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Successful recovery of native plants post-invasive removal in forest understories is driven by native community features

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Abstract

Temperate forest understories hold the majority of the plant diversity present in these ecosystems and play an essential role in the recruitment and establishment of native trees. However, the long-term persistence of diverse and functional forest understories is threatened by the impacts of invasive plants. As a result, a common practice is the removal of the agent of invasion. Despite this, we know little about the success of these practices and lack a comprehensive understanding of what intrinsic and extrinsic factors shape the recovery. In a multiyear field experiment, we investigated (Q1) whether native propagule availability drove native community recovery, (Q2) what the characteristics of successfully recovering communities were, and (Q3) under which environmental conditions native community recovery rates were faster. After initial removal of invasives, we seeded native species to manipulate assembly history and mimic restoration practices, we also implemented a repeated, versus once, removal treatment, all in a full-factorial design. We collected data on plant species composition and abundance (i.e., species level percent cover) and on environmental conditions (i.e., light and soil water availability) in the three subsequent summers. Our results show that native community recovery rates were independent of seeding additions or frequency of invasive plant removal. The fastest rates of recovery were associated with high native species richness, native communities with higher values of specific leaf area (SLA), and low drought stress years. Our results suggest that restoration practices post-invasive plant removal should be tailored to enhance natural dispersal, or artificial addition if the resident community is species-poor, of native species with traits compatible with high resource availability, such as species with high SLA. In addition to the importance of the native community characteristics, our results underscore the need for assessing environmental conditions, favoring management practices during years of low drought stress to maximize native community recovery.

INTRODUCTION

Forest ecosystems provide a wide range of functions, processes, and services (Decocq et al., 2016; Gauthier et al., 2023; Liang et al., 2016; Thompson et al., 2011). However, these ecosystems are increasingly jeopardized as forested lands within human-modified landscapes face a variety of novel stressors, including fragmentation, pollution, and the introduction of invasive species (Vilà & Ibáñez, 2011). Among these stressors, invasive plant species pose a significant threat to the recruitment of native plants as they establish and spread in forest understories (Link et al., 2018). The understory is critical for the regeneration of native tree species, which is the precursor to the long-lived canopy layer, and is especially important in forests of the eastern United States, where up to 80% of plant species richness is found (Gilliam, 2014). Unfortunately, these temperate deciduous forests are also estimated to experience the highest levels of plant invasion compared with other forest types within the contiguous United States (Oswalt et al., 2015). Specifically, these understories are frequently invaded by herbs such as *Alliaria petiolata*, which, due to its unmatched phenology compared with co-occurring natives, can exploit extended periods of carbon gain across multiple seasons (Heberling et al., 2019), and by shrubs like *Rosa multiflora*, which take advantage of canopy gaps and disturbed soil to establish and expand (Emsweller et al., 2018). As a result, managers face the significant challenge of maintaining healthy forest ecosystems in the face of ongoing multispecies plant invasions.

The typical approach to managing invasive understory shrubs and herbs involves mechanical removal of their biomass, eventually followed by chemical control though rarely by native species addition or repeated removal efforts (Kettenring & Adams, 2011). These common practices often assume the system will undergo successful passive restoration. However, unassisted recovery of the system after invader removal frequently encounters significant challenges. A major issue is the potential for the same invasive species, or others non-targeted by management practices present at low abundances, to (re-)establish and exploit the temporary reduction in competitive interactions and increase in resource availability following plant removal (secondary invasion; Pearson et al., 2016). Such (re-)establishment is facilitated by the persistence of a seed bank left behind after the physical removal of invasive species, leading to reinvasion (D'Antonio & Meyerson, 2002). The presence of a persistent seed bank allows new recruits to exploit the release of resources (Moore et al., 2023; Schuster et al., 2023), particularly light and soil water, which are limiting in forest understories due to intense competition from the tree canopy (Landuyt et al., 2019). Also, removal practices commonly ignore the invader's root system, which may lead to resprouting (Luken & Mattimiro, 1991), further reducing management efficiency (Diaz-Toribio & Putz, 2017; Enloe et al., 2018).

Given these challenges, two management approaches present ecology-driven alternatives to current practices. First, actively promoting an early arrival of native species through seed addition after invasive removal could prevent reinvasion and boost the recovery of the native community by exploiting priority effects (Byun et al., 2018; Fukami et al., 2016). That is the early establishment of the native community could have long-lasting impacts on community assemblage if the species that first colonize a site are highly competitive tapping into recently available limiting resources and establishing a strong dominance over the late arrivals. Even if early arrival species lose their competitive edge over time, early establishment of native species may still "buy time" to other native species to establish later (Margulies et al., 2017). Second, repeated removal might effectively decrease invasive shrubs' survival, particularly under the low-light environments of forest understories (Luken & Mattimiro, 1991). However, there is little empirical evidence that adding species early after invasive removal and prior to reinvasion coupled with repeated removal would be sufficient to restore forest understories after multispecies invasive plant management (Fukami et al., 2016; Weidlich et al., 2021).

Despite being a critical stage for maintaining forest composition and function (Clark et al., 1999; Green et al., 2014; Grubb, 1977), another major issue is the slow or scarce recovery of native species after the removal of understory invaders (Flory & Clay, 2009). This lack of native species recovery can be attributed to several factors, including the persistence of altered soil conditions, disrupted mutualistic relationships, and novel stressors, which decrease seed arrival and their ability to establish. Some invasive plants modify soil chemistry and microbial communities in ways that disadvantage native species,

even after the invaders are removed (soil legacy effects; Ehrenfeld et al., 2001; Kourtev et al., 2002). For instance, invasive plants such as *A. petiolata* release allelopathic chemicals that inhibit the growth of native species and disrupt mycorrhizal fungi essential for native plant nutrient uptake (Stinson et al., 2006). Additionally, novel stressors such as rapidly changing climate, modified landscapes, and new species assemblages further hinder recovery efforts (Dyderski & Jagodzinski, 2018; Vasquez-Grandon et al., 2018). Specifically, forest fragmentation reduces seed availability and alters microclimate conditions, creating less favorable environments for establishment (Haddad et al., 2015; Smith et al., 2019). Collectively and over time, these stressors may hamper forests' long-term existence (Ward et al., 2018). Giving native species the advantage from early arrival via seed additions could be an effective strategy to recover plant communities after invasive species removal. However, the conditions under which sowing would successfully contribute to the recovery of the native community remain unclear.

The characteristics of early establishing native plant species may play a vital role in determining the success of recovery efforts in forests. Specifically, growth form and plant functional traits of added species are particularly important factors to consider during active restoration practices (Ostertag et al., 2015). For example, there is growing evidence that tree planting and passively regenerated forests are ineffective in promoting native understory regeneration of shrubs and herbs (Aubin et al., 2008; Kremer & Bauhus, 2020), critical components of plant diversity in temperate forests (Spicer et al., 2020). Incorporating understory regeneration into restoration plans is then crucial for ensuring biodiversity and ecosystem function (Hupperts et al., 2019). In addition to restoring a diversity of growth forms, understanding plant functional traits can help predict successful restoration via plant growth rates and resource use efficiency (Ostertag et al., 2015). Species with acquisitive traits, like higher specific leaf area (SLA: area per dry mass), tend to have faster growth rates, making them ideal for early establishment when resources are abundant (Dahlgren et al., 2006). However, these species may also be more susceptible to drought stress, potentially stalling the recovery process if conditions are not optimal (Greenwood et al., 2017; Wellstein et al., 2017). By considering growth forms and leaf traits, restoration practitioners can select native species that are better adapted to the environmental conditions of the restoration site, increasing the likelihood of successful restoration outcomes (Laughlin et al., 2017).

Despite the possible benefit of promoting the early arrival of native species to enhance forest community recovery after invasive species removal, this mechanism has been studied primarily in grasslands and controlled settings (Weidlich et al., 2021). Only recently have studies in temperate forests begun testing seeding approaches after invasive removal with promising results (Moore et al., 2023), but little attention has been given to the features of the native community and the environmental context that may be driven the success, or failure, of those treatments. To address this knowledge gap, we investigated the role of propagule addition of native species in the community assembly of temperate forests under restoration, by deliberately giving native seeds the advantage of arriving first after removing invasive plants. Specifically, we aimed to answer: (Q1) Could seed additions and repeated clipping be a successful practice driving community assembly after invasive plant removal? (Q2) What are the characteristics of the native plant community associated with faster recovery? Lastly, (Q3) how is the recovery of the native community affected by environmental conditions, specifically, light and soil water availability? Answers to these questions can inform both the mechanisms of community assembly after disturbance due to management practices and the effectiveness of common restoration practices implemented after invasive plant removal.

MATERIALS AND METHODS

We carried out a multiyear field experiment in which we removed all invasive plants of all growth forms (i.e., herbaceous, woody, and lianas; for a complete list of species and respective growth forms, see Appendix S1: Table S1), once or multiple times, and seeded the plots with two different native species' seed mix. Three years following the implementation of the treatments, we collected data on the vegetation and on key environmental variables (such as light and soil water) during the growing season, which we then analyzed to answer our research questions.

Study locations

We carried out this study in four forests in southeastern Michigan, USA (for detailed coordinates of forest locations refer to Appendix S1: Figure S1, Table S2). All forests are characterized by temperate broadleaf species common in dry-mesic southern forests (Kost et al., 2007). Climate is similar across all four forests. Climate data based on measurements taken from 1991 to 2020 (Arguez et al., 2010) for the region indicates that the mean annual

temperature is 8.7°C, with a minimum mean temperature in January of −5.4°C and a maximum in July of 22°C. The average annual rainfall is 822 mm.

Field experimental setup

In the summer of 2019, in each forest, we selected two to four sites and at each site, we set up three sets of 3×2 m plots in areas occupied by invasive species. Each plot was divided into six 1-m^2 subplots where treatments were applied in a full factorial design (Figure 1). Late that first summer (August–October), we recorded invasive species identity at the subplot level (for a list of the invasive plant species recorded, see Appendix S1: Table S1), and we clipped all invasive species stems at the soil surface level (roots were not removed to avoid additional disturbance). From 2020 to 2022, in half of the subplots, we clipped invasive species monthly over the growing season (from June to August), that is, one-year versus multiyear invasive species removal; the other half of the subplots were left unclipped.

To identify whether native seed additions drive community assembly, we left one-third of the subplots untreated (control treatment), and to a third of the subplots we added a native forb seed mix between October 9 and 12, 2019 (forbs added treatment; density of 1.5 g of seeds/m^2), to another third, we added a mixture of forb and grass seeds between October 17 and 20, 2020 (mixture added treatment; density of 1.5 g and 2.4 g of seeds/m^2 of forbs and grass, respectively) (Figure 1). The grass mix contained cool and warm season grasses to span as much of the growing season as possible. We used a mixture of forbs and grasses because native grasses usually establish faster than forbs, which need 2–3 years after seeding to achieve higher cover percentages. All seed mixes were purchased from Michigan Wildflower Farm, a local seed producer that sources seeds primarily from Michigan, and occasionally from the broader Great Lakes region. The original mixes were preselected species by the supplier as a "woodland edge mix," designed specifically for restoration purposes and containing both forbs and grasses. To implement our treatments, we requested the forb and grass components be sold separately. We chose to use a commercially available seed mix to ensure our treatments closely reflect the types of products that land managers would typically have access to for similar restoration projects. Refer to Appendix S1: Table S3 for the complete list of seeded forbs and grass species. In total, we surveyed, yearly, 216 1 m^2 subplots (4 forests × 3–4 sites per forest × 3 plots per site × 6 subplots), with 36-m^2 subplots (or 36 replicates of 1 m^2 each) per removal (one-year and multiyear) and seeding (control, forbs added, and mixture added) combination.

Plant data

Response variable

In 2019, before implementing treatments, we collected data on the percent cover of native and invasive plants. Since we had preinvasive removal data on native cover, we used the changes in native cover as our metric to assess the native community's response to the treatments. After treatments, in 2020–2022, at each 1 m^2 subplot we collected monthly data at the species level on percent cover (ocular estimation; precision to 1%, maximum of 100% cover per subplot) over the growing season (June to August). The summed percent cover of native species at each subplot was used as our response variable. Additionally, we calculated the difference in native species cover at the subplot level between the last year of sampling (2023) and the pre-invasive removal data (2019).

Predictor variables

We derived the native richness of all species within a subplot (including both the resident community and seeded
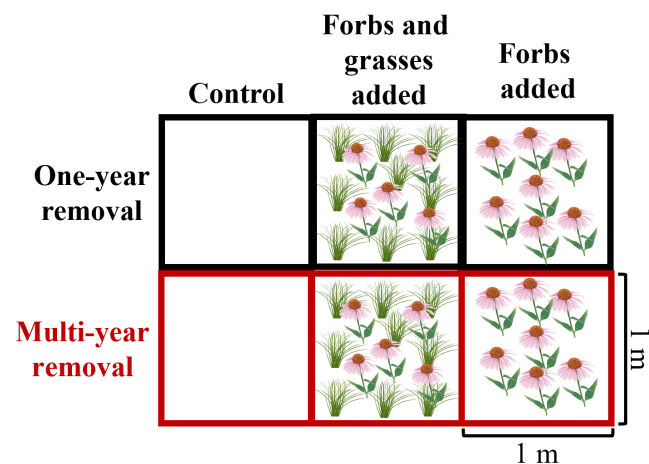

FIGURE 1   Experimental setup representing all removal and seeding treatments used to investigate the role of priority effects in recovery of recently managed invaded forest understories. The actual location of each subplot within a plot was randomized and adjusted depending on its slope to avoid runoff of added seeds to control subplots. Illustration credits: Dylan Taillie (grass), Kim Kraeer, and Lucy Van Essen-Fishman (forb), available from the Integration and Application Network (ian.umces.edu/media-library).

species) from species-level data collected in June, the earliest month surveyed each year from 2020 to 2022. We also recorded invasive species density, and in the multiyear removal subplots, we estimated the biomass of clipped resprouts. Clipped biomass was dried at 60°C until a constant weight was achieved. Data collection spanned June, July, and August from 2020 to 2022 for added forbs seed treatment, and from 2021 to 2022 for the added mixture seed treatment. We harmonized species names using Taxonomic Name Resolution Service (Boyle et al., 2013) and assigned native status following Reznicek et al. (2014). We obtained SLA values from TRY database (Kattge et al., 2011) and growth form from USDA PLANTS (USDA and NRCS 2022). We calculated the community weighted mean of SLA of all native species within a subplot (similar to the criteria used for determining native richness) using the "FD" package (Laliberté et al., 2014). For species without SLA values (18% of species), we assigned genus-level values. We aggregated the original growth form categories into three groups, "graminoids," "forbs," and "woody," and determined the proportion of the total cover occupied by each group at the subplot level.

Environmental data

We collected data on three environmental variables, all of which are limiting resources for plant growth and survival in forest understories and could impact the management treatments we implemented. These variables include light availability under the canopy and soil moisture, measured at the subplot scale, and soil nutrients, measured at the forest scale. Additionally, vapor pressure deficit (VPD) was calculated post hoc to help explain the model results.

Predictor variables

Each summer, we estimated light availability once the canopy had fully closed by taking canopy photos at the peak of greenness (July) in the center of each subplot using a fish-eye lens attached to a tripod-mounted smartphone at a height of 1.2 m. We analyzed the photos following the methods outlined by Bianchi et al. (2017). We measured soil moisture monthly from June to August each year using the Fieldscout TDR300 Soil Moisture Meter at the center of each subplot, but only used data from July, the driest month, because water stress constrains growth. We estimated soil nutrient availability by deploying ion-exchange resin capsules at each site (three

to four sites at each forest), purchased and analyzed from UNIBEST.

Additional variable for model interpretation

To calculate VPD values between 2020 and 2022 at the forest level, we used hourly temperature (in degrees Celsius) and relative humidity (in percentage) data from HOBO U23 Pro v2 data loggers (Onset Computer Corp.) placed under the forest canopy at each forest. We then obtained daily averages from May to August and calculated the cumulative sum of VPD per year. For VPD calculations, we utilized the package "pvldcurve" (Raesch, 2020). We performed all data wrangling using the family of packages "tidyverse" (Wickham et al., 2019) in R (R Core Team, 2024).

Data analysis

To answer whether native seed addition and repeated invasive removal affected community assembly after invasive removal we analyzed native percent cover (Cover) in August for each subplot (i) and year (t). Percent cover in year t was estimated as a function of cover the year before (i.e., autoregressive dependency, differentiated by growth form) for each sowing and removal combination, and to account for year-to-year variability in this dependency, we estimated this effect for each year ($\beta_{\text{treatment},t}$). We also included features of the native community and environmental conditions that could have contributed to native cover recovery, that is, native richness (estimated early in the June census of the same year; a proxy for higher probability of including native species better suited for growth), SLA community weighted mean of the native community (CWMSLA; a proxy for community functionality), soil moisture and light measures taken that summer (factors that directly affect plant growth). Being the likelihood:

$$\text{Cover}_{(i,t)} \sim \text{Normal}\left(C_{i,t}, \sigma^2\right)$$

Being the process model:

$$\begin{aligned} C_{i,t} = \beta_{\text{treatment}(i),t} \cdot (&w_1 \cdot \%\text{Graminoids}_{t-1} \\ &+ w_2 \cdot \%\text{Forbs}_{t-1} + w_3 \cdot \%\text{Woody}_{t-1}) \\ &+ \alpha_1 \text{NativeRichness}_{(i,t)} + \alpha_2 \text{CWM}_{\text{SLA}(i,t)} \\ &+ \alpha_3 \text{Light}_{(i,t)} + \alpha_4 \text{SoilMoisture}_{(i,t)} \end{aligned}$$

Parameter β represents the rate of native cover recovery per seeding treatment and removal frequency,

estimated for each year. Parameter ω are weights given to each growth form (graminoids, forbs, woody) to assess their specific contribution to recovery ($\sum w_k = 1$). Note that growth forms were not included in the 2020 analysis, because in 2019, we only recorded overall native community cover, using this measurement instead. We estimated all parameters from noninformative prior distributions, $\alpha_*, \beta_* \sim \text{Normal}(0,100)$ and $\omega_* \sim \text{Dirichlet}(1)$, and variance $1/\sigma^2 \sim \text{Gamma}(0.0001, 0.0001)$. We ran multiple iterations of the process models, which incorporated variables associated with the invasive community (i.e., percent cover, biomass, density) and with soil nutrients, particularly soil nitrogen, phosphorus, and potassium, as explanatory variables, selecting the model structure with the lowest deviance information criterion (DIC) value. Based on the model structure, the β_* parameters represent the outcomes for Q1, α_1 and α_2 parameters reflect the results for Q2, while those for Q3 are reflected by α_3 and α_4 parameters.

We also explored residuals to ensure that variables excluded from the final model based on the selection process, but considered important due to the study design or biological relevance, were not biasing results or missing key relationships or interactions. In an exploratory analysis of the model residuals, we examined their associations with invasive species identity and initial cover, forest, and plot. To elucidate potential explanations for the observed variations across years, $\beta_{treatment,t}$, we conducted additional investigations into environmental conditions that could explain these differences, for example, VPD. We retrieved posterior distribution and parameter values after convergence, using the least 50,000 iterations with a thinning interval of 100. Model convergence was checked by visual inspection of trace and density plots. We ran the auto-regressive mixed-effects models in JAGS (Plummer, 2003) through R using "rjags" (Plummer, 2022).

To assess whether added seeds had differential effects across levels of native richness, we calculated an effect size (ES) of native cover across the treatments of seed addition by invasive species removal. ES was calculated as $ES = (\text{native cover}_{\text{seed addition}} - \text{native cover}_{\text{control}}) / |\text{average}|$, following Ibáñez et al. (2021). A positive ES value for each combination of seed mix and invasive species removal treatment indicates that the combination aided native cover, while an ES value close to zero implies that the combination had no impact on the native cover. The complete dataset and associated files can be found in DRYAD (https://doi.org/10.5061/dryad.mpg4f4r5w), and reproducible modeling code along with the full list of packages used can be found on Zenodo: https://doi.org/10.5281/zenodo.14665596.

RESULTS

The total percent cover of the native community within a plot varied from 0% (16 subplots in 2019 to one in 2022) to 100% (three in 2022). We recorded a total of 132 native species across all forests. At the subplot level and across years, light availability ranged from 5.83% to 70.2% of full sunlight, and soil moisture, measured as volumetric water content, ranged from 0% to 43.4%. We were only able to calculate complete VPD values at two of our forests due to sensor failure, but year-to-year variation in climatic conditions is similar across the study area (Arguez et al., 2010). All parameter values from the analyses are reported in Appendix S1: Table S4 and model fit in Appendix S1: Figure S2. Exploration of model residuals can be found in Appendix S1: Figures S3 and S4.

(Q1) *Could seed additions and repeated clipping be a successful practice driving community assembly after invasive plant removal?* Recovery rates (i.e., rate of increase in native cover) of the native community were not significantly different between control and seeded treatments (i.e., forbs added, or mixture added; Figure 2) within a year. Although multiyear removal subplots tended to have a higher recovery rate than one-year removal subplots, these were not statistically different from one another except in the forbs added treatment in 2021 (Figure 2). In that year, the mean native recovery in the multiyear removal treatment was 63.86% higher than in the one-year removal treatment when forbs were added. The mean native community recovery rates were 112% higher in 2021 compared with 2020, and 59% higher compared with 2022 for all treatments (Figure 2). Additionally, calculations of mean percent native cover for each forest across treatments and years combinations showed that no combination was significantly different from each other as all confidence intervals overlap (Appendix S1: Figure S5). Richer forests (i.e., Forests 1, 2, and 3) consistently exhibited higher total native cover for multiyear removal treatments, regardless of seed addition, in 2021 and 2022. Specifically, the percent change in total native cover between multiyear and one-time removal treatments within each year was four to five times higher in 2021 and 2022 compared with 2020. Forest 1 (native richness = 94) and Forest 3 (native richness = 78) showed significant positive total native cover in both years, while Forest 2 (richness = 79) displayed a similar pattern, but only in 2021 (Appendix S1: Figure S5).

The difference in native cover between the last year of data collection and the pre-invasive removal period showed an increase in native cover across all treatments, irrespective of seed addition, consistent with model results. Specifically, multiyear removal had a significantly higher increase in native cover overall (ANOVA,
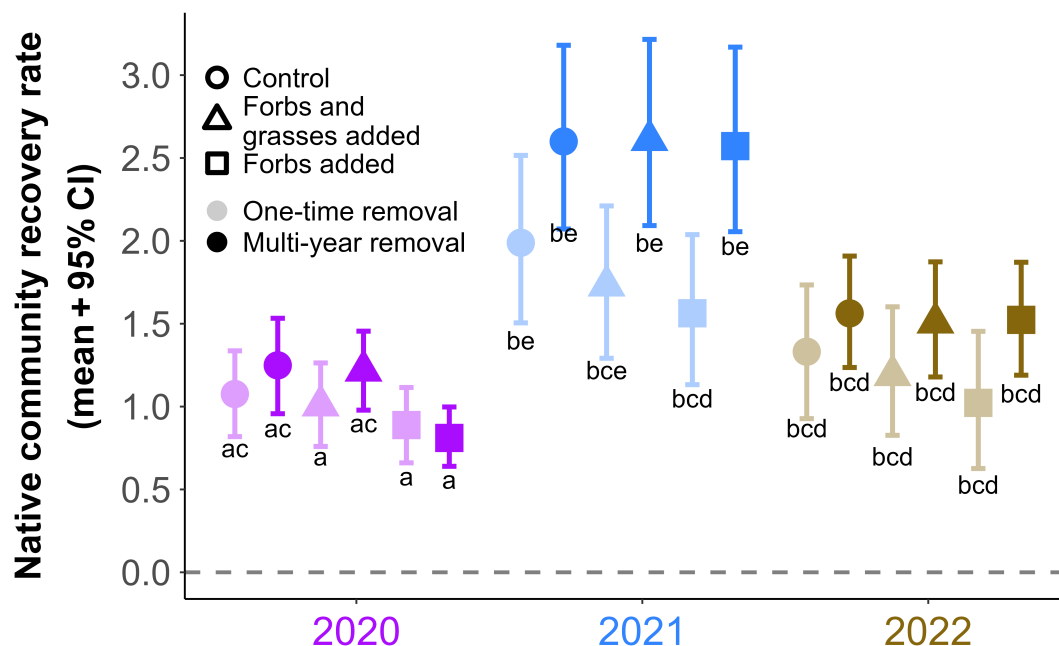
FIGURE 2 Native community cover recovery rates (β parameters) across years, seeding treatments, and removal frequencies. Parameters with 95% credible intervals (CI) that do not overlap are considered statistically different from one another, that is, different letters.

$F_{1,210} = 24.9$, $p < 0.05$; Appendix S1: Figure S6). Lastly, out of the 17 forb species seeded, 12 established during our experiment, resulting in a 70% establishment rate. Of the four grass species seeded, only two established (50% establishment; Appendix S1: Table S3).

(Q2) *What are the characteristics of the native plant community associated with faster recovery?* Our analysis revealed that native richness was significantly and positively, associated with the recovery of the native community following invasive species management (Figure 3A). Specifically, one additional native species led to an average 2.28% increase in native cover. This coefficient was the strongest of the variables considered. When analyzing sowing treatment ES as a function of native richness, we did not find any patterns, that is, sowing did not make a difference across all levels of native richness (Appendix S1: Figure S7). Recovery was also higher among subplots with a higher community weighted mean of SLA (CWMSLA), with a 0.11% increase in native cover per unit increase in CWMSLA (Figure 3A). To investigate further, we compared the SLA values of seeded species that were established versus those that failed to establish (i.e., species that were not recorded in any subplot at any given time-point of the experiment). Although not significantly different (as the ranges overlap), our results suggest that the seeded forbs and grasses that were established tended to have higher SLA values compared with those that did not. On average, established forbs had SLA values that were 79% higher, while established grasses had SLA values that were 56%

higher (Figure 4A,B). And among the seeded species that established, those with higher SLA tended to establish in higher densities. Specifically, one unit increase in SLA values of established seeded natives was associated with, on average, 2.97 more occurrences (Figure 4C; linear regression, β = 2.97 [confidence intervals: 0.942–4.99], $p = 0.00849$). Lastly, growth form categories contributed similarly to native community recovery (parameters ω, Appendix S1: Figure S8).

(Q3) *How is the recovery of the native community affected by environmental conditions, specifically, light and soil water availability?* Subplots with higher available light had higher native recovery rates, with each 1% increase in canopy openness associated with a 0.12% increase in native cover (Figure 3A). Soil moisture availability at the subplot level did not have a significant effect on the native recovery rate (Figure 3A). However, in further exploration of environmental conditions that differed across years while our experiment was in place, 2021 had lower cumulative values of VPD compared with the other years, indicating lower atmospheric water demand (Figure 3B).

DISCUSSION

Invasive plants, along with other stressors, threaten the long-term persistence and function of forest ecosystems by negatively impacting forest regeneration and the maintenance of a healthy understory (Link et al., 2018;
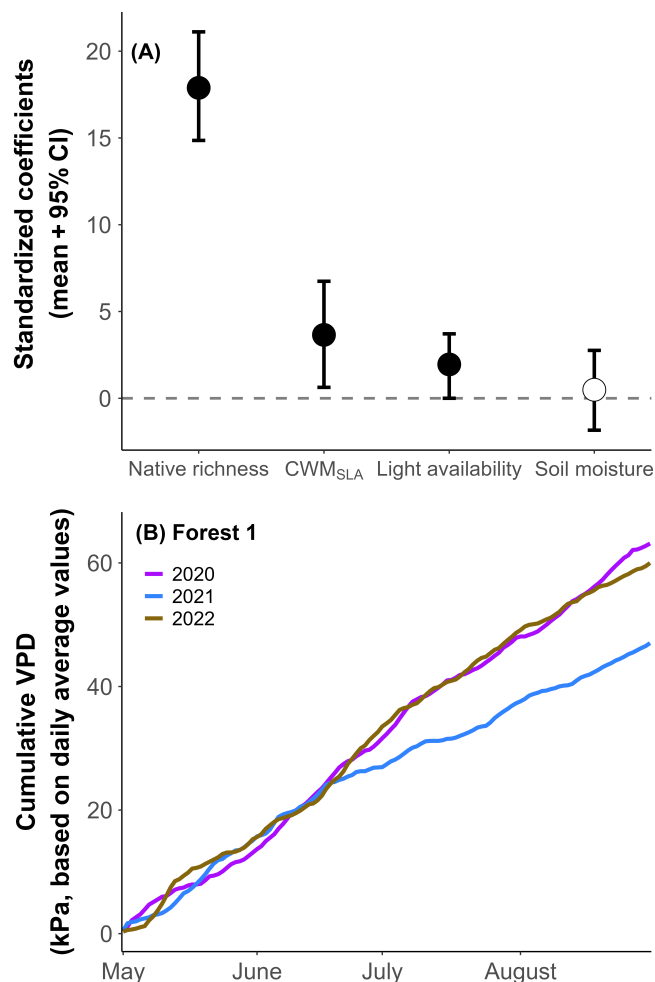
FIGURE 3 (A) Posterior means and 95% CI of parameter values (standardized for comparisons) from the additional covariates included in the analysis. CWMSLA: community weighted mean of specific leaf area. Credible intervals (CI) that do not cross zero are statistically significant (solid symbols). (B) Cumulative vapor pressure deficit (VPD) from one of the Forest's environmental sensors.

FIGURE 4 (A, B) Distribution of specific leaf area (SLA) values among naturally occurring native species (black line) and range of SLA values of (A) seeded forbs and (B) seeded grasses differentiated as a function of having successfully established or not (colors). (C) Relationship between established seeded native species and their SLA values ($\beta = 2.97$ [CI: 0.942–4.99], $p = 0.00849$).

Simberloff et al., 2013; Ward et al., 2018). Despite extensive restoration efforts after invasive plant removal, successful native recovery is rarely achieved while reinvasion is common (Kettenring & Adams, 2011). We examined native plant community assembly following the removal of invasive species and the addition of native propagules to better understand the recovery process (in this study, evaluated as changes in native plant cover). We found that neither seed additions nor multiyear invasive removal speeded native community recovery; the fastest recovery rates resulted from a combination of high native richness, a native community with relatively high SLA,E and low drought stress. This suggests that native species with leaf traits similar to those of the invaders were more successful in recovering after removal, while species better suited to
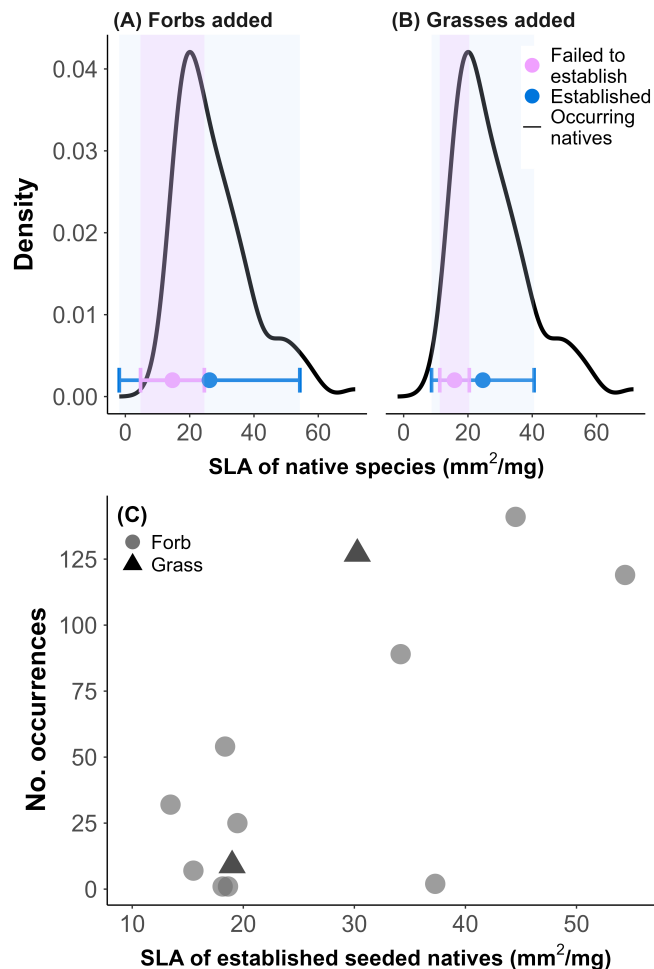
low-light environments, typical of temperate forest understories, lagged behind. Overall, our results provide valuable information to assess the viability of invasive removal practices and to guide the implementation of more effective restoration aimed at the native plant recovery of temperate forest understories.

(Q1) Could seed additions and repeated clipping be a successful practice driving community assembly after invasive plant removal?

Removal practices decrease the abundance of targeted invasive species and generally restart community assembly by reducing plant density and increasing resource availability, leading to the assumption that priority

effects, or the ability to establish first, could be the driving factor of community assembly (Byun et al., 2018; Fukami et al., 2016). Due to the potential lack of native propagules as a consequence of degradation (Schuster et al., 2018) and direct competition from invasive plants (Collier et al., 2002; Ward et al., 2018), seeding practices are common to supplement native propagules (Copeland et al., 2019).

Contrary to the expected effect of seed additions, our results showed that, in the temperate forest understories of our study region, native species recovery rates were similar between the control (i.e., no native seed addition) and treatment groups (added native seeds; Figure 2; Appendix S1: Figure S5). This finding suggests that in our study system, native propagules are not a limiting factor for restoration. In contrast, a recent experiment in a temperate deciduous forest in Eastern United States found that native seed addition enhanced native species richness and abundance, and reduced invasive shrub abundance, particularly at sites with medium and low invasion intensities (Moore et al., 2023). However, 2 years after treatment, secondary invasion in some of those communities resulted in plant community compositions similar to those observed in control plots (Moore et al., 2023). These disparate results suggest that temperate forests may not always provide sufficient native propagules to promote rapid native community recovery, and that artificial seed addition might or not improve recovery rates. Therefore, the context dependencies associated with the effects of adding seeds to recently managed forest understories need further investigation to more accurately guide management decisions.

(Q2) What are the characteristics of the native plant community associated with faster recovery?

Functionally diverse communities with complementary resource-use strategies are better equipped to exploit available resources (Byun et al., 2018; Davis et al., 2000; Funk et al., 2008). This resource-use efficiency can be driven by niche complementarity, where different species utilize distinct resources or occupy different ecological niches, thereby maximizing resource capture. At the same time, sampling effects may also contribute, as diverse communities are more likely to contain one or more particularly competitive species that excel under a given set of environmental conditions (Funk et al., 2008; Tilman, 2001; Tilman et al., 2014). Specifically in forest understories, a richer native community could be more likely to have strong native competitors adapted to the shaded understory (Gomez et al., 2019; Vojik & Boublik, 2018), while

also including species that respond rapidly to pulses of resources that are often found after disturbance or invasive removal (Driscoll, 2017; Moles et al., 2012).

Our results show that the recovery of native understory plant communities, in terms of percentage cover, was positively associated with two key variables: native richness and community-level SLA (Figure 3A). The strongest relationship was observed with native richness, supporting the idea that niche complementarity could be in place. As a result, richer communities would exploit unused resources more efficiently following the removal of invasive species. Such a community feature is particularly relevant in the context of recently managed invaded forests, where the reduction of invader plant density leaves unutilized resources over time and space. These unused resources could then be explored by richer native communities given the greater potential of interspecific complementarity, as discussed above.

The ability to explore post-management site resource pulses and local environmental conditions of forest understories are also tightly linked to intra and interspecific variation in resource-use strategies. Resource-use strategies can be inferred from plant leaf traits, as described in the leaf economic spectrum (LES; Diaz et al., 2016; Wright et al., 2004). On one end of the LES, species with acquisitive leaves have high SLA, N content, light demands, and maximum photosynthetic rates, but low investment in leaf tissue mass relative to area (or SLA), low survival rates, and shorter leaf lifespan (Diaz et al., 2016; Wright et al., 2004). On the other end, conservative species tend to be shade-tolerant, investing heavily in leaf tissue, and have leaves with longer lifespan, and slower carbon processing rates (Diaz et al., 2016; Wright et al., 2004). The LES is a generalizable framework and holds across growth forms, plant functional groups, or biomes (Diaz et al., 2016; Wright et al., 2004). Our analysis shows that rates of native community recovery following invasive species removal were dependent on overall native community leaf trait composition (Figure 2). Specifically, our results suggest that native communities with higher CWMSLA were linked to faster native cover recovery rates (Figure 3A), and that seeded species with higher SLA values were more likely to establish (Figure 4). Plants with higher SLA values are more adapted to high-resource environments (Maracahipes et al., 2018; Pérez-Harguindeguy et al., 2016 but see Gommers et al., 2013; Liu et al., 2016) and disturbed areas, such as sites after management interventions (Gong & Gao, 2019; Ibáñez et al., 2021; Ordonez & Olff, 2013).

Our SLA results suggest that the diversity effect in native community recovery may partly arise from a higher likelihood of including species with higher SLA values. This relationship is relevant because richer communities

increase the likelihood that key functional traits, such as high SLA, are present within the community. Therefore, if artificial seed addition is needed, selecting plant species based on their trait values can be an important tool to create resilient native communities given site-specific characteristics (Laughlin et al., 2017) that could increase their native coverage in response to the removal of invasive species. Such approach can greatly improve restoration success to control invasive species (Ostertag et al., 2015).

(Q3) How is the recovery of the native community affected by environmental conditions, specifically, light and soil water availability?

In temperate broadleaf forests, understory growth is mainly limited by light availability (Axmanová et al., 2011; Landuyt et al., 2020). In these shaded environments, some understory plants acquire most of their carbon before the canopy leafs out and after canopy leaf senescence (Jolly et al., 2004; Lee & Ibáñez, 2021). Our results support a positive response in native cover recovery with increasing light availability, matching the higher establishment of species with higher SLA. Species with higher SLA values characterize acquisitive leaves which are better equipped to rapidly intercept light, which in turn leads to higher carbon fixation and faster growth (Wright et al., 2004). Our finding is also consistent with previous studies that have demonstrated strong correlations between both understory plant richness and cover, and light availability and heterogeneity in temperate forests (Dormann et al., 2020; Helbach et al., 2022). Although our invasive removal treatments did not directly affect the canopy structure, our experimental plots were established across sites with substantial variation in light availability within the canopy. Furthermore, the removal of a dense shrub layer, as we performed through clipping, is known to enhance light availability to the forest floor (Kaye & Hone, 2016).

While our analysis did not reveal a significant effect of soil moisture (based on measurements taken at one particular time each month), the year-to-year differences on native cover recovery rate align with those in VPD values (Figures 2 and 3). Plants regulate evapotranspiration rates based on the non-linear relationship between temperature and relative humidity, or VPD (Grossiord et al., 2020; McAdam & Brodribb, 2015). This regulation directly affects photosynthesis rates: high temperatures in combination with low relative humidity (i.e., high VPD values) induce stomata closure, thereby suspending photosynthesis to avoid hydraulic failure (McAdam & Brodribb, 2015; Novick et al., 2016). Together, these results suggest that to achieve higher and lasting native cover

recovery rates in the native community optimal growing conditions are essential. Years of lower water stress levels in the warmest months in the growing season, such as 2021, play a disproportionately important role in promoting native plant recovery, and in our study, this was particularly prominent in sites with higher richness (Appendix S1: Figure S5). While extreme weather events are expected to become more frequent, our study did capture important year-to-year variability in water-limiting conditions. However, a longer timeframe would have provided a more comprehensive understanding of how, following invasive species removal, the reassembling of understory native communities responds to prolonged periods of fluctuating water availability.

Dominant invader versus invasive plant community

Current management practices for controlling or attempting to eradicate invasive species typically involve targeting a focal nuisance plant with significant impacts (D'Antonio et al., 2017). For example, in our region, one example is garlic mustard (*A. petiolata* (M. Bieb.) Cavara & Grande), which is well known for its allelopathic effects and usually draws significant control efforts and resources from managers, practitioners, and landowners (Blossey et al., 2021; Cipollini et al., 2012; Portales-Reyes et al., 2015). Given the species-specific usual focus, we further investigated whether the unexplained variability by our model's predictors could be attributed to the identity of the dominant invasive species. However, we found no clear associations, which suggests that the management of invaders could shift from an invasive species-focused to a native community-level approach. Improving the ability of native community to take advantage of the removal of an invasive species could, then, help prevent secondary invasions or the reinvasion by low abundance species already present at a site (Kuebbing et al., 2013; Pearson et al., 2016). Invasive species often have intrinsic advantages over co-occurring natives, for example, larger carbon gain per leaf area, longer leaf lifespan, and extended leaf phenology (Fridley, 2012; Fridley & Craddock, 2015; Heberling & Fridley, 2013). So, adopting a community-level approach where the richness and functionality of the native vegetation are evaluated before invasive removal could prevent reinvasion and ensure restoration success.

CONCLUSIONS

The scientific literature on invaded ecosystems primarily focuses on the agent of the impact: the invasive plants

harming the native community (Ibáñez et al., 2021; McGeoch et al., 2016). Here, we switched the research focus from the invasive species to the affected community by studying mechanisms of community assembly of temperate forest understories. Specifically, we investigated the role of priority effects in structuring such communities, the features of this recently assembled community, and the environmental conditions aiding native community recovery. We performed our study after the management of invasive species, a restoration practice that is rarely successful past the removal stage (Kettenring & Adams, 2011). Thus, our results could be beneficial to managers and practitioners on the ground by allowing them to tailor and adapt their current approaches to potentially increase native community recovery success in forested systems. Specifically, management of invaded forest understories could be targeted to increase the native richness of the incoming community if native propagules are limited, choosing species with higher SLA or more acquisitive strategies to supplement local native propagules. Additionally, managers should consider assessing whether the environmental conditions are optimal for removal, particularly with respect to predicted drought levels. Therefore, future research should investigate whether alternative or customized seed mixes containing species with such characteristics can enhance native establishment and recovery rates, as well as the long-term monitoring of treatments—an area where data remain scarce in the management of forest understory invasions. Such studies would help expand our understanding of the context dependencies of native plant recovery and how year-to-year weather variability influences plant community assembly outcomes following invasive species removal.

AUTHOR CONTRIBUTIONS

Laís Petri and Inés Ibañez conceptualized the study, developed the methodology, collected and analyzed the data, and contributed to writing, review, and editing. Laís Petri implemented the field experiment, and collected, curated, and visualized the data.

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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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