Engineering Invasion: Do Canopy Gaps Created By The North American Beaver (*Castor canadensis*) Facilitate Terrestrial Plant Invasions?

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Abstract

The North American beaver (*Castor canadensis*) is a keystone ecosystem engineer whose dam-building and foraging activities create or sustain riparian habitats. Beavers influence the competitive dynamics of the forest understory through tree felling, which creates canopy gaps with increased light availability. Although invasive vegetation is common in riparian ecosystems across the United States, it is unknown whether the canopy gaps created by beavers promote terrestrial plant invasions. Our objectives were to assess: (1) the extent to which beaver felling influenced light availability, (2) whether canopy gaps created by beaver felling facilitated the spread of non-native herbaceous plants and woody shrubs, and (3) which invasive species took advantage of these gaps. This study took place at the Huyck Preserve and Biological Research Station in east-central New York State. We surveyed five-meter radial plots around a total of 38 beaver-felled and unfelled control trees, measuring tree diameter, canopy openness, soil pH, and the percent abundance of invasive plant species present. Plots with beaver-felled trees had significantly higher light levels than unfelled control plots. The total percent abundance of invasive herbaceous plants and shrubs was significantly higher in beaver-felled plots than in controls. However, only three of the ten invasive species surveyed were drivers of this difference (*Celastrus orbiculatus, Lonicera spp.*, and *Berberis thunbergii*). These results reinforce the importance of light availability resulting from canopy disturbance, and facilitated by beaver activity, in enabling terrestrial plant invasions.

Introduction

North American beavers (*Castor canadensis*) mold the riparian ecosystems they engineer and inhabit. Through selective foraging and the use of woody vegetation for dam and lodge creation, they can significantly impact the composition and structure of near-shore canopy and understory (Donkor & Fryxell, 1999; Rosell et al., 2005). Reduced tree density creates gaps that allow for greater light penetration through the forest canopy while decreasing competition for soil and nutrients (Barnes & Dibble, 1988; Johnston & Naiman, 1990).

Invasions of non-native plants have been demonstrated to increase in frequency and severity in the wake of canopy disturbance (Belote et al., 2008; Lee & Thompson, 2012). In Pennsylvania and New Jersey, Eschtruth and Battles (2009) found that canopy disturbances resulting from hemlock woolly adelgid (*Adelges tsugae*) infestation and propagule pressure were associated with intensified invasions of garlic mustard (*Alliaria petiolata*), Japanese barberry (*Berberis thunbergii*), and Japanese stiltgrass (*Microstegium vimineum*). Gaps created by logging in Hawaiian forests resulted in greater availability of light and nitrogen that promoted the spread of invasive plants (Loh et al., 2008). In California's redwood forest, increased light availability was also a vital resource in plant species invasions, as unshaded plots had a greater proportion of invasive species than nearby shaded plots (Blair et al., 2010).

Although beavers are considered generalist herbivores, their preference for more palatable woody plant species, such as willows and poplars, has earned them recognition as choosy, opportunistic foragers (Haarberg & Rosell, 2006; Vorel et al, 2015). A well-documented effect of selective and choosy herbivory is the proliferation of non-preferred vegetation, as herbivores with a stronger preference for native species over non-native species can encourage invasions (Augustine & McNaughton, 1998; Keane & Crawley, 2002). Previous studies have demonstrated a relationship between beaver foraging preferences and invasions of non-native trees and shrubs. In Hungary, the Eurasian beaver (*Castor fiber*) may expedite the shift in canopy composition toward non-native hardwood shrubs through its preference for softwood species (Juhasz et al., 2022). Beavers in Ohio may aid amur honeysuckle (*Lonicera maackii*) invasion by selectively felling its competition (Deardorff & Gorchov, 2020). Invasive tamarisk trees (*Tamarix ramosissima*) thrive where beavers are abundant in the Grand Canyon National Park (Mortenson et al., 2008).

While invasive vegetation is common in the riparian ecosystems of the northeastern United States, whether the canopy gaps created by beavers promote invasions of non-native herbaceous plants and shrubs has yet to be thoroughly investigated. In this study, we examined the influence of beavers on facilitating invasive colonization and spread at the Huyck Preserve and Biological Research Station in New York. Lincoln Pond, situated within the Preserve, has a long history of beaver activity, making it an ideal location for this study (Muller-Schwarze et. al, 1983; Tevis 1949; Tevis, 1950).

Our objectives were to determine: (1) the extent to which beaver felling influenced light availability, (2) whether canopy gaps created by beaver felling facilitated the spread of non-native herbaceous plants and woody shrubs, and (3) which invasive species took advantage of these gaps. To investigate these questions, we surveyed plots centered around beaver-felled trees and unfelled controls to characterize canopy openness, soil pH, and percent abundance of invasive species. Since beaver-felled gaps increase light availability—potentially creating conditions conducive to the spread of non-native species—we hypothesized that beaver herbivory promotes the spread of invasive herbaceous plants and shrubs at the Preserve.

Methods

Study Site

This study took place at the Huyck Preserve and Biological Research Station in east-central New York State (Fig. 1a). Beavers are well-established on Lincoln Pond, with evidence of their presence first being recorded by Eugene P. Odum in 1939 (Tevis, 1950). By 1947, two beaver lodges were observed nested along the banks of the 4 hectare-pond (Odum, 1939; Tevis, 1950). Since then, a third has been established. Over this timeframe, beavers have had a marked effect on the landscape. In a preliminary survey of beaver activity surrounding the pond, 835 trees with evidence of beaver interaction (felling or gnawing) were identified (Fig. A1, Campbell & Velicer, 2024).

The north and east sides of Lincoln Pond are dominated by old-growth eastern hemlock (*Tsuga canadensis*). Marshes and alder (*Alnus incana*) thickets cling to the north, west, and, to a lesser extent, east shorelines. The southwest shore is characterized by a red pine plantation dating back to 1928 (Tevis, 1950) that is now overgrown with mixed deciduous hardwood, namely sugar maple (*Acer saccharum*), American hornbeam (*Carpinus caroliniana*), American hophornbeam (*Ostrya virginiana*), and white ash (*Fraxinus americana*).

Invasive species are actively managed on the Preserve, through the use of a variety of techniques from manual cutting to spot-torching. Fieldwork for this study was conducted in the summer of 2024 before the annual management of invasive herbaceous plants and shrubs began around the pond area.

Field Sampling

Five-meter radial plots were surveyed around a total of 38 selected trees—19 felled and 19 unfelled control trees (Fig. 1b). Felled tree plots were selected based on the initial assessment of beaver activity around Lincoln Pond (Fig. A1, Campbell & Velicer, 2024). Only woody stems greater than 15 cm were considered, as felled trees of that size created a canopy gap large enough to alter the understory light environment. Plots were selected to avoid overlaps with a hiking trail surrounding the pond to minimize the effects of increased light availability from the path. Due to the high levels of beaver activity immediately surrounding the pond, randomly selected unfelled controls were, on average, farther from the pond than felled trees, but still within the riparian zone.

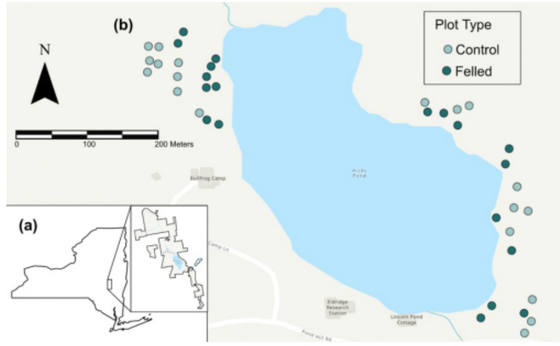

Figure 1. (a) Location of the Huyck Preserve and Biological Research Station in east-central New York State. (b) Location of surveyed plots (n=38) around Lincoln Pond, summer 2024 (plot symbols not to scale).

Within each plot, we estimated the percent abundance of all invasive terrestrial herbaceous plants and shrubs. Invasive trees were not present at the study location, and therefore not included in the study design. While observed in some plots, aquatic invasive species were not considered in this analysis. The abundance and growth form of some non-native species, particularly the Asiatic bittersweet (*Celastrus orbiculatus*), rendered counts impractical. Tree diameters were measured 20 cm from the ground, which is below beaver felling height (Belovsky, 1984; Janiszewski, 2017). We used Avenza Maps version 5.3.3 (243.1) to record tree location and a spherical densiometer to measure canopy openness. Soil samples were taken at the base of each tree, and their pH was measured with a HANNA H198107 pH meter in the lab. This controlled for differences in soil pH between plot types that may have accounted for observed differences in invasive species abundance.

Statistical Analysis

Analysis of Variance (ANOVA) was performed in R version 4.3.2 (R Core Team, 2023) to test whether the mean percent abundance of invasive plants varied according to soil pH or canopy openness. Student's t-tests were conducted to determine whether the total percent abundance of invasive species, soil pH, and canopy openness were significantly different between felled and control plots. A simple linear regression model was used to assess how well canopy openness predicted the total percent abundance of invasive species plants across all plots.

Results

Plots centered around a total of eight different tree species were surveyed (Table 1). Two felled trees could not be identified due to significant rotting. The vast majority of felled plots were centered around deciduous trees, with eastern hemlock encompassing only ~11% of felled trees surveyed. In contrast, ~68% of control trees were eastern hemlock (Table 1). This difference can be attributed to diet preferences, as beavers generally favor more easily digestible deciduous trees over conifers (Fryxell & Doucet, 1993; Gallant et al., 2004). The study site's high levels of beaver activity, undoubtedly a consequence of prolonged beaver residency at Lincoln Pond, rendered very few large deciduous trees left standing within the riparian zone that could serve as controls.

There were no significant interactions between plot type, soil pH, and canopy cover. However, canopy cover was highly correlated with plot type (Table 2, Fig. A2). Plots with beaver-felled trees exhibited gaps in the forest canopy, resulting in significantly higher light levels than unfelled control plots (~74% versus ~91%, respectively; Fig. 2). The total percent abundance of invasive species decreased as canopy cover increased (Fig. 3), with canopy cover explaining ~41% of the variability in the total percent abundance of invasive species ($p < 0.001$; Table 3).

Plot Type	Species	Common Name	Species Code	Relative Abundance (%)	Average Diameter (cm)
Felled	*Acer saccharum*	Sugar maple	ACSA	5.26	29.60
	Betula alleghaniensis	Yellow birch	BEAL	10.53	23.85
	Carpinus caroliniana	American hornbeam	CACA	5.26	17.00
	Ostrya virginiana	American hophornbeam	OSVI	31.58	25.79
	Tilia americana	Basswood	TIAM	21.05	42.93
	Tsuga canadensis	Eastern hemlock	TSCA	10.53	26.00
	Ulmus ruba	Slippery elm	ULRU	5.26	23.50
	Unknown	N/A	N/A	10.53	37.00
Control	*Acer saccharum*	Sugar maple	ACSA	5.26	20.85
	Ostrya virginiana	American hophornbeam	OSVI	5.26	20.30
	Quercus rubra	Red oak	QURU	21.05	46.28
	Tsuga canadensis	Eastern hemlock	TSCA	68.42	28.23

Table 1. Average relative abundance and size of tree species found in the felled (n=19) and control plots (n=19).

Variable	Sum of Squares	df	Mean Square	F value	Pr (>F)
Plot type	5338	1	5338	32.352	< 0.001***
Soil pH	361	1	361	2.118	0.150
Canopy cover	1387	1	1387	8.403	< 0.01**
Plot type x Soil pH	177	1	177	1.072	0.309
Plot type x Canopy cover	57	1	57	0.345	0.561
Soil pH x Canopy cover	459	1	459	2.779	0.106
Plot type x Soil pH x Canopy cover	6	1	6	0.037	0.848
Residuals	4950	30	165		
** p < 0.01, *** p < 0.001					

Table 2. Percent abundance of invasive plants as a function of soil pH and canopy cover, tested using an ANOVA.

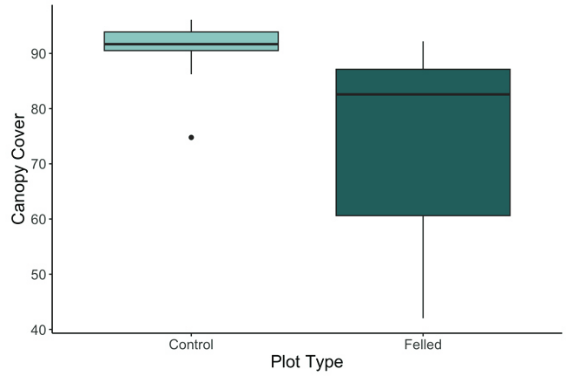

Figure 2. A boxplot of canopy cover (%) between control and felled plots ($p < 0.001$). Thick black line indicates the median value. Boxes represent the 1st to 3rd quartile range. Whiskers extend to the most extreme values within 1.5 times the interquartile range. Outliers are represented by black dots.

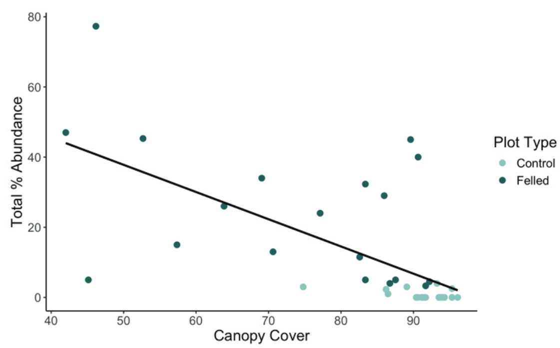

Figure 3. A scatterplot of canopy closure as a predictor of total percent abundance of invasive species plants across all plots. The line represents the fitted values from the linear regression.

Variable	Estimate	Standard Error	p-value
Intercept	76.5951	12.8657	< 0.001***
Canopy cover	-0.7759	12.8657	< 0.001***
*** p < 0.001			

Table 3. Estimated regression parameters, standard errors, and p-values for the simple linear regression model (R Square = 0.4148).

The total percent abundance of invasive herbaceous plants and shrubs was significantly higher and more variable in beaver-felled plots than in controls ($p < 0.001$; Fig. 4, Table 4). However, of the ten invasive species identified, only Asiatic bittersweet, honeysuckles (*Lonicera spp.)*, and Japanese barberry were significantly more prevalent in felled plots than in control plots (Figure 5; Table 5). Thus, only a small portion of the invasive species surveyed are drivers of the difference in invasive species prevalence by plot type.

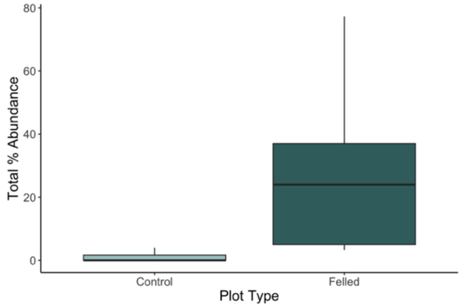

Figure 4. A boxplot of total percent abundance of invasive herbaceous plants and shrubs between control and felled plots ($p < 0.001$). The thick black line indicates the median value. Boxes represent the 1st to 3rd quartile range. Whiskers extend to the most extreme values within 1.5 times the interquartile range. Outliers are represented by black dots.

T-test	t-value	p-value
Total % abundance	-5.097	< 0.001***
Canopy cover	4.267	< 0.001***
Soil pH	-2.253	0.031*
* p < 0.05, *** p < 0.001		

Table 4. T-test for differences in total percent abundance of invasive species, canopy openness, and soil pH between felled and control plots.

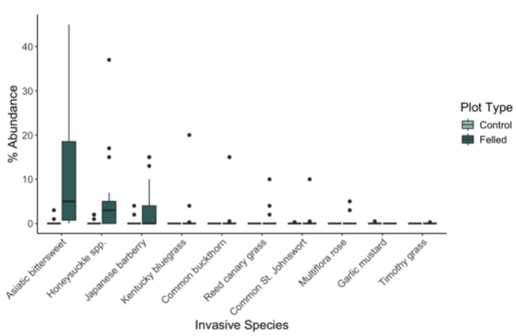

Figure 5. A boxplot of percent abundance of observed invasive herbaceous plant and shrub species between control and felled plots ($p < 0.001$). A thick black line indicates the median value. Boxes represent the 1st to 3rd quartile range. Whiskers extend to the most extreme values within 1.5 times the interquartile range. Outliers are represented by black dots.

Species	Common Name	t-value	p-value
Celastrus orbiculatus	Asiatic bittersweet	-3.538	0.002**
Lonicera spp.[a]	Honeysuckle spp.	-2.643	0.016*
Berberis thunbergii	Japanese barberry	-2.236	0.037*
Poa pratensis	Kentucky bluegrass	-1.205	0.244
Rhamnus cathartica	Common buckthorn	-1.035	0.315
Phalaris arundinacea	Reed canary grass	-1.509	0.149
Hypericum perforatum	Common St. Johnswort	-1.084	0.293
Rosa multiflora	Multiflora rose	-1.407	0.177
Alliaria petiolata	Garlic mustard	1.000	0.331
Phleum pratense	Timothy grass	-1.000	0.331

[a]There are potentially up to three species of invasive honeysuckle (*Lonicera morrowii*, *Lonicera tatarica*, and *Lonicera xylosteum*) located at the study site which were not able to be practically distinguished in the field.
* p < 0.05, ** p < 0.01

Table 5. Student's t-tests comparing the mean percent abundance of each invasive herbaceous plant and shrub species in felled versus control plots.

Discussion

Beaver-created canopy gaps exhibited significantly increased understory light availability, a finding consistent with previous observations in the midwestern United States (Barnes & Dibble, 1988; Johnston & Naiman, 1990). As predicted, higher light levels, resulting from beaver felling, were associated with a greater prevalence of invasive herbaceous plants and woody shrubs. This observed correlation between canopy openness and invasive species abundance reinforces light as a crucial resource for invasive species proliferation (Blair et al., 2010). Other studies have also highlighted the association between increased light availability due to canopy disturbance and the spread of invasive plants (Belote et al., 2008; Eschtruth & Battles, 2009; Lee & Thompson, 2012).

The dominance of Asiatic bittersweet, honeysuckles, and Japanese barberry in driving the observed differences in total invasive species abundance between plot types suggests that not all invasive plants are equally skilled in exploiting the gaps created by beavers. The success of the most prevalent invader in felled plots, Asiatic bittersweet, is likely bolstered by its rapid seed production, high germination rates, and rapid growth in high-light environments (Ellsworth, 2003). The hardy invader may endure years in heavily shaded understory before rapidly colonizing canopy gaps created by disturbance—likely giving it an advantage over other invaders such as common St. Johnswort (*Hypericum perforatum*), whose seedlings are small and slow-growing, or even common buckthorn (*Rhamnus cathartica*), whose growth rate is considered medium to fast (Campbell, 1985; Dirr, 1998; Patterson, 1974).

The honeysuckles found on the Preserve are also fast-growing and tolerant of a wide range of light conditions. Their seeds are readily dispersed by white-tailed deer populations, and, like the seeds of Asiatic bittersweet and Japanese barberry, by frugivorous birds. Morrow's honeysuckle (*Lonicera morrowii*), one of the Preserve's invasive honeysuckle species, can germinate beneath 2 inches of leaf litter (Hidayati, 2000). This ability may provide it the edge needed to invade dense hemlock forest, where thick leaf litter typically inhibits colonization by most herbaceous plants and shrubs. While not a particularly fast grower, Japanese barberry has been observed exploiting canopy gaps in hemlock forest, and its seedling survival and growth rate is also positively correlated with light level (D'Appollonio, 2006; Eschtruth & Battles, 2009; Silander, 1999).

In contrast to the more successful invaders, garlic mustard is most competitive in well-shaded understory (Dhillion, 1999), and was only observed in a single control plot in this study. Reed canary grass (*Phalaris arundinacea*) and timothy grass (*Phleum pratense*) were restricted to plots on a thin strip of wetland sandwiched between the pond's edge and the beginning of hemlock forest. Thus, the non-significant increase in the percent abundance of these grasses in felled plots may be influenced by the slight difference in distance from the pond between felled and control plots.

The lack of significant interactions between soil pH and invasive species abundance further underscores the dominant role of light availability in facilitating non-native plant invasions. Soil pH was measured to account for any possible confounding effects of soil chemistry on invasive colonization across plot types. Although, it is possible that the increased presence of invasive plants may also be a contributing factor to the higher soil pH levels observed in felled plots. Asiatic bittersweet and Morrow's honeysuckle have been observed to significantly increase soil pH (Hicks, 2004).

While beavers are typically recognized as wetland engineers with positive impacts on biodiversity and are often introduced to habitats as part of ecological restoration efforts (Law et al., 2019; Smith & Mather, 2013; Stringer & Gaywood, 2016), this research sheds light on an understudied aspect of their ecological impact: their potential to aid terrestrial plant invasions. Common invaders in the northeastern United States, such as Asiatic bittersweet and Japanese barberry, are known to monopolize resources and reduce biodiversity by out-competing native vegetation (Delisle & Parshall, 2018; Dibble & Rees, 2005; Ellsworth, 2003; McNab and Meeker, 1987).

The findings of this study may be context-dependent based on forest type and the legacy of invasive plants in the area. More studies, particularly across larger sites without annual invasive plant management, are needed to gain a more comprehensive understanding of the possible long-term impacts of beaver felling on plant invasions and implications for invasive plant management at a broader scale. Investigating the relationship between near-shore tree felling and aquatic invasive species abundance also warrants further consideration. Beavers' influence on invasive plant spread may be important to consider in wetland restoration and management.

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About the Author

Carlina Velicer is a third-year undergraduate majoring in ecology and evolutionary biology and minoring in environmental humanities. She conducted this research during her time as an Odum field ecology intern at the Huyck Preserve and Biological Research Station, located near Albany. Her interests lie in research that informs conservation efforts and our understanding of ecological responses to abiotic and biotic disturbances such as climate change, habitat loss, and invasions of non-native species.

Appendix

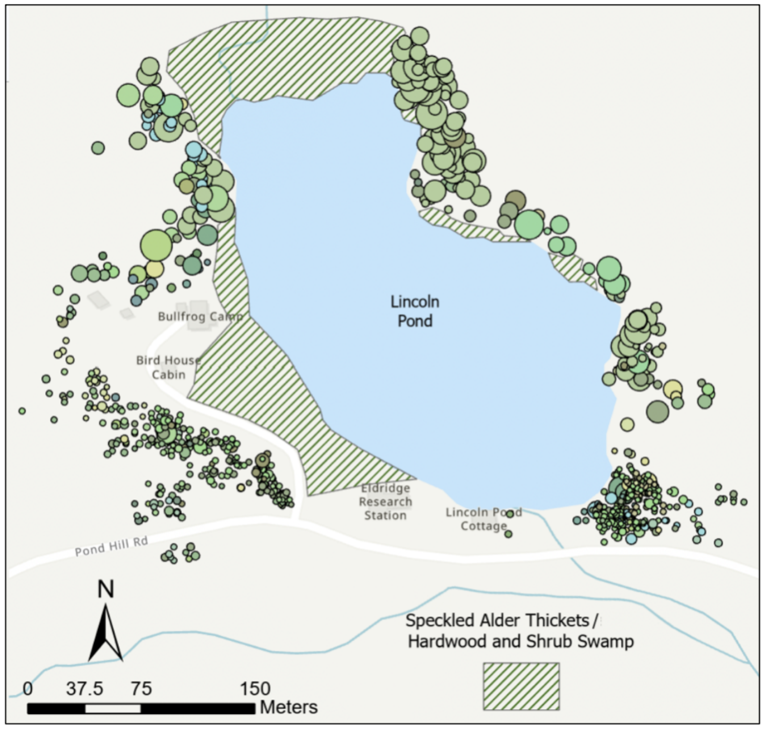

Figure A1. Map of trees fully felled (n=627) and gnawed (n=208) by beavers surrounding Lincoln Pond, summer 2024. Dot color corresponds to tree species (n=22) and dot size corresponds to tree size (Campbell & Velicer, 2024).

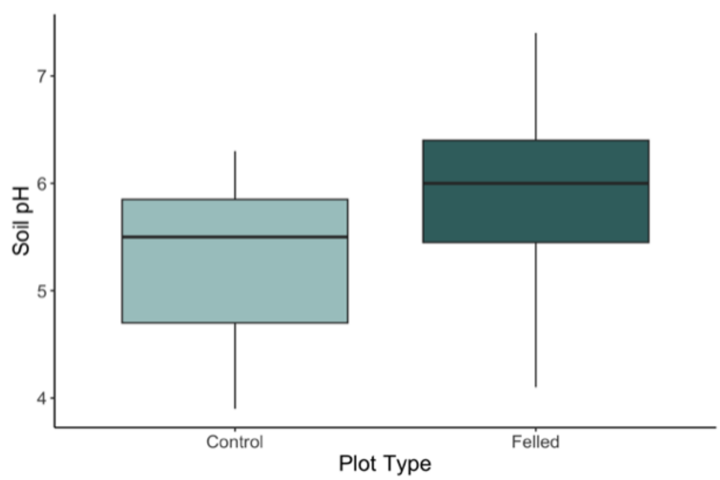

Figure A2. Boxplot of soil pH between control and felled plots ($p < 0.05$). Thick black line indicates the median value. Boxes represent the 1st to 3rd quartile range. Whiskers extend to the most extreme values within 1.5 times the interquartile range. Outliers represented by black dots.