

ARTICLE

Multiple stressors prevent gains in native plant diversity following invasive species removal

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Abstract

Land managers spend substantial resources managing invasive species to mitigate their negative ecological and economic impacts. However, invasive species management is seldom coupled with empirical assessments of management outcomes or the ecological impacts of the target species. Additionally, the study of invasive species has, until recently, neglected to acknowledge co-stressors on native communities, which often are the drivers of ecological degradation. We assessed the effects of the invasive plant *Vincetoxicum rossicum* and its removal on understory plant communities, as well as whether these effects were mediated by deer and invasive earthworms. We used paired fenced and open plots with *V. rossicum* and an open plot without *V. rossicum* at each of the three forested sites in New York State Parks from 2017 to 2020. Following a nested design, we located paired sets of open and fenced plots in areas where *V. rossicum* was experimentally removed and in areas where it was unmanaged. After three years of *V. rossicum* removal, *V. rossicum* significantly declined. However, the ultimate goal of management was native plant recovery. Contrary to this aim, native plant diversity and cover increased if *V. rossicum* was left unmanaged but did not change with *V. rossicum* removal. Thus, we provide strong evidence that reducing target species abundance does not always translate into native plant recovery. This disparity may be because deer and invasive earthworms are stronger drivers of understory plant communities than *V. rossicum*, as native plant cover and diversity were lower the more earthworms were in a plot and invasive plant species declined after fencing to exclude deer. Management that prioritizes reducing deer and earthworm impacts over invasive plant removal is therefore worth exploring, especially when coupled with continued monitoring to assess if these actions result in the desired management outcomes. Overall, our findings underscore the need to collect data to test management assumptions: reducing the abundance of an invader may not always result in native plant recovery, especially if other stressors are the ultimate drivers of change in invaded communities.

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KEYWORDS

invasive earthworms, invasive plants, management, multiple stressors, understory plant community, *Vincetoxicum rossicum*, white-tailed deer

INTRODUCTION

Invasive species management is a cornerstone of conservation and restoration efforts worldwide (Kopf et al., 2017). As the demand to prevent and mitigate negative impacts of non-native species grows, evidence that can guide managers to assess whether actions effectively lead to ecosystem recovery is increasingly needed (Simberloff et al., 2013). However, data on the outcomes of invasive species management are rarely collected (Kettenring & Adams, 2011), and when collected often reveal management has limited success (García-Díaz et al., 2021; Martin & Blossey, 2013) or unintended negative consequences on native taxa (Kopf et al., 2017; Rinella et al., 2009; Zarnetske et al., 2010). Further, even if management does not impact native taxa directly, native diversity or ecosystem function may not increase following removal of an invasive plant because of legacy effects (Cuddington, 2011; Reynolds et al., 2017) or because other invasive species may colonize empty space created by removal efforts (Kuebbing et al., 2013; Luken et al., 1997). Addressing this knowing-doing gap is therefore critical to effective and efficient management and is of great interest to land managers, who consistently face the dilemma of how to allocate limited resources given the extraordinarily high cost of managing invasive species (Crystal-Ornelas et al., 2021; Gren, 2008).

However, understanding what factors underlie management success is often hindered by failure to identify the drivers of ecosystem change (MacDougall & Turkington, 2005), as many co-occurring stressors—not just invasive species—may impact native plant communities (Dávalos et al., 2014; Fisichelli & Miller, 2018; Kuebbing et al., 2013). In forests in the northeastern United States, white-tailed deer (*Odocoileus virginianus* Zimmerman) and invasive earthworms introduced from Europe (Lumbricidae) and Asia (Megascopidae) are known stressors that alter plant communities (Bradshaw & Waller, 2016; Chang et al., 2021; Dávalos et al., 2015a; Frelich et al., 2019). Deer are selective herbivores and, when prevalent, may reduce the abundance of highly preferred plant species (often forbs and woody saplings), leading to the dominance of less preferred plants (often graminoids and ferns) (Averill et al., 2016; Nuttle et al., 2014; Rooney, 2009). Deer also impact plant communities through indirect nonconsumptive effects, such as by altering physical and chemical soil conditions (Kardol et al., 2014; Sabo et al., 2017). Deer management may therefore play a crucial role in the restoration of invaded

communities, especially as deer have also been implicated in facilitating multiple invasive plant species, including *Alliaria petiolata* (Bieb.) Cavara Grande, *Berberis thunbergii* D.C., and *Microstegium vimineum* (Trin.) A. Camus (Dávalos et al., 2015b; DiTommaso et al., 2014; Kalisz et al., 2014; Knight, Dunn, et al., 2009; Shen et al., 2016).

Introduced earthworms are similarly strong drivers of community-level change. Earthworms alter the chemical and physical characteristics of soil, leading to cascading impacts on understory plant and animal communities (Frelich et al., 2019; Moore et al., 2018; Tiunov et al., 2006). In North America, greater earthworm abundance and diversity are also associated with lower plant diversity and more graminoids (Craven et al., 2017). Additionally, earthworms alter competitive outcomes of interactions between native and invasive species (Nuzzo et al., 2009; Whitfeld et al., 2014) and may become more abundant in the presence of deer (Dávalos, Simpson, et al., 2015; Mahon & Crist, 2019). Invasive plants, earthworms, and white-tailed deer may therefore interact with each other (Dávalos et al., 2014; Fisichelli & Miller, 2018) to drive plant community change in forests in the northeastern United States. However, the combined effects of these stressors remain understudied, particularly in the context of invasive plant management.

Here we use a multiple-stressor framework to assess how deer, invasive earthworms, and invasive plant management influence understory plant communities. We use *Vincetoxicum rossicum* (Kleopow) Barbarich (pale swallowwort) as a case study, as it is an active management priority in northeastern North America. Introduced from eastern Europe in the late 1800s, *V. rossicum* is a creeping vine that forms dense monocrops in both open-field and understory habitats (DiTommaso et al., 2005; Sheeley & Raynal, 1996) and is associated with reduced plant richness and functional diversity (Carboni et al., 2021; Sodhi et al., 2019), lower arthropod diversity (Ernst & Cappuccino, 2005), and distinct microbial communities (Bugiel et al., 2018). In addition, *V. rossicum* acts as an oviposition sink for *Danaus plexippus* L. (monarch butterfly) (Casagrande & Dacey, 2007) and is abundant in endangered alvar communities in New York State and known to encroach habitat of *Asplenium scolopendrium* var. *americanum* (Fernald) Kartesz & Gandhi (American hart's-tongue fern), a federally threatened species. Yet the mechanism by which *V. rossicum* drives declines in community diversity—and indeed, whether *V. rossicum* is the ultimate driver or

merely the passenger of change—remains less well understood (DiTommaso et al., 2005; but see Carboni et al., 2021). Thus, understanding whether common stressors such as deer and earthworms independently drive declines in community diversity or mediate the impact of *V. rossicum* and its management is particularly important in this system.

Further, conventional management of *V. rossicum* is costly and has limited efficacy. Managers are therefore expending valuable resources to implement tools that have limited success at controlling the spread and reducing the abundance of *V. rossicum*, making the knowing-doing gap especially critical. Manual and mechanical management of *V. rossicum* requires consistent treatment over multiple years to drive declines in target plant populations, likely due to persistence via belowground structures and the seedbank (Biazzo & Milbrath, 2019; Milbrath et al., 2016). Chemical management using glyphosates or triclopyr herbicides can significantly reduce populations but still requires continued applications to reduce the seedbank and prevent new colonization events (DiTommaso et al., 2013). Chemical management also risks negative population-level impacts on native plants (Rinella et al., 2009; Smith et al., 2006). In addition to chemical control, the defoliating moth *Hypena opulenta* Christoph has been introduced as a biocontrol. However, five years after releases of *H. opulenta* in Ontario, Canada, reported damage is well below the level necessary to control *V. rossicum* populations (Bourchier et al., 2019; Livingstone et al., 2020).

To address this knowing-doing gap, we used understory vegetation surveys at three forested sites in New York in which *V. rossicum* has been identified as a management priority. Specifically, we quantified the impact of *V. rossicum* by comparing plant community composition and diversity between neighboring uninvaded and invaded plots and we quantified the impact of *V. rossicum* removal by comparing neighboring invaded plots with and without management. We also explored whether differences between these plots were associated with earthworms and deer, two major ecological drivers in the system.

In line with previous findings (Table 1), we hypothesized that *V. rossicum*, management to remove *V. rossicum*, deer, and earthworms are all major drivers of change in understory plant communities. We predicted that cover, diversity, and composition of plants other than *V. rossicum* would be negatively affected by each stressor and that *V. rossicum* cover would be positively affected by deer and earthworms. Further, invasive species management is motivated by the expectation that management will ameliorate the negative impacts of the invader, despite limited evidence for this expectation (Kettenring & Adams, 2011; Quirion et al., 2018). Thus, we also predicted that

management would be successful, such that over time, managed plots with *V. rossicum* and plots without *V. rossicum* should become increasingly similar in plant community composition and native plant diversity. Finally, we designed our models to account for potential interactive effects, such as whether earthworms and deer mediate the effects of *V. rossicum* and *V. rossicum* removal. We did not make a priori predictions regarding the direction of these hypothesized interactive effects, as how these stressors mediate management and plant invasions remains understudied.

METHODS

We conducted research at three NYS Parks (Figure 1a): Buttermilk Falls, Ithaca (42.429370, −76.521641), Green Lakes, Fayetteville (43.063065, −75.972341), and Taughannock Falls, Trumansburg (42.550822, −76.60726). The study area is situated in the Allegheny Plateau (Buttermilk Falls and Taughannock Falls) and Onondaga escarpment (Green Lakes) of the Appalachian Plateau. Locations targeted for *V. rossicum* removal were based on management priorities of the parks and available funding. We selected sites with a comparable nearby area with *V. rossicum* that would remain unmanaged for the duration of the study. Since their establishment in the 1920s, all parks have been under mixed management prioritizing conservation and recreation. Forests remain fragmented and with significant trail-forest edge habitat. We selected sites in secondary mixed hardwood forests dominated by *Acer* spp., *Fraxinus* spp., and *Pinus strobus* L under 70%–90% canopy cover and with similar initial *V. rossicum* cover (10%–44% cover, on average, for each open or fenced plot).

We balanced investigating the ecological effects of multiple stressors with the reality of local management priorities and site limitations. We therefore did not conduct a fully factorial design, but instead prioritized quantifying the impact of *V. rossicum* and *V. rossicum* removal, and whether the impact of each is mediated by earthworms or by fencing to exclude white-tailed deer. In June 2017, within each site, we selected two areas that contained *V. rossicum* (ranging from 10.00% to 44.48% cover): one area to be managed for *V. rossicum* and one area to be left unmanaged (spaced 0.8–2.4 km apart). We selected areas that were similar in canopy cover, slope, and land use history. Within each area, we established two paired 15 × 15 m plots (spaced 10–15 m apart) and randomly assigned one plot to be fenced to exclude white-tailed deer and one to be open to allow deer access. We constructed fences in summer 2018 using black polypropylene fencing (2.6 m high, 3.8 × 5 cm cell size,

TABLE 1 Summary of previously reported trends of how each of our tested four stressors (deer, earthworms, *Vincetoxicum rossicum*, and management of *V. rossicum*) impact understory plant community composition.

Stressor	Previously reported trends	Does our study support these trends?	Our findings
<i>V. rossicum</i>	Areas with <i>V. rossicum</i> have different plant community composition and less native plant diversity than areas without <i>V. rossicum</i> (Carboni et al., 2021; Sodhi et al., 2019)	No	Native plant cover and total species richness, diversity, and evenness did not differ between open plots with <i>V. rossicum</i> and open plots without <i>V. rossicum</i> (plot type was dropped from our models because it was not significant). However, presence of <i>V. rossicum</i> alters plant community composition, but this effect is mediated by the impacts of management and time (three-way interaction between <i>V. rossicum</i> , management, and time: $p < 0.01$).
Management of <i>V. rossicum</i>	Management of <i>V. rossicum</i> alters plant community composition, increases plant diversity, and decreases abundance of <i>V. rossicum</i> (Biazzo & Milbrath, 2019)	Partially ✓	Changes in plant community composition over time were greater for managed areas than for unmanaged areas (Figure 5); however, native plant cover and total species richness and diversity increased over time for unmanaged plots, but did not change over time for managed plots (Figure 3) In managed plots, <i>V. rossicum</i> cover decreased over time ($p < 0.001$; Figure 3a,c)
Fencing	Fencing to exclude deer alters plant community composition, increases native plant diversity and reduces cover of unpalatable invasive species (Gorchov et al., 2021; Kalisz et al., 2014; Knight, Caswell, & Kalisz, 2009)	Partially ✓	Fencing altered plant community composition (Figure 5; $p < 0.001$), but did not significantly change native plant diversity In unmanaged areas, fencing decreases <i>V. rossicum</i> cover (Figure 2d; $p = 0.01$); fencing also decreases cover of another invader— <i>Alliaria petiolata</i>
Earthworms	As earthworms become more abundant, plant community composition changes and contains less diversity, higher proportion of sedges and grasses, and more invasive plants (Craven et al., 2017; Frelich et al., 2019; Hale et al., 2006; Nuzzo et al., 2009)	Partially ✓	Earthworm abundance was associated with plant community composition ($p < 0.001$), but was not correlated to differences in plant diversity or evenness over time; however, the less earthworms were in a plot the more native plant cover ($p = 0.01$) and total species richness ($p = 0.03$) increased between 2018 and 2020 <i>V. rossicum</i> cover increased with earthworm abundance ($p = 0.005$)

Note: We pair each previously reported trend with an explanation of how our findings support (or fail to support) the impact of each stressor (row label on left) on plant community composition, plant diversity, and cover of *V. rossicum*.

408 kg breaking strength, Deer Busters, Frederick, MD). In each area, we also established an additional 15×15 m open plot without *V. rossicum* and without fencing (located up to 250 m from the previously paired plots). This allowed us to compare understory plant communities with and without *V. rossicum* in both the managed and unmanaged areas, in presence of deer (Figure 1b). Within each plot, we established nine 1×0.5 m permanent quadrats, stratified randomly along three equidistant transects.

Beginning in July 2017, NYS Parks staff used a mixed-management method to control *V. rossicum*. Annual

application of 2% triclopyr with a backpack sprayer was followed by manual removal of *V. rossicum* with hand trowels by interns with the Friends of Recreation, Conservation, and Environmental Stewardship (FORCES) program.

From 2017 to 2020, we recorded percent cover of *V. rossicum* in each of our 1×0.5 m permanent quadrats within paired plots containing *V. rossicum*. In 2018 and 2020, we conducted understory vegetation surveys in permanent quadrats across all sites (9 quadrats \times 3 plots \times 2 areas \times 3 sites = 162 surveys; see Appendix S1: Table S1

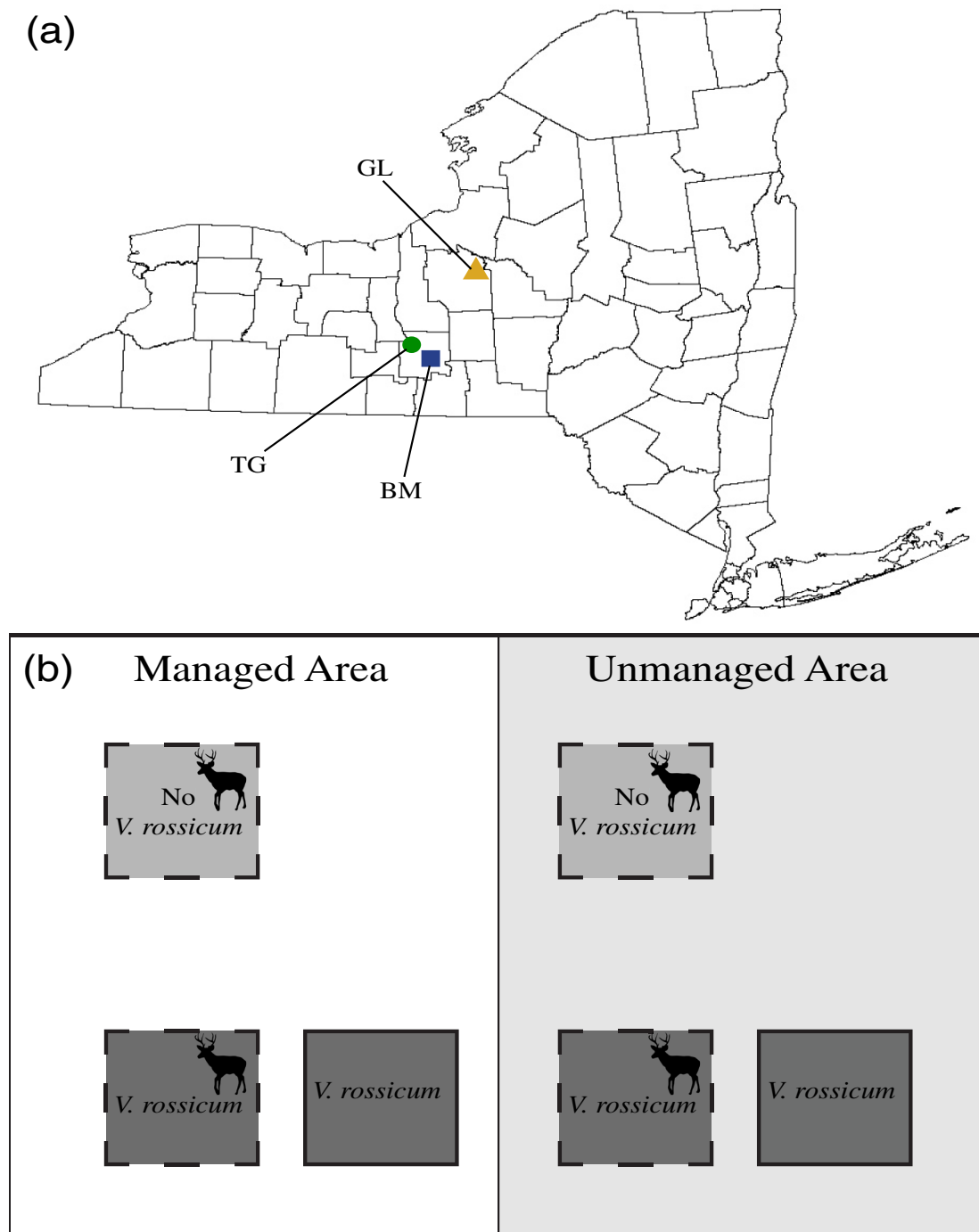


FIGURE 1 (a) Location of study sites at three New York State Parks (BM, Buttermilk Falls; GL, Green Lakes; TG, Taughannock Falls). (b) Study site design. In each site, *Vincetoxicum rossicum* was managed through manual removal and herbicide application. In both managed and unmanaged areas, we established three 15 × 15 m plots: two with *V. rossicum* present and one without *V. rossicum*. We erected a deer exclosure around one plot with *V. rossicum* present (solid border) and left the other two plots open (dashed border).

for specific timing of data collection). We conducted surveys of vegetation <120 cm tall by estimating total vegetation percent cover, total cover by life-form (i.e., woody, forb, graminoid, and fern), and total cover by species using intervals of 0%–5%, >5%–25%, >25%–50%, >50%–75%, and >75%–100%. We also identified each

vascular plant species to the lowest taxonomic resolution possible using Gleason and Cronquist (1991) as well as a digital key to the Asteraceae of New York (New York Flora Association, 2020; Tal, 2018; USDA NRCS, 2017).

Each summer from 2017 to 2020, we also sampled earthworms at five locations stratified randomly

throughout each open and fenced plot with *V. rossicum*. We sampled earthworms in open plots without *V. rossicum* in 2018 only. We placed a 0.5×0.5 m metal frame on the ground, removed leaf litter within the frame, and collected any earthworms found in the leaf litter. We then slowly poured 3.8 L of a mustard solution (15 g/L) evenly across the area within the frame (Lawrence & Bowers, 2002) and collected all earthworms that emerged from the soil within a 10-min period. We stored earthworms in 2% formalin in the field and then transferred earthworms to 75% ethyl-ethanol 7–10 days later. We identified individuals to the lowest taxonomic level possible (species for adults and genus for most juveniles; Reynolds, 1977), counted the number of earthworms in each sample, and obtained fresh biomass (in grams) per sample.

Statistical analyses

We ran all statistical analyses in R (R Core Team, 2021) using the glmmTMB package (Brooks et al., 2017). We conducted type III analysis of variance and Wald χ^2 tests using the car package (Fox & Weisberg, 2019) and ran pairwise comparisons with Tukey tests using the emmeans package (Lenth, 2022). We backward eliminated nonsignificant terms via log-likelihood tests (all full and reduced models listed in Appendix S1: Table S2). We estimated conditional and marginal R^2 with MuMIn package (Bartón, 2020), estimated predictions with the ggeffects package (Lüdtke, 2018), and checked model assumptions using the DHARMA package (Hartig, 2022). We considered $p < 0.05$ as statistically significant.

Earthworm biomass and earthworm counts were significantly correlated (Spearman's correlation = 0.88, $p < 0.001$). Average earthworm counts had higher explanatory power than biomass. To evaluate differences in mean earthworm counts among the three study sites, we averaged earthworm counts per plot, site, and year ($N = 5$ samples per plot \times 4 plots per site; 2017–2020) and fit a linear model with site as a fixed effect followed by pairwise comparisons with a Tukey test.

To determine the effects of management, fencing, and earthworm abundance on cover of *V. rossicum* over time (2017–2020), we constructed a generalized linear mixed-effects model and fit the model to only data from plots with *V. rossicum*. We included fixed effects for number of years since management started, management (managed or unmanaged), fencing (fenced or open), earthworm counts (average per plot in each sampling year, log-transformed), a three-way interaction between number of years since management started, management, fencing,

and all possible two-way interactions. To account for the hierarchical structure of the data and repeated measures per quadrat, we also included site, area nested within site, plot nested within area, and quadrat nested within plot as random intercept effects. Preliminary analyses indicated a disproportionate number of zero values in managed areas. We therefore evaluated model fit assuming Poisson and negative binomial distributions and including a zero-inflation component (Poisson only). Residual evaluation and AIC values indicated a negative binomial distribution (nbimom2 in glmmTMB package, variance = $\mu(1 + \mu/k)$, where μ = mean and k = overdispersion parameter) was a better fit than Poisson or quasi-Poisson (nbinom1, variance = $\phi\mu$, μ = mean, and ϕ = overdispersion parameter) (Appendix S1: Table S3).

To evaluate the effects of management, fencing, and earthworms, we fit independent linear mixed-effects models (Gaussian errors) to data on change in native plant cover (in percentage) as well as in native species richness, diversity (Shannon index), and evenness (Pielou index). In these analyses, we included community vegetation data collected in 2018 and 2020 from all plots, both with and without *V. rossicum*. To evaluate the change between initial and final collection years, we calculated the difference between 2020 and 2018 for each metric and used this difference as the response variable. Thus, a positive difference indicates an increase in the diversity metric, whereas a negative difference indicates a decrease in the diversity metric. In all models, we included fixed effects of the initial value of each diversity metric and management (managed or unmanaged), plot type (fenced with *V. rossicum*, open with *V. rossicum*, or open without *V. rossicum*), earthworm counts (average counts per plot in 2018), and all possible three- and two-way interactions between management, plot type, and earthworm count. We included nested random intercept effects (site, area nested within site, and plot nested within area) to account for the hierarchical structure of the data. We planned post hoc comparisons of “plot type” to evaluate the effect of (1) fencing (by comparing paired fenced and open plots that both contain *V. rossicum*) and (2) *V. rossicum* (by comparing open plots with *V. rossicum* to open plots without *V. rossicum*). Plot type was not significant in any of the models and therefore we did not conduct post hoc comparisons.

To evaluate trends in understory plant community composition excluding *V. rossicum* (but including native and non-native species), we fit generalized linear models to multivariate data with the mvabund package (Wang et al., 2012) using a negative binomial distribution. In all models, we included fixed effects of year (2018 or 2020), management (managed or unmanaged), and earthworm count in 2018. We fit models in two different ways. To assess the effect of deer, we fit models only to

community composition data from plots invaded by *V. rossicum* and included fencing (fenced or open) as an additional fixed effect. We included a three-way interaction between year, management, and fencing and two-way interactions between year and both management and fencing and between management and fencing. Similarly, to assess the effect of *V. rossicum*, we fit models only to community composition data from open plots and included *V. rossicum* (invaded or uninvaded) as an additional fixed effect. We also included all possible three-way and two-way interactions between year, management, and *V. rossicum*. We tested significance of model terms via nested log-likelihood ratio (LR) tests with permutations. The mvabund function does not account for random effects. Thus, we used restricted permutations to account for the lack of independence of samples within site, plot, and year (Szöcs et al., 2015). To visualize trends, we used distance-based redundancy analysis (dbRDA) using Bray–Curtis dissimilarities in the vegan package (Oksanen et al., 2019).

RESULTS

We identified 84 vascular plant species across 72 genera and 46 families. Fifty-five of these species were native to New York State and 14 were non-native, 8 of which are classified as invasive by New York State legislation (NYS Department of Environmental Conservation, n.d.). We did not identify the remaining 15 taxa to sufficient resolution to determine their origin. The most common species were *Acer saccharum* Marshall, *Fraxinus* sp., and *V. rossicum*. We did not find any New York State threatened or endangered species within our plots (Appendix S2: Table S1). Within sites, cover of *V. rossicum* was not statistically different among plots at the beginning of the study (Appendix S1: Table S4; Tukey test: $p > 0.05$ for all comparisons) but diversity metrics tended to be higher in unmanaged than managed areas (Figure 2a–c).

Across all three sites, we found megascolecid earthworms (genus *Amyntas* and *Metaphire*) native to Asia and identified three earthworm species native to Europe:

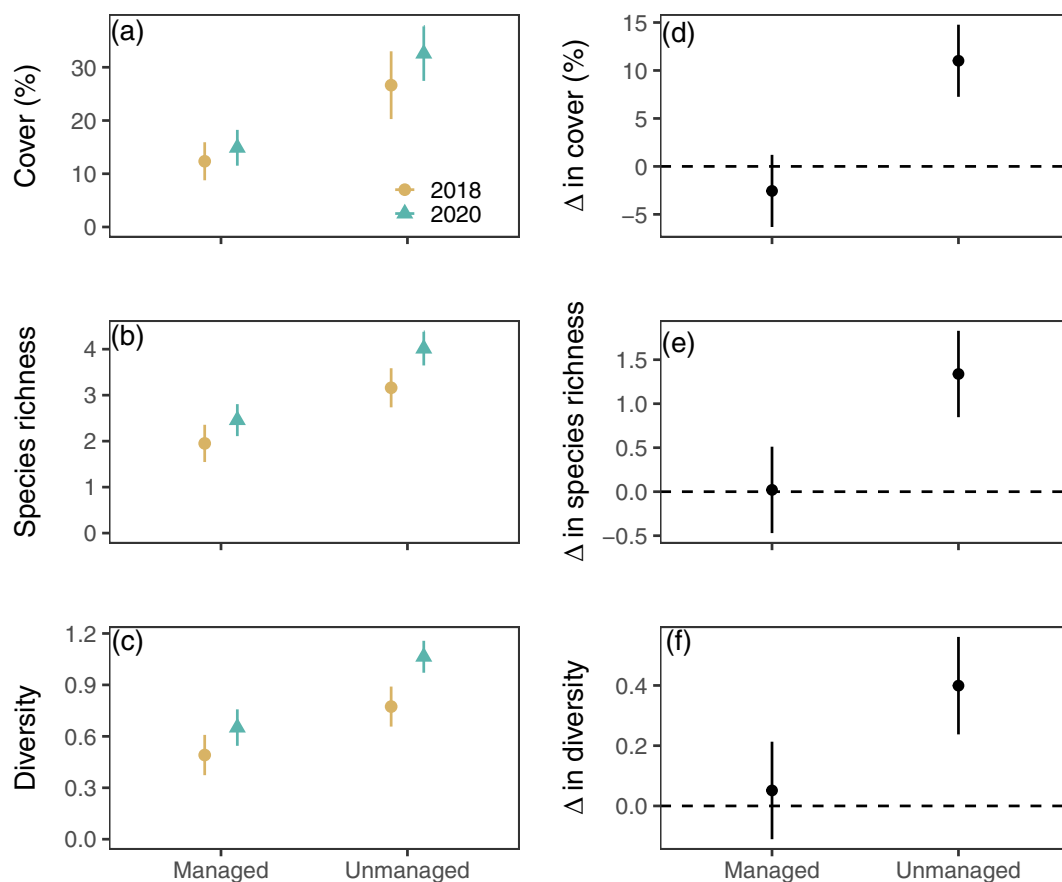


FIGURE 2 (a) Plant cover, (b) species richness, and (c) Shannon diversity index in managed and unmanaged areas during the study period (means \pm 2SE). Effect of management (managed or unmanaged) on the difference between 2020 and 2018 in native (d) plant cover, (e) species richness, and (f) Shannon diversity index. Positive values show an increase in the measure over time; values less than zero show a decrease in the measure over time. Data depict predictions and 95% CI from linear mixed models including random effects for site, area nested within site, and plot nested within area.

Lumbricus rubellus Hoffmeister, *L. terrestris* L., and *Octolasion tyrtaeum* Savigny. Earthworm counts varied over the four years of sampling (Appendix S1: Figure S1), with each plot containing earthworms during at least one sampling period. Earthworms were less abundant at Buttermilk Falls than at Green Lakes (Tukey test, difference [SE] = -4.93 [1.41], $p = 0.02$), but did not significantly differ between Buttermilk Falls and Taughannock Falls (difference [SE] = -3.35 [1.41], $p = 0.09$) or between Taughannock Falls and Green Lakes (difference [SE] = 1.57 [1.41], $p = 0.53$).

Cover of *V. rossicum* varied across study sites and sampling years (Appendix S1: Figure S2). We found a significant interactive effect among year, management, and fencing on *V. rossicum* cover (Table 2; Appendix S1: Table S5; conditional $R^2 = 0.52$; marginal $R^2 = 0.67$). In 2017, *V. rossicum* cover was similar (mean \pm 1SE: $19.5\% \pm 1.9$) across all management and fencing treatments (Tukey test; $p > 0.05$ for all comparisons; Appendix S1: Table S4). By 2020, management significantly reduced average *V. rossicum* cover to less than 1% (Figure 3a; Tukey test, difference [SE] = -3.49 [0.47]; $p < 0.001$) in both open and fenced plots (Figure 3b; Tukey test, difference [SE] = 0.80 [0.59]; $p = 0.52$). In contrast, for unmanaged plots, *V. rossicum* percent cover was lower for fenced plots (mean \pm 2SE: $5.63\% \pm 5.42$) than for open plots ($12.07\% \pm 5.28$) by 2020 (Figure 3c,d; Tukey test, difference [SE] = -3.49 [0.47]; $p = 0.01$). Cover of *V. rossicum* was positively correlated with earthworm counts in managed areas, but negatively correlated with earthworm counts in unmanaged areas (Table 2; Appendix S1: Table S5, Figure S3).

TABLE 2 Effects of management (managed or unmanaged) and fencing (fenced or open) on percent cover of *Vincetoxicum rossicum* at three New York State Parks between 2017 and 2020.

Factor	$\chi^2_{df=1}$	Pr(> χ^2)
Intercept	40.56	<0.001
Years since management started	110.65	<0.001
Management (M)	1.33	0.25
Fencing (F)	0.76	0.38
Earthworm count	14.01	<0.001
Earthworm \times M	12.79	<0.001
Year \times M	22.95	<0.001
Year \times F	0.47	0.49
M \times F	0.05	0.82
Year \times M \times F	5.21	0.02

Note: Results of Type III Wald χ^2 of generalized linear mixed model with negative binomial errors. Model included random effects for site, area within site, plot within area, and quadrat within plot. Significant effects appear in boldface. Table shows the results from the reduced model.

Overall, fencing (comparison between fenced plots with *V. rossicum* and open plots with *V. rossicum*) and *V. rossicum* presence (comparison between open plots with *V. rossicum* and open plots without *V. rossicum*) had no significant effect on any of the diversity measures (plot type was not significant and dropped from reduced models). However, percent cover of native species experienced greater increases between 2018 and 2020 for plots with initially lower native cover in 2018 ($\chi^2 = 106.59$, $df = 1$, $p < 0.001$; conditional $R^2 = 0.41$; marginal $R^2 = 0.41$) and for plots with fewer earthworms ($\chi^2 = 6.36$, $df = 1$, $p = 0.01$; Figure 4). Changes in native percent cover significantly varied with management ($\chi^2 = 23.42$, $df = 1$, $p < 0.001$): percent cover of native species did not change between 2018 and 2020 for managed areas (difference estimate overlaps with zero), but significantly increased in unmanaged areas (difference is positive; Figure 2d).

The same factors were associated with changes in species richness. Species richness also increased more strongly between 2018 and 2020 for plots with initially lower species richness in 2018 ($\chi^2 = 96.50$, $df = 1$, $p < 0.001$; conditional $R^2 = 0.56$; marginal $R^2 = 0.45$) and for plots with fewer earthworms ($\chi^2 = 4.62$, $df = 1$, $p = 0.03$; Figure 4). Changes in species richness significantly varied with management ($\chi^2 = 13.14$, $df = 1$, $p < 0.001$). While species richness did not change (difference overlaps with zero) in managed areas, it increased (difference was positive) when *V. rossicum* was unmanaged, indicating that it increased over time (Figure 2e). Gains in species richness per quadrat were mostly driven by *Acer* spp., *Ulmus* spp., and *Pinus strobus*.

Changes in diversity (Shannon index) were, again, negatively associated with initial diversity in 2018 ($\chi^2 = 133.22$, $df = 1$, $p < 0.001$; conditional $R^2 = 0.62$; marginal $R^2 = 0.48$) but were not associated with earthworm abundance. Changes in diversity also, again, depended on management ($\chi^2 = 8.90$, $df = 1$, $p = 0.003$): between 2018 and 2020, diversity did not change in managed areas, but increased in unmanaged areas (Figure 2f). Similarly, changes in evenness (Pielou index) were negatively correlated with initial evenness ($\chi^2 = 194.24$, $df = 1$, $p < 0.001$; conditional $R^2 = 0.66$; marginal $R^2 = 0.64$). However, changes in evenness were not associated with any other investigated factor.

Plant community composition was highly site specific (Appendix S1: Figure S4), with Buttermilk Falls containing the most species and Green Lakes the least. Twenty-nine percent of all species occurred at all three sites, whereas 42% occurred at just one site. Accordingly, most species showed site-specific trends in their responses to invasion and fencing, although the

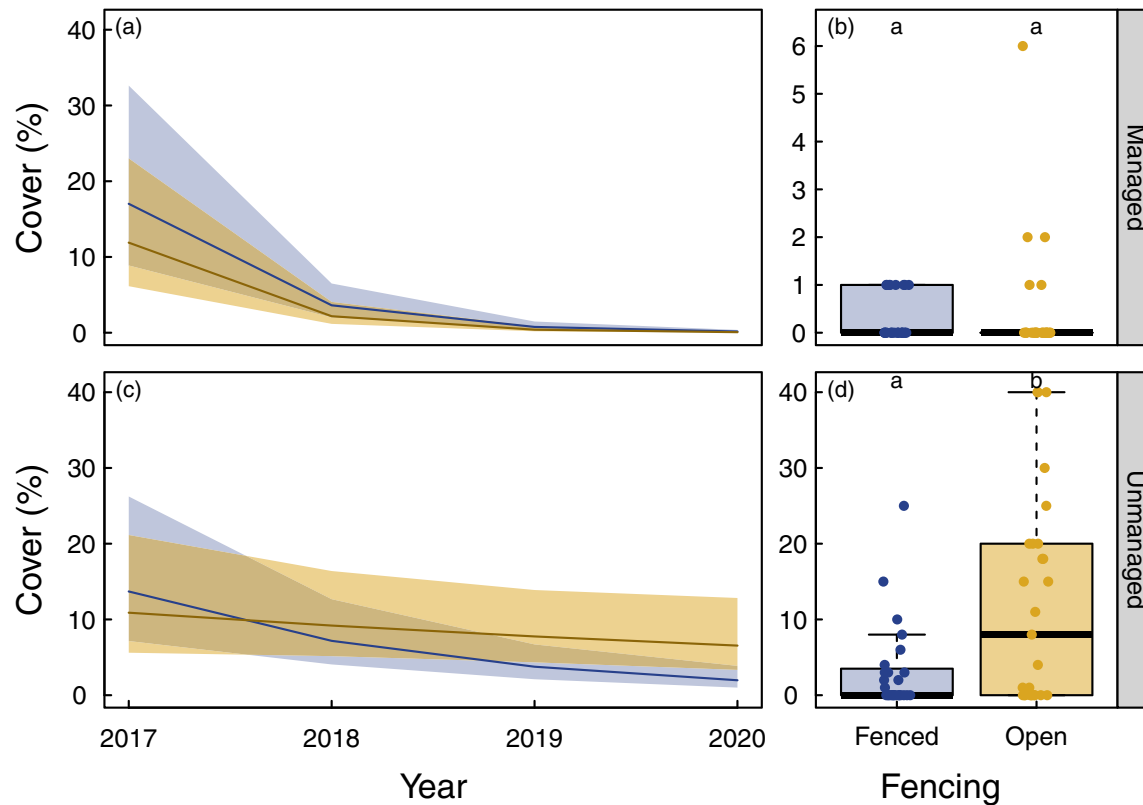


FIGURE 3 Effects of management (managed or unmanaged) and fencing (fenced or open) on *Vincetoxicum rossicum* cover over time. Panels (a) and (c) depict marginal effects (estimates and 95% CI) according to a mixed generalized linear model with negative binomial errors. Model included site, area nested within site, and plot nested within area as random effects. Panels (b) and (d) depict *V. rossicum* cover in fenced and open plots in 2020 after three years of management and two years of deer exclusion through fencing. Letters indicate significant differences among means (Tukey test, $\alpha = 0.05$). Note different y-axis scale on (b). In panels (b) and (d), the box plot midline represents the median, the box limits represent the interquartile range, the whiskers represent the minimum and maximum without outliers, and the points represent the outliers.

abundance of *A. petiolata* consistently increased across the study period, more so in open plots than in fenced plots. Further, despite site-to-site variation, when assessing differences between fenced and open plots, we found a significant interactive effect of management and year ($p < 0.001$, deviance = 11.0) as well as of fencing ($p < 0.001$, deviance = 319.7) and earthworm count ($p < 0.001$, deviance = 385.1). Specifically, managed areas experienced greater changes in plant communities over time than unmanaged areas (Figure 5), which was largely driven by changes in native species composition, especially changes in *Lindera benzoin* (univariate model: $p = 0.003$; Appendix S1: Figure S5). *Lindera benzoin* also strongly contributed to variation in plant community composition due to fencing and was significantly more abundant in fenced versus open plots (univariate model: $p = 0.02$; Appendix S1: Figure S6). The effect of earthworm count was significant for three univariate models: earthworm abundance was negatively correlated with the abundance of *Ostrya virginiana* ($p < 0.01$), but positively correlated to the abundances of *Geranium maculatum*

($p < 0.01$) and *Myosotis sylvatica* ($p < 0.01$) (Appendix S1: Figure S7).

In a separate model where we assessed the effect of *V. rossicum*, we found a significant interactive effect of management, invasion, and year ($p < 0.01$, LR = 20.58; Figure 5), with greater changes in plant communities over time for managed plots than unmanaged plots, but only for plots invaded rather than uninvaded by *V. rossicum*. Native *Fraxinus* sp. explained much of the variation captured by this interactive effect (univariate model: $p < 0.01$; Appendix S1: Figure S8). We also found a significant effect of earthworm count ($p < 0.001$, LR = 481.1) on plant community composition (Figure 5), which was also largely driven by native species (Appendix S1: Figure S9), with the abundances of *G. maculatum* ($p < 0.01$), *Solidago flexicaulis* ($p = 0.02$), and *Fraxinus* sp. ($p = 0.04$) all positively correlated with earthworm counts. Overall trends in plant community responses were similar when assessing the whole plant community versus just the native plant community (see Appendix S3 for results of the native plant community analyses).

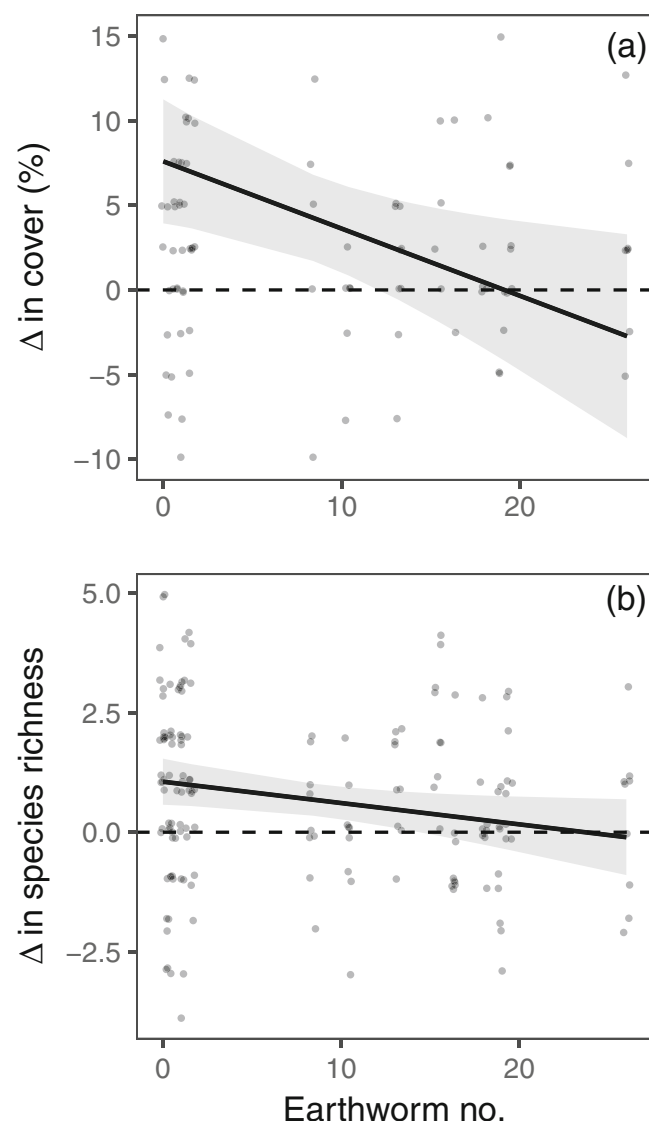


FIGURE 4 Effect of earthworm abundance on the difference between 2020 and 2018 in native (a) plant cover and (b) species richness. Data depict individual observations and predictions and 95% CI from linear mixed models including random effects for site, area nested within site, and plot nested within area.

DISCUSSION

Overall, *V. rossicum* removal does not lead to recovery of native plant communities—the ultimate goal of management at our study sites. NYS Parks management is effectively lowering *V. rossicum* abundance through manual removal and herbicide application, but native plant diversity remained consistently low in areas where *V. rossicum* was managed while plant diversity increased in neighboring areas where *V. rossicum* remained unmanaged. Thus, invasive plant management not only failed to increase native plant diversity but actually impeded it: native plant diversity fared better in areas where *V. rossicum* was left unmanaged.

This finding speaks to a need for increased understanding not just of the impacts of invasive species but of their management. Indeed, despite repeated calls to action and substantial increases in research on biological invasions (Blossey, 1999; Kumschick et al., 2015; Pergl et al., 2020), our understanding of the impacts of invaders and their management often remains unclear, especially regarding impacts on native communities. For example, across 50 years of the literature on invasive plants, nearly 2000 articles were published on invasive *Phragmites australis*, but only 11 documented the impacts of its management (Kettenring & Adams, 2011). Instead, management decisions are often based on the assumption that the invader's negative impacts decrease following declines in the invader's abundance. Yet, as our findings underscore, the relationship between an invader's abundance and its impacts is highly context dependent and difficult to predict (Sofaer et al., 2018; Thiele et al., 2010). Further, invasive plant management itself—including hand-pulling plants (Kettenring & Adams, 2011)—is often a strong disturbance that disrupts native plant communities and creates empty niches ripe for reinvasion by the same or new plant species (Hazelton et al., 2014; Skurski et al., 2013). Monitoring that assesses the impacts of plant invasions, and whether those impacts are mitigated following management, is therefore critical, especially if monitoring simultaneously assesses multiple ecosystem stressors. Such an approach would allow managers to better prioritize management techniques that will effectively target the ultimate drivers of ecological degradation (Armitage et al., 2009; Barney et al., 2015; Gorchoff et al., 2021; Lindenmayer et al., 2015; Martin & Blossey, 2013).

To this end, we find that stressors other than *V. rossicum* may be the most important drivers of understory plant community composition within our sites. For example, at the beginning of our study in 2018, our sites were already depauperate of native plants. However, native plant diversity was especially low in areas targeted for *V. rossicum* removal, suggesting that other stressors were responsible for driving plant diversity to such low levels. Indeed, as hypothesized, we found that plots with more earthworms had less native plant cover and total species richness. We also found that plots with more earthworms had more *V. rossicum*, which supports previous findings that earthworms facilitate plant invasions (Hopfensperger et al., 2011; Nuzzo et al., 2009). Thus, invasive earthworms may impede the recovery of native plant diversity. This finding is perhaps unsurprising, as earthworms are well known to reduce leaf litter accumulation and transform soil density, water retention, and pH (Fahey et al., 2021; Richardson et al., 2022; Suárez et al., 2006). They reduce mycorrhizal associations and may positively or negatively affect germination by vertically transporting seed through

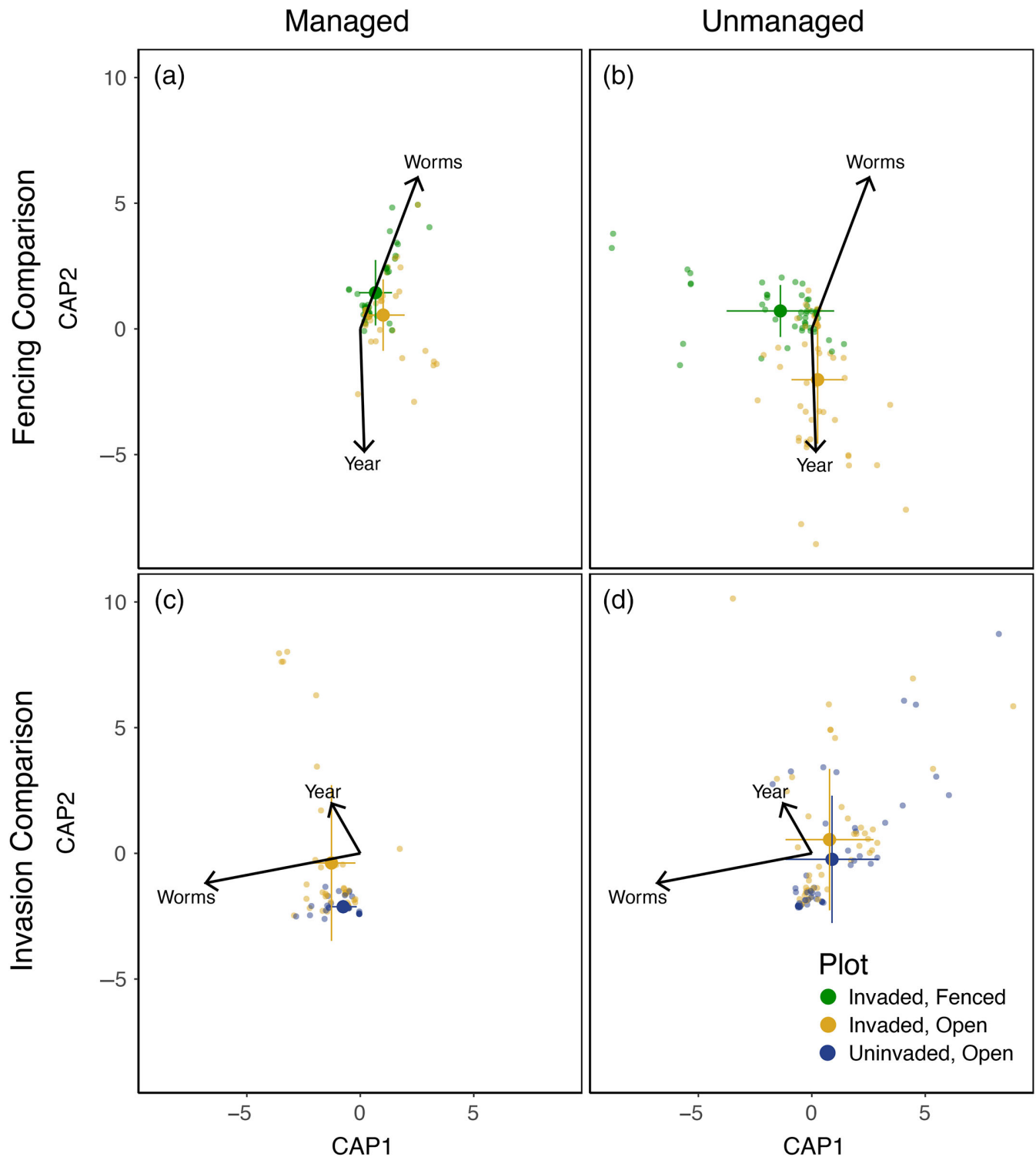


FIGURE 5 Distance-based redundancy analysis was performed using Bray–Curtis dissimilarities. (a, b) To assess deer fencing effects, we fit the model to plant community data only for plots invaded by *Vincetoxicum rossicum* and plotted the results of fencing separately for (a) managed areas and (b) unmanaged areas. (c, d) To assess *V. rossicum* effects, we fit the model to plant community data only for unfenced plots and plotted the results of *V. rossicum* invasion separately for (c) managed and (d) unmanaged areas. Smaller, semitransparent points display the scores for individual quadrats, whereas larger, solid points display the scores averaged across area and plot. Arrows represent the association between plant community composition and earthworm abundance and year. Error bars represent one standard deviation.

the soil and damaging seed during digestion, which in turn impacts seedling survival and plant community composition (Clause et al., 2017; Craven et al., 2017; Eisenhauer et al., 2009; Forey et al., 2011; Milcu et al., 2006). Managing invasive earthworms, not invasive *V. rossicum*, may therefore be the key to successful recovery of native plant communities.

Unfortunately, our understanding of how to control invasive earthworms within natural areas remains limited (Chang et al., 2021; Frelich et al., 2019). However, strong correlational evidence suggests that earthworms decline following fencing to exclude deer in northeastern forests (Dávalos, Simpson, et al., 2015; Mahon & Crist, 2019). Fencing to exclude deer may therefore be beneficial, especially as we also found that fencing decreased *V. rossicum* as well as *A. petiolata*, another common plant invader. Yet, as our data underscore: decreased abundance of *V. rossicum* does not always translate into recovery of plant communities. Indeed, fencing did not increase native plant diversity in our study, but this could be because deer browsing results in many species becoming locally extirpated or existing only as dormant seeds in the seedbank (Begley-Miller et al., 2014). After fencing, increases in diversity may therefore only occur from germination of dormant species in the seedbank or dispersal of species from local refugia. Such processes may only be captured across time periods longer than our study, especially for long-lived herbaceous plants (Pendergast et al., 2016). Further, other studies find that fencing to exclude deer increases the abundance of palatable (often native) species (Averill et al., 2016; Nuttle et al., 2011; Rooney, 2009).

Prioritizing management that simultaneously focuses on reducing deer and transplanting native species to restore native plant communities is therefore a strategy that is worth exploring. However, our findings emphasize that future management should be coupled with continued monitoring to assess whether predicted management outcomes match reality. Specifically, we find the same result as previous studies—that *V. rossicum* abundance declines following management of *V. rossicum*—but come to a very different conclusion. While previous studies have touted the success of sustained mixed management in combatting *V. rossicum* invasions (Averill et al., 2008; DiTommaso et al., 2013), we find that management of *V. rossicum* removal does not lead to recovery of native plant communities. Thus, future management efforts should continue to be integrated with monitoring. For example, assessing the impacts of fencing on plant communities, not just on the abundance of target invasive species, would allow managers to adaptively assess whether management actually achieves the desired outcome: in this case, recovery of native plant communities.

Finally, our monitoring efforts enabled us to detect an association between plant communities and forest stressors, but interpretation was complicated by the strong association between community composition and site. Several processes, including long-lasting impacts of deer herbivory and previous land use (Tanentzap et al., 2012), drive plant community composition to be highly localized (Vellend, 2010). Thus, management practitioners may want to utilize a monitoring method that is more comparable across sites despite variation in community composition. For example, transplanting select sentinel species into sites may allow practitioners to avoid site dependencies of plant communities while easily assessing the impacts of multiple stressors (Nuzzo et al., 2017). This strategy also depends less on expert knowledge than traditional vegetation surveys and can thus be carried out by land managers or private landowners (Blossey et al., 2019).

CONCLUSIONS

Our results show that reducing the abundance of a target species may not always lead to recovery of native plant diversity, underscoring calls to manage the impacts of invasive species rather than the species itself (García-Díaz et al., 2021). This disparity may be due to stressors other than plant invasions driving declines in native plant diversity. Thus, our findings contribute to a growing body of literature that questions the assumed role of invasive plants as drivers of ecological change. Here, we find correlational evidence that earthworms may drive change in understory communities, as native plant cover and plant diversity were negatively correlated with the number of earthworms in a plot. We also find that deer may facilitate plant invasions, as invasive plant species declined after fencing. Our findings highlight that our current management efforts are not producing the desired outcome and that a change in management strategy is worth exploring but should be coupled with continued monitoring to assess whether new efforts led to better recovery of native plant communities. Overall, efforts to monitor invasive species management with empirical methods that consider the individual and combined effects of multiple stressors are important for ensuring successful outcomes of invasive plant management and of species conservation more broadly.

AUTHOR CONTRIBUTIONS

Jeremy Collings and Andrea Dávalos contributed to the design and data collection. All authors contributed to the analyses and manuscript preparation. Jeremy Collings prepared the first draft of the manuscript, which was edited by Andrea Dávalos and Stacy B. Endriss.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Collings & Dávalos, 2020) are available from Figshare: <https://doi.org/10.6084/m9.figshare.13376888.v1>.

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SUPPORTING INFORMATION

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

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