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Positive regeneration responses of oak, hickory, and american chestnut to repeated prescribed fires and mechanical thinning 22 years after study initiation

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ABSTRACT

Since the 1960s, there has been an increasing trend in oak (*Quercus* spp.) dominated forests exhibiting poor oak regeneration and recruitment, and associated hickories (*Carya* spp.) are likely undergoing a similar trend. Additionally, American chestnut (*Castanea dentata*) responses to management have been poorly studied. Silvicultural treatments to increase oak regeneration include prescribed fires and stand thinning, but often show mixed results. One potential issue is grouping oaks and hickories when analyzing treatment responses. This may obscure species- or genus-specific responses, making the long-term efficacy of silvicultural treatments difficult to identify. Thus, oak and hickory seedling and sapling responses to mechanical thinning, repeated prescribed burning, combined thinning and burning, and unmanipulated controls were analyzed at the species and genus level. Treatment plots also included American chestnut regeneration, were included in the genus-specific analyses. There was no evidence of species-specific responses to individual treatments in oak, while species-specific responses were observed in sapling hickories with *Carya glabra* and *Carya tomentosa* densities being 2.5 times greater than *Carya ovata*. When grouped by genus, oak and hickory have similar responses to individual treatments, thus analyzing their responses as a collective group is appropriate. The combined burning and thinning treatment was most effective with average sapling densities increasing by 2362 %, 1277 %, and 500 % for oak, hickory, and American chestnut, respectively, as of 2022 compared to 2000 (pre-treatment). Long-term forest management to increase understory light levels and decrease the competitive strength of mesophytes appears equally capable of promoting oak, hickory, and potentially American chestnut regeneration.

1. Introduction

Together, oak, hickory, and chestnut maintain a place of great economic, ecological, and cultural value to eastern North America. From an economic standpoint, these hardwoods represent a valuable, high-quality wood source. For example, white oak (*Quercus alba*) timber is critical to the increasing global demand of white oak barrels for the aging and finishing of high-quality spirits (Dhungel et al., 2023). Ecologically, all have functioned as foundational species in that they provide food, habitat, and structure that is essential to maintaining overall forest biodiversity (Burns and Honkala, 1990; Fralish, 2004). Culturally, oak acorns and chestnut/hickory nuts were utilized as important food sources to indigenous eastern North American groups and were likewise used by early European settlers (Abrams and Nowacki, 2008). The chestnut blight decimated American chestnut during the early 1900s, and poor regeneration of oak (*Quercus* spp.) in eastern North American forests has been recognized for decades (Larsen, 1953; Johnson, 1979; Lorimer, 1984). While studied to a lesser degree, hickory (*Carya* spp.) is closely associated with oak in the landscape and has also been experiencing poor regeneration (McCarthy and Wistendahl, 1988; Evans and Keen, 2013; Cowden et al., 2014; Lefland et al., 2018). Given the tendency for oak, formerly chestnut, and hickory to co-occur and be major components of several forest types, understanding the mechanisms behind poor regeneration, along with how to reverse this trend is

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of the utmost importance.

Poor oak and hickory regeneration is likely due to several interacting phenomena, although the widespread implementation of forest fire suppression strategies in the early 1900's is likely a primary factor (Nowacki and Abrams, 2008; Hanberry et al., 2020; Alexander et al., 2021). The reduction of fire on the landscape coincides with the first reports of poor oak regeneration (Brose et al., 2001; McCarthy et al., 2001; Sutherland and Hutchinson, 2003) and has also been identified as a driving force behind forest mesophication. The process of forest mesophication has been described as a combination of fire exclusion and vigorous regeneration of fire-sensitive mesophytes that outcompete and replace xeric-adapted species in the forest understory (Nowacki and Abrams, 2008; Aleander et al., 2021). Without fire as a disturbance agent allowing increased levels of light to the forest floor, fire-sensitive species (e.g., *Acer rubrum* and *A. saccharum*) can persist in forest understories at higher densities. The resulting shift to the less flammable leaf litter of mesophytes reduced the frequency and intensity of fire, when fire did occur (Nowacki and Abrams, 2008; Alexander and Arthur, 2014; Dickinson et al., 2016). The concern is that, eventually, the fire-sensitive species could cause exclusion of fire-adapted species (i.e., *Quercus* spp. and *Carya* spp.) from the sub-canopy forest layers, and unmanaged stands may undergo shifts in forest type (Nowacki and Abrams, 2008; Dyer and Hutchinson, 2019; Hanberry, 2019).

There is also evidence that climate change has played a role in the decline of oak and hickory regeneration (McEwan et al., 2011; Pederson et al., 2015; Clark et al., 2016). While difficult to detangle the proportional impacts of climate change versus forest mesophication as both occur at similar temporal and spatial scales, regional trends in climate cannot be ignored as a major driver behind recent forest regeneration patterns. Eastern North America has experienced increasingly wet growing season conditions over the last century, while also experiencing less frequent and less intense droughts (Ficklin et al., 2015; Pederson et al., 2015). Growing season site water balance has been repeatedly demonstrated to be important for tree growth and health for a variety of species in the region (Speer et al., 2009; Martin-Benito and Pederson, 2015; LeBlanc et al., 2020; Rudolph and LeBlanc, 2020), but increasingly wet growing season conditions over the last century have likely benefitted mesophytic species like *Acer saccharum* over xeric-adapted oaks and hickories (Pederson et al., 2015; Clark et al., 2016). However, regional climate change patterns project higher growing season temperatures and more frequent drought, thus, it is possible that environmental conditions will eventually favor xeric-adapted species again (Clark et al., 2016; Iverson et al., 2019; Anderegg et al., 2020). The likelihood of reversing current trends in forest regeneration due to climate change likely depends on the intensity of future shifts in climate and future forest compositions may not reflect those recorded prior to the 20th century (Iverson et al., 2019). Controlled manipulations of the forest environment through silvicultural management will likely be critical in returning oak and hickory regeneration to historical levels.

Forest management strategies aimed at increasing understory oak and hickory often use prescribed fire as a tool to increase understory light levels and decrease densities of species like *Acer saccharum* and *A. rubrum* through top-killing small trees. Given the variety of burning regimes and variations in local forest conditions over the ranges of eastern North American oaks and hickories, results have been mixed. Single prescribed fires appear unlikely to reduce densities of fire-sensitive species in the forest understory, although a single fire can increase fire-adapted species in some cases (Albrecht and McCarthy, 2006; Blankenship and Arthur, 2006; Alexander et al., 2008; Brose et al., 2013). There is evidence that a single prescribed fire may have the opposite effect in the short term by increasing the density of vigorous stump-sprouting, fire-sensitive species like *Acer rubrum* (Albrecht and McCarthy, 2006; Izbicki et al., 2020). However, other studies have found increased levels of oak and hickory regeneration over competitors several years after a single prescribed burn (Dems et al., 2021; Bataineh et al., 2022).

Long-term management plans with multiple prescribed fires, and potentially selective overstory and midstory thinning, may have a greater ability to shift the physical environmental in a way that allows for a brighter, drier, and more flammable forest floor that mimics historic oak-dominated forest conditions by continually reducing the density of mesic-adapted species (Fan et al., 2012; Hutchinson et al., 2012, 2024; Knapp et al., 2015; Iverson et al., 2017; Izbicki et al., 2020). Specifically in southeast Ohio where this study is located, surveys immediately following the initial treatments did not appear successful in enhancing oak and hickory regeneration due to the extreme proliferation of early-successional species (Albrecht and McCarthy, 2006). The application of additional burns in this location became increasingly successful in enhancing oak and hickory regeneration over time, even as competition with species like *Acer rubrum*, *Liriodendron tulipifera*, and *Sassafras albidum* remained intense (Iverson et al., 2008; Hutchinson et al., 2024). Long-term studies in the more xeric Missouri Ozarks region have also found broad trends in successful oak and hickory regeneration in response to multiple prescribed burns, but fire frequency greatly influenced this broad success (Knapp et al., 2015, 2017). In some locations, a century or more of little to no fire in historically oak and hickory dominated forests has passed. Thus, expectations for management strategies to be quickly impactful are best tempered.

Due to their close association in several forest types throughout the region, oak and hickory are commonly treated as a single functional group when determining the efficacy of forest management (e.g., Burns and Honkala, 1990; Knapp et al., 2015; Iverson et al., 2017; Hutchinson et al., 2024). Despite their close landscape association, genus-specific differences exist between oak and hickory reproduction, life history, and growth strategies. These differences may result in separate responses to forest management. In general, hickories have been shown to tolerate lower light levels in the forest understory, surviving for decades and even exceeding a century (Burns and Honkala, 1990; Lefland et al., 2018; Pile Knapp et al., 2021; Rudolph et al., 2024), which is a trait not commonly observed in suppressed oaks. Oak and hickory are both masting species, however hickories have shown a more consistent capacity to develop advanced regeneration (saplings) in low light conditions compared to oak (Nixon et al., 1983; Lefland et al., 2018; Pile Knapp et al., 2021). In general, mature hickories are also more susceptible to fire compared to oak, as their bark and bud structure do not prevent damage to living tissues to the same degree as oaks (Burns and Honkala, 1990). Hickories and oaks may also differ in their drought tolerance strategies and in their hydraulic behaviors (Burns and Honkala, 1990; Au and Maxwell, 2022; Bryant et al., 2022). The tendency for hickory to take a more conservative growth and reproductive strategy, along with increased susceptibility to fire damage compared to oak may result in different responses to forest management when observed in the long term.

An additional source of variation when considering oak and hickory regeneration responses to silvicultural management may be caused by species-specific differences. Among the major oak species in the region, white oak (*Quercus alba*) has a higher shade tolerance and lower juvenile growth rate compared to red and black oak (*Q. rubra* and *Q. velutina*) and even other members of the white oak subgenus (*Quercus* subg. *Quercus)* like chestnut oak (*Q. montana*) (Burns and Honkala, 1990; Rebbeck et al., 2011; Johnson et al., 2019). The major hickory species in the region also show species-specific responses to their environment. For example, shagbark hickory (*Carya ovata*) is more shade tolerant throughout its life cycle compared to pignut hickory and mockernut hickory (*C. glabra* and *C. tomentosa*, respectively) (Burns and Honkala, 1990). While these three species can all respond quickly to canopy openings, shagbark hickory has a slower, more conservative growth strategy (Burns and Honkala, 1990; Cowden et al., 2014). Species-specific differences in drought tolerance and habitat preferences also exist in hickory. For example, mockernut hickory tolerates dry-upland conditions well, while shagbark hickory can tolerate a wider range of environmental and habitat conditions (Burns and Honkala, 1990). By understanding how fire-related management strategies affect individual oak and hickory species, the overall efficacy of management plans and the appropriateness of grouping oak and hickory can be better assessed.

Other species-specific differences like drought tolerance and preferred topographic position also vary among the major oak species, which may impact regeneration and recruitment responses to management regimes (Burns and Honkala, 1990; Dey, 2002; Johnson et al., 2019). For example, the success of fire-based management approaches to increase oak regeneration in southeast Ohio varies along topographic and moisture gradients (Hutchinson et al., 2005, 2024; Iverson et al., 2017; Radcliffe et al., 2021). Oak regeneration on mesic sites was extremely poor and management only produced positive results in intermediately dry and xeric sites (Albrecht and McCarthy, 2006; Iverson et al., 2008, 2017; Hutchinson et al., 2024). In more mesic environments, the competitive abilities of mesic-adapted species like *Acer saccharum*, and *Acer rubrum* are too strong to be significantly impacted by burning (Iverson et al., 2008; Hutchinson et al., 2024).

As a historic component of several fire-prone eastern North American forest types (Collins et al., 2017; Kane et al., 2020), American chestnut (*Castanea dentata*) may also benefit from silvicultural treatments aimed at increasing oak and hickory regeneration. As the decline of American chestnut coincided with the start of forest fire suppression in the early-1900's (McEwan et al., 2011; Collins et al., 2017), scant evidence exists for how American chestnut responds to fire. It has been suggested that American chestnut would have similar responses as oak due to similar growth strategies, bark anatomy, and phylogenetic relatedness (Kane et al., 2020). Limited observation of American chestnut sprouts in areas subjected to prescribed burns and competition release support this idea, as chestnut had the same positive responses as oaks to silvicultural treatments (McCament and McCarthy, 2005; Belair et al., 2014). Thus, locations within the historic range of American chestnut where management strategies are aimed at increasing oak regeneration may also serve as prime locations to reintroduce and promote American chestnut regeneration.

Overall, this research analyzed long-term regeneration surveys in response to silvicultural treatments to assess the effectiveness of long-term management plans. This manuscript aims to address the following research questions. (1) Within genera, do oak and hickory exhibit species-specific responses to repeated prescribed burning and a mechanical thinning treatment? (2) Across genera, do oak and hickory respond differently to silvicultural treatments? (3) Have oak and hickory sapling stem densities increased beyond pre-treatment densities 22 years after the first treatments were applied? (4) Due to the presence of *Castanea dentata* saplings occurring in survey plots, it was asked post-hoc if *Castanea dentata* sapling regeneration also responds to silvicultural treatments.

2. Methods

2.1. Study area

This research utilized two of the long-term USDA Forest Service Fire and Fire Surrogate (FFS) study locations at Vinton Furnace Experimental Forest (39.33°, −82.65°) and Zaleski State Forest (39.58°, −82.62°) in southeast Ohio. Permanent, experimental forest plots were established in 2000, to determine forest understory regeneration responses to mechanical thinning and prescribed burning. The four treatments were mechanical thinning only, prescribed burning only, a combination of mechanical thinning and prescribed burning, and a control unit subjected to no active silvicultural management over the course of the experiment. The treatment areas are located within the unglaciated Allegheny Plateau and were located across a range of aspects and slope positions, as well as both dry and mesic areas. South-facing and ridgetops are currently composed of mixed oak forest, while north-facing and ravine locations are primarily mixed-mesophytic (Iverson et al., 2017). Pre-treatment stand overstory basal areas were dominated by oak (81.5 %) with a minor hickory component (3.5 %). The pre-treatment sapling layer was dominated primarily by *Acer rubrum* and *Nyssa sylvatica*, while the seedling layer was primarily *Acer rubrum* (Albrecht and McCarthy, 2006). Additionally, deer herbivory (often thought to contribute to oak regeneration failure), has been found to be negligible in the study area due to lower white-tailed deer densities (Apsley and McCarthy, 2004).

After pre-treatment surveys in 2000, thinning occurred from late 2000 to early 2001. Commercial thinning operations reduced basal area by 20–30 % from a pre-treatment basal area of 29 m^2 h^{-1}, primarily focusing on midstory-occupying trees with a diameter at breast height of 15–35 cm (Iverson et al., 2004; Albrecht and McCarthy, 2006; Hutchinson et al., 2024). The thinning operation maintained the overstory dominance of reproductively mature oaks, while enhancing canopy gap structure to promote seedling regeneration (Albrecht and McCarthy, 2006).

Prescribed burning occurred in 2001, 2005, 2010, and 2016. All burns were conducted in the spring dormant season (late-March to mid-April) and ignited via hand-sources and some helicopter-based ignitions (Hutchinson et al., 2024). The initial prescribed burn was low intensity with flame lengths less than 1 m, consuming leaf litter and occasional 1-hour fuels (Iverson et al., 2004; Albrecht and McCarthy, 2006). The 2005, 2010, and 2016 prescribed burns were conducted under drier conditions, resulting in 1–2 m flame lengths and overstory mortality (Iverson et al., 2017; Hutchinson et al., 2024). Typical representations of each treatment type can be seen below in Fig. 1.

2.2. Field data collection

Both study locations were subjected to the four treatments, with each treatment area containing ten long-term plots. Each study plot measured 20 × 50 m and was separated into ten 10 × 10 m subplots, from which three 10 m x 10 m subplots were used to survey sapling regeneration (240 subplots total). Saplings were defined as trees taller than 1.4 m and with a diameter at breast height (DBH) between 3.0 and 9.9 cm. To survey saplings, each individual stem present in the three 10 m x 10 m subplots was tallied and identified by species. Seedling regeneration was surveyed in 1 m^2 quadrats (1600 quadrats total). Each 10 m x 10 m subplot contained two seedling regeneration quadrats, for a total of 20 x 1 m^2 quadrats per study plot. Seedlings were identified to species and separated into three size classes by height (0–9.9 cm, 10–49.9 cm, 50–139.9 cm). Field surveys in 2000, 2001, 2004, and 2022 (the sixth growing season after the last burn) identified all stems to species. Surveys in 2007, 2009, 2011, 2014, and 2017 identified stems to species in most cases with several species being grouped by genera, for example identifying *Carya* only to genus.

2.3. Data analysis

2.3.1. Species-specific responses

All statistical analyses were completed with R v. 4.4.4 (R Core Team, 2021). To determine species-specific regeneration responses of oak and hickory, only the most common species were used (*Quercus alba*, *Q. montana*, *Q. rubra*, *Q. velutina*, *Carya glabra*, *C. tomentosa*, and *C. ovata*). Only sapling and seedling count data from the pre-treatment survey in 2000, and the post-treatment surveys 2001, 2004, and 2022 surveys were included in this analysis as they identified hickory to species as all other sapling surveys grouped hickory as *Carya* spp.

To determine if species-specific differences in regeneration response to the treatments in oak exist, zero-inflated negative binomial (ZINB) models were constructed using the "zeroinfl" function from the R package pscl (Zeileis et al., 2008). This type of model was justified due to the use of count data, and specifically count data where true zeroes were plentiful, meaningful, and sapling counts varied greatly within and among treatment groups. Two separate models were fitted separating

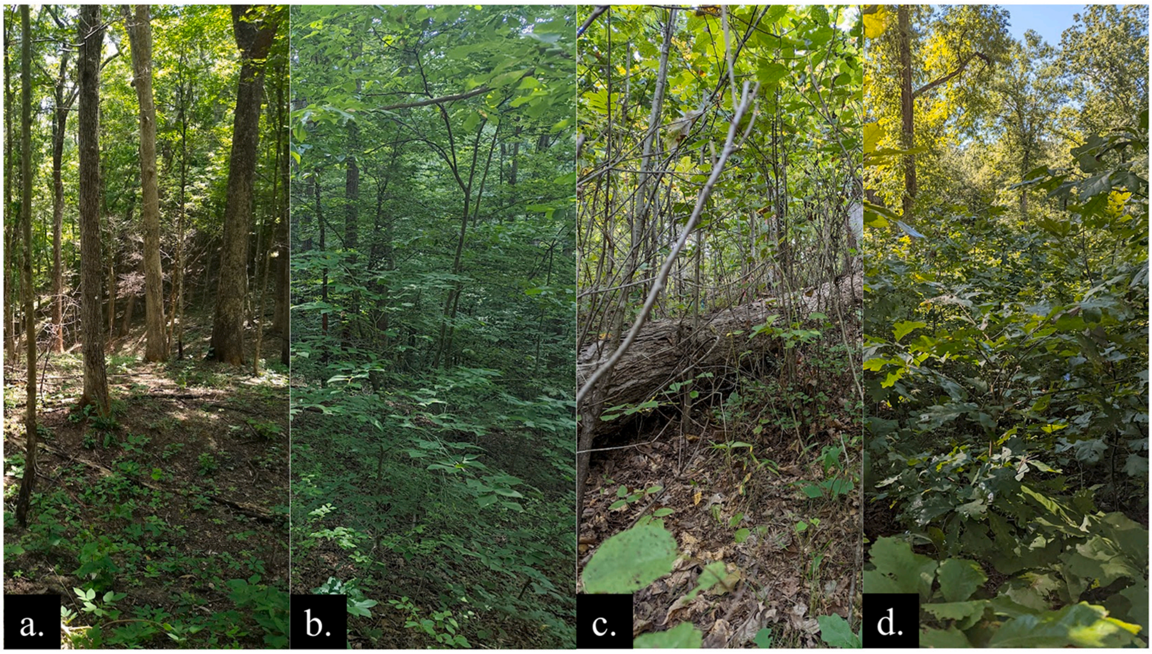

Fig. 1. Example of each treatment type as of Summer 2022. Letter codes are as follows: a.) Control, b.) Thin-only, c.) Burn-only, d.) Thin and Burn.

oak saplings (DBH between 3.0 – 9.9 cm) from oak seedlings (Height up to 139 cm), and in each case the response variable was stem counts summed by plot. Fixed explanatory variables used in the oak sapling model included treatment year, the type of silvicultural treatment, oak species, an interaction between oak species and treatment, an interaction between oak species and year, and an interaction between treatment and year, and site of the treatments as a random effect. Given the simplicity of the statistical model, the only model considered is the full model with all explanatory variables and their interactions. For the seedling counts, the following model structure was used: Fixed explanatory variables in the oak seedling model included treatment year, the type of silvicultural treatment, oak species, seedling size class, an interaction between oak species and treatment year, an interaction between species and treatment type, an interaction between seedling size class and treatment type, and site of the treatments as a random effect.

An identical process was used to model species-specific responses of hickory sapling and seedling regeneration to silvicultural treatments. The number of non-zero sapling counts for hickory were satisfactory for use in zero-inflated negative binomial models but was not enough to include interactions without resulting in model singularity. Thus, the final model for hickory saplings was: treatment year, the type of silvicultural treatment, hickory species site of the treatments as a random effect. For hickory seedling counts, the final model included the following fixed and random effects: treatment year, the type of silvicultural treatment, hickory species, seedling size class, an interaction between hickory species and treatment year, an interaction between species and treatment type, an interaction between seedling size class and treatment type, and site of the treatments as a random effect. To determine pairwise species-specific differences in stem density of oak and hickory, respectively, the function "emmeans" from the R package emmeans was used with a Tukey adjustment to account for multiple comparisons (Lenth 2023). The "emmeans" function allows for pairwise comparison of species responses in the zero-inflated negative binomial models that include factors. For both oak and hickory, the resulting model predictions of stem count were then converted into predicted stem densities (stems/ha).

2.3.2. Genus-specific responses

To determine if oak and hickory on a genus-level respond differently to silvicultural treatments, and if oak and hickory stem densities have significantly increased compared to pre-treatment densities, zero-inflated gamma distribution models with a logistic link were constructed using the "glmmTMB" function from the package glmmTMB (Brooks et al., 2017). This type of model was chosen since the response variable was stem densities (a continuous numerical variable), large variation in stem densities, and numerous real zeroes in the dataset. A transformation of adding 1.0×10^{-7} to each stem density value was applied to satisfy the necessary requirement of modeling positive, non-zero data. For saplings, three genera were included in the stem density data (*Quercus*, *Carya*, and *Castanea)*. *Castanea* was included in this grouping due to sufficient numbers of saplings identified during surveys and general lack of knowledge on *Castanea* responses to silvicultural management. Only *Quercus* and *Carya* were included in the seedling model. However, in both models stem densities were summed per plot. For sapling stem density, the model included survey year (2000, 2001, 2004, 2007, 2009, 2011, 2014, 2017, and 2022), genus, treatment type, all possible interactions, and site location as a random variable. The seedling stem density model included survey year (2000, 2001, 2004, 2022), genus, treatment type, seedling size class, all possible interactions, and site location as a random variable. These were the only years of seedling survey data available at this time. To determine pairwise differences in stem density by genus and by treatment year, the function "emmeans" from the R package emmeans was used (Lenth 2023).

3. Results

3.1. Sapling oak species-specific responses

There were no significant differences among the four oak species within treatments 22 years after the initial treatment (Fig. 2a, Table 1b). While the control treatments experienced virtually no sapling recruitment over the past 22 years, each oak species had significantly higher stem densities in the treatments compared to the control (Fig. 2a). In addition, the silvicultural treatments were not significantly different from each other. However, even though the thin only treatment was not significantly different from the treatments that included burning, this likely was caused by a single thinned plot that contained a high density

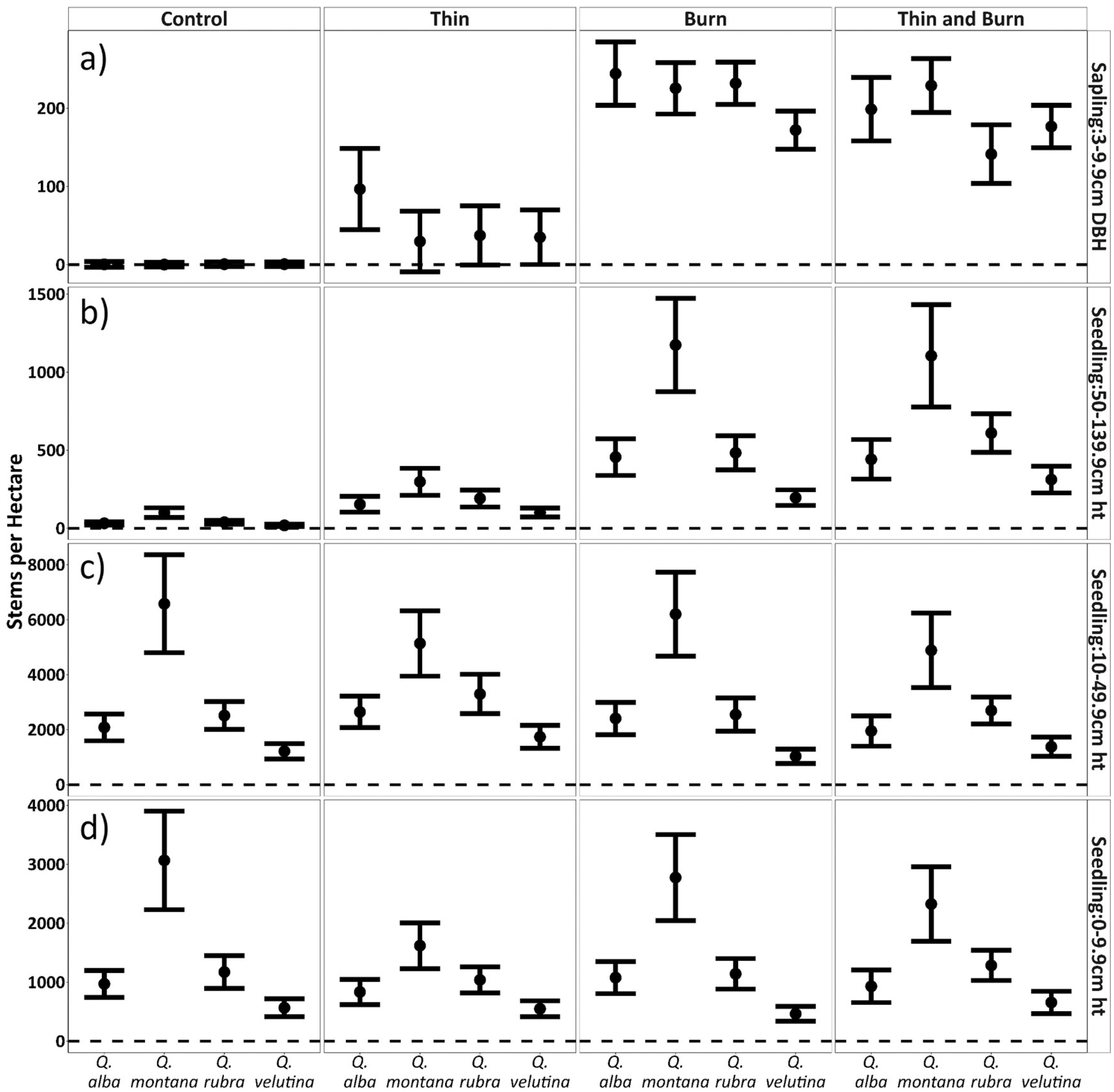

Fig. 2. *Quercus* sapling and seedling stem density per hectare model predictions (mean and standard error) of four oak species for the 2022 sampling year by silvicultural treatment.

of oak saplings. In 2022, 95 % of the thin only plots contained seven or less oak saplings and had median oak sapling count of 2 per plot. However, there was a single plot that contained 72 oak saplings. In contrast, the burn only and thin + burn plots consistently had a greater number of oak saplings with median sapling count values of 16 and 19, respectively.

3.2. *Seedling oak species-specific responses*

Oak seedlings, regardless of size class, did demonstrate significant species-specific differences in regeneration response to the four treatments (Fig. 2b, c, d, Table 1a). Post-hoc analyses revealed that *Quercus montana* generally had the strongest positive regeneration responses among all treatments and size classes, but this difference decreased as size class increased (Fig. 2b, c, d). Within species in the small and medium seedling size classes, comparisons of silvicultural treatments did not result in higher seedling stem densities after 22 years. In the largest seedling size class, all oak species in the treatments had significantly higher oak seedling regeneration levels compared to the controls after 22 years of management. In addition, the number of large seedlings for all oaks were significantly higher in the burn only and thin/burn treatment, compared to the thin only treatment.

3.3. *Sapling hickory species-specific responses*

Unlike the oaks, hickory saplings did show species-specific responses within treatments (Fig. 3a, Table 1d). Post-hoc analyses revealed that in all four treatments, *Carya ovata* stem densities were on average 87 % lower than either *Carya glabra* or *Carya tomentosa,* while there was only a 0.35 % difference in stem densities between *Carya glabra* and *Carya tomentosa* (Fig. 3a). Similar to the oaks, all three hickory species had significantly higher stem densities in the silvicultural treatments, compared to the control. However, all hickory species maintained a presence as saplings in the control treatment (Fig. 3a).

3.4. *Seedling hickory species-specific responses*

As with the saplings, hickory seedling regeneration responses were found to have species-specific differences within individual treatments. Significant species-specific responses were present in all seedling size classes for the control, thin only, and burn only treatments (Fig. 3b, c, d, Table 1c). However, there were no differences between the three species within the thin and burn treatment.

Table 1
Statistical model outputs for a) Oak seedling species-specific regeneration responses, b) Oak sapling species-specific regeneration responses, c) Hickory seedling species-specific regeneration responses, d) Hickory sapling species-specific regeneration responses, e) Seedling genus-specific regeneration responses, and f) Sapling genus-specific regeneration responses.

Oak seedling species-specific regeneration					Oak sapling species-specific regeneration			
a.) Fixed variables	χ^2	*df*	*p*	**b.)**	**Fixed Variables**	χ^2	*df*	*p*
Year	31.9	3	< 0.001		Year	94.8	3	< 0.001
Oak species	161.3	3	< 0.001		Oak Species	3.7	3	0.290
Treatment	98.5	3	< 0.001		Treatment	6.3	3	0.098
Seedling size	120.5	1	< 0.001		Year*Species	14.7	9	0.100
Year*Oak species	116.6	9	< 0.001		Treatment*Oak species	12.2	9	0.200
Treatment*Oak species	15.5	9	0.0783		Year*Treatment	85.4	9	< 0.001
Treatment*Seedling size	119.8	6	< 0.001					
Hickory seedling species-specific regeneration					Hickory sapling species-specific regeneration			
c.) Fixed variables	χ^2	*df*	*p*	**d.)**	**Fixed Variables**	χ^2	*df*	*p*
Year	24.6	3	< 0.001		Year	97.3	3	< 0.001
Hickory species	11.0	2	0.004		Hickory species	22.2	2	< 0.001
Treatment	7.1	3	0.068		Treatment	33.1	3	< 0.001
Seedling size	68.5	2	< 0.001					
Treatment*Hickory species	19.1	6	0.004					
Treatment*Seedling size	13.3	6	0.038					
Seedling genus-specific regeneration					Sapling genus-specific regeneration			
e.) Fixed variables	χ^2	*df*	*p*	**f.)**	**Fixed Variables**	χ^2	*df*	*p*
Year	10.0	3	0.018		Year	88.6	9	< 0.001
Genus	122.6	1	< 0.001		Genus	244.7	2	< 0.001
Treatment	8.7	3	0.033		Treatment	232.4	3	< 0.001
Seedling size	553.0	2	< 0.001		Year*Genus	24.6	18	0.136
Year*Genus	136.3	3	< 0.001		Treatment*Genus	112.2	6	< 0.001
Year*Treatment	48.7	9	< 0.001		Year*Treatment	130.6	27	< 0.001
Year*Seedling size	343.1	6	< 0.001					
Treatment*Genus	13.8	3	0.003					
Genus*Seedling size	162.5	2	< 0.001					
Treatment*Seedling size	71.7	6	< 0.001					

3.5. Sapling genus-specific responses

Within silvicultural treatments, there was not a significant difference between oak and hickory stem densities in 2022 (Fig. 4, Table 1f). However, when comparing oak and hickory within the control, the average stem density of hickories in the sapling regeneration layer was significantly higher than oak in 2022 (*Quercus* 4 stems/ha versus *Carya* 72 stems/ha). While stem densities between oak and hickory were not statistically different from each other in 2022 for the other three treatments, oak had higher average stem densities in the burn only treatment (*Quercus* 887 stems/ha versus *Carya* 576 stems/ha), and thin/burn treatment (*Quercus* 1920 stems/ha versus *Carya* 661 stems/ha), while hickory had higher stem densities in the thin only treatment (*Quercus* 103 stems/ha versus *Carya* 153 stems/ha).

When comparing stem densities within a treatment (i.e., 2000 vs 2022), only the combined thinning and burning treatment had significantly higher predicted stem densities of oak and hickory (Fig. 4, Table 2). The burn only and thin only treatments did have higher stem densities in 2022 compared to 2000, but the differences were not statistically significant. The control group maintained a pattern of virtually no oak saplings with a small number of hickory saplings over the 22 years (Fig. 4, Table 2).

3.6. Seedling genus-specific responses

There were significant differences in seedling stem density between oak and hickory for all size classes in all treatments, as oak consistently had higher stem densities (Fig. 5). For oak, all treatments resulted in significantly higher stem densities in the large and small seedling size classes in 2022 compared to 2000 (Fig. 5). In the medium seedling size class for oak, stem densities in the burn only and thin/burn treatments were not significantly different from pre-treatment levels. For hickory seedling stem densities, there was a significant decrease in 2022 compared to pre-treatment levels for the small and medium size classes in all treatments. Additionally, predicted hickory stem density in the small size class was less than one stem per hectare in 2022, resulting in negative stem density values in Fig. 5 as a result of the logarithmic transformation necessary to visualize potential genus-specific differences. In the large seedling size class, significant increases in hickory seedling stem densities were observed in control and thin only treatments, but not in the burn only and thin/burn treatments (Fig. 5).

3.7. Sapling Castanea dentata regeneration responses

American chestnut sapling regeneration responses to the treatments reflected a similar pattern to the oaks and hickories. Post-hoc testing using asymptotic Z testing from the R package "emmeans" showed that sapling stem densities in 2022 in the burn only (z ratio = 5.5, $P < 0.001$) and thin/burn treatments (z ratio = 4.3, $P < 0.001$) were significantly higher than stem densities in the control treatment. Post-hoc testing revealed that changes in stem densities within treatments between 2000 and 2022 were not significantly different. However, all treatments did have significantly higher stem densities from pre-treatment densities in 2021 (Fig. 6).

4. Discussion

This study had a broad objective of evaluating the feasibility of treating oak and hickory as a single function group in management plans aimed at enhancing regeneration. Specifically, this study utilized statistical modeling based on long-term regeneration surveys and determined, within a genus, that oak did not exhibit species-specific regeneration responses to mechanical thinning and repeated prescribed burning silvicultural treatments while species-specific differences were

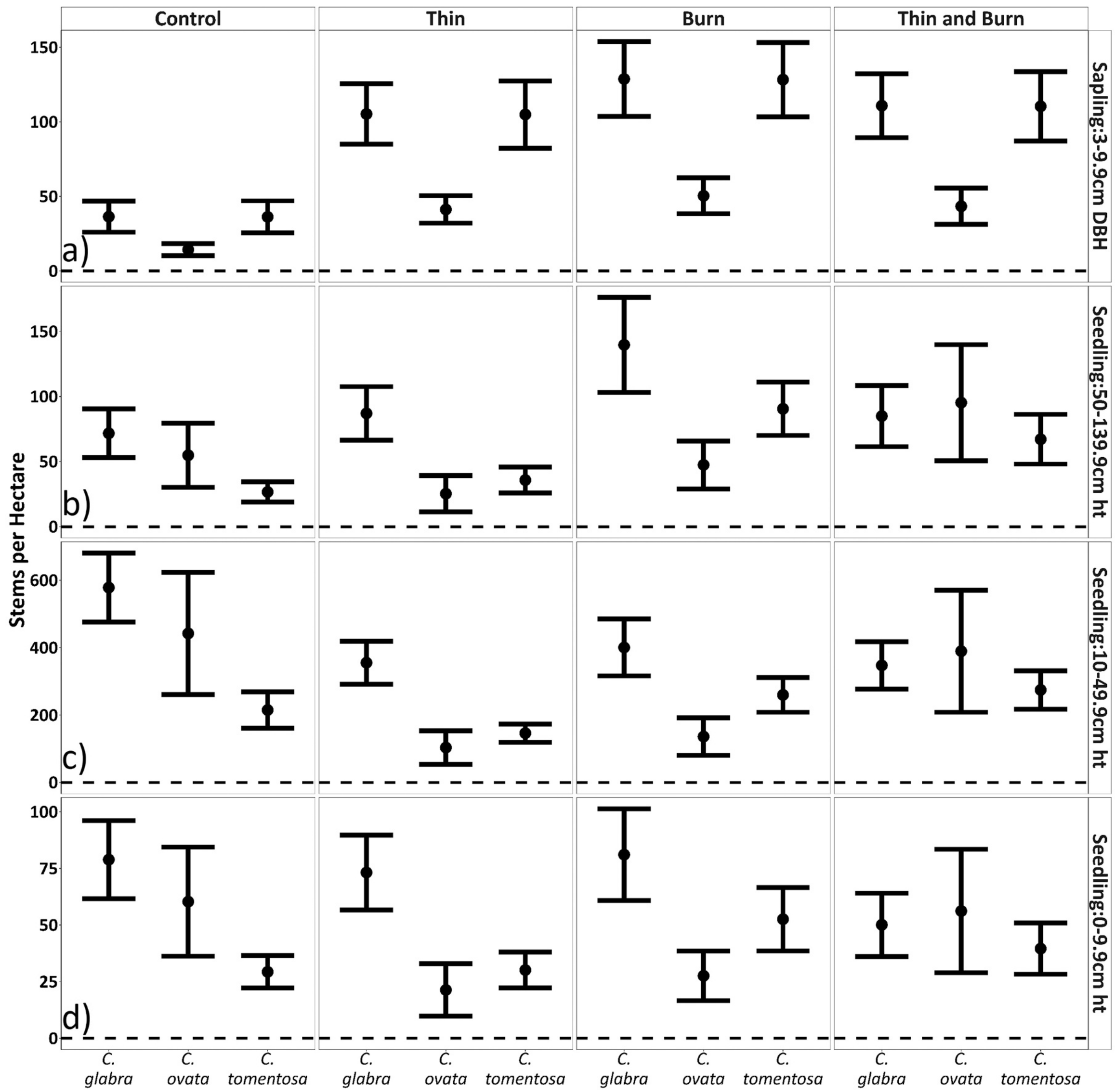

Fig. 3. *Carya* sapling and seedling stem density per hectare model predictions (mean and standard error) of three hickory species for the 2022 sampling year by silvicultural treatment.

detected in hickory. The regeneration responses of oak and hickory were evaluated on a genus-specific level which found no difference in regeneration responses, justifying their grouping in management plans. Additionally, American chestnut regeneration also appeared to respond positively to the treatments that incorporated burning. Finally, the long-term efficacy of managing oak and hickory regeneration is successful when combining mechanical thinning with repeated prescribed burns, although positive results can take over a decade to emerge.

4.1. Species-specific responses

Despite differences in shade tolerances, habitat preferences, and stress tolerances, species-specific responses of oaks to the silvicultural treatments that were found in the seedling size classes were not present in the sapling stage. This is in contrast with other studies, such as in upland forests in Missouri where the white oak subgenus responded better to burning compared to oaks from the red oak subgenus (Fan et al., 2012; Knapp et al., 2015). The Missouri studies included post oak (*Q. stellata*), scarlet oak (*Q. coccinea*), and southern red oak (*Q. falcata*), that typically occupy dry, poor-quality ridgetops (Burns and Honkala, 1990; Fan et al., 2012; Knapp et al., 2015). The inherent species differences among these three oaks in Missouri may be greater than that of the four oak species analyzed in this study from southeast Ohio. Given the diversity of oaks in eastern North America, species-specific responses to silvicultural management are likely to exist in some locations, for some species, but this assumption requires additional study. Additionally, apparent differences between oaks stem densities in the seedling layer (i.e. greater densities of *Quercus montana* despite being the second most common oak in the study area) which do not carry into the sapling layer may be a result of short-term masting patterns. From a management perspective, the lack of species-specific responses observed in this study may be welcomed for maintaining and restoring a diverse representation of oaks in the landscape. However, if increased regeneration of a specific oak species is the goal of management, additional strategies may need to be explored that would benefit the regeneration of one oak species over another.

This study did find differences among the hickory species in response to treatments, which does align with the current understanding of hickory ecology (Burns and Honkala, 1990; Lefland et al., 2018; Pile Knapp et al., 2021) but is also likely related to overstory abundance of hickories in the study locations. Positive shagbark hickory responses to the treatments were muted compared to the other two species. This may

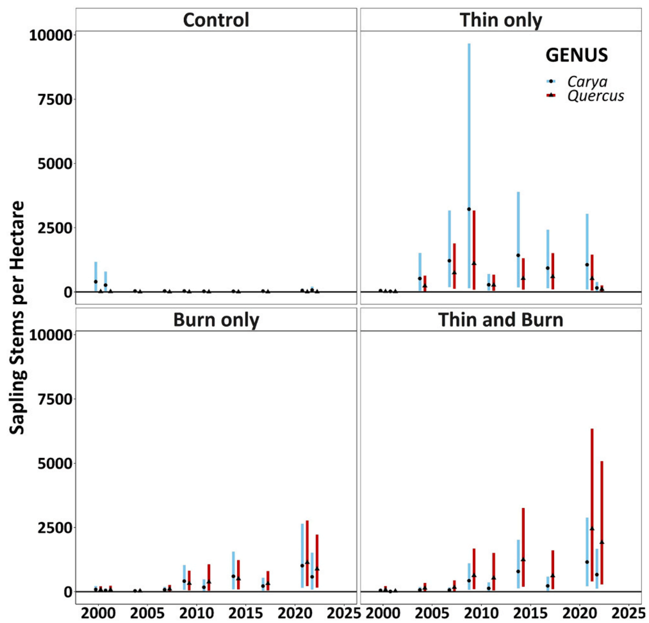

Fig. 4. Sapling stem density per hectare model prediction standard error ranges comparing *Quercus* and *Carya* for sampling years by silvicultural treatment.

be explained by shagbark hickory only making up 6 % of the hickories in the Vinton Furnace Experimental Forest area. Additionally, it may be that having a wider tolerance to varied habitats compared to other hickories, combined with the wetter climate conditions of recent decades has allowed shagbark seedlings to be at similar densities to pignut and mockernut hickory (Burns and Honkala, 1990; Cowden et al., 2014; Pile Knapp et al., 2021).

4.2. Genus-specific responses

Evidence of oaks and hickories having a similar response to silvicultural treatments may be a positive result for certain management goals where promoting oak-hickory forest types in general are desired. The success regenerating oak and hickory together in other long-term studies that have applied repeated burns seems to be tied to the timing between burns (Fan et al., 2012; Knapp et al., 2015, 2017). When burns were applied too frequently (i.e., annually), hickory regeneration remained poor compared to oak, while waiting several years between burns yielded a more equal response (Knapp et al., 2015, 2017). In this case, the damage to hickory caused by fire likely overrode any ability to positively respond to increased light levels. In this study, a five-year interval between fires appears to strike the right balance between disturbance and recovery period to promote oak and hickory together.

Although not significantly different, the thin only treatment slightly favored hickory regeneration compared to treatments that included prescribed burning. This may reflect the increased shade tolerance and decreased fire tolerance of hickory compared to oak (Burns and Honkala, 1990; Knapp et al., 2015). Additionally, the higher abundance of hickory in the control treatments supports the assertion that hickory is more shade tolerant than oak (Lefland et al., 2018; Pile Knapp et al., 2021). These findings were also supported in oak-hickory forests in Missouri where non-burned forest areas generally had higher levels of hickory regeneration compared to oaks (Knapp et al., 2015, 2017).

4.3. Implications for American chestnut

American chestnut regeneration also responded positively to increased light levels and repeated burns. This result supports the hypothesis that American chestnut populations may have benefitted by historical fire-regimes within their native range. This positive response to fire is consistent with the few other studies analyzing American chestnut responses to management (McCament and McCarthy, 2005; Belair et al., 2014). Focusing regeneration efforts on locations that currently experience regular fire within the historical range of American chestnut may increase chances of successful reintroduction. Although anecdotal, it is worth noting that American chestnut saplings found throughout the burn only and thin and burn treatments were generally larger and appeared to be surviving longer before succumbing to *Cryphonectria parasitica* infection compared to unburned areas. Historical accounts (pre-European settlement) of the study area did not deem American chestnut as a dominant overstory species but may have benefitted from the logging practices of the late 1800's to early 1900's (Dyer and Hutchinson, 2021). However, additional research would be necessary to determine if American chestnut longevity is increased in areas subjected to repeated burns and if this positive response is due to increased light availability, or that repeated burning lowers blight spore loads.

Table 2
Mean predicted ± SE of *Quercus*, *Carya*, and *Castanea* saplings in each silvicultural treatment comparing pre-treatment (2000) stem densities versus the most recent (2022) sapling regeneration survey.

Treatment	Predicted Model Stem Densities per hectare								
	2000					2022			
Control	Genus	Mean density	Density range			Mean density	Density range		
	Quercus	10	2.0	-	24.3	4	0.3	-	9.0
	Carya	396	29.3	-	1169.9	72	6.4	-	203.9
	Castanea	4	0.4	-	9.3	1	0.1	-	1.1
Mechanical thinning	*Quercus*	18	2.5	-	44.6	103	17.8	-	259.3
	Carya	46	8.5	-	110.9	153	27.5	-	385.9
	Castanea	1	0.1	-	0.2	1	0.1	-	0.3
Prescribed burning	*Quercus*	76	7.9	-	210.2	887	157.2	-	2223.5
	Carya	87	13.6	-	223.1	576	84.2	-	1517.8
	Castanea	8	1.2	-	17.4	33	4.4	-	87.0
Thinning and burning	*Quercus*	78	8.4	-	217.6	1920	284.7	-	5081.1
	Carya	48	7.0	-	124.3	661	118.8	-	1669.3
	Castanea	2	0.2	-	3.1	12	1.6	-	33.0

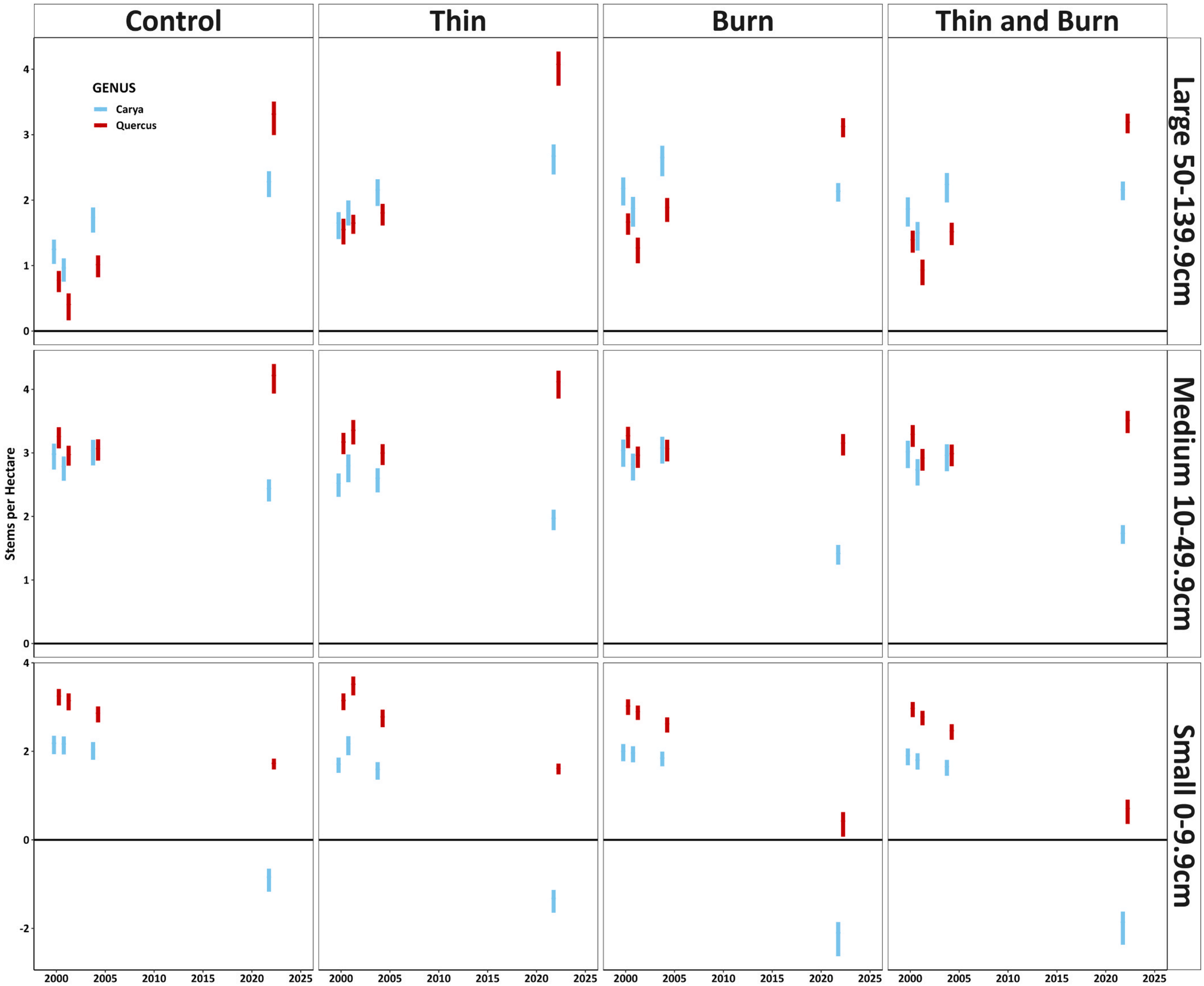

Fig. 5. Base-10 logarithmic transformed seedling stem density per hectare model standard error prediction ranges separated by seedling size class comparing *Quercus* and *Carya* for sampling years by silvicultural treatment.

4.4. Long-term efficacy

Sustained increases in oak and hickory sapling regeneration due to silvicultural treatments including repeated prescribed burns appears successful yet has taken nearly two decades to demonstrate its long-term effectiveness. This positive result continues to reflect the positive outlook on oak and hickory regeneration in response to management as described in Iverson et al. (2017). Repeated burning and thinning as a tool to increase understory light levels appears to be the most effective achieving oak and hickory management goals while simultaneously increasing the competitive ability of these species. Although this study recognizes the importance of topography on the efficacy of these silvicultural management techniques, specifically in southeast Ohio (Albrecht and McCarthy, 2006; Iverson et al., 2008, 2017; Hutchinson et al., 2024), taking a broader approach without considering topography to analyzing species- and genus-specific regeneration responses to management can make these results more applicable to a wider variety of locations in the eastern United States. The conclusions of this analysis continue to support the need for long-term planning of oak and hickory regeneration, despite the challenges of regularly applying prescribed burns, and that the time required to see positive results can take a decade or more.

Decades of fire exclusion practices, forest mesophication, and an increasingly wet climate resulting in the current lack of oak and hickory regeneration will take significant time to correct with repeated prescribed fires and likely the addition of mechanical density reduction (Blankenship and Arthur, 2006; Alexander et al., 2008; Brose et al., 2013; Hutchinson et al., 2024). Additionally, impacts of climate change will likely influence seed production patterns (masting events) of oak and hickory that rely partly on weather patterns (Smith et al., 2021; Bogdziewicz et al., 2024). Depending on the severity of climate change impacts on masting, increasing oak and hickory via silvicultural manipulation could be further hampered by challenges to seed production. Determining the impacts of these interacting and likely synergizing forces will only increase in importance as climate change progresses through the coming decades and centuries. Additionally, understanding the best practices for regeneration and sustaining oak and hickory on the landscape should provide resiliency to a hotter and drier future climate.

5. Conclusions

The positive regeneration responses of all oak species observed in this study supports the ability of long-term management for maintaining

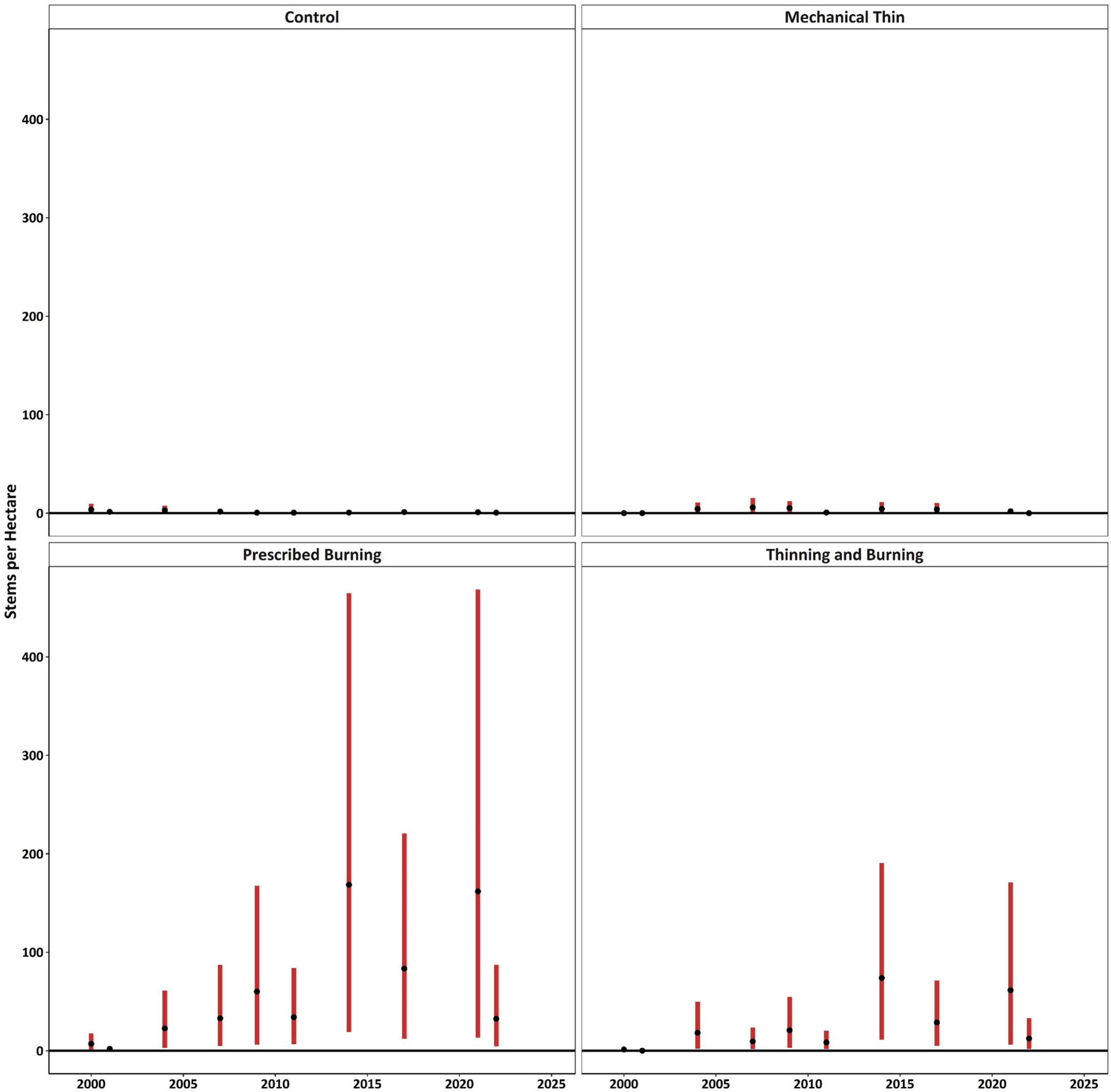

Fig. 6. Sapling stem density per hectare model prediction ranges for *Castanea dentata* for sampling years by silvicultural treatment. Overlapping bars are not statistically different ($\alpha = 0.05$).

the diversity of oaks present in eastern North American forests. While regeneration responses were different among hickory species, their overall response was positive and mirrored that of the oaks suggesting their common responses to increased forest floor light levels. The similar long-term responses of the genera to mechanical thinning and repeated prescribed burns justify their grouping when planning to increase regeneration levels of fire-adapted species. Additionally, this management strategy also increased American chestnut regeneration which may prove beneficial to restoration efforts. Although a lengthy process, the utilization of repeated fire and mechanical thinning appears to bring forest conditions closer to historic norms that promoted oak and hickory regeneration and can be a successful strategy, especially when tailored to local conditions.

CRediT authorship contribution statement

McCarthy Brian C: Writing – review & editing, Supervision, Methodology, Conceptualization. **Rudolph Aaron J:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Snell Rebecca S:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Hutchinson Todd F:** Writing – review & editing, Conceptualization.

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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Data availability

Data will be made available on request.

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