MANAGEMENT OF A SECONDARY, TEMPERATE FOREST IMPACTS POPULATION AND COMMUNITY DYNAMICS IN UNDERSTORY WOODY PLANTS

by

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Management of a Secondary, Temperate Forest Impacts Population and Community Dynamics in Understory Woody Plants

Abstract

By

ALEXA WAGNER

A majority of forested land in the eastern United States is secondary growth, previously having been cleared for agriculture or logging. These second-growth forests, when left unmanaged, tend to exist in a state of lower species and structural diversity as compared to their old growth counterparts. Forest management can be used to accelerate the transition of these young forests from even-aged forest stands of densely-spaced long-lived pioneer species to more resilient forest stands characterized by mixed ages of diverse tree species. In particular, low-impact management – including overstory thinning through removal of select trees – can be employed to release crowded trees from competition and subsequently increase structural heterogeneity within the forest and productivity of residual trees. Many young forests located in the eastern United States are also invaded by nonnative species, which degrade habitat and threaten native species. As a result, in addition to overstory thinning, management of nonnative species is a key component of forest management. However, in order to understand best practices in the management of secondary forests, more information is need on how these common management strategies drive dynamics, and ultimately composition, within the forest understory.

There are several pathways via which forest management may influence the forest understory, regulated by both abiotic and biotic changes within the forest. For instance,

management strategies that open up the forest overstory can increase light levels in the understory, potentially fostering new growth. Though overstory thinning improves resource availability, additional removal of nonnative competitors in the understory is needed to effectively stimulate recruitment and regeneration of diverse woody communities. Such changes in forest conditions will affect recruitment, growth, and mortality variably across species, increasing the likelihood of compositional shifts within managed forests. Specifically, species that respond positively to management will likely “win” out over other species that are not as quick to take advantage of new resources or respond to management-induced changes.

As a dynamic and context-dependent process, responses by understory vegetation to common management practices such as overstory thinning and nonnative shrub removal are likely quite nuanced. Here I investigate the response of understory woody communities to common forest management strategies including overstory thinning and overstory thinning done in tandem with the removal of nonnative shrubs. Specifically, I assess the impacts of these management strategies on survival, growth, productivity, dispersal rates, seedling abundance and diversity of woody species within the forest understory. To understand drivers of, and contingencies in, responses of these parameters to management, I also monitored abiotic factors including light availability, soil moisture, and litter depth across the forest landscape. Broadly, the research outlined in this dissertation explores the impacts of forest management on composition and dynamics within the understory woody plant community.

Chapter 1

Introduction

Forests comprise a large and critical component of the landscape; sequestering carbon, providing key habitat, and supporting economies through timber production (Chaudhary et al., 2016). In Ohio, 38% of the land is covered by forest, a number reflective of forest cover in the US as a whole (Forest and Snapshot, 2014, US Forest Service, 2022). A majority of these forests are regenerating, second-growth stands that were previously cleared for agriculture or other development in the early 1900s (Flinn and Vellend, 2005). Due to the legacies of past anthropogenic land use, these secondary forests tend to be less biodiverse and less structurally complex (e.g., course woody debris and presence of standing dead wood, diversity of tree ages and sizes) than are old growth forests (Silver et al., 2013). Their understories also often contain stands of nonnative shrubs (Motzkin et al., 2002; Trammell et al., 2020). Forests are threatened by a number of factors including drought, raising temperatures, increased invasion of nonnative species, and increased incidence of insect and disease outbreaks (Evans and Perschel, 2009). The low levels of structural and biotic diversity can make these young forests particularly susceptible to such disturbances. For instance, increases in temperature are predicted to shift insect and pathogen ranges northward, which will impact tree survival and productivity (Evans and Gregoire, 2007). This is particularly worrisome in young forests in which low tree diversity and high densities of vulnerable tree species can be particularly at risk (Desprez-Loustau et al., 2018). Forest management is being used to increase the resistance of these second-growth forests to environmental changes by increasing biodiversity and structural complexity in both the overstory and understory (Salonius, 2007; Webster et al., 2018).

Forest management fosters resilience via several pathways, including increasing the diversity of native species, promoting recruitment of desired species, fostering productivity of overstory trees, and enhancing the physical complexity of the forest (Evans and Perschel, 2009; Gough et al., 2021; Webster et al., 2018). Common management techniques employed to achieve these goals include thinning of the forest overstory and removal of nonnative species, both of which can foster regeneration in the forest understory, ultimately promoting native species (Duguid and Ashton, 2013; Nerfa et al., 2022; Walters et al., 2016). As forest management is increasingly employed to protect biodiversity and increase productivity, more research is needed to increase understanding of the outcomes of these practices on demographic processes and ultimately compositional shifts within the forest understory. Demographic processes, such as recruitment, mortality, growth, productivity, and dispersal of individual species can be impacted by management via changes in resource availability. Many environmental factors can play a role in driving these processes for specific species. These include, but are not limited to, microclimate, soil nutrients, soil structure, light, water, and available space; all of which can be impacted by management.

The research described in this dissertation was conducted within a nine-hectare forest management manipulation known at the Working Woods Learning Forest (hereafter Working Woods), located the Holden Arboretum. Working Woods is a young forest, previously used for row-crop farming until the late 1960s. Working Woods was managed using the following three common forest management treatments: control, overstory thinning, and overstory thinning coupled with removal of nonnative shrubs. This young forest simultaneously serves as a public demonstration of management practices and a living laboratory used to quantify the impacts of common forest management techniques on key management objectives including biodiversity, native recruitment, and plant growth. Knowledge generated in this experimental forest is shared with the public via programming, including workshops, that convey research findings on the impacts of forest management to the general public.

My research details the impacts of the forest management techniques demonstrated within Working Woods on forest demographics and community composition. In particular, I explored important demographic processes driving the composition of plant communities, including reproductive output, recruitment, growth, mortality, and dispersal. Specifically, I monitored the recruitment, growth, and mortality of 1,540 naturally-occurring woody seedlings over the course of four years following initiation of forest management. I also examined how treatment impacted fruit production in two common shrub species within the forest understory. I explored the potential for management to influence rates of seed dispersal in species dispersed via fleshy fruits – a common dispersal strategy for many of the woody shrubs present at the site – using artificial fruit models. Finally, I explored how management ultimately altered the richness of species recruiting in the understory, across the understory using patterns of beta diversity, and through time using temporal patterns of species turnover.

Dispersal is a critical process influencing plant composition within the forest understory (Dieckmann et al., 1999). The dispersal of plant propagules within the forest can by impacted by management if changes in habitat associated with either overstory thinning or nonnative shrub removal impact the activity levels or behavior of important dispersers (e.g., birds), altering rates of dispersal in managed areas. In chapter 2, I review the response of fruit production and dispersal to forest management. Specifically, I measured fruit production on two species of naturally-occurring understory shrubs (native: *Lindera benzoin* and nonnative *Rhamnus frangula*) across forest management treatments. Then, I use artificial fruit models as a proxy for fleshy fruits to determine rates of fruit removal in the system. In areas managed with canopy thinning, I observed an increase in fruit production of nonnative glossy buckthorn (*Rhamnus frangula*), as well as increased removal of artificial. Interestingly, plots managed with overstory thinning done in tandem with nonnative shrub removal did not exhibit these same levels of increased fruit removal. Rates of fruit removal were further modified by fruit color, but not by density of fruit displays. Fruit removal by birds may be impacted by management-induced changes to habitat structure such as removal of nonnative understory plants and/or the availability of naturally occurring fruit also present in those locations.

In chapter 3, I report the impacts of forest management on the recruitment, growth, mortality, and richness of woody seedlings occurring over the four years following initial management. I found higher recruitment, mortality and richness across all species in areas where the overstory was thinned and nonnatives were removed from the understory compared to thinned-only areas. This confirms that overstory thinning done without nonnative removal is insufficient for effectively stimulating these important demographic processes in the first few years of management. Management impacts were, unsurprisingly, variable across species. For example, *Liriodendron tulipifera* (tulip poplar) and *Acer rubrum* (red maple) recruited more readily under management involving overstory thinning done in tandem with nonnative shrub removal. *Prunus serontina* (black cherry) exhibited slower growth in plots with overstory thinning and understory nonnative removal compared to areas with no management while growth in other species (*Acer saccharum* [sugar maple], *Fraxinus americana* [white ash], and *Rhamnus frangula* [glossy buckthorn]) was not impacted by treatment. Although more time is needed to determine which species will become more successful following management, I suggest that certain species – with faster growth rates and more resource acquisitive strategies – are likely to be more successful under managed conditions. Collectively, I found that richness of newly recruited woody plants was highest in areas managed with both overstory thinning and nonnative shrub removal, as compared to plots managed with just overstory thinning.

In chapter 4, I explore the impacts of forest management on the composition of woody communities recruiting following management, as well as variability in communities through space and time, as measured by beta diversity and temporal turnover, respectively. Management drove compositional differences in newly recruited woody plant communities, but did so variably across years. Beta diversity, too, was influenced by forest management. Specifically, beta diversity was lowest in areas managed with overstory thinning done in tandem with nonnative shrub removal, though this result was only significant in 2020. That is to say, forest plots across these managed landscapes tended to be more heterogeneous than those in unmanaged plots. The composition of newly recruited communities changed over time in both control plots and areas managed with overstory thinning done in tandem with nonnative shrub removal, but not in thinned-only plots. Temporal turnover was robust to changes through time due to management, which may be related to lagging abiotic and biotic changes associated with management.

In chapter 5, I summarize my results, emphasizing the important implications of this research for restoration practitioners. I found forest management to be a driver of understory demographics and community composition, with variable impacts across species and through time. This matters for managers whom often actively seek to remove certain (mostly nonnative) species in their system while promoting others (mostly native). The goals of forest managers can be highly variable, and can include (but are certainly not limited to): increasing rates of carbon sequestration, improving habit for wildlife, increasing biodiversity, improving ecosystem services, and/or increasing rates of timber growth for future harvest. My research demonstrated changes in fruit production and dispersal of fleshy-fruited shrubs associated with management, with increases in these processes in areas where the overstory was thinned. This suggests that managers should strongly consider the removal of nonnative shrubs in managed areas in which their spread may be enhanced. Both recruitment and mortality of newly recruiting seedlings were highest in areas managed with both overstory thinning and nonnative shrub removal. These dynamics drove community level responses in plant composition and patterns of diversity. These findings provide further evidence that removal of nonnative shrubs is likely a critical component of the management of many secondary forests in order to effectively stimulate the regeneration of woody species quickly. Other responses, such as growth, were species-specific, with some species expressing slowed growth in response to management while others expressed increased growth. This research demonstrates that shifting dynamics associated with forest management can be nuanced and difficult to predict. The long-term consequences of forest management on compositional shifts in woody seedlings is largely undescribed and worth examining as important indicators of restoration success, and probable bellwethers of future forest composition.

Chapter 2

Overstory thinning impacts fruit production and frugivory of understory shrubs in a post-agricultural temperate forest

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Abstract

Forest management has the potential to drive demographic shifts among woody plants in the forest understory, which can determine future trajectories of forest communities. Here, we consider the relationships between fruiting shrubs, frugivores, and forest management practices in a young mixed mesophilic hardwood forest, exploring how forest management influences both fruit production and bird-mediated fruit removal in shrubs within the forest understory. Specifically, we measured fruit production and removal within one-hectare forest plots treated with one of three management treatments: 1) overstory thinning (thinning of the forest canopy trees by 20% using a mix of girdling and selective-felling), 2) overstory thinning coupled with nonnative shrub removal, or 3) unmanaged control. We find forest management to be a driver of both fruit production on and removal from shrubs, with higher productivity and rates of fruit removal in areas with overstory thinning relative to controls. These shifts in demographic processes have the potential to serve as a pathway via which forest management may alter trophic interactions.

Keywords

forest management • frugivory • fruit production • plant community • shrub dispersal

Introduction

Forest management is often employed to enhance forest resiliency by increasing native diversity and structural complexity (Kern et al., 2017; Muzika, 2017). Land-use histories dominated by anthropogenic activity (e.g., agricultural land use, deforestation, biotic invasion), often result in even-aged stands of densely spaced trees and understories dominated by nonnative species. These conditions are important drivers of both early and late life stages of plant species within the forest understory. Forest management can be used to control nonnative species, reduce overcrowding, and promote recruitment and survival in the understory (McKenzie et al., 2000; Messier et al., 2016; Millar et al., 2007). Selective silviculture involving the removal of a small number of mature trees to thin the forest canopy is one commonly used practice. Additionally, control of nonnative shrubs in the forest understory can be used to bolster native diversity within the forest understory. Combining both thinning of the forest overstory and removal of nonnative species can free up resources within the forest, stimulating recruitment and promoting survival of species remaining in the forest understory (De Lombaerde et al., 2021; Ding and Zang, 2021; Kermavnar et al., 2019).

Plants in the understory may be particularly vulnerable to the pressures imposed by dense overstory stands. Overstory thinning increases availability of resources such as water, light, and nutrients within the forest understory (Denslow et al., 1998; Scharenbroch and Bockheim, 2007). As such, overstory thinning can be an important tool to promote recruitment dynamics within the forest understory (Ares et al., 2010). However, gaps created by overstory thinning can also increase the fitness and establishment of mature (fruit-producing) nonnative shrubs like *Rhamnus frangula* and *Rosa multiflora*, ultimately increasing their abundance (Burnham and Lee, 2010; Dlugos et al., 2015).

Just as dense forest canopies can influence resource availability in the understory, thickets of nonnative shrubs tend to crowd neighboring woody plants, which leads to slower growth, reduced abundance, and lower fecundity (Maynard-Bean and Kaye, 2019; Miller and Gorchov, 2004). Removal of dense nonnative vegetation can positively impact the recruitment and survival of neighboring understory species by creating space and decreasing competition for resources. However, species trajectories within managed forests are also dependent on overstory conditions and species composition (De Lombaerde et al., 2021). For instance, the magnitude and identity of recruited individuals is influenced by the identity and abundance of reproductive individuals present in the surrounding environment (Minor and Kobe, 2019a).

Forest management also has the potential to influence key interactions between understory shrubs and their dispersers. As management mediates fruit production, habitat use by avian dispersers may be influenced, which could alter the probability of fruit removal, dispersal, and recruitment of those plant species across the forest landscape. Frugivorous birds, in particular, are important drivers of mid and long-distance dispersal for many fruit-producing plants (Butler et al., 2007) and influence plant demographics within the forest understory (Garcia et al., 2010). Habitat changes due to management (e.g., increased dead standing woody debris, decreased vegetative cover, etc.) are likely to impact these biotic relationships by promoting or discouraging activity by various bird species within the forest (Lane et al., 2015; Zhang et al., 2022). Further, forest management may impact seed dispersal variably across fruit-bearing species, dependent on plant traits. For example, fruit color and abundance can impact frugivore preference (Denslow and Moermond, 1982; Gleditsch and Carlo, 2011; McCarty et al., 2002). However, additional study is needed detailing the relationships between plants and their mutualists within the context of forest management in order to better understand the dynamics responsible for driving plant communities in managed forests (Gosper et al., 2005; Link et al., 2018).

Here, we investigate the effects of forest management on fruit production, as well as rates of fruit removal, in understory shrubs. Specifically, we measured the impact of overstory thinning on fruit production in two common shrub species: the native *Lindera benzoin* and the nonnative *Rhamnus frangula*. We also measured the impacts of overstory thinning and overstory thinning plus nonnative shrub removal on rates of fruit removal at high and low densities of red and blue fruit. We asked whether (1) overstory thinning increased fruit production in two shrub species; (2) if forest management involving overstory thinning and nonnative removal increased the handling of fruit by avian-dispersers; (3) if higher fruit abundances would increase fruit handling; and (4) if avian-dispersers preferred red fruit to blue fruit.

Methods

Study Site

Research was conducted in a mid-successional forest located at The Holden Arboretum (41.605589 ° N, -81.296129 ° W) in Lake County, Ohio. The site had been used for row-crop agriculture until approximately the 1960s. This mid-successional forest is comprised of mixed mesophilic overstory trees including: *Acer rubrum*, *Acer saccharum*, *Fagus grandifolia*, *Fraxinus americana*, *Liriodendron tulipifera*, *Nyssa sylvatica*, and *Quercus rubra*. *Acer rubrum* and *Liriodendron tulipifera* are the most common trees in the upper canopy. The understory is dominated by avian-dispersed shrubs, both native and nonnative. Common native shrubs include *Cornus florida*, *Lindera benzoin*, and *Viburnum* spp., while common nonnative shrubs include *Celastrus orbiculatus*, *Euonymus alatus*, *Ligustrum vulgare*, *Lonicera morrowii*, *Rhamnus* *frangula*, and *Rosa muiltiflora*. The bird community consists of the following species: *Baeolophus bicolor*, *Contopus virens*, *Cyanocitta cristata*, *Empidonax virescens*, *Melanerpes carolinus, Picoides pubescens*, *Poecile atricapillus, Setophaga citrina*, *Setophaga ruticilla*, *Sitta carolinensis, Spinus tristis*, *Turdus migratorius*, and *Vireo olivaceus* (personal communication, Mike Watson 2020).

In 2018, we established nine 1-hectare plots, each receiving one of three management treatments: overstory thinning, overstory thinning and nonnative removal, or control. Each management treatment was replicated three times. Thinning was accomplished with a combination of girdling or felling such that approximately 20% of overstory trees were either girdled or felled. A majority (~90%) of these trees were girdled, with felling reserved for trees that posed greater risk for damage due to their proximity to hiking trails or desirable crop trees. Girdling is a commonly used thinning technique and involves stripping (cutting) the bark of a tree past the cambium layer in order to cut off the supply of nutrients from root system, ultimately killing the tree over the course of several years. This technique keeps woody material *in-situ* while creating incremental increases in light availability as the tree dies. As opposed to the more immediate changes in light as a results of intense logging, incremental changes are shown to discourage aggressive recolonization of certain nonnative plant species (Loh and Daehler, 2008). Additionally, selective thinning can increase the diversity of woody debris present in the forest, which serve as habitat for a variety of avian-frugivore species (Atlegrim and Sjöberg, 2004; Versluijs et al., 2020). Nonnative removal was accomplished by removing all nonnative shrubs, along with grapevines within plots using mechanical removal followed by treatment with a chemical herbicide (*Aquaneat*, glyphosphate-based). Control plots were left unmanaged.

Field Monitoring – Fruit Production

To quantify the impact of management on fruit set, we counted the number of fruits produced by the native shrub *Lindera benzoin* and the nonnative shrub *Rhamnus frangula*, two of the most abundant understory shrubs found at the site. One to eleven shrubs of each species were monitored per 1-hectare plot, depending on shrub abundance within a plot. Plots that did not contain any representatives of a certain species were excluded. Shrubs greater than 1 m in height were randomly selected within management plots (*L. benzoin*: IC: *n*=21, C *n*=3; *R. frangula*: IC: *n*=48, *C*: *n*=31). We did not sample fruit production in plots with thinning and nonnative removal as this treatment involved the removal of all nonnative shrubs and, thus, the plots lacked *Rhamnus frangula*. For each shrub, we counted total number of fruits for the entire plant. We counted *R. frangula* fruits in July of 2021 (three years following management) and *L. benzoin* fruits in August of 2021 to coincide with peak fruit production. Shrub height was estimated using height classes between 1 and 4 (1 = 0.5 to1 m, 2 = 1 to1.5 m, 3 = 1.5 to 2 m, 4 = > 2 m).

To calculate the level of canopy openness experienced by each shrub we took hemispherical photos of the forest canopy l meter north of each shrub using a Nikon D5600 digital SLR camera with a Sigma 4.5mm f/2.8 EX DC HSM Circular Fisheye Lens. This was done at the time of fruit surveys. Canopy openness was digitally estimated using Gap Light Analyzer (Copyrighted by Cary Institute of Ecosystem Studies) to calculate percent area in each photo displaying open sky (Frazer et at., 1999). Volumetric water content (VWC) was measured at the location of each hemispherical photo using a *HydroSense II* Campbell Scientific hand-held probe. VMC was taken at the time of fruit surveys.

Fruit Removal

To test the impacts of management on bird-mediated fruit removal, we monitored the removal of artificial fruits by birds within the management plots. Odorless and edible artificial fruits were made with flour, butter, food coloring, and gelatin (Wennersten and Forsman, 2009). Artificial fruits were round and 1-1.5 cm in diameter (Supp. Fig. S1). They were refrigerated at 5°C for approximately 24 hours before use in the field. Artificial fruits were colored blue or red, mimicking the colors of common understory shrubs (blue nonnatives: *Ligustrum vulgare* and *Rhamnus frangula*; blue natives: *Viburnum acerifolium*, *Viburnum dentatum*, and *Vitis vinifera*; red nonnatives: *Lonicera* spp. and *Rosa multiflora*; red natives: *Cornus florida*, *Lindera benzoin*, and *Malus* spp.).

Forty-eight subplots were haphazardly nested within the three southernmost 1-hectares (one 1-ha plot per management treatment) for display of artificial fruits. Each subplot was 10 m in diameter. Subplots were assigned to display either red or blue fruit at either high (20 fruits per subplot) or low (5 fruits per subplot) densities. Four replicates of each of four fruit display treatments (Red Fruit:High Density, Red Fruit:Low Density, Blue Fruit:High Density, and Blue Fruit:Low Density) were set out in each 1-hectare management plot (with sixteen subplots per 1-hectare), and were positioned a minimum of 20 m from one another. Natural fruit density in these areas was very low, with no fruit observed within 20 m of our fruit displays. Over a 10-day period in mid-July 2020, artificial fruits were haphazardly scattered on branches between 0.5 to 2 m above the surface of the ground across multiple woody shrubs or saplings within each 10 m subplot. Prior to display, fruits were remolded in the field using nitrile gloves to create a smooth surface before being threaded with 1 mm silver copper wire that held fruit less than 10 cm from display branch. Twenty-four hours after placement in the plots, artificial fruits were scored as having been handled by a bird, or not (Supp. Fig.1). An artificial fruit was considered to have been handled by a bird if it showed beak marks, evidence of pecking/biting, or if fruit was completely removed (Lopes, 2001).

Analysis – Fruit Production

To test the impact of forest management on the fruit production of *Rhamnus frangula* in 2021, we used negative binomial regression (function:*glm.nb*, package “MASS”) to examine the total number of fruits produced as a function of forest management treatment (IC and Control) with canopy openness, soil moisture, and shrub height class included as covariates in all fruit production models. Note that the IC treatment can indirectly affect fruit production by altering canopy openness. Thus, we also report the results of this model without canopy openness and soil moisture as covariates, allowing potential indirect effects of IC that are mediated through those environmental factors to be attributed to the treatment term in the model (Supp. Table S1.). We chose a negative binomial regression model in order to account for over dispersion of our count data. Significance of individual factors within the models was determined using Chi-square tests (a non-parametric analysis) (function: *anova*). Note that we do not statistically analyze the impacts of management on *Lindera benzoin* due to small sample sizes within the control plots.

Fruit Removal

To test the effects of forest management on rates of fruit removal across forest management treatments for artificial fruits of two colors, hung at two densities, we calculated the proportion of bird-handled fruit out of the total displayed fruit at each subplot. We analyzed the proportion of bird-handled fruits as a function of management, density (High, Low), and color (Blue, Red) as predictors using a general linear model (function: glm()) with quasipoisson distribution to account for over dispersion. Post-hoc significance of models was determined using Tukeys post-hoc analysis (function: TukeyHSD()). Canopy openness and soil moisture were not significant when included as covariates, therefore these terms were removed from our model (Supp. Table S2.). There is no significant interaction between treatment and fruit color, which could have indicated that birds have different color preferences depending on which treatment type was being considered. As such, the interaction term was also removed from our model.

Results

Fruit Production

Lindera benzoin plants produced slightly more fruits in IC plots relative to control plots on average, but there were notably fewer plants within the control plots and we did not explore statistical differences among treatments for this this species (Fig. 2.1.). *Rhamnus frangula* also produced more fruit in thinned plots ($\chi^2_{1,77} = 10.5$, $p<0.01$) when accounting for modeled effects of canopy openness ($\chi^2_{1,75} = 67.3$, $p=0.17$), soil moisture ($\chi^2_{1,74} = 67.7$, $p=0.55$), and shrub height ($\chi^2_{1,76} = 10.5$, $p<0.001$). The effect of management treatment was similar in models without canopy openness as a covariate ($\chi^2_{1,\ 77} = 10.12$, $p=<0.01$).

Fruit Removal

Treatment ($\chi^2_{2,48} = 18.88$, $p<0.001$) and fruit color ($\chi^2_{2,48} = 11.39$, $p<0.001$) impacted the handling of fruit by birds. Birds handled more artificial fruit in areas with overstory thinning compared to control areas ($p<0.01$; Fig. 2.2.) and areas with both overstory thinning and nonnative removal ($p<0.001$; Fig. 2.2.). On, average 44% of available fruits were handled in thinned plots while approximately 20% and 13% were handed in control plots, and plots with thinning plus nonnative removal, respectively. Red fruit were preferred to blue fruit ($\chi^2_{1,48}= 13.3$,

$p<0.001$; Fig. 2.2.). Fruit handling was unaffected by the density of fruit in display clusters ($\chi^2_{1,48} = 2.2$, $p= 0.13$; Fig. 2.2.).

Discussion

Forest management is often used to create opportunity for new recruitment in the understory via multiple pathways, including by influencing the productivity and dispersal of species already present in the forest understory. We show fruit production and removal can be affected by forest management manipulating both the overstory and understory. *Rhamnus frangula* (a nonnative shrub), produced a greater number of fruits following overstory thinning compared to unmanaged controls. Low sample sizes limited out ability to statistically explore differences in fruit production of *Lindera benzoin* (a native species) across the management treatments, though the general trend for the species was similar to that seen in the nonnative shrub, with somewhat higher fruit production in plots treated with overstory thinning. Further, we observed the highest rates of fruit removal in areas with overstory thinning relative to control and plots with both overstory thinning and nonnative removal. However, plots treated with overstory thinning in tandem with nonnative removal had lower rates of fruit removal than controls.

Fruit production is often higher in areas with greater light availability (Silander and Klepeis, 1999). As a result, thinning the forest canopy could be expected to result in higher fruit production in shrubs. This is consistent with our finding that *Rhamnus frangula* produced more fruit in areas managed with overstory thinning, although treatment also seems to have an effect beyond that explained directly by the measured variability in canopy openness (as well as soil moisture). We see a positive (though insignificant) trend between fruit production and canopy openness (Supp. Fig. S2). This is similar to the findings of Cipollini et al (1994) which found *Lindera benzoin* to be more productive in full light conditions, relative to the forest understory, but did not vary in productivity across a range of light intensities within the forest (Cipollini et al., 1994). Management may also be impacting fruit production through pathways beyond the increase in light availability. Additional mechanisms potentially mediating the effects of management could include changes in nutrient availability (Yu et al., 2022) or the competitive effects imposed by neighboring vegetation (Minor and Kobe, 2019). For instance, thinning of canopy trees may increase nutrient availability for the remaining vegetation, which could impact fruit production.

Dispersal can also be an important determinant of local plant communities, and can, itself, be driven by environmental heterogeneity. As such, possible shifts in dispersal dynamics could be key drivers of responses to forest management in the understory community. Habitat use by frugivores, and ultimately rates of seed dispersal, can be influenced by the presence and distribution of canopy gaps (Cipollini et al 1994; Germaine et al., 1997; Levey, 1988; Stribling et al., 1990). We found fruit removal by birds to be highest in forests managed by overstory thinning alone relative to areas managed with overstory thinning in combination with removal of nonnative shrubs or unmanaged areas. The increase in fruit removal in areas with overstory thinning relative to areas in which the canopy was thinned in tandem with removal of nonnative shrubs is presumably a result of changes in understory vegetation. Avian richness in known to decrease as tree cover and fruit abundance decrease (Albrecht et al 2012). However, tree thinning can promote early successional, fruit-eating bird species like buntings (*Passerine* spp.), chats (*Granatellus* spp.), pee-wee (*Contopus* spp.), and vireos (*Vireo* spp.) (Campbell et al., 2007; Gram et al., 2003). Habitat structure (e.g. woody plant abundance, canopy cover, number of dead standing trees, etc.) can also influence avian space use, sometimes regardless of landscape scale (Jayapal et al., 2009; Mitchell et al., 2006, 2001), although the nature of these relationships is typically species and context-dependent. In general, bird richness decreases as the density of nonnative shrubs increases, although bird abundance tends to be unaffected (Nelson et al., 2017). We observed increased fruit removal when we thinned the forest canopy, but this effect disappeared when we also removed nonnative shrubs. It is possible that birds are responding to this disturbance (shrub removal) by moving away from these areas (Stribling et al., 1990), or that the potentially negative effect of lower fruit abundance on bird abundance outweighs the potentially positive effects of both shrub removal and overstory thinning on bird diversity (or abundance), and subsequent frugivory. As girdled trees die and dead standing wood increases over time, bird habitat use may respond positively to increased spatial complexity of the understory habitat in plots with both overstory thinning and nonnative shrub removal (Germaine et al., 1997). Given the observed sensitivity of mutualists to forest management, restoration attempts aiming to increase the integrity of early successional forests should consider the composition and behavior of dispersers present within a system (Pinotti et al., 2012).

In addition to the importance of habitat, plant traits are also important drivers of dispersal. Consistent with other studies of eastern forests in North America, we found that red fruit were removed more readily than were blue fruit (Arruda et al., 2008; Duan et al., 2014). The preference for red fruit was consistent across all management treatments. In our forested system, common native red-fruiting shrubs include *Cornus florida* and *Lindera benzoin*, while nonnative red-fruiting shrubs include *Celastrus orbiculatus*, *Euonymus alatus*, *Lonicera morrowii*, and *Rosa muiltiflora*. Native blue-fruiting shrubs include *Viburnum acerifolium* and *Viburnum dentatum*, while common nonnative shrubs with blue fruit include *Ligustrum vulgare* and

Rhamnus frangula. In our site, red-fruiting shrubs are generally more common than blue-fruiting shrubs (*e.g.*, *L. benzoin* is more common than any blue-fruited native shrub [including *Ligustrum vulgare* and *Viburnum dentatum*], and *R. multiflora* is more common than *R. frangula* and any other blue-fruited nonnative shrub [including *Viburnum acerifolium*, and *Vitis riparia*]). This suggests that interactions between fruit color and avian dispersal could be important drivers of understory community composition, both in the past and into the future. Contrary to our expectations, we did not find density of fruit display (high vs. low abundance) to strongly impact fruit removal. However, others have found that fruit removal by birds decreases with decreasing fruit abundance (Albrecht et al., 2012; Quitián et al., 2019), though these dynamics can differ across shrub species and frugivore guilds (Mokotjomela et al., 2013). We found fruit handling to be marginally lower at lower fruit densities, which may be related to our observation of lower fruit removal in plots where the understory has been removed as presumably these forested sections contain lower overall fruit densities as a direct result of shrub removal. It is possible that our “low” and “high” fruit display densities were not drastic enough for us to detect the difference in bird preference.

Our study is limited by the number of wild-occurring individuals at our site. In the context of our forest, additional replicates and species would provide a greater understanding of management’s impact on fruit production, especially in native versus nonnative species, broadly. Additionally, the slow death of canopy trees via girdling (Matsushita et al., 2022) may mean our results will become stronger over time as these girdled trees become less robust over time and ultimately die.

Forest management influences dynamics within the forest understory via both biotic and abiotic drivers of understory fruit production and removal. However, these dynamics are likely to vary across plant species and types of forest management. Understanding these nuanced dynamics will play a key role in the ability of scientists and managers, alike, to predict the successes and failures of understory plant species. We conclude forest management has the potential to influence key demographic processes responsible for maintaining plant populations, prompting the need for basic research to fully understand how forests are likely to respond to management now and into the future.

Figures:

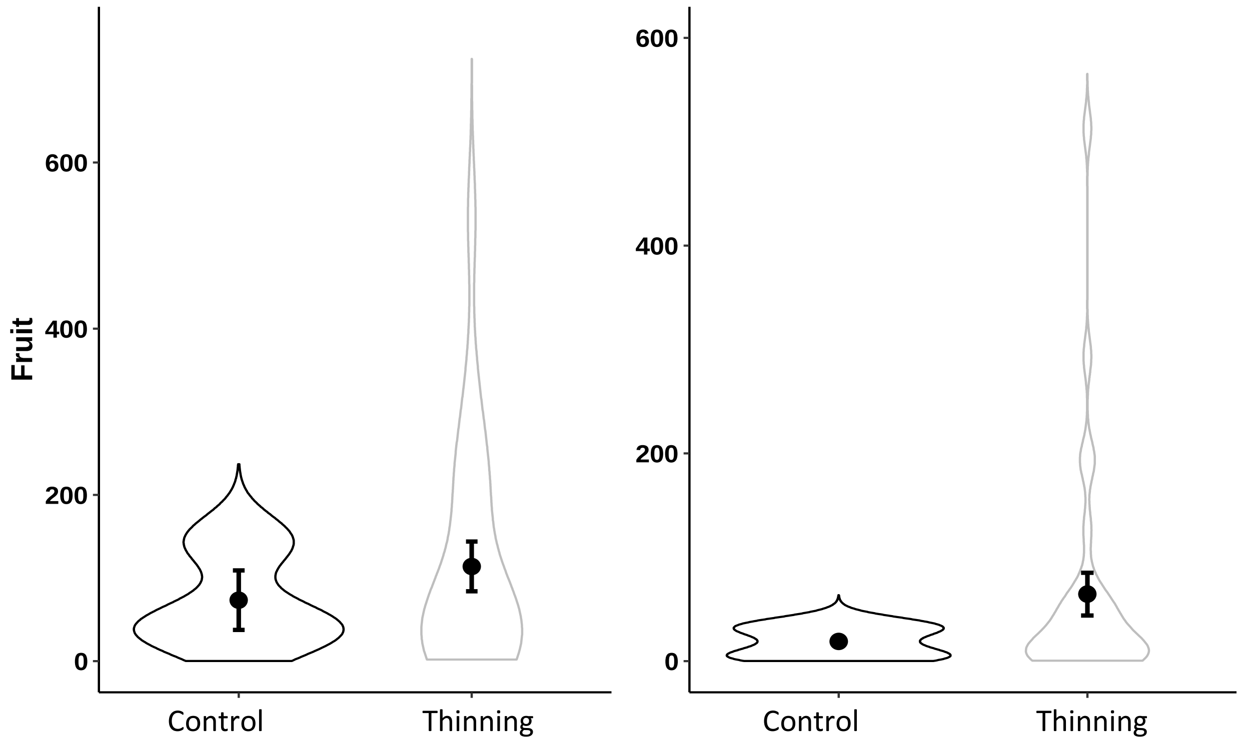


Figure 2.1. The total number of fruits produced by Spicebush (*Lindera benzoin*) (left) and Buckthorn (*Rhamnus frangula*) (right), across control and thinned plots. Error bars show standard error around the mean while ‘violins’ represent the shape of the distribution.

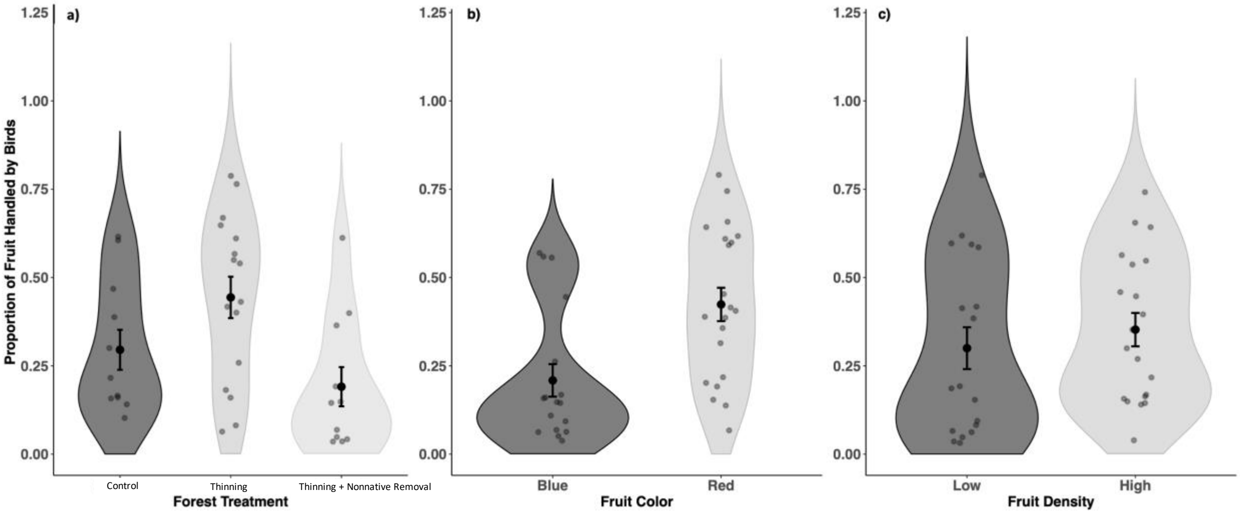


Figure 2.2. Average proportion of artificial fruits handled by birds: a) in control plots, thinned plots, and thinned plots with nonnative removal; b) for blue fruits and red fruits; and c) for fruits hung at low or high densities. Error bars show standard error around the mean while 'violins' represent the shape of the distribution.

Chapter 3

Woody seedling recruitment, mortality and richness influenced by forest overstory thinning and nonnative shrub removal

Abstract

Forest management can be used to accelerate the progression of young and unhealthy secondary-growth forests toward systems more closely resembling old-growth forests in terms of structure and function. Future trajectories of such forests are determined, in part, by demographic shifts among woody species in the forest understory in response to management. Such management commonly includes thinning of the forest overstory and removal of nonnative species from the understory. Here, we explore the impacts of these common forest management techniques on woody seedling demographics within the understory of a central hardwood forest recovering after agricultural use. Specifically, we treated forest plots with one of three management treatments: 1) overstory thinning (girdling of approximately 20% of trees to open the canopy), 2) overstory thinning coupled with nonnative shrub removal, or 3) unmanaged control. We monitored recruitment, growth, and mortality of native and nonnative woody seedlings across these management treatments. We found that management pairing overstory thinning with nonnative shrub removal boosted seedling recruitment but also mortality. Richness of these woody recruits was also higher in areas managed with this combined treatment. However, species recruitment, growth and mortality responses tended to be species-specific, with many individual species not responding to management. Overall, we found that management impacted important demographic responses during the first few years following application, and did so in ways that increased the richness of newly recruiting communities. However, we also noted that nonnative shrub removal was a critical component of management, driving changes above and beyond what was seen in forests managed with overstory thinning alone.

Key words:

Forest management • recruitment • mortality • plant communities • species richness

Introduction

A legacy of past anthropogenic land use across a majority of forested land in the United States has left many of our forests less productive and biodiverse than their old growth counterparts (USDA, 2020). Critically, the lower diversity and structural complexity of these previously disturbed forests can make them less resilient to disturbances including wind, fire, and disease compared to old-growth forests (Seidl et al., 2014). Management of these young forests can increase resiliency by increasing species diversity, promoting a greater range of tree age classes and recruitment stages, and discouraging densely-packed stands (Ibáñez et al., 2019; McCarthy and Bailey, 1994; Webster et al., 2018). Proper forest management also promotes long-term carbon storage (Fargione et al., 2018; Tappeiner et al., 1997) and provides important wildlife habitat (Simard et al., 2018).

To promote the recruitment and survival of a diverse array of native species there are a number of forestry techniques that can be employed, many of which focus on thinning the forest canopy. Thinning the forest canopy can be key to freeing up resources such as water, light, and nutrients, increasing productivity and survival for both the remaining forest vegetation and future seedlings (Cipollini et al., 1994; Denslow et al., 1998; Ding and Zang, 2021; Fujii et al., 2021; Kermavnar et al., 2019; Scharenbroch and Bockheim, 2007; Zhu et al., 2014). Forest managers often thin dense canopies by selectively felling (and subsequently removing for timber) a subset of mature trees. Tree girdling is another technique that can be useful, particularly when a timber harvest is not desired (Pariona et al., 2023). Girdling is used to kill trees by disrupting sap transport through the phloem by creating a shallow cut (~2-5 cm depth) around the entire circumference of a tree. Death of girdled canopy trees is slow compared to felling, which creates immediate canopy gaps as trees fall. In girdled trees, death typically occurs between one and four years following girdling (Gough et al., 2021, 2013; Merceron et al., 2016; Schroder and Ward, 2022). Unlike timber harvest, managers thinning the forest canopy via girdling leave the dead trees standing on the landscape. Girdling has many benefits as a forest management technique. For instance, the increase in standing dead trees (snags) within the forest provides habitat for wildlife and woody material left within the forest further increases structural complexity (Stribling et al., 1990). Leaving standing dead wood on the site also increases carbon storage within the forest (Ameray et al., 2021). Both the ability of a system to store carbon and maintain structural complexity via diverse tree ages are important factors for forest resiliency against climatic threats (Gough et al., 2021; Grigri et al., 2020; Niedermaier et al., 2022). However, more research is needed to determine how thinning of the forest canopy by selectively girdling trees impacts forest dynamics, including demographic processes. Such knowledge will foster a better understanding of how this management practice may shape future forest communities.

Thinning of the forest canopy (either by girdling or other management techniques such as selective harvest) is often done in tandem with removal of nonnative shrubs in the forest understory as secondary forests are often heavily invaded by nonnative shrubs (Collier et al., 2002; Holmes and Matlack, 2017). Removal of nonnative shrubs can be a critical component of forest management in many young forests and can impact species recruitment above and beyond any changes associated with overstory thinning alone (Ali et al., 2019; Beckage et al., 2017). Removal of nonnative shrubs can decrease competition and increase suitable habitat within the forest understory, creating conditions favorable to new recruitment of native woody plants (De Lombaerde et al., 2021). Such management can boost native species within the forest and can have the added benefit of increasing the diversity of ages of trees represented within the forest by promoting new recruitment. However, our understanding of how understory dynamics respond to nonnative shrub removal when done in tandem with overstory thinning is currently lacking (Landuyt et al., 2019). Management techniques removing nonnative plants and those creating canopy gaps are both known to change environmental conditions, potentially impacting the survivorship and growth of tree seedlings (Beckage and Clark, 2003). Understanding which plant species experience enhanced survival and growth as a result of management allows us to make predictions about future forest communities.

Here, we explore the impacts of forest management on the recruitment, growth, survival, and richness of woody seedlings. We predicted that forest management would promote overall higher rates of recruitment, growth, and survival of woody seedlings in plots with overstory thinning and nonnative removal in the understory compared to plots managed with just overstory thinning. We further expected that responses in recruitment, growth and survival to management would differ across species, with some species responding more strongly to forest management than others. Together, we predicted that these responses would drive increased richness of woody seedlings in managed plots.

Methods

Site and Design

We established a forest management manipulation within in a maple-dominated central hardwood forest located at the Holden Arboretum (-81.296129, 41.605589) in Lake County, Ohio. The average monthly temperature in the area typically ranges from 6-26 °C across the year, with a mean annual temperature of 10.7 °C. The average monthly precipitation is typically between 5-10 cm across the year with mean annual precipitation of 99.23 cm (US Climate Data, 2022). Released from agriculture approximately sixty years ago, the overstory of this mid-successional forest is dominated by (in order of relative abundance): *Acer rubrum*, *Acer saccharum*, *Liriodendron tulipifera*, *Fagus grandifolia*, *Quercus rubra*, and *Quercus alba*. Common woody shrubs within the forest include *Rosa multiflora*, *Rhamnus frangula*, and *Lindera bezoin*. Common woody seedlings found in the forest understory include *Fraxinus americana*, *Acer rubrum*, *Acer saccharum*, *Liriodendron tulipifera*, *Rhamnus frangula*, *Rosa multiflora*, *Ligustrum vulgare*, *Lonicera morrowii*, *Lindera benzoin*, *Viburnum acerifolium*, and *Viburnum dentatum*.

We established nine 1-hectare plots, each receiving one of three management treatments: overstory thinning, overstory thinning with nonnative removal in the understory, or unmanaged control, with three replicates of each management treatment. We implemented the overstory thinning by selectively targeting canopy trees using a combination of girdling (~90% of thinned trees) and felling (~10% of thinned trees). Girdling was preferred in order to retain standing dead biomass in the system, but some trees were felled if they posed a threat to neighboring trees or trails. For the overstory thinning and nonnative removal, all nonnative shrubs in the forest understory, along with *Vitis* spp. (wild grapevine), were removed with a mixture of hand pulling, rototilling and herbicide application (*Aquaneat*, glyphosphate-based). Large grapevines were cut and stamped with *Aquaneat*. Continued management of nonnative shrubs was implemented annually in the fall to limit reestablishment of nonnative shrubs.

In 2018, we haphazardly selected 116 mature (DBH>20) trees across all management plots. All selected trees were one of three species: *Acer rubrum*, *Acer saccharum*, or *Liriodendron tulipifera*. One and a half meters due north from the trunk of each selected tree we established a 1-m^2 subplot. This resulted in 8 to 17 subplots per 1-hectare management plot.

Biotic Monitoring

Twice per growing season, beginning in June 2019, we censused all seedlings growing within the subplots. Censuses occurred toward the beginning and end of each growing season (June and August) from 2019 to 2022. During these censuses, all woody seedlings < 60 cm in stem height occurring within a subplot were individually tagged with a uniquely numbered small butt-end aluminum band (National Band and Tag Company). We recorded a seedling as dead if we observed that the individual lacked leaves and had a brittle stem at a census. Sometimes individuals that had been censused previously were not observed at a census. We considered these "lost" seedlings to be dead if that individual was missing for more than three years. In these cases, we considered the year of death to be the first census in which the individual did not appear.

Abiotic Monitoring

Canopy openness, litter depth, and soil moisture were measured 2.5 m from the trunk of the selected tree in each cardinal direction. To measure canopy openness, we took hemispherical photos of the forest canopy. A Nikon D5600 digital SLR camera with a Sigma 4.5 mm f/2.8 EX DC HSM Circular Fisheye Lens was positioned 1.5 m above the forest floor and a photo was taken of the forest canopy directly overhead. Photos were acquired between June and August of 2020. Photos were processed using ImageJ with the Hemispherical 2.0 plugin to set contrast between sky and forest canopy. These images were then analyzed using Gap Light Analyzer to measure canopy openness (Cary Institute), providing an estimate of percent area not occupied by leaves or branches (the area of the photo showing open sky). Canopy openness was averaged across all four points surrounding each adult tree to generate a single estimate of canopy openness for each subplot. In August 2022, we measured litter depth at the same four hemispherical photo locations surrounding the selected tree (2.5 m due N, E, S, and W from the tree trunk). The four litter depth measurements were averaged to generate a single value for each subplot. Volumetric water content (VWC) was measured at the same four locations in July 2020, using a HydroSense II Campbell Scientific hand-held probe. Given the number of plots and their spatial distribution, we had to measure soil moisture across a period of 4 weeks. To understand the relative distribution of soil moisture levels across plots correcting for day-to-day variability in soil moisture levels across the sampling period, we standardized field measurements using soil moisture measurements taken each day at each of four "standard" locations located approximately 2-meter from edge of forest. We averaged these four standard soil moisture measurements daily to create a reference VWC for each day and also calculated a maximum soil moisture value for the season taken across the four standard points. These values were then used to scale the field measurements as a function of the relative wetness experienced on the specific day of each field VWC measurement.

$$standardized\ VWC = VWC * \left(2 - \frac{reference\ VWC\ (on\ date\ of\ measurement)}{\text{maximum}\ \ reference\ VWC\ (across\ all\ dates)}\right)$$

This standardized soil moisture value was then averaged across the four points surrounding each adult tree.

Analysis – Field Parameters

Statistical analyses were conducted in Rstudio (Version 1.3.1093). To calculate seedling recruitment within each subplot we used the June 2019 census as a starting point, and counted any new seedling appearing over the next seven censuses (through August of 2022) as a new recruit. This provided us with the number of new individuals appearing within each subplot from initiation of treatments through the end of the 2022 growing season. To explore seedling growth rates, we examined the change in stem height from June 2019 to August 2022 for all individual seedlings present in both of these censuses. We did not include individuals that recruited after June 2019 or died prior to August 2022. To calculate mortality, we counted the number of individuals of each species that died from August 2019 through August 2022 (no death was recorded in June 2019 as this was the initial year of banding) within each subplot. To correct mortality rates for the total number of seedlings present, we divided the total number of seedlings that died by the total number of seedlings ever present within each subplot. Note that plants tagged in June 2019 included individuals that were present before the experiment began.

Effects of Management on Recruitment and Mortality

We explored the impacts of forest management on recruitment of seedlings in the understory using general linear models. Specifically, we used a general linear model (function: glm()) to explore the number of newly recruited individuals between 2019 and 2022 as a function of forest management treatment. We also used a general linear model to test the proportion of individuals that died in this time period as a function of management. Significance of all models (recruitment and mortality) was tested using ANOVA (function: Anova(), package: "car") (Fox and Weisberg 2019). Tukey post-hoc analysis was used to evaluate pairwise differences among treatments (function: TukeyHSD()). We report model results with (Table S3.1) and without canopy openness, soil moisture, and litter depth as covariates. These covariates can be directly influenced by treatment, and thus their inclusion limits our ability to detect treatment effects, but can also can help to identify drivers of and contingencies in responses to forest management.

Species-Specific Effects of Management on Recruitment, Growth, and Mortality

We also explored responses of recruitment, growth, and mortality to management treatment for each of the seven most abundant woody species (*Acer rubrum*, *Acer saccharum*, *Fraxinus americana*, *Liriodendron tulipifera*, *Prunus serotina*, *Rhamnus frangula*, and *Vitis* spp.) within our seedling surveys. For each species, we ran a general linear model glm() to determine the impact of forest management on each variable (recruitment, growth, and mortality) from 2019 to 2022. We did not model the effects of treatment on mortality for *Rhamnus frangula* and wild grape *Vitis* spp. since management involved the removal of each. We did not model the effects of treatment on growth for *Acer rubrum*, *Liriodendron tulipifera*, or *Vitis* spp. due to low sample size of individuals surviving from 2019 to 2022. In each species model, we included canopy openness, soil moisture, and litter depth, in addition to management treatment, as fixed effects to account for environmental variability (Table S3.2). We also ran these models without canopy openness, soil moisture, and litter depth as covariates (Table S2.3).

Effects of Management on Richness

To test for treatment effects on plant richness, we tested the number of species that recruited from 2020-2022 in each subplot as a function of management treatment using a general linear model. Significance of richness models was tested using ANOVA (function: Anova(), package: “car”). Differences among management treatments were evaluated using Tukey post-hoc analysis (function: TukeyHSD()).

Results

Seedling recruitment from aggregating data across all species responded to forest management ($F_{2,91}$=132.24, p=0.01). Specifically, recruitment was higher in plots with combined overstory thinning paired with nonnative shrub removal, as compared to plots with thinning alone (p=0.02) (Fig. 3.1). Control plots had marginally lower recruitment compared to plots with combined overstory thinning and nonnative removal ($p=0.06$) (Fig. 3.1). However, controls did not differ from plots with overstory thinning ($p=0.87$) (Fig. 1).

Mortality responded to forest treatments four years post-management ($F_{2,86}=3.51$, $p=0.03$) (Fig. 1). Specifically, mortality was higher in plots with combined overstory thinning paired with nonnative shrub removal, as compared to plots with thinning alone ($p<0.01$) (Fig. 3.1). In control plots, mortality did not differ from plots with overstory thinning ($p=0.57$) (Fig. 3.1) and was slightly lower compared combined overstory thinning and nonnative removal ($p=0.11$) (Fig. 3.1).

Recruitment of newly established seedlings from 2019 to 2022 was highest in plots with overstory thinning and removal of nonnative shrubs compared to plots with overstory thinning or no management for *Acer rubrum* ($F_{2,87}=3.95$, $p=0.02$) (Fig. 3.2) and *Liriodendron tulipifera* ($F={}_{2,87}8.19$, $p<0.001$). Management did not affect the recruitment of the remaining five species (*Fraxinus americana*: $F_{2,87}=0.75$, $p=0.48$; *Acer saccharum*: $F_{2,87}=0.68$, $p=0.51$; *Rhamnus frangula*: $F_{2,87}=0.82$, $p=0.44$; *Prunus serotina*: $F_{2,88}=0.945$, $p=0.41$; *Vitis* spp.: $F_{2,87}=1.68$, $p=0.19$) (Fig. 3.2). Management did not impact the mortality of any species (*Fraxinus americana*: $F_{2,83}=0.93$, $p=0.34$; *Acer saccharum*: $F_{2,26}=1.35$, $p=0.28$; *Acer rubrum*: $F_{2,25}=2.42$, $p=0.11$; *Liriodendron tulipifera*: $F_{2,40}=0.37$, $p=0.11$; *Prunus serotina*: $F_{2,32}=0.52$, $p=0.69$; *Vitis* spp.: $F_{2,8}=0.37$, $p=0.71$) (Fig. 3.2). Management impacted the growth of *Prunus serotina* ($F_{2,9}=4.32$, $p=0.04$) (Fig. 3.2). Management did not impact the growth of the remaining three species (*Fraxinus americana*: $F_{2,41}=1.45$, $p=0.25$; *Acer saccharum*: $F_{2,5}=0.13$, $p=0.37$; *Rhamnus frangula*:$F_{2,12}=10.31$, $p=0.26$) (Fig. 3.2).

Forest management impacted richness of newly recruited woody seedlings ($F_{2,90}=4.81$, $p=0.01$) (Fig. 3.3). Specifically, richness was higher in plots managed with both overstory thinning and nonnative shrub removal as compared to plots managed with overstory thinning alone (p<0.01). However, richness in these plots did not differ from that found in unmanaged controls (p=0.41). Unmanaged control plots also did not differ from plots managed with overstory thinning alone (p=0.18).

Discussion

Demographics of tree seedlings in the forest understory play a key role in long-term forest dynamics (Harmon et. al., 2015). We found that forest management affected seedling recruitment, mortality, and growth within our secondary deciduous forest. These results ultimately influenced seedling richness, with more seedling species recruiting in managed plots. Specifically, the combined effects of overstory thinning and removal on nonnative shrubs increased woody seedling recruitment. However, this management treatment also increased mortality rates among these seedlings. Collectively, these processes can contribute to the nature of reassembling plant communities. Ultimately, we found richness of these woody seedlings to be highest in plots managed with overstory thinning done in tandem with nonnative management. Species-specific patterns were variable across management strategies. Growth rates of young woody seedlings were unchanged across treatments for most species, though we observed a decrease in stem height of *Prunus serotina* in the combined management treatment type and higher growth rates in species including: *Fraxinus americana*, *Liriodendron tulipifera*, and *Rhamnus frangula*.

Over the course of the first four years following forest management initiation, we found higher recruitment of woody seedlings in areas managed with overstory thinning done in tandem with nonnative shrub removal. Shade-tolerant species (Humbert et al., 2007) already dominant within the mature trees within the forest – such as *Acer rubrum*, *Acer saccharum*, and *Liriodendron tulipifera* – were among the most commonly recruited species across our subplots. The relatively high recruitment of these species is likely promoted by a high input of seeds from abundant nearby adults, combined with the generally resource acquisitive traits of these species. Although a highly stochastic process, we expected recruitment to respond to changes in overstory stand structure, as these effects can be mediated by interactive effects between changing light levels and the shade tolerance of species in the forest understory (Käber et al., 2021). We found the highest rates of recruitment in areas with overstory thinning and nonnative removal. Both forest management and nonnative shrub removal have been shown to influence the dynamics of woody seedlings in the overstory. Overstory thinning, for example, has been shown to increase recruitment of tree seedlings relative to unmanaged areas (Coates, 2002; Gutiérrez and Trejo, 2022; Zhang and Yi, 2021). Similarly, removal of nonnative shrubs has been found to promote the survival of seedlings (De Lombaerde et al 2021). We found seedling survival to be lower in areas with combined overstory thinning and nonnative shrub removal relative to areas managed with overstory thinning alone, though the combined management treatment did not differ from control plots.

With variability in traits (such as shade-tolerance) across species, we expected individual species to respond variably to forest management. We found that overstory thinning coupled with nonnative shrub removal drove higher recruitment rates in early successional species such as *Liriodendron tulipifera* and *Acer rubrum*. Forest management also slowed the growth of *Prunus serotina*, although did not impact the remaining species (*Acer saccharum*, *Fraxinus americana*, and *Rhamnus frangula)*. We do not observe species-specific responses in terms of mortality across our species. In contrast to our results, Beckage and Clark (2003) did find species-specific responses to forest management, with differential mortality of (in decreasing order of mortality) *Quercus rubra, Acer rubrum* and *Liriodendron tulipifera* following removal of understory vegetation, although these results are likely dependent on environmental context, including resource availability, within managed sites. More time may be required to fully understand how variability in species-level responses to management will influence competitive dynamics among species, and ultimately the composition of future communities. For instance, Beckage et al., (2017) demonstrated the differential responses of common temperate understory species such as *Acer rubrum* and *Liriodendron tulipifera* were mediated by context-specific factors such as nutrient availability. Our research adds to our understanding that the combined forest management of the forest overstory and understory can dictate the magnitude of demographic responses within young woody seedlings during the first few years following management. Tracking species-specific dynamics in the forest understory in response to management into the future will facilitate our ability to predict the composition of future forest communities.

Along with species-specific responses, community changes will also play a key role in regulating understory dynamics, ultimately shifting trajectories for plant communities undergoing restoration efforts. Increasing the diversity of plant communities is of concern for managers aiming to improve the integrity of their system (Muzika, 2017). We found the richness of newly recruited woody seedlings to be higher in areas managed with overstory thinning done in tandem with nonnative shrub removal. Other studies also demonstrate increased richness as a result of canopy gap creation (Walters et al., 2016) or removal of nonnative understory shrubs (Moore et al., 2023).

Lack of responses to management in some species may be due to time lags between the implementation of forest management and changes in environmental conditions in the understory. For example, girdled trees may be slow to die, often taking years. The slowness of this process results in a situation in which environmental changes associated with the management action, such as increased light levels in the forest understory, take place slowly. The time that it takes a forest to respond to assisted succession via forest management can vary from 1-7 years (Beckage et al., 2017; Duah-gyamfi et al., 2014; Harmon and Pabst, 2015). As such, we might expect slow shifts in species demographics (Kern et al., 2017).

Managers often aim to increase the abundance and variety of desired species (e.g., encourage native regeneration), while decreasing weedy species. We demonstrated the ability of forest management to influence key demographic components in the understory. This understanding can inform land managers aiming to restore specific species, as well as overall diversity, in degraded, secondary forests. These results illustrate the value of studying population dynamics among woody seedlings, which, as quick responders to management, likely provide early evidence of management's impacts within forests.

Figures:

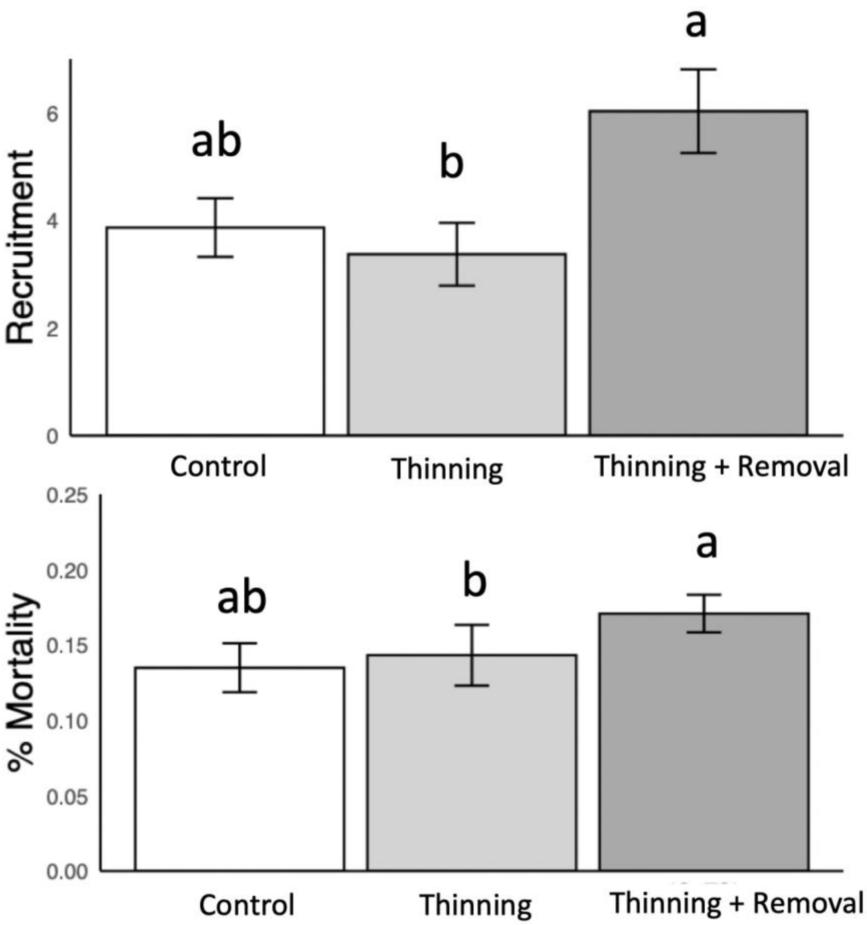


Figure 3.1. Average number of woody seedlings that recruited (top) and the proportion of woody seedlings that died (bottom) in each forest management treatment from 2019 through 2022. Letters indicate significant differences across treatments based on Tukey multiple comparison test.

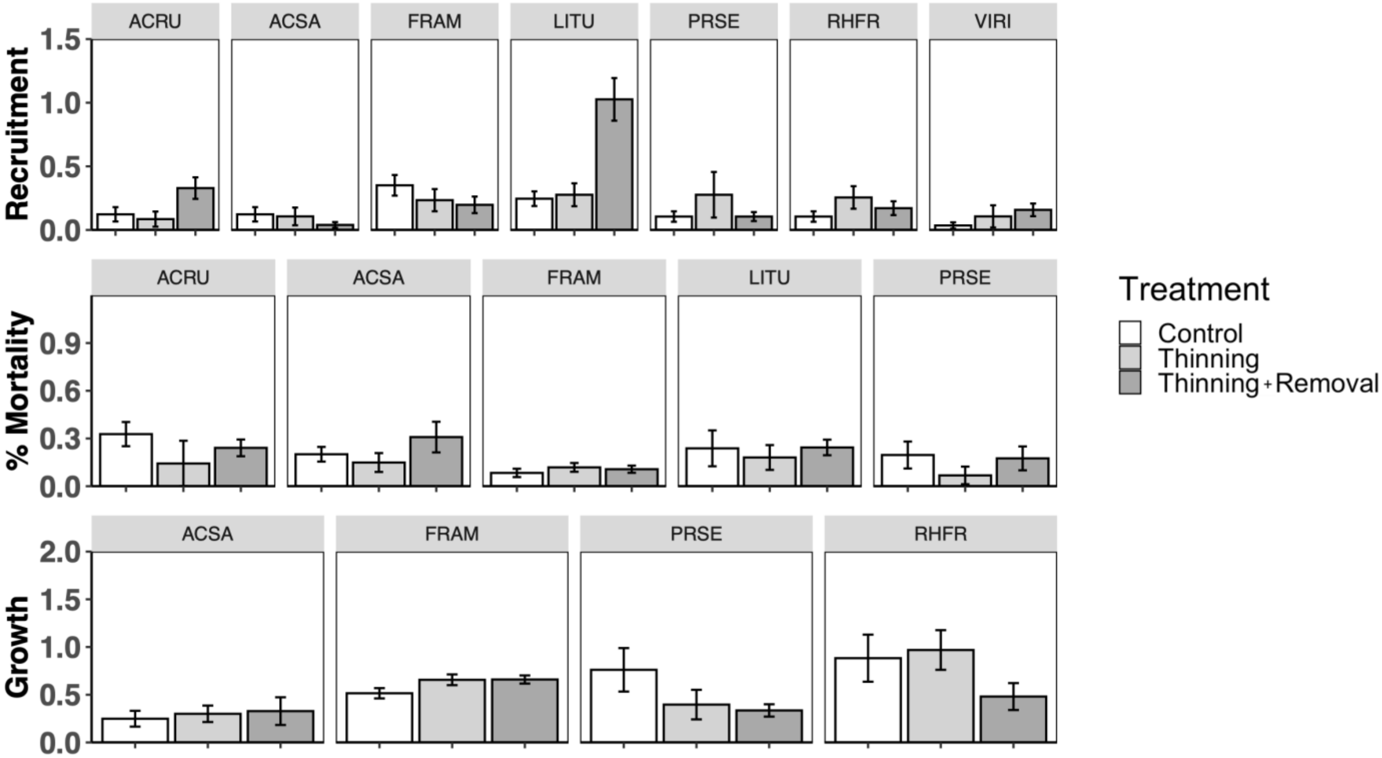


Figure 3.2. Average number of seedlings recruited (top), average proportion of seedlings that died (middle), and average growth in height from 2019-2022 (bottom) for each species across forest treatment plots. Species codes are as follows: *Acer rubrum* (ACRU), *Acer saccharum* (ACSA), *Fraxinus americana* (FRAM), *Liriodendron tulipifera* (LITU), *Prunus serotina* (PRSE), *Rhamnus frangula* (RHFR), *Vitis spp.* (VIRI).

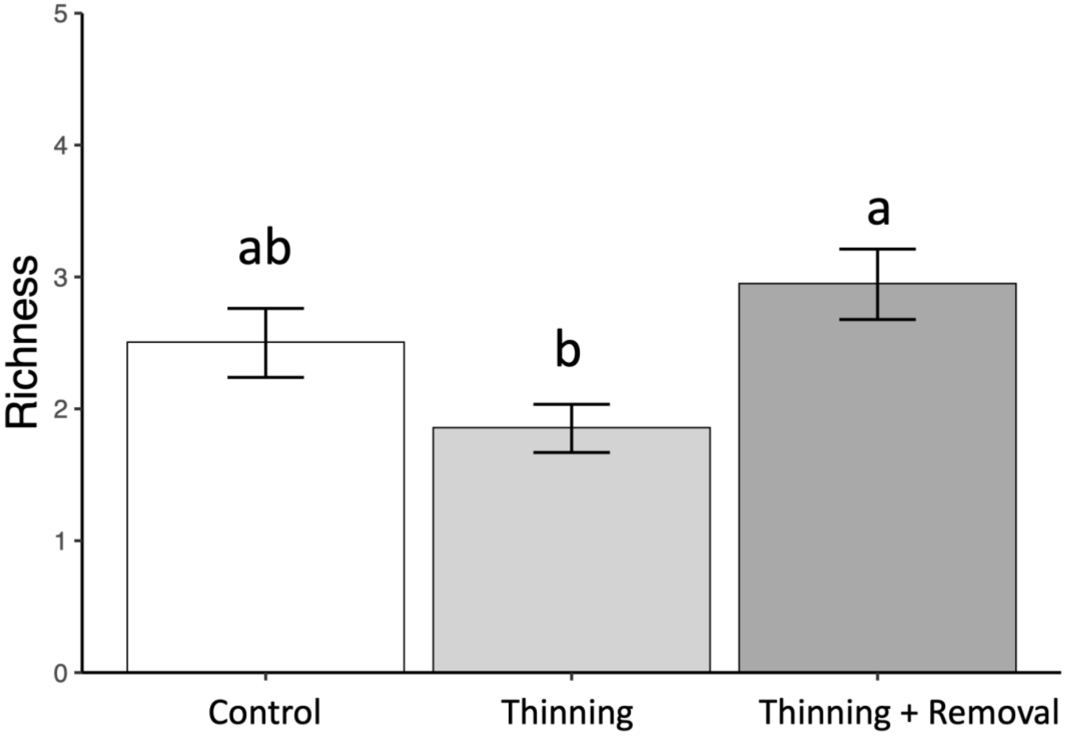


Figure 3.3. The average number of newly recruited woody species across management treatments from 2020-2022.

Chapter 4

Effect of overstory tree thinning with and without nonnative shrub removal on beta diversity and temporal turnover in newly recruited woody plant communities

Abstract

Second-growth forests tend to be less diverse than their older-growth counterparts. Forest management can be used to encourage diversity in young forests, enhancing resilience of these forests to various threats including pests and pathogens, as well as climate change. Understanding the impacts of forest management on spatial and temporal variability in newly establishing plant communities is key to predicting resultant patterns of biodiversity across the forest landscape. Two critical measures of the spatial and temporal aspects of biodiversity are beta diversity and temporal turnover. Beta diversity quantifies variability in composition of species across space, while temporal turnover quantifies temporal changes in species composition. We monitored the impacts of three common forest management techniques (selective overstory thinning done alone, selective overstory thinning done in tandem with removal of nonnative shrubs, and unmanaged control) on composition, beta diversity, and temporal turnover in communities of newly recruited woody seedlings within a second-growth forest in Northeast Ohio. Management impacted the composition of newly recruiting woody seedlings in the first two years of study (2020 and 2021), though there was no signal of management treatment on community composition in the third (2022). We found that beta diversity was lower in areas with overstory thinning done with nonnative shrub removal, compared to forests with no management or managed with overstory thinning alone, indicating that variability in community composition was lower within these managed areas. Community composition of newly recruited woody seedlings varied across years (from 2020 to 2022) in plots managed with overstory thinning paired with nonnative shrub removal, as well as unmanaged plots. Interestingly, composition across these three years was relatively consistent in plots managed with overstory thinning alone. Temporal turnover from 2020 to 2022 did not differ across management treatments. Our findings indicate that management has the potential to drive community composition in newly recruiting woody plant communities, including patterns of diversity across the forest landscape. These effects were more pronounced in the treatment including overstory thinning done in tandem with understory removal of nonnatives. However, there were notable differences in management effects across years.

Key words:

Biodiversity • beta diversity • forest management • heterogeneity • temporal turnover

Introduction

Across North America, second-growth forests form dense stands that tend to be less biodiverse and more spatially homogenous as compared to older-growth forests (Goebel et al., 1996; Oliver, 1980; Shifley et al., 1995). Management of these second-growth forests often aims to increase biodiversity, and while impacts of such management is often measured at the plot-level, important aspects of biodiversity are also underpinned by the heterogeneity of that biodiversity across the forest (i.e., beta diversity) (Burrascano et al., 2018). Beta diversity quantifies the differences in composition of species across communities in a defined spatial scale (Whittaker, 1972). Moreover, critical shifts in biodiversity through time (in response to management or other factors) are driven by temporal changes in the biotic community (hereafter referred to as “temporal turnover”) (Shurin, 2007). Temporal turnover can be a slow and continual process in some cases (Laliberté et al., 2009), or fast in others (Van Breugel et al., 2007). Disturbance (including management actions) that speed up demographic processes and create opportunities for new recruitment tend to lead to faster rates of temporal turnover (Battles et al., 2001). As such, temporal turnover can be a critical driver of community composition across spatial scales, ultimately influencing beta diversity.

Beta diversity is a key, though often under-considered, component of community composition across the landscape (Socolar et al., 2016). Increased beta diversity can promote ecosystem resilience by creating a heterogenous mosaic of plant communities within forests (Churchill et al., 2013). Forest management actions, while often applied over large swaths of land, often have variable impacts on environmental conditions throughout forests, resulting in a mosaic of microsite conditions (Churchill et al., 2013). Ultimately, these changes have the potential to alter beta diversity in managed forests. The relationship between beta diversity and forest management can also be indicative of the effectiveness of silvicultural practices that aim to conserve or restore plant diversity (Sabatini et al., 2014).

Forest management often aims to harness novel abiotic conditions to promote seedling recruitment and assemblage of diverse communities. Increasing structural and habitat complexity via changes induced by tree thinning can create greater variability in plant community composition (Ares et al., 2009). Nonnative plant removal, along with overstory thinning, can further influence understory environmental conditions by reducing competition for space, light, and nutrients. These environmental changes lead to altered abiotic conditions through time, both when comparing conditions immediately before and after the management action, as well shifts in conditions more slowly through time following the management action (Dyderski and Jagodziński, 2021). But, while these environmental conditions vary through time (almost by definition of the disturbance), they also vary across space. For example, a tree felled as a part of management will increase light availability on the forest floor, but not equally throughout the forest. Conditions very close to a felled tree are likely to experience significantly brighter conditions, while conditions a short distance away may experience very little change in light conditions. Environmental characteristics such as soil structure, and water, light and nutrient availability can impact species distributions across the forest, as well as the speed and extent to which community composition shifts after disturbance (Hérault and Piponiot, 2018). Information detailing how plant communities respond to environmental heterogeneity driven by forest management is needed to help us understand mechanisms driving responses to such management (Coates and Burton, 1997). Further, more information is needed on how tree recruitment responds to environmental drivers in order to forecast which communities will be present under various climate scenarios (Lee and Ibáñez, 2021).

Although increased complexity in microsite conditions brought about by management practices may facilitate temporal turnover and beta diversity, community composition (and changes therein) will also depend on the ability of individuals in the species pool to fill available niches, as this determines which species ultimately establish themselves (Pickett and White, 1985, Darwin 1859, Rosenzweig, 1995). Management that alters the nature of available niches will also be responsible for shifts (both spatial and temporal) in plant communities. For instance, temporal turnover can increase due to disturbance such as fire if the fire changes the suite of available niches, but if such disturbance affects the landscape relatively uniformly, the variety of niches available on the landscape may be narrowed, leading to lower beta diversity (Heydari et al., 2017). Monitoring compositional shifts in recruiting woody seedling communities across both space and time during the initial years following management is valuable for managers that may need to quickly adapt strategies due to short timelines or funding limitations.

Using a landscape-scale forest management manipulation, we managed forested plots with light thinning of the forest canopy or light thinning of the forest canopy paired with removal of nonnative shrubs. Additional plots were left as unmanaged controls. Here we explore the community composition of newly recruited woody seedlings across forest management treatments. We also report the effects of forest management on the beta diversity of these newly recruited communities as well as the temporal variability (temporal turnover) over the first three years following management. We expected that both overstory thinning and overstory thinning with nonnative shrub removal would impact community composition and increase beta diversity within the forest. We further predicted that these management actions would drive changes in composition from year to year within plots and would increase temporal turnover.

Methods

Study site

This research was conducted within a second-growth, deciduous forest at the Holden Arboretum (-81.296129, 41.605589), located in Lake County, Ohio. The forest, released from agriculture approximately 60 years prior, is characterized by a densely-packed even-aged stand a canopy. The understory is characterized by native species including *Acer rubrum*, *Acer saccharum*, *Fraxinus americana*, *Liriodendron tulipifera*, *Lindera benzoin*, *Viburnum acerifolium*, *Viburnum dentatum* and nonnative species including: *Celastrus orbiculatus*, *Ligustrum vulgare*, *Lonicera morrowii*, *Rhamnus frangula*, and *Rosa multiflora*. Mean annual temperature averages 10.7 °C with mean annual precipitation of 99.2 cm (US Climate Data, 2022).

Field Methods

We explored the impacts of three forest management strategies on community composition, beta diversity, and temporal turnover of newly recruiting woody species within the forest understory. In 2019, we established nine 1-hectare plots, each receiving one of three management treatments: control (no management), overstory thinning, and overstory thinning coupled with removal of nonnative shrubs in the understory. We established three replicates of each treatment for a total of nine 1-ha plots. The overstory thinning treatment involved killing select overstory trees through a combination of girdling (~90% of killed trees) and felling (~10% of killed trees) such that the canopy was thinned by approximately 20%. In the overstory thinning with removal of nonnative shrubs treatment, selective killing of canopy trees was combined with removal of all nonnative shrubs in the forest understory, as well as removal of wild grape (*Vitis* spp.). In this management treatment, all nonnative shrubs and wild grapevine were removed on a yearly basis (during fall months) by hand cutting or pulling and then applying herbicide to inhibit regrowth (*Aquaneat*, glyphosphate-based).

In 2018, we haphazardly established 116 subplots collectively across the 1-ha management plots. Subplots were 1-m^2 and located 1.5 m north of the trunk of a healthy tree of one of the following species: *Acer rubrum*, *Acer saccharum*, or *Liriodendron tulipifera*. This resulted in 8 to 17 subplots per 1-hectare management plot. Starting in June 2020, all newly recruited woody seedlings within a subplot were individually tagged with a uniquely numbered small butt-end aluminum band (*National Band and Tag Company*). We censused for recruited individuals twice annually (June and August) from 2020 to 2022, following an initial survey in June 2019. These biannual censuses allowed us to determine what individuals had newly recruited each year. Using these census data, we compiled the number of seedlings of each species recruiting to each subplot in each year.

Analysis

Statistical analyses were conducted in Rstudio (Version 1.3.1093). We assessed variation in community composition of newly recruited woody seedlings as a function of management treatment (control, thinning, and thinning with nonnative removal) using a three-way permutational analysis of variance (PERMANOVA) (package: “vegan”) based on a Bray-Curtis dissimilarity index of species abundance, calculated separately for each year (Oksanen et al., 2015). That is, we explored differences in woody seedlings that were newly recruited in the 2020, 2021, and 2022 censuses across management treatments. We removed species with only one occurrence (singletons) in each year to reduce multidimensional error. We used non-metric multidimensional scaling (NMDS) to visualize community structure across treatments.

To test if beta diversity differed across management treatments, we calculated beta diversity within 1-ha management plots using the multivariate homogeneity of group dispersions metric (Anderson et al., 2011). Specifically, beta diversity was calculated as the distance (variance) of each individual subplot to the centroid of its respective treatment group (control, thinning, and thinning with nonnative removal). We calculated this distance using the betadisper() function in the ‘vegan’ package separately for each of our sampling years (2020-2022). To explore differences in beta diversity across the three management treatments, we tested for significant differences in beta diversity using a general linear model with management treatment as the explanatory variable (function: glm()). Significance of this model was tested using ANOVA (function: Anova(), package: “car”). Analyses were done separately for each of the three sampling years in order to explore the impacts of forest management on beta diversity through time.

To explore differences in the magnitude of compositional changes among communities of newly recruited woody seedlings across management treatments over time, we ran a PERMANOVA exploring compositional differences (as measured by Bray-Curtis) as function of year (2020, 2021, and 2022), separately for each of the three management treatments (control, thinning, and thinning with nonnative removal). As in the above analysis exploring community change across management treatments, we removed species with only one occurrence (singletons) in each year to reduce multidimensional error. We used non-metric multidimensional scaling (NMDS) to visualize community structure across treatments.

To investigate temporal turnover of newly recruited woody plant communities, we calculated the Bray-Curtis dissimilarity of each subplot compared to itself in the first and last sampling years (2020 and 2022). We ran a regression analysis on the dissimilarity values of each subplot using a general linear model with management treatment as the explanatory variable (function: glm()). Significance of this model was tested using ANOVA (function: Anova(), package: “car”).

Results

In both 2020 and 2021, we observed significant differences in the composition of recruited communities across management treatments (2020: $F_{2,69}$=2.02, p=0.01; 2021: $F_{2,55}$=1.88, p=0.03) (Fig. 4.1). In 2022, however, composition did not differ across management treatments (2022: $F_{2,40}$=1.44, p=0.16) (Fig 4.1).

In 2020, beta diversity of newly recruited woody seedlings varied across management treatments ($F_{2,67}$=6.35, p<0.01) (Fig. 4.2). Specifically, beta diversity was lower in plots with overstory thinning paired with nonnative removal as compared to areas with no management (p=0.01), though beta diversity within these plots with thinning plus nonnative shrub removal was not significantly different from that seen in plots with overstory thinning alone (p=0.11). Beta diversity within control and overstory thinning plots did not differ from one another (p=0.71) (Fig. 4.2). In 2021, beta diversity of newly recruited woody seedlings varied marginally across management treatments ($F_{2,53}$=2.91, p=0.06) (Fig. 4.2). Beta diversity continued to be lower in plots with overstory thinning paired with nonnative removal as compared to areas with no management (p=0.11) and areas with overstory thinning alone (p=0.16), although these results were not significant for either treatment pairing (Fig. 4.2). Beta diversity within control plots did not differ from plots with overstory thinning (p=0.15) (Fig. 4.2). In 2022, beta diversity did not vary across management treatments ($F_{2,38}$=1.79, p=0.18) (Fig. 4.2).

Composition of newly recruited woody communities differed significantly across the three survey years in both overstory thinning plus nonnative shrub removal plots and in control plots (Thinning and Removal: $F_{2,69}=2.23$, $p=0.02$; Control: $F_{2,52}=1.85$, $p=0.03$) (Fig. 4.3). In plots with overstory thinning alone, we did not observe significant differences in community composition of newly recruited woody individuals through time (Thinning: $F_{2,40}=1.26$, $p=0.23$) (Fig 4.3).

Treatment did not have an effect on temporal turnover in newly recruited woody communities from 2020 to 2022 ($F_{1,28}=0.81$, $p=0.46$) (Fig. 4.4).

Discussion

We found that forest management drove changes in the community composition of newly recruited woody seedlings within our system in two of the three years studied. Further, beta diversity was lower in areas managed with both overstory thinning and nonnative shrub removal as compared to areas without management or areas managed with overstory thinning alone, but only in 2020 and 2021. Within management treatments, we observed significant differences in the composition of newly recruited seedlings across the three years in thinning plus nonnative removal and control plots. Despite this, the magnitude of temporal turnover within subplots from 2020 to 2022 did not differ across management treatments.

Our findings suggest that the combination of overstory thinning and nonnative shrub removal during forest management can influence the suite of woody species recruiting into the forest within at least the first few years following management. Interestingly, overstory thinning when done without nonnative shrub removal did not influence the community of newly recruiting woody seedlings. Previous studies exploring the effects of management techniques that employ overstory thinning on understory plant diversity have resulted in mixed findings. Some studies have found overstory thinning to promote diversity in the understory (Thomas et al., 1999), while others have found declines in diversity (Wyatt and Silman, 2010), and some have suggested there is no impact of overstory thinning on understory diversity at all (Duguid and Ashton, 2013). Site-specific qualities such as resource availability and environmental variation are likely to play a larger role in determining the composition of plant communities, than the management itself (Duguid and Ashton, 2013). More studies on woody seedlings in particular are needed to predict how management is likely to drive spatial and temporal changes in community composition (Cavers and Cottrell, 2015).

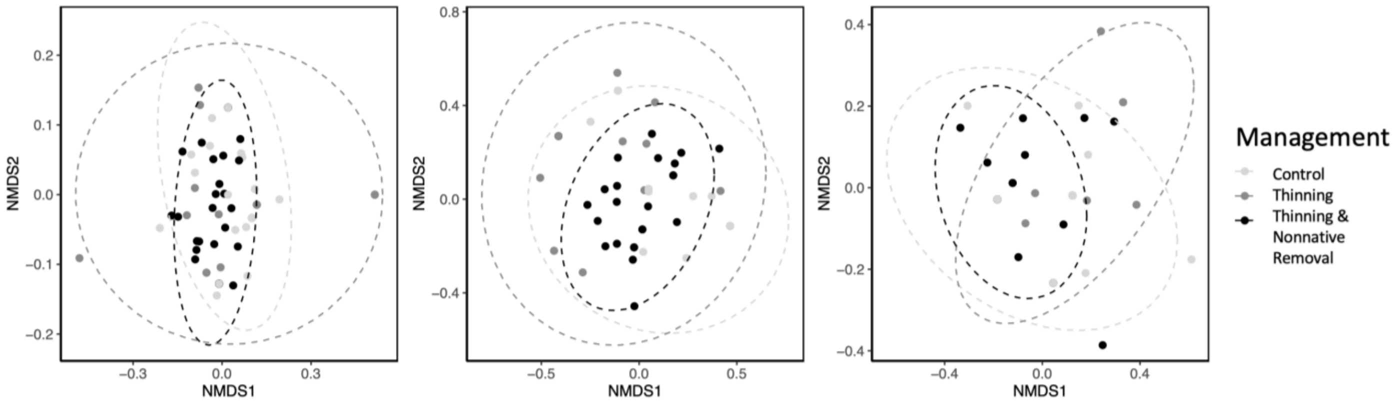
In addition to these compositional differences across management treatments, we also found variability in beta diversity (spatial heterogeneity), with lower levels of beta diversity in forested areas managed with overstory thinning and understory nonnative management compared to areas with no management, as well as areas managed with overstory thinning alone (though this result was not significant). Such spatial heterogeneity in communities of newly recruiting woody plants associated with management combining thinning of the overstory with removal of nonnative shrubs may be driven by various niche-level processes that can occur on fine spatial scales (Fernandez-Going et al., 2013). Removal of nonnative competitors may be a driver of this result by decreasing the richness of nonnative species, while increasing the richness of native species (Moore et al., 2023). Further, nonnative shrubs are often patchily distributed within our forests and, as such, their presence may actually lead to increased beta diversity (Petsch et al 2022).

Community composition of newly recruited seedlings changed over the course of three years in areas managed with overstory thinning and nonnative removal, and interestingly, in the control plots. Forests managed with overstory thinning did not experience significant compositional shifts in the seedling community over the same three years. Our finding that compositional changes occurred in plots with overstory thinning plus nonnative removal is supported by literature showing increases in both abundance (Copeland et al., 2019) and richness (Moore et al., 2023) of native plants following removal of nonnative species. In our case, overstory thinning served as an applied disturbance, similar to natural disturbances such as tree or shrub mortality from wind storms or insect outbreak (Grigri et al., 2020). Disturbance can change resources availability and, ultimately, the composition of individuals present in the community (Ares et al., 2009; Hérault and Piponiot, 2018). Whether a result of management or natural disturbance, overstory gaps lead to increase light availability in the understory in which plant communities are likely to respond (Dormann et al., 2020; Tsai et al., 2018). Contrary to expectations, thinning alone did not drive compositional changes at our site, and the removal of nonnative shrubs was required in tandem with overstory thinning to shift communities in the first several years. A delayed response in areas without nonnative removal, is likely due to the slow rate of death of overstory trees over the course of the study. Girdled trees often take 1-5 years to die (Fassnacht and Steele, 2016; Merceron et al., 2016) and so while nonnatives are instantly removed from the system, resulting in quicker impacts, girdling of overstory trees will likely be slower to impact understory communities. Notably, there were significant shifts in the newly recruited seedling community in control plots. Such shifts might come about as communities change through time with succession (Miceli et al., 1977). More likely influencing our results, seedlings are particularly susceptible to interannual variation in environmental conditions (Wang et al., 2018), which can lead to changes in the community of newly recruited seedlings across years.

Management often increases the availability of limiting resources. Such changes can be evident immediately after a management action, or can shift slowly in the years following management. As such, management can influence the rate at which species composition changes across the forest landscape (Myers et al., 2013). However, we did not observe a significant response of temporal turnover to forest management. This is dissimilar to other studies which have documented rapid increases in temporal turnover of woody communities following forest disturbance (Ravnjak, 2022). As management continues to promote changes in the forest environmental over time, we expect to begin to see increased rates of temporal turnover within managed plots, with the greatest shifts most likely in plots managed with overstory thinning done in tandem with nonnative shrub removal, as this treatment generates the greatest changes in the environment and has driven the biggest shifts in community composition and beta diversity. Other factors beyond the scope of the environmental factors that shift soon after management, such as limited local dispersal (e.g., small species pool), will also likely impact rates of temporal turnover (Gilbert and Lechowicz, 2004). Further analysis detailing the degree to which environmental cues shift over time following management will provide more information as to how quickly and to what degree communities are likely to shift in composition.

Our results suggest that forest management can influence the composition of woody seedling communities. We found that management can drive compositional shifts in woody seedling communities present in the forest understory in the first few years following management, but these results varied across treatments. We also showed that management can increase beta diversity. Temporal turnover was not responsive to management over the first few years following management, but long-term monitoring is needed to determine if management will cause communities to begin shifting more rapidly over time. Additional time will also reveal whether community composition will continue to become more heterogeneous within managed plots. Improved understanding of spatial and temporal shifts in community composition through time can inform management and restoration efforts that aim to improve system resiliency by increasing diversity as well as heterogeneity across the landscape.

Figures:



2020 2021 2022

Figure 4.1. NMDS of newly recruited woody seedling communities in 2020 (left), 2021 (middle) and 2022 (right) for each of the three management treatments.

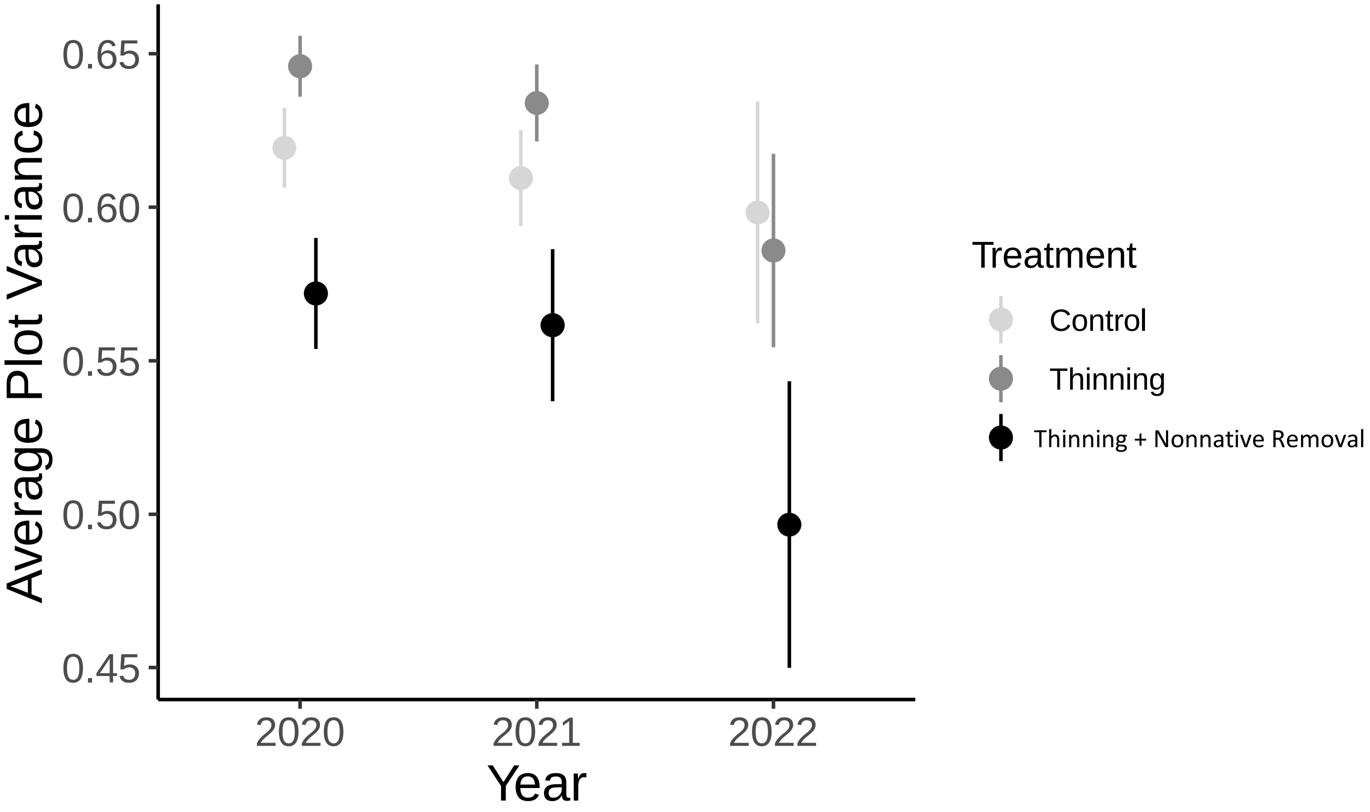
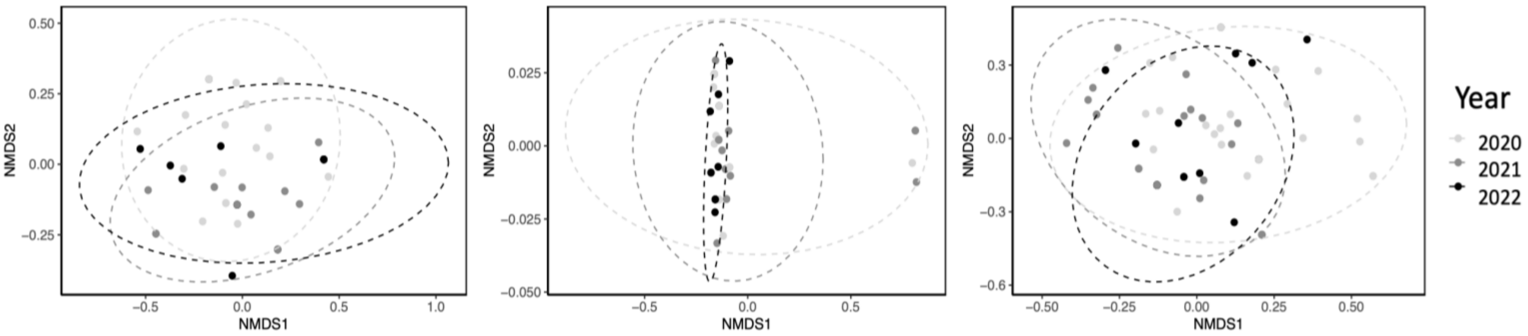


Figure 4.2. Average beta diversity of newly recruited woody seedlings (distance of each subplot to its respective treatment centroid) for each forest management treatment (Light Gray = Control, Medium Gary = Thinning, Dark Gary = Thinning and Nonnative Removal) across the first three years following management.



Control

Thinning

Thinning and Removal

Figure 4.3. NMDS of newly recruited woody seedlings recruited in control (left), overstory thinning (middle) and overstory thinning plus nonnative removal (right) plots across three years (Light Gray = 2020, Gray = 2021, Black = 2022).

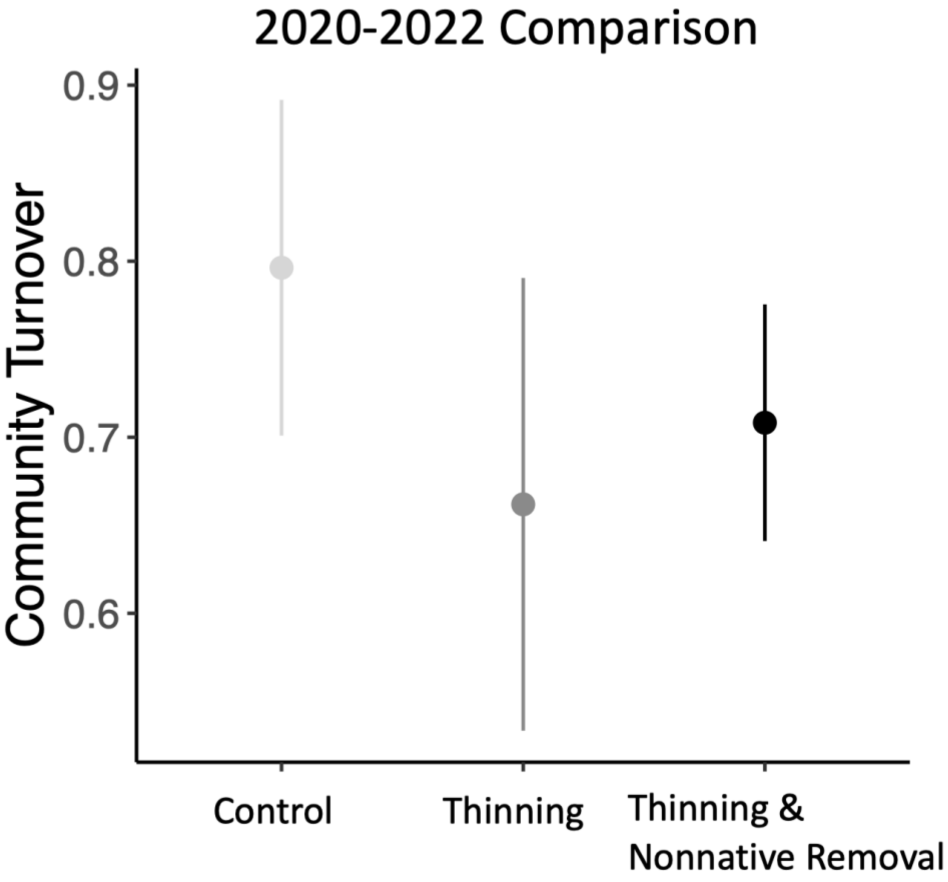


Figure 4.4. The average Bray-Curtis Dissimilarity of subplots in 2020 compared to 2022 across each forest treatment (Control = Light Gray, Thinning = Gray, Thinning and Nonnative Removal = Black). Bray-Curtis dissimilarity is bound between 0-1, with a score of zero indicating identical composition and a score of one indicating complete dissimilarity. Error bars represent 95% confidence intervals.

Chapter 5

Discussion

I evaluated the impacts of forest management on the population and community dynamics of woody species within the understory of a secondary growth forest. Specifically, I evaluated the effect of management using overstory thinning, with and without removal of nonnative shrubs, in the forest understory. Broadly, I determined that management can mediate changes in key demographic process such as recruitment, growth, and mortality in seedlings and productivity and dispersal of shrubs leading to important changes in community composition and patterns of biodiversity.

In chapter 2, I explored the impacts of management on fruit production in two common shrub species as a function of forest management. I also explored rates of removal of artificial fruits as a proxy for how management may affect fruit removal rates by avian dispersers. I found that glossy buckthorn (*Rhamnus frangula*), a nonnative species commonly found in our sites, produced more fruit in areas where the forest overstory was thinned as compared to both unmanaged forest and forest with overstory thinning and removal of nonnative shrubs. Similarly, rates of artificial fruit removal by birds were also highest in these areas managed with overstory thinning. Inversely, I found fruit removal to be lowest in areas in which nonnative shrubs were removed from the understory in tandem with overstory thinning. Increases in fruit removal in areas managed with overstory thinning may influence dispersal and ultimately future recruitment of species. Many invasive shrubs themselves are bird-dispersed, which may mean that birds will facilitate their spread over time. My research suggests that the impacts of management on interspecific interactions should be considered when predicting how woody, fruit-bearing species are likely to respond to forest management. Notably, as management has capacity to drive increases in both reproductive output as well as dispersal of forest shrubs, including nonnative species, managers should plan continued removal of undesired species for several years following overstory thinning.

In chapter 3, I found higher recruitment and mortality across all seedlings after four years in areas with managed with both overstory thinning combined with nonnative removal. This additionally resulted in higher species richness in those areas. Beyond these broad demographic patterns, we uncovered important species-specific responses to management in processes including recruitment and growth. Species-specific responses to management can play a key role in regulating understory dynamics, ultimately shifting trajectories for plant communities undergoing restoration efforts. Overstory thinning coupled with nonnative shrub removal drove higher recruitment rates in early successional species such as *Acer rubrum* (red maple). Seedling growth rates were similarly variable across species, with slower *Prunus serotina* growth in managed plots, although others (*Acer saccaharum, Fraxinus americana, Rhamnus frangula*) were unresponsive to treatment. Management goals often include increases in desired species (e.g., encourage native regeneration). I demonstrate that monitoring the growth and demography of individual species in the first years following management can reveal patterns of success and failure that may be important for understanding forest responses to management.

In chapter 4, I characterized how management drove plant community composition across the forest. I found community composition of newly recruited woody seedlings to shift in response to forest management. Specifically, overstory thinning paired with nonnative removal drove a change in community composition relative to the control. However, management effects varied through with treatment effects observed in the first two years following management, but not in the third. In addition, beta diversity was lower in areas with overstory thinning and nonnative removal, compared to forest with no management or overstory thinning alone, though, as with compositional differences, only in 2020 and 2021. Community composition varied through time in plots managed with overstory thinning combined with nonnative removal and, interestingly, in control plots, but not plots managed with overstory thinning alone. Although not significant, temporal turnover was lower in areas managed overstory thinning alone. Additional monitoring of the impacts of management on environmental variables will likely illuminate the mechanisms behind demographic shifts in understory woody plant communities. In sum, management that improves the availability of limiting resources including light, soil moisture, and litter depth across the landscape may influence the rate at which communities assemble following management. This research demonstrates that mangers seeking to improve the diversity of plant communities found in secondary forests can do so by manipulating the structure of the forest via both thinning the overstory while simultaneously removing nonnatives in the understory. The long-term effects of management are likely to be dynamic and understanding them will require a nuanced understanding of the system.

The research presented in this dissertation highlights three key findings. 1) Forest management involving overstory thinning drives increases in fruit production of Rhamnus frangula (nonnative), while birds were also more attracted to fruit mimics in these areas compared to unmanaged areas. This suggests that managers should strongly consider the removal of nonnative shrubs during overstory thinning to lessen the probability of their dispersion by birds. 2) Relative to control and thinned-only, forests managed with both overstory thinning and nonnative shrub removal had greater recruitment, mortality and richness of newly recruited woody plants, although responses were variable across species. This suggests that managers can expect young woody seedlings to respond quickly to management (especially when nonnatives are removed) with certain species succeeding over others. 3) The effect of forest management on plant community composition varies from year to year, with the removal of nonnative shrubs being a critical component to changes in community structure, including increases in beta diversity across the forest landscape. This leads to interesting follow-up questions that investigate long-term patterns of community change over time and spatial variability, which will help managers predict the impacts of their efforts. Understanding the effects of forest management on young woody plants is important for determining the structure and composition of future forest communities. In conclusion, long-term monitoring can provide important insight into on how forests will respond to changes induced by management or other disturbances.

Appendix A: Chapter 2 Supplemental Material

Table S2.1 Table of model results testing the impact of management on fruit production for *Rhamnus frangula* without canopy openness and soil moisture covariates (includes height).

	χ^2	**Df**	**Pr(>Chi)**
Treatment	10.12	1	**<0.01**
Height	63.362	1	**<0.001**

Table S2.2 Table of model results testing the impact of treatment on fruit removal with canopy openness and soil moisture included as covariates.

	χ^2	**Df**	**Pr(>Chi)**
Treatment	15.83	2	<0.001
Color	12.27	1	<0.001
Density	2.21	1	0.14
Canopy Openness	0.09	1	0.76
Soil Moisture	0.16	1	0.69

Figure S2.1 Examples of artificial fruit with marks that were consider to be “removed” by a bird.

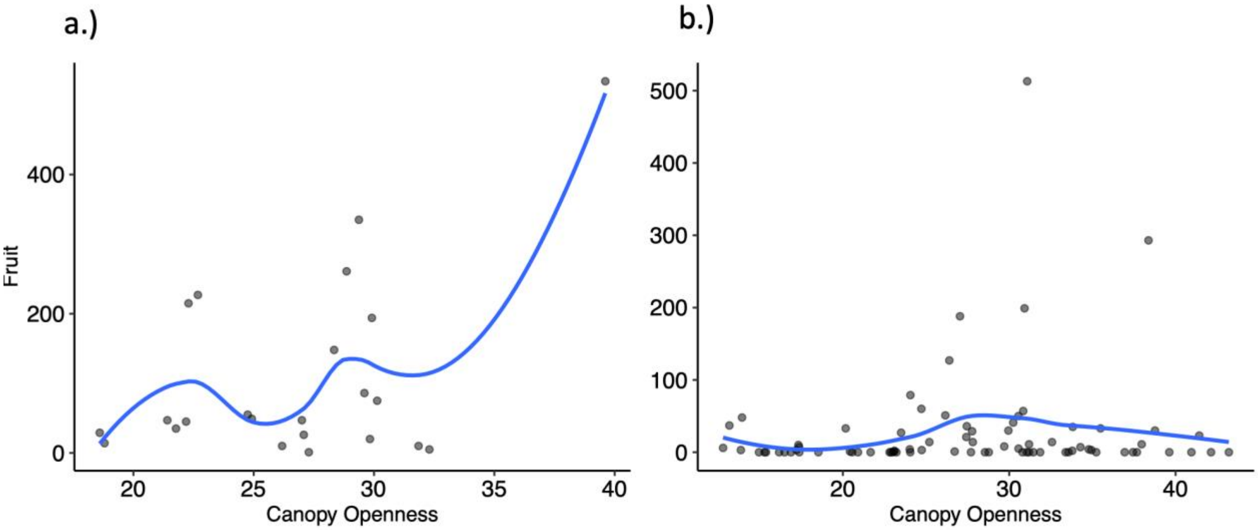


Figure S2.2 Total number of fruits of *Lindera benzoin* (left) and *Rhamnus frangula* (right) as a function of canopy openness. Blue lines represent fitted values from linear model (function: geom_smooth(); package: “ggplot2”).

Appendix B: Chapter 3 Supplemental Material

Table S3.1. ANOVA results for seedling recruitment and mortality across all individuals (species combined) without covariates included.

	Predictors	**F**	**Df**	**Df.res**	**Pr(>F)**
Recruitment					
	Treatment	132.24	2	4.80	0.01
	Residuals	1254.74	91		
Mortality					
	Treatment	153.54	2	5.07	0.01
	Residuals	1347.12	89		

Table S3.2. Analysis of Variance (ANOVA) results for species-specific recruitment, mortality, and growth with covariates included.

Model	**Predictor**	**Sum Sq**	**Df**	**F value**	**p**
Recruitment					
Ash					
	Treatment	1.36	2	0.75	0.48
	Canopy Openness (2020)	0.27	1	0.29	0.59
	Soil Moisture	1.55	1	1.71	0.19
	Litter	0.14	1	0.15	0.7
	Residuals	79.74	87		
Sugar					
	Treatment	0.39	2	0.68	0.51
	Canopy Openness (2020)	0.15	1	0.52	0.47
	Soil Moisture	0.5	1	1.72	0.19
	Litter	0.01	1	0.05	0.82
	Residuals	25.35	87		
Red					
	Treatment	5.85	2	3.95	**0.02**
	Canopy Openness (2020)	0.03	1	0.05	0.83
	Soil Moisture	0.52	1	0.7	0.4
	Litter	2.91	1	3.93	0.05
	Residuals	65.18	87		

Buckthorn					
	Treatment	1.14	2	0.82	0.44
	Canopy Openness (2020)	1.42	1	2.06	0.15
	Soil Moisture	0.21	1	0.31	0.58
	Litter	1.65	1	2.4	0.13
	Residuals	60.69	87		
Poplar					
	Treatment	63.13	2	8.19	**<0.001**
	Canopy Openness (2020)	0.01	1	0.003	0.95
	Soil Moisture	0.004	1	0.001	0.97
	Litter	0.16	1	0.04	0.84
	Residuals	339.03	87		
Cherry					
	Treatment	1.76	2	0.94	0.41
	Canopy Openness (2020)	0.33	1	0.36	0.55
	Soil Moisture	0.46	1	0.49	0.49
	Litter	0.29	1	0.31	0.58
	Residuals	82.66	87		
Grape					
	Treatment	1.33	2	1.68	0.19
	Canopy Openness (2020)	0.35	1	0.88	0.35
	Soil Moisture	0.68	1	1.71	0.19
	Litter	0.09	1	0.23	0.63

Residuals	34.97	87		
Mortality				
Ash				
Treatment	0.11	2	0.93	0.34
Canopy Openness (2020)	<0.01	1	0.05	0.83
Soil Moisture	<0.01	1	0.09	0.77
Litter	0.01	1	0.21	0.67
Residuals	5.02	83		
Sugar				
Treatment	0.35	2	1.35	0.28
Canopy Openness (2020)	0.06	1	0.47	0.5
Soil Moisture	0.22	1	1.69	0.2
Litter	0.08	1	0.62	0.44
Residuals	3.38	26		
Red				
Treatment	0.8	2	2.42	0.11
Canopy Openness (2020)	0.03	1	0.2	0.65
Soil Moisture	0.23	1	1.42	0.24
Litter	0	1	0.02	0.9
Residuals	4.83	37		
Poplar				
Treatment	0.11	2	0.37	0.69
Canopy Openness (2020)	0.14	1	0.96	0.33

	Soil Moisture	0.16	1	1.08	0.3
	Litter	0.02	1	0.16	0.69
	Residuals	5.81	40		
Cherry					
	Treatment	0.13	2	0.52	0.61
	Canopy Openness (2020)	0.22	1	1.84	0.18
	Soil Moisture	0.14	1	1.11	0.3
	Litter	0.07	1	0.54	0.47
	Residuals	3.9	32		
Grape					
	Treatment	0.21	2	0.37	0.71
	Canopy Openness (2020)	0.07	1	0.25	0.63
	Soil Moisture	0.05	1	0.18	0.68
	Litter	0.03	1	0.1	0.76
	Residuals	2.25	8		
Growth					
Ash					
	Treatment	25.37	2	1.46	0.25
	Canopy Openness (2020)	129.42	1	14.85	**<0.001**
	Soil Moisture	0.53	1	0.06	0.81
	Litter	31.4	1	3.6	0.06
	Residuals	357.4	41		
Sugar					

	Treatment	0.13	2	1.22	0.37
	Canopy Openness (2020)	0.64	1	12.28	0.02
	Soil Moisture	0.07	1	1.41	0.29
	Litter	0	1	0	1
	Residuals	0.26	5		
Buckthorn					
	Treatment	10.31	2	1.49	0.26
	Canopy Openness (2020)	0.12	1	0.04	0.85
	Soil Moisture	0.07	1	0.02	0.89
	Litter	11.7	1	3.38	0.09
	Residuals	41.59	12		
Cherry					
	Treatment	4.32	2	4.91	**0.04**
	Canopy Openness (2020)	1.03	1	2.33	0.16
	Soil Moisture	0.48	1	1.1	0.32
	Litter	1.69	1	3.83	0.08
	Residuals	3.96	9		

Table S3.3. Analysis of Variance (ANOVA) results for species-specific recruitment, mortality, and growth without covariates.

Model	Predictor	Sum Sq	Df	F value	p
Recruitment					
Ash	Treatment	1.31	2	0.72	0.49
	Residuals	81.94	90		
Sugar	Treatment	0.39	2	0.67	0.51
	Residuals	26.19	90		
Red	Treatment	5.65	2	3.72	**0.03**
	Residuals	68.41	90		
Buck	Treatment	0.89	2	0.63	0.53
	Residuals	63.77	90		
Poplar	Treatment	63.24	2	8.39	**<0.001**
	Residuals	339.21	90		
cherry	Treatment	1.40	2	0.75	0.47
	Residuals	83.76	90		
grape	Treatment	1.18	2	1.47	0.23
	Residuals	35.94	90		
Mortality					
Ash	Treatment	0.12	2	1.07	0.35
	Residuals	5.16	91		
Sugar	Treatment	0.35	2	1.38	0.27
	Residuals	4.08	32		

Red	Treatment	1.35	2	4.68	**0.02**
	Residuals	4.34	30		
Poplar	Treatment	0.20	2	0.67	0.52
	Residuals	6.67	44		
cherry	Treatment	0.11	2	0.42	0.66
	Residuals	4.60	36		
Growth					
Ash	Treatment	2.15	2	0.10	0.91
	Residuals	515.99	48		
sugar	Treatment	0.009	2	0.03	0.97
	Residuals	1.61	9		
Buck	Treatment	6.53	2	0.92	0.42
	Residuals	53.47	15		
cherry	Treatment	2.09	2	1.50	0.26
	Residuals	9.04	13		

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