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Common buckthorn (*Rhamnus cathartica*) invasion exacerbates white-tailed deer (*Odocoileus virginianus*) browsing on native woody plants

Research Article

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Abstract

Selective feeding by overabundant herbivores can considerably alter plant community composition and structure, often benefiting non-native species. White-tailed deer (*Odocoileus virginianus*) are a dominant herbivore in North America, known for their preference for native plants over unpalatable invasive species. Common buckthorn (*Rhamnus cathartica L.*), a widely invasive shrub, is largely avoided by deer, potentially facilitating its competitive advantage against native plants. This study investigates the interactive effects of *R. cathartica* invasion and deer browsing on native woody plants within a postindustrial urban forest undergoing restoration. Specifically, we employed both a long-term observational tree survey and an experimental shrub study to assess *R. cathartica* impacts on native trees and shrubs, and to investigate whether *R. cathartica* presence intensifies deer browsing. For the tree study, we surveyed 10 native tree species planted in areas with varying levels of *R. cathartica* invasion to assess tree health as a function of *R. cathartica* and canopy tree cover. For the shrub study, we examined deer and insect herbivory on five deer-resistant native shrubs with and without deer exclusion and *R. cathartica* removal. We found that increased *R. cathartica* cover correlated with reduced health in native tree species, a relationship not found between the trees and native canopy tree cover. We also found that all five planted native shrub species experienced considerable browsing, with deer and insect damage intensifying in the presence of *R. cathartica*. This study highlights the complex interplay between non-native plant invasions and native herbivore activity, demonstrating that *R. cathartica* indirectly facilitates increased deer herbivory on native species. These findings emphasize the need for integrated forest restoration strategies that address both invasive plant removal and herbivore management to support native species recovery.

Introduction

Large mammalian herbivores can drive landscape-level shifts in plant community composition and structure through selective feeding (Nomiya et al. 2003; Perrin et al. 2006; Vavra et al. 2007). By preferentially consuming palatable plant species while avoiding less preferred ones, herbivores may confer a competitive advantage to unpalatable species (Averill et al. 2018; Bergvall et al. 2006; Rossell et al. 2005). In much of North America, white-tailed deer (*Odocoileus virginianus*; hereafter "deer") are the dominant, often overabundant, wild herbivore (McCabe and McCabe 1997; Ramirez et al. 2018; VerCauteren 2003). Elevated deer populations can cause considerable ecological and economic damage, including impaired forest regeneration and reduced native plant diversity (Bradshaw and Waller 2016; Bressette et al. 2012; McShea 2012).

Deer herbivory and non-native plant invasion often co-occur and may interact to affect native plant communities (Averill et al. 2018; Eschtruth and Battles 2009; Kalisz et al. 2014). These interactions generally fall into two categories (Gorchov et al. 2021): (1) In most interactions, the combined negative impact of deer and invasive plants is equal to or less than the sum of their individual effects, often because both stressors act on similar ecological processes (Bourg et al. 2017; Haffey and Gorchov 2019; Waller and Maas 2013). (2) But sometimes, synergistic negative interactions occur when the presence of an unpalatable plant invader may displace deer browsing pressure onto more palatable native species, thereby exacerbating the deer herbivory (Haffey and Gorchov 2019; Kalisz et al. 2014).

Common buckthorn (*Rhamnus cathartica* L.) is an invasive non-native shrub that disrupts native plant communities with allelopathic chemicals and dense monotypic growth (Knight et al. 2007; Pinzone et al. 2018; Warren et al. 2017). Whereas deer sometimes preferentially browse on non-native plant species (Averill et al. 2016; Donoso et al. 2024; Rossell et al. 2007), they appear to avoid eating *R. cathartica* and are less populous in *R. cathartica*–invaded landscapes (Aday and Wyckoff 2010; Nitzsche et al. 2019; Vernon et al. 2014). The individual

Management Implications

The findings of this study underscore the need for integrated restoration strategies that simultaneously address invasive shrub removal and herbivore management. Common buckthorn *(Rhamnus cathartica* L.) not only suppresses native plant growth through direct competition but also indirectly amplifies herbivory by native deer and insects. Because *R. cathartica* is largely avoided by deer, its presence redirects browsing pressure onto co-occurring, more palatable native plants—intensifying damage and reducing survival even among species considered deer resistant. This synergistic interaction between *R. cathartica* invasion and white-tailed deer overabundance creates a feedback loop that can undermine native vegetation recovery and forest restoration efforts. For land managers, these results highlight that partial control of either stressor—*R. cathartica* or deer—is unlikely to yield long-term restoration success. Removal of *R. cathartica* alone may not reduce browsing impacts, whereas deer exclusion without invasive shrub control may still permit *R. cathartica* to competitively suppress native species. Instead, restoration success will depend on concurrent implementation of both invasive species removal and deer population management. Practitioners should also consider prioritizing the removal of *R. cathartica* in areas where native vegetation is already under deer pressure, as these locations may experience the most severe compounding effects.

negative effects of deer overabundance (Blossey et al. 2017; Cote et al. 2004) and *R. cathartica* invasion (Knight et al. 2007; Warren et al. 2017) on plant communities are well established, but their potential synergistic impact remains less understood.

We investigated how the presence of *R. cathartica* influenced deer browsing on native woody species in a postindustrial forest undergoing ecological restoration. Specifically, we examined the interactive effects of *R. cathartica* invasion and deer exclusion on the condition and herbivory of native saplings and shrubs. In addition, given that native-range herbivorous insects generally avoid consuming invaded-range *R. cathartica* (Grunzweig et al. 2015; Schuh and Larsen 2015; Tallamy and Shropshire 2009), we assessed insect herbivory as an independent indicator of herbivore pressure, as insect activity is not directly influenced by deer presence. We first conducted an observational survey of planted native tree saplings (hereafter the "tree survey") to evaluate their baseline condition in relation to *R. cathartica* and canopy tree cover. We then performed a manipulative experiment (hereafter the "shrub experiment") using deer exclosures and *R. cathartica* removal to test for interactive effects on herbivory and plant condition. We hypothesized that, if *R. cathartica* is unpalatable and displaces deer from itself toward neighboring native shrubs, its presence would redirect deer browsing pressure, thereby amplifying herbivory on native shrubs—a synergistic effect of *R. cathartica* and deer. Alternatively, if *R. cathartica* is equally palatable to deer or does not displace their browsing behavior (i.e., impacts are independent or merely additive), then herbivory levels should reflect the sum of individual effects, and deer exclusion would not alter herbivory levels across *R. cathartica* treatments.

Material and Methods

Study Site

The Tifft Nature Preserve (hereafter "Tifft") is a 107-ha urban nature preserve comprising woodlands, wetlands, and grasslands, administered by the Buffalo Society of Natural Sciences on the eastern shore of Lake Erie (42.84°N, 78.85°W). Historically, Tifft was a hub for railroad and barge shipping before being repurposed as an industrial and municipal dump. It was converted into a nature preserve in the early 1970s. Following abandonment, vegetation established in a soil layer consisting of thin humus over mineral soil mixed with industrial dredge, building debris and residential waste. Historic aerial photographs indicate that trees began colonizing Tifft in the 1950s. The dominant canopy species in the woodland areas is eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall), with some willow (*Salix* L.). The understory is primarily composed of *R. cathartica*, Japanese knotweed (*Polygonum cuspidatum* Siebold & Zucc.), and honeysuckle (*Lonicera* L.) with minimal natural regeneration of native woody species (Labatore et al. 2017). Deer are overabundant at the site and in the surrounding urban/suburban areas (Booth-Binczik and Hurst 2018; Spiering 2009). Although direct measurements of deer density at Tifft are unavailable, observations of single herds exceeding 30 individuals, along with extensive browsing and a near absence of tree regeneration, suggest that deer densities are well above natural levels for the region (Spiering 2009).

Tree Survey

Between 2010 and 2013, approximately 2,000 saplings from 31 species were planted across 40 ha of forested areas as part of the Tifft management plan (Spiering 2009). To mitigate losses from deer browsing, saplings (1- to 2.5-cm diameter at breast height, >1-m height) were protected with wooden and wire fencing or plastic tree tubes. With time, many of these protective measures failed, but some trees reached sufficient height to withstand browsing (Goetsch et al. 2011). *Rhamnus cathartica* was mechanically cleared before trees were planted but was not managed since then. In 2018, we haphazardly surveyed a subset ($n = 289$, ~23% of the 1,279 planted trees) of the 10 most common planted trees: red maple (*Acer rubrum* L.) ($n = 48$), silver maple (*Acer saccharinum* L.) ($n = 19$), shagbark hickory [*Carya ovata* (Mill.) K. Koch] ($n = 15$), hackberry (*Celtis occidentalis* L.) ($n = 18$), butternut (*Juglans cinerea* L.) ($n = 19$), *P. deltoides* ($n = 27$), sycamore (*Platanus occidentalis* L.) ($n = 59$), swamp white oak (*Quercus bicolor* Willd.) ($n = 36$), black willow (*Salix nigra* Marshall) ($n = 18$), and basswood (*Tilia americana* L.) ($n = 30$). Tree height was measured, and each tree was rated with an ordinal index of health (0 to 5) based on relative size, bark and wood condition, and growth form/sturdiness with 0 = dead, 1 = least healthy, 2 = less than average health, 3 = average, 4 = more than average, and 5 = most healthy. We also assessed *R. cathartica* cover (percent cover in a 1-m^2 circle surrounding the target tree) and non-*R. cathartica* canopy tree cover using a spherical densiometer.

Shrub Experiment

Following the approach of similar restoration studies (e.g., Wragg et al. 2021), we utilized existing management structures for this research. Two deer exclosures were available to examine deer impacts. The exclosures ("deer excluded") were in forested areas 1 km apart and enclosed by continuous 3-m-high fencing. The smaller exclosure ("buckthorn regrowth") covered 56 m^2, while the larger ("buckthorn removed") encompassed 15,330 m^2. No evidence indicated deer penetration into the exclosures during the experiment. The area immediately outside each exclosure, where deer were unrestricted and frequently observed, served as a control ("deer present").

For the buckthorn removed treatment, all *R. cathartica* plants were cut to the ground in the dormant season before the experiment. All brush was removed from within the planting area and at least 1 m from the perimeter of the plantings. The *R. cathartica* stumps were treated with the herbicide Pathfinder II™ (triclopyr ester; Paizo Inc., Redmond, WA, USA) at 100% concentration after being cut, and foliage from resprouts was sprayed with Garlon 3A™ (triclopyr amine salt; Dow AgroSciences LLC, Indianapolis, IN, USA) at 5% concentration during the following growing season. For the buckthorn regrowth treatment (small exclosure), *R. cathartica* dominated inside and outside the deer exclosure. To minimize immediate shading as a confounding variable, *R. cathartica* plants >1 m were cut (but not treated) immediately before the experiment, leaving plants of similar height (0.5 to 1 m) as the study shrubs.

In October 2018, we planted 20 individuals of five native woody species ($n = 100$ total) within each of the four treatment combinations ($n = 25$ plants per treatment: deer present/buckthorn regrowth, deer present/buckthorn removed, deer excluded/buckthorn regrowth, deer excluded/buckthorn removed). Plant spacing and arrangement were standardized across treatments, with clusters of five plants (one of each species) arranged in a quincunx formation, spaced 3.5 m apart (Figure 1). Each cluster was positioned at least 1 m from the exclosure fencing. Based on previous research and site observations, we selected shrub species moderately resistant to deer browsing (Fargione et al. 1999; Nitzsche et al. 2019; Sample et al. 2023) to increase the chance we would have measurable target plants through the end of monitoring. The native shrubs were elderberry [*Sambucus nigra* L. ssp. *canadensis* (L.) R. Bolli], winterberry [*Ilex verticillata* (L.) A. Gray], red-osier dogwood (*Cornus sericea* L.), buttonbush (*Celtis occidentalis* L.), and spicebush [*Lindera benzoin* (L.) Blume]. All plants were 0.5- to 1-m tall when planted.

We monitored herbivory damage on the plants in October 2018, May 2019, July 2019, and October 2019. Leaf/stem damage was visually estimated as damage classification bins: 0%, 20%, 40%, 60%, 80%, or 100% herbivory damage (100% = mortality). We categorize damage type as deer (jagged edges, tearing, height) or insect (holes, chewed edges, skeletonized leaves, tunnels).

Data Analysis

We analyzed the effects of *R. cathartica* cover (%) and canopy tree cover (%) on tree sapling health using a cumulative link mixed model (CLMM) implemented in the ORDINAL package in R (R Core Team 2025). To account for potential non-independence associated with planting effort and timing, we included planting date as a random effect. To assess variation in sapling health across species, we fit a second CLMM including species identity as a fixed effect, with planting date again treated as a random effect. When a categorical predictor, like species, is analyzed in a CLMM model, estimating all species would create multicollinearity, so we used a reference level for comparison. Because *A. saccharinum* exhibited the lowest average health rating, it was specified as the reference category. We evaluated the contribution of species identity to model fit using a likelihood ratio test comparing the full model (with species) with a reduced model excluding species.

For the shrub experiment, we evaluated the percentage of deer leaf/stem damage as a function of deer exclusion, *R. cathartica* removal and species identity using a Generalized linear mixed model (GLMM), assuming a beta error distribution. We used the beta distribution as it is well suited for modeling proportions bounded between 0 and 1. We also included a deer by *R. cathartica* interaction term to account for synergistic effects between deer exclusion and *R. cathartica* removal. We used the GLMMTMB package and fit the models using an analysis of deviance (ANODEV) approach. To account for repeated observations and clustered plantings, we included date and cluster as random effects. We also evaluated insect herbivory as a function of *R. cathartica* removal, deer exclusion, and species identity using a GLMM, assuming a beta error distribution and fit with an ANODEV approach. We included month and cluster as random effects.

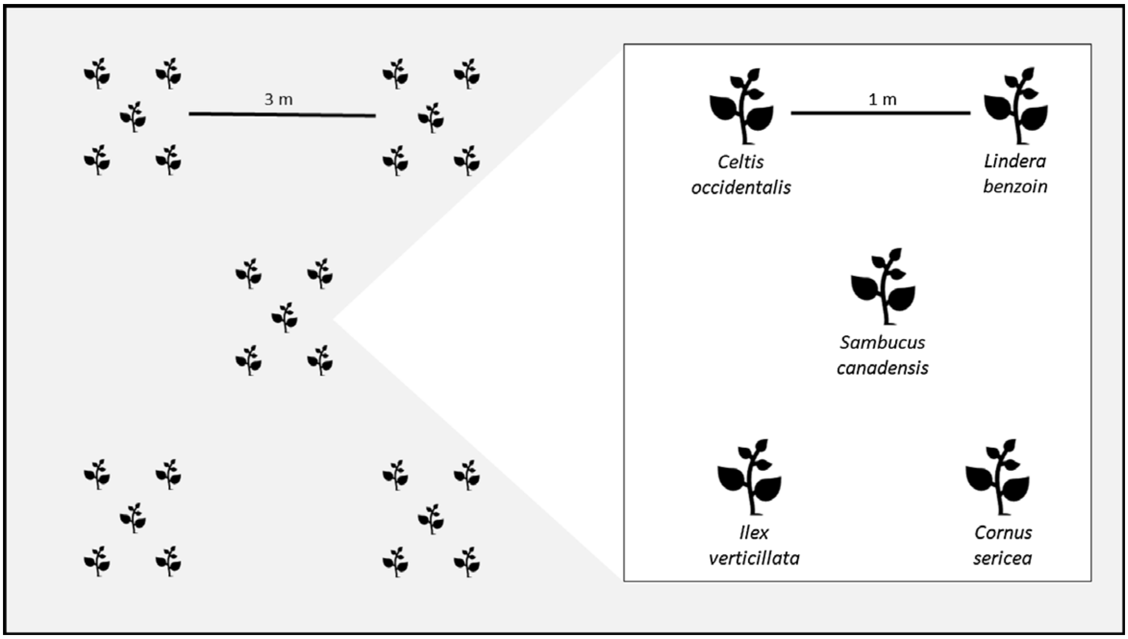

Figure 1. Each shrub treatment cluster contained five groupings of 5 native woody shrubs in the shape of a quincunx. Each group was 3 m apart, and plants within each group were 1 m apart. The native shrubs were elderberry (*Sambucus nigra* ssp. *canadensis*), winterberry (*Ilex verticillata*), red-osier dogwood (*Cornus sericea*), buttonbush (*Celtis occidentalis*), and spicebush (*Lindera benzoin*).

Results and Discussion

Tree Survey

Tree health declined with increasing *R. cathartica* cover (Figure 2; estimate = −0.021, SE = 0.006, z-value = −3.291, P-value = 0.001), but showed no clear association with canopy tree cover (estimate = −0.003, SE = 0.004, z-value = −0.763, P-value = 0.445). The mean (±SE) tree health index across all species was 2.71 ± 0.01, with *A. saccharinum* exhibiting the lowest mean health score (1.94 ± 0.06) (Supplementary Material 1). Tree species identity accounted for variation in sapling health ratings ($\chi^2 = 95.7$, df = 9, $P < 0.0001$), indicating that species differed in their likelihood of receiving higher condition scores. *Salix nigra*, *Q. bicolor*, *P. occidentalis*, and *C. occidentalis* exhibited higher average health ratings than *A. saccharinum*, *A. rubrum*, *T. americana*, *P. deltoides*, *J. cinerea*, and *C. ovata* (Supplementary Material 1).

Shrub Experiment

Of the 100 shrubs planted in October 2018, 79% survived until November 2019. The interaction between *R. cathartica* removal and deer exclusion revealed that herbivory damage was higher in plots where deer were present (59.8 ± 2.67%), and this effect was further amplified when *R. cathartica* also was present (69.4 ± 2.70%) (Figure 3; df = 1, $\chi^2 = 6.221$, P-value = 0.012). In contrast, herbivory levels remained consistently low in deer-excluded plots regardless of *R. cathartica* presence. Whereas the GLMM model suggested that deer herbivory damage differed by shrub species (df = 5, $\chi^2 = 18.430$, P-value < 0.001), post hoc analysis did not (Supplementary Material 2a), suggesting that the differences between groups are not clearly localized to any specific pair.

Insect herbivory was higher with *R. cathartica* regrowth (30.55 ± 3.61%) than where it was removed (23.72 ± 2.13%) (Figure 4; df = 1, $\chi^2 = 6.910$, P-value = 0.008), and insect damage differed by shrub species (Supplementary Material 2b; df = 4, $\chi^2 = 25.022$, P-value < 0.001). The post hoc analysis indicated that *S. canadensis* experienced greater insect herbivory (43.33 ± 5.01%) than any of the other shrubs (23.88 ± 0.93%) (Supplementary Material 2b). Insect herbivory was not affected by deer exclusion (df = 1, $\chi^2 = 0.207$, P-value = 0.648).

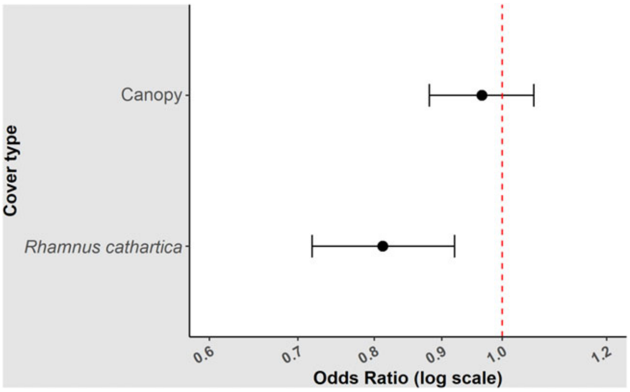

Figure 2. Odds ratios (±95% confidence intervals) for the effects of common buckthorn (*Rhamnus cathartica*) and canopy tree cover (%) on tree health. Tree health was rated based on relative size, bark and wood condition, and growth form/sturdiness, with 0 = dead, 1 = least healthy, 2 = less than average health, 3 = average, 4 = more than average, and 5 = most healthy.
Odds ratios are plotted on a $\log_{10}$ scale. The dashed horizontal line at 1 represents the null expectation of no effect.

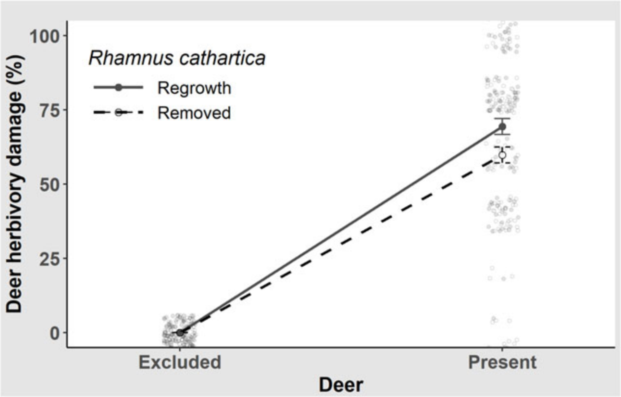

Figure 3. Deer herbivory damage (%) on tree saplings as a function of white-tailed deer (*Odocoileus virginianus*) presence and common buckthorn (*Rhamnus cathartica*) removal. Lines connect group means (±SE) to aid interpretation of interaction patterns. (Lines are included for interpretative clarity and should not be interpreted as continuous interpolations.) Points were jittered to avoid overplotting. The interaction term indicates that deer damage was low with deer excluded regardless of *R. cathartica* removal, but was considerably higher with deer present and higher still where both deer and *R. cathartica* were present.

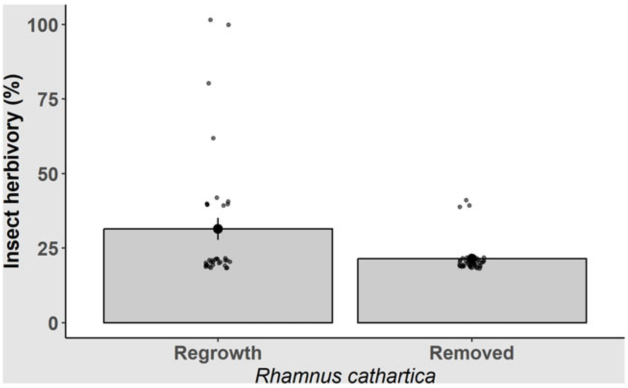

Figure 4. Bar plot showing insect herbivory damage as a function of common buckthorn (*Rhamnus cathartica*) exclusion. Herbivory damage was visually estimated as 0%, 20%, 40%, 60%, 80%, or 100% (with points jittered to avoid overplotting).

Summary of Research Findings

Our results demonstrate a synergistic negative interaction between overabundant deer and *R. cathartica* invasion, whereby the combined presence of both stressors amplified herbivory damage to native woody plants more than either factor alone. *Rhamnus cathartica* and deer each negatively affected native plant health, but our findings revealed that *R. cathartica* exacerbated deer browsing pressure by 16.1% and insect herbivory by 28.7%. We also found *R. cathartica* cover negatively associated with native tree health, an effect not mirrored by native canopy tree cover, suggesting a direct competitive effect. That *R. cathartica* also facilitates increased deer herbivory on native shrubs, likely because it is unpalatable and forces herbivores to focus on nearby, more palatable native plants, suggests indirect competitive effects. Whereas most prior studies reported sub-additive interactions between deer and invasive plants (e.g., Bourg et al. 2017; Waller and Maas 2013) our results support a contrasting pattern in which *R. cathartica* facilitates intensified herbivory.

Seedling mortality is particularly high during the early recruitment stage (Albrecht and McCarthy 2009; Harper 1977; Warren and Bradford 2011), and *R. cathartica* invasion further inhibits seedling establishment (Fagan and Peart 2004; Knight et al. 2007; Warren et al. 2017). In native plant restoration, then, the seed stage often is skipped for larger life stages that are more likely to survive deer browsing (Goetsch et al. 2011). *Rhamnus cathartica* allelochemicals directly suppress competitor seed germination and seedling growth (Knight et al. 2007; Pinzone et al. 2018; Warren et al. 2017), but their effects on larger plants are unknown. Our results provide strong evidence that *R. cathartica* directly suppresses larger plants as well, which could be attributed to shading from rapid regrowth (despite *R. cathartica* being cut to the ground before tree planting), allelopathy, or altered herbivore pressures. Indeed, our results showed greater herbivory damage on planted native shrubs in the presence of *R. cathartica*, suggesting that *R. cathartica* redirects deer browsing toward more palatable native plants. Additionally, we detected greater insect herbivory on native shrubs in the presence of *R. cathartica*, suggesting that insect herbivores, like deer, may shift feeding preferences away from the invasive species (Grunzweig et al. 2015; Knight et al. 2007; Schuh and Larsen 2015).

The finding that native shrubs experienced greater herbivory in the presence of *R. cathartica* aligns with "neighbor contrast susceptibility," in which herbivores disproportionately attack a focal plant that stands out from its immediate neighbors due to differences in palatability, morphology, or chemical traits (Barbosa et al. 2009; Bergvall et al. 2006), although evidence for this phenomenon appears scale and context dependent (Underwood et al. 2014; Wright et al. 2019). In the *R. cathartica* case investigated here, the less palatable and structurally dominant *R. cathartica* may have intensified both vertebrate and invertebrate herbivory on co-occurring native shrubs by increasing their apparent contrast, thereby concentrating herbivore browsing and feeding pressure. Such a shift could facilitate *R. cathartica* invasion and persistence by enabling greater allocation of resources toward growth and reproduction, thus enhancing its competitive advantage.

Our study leveraged two preexisting deer exclosures—one in a buckthorn regrowth location and one in a buckthorn removal location—to assess the interactive effects of invasive shrub management and deer exclusion. Although informative, this design presents important limitations. Each treatment combination (deer by *R. cathartica*) occurred at only one location, precluding true replication of treatment conditions and introducing potential confounding with local characteristics. From a statistical perspective, this represents a lack of independent replication so that treatment effects cannot be cleanly separated from site-specific environmental variation. Ideally, a fully replicated factorial design with multiple sites per treatment would be employed to disentangle these effects. We note, however, that our use of independent insect herbivory data, unaffected by deer exclusion, provided a secondary line of evidence supporting the observed treatment patterns. Such limitations are common in retrospective ecological studies and reflect the practical challenges of conducting research within established land management frameworks (Wragg et al. 2021). Ideally, restoration experiments would be co-designed by researchers and land managers to ensure consistency in treatment application and experimental structure (Copeland et al. 2019; Wragg et al. 2021), but logistical constraints often require scientists to work within the boundaries of ongoing management efforts. Despite inherent limitations, retrospective analyses like ours remain valuable for evaluating restoration outcomes in complex, degraded ecosystems, where invasive species and overabundant herbivores pose persistent management challenges (Löf et al. 2019; Oldfield et al. 2013).

Our findings suggest that non-native species dominance amplifies deer herbivory, further undermining native vegetation recovery. Although planting larger individuals with protective barriers reduced browsing pressure, our results indicate that without thorough *R. cathartica* eradication, native tree species remained suppressed by regenerating *R. cathartica*. Moreover, in the absence of deer exclusion, species reported as deer-resistant experienced considerable herbivory, with *R. cathartica* compounding these effects. These outcomes underscore the necessity of an integrated restoration approach that simultaneously targets invasive plant control and herbivore population management to achieve meaningful ecological recovery.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/inp.2025.10023.

Data availability statement. The data generated and analyzed for the current study are available in the Dryad data repository: https://datadryad.org/dataset/doi:10.5061/dryad.wstqjq2zp.

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Competing interests. The authors declare no conflicts of interest.

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