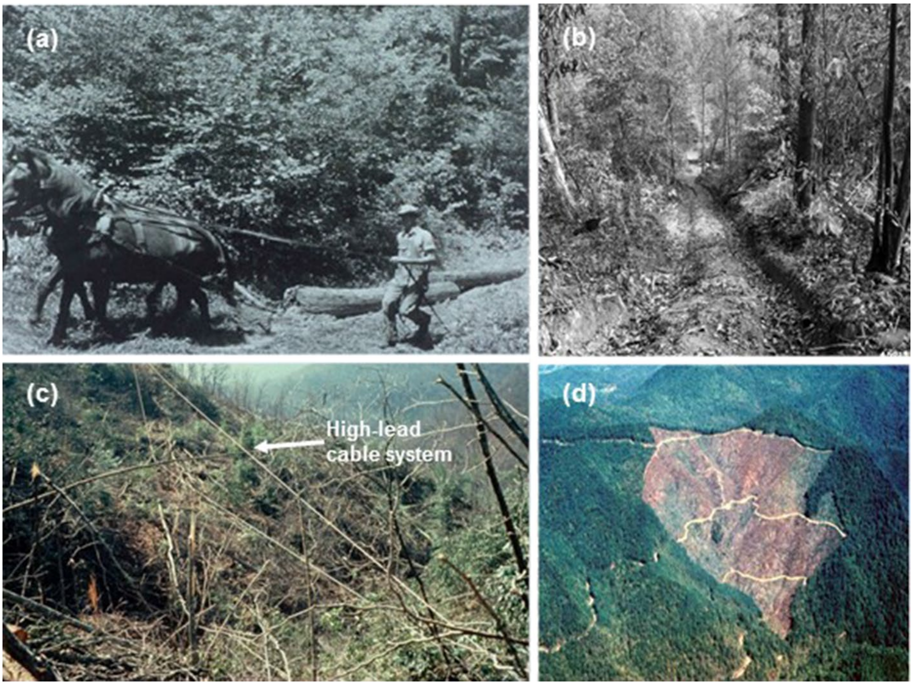

Fig. 2 Historical photos of partial-cut and clear-cut watersheds (from Coweeta photo archives). **a** Partial-cut, dragging logs using mule team; **b** partial-cut, dragging log bundles created deep, wide channels; **c** clear-cut, high-lead cable system suspends logs above the ground; **d** clear-cut, aerial photo taken 1st year after cutting, roads were installed perpendicular to streams

approximately north–south transects (330°) at 200 m intervals spanning the Coweeta Basin (Douglass and Hoover 1988). All permanent plots in the Coweeta Basin were originally inventoried in 1934. In later years, the partial-cut watershed was re-inventoried in 1952 and 2014; the clear-cut in 1974, 1984, 1993, 1997 and 2008; and the reference watershed in 1969, 1993 and 2009. All woody stems (trees and shrubs) ≥ 2.5 cm dbh were measured and recorded by species in each permanent plot. Inventory data from the earlier survey periods have been published for the clear-cut (Elliott et al. 1997). Inventory data for the partial-cut has never been published and the most recent survey of the permanent plots (2014) was conducted for this study (Appendix 1 in Electronic Supplementary Material, ESM). The reference watershed was inventoried as part of the overall Coweeta Basin surveys (Elliott et al. 1999; Elliott, unpublished). In 1974 before the clear-cut, trees were inventoried from 20-m × 40-m plots, perpendicular to the Coweeta Basin permanent plot network. In subsequent years after clear-cutting (1984, 1993, 1997, 2008), 24 of these original plots were re-measured (Elliott et al. 1997). The number of plots surveyed in each watershed is provided in Table 1. The last survey years (partial-cut, 2014; clear-cut, 2008; and reference, 2009) will be referred to as the 2010s for ease of comparisons among these three watersheds. In our case study, the experimental treatments were applied across the entire watershed (Table 1) and could not be replicated. Here, we define the population as the whole watershed, and draw samples (plots) over time in each of the three watersheds. Hence, our statistical analyses only compare differences between watersheds and within watersheds over time to address the concern of pseudoreplication (Stewart-Oaten et al. 1986; Oksanen 2001; Davies and Gray 2015; Colegrave and Ruxton 2018).

Data analysis

For all inventories in each watershed, we calculated density (stems ha^{-1}), basal area ($\mathrm{m}^2\ \mathrm{ha}^{-1}$), foliage biomass (kg ha^{-1}), total aboveground biomass (kg ha^{-1}) and importance value (IV, relative density + relative basal area ÷ 2). We used species-specific allometric equations from Martin et al. (1998) to calculate aboveground biomass (foliage and total) of deciduous trees, equations from Santee and Monk (1981) and Miniat (unpublished) for eastern hemlock (*Tsuga canadensis* (L.) Carr.) and equations from McGinty (1972) for rosebay rhododendron and mountain laurel. To evaluate changes in diversity, we used species richness (*S*, number of species) and Shannon-Weiner index of diversity (H′), a simple quantitative expression that incorporates both species richness and the evenness of species abundance (Magurran 2004). H′ was calculated for each plot on the basis of basal area ($\mathrm{H'_{basal\ area}}$), total biomass ($\mathrm{H'_{biomass}}$) and IV ($\mathrm{H'_{IV}}$).

We compared density, basal area, foliage biomass, total biomass and diversity (*S*, $\mathrm{H'_{basal\ area}}$, $\mathrm{H'_{biomass}}$ and $\mathrm{H'_{IV}}$) across watersheds in each year, and within watersheds across time using the general linear model procedure (PROC GLM, SAS v9.4, 2002–2012). If the overall *F*-test was significant ($p \leq 0.05$), we used Ryan-Einot-Gabriel-Welsh Multiple Range Test. For the last survey (2008, 2009, 2014), we used analysis of covariance where the covariate was the initial condition (1934 survey) to compare differences among watersheds. The covariate was only significant for $\mathrm{H'_{basal\ area}}$, $\mathrm{H'_{biomass}}$ and $\mathrm{H'_{IV}}$ where the covariate was initial $\mathrm{H'_{basal\ area}}$, $\mathrm{H'_{biomass}}$ and $\mathrm{H'_{IV}}$ in 1934, respectively (PROC GLM, SAS v9.4, 2002–2012).

In order to assess the implications of species compositional changes on hydrology and biogeochemistry, species were classified into functional groups based on their water use and nutrient acquisition traits and shade tolerance. Water use largely depends on xylem anatomy (Taneda and Sperry 2008; Ford et al. 2011); groups included diffuse-porous (tulip poplar, black birch (*Betula lenta* L.), blackgum *(Nyssa sylvatica* Marsh.), red maple and others), ring-porous (hickories, oaks, sourwood (*Oxydendrum arboreum* (L.) De Candolle) and others), non-porous evergreen trees (pitch pine and eastern hemlock), evergreen shrubs (rosebay rhododendron and mountain laurel) and black locust (*Robinia pseudoacacia* L.). Diffuse-porous species have the highest daily water use (DWU); ring-porous species have the lowest DWU compared to other tree species (Ford et al. 2011). Even though black locust has ring-porous xylem, it is isohydric (i.e., maintaining stable leaf water potentials as soil water potentials drop, Klein 2014) and has higher DWU than oaks or hickories (Miniat and Hubbard, unpublished). Nutrient acquisition traits largely depend on mycorrhizal associations (Phillips et al. 2013); groups included arbuscular mycorrhizal (AM), ectomycorrhizal (ECM), the ericoid mycorrhizal (ERM) tree sourwood (*Oxydendrum aboreum* (L.) De Candolle), evergreen trees, evergreen shrubs and the nitrogen (N) fixing tree black locust (Wurzburger and Miniat 2014). Evergreen shrubs, rosebay rhododendron and mountain laurel, also have ericoid mycorrhizal associations. However, their sclerophyllous leaves have lower nutrient concentrations and slower decomposition rates (Wright and Coleman 2002); subsequently, nutrient cycling rates are slower than deciduous leaves. Shade-tolerance is associated with a wide range of physiological and morphological traits (Valladares and Niinemets 2008); however, we grouped species into the simplest categories according to the “carbon gain hypothesis” (Givnish 1988) that relates to the ability to tolerate low light levels and compete for light according to Burns and Honkala (1990); groups included intolerant, intermediate, tolerant and evergreen shrubs. We compared the proportional distribution of these functional groups among watersheds.

Results

Aboveground biomass

In 1934, the aboveground biomass across all watersheds was similar (Fig. 3). In the 2010s, the aboveground biomass was marginally different among watersheds ($F_{2,\ 94} = 2.61$, $p = 0.079$), with lower biomass in the clear-cut watershed compared to the other two watersheds. Between these years, decreases in biomass were observed in the partial-cut

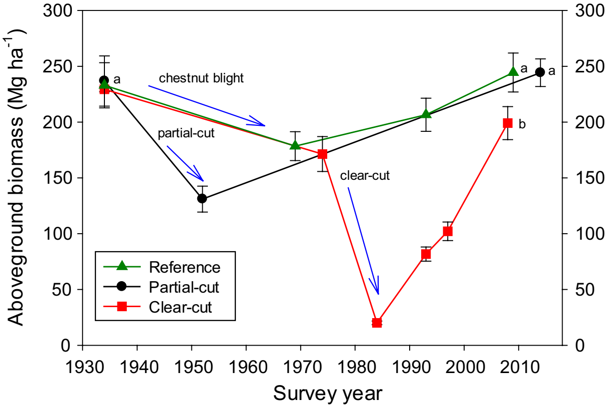

Fig. 3 Mean (± se bars) aboveground biomass over time for the three watersheds: reference, partial-cut, and clear-cut. In 1934, watershed values with different letters (a, b) were significantly different ($p \le 0.05$). For the 2010s, watershed values with different letters (a, b) were significantly different ($p = 0.079$)

watershed due to the partial harvest logging, in the clear-cut watershed due to chestnut blight and cutting, and in the reference watershed due to chestnut blight (Fig. 3). In contrast, in the 2010s, density and basal area were greater in the clear-cut watershed than the partial-cut and reference watersheds (Table 2). Contrary to our expectations, the partial-cut watershed recovered to reference watershed levels of aboveground biomass and species composition.

Species composition

In 1934, American chestnut was the most abundant species (102.6–124.8 Mg ha^{-1} biomass) in all watersheds. By the 2010s, eight species (chestnut oak, white oak, scarlet oak, northern red oak, black oak, hickories, red maple and tulip poplar) accounted for 74–79% of the total aboveground biomass (Appendices 1–3 in ESM). The partial-cut and reference watersheds had a similar pattern of species composition over time (Fig. 4a, b). The white oak group (*Quercus* subgenus Leucobalanus; chestnut oak and white oak) became the most abundant after 1934 following the loss of American chestnut, with the red oak group (*Quercus* subgenus Erythrobalanus; northern red oak, black oak and scarlet oak) and red maple the second and third most abundant, respectively (Fig. 4a, b). By the 2010s, the white oak group comprised 37% and 31% of the total aboveground biomass in the partial-cut and reference watersheds, respectively.

In the clear-cut watershed, before cutting (1974), the red oak and white oak groups were the most abundant, followed by hickory. By the 2010s, tulip poplar became the most abundant species accounting for 31% (62.5 ± 18.1 Mg ha^{-1}) of the total aboveground biomass, and the white oak group (18%) and red maple (11%) were the second and third most abundant, respectively (Fig. 4c). The white oak group had lower biomass in the clear-cut watershed compared to the partial-cut or reference watersheds. Black locust and tulip poplar had greater biomass in the clear-cut watershed than either the partial-cut or reference

Table 2 Mean (± se) density (stems ha^{-1}), basal area (m^2 ha^{-1}), and foliage biomass (kg ha^{-1}) for each watershed treatment (reference, partial-cut, and clear-cut) and survey years (pre- and post-harvest noted). Trees and evergreen shrubs (stems ≥ 2.5 cm dbh)

Treatment	Survey year	Density	Basal area	Foliage
Reference	1934	3673 (167)b	29.78 (1.54)b	4964 (317)a
	1969	6067 (480)a	25.95 (1.11)b	3586 (168)b
	1993	3829 (566)b	29.43 (1.52)b	3861 (195)b
	2009	3649 (322)b,y	36.90 (1.85)a,y	4170 (227)b,y
Partial-cut	1934-pre	3010 (128)a	29.86 (1.53)b	4490 (216)a
	1952-post	3751 (250)a	21.20 (1.24)c	2655 (160)b
	2014-post	3327 (308)a,y	36.04 (1.15)a,y	4255 (157)a,y
Clear-cut	1934-pre	2660 (187)c	28.82 (2.01)b	3850 (271)b
	1974-pre	2787 (417)c	25.26 (1.51)b	3216 (203)b
	1993-post	17,982 (2328)a	22.86 (1.36)b	3786 (298)b
	2008-post	11,348 (1548)b,x	42.21 (2.11)a,x	5807 (370)a,x

Values within watersheds followed by different letters denote significant differences ($p \leq .05$) over time based on Ryan-Einot-Gabriel-Welsh Multiple Range Test. For the last survey (2008, 2009, 2014), values followed by different letters (x, y, z) denote significant differences ($p \leq 0.05$) among watersheds

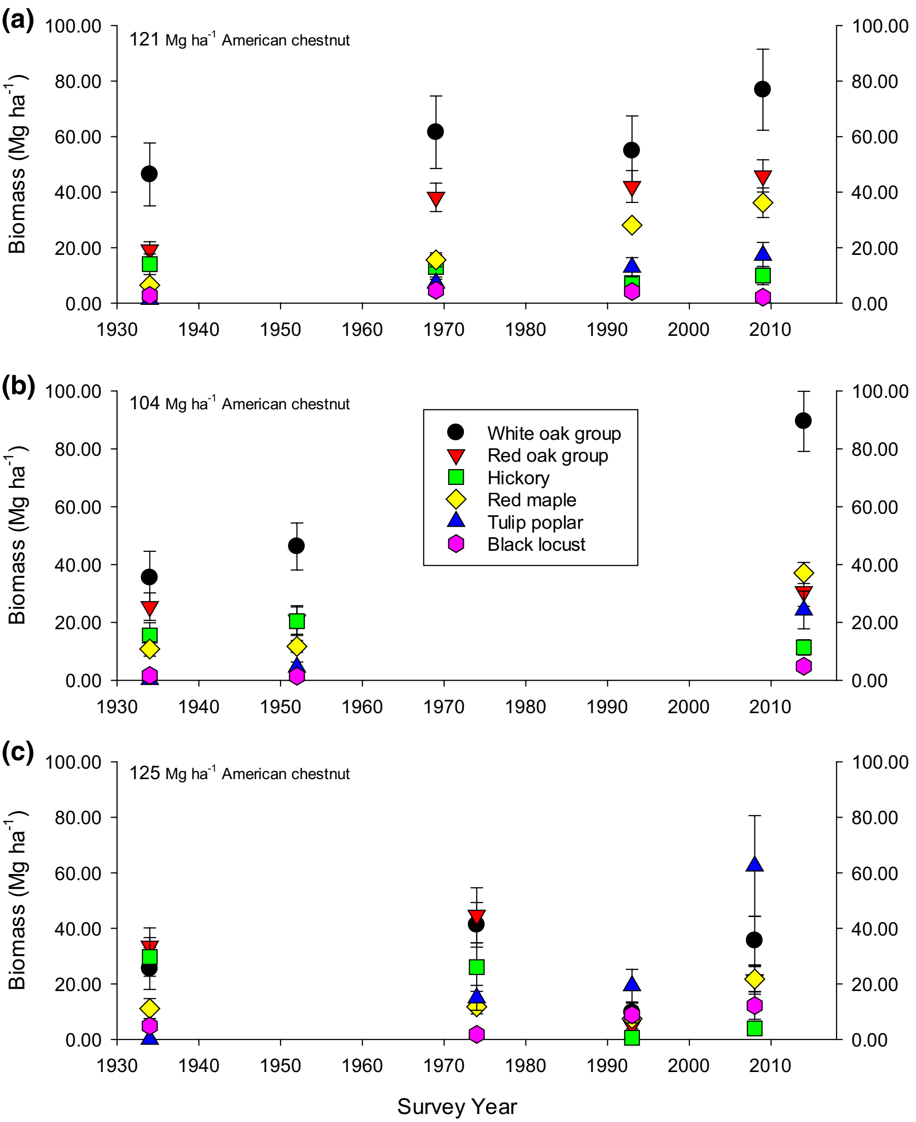

Fig. 4 Species composition over time for all watersheds: **a** reference; **b** partial-cut; and **c** clear-cut. Values are mean (± se bars) aboveground biomass. Species are American chestnut (*Castanea dentata*); white oak group = chestnut oak (*Quercus montana*) and white oak (*Q. alba*); red oak group = northern red oak (*Quercus rubra*), scarlet oak (*Q. coccinea*) and black oak (*Q. velutina*); hickory (*Carya* spp.); red maple (*Acer rubrum*); tulip poplar (*Liriodendron tulipifera*); and black locust (*Robinia pseudoacacia*). Estimated values of American chestnut biomass in 1934 were based on diameter measurements from standing dead and dying trees

watersheds. Red maple biomass was lower in the clear-cut watershed than the other two watersheds (Fig. 4a–c).

Tree species diversity

Across the three watersheds we found 34 tree species and two evergreen shrubs (Appendices 1–3 in ESM), with an average of 12–17 species per plot (Table 3). H'_{biomass} and $H'_{\text{basal area}}$ increased over time in the partial-cut and reference watersheds, but not in the clear-cut watershed (Fig. 5, Table 3). This increased diversity can be attributed to the loss of the dominant American chestnut, which accounted for 51–53% of the total aboveground biomass in 1934. H'_{biomass} was greater in reference watershed than the partial-cut and clear-cut watersheds in the 2010s. The increased diversity in the reference watershed over time was due to greater species evenness (Fig. 5), after the loss of American chestnut, rather than changes in species richness (Table 3). In the clear-cut watershed, H'_{IV} showed a significant decline over time, while $H'_{\text{basal area}}$ and H'_{biomass} did not significantly change over time (Table 3). The clear-cut watershed had fewer species (S/plot) in the 2010s than in 1934. In the 2010s, the partial-cut watershed had fewer species than the reference watershed, but there was no difference between the partial-cut and clear-cut watersheds (Table 3).

Distribution of functional groups

The proportional basal area of diffuse-porous species increased, while ring-porous species decreased over time in all watersheds (Fig. 6a, b). By 2010s, partial-cut and reference watersheds had similar proportions of diffuse-porous and ring-porous basal area, while the clear-cut watershed had significantly less ring-porous species than the partial-cut or

Table 3 Mean (± se) species richness, *S*/plot; and Shannon's index based on basal area, $H'_{\text{basal area}}$; importance value, H'_{IV} (where IV = relative density + relative basal area ÷ 2); and total aboveground biomass, H'_{biomass} for each watershed treatment (reference, partial-cut, and clear-cut) and survey years (pre- and post-harvest noted)

	Survey year	*S*/plot	$H'_{\text{basal area}}$	H'_{IV}	H'_{biomass}
Reference	1934	16.3 (0.6)a	1.83 (0.07)b	1.92 (0.06)a	1.43 (0.07)b
	1969	17.2 (0.5)a	2.05 (0.05)a	2.03 (0.05)a	1.73 (0.07)a
	1993	14.7 (0.6)a	1.95 (0.05)ab	1.97 (0.05)a	1.71 (0.06)a
	2009	15.2 (1.1)a,x	1.92 (0.04)ab,x	1.90 (0.05)a,x	1.73 (0.05)a,x
Partial-cut	1934-pre	11.5 (0.4)b	1.37 (0.06)b	1.68 (0.05)b	1.12 (0.07)b
	1952-post	13.0 (0.3)a	1.66 (0.04)a	1.97 (0.04)a	1.35 (0.06)a
	2014-post	12.6 (1.4)b,y	1.61 (0.03)a,y	1.84 (0.04)a,x	1.37 (0.04)a,y
Clear-cut	1934-pre	15.5 (0.5)a	1.78 (0.06)a	1.93 (0.06)a	1.46 (0.08)a
	1974-pre	12.7 (0.6)b	1.81 (0.04)a	1.91 (0.04)a	1.54 (0.06)a
	1993-post	14.6 (0.7)ab	1.75 (0.07)a	1.88 (0.06)ab	1.50 (0.08)a
	2008-post	13.2 (0.7)b,y	1.73 (0.09)a,y	1.75 (0.06)b,y	1.49 (0.09)a,y

Values within watersheds followed by different letters (a, b) denote significant differences ($p \leq 0.05$) over time based on Ryan-Einot-Gabriel-Welsh Multiple Range Test. For the last survey (2008, 2009, 2014), we used analysis of covariance for $H'_{\text{basal area}}$, H'_{IV}, and H'_{biomass}, where the covariate was initial $H'_{\text{basal area}}$, H'_{IV}, and H'_{biomass} in 1934, respectively (PROC GLM, SAS v9.4, 2002–1012); values followed by different letters (x, y) denote significant differences ($p \leq 0.05$) among watersheds

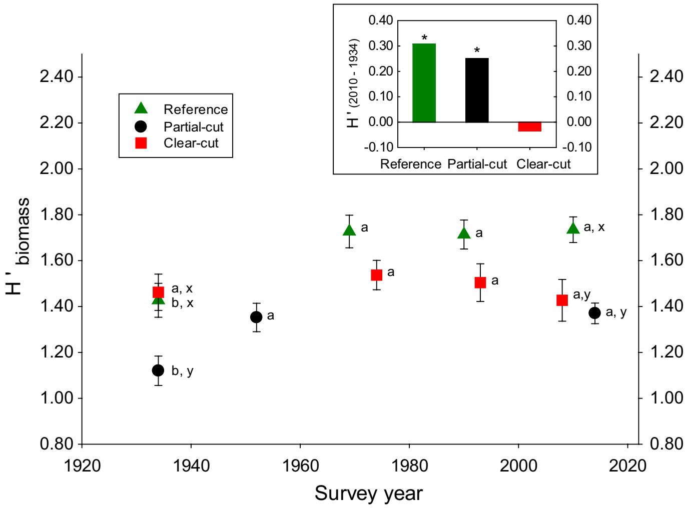

Fig. 5 Changes in diversity (Shannon's index based on total biomass, H'_{biomass}) over time since 1934 for all watersheds (reference, partial-cut, and clear-cut). Within watersheds, values across years with different letters (a, b) are significantly different ($p \leq 0.05$). In the 2010s, values across watersheds followed by different letters (x, y) are significantly different ($p \leq 0.05$) based on analysis of covariance, where the covariate was initial H'_{biomass} in 1934 (PROC GLM, SAS v9.4, 2002–1012). Inset shows the H'_{biomass} difference values between the 2010s last survey and 1934 survey for each watershed, asterisk denotes significant ($p \leq 0.05$) change

reference watersheds (Fig. 6b). In the clear-cut watershed, we saw a 25% increase in diffuse-porous and a 36% decrease in ring-porous species over time (Fig. 6b). This substantial increase can be attributed to the dominance of tulip poplar, a diffuse-porous species, in the clear-cut watershed. By 2010s, basal area of evergreen shrubs increased by 8–11% across all watersheds since 1934. The clear-cut watershed had greater proportional basal area of black locust and non-porous evergreen trees than the reference watershed in the 2010s. Functional group distributions based on nutrient acquisition traits (Appendix 4 in ESM) and shade tolerance (Appendix 5 in ESM) had similar patterns to those of water use traits (Fig. 6a, b), largely because most ring-porous species are also those with ectomycorrhizal associations and intermediate shade tolerance. AM species were greater and ECM species were lower in the clear-cut watershed than the partial-cut or reference watersheds (Appendix 4 in ESM).

Discussion

Our long-term case study provided evidence that point to the benefits of partial-cutting over clear-cutting in the southern Appalachian Mountains. Contrary to expectations, the partial-cut watershed returned to the reference watershed levels in terms of aboveground biomass, species composition, and the distribution of functional groups; and tree diversity increased over time. In contrast, in the clear-cut watershed, species composition and the distribution of functional groups shifted, and tree diversity was reduced. These results are

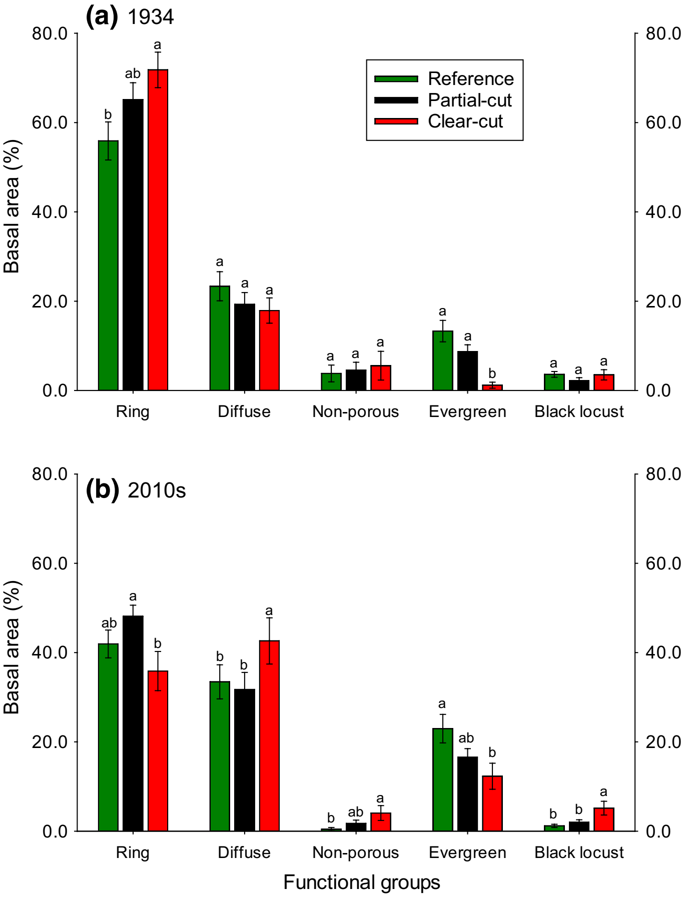

Fig. 6 Distribution of functional groups by percent basal area in **a** 1934 and **b** the 2010s for all watersheds (reference, partial-cut, and clear-cut). Functional groups represent differences in water use strategies: ring-porous xylem; diffuse-porous xylem; non-porous xylem, pitch pine (*Pinus rigida*) and eastern hemlock (*Tsuga canadensis*); evergreen shrubs, mountain laurel (*Kalmia latifolia*) and rosebay rhododendron (*Rhododendron maximum*); and black locust (*Robinia pseudoacadia*). Within panels (years), watershed values with different letters (a, b) are significantly different ($p \leq 0.05$)

discussed in the text below using ecological and functional perspectives with additional considerations of ecosystem services impacts.

Aboveground biomass recovery

The partial-cut method in our case study predated BMPs; the logging operation resulted in extensive soil exposure, soil erosion and sediment transport, and scoured stream channels (Hoover 1952); thus, we expected that these exploitive logging practices in the partial-cut watershed would impede or delay forest recovery. Contrary to this expectation, our results showed that aboveground biomass in the partial-cut watershed was comparable to the reference watershed by the last survey period (2010s). This suggests that light levels regulated by residual basal area could be more important than soil disturbance, particularly in forests where hardwood stump sprouting is common and accelerates growth and development (Elliott et al. 1997; Keyser and Zarnoch 2014; Keyser and Loftis 2015). Because hardwood species likely regenerated primarily by stump sprouting, even if the seed bank and seed germination were disrupted following extreme soil disturbance in the partial-cut watershed, vegetative reproduction likely obviated the need for sexual reproduction and lessened the potentially negative, long-term soil disturbance impacts on vegetative recovery. While aspect could have contributed to the rapid recovery of the south-facing, partial-cut watershed compared to the north-facing, reference watershed, we found greater differences between the partial-cut and clear-cut watersheds, both of which are south-facing.

Maintenance of canopy species composition and functional groups

In our case study, the partial-cut watershed was not different from the mature, reference watershed in species composition and the distribution of functional groups (Fig. 6). This result was likely mediated by light levels in the post-cut forests. Hardwood species differ in their shade tolerance (Burns and Honkala 1990). Competition for light varies among oaks, maples and tulip poplar, with red maple being the most shade tolerant, chestnut oak, northern red oak, black oak and hickories being intermediate, and tulip poplar and black locust being shade intolerant (Burns and Honkala 1990; Gottschalk 1994; Kobe et al. 1995). Tulip poplar is a fast-growing, shade intolerant species, and in high light, such as that created by clear-cutting, it can quickly overtop and out-compete these other species. This is particularly true when there is an abundance of the N-fixing black locust. Recent work has shown that greater aboveground biomass of black locust is associated with greater total soil N content and availability, and productivity of non-fixing trees such as tulip poplar (Boring et al. 2014; Minucci et al., in review). In contrast, in lower light and soil moisture conditions, tulip poplar does not compete well with oak species (Iverson et al. 2017). Once established in a dominant crown position, however, long-lived tulip poplar can remain a canopy dominant (Elliott and Swank 1994; Elliott et al. 1998; Brashears et al. 2004).

Long-term data at Coweeta Hydrologic Laboratory show that forest species composition has been gradually changing from dominance by oaks and hickories in the 1970s to greater abundance of red maple and tulip poplar in the 2010s (Vose and Elliott 2016). The increase in red maple and tulip poplar may be the result of a suite of factors including forest cutting practices (Yarnell 1998; Wang et al. 2015), fire exclusion (Abrams 1992, 1998; Knott et al. 2018), changing climate (Pederson et al. 2015; Caldwell et al. 2016), and increases in herbivores and frugivores (Dey 2014; Dolin and Kilgore 2018; Knott et al. 2018). Here we show that this pattern has been accelerated in a watershed that was clear-cut and harvested, but not on a watershed that was partial-cut and harvested. This lends support for the important role that cutting practices may be playing in the long-term pattern. Importantly, unlike black locust, tulip poplar is not just an early-successional species; it can dominate forests at early and late successional stages of development (Boring et al. 2014). Thus, clear-cutting forests could permanently shift species composition from oak-dominated forests to tulip poplar-dominated forests.

Maintaining species composition as an oak-dominated forest has important impacts on ecosystem services, such as timber value, water quantity, and nutrient cycling. Over time, the proportional abundance of low-commercial value species has increased, proportional abundance of high-commercial value species has decreased in all three watersheds, but more so in the clear-cut watershed than the partial-cut or reference watersheds

(Appendices 6 in ESM). In the partial-cut watershed, high-value commercial species (Timber Mart-South 2018), such as chestnut oak, white oak and red oak, increased in basal area by 9.41 m^2 ha^{-1} between 1934 and 2010s (Appendices 1–3 in ESM); while their increase in the clear-cut watershed was 6.04 m^2 ha^{-1}. Less valuable tulip poplar increased by 10.17 m^2 ha^{-1} in the clear-cut watershed between 1934 and 2010s, and increased by only 3.27 and 2.00 m^2 ha^{-1} in the partial-cut and reference watersheds, respectively (Appendices 1–3 in ESM). Abundance of non-commercial species was comparable among all three watersheds, but increased over time (Appendix 6 in ESM). For example, red maple, a shade tolerant species, is considered an undesirable, non-commercial species (Keyser and Loftis 2013). Its basal area increased by 3.31–3.46 m^2 ha^{-1} between 1934 and 2010s, regardless of the harvest treatment. While our simple grouping of species into commercial-value does not take into account tree grade and size (Brandeis 2017), it gives a general sense of how shifting species composition can influence economic value. Based on the comparable proportions of high- and lower-value commercial species, the partial-cut watershed could regain its potential economic value similar to the reference watershed even though it experienced the exploitive logging practices of the 1940s.

Similar species composition between the partial-cut and reference watersheds suggests that evapotranspiration and water yield may also be comparable; whereas, the different species composition in the clear-cut watershed with a much higher proportion of diffuse-porous species has increased water use and subsequently reduced water yield compared to the other watersheds (Elliott et al. 2017; Jackson et al. 2018). This is an important finding because changes in water yield due to forest treatment have significant implications for climate change and domestic water supply (Ford et al. 2011; Caldwell et al. 2016).

Nutrient acquisition traits, specifically their mycorrhizal associations, were also similar between the partial-cut and reference watersheds (Appendix 4 in ESM). In both watersheds, while species with AM fungal associations increased over time, ECM species, primarily oaks and hickories, still had the largest proportional abundance. In the clear-cut watershed, AM species increased over time and had higher proportional abundance than ECM species. Trees with AM associations are more dominant on sites with higher soil N and lower C:N, relative to trees with ECM associations (Phillips et al. 2013; Averill et al. 2018; Zhu et al. 2018; Mushinski et al. 2019) and high light may also have played an amplifying role. Nitrogen fixation by black locust, the early-successional shade-intolerant species, in the clear-cut watershed was 10 kg N ha^{-1} $year^{-1}$ (Boring et al. 2014), and this likely enhanced forest regeneration and provided a legacy of residual N to the later successional forest. Black locust basal area increased by 0.35 m^2 ha^{-1} in the partial-cut watershed; while its basal area increased by 1.76 m^2 ha^{-1} in the clear-cut and decreased by 0.21 m^2 ha^{-1} in the reference between 1934 and 2010s (Appendices 1–3 in ESM). In forests where disturbances remove less than half of the canopy basal area, maintain the understory light conditions, and deposit pulses of N through organic matter input, species-specific responses ensue. Fast-growing species that associate with ectomycorrhizal fungi (ECM), such as northern red oak, scarlet oak and pitch pine (Dharmadi et al. 2019), are promoted in these cases while those that associate with arbuscular mycorrhizae are not (Elliott et al. 2017).

Greater species diversity

While diversity (regardless of the metric used, $H'_{\text{basal area}}$, H'_{IV}, and H'_{biomass}) in the partial-cut watershed substantially increased after harvest (Fig. 5, inset), it remained lower than the reference watershed. The clear-cut watershed, however, showed reduced tree diversity (species richness, H'_{IV}). Clear-cuts followed by increases in shade-intolerant species often decrease tree species diversity (Jenkins and Parker 1998; Brashears et al. 2004), a pattern that has also been shown on other clear-cut watersheds in the Coweeta Basin (Elliott and Swank 1994; Elliott et al. 1998). In contrast, Schuler (2004) found that diversity (H′) decreased in both partial-cut (residual basal area 8–15 m^2 ha^{-1}) and reference stands compared to diameter-limit cuts (trees cut > 43 cm dbh) over a period of 50 years since harvest. Diameter-limit harvests, where only large trees are cut, usually remove commercially-valuable timber and leave the rest, and this remains the dominant harvesting practice in the central Appalachians (Schuler 2004). In a later study, Schuler et al. (2017) investigated various levels of partial-harvests, with cuts repeated over 10- and 20-year cutting cycles, compared to clear-cut and reference forests; they found that partial-cutting leaving low residual basal area accelerated the decline in H′ and species richness over time. In our study, the uncut reference forest had the highest H′ and species richness compared to the other two watersheds, even though H′ increased over time in the partial-cut watershed. Variability among results could be attributed to a number of factors including initial stand condition and species composition, localized differences in physiography and climate, harvest method, and residual basal area after harvest (i.e., harvest intensity). In a meta-analysis of nineteen studies, Clark and Covey (2012) showed an overall significant negative effect of logging on tree species richness, however, the reported studies varied with no change, positive and negative effects. They proposed that the variability in results were driven by differences in biome, characteristics among trees and their functional attributes, and selection harvesting practices.

Considerations and conclusions

In the southern Appalachian region, on National Forest lands, current harvest regimes are dominated by partial-harvesting, which can vary by frequency and intensity (Canham et al. 2013; Brown et al. 2018). The most prominent partial-cutting practice is the two-age regeneration harvest, and while it is an alternative to clear-cutting, it creates similar regeneration conditions with nearly full sunlight reaching the forest floor following harvest (Atwood et al. 2011; Grayson et al. 2012; Elliott and Vose 2016). The two-age (retaining 2.3–6.9 m^2 ha^{-1}) and shelterwood (retaining 12–14 m^2 ha^{-1}) harvests remove 60–80% of the stand basal area (Loftis 1990, Belote et al. 2012). In contrast, the partial-cut watershed in our case study only removed 29% of the basal area, leaving 21 m^2 ha^{-1} residual basal area (Table 2). The high light conditions created by removing > 60% of the basal area promotes the growth and dominance of shade-intolerant species such as tulip poplar and black locust in the southern Appalachians (Miller et al. 2006; Elliott and Vose 2016). Based on our case study, if managers partially-cut an oak-dominated forest *leaving* 60–70% residual basal area, instead of removing that amount or more through clear-cutting or high-intensity partial-cutting, they might expect to maintain similar species composition over time rather than shifting it towards one dominated by shade-intolerant (non-oak species). Similar results have been shown across 126 non-industrial private forests (NIPF) sites in the eastern USA; only minor post-harvesting differences in tree species composition resulted under low harvesting intensities, e.g., approximately one-fifth of the stand volume (McDonald et al. 2008).

Our case study revealed that partial-cutting a watershed, in the southern Appalachians, even with extreme soil disturbance and high sediment transport, does not alter long-term vegetation dynamics as significantly as clear-cutting a watershed with cable logging and following BMPs. Total aboveground biomass, species composition, and the distribution of functional groups (and thus, potentially water yield) were unaffected in the partial-cut watershed; while diversity increased over time on the partial-cut watershed, H'_{biomass} remained lower than the mature reference watershed. The partial-cut watershed had fewer long-term effects than the clear-cut watershed. These results may help to understand how historical harvesting practices affected present-day forest composition and diversity, and this understanding could aid forest managers, conservationists, and hydrologists in making informed decisions when designing management strategies for southern Appalachian forests. Future research could further establish the relationship between partial-cutting and ecosystem services such as water yield, nutrient cycling and productivity within the Coweeta Basin and the greater southern Appalachians. Other silvicultural systems such as spatial arrangements of residual trees (Fahey et al. 2018, Guldin 2019) and retention harvests (Lindenmayer et al. 2012; Curzon et al. 2017) could be explored to create complexity and provide continuity of ecosystem structure, function, and species composition (Dumroese et al. 2015).

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