Individual and interactive effects of white-tailed deer and woody invasive plants on native tree seedlings in an early successional forest

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Abstract

Regeneration failure is a pressing issue endangering the health of many forests in North America. Invasive plants and white-tailed deer (*Odocoileus virginianus*) contribute to regeneration failure by impacting tree seedling growth and survival. This study investigated the individual and interactive effects of deer and woody invasive plants on seedlings in an early successional forest. In a stand of *Juniperus virginiana* near Oxford, OH, we initiated a factorial experiment with each combination of deer access/exclosure and invasive woody plants removed/not removed. In June 2022, we applied treatments by placing deer exclosures, 2.13m tall fences using four trees as corner posts, and by removing all woody invasive shrubs and vines. We planted native tree seedlings and monitored natural regeneration (tree seedlings 0.3–2 m) in each plot. Change in height for planted seedlings was significantly impacted by deer and the interaction: excluding deer resulted in less height loss and this effect was greater where invasives were present. Change in height of natural regeneration was significantly affected by deer; seedlings grew taller in deer exclosures. The total number of seedlings recruiting per plot did not differ among treatments. However, the number of recruits excluding *F. americana* seedlings showed a marginally significant interaction: number of recruits was greatest where deer and invasives were removed. Overall, deer had a greater impact than invasives on natural regeneration and planted seedling. These small exclosures required minimal cost, installation time, and maintenance. These findings lead us to recommend this method to land managers.

Introduction

Many stressors threaten the composition, structure, and long-term health of forests in eastern North America and elsewhere (Dey et al. 2019). One of the greatest threats to forest health, regeneration failure, is a widespread issue throughout North America (Dey et al. 2019, Miller and McGill 2019, Miller et al. 2023). Canopy trees provide structure, habitat, and food sources, so their lack of regeneration poses ecological catastrophe. Tree regeneration is also crucial to combating global climate change, as trees capture and sequester vast amounts of carbon. One factor driving regeneration failure in the deciduous forests of eastern North America is high density of white-tailed deer (*Odocoileus virginianus)* (hereafter 'deer'). In many areas, densities are much greater than pre-European settlement (Rooney 2001). Deer impact tree establishment and persistence through their browsing patterns, selectively feeding upon seedlings of palatable woody species (Rooney and Waller 2003, Cote et al. 2004, Bradshaw and Waller 2016). This selective browsing results in widespread shifts in composition from palatable to unpalatable plant species (Bradshaw and Waller 2016).

Invasive non-native plant species also contribute to regeneration failure, as these have increased in eastern forests since the early to mid-1800s (Webster et al 2006). Certain invasive species suppress the growth of tree seedlings both directly and indirectly (Boyce 2009). Forests invaded by the non-native shrub, *Lonicera maackii*, have seedling and sapling layers with lower densities and species richness than uninvaded forests (Hartman and McCarthy 2008). Stinson et al. (2006) found *Alliaria petiolata* suppressed growth of native tree seedlings by disrupting mutualisms between the native trees and arbuscular mycorrhizae. Younger forests are generally more susceptible to invasion (Mosher et al. 2008, Kuhman et al. 2010) and have been shown to have significantly more invasive species than older forests (Trammell et al. 2020), likely due to greater light availability (Davis et al. 2000, Trammell et al. 2020).

While the individual negative effects of abundant deer and invasive plant species on native tree regeneration are well known, their interactive effects are not as well understood. Owings et al. (2017) found that both deer and *L. maackii* individually had negative impacts on the survival of underplanted seedlings, but they did not find many interactive effects. Donoso et al. (2024) found that deer, but not *L. maackii*, reduced density and species richness of tree seedlings. However, a literature review identified several cases of synergistic effects of deer and invasive plants: removal of both enhanced native plant responses, but there was no benefit to only removing invasives or only excluding deer (Gorchov et al. 2021). Removal of just invasive shrubs increases deer browse on some native tree seedlings (Peebles-Spencer and Gorchov 2017) and may trigger invasion of other plants (Kuebbing and Nuñez 2014). Conversely, deer feed on some invasives such as *L. maackii*, so their exclusion increases the negative impacts of these species (Peebles-Spencer et al. 2018). Indeed, Jenkins and Howard

(2021) found that reducing deer populations increased the density of nonnative (as well as native) woody plants due to reduced browse pressure.

Artificial regeneration methods such as enrichment planting may be necessary to restore degraded forests and promote the establishment of desired tree species (Dey et al. 2012). However, many enrichment plantings and forest restoration projects have failed due to a variety of ecological factors, including deer browse and competition with invasive plant species (Löf et al. 2019, Thyroff et al. 2019, Davis and Pinto 2021). Measures can be taken to combat these ecological factors (e.g. fencing or caging of planted seedlings and removal of invasive plants), but the need for both is not as well understood and may not be necessary (Löf et al. 2019, Davis and Pinto 2021).

In this study, we aim to understand the impact of deer and invasive plant species on tree regeneration in an early successional forest. We hypothesize that the exclusion of deer and the removal of invasive woody species will yield the greatest growth and survival of tree seedlings, while the removal of just deer will have a smaller positive effect on the seedlings. We also aim to assess the practicality and cost of creating small exclosures that use large trees as the corner posts. This information can be utilized by land managers to promote tree establishment and persistence in early successional forests, by modifying the management of both invasive plants and deer.

Materials and Methods

Study site

This study was conducted in an early successional forest in the Bachelor Preserve, in Miami University's Natural Areas system in Oxford, Ohio, USA (39° 31 '13.6"N 84° 42' 14.9"W). This area was livestock pasture until about 1950 and began transitioning to forest around 1975 (Lash 2018). Soil type ranged from silt loam to clay loam and silty clay loam. Average pH of the soil samples was 6.5 and organic matter ranged from 2.89–4.82% (Hay 2023). The study site is a stand of early successional *Juniperus virginiana* forest with only a few other species represented in the canopy, including *Maclura pomifera, Fagus grandifolia*, and *Juglans nigra* (Hay 2023). The understory tree (2.5–5 cm diameter at breast height (DBH) density was 225/ha, also mainly (78%) composed of *J. virginiana*, while the sapling (2.5–5 cm DBH) layer was almost nonexistent (50 trees/ha) (Hay 2023). Seedling (0.3–1.5 m) density was 12,000 stems/ha, but 96% are *Fraxinus* spp. (Hay 2023), which will not grow beyond 2.5 cm dbh due to Emerald Ash Borer (Herms et al. 2010).

The site was heavily invaded (3.23 m^2/ha) by non-native shrubs, particularly *L. maackii* (1.23 m^2/ha) and *Ligustrum obtusifolium* (0.75 m^2/ha), and the invasive vine *Celastrus orbiculatus* (0.38 m^2/ha) (Hay 2023). In 2014, deer density in Bachelor Preserve was estimated at 13 deer/km^2 in summer and 13.7 deer/km^2 in winter (Barrett 2014). Density was later measured as 18.2 deer/km^2 in spring 2017 and 9.5 deer/km^2 in summer 2017 (Peterson 2018). Archery-based deer management was initiated in winter 2022/23, and in summer 2023 density was 4.4–7.5 deer/km^2 (Cooper 2024). We note that these estimates were for the entire Bachelor Preserve, not the smaller, earlier successional stand used in this study. Densities greater than 8 deer/km^2 have been shown to cause dramatic shifts in vegetation (Horsley et al. 2003). Similarly, Tilghman (1989) suggested maintaining deer populations at 7 deer/km^2 to ensure tree regeneration.

To examine the individual and interactive effects of deer and invasive plants, we used a factorial experimental design with 10 plots of each combination of deer exclosure/access and invasive woody plants removed/not removed, for a total of 40 plots. Plots were randomly assigned to treatments and treatments were applied in June 2022. Plots were created so that four trees > 10 cm dbh served as the corners of each plot, resulting in plots approximately 3.5m x 3.5m. No plot had a side less than 2m in length. Plots were ≥ 20 m from trails and ≥ 8 m from one another. Plot locations were selected to avoid inclusion of any tree > 20 cm dbh.

Exclosure plots had fences constructed around them, with the four corner trees serving as the fence posts. The exclosures were constructed by combining 1.22 m and 0.91 m tall 20-gauge galvanized steel poultry wire with 25.4 mm mesh to create

2.13 m tall fences (Fig. 1), within the height range recommended to prevent deer from jumping over the fence (Curtis et al. 1994, Redick and Jacobs 2020). This material was selected due to its relatively low cost and maintenance as well as its high efficacy (VerCauteren et al. 2006, Redick and Jacobs 2020). Redick and Jacobs (2020) found that wire and mesh fencing were both more effective at reducing browse than other materials, including electric fences. Flagging was applied to the fences to enhance visibility and deter deer from running into and potentially breaking the fence (Redick and Jacobs 2020). Construction of all 20 fences took three people approximately 25–30 hours total, so a team of three could be expected to construct about six fences per 8-hour day. Fences were checked monthly during the summers and after major storms in other seasons to check for damage and repair when necessary.

Plots designated for invasive removal had all woody invasive shrubs and vines removed via cutting and stump application of 41% glyphosate herbicide (Compare-N-Save Grass and Weed Killer 41% Glyphosate Concentrate), which is appropriate for all invasive shrub and tree species observed at this site (NRCS n.d., USFS n.d.). Regardless of the dimensions of the plot, all invasives were removed from a uniform 3.5 m x 3.5 m square. Cut stems were placed a short distance outside plots. Invasive removal plots were re-treated in September 2022 when all invasive resprouts were cut and treated with herbicide. In June 2023, all invasive resprouts greater than 0.3 m in height were identified, measured, and treated. However, there was minimal resprouting, with an average of 3.5 stems per plot. *Celastrus orbiculatus* accounted for the majority (71.4%) of these resprouts requiring treatment.

Estimates of canopy cover were made with the 'modified canopy cover index' of the mobile app GLAMA (Gap Light Analysis Mobile Application) as recommended by Tichý (2016). The GLAMA program estimates canopy cover from hemispherical photographs taken on an Android phone. Two photographs were taken from the center of each plot, one 0.3m and one 2m above the ground. The 0.3m photo is used to quantify the effects of deer and invasive treatments on light availability at the seedling level, while the 2m photos provided an estimate of tree canopy cover of the site. To ensure photos were taken completely horizontal to the ground, the Samsung phone was placed on a clipboard with an Apple iPhone. The iPhone application called "Measure" was used because it has a "Level" function that tells if an object is level. All photos were taken on the same day in August 2022, and analyzed using the recommended settings on the app.

Tree species for underplanting

Successful artificial regeneration requires selecting species that can persist in the future climate of the site (Löf et al. 2019, Davis and Pinto 2021). Seedlings typically escape deer browse and shrub effects as they grow > 2m (Walters et al. 2020). Therefore, tree species were selected based on two criteria: fast growth and ability to withstand the future climate. To determine species that are relatively fast-growing, we used Burns and Honkala (1990). To determine which species could persist in future climate conditions, we used the 1x1 degree grid summary (N39 E84) from the USFS Climate Change Atlas (USFS 2018). We restricted the list of fast-growing species to those that had ratings of fair or better in the capabil45 category. This is an estimate of the capability of the species to cope with the changing climate at RCP 4.5 (moderate emissions scenario) and is based on its current abundance in the area, change class (potential change in habitat suitability by 2100), and adaptability (based on disturbance and biological characteristics of the species) (USFS 2018). Northern Red Oak (*Quercus rubra*), Yellow-poplar (*Liriodendron tulipifera*), Black Walnut (*Juglans nigra*), and Bitternut Hickory (*Carya cordiformis*) were planted in 2022, and Sweetgum (*Liquidambar styraciflua*) was planted in 2024. Few *C. cordiformis* established and these are excluded from analysis. *Juglans nigra* seedlings were grown from collected seeds while 50 bare root seedlings of the other tree species were purchased from Cold Stream Farm (Free Soil, MI, USA). *Quercus rubra* and *L. tulipifera* seedlings were 0.6–0.9 m in height. *Liquidambar styraciflua* seedlings were 0.7–1.1 m in height. *Juglans nigra* seedlings were 0.1–0.4 m in height.

One seedling of each species was planted in each plot in June 2022; seedlings were planted ≥ 1 m apart. Seedlings were checked approximately 5 days after planting and any uprooted seedlings were replanted. Due to uprooting of planted seedlings, trail cameras were placed in four of the plots to determine the cause of uprooting. Several images and videos showed racoons digging in the plots, so they were likely responsible for uprooting the seedlings. The extra *L. tulipifera* and *Q. rubra* seedlings were planted in selected plots.

Due to low survival of planted seedlings (Hay 2023), additional seedlings were planted in October 2022 (*L. tulipifera*), May 2023 (*J. nigra*), and November 2024 (*Liquidambar styraciflua*). *J. nigra* were grown from seed as above, and the other species planted as bare-root seedlings purchased from Cold Stream Farm. To prevent uprooting by raccoons, cages were placed around the seedlings. Cages were 20-gauge galvanized steel poultry wire with 25.4 mm mesh and were approximately 0.5 m tall with a diameter of 0.2 m. Cages were anchored into the ground using four landscape staples and were removed from seedlings 3–4 weeks after planting.

Natural Regeneration

In June 2022, natural regeneration in the plots was censused by tagging, identifying, and measuring the height and basal diameter of each tree seedling between 0.3 m and 2.5 m in height. We tagged, identified, and measured new recruitment (i.e. any untagged seedlings that had passed the 0.3m threshold) in May 2023, June 2024, and June 2025.

Measurement of Tree Seedling Responses

Height and basal diameter of each planted tree seedling was measured at planting and of each natural regeneration stem when first tagged. Survival and height were recorded monthly through October 2022. Height and survival of all seedlings were recorded in June 2023, May 2024, and June 2025.

Data analysis

All analyses were done using Rstudio 2025.05.1 + 513.

To test the effects of deer, invasive plants, and their interaction on modified canopy cover at 0.3m and 2m height, we used two-way analysis of variance (ANOVA, using aov in R). We confirmed the appropriateness of this ANOVA and each other linear model (below) by testing normality of residuals using the Shapiro-Wilks test.

To test the effects of deer, invasive plants, and their interaction on survival of each species of planted seedlings, we used a binomial regression with glm. To test the effects of deer, invasive plants, and their interaction on change in height from time of planting to 2025 for planted seedlings, we used two-way generalized linear models (GLMs, using glm in R) with species (*Q. rubra, L. styraciflua, J. nigra*, and *L. tulipifera*) as a fixed effect.

To test the effects of deer, invasive plants, and their interaction on plot-level survival of natural regeneration (percent of seedlings tagged in 2022 that were alive in 2025), we used ANOVA on ranks (ARTool package in R), because residuals from aov failed the Shapiro-Wilks test for normality. To test the effects of deer, invasive plants, and their interaction on height change from 2022 to 2025 of all surviving natural regeneration stems, we used a two-way mixed effects model (lme, using nlme in R) with Plot as a random factor. We also singled out the seedling with the greatest height gain (from 2022 to 2025) in each plot, and tested the effects of deer, invasive plants, and their interaction on height change using two-way ANOVA with aov.

To test the effects of deer, invasive plants, and their interaction on recruitment (number of recruits per plot), we used Poisson regression with a log link function in glm. After analyzing all recruitment data together, we excluded *F. americana* seedlings, since they will not grow beyond 2.5 cm dbh due to Emerald Ash Borer (Herms et al. 2010). To test the effects of deer, invasive plants, and their interaction on the number of non-*Fraxinus* recruits per plot, we used Poisson regression with glm.

To test the effects of deer, invasive plants, and their interaction on plot-level seedling species richness (number of tree species with at least 1 stem 0.3–1.5 m in 2025), we used Poisson regression using glm.

Results

Canopy Cover

Average canopy cover across plots at 2 m was 78.4%, with no effect of deer or invasives, as well as no interaction (Table 1). However, at 0.3 m above ground level, invasive removal resulted in significantly lower canopy cover ($p = 0.014$). Average canopy cover with invasives present was 80.6%, while average canopy cover without invasives was 76.9% (Fig. 2).

Table 1
Statistics (F, p) for two-way analyses of variance (ANOVAs) of canopy cover and height change of natural regeneration. Bold denotes statistical significance. Max. height change is the change in height, from 2022 to 2025, of the natural regeneration seedling with the greatest growth in each plot. Degrees of freedom for F were 1, 36 for canopy cover and 1, 35 for Max. height change (1 plot had no natural regeneration).

	Deer treatment		**Invasive treatment**		**Interaction**	
Response	F	p	F	p	F	p
Modified canopy cover, 2.0 m	0.010	0.921	0.261	0.613	0.780	0.383
Modified canopy cover, 0.3 m	0.204	0.655	6.758	**0.014**	0.445	0.509
Max. height change	6.352	**0.017**	0.259	0.614	0.393	0.535

Planted Seedlings

Survival of planted seedlings was not significantly affected by deer, invasives, or their interaction This was true of each species of planted seedling (*Q. rubra, L. styraciflua, J. nigra*, and *L. tulipifera)* (Table 2).

Table 2
Binomial logistic regression statistics for survival of planted seedlings to June 2025. One seedling of each species was planted in each plot (n = 40) with replacement of some seedlings that died within the first week.

Species	**Month planted**	**# alive June 2025**	**Deer**		**Invasives**		**Interaction**	
			z	p	z	p	z	p
Quercus rubra	June 2022	4	0.003	0.998	0.000	1.000	0.000	1.000
Juglans nigra	June 2022, May 2023	12	1.001	0.317	0.128	0.898	0.680	0.497
Liriodendron tulipifera	June 2022, October 2022	7	0.187	0.852	-0.321	0.748	0.274	0.784
Liquidambar styraciflua	November 2024	26	-0.905	0.365	0.514	0.608	-0.096	0.923

Change in height from 2022–2025 for planted seedlings was significantly impacted by deer ($p < 0.0001$) and the interaction of deer and invasives ($p = 0.042$) (Table 3, Fig. 3). Excluding deer resulted in less height loss in planted seedlings. This effect of deer exclosure was greater where invasives were present. Change in height was also different across species ($p < 0.0001$).

Natural Regeneration

Percent survival of natural regeneration from 2022–2025 tended to be greater where invasive plants were present ($p = 0.075$) but was not affected by deer exclusion (Table 3, Fig. 4). Change in height of natural regeneration was significantly affected by deer ($p = 0.004$), but not invasives or the interaction (Table 3). Seedlings grew taller where deer were excluded (Fig. 5). For the seedling in each plot with the greatest height growth, change in height was significantly affected by deer ($p = 0.017$), but not invasives or the interaction (Table 2, Fig. 6). Where deer were excluded, seedlings grew on average 7.7 cm (deer excluded, invasives present) to 12 cm (deer excluded, invasives removed) centimeters taller than seedlings in deer access plots.

Table 3
Statistics (F, p) for two-way generalized linear model (GLM) for change in height for planted seedlings, linear mixed effects model (lme) for height change for natural regeneration, and analysis of variance (ANOVA) on ranks for survival of natural regeneration. All significant values are bolded ($p \leq 0.05$)

		Deer treatment		Invasive treatment		Interaction		Species	
Statistical test	**Response**	F	p	F	p	F	p	F	p
Two-way GLMs	Change in ht, planted seedlings	$F_{1,50}=23.459$	**< 0.001**	$F_{1,49}=0.432$	0.515	$F_{1,44}=4.365$	**0.043**	$F_{4,45}=22.212$	**< 0.001**
lme	Ht change all natural regen	$F_{1,34}=9.61$	**0.004**	$F_{1,34}=1.879$	0.179	$F_{1,34}=0.158$	0.693	n/a	n/a
ANOVA on ranks	Survival, natural regen	$F_{1,35}=1.533$	0.224	$F_{1,35}=3.356$	*0.075*	$F_{1,35}=0.247$	0.622	n/a	n/a

The number of all recruits per plot was not affected by deer, invasive plants, or the interaction (Table 4). However, when *F. americana* seedlings were removed from analysis, the number of recruits showed a marginally significant interaction ($p = 0.066$): where deer were excluded and invasives removed, the average number of recruits was greatest (Table 4, Fig. 7). Species richness of seedlings per plot was not significantly affected by deer, invasives, or their interaction (Table 4), but richness was slightly greater where both deer and invasives were removed (2.6 seedling species per plot compared to 1.8 where deer only were excluded, 1.6 where invasives only were removed, and 1.9 in control plots).

Table 4
Statistics (z, p for Poisson regressions (using GLM) for per plot numbers of tree seedling recruits, number of seedling recruits excluding *F. americana*, and species richness of tree seedlings

	Deer treatment		Invasive treatment		Interaction	
Response	z	p	z	p	z	p
All recruitment	1.235	0.217	0.919	0.358	1.307	0.191
non-FRAM recruitment	0.242	0.809	-0.533	0.594	1.835	*0.066*
Species richness	-0.143	0.887	-0.477	0.634	1.150	0.250

Discussion

Planted Seedlings

Mortality of planted seedlings was high due to uprooting by raccoons (for seedlings planted in 2022, discussed later) and transplant shock of bare root seedlings *(J. nigra*, the only species not planted as bare root nursery stock, had the highest survival).

Deer access resulted in seedlings having greater decreases in height over time, likely due to browse of apical shoots. Other studies have similarly found deer access to decrease growth of planted seedlings (Owings et al. 2017, Truax et al. 2018, Redick et al. 2020). Removal of woody invasives reduced growth in exclosures, but mitigated height loss in deer access plots, contrary to previous studies that found invasives facilitate seedling growth under high deer pressure (Peebles-Spencer and Gorchov 2017).

Although we selected relatively fast-growing species, none of our planted seedlings surpassed the 2m height threshold by the end of the study;the tallest seedling in 2025 was a 1.13 m *L. styraciflua*). Seedlings will continue to be monitored: if they grow 8 cm per year (largest *L. styraciflua* height increase seen in this study) in deer exclosures, the tallest will reach 2m in about 12 years.

Natural regeneration and recruitment

The greater height growth of natural regeneration stems where deer were excluded is attributable to the absence of browse. Many seedlings in deer access plots had apical browse damage, often with multiple browse events over the 3-year study.

Recruitment of native seedlings excluding *Fraxinus* spp. was greater where both deer and invasives were removed, although only marginally. This indicates that both exclusion of deer and invasive removal are important for recruitment. Other studies have reported correlations between density of natural regeneration (seedlings and saplings) and deer browse impacts/deer density (Russell et al. 2017, Miller and McGill 2019, Miller et al. 2023). However, deer also browse on invasive plants (Peebles-Spencer et al. 2018), so deer exclosure only could result in increased density of invasive plants (Jenkins and Howard 2021), lowering natural regeneration if invasive plants are not also removed.

We investigated recruitment of seedlings other than *Fraxinus* spp. because *Fraxinus* will not grow beyond 2.5 cm dbh due to the Emerald Ash Borer (*Agrilus planipennis*) (Herms et al. 2010). The scarcity of species other than *Fraxinus* spp. in the seedling layer therefore poses a serious threat to the forest health. Our findings that non-*Fraxinus* recruitment, and species richness of recruitment, tended to be greatest where deer were excluded and invasive woody plants removed suggest management of both deer and invasives is necessary to overcome regeneration failure in these sorts of early successional stands. The low diversity in naturally occurring seedlings may be due to preferential browsing by deer. Selective browsing by deer often results in species composition shifts from preferred to non-preferred species, where preferred species can be virtually eliminated from the seedling layer (Rooney and Waller 2003, Bradshaw and Waller 2016, Cote et al. 2004, Miller and McGill 2019).

Indeed, changes in the naturally occurring vegetation (e.g. changes in species composition) may need multiple years to manifest. The impacts of deer exclosure and/or reduction of deer densities on native vegetation often take many years to manifest due to legacy effects of deer (Tanentzap et al. 2012, Nuttle et al. 2014). Similarly, invasive plants can have long lasting impacts after they have been removed, especially on the soil (e.g. nutrient cycling, microbial composition) (Afzal et al 2023, Corbin and D'Antonio 2012). While we did see differences of deer exclusion and invasive removal after just three years, the forest stand still lacks the diversity of seedlings and saplings that are needed for canopy replacement (Miller et al. 2023).

The positive, marginally significant, effect of invasives on survival of natural regeneration was unexpected because removal of invasive plants increased light availability (i.e. lower modified canopy cover) and invasive shrubs directly negatively affect forest regeneration by shading out native seedlings (Boyce 2009). Notably, average survival was lowest where deer had access and invasives were removed. Invasives may provide protection to native tree seedlings by decreasing deer access, as reported for *Acer saccharum* seedlings under the canopy of *L. maackii* (Peebles-Spencer and Gorchov 2017). This facilitation effect of invasive shrubs is expected only where deer browse impact is high (e.g., deer are overabundant).

Exclosures and cages

This was the first study to our knowledge that created small deer exclosures that utilized naturally occurring large trees as fence posts. An objective of our study was to determine the efficacy, practicality, and cost of this exclosure method. Land managers often have limited resources (money, time, labor); therefore, finding an inexpensive material and method for building exclosures is crucial.

The galvanized mesh fencing used to construct our exclosures was selected due to its relatively low cost and maintenance. To make 20 exclosures, we spent approximately $1,670, which equates to about $83.50 per exclosure. The galvanized mesh fencing we used cost about $4.60/m, less than many other types of fencing (VerCauteren et al. 2006). The prices listed in VerCauteren et al. (2006) also included cost of labor. We found our fencing technique to be easily achievable with only 2–3 people and estimated cost of labor to be approximately $1/m, putting the total price of construction at $5.60/m, still less than many other fencing types. Further, VerCauteren et al. (2006) found wire fencing to have relatively high efficacy (90–99%) and longevity (30–40 years) compared to other fencing types.

Over the course of three years, we needed to make 17 repairs on exclosures (so about 0.3 repairs per exclosure per year). Most commonly, one side sagged (e.g. due to branch fall) and the repair involved adding a top line of ¼-inch twisted nylon rope and securing the poultry wire to it with zip-ties. Had we added this top line to each exclosure, this would have added about 30 min. and $10 (for 16 m of rope). In addition, 12-inch heavy duty tent pegs were used to anchor the bottom of the poultry wire where needed on some exclosures, so we recommend planning for 4 pegs ($12) per exclosure.

Since these exclosures did not require much assembly time and cost and required minimal repairs over the course of three years, we recommend this method to land managers. These exclosures could be disassembled after tree seedlings have surpassed the 2 m “shrub-deer bottleneck” and reassembled in other locations, using trees as corners in the same stand, a type of ‘rotational fencing.’ Growth models indicated that rotational fencing for 10 years would be sufficient to restore densities of tall shrubs in deciduous woodland in Wyoming with high deer impacts (Merrill et al. 2003). Based on the 8 cm/year growth of our fastest growing species, we estimate 12 years would be needed before exclosures were moved.

However, survival was extremely low across all treatments for seedlings planted in June 2022. Most seedlings (51%) were uprooted 3–5 days after they were first planted, and trail cameras at different plots revealed that raccoons were uprooting the seedlings. This uprooting occurred even in fenced plots, revealing that exclosures did not keep out raccoons (and likely other small mammals). In contrast, survival of *L. styraciflua* seedlings planted in November 2024 with cages was much greater, with 65% surviving by June 2025 across treatments. The cages for the planted seedlings did not take much time to assemble (approximately 5 hours total for 40 cages), were made of leftover fencing material (meaning low cost), and were able to be reused in other plantings. Due to this, we recommend pairing the exclosures with protective cages or some other additional protective measures (e.g. stronger ground anchors to prevent access under fences) if planting seedlings. We found leaving cages in place for 3–4 weeks to be effective.

Conclusions

Overall, deer had the greatest impact on planted seedlings and affected natural regeneration. Deer exclosure increased recruitment of native seedlings, with greatest recruitment in deer and invasive removed plots, and increased height growth in natural regeneration. Removal of invasive shrubs and vines is not needed to enhance seedling growth and recruitment.

These small exclosures that utilized trees as corner posts required minimal cost, installation time, and maintenance. These findings, in conjunction with the positive effects on native tree seedlings, lead us to recommend this method to land managers. Our fencing method could also be easily used for rotational fencing. However, due to predation by small/medium mammals, we recommend these exclosures be paired with other protective measures (e.g. caging) when conducting underplanting. In comparable early-successional forests, we suggest that land managers focus efforts on alleviating deer pressure as opposed to focusing on invasive plant species removal. We expect that with a longer time frame, more pronounced treatment effects would arise. We also expect the facilitative effect of invasive shrubs protecting tree seedlings from deer browse may be erased with the alleviation of deer pressure, which may then warrant invasive removal.

Declarations

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Author Contribution

AH and DG wrote and reviewed the manuscript and completed all data analysis and creation of figures.

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Figures

Figure 1

One of the deer exclosure plots in an early successional stand in the Miami University Natural Areas near Oxford, Ohio. The exclosures were constructed by combining 1.22 m and 0.91 m tall 20-gauge galvanized steel poultry wire with 25.4 mm mesh to create 2.13 m tall fences. Four naturally occurring trees were used as the corner posts for each exclosure. Flagging was applied to the fences to enhance visibility and deter deer from running into the fence.

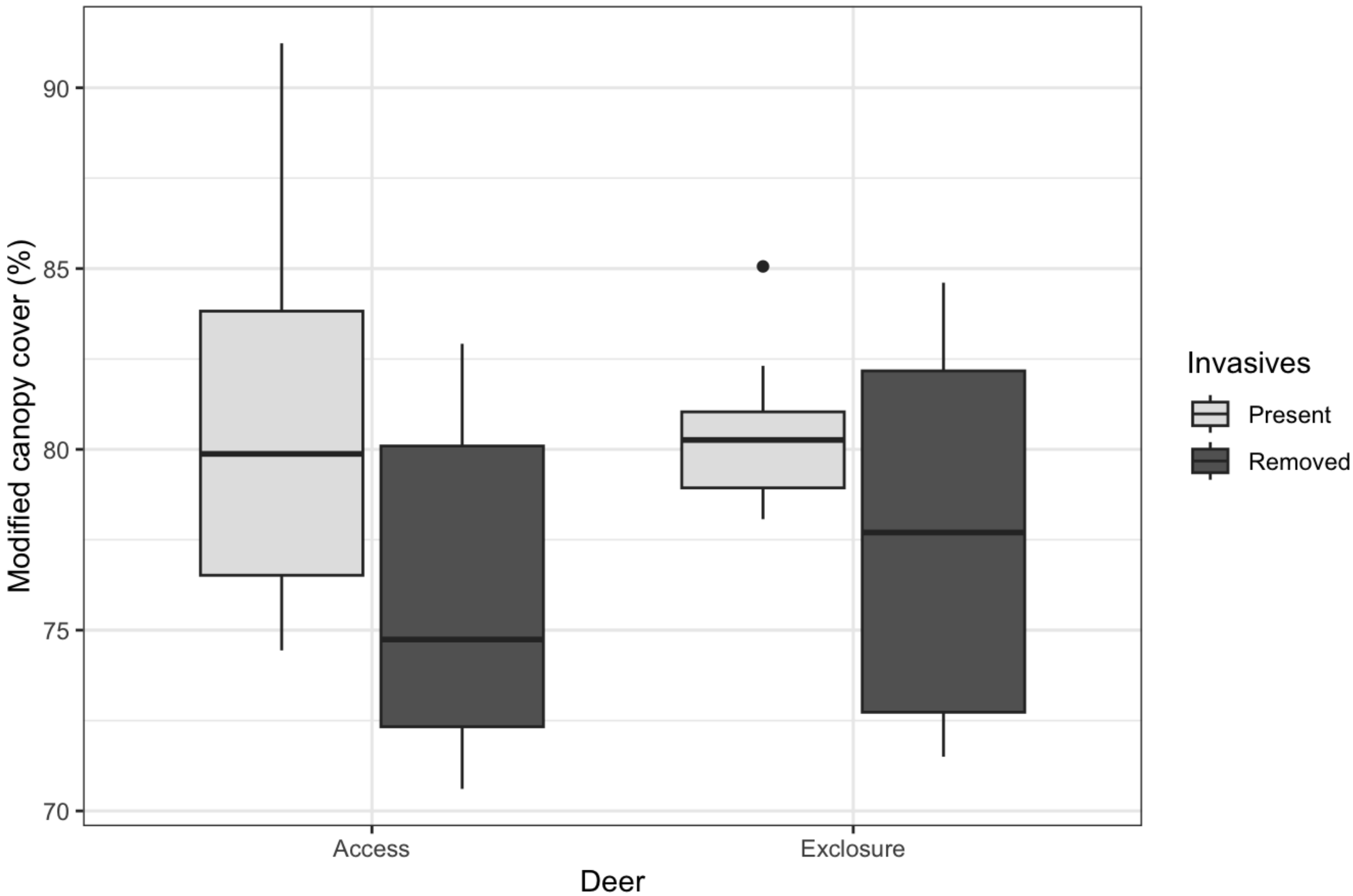

Figure 2

Boxplot of Modified Canopy Cover index values at 0.3 m by deer and invasive treatment. Canopy photographs were taken in the center of each plot at 0.3 m above ground and analyzed in the GLAMA app.

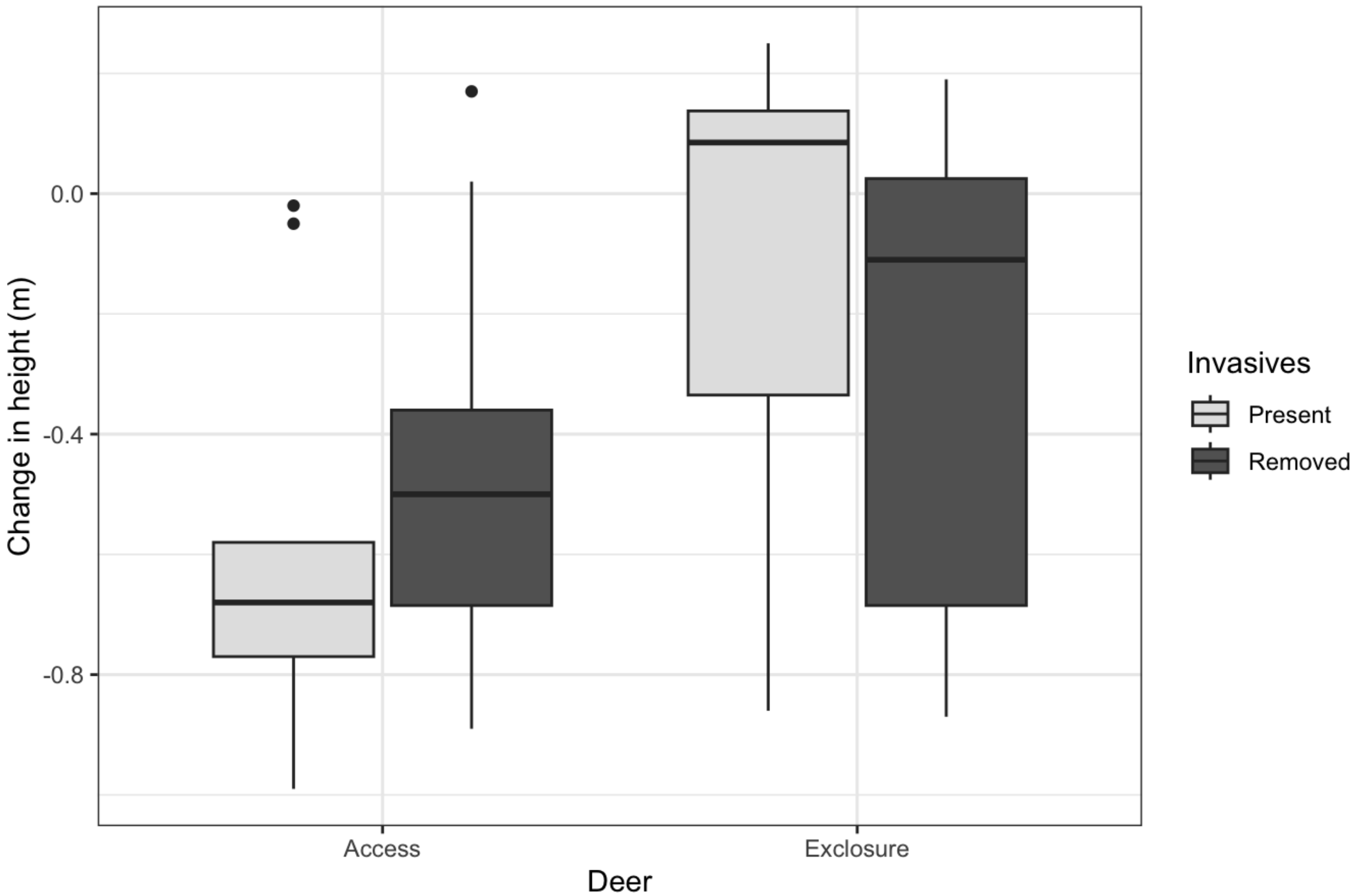

Figure 3

Boxplot of change in height for planted seedlings. Values are change in height from time of planting (Table 1) to June 2025.

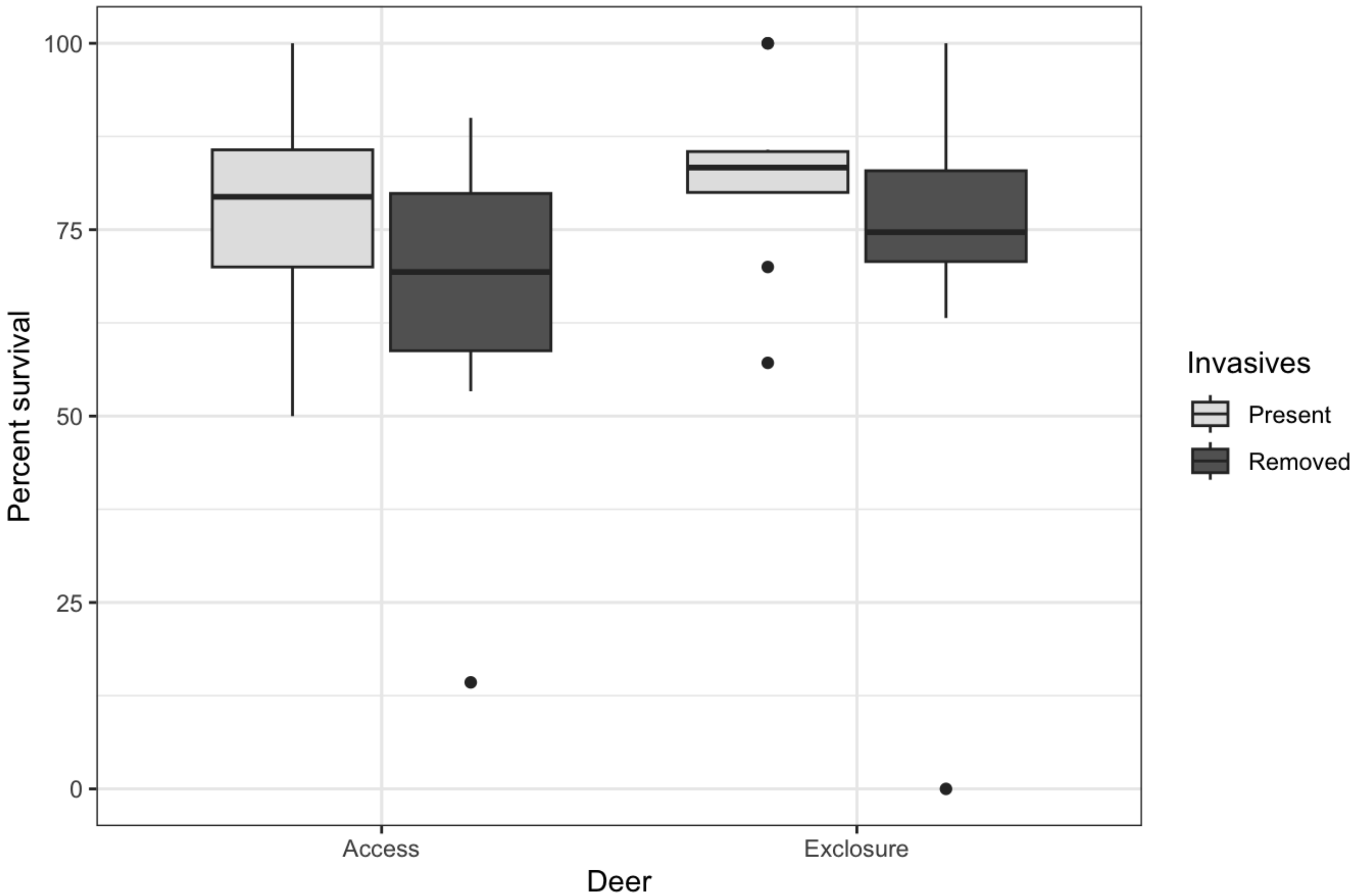

Figure 4

Boxplot of percent survival of all natural regeneration. Percent survival is the percent of naturally occurring seedlings tagged in June 2022 in a plot that were still living by June 2025.

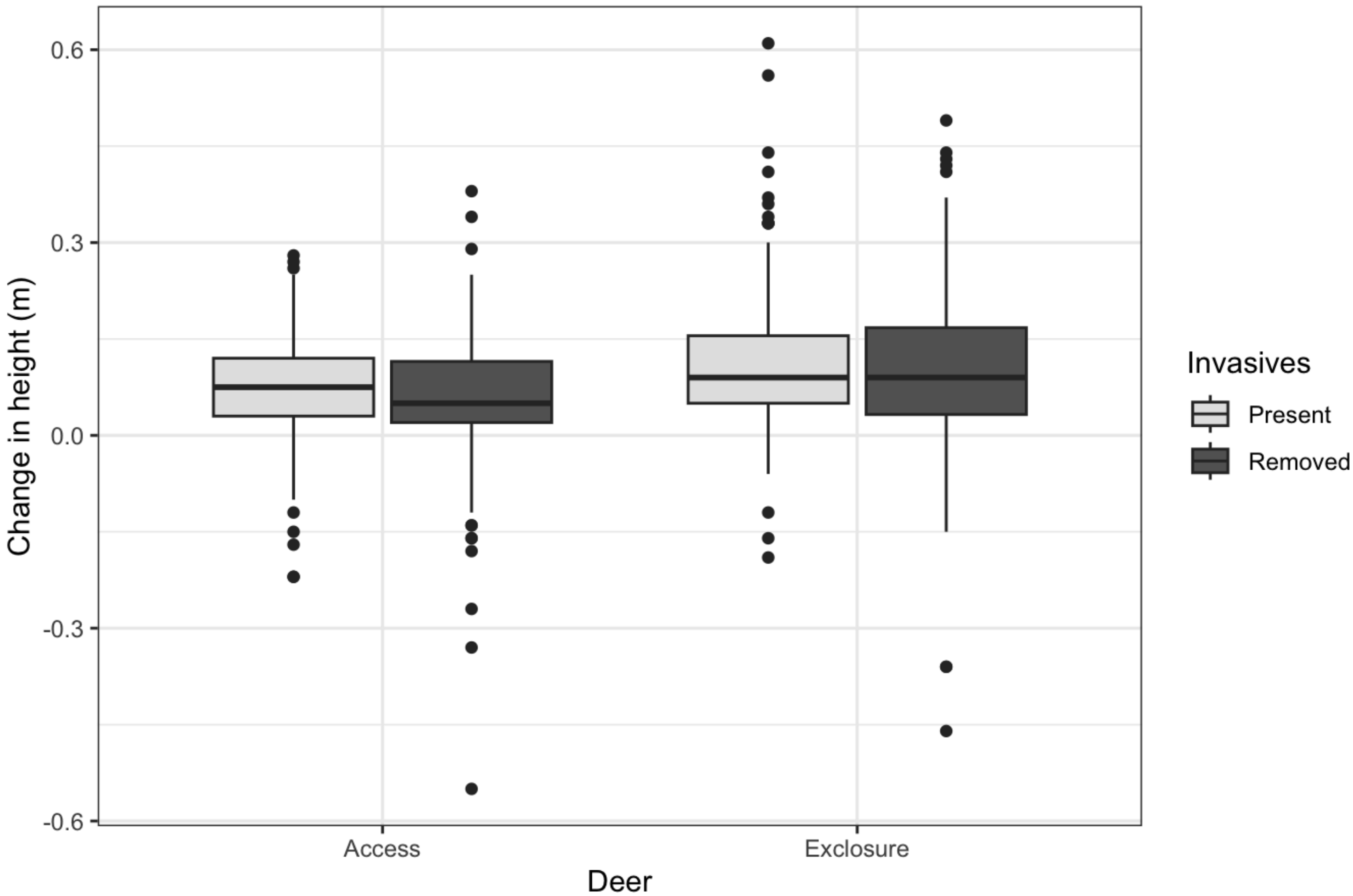

Figure 5

Boxplot of change in height of natural regeneration by deer and invasive treatment between June 2022 and June 2025. Heights analyzed for each native tree seedling 30 cm<ht<2.5m still alive in 2025.

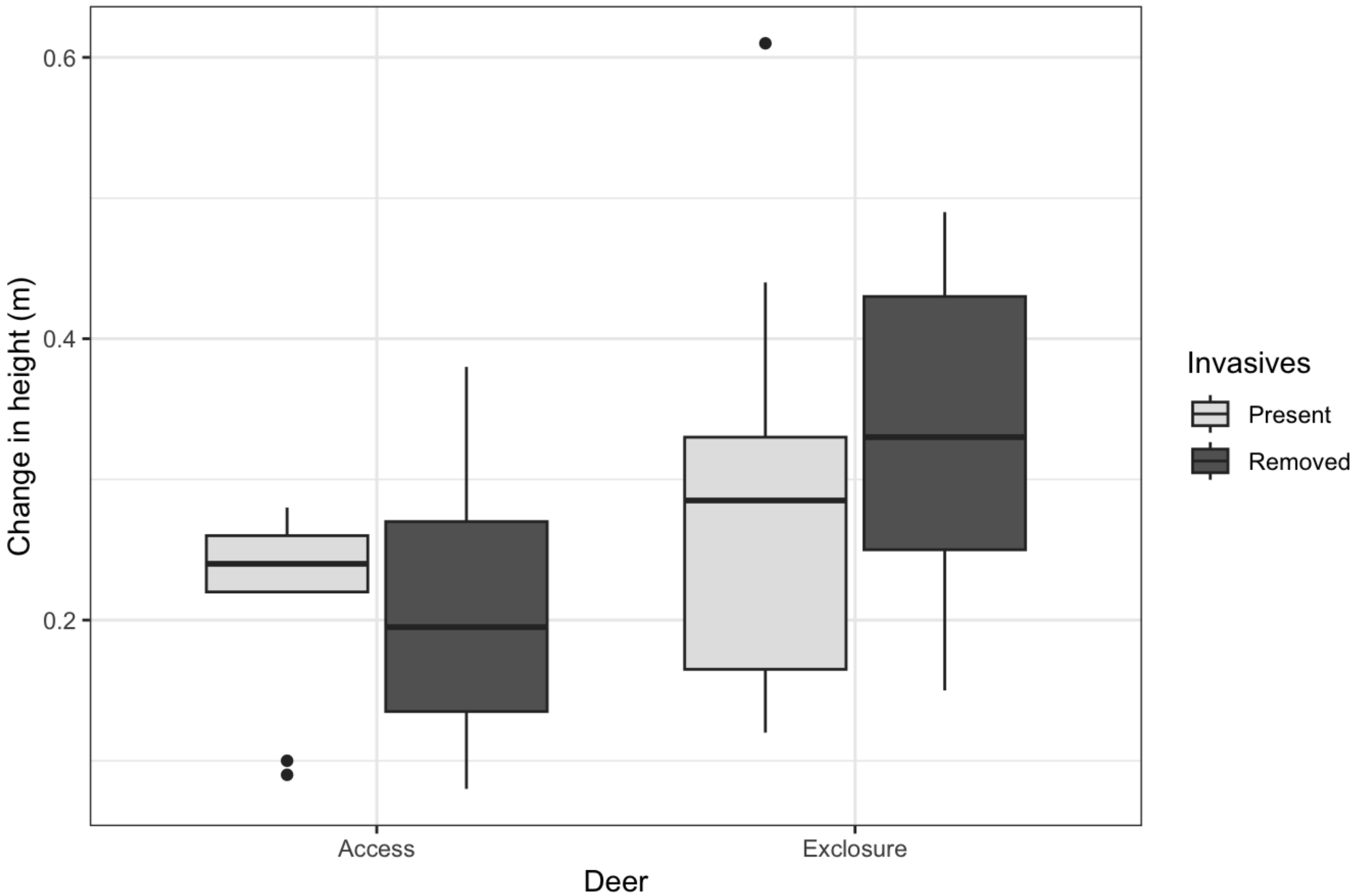

Figure 6

Boxplot of change in height (2022-2025) for the natural regeneration seedling in each plot with the greatest height growth.

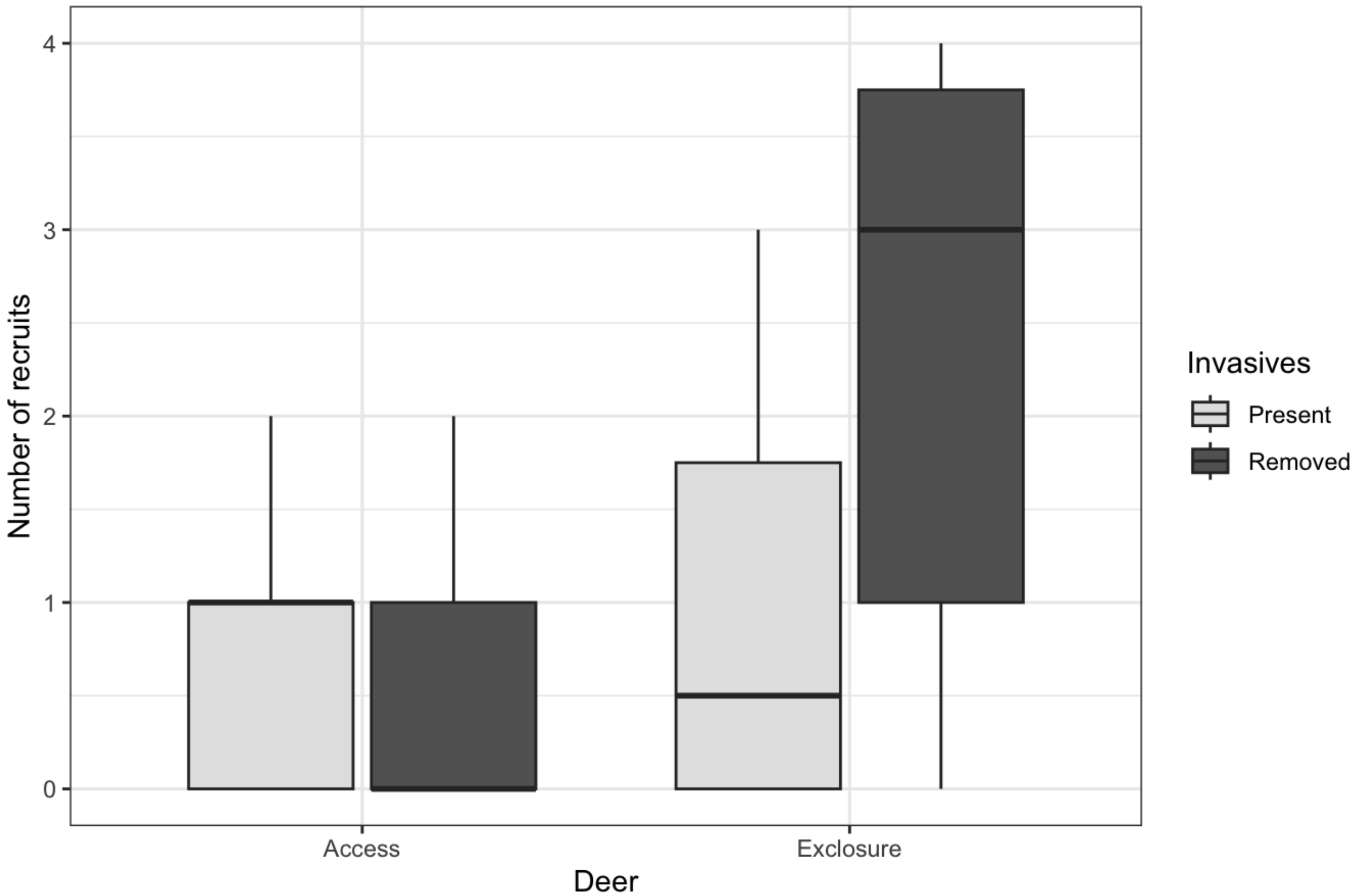

Figure 7

Boxplot of recruitment of native seedlings per plot by 2025, excluding *F. americana,* by deer and invasive treatments. New recruits were native seedlings that passed the 0.3m height threshold in each plot after June 2022.