Received: 12 August 2022 | Accepted: 22 August 2022

DOI: 10.1002/ecs2.4351

ARTICLE

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Plant community dynamics following non-native shrub removal depend on invasion intensity and forest site characteristics

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Funding information
Delaware Environmental Institute (DENIN); University of Delaware Research Foundation; USDA Forest Service, Grant/Award Number: 16-JV-11242308-122

Handling Editor: Debra P. C. Peters

Abstract

Globally, temperate deciduous forests are threatened by invasion of non-native (exotic) plant species. In the eastern United States, *Rosa multiflora* is a dominant shrub invader in forests, which often forms dense thickets that reduce sunlight availability in the understory, where decreased native plant diversity and abundance are observed. Management and restoration are difficult but desirable, especially when invasion intensity is still low. Few studies have examined the relative success of different management strategies under varying invasion intensities. Our study objectives were to conduct a *R. multiflora* removal experiment in three forest sites experiencing different invasion intensities and to restore native plant biodiversity while preventing secondary invasion. We utilized three management strategies: invasive plant removal, removal followed by native seed addition, and removal plus native seed and mulched invasive stem addition. We investigated the similarity between seed bank species composition and existing vegetation before and after removal to assess the potential for passive restoration. Two seasons after removal, we found that simply removing roses increased native species richness, native floristic quality assessment ($FQAI_N$), and native shrub abundance in our medium invasion site, and total species richness in our low and medium invasion sites. Compared to removal alone, native seed addition, with and without mulch addition, resulted in larger native and total species richness and $FQAI_N$ increases at all sites, larger increases in native shrub abundance and exotic species richness in our medium invasion site, and larger reductions in exotic and total shrub abundance in our low and medium invasion sites. Following removal, species similarity between the seed bank and vegetation improved for all three sites. Our results indicate that removal of *R. multiflora* alone increased native plant biodiversity in the medium invasion scenario, but the seed bank may not provide a large native species pool. Additional management strategies lead to improved outcomes, especially in our most invaded forest, demonstrating the need to conduct multiple plant removal treatments

across forests with varying site conditions and plant invasion intensity to improve management recommendations.

KEYWORDS
floristic quality assessment, invasive plant management, non-native plant invasion, *Rosa multiflora*, temperate deciduous forest, woody plant community

INTRODUCTION

Non-native invasive (hereafter "invasive") species are widely recognized as one of the greatest threats to biodiversity worldwide (e.g., Mack et al., 2000; Vitousek, Mooney, et al., 1997). The effects of plant invasions on ecosystem structure and function are well-documented (Brooks et al., 2004; Pyšek et al., 2012; Trammell et al., 2012; Vitousek, D'Antonio, et al., 1997). Specifically, invasive plants can alter nitrogen (Corbin & D'Antonio, 2004; Ehrenfeld, 2003; Ehrenfeld et al., 2001) and carbon cycling (Liao et al., 2008), native plant community composition (Link et al., 2018; Pearson et al., 2016; Trammell & Carreiro, 2011), and soil microbial communities (Hawkes et al., 2005; Kourtev et al., 2002). Beyond ecological threats, invasions have considerable economic impacts (Holmes et al., 2009; Pimentel et al., 2005). Costs associated with control of invasive species and the damage they cause were estimated to exceed $120 billion in the United States alone, and invasive plants contributed nearly $35 billion to that total (Pimentel et al., 2005). Developing mitigation strategies that address the combined ecological–economic effects of invasive species is critical to sustaining ecosystems and economies worldwide.

Invasion of non-native plant species in forest ecosystems is widespread, and many forest species native to one continent are now invasive in forests on other continents (e.g., Brus et al., 2019; Fridley, 2008; Langmaier & Lapin, 2020; Schulz & Gray, 2013; Shifley et al., 2012; Shifley & Moser, 2016; Wagner et al., 2017; Webster et al., 2006; Xu et al., 2012; Zhang et al., 2021). The temperate deciduous forest biome covers 5% of the earth's landmass, yet 25% of the global population resides on this land (United Nations, 2013). Additionally, these forests occur in wealthy nations with extensive global trade networks, which has facilitated the spread of invasive species from their native ranges (e.g., Holmes et al., 2009; Pimentel et al., 2005). While invasive species occur across all forest strata worldwide, we focus on the United States as a case study, where the dominant invasive forest species are shrubs and vines in the understory (Trammell et al., 2020; Trammell & Carreiro, 2011; Webster et al., 2006).

In forests of the northeastern and north-central United States, the most common invaders are the shrub *Rosa multiflora* (multiflora rose) followed by the vine *Lonicera japonica* (Japanese honeysuckle; Kurtz & Hansen, 2013; Schulz & Gray, 2013; Trammell et al., 2020). These and similar invasive plants possess traits that offer a competitive advantage with respect to the native understory community, such as unpalatability to herbivores, increased rates of germination and colonization, and a longer growing season due to earlier leaf out in spring and later leaf senescence in autumn (Fridley, 2012; Smith, 2013; Trammell et al., 2012; Ward et al., 2013). Invasive shrub and vine dominance in native forests may suppress native herbaceous, shrub, and tree species, leading to diminished or failed forest regeneration in the long term (Aronson & Handel, 2011; Collier et al., 2002). Moreover, the understory is the most biodiverse layer in many forest ecosystems due to the high richness in herbaceous species (Gilliam, 2007, 2014; Huebner, 2003; Huebner et al., 1995; Wavrek et al., 2017) and is the increasing focus of invasive plant management and restoration efforts (Weidlich et al., 2020).

Removal of invasive plant species can be successful in restoring native plant diversity (Maynard-Bean & Kaye, 2019), especially when the removal is followed by planting of desirable native species (Flory & Clay, 2009; Hartman & McCarthy, 2004; Johnson & Handel, 2016), including reintroduction of locally extirpated species (Ward et al., 2013). However, in the absence of continuing follow-up management, the initial target species may reinvade and establish at or near preremoval levels within a few years (Hopfensperger et al., 2019; Ward et al., 2013). Likewise, other non-native plants may inadvertently benefit from the removal and become established, leading to secondary invasions (Kettenring & Adams, 2011; Pearson et al., 2016). This phenomenon, often called an "invasive species treadmill" (Thomas & Reid, 2007), is one of several challenges land managers face in forest restoration efforts.

Current techniques used in removal and restoration are costly, require large numbers of personnel, and may fail to prevent reinvasion/secondary invasions of non-native plants (Hopfensperger et al., 2019; Kettenring & Adams, 2011).

This is especially true in landscapes with isolated forest patches and where land managers often lack the resources to develop long-term restoration strategies that focus on controlling abundant invaders (Pearson et al., 2016). Furthermore, studies often focus on the restoration of sites that are already highly degraded and/or invaded and do not evaluate the potential success under lower invasion scenarios. Thus, there is a growing need for efficient, cost-effective management strategies that contain and successfully eradicate invasive plants under a variety of conditions and locations while restoring native ecosystems to ensure they are resilient to future invasions.

To address the need for experimental, manipulative studies in diverse settings (i.e., multiple sites), we replicated an invasive plant removal experiment in three forests located in northern Delaware and southeastern Pennsylvania, each experiencing different amounts of multiflora rose invasion. Specifically, we asked the following questions: (1) How does community composition change following invasive plant removal in forests with different invasion intensities? (2) How does the plant community respond to additional management treatments (i.e., seed mix addition and mulch addition) in forests with different invasion intensities? (3) Is the seed bank composition similar to the existing vegetation, and does similarity change following invasive plant removal? While we conducted this study in eastern US temperate deciduous forests, the answers to these questions are informative for plant invasions in forests across the world.

Previous sampling of these sites indicated differences in invasion intensity (i.e., the number of non-native stems per hectare); tree, shrub, and vine species composition; and forest age at the site level (Trammell et al., 2020). Multiflora rose was present in all three locations at varying abundance; however, we established our experimental study sites at maximum rose cover and density within each forest. Following invasive plant removal, we expected declines in invasive plant richness and invasive shrub abundance, and subsequent increases in native species richness and native species abundance. We hypothesized that additional management treatments would result in enhanced stimulation of the native plant community and inhibition of invasive plant reoccurrence. Previous studies of forest ecosystems have shown little similarity between existing vegetation and the seed bank, which tends to be dominated by pioneer species and/or exotic species that are absent in standing vegetation (Beauchamp et al., 2013; Hopfensperger, 2007; Kostel-Hughes et al., 1998). Therefore, we did not expect the seed bank and vegetation at a site to be similar across our study forests, though we expected similarity to increase postremoval as increases in resource availability (i.e., sunlight, space, water, nutrients) and altered soil conditions (i.e., temperature, pH, soil moisture) would have stimulated germination and increased seedling emergence rates.

METHODS

Site selection and study design

In this study, we selected three forest sites that are part of a long-term ecological study of forests in and around urban areas called the FRAME (FoRests Among Managed Ecosystems; https://sites.udel.edu/frame/). In 2015, vegetation sampling of all 38 FRAME sites was conducted, and the abundance of non-native woody plants (i.e., the number of non-native woody stems) was used to rank sites along a gradient of invasion (Trammell et al., 2020). Thus, sites could be classified along this gradient as experiencing low (0.2–25 non-native stems ha^{-1}; $n = 11$), medium (26–80.5 non-native stems ha^{-1}; $n = 11$), or high (>80.5 non-native stems ha^{-1}; $n = 11$) or no invasion (0 non-native stems ha^{-1}; $n = 5$). Based on this classification, we selected one site from each of the low, medium, and high invasion categories to conduct a manipulative invasive plant removal experiment. Sites ranged in rose stem size and age of rose invasion in accordance with their invasion (i.e., our low invasion site had the smallest and youngest rose stems, medium invasion had intermediate stem sizes and age, and high invasion had the largest and oldest rose stems), and sites were located in the Piedmont region of northern Delaware and southeast Pennsylvania within 13 km of one another.

In March 2017, we surveyed each study forest ($n = 3$) for potential invasive plant removal locations. Each removal area had to meet certain criteria: (1) invasive plant cover, particularly of shrubs and specifically *R. multiflora*, must be dense enough such that nine 4-m^2 treatment plots could be established within the removal area; (2) plots must contain at least 75% cover of invasive plant species; (3) plots must be placed at least 1 m away from any other subplot and/or tree; and (4) invasive plant cover should extend beyond the perimeter of the removal area to allow the establishment of control plots, in which no manipulation (i.e., invasive plant removal) would be performed. Additionally, an area with little or no invasive species presence was located nearby, beyond the boundary where invasion density was visually evident. Here, a 16-m^2 (4 m × 4 m) reference plot was established to assess the native plant community composition and to monitor potential changes in the plant community and/or detection of newly arriving or dispersing non-native species at the site (Figure 1).

Four strategies (one control and three treatments) were adopted for this experiment, representing approaches

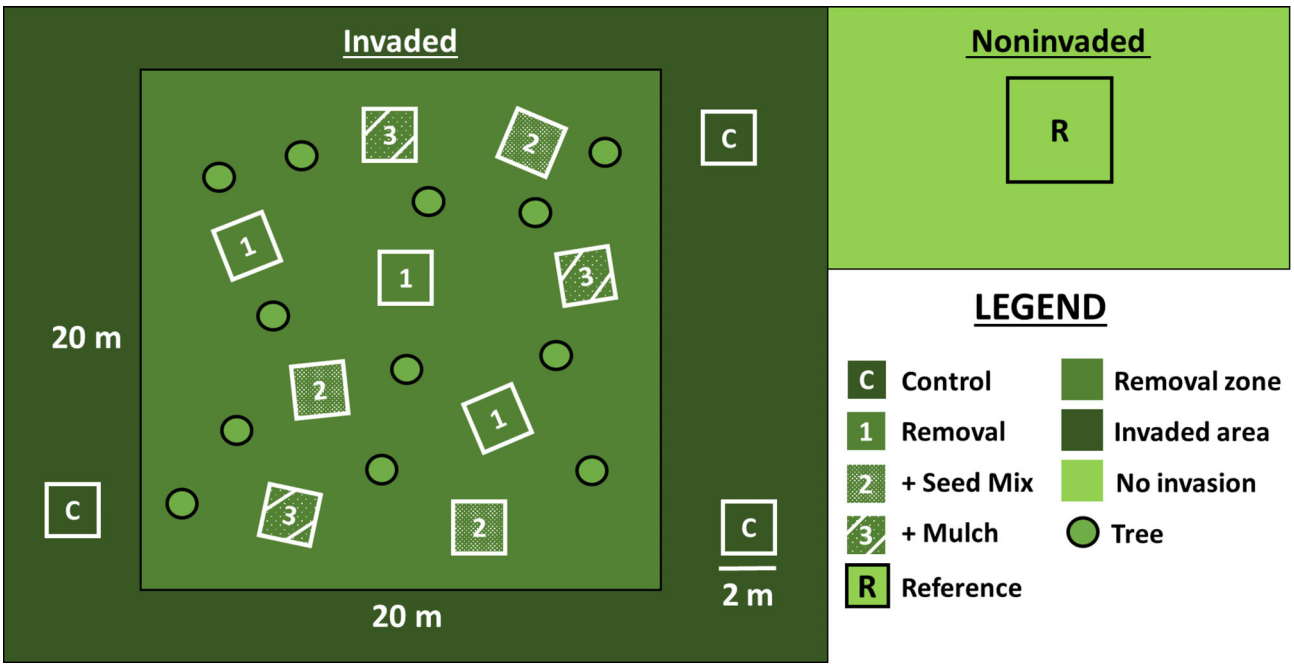

FIGURE 1 Study design for rose removal experiment. A large area of invasive shrub cover (mostly *Rosa multiflora*) with a clear boundary between invaded and noninvaded forest was located in each forest site. Within the invaded area, a 400-m^2 (20 m × 20 m) "removal zone" was established for invasive plant removal, except in the low invasion site, where there were two removal zones. In the removal zone, nine 4-m^2 (2 m × 2 m) treatment plots were established consisting of (1) invasive plant removal only ($n = 3$), (2) invasive plant removal plus a native seed mix addition ($n = 3$), and (3) invasive plant removal plus seed mix and mulched *R. multiflora* stems. Beyond the removal zone but within the invaded area, three 4-m^2 control plots (C) were established to monitor the plant community under invaded conditions. Within the uninvaded area, a 16-m^2 (4 m × 4 m) reference plot (R) was established to monitor the plant community in the absence of invasive shrub cover.

that could be implemented by landowners, managers, and restoration project designers. For each treatment, three 4-m^2 (2 m × 2 m) plots were established within each site ($n = 9$ plots $site^{-1}$) for a total of 27 treatment plots across the three forest sites. Additionally, three 4-m^2 (2 m × 2 m) control plots were established outside of the removal area ($n = 36$ total treatment and control plots). Treatment strategies were additive, such that each subsequent strategy used the methods of the previous strategy. The strategies were: (1) no invasive plant management (hereafter "control"), (2) invasive plant removal using hand pulling or mechanical means (cutting) followed by stump treatment with the herbicide glyphosate (hereafter "removal-only treatment"), (3) strategy 2 plus the addition of a native plant seed mix (hereafter "seed mix treatment"), and (4) strategy 3 followed by the addition of chipped invasive stems six weeks later (hereafter "mulched treatment"); stems were previously cut and allowed to dry on-site.

Vegetation sampling

In 2017, we sampled all vegetation and measured canopy cover in each treatment plot ($n = 12$ plots $site^{-1}$) and one reference plot ($n = 1$ plot $site^{-1}$) at each forest site, prior to invasive plant removal. All subplots were revisited for postremoval vegetation sampling and canopy cover measurements in 2018 and 2019 to assess the responses of the plant community to the various treatments. Forb and tree species were identified, and individuals were counted, whereas individual stems were counted for all shrub species. For vines, graminoids (grasses and sedges), and ferns, the percent ground cover was estimated since it is often difficult or impossible to determine individuals. Spring ephemeral plants were counted every year from mid-March to mid-May, and all other plants were sampled in peak growing season starting in July.

Invasive plant removal experiment

From February to March 2018, invasive plants were removed within the removal zone at all three forest sites. Small invasive shrubs were hand pulled, taking great care to remove all root tissues. Larger plants were cut with pruning shears or loppers at approximately 10 cm above ground, and a 50.2% glyphosate herbicide solution was applied to the resulting stump immediately afterward.

Cut stems were gathered and air-dried for at least 6 weeks at the study site prior to chipping/mulching in May 2018.

In March 2018, a customized native seed mix (Prairie Moon Nursery, Winona, MN) was applied to plots in treatment strategies 2 and 3. The seed mix included plant species present at the site or nearby sites but excluded species that are known to be palatable to deer (e.g., *Trillium* spp.). The seed mix consisted of 29 herbaceous and 7 graminoid species in densities based on seed size (Appendix S1: Table S1). All plots ($n = 18$ total; 6 plots site^{-1}) were seeded with 26.96 g of seed (6.74 g m^{-2}) via hand scattering in March 2018.

We used a Tazz K32 Chipper Shredder to chip the cut and dried *R. multiflora* stems. Due to the large volume of entangled woody debris removed, stems of other invasive species such as *Berberis thunbergii* (Japanese barberry), *Celastrus orbiculatus* (Asian bittersweet), and *Rubus phoenicolasius* (wineberry) may have unintentionally been chipped as well, though we minimized their inclusion to the best of our ability. At each site, the resulting weight of the chipped biomass was similar (low invasion = 10.55 kg, medium invasion = 10.65 kg, and high invasion = 10.55 kg). In early May 2018, we applied 3.5 kg of chipped stems by hand to each plot of treatment strategy 3, the mulch treatment group ($n = 9$ total; 3 plots site^{-1}), forming a layer ~2 cm thick on the soil surface.

Floristic quality assessment index

A floristic quality assessment (FQA) was performed for all treatment plots at each forest site following the equation for native FQA described in Freyman et al. (2016). The FQA relies on coefficients of conservatism (*C*), originally developed by Swink and Wilhelm (1994), which are values between 0 and 10 assigned for all plant species within a given region or state. Invasive plant species, by definition, have a *C* of 0. Low FQA values represent species that are disturbance tolerant and lower quality habitat tolerant (i.e., weedy or ruderal species). High FQA values indicate plant species that occur in pristine, undisturbed, or true remnant habitats (i.e., not disturbance tolerant). Floral databases for Pennsylvania and Delaware (McAvoy, 2018), which include native status of plants and coefficients of conservatism (*C*), were accessed and downloaded from the Universal FQA Calculator (https://universalfqa.org/; Freyman et al., 2016). Seven taxa were only identified to genus and were not included in FQA calculations (hereafter $FQAI_N$; see Appendix S1: Table S2 for native status and *C* of plants identified in this study).

Soil seed bank

Soil collection for seed bank evaluation was conducted in April 2018. At each site, 10 soil cores were taken at random points along each edge (0–20 m) of the removal zone's perimeter, with each sample taken at least 1 m away from the previous one ($n = 40$ cores site^{-1}). Soil cores were collected with an 8 cm diameter soil auger to a depth of 10 cm, which is a sufficient sampling depth for capturing viable seeds in forest soils (Decocq et al., 2004; Kostel-Hughes et al., 1998; Leckie et al., 2000; Wódkiewicz & Kwiatkowska-Falińska, 2010). Soil was bulked and homogenized in the field using a 5-L bucket at each forest site. Soils were transported on ice to the University of Delaware's Fischer Greenhouse and stored at 2°C.

In preparation for the seed germination study, soils were gently sieved (4.75 mm) to remove rocks and other debris, and no seeds larger than 4.75 mm were present in the soil. The resulting sieved soil was then divided into eight flats (54 × 26 cm) per forest site, with 1.5 cm of soil (2.3 L flat^{-1}) placed over 3 cm of sterile potting mix (Metromix 852, Sun Gro Horticulture, Agawam, MA). In addition, six control flats contained an equivalent volume of sterile potting mix (4.5 L flat^{-1}). Each tray was watered to moisten both soil and potting mix, and soils were watered every other day, or when dry to the touch, with 700–800 ml of tap water for the duration of the study. Daytime and nighttime temperature (28 and 26°C, respectively) and relative humidity (50% and 60%, respectively) were set to mimic peak growing season conditions in the region. Seedlings grew until they could be identified, or until their growth impeded subsequent seedling growth. Seedlings that required longer growth for positive identification were transplanted into individual containers until identified. Specimens of each species were pressed and archived for future use.

In the winter, flats were moved from the growth chamber to a covered shade house at the University of Delaware Botanic Gardens. This transfer assists with physiological dormancy for species that require a second cold stratification. All flats were covered for protection from weather, potential seed predation, and wind-blown seeds. The following spring (April 2019), flats were transferred back to a growth chamber under the same environmental conditions as the previous year. After a period of two weeks with no seed germination, flats were fertilized with 800 ml of 173 ppm potassium nitrate to mimic natural N addition to soils in field conditions (Beauchamp et al., 2013; Benech-Arnold et al., 2000; Decocq et al., 2004; Finch-Savage & Leubner-Metzger, 2006). After two more weeks with no germination, soils were discarded. The study concluded in July 2019.

Statistical data analysis

All data analyses were performed in R (version 3.6.3; R Core Team, 2019) using the rstatix package (Kassambara, 2020) to test for statistical significance, considered at $\alpha = 0.05$. Trends toward significance were considered at $\alpha = 0.10$ for pairwise comparisons following post hoc analyses. To aid comparisons in abundance of the full plant community, taxa were placed into three forest strata: herbaceous (forbs, excluding herbaceous vines, measured as number of individuals), woody plants (trees, measured as individuals, and shrubs, measured as number of stems), and ground cover (herbaceous and woody vines, graminoids, and ferns; measured as percent ground cover). Within each forest site and prior to invasive plant removal, there were no differences in vegetation metrics between the treatment groups ($p > 0.10$; data not shown).

To assess plant community differences between the control and treatment strategies following invasive plant removal, we first calculated net change between the pre- and postremoval (2017 vs. 2019) plant communities in absolute values (as opposed to relative values) of native, exotic, and total shrub abundances; native, exotic, and total species richness of the full plant community; and a native FQA index. We used Welch's ANOVA followed by the Games–Howell post hoc test to determine significant differences in native, exotic, and total shrub abundances due to heteroscedasticity of the data. To determine significant differences in native, exotic, and total species richness and the native FQA index, we performed a one-way ANOVA followed by the Tukey honestly significant difference post hoc test. We tested for the effect of management strategy on all response variables (native, exotic, and total shrub abundances; native, exotic, and total species richness; and the native FQA index) separately for each forest patch.

To evaluate change over time in the plant community as a whole, we used the rank abundance curve change (RAC_change) function within the codyn R package (Avolio et al., 2019; Hallett et al., 2020). The RAC_change function calculates the relative change in species abundance of all species over time in several important ecological metrics: species richness, community evenness, rank abundance, species gains, and species losses. Relative (proportional) species abundance was calculated at the treatment level (by pooling the three replicate plots from each treatment) and separated by forest stratum (herbs, woody plants, and ground cover species). Three years of species abundance data were used in the analysis: preremoval (2017), the first growing season postremoval (2018), and two growing seasons postremoval (2019). To test for significance, we used the nonparametric Kruskal–Wallis test followed by Dunn's post hoc multiple comparison test, and each of the five metrics was analyzed separately. To further visualize how species ranks and abundances changed in response to management strategies, RACs were generated for each forest stratum at each site, for each year.

To determine similarities in vegetation structure among the control and treatment groups, we used the metaMDS function in the vegan R package for nonmetric multidimensional scaling (NMDS) with the Sørensen (Bray–Curtis) distance measure and a random starting configuration (Oksanen et al., 2020). Each site was analyzed separately. To minimize stress and maximize correlation between species with ordination configuration, a two-dimensional NMDS ordination solution with final stress values (<0.2) for all three sites was selected. Pearson correlation coefficients between relative species abundance and NMDS dimensions were used to assess species contributions in explaining community composition along different NMDS dimensions.

Due to differences in sampling methodology, statistical analyses were not performed between seed bank and vegetation communities; however, appropriate descriptive statistics were calculated and used to compare the two communities. Native, exotic, and total species richness, as well as Simpson's evenness (E) of seed bank species were calculated. Sørensen's index of similarity (C_S), which measures similarity based on shared species between two communities, was used to assess the similarity of the seed bank with the vegetation community pre- and postremoval and is calculated as follows:

$$C_S = \frac{2\,|A \cap B|}{|A| + |B|},$$

where A and B are the species richness of the seed bank and vegetation community, respectively. RACs were generated to examine the proportional distribution of species within the seed bank.

RESULTS

Across our forest sites, a total of 60 plant taxa (42 native, 15 exotic, and 3 unknown) were found in 2017, which consisted of 25 herbs (23 native, 1 exotic, and 1 unknown), 4 ferns (all native), 1 graminoid (exotic), 12 vines (8 native and 4 exotic), 12 shrubs (3 native, 8 exotic, and 1 unknown), and 6 trees (4 native, 1 exotic, and 1 unknown). In 2019, a total of 92 plant taxa (70 native, 18 exotic, and 4 unknown) were found across our forest sites; of those, there were 43 herbs (40 native, 2 exotic, and 1 unknown), 5 ferns (all native),

3 graminoids (1 of each status), 13 vines (9 native and 4 exotic), 13 shrubs (4 native, 8 exotic, and 1 unknown), and 15 trees (11 native, 3 exotic, and 1 unknown).

Plant compositional change following invasive species management

Net changes in shrub abundance, species richness, and native floristic quality

There were significant changes in shrub abundance, species richness, and native floristic quality following invasive plant management (Figures 2 and 3). In the low and high invasion sites, net change in native shrub abundance did not differ among the four strategies (Figure 2a,g). However, in the high invasion site, there was a significant reduction in exotic ($F_{3,3.80} = 235.91$, $p < 0.01$) and total ($F_{3,3.92} = 440.25$, $p < 0.01$) shrub abundance in the mulched treatment (exotic = -54.3 ± 2.2, total = -51.7 ± 1.5, $p < 0.01$) and a trend toward reduction in the removal-only treatment (exotic = -46.0 ± 12.6, total = -47.0 ± 11.0, $p < 0.10$) compared to the control (exotic = $+21.7 \pm 1.2$, total = $+22.0 \pm 1.0$; Figure 2h,i). Similarly, in the low invasion site, there was a significant reduction in total ($F_{3,4.06} = 12.63$, $p = 0.02$) shrub abundance in the removal-only treatment (-56.7 ± 8.4, $p = 0.04$) and a trend toward reduction in the seed mix treatment (-47.3 ± 8.7, $p = 0.07$) compared to the control (-5.0 ± 4.4; Figure 2c). Additionally, there was a trend toward reduced exotic ($F_{3,4.06} = 9.95$, $p = 0.02$) shrub abundance in the removal-only (-60.7 ± 10.3, $p = 0.051$) and seed mix (-49.7 ± 10.4, $p = 0.09$) treatments compared to the

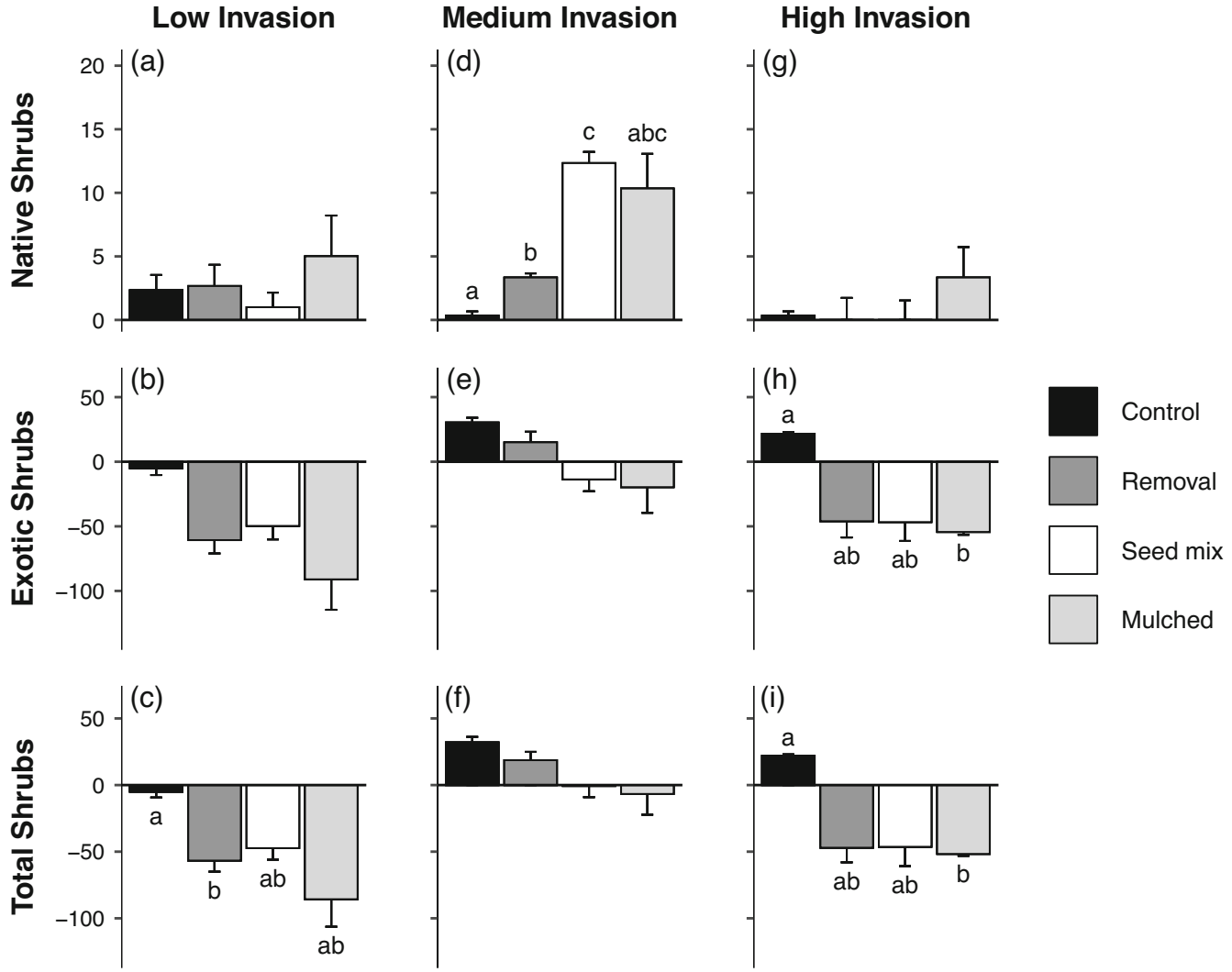

FIGURE 2 Mean net change (2017–2019) in native, exotic, and total shrub abundance among different treatment groups at all three sites. Letters indicate significant differences within each sub-panel; trends ($p < 0.10$) are reported in text. Note different *y*-axis scale for the native shrubs.

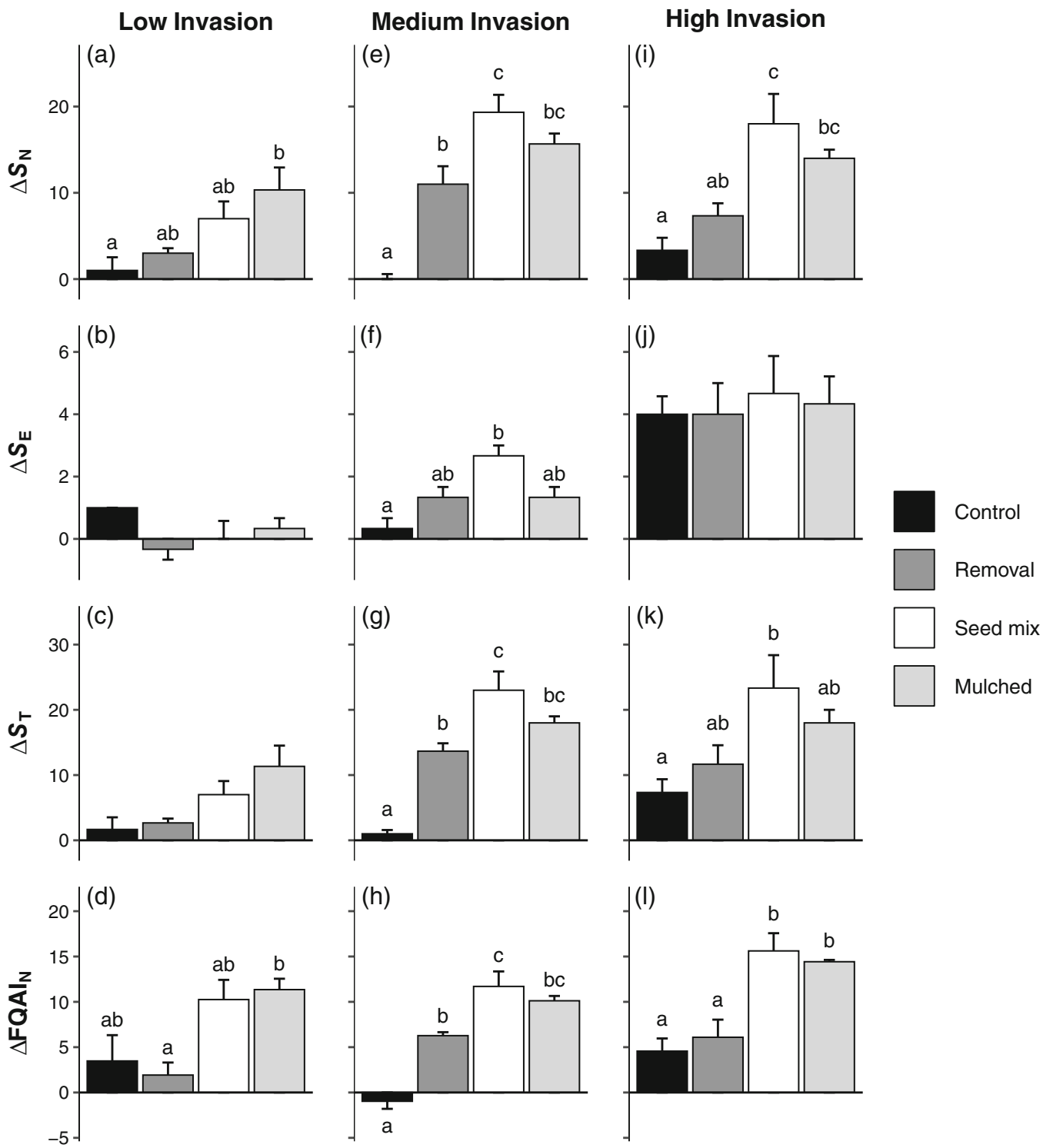

FIGURE 3 Mean net change (2017–2019) in total ($\Delta\overline{S}_T$), native ($\Delta\overline{S}_N$), and exotic species richness ($\Delta\overline{S}_E$) and native floristic quality assessment ($\Delta\overline{FQAI}_N$) among different treatment groups at all three sites. Letters indicate significant differences within each sub-panel; trends ($p < 0.10$) are reported in text. Note different *y*-axis scales.

control (-5.0 ± 5.3) in the low invasion site (Figure 2b). In contrast, in the medium invasion site, net change in native shrub abundance ($F_{3,4.11} = 45.53$, $p < 0.01$) was significantly greater in the removal-only treatment ($+3.3 \pm 0.3$) compared to the control ($+0.3 \pm 0.3$, $p = 0.01$) and in the seed mix ($+12.3 \pm 0.9$) compared to the removal-only treatment ($p = 0.01$) and control ($p < 0.01$; Figure 2d). There was a trend toward reduction

in exotic ($F_{3,3.92} = 6.30$, $p = 0.06$) shrub abundance in the seed mix treatment (-13.7 ± 9.2) compared to the control ($+30.3 \pm 3.7$, $p = 0.07$; Figure 2e), yet there were no significant changes in total shrub abundance among the strategies in the medium invasion site (Figure 2f).

In the low invasion site, the $\Delta\overline{S}_N$ ($F_{3,8} = 5.16$, $p = 0.03$) was significantly higher in the mulched treatment (10.3 ± 2.6) compared to the control (1.0 ± 1.5, $p = 0.03$) and showed a trend compared to the removal-only treatment (3.0 ± 0.6, $p = 0.08$; Figure 3a). There were no significant differences in $\Delta\overline{S}_E$ or $\Delta\overline{S}_T$ between the treatments (Figure 3b,c), though there were trends toward higher $\Delta\overline{S}_T$ ($F_{3,8} = 4.28$, $p = 0.04$) in the mulched treatment (11.3 ± 3.2) compared to the control (1.7 ± 1.9, $p = 0.051$) and removal-only treatments (2.7 ± 0.7, $p = 0.08$). The $\Delta\overline{FQAI}_N$ ($F_{3,8} = 5.57$, $p = 0.02$) was significantly higher in the mulched treatment (11.4 ± 1.2) compared to the removal-only treatment (1.9 ± 1.4, $p = 0.04$) and showed a trend compared to the control (3.5 ± 2.8, $p = 0.09$); additionally, a similar trend toward higher $\Delta\overline{FQAI}_N$ was also observed in the seed mix treatment (10.3 ± 2.2) compared to the removal-only treatment (1.9 ± 1.4, $p = 0.07$; Figure 3d).

In the medium invasion site, $\Delta\overline{S}_N$ ($F_{3,8} = 27.55$, $p < 0.01$), $\Delta\overline{S}_T$ ($F_{3,8} = 31.93$, $p < 0.01$), and $\Delta\overline{FQAI}_N$ ($F_{3,8} = 33.13$, $p < 0.01$) were significantly higher in the removal-only ($\Delta\overline{S}_N = 11.0 \pm 2.1$, $\Delta\overline{S}_T = 13.7 \pm 1.2$, $\Delta\overline{FQAI}_N = 6.3 \pm 0.4$), seed mix ($\Delta\overline{S}_N = 19.3 \pm 2.0$, $\Delta\overline{S}_T = 23.0 \pm 2.9$, $\Delta\overline{FQAI}_N = 11.7 \pm 1.7$) and mulched ($\Delta\overline{S}_N = 15.7 \pm 1.2$, $\Delta\overline{S}_T = 18.0 \pm 1.0$, $\Delta\overline{FQAI}_N = 10.1 \pm 0.5$) treatments compared to the control ($\Delta\overline{S}_N = 0.0 \pm 0.6$, $\Delta\overline{S}_T = 1.0 \pm 0.6$, $\Delta\overline{FQAI}_N = -1.0 \pm 0.8$, $p < 0.01$), and in the seed mix compared to the removal-only treatment ($p < 0.03$; Figure 3e,g,h). Additionally, there was a trend toward higher $\Delta\overline{FQAI}_N$ in the mulched treatment compared to the removal-only treatment ($p = 0.09$; Figure 3h). The $\Delta\overline{S}_E$ ($F_{3,8} = 8.25$, $p < 0.01$) was significantly higher in the seed mix treatment (2.7 ± 0.3) compared to the control (0.3 ± 0.3, $p < 0.01$), and trends toward higher $\Delta\overline{S}_E$ compared to the removal-only (1.3 ± 1.3, $p = 0.08$) and mulched (1.3 ± 0.3, $p = 0.08$) treatments (Figure 3f).

In the high invasion site, the $\Delta\overline{S}_N$ ($F_{3,8} = 10.05$, $p < 0.01$) was significantly higher in the seed mix (18.3 ± 3.8, $p < 0.01$) and mulched (14.0 ± 1.0, $p = 0.03$) treatments compared to the control (3.3 ± 1.5) and in the seed mix treatment compared to the removal-only (7.3 ± 1.5, $p = 0.03$) treatment (Figure 3i). The $\Delta\overline{S}_T$ ($F_{3,8} = 4.71$, $p = 0.04$) was significantly higher in the seed mix treatment (23.3 ± 5.0) compared to the control (7.3 ± 2.0, $p = 0.03$; Figure 3k). The $\Delta\overline{FQAI}_N$ ($F_{3,8} = 13.35$, $p < 0.01$) was significantly higher in the seed mix (15.6 ± 2.0) and mulch treatments (14.4 ± 0.2) compared to the control (4.6 ± 1.4, $p < 0.01$) and removal-only treatments (6.1 ± 1.9, $p \leq 0.02$; Figure 3l). There were no significant differences in $\Delta\overline{S}_E$ between any of the groups in the high invasion site (Figure 3j).

Multivariate plant community analysis

Results of ordination analysis revealed the shift in plant community composition following invasive plant removal (Figure 4). In the low invasion site, all preremoval (2017) plots clustered in plant composition, yet demonstrated dissimilar plant communities in response to management (Figure 4a). The control community showed little change in 2018, but shifted in the positive direction along both NMDS axes in 2019. The seed mix and mulched treatment plant communities became more dissimilar from one another and from the removal-only and control communities in 2018. However, in 2019, the seed mix and mulched plant communities were nearly identical to one another and similar to the removal-only community along NMDS Axis 1 yet, dissimilar to the removal-only community along Axis 2, though all three were still dissimilar to the control community (Figure 4a). Variation along NMDS Axis 1 was related to the native vine *Rubus flagellaris* ($r = -0.55$, $p < 0.01$) and other unidentified *Rubus* spp. ($r = -0.58$, $p < 0.01$) on the negative side, while the positive side was related to the invasive woody vine *L. japonica* ($r = 0.53$, $p < 0.01$). Variation along NMDS Axis 2 was associated with the native herb *Symplocarpus foetidus* ($r = -0.61$, $p < 0.01$) on the negative side, while the positive side was associated with the native shrub *Viburnum dentatum* ($r = 0.40$, $p = 0.02$) and native herbs *Hydrophyllum virginiana* ($r = 0.51$, $p < 0.01$) and *Polymnia canadensis* ($r = 0.46$, $p < 0.01$).

In the medium invasion site, all preremoval (2017) plots had similar plant communities (Figure 4b). In 2018 and 2019, control and removal-only plots remained similar to their respective preremoval plots due to considerable overlap in community dispersion between the preremoval (2017) and postremoval (2018 and 2019) plots (Figure 4b). The seed mix and mulched treatment plant communities became more dissimilar from one another in 2018, and there was greater dissimilarity between the removal-only and control plant communities in the mulched treatment plant community than in the seed mix plant community. However, in 2019, the seed mix and mulched communities were more similar to one another and shifted along NMDS Axis 1 toward the control and their respective preremoval communities (Figure 4b). The negative side of NMDS Axis 1 was associated with the native vines *Dioscorea villosa* ($r = -0.53$,

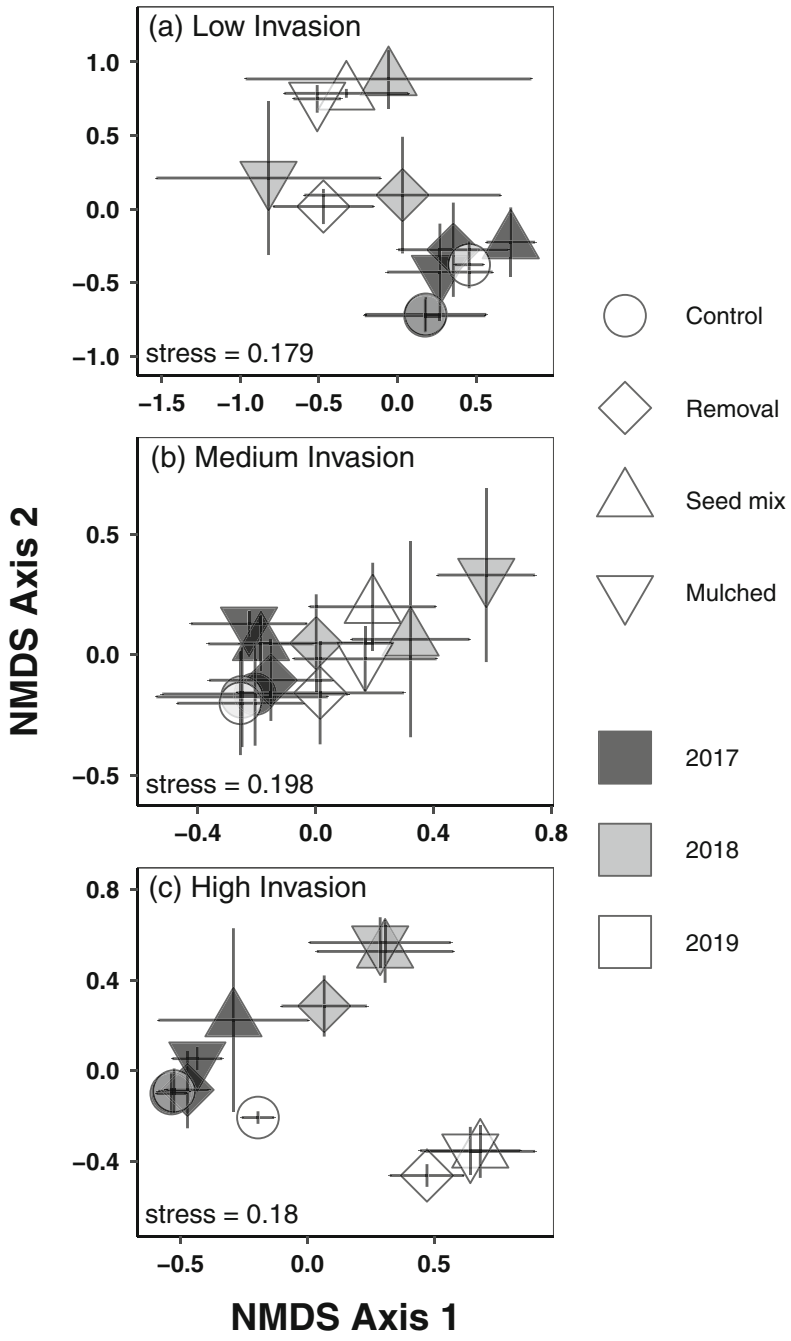

FIGURE 4 Nonmetric multidimensional scaling (NMDS) shows plant community composition (centroids and dispersion) of each treatment group over time within the low (a), medium (b), and (c) high invasion sites, before and after invasive plant removal (2017–2019). Note the different axis scales in each panel.

$p < 0.01$) and *Parthenocissus quinquefolia* ($r = -0.49$, $p < 0.01$), while the positive side was associated with the invasive grass *Microstegium vimineum* ($r = 0.50$, $p < 0.01$), the native tree *Carpinus caroliniana* ($r = 0.38$, $p = 0.02$), and the native shrub *Viburnum acerifolium* ($r = 0.33$, $p = 0.05$). Variation along NMDS Axis 2 was related to the native herb *Podophyllum peltatum* ($r = -0.50$, $p < 0.01$) and the native vine *Toxicodendron radicans* ($r = -0.44$, $p < 0.01$) on the negative side, while the positive side was associated with the native fern *Botrypus virginianus* ($r = 0.44$, $p < 0.01$).

In the high invasion site, all preremoval treatment plots (2017) had similar plant communities, which diverged following invasive plant management (Figure 4c). The control community showed little change in 2018, but shifted toward the positive direction along NMDS Axis 1 in 2019. All three treatment communities shifted in the positive direction along both NMDS axes in 2018, though

less so in the removal-only community, and the seed mix and mulched communities became nearly identical. The treatment communities shifted in the negative direction along NMDS Axis 2 in 2019 and became more similar to one another in 2019, yet remained dissimilar from the control community (Figure 4c). NMDS Axis 1 was associated with the invasive woody vines *C. orbiculatus* ($r = -0.58$, $p < 0.01$) and *L. japonica* ($r = -0.34$, $p = 0.04$) on the negative side, while the positive side was associated with the native herbs *P. canadensis* ($r = 0.57$, $p < 0.01$), *Mertensia virginica* ($r = 0.57$, $p < 0.01$), and *H. virginiana* ($r = 0.50$, $p < 0.01$). NMDS Axis 2 was associated with the native herbs *Pilea pumila* ($r = -0.52$, $p < 0.01$) and *Sanicula odoratus* ($r = -0.49$, $p < 0.01$) on the negative side and the native herbs *Claytonia virginica* ($r = 0.58$, $p < 0.01$) and *Anemone virginiana* ($r = 0.40$, $p = 0.02$) on the positive side.

Rank abundance

Across the forest strata, species rank and abundance of individual plants in the control group remained similar throughout the study (Appendix S1: Figure S1 and Table S3). However, we found shifts in rank and abundance of plant species following invasive plant removal in the first and second seasons postremoval (2018 and 2019), though changes accelerated in 2019; therefore, we report changes observed in 2019 only. Analysis of the full plant community using the codyn R package revealed a significant reordering of mean species ranks ($\chi^2 = 8.74$, $p = 0.03$) at the medium invasion site only (Figure 5). There were significantly more rank shifts between species in the seed mix treatment group (+0.27) compared to the control group (+0.10, $p = 0.03$) in 2019, two growing seasons after invasive plant removal was completed. No other trends or significant differences in (relative values, as opposed to absolute values) species richness change, evenness change, gains, or losses were observed ($p > 0.10$).

RACs for each site further illustrate rank shifts within the forest strata (e.g., woody, herbaceous, and ground cover) with additional management treatments following invasive plant removal. In the control group, *R. multiflora* remained the most abundant species in the woody plant layer at all three sites (Appendix S1: Figure S1 and Table S3). In 2017 and 2019 control plots, of the five-most abundant woody plant species, two were invasive in the low invasion site, three in the medium invasion site, and four in the high invasion site. In the herbaceous layer, the native herb *S. foetidus* was the only species present in control plots at the low invasion site in 2017; however, no herb species were present in 2019. In the medium and high invasion sites, the most abundant herb species in 2017 remained as such in 2019, though relative abundance of the native herb *Arisaema triphyllum* decreased by more than 50% in the high invasion site. In the ground cover layer, the invasive grass *M. vimineum* and invasive vine *L. japonica* displaced the native vine *Smilax rotundifolia* as the most abundant species at the low invasion site in 2019. In the medium and high invasion sites, the invasive woody vine *C. orbiculatus* was the most abundant ground cover species in 2017, though it was displaced by the exotic herbaceous vine *Stellaria media* as the most abundant in 2019 at the high invasion site.

In the removal-only treatment group (Appendix S1: Figure S2 and Table S4), *Lindera benzoin* became the most abundant plant species at the low invasion site in 2019, and the native tree *Acer rubrum* was gained. In the low invasion herbaceous layer, only *S. foetidus* was present in 2017, but an additional native species, *Erechtites hieraciifolius*, arrived and became abundant in 2019. In the low invasion ground cover layer (in rank order), the native woody vine *P. quinquefolia* became the most abundant species, followed by native woody vines *S. rotundifolia* and *T. radicans* in 2019. In the medium invasion site, invasive shrubs were the only woody species present in 2017 (Appendix S1: Figure S2 and Table S4), but the native tree species *Cornus alternifolia* arrived in the top five ranks in removal-only treatment plots along with 10 additional native trees gained at lower ranks. In the herbaceous layer, the top three species remained unchanged in 2019. In the ground cover layer, an exotic vine was replaced by a native herbaceous vine as the most abundant species in 2019. In the high invasion site, invasive shrubs remained the two-most abundant woody species in 2019, though a native tree species became the third-most abundant (Appendix S1: Figure S2 and Table S4). In the herbaceous layer, new native species were the three most abundant species in 2019, and one new invasive plant species arrived and displaced the previously abundant herbs. In the ground cover layer, the most abundant species remained exotic invasive species in 2019.

In the seed mix treatment group (Appendix S1: Figure S3 and Table S5), the most abundant species in the woody and ground cover strata at the low invasion site remained the same between 2017 and 2019; however, there were new native species present across all strata at the site in 2019. Similarly, exotic invasive species remained abundant at the high invasion site in the woody layer, yet many new native species were present in the herbaceous and ground cover strata two seasons after invasive plant removal with additional seed mix.

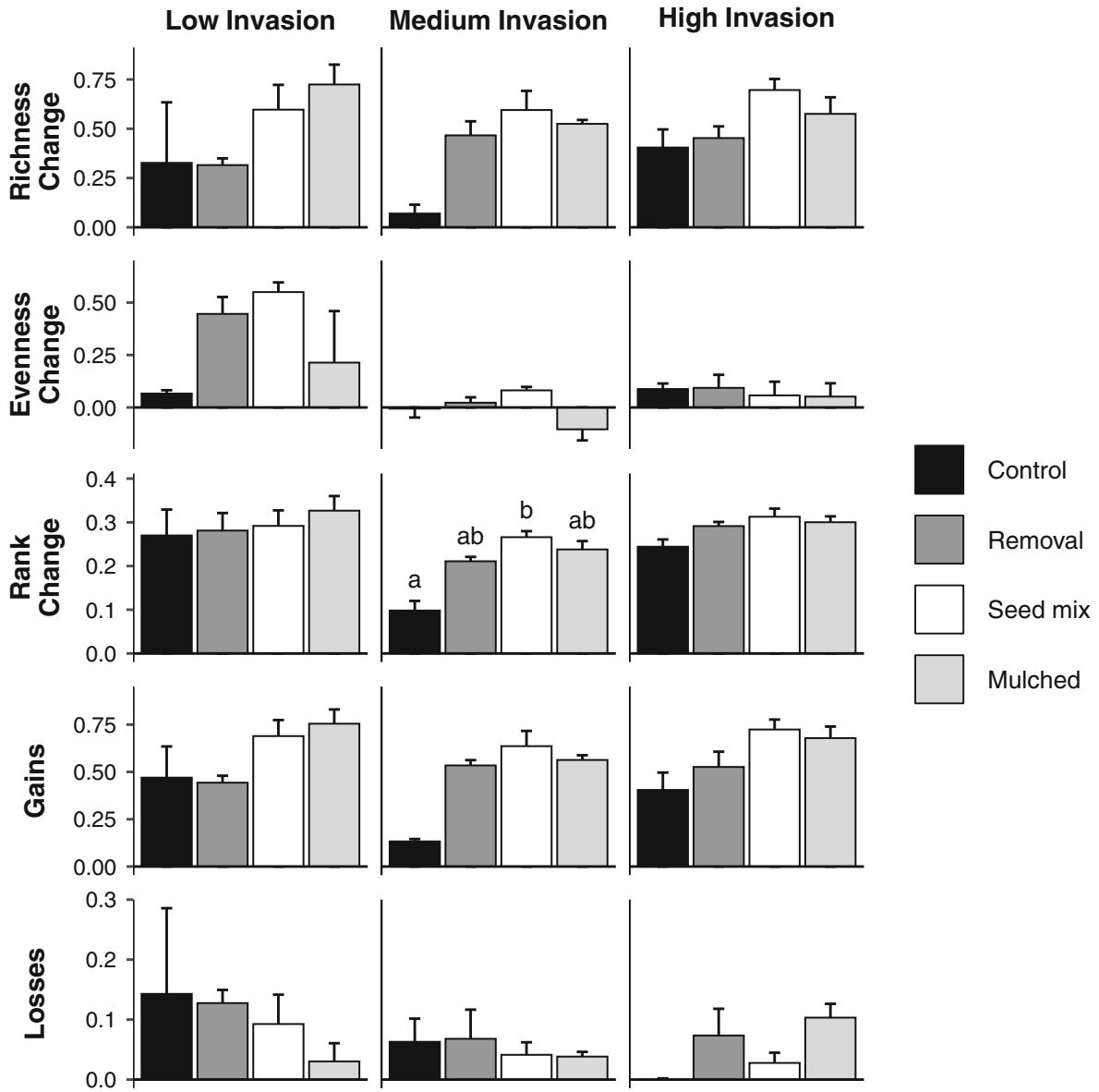

FIGURE 5 Results of community analysis from R package codyn, showing net change (2017–2019) in species richness, evenness change, rank change, and species gains and losses. Means and standard errors are shown. Letters denote significant differences among treatment groups.

In the medium invasion site, the invasive shrubs *R. multiflora* and *B. thunbergii* remained the two-most abundant species of the woody plant layer, but new native shrubs *V. dentatum* and *L. benzoin* and a new native tree *Prunus serotina* were the third-, fourth-, and fifth-most abundant species, respectively. Though woody species richness more than tripled at the medium invasion site, 7 of 20 were exotic species. In the herbaceous layer, 10 new native species were added, and the native spring ephemeral *Erythronium americanum* remained the most abundant species, followed by a new species from the native seed mix, *Mertensia virginiana*. In the ground cover layer, a native species (*Amphicarpaea bracteata*) replaced an invasive as the most abundant species, and five new native species were added.

In the mulched treatment group (Appendix S1: Figure S4 and Table S6), *R. multiflora* remained the most abundant woody species across sites following invasive plant removal. New species appeared in all strata except at the high invasion site, where fewer woody plant species were found in 2019; however, this site had the largest increase in herbaceous species (+17 species) and added native taxa to the ground cover layer (*Elymus* spp.). In the low invasion site, a single exotic species, found in the woody plant layer, was added; nonetheless, six new native woody species were added, along with nine native

herbs and five native ground cover species. In the medium invasion site, the two-most abundant species in each stratum remained the same, though 7 new native species appeared in the woody and herbaceous strata and 11 native species in the ground cover layer. In general, the woody, herbaceous, and ground communities gained species, with more even abundance across the ranks.

Seed bank composition and similarity to vegetation

Across the three forest sites, a total of 1905 individuals from 48 taxa emerged from the seed bank; 45 of the taxa were identified as species. The seed bank contained 29 herb/forb, three vine, five tree, four shrub, and seven graminoid species. There were 30 native species, 16 exotic species, and 2 of unknown status (Appendix S1: Table S2). The most abundant seed bank species was a non-native tree species, *Paulownia tomentosa* (58.8% of all seedlings), and it was absent from existing vegetation in our study plots. The next most abundant species were native: the herb *Phytolacca americana* (8.5% of all seedlings) and the vine *Potentilla canadensis* (4.7% of all seedlings). In the seed bank, native and total species richness was the lowest at the low invasion site (Figure 6), followed by the medium (Figure 7) and high (Figure 8) invasion sites (Table 1). The high invasion site also had the highest Simpson's evenness (E), followed by the low invasion and the medium invasion sites (Table 1).

Prior to invasive plant removal in the forests, the medium invasion site had the greatest total and native species richness, followed by the high invasion site and then the low invasion site, whereas the high invasion site had the greatest number of exotic species, followed by the medium and low invasion sites (Table 1). In 2019, two seasons after invasive plant removal, this pattern remained unchanged, though the high invasion site had the greatest absolute increase in native and total species (native = +24, total = +29), followed by the medium invasion site (native = +20, total = +25), and the low invasion site (native = +17, total = +21; Table 1; Appendix S1: Tables S7–S9). Seed bank species composition became more similar to standing vegetation species composition (i.e., in situ plant community) following invasive plant removal in the low ($\Delta C_S = +0.024$) and high invasion ($\Delta C_S = +0.074$) sites, but similarity decreased in the medium invasion site ($\Delta C_S = -0.046$; Table 1). However, the number of shared taxa between the seed bank and in situ plant community increased across all the sites (Tables 1 and 2). Five tree species

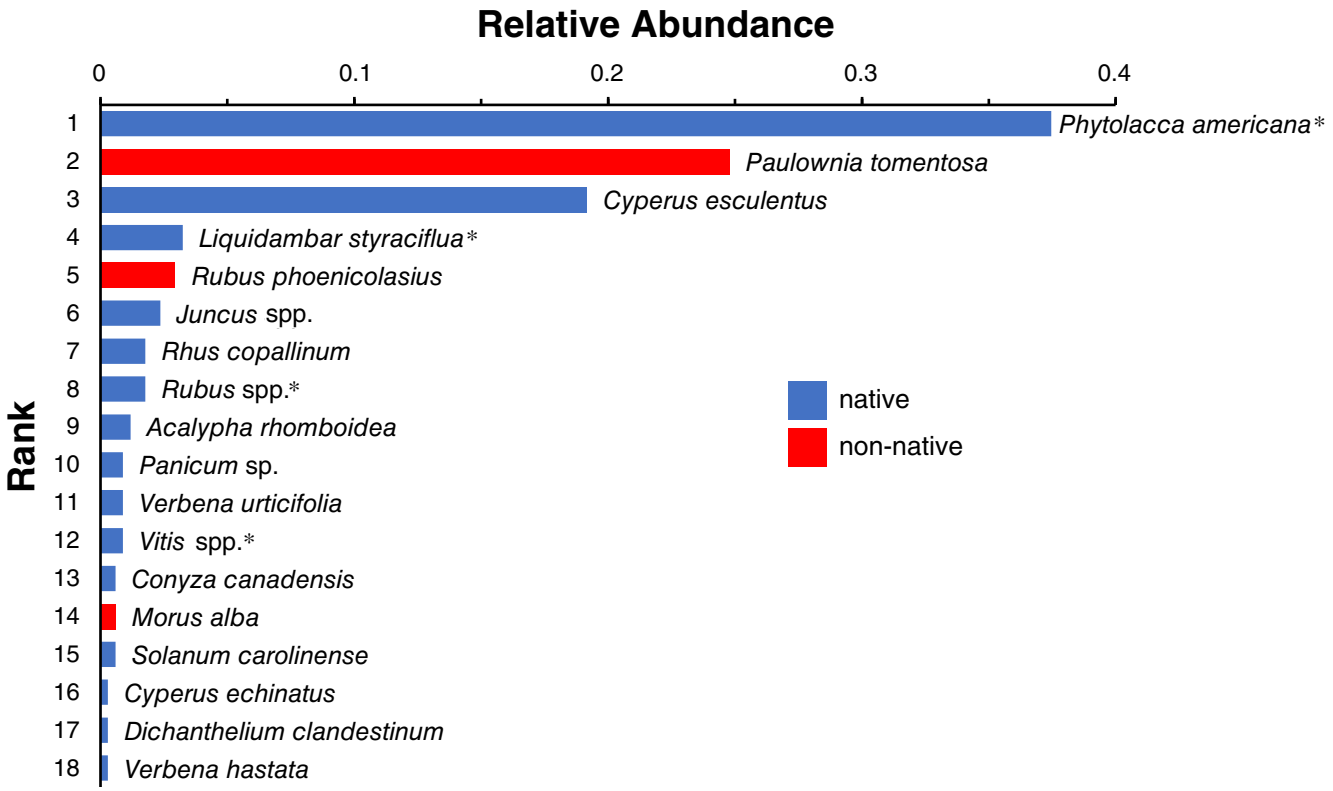

FIGURE 6 Rank abundance bar chart showing species identified in the seed bank at the low invasion site. Red bars indicate exotic species. *Denotes species found in the existing vegetation.

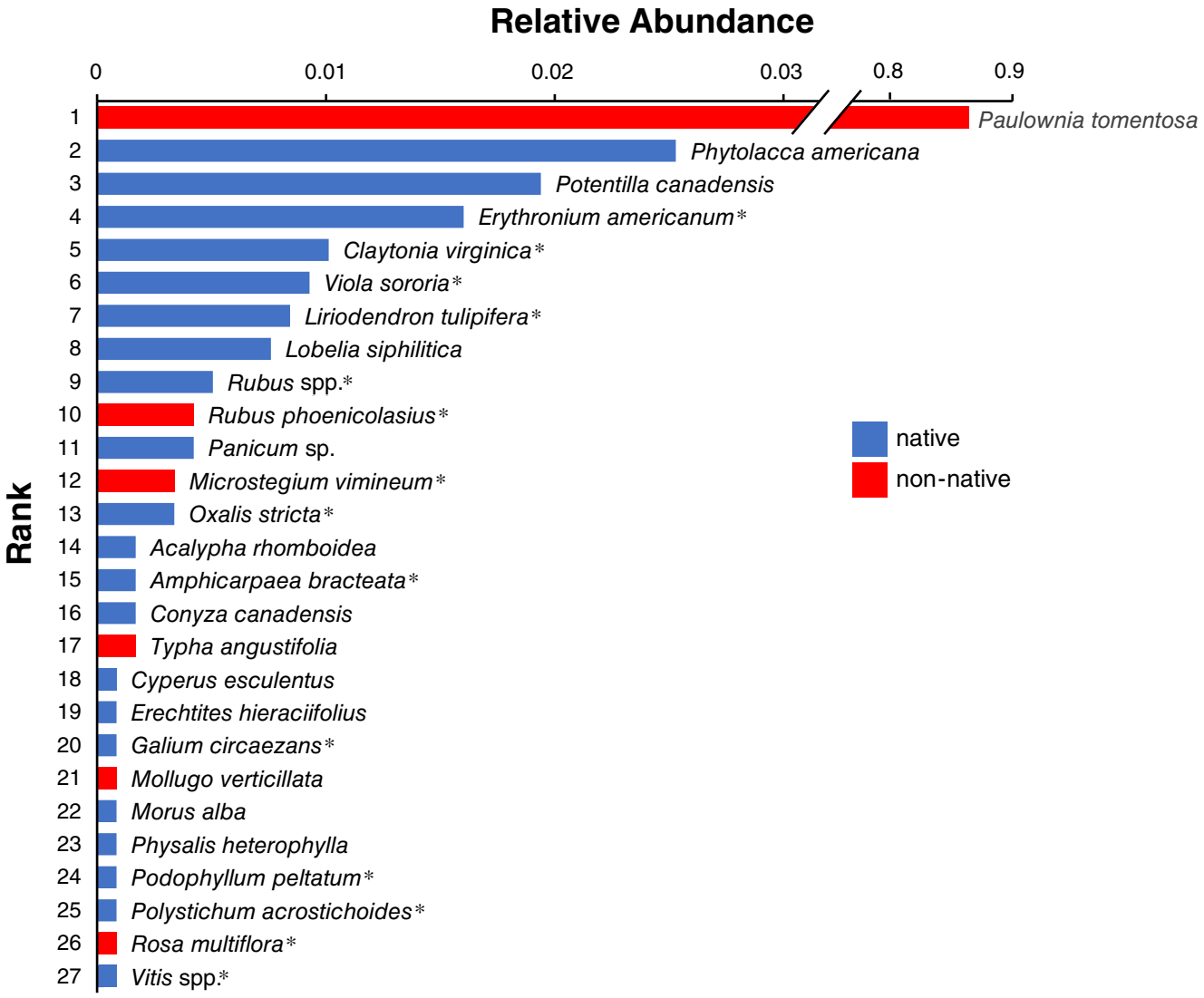

FIGURE 7 Rank abundance bar chart showing species identified in the seed bank at the medium invasion site. Red bars indicate exotic species. *Denotes species found in the existing vegetation.

germinated from the seed bank, and though none were present in the vegetation prior to invasive plant removal, three of these tree species were found in the vegetation after invasive plant removal (native *Liquidambar styraciflua* at the low invasion site, native *Liriodendron tulipifera* at the medium and high invasion sites, and the invasive *Ailanthus altissima* at the high invasion site; Table 2).

DISCUSSION

In general, invasive plant removal increased native plant richness and floristic quality and decreased the abundance of exotic invasive shrubs, yet additional management efforts further enhanced native richness and quality across our forest sites. Conducting invasive plant removal experiments across three forests with varying invasive plant abundance demonstrated complex responses to management efforts. For example, postremoval the low and high invasion sites had fewer total and exotic shrubs, yet the medium invasion site had significantly more native shrubs (Figure 2). Furthermore, the mulched experimental treatment resulted in greater native species richness and floristic quality in the low invasion site, whereas the seed mix resulted in greater native and total species richness and floristic quality in the medium and high invasion sites (Figure 3). Differential plant community responses to our experimental manipulations demonstrate the necessity of studying experimental management efforts across many different forest sites simultaneously, as well as the importance of understanding plant community composition within forests prior to invasive plant management.

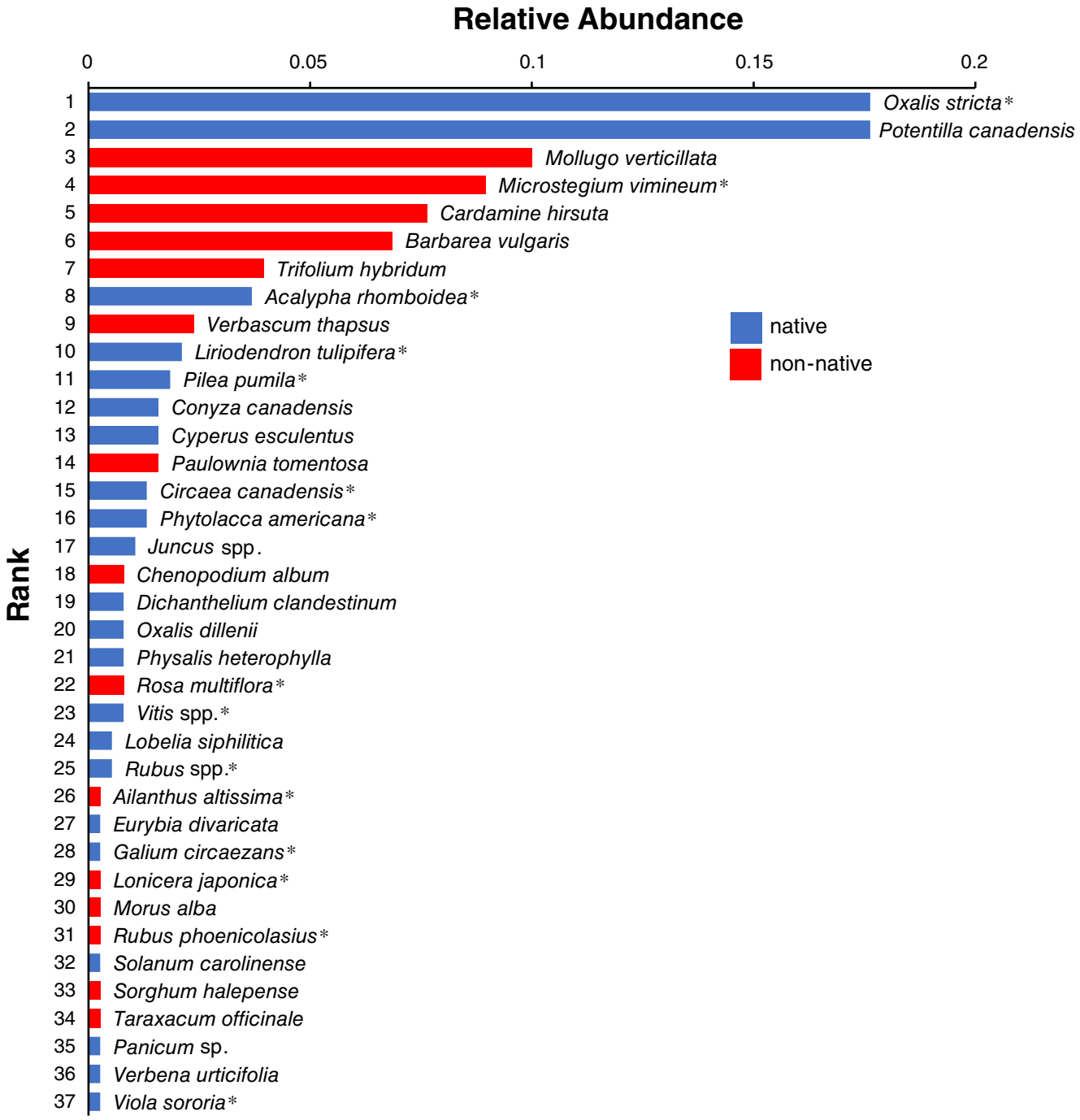

FIGURE 8 Rank abundance bar chart showing species identified in the seed bank at the high invasion site. Red bars indicate exotic species. *Denotes species found in the existing vegetation.

Plant community dynamics

Plant community change without management intervention

Plant community composition changes over time in forest ecosystems without human interventions, and the plant community dynamics in our control (invaded) and reference (noninvaded) plots provide insight on how plant composition naturally shifts over time. Two seasons after invasive plant removal (in 2019), *R. multiflora* was still the most abundant woody plant species across the three forest sites, though stem counts of *B. thunbergii* increased by 270%, accounting for the slight reduction in *R. multiflora* relative abundance across sites. Despite the continued dominance of exotic invasive shrubs in our forests, total, native, and exotic species richness increased or remained stable over time in our sites (Figure 3),

TABLE 1 Total (S_T), native (S_N), and exotic taxa richness (S_E), and Simpson's evenness (E; seed bank only) of preremoval (2017) and postremoval (2019) vegetation, and the seed bank (number of species of unknown native status not reported) at the low, medium, and high invasion forest sites.

Metric	Low	Medium	High
2017			
S_T	12	44	29
S_N	9	33	15
S_E	3	9	12
2019			
S_T	33	69	58
S_N	26	53	39
S_E	5	12	16
Seed bank			
S_T	18	27	37
S_N	13	19	20
S_E	3	7	15
E	0.229	0.049	0.28
C_S			
2017	0.133	0.338	0.242
2019	0.157	0.292	0.316
Shared taxa			
2017	2	11	7
2019	4	14	15

Note: For vegetation, evenness was calculated by growth habit and is not reported here. Sørensen's index of similarity (C_S), and number of shared taxa (found in both the seed bank and existing vegetation) preremoval (2017) and postremoval (2019). See Table 2 for a list of shared taxa by site and year.

indicating new species are still arriving in these invaded forests. At the low invasion site, *Quercus rubra* (red oak) seedlings were no longer present in the noninvaded reference plot but were gained in control plots; additionally, two native species were lost in the medium invasion reference plot but remained in control plots, suggesting a potential protective effect of exotic shrub cover from deer browse. *R. multiflora* is somewhat palatable to white-tailed deer, but its prickles can provide some defense against herbivory (Averill et al., 2016). Thus, shrub cover may indirectly protect small native plants co-occurring beneath the shrubs, but this is also dependent on the palatability of the native species (Peebles-Spencer & Gorchov, 2017).

The addition of native species can enhance native plant community composition, but only if there are no equal losses of native species. Without management (i.e., control plots), the only native herbaceous species present at the low invasion site was lost by 2019, and

TABLE 2 Taxa found in both the existing vegetation and in the seed bank preremoval (2017) and postremoval (2019) at the low, medium, and high invasion forest sites.

Invasion intensity	2017	2019
Low		
		LIQSTY
		PHYAME
	RUBSPP	RUBSPP
	VITSPP	VITSPP
Medium		
	AMPBRA	AMPBRA
	CLAVIR[a]	CLAVIR[a]
	ERYAME[a]	ERYAME[a]
	GALCIR	GALCIR
		LIRTUL
	MICVIM	*MICVIM*
		OXASTR
	PODPEL[a]	PODPEL[a]
	POLACR[a]	POLACR[a]
	ROSMUL[a]	*ROSMUL*[a]
	RUBPHO	*RUBPHO*
	RUBSPP	RUBSPP
	VIOSOR	VIOSOR
	VITSPP	VITSPP
High		
		ACARHO
		AILALT
		CIRCAN[a]
	GALCIR	GALCIR
		LIRTUL
	LONJAP[a]	*LONJAP*[a]
	MICVIM	*MICVIM*
		OXASTR
		PHYAME
		PILPUM
	ROSMUL[a]	*ROSMUL*[a]
	RUBPHO	*RUBPHO*
	RUBSPP	RUBSPP
	VIOSOR	VIOSOR
	VITSPP	VITSPP

Note: See Appendix S1: Table S2 for the complete list of species codes. Taxa in boldface are trees. Taxa in italics are exotic; RUBSPP may or may not contain exotic species.

[a]Denotes species that were growing at the exact location where a soil core was taken; though it is assumed that they germinated from the seed bank, these species never appeared when soil was placed in the growth chamber.

herbaceous species richness declined by 20% in the medium invasion site, where herbaceous richness was previously highest. Most herbaceous plants we identified across the three forest sites were spring ephemeral species (76%), which many native insect specialists depend on as their sole source of nutrition when they emerge in the spring (Kudo & Cooper, 2019; Parker et al., 2016). Thus, the loss of these native primary producers could have cascading effects that lead to the loss of native biodiversity beyond the plant community. In contrast, herbaceous species richness increased at the high invasion site, which may be related to the abundance of exotic woody stems and any protective effect they might provide against herbivory (Moore, 2022). Future studies could continue long-term monitoring of invaded, unmanaged plots where deer are present to examine this potential dynamic more thoroughly. While new native species were observed in control plots in all forest sites over the three years, the relative abundance of native species decreased in most forest strata (Appendix S1: Table S6 and Figure S1). This suggests exotic species abundance will increase and native species abundance will decrease over time without management in our forest sites; however, these changes may depend on invasion intensity and plant–pathogen interactions (Chiuffo et al., 2018; Ericson et al., 2017; Flory et al., 2011, 2018; Flory & Clay, 2013; Policelli et al., 2018; Stricker et al., 2016).

The abundance of problematic invasive woody plants increased at the medium and high invasion sites in 2019 without invasive plant management. Seedlings and saplings of invasive shrubs at the medium invasion site nearly doubled, and seedlings of the only native tree species, the critically endangered ash (*Fraxinus americana* or *F. pennsylvanica*; Jerome et al., 2017; Westwood et al., 2017), were no longer present (*Fraxinus* spp. [FRASPP]; Appendix S1: Figure S6). Similarly, at the high invasion site, all exotic woody plants increased, and *B. thunbergii* was now present in both the seedling and sapling layers (Appendix S1: Figure S7). This may indicate that invasion intensity is becoming more severe at these sites, with competition between invasive shrubs and native tree species threatening forest regeneration (e.g., Link et al., 2018; Ward et al., 2013), making potential management ever more important while potentially more difficult in the future.

Plant community change with management

To increase and maintain native species in our forests, we removed exotic invasive shrubs across a low, medium, and high invasion forest. We found that simply removing invasive plants without any further treatment decreased total shrub abundance in the low invasion site and increased native shrub abundance in the medium invasion site, where it was the lowest prior to removal (Figure 2). We observed trends toward decreased exotic shrub abundance in the low and high invasion sites, suggesting removal alone may be a valuable investment when the exotic species spread is in the early or late stages of invasion, though it remains unclear whether repeated removal of invasive plants would have enhanced the effect. In contrast, we found that removal alone increased mean native and total species richness and $FQAI_N$ at the medium invasion site (Figure 3e,g,h) suggesting exotic shrub removal increases the value of the plant community even when exotic shrubs (<1 m in height; seedling layer; Appendix S1: Figure S6) increase in abundance. Since exotic shrub abundance did not decrease, simply removing invasive plants has the same effect as doing nothing at all with respect to exotic shrubs in the medium invasion forest site. For land managers with limited resources and personnel, this is an important finding, as attempting to reduce exotic and/or total shrub abundances by a single removal is not an effective use of time, money, and people power.

The addition of native seed mix further increased native shrub abundance in the medium invasion site. Given that native shrub abundance was the lowest at this site prior to removal and that we observed unexpected increases in exotic shrub abundance with the removal-only treatment, a native seed mix could enhance the native plant community without exotic plant increases. Moreover, we found seed mix addition significantly increased native species richness and $FQAI_N$ at the medium and high invasion sites, yet had no effect on the species richness at the low invasion site (Figure 3), though there was a trend toward increased $FQAI_N$. These findings suggest some other environmental factors (e.g., soil conditions, land-use history) at the low invasion site may contribute to low native seed germination in this forest.

The addition of C-rich mulched stems had the greatest effect at the low invasion site, where we observed the largest increases in native species richness and floristic quality compared to other treatment strategies (Figure 3). Our low invasion site has the most recent forest canopy closure (Trammell et al., 2020) and may be experiencing altered soil conditions from previous land-use activities (e.g., agriculture), which may explain why we observed these patterns after enriching soil C. For managers questioning whether a seed mix addition alone is enough to reach their management goals, our results suggest this is dependent on forest invasion

intensity as well as other forest site conditions and land-use history. In the medium and high invasion sites, the mulch addition still resulted in significant improvements in species richness and floristic quality compared to the control group, but the effect was marginally suppressed when compared to the seed mix treatment (Figure 3). In the high invasion site, the mulch treatment led to large decreases in exotic and total shrub abundances, suggesting that the addition of a carbon-rich substrate may alter soil properties and ecosystem processes (i.e., soil-N cycling and decomposition) that would otherwise promote exotic shrub growth at the site.

The plant communities within a forest site (i.e., control and the three treatment groups) were similar prior to invasive plant removal, as expected (Figure 4). However, the low and high invasion sites show the most distinct and consistent responses to management, shifting away from the control plots, whereas the medium invasion site shows greater dispersion and overlap among pre- and postmanagement communities. This shift back to preremoval communities in the medium invasion site is in part due to the increased presence and abundance of the invasive grass *M. vimineum*, a shade-tolerant species that easily invades disturbed forests and is difficult to control once established (Fryer, 2011; Gibson et al., 2002). *M. vimineum* was present in a single treatment plot prior to removal and by 2019 had spread to all but one treatment plot, yet it remained absent from control plots, where the lack of sunlight under dense shrub cover likely prevented *M. vimineum* establishment and spread (Huebner, 2010a, 2010b; Schramm & Ehrenfeld, 2010). Thus, our management efforts likely facilitated this secondary invasion by increasing sunlight and disturbing the soil and leaf litter layer (Marshall & Buckley, 2008; Nord et al., 2010; Oswalt & Oswalt, 2007) in a forest where this particularly problematic invasive species was already present. These findings demonstrate the need to identify existing species and assess plant communities prior to implementing management practices that can disturb soil and ground cover.

Seed bank and similarity to vegetation

Within each site, we found that the initial in situ plant community differed from seed bank species composition, but the low and high invasion sites became more similar to their seed banks following invasive plant removal (Table 1). The forest with the highest species richness (i.e., medium invasion site) became less similar following invasive plant removal due to the increase in species richness in postremoval vegetation that was not shared with the seed bank. The most abundant species, by far, in the seed bank across the three forest sites was the invasive tree *P. tomentosa*. The potential threat posed by *P. tomentosa* is substantial, as it accounted for nearly 87% of all germinants in the seed bank at our medium invasion site (Figure 7) and 25% at our low invasion site (Figure 6). The forest canopy consists primarily of native species (e.g., Trammell et al., 2020; Trammell & Carreiro, 2011), but *P. tomentosa* can become invasive when established, and at least 15 US states include it on their invasive species watchlist (https://www.invasive.org). While mature trees of this species were common along the forest's edge, *P. tomentosa* was not present in our forest plant communities. Thus, the prevalence of *P. tomentosa* in the seed bank demonstrates the potential threat of this exotic invasive tree to the forest if/when canopy gaps form due to extreme weather events or exotic pests.

Implications for forest management

Removal alone was the most effective strategy for limiting reinvasion of exotic shrubs that were present before invasive plant removal in the low invasion site (Appendix S1: Figure S5). Under a medium invasion scenario, removal alone may be an effective strategy for increasing native shrub abundance (Figure 2), species richness, and $FQAI_N$ (Figure 3). This strategy may be most appealing to landowners or managers of smaller properties, or those with smaller budgets, because of the ease with which it can be implemented—it is the quickest, cheapest, and easiest strategy to repeat—and may make subsequent follow-up treatments more feasible. Over several years, removal and monitoring, without additional management, may be enough to counteract the reinvasion we observed in the medium invasion site.

If managers are less constrained by financial resources, then hand-sowing a native seed mix after invasive plant removal could result in even larger increases in native shrub abundance under medium invasion scenarios (Figure 2) and improved native plant richness and floristic quality under medium and high invasion scenarios, especially in the woody and herbaceous forest strata (Appendix S1: Figure S3). Since seeds can easily be transported to field locations and no further equipment is necessary for hand sowing, this strategy may appeal to managers with larger budgets grappling with medium- to high-intensity invasions. Our seed mix included only herbs, grasses, and sedges, and future research could examine how the incorporation of native woody seeds or direct sowing (i.e., planting) affects the resulting plant community.

We found that mulching and applying invasive stems (plus addition of native seed mix) was the best strategy for improving the native plant community and reducing exotic shrubs at the low invasion site (Figures 2 and 3). Additionally, richness across all three forest strata at the site was the highest with this strategy (Appendix S1: Figure S4). Conversely, at the medium and high invasion sites, this strategy depressed richness and $FQAI_N$ relative to the seed mix addition treatment and led to smaller increases in richness in the three forest strata, though there was a significant reduction in exotic and total shrub abundance at the high invasion site. If management goals mainly involve reducing exotic or total shrub abundance, which may help stimulate tree germination and increase survival, this strategy could prove useful in highly invaded areas. Transporting and using a chipper/mulcher on-site may be difficult but still feasible if trails or other points of entry provide access to forest interiors, as was the case at our sites. However, more significant improvements would be made in sites experiencing a low amount of invasion, and this strategy would be more easily executed where density of shrubs does not impede movement. Ultimately, knowledge of the existing plant community, seed bank, and current constraints should inform land managers about which strategy is appropriate for achieving their desired goals.

CONCLUSIONS

While all three treatment strategies improved native plant richness and floristic quality in the plant community, the effects were site dependent. Application of mulched stems plus a native seed mix improved the native plant community the most in a younger, less invaded forest and reduced the shrub invasion in a highly invaded forest. In contrast, native seed mix alone provided the greatest improvement to the native plant community in our medium and high invasion sites. The results of this research may have broad implications for land managers and other professionals involved in restoration projects. When considering management strategies, it is best to weigh these benefits and trade-offs and choose the one that is most appropriate for the desired management goals. This determination will likely be made based on existing financial and personnel limitations, presence and abundance of invasive shrub species, and existing native biodiversity. Depending on forest type (i.e., invasion intensity) and management strategy, these easy-to-implement and cost-effective treatments show improved native plant communities with management. However, a lack of management leads to increased invasion, regardless of forest type, demonstrating that these invaded forests will continue to experience reductions in native species and increased dominance of plant invaders in the understory. To maintain native forest ecosystems, management efforts are needed to restore and enhance future trajectories of the plant community.

AUTHOR CONTRIBUTIONS

Eric Moore and Tara L. E. Trammell formulated the idea and developed methodology. Eric Moore analyzed data and wrote the manuscript. Tara L. E. Trammell assisted with data analysis and manuscript revision. Vincent D'Amico established a long-term urban forest study, developed methodology, and contributed to revision.

ACKNOWLEDGMENTS

We thank Meghan Avolio for reviewing the manuscript. We also thank Aubrey Inkster for field and greenhouse assistance, and Maggie Bayalis, Samantha Nestory, Nathaly Rodriguez, Gavin Rosier, and Noah Totsline for field assistance. We acknowledge the University of Delaware Research Foundation and USDA Forest Service (#16-JV-11242308-122) for funding. We thank the Delaware Environmental Institute for the fellowship awarded to Eric Moore.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Moore et al., 2022) are available from the EDI Data Portal: https://doi.org/10.6073/pasta/cef7ba55f59a03594f24f84623709e12.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Moore, Eric, Vincent D'Amico, and Tara L. E. Trammell. 2023. "Plant Community Dynamics Following Non-Native Shrub Removal Depend on Invasion Intensity and Forest Site Characteristics." *Ecosphere* 14(1): e4351. https://doi.org/10.1002/ecs2.4351