Understanding the causes of biodiversity decline in temperate forests: Disentangling the impacts of browsing and nonnative species

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Submitted to the Graduate Faculty of the

Dietrich School of Arts and Sciences in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

University of Pittsburgh

2022

UNIVERSITY OF PITTSBURGH

DIETRICH SCHOOL OF ARTS AND SCIENCES

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Several factors contribute to the loss of biodiversity in forests worldwide. Among these are habitat fragmentation and urbanization, fire suppression regimes, loss of old-growth forests, increases in deer densities, and invasions by nonnative species. In many areas of the US, deer densities have increased three to five-fold over the past several decades. Besides loss of species richness and diversity, this has caused forest communities to shift over time such that communities now consist largely of browse-tolerant and shade-tolerant species. Moreover, native wildflowers and understory shrubs have been locally extirpated in many areas. Because deer have been overabundant on the landscape for such a long period of time, this has led to legacy effects wherein native species that are largely absent or have been locally extirpated fail to regenerate because there are no nearby seed or propagule sources for recruitment.

Human activities have led to the introductions of species to foreign ecosystems all over the world. The increase in rate of spread of non-native plants has coincided with a global decrease in biodiversity. While the majority of non-native species do not establish or become invasive, the small percent that do establish and proliferate pose substantial threats to native ecosystems. Anthropogenic factors that contribute to the spread of species include physical movement of propagules, alterations of disturbance regimes, and changing limiting resources through fragmentation across entire landscapes. The annual costs of mitigating or eradicating invasive plant and animal species exceed billions of dollars for many nations.

Invasive plant species now cover vast areas of the eastern United States. Habitats within the Eastern Deciduous Forest Biome have experienced declines in diversity of both herbaceous and woody species. Canopy trees are not self-replacing and often fail to recruit in the understory. Furthermore, fire-tolerant species, such as oaks, and browse-intolerant species are failing to recruit at regional landscapes due to fire suppression practices and deer overbrowsing. It is unclear how processes such as exotic invasions and deer overbrowsing interact in causing largescale diversity loss in eastern deciduous forests.

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Treefalls cause the formation of large tip-up mounds that create unique microsites, potentially promoting diversity in forests worldwide. Distinct plant assemblages may rapidly form on these microsites, but evidence is scant. We tested the hypothesis that novel plant communities would establish on young treefall mounds using field surveys in three temperate forests combined with a literature review. In two forests, a distinct woody plant assemblage formed on mounds whereas ferns dominated reference plots. In the other forest, a single woody species dominated mounds and was nearly absent off mounds. Our review revealed that sometimes distinct communities fail to develop on mounds, but when they do, the woody colonizers shared key traits; they were fast-growing, seed-banking, browse-sensitive, and avian or wind-dispersed. A small number of studies exist of early succession on tip-up mounds (22), but these have been plagued by variable methodologies and the inconsistent use or non-use of reference sites. Our review identified six unique microsites typically created by treefalls. We recommend that future studies consider these microsites and consistently use two reference sites: one on undisturbed soil adjacent to the mound and one further away beneath closed canopy forest. This approach will allow a comprehensive evaluation regarding the degree that pit and mound topography associated with treefalls promotes forest diversity worldwide.

1.1 Introduction

When trees fall with the trunk intact, the roots pull soil up with them, creating a mound structure and corresponding pit where the roots and soil had been (Beatty and Stone 1986). Weather events including windstorms or heavy ice and snow can uproot at widely varying scales, from single trees to massive blowdowns, and this is often correlated with the species of the uprooted tree (Foster et al. 1998; Pickett and White 1985; Schaetzl et al. 1988; Ulanova 2000). For example, single treefalls are more common in spruce-dominated forests than beech-dominated forests due to shallow root systems of spruce trees (Pawlik et al. 2017). Besides dominant canopy tree species, general climate, soil depth differences, tree health, and age of forests cause variation in the size and frequency of treefall events between biomes and forest types (Barker Plotkin et al. 2017; Beatty and Stone 1986; Krisans et al. 2020; Lindemann and Baker 2001; Samariks et al. 2021; Sobhani et al. 2014). Regardless, tree toppling is a continuous process in all forest types and most often caused by windthrow (Beatty and Stone 1986). Climate change is predicted to increase the frequency and severity of windthrow events and could therefore increase or alter regeneration patterns worldwide (Bussotti and Pollastrini 2017; Haarsma 2021; Peltola et al. 2010; Sobhani et al. 2014; Turner et al. 1998). It is well known that pit and mound topography can lead to decades or centuries-long landscape legacies, but what is less known are the dynamics, patterns, and rates of regeneration on newly created mound and pit microsites (i.e. ≤25 years) (Harrison-Day and Kirkpatrick 2019; Jonsson and Esseen 1990; Kulakowski and Veblen 2003; Schaetzl et al. 1990; Schaetzl et al. 1989).

The disturbance from uprooting leads to fundamental differences in abiotic conditions of soil microsites between mounds, pits, and the remaining intact forest floor (Peterson et al. 1990; Yoshida 2021). Mounds typically have higher exposed mineral soil with larger sediments and lower soil moisture compared to pits which can have around four times as much organic soil than mounds (Peterson et al. 1990; Schaetzl et al. 1990; Yoshida 2021). Pits also accrue many times more leaf litter than mounds do and contain deeper snow accumulation in the winter (Beatty and Stone 1986; Schaetzl et al. 1990). The lack of litter and snow accumulation on mounds increases temperature variability on mounds with lower temperatures in winter and higher temperatures in summer than pits or undisturbed soil sites (Beatty 1984; Beatty and Stone 1986; Peterson et al. 1990; Yoshida 2021). Mounds are also prone to having low soil stability and experience soil sloughing that adds to rapid soil accumulation in pits (Peterson et al. 1990). Intact sites sometimes exhibit intermediate soil moisture and horizon properties when compared with mounds and pits, but several studies have shown that they have higher soil moisture and lower light than disturbed microsites (Peterson et al. 1990; Schaetzl et al. 1990; Yoshida 2021).

Because soil on new mounds is often nutrient poor, and prone to freezing, thawing, and soil sloughing, which may be inimical to successful plant recruitment, the development of mound assemblages may be slow (Beatty 2003; Beatty and Stone 1986; Clinton and Baker 2000; Peterson et al. 1990). Regardless, fairly unique vegetation often occurs on older mounds many decades following mound formation and after mound habitats stabilize (Beatty 1984; Beatty 2003). What remains poorly understood is whether distinct assemblages form rapidly on younger tip-up mounds in the early years after their formation when mounds are less stable. Evidence is mixed and scant; Peterson et al. (1990) found that 4-year old mounds were highly impoverished unstable habitats and Spicer et al. (2018) found that distinct assemblages did not form on recently created tip-up mounds (4 years old). Rather, the vegetation on mounds was "a slightly impoverished subset of the vegetation growing on adjacent reference sites" (Spicer et al. 2018). However, Hutnik (1952) found distinct communities on mounds twelve growing seasons after a blowdown (see also Nakashizuka 1989 and Table 1).

Among windthrow microsites, mounds are particularly unique because even though they exhibit abiotic characteristics adverse to plant establishment, they create elevated microsites within the vertical structure of the forest. Besides substantially increasing light availability, the exposed mineral soil can release seeds from the seed bank and mounds can capture light-seeded species such as *Betula spp.* (Carlton and Bazzaz 1998a; Carlton and Bazzaz 1998b; Putz 1983; Schaetzl et al. 1988; Yoshida 2021). This suite of characteristics can promote the development of distinct pioneer plant communities within the first couple decades in most forest types worldwide (Carlton and Bazzaz 1998a; Kuuluvainen and Juntunen 1998; Nakashizuka 1989; Putz 1983; Yoshida 2021). The vertical structure of mounds can also provide a refuge to plants from many detrimental factors including vertebrate browsing, water inundation, and fungal pathogens (Battaglia et al. 1999; Long et al. 1998; Peterson and Pickett 1990; Yoshida 2021). Moreover, they serve as avian landing and nesting sites and provide favorable habitats for pollinators such as ground-nesting bees, which can promote the dispersal and proliferation of flowering and fruiting species (Campbell et al. 2017; Thompson 1980; Wojton and Pitucha 2020). Consequently, the ecological conditions on mounds may favor the rapid formation of plant communities that are distinct from areas adjacent to tip-up mounds and also distinct from the surrounding forest matrix. If so, then mounds may commonly promote diversity because they provide unique and fairly open microsites that form repeatedly and patchily throughout forests (Beatty 1984; Nakashizuka 1989; Riera 1985). This may be particularly true in old-growth forests that have little opportunity otherwise for the establishment and maintenance of early-successional species.

Here, we tested the hypothesis that distinct plant communities will develop rapidly on newly formed tip-up mounds versus adjacent reference sites on the intact forest floor. We predicted that mounds will not only develop unique plant assemblages, but they also will have higher plant species richness and diversity. In addition, we reviewed the literature on newly formed tip-up mounds in forests worldwide to synthesize what is known about early community development and patterns of biodiversity on these microsites. Based on our synthesis of the literature, we outline and briefly discuss five mechanisms that potentially underlie distinct community development immediately following tip-up mound formation. Finally, we describe how treefalls and their associated tip-up mounds cause the formation of six unique microsites and make the case that future studies of pits and mounds should consistently measure all of these microsites as well as two contrasting types of reference sites.

1.2 Methods

1.2.1 Study Sites

We studied tip-up mounds in the Upper Peninsula of Michigan within three blowdowns that are all surrounded by continuous forest cover. All forests are part of the Hemlock-White Pine-Northern Hardwoods Association (Braun 1950; Vankat 1979). Regional climate is continental, with summer temperatures occasionally exceeding 30˚C and winter temperatures regularly below -25˚C.

One of our focal blowdowns occurred in the Sturgeon River Gorge Wilderness located within in the Ottawa National Forest (46˚ 36’ 5.38” N latitude, 88˚ 42’ 37.41” W longitude). This windthrow occurred either in 2011 or 2012 (based on aerial imagery, and T. Strietzel, US Forest Service, *pers. comm.*). This storm created tree tip-up mounds typically greater than 1.5 m in height and 3 m long. Most of the windthrown trees were *Populus grandidentata* Michx. Common tree species in this fairly mature second-growth stand included *Acer saccharum* Marsh., *Acer rubrum* L., *Betula alleghaniensis* Britton., *Tilia Americana* L., *Picea glauca* (Moench) Voss, and *Abies balsamea* (L.) Mill.

The second windthrow occurred in 2012 on a north-facing upper-mid slope of Mt. Huron at a private 2500-ha reserve on the shore of Lake Superior (Huron Mountain Club, 46˚ 52’ 47” N latitude, 87˚ 54’ 36” W longitude). The Huron Mountain Club contains one of the largest tracts of old-growth forest left within the Eastern Deciduous Forest Biome. The topography is notably more rugged than that surrounding the Sturgeon River Gorge, with relief of up to 270 m above Lake Superior (Woods 2000). The forest was dominated by *Tsuga canadensis* (L.) Carrière, *Tilia americana*, *Betula alleghaniensis*, and *Acer saccharum*. For more details regarding soils, climate, and geology of these two sites see Woods (2000; 2008).

The third blowdown occurred in July of 2017 in a forest that is part of the University of Notre Dame Environmental Research Center (UNDERC) in the Northern Highland Province (46° 13' N, 89° 32' W), south of the Ottawa National Forest. The forest is largely second-growth and consists mainly of *B. alleghaniensis*, *A. saccharum*, *Abies balsamea*, *Betula papyrifera*, *Pinus strobus*, *Populus grandidentata*, and *Populus tremuloides*. Local altitude ranges from 500 to 520 meters.

1.2.2 Vegetation sampling

In June 2016 at the Sturgeon River Gorge, we selected ten tip-up mounds. Because this was a small, highly localized blowdown, we sampled nearly all the mounds at the site. We measured height, length, and width of each mound, and estimated area as the product of the length and width. We then randomly selected an undisturbed reference site of the same size on intact soil adjacent to each mound (but avoiding pits). The reference plots were at least 1 meter away, though not more than 3 meters away from the focal mound, and all reference plots were beneath the canopy gap created by the treefall. We visually estimated the cover of all vascular plant species on each mound and within each reference site. For woody species, we recorded if any of the individuals were reproductive (yes or no; based on the presence of buds, flowers, or fruits) on the mound or adjacent reference site and the total number of stems that were taller than 50 cm. Our goal was to use these measures as a metric of plant performance.

In July of 2014 at the Huron Mountain Club, we selected 14 tip-up mounds that occurred on either side of a narrow foot trail that went to the summit of Mt. Huron. Similar to the Sturgeon River Gorge, we ended up surveying the majority of the mounds because this too was a small localized blowdown. Reference sites and reproductive status were assigned as above. We could not visually estimate cover of all plant species because the height of the mounds precluded us from ascending them. Thus, we quantified plant density for the only 3 woody species that occurred on the mounds or reference sites. We also quantified the percent of individuals that were reproductive and the percent over 50 cm tall.

In July of 2019, we sampled 25 tip-up mounds and paired refence plots within a blowdown at UNDERC and recorded percent cover of all vascular plant species. We chose reference plots using the same protocol as at the other two sites. We measured the length and width of each mound, and estimated area as the product of the length and width.

1.2.3 Statistical analyses

We analyzed data from Sturgeon River Gorge and UNDERC together because they include data on all vascular plant species. The area of plots varied by more than one order of magnitude in some cases and was strongly bimodal and we were not able to find a data transformation to make the distribution more normal. Because of this and after graphical exploration showed no apparent relationship between area and differences in response variables, we did not include area as a factor in our models. To test for differences in total cover, species richness, and Shannon diversity, we conducted linear models. We included microsite (tip-up mound or reference) and tip-up mound plot pairs nested within site (Sturgeon River Gorge or UNDERC) as fixed factors.

We used non-metric multidimensional scaling (NMDS) employing the Bray-Curtis dissimilarity of species percent coverage matrix (R package, *vegan*) and a permutational ANOVA (PERMANOVA) to evaluate differences between communities on tip-up mounds versus reference plots (Oksanen 2015). We used a PERMDISP analysis to test for differences in beta diversity between microsite groups (Anderson et al. 2006). We also performed an indicator species analysis to identify species that were statistically associated with either microsite (*vegan*). For the Huron Mountain Club dataset, we compared stem density of *Sambucus racemosa* L. (the only common woody species represented by more than a few single stems) between mounds and reference plots using paired Mann-Whitney-Wilcoxon tests. All analyses were conducted using R version 3.4.2 (R Core Team).

1.2.4 Literature Review

We searched separately “pit-mound topography”, “tip-up mound*” and “root plate*” on Web of Science, combined with an exhaustive traditional review of the literature on treefalls and tip-up mounds (Table 1). Root plate is a common term for tip-up mound in the European literature. Because our interest was in the early colonization of tip-up mounds, we reviewed only studies that reported plant species diversity, richness, or abundance on tip-up mounds or pit-mound complexes equal to or less than 25 years old. We found 21 relevant publications (not including the current study). We only included publications where the authors were able to reliably date the age of the mound to within a few years. For example, we did not include Beatty (1984) or Simon et al. (2011) because ages of mounds or associated treefalls were not specified or were quite old. Because only ten of the twenty-one total studies reported any measure of variation, and three of these came from one location (Long et al. 1998; Peterson et al. 1990; Peterson and Pickett 1990), it was not possible to conduct a rigorous meta-analysis.

1.3 Empirical Results

1.3.1 Sturgeon River Gorge and UNDERC

Including tip-up mounds and reference plot pairs from Sturgeon River Gorge and UNDERC, total plant cover was marginally higher on tip-up mounds (Figure 1.1, linear model, $p = 0.067$). Species richness and Shannon diversity did not differ between mound and reference plots (Figure 1.1). The plant assemblages on tip-up mounds contrasted sharply with those on adjacent reference plots (Figure 1.2, PERMANOVA, p = 0.001). There were significant differences in community composition between Sturgeon River Gorge and UNDERC sites (PERMANOVA, p = 0.001), but beta diversity of tip-up mounds was lower than beta diversity of reference plots (PERMDISP, p = 0.002). This suggests that, overall, plant communities on tip-up mounds were more similar to each other than reference plots were similar to each other.

The plant assemblages that occurred on tip-mounds contrasted sharply with those on adjacent reference sites (Figures 1.2 and 1.3). More importantly, mounds were dominated by three fruit-bearing woody species, whereas reference sites were dominated by four fern species, as well as sugar maple seedlings and small saplings (Figures 1.3 and 1.4). Indicator species analyses confirmed that three woody species, *Prunus pensylvanica*, *Rubus idaeus,* and *S. racemosa*, characterized the vegetation on tip-up mounds while two woody species, *Fagus grandifolia* and *Fraxinus pennsylvanica*, characterized the vegetation in reference plots (Table 1.2).

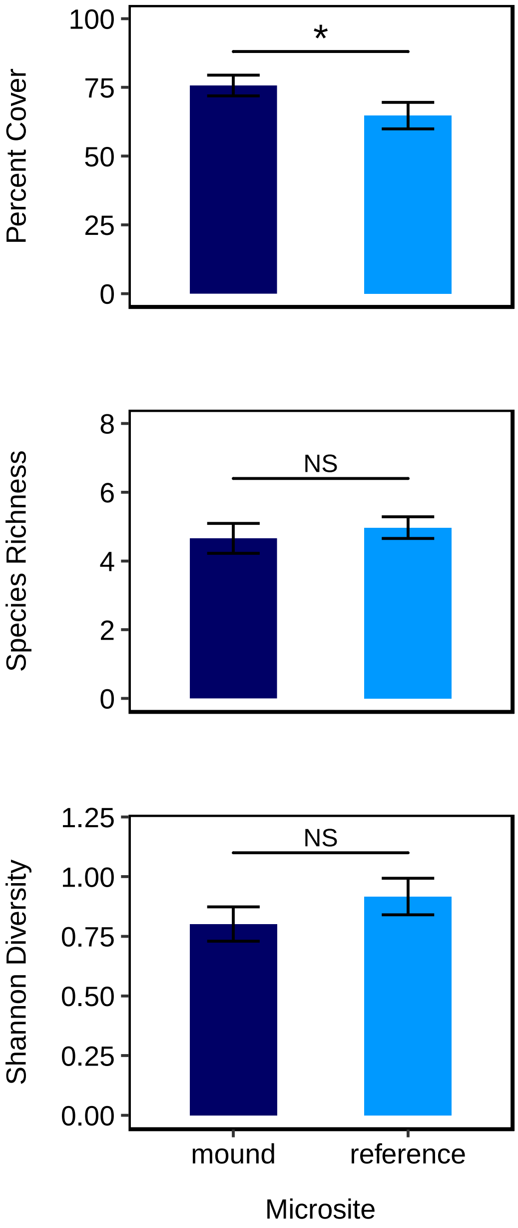

Percent Cover
100
75
50
25
0
*
Species Richness
8
6
4
2
0
NS
Shannon Diversity
1.25
1.00
0.75
0.50
0.25
0.00
NS
mound
reference
Microsite

Figure 1.1

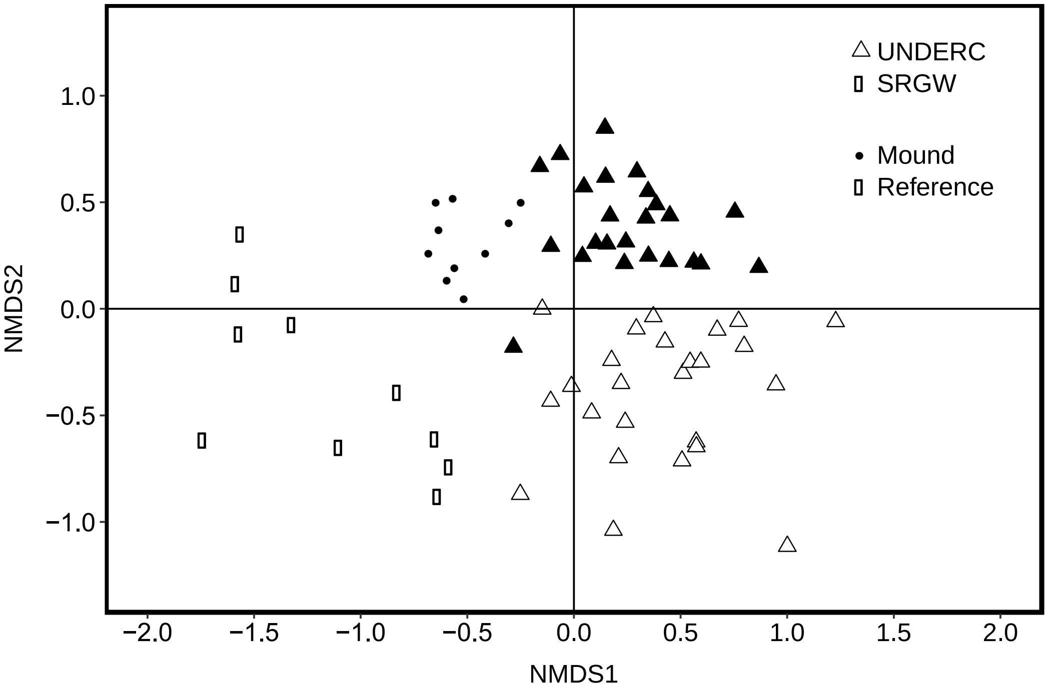
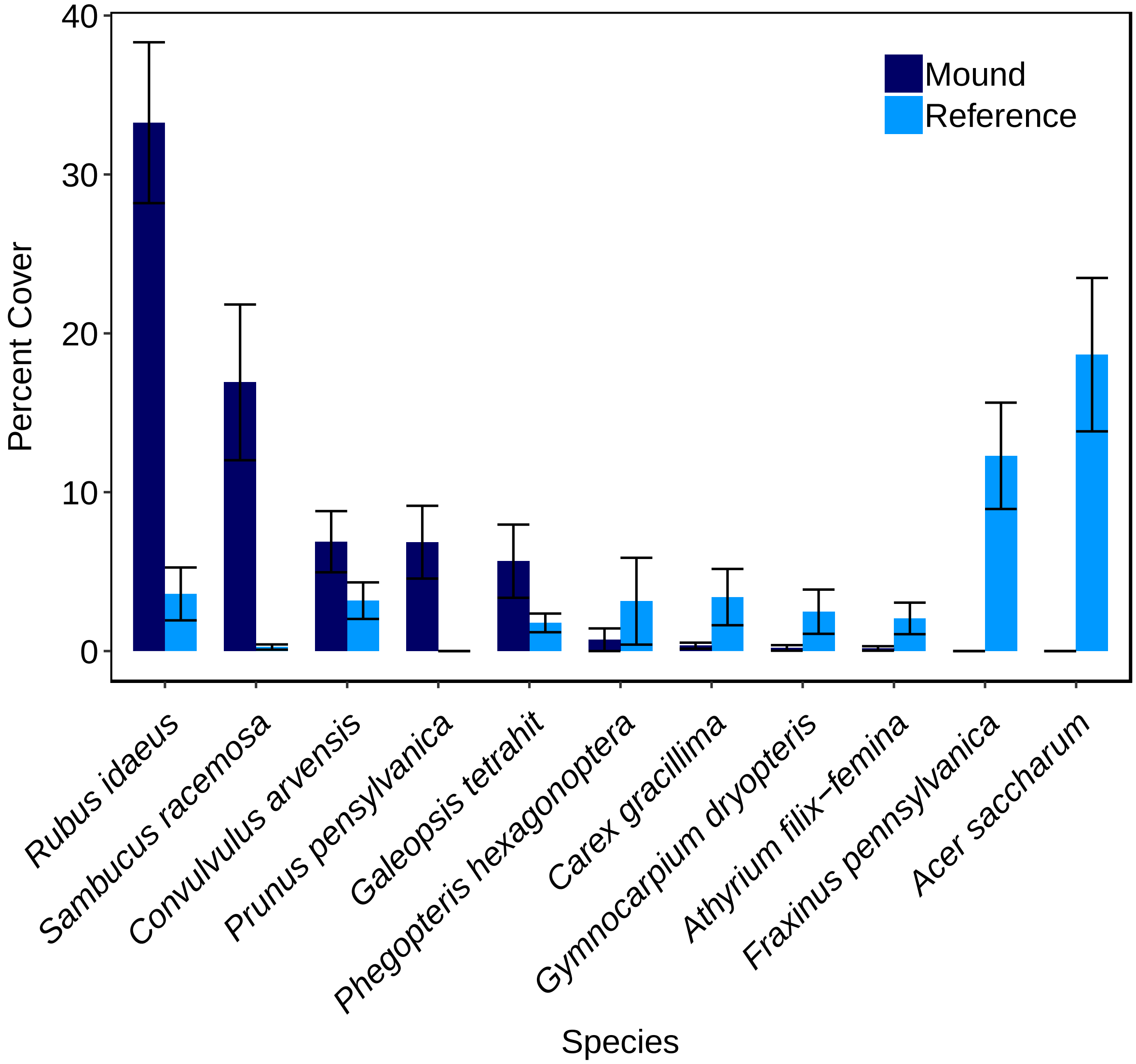

UNDERC
SRGW
Mound
Reference
1.0
0.5
0.0
−0.5
−1.0
NMDS2
−2.0
−1.5
−1.0
−0.5
0.0
0.5
1.0
1.5
2.0
NMDS1

Figure 1.2



40
30
20
10
0
Percent Cover
Mound
Reference
Rubus idaeus
Sambucus racemosa
Convulvulus arvensis
Prunus pensylvanica
Galeopsis tetrahit
Phegopteris hexagonoptera
Carex gracillima
Gymnocarpium dryopteris
Athyrium filix−femina
Fraxinus pennsylvanica
Acer saccharum
Species

Figure 1.3

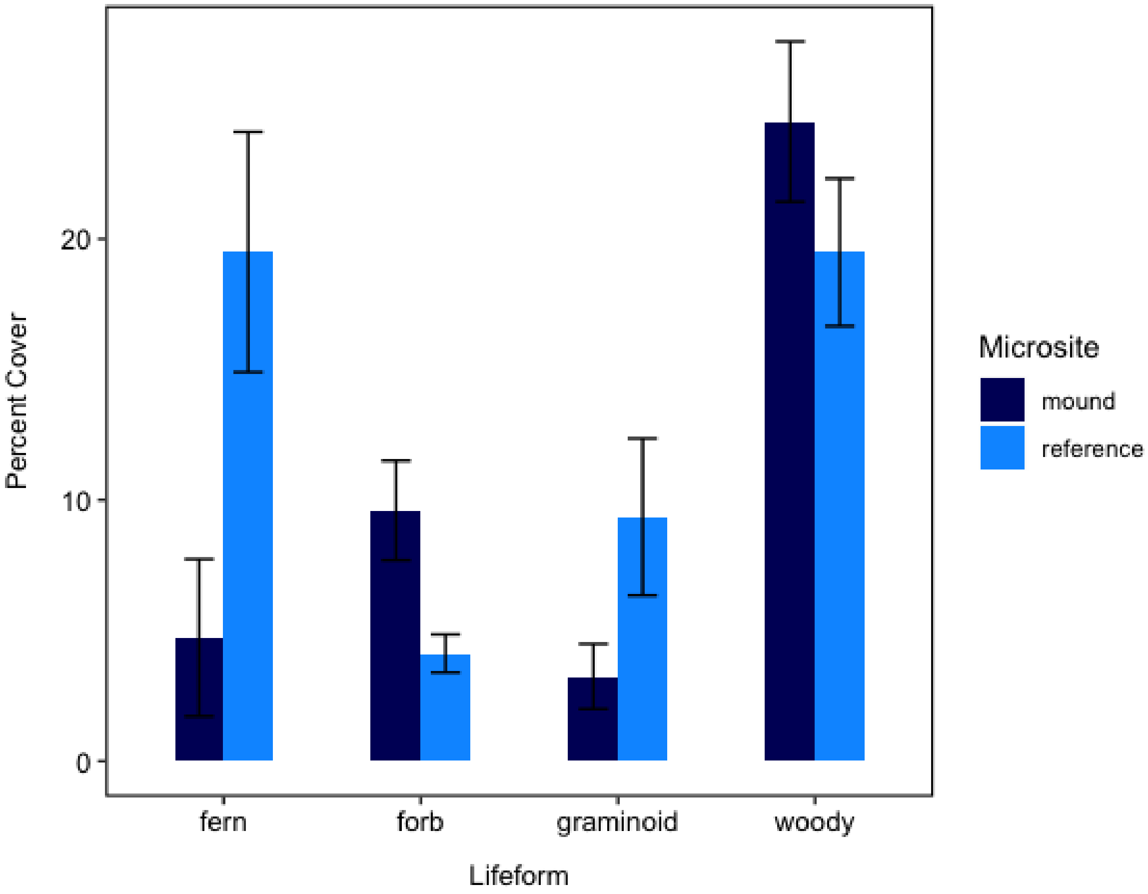


Figure 1.4

1.3.2 Huron Mountain Club

At Huron Mountain Club, *S. racemosa* was seven times denser on mounds versus adjacent reference plots (Figure 1.5). Thirty-one percent of *S. racemosa* were reproductive on tip-up mounds while zero percent were reproductive on reference sites. Of total *S. racemosa* stems, 86% were greater than 50 cm tall on mounds versus 57% in reference plots. Thus, individual stems of *R. racemosa* were fairly tall, and nearly a third, were reproductive on mounds. In contrast with mound vegetation at Sturgeon River Gorge, we found only a single *P. pensylvanica* on a tip-up mound and three stems of *Rubus* sp.; one on a tip-up mound and two in reference plots.

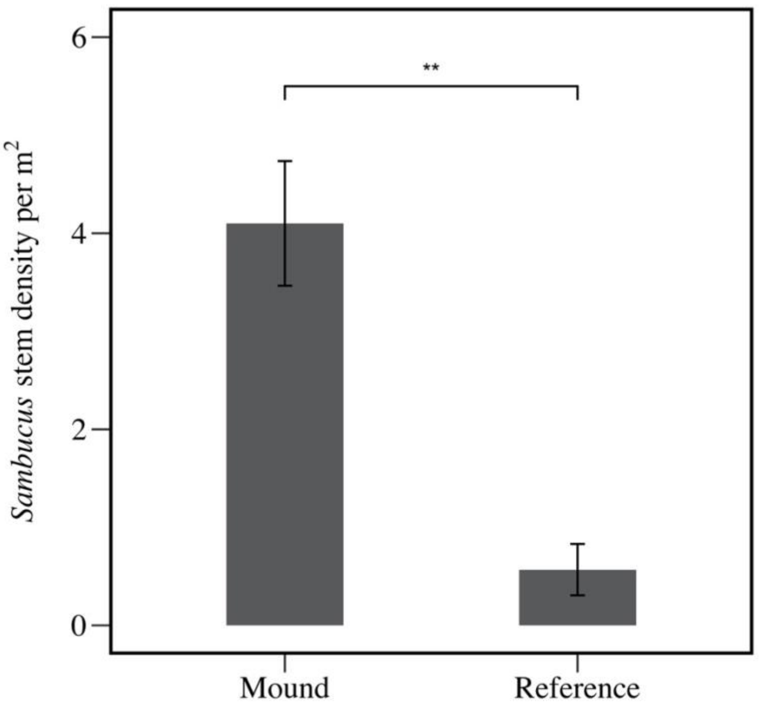


Figure 1.5

1.4 Discussion

1.4.1 Key Empirical Findings

We demonstrate that entirely distinct plant assemblages can form rapidly (4-5 years) on tree tip-up mounds at Sturgeon River Gorge and UNDERC (*cf*. Spicer et al. 2018). At Sturgeon

River Gorge and UNDERC, three fast growing woody species were thriving on mounds (abundant, tall, and often reproductive) and were absent from adjacent reference sites. Intact reference sites, on the other hand, hosted abundant ferns and species that are shade-tolerant and grow more slowly. At the Huron Mountain Club, mounds were characterized by moderately dense stands of *S. racemosa* that were uncommon in adjacent areas. Thus, at all sites, mounds enhanced total forest beta diversity by creating unique microsites that were rapidly colonized by species that rarely or never occurred in our adjacent reference sites. Our results add to the small number of studies that clearly demonstrated the formation of unique communities on recently formed mounds (Hutnik 1952; Nakashizuka 1989, Table 1.1, Figure 1.8).

1.4.2 Literature Review

We identified a total of 22 studies (including this study) that explored species colonization of tip-up mounds within 25 years of their formation (Table 1.1, Figures 1.7, 1.8, 1.9). Nine of these focused unequivocally on very young mounds that were equal to or less than ten years old (Battaglia et al. 1999; Carlton and Bazzaz 1998a; Peterson et al. 1990; Peterson and Pickett 1990; Spicer et al. 2018; Vodde et al. 2015; Waldron et al. 2014; Yoshida 2021, Fig. 9). In contrast to our results, these studies found that communities on mounds were impoverished, with much lower species diversity, richness, and plant abundance versus reference sites. Of the 22 studies, only 6 reported diversity metrics and 9 reported species richness (Figures 1.7 and 1.8). Only one-third of the studies that reported diversity found higher diversity on mounds than pits or mounds than intact sites (Figure 1.8). Similarly, one-third of the studies that reported species richness found more species overall on mounds vs. pits, and less than half found more species on mounds than intact sites (Figure 1.8). Interestingly, although few studies reported higher overall diversity or species richness on mounds, 15 of the 22 studies we include here found unique species or plant assemblages on mounds vs. other microsites (Figure 1.8, Table 1.1). Many of these same studies, and others, identified single, or in some cases, a few woody species, that were more abundant on mounds (Battaglia et al. 1999; Carlton and Bazzaz 1998a; Kern et al. 2019; Krueger and Peterson 2006; Long et al. 1998; Mollaei Darabi et al. 2014; Peterson and Pickett 1990; Vodde et al. 2015). These woody species were typically fast growing, early successional species (e.g., *Betula spp*, *Sorbus aucuparia*, *Prunus pensylvanica*). Similarly, we also found early successional woody species dominated our mounds (Figure 1.3). These results *suggest* that relatively young mounds may commonly promote the establishment and persistence of fast growing woody pioneers (see Kern et al. 2019; Putz 1983 and Riera 1985 for tropical forests). Kern et al. (2019) found that these saplings can escape browsing pressure (> 2 m) in thirteen years or less and that by growing on mounds, saplings are 30% closer to reaching canopy height than off mounds. Yoshida (2021) showed that even though density of the smallest height class (<25cm) of *Abies sachalinensis* was much higher in pits, there were more in the 50cm height class found on mounds in the tenth growing season post-windthrow. Coupled with support that saplings can grow faster on mounds, these results suggest that mounds are paramount to promoting regeneration following wind disturbances (Vodde et al. 2010). Nonetheless, young mounds often remain fairly open with low plant abundance and diversity (Peterson and Pickett 1990; Spicer et al. 2018; Vodde et al. 2015). Peterson et al. (1990) found that mounds remained strikingly depauperate 4 years after their formation; thus, they remain relatively open habitats available for subsequent plant colonization years after mound formation (see also Spicer et al. 2018).

Why do young mounds often remain open and depauperate? One key is likely the degree that the soil on mounds is stable; excessive erosion and sloughing may reduce successful establishment and delay community development (Peterson et al. 1990). Both Peterson et al. (1990) and Spicer et al. (2018) studied mounds that occurred within large blowdowns (> 3.0 ha) where the action of wind, precipitation, and exposure to excessive freezing and thawing may be greater than in smaller blowdowns or beneath a single treefall (see also Nakashizuka 1989). On mounds that were a decade older (20-25 years) and likely more stable, Lang et al. (2009) found that mound communities not only differed from reference sites but also had higher diversity (Table 1). Depauperate mounds may also reflect a legacy of overbrowsing, which may cause dispersal limitation by reducing the nearby supply of propagules of plant species vulnerable to browsers (Pendergast et al. 2016). In addition, plant succession on mounds in old-growth or mature forests may be delayed (e.g., Peterson et al. 1990; Spicer et al. 2018) because soil seed banks may contain few viable seeds of early successional woody species (Peterson and Carson 1996). Finally, the mounds of some tree species or soil types may be inherently more stable than others, and thus rapid succession on mounds may be dependent upon the species of tree that created the mound or local variation in soil type (e.g., Lohmus et al. 2010; Vodde et al. 2010). Future research will be required to distinguish among these and other potential explanations.

Table 1.1

Location of study, *forest type*	**Time since windthrow**	**Microsites measured**	**Focus of study**	**Relevant Findings**	**Source**
Northern Sweden, ***Boreal spruce forest***	Variable, median treefall age was 21 years.	Disturbed soil (mounds + pits)	Bryophyte assemblage composition and diversity on pits, mounds, and undisturbed soil	Disturbed soil had higher bryophyte diversity than adjacent reference sites.	Jonsson and Esseen (1990)
Northeast Estonia, ***Hemiboreal mixed spruce-hardwood***	1-10 years	Mounds, pits, intact soil sites	Woody species regeneration following storms	Regeneration densities lowest on mounds and highest on intact soil sites. Species differentially colonized pit and mound sites.	Vodde et al. (2015) *See also* Ilisson et al. (2007)
Estonia, ***Hemiboreal mixed mesotrophic and drained swamp forests***	Variable	Mounds	Lichen abundance and community properties on mounds	Lichen abundance increases with treefall age. Mounds hosted several rare lichen	Lohmus et al. (2010)

				species and some lichen species specialize on mounds.	
Müritz National Park, Mecklenburg-Western Pomerania, North–East Germany, ***Central European beech forest***	<12 years, 12-24 years, >24 years	Mounds, intact soil sites	Vascular and bryophyte species richness and community composition on mounds and undisturbed soil	Species richness and number of species with persistent seed banks were higher on mounds for vascular and nonvascular plants. Young mounds hosted unique vascular species. Vascular species richness decreased as mound age increased. *Rubus idaeus* only found on young mounds. Plant community composition differed between mounds and reference sites.	von Oheimb et al. (2007)

North Shore administrative region, Quebec, Canada, ***Boreal eastern black spruce-moss forest***	4 years	Mounds, pits, intact soil sites	Regeneration of herbaceous and woody species in windthrow and windthrow-salvage logged plots	Species richness was highest on undisturbed sites, intermediate on mounds, and lowest in pits, regardless of salvage treatment. White birch was associated with mounds.	Waldron et al. (2014)
Upper Peninsula, Michigan, ***Mature and old-growth Temperate northern hardwood***	4-5 years	Mounds, intact reference sites	Plant species regeneration on mounds versus intact adjacent reference sites	Mounds were characterized by woody plant communities distinct from reference sites.	Current study
Northern Wisconsin, ***Old growth hemlock-northern hardwood***	10-15 years post windthrow	Mounds, intact reference sites	Regeneration of light-seeded and browse-sensitive tree species on mounds vs. closed forest sites	More browse damage in recently disturbed plots than in intact forest sites, but less browsing occurred on trees < 2 m tall on mounds than off mounds within the blowdown. In the	(Kern et al. 2019)

				understory, *Acer saccharum* was more common off mounds and *Betula alleghaniensis* and tall light-seeded species were more common on mounds.	
Flambeau River State Forest, Wisconsin, ***Old growth hemlock-northern hardwood***	25 years post windthrow	Mounds (top, upper surface, lower surface), pits, intact reference plots	Species richness in pit-mound microsites in salvaged and unsalvaged sites.	Mounds had higher species richness and cover than other microsites. *Maianthemum canadense, Poa spp.*, and *Trientalis borealis* had higher cover on mounds than in pits.	Lang et al. (2009)
Cedar Creek Natural History Area, Central Minnesot**a,** ***Temperate pine forest***	1-14 years post windthrow (repeated sampling	Mounds (upper surface, lower surface),	Presence of vascular plants	New soil (lower surface) sites on mounds had most distinct assemblage. They	Palmer et al. (2000)

		pits, intact soil plots		were distinguished by ruderal species, spread of vines, and *Rubus idaeus*. Within the mound microsites, the old soil (upper surface) initially had more species than the new soil, but this reversed within two years following windthrow. All microsites converged in composition within 14 years.	
Uryu Experimental Forest, Hokkaido Japan, ***Temperate mixed forest***	2 and 10 years post windthrow	Mounds, pits, intact reference plots (reference plots only 2 years post windthrow)	Regeneration of woody species on treefall microsites	Density of all species (*Abies sachalinensis, Picea glehnii, Betula spp.*, *Picea amurense, Quercus crispula*) on mounds was lower than in pits	Yoshida (2021)

				but higher than on undisturbed ground 2 years post-windthrow. At 10 years post-windthrow, density of seedlings on mounds substantially decreased for all species except *Betula spp.*	
Northeastern Forest Experiment Station, New Hampshire, ***Temperate northern hardwood***	12 years post hurricane	Mounds (top edge, upper surface, lower surface), pits	Reproduction of woody seedlings on treefall microsites	Most reproductive seedlings on mounds. Different community composition on mounds than in pits. *Prunus pensylvanica* and *Sambucus racemosa* found only on mounds and not in pits. Did not include adjacent	Hutnik (1952)

				undisturbed reference sites, but noted that *Betula papyrifera* was not present in any undisturbed area of surrounding forest.	
Harvard Forest, North-central Massachusetts, ***White pine-hemlock hardwood***	1-3 years post experimental blowdowns	Mounds (top wall, top edge), pits, open intact sites, fern cover sites	Birch regeneration on pit-mound microsites	Birch seedlings (from seed) had greatest survival on mounds. The tallest of transplanted seedlings were located on mounds.	Carlton and Bazzaz (1998a)
Allegheny National Forest, Pennsylvania**,** ***Temperate old growth hemlock-northern hardwood***	4 years post windthrow	Mounds, pits	Plant community composition comparisons between mounds and pits on elevational gradient	Higher species richness, biomass, and stem density in pits. *Prunus pensylvanica* had higher densities on mounds.	Peterson and Pickett (1990)

Allegheny National Forest, Pennsylvania, ***Temperate old growth hemlock-northern hardwood***	4 years post windthrow	Mounds (top), pits (center, wall), intact sites opposite mounds	Soil properties, environmental conditions, and plant colonization on pit-mound microsites.	Mounds had lower species richness and lower herbaceous and total plant cover than other microsites. Tree cover was similar on mounds to pit and wall sites. Undisturbed sites had highest tree and total cover.	Peterson et al. (1990)
Allegheny National Forest, Pennsylvania, ***Temperate old growth hemlock-northern hardwood***	9 years post windthrow	Mounds, surrounding area	Hemlock regeneration on mounds vs. adjacent reference sites.	Hemlock occurred primarily on mounds because mounds were a refuge from browsing by whitetail deer.	Long et al. (1998)
Allegheny National Forest, NW Pennsylvania,***Temperate old growth hemlock-northern hardwood***	18 years post windthrow	Mounds, pits, points along transects	Hemlock regeneration on mounds vs. surrounding areas	Hemlock persisted on mounds 9 years after Long et al. (1998).	Krueger and Peterson (2006)

Powdermill Nature Reserve, South-central Pennsylvania, ***Mature temperate mixed mesophytic***	3 years post windthrow	Mounds, intact reference plots	Community composition comparisons between mounds and intact soil in salvaged vs. unsalvaged sites.	There was little difference in community composition between plant communities on tip-up mounds and reference plots.	Spicer et al. (2018)
Mazandaran province, Northern Iran, ***Temperate beech forest***	Variable (1 to >15 years)	Mounds, pits, intact closed canopy plots	Community composition comparisons between pit-mound microsites along age gradient in gaps and versus intact closed canopy sites	Communities differed between pit-mound sites and closed canopy sites, with species such as *Sambucus ebulus* only found in disturbed sites. Herbaceous and regeneration composition on pits and mounds changed over time. Mounds had the most diversity at younger stages and were colonized by disturbance	Mollaei Darabi et al. (2014)

				specialists such as *Rubus spp.*	
Ohdaigahara, western Japan, ***Old growth beech-fir***	Variable	Mounds, pits, fallen boles	Distribution of seedlings and saplings in gap and closed canopy microsites	Species richness and diversity of woody seedlings was highest on mounds. Mounds may have provided refuge from dwarf bamboo recalcitrant understory layer.	Nakashizuka (1989)
Congaree Swamp National Park, South Carolina**,** ***Old growth mixed bottomland hardwood and Pinus taeda bottomland hardwood***	5 years post hurricane	Mounds, pits, intact sites	Seedling establishment and survival following Hurricane Hugo	*Liquidambar styraciflua* and *Acer rubrum* seedlings had positive correlation with number and area of mounds. *Asimina triloba* had negative correlation with number of mounds.	Battaglia et al. (1999)

Barro Colorado Island, Republic of Panama ***Tropical semi-deciduous moist forest***	6 years or less	Disturbed soil (mounds + pits)	Pioneer tree distribution on disturbed soil and other gap microsites.	Pioneer trees were more common on disturbed soil. There were several viable seeds of pioneer tree species in the seed bank.	Putz (1983)
Piste de St. Elie study site, French Guiana ***Tropical rain forest***	1-20 years post windthrow	Mounds, ground sites	Regeneration on tip-up mounds	A pioneer species (*Cecropia obtusa*) germinated and persisted better on tip-up mounds than surrounding ground areas.	Riera (1985)

Table 1.2

Species	**Plot type association**	**Indicator species statistic**	**p-value**
Rubus idaeus	Tip-up mounds	0.922	0.005
Sambucus racemosa	Tip-up mounds	0.671	0.005
Prunus pensylvanica	Tip-up mounds	0.655	0.005
Acer saccharum	Reference plots	0.775	0.005
Fraxinus pennsylvanica	Reference plots	0.697	0.005

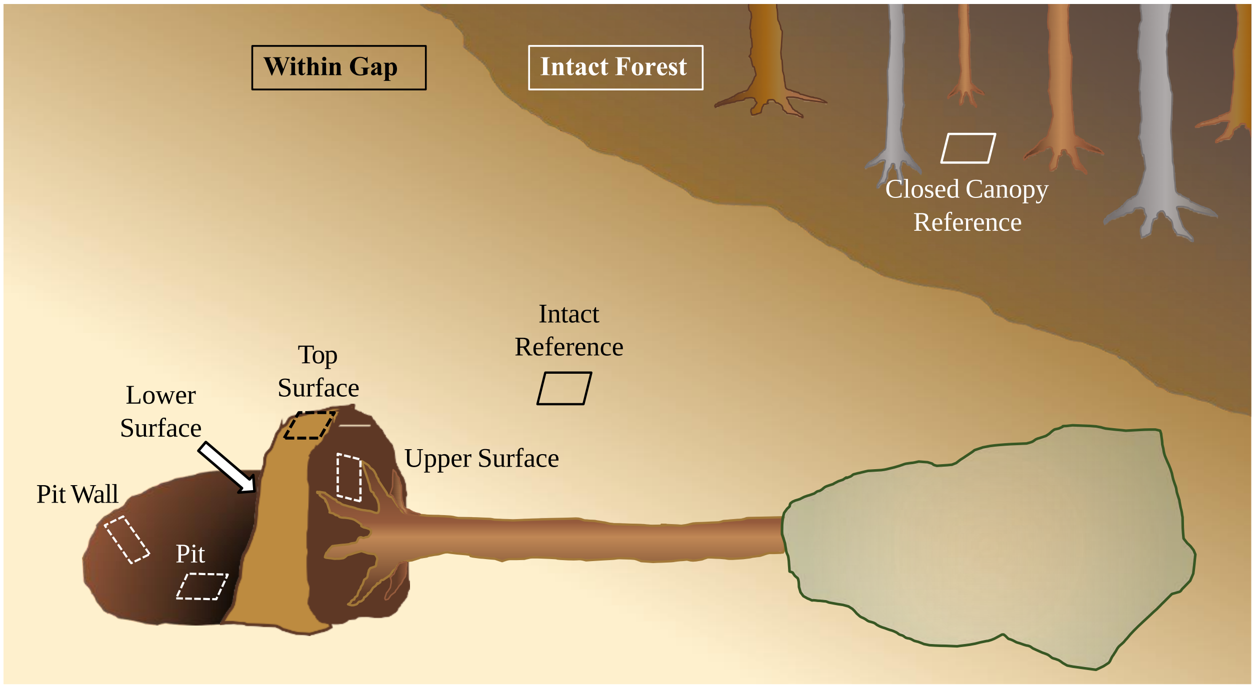


Figure 1.6

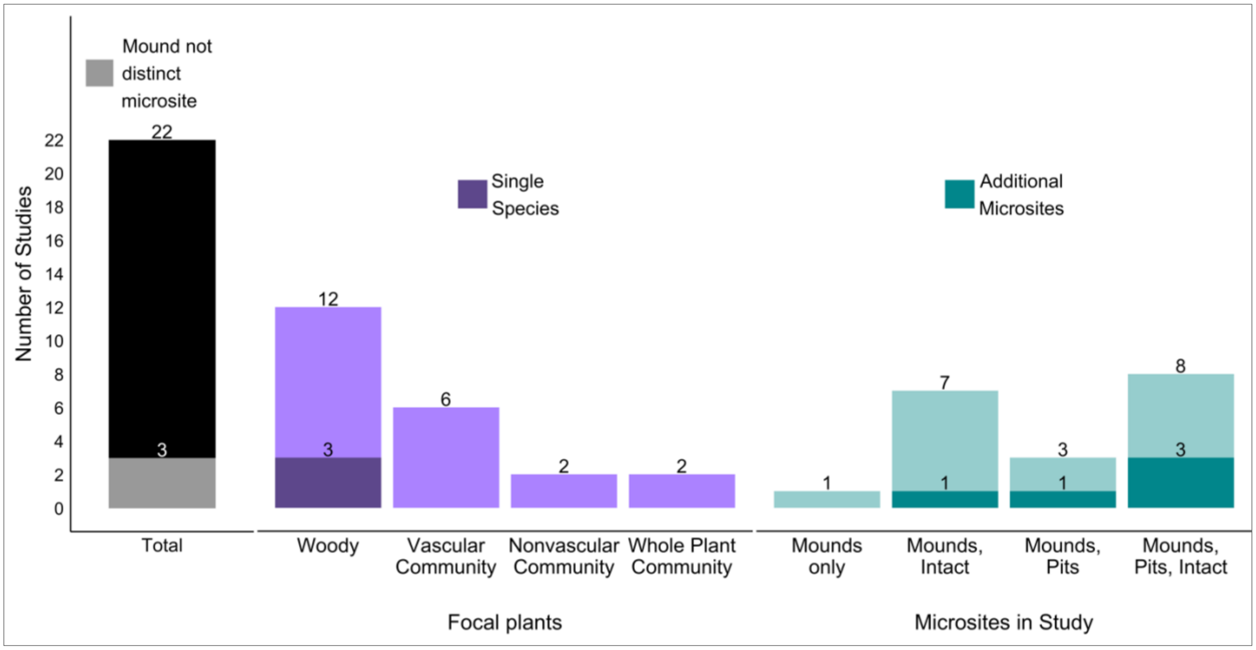


Figure 1.7

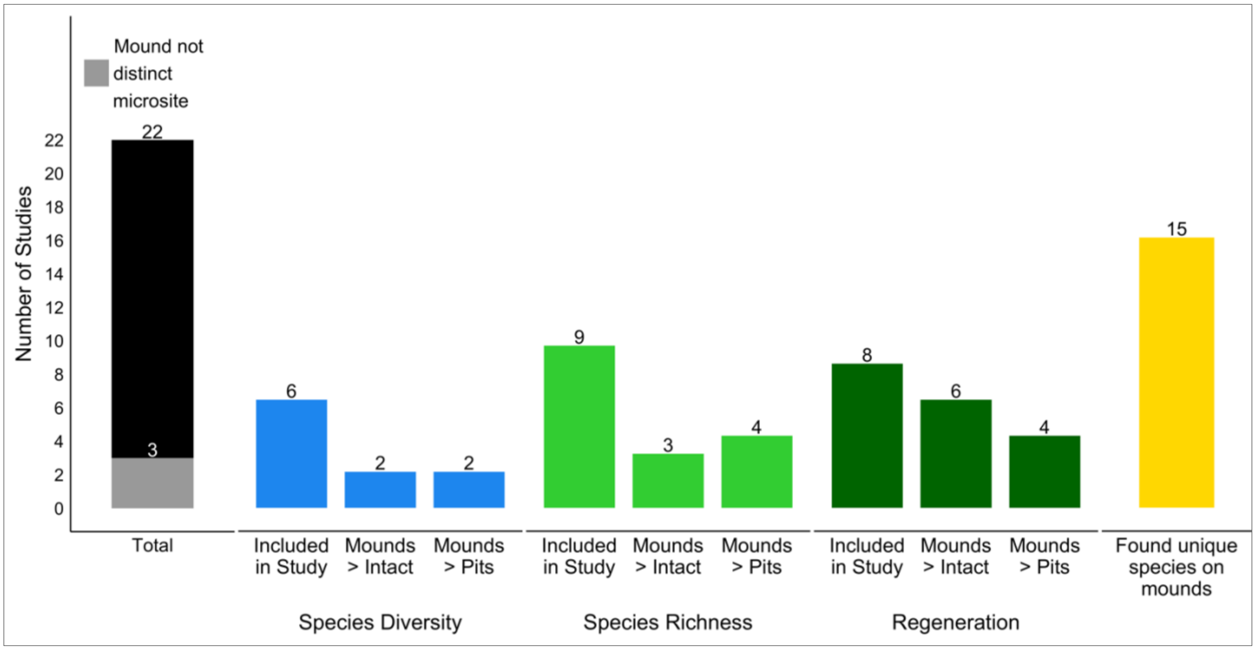

Mound not distinct microsite
Number of Studies
0
2
4
6
8
10
12
14
16
18
20
22
22
3
6
2
2
9
3
4
8
6
4
15
Total
Included in Study
Mounds > Intact
Mounds > Pits
Included in Study
Mounds > Intact
Mounds > Pits
Included in Study
Mounds > Intact
Mounds > Pits
Found unique species on mounds
Species Diversity
Species Richness
Regeneration

Figure 1.8

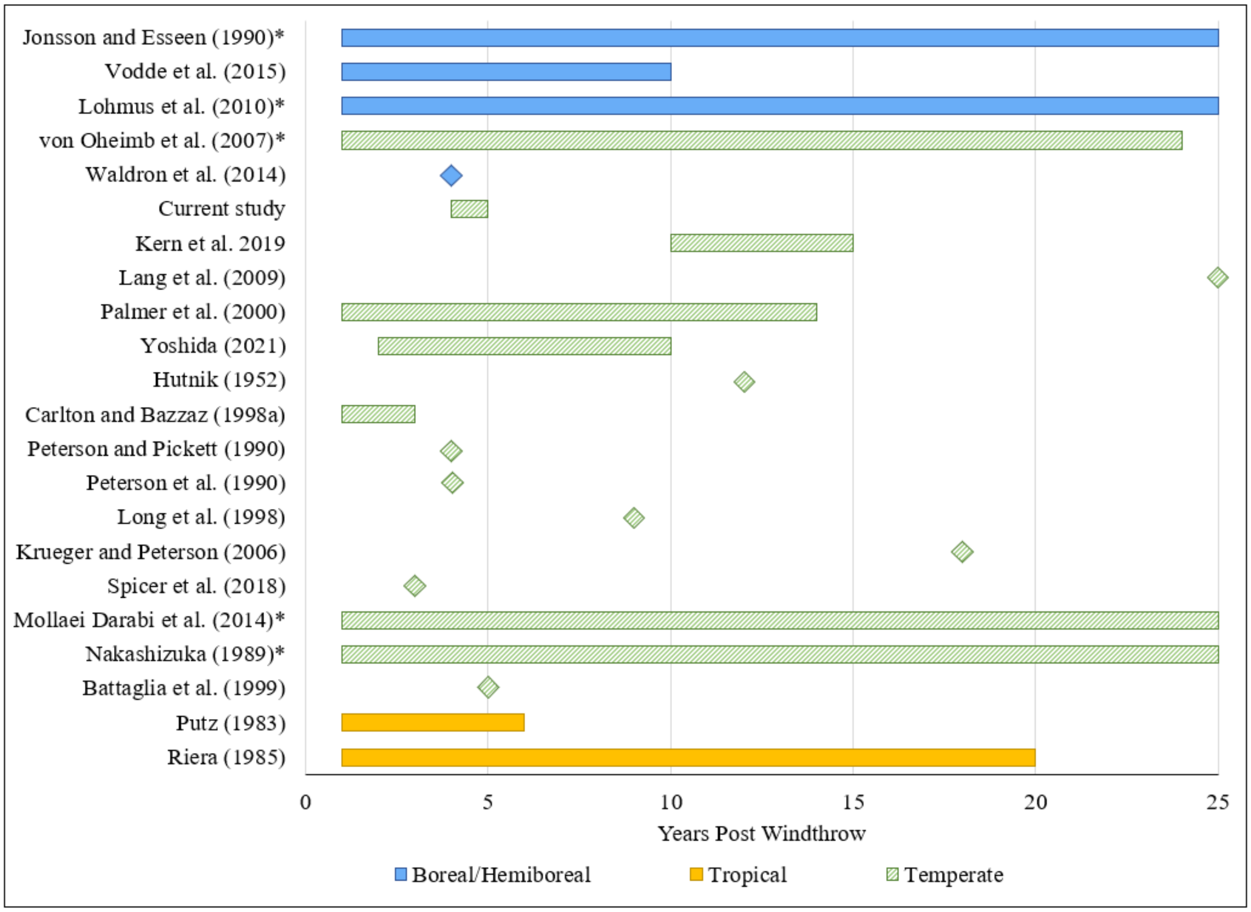

Jonsson and Esseen (1990)*
Vodde et al. (2015)
Lohmus et al. (2010)*
von Oheimb et al. (2007)*
Waldron et al. (2014)
Current study
Kern et al. 2019
Lang et al. (2009)
Palmer et al. (2000)
Yoshida (2021)
Hutnik (1952)
Carlton and Bazzaz (1998a)
Peterson and Pickett (1990)
Peterson et al. (1990)
Long et al. (1998)
Krueger and Peterson (2006)
Spicer et al. (2018)
Mollaei Darabi et al. (2014)*
Nakashizuka (1989)*
Battaglia et al. (1999)
Putz (1983)
Riera (1985)
0
5
10
15
20
25
Years Post Windthrow
Boreal/Hemiboreal
Tropical
Temperate

Figure 1.9

1.4.3 Mechanisms underlying rapid colonization of mounds

While there may be additional mechanisms, we propose five general, non-mutually exclusive mechanisms, that underlie the rapid formation of novel plant communities on mounds. These include: 1. Mounds typically have disturbed and exposed mineral soil, which likely promotes germination and establishment from the seed bank or from wind or avian dispersed seeds (Riera 1985; Sauer and Struik 1964). 2. Mounds enhance the establishment and growth of early successional species because these elevated habitats receive more light than adjacent microsites on the soil surface (Barker Plotkin et al. 2017; Carlton and Bazzaz 1998b; Clinton and Baker 2000; Putz 1983). 3. Avian frugivores may perch on mounds thereby concentrating seed dispersal on top of mounds (Thompson 1980). 4. Both above and below ground competition with a recalcitrant understory layer may be mitigated because mounds are perched above these dense plant layers (Kulakowski and Veblen 2003; Nakashizuka 1989; Royo and Carson 2006). 5. Mounds are refugia from vertebrate herbivores, particularly white-tail deer (Kern et al. 2019; Krueger and Peterson 2006; Long et al. 1998). An additional mechanism may be common in wetland or bottomland forests, where mounds serve as refuge from overly hydric conditions on the soil surface (Battaglia et al. 1999; Peterson and Pickett 1990; Titus 1990).

With the above mechanisms in mind, we note that the species that rapidly colonized mounds in this study and elsewhere (e.g., *S. racemosa*, *R. idaeus*, and *P. pensylvanica*) shared a suite of unique traits. They were all fast-growing pioneers, that likely benefit from reduced competition on elevated mounds, are avian dispersed, seed banking, and preferred by deer. Consequently, any species that share at least some of these traits may commonly establish on mounds in many forest types or geographic regions (Barker Plotkin et al. 2017; Hutnik 1952; Long et al. 1998; Nakashizuka 1989; Putz 1983).

1.4.4 Limitations of previous studies and a way forward

We identify a number of limitations in past studies in terms of methodologies (e.g., ability to reliably date mound age), location and recognition of unique microsites, failure to distinguish among contrasting microsites, and use of reference sites (Figures 1.6, 1.7, and 1.8, Table A-1). Five of the twenty-two studies did not have an intact reference site adjacent to the mound and only two of the eighteen used a closed canopy reference site (Appendix A, Table A-1). In addition, studies varied substantially regarding which unique microsites they recognized or surveyed (Figures 1.6 and 1.7, Appendix A). Furthermore, the limited number of studies to date vary in focal species or communities (e.g. woody species or communities, forbs, nonvascular plants), making it difficult to reach conclusions about overall plant community diversity or species richness (Figures 1.7 and 1.8, Table 1). In some cases, studies sampled or reported the pit and mound together as a single, relatively large microsite (e.g., Jonsson and Esseen 1990; Mollaei Darabi et al. 2014; Putz 1983).

From the studies in Table 1.1, we have distinguished five distinct microsites that typically accompany treefalls and their associated pits and mounds (Figure 1.6). We recommend that future studies of habitats associated with tip-up mounds sample all five of these microsites, which builds upon both Hutnik (1952) and Peterson et al. (1990). We also strongly recommend the use of two reference sites: one on undisturbed soil adjacent to the pit and mound, and another beneath nearby intact forest, located away from the treefall or blowdown to avoid edge effects (Figure 1.6, see also Simon 2011). The use of these two types of reference sites distinguishes the effect of the mound from the intact soil surface adjacent to the mound, and in addition, how these microsites differ from nearby plant communities that occur in undisturbed intact forest. No study sampled more than four of the five. Finally, only Peterson et al. (1990) distinguished the pit wall from other microsites. The pit wall microsite may contrast sharply with other microsites, particularly in mature or old-growth forests, because the fall of large trees creates large and very deep pits (Peterson et al. 1990). In contrast to the pit wall, deep pits periodically fill with standing water at the bottom, sometimes becoming anaerobic (Beatty and Stone 1986) and may have a depauperate soil seed bank, which was uplifted within the soil onto the corresponding mound.

Our review revealed that the geographic distribution of studies was biased towards temperate forests (16 studies, Figure 1.9), twelve of which were in the United States (Table 1.1). There were only four studies from boreal or hemi-boreal regions and just two from tropical forests, both Neotropical (Table 1.1, Figure 1.9). Clearly, studies are needed in forests on other continents (e.g., Africa) and south of the equator, to fully evaluate the degree that the microhabitats associated with treefall pits and mound promote forest-wide diversity.

1.5 Conclusions

Distinct plant communities can rapidly develop on newly formed tree tip-up mounds, though this often fails to occur. When it does occur, these plant assemblages are commonly colonized by fast growing, early successional, seed-banking, avian-dispersed, and browse-preferred woody species. Thus, mounds can serve as a foci for woody species that may be scarce within the nearby intact forest matrix; in this way, mounds contribute to the maintenance of forest-wide diversity. Our review of the literature identified only 22 studies of early succession (25 years old or less) on tip-up mounds. Despite many studies reporting lower overall diversity or species richness on mounds, more than two-thirds of the studies in our review identified unique species or plant assemblages on mounds vs. surrounding areas and other microsites. The studies varied widely in approaches and methodologies, and were restricted to a few geographic regions, primarily the eastern U.S. (Table 1.1). We recommend that future studies of the habitats associated with young pits and mounds recognize and survey five unique microsites (Figure 1.6, Appendix A). We also recommend the use of two reference sites: one adjacent to the fallen tree on undisturbed intact soil but within the canopy gap, and one beneath nearby intact closed canopy forest (Figure 1.6, Appendix A). We hope that this integrated approach may contribute to a more comprehensive understanding of the degree to which early vegetation dynamics on newly formed pit and mound complexes contributes to the maintenance of diversity in forests, regardless of biome.

2.0 Do invasive species provide a refuge from browsers?: A test of associational resistance in a peri-urban habitat plagued by deer

White-tailed deer (*Odocoileus virginianus*) overbrowsing over the past several decades has caused substantial changes to plant communities in eastern deciduous forests. Deer-preferred species have declined or become locally extirpated in many areas while deer-tolerant species have greatly increased in abundance. Moreover, the abundance of nonnative invasive species has also increased over the last few decades, outcompeting many native species. Native shrubs such as *Sambucus canadensis* (American elderberry) are now much less common, particularly in urban forests and forests with high deer densities. Here, we performed a short-term study in which we introduced propagations of a native shrub into a replicated field experiment in which we factorially manipulated deer presence or absence and invasive species presence or absence by using exclosures and removing invasive species. We monitored metrics of *S. canadensis* fitness including leaf count and plant height over two growing seasons. Browsing substantially reduced survival whereas invasive species provided a modest degree of associational resistance. Browsing significantly decreased both leaf count and plant height. By the end of the study, individuals within exclosures had over twice the number of leaves, were five times taller, and had much lower mortality versus those exposed to browsing. Removing invasive species did not change plant height, however, *S. canadensis* individuals experienced marginally higher leaf counts inside exclosures where we had removed invasive species. This trend was opposite in individuals outside of fences such that those growing within patches where invasive species remained had slightly higher leaf counts, especially during the first growing season. Until the final census date, elderberry growing within patches of invasive species had slightly lower mortality versus those growing in patches where invasive species had been removed. The results from our short-term study indicate that browsing is more inimical to a native shrub than competition from invasive species and we did not find evidence of associational resistance to browsing from invasive cover.

2.1 Introduction

Peri-urban forests exist between urban and rural areas, or at the urban-rural interface, and often face the same biodiversity threats as older, intact forests, but with the added complexities of being near metropolitan areas. Peri-urban forests experience considerable habitat fragmentation, edge effects, patchworks of differing land use history, and frequent invasions by nonnative plant species (Davis, Singh, Thill, & Meentemeyer, 2016; Dolan, Stephens, & Moore, 2015; La Sorte, McKinney, & Pysek, 2007). Residential propagule pressure from intentional or unintentional introductions of ornamental and nonnative species as well as high amounts of patchy areas with higher light levels of peri-urban forests increase the invasibility of these habitats (Chytry et al., 2008; Martin, Canham, & Marks, 2009; Tanentzap & Bazely, 2009). Moreover, in areas with high deer densities, deer can home in on and easily exploit fragmented forest patches by overbrowsing native herbs and shrubs (George & Crooks, 2006; Soultan, Attum, & Lahue, 2021).

The extirpation of apex predators and lax game management have often caused deer densities to increase to three to five times their pre-European settlement levels throughout much of the Eastern Deciduous Forest Biome of the US (Flagel, Belovsky, & Beyer, 2016; Ward & Williams, 2020). Consequently, overbrowsing by ungulates, particularly white-tailed deer

(*Odocoileus virginianus*) has caused declines in both biodiversity and abundance of browse-sensitive native plant species (Cote, Rooney, Tremblay, Dussault, & Waller, 2004; Nuttle, Royo, Adams, & Carson, 2013; Rooney, 2001; Royo & Carson, 2006). This overbrowsing of preferred species often causes the formation of depauperate and recalcitrant understory layers (sensu Royo & Carson, 2006) that are inimical to forest recovery even if herbivores are reduced in abundance for decades (T. H. t. Pendergast, D. J. Burke, & W. P. Carson, 2013). Delays in forest recovery, referred to as legacy effects or the ghost of herbivory past (sensu Banta, Royo, Kirschbaum, & Carson, 2005; Howe, Brown, & Zorn-Arnold, 2002) occur, at least partly, because of a lack of nearby seed sources or propagules for species driven to local extinction by overbrowsing (Pendergast, Hanlon, Long, Royo, & Carson, 2016; Royo, Stout, deCalesta, & Pierson, 2010). In total, overbrowsing has led to widescale shifts in both herbaceous and woody understory species, as well as declines in tree diversity in the overstory (R. C. Anderson & Katz, 1993; Casabon & Pothier, 2007; Cote et al., 2004; Kelly, 2019; Rooney, 2009; Rooney & Waller, 2003; Royo & Carson, 2006).

The establishment of nonnative plant species is increasingly common and often pervasive in temperate forests, and acting simultaneously with overbrowsing, may also cause declines in the abundance and diversity of native plant species (A. Kulmatiski, 2006; Nuñez & Paritsis, 2018; Pysek et al., 2012; Xu et al., 2020). Nonnative invasive species are often superior competitors because they typically escape enemies, introduce novel secondary metabolites and allelochemicals, cast deep shade, and exhibit longer leaf phenology than natives (Alexander & Levine, 2019; Blossey & Notzold, 1995; Callaway & Ridenour, 2004; Kalisz, Kivlin, & Bialic-Murphy; Siemann, DeWalt, Zou, & Rogers, 2017; Siemens & Blossey, 2007; Smith & Hall, 2016). Moreover, they can alter soil properties and microbes in a way that makes it difficult for native species to reestablish if they had been locally extirpated (Pringle et al., 2009; Tanner & Gange, 2013; van der Putten, Klironomos, & Wardle, 2007; Vogelsang & Bever, 2009). Overbrowsing can facilitate invasion and spread of nonnative species, thus the combination of these drivers can be exceedingly detrimental to native plant communities (Averill et al., 2018; Burke et al., 2019; Knight, Dunn, Smith, Davis, & Kalisz, 2009; Vavra, Parks, & Wisdom, 2007). White-tailed deer often avoid herbaceous and woody nonnative species, potentially creating a positive feedback whereby invasive plant abundance increases while native abundance and diversity decreases (Arcese, Schuster, Campbell, Barber, & Martin, 2014; Kelly, 2019; Link, Turnblacer, Snyder, Daugherty, & Utz, 2018).

It is possible, however, for palatable species to "hide" in relatively dense patches of unpalatable species, an interaction termed associational resistance (Barbosa et al., 2009). Here, palatable species are either less detectable or less accessible to herbivores chemically, visually, or physically (Atsatt & Odowd, 1976; Barbosa et al., 2009; Callaway, Kikodze, Chiboshvili, & Khetsuriani, 2005; Waller & Maas, 2013). For example, McNaughton (1978) found that in the Serengeti, browsing was reduced on palatable grasses when they were growing in dense swards of unpalatable grasses (McNaughton, 1978). Many nonnative plant species, particularly invasive shrubs, are unpalatable, thorny, and grow in dense thickets; these thickets may protect browse-sensitive native plants when browsers are abundant (Atwater, Bauer, & Callaway, 2011; Baraza, Zamora, & Hodar, 2006; Cipollini, Ames, & Cipollini, 2009). For example, Gorchov and Trisel (2003) found that dense stands of the invasive shrub, *Lonicera maackii*, reduced deer browsing on native tree seedlings in a temperate hardwood forest. Thus, under high browsing regimes, it remains unclear whether nonnative invasive species are, in fact, always inimical to native species. If associational resistance frequently occurs, where native species find refuge from herbivores near nonnative species, nonnative species could potentially protect vulnerable native species from local extirpation. In other words, nonnative species can potentially sustain viable seed and propagule sources or facilitate growth above the browse line of browse-sensitive native species.

In this experiment, we introduced propagated individuals of a browse-sensitive native shrub, *Sambucus canadensis*, into established plots in which we factorially manipulated deer presence or absence and nonnative invasive species presence or absence. This species was historically present but has now been locally extirpated from the immediate region. We then monitored the growth and fitness of each individual at different time points throughout two growing seasons. Here, we present four hypotheses: 1) Deer browsing will decrease the survivorship and fitness of *S. canadensis,* 2) Dense cover by invasive plant species will decrease the survivorship and fitness of *S. canadensis*, and 3) The combination of deer browsing and cover by invasive plant species will decrease fitness more than either driver alone (i.e. additively or synergistically), and alternatively, 4) Dense cover by invasive species will confer protection from deer browsing and increase survivorship and performance of *S. canadensis* in deer access plots.

2.2 Materials and Methods

2.2.1 Study Site

We conducted our study within an 86-ha closed canopy, second-growth forest at the Eden Hall Campus of Chatham University located approximately 20 kilometers north of Pittsburgh, Pennsylvania, USA (40.6638N, 79.9559W). White-tailed deer have been over-abundant for decades throughout this forest and region (Adams & Villarreal, 2020; Carson, Royo, & Peterson, 2014; Redding, 1995; Rushing et al., 2020). The forest occurs at the urban-rural fringe and the landscape surrounding the forest is composed of patches of second-growth forest, old-fields, agricultural lands, a golf course, a grade school, and fairly extensive urban development (Link et al., 2018). The forest is part of the Mixed Mesophytic Association (Vankat, 1979) of the Eastern Deciduous Forest Biome; common overstory trees include *Quercus* spp., *Prunus serotina*, *Sassafras albidum*, and *Acer rubrum* (Link et al., 2018). Soils are a patchwork of various well drained loams and average annual precipitation is 970 mm (Hopkins, Bain, & Copeland, 2014; Link et al., 2018).

Multiple nonnative species dominate the forest understory (mean percent cover = 78.4 ± 8.0 S.E.); in decreasing order of abundance these were *Ligustrum sinese, Berberis thunbergii, Rosa multiflora,* and *Microstegium vimineum* (Appendix A). Other abundant nonnative species include *Celastrus orbiculatus*, *Lonicera spp.* (multiple species), and *Alliaria petiolata* were also abundant. More than a dozen other non-native species occur in the understory. Common native understory species (mean percent cover = 65.3 ± 6.3 S.E.) in decreasing order of abundance were *Lindera benzoin*, *Rubus* spp., *Impatiens capensis*, *Polystichum acrostichoides, and Persicaria virginiana* (Appendix A). The combination of both native and non-native species created a dense understory layer (Appendix A).

In general, Pennsylvania has a long history of deer overpopulation (Leopold, Sowls, & Spencer, 1947). This study site is located within Allegheny County, Pennsylvania, where deer densities have increased at least threefold in the past four decades (Hanberry & Hanberry, 2020). Current deer density estimates are between 11.6 and 17.4 deer/km^2 in Allegheny County (US Forest Service QDMA), which is considered moderately high. The broad absence of deer-preferred species such as *Trillium* and apparent browse lines on native shrubs at our study site suggest that deer are overpopulated in this area.

2.2.2 Experimental Design

We identified five widely scattered and fairly level sites throughout the forest and in a randomly selected half of each of the five sites, we erected 2.2m tall fences that were paired with adjacent control plots of the same size (plots ranged in size from 200m^2 to 400m^2). Plots varied in size because of uneven and steep terrain. We divided each larger plot into 25m^2 subplots. We performed complete vascular plant vegetation surveys the first growing season the fences were in place and prior to any plant removals. Working in teams of at least two to increase accuracy and minimize bias, we visually measured percent cover of all vascular plant species in each subplot using reference frames and recorded all values above 0.25% mostly in increments of a quarter percent. For any species present in a subplot under 0.25% cover, we labeled them as “trace” and later assigned a value of 0.1% for analyses.

We removed all invasive plant species from a randomly selected half of each exclosure and control plot during May 2019. Similar to Maynard-Bean and Kaye (2019), we hand pulled smaller individuals, but for larger plants, we cut the stem near the base, and using paint brushes, we carefully applied glyphosate to the exposed stems and leaves. Weeded invasive biomass was placed outside the plots. We did not repeat invasive removal treatments following the initial removal. In June 2020, invasive cover in removal treatment plots was less than 10% on average with little difference between subplots in fences and subplots outside of fences (5.9 ± 0.95 S.E. total, 5.4 ± 1.1 S.E. in fences, 6.3 ± 1.6 S.E. outside of fences, Fig. S1). Invasive plants had reestablished in 38% of the invasive removal treatment subplots. In total, we had four treatments: 1) deer excluded with invasive species removed, 2) deer excluded with invasive species present, 3) deer present with invasive species removed, and 4) deer present and invasive species present (control).

2.2.3 Focal shrub species

We chose *Sambucus canadensis* (American elderberry, Adoxaceae) as our focal understory species for multiple reasons. First, it is a geographically widespread species, native to the eastern U.S., eastern Canada, and Mexico (Applequist, 2015; Charlebois, Byers, Finn, & Thomas, 2010). Applequist (2015) and Bolli (1994) classify *S. canadensis* a subspecies of *S. nigra*, which occurs throughout Europe (Atkinson and Atkinson 2002). Second, like many shrubs and small trees (Table 1), *S. canadensis* is palatable and likely vulnerable to browsing (Arcese et al., 2014; Shrestha & Lubell, 2015). Third, it occurs in a wide variety of habitats from roadsides, to woodlands, to closed canopy forests where it can grow to over five meters (Charlebois et al. 2010). Finally, it is important ecologically because its leaves and berries (drupe) are consumed and dispersed by numerous species of birds and mammals (Charlebois et al. 2010). As of 2019, it did not occur at our study site but occurred in the surrounding region. We purchased 120 individuals of *S. canadensis* (roots and leafless stem ~40-50cm tall) from a commercial greenhouse (Cold Stream Farm, MI, USA), and on June 14, 2019, haphazardly planted six individuals into locations within all four of our treatments. All transplants were at least 2m apart and at least 1.0m away from the edge of the plot or fence. The only instances in which we would not use a haphazardly chosen spot is if it contained a tree or downed log that prevented planting there. We quantified survivorship, height, and leaf count five times from August 2019 to April 2021, however, we had to exclude leaf count data from one census due to sampling error.

2.2.4 Statistical Analysis

We analyzed the performance of *S. canadensis* for the duration of the experiment using linear mixed-effects (LME) or generalized linear mixed-effects (GLME) models. Fixed effects in all models included census date, exclosure treatment, invasive removal treatment, and an interaction effect (invasive removal x exclosure). A nested random effect term, consisting of plant individual nested within subplots within plots, was included to account for both the repeated measures on individuals and potential plot- or subplot-level effects (although preliminary analyses indicated that variables did not significantly differ among plots). We assessed survivorship and height using a GLME model with binomial error distribution and an LME model, respectively. Height data were ln-transformed to better approximate normality. Additionally, we performed an ANOVA for survivorship, height, and leaf count data from the final census date (April 2021) following two growing seasons. All statistical analyses were conducted in R Studio using the LMER package (Bates et al., 2020; R Core Development Team, 2020).

2.3 Results

2.3.1 Survivorship

At one of our five sites, all but one *S. canadensis* transplant died within three months of planting (June 2019) both inside the exclosure and adjacent control plot, therefore we removed this site from our analyses. We speculate that a more open canopy and dry soil conditions at this location could have led to dessication. Forty-eight of 120 individuals (40%) survived to the end of the study. Deer browsing reduced survivorship of *S. canadensis* by two thirds (~75% vs. <25%), whereas removing invasives never had a significant effect on survivorship (Figure 2.1, Tables 2.1 and 2.2).

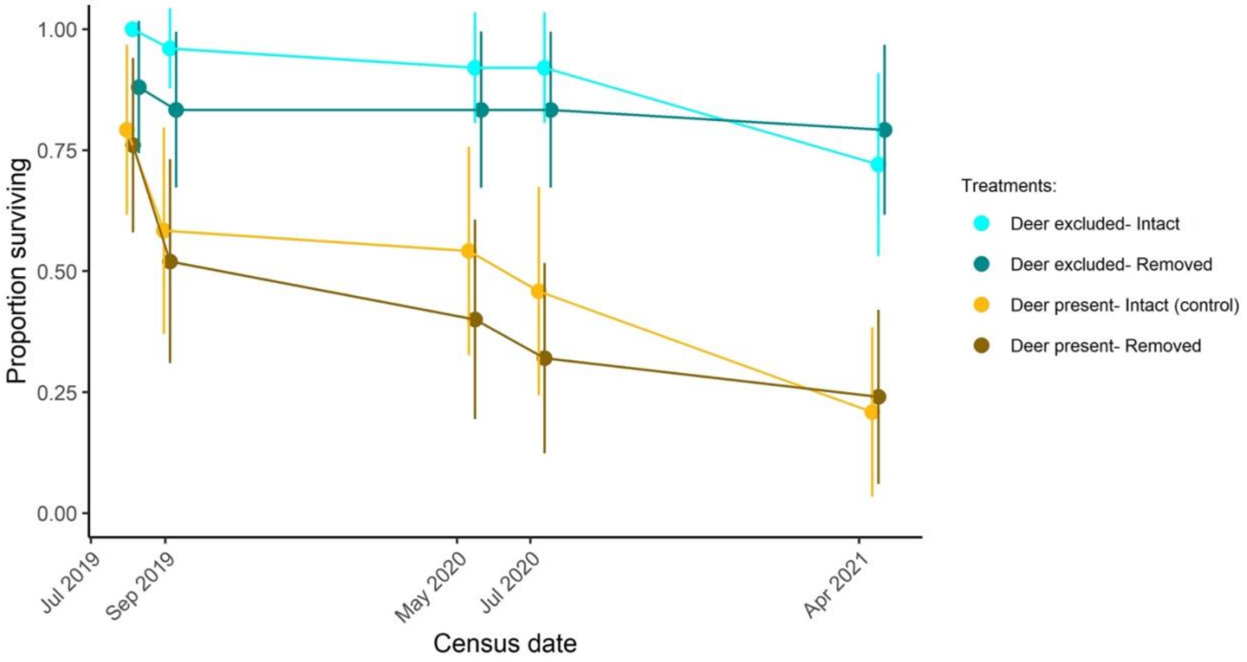

Proportion surviving
1.00
0.75
0.50
0.25
0.00
Jul 2019
Sep 2019
May 2020
Jul 2020
Apr 2021
Census date
Treatments:
Deer excluded- Intact
Deer excluded- Removed
Deer present- Intact (control)
Deer present- Removed

Figure 2.1

2.3.2 Height

Excluding deer increased the height of *S. canadensis* three to five-fold whereas removing invasives did not have a significant effect on height over the duration of the study (Figure 2.2, Table 2.1). However, excluding deer and removing invasives both increased height by the final census date (Figure 2.2, Table 2.2). Outside the exclosures, stems on average were roughly 10cm tall (range 5.1 – 20.9cm) versus more than 55cm (range 2.5 – 170.5cm) inside the exclosures. Excluding deer and removing invasives together nearly doubled the height of *S. canadensis* versus areas inside the exclosures where we left invasive species intact (Figure 2.2, Table 2.2). Finally, stems across all treatments lost height during each winter (Figure 2.2, Table 2.1, compare Sept. 2019 to May 2020 and July 2020 to April 2021). Such winter dieback is common in this species, particularly in the northern part of its range (Charlebois et al. 2010, Shrestha & Lubell 2015).

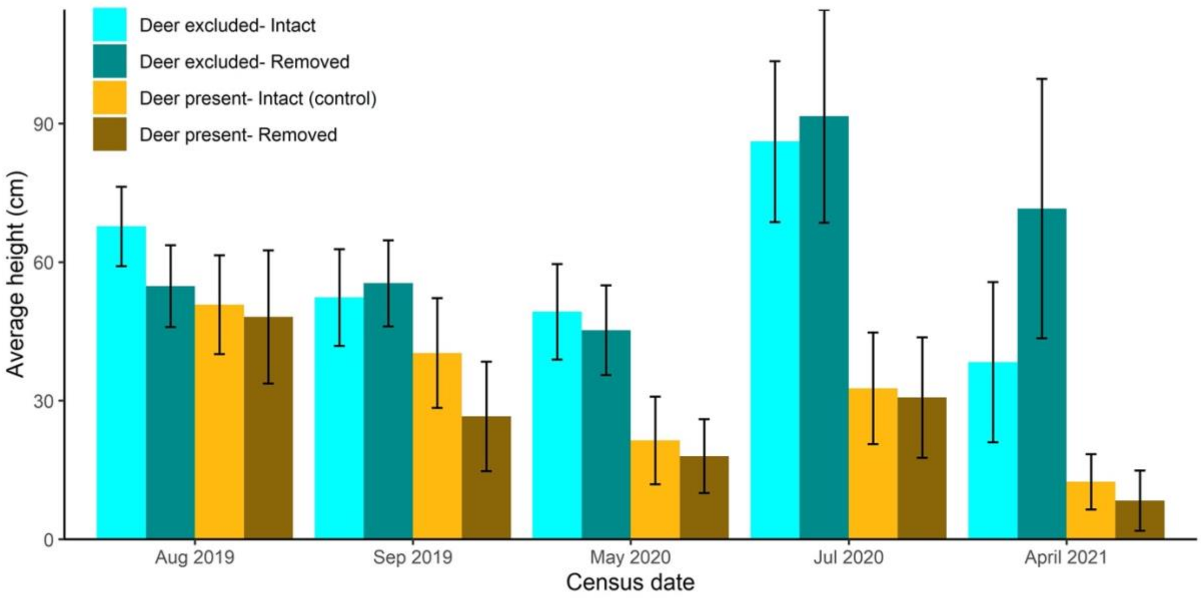


Figure 2.2

2.3.3 Leaf count

Leaf counts were significantly higher in individuals where deer were unable to browse but only marginally where invasive plants had been removed when considering all census dates (Figure 2.3, Table 2.1). However, by the end of the study, excluding deer and removing invasives both significantly increased leaf count (Figure 2.3, Table 2.2). Individuals within deer exclosures had higher leaf counts where invasive plants had been removed.

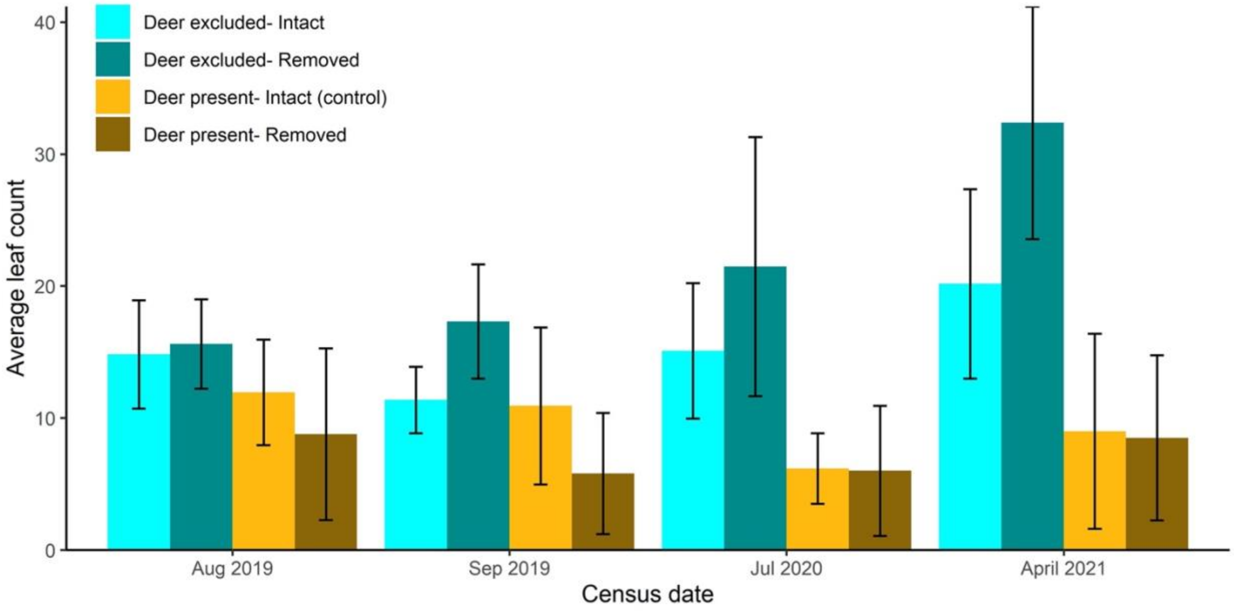


Figure 2.3

Table 2.1

Model and terms	χ^2	df	p
Survivorship			
Deer exclosure	9.5	1	0.0020
Invasive removal	1.0	1	0.7456
Census date	54.5	4	<0.0001
Deer exclosure × Invasive removal	0.1	1	0.8582
(ln) Height			
Deer exclosure treatment	12.8	1	0.0003
Invasive removal treatment	2.3	1	0.1303
Census date	29.1	4	<0.0001

Deer exclosure × invasive removal	2.0	1	0.1512
Leaf count			
Deer exclosure treatment	6.3	1	0.0119
Invasive removal treatment	3.3	1	0.0700
Census date	48.4	4	<0.0001
Deer exclosure × invasive removal	7.7	1	0.0653

Table 2.2

Model and terms	χ^2	df	p
Survivorship			
Deer exclosure	9.5	1	<0.0001
Invasive removal	1.0	1	0.6440
Deer exclosure × Invasive removal	0.1	1	0.9255
Height			
Deer exclosure treatment	12.8	1	0.0033
Invasive removal treatment	2.3	1	0.0536
Deer exclosure × invasive removal	2.0	1	0.2157
Leaf count			
Deer exclosure treatment	6.3	1	0.0010
Invasive removal treatment	3.3	1	0.0372
Deer exclosure × invasive removal	7.7	1	0.2253

2.4 Discussion

We investigated how a native shrub species that had been nearly locally extirpated in a peri-urban forest community responded to treatments including excluding white-tailed deer and removing nonnative invasive species. Our results reinforce consistent evidence that browsing by white-tailed deer suppresses the regeneration of sensitive native plant species and acts as a primary filter driving changes in community composition (R. C. Anderson, 1994; Knight et al., 2009; Nuttle et al., 2013; Ward, Williams, & Linske, 2018). These results were immediately evident. Conversely, invasive species presence independently had no effect on the survival of *S. canadensis*, and invasive removals did not cause an increase in performance until the final census date (see Table 2.2).

Elderberry survival inside of deer exclosures was high and remained steady throughout the experiment. There was roughly 75% survival in the deer exclusion treatments regardless of invasive removal treatment. The initial drop in survival among individuals subject to browsing (between Aug 2019 and Sept 2019) was most likely due to a combination of establishment failure and herbivory. Until the final census date, there was a trend of individuals persisting slightly better in treatments that did not undergo invasive removals vs. those where we had removed invasives. However, this was not significant and regardless of browse treatment, suggesting against associational resistance wherein individuals could potentially be "hiding" from browsing among unpalatable and dense stems of invasive plants. One limitation of this short-term study is that shrubs occasionally appear to be dead, but send active shoots in a subsequent growing season. We did find 13 instances of this in our data in which an individual was marked as dead and then later recorded as being alive. We adjusted this in our dataset and acknowledge the possibility that some individuals that were not counted as surviving during the final census could send live shoots in future growing seasons; however, we are confident they did not grow or photosynthesize during the 2021 growing season.

The deer exclusion treatment caused the differences in heights of individuals to consistently diverge over time. By the end of the study, individuals that were protected from browsing were roughly five times taller than those subject to deer browsing. The lack of overall response in stem height to removing invasive plant cover is consistent with meta-analytic findings that removing dense understory often does not increase stem height or diameter, but rather causes an increase in biomass (De Lombaerde et al., 2021). However, at the final census date, individuals that were protected from browsing were nearly twice as tall if growing where invasives had been removed vs. where they remained intact. Thus, invasive species cover indeed limits one or more resources (e.g. nutrients, light, soil moisture) and hinders the growth of native individuals.

We used leaf count as another performance metric to monitor *S. canandensis* individuals over time. It is important to note that leaf size was fairly consistent for elderberry individuals. Similarly to height metrics, individuals that were protected from deer consistently had more leaves over time. However, unlike stem height, leaf count was consistently higher in invasive removal treatments where they were also protected from deer browsing. This suggests that, similar to height, presence of invasive species substantially reduce native plant biomass (e.g. leaf count), but that deer browsing is an overwhelming filter for plant performance or regeneration in areas with high deer densities.

A considerable limitation to this study was its brevity (a total of 22 months). Long-term survival and growth performance could differ from the results presented here, particularly in studies regarding woody species. For example, woody plants might lie dormant for one or more growing seasons and show increased performance, reproduce, and ultimately succeed after being established for several seasons. Another factor to consider is that plants acquired from commercial greenhouses or nurseries may have different nutrient content or secondary metabolite levels than wild plants. Thus, it is possible that wild *S. canadensis* could respond differently than the transplants used in this study. For example, if propagated plants contain higher nutrient or starch contents, this would give them the ability to better tolerate browse damage, however, it may also make them more susceptible to herbivores.

Despite the lack of evidence for associational resistance in this study, it is still possible that this phenomenon occurs on these urban landscapes. Here, general high mortality outside of deer fences inherently caused low replication in treatments where deer were present and where one would expect to see evidence of associational resistance. Gorchov and Trisel (2003) found that *Lonicera maackii*, which is broadly present at this site, has been shown to prevent browsing on native species in forests. It may be that only particular invasive species can provide substantial refuge from browsing. Thus, any follow-up studies will include higher sample sizes, more native response species, and separation of individual invasive species to test for possible associational resistance from specific invasive species, particularly shrubs and allelopathic *Alliaria petiolata*. Besides the identities of invasive species, the response of native species in a given area would also depend on deer pressure, deer palatability, and preference depending on the diversity and identity of the species growing there. In areas with low deer pressure, invasive species may, in fact, be the overwhelming barrier to native plant diversity and regeneration of deer-preferred species. When considering native species that are not browse-sensitive, invasive species are almost certainly the dominant negative pressure. The relative importance of associational resistance for management applications would depend on the management goals and in consideration of deer pressure and the native plant community makeup in a given area. If associational resistance does occur with particular invasive species, leaving some dense patches of invasives thoughtfully in a forest matrix during invasive plant management could perhaps foster the regeneration of browse-sensitive native plant species. Native woody species targeted for regeneration could potentially persist long enough among invasive species (for example, until they grow above the browse line) for them to escape threat of mortality from herbivory and succeed long-term. Managers could then remove the patches of invasive species at that point and allow native species to grow unhindered. Herbaceous plants might be able to persist among invasive patches as a seed source to connect naturally occurring refugia such as steep slopes and tree tip-up mounds. However, it may not make sense to introduce (or re-introduce) highly preferred native species to an area with very high deer pressure. Most likely, these practices would have to be done in conjunction with strategies to reduce deer densities and set long-term goals to eventually mitigate invasive plant cover when it is no longer beneficial.

2.5 Conclusions

Deer browsing continues to be an overwhelming primary filter to the regeneration of browse-sensitive native plant species, particularly in peri-urban habitats where deer are both overabundant and easily able to home in on fragmented forest patches. Our results also demonstrate that dense presence of invasive species is inimical to the growth of native species. We did not find evidence of associational resistance to deer browsing by invasive species in this study. If associational resistance does occur, its use in management strategies to promote native regeneration would be highly dependent on the site and variables such as deer pressure, plant palatability, and long-term goals for plant communities. This might be particularly relevant in urban or peri-urban habitats where deer and invasive species both have a substantial presence. The relative negative impacts of deer browsing and invasive species, however, are largely site-specific wherein invasive species could be the dominant repressor of deer-preferred native plants in areas with low deer pressure.

3.0 Chapter 3: Invasive species interactions with deer browsing and their impact on forest diversity, richness, and community makeup

Invasive plant species have increased in abundance worldwide over the past several decades and caused profound changes to native plant communities. In many areas of the Eastern US, increases in invasive species co-occurred with increases in white-tailed deer densities. Deer overbrowsing has been shown to decrease native plant richness, diversity, and abundance, particularly in temperate forest understories. Here, we used large deer fences in a heavily invaded peri-urban forest in western Pennsylvania and performed invasive species removals in a split plot design. We aimed to test for individual effects of each factor to the native plant communities as well as whether or not deer browsing and invasive species potentially act additively, synergistically, or antagonistically. We performed full vascular plant surveys nearly four growing seasons following deer exclusion and two growing seasons following invasive removals. There were no changes in overall plant species or native plant species richness or diversity between any of the treatments. There was higher overall plant cover in invasive treatment plots where invasive species remained intact. Despite hardly any difference at the community metric level, we did find that plant communities differed between both invasive removal treatments and deer exclosure treatments, but this was fairly site-specific regarding the location of fences within the forest. We found higher than 50% cover of invasive species in plots where we did not perform removals and higher native plant cover in the fence and invasive removal treatment combination. This short-term study

3.1 Introduction

Browsing by white-tailed deer (*Odocoileus virginianus*) has caused profound changes to forest plant communities across large regions of the Eastern United States since becoming overabundant over much of the landscape during the mid-20th century (Cote et al., 2004; Leopold et al., 1947). Deer densities are up to five times higher in some areas of the United States than they were prior to European settlement (Flagel et al., 2016). Following long sustained herbivore pressure, many eastern deciduous forests now have lower species richness and diversity in addition to shifts in overall plant community makeup (Goetsch, Wigg, Royo, Ristau, & Carson, 2011; Nuttle et al., 2013; Rooney, 2001). Populations of wildflowers, oak trees, and other browse-sensitive herbs and shrubs have declined while dense monocultures of ferns, beech sprouts, and maples sprouts have increased (Royo & Carson, 2006). Because browse-sensitive plant and wildflower abundances continued to diminish over time, local extirpation and legacy effects from overabundant deer now plague forests (Pendergast et al., 2016). Even if there is relief from browse pressure, a lack of nearby seed and propagule sources could preclude populations of these species from returning to the landscape (Aronson & Handel, 2011; Royo et al., 2010).

Increases in the invasion and spread of nonnative plant species have coincided with high deer densities for the better part of the last century and similarly caused detrimental effects to many forest communities (A. Kulmatiski, 2006). An ever-increasing degree of globalization has led to proliferating shipping routes and traffic (Perrings, 2010). This can cause unintentional nonnative species introduction and subsequent re-introduction events (Le Maitre, Richardson, & Chapman, 2004). If a nonnative species establishes and becomes invasive, it is likely to outcompete many native species due to a variety of characteristics or mechanisms (Liebhold et al., 2017). Invasive species often exhibit extended leaf phenology, allelopathy, high reproductive yields, and the ability to clonally spread (Murrell et al., 2011; Roche et al., 2021; Smith & Hall, 2016). They sometimes exhibit hybrid vigor from interspecific hybridization with native species or other nonnative invasive species, or from intraspecific hybridization with different genotypes from multiple or repeated introductions (Ellstrand & Schierenbeck, 2000; Geiger, Pratt, Wheeler, & A. Williams, 2011; Vila & D'Antonio, 1998). Furthermore, nonnative plants tend to be less susceptible or less likely to succumb to bacterial and fungal infections introduced ranges (Keane & Crawley, 2002; Mordecai, 2011; Power & Mitchell, 2004). Similarly, they often escape insect and mammalian herbivore pressure in introduced areas because the herbivores did not evolve to overcome or adapt to the plant’s nonnative secondary metabolites (Kirichenko, Péré, Baranchikov, Schaffner, & Kenis, 2013). Being able to escape enemies in new ranges creates further opportunities to effectively proliferate and outcompete natives because invasive species can afford to spend less energy on defenses and allocate more energy towards growth and reproduction (Siemann et al., 2017).

Studies have shown that the combination of invasive plant species and white-tailed deer browsing can interactively increase detrimental impacts to native plant communities compared to either cause on its own (Bourg, McShea, Herrmann, Stewart, & Blossey, 2017; Burke et al., 2019; Vavra et al., 2007). Because deer often avoid browsing invasive species and overbrowse many native species, overabundant deer can facilitate and exacerbate invasive plant spread and establishment (Arcese et al., 2014; Averill et al., 2018; Kelly, 2019; Rooney, 2009; Shen, Bourg, McShea, & Turner, 2016; Vavra et al., 2007). Knight et al. (2009) found that five years after excluding deer in a Pennsylvania forest, native species richness and abundance dramatically decreased in deer access plots. Furthermore, those that did persist in deer access plots rarely became reproductive compared to those protected from deer, while invasive species were more abundant and reproductive in deer access plots. Nuzzo, Dávalos, and Blossey (2017) found evidence that native cover increased while nonnative cover decreased in the few years following deer culling, but the trend faded as deer populations returned to the landscape. Furthermore, concurrently competing with invasive plant species and creating defenses against herbivory can come a physiological cost to woody seedlings and their ability to successfully reach the canopy (Morrison, Roche, & Veatch-Blohm, 2022).

Native plant communities are particularly at risk of degradation due to both nonnative plant invasions and deer browsing in urban, suburban, and peri-urban forests (Morrison, 2017). These forests are fragmented and experience considerable edge effects (Aronson & Handel, 2011; La Sorte et al., 2007; Morrison, Fertitta, Zymaris, DiBartolo, & Akparanta, 2022). Forest patches near moderate to extensive human activity are frequently disturbed, highly invasible, and near gardens and homes from which nonnative ornamental plants can escape (Chytry et al., 2008; Dolan et al., 2015; Tanentzap & Bazely, 2009). Additionally, human car and foot traffic can exacerbate the spread of invasive species (Schramm & Ehrenfeld, 2012). Moreover, forests that have extensive edges patches of open or early successional areas including moderately disturbed suburban forests are preferred habitats for deer (Alverson, Waller, & Solheim, 1988; Potapov, Bedford, Bryntesson, & Cooper, 2014).

Here, we experimentally manipulated deer browsing and invasive plant cover in a peri-urban forest and monitored the plant communities over time. By using deer exclosure fences and performing invasive plant removals, we tested two hypotheses: 1.) Deer browsing reduces plant cover, species richness, and diversity, and 2.) Dense invasive plant cover prevents the recovery of native plant communities. We predicted that excluding deer would cause increased plant abundance and diversity in the overall plant community as well as the native plant community. We also predicted that removing invasive species would increase native plant abundance and diversity. In conjunction, we predicted that the native community might require the exclusion of deer and the removal of invasive competition to substantially recover. Thus, we predicted that native communities would have the highest abundance, richness, and diversity when both free from deer browsing and invasive plant cover.

3.2 Methods and Statistical Analyses

3.2.1 Study site

This study was conducted at Chatham University Eden Hall Campus in Gibsonia, Pennsylvania (40.6638N, 79.9559W). The campus is located amongst extensive patches of second growth forests. The forest at this campus is a peri-urban, mixed mesophytic second growth forest with closed canopy stands of varying ages with *Acer rubrum*, *Quercus* spp, and *Prunus serotina* being common in the overstory. Common native shrubs include *Lindera benzoin* and *Rubus* spp., and the most common native forbs are *Impatiens capensis*, *Persicaria virginiana*, and *Prunella vulgaris* (Betras, de Cortie, Carroll, Utz, & Carson, 2022). The campus forest is located amongst other extensive patches of second growth forests. The soil is mostly loamy and well draining (Hopkins et al., 2014). Mean annual precipitation is 970mm (Hopkins et al., 2014). There are old-fields, agricultural fields, a golf-course, a public school, houses, and developed areas nearby (Betras et al., 2022; Link et al., 2018). Deer populations have been high in this region for several decades and the forest contains extensive cover by numerous invasive plant species, particularly shrubs. Nonnative invasive species with the highest cover in the forest include *Ligustrum sinese*, *Berberis thunbergii*, *Rosa multiflora*, *Microstegium vimineum*, *Celastrus orbiculatus*, multiple *Lonicera* spp., and *Alliaria petiolata* (Betras et al., 2022).

3.2.2 Experimental Design

We factorially manipulated deer browsing and invasive species presences by using deer exclosure fences and performing invasive species removals. Five large fences were built in Spring of 2017 that spanned over a large area of the campus in different locations. Due to hilly and steep terrain, high tree density, or unevenly spaced large trunks in some areas, the size and shape of the fences varied somewhat and not all fences were completely square. We divided the plots into as many 25m^2 subplots as possible while still allowing for a small buffer between subplots and the fences. To maximize the number of subplots, we divided fenced plots into either 5m x 5m square subplots or 6.25m x 4m rectangular subplots depending on the size and shape and the fence. It was important to keep the area of the subplots the same to perform consistent percent cover estimates. We also tried to minimize any edge effects by keeping the perimeters as similar as possible and at these dimensions, the rectangular plots only had a 2.5% longer perimeter than the square plots. We then established a paired plot outside of each fence equal in size and shape to the ones inside of the fences on a randomly designated side of each fence with a buffer in between (Figure 3.1).

In May of 2019, we performed invasive species removals in half of each fenced and paired unfenced plot (Figure 3.1). We randomly chose which side would receive the removal treatment as well as which direction to split the plot. However, if the plot was on a slope, we divided the plot in the same direction as the slope so that each treatment had a slightly higher and lower side to minimize any differences from soil moisture or runoff. To avoid major soil perturbation, we removed most nonnative invasive plants by cutting the stems at the base and carefully applying glyphosate to the exposed stem. For very small plants or species with shallow roots, such as *Alliaria petiolata*, we carefully pulled them from the soil by hand. With the exception of one minor touch-up in November 2019, we did not repeat the invasive removal treatment. In June of 2020, mean percent cover of invasive plants in removal treatment plots was roughly 5% while mean invasive cover in non-removal plots was more than 20% (Betras et al., 2022).

This experimental design included four treatments: 1.) deer accessible and invasive plants intact, 2.) deer accessible and invasive plants removed, 3.) deer excluded and invasive plants intact, and 4.) deer excluded and invasive plants removed. Additionally, we introduced individuals of *Sambucus canadensis* within all of the treatments in 2019 and monitored their performance for two growing seasons (results published in Betras et al., 2022).

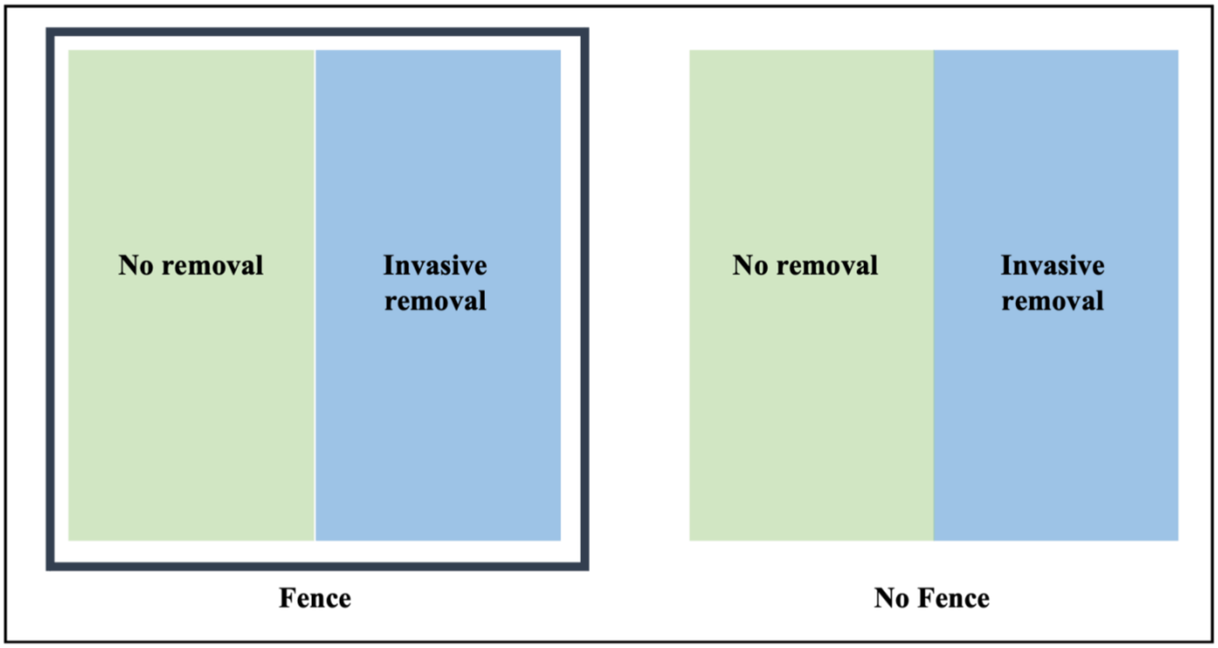


Figure 3.1

We performed a complete understory plant survey of between the end of July and the beginning of August 2018, almost two full growing seasons post-fence construction (and pre-removals). To estimate percent cover, we worked in teams with a minimum of two people people per team for accuracy and to minimize bias. We constructed reference frames that represented 0.25%, 0.5%, and 1% of the subplot area (25cm x 25cm, 35.4cm x 35.4cm, and 100cm x 100cm respectively) and used them to visually estimate the percent cover of every vascular species present. If a species covered less than 0.25% of a subplot, we considered it “trace” and assigned values of 0.1% cover to perform analyses. We identified common graminoid species such as *Poa pratensis*, *Carex sect. stellulatae*, *Carex albursina*, *Carex intumescens* and invasive *Microstegium vimineum*, but designated obscure graminoids as ‘graminoid’ in our data. We also estimated percent cover of moss but did not differentiate any nonvascular species. We used this method for every subsequent sampling effort. We resurveyed all plots between the end of August and the beginning of October 2019, at the end of the growing season that immediately followed the removal treatment. We performed another complete survey during the subsequent growing season in June 2020. Although we performed a census at the end of the 2019 growing season, all analyses presented here are from the 2020 census to minimize any potential effect from removal treatment on plant cover within the same year.

3.2.3 Statistical Analyses

We analyzed plant community metrics using linear mixed models or generalized linear models in a nested, split-plot design. We tested for differences in percent cover and Shannon diversity using linear models and differences in species richness using generalized linear models. Fixed factors included deer exclusion treatment and invasive species with an interaction term and random factors included the deer exclusion treatment nested within the five plot sites and the invasive treatment nested within the deer exclusion treatment (R package *nlme* for LMMs and *lme4* for GLMMs). Percent cover data was log-transformed to normalize residuals. We also separately analyzed the data to include only native species to test for differences in native species cover, richness, and Shannon diversity between treatments. We used the R package *vegan* to calculate plant community metrics and to create an NMDS (non-metric multidimensional scaling) ordination using the Bray-Curtis dissimilarity of species percent coverage matrix. We used a permutational ANOVA (PERMANOVA) to evaluate plant community similarity or non-similarity between treatments and site locations (Oksanen, 2015) We used a PERMDISP analysis (*vegan* package) to test for differences in beta diversity between groups within each treatment (M. J.

Anderson, Ellingsen, & McArdle, 2006). All analyses were performed using R version 3.4.1 (R Core Development Team, 2020).

3.3 Results

Percent cover did not differ between deer exclosure treatments, but was higher where native species were left intact (p=0.03, Figure 3.2). There were no differences in species richness or Shannon diversity between any treatments (Figure 3.2).

For native plants, there was no difference in percent cover, species richness, or Shannon diversity between any of the treatments (Figure 3.3), but there were again strong site effects for percent cover and species richness (p<0.001, Table 3.1). Although there were no differences in these community metrics, some particular native species responded differently to treatments. *Rubus spp.* had higher cover in fences where deer did not have access (mean percent cover = 11.02 ± 1.91 SE) vs. outside of fences (mean percent cover = 5.61 ± 1.03 SE). In invasive removal plots, *Impatiens capensis* had more than two times mean cover than plots with intact invasive species (mean percent cover = 18.86 ± 3.94 SE, and 7.67 ± 2.29 SE, respectively).

Plant community composition showed a significant three-way interaction between the fence treatments, invasive removal treatments, and sites (PERMANOVA, p<0.001 for all individual treatments, pairwise combinations, and three-way interaction, Figure 3.4). Here, the plant communities responded differently to different treatments based on their location in the forest. For example, plant communities in Site 2 and Site 3 separated more between invasive removal and invasive intact plots than between fenced and unfenced plots (Figure 3.4.).

Conversely, plant communities in Site 4 and Site 5 separated more between fenced and unfenced plots than between invasive removal and invasive intact plots (Figure 3.4). Site 1 plant communities showed little to no separation between either fence or removal treatments. Throughout the forest, plant communities in fenced plots where deer did not have access had similar homogeneity to unfenced plots vulnerable to browsing (PERMDISP, $p = 0.76$). However, plant communities were more homogenous in plots with intact invasive plants than in invasive removal plots (PERMDISP, $p = 0.047$).

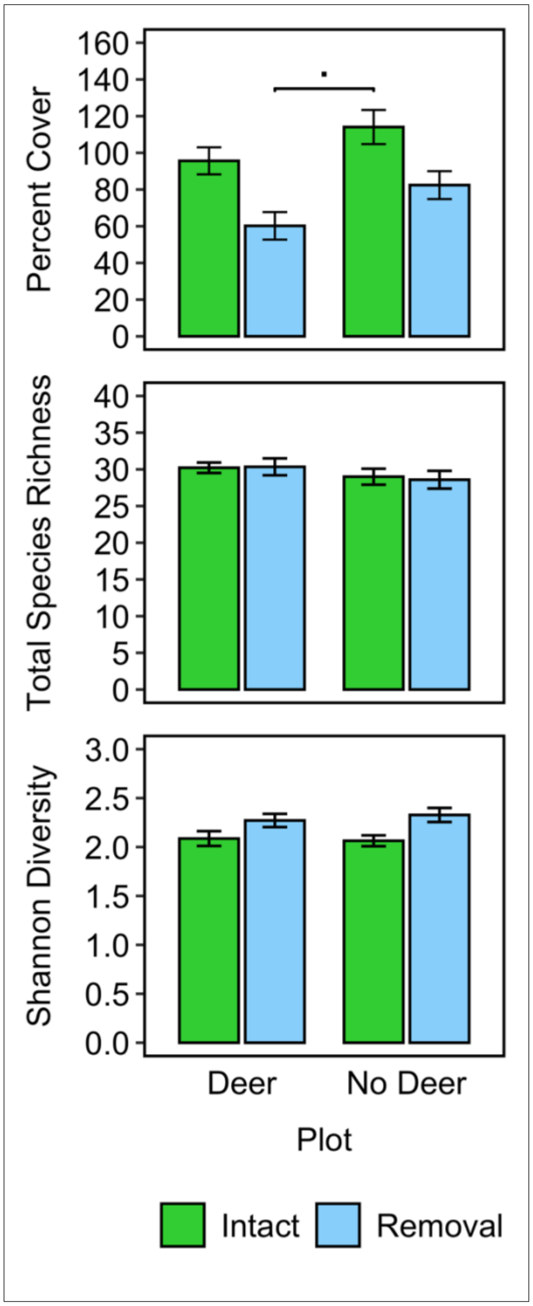

Percent Cover
160
140
120
100
80
60
40
20
0
.
Total Species Richness
40
35
30
25
20
15
10
5
0
Shannon Diversity
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Deer
No Deer
Plot
Intact
Removal

Figure 3.2

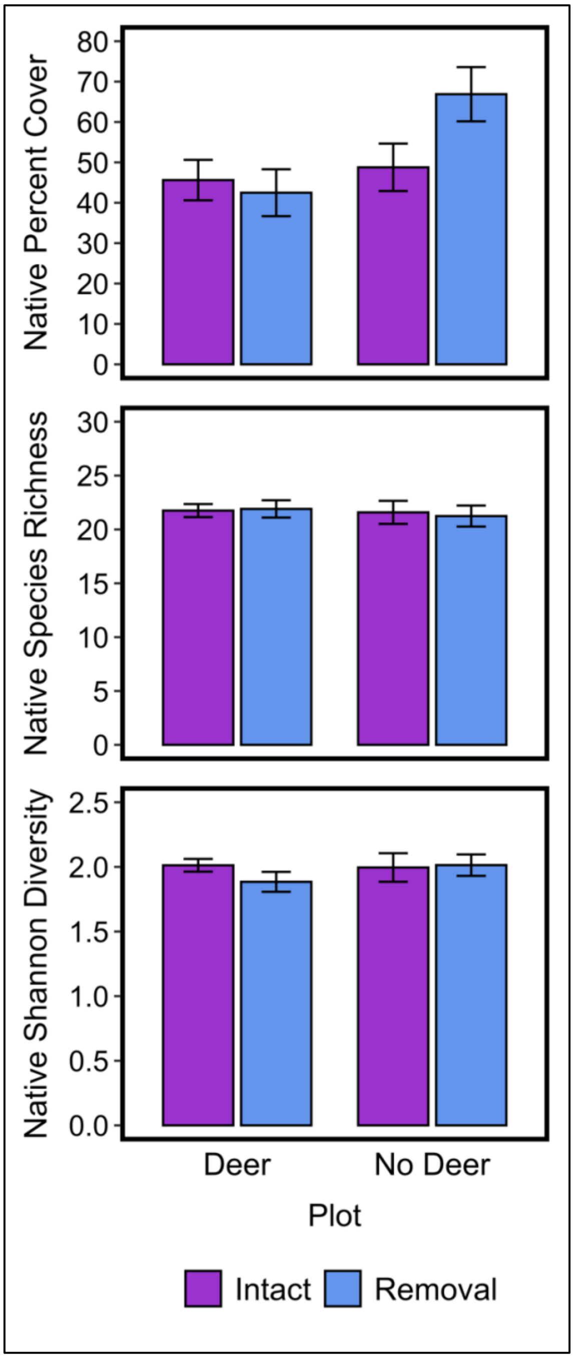

Native Percent Cover
0
10
20
30
40
50
60
70
80
Native Species Richness
0
5
10
15
20
25
30
Native Shannon Diversity
0.0
0.5
1.0
1.5
2.0
2.5
Deer
No Deer
Plot
Intact
Removal

Figure 3.3

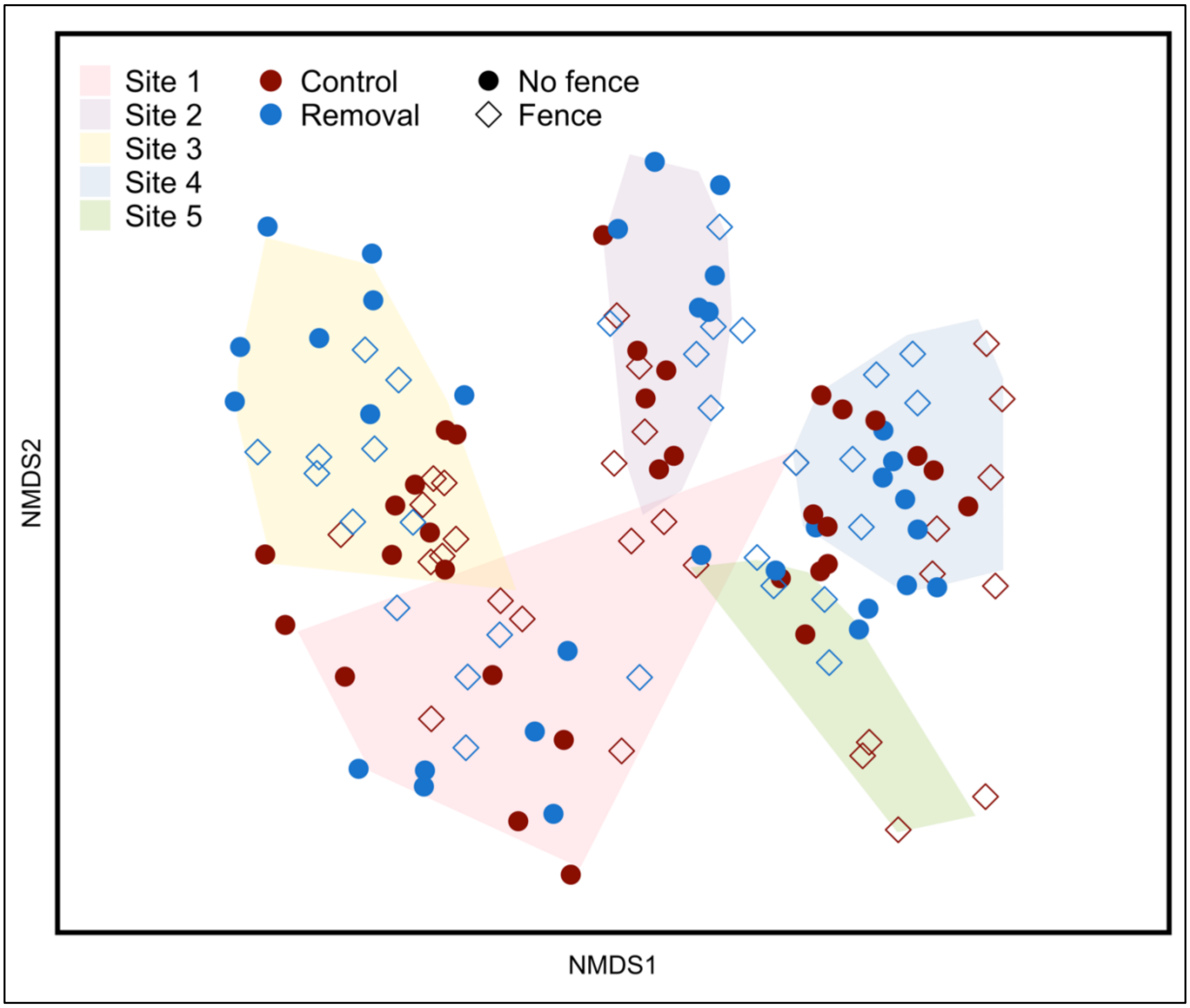


Figure 3.4

3.4 Discussion

We examined how deer browsing and invasive species cover impact native plant understory communities in a peri-urban forest by experimentally removing them in a factorial design. We found little evidence of treatment effects to richness or diversity three years after excluding deer and one year after removing invasive species (mid-second growing season), however there were some noticeable changes to plant community composition.

Neither removing invasive species nor excluding deer browsing caused changes to plant richness or diversity. The higher total plant cover in plots that had intact invasive species highlights how dense the invasive cover is in this forest. Native plants accounted for less than half of total cover in plots where invasive species remained intact (Figures 3.2 and 3.3). It could also be that native species did not have enough growing time to fill as much space as established invasive shrubs in removal plots. Within removal treatments, higher cover inside of fences potentially supports our hypothesis that native understory species will require relief from both deer browsing and invasive cover to recover. Bourg et al. (2017) concluded in a similar study that both excluding deer and removing invasives were required to increase species richness in the herbaceous community, and removing either factor alone was insufficient (see also Aronson & Handel, 2011 pertaining to woody communities). Bourg et al. (2017) also found a large decrease in cover of the invasive grass *M. vimineum* within fenced plots by the end of their study, supporting findings from other studies that deer facilitate the spread of invasive species (Averill et al., 2018; Knight et al., 2009; Shen et al., 2016).

The results presented here are rather soon after initial treatments (1-3 years) while similar studies with published results lasted at least five years (Bourg et al., 2017; Knight et al., 2009). Interestingly, invasive removal plots significantly differed from non-removal plots in beta diversity whereas fenced and unfenced plots were more homogenous even though the fence treatment had been up longer. Furthermore, although there was no overall treatment effect on native percent cover, cover was highest in removal plots inside of fences. These findings further indicate the importance of coupling invasive removals with deer exclusion to release and restore the native community.

In another similar study, Nuzzo et al. (2017) did not find strong community level effects from treatments such as deer exclusion (e.g. percent cover), but argued that community level metrics often fail to capture the whole picture. For example, though cover remained the same, the composition between native and nonnative species changed and cover of individual species such as *Trillium* also increased. They additionally monitored individuals of deer-preferred species over time and found they grew taller and reproduced more, which would be missed in broad community level responses. Similarly and within our experimental design, introduced individuals of *Sambucus canadensis*, a deer-preferred native shrub, performed exceedingly better when protected from deer browse and only slightly better in the removal treatment (Betras et al., 2022). Here, in the native community, *Rubus spp.* cover was higher inside of fences where deer could not browse them vs. deer access plots, and *Impatiens capensis* was higher in invasive removal plots vs. intact invasive plots. Deer often browse and prefer *Rubus*, which can be an indicator species for deer browse pressure. Thus, despite the lack of significant community level metric differences, the communities themselves differed.

The NMDS ordination revealed distinct divergences between treatments, but some diverged between fenced and unfenced plots while others diverged between invasive removal and invasive intact plots, depending on the site location (Figure 3.4). For example, Sites 2 and 3 separated more depending on invasive removal vs. intact treatment while Sites 4 and 5 separated more based on deer access vs. exclosure treatment. There were pronounced differences between sites. Percent cover did not differ between any treatments at one of the five sites. Two of the sites had much higher plant cover in treatments where there was no invasive removal, both inside and outside of fences. The other two plots showed higher plant cover where there was no invasive removal, but only either inside or outside of fences. The notable differences in plant cover and richness in addition to differences in community composition could be due to the differences in forest ages and locations of the sites. Sites 4 and 5 were located in a fairly mature forest patch while Sites 1, 2, and 3 were located in a younger forest patch with a road and buildings separating them from Sites 4 and 5. Accordingly, Site 4 and Site 5 are grouped near each other in ordination space and somewhat separated from Sites 1, 2, and 3 (Figure 3.4). Other studies have found that only species present before deer exclusion treatments remained following deer exclusion with no recovery of deer-preferred species, even after decades (Nuzzo et al., 2017; Pendergast et al., 2016; Royo et al., 2010). In this study, it is likely that plant communities at these locations differed prior to this experiment, especially because the current forest is growing on a patchwork of differing land use histories including horse pastures and agricultural fields among others.

3.5 Conclusions

Numerous past studies have demonstrated that overabundant deer have overwhelmingly changed and degraded forest understory communities. Similarly, studies worldwide have shown that nonnative invasive species can have a devastating impact on native plant communities. Although in this experiment, community level metrics largely did not detect effects of excluding deer or removing invasive species, we did find differences in either individual species abundance or plant community composition between treatments. One deer-preferred shrub was more abundant in fenced plots vs. deer access plots while a native herb was more abundant in invasive removal plots than intact invasive plots. More than half of the plant cover in plots that did not undergo removals is cover by invasive species, and native species cover was higher in the fence and invasive removal treatment combination. This study is limited by a short timeframe, but it is likely that the combination of excluding deer and removing invasive plant cover would be required to restore a diverse and abundant native understory.

4.0 Soil feedbacks as a mechanism underlying exotic plant invasions in riparian forests: using mesocosms to evaluate plant-soil-feedbacks

Invasive plant species have become increasingly abundant over the past century. Although several mechanisms have been shown to contribute to their ability to readily spread, there has been more focus on plant-soil feedbacks as an invasion mechanism in the past few decades. Plant-soil feedbacks refer to how soil changes after a plant grows in it and how those biotic or abiotic changes drive subsequent colonization and fitness of either conspecific or heterospecific species. Plants often cause shifts in soil microbial communities or cause abiotic changes to soil such as acidification. Plant-soil feedback experiments are commonly performed in rich, loamy soils, however it's unclear whether plants can exhibit strong feedbacks in well-draining, coarse soil. Here, we performed a replicated mesocosm experiment to test for plant-soil feedbacks between two native species and two invasive species commonly found on young landforms in coarse-sediment streams. We hypothesized that nonnative invasive species successfully colonize nascent landforms via shifting soil conditions in ways that can inhibit the colonization of native pioneer species. We grew each of the focal species in mesocosms for roughly two seasons and then performed transplants in all one-to-one species combinations. We monitored plant growth during the feedback phase over one growing season. The strongest feedbacks occurred in soil conditioned by Bohemian knotweed for all treatment combinations, but the most negative feedback was when knotweed grew in its own conspecific-conditioned soil. These results are contrary to the evidence from other soil feedback experiments on invasive species wherein invasive species demonstrated positive feedbacks with themselves. We also found that native Eastern cottonwood exhibited negative feedbacks with itself. We did not find feedback effects from any species growing in soil conditioned by American Sycamore. A nonnative bush honeysuckle species grew tallest in native-conditioned soil. Although we cannot attribute differences to specific mechanisms, we demonstrated that plant soil-feedbacks can readily occur in coarse, well-draining soil and provided evidence of strong negative feedbacks from a nonnative species in its own conspecific-conditioned soil.

4.1 Introduction

Nonnative invasive plant species often become dominant, thereby excluding native species and forming near monospecific patches and stands that can persist for decades (A. Kulmatiski, 2006; Nuñez & Paritsis, 2018). A variety of mechanisms potentially underlie the success of exotic species and multiple mechanisms may operate at the same time. These include casting deep shade, escaping enemies, altered phenology, and enhanced rates of seed and clonal dispersal relative to natives (Alexander & Levine, 2019; Blossey & Notzold, 1995; Lamberti-Raverot, Piola, Vallier, Gardette, & Puijalon, 2019; Siemann et al., 2017; Siemens & Blossey, 2007). Exotic species may also use “novel weapons” in the form of chemical root exudates that are harmful to both native plant and microbial communities because these communities lack an evolutionary history with these exudates (Becerra et al., 2018; Callaway & Ridenour, 2004). What remains far less understood is the degree that plant-soil feedbacks either promote or delay the invasion of exotic plant species and the specific mechanisms that potentially underlie this.

Plant-soil feedbacks are likely central to patterns of relative abundance and species composition in plant communities. Plant-soil feedback refers to the performance of plants after they have altered the physical and biotic composition of the soil they occupy (van der Heijden, Bardgett, & van Straalen, 2008; van der Putten, 2003). Thus, plants first condition soil, and the conditioned soil properties can increase or decrease subsequent plant growth and fitness (James D. Bever, 1994; J. D. Bever, Westover, & Antonovics, 1997; Kardol, Cornips, van Kempen, Bakx-Schotman, & van der Putten, 2007; Reinhart, 2012). In positive plant-soil feedbacks, conspecific (growth in own soil) growth rates increase in conditioned soil, or the positive soil associations outweigh the negative ones (Brinkman, Van der Putten, Bakker, & Verhoeven, 2010; A. Kulmatiski, 2018; A. Kulmatiski, Beard, Stevens, & Cobbold, 2008; Suding et al., 2013). Conversely, in negative plant-soil feedbacks, growth rates decrease, or the negative soil associations are greater than positive ones. Plant-soil feedbacks and directions may also be framed in the context of heterospecific comparisons such that a positive feedback occurs when a plant species does better in conspecific-conditioned soil (“home” soil) versus heterospecific-conditioned soil (“away” soil), or pairwise growth rate comparisons (James D. Bever, 1994; Dukes, Koyama, Dunfield, & Antunes, 2019; Kardol et al., 2007; Klironomos, 2002; T. H. Pendergast, D. J. Burke, & W. P. Carson, 2013; van der Putten et al., 2013).

Positive plant-soil feedbacks can result from a variety of mechanisms including beneficial associations with soil microbes such as mycorrhizal fungi or rhizobacteria; these mutualists and their hosts exchange resources such as soil nutrients and carbohydrates (Bulgarelli, 2018; Bulgarelli et al., 2015; Fitzpatrick et al., 2018; Hacquard et al., 2015). These soil microbes may confer synergistic advantages to their hosts through plant-fungal-bacterial associations (Larimer, Clay, & Bever, 2014; van der Heijden, de Bruin, Luckerhoff, van Logtestijn, & Schlaeppi, 2016). Additional studies of plant microbiomes, however, have elucidated several other physiological benefits that microbes may provide to plants such as producing growth hormones (e.g., auxin) and providing immunity to infection by pathogens (J. D. Bever, 2015; Bulgarelli, Schlaeppi, Spaepen, van Themaat, & Schulze-Lefert, 2013; Hacquard, Spaepen, Garrido-Oter, & Schulze-Lefert, 2017; Malik, Dixon, & Bever, 2016; Yuan et al., 2018). Berendsen et al. (2012; 2018) demonstrated that plants can actively recruit beneficial microbes when under attack by insects or pathogens. Some plant species may also create positive feedbacks by serving as a "sink" or source to promote the dispersal of generalist pathogens that negatively impact nearby heterospecifics (Facelli, McKay, Facelli, & Scott, 2018; Mordecai, 2011; Power & Mitchell, 2004).

Negative feedbacks mostly occur through pathogen accumulation, nutrient or mutualist disruption or depletion, or via phytochemical exudates of neighboring plants (e.g., allelochemicals). Plants often accumulate species-specific pathogens in roots or in the rhizosphere, making the soil increasingly inimical to conspecific establishment and growth (Clay et al., 2008; Mills & Bever, 1998; Mordecai, 2011; Packer & Clay, 2000). Klironomos (2003) demonstrated that while mycorrhizal fungi had classically been considered plant mutualists, these interactions could occur along a mutualism to parasitism continuum. At the community-level, negative plant-soil feedbacks can often promote species diversity by means of negative frequency-dependent mechanisms (Klironomos, 2002; Mack & Bever, 2014; Mack, Eppinga, & Bever, 2019; Mangan et al., 2010; Reinhart, 2012). Negative-frequency dependence via soil pathogens is currently the best explanation for the maintenance of diversity in hyper-diverse tropical forests as well as other community types (see also Mack et al., 2019; Mangan et al., 2010).

The degree to which soil feedbacks regulate the invasion of nonnative species is an area of active research though there seems little doubt that soil-feedbacks likely directly or indirectly facilitate the invasion of nonnatives (A. Kulmatiski, 2018; Levine, Pachepsky, Kendall, Yelenik, & HilleRisLambers, 2006). Inderjit and van der Putten (2010) proposed three general mechanisms by which plant-soil feedbacks may contribute to invasive success. (1) Invasive plants experience neutral to positive feedbacks in their introduced range, while native plants mostly experience negative feedbacks. (2) Invasive species may change the native plant-soil associations by increasing pathogen loads or disrupting beneficial associations. (3) Invasive plants release toxic allelochemicals that native soil communities cannot detoxify and can even increase the toxicity of these allelochemicals. Studies have shown that nonnative invasive plants can experience neutral to positive feedbacks in new ranges because they escape from their natural soil enemies in their native range (Callaway, Thelen, Rodriguez, & Holben, 2004; Keane & Crawley, 2002; Klironomos, 2002; Reinhart, Packer, Van der Putten, & Clay, 2003; van der Putten et al., 2013; Zuppinger-Dingley et al., 2011). Regarding the second mechanism, there is strong support that invasive plants alter soil microbial community composition, and can in some cases alter the total abundances of microbes in the soil (Dassonville, Guillaumaud, Piola, Meerts, & Poly, 2011; Shannon, Bauer, Anderson, & Reynolds, 2014; Sielaff et al., 2018; Suseela, Alpert, Nakatsu, Armstrong, & Tharayil, 2016; P. Zhang, Li, Wu, & Hu, 2019). Vogelsang and Bever (2009) proposed the “degraded mutualist hypothesis” and found that invasive plant species can benefit from disrupting associations between native plants and their microbial mutualists (e.g., mycorrhizal fungi). This mechanism may be particularly potent when the nonnative species does not depend on these mutualisms, but native species do. Conversely, invasive species might also accumulate native pathogens that are more harmful to native species than introduced ones (but see Dukes et al., 2019; Mangla, Inderjit, & Callaway, 2008). The third mechanism is adapted from the “novel weapons hypothesis” whereby nonnative plants exude allelochemicals that are novel and detrimental to the native community (Callaway & Ridenour, 2004). Due to a lack of coevolutionary history, native plants are vulnerable to these toxins whereas co-occurring species from the nonnative's native range are not (Thorpe, Thelen, Diaconu, & Callaway, 2009). Furthermore, native microbial communities might enhance negative allelopathic impacts to native plants by increasing toxicity (Bains et al., 2009). Both Bains et al. (2009) and Fan, Marston, Hay, and Hostettmann (2009) found that nonnative invasive species produce different levels of potentially toxic chemical compounds (i.e. phenolics and tannins) in their introduced range compared to their native ranges. One area that has received less attention is the degree to which soil feedbacks of co-occurring exotic invasive species facilitate or inhibit each other and impact overall invasive spread (S. E. Kuebbing & Nuñez, 2016; Sara E. Kuebbing, Nuñez, & Simberloff, 2013; Rauschert & Shea, 2017).

Because the vast majority of plant-soil feedback studies pertain to grassland species and are often performed in short-term greenhouse experiments, it is critical to determine (1) if general plant-soil feedback trends are consistent across ecosystems, soil types, and lifeforms, and (2) if feedback dynamics change in the presence of co-occurring or codominant invaders. For example, there is compelling evidence that plant-soil feedbacks become increasingly positive and accrue more species-specific mutualisms over time, accelerating succession in grassland systems (Bauer, Mack, & Bever, 2015; Kardol, Bezemer, & van der Putten, 2006; Koziol & Bever, 2016, 2017, 2018). It is unclear, however, whether this dynamic applies to forest systems that ultimately serve as global carbon sinks. Moreover, Kuebbing et al. (2015; 2015; 2014; 2016) found that invasive codominant woody shrubs not only perpetuate their codominance through plant-soil feedbacks, but these co-occurring invasives also facilitate the persistence of a third invasive shrub in eastern deciduous forests. Thus, it is important to determine if invasive species act synergistically or additively in invasion dynamics. Furthermore, little work has been done comparing the strength of soil feedbacks in different soil textures (but see Schradin & Cipollini, 2012). Tran, Watts-

Williams, Smernik, and Cavagnaro (2021) recently found that “coarse substrate” sandy soil leaches more phosphorous and dissolved organic content than fine substrate sandy soils and that leaching is mediated by arbuscular mycorrhizal fungi (AMF). In testing for feedbacks, greenhouse experiments allow for tightly-controlled conditions that can be useful for determining plant-soil feedback magnitude and direction, however, it remains unclear the degree to which they are important *in situ* (De Long, Fry, Veen, & Kardol, 2019; Gundale, Wardle, Kardol, & Nilsson, 2019; Andrew Kulmatiski & Kardol, 2008). Thus, different approaches that incorporate somewhat less-controlled, but more realistic environmental factors would be beneficial.

Aggressive nonnative plant invasions are common on newly emergent landforms that occur throughout coarse sediment riparian areas of the northeastern US. These landforms undergo rapid primary succession to native woody species, however, aggressive invasion byexotic species has increasingly led to near monocultures of non-native species. Here, we tested plant soil feedbacks between two native species and two invasive species commonly found on young landforms by using large mesocosms in a multi-year field experiment. We hypothesized that nonnative invasive species successfully colonize young landforms by altering the soil in such a way that native species cannot colonize well. We predicted that native species would not perform well in conspecific-conditioned soil or soil that had invasive plant conditioning treatments. We also predicted that invasive species would perform well in both invasive-conditioned and native-conditioned soils. Alternatively, we hypothesized that feedbacks could be weak, in general, in coarse sediment well-draining soil that could be prone to substantial leaching.

4.2 Materials and Methods

4.2.1 Model System and focal species

We designed this experiment to model communities of three previously studied riparian sites that are in close proximity in Western NY and Northwest PA (Zoar Valley, Eighteenmile Creek, and Chautauqua Gorge). Forests within these riparian corridors undergo primary succession whereby pioneer trees establish in the first few years on emergent cobble bars (Diggins, 2013). These native pioneer tree species include sycamore (*Platanus occidentalis*), eastern cottonwood (*Populus deltoides*), and black locust (*Robinia pseudoacacia*). We chose to omit black locust in this study because of its N-fixing capacity. Invasive species have been increasingly colonizing nascent landforms in these river corridors over the past two decades. Two putatively troublesome invaders of Eastern US riparian zones, Morrow's honeysuckle (*Lonicera morrowii*) and Bohemian knotweed (*Fallopia x bohemica*), are the focal nonnative invasive species in this study. The former is a woody shrub, the latter is a long-lived herbaceous species, which is particularly pernicious because it forms a persistent network of underground rhizomes that resist displacement by natives. Regardless, both can form 2–4 meter tall nearly monospecific canopies. Furthermore, knotweed is typically nonmycorrhizal and does not rely on mycorrhizal fungi in the soil, however, it has been shown to be facultatively mycorrhizal (Wu, Isobe, & Ishii, 2004). Conversely, Morrow's honeysuckle associates with arbuscular mycorrhizal fungi and can reduce colonization of arbuscular mycorrhizal fungi in roots of native plants (Shannon et al., 2014). In addition to Japanese knotweed being nonmycorrhizal, it is also known to release tannins and polyphenols into the soil that often cause long-term changes to soil chemistry (Z. L. Zhang, Bhowmik, & Suseela, 2021).

4.2.2 Experimental Design

This design consisted of a 1-year conditioning phase (Phase 1) in which focal species grew in monospecific mesocosms (30 mesocosms per species). We began the feedback phase (Phase 2) partly into the growing season the following year. Treatments included all pairwise conditioning and feedback combinations such that each focal species would grow in soil conditioned by every other species, including conspecific-conditioned for a total of 16 treatment combinations (Figure 4.1). We randomly designated mesocosms for each species for Phase 1. We then randomly designated mesocosms from each conditioning group to each four Phase 2 treatments. Although we intended to have between 7 and 8 replicates per treatment combination, we ended up having a handful of treatment combinations with either 6 or 9 replicates. During phase 2, we monitored plant growth metrics including height and leaf count over multiple timepoints in addition to recording an initial and final root length per individual.

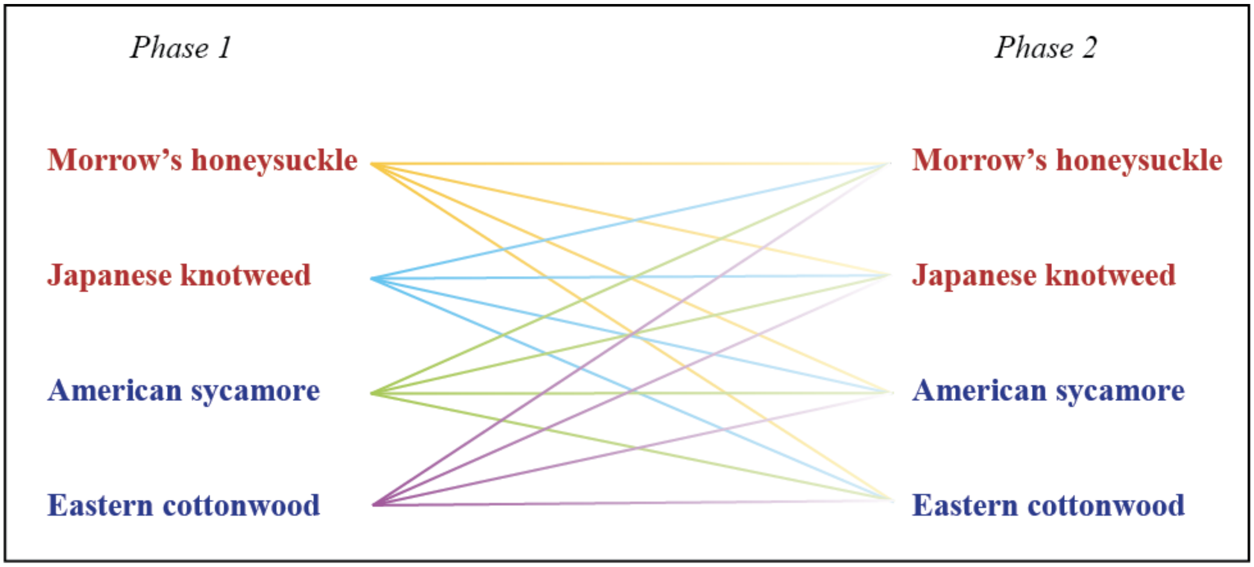


Figure 4.1

4.2.3 Mesocosm Location and Setup

We performed this experiment in an open old-field at University of Pittsburgh's Pymatuning Laboratory of Ecology in Linesville, Pennsylvania. We used round cattle tanks as mesocosms that were roughly 1.5m in diameter and nearly 0.75m high. We placed the mesocosm in an array in which there were three parallel sets of two rows of 20 mesocosms (6 rows, 120 mesocosms total) where mesocosms in rows (2x20) were slightly over 0.5m apart, on average (see Appendix D, Figure D-1). The three sets of rows were over 5m apart. In June 2018, we used machinery to layer three different types of substrates into the mesocosms that closely resemble the substrate composition of the model system. The bottom layer consisted of 2b gravel, the second layer consisted of friable shale, and we used bank gravel on the top. We used nearly 0.5 tons of each substrate type per mesocosm. We installed valve drains about 6-8" from the ground to be able to drain excess water following excessive precipitation, if necessary. We also drilled overflow holes slightly above the substrate line in each tank to prevent complete inundation.

4.2.4 Conditioning Phase (Phase 1)

In June 2019, to inoculate the mesocosms with a base microbial community, we collected 120L of substrate from each creek in the model system to use as whole soil inoculum. We transported the substrate from the landforms in plastic bags and then transferred them to 5-gallon buckets. We homogenized all the substrate from one creek in an empty mesocosm by mixing it before using plastic measuring buckets to put 1L of substrate into every mesocosm. We put 1L substrate from each creek into every mesocosm for a total of 3L per mesocosm.

We attempted to establish plants in the mesocosms from cuttings by using rooting powder between June and August 2019, however, there was extremely high mortality over the winter, especially in native species. Therefore, we repeated the conditioning phase in 2020. In spring and summer, we located and collected very young cottonwood and sycamore individuals from near focal creeks and local areas around the field station to transplant into the mesocosms. We carefully dug up seedlings using a trowel and rinsed the roots before planting them into the mesocosms to condition the soil. We grew at least 15, but more often around 20 individuals growing in each tank for Phase 1. To supplement honeysuckle conditioning tanks, we collected and planted local Morrow's honeysuckle seeds. We collected local knotweed rhizomes and planted roughly 2" ramets in knotweed conditioning mesocosms. We weeded and maintained the plants for the duration of the 2020 growing season.

We continued to let Phase 1 plant grow into the next growing season, through June 2021. We used seed tags to label all individuals from Phase 1 and their location in the mesocosms. We inventoried plant height and leaf count for each individual. When we ended Phase 1 and began Phase 2, we collected bulk soil samples, rhizosphere rinsate, and root samples from 3 randomly chosen individuals for each mesocosm from the conditioning phase (Phase 1). We changed gloves and bleach-sterilized trowels between every mesocosm. We put samples in a -20°C freezer to use in future microbial analyses. We cut all Phase 1 stems below the soil line to minimize soil perturbation and collected aboveground biomass for each tank that we later dried and weighed.

4.2.5 Feedback Phase (Phase 2)

To have seedlings ready to plant for Phase 2 and to reduce variation for between Phase 2 individuals, we grew sycamore, honeysuckle, and knotweed individuals from seed in the greenhouse at the University of Pittsburgh. We grew 800 seeds per species in cell trays. We sowed seeds directly into Old Castle C/B media because stratification was not necessary for these species. We placed humidity domes over the trays. Lights were on for 8 hours/day with a daytime temperature range of 72-77°F and a nighttime temperature range of 60-65°F. Plants were watered daily and grew from 3/3/2021-5/27/2021. Because cottonwood seeds are only viable for days after falling, there has been very little success in drying and storing them. Thus, they are also not able to be purchased. We planned to collect cottonwood seeds once they started to fall and immediately plant them into sand to germinate before transplanting them into the mesocosms. Although we collected and germinated roughly 1000 cottonwood seeds, we had one mortality event from soil drying on a hot day and lost over half of the seedlings. To replace those individuals, we collected newly germinated seedlings from a beach near Erie, PA where we found over 100,000 seedlings growing from an obvious recent seed rain event. All the seedlings were comparably sized. We used a trowel to carefully remove at least 800 seedlings from the sand and placed them in plastic bags for transport. To avoid another mortality event, we rinsed seedlings and refrigerated them until we were ready to plant them in mesocosms.

We began the feedback phase (Phase 2) in July 2021. We cut all Phase 1 plants below the soil line and left the Phase 1 roots in the mesocosms. We immediately planted Phase 2 individuals in mesocosms at least 20cm from another individual. Because of some mortality in the greenhouse or between moving plants from the greenhouse and planting for Phase 2, we used 13 individuals per mesocosm for sycamore and knotweed feedbacks. We planted 15 cottonwood and honeysuckle individuals per mesocosms for those treatments. All individual plants had unique labels and we recorded the specific (removed) Phase 1 individual nearest to each Phase 2 individual we planted. We recorded the initial root length, height, and leaf count. We changed gloves and bleach-sterilized trowels between every mesocosm.

We collected height and leaf count data on every individual for at least two timepoints before the harvest timepoint, but the timing differed between species. As an additional metric, we counted the number of stems per honeysuckle individual. We continually weeded the mesocosms and watered the plants when necessary. In October 2021, we destructively harvested all Phase 2 individuals. We again collected bulk soil from each mesocosm and rhizosphere rinsate and root samples from 3 random invidividuals in each mesocosm and stored them in a -20°C freezer for future microbial analyses. We recorded final height, root length, and leaf count. Additionally, we recorded stem count for honeysuckle. We separated roots from shoots and put aboveground biomass and belowground biomass in bags per mescocosm to dry and weigh (results not shown here). We used some of the bulk soil from each tank to measure soil pH and percent organic carbon.

4.2.6 Statistical Analyses

We analyzed performance of plant species across conditioning treatments using linear mixed effects models and generalized linear mixed effects models. We performed separate analyses for each species. We tested for differences in height and root length using linear mixed effects models and leaf count using generalized linear mixed effects models. We included treatment as a fixed factor and mesocosm number as a random factor. Preliminary analyses on soil variables using linear models showed no effect of conditioning treatment on soil pH or percent organic carbon, so we did not include those as terms in the species models. All statistical analyses were performed using R statistical software, Version 4.0.3. (R Core Team, 2020).

4.3 Results

4.3.1 Eastern cottonwood

Cottonwood height did not differ between any soil conditioning treatment (Figure 4.2, Table 4.1). There was a significant treatment effect in cottonwood root length (p=0.0135, Figure 4.2, Table 4.1). Cottonwood roots grew almost two times longer in knotweed-conditioned soil (12.53 cm ± 0.78 S.E.) than in conspecific conditioned soil (7.49 cm ± 0.58 S.E., post-hoc pairwise comparison p=0.0173, Figure 4.2).

4.3.2 American sycamore

Sycamore did not show differences in any response variables including height, root length, or leaf count between conditioning treatments (Figure 4.2, Table 4.1).

4.3.3 Morrow’s honeysuckle

Honeysuckle showed a significant feedback response in height and stem count (p=0.015 and p=0.038, respectively, Figures 4.3 and 4.4, Table 4.1). Honeysuckle plants grew taller in sycamore-conditioned soil (12.53 cm ± 1.88 S.E.) than in cottonwood-conditioned soil (10.18 cm ± 0.33 S.E., post-hoc pairwise comparison p=0.026, Figure 4.3). Honeysuckle grew marginally taller in sycamore-conditioned soil than in the knotweed conditioning treatment (10.45 cm ± 0.29 S.E.).

Honeysuckle also showed higher mean stem counts per individual in the sycamore conditioning treatment (3.95 ± 0.27 S.E.) compared to knotweed-conditioned soil (2.53 ± 0.17 S.E., post-hoc pairwise comparison p=0.043, Figure 4.4). Additionally, there were marginally more honeysuckle stems per individual growing in conspecific-conditioned soil (3.83 ± 0.28 S.E.) than in the knotweed conditioning treatment (post-hoc pairwise comparison p=0.070, Figure 4.4).

4.3.4 Bohemian knotweed

Knotweed showed significant feedback responses to conditioning treatment for height and leaf count (<0.001 for both, Figure 4.3., Table 4.1). Knotweed plants grew taller in the cottonwood conditioning treatment (11.63 cm ± 0.61 S.E.) and the sycamore conditioning treatment (10.68 cm ± 0.54 S.E.) than in its own conspecific conditioned soil (7.34 cm ± 0.40 S.E., post-hoc pairwise comparison p=0.001 and p=0.008, respectively, Figure 4.3). Knotweed also grew marginally taller in the cottonwood conditioning treatment than in the honeysuckle conditioning treatment (9.12 cm ± 0.56 S.E., post-hoc pairwise comparison $p=0.083$, Figure 4.3).

Knotweed showed similar responses in leaf count such that individuals produced more leaves on average in cottonwood conditioned soil (10.25 ± 0.85 S.E.), sycamore-conditioned soil (9.77 ± 0.79 S.E.), and honeysuckle-conditioned soil (7.59 ± 0.78 S.E.) than in its own conspecific-conditioned soil (4.10 ± 0.35 S.E., post-hoc pairwise comparison $p<0.001$ for all, Figure 4.3).

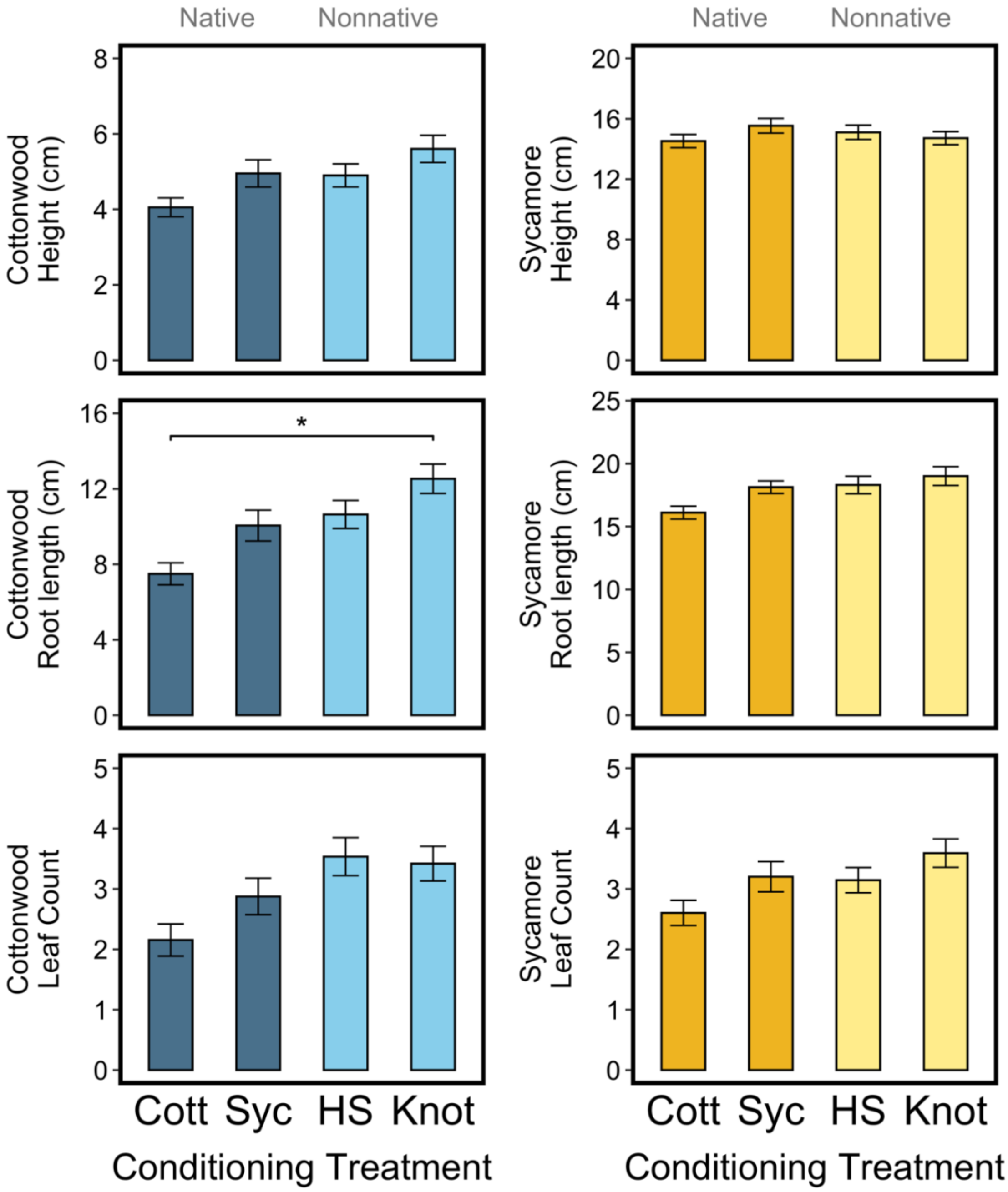

Native
Nonnative
Native
Nonnative
Cottonwood Height (cm)
0
2
4
6
8
Sycamore Height (cm)
0
4
8
12
16
20
Cottonwood Root length (cm)
0
4
8
12
16
*
Sycamore Root length (cm)
0
5
10
15
20
25
Cottonwood Leaf Count
0
1
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Figure 4.2

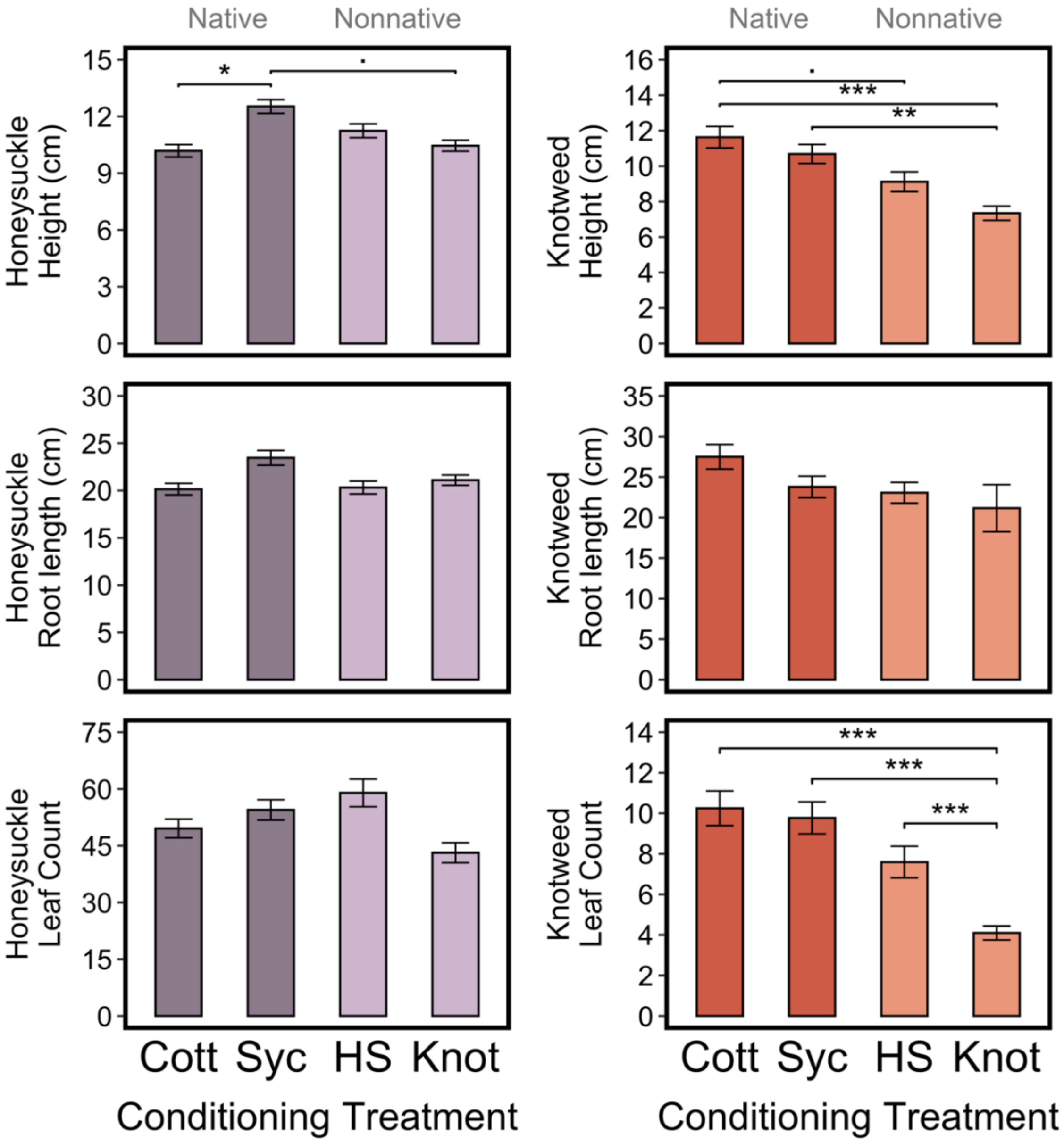
Native
Nonnative
Honeysuckle Height (cm)
Knotweed Height (cm)
Honeysuckle Root length (cm)
Knotweed Root length (cm)
Honeysuckle Leaf Count
Knotweed Leaf Count
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Figure 4.3

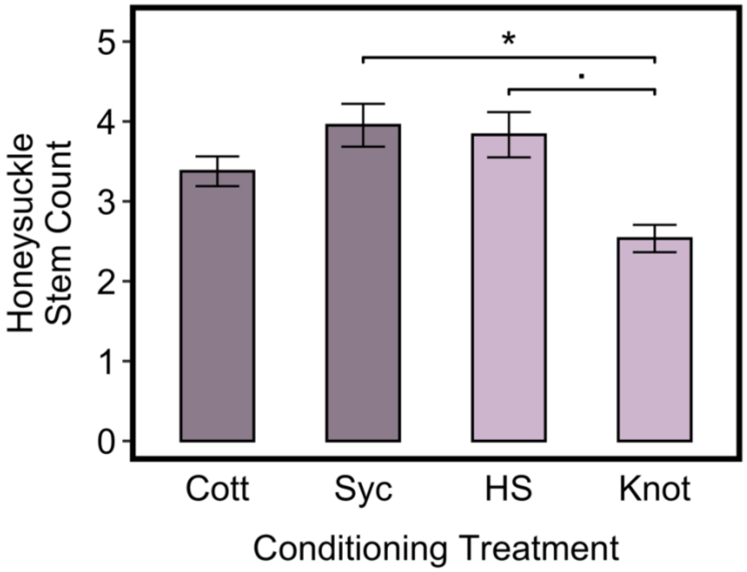

Figure 4.4

Table 4.1

Models	**Chisq**	**df**	**Pr(>Chisq)**
Cottonwood			
Height (cm)	4.5237	3	0.2102
Root length (cm)	10.698	3	**0.0135**
Leaf count	6.6815	3	0.0827.
Sycamore			
Height (cm)	1.9738	3	0.5779
Root length (cm)	5.0717	3	0.1666
Leaf count	4.5375	3	0.209
Honeysuckle			
Height (cm)	10.462	3	**0.015**

Root length (cm)	5.4808	3	0.1398
Leaf count	4.613	3	0.2024
Stem count	8.4434	3	**0.0377**
Knotweed			
Height (cm)	24.031	3	**<0.001**
Root length (cm)	3.9018	3	0.2723
Leaf count	39.29	3	**<0.001**

4.4 Discussion

Here we sought to test how plant-soil feedbacks could potentially be contributing to invasion patterns in a riparian study system with coarse and sandy soils by using a somewhat hybrid experiment. We grew plants in large outdoor mesocosms where conditions cannot be controlled like in a greenhouse, yet they offer more access, control, and feasibility than performing an experiment directly in the model system. We expected to see invasive species perform similarly across conditioning treatments because they are known to exhibit positive soil feedbacks in introduced ranges (Beckstead & Parker, 2003; Inderjit & van der Putten, 2010). We also expected to see native species perform poorly in conspecific and invasive conditioned soils.

Our results showed that species responded with different metrics in exhibiting feedbacks. For example, cottonwood showed significant differences in root length while honeysuckle showed responses to conditioning treatments in height and stem count. Knotweed had significant responses in both height and leaf count. Because of the nature of the experiment, this makes sense to a degree. Cottonwood responses may have been stronger in height and leaf count, however, they went through a fairly substantial dieback phase and lost several leaves before re-establishing, potentially because of their small size when we planted them. The roots, however, were protected from sun shock and likely remained healthy and growing for the duration of the experiment. The lack of response in knotweed root length when the other response variables showed such stark differences could be due to the growth structure and energy storage in its rhizomes that sometimes grow wide before growing very long. It is also possible that we simply did not have robust enough replication to pick up on subtler effects.

It was unexpected that cottonwood showed the most root growth in knotweed conditioning treatments because knotweed is such an aggressive invader that can disrupt mutualists and release phytochemicals into the soil (Dommanget et al., 2014; Murrell et al., 2011). It also presents evidence counter to our hypothesis that these invasives are successful because of soil-feedbacks, however it's entirely possible that in this system, knotweed is so competitive because of clonal growth and shading out other plants (Siemens & Blossey, 2007). Perhaps the most surprising of our results was the marked negative conspecific feedback that knotweed exhibited in its own soil. We did not expect invasive species to have really strong differences between any treatments because of how commonly they escape negative feedbacks and we expected the strongest conspecific feedback in native species. For example, honeysuckle responded as we might predict, where it performed slightly better in native conditioned mesocosms, but exhibited no strong negative feedbacks in its own conditioned soil.

We did have an alternative hypothesis that feedbacks might not be strong overall in such coarse sandy soils and our results seem to support that to a degree. No differences were found in sycamore between any conditioning treatments. However, knotweed showed strong differences to treatments. Very few studies have been done on sandy soils or soil textures with large granules. It is interesting that Tran et al. (2021) found that coarse substrate sandy soil leaches P and dissolved organic content readily, but that this can be mediated to an extent by AMF. In fact, Schradin and Cipollini (2012) compared feedbacks of similarly invasive congener of the focal honeysuckle in this experiment with two native species in a loamy soil and an acidic sandy soil. They reported that the invasive honeysuckle performed well in all loamy soils regardless of conditioning treatment or sterilization and that it fared well in inoculated sandy soil, but the feedback turned negative in sterilized sandy soil. Future research on soil feedbacks in sandy soils, and particularly the role that AMF might play in them would further our understanding and even predictions of when to expect strong feedbacks or in what direction.

Unfortunately, we do not currently have information on the microbial communities from this experiment. Knowing about the microbial community structures in the soil and in the roots would shed more light on our findings here and if our results are driven more by native vs. nonnative differences, soil type, or other factors. One major limitation of this outdoor mesocosm study is that we were not definitively able to attribute growth differences to the microbial community like is possible in greenhouse experiments with microbial inoculum. It remains unclear if microbial aspects in the soil would be as susceptible to washing away as nutrients and dissolved organic carbon are in leaching from sandy soils. Our results so far fail to completely explain the extensive invasion dynamics currently seen in coarse sediment riparian forest systems.

4.5 Conclusion

We found that a nonnative invasive species had lower growth in its own conspecific conditioned soil, contrary to may study findings on invasions and plant soil feedbacks to date. Our outdoor mesocosm experiment provided more realistic environmental variation than greenhouse experiments, however, it requires other linking information to be able to confidently explain the mechanisms behind our results. Incorporating genetic sequencing tools, examining more soil types and textures, and implementing experimental designs that link greenhouse and natural dynamics would go a long way in furthering our understanding of how plant-soil feedbacks contribute to plant invasions.

Appendix A

Literature Review: Microsites Studied

Table A-1

	Microsites measured							
Study	Mound Top	Upper Surface	Lower Surface	Mound Overall	Pit	Pit Wall	Intact Ref. Site	Closed Canopy Ref. Site
Hutnik 1952	🟦	🟦	🟦		🟦			
Putz 1983				-	-		🟦	
Riera 1985	🟦							
Nakashizuka 1989				🟦	🟦			🟦
Peterson & Pickett 1990				🟦	🟦			
Peterson et al. 1990	🟦				🟦	🟦	🟦	
Carlton & Bazzaz 1998	🟦	🟦			🟦		🟦	
Long et al. 1998				🟦	-		-	
Battaglia et al. 1999				🟦	🟦		🟦	
Palmer et al. 2000		🟦	🟦		🟦		🟦	
Krueger & Peterson 2006				🟦	🟦		🟦	

von Oheimb et al. 2007				🟦			🟦	
Lang et al. 2009	🟦	?	?		🟦	?	🟦	
Lõhmus et al. 2010				🟦				
Mollaei Darabi et al. 2014				🟦	🟦			🟦
Waldron et al. 2014				🟦	🟦		🟦	
Vodde et al. 2015				🟦	🟦		🟦	
Jonsson & Esseen 2016				-	-		🟦	
Spicer et al. 2018				🟦			🟦	
Kern et al. 2019				🟦			🟦	
Yoshida 2021				🟦	🟦		🟦	
Current Study				🟦			🟦	

Appendix B

Common Species at Chatham University Eden Hall Campus

Table B-1

Species	**Growth form**	**Mean cover (%)**	**S.E. cover**
Native		65.3	6.3
Lindera benzoin	shrub	8.5	1.8
Rubus spp.	shrub	7.9	1.9
Impatiens capensis	forb	5.2	1.8
Grasses (excluding *Microstegium vimineum*)	graminoid	4.2	1.9
Polystichum acrostichoides	fern	2.7	0.6
Persicaria virginiana	forb	2.7	0.6
Prunella vulgaris	forb	2.4	0.6
Nonnnative		78.4	8.0
Ligustrum sinese	shrub	19.7	3.8
Berberis thunbergii	shrub	9.7	2.8
Rosa multiflora	shrub	7.4	1.9
Microstegium vimineum	graminoid	7.3	2.8
Celastrus orbiculatus	vine	6.6	0.8
Lonicera spp.	shrub	5.5	1.4
Alliaria petiolata	forb	1.4	0.3

Appendix C

Percent Cover of Most Abundant Species at Chatham University Eden Hall Campus

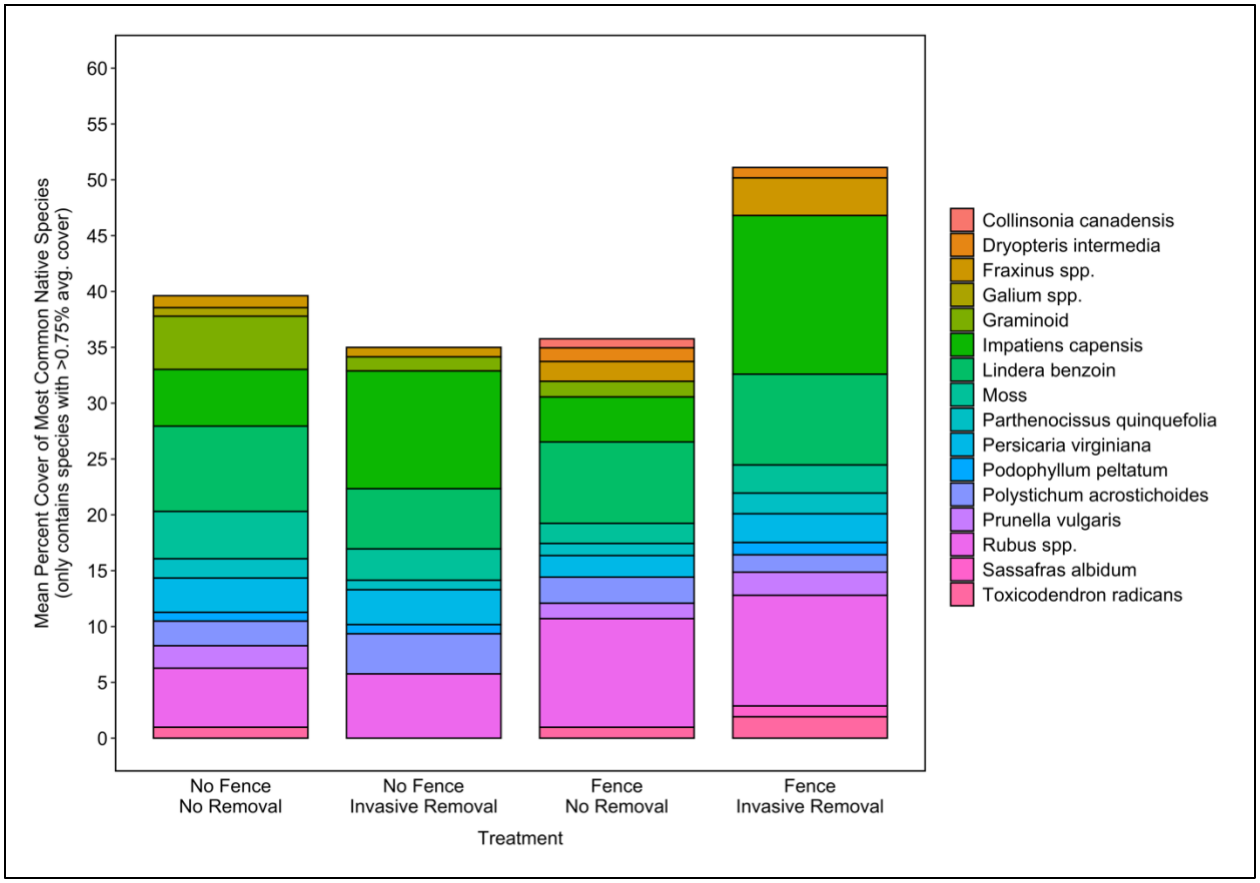

Figure C-1

Appendix D

Mesocosm Array for Soil Feedback Experiment

Figure D-1

Image of the mesocosm setup at University of Pittsburgh Pymatuning Laboratory of Ecology in Linesville, Pennsylvania.

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