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Invader removal restructures multitrophic communities and triggers secondary invasion

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Research Article

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Abstract

Invasive, non-native plants frequently restructure ecosystems by homogenizing vegetation and altering trophic interactions, but the ecological consequences of invader removal are less predictable. Removal can redistribute light, nutrients, and detrital resources, initiating community reassembly that extends beyond vegetation recovery and may facilitate secondary invasions. We used a single-site invasive-removal field study to examine how management of European buckthorn (*Rhamnus cathartica* L.) reshaped vegetation structure, litter accumulation, and faunal communities in a postindustrial forest preserve in western New York State, USA. Across 18 plots representing managed, not-treated, and regrown *R. cathartica* conditions, we quantified herbaceous vegetation, leaf litter biomass, and the abundance of arthropods, pollinators and small mammals. *Rhamnus cathartica* removal was associated with a 10-fold increase in herbaceous plant cover and species richness, producing structurally complex understories and higher arthropod and pollinator abundance. However, managed plots also supported 3- to 5-fold higher densities of the invasive European fire ant (*Myrmica rubra*)—corresponding with increased leaf litter in managed plots. Ant abundance was positively associated with thicker, more persistent litter layers rather than canopy openness, and increasing *M. rubra* density, in turn, corresponded with reduced pollinator abundance. Detritivore and rodent responses were more closely linked to vegetation structure and litter conditions than to ant abundance.

Introduction

Invasive, non-native plants can form dense, homogeneous patches that displace native flora and alter ecosystem structure (Archibold et al. 1997; Ferdinands et al. 2005; Jo et al. 2017). By monopolizing light, space, and soil resources, often aided by enemy release and altered biotic interactions, invaders suppress seedling regeneration and shift community composition (Broadbent et al. 2018; Tanner and Gange 2013; Warren et al. 2017). This structural homogenization reduces biodiversity and restructures trophic interactions across ecosystems, with cascading effects on pollinators, herbivores, predators, and decomposers (Holl et al. 2022; McKinney and Lockwood 1999; Olden and Rooney 2006). Ecosystem dynamics can be further altered when invasive plants are removed (Pearson et al. 2016; Rivas-Torres et al. 2024; Shen et al. 2023). As a disturbance, removal redistributes light, water, and nutrients, potentially facilitating opportunistic secondary invasions (Flory and Bauer 2014; Mack et al. 2000; Pearson et al. 2016).

Invader-induced changes in structure and resources extend beyond vegetation, cascading through higher trophic levels as invaders alter herbivore foraging, pollinator visitation, and decomposer pathways (Grunzweig et al. 2015; Iqbal et al. 2021; Tallamy and Shropshire 2009). The absence of specialist herbivores can enhance invader success by allowing greater allocation to growth and reproduction (Joshi and Vrieling 2005; Sun et al. 2023; Tallamy and Shropshire 2009). At the same time, palatable native plants often receive disproportionate browsing pressure when generalist herbivores avoid invasive species, intensifying damage and reducing their competitive ability (Eschtruth and Battles 2009; Haffey and Gorchov 2019; Warren et al. 2025).

Invasive plants can also disrupt native plant reproduction by reshaping pollinator assemblages (Brett et al. 2024; Wang et al. 2024; Yang et al. 2024). Such shifts often reflect evolutionary mismatches, as floral cues, morphology, or resource quality of invaders fail to meet native pollinator requirements (Aizen et al. 2008; Howard and Symonds 2023; Parra-Tabla et al. 2015). Invaders that produce abundant floral rewards may attract large numbers of pollinators but, in doing so, divert them from native plants (Brett et al. 2024; Cuadra-Valdés et al. 2021; Wang et al. 2023). These effects can be further compounded when invasive plants form dense stands that shade native flowers and degrade habitat quality for thermophilic pollinators (Herrera 1997; Valladares et al. 1997; Wiatrowska et al. 2023).

Plant defensive chemistry also can reshape detrital pathways. Non-native leaf litter can be unpalatable when defensive compounds persist after senescence or when nitrogen content is low

Management Implications

Removal of *Rhamnus cathartica* (European buckthorn) promotes strong native herbaceous recovery but also alters ground conditions in ways that can favor secondary invaders. At Tifft Nature Preserve, removal corresponded with a 10-fold increase in herbaceous cover and native plant richness, yet it also corresponded with thicker, more persistent leaf litter layers that appeared to support high densities of invasive *Myrmica rubra* (European fire ant). The elevated ant abundance coincided with reduced pollinator abundance, suggesting that post-removal habitat changes can constrain faunal taxa even as vegetation rebounds. Whereas effective *R. cathartica* management already requires follow-up chemical treatment to prevent resprouting, comparable, landscape-scale control options for invasive ants are limited. Consequently, managers might weigh the benefits of vegetation recovery against the risk of secondary invasion and prioritize integrated post-removal monitoring of both plants and fauna. Where invasive ants are present, targeted local suppression may help preserve restoration gains; where suppression is infeasible, managers may face a trade-off between tolerating an invasive shrub or accepting invasive ants as the lesser of two evils.

(Di Sabatino et al. 2020; Guo et al. 2023; Mayer et al. 2005). Some invaders actually accelerate decomposition by producing nitrogen-rich foliage, altering soil nutrient dynamics and favoring themselves and other non-natives (Allison and Vitousek 2004; Heneghan et al. 2006; Li et al. 2017). Although high-nitrogen litter can briefly boost detritivore abundance, such pulses may shift arthropod community composition and lead to long-term declines (Heneghan et al. 2002; Litt et al. 2014; Woodworth et al. 2020).

By altering understory food resources, litter, and protective cover, invasive plants can also affect seed predators and other small mammals. Dense invasive cover can increase rodent activity by providing refuge from predators (Johnson and León 2015; Mattos and Orrock 2010). Where non-native seeds and fruits are avoided, seed predators such as the white-footed/deer mouse (*Peromyscus* spp.) may concentrate foraging on native seeds, further constraining native regeneration (Knight et al. 2007; Shahid et al. 2009). Increased rodent activity can also reshape lower trophic levels through predation on soil arthropods, with consequences that propagate through the food web (Hamilton 1941; McCay and Storm 1997).

European buckthorn (*Rhamnus cathartica* L.) is a woody species introduced to North America in the 1800s for medicinal and ornamental purposes (Kurylo and Endress 2012). It vigorously invades forest understories, forming dense monotypic stands that monopolize light and space and are associated with declines in native plant richness and abundance and shifts in community composition (Klionsky et al. 2011; Knight et al. 2007; Mascaro and Schnitzer 2007). *Rhamnus cathartica* produces nitrogen-rich leaves that decompose rapidly, accelerating nutrient cycling and releasing nitrogen into the soil (Heneghan et al. 2006; Klionsky et al. 2011). Together, these traits restructure microhabitats and food webs, reducing the abundance of native plants and animals and motivating management removal efforts (Lamb et al. 2022; Schuster et al. 2024; Wragg et al. 2021).

European fire ant (*Myrmica rubra*), native to Europe and parts of Asia, has established invasive populations in North America, particularly in the northeastern United States and southeastern Canada (Groden et al. 2005; Wetterer 2011; Wheeler 1908). It prefers moist, shaded habitats such as woodlands and gardens but can persist in disturbed areas that do not become excessively dry (Chen and Adams 2018; Groden et al. 2005; Warren et al. 2019). Its invasion has been associated with declines of up to 90% in native ant populations, as well as reductions in some native arthropods on which it preys (Gammans et al. 2018; Goodman and Warren 2019; Reznikova and Panteleeva 2001).

We evaluated how *R. cathartica* removal alters multi-trophic interactions among plants, arthropods, pollinators, and rodents, focusing on whether removal-driven changes in vegetation structure and litter dynamics affect the invasive *M. rubra* and cascade across trophic levels. This field study in a single post-industrial forest system tests mechanistic links among management, habitat structure, and faunal responses. We predicted that reduced canopy cover following removal would lower *M. rubra* abundance given its preference for moist, shaded microhabitats, and that release from *R. cathartica* suppression would increase herbaceous cover and richness, enhancing floral resources for pollinators and structural microhabitats for other arthropods. For higher trophic levels, we tested competing mechanisms: pollinators would increase with greater floral availability but could decline if removal eliminated an attractive generalist resource, detritivores would increase if chemically defended litter was removed but could decline if loss of nitrogen-rich litter reduced resource quality, and rodents would increase with greater plant and arthropod resources but could decrease if reduced cover elevated predation risk.

Materials and Methods

Study Site

Tifft Nature Preserve is a 107-ha forest and wetland complex near the eastern shore of Lake Erie in Buffalo, NY, USA (42.84651°N, 78.85951°W). The site was historically a floodplain wetland, later converted to farmland, then used as an industrial transshipment and storage area where bulk materials such as iron ore, lumber, and coal were unloaded, stored, and redistributed. Subsequently, Tifft was used as an industrial and municipal dumping site before restoration as a nature preserve in the 1970s. The terrestrial soils are highly modified and mapped primarily as urban land, Haplaquolls, and covered landfill (Soil Survey Staff 2018). Consistent with this classification, the soil base includes mixed natural and man-made materials so that soil components and properties are variable across the preserve and can change dramatically over short distances, both horizontally and vertically; however, the alkaline soils have a narrow pH range (7.6 to 7.8) and consistently high calcium concentrations (Spiering 2009).

The woodland canopy is dominated by eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall) with some willow (*Salix* spp.) and tree-of-heaven [*Ailanthus altissima* (Mill.) Swingle]. The understory is dominated by *R. cathartica* (with alder buckthorn [*Frangula alnus* Mill.] in wetter areas), Japanese knotweed (*Polygonum cuspidatum* Siebold & Zucc.; syn.: *Reynoutria japonica* Houtt.), dogwood (*Cornus* spp.), and honeysuckle (*Lonicera* spp.), with limited natural regeneration of native woody species (Labatore et al. 2017). White-tailed deer (*Odocoileus virginianus*) are overabundant at Tifft and in surrounding urban and suburban areas (Booth-Binczik and Hurst 2018; Spiering 2009). Invasive *M. rubra* has colonized mesic areas

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in the preserve (Warren et al. 2019). As part of a site restoration plan implemented between 2010 and 2013, there were 31 native tree species planted across 40 ha of forested areas following mechanical removal of *R. cathartica*.

Study Plots

In June 2021, we established 18 plots (10 by 10 m, 100 m^2; mean inter-plot distance = 75 m) at Tifft, distributed among three *R. cathartica* management treatments ($n = 6$ per treatment) Supplementary Material 1 (site map). Treatments were stratified by preexisting management units and site logistics, a common outcome within established land management frameworks (Wragg et al. 2021). Plots were located to fall entirely within a single management unit, avoid obvious edge effects and active disturbance, and span the range of canopy cover and ground-layer conditions present within each unit. "Not-treated" plots were areas where *R. cathartica* was never removed and had matured into tree-dominated stands with minimal understory vegetation Supplementary Material 2 (plot photos). "Regrown" plots were areas mechanically cut in 2012 but not subsequently treated, resulting in dense regrowth by 2021. "Managed" plots were areas mechanically cut and mulched in 2020, followed by targeted cut-stump herbicide treatment in which Pathfinder II™ (triclopyr ester; Corteva Agriscience, Indianapolis, IN, USA) was directly applied to freshly cut *R. cathartica* stumps at 100% concentration. In early 2021, resprouting *R. cathartica* was treated using spot application to foliage with Garlon 3A™ (triclopyr amine salt; Corteva Agriscience) at 5%, avoiding broadcast application to the surrounding vegetation. Treatments therefore differed in both removal approach and time since intervention, with regrown plots last treated in 2012 and managed plots treated in 2020 to 2021. All plots contained native trees planted between 2010 and 2013 as part of restoration efforts, and approximately 90% of the surviving native trees were planted individuals (primarily maple [*Acer*], but also oak [*Quercus*], basswood [*Tilia*], and birch [*Betula*]), with limited volunteer native tree recruitment (primarily *P. deltoides*).

Floral and Faunal Surveys

Plot vegetation was sampled in June and September 2021. Diameter at breast height (DBH) and stem counts for small-diameter woody stems (DBH < 10 cm) were measured along a 14-m plot-diagonal transect using a caliper, and tree-sized stems (DBH ≥ 10 cm) were measured with a DBH tape. Herbaceous-layer vegetation was sampled in four 0.25-m^2 subplots per plot, positioned 1 m inward from each corner. Litter biomass was quantified from the same four 0.25-m^2 subplots by collecting leaf material at the litter–soil interface, removing coarse woody fragments (e.g., twigs, bark), drying samples for 72 h at 65 C, and weighing to obtain dry mass. At the time of sampling, no coarse remnants of *R. cathartica* mulch were evident.

Pollinators were collected three times (June, July, and August 2021) using blue vane traps (SpringStar, Woodinville, WA, USA). Each trap consisted of a plastic container (15-cm diameter by 15-cm height) with a blue screw funnel and cross vanes, filled with water plus a drop of detergent, and suspended 1.2 m above ground using a shepherd's hook. One trap was deployed per plot per sampling period and remained in place for 7 consecutive days (18 traps per period; 54 trap deployments total). Tree-dwelling arthropods were collected three times (June, July, and August 2021) using a 1-m^2 canvas beat sheet placed beneath low branches of three focal trees per plot (54 beat sheet samples per period); the same trees were sampled each period. A PVC stick was used to shake four branches for 15 s each to dislodge arthropods onto the canvas for collection. Leaf litter arthropods were sampled three times (June, July, and August 2021) by collecting leaf litter and decaying organic material at the litter–soil interface from the four 0.25-m^2 vegetation subplots per plot and pooling material into a single sample per plot per period (54 pooled litter samples total). Samples were processed using Berlese-Tullgren funnels under tungsten bulbs for 7 d, and extracted arthropods were preserved in alcohol. *Myrmica rubra* foragers were collected arboreally in the beat-sheet sampling and terrestrially in the leaf-litter samples.

Rodents were live-trapped twice (June and July 2021) for 1 night per sampling period using Sherman traps (H.B. Sherman, Tallahassee, FL, USA). Four traps were placed 1 m inward from each plot corner at dusk and checked at dawn (144 trap-nights total). Traps were baited with a seed mixture and freeze-dried mealworms. Captured rodents were transferred to a cloth bag, identified as *Peromyscus* spp. and released at the point of capture; individuals were not marked, so captures were interpreted as relative activity. All trapping and handling procedures were approved by the New York State Department of Environmental Conservation (License to Collect), the Buffalo Museum of Science, and the Buffalo State Institutional Animal Care and Use Committee. Fauna were identified to order (pollinators to family) and flora to family (Bland and Jaques 1978; Brown 2020; Del Tredici 2020; Neal et al. 2023)

Data Analysis

We analyzed vegetation richness and herbaceous cover as functions of *R. cathartica* treatment using generalized linear mixed models (GLMMs) in the R statistical program (R Core Team 2025). Treatment was included as a fixed effect and plot as a random intercept to account for plot-level heterogeneity. Fixed effects were evaluated with type II Wald χ^2 tests (CAR package), model fit was assessed using dispersion parameters, and pairwise differences among treatments were evaluated with Tukey post hoc comparisons (MULTCOMP package). We did not include *M. rubra* abundance as a predictor in vegetation models because we had no a priori expectation that ant abundance would directly influence plant cover or richness. Vegetation responses were modeled with Poisson GLMMs, whereas faunal responses were modeled with negative binomial GLMMs to accommodate aggregation and excess variance typical of animal count data.

We modeled *M. rubra* abundance as a function of treatment, centered and scaled litter biomass (g), and their interaction using a negative binomial GLMM, with a random intercept for plot. We also fit an additive model without the interaction term to evaluate the partial effect of litter while controlling for treatment. For both models, fixed effects were evaluated with type II Wald χ^2 tests, and Tukey post hoc comparisons were used to examine treatment differences where appropriate. Marginal and conditional pseudo-R^2 values were calculated using the MuMIn package.

Arthropod, pollinator, detritivore, and rodent capture responses were analyzed using negative binomial GLMMs with fixed effects for *R. cathartica* treatment, centered and scaled *M. rubra* abundance, and their interaction and a random intercept for plot. Total arthropod abundance was modeled as before, and arthropod taxonomic richness was analyzed using a parallel zero-inflated model fit with GLMMTMB. Pollinator abundance was defined as the summed abundance of bees from four families (Apidae, Megachilidae, Andrenidae, and Halictidae) captured in blue vane traps. Detritivore abundance was defined as the

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combined abundance of Diplopoda, Isopoda, and terrestrial Gastropoda; and rodent activity was quantified as total *Peromyscus* captures across trapping sessions.

Because not-treated habitat occurred primarily within one portion of the site, 5/6 not-treated plots were located within the same general area and not fully interspersed with the other treatments. As such, we conducted two sensitivity analyses to evaluate whether results were driven by unusually homogeneous or influential plots. First, we compared within-plot variability in *M. rubra* abundance among treatments using a Fligner-Killeen test applied to plot-level variances. Second, we conducted a leave-one-plot-out analysis in which the primary model was refit after removing each plot in turn. Treatment inference was considered robust if the treatment effect remained supported across all refits and if the direction of treatment coefficients remained consistent.

Results and Discussion

Plant Communities

Native woody basal area was negligible across treatments (<0.01 m^2 ha^{-1}). In contrast, *R. cathartica* basal area was higher in regrown plots (mean ± SE; 18.95 ± 1.04 m^2 ha^{-1}) than in not-treated plots (0.73 ± 0.06 m^2 ha^{-1}), and it was absent from managed plots. Leaf litter biomass was similar in managed (201.54 ± 13.62 g m^{-2}) and regrown (212.65 ± 4.51 g m^{-2}) plots but lower in not-treated plots (98.31 ± 7.96 g m^{-2}).

Herbaceous layer cover was highest in managed plots (mean ± SE; 96.33 ± 1.98%), intermediate in not-treated plots (36.66 ± 10.89%), and lowest in regrown plots (1.33 ± 0.72%; $\chi^2 = 27.345$, df = 2, P-value < 0.001). Herbaceous species richness showed the same pattern, with the highest richness in managed plots (14.33 ± 1.09 species), intermediate in not-treated plots (6.16 ± 1.22 species), and lowest in regrown plots (0.50 ± 0.18 species) ($\chi^2 = 36.285$, df = 2, P-value < 0.001). Managed plots were dominated by native species (87%) such as marsh horsetail (*Equisetum palustre* L.; 26% cover), foxtail (*Setaria* sp.; 18%), and slender rush (*Juncus tenuis* Willd.; 11%), each exceeding 10% cover. Not-treated plots were dominated by introduced species and invasive natives (95%), primarily fescue (*Festuca* spp.; 31% cover), catchweed bedstraw (*Galium aparine* L.; 27%), birdsfoot trefoil (*Lotus corniculatus* L.; 21%), and orchardgrass (*Dactylis glomerata* L.; 12%). Vegetation was nearly absent in regrown plots, with sparse cover of eastern enchanter's nightshade [*Circaea canadensis* (L.) Hill; 7%] and bulbous buttercup (*Ranunculus bulbosus* L.; 1%).

Rhamnus cathartica by European Ant Impacts

Rhamnus cathartica treatment and leaf litter biomass both influenced *M. rubra* abundance, with no evidence of a treatment by litter interaction ($\chi^2 = 1.285$, df = 2, P-value = 0.525). Managed plots supported higher (mean ± SE) *M. rubra* abundance (Figure 1A; 43.9 ± 8.5 workers m^{-2}; Tukey P-value < 0.012) than the regrown (16.4 ± 4.5 workers m^{-2}) and not-treated (7.8 ± 2.3 workers m^{-2}) plots, which did not differ (Tukey P-value < 0.117) ($\chi^2 = 13.829$, df = 2, P-value < 0.001). *Myrmica rubra* abundance also increased with leaf litter biomass (Figure 1B; $\chi^2 = 4.804$, df = 1, P-value < 0.028), which explained approximately 16% to 25% of the variance in *M. rubra* counts (pseudo-R^2). After treatment effects were accounted for, leaf litter remained a positive predictor of *M. rubra* abundance ($\chi^2 = 4.680$, df = 1, P-value = 0.030), indicating that the litter effect was independent of treatment differences.

Rhamnus cathartica treatment and *M. rubra* abundance both influenced arthropod abundance, but there was no interaction between the two ($\chi^2 = 1.178$, df = 2, P-value = 0.554). Arthropod abundance (mean ± SE) was higher (Tukey P-value < 0.001) in managed plots (Figure 2A; 254.6 ± 30.8 individuals m^{-2}) compared with both regrown (90.8 ± 14.2 individuals m^{-2}) and not-treated plots (103.1 ± 11.3 individuals m^{-2}), which did not differ (Tukey P-value = 0.316) ($\chi^2 = 20.131$, df = 2, P-value < 0.001). Arthropod abundance also increased with *M. rubra* abundance (Figure 2B; $\chi^2 = 10.417$, df = 1, P-value = 0.001) and explained approximately 31% to 36% of the variance in arthropod counts (pseudo-R^2). Arthropod richness was influenced by *R. cathartica* treatment ($\chi^2 = 8.263$, df = 2, P-value < 0.001), but it was not affected by *M. rubra* abundance ($\chi^2 = 0.095$, df = 1, P-value = 0.757), and there was no interaction between the two ($\chi^2 = 1.406$, df = 2, P-value = 0.495). Arthropod richness was higher in the managed (12.3 ± 0.3) than in the regrown (8.7 ± 0.5) plots (Tukey P-value = 0.003) but did not differ compared with the not-treated plots (10.2 ± 0.4; Tukey P-value = 0.143), nor was there a difference between the regrown and not-treated plots (Tukey P-value = 0.338).

There was marginal evidence for an *R. cathartica* treatment by *M. rubra* interaction, suggesting that the relationship between pollinator abundance and *M. rubra* abundance differed among treatments (Figure 3; $\chi^2 = 5.778$, df = 2, P-value = 0.055). In not-treated plots, pollinator abundance (0.06 ± 0.06 individuals $trap^{-1}$) declined steeply with increasing *M. rubra* abundance, whereas in regrown plots, pollinator abundance (9.16 ± 4.15 individuals $trap^{-1}$) was consistently low regardless of *M. rubra* density. Managed plots supported higher pollinator numbers overall, but pollinator abundance (16.05 ± 2.28 individuals $trap^{-1}$) also declined with increasing *M. rubra* abundance.

Detritivore abundance varied among *R. cathartica* treatments (Figure 4; $\chi^2 = 22.118$, df = 2, P-value < 0.001) but was not related to *M. rubra* abundance ($\chi^2 = 0.504$, df = 1, P-value = 0.477), and there was no treatment by *M. rubra* interaction ($\chi^2 = 1.730$, df = 2, P-value = 0.420). Detritivores were less abundant in not-treated plots (1.9 ± 0.7 individuals m^{-2}) compared with both regrown plots (15.9 ± 3.4 individuals m^{-2}; Tukey P-value < 0.001) and managed plots (18.1 ± 4 individuals m^{-2}; Tukey P-value < 0.001). Managed and regrown plots did not differ in detritivore abundance (Tukey P-value = 0.921).

Rodent captures ($n = 28$ *Peromyscus* spp., 1 *Microtus* sp.) varied among *R. cathartica* treatments (Figure 5; $\chi^2 = 13.387$, df = 2, P-value = 0.001) but were not related to *M. rubra* abundance ($\chi^2 = 2.474$, df = 2, P-value = 0.115), and there was no treatment by *M. rubra* interaction ($\chi^2 = 2.254$, df = 2, P-value = 0.323). Rodent captures were higher in regrown plots (1.1 ± 0.2 individuals $trap^{-1}$) compared with both not-treated plots (0.1 ± 0.1 individuals $trap^{-1}$; Tukey P-value = 0.004) and managed plots (0.2 ± 0.1 individuals $trap^{-1}$; Tukey P-value = 0.010). Managed and not-treated plots did not differ (Tukey P-value = 0.758).

Within-plot variance in *M. rubra* abundance did not differ among treatments (Fligner-Killeen; $\chi^2 = 5.11$, df = 2, P-value = 0.078). Leave-one-plot-out sensitivity analysis indicated that the treatment effect was robust to removal of any single plot (P-value range = <0.001 to 0.004; median = 0.002). Treatment coefficient estimates were directionally consistent across refits.

Rhamnus cathartica removal reshaped communities across trophic levels, yielding both restorative and unexpected outcomes. As predicted, removal promoted strong vegetation recovery, with herbaceous cover and species richness increasing more than 10-fold relative to invaded plots. This rebound was accompanied by

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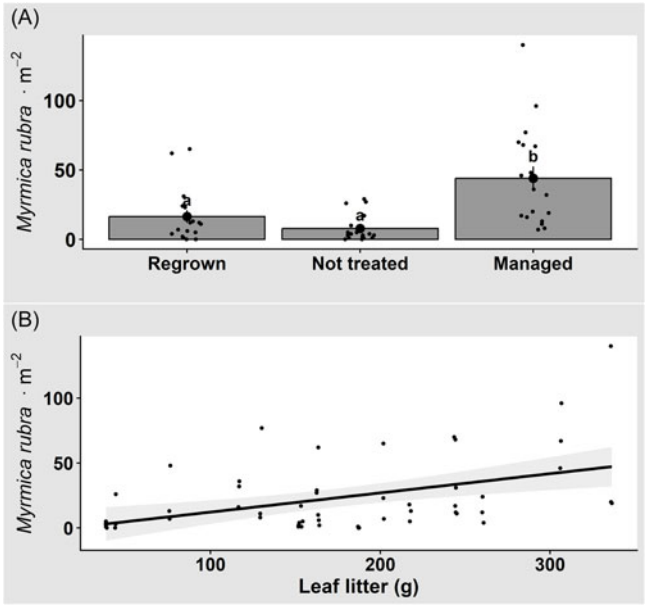

Figure 1. *Myrmica rubra* abundance (mean ± SE) as a function of (A) *Rhamnus cathartica* treatment and (B) leaf litter biomass. The *R. cathartica* treatments were: regrown (*R. cathartica* removed and resprouted as dense shrubbery), not-treated (mature *R. cathartica* untreated), and managed (*R. cathartica* mechanically and then chemically removed). Letters summarize Tukey-adjusted pairwise comparisons controlling the family-wise error rate at $\alpha = 0.05$. *Myrmica rubra* abundance was higher in managed plots than in regrown and not-treated plots and increased with leaf litter biomass.

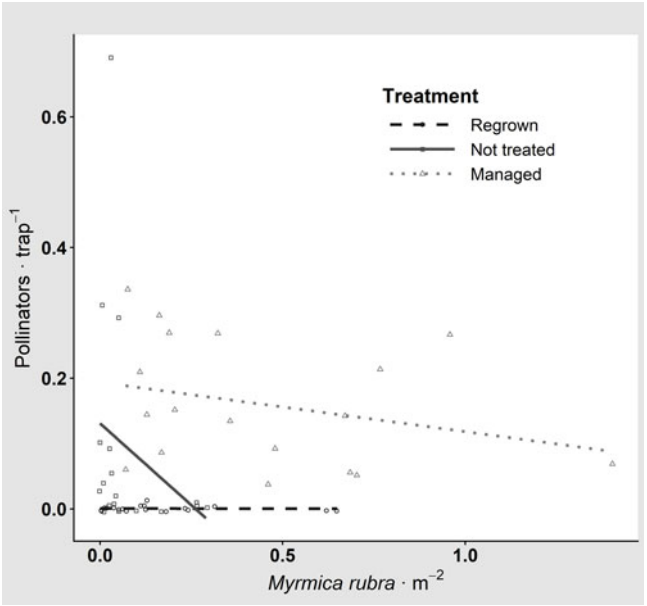

Figure 3. Pollinator abundance in relation to *Myrmica rubra* abundance across *Rhamnus cathartica* treatments. Pollinator abundance was highest in managed plots, intermediate in not-treated plots, and nearly absent in densely regrown plots. Pollinator abundance tended to decline with increasing *M. rubra* abundance, with the steepest decline in not-treated plots. Managed plots supported higher pollinator abundance overall, but pollinator abundance also decreased as *M. rubra* abundance increased.

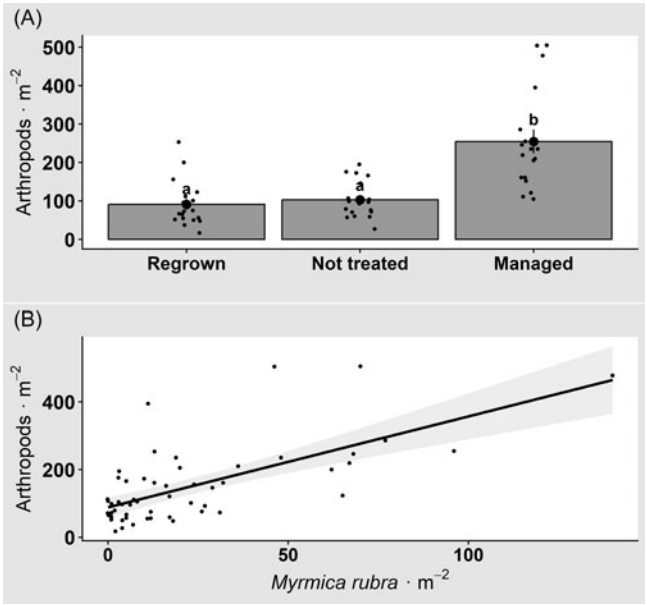

Figure 2. Arthropod abundance (mean ± SE) in relation to (A) *Rhamnus cathartica* treatment and (B) *Myrmica rubra* abundance. Letters summarize Tukey-adjusted pairwise comparisons controlling the family-wise error rate at $\alpha = 0.05$. Arthropod abundance was highest in managed plots and was positively associated with *M. rubra* abundance.

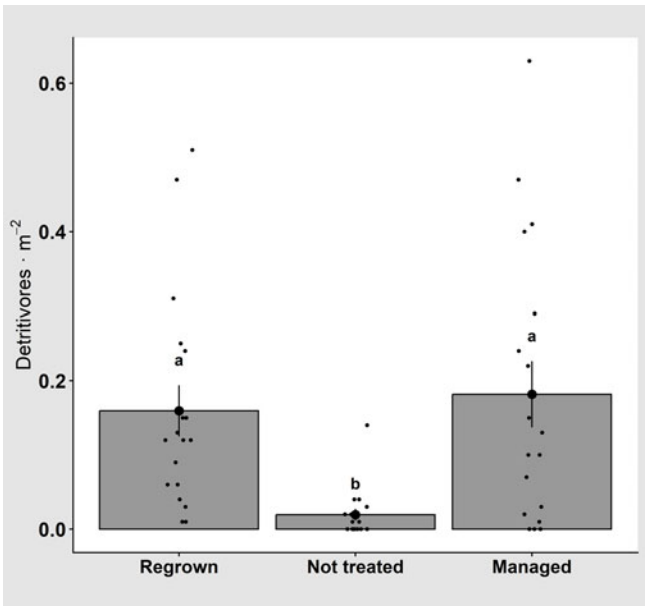

Figure 4. Detritivore abundance (mean ± SE) across *Rhamnus cathartica* treatments. Detritivores were less abundant in not-treated plots than in regrown or managed plots. Letters summarize Tukey-adjusted pairwise comparisons controlling the family-wise error rate at $\alpha = 0.05$. Individual observations are shown with jittered residuals to avoid overplotting.

higher pollinator and arthropod abundance, consistent with increased light availability and altered litter conditions that improved habitat structure and resource availability. However, these gains coincided with a 3- to 6-fold increase in invasive *M. rubra* ants, which were most abundant in recently managed plots. Rather than declining with the increased openness following removal, *M. rubra* appeared to exploit the thicker litter layers that developed after *R. cathartica* removal. These results indicate that invader removal can simultaneously foster native recovery and facilitate secondary invasion, suggesting that restoration in

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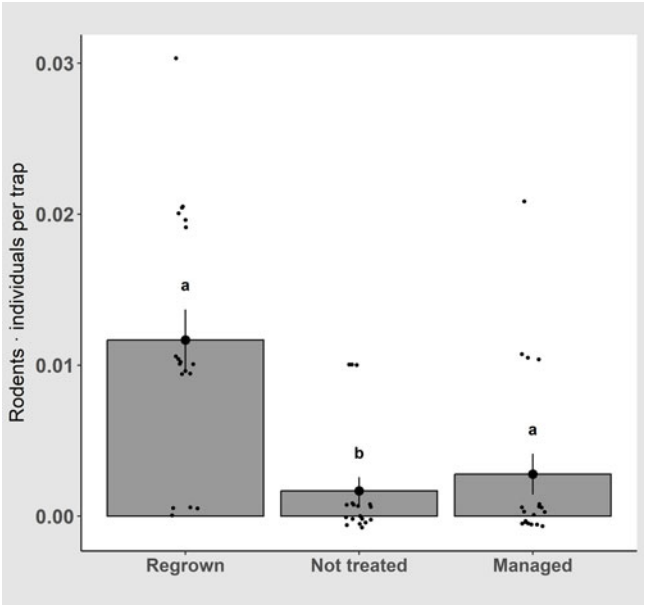

Figure 5. Rodent abundance (mean ± SE) across *Rhamnus cathartica* treatments. Rodents were most abundant in densely regrown plots. Letters summarize Tukey-adjusted pairwise comparisons controlling the family-wise error rate at $\alpha = 0.05$. Individual observations are shown with jittered residuals to avoid overplotting.

already-invaded ecosystems may redirect, rather than reverse, invasion-driven community change.

Contrary to expectations, *M. rubra* was three to six times more abundant in managed plots than in *R. cathartica*–dominated areas. Rather than declining after *R. cathartica* removal, *M. rubra* abundance was positively associated with leaf litter accumulation, which increased in managed plots. *Rhamnus cathartica* leaves decompose rapidly due to their high nitrogen content (Heneghan et al. 2002), producing little litter buildup in invaded areas, whereas managed plots accumulated thicker, more stable litter layers that provide ant nesting substrate and microclimatic buffering (Groc et al. 2009; Vasconcelos et al. 2009). Overall arthropod abundance increased with *M. rubra* density, consistent with shared habitat preferences rather than facilitation. Pollinator abundance, in contrast, declined with increased *M. rubra*, suggesting potential interference or avoidance effects, whereas detritivores were largely unaffected. Together, these patterns indicate that *R. cathartica* removal improved habitat conditions that supported greater arthropod abundance overall, but the simultaneous rise of *M. rubra* produced mixed responses across trophic groups. Similar context-dependent outcomes have been reported elsewhere, where invasive ants, including *M. rubra*, have effects on native arthropods that range from strongly negative (Holway et al. 2002; Lach 2007) to neutral or even positive depending on habitat and resource structure (Garnas et al. 2014; Goodman and Warren 2019; Krushelnycky and Gillespie 2008).

Herbaceous cover and species richness increased in managed plots relative to *R. cathartica*–dominated areas, and vegetation shifted toward native dominance, consistent with *R. cathartica* removal facilitating plant community recovery (Lamb et al. 2022; Larkin et al. 2014; Wragg et al. 2021). In contrast, plots where *R. cathartica* regrew after earlier removal supported sparse, depauperate vegetation, indicating that sustained management is essential to prevent reinvasion (Lamb et al. 2022; Wragg et al. 2021). In our study, herbaceous cover and richness in removal plots were more than twice those in not-treated plots and roughly 14 times those in regrown plots, and vegetation composition shifted from 95% non-native in not-treated plots to 87% native in removal plots. The not-treated plots were dominated by non-native *Festuca* spp., *G. aparine*, and *L. corniculatus*, suggesting that self-thinning of mature *R. cathartica* canopies (Knight et al. 2007; Schuster et al. 2022) may allow secondary colonization by disturbance-tolerant herbs but not native perennials. At Tifft, *O. virginianus* appears to use not-treated stands for bedding, which may further suppress palatable herbaceous species through selective browsing (Warren et al. 2025). These patterns suggest that post-removal plant community composition is shaped by both residual *R. cathartica* legacies and herbivore pressure.

Given the strong links between floral diversity and pollinator communities, we expected pollinator abundance and richness to increase following *R. cathartica* removal. Pollinator abundance and richness were indeed higher in managed plots than in not-treated or regrown plots, with abundance in managed plots more than triple that in not-treated plots and over an order of magnitude higher than in densely regrown plots. This pattern mirrors results from removal of other invasive shrubs, including *F. alnus*, Amur honeysuckle [*Lonicera maackii* (Rupr.) Maxim.], and Chinese privet (*Ligustrum sinense* Lour.), where pollinators and native plant communities rebounded rapidly (Fiedler et al. 2012; Hanula and Horn 2011; Hartman and McCarthy 2004). Although studies directly testing pollinator responses to *R. cathartica* removal appear limited, removal of the closely related *F. alnus* has been associated with increases in generalist pollinators, consistent with rapid recolonization after shrub removal (Fiedler et al. 2012).

At our site, *M. rubra* forms large foraging swarms that blanket the ground and extend into woody vegetation, a pattern consistent with invasive ants that disrupt native arthropod communities. High densities of invasive ants can restructure co-occurring arthropod communities, particularly pollinators that nest in or forage near the ground (Goodman and Warren 2019; Lach 2007; Plentovich et al. 2021). For example, invasive ants were a primary cause of nest failure in the endangered yellow-faced bee (*Hylaeus anthracinus*) (Plentovich et al. 2021), and the invasive Asian needle ant (*Brachyponera chinensis*) appears linked to declines in bees and butterflies (Ulyshen and Horn 2023). In our study, *R. cathartica* removal coincided with increased pollinator abundance, but higher *M. rubra* abundance within those plots appeared to dampen these gains. Whereas both *M. rubra* and pollinators increased with *R. cathartica* removal, pollinator abundance declined as ant abundance increased, suggesting that secondary invasion by invasive ants can constrain restoration benefits.

The spatial independence of pollinator samples depends on pollinator foraging range, trap attractiveness, and landscape heterogeneity. Our 75-m plot spacing falls within the 50- to 100-m range used in comparable field studies (Kremen et al. 2002; Williams et al. 2010) and below the 100- to 300-m foraging distances typical of many native bees (Greenleaf et al. 2007; Zurbuchen et al. 2010). However, blue vane traps have relatively limited effective attraction radii (approximately 25 to 50 m) and largely intercept local bee activity rather than drawing individuals from long distances (Cane et al. 2000; Kimoto et al. 2012). In heterogeneous landscapes, vegetation structure can further localize bee movement, with foraging in dense vegetation and along forest edges occurring over shorter distances than in open habitats (Kimoto et al. 2012; Steffan-Dewenter and Tscharntke 2000; Taki et al. 2007). Thus, in our structurally diverse system, 75-m spacing likely captured distinct pollinator assemblages. However, because

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blue vane traps are biased toward bees, Lepidopteran pollinators likely were underrepresented (Short et al. 2023; Westerberg et al. 2021).

We found that leaf litter biomass was roughly half as great in not-treated plots as in managed and regrown plots. Although *R. cathartica* leaves decompose rapidly due to their high nitrogen content (Ewing et al. 2015; Heneghan et al. 2006; Knight et al. 2007), managed plots accumulated more leaf litter despite supporting substantially less woody cover, suggesting longer persistence of native tree litter. Managed plots accumulated predominantly native tree litter, which likely is more recalcitrant than *R. cathartica* litter and therefore persisted longer, forming thicker layers. Consistent with these patterns, detritivore abundance tracked litter accumulation, with not-treated plots supporting about half the detritivore abundance of regrown and managed plots. *Myrmica rubr*a abundance increased with litter biomass, but detritivores did not respond to *M. rubra*, suggesting that variation in litter biomass acted as the primary driver of detritivore abundance across treatments.

Rhamnus cathartica invasion has been linked to reduced mammal abundance where rodents avoid its unpalatable nonnative seeds and fruits (Knight et al. 2007; Shahid et al. 2009; Vernon et al. 2014). Because ground-dwelling arthropods are a key food resource for omnivorous rodents, and we expected increased arthropod abundance following *R. cathartica* removal, we expected higher rodent (*Peromyscus* spp. in this case) activity in managed plots. Instead, rodents were most abundant in densely regrown plots, likely because *R. cathartica* regrowth provides thick understory cover that reduces predation risk (Johnson and León 2015; Mattos and Orrock 2010).

Although mulched *R. cathartica* material was left on-site following removal, *R. cathartica* litter decomposes rapidly due to its high nitrogen content, suggesting that elevated litter biomass in managed plots within the first year after treatment reflected accumulation of native tree litter and persistent ground-layer detritus rather than residual *R. cathartica* debris. Consistent with this interpretation, *R. cathartica*–dominated plots exhibited lower litter biomass despite continuous *R. cathartica* leaf input, indicating that decomposition rates, rather than litter production per se, governed standing litter biomass. Although herbicide application may have influenced vegetation dynamics, several factors suggest it was not the primary driver of observed patterns. Application consisted of cut-stump treatments after mechanical *R. cathartica* removal rather than broadcast spraying. Managed plots supported the highest herbaceous cover (96%) and richness (14 species), with 87% native composition—a pattern more consistent with competitive release from *R. cathartica* than herbicide-induced suppression. However, because managed and regrown plots differed in both herbicide use and time since treatment, we cannot fully separate the effects of chemical follow-up from recovery time. Because of the management history constraints on study design, our treatment plots were imperfectly interspersed, but our sensitivity checks indicated that inference was not driven by unusually low within-plot variability in the clustered treatment or by any single influential plot.

Our inferences derive from a single, postindustrial preserve with alkaline soils, deer overabundance, and an established *M. rubra* population. As such, our study clarifies general processes, but not general magnitudes. The key pathway we documented is that *R. cathartica* removal increased herbaceous cover and litter mass, which likely provided nesting substrate and a buffered microclimate favoring *M. rubra*. At the same time, increased openness and light availability increased arthropod and pollinator abundance. Responses documented here reflect relatively early post-removal dynamics. Vegetation recovery, litter accumulation, and faunal responses may continue to shift as succession proceeds, *R. cathartica* resprouts are suppressed or recolonization continues, and litter inputs stabilize under regenerating canopy conditions. Some responses observed here, such as elevated herbaceous cover or increased abundance of disturbance-associated fauna, may strengthen or reverse as competitive interactions and habitat structure change. Long-term monitoring will be necessary to determine whether these early patterns persist or shift toward later-stage community trajectories.

These results illustrate that invader removal can function as an ecological disturbance that reorganizes community structure rather than simply reversing the effects of invasion. The post-removal proliferation of *M. rubra* suggests that removal can generate new resource regimes and habitat configurations that favor disturbance-adapted or opportunistic species. This outcome aligns with models of secondary invasion and succession, in which restoration-driven shifts in light, litter, and soil conditions act as disturbance pulses that reset competitive hierarchies and open colonization windows (Flory and Bauer 2014; Mack et al. 2000; Pearson et al. 2016). In this sense, restoration and invasion represent linked phases of ecosystem reorganization: both redistribute resources, restructure trophic interactions, and initiate novel successional pathways. The patterns observed here emphasize that post-removal community trajectories are governed less by a return to preinvasion states than by emergent post-disturbance assembly dynamics.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/inp.2026.10041

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