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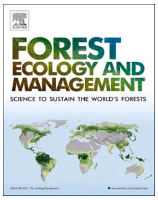

Long-term effects of alternative partial harvesting methods on the woody regeneration layer in high-elevation *Quercus rubra* forests of the southern Appalachian Mountains, USA

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ABSTRACT

High-elevation *Quercus rubra* forests in the Appalachian Mountains represent a transition zone between temperate mixed-*Quercus* forests that dominate lower elevations (<1350 m) and *Picea-Abies* forests at high (>1530 m) elevations. Little information exists specific to the response to disturbance, including timber harvesting, in these forests. In this study, we examined the long-term (22 years) effects of alternative regeneration methods – group selection harvests (GSH) and shelterwood with high (SWH; 9.0 m^2/ha) and low (SWL; 5.0 m^2/ha) residual basal area, and undisturbed control (CON) – on the development of the regeneration layer in high-elevation *Q. rubra* forests in the Appalachian Mountains. Treatments affected the density of the regeneration layer (stems ha^{-1}; SPH), but results varied by species group. Density of *Q. rubra* saplings (stems $\geq$ 3.8 cm dbh and <10.9 cm dbh) was significantly greater in GSH (250 SPH), SWH (85 SPH), and SWL (121 SPH) than CON (0 SPH). For shade-tolerant species, density averaged 1095 SPH in SWH and SWL and was significantly greater than in CON. Shade-tolerant *Acer rubrum* was the most abundant species in the sapling layer 22 years post-harvest. Survival of individuals tagged and followed over time was unaffected by treatment, however, height of *Quercus* seedlings was greatest in treatments with lower residual basal area (GSH and SWL). At Y22, the relatively low density of successfully regenerated *Quercus* stems in the regenerated stands suggests that additional treatments, including crown-touch release and/or prescribed burning, may be necessary to secure the continued recruitment of *Quercus* in these high-elevation *Q. rubra* forests.

1. Introduction

In the northern hemisphere, the ecological importance of the *Quercus* L. genus is unparalleled. Containing over 400 species on five continents, *Quercus* dominates myriad ecological habitats, including upland, riparian, bottomland, and coastal environments in temperate, subtropical, and tropical forest systems (Nixon, 2006; Cavender-Bares, 2019). In the eastern United States, *Quercus* forests comprise approximately 75.5 million ha of forestland (Dey, 2014). One of the more unique *Quercus* ecosystems in the eastern United States, high-elevation *Quercus rubra* L. forests in the southern and central Appalachian Mountains, represent a transition zone between temperate mixed-*Quercus* forests that dominate lower elevations (<1350 m) and remnant *Picea* – *Abies* (*Picea rubens* Sarg-*Abies fraseri* (Pursh) Poir) forests located at high (>1530 m) elevations (Cogbill and White, 1991). Along with northern hardwood and *Picea* – *Abies* forests, high-elevation *Q. rubra* forests, which occupy approximately 70,110 ha in the southeastern US (from Georgia to Virginia) are one of three principle high-elevation cover types in the southern Appalachians. The juxtaposition of high-elevation *Q. rubra* forests with other high-elevation forest types means these forests often provide and maintain critical wildlife habitat for a variety of bird and mammal species that are reliant on other higher elevation habitats, such as the *Glaucomys sabrinus* Sjaw. Furthermore, similar to lower-elevation mixed-*Quercus* forests, hard mast production in high-elevation *Q. rubra* forests is a critical wildlife food resource for myriad of wildlife species, including *Meleagris gallopavo* Linnaeus, *Ursus americanus* Pallas, and *Odocoileus virginianus* Zimmermann (McShea et al., 2007).

The maintenance of *Quercus*-dominated forests across spatial and

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temporal scales is reliant on frequent disturbance, as *Quercus* species are mid-tolerant of shade and preferentially store carbohydrates below- rather than above-ground (Brose and Rebbeck, 2016). Disturbances commonplace during the time period when most present-day *Quercus* forests regenerated (late 1880s – early 1900s), including high-elevation *Q. rubra* forests, included frequent anthropogenic burning, grazing, and repeated, often exploitive timber harvesting (Dey 2014; McEwan et al., 2011). Co-occurring with these anthropogenic disturbances was the loss of a foundational species, *Castanea dentata* (Marshall) Borkh.*),* from the landscape as a result of the introduced fungal pathogen, *Cryphonectria parasitica* (Murrill) Barr, which further promoted successful regeneration and recruitment of *Quercus* in both low- (Elliott and Swank, 2008; Woods and Shanks, 1959) and high-elevation (van de Gevel et al., 2012) deciduous broadleaved forest types. This multi-decadal period of frequent, moderate to high-intensity disturbance was followed by land abandonment and a concomitant period of reduced, often non-existent anthropogenic disturbance that exists through present day (Buchanan and Hart, 2012; Hart and Grissino-Mayer, 2008). Natural disturbances that influence forest structure and function are common and consist of those typical of southern Appalachian forests, including wind-throw, drought, and, given the elevation, frequent and often severe ice storms (Clinton and Boring, 1993; Clinton and Baker, 2000; Lafon, 2006; Greenberg et al., 2011a; van de Gevel et al., 2012).

The pattern of land-uses that facilitated successful *Quercus* regeneration and recruitment has homogenized forest structure across *Quercus* and non-*Quercus* forests that comprise the eastern United States (Hanberry et al., 2012; Schulte et al., 2007). In the Appalachian Mountains of western North Carolina, for example, 94% of high-elevation *Q. rubra* forests are in a structurally closed-canopied condition (Ponder, 2014). In comparison, models that focus on the historical range of variability of structure suggest the majority of high-elevation *Q. rubra* forests existed in conditions that were more open-canopied (57%) than close-canopied (43%), with open conditions represented by early seral (5%), open mid- (7%), open late- (6%), and open old-growth (39%) seral conditions (Kelly, 2013). Close-canopied conditions at landscape-levels can negatively affect habitat for a variety of species whose populations in the region are in decline or are of particular management concern, including *Bonasa umbellus* Linnaeus (Jones et al., 2008) and *Vermivora chrysoptera* Linnaeus (Klaus and Buehler, 2001).

Deficits in open and young forest conditions are easily ameliorated through active forest management that includes a variety of silvicultural tools, such as timber harvesting via thinning and/or regeneration harvests and repeated prescribed burning. Little information exists specific to the regeneration response to disturbance, including silvicultural regeneration harvests, in high-elevation *Q. rubra* forests. Of particular importance is how well regeneration methods promote and maintain the *Quercus* component of these forested system, as the maintenance of *Quercus* across the landscape is vital to the sustained production of a wide array of ecosystem goods and services. For example, decreased acorn production associated with aging *Quercus* forests (Goodrum et al., 1971) may negatively affect population dynamics of both game and non-game wildlife species (McShea et al., 2007). Similarly, as *Quercus* fails to regenerate and mesophytic species increase in abundance and importance, annual water yield decreases (Caldwell et al., 2016). In fact, successful regeneration, recruitment, and maintenance of *Quercus* is tied to overall biodiversity and ecosystem functioning at the stand- and landscape-levels in a variety of mixed-*Quercus* forest types that dominate much of the eastern United States (Alexander and Arthur, 2014; Kreye et al., 2018; Rodewald and Abrams, 2002; Sierzega and Eichholz, 2019).

When pressure from native browsers (e.g., *O. virginianus*) is low (Thomas-Van Gundy et al. 2014), successful regeneration of *Quercus* following regeneration harvests conducted at lower elevations in the Appalachian Mountains is dependent on the size of advance reproduction (i.e., seedlings present prior to harvest) prior to disturbance (Loftis, 1990a), as small *Quercus* advance reproduction is outcompeted by co-occurring mesic species, including *Acer rubrum* L., *Betula lenta* L., and *Liriodendron tulipifera* L. (Beck and Hooper, 1986; Miller et al., 2006; Swaim et al., 2018). *L. tulipifera*, which is one of the primary competitors with *Quercus* on lower-elevation sites in the southern Appalachians (Brashears et al., 2004; Loftis, 1983), is less abundant (and often absent) and less competitive at higher elevations (Beck and Della-Bianca, 1981). The lack of competition from *L. tulipifera* following disturbance in these higher-elevation forests may alleviate many of the issues that make successful regeneration and recruitment of *Quercus* difficult in lower-elevation forests throughout the Appalachian region.

In this study, we examined the effects of alternative regeneration methods, conducted primarily to create structural diversity and improve wildlife habitat and regenerate and recruit a new *Quercus* cohort, on the development of the woody regeneration layer in high-elevation *Q. rubra* forests in the southern Appalachian Mountains. Specifically, in an effort to understand the response of these under-studied, but ecologically important forest systems to managed disturbance, we quantified the effects of three partial harvest regeneration methods – group selection, shelterwood with reserves with low level of retention, and shelterwood with reserves with high level of retention on (1) the regeneration and recruitment of *Q. rubra* and other, co-occurring species up through 22 years post-harvest, and (2) the survival and growth of individual *Q. rubra* seedlings 22 years post-harvest. Results from this study will provide some of the only quantitative information regarding the response of these unique and relatively rare high-elevation forest systems to silvicultural disturbance and will help guide restoration and sustainable management of these systems for a variety of ecosystem services into the future.

2. Methods

2.1. Study area

This study was conducted on the Wayah Ranger District on the Nantahala National Forest in western North Carolina, USA (35°81′N, 83°35′W) (Fig. 1). The study area, which was located within the Wine Spring Creek watershed, lies within the Southern Blue Ridge Mountains Subsection of the broader Central Appalachian Broadleaf Forest-Coniferous Forest Province (Cleland et al., 2007). Soils within the study are mesic Typic Dystrudepts (Edneyville and Chestnut soil series), mesic Typic Humudepts (Callasaja and Tuckasegee soil series), rigid Tyipc Humudepts (Burton soil series), and frigid Lithic Humudepts (Craggey soil series) (Soil Survey Staff, Soil Web Survey). Soils in these high-elevation *Quercus rubra* L. forest types are thin, low in organic matter, and nutrient-poor (Simon et al., 2011). Annual precipitation averages 176 cm, with January and July temperature averaging 3.3 and 22.2 °C, respectively (McNab and Browning, 1992). Vegetation is described as dry, high-elevation *Q. rubra* based on the classification system developed by McNab and Browning (1992).

2.2. Experimental design and data collection

In 1994 (prior to treatment), 11 stands (i.e., experimental units) that ranged in size between 3.9 and 7.6 ha were located throughout the Wine Spring Creek watershed. Average slope of the stands varied between 35 and 46%, with aspect predominantly west to south-west facing. Average elevation of each stand ranged between 1333 and 1508 m and stand age at the time the study was initiated averaged 86 years.

Treatments that included group selection harvest (GSH), shelterwood with a high level of residual basal area (SWH), shelterwood with a low level of residual basal area (SWL), and control (CON) were randomly assigned to each stand. Each treatment was replicated in three stands, with the exception of GSH, which was replicated in two stands. It should be noted that the GSH treatment was initially assigned to three replicate stands while the CON treatment was initially assigned to two replicate stands. However, in the third GSH replicate stand, no sampling plots were located within actual gaps; instead all plots were located at

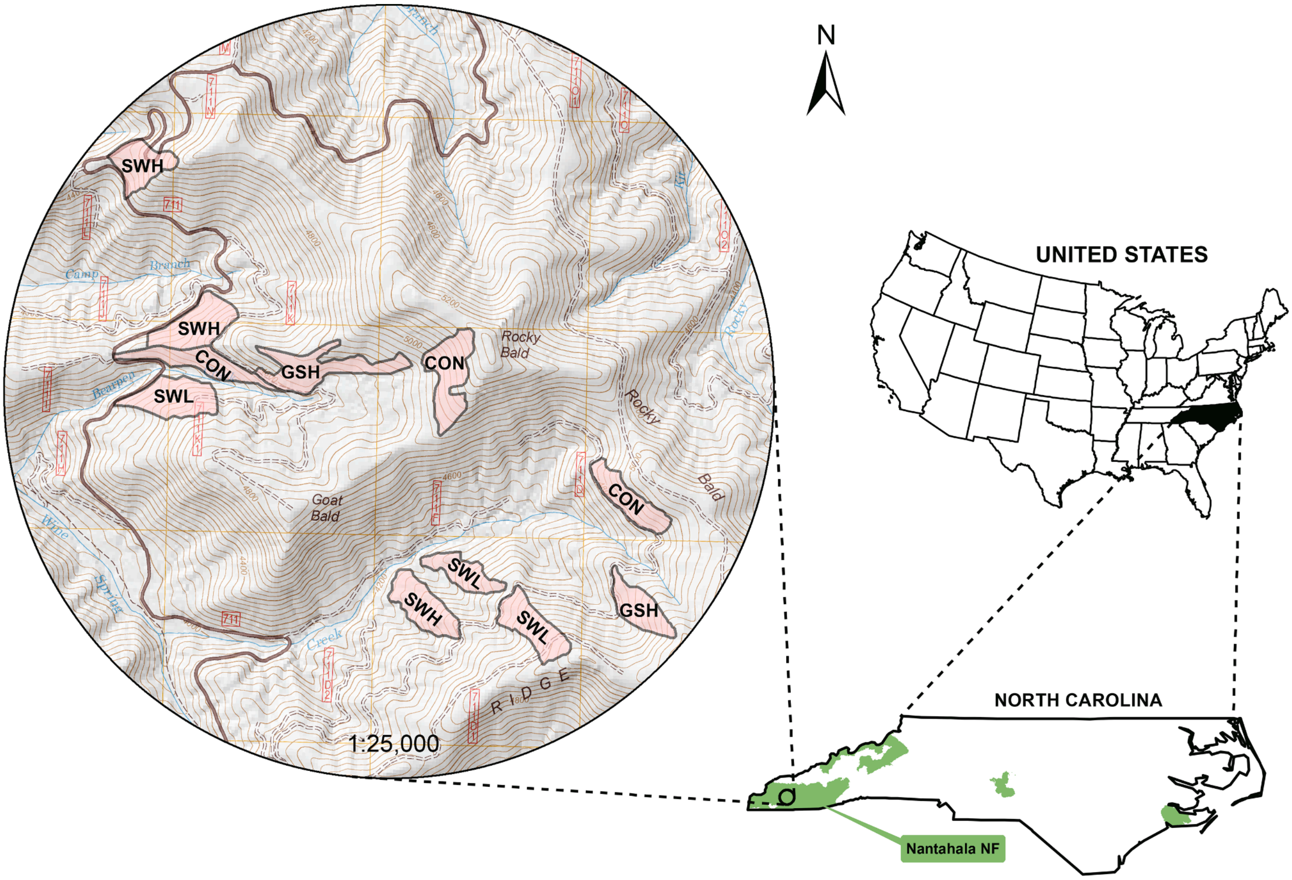

Fig. 1. Location of the 11 experimental stands within the Wine Spring study area. CON = control, GSH = group selection harvest, SWH = shelterwood with high residual basal area, SWL = shelterwood with low residual basal area.

least two tree lengths (60 m) away from any silviculturally-created gap and displayed no evidence of harvest-related disturbance (no cut trees, no skid trail or road construction). Therefore, we considered the third replicate of the GSH treatment to be a CON, decreasing the sample size of GSH from three to two replicates and increasing the sample size of CON from two to three replicates.

The SWH treatment consisted of a harvest that left, on average, 9.0 m^2/ha of residual basal area while the SWL consisted of a harvest that left, on average, 5.0 m^2/ha of residual basal area (Elliott and Knoepp, 2005). In both the SWL and SWH treatments, *Q. rubra* was the preferred leave tree. In the GSH treatment, 25% of the stand area was harvested in group openings between 0.10 and 0.20 ha in size (Elliott and Knoepp, 2005), with no residual basal area retained in the openings.

Prior to treatment, we randomly established up to 13 subplots in each stand, with subplot centers permanently marked for re-measurement. The number of subplots established within each replicate was proportional to stand size, with between six and 13 subplots located in each replicate stand of the CON, SWL, and SWH treatments. Although prior to treatment, we established six subplots in one GSH replicate and nine subplots in the other GSH replicate, only two subplots in each of the GSH replicates were measured post-harvest, as these were the only subplots of the original six that fell within harvested gaps. At each subplot, we conducted a pre-treatment inventory of arborescent vegetation ≥10.9 cm dbh using a 2.3 m^2 ha^{-1} factor prism to describe pretreatment structure and composition. For each sample tree, we recorded species and diameter at breast height (dbh; cm).

At each subplot, we used a 0.004 ha regeneration subplot to quantify and describe the woody regeneration layer prior to treatment (Y0) and again 4 (Y4; 2001) and 22 years post-treatment (Y22; 2019). In each regeneration subplot, we enumerated arborescent stems by species into one of four size classes: small seedlings (stems < 0.6 m); medium seedlings (stems ≥ 0.6 m and <1.2 m), large seedlings (stems ≥ 1.2 m and <3.8 cm dbh), and saplings (stems ≥ 3.8 cm and <10.9 cm dbh).

At each subplot, up to five seedlings were permanently tagged and stem-mapped to facilitate re-location. Status (live/dead) and height (m) of each seedling were recorded in Y0 and Y22.

2.3. Data analysis

Analysis of variance (ANOVA) ($\alpha = 0.05$) under a completely random design with repeated measures was used to analyze the effects of treatment (CON, GSH, SWH, SWL), year (Y0, Y4, Y22 years post-treatment), and the interaction between treatment and year on stems ha^{-1} (SPH) of five distinct species groups (Table 1) in the small seedling, medium seedling, large seedling, and sapling size classes. The five species groups were: (1) QURU (*Q. rubra*), QUCA (other *Quercus* and *Carya* species), INTO (shade-intolerant species), MIDT (species mid-tolerant of shade), and TOLE (shade-tolerant species). A similar analysis was conducted on the relative abundance of each species group in the sapling layer, species richness (number of species at each subplot) of the sapling layer, and height of tagged *Quercus* seedlings and all other species combined (OTHER). Species were combined into these two broad categories because sample sizes were insufficient to analyze the specific species groups utilized in this study (Table 1). Due to unequal sampling intervals, a spatial power covariance structure was used to account for the correlation among years. The effects of treatment on survival of tagged *Q. rubra* and OTHER seedlings between Y0 and Y22 was analyzed using a one-way ANOVA. When necessary, data were transformed in instances where residuals did not meet assumptions of normality and homogeneous variance. Treatment effects, when part of a significant

Table 1
Species within the *Quercus rubra* (QURU), *Quercus-Cayra* (QUCA), shade-intolerant (INTO), mid-tolerant (MIDT), and tolerant (TOLE) species groups.

QURU	QUCA	INTO	MIDT	TOLE
Quercus rubra L.	*Carya* Nutt.	*Betula lenta* L.	*B. alleghaniensis* Britton	*Acer pensylvanicum* L.
	Q. alba L	*Liriodendron tulipifera* L.	*Castanea dentata* (Marshall) Borkh.	*A. rubrum* L.
	Q. coccinea Münchh.	*Prunus serotina* Ehrh.	*Fraxinus americana* L.	*A. saccharum* Marshall
	Q. montana Willd.	*P. pensylvanica* L. f.	*Magnolia fraseri* Walter	*Aesculus flava* Aiton
	Q. velutina Lam.	*Robinia pseudoacacia* L.	*M. acuminata* (L.) L.	*Amelanchier* spp.
		Sassafras albidum (Nutt.) Nees	*Pinus strobus* L.	*Cornus* spp.
				Fagus grandifolia Ehrh.
				Halesia tetraptera Ellis
				Oxydendrum arboretum (L.) DC.
				Tilia heterophylla (Vent.) Loudon
				Tsuga canadensis (L.) Carrière

interaction (treatment × year), were examined using the SLICE option. Post-hoc comparisons were adjusted using a False Discovery Rate (Benajmini and Hockberg, 1995). Analyses were conducted using the MIXED procedure in SAS v. 9.4 (SAS Institute INC., Cary, NC, USA).

3. Results

3.1. Pre-treatment structure and composition

Prior to harvest, basal area (BA) of the overstory (stems ≥ 10.9 cm dbh) averaged (standard deviation) 24.3 (2.8) m^2 ha^{-1}. No significant differences in basal area prior to treatment were detected ($p > 0.05$). Overall, *Q. rubra* dominated the overstory (29.4% of BA), followed by species in the *Acer* genus (*A. rubrum* and *A. saccharum*) (24.5% of BA), and *Q. montana* (14.8% of BA).

Across stands, SPH of the woody regeneration layer (stems < 10.9 cm dbh) decreased as size class increased prior to treatment. Regardless of size class, species in the TOLE group dominated the regeneration layer, comprising between 48 and 70% of overall SPH. In comparison, QURU comprised 19, 12, 14, and 7% of the small, medium, and large seedling, and sapling size classes, respectively. The QUCA group comprised 5, 3, 13, and 6% of the small, medium, and large seedling, and sapling size classes, respectively.

3.2. Posttreatment – small seedling layer

We observed a significant main effect of year on SPH of small QURU ($p = 0.0375$) and TOLE ($p = 0.0056$) seedlings. For QURU, SPH in Y4 (2635 ± 690) was significantly greater than Y0 (752 ± 138), but similar to Y22 (1360 ± 410). For the TOLE group, SPH in Y0 (1849 ± 365) was significantly lower than in Y4 (4124 ± 832), but similar to Y22 (1959 ± 281). For the MIDT, QUCA, and INTO species groups, neither treatment nor year had any significant effect on small seedling density, with density, across treatments and years, averaging 512 (71), 255 (49), and 474 (106) SPH, respectively.

Prior to treatment, *Q. alba* (56%), *Sassafras albidum* (51%), *Magnolia acuminata* (39%), and *Acer pensylvanicum* (36%) comprised the greatest proportion of the QUCA, INTO, MIDT, and TOLE groups in the small seedling layer, respectively. In Y22, *Q. alba* (49%), *S. albidum* (52%), *M. acuminata* (41%), and *Amelanchier arborea* (31%) comprised the greatest proportion of the QUCA, INTO, MIDT, and TOLE groups in the small seedling layer, respectively.

3.3. Posttreatment – medium seedling layer

The interaction between treatment and year significantly affected SPH of medium seedlings in the QURU ($p = 0.0023$), INTO ($p = 0.0133$), and TOLE ($p = 0.0374$) species groups, although significant treatment differences occurred only in Y4 (Table 2). The main effect of year significantly influenced SPH of MIDT species ($p = 0.0115$), while neither treatment, year, nor the interaction between treatment and year significantly influenced SPH of medium seedlings in the QUCA group.

Prior to treatment, *Q. alba* (58%), *S. albidum* (57%), *C. dentata* (64%), and *Fagus grandifolia* (36%) comprised the greatest proportion of the QUCA, INTO, MIDT, and TOLE groups across treatments in the medium seedling layer, respectively. In Y22, *Q. alba* (55%), *S. albidum* (50%), *C. dentata* (64%), and *F. grandifolia* (25%) comprised the greatest proportion of the QUCA, INTO, MIDT, and TOLE groups in the medium seedling layer, respectively.

3.4. Posttreatment – large seedling layer

The interaction between treatment and year significantly affected SPH of large seedlings in the QUCA ($p = 0.0106$) and MIDT ($p < 0.0001$) species groups, although significant treatment differences occurred only in Y4 (Table 3). For the QURU ($p = 0.0003$) and INTO ($p = 0.0005$) groups, only the main effect of year significantly affected SPH of large seedlings. For the TOLE group, the main effects of treatment ($p = 0.0020$) and year ($p < 0.0001$) significantly influenced density, with CON having lower density of TOLE stems than both SWH and SWL.

Prior to treatment, *Q. alba* (40%)/*Q. montana* (40%), *B. lenta* (27%)/*S. albidum* (27%)/*R. psuedoacacia* (27%), *C. dentata* (74%), and *F. grandifolia* (38%) comprised the greatest proportion of the QUCA, INTO, MIDT, and TOLE groups in the large seedling layer, respectively.

Table 2
Stems ha^{-1} of medium seedlings (stems ≥ 0.6 and <1.2 m) by species group prior to treatment (Y0) and 4 (Y4) and 22 (Y22) years posttreatment. Uppercase letters indicate significant differences among treatments within a given species group and year; lowercase letters indicate significant differences among years within a given treatment and species group. Values represent the mean (standard error). Species groups defined in Table 1.

	CON	GSH	SWH	SWL	AVG
Y0					
INTO	52 (22)	0 (0)	37 (37)^{a}	0 (0)^{a}	24 (12)
MIDT	237 (73)	500 (500)	403 (88)	303 (90)	348 (81)^{ab}
QURU	87 (43)^{a}	125 (125)	78 (41)^{a}	165 (81)^{a}	113 (31)
QUCA	38 (38)	0 (0)	56 (56)	31 (16)	34 (17)
TOLE	101 (60)	1625 (1625)	267 (127)	306 (32)^{a}	479 (281)
Y4					
INTO	55 (19)^{A}	375 (375)^{AB}	427 (95)^{Bb}	150 (49)^{ACb}	241 (75)
MIDT	727 (197)	375 (250)	575 (130)	514 (60)	564 (76)^{a}
QURU	185 (30)^{Ab}	188 (188)^{AB}	574 (228)^{BCb}	901 (150)^{Cb}	487 (117)
QUCA	55 (41)	0 (0)	61 (11)	73 (39)	52 (16)
TOLE	396 (187)^{A}	1125 (1125)^{AB}	1060 (368)^{AB}	1899 (388)^{Bb}	1120 (267)
Y22					
INTO	73 (73)	125 (0)	71 (20)^{a}	16 (8)^{a}	66 (21)
MIDT	251 (79)	63 (63)	243 (26)	194 (32)	199 (31)^{b}
QURU	161 (49)^{ab}	63 (63)	139 (15)^{ab}	172 (45)^{a}	140 (22)
QUCA	40 (22)	0 (0)	28 (28)	6.4 (6.4)	20 (10)
TOLE	321 (121)	0 (0)	509 (248)	338 (102)^{a}	319 (87)

Table 3
Stems ha^{-1} of large seedlings (stems $\geq$ 1.2 m and <3.8 cm dbh) by species group prior to treatment (Y0) and 4 (Y4) and 22 (Y22) years posttreatment. Uppercase letters indicate significant differences among treatments within a given species group and year; lowercase letters indicate significant differences among years within a given treatment and species group. Values represent the mean (standard error). Species groups defined in Table 1.

	CON	GSH	SWH	SWL	AVG
Y0					
INTO	41 (12)	0 (0)	39 (9)	6 (6)	24 (7)^{a}
MIDT	444 (66)^{a}	125 (125)	588 (48)^{a}	543 (134)^{a}	452 (66)
QURU	83 (30)	250 (125)	141 (85)	149 (80)	147 (37)^{a}
QUCA	13 (13)	63 (63)	53 (43)^{a}	25 (16)	36 (15)
TOLE	165 (85)	938 (938)	460 (122)	1026 (418)	620 (198)^{a}
Y4					
INTO	142 (117)	813 (562)	847 (360)	640 (352)	592 (169)^{b}
MIDT	1185 (62)^{Ab}	813 (813)^{AB}	2549 (159)^{Bb}	1318 (243)^{Ab}	1526 (243)
QURU	205 (108)	938 (688)	587 (166)	879 (381)	626 (165)^{b}
QUCA	19 (19)^{A}	63 (63)^{AC}	492 (129)^{Bb}	298 (178)^{BC}	232 (80)
TOLE	591 (143)	3000 (2750)	4565 (1899)	4772 (773)	3253 (820)^{b}
Y22					
INTO	6 (6)	125 (125)	245 (16)	103 (76)	119 (37)^{a}
MIDT	408 (65)^{a}	125 (125)	374 (86)^{c}	284 (89)^{c}	313 (49)
QURU	20 (12)	125 (0)	117 (55)	182 (43)	110 (25)^{a}
QUCA	54 (37)	0 (0)	69 (40)^{a}	6 (6)	35 (16)
TOLE	236 (79)	688 (563)	840 (147)	1486 (841)	824 (260)^{a}
AVG					
INTO	63 (40)	312 (218)	377 (160)	250 (143)	245 (71)
MIDT	679 (131)	354 (259)	1170 (350)	715 (177)	764 (127)
QURU	103 (42)	438 (241)	282 (95)	403 (164)	294 (69)
QUCA	29 (14)	42 (26)	204 (83)	110 (70)	101 (31)
TOLE	330 (85)^{A}	1542 (894)^{AB}	1955 (856)^{B}	2428 (686)^{B}	1566 (355)

In Y22, *Q. montana* (50%), *B. lenta* (77%), *C. dentata* (58%), and *F. grandifolia* (52%) comprised the greatest proportion of the QUCA, INTO, MIDT, and TOLE groups in the large seedling layer, respectively.

3.5. Posttreatment – Sapling layer

The main effect of year significantly affected SPH of saplings in the QUCA ($p = 0.0001$), INTO ($p = 0.0214$), and MIDT ($p = 0.0415$) species groups (Fig. 2). A significant interaction between treatment and year was observed for QURU ($p = 0.0204$) and TOLE ($p = 0.0105$). In Y22, QURU saplings in CON averaged 0 SPH compared to an average of 250, 85, and 121 SPH in the GSH, SWH, and SWL treatments, respectively (Fig. 2). In Y22, density of the TOLE group in the SWH and SWL averaged 1095 SPH and was significantly greater than in CON.

Relative abundance of the INTO and TOLE groups in the sapling layer was unaffected by treatment or year, while we observed a significant interaction between treatment and year for the MIDT group ($p = 0.0285$) (Fig. 3). By Y22, relative abundance of MIDT was significantly lower in the SWH and SWL than in CON. The main effect of year significantly affected the relative abundance of QUCA ($p = 0.0002$) and QURU ($p = 0.0078$).

Species richness of the sapling layer was affected by the interaction between treatment and year ($p = 0.0097$). Prior to treatment, richness did differ between CON and SWH, and richness in GSH and SWL did not differ from each other (Fig. 4). Richness within the GSH, SWH, and SWL treatments decreased in Y4. By Y22, however, richness returned to pretreatment levels, with richness in all three active management treatments significantly greater than in CON.

Prior to treatment, *Q. montana* (63%), *R. pseudoacacia* (41%), *C. dentata* (50%), and *A. rubrum* (42%) comprised the greatest proportion of the QUCA, INTO, MIDT, and TOLE species groups, respectively. In Y22, across all treatments, *Q. montana* (58%), *R. pseudoacacia* (33%), *C. dentata* (25%), and *A. rubrum* (39%) were the most prominent species within the QUCA, INTO, MIDT, and TOLE groups, respectively.

3.6. Individual tagged seedling dynamics

A total of 139 *Quercus* seedlings were tagged in Y0, of which 135 were successfully relocated in Y22. Survival of *Quercus* seedlings between Y0 and Y22 was not significantly affected by treatment, with survival averaging 31.0% (10.6), 53.3% (13.3), 18.2% (12.5), and 20.3% (15.1) in the CON, GSH, SWH, and SWL treatments, respectively. A total of 234 OTHER seedlings were tagged in Y0, of which 234 were relocated in Y22. For OTHER, survival did not significantly differ among treatments, with survival averaging 75.8% (15.6), 25.0% (25.0), 40.6% (0.3%), and 48.9% (4.2) in the CON, GSH, SWH, and SWL treatments, respectively.

Height of the tagged *Quercus* ($p = 0.0021$) and OTHER ($p = 0.0005$) seedlings was significantly affected by the interaction between treatment and year. No differences in *Quercus* seedling height among treatments were detected until Y22, at which time seedling height in GSH was significantly greater than in all other treatments (Fig. 5). No difference in tagged *Quercus* seedling height between the SWH and SWL treatments was observed, but height in SWL was greater than CON. For OTHER tagged seedlings, significant differences in seedling height among treatments were limited to Y22 at which time, the average height of tagged OTHER seedlings was significantly greater in SWL than in CON and GSH.

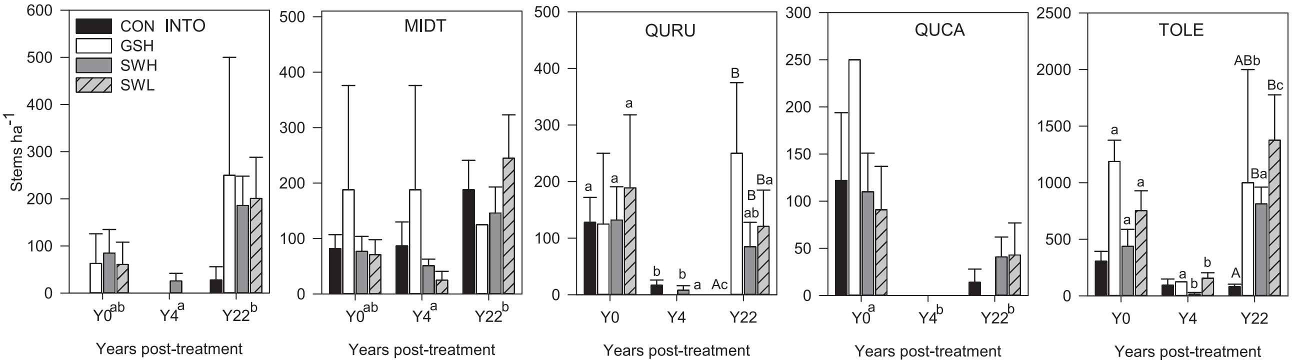

Fig. 2. Density (stems ha^{-1}) of sapling sized stems (stems $\geq$ 3.8 cm and <10.9 cm dbh) in the intolerant (INTO), mid-tolerant (MIDT), *Quercus rubra* (QURU), *Quercus-Carya* (QUCA), and tolerant (TOLE) species groups prior to treatment (Y0) and four (Y4) and 22 (Y22) years posttreatment. Uppercase letters above bars indicate significant differences among treatments within a given year. Lowercase letters above bars indicate significant differences among years within a given treatment. Lowercase letters along x-axis indicate significant differences among years averaged across treatments (i.e., significant main effect of year). Values and error bars represent the mean and standard error, respectively.

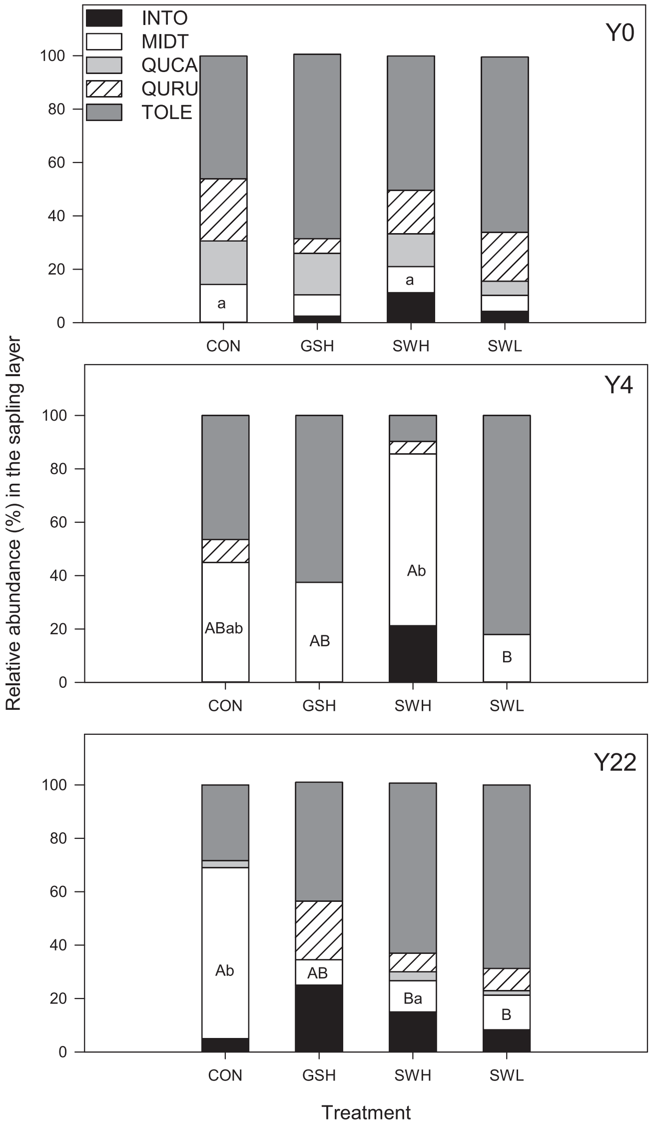

Fig. 3. Relative abundance of intolerant (INTO), mid-tolerant (MIDT), *Quercus rubra* (QURU), *Quercus-Carya* (QUCA), and tolerant (TOLE) species groups in the sapling sized regeneration layer (stems $\geq$ 3.8 cm and $<$10.9 cm dbh) prior to treatment (Y0) and four (Y4) and 22 (Y22) years posttreatment in the CON, GSH, SWH, and SWL treatments. Uppercase letters indicate significant differences among treatments within a given year. Lowercase letters indicate significant differences among years within a given treatment.

4. Discussion

Forested ecosystems in the southern and central Appalachian Mountains contain some of the highest levels of biological diversity and endemism of both plant and animal species in the United States (Pickering et al., 2003; Stein et al., 2000). Once thought to be a landscape dominated by mature, closed-canopied forests sustained through gap-phase dynamics (Clebsch and Busing, 1989; Lorimer, 1980), there is now recognition of the role that exogenous disturbances, both anthropogenic (e.g., fire, timber harvesting/biomass extraction, grazing) and natural (e.g., wildfire, wind, ice, drought), have in the maintenance and conservation of biodiversity across trophic levels in temperate broadleaved deciduous forests in the eastern United States, including those in the Appalachian Mountains (Aldinger et al., 2017; Greenberg et al., 2011b; Hanson and Lorimer, 2007; McCord et al., 2014; Roberts and Milam, 2017; Swanson et al., 2011; Vander Yacht et al., 2016). As such, there is an increased focus on implementing forest management activities for purposes other than extraction of provisioning ecosystem services, such as timber and fiber.

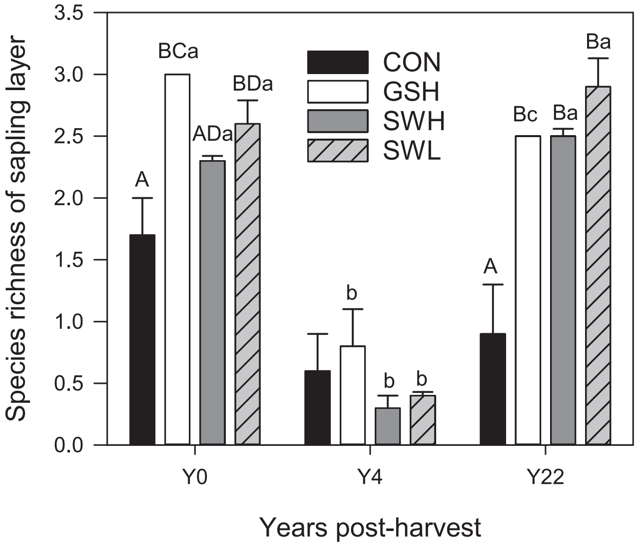

Fig. 4. Species richness of sapling sized stems (stems $\geq$ 3.8 cm and $<$10.9 cm dbh) prior to treatment (Y0) and four (Y4) and 22 (Y22) years posttreatment. Uppercase letters indicate significant differences among treatments within a given year. Lowercase letters indicate significant differences among years within a given treatment. Values and error bars represent the mean and standard error, respectively.

Active management in high-elevation *Q. rubra* forests has been limited relative to lower-elevation counterparts primarily because stems in high-elevation forests tend to be stunted, wind-swept, and of low quality due to frequent wind and ice storms associated with these high-elevation environments (Natural Heritage Program, 2020). Consequently, we know little about how these high-elevation *Q. rubra* stands respond to disturbance, including silvicultural regeneration harvests implemented to regenerate a new *Quercus* age cohort and promote and restore structural and ecological complexity within the community.

Similar to lower-elevation, montane *Quercus* forests in the Appalachian region (Hutchinson et al., 2016; Iverson et al., 2008; Keyser et al. 2017), density of the woody regeneration layer in these mature, high-elevation *Q. rubra* forests prior to harvest decreased from the small seedling to sapling size classes, with the regeneration layer, regardless of size class, dominated by shade-tolerant species; particularly abundant were *A. pensylvanicum* (small seedling), *F. grandifolia* (medium and large seedling), and *A. rubrum* (sapling). The development of a dense and well-developed understory and midstory dominated by shade-tolerant species is commonplace in *Quercus* forests and is a contributing factor to widespread *Quercus* regeneration and recruitment problems in the eastern United States (Dey, 2014). Dense, shade-tolerant understories intercept light and limit development of *Quercus* seedlings (Grayson et al., 2012; Schweitzer and Dey, 2011) into large seedlings and saplings (stems $>$ 1.2 m) capable of competing with existing seedling and sapling pool as well as shade-intolerant species, such as *B. lenta* and *L. tulipifera* (Miller et al., 2006), that become established shortly after disturbance.

Long-term (22-year) results from this study revealed that, like their low-elevation counterparts, high-elevation, *Quercus* forests are readily regenerated through a variety of silviculture regeneration methods, including group selection and shelterwood methods, but that conserving pre-harvest species composition remains problematic due, in part, to the lack of large, competitive *Quercus* seedlings prior to harvest (Loftis, 1983; Loftis, 1990a; Weigel and Parker, 1997). Unlike their lower-elevation counterparts in the southern Appalachians, however, these high-elevation *Q. rubra* forests were not dominated by shade-intolerant *L. tulipifera* or *B. lenta* following shelterwood and group selection harvests (Beck and Hooper, 1986; Jenkins and Parker, 1998; Miller et al.,

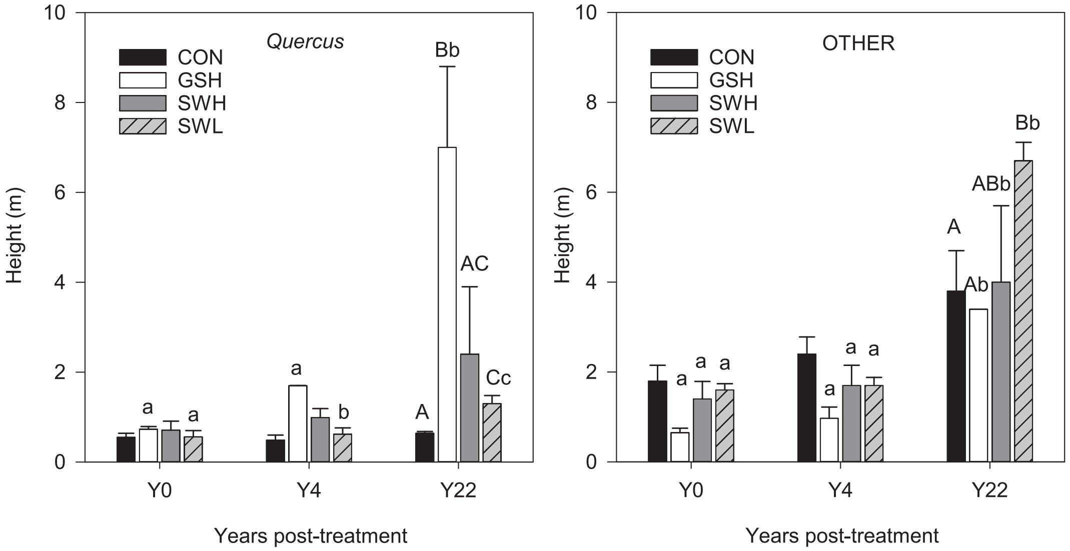

Fig. 5. Height (m) of individually tagged *Quercus* and OTHER seedlings prior to treatment (Y0) and four (Y4) and 22 (Y22) years posttreatment. Uppercase letters indicate significant differences among treatments within a given year. Lowercase letters indicate significant differences among years within a given treatment. Values and error bars represent the mean and standard error, respectively.

2006; Royo et al., 2019). Instead, after 22 years, these high-elevation *Q. rubra* forests subjected to partial harvesting were dominated by shade-tolerant species, primarily, *A. rubrum* and *F. grandifolia*, confirming that shade-tolerant species present in the regeneration layer prior to harvest limit successful *Quercus* regeneration and recruitment following managed regeneration events (Hackworth et al., 2019; Schweitzer, 2019; Steiner et al., 2018; Thomas-Van Gundy et al., 2014).

To secure future *Quercus* regeneration and recruitment, the shade-tolerant, often recalcitrant understory must be managed and controlled post-harvest via various cultural treatments that may include chemical, mechanical and/or fire. Although chemical treatments are highly effective in controlling competition, chemical and labor costs at larger, stand-level scales are costly (Kochenderfer et al., 2011; Schweitzer et al., 2020). Conversely, although prescribed fire is a cost-effective option, the ability of fire to control shade-tolerant competition in the understory is inconsistent and requires repeated application (Alexander et al., 2008; Green et al., 2010; Keyser et al., 2017). An often overlooked treatment, mechanical soil scarification, can reduce competition from both shade-tolerant and shade-intolerant species and favor *Quercus* and other mid-tolerant species (Zaczek, 2002; Lhotka and Zacek, 2003; Felton et al., 2006; Shabaga et al., 2019), but efficacy and operability are likely limited in mountainous terrain with steep slopes (>30%) and rocky soils (USDA, 2012).

Left undisturbed, small *Quercus* seedlings rarely develop into large seedlings or saplings (Crow, 1992). In these high-elevation *Q. rubra* forests, in CON, relative abundance of sapling-sized QURU seedlings dropped from ~24% in Y0 to 0% in Y22, while the relative abundance of QUCA saplings dropped from 16% to 2% between Y0 and Y22. Although the sapling layer of the partial harvesting treatments, which will likely form the dominant and co-dominant canopy layers over time, was dominated by shade-tolerant species, regardless of the regeneration method implemented, QURU and/or QUCA saplings were present in Y22 at a greater abundance than in CON, affirming that canopy disturbance is critical to the survival and recruitment of understory *Quercus* over time (Buchanan and Hart, 2012; Hart et al., 2015).

Interestingly, survival of tagged seedlings of neither *Quercus* nor competing species was influenced by treatment. These results, at least for *Quercus* species, contrast with research that suggests seedling survival increases with decreasing overstory density (Crow, 1992; Loftis, 1990b). Overstory density was completely removed in small patches in GSH, while density was reduced to 9.0 and 5.0 m^2/ha in SWH and SWL, respectively. Although reduction in density did not affect survival of *Quercus* individuals, average height of tagged *Q. rubra* seedlings in both GSH and SWL treatments was significantly greater than in CON. Although there are relative differences in shade-tolerance within the *Quercus* genus, in general, *Quercus* species are categorized as mid-tolerant of shade; as such, residual basal area in the SWH treatment may have been high enough to inhibit the growth of *Quercus* seedlings (Miller et al., 2006) relative to more open conditions in GSH and SWL.

4.1. Conclusions

High-elevation *Q. rubra* forests of the southern and central Appalachians are unique in structure and composition relative to the broad-leaved deciduous forests that dominate lower elevations. Although management, including harvesting is rarely conducted in efforts to manage for timber, lack of disturbance has led to a decrease in landscape-level structural diversity and young forest habitat required or preferred by a variety of wildlife species of importance and conservation concern. Regeneration harvests, including the partial regeneration harvests conducted in this study, have been shown to create the structural heterogeneity and young forest habitat preferred by a variety of game and non-game wildlife species in the region (Jones et al., 2008; Klaus and Buehler, 2001; McDermott and Wood, 2009). However, regeneration harvests conducted without regard to *Quercus* ecology can decrease abundance and importance of *Quercus* across a variety of spatial scales (Fei et al., 2011; Swaim et al., 2018). Given the ecological significance of *Quercus* (e.g., McShea et al., 2007; Cavender-Bares, 2016; Kreye et al., 2018), it is, therefore, imperative that management activities, including regeneration harvests facilitate the long-term regeneration and recruitment of *Quercus* dominant and co-dominant canopy positions.

At Y22, the relatively low density of successfully regenerated (i.e., sapling-sized) QURU and QUCA stems in the partial harvest regeneration treatments coupled with the observation that the height of individually tagged *Quercus* seedlings was generally shorter than that of competing species suggests that additional cultural treatments, including intermediate treatments such as crown-touch release methods, may be necessary to secure the continued recruitment of *Quercus* individuals in these high-elevation *Q. rubra* forests (Gottschalk et al., 2014). It is apparent that, although regeneration harvests secured greater *Q. rubra* saplings than CON, at maturity, *Q. rubra* will represent a proportionally lower amount of overstory basal area than prior to harvest. Although incidences of browse were not specifically recorded, *O. virginianus* density throughout the study area is low relative to other areas of the eastern United States (e.g., Pennsylvania, Wisconsin, Michigan, West Virginia) (Walters et al., 2016), where browse pressure by *O. virginianus* severely limits the success of *Quercus* regeneration (Nuttle et al., 2013; Thomas-Van Gundy et al., 2014; Granger et al., 2018). Prescribed fire, although historically not as frequent as in lower elevation *Quercus* forests, could be used alone, or in combination with harvesting or chemical treatments, to reduce competition with shade-tolerant competitors (Brose, 2010; Keyser, 2019) and promote more open understory conditions that are more representative of more historic conditions (Kelly, 2013).

CRediT authorship contribution statement

Tara L. Keyser: Formal analysis, Data curation, Investigation, Writing - original draft, Writing - review & editing. **David L. Loftis:** Conceptualization, Methodology, Data curation, Writing - review & editing.

Declaration of Competing Interest

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

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