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Invasion Shadows: The Accumulation and Loss of Ecological Impacts from an Invasive Plant

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Ecological impacts from invasive plants that have been identified include reductions in biodiversity, changes in resource cycling, and disruptions of ecosystem function. To mitigate these negative ecological impacts, managers work to remove invasive plants. However, removal does not necessarily immediately lead to a return to the uninvaded ecological state. Similarly, the accumulation rate of ecological impacts following invader establishment is almost entirely unknown for most species, hindering identification of optimal management times. The accumulation and loss (so-called legacy effects) of impacts following invader establishment and removal represent an "invasion shadow." To begin to understand invasion shadows, we measured the changes in biotic and abiotic ecological impacts during establishment and following removal of the forest understory invader Japanese stiltgrass. We found that when the abiotic metrics were considered, seeded areas became more functionally similar to the invaded landscape and removed areas became more similar to the uninvaded landscape. However, while the plant community did not change in a 3-yr period during a new invasion, following invader removal, it became less similar to both the invaded and uninvaded landscape altogether, suggesting legacies. Surprisingly, all changes occurred almost immediately and persisted following invader establishment and removal. Our results show, at least in a 3-yr period, that ecosystems can respond to changes in invader abundance, and in some cases simply removing the invader could result in long-term changes to the resident plant community.

Nomenclature: Japanese stiltgrass (Mary's-grass), *Microstegium vimineum* (Trin.) A. Camus.

Key words: Global Invader Impact Network (GIIN), impact, legacy effect, multivariate, species similarity.

Significant resources are allocated for prevention, management, and eradication of invasive plants to ameliorate their negative ecological impact. Although most land managers desire to permanently remove (i.e., eradicate) invasive plants, in most cases eradication is not a feasible option for established populations (Rejmánek and Pitcairn 2002). Therefore, invasive plant populations are managed in an ongoing effort to reduce population sizes and their contribution to future generations. Unfortunately, management itself can cause negative externalities, such as reduced native plant cover (Rinella et al. 2009) and establishment of secondary invaders (Pearson et al. 2016; Skurski et al. 2013). Therefore, in certain circumstances, managing to mitigate impacts may not result in a net positive impact to the ecosystem.

However, in some instances, local extirpation of an invasive population is possible (Simberloff 2003). Assuming the invasive plant was responsible for the undesirable ecosystem effects (i.e., a driver of change; MacDougall and Turkington 2005), a return to a pre-invasion state should follow once the invasive plant is removed. Thus, invader eradication is often assumed to be analogous with restoration (Corbin and D'Antonio 2012). Unfortunately, there is very little evidence of successful eradication leading immediately to an ecosystem functioning as an uninvaded state. Therefore, although restoration is most often the goal of land managers, as Corbin and D'Antonio (2012: 117) explain, "Even where local eradication is achieved, removal by itself is unlikely to allow restoration of broader community or ecosystem characteristics." This lack of restoration following invader removal could be attributed to the invaders not being the drivers of change, though increasing evidence suggests otherwise (Vilà et al. 2011), or their changes being persistent.

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Management Implications

Invasive plants can have costly and undesirable ecological impacts. Therefore, a top priority of many natural resource managers is to remove invasive plants with the intent of eventual extirpation and mitigation of their impacts. Impact mitigation is contingent on the assumption that removing the invader will also remove all of its impacts and return the system to an uninvaded state. However, invader impacts may persist (so-called legacy effects), suggesting that removal alone will not meet management objectives.

More broadly, if invasive plant impacts are temporally dependent, not only could legacy effects be an important management consideration, but so too would the accumulation of impacts following a nascent invasion be important, especially in determining when to manage new invasions. Thus, if reducing the impacts of an invasive plant is the desired outcome, understanding both the accumulation and loss of impacts could directly influence management practices and timelines. However, these "invasion shadows" are poorly understood for most invasive plants. We studied the accumulation and loss of biotic and abiotic impacts of the common understory invader Japanese stiltgrass (*Microstegium vimineum*).

Our results show that ecological impacts depend on the duration of Japanese stiltgrass invasion, particularly for soil biogeochemistry. Depending on management goals, the period of time in which management is most effective may vary. For example, newly established invasions did not impact biogeochemistry as greatly as established invasions, and when the invader was removed, those impacts declined. Therefore, in this case, management can occur throughout the invasion and still potentially be effective. Conversely, the plant community remained unchanged in the early stage of invader establishment but experienced significant legacy effects during invader removal (i.e., the plant community did not return to an uninvaded state). Overall, we have shown that biotic and abiotic ecosystem properties vary in their temporal dynamics following invader establishment and removal, which should be considered when developing management strategies.

Although the physical presence of the invader may be removed through management, residual impacts may remain. Instead of an instantaneous return to an uninvaded ecological state, invader-mediated changes may persist, resulting in a "shadow" of the invader. For example, although a species that increases soil pH may have been locally eradicated, this increase in pH may remain long after the plant material is removed. Impact persistence, termed "legacy effects," can vary in temporal persistence (Marchante et al. 2015) and may have unequal effects across an ecosystem (Cuddington 2011). In some instances, legacy effects may persist in perpetuity unless an intervention is made (Hobbs et al. 2009). Despite the importance of these temporal dynamics, our understanding of legacy effects is limited but may have implications for achieving management goals.

In addition to the "back end" of invasion leading to potential legacy effects, even less is known about the accrual of invasive plant impacts following establishment of a nascent invasion. Over time, nascent invasions will increase in size and density, two factors that we know influence the magnitude of ecological impacts in some circumstances (Barney et al. 2013). However, invasive plant impacts have been studied almost exclusively using established populations, usually of unknown age, precluding identification of how impacts change with time (Kumschick et al. 2015). Understanding whether impacts occur immediately or accrue slowly with population age will aid development of appropriate management objectives based on impact dynamics (Barney 2016).

Temporal effects of invasive plant impacts are an important yet poorly understood element of invasion dynamics with potential implications for management and restoration. First, because management itself can have negative impacts, and invasive plants can have legacy effects, the choice to manage invasive plants should be carefully considered and driven by an understanding of invader impacts (Barney 2016). Some studies have shown legacy effects in single-metric impacts (e.g., Grove et al. 2015; Holdredge and Bertness 2010), but no study to date has looked at both biotic and abiotic characteristics of the environment following invader removal or impact accrual following establishment. In fact, few studies consider temporal effects at all either on the front end or back end of an invasion (unpublished data). Here we determine whether Japanese stiltgrass (*Microstegium vimineum*) has temporal impacts on biotic and abiotic environmental characteristics and, if so, at what rate they change following both removal and establishment.

Materials and Methods

Three sites were established across the Virginia section of the Ridge and Valley at Pandapas Pond Recreation Area in Montgomery County, VA (37.281088°N, 80.475236°W), Peaks of Otter Recreation Area in Jefferson National Forest, Bedford County, VA (37.442586°N, 79.612103°W), and Babbling Springs Recreation Area in George Washington National Forest, Rockbridge County, VA (37.926001°N, 79.605503°W), as described in Tekiela and Barney (2015). The experimental design of Barney et al. (2015) was followed in accordance with the Global Invader Impact Network (GIIN) and described in Tekiela and Barney (2015); however, a summary of methods follows. In 2013, at each location, four treatments were established: two randomly placed within the invasion and two within the uninvaded site. Within the invasion we installed spatially paired 1.75 by 1.75 m invaded (IN) and removal (RE) plots (i.e., 3.50 by 1.75 m) for a total of 22 replicates. IN plots were left unmanipulated for the duration of the study. RE plots were managed in June of each year to remove all *M. vimineum* individuals by hand pulling, and then remanaged in July to

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remove any new seedlings. Within the uninvaded site, we installed uninvaded (UN) and seeded (SE) plots. UN plots were left unmanipulated to represent an uninvaded forest understory. SE plots were sown with *M. vimineum* seed at the same density as the surrounding invasion in May 2013.

Data collection occurred in late July of 2013 through 2015, approximately at peak growing season, to capture the greatest influence of *M. vimineum*. Each vascular plant in each plot was identified to species, and the percent ground cover was assessed to the nearest 1%. Five 1-cm-diameter by 10-cm-deep soil samples were collected in each plot and homogenized. These samples were then dried, sieved (4-mm sieve), and analyzed for soil macro- (N, P, and K) and micro- (Ca, Mg, Zn, Mn, Cu, Fe, and B) nutrients, pH, and cation exchange capacity. Soil moisture was measured using three subsamples of an electronic soil moisture probe, and soil infiltration rate was calculated using a randomly placed single 10-cm-diameter ring driven 10 cm into the ground and infiltrated with 600 ml of water. Additionally, light penetration was calculated by measuring photosynthetic active radiation (PAR) above and below the forest understory layer across three equidistant transects within each plot.

To test the effect of removals and seeding on individual ecosystem metrics, plant richness, native richness, and invasive richness were measured. An analysis of variance (ANOVA) was run on each dependent variable using removal year (1, 2, or 3), treatment, site, and the interaction of treatment by removal year as fixed effects (Bolker et al. 2009). Means were separated using post hoc Tukey's honest significant difference (HSD).

We also wanted to compare the similarities between plant communities in both species identity and abundance, which is not possible with standard richness or biodiversity metrics. Similarity metrics can compare unique species among plots, but they only consider presence/absence of species and are not capable of considering abundance/prevalence (Ricotta and Szeidl 2006). Biodiversity metrics are capable of describing the relative abundance within an area but are not capable of making species composition comparisons. Both elements are important for comparing plant community composition. Therefore, we developed a new method to estimate the similarity of species composition, similar to a TWINSPAN analysis (Hill 1979), that explicitly accounts for species identity and abundance by describing the "plant community distance" between each treatment.

First, all resident plant species percent cover data, excluding data for *M. vimineum*, were subjected to a principal component analysis that was varimax rotated to center. Then, a factor analysis was used to reduce the complexity of the data by removing any components with variance explained <1. This reduced the plant community from 148 species to 60 components. Because of the flexibility of this analysis, we used the same method to incorporate and reduce complexity of all abiotic metrics, which reduced 15 ecosystem properties to 6 components to also test the similarity between overall ecosystem characteristics.

We analyzed plant community and ecosystem metric data sets separately. The center of mass (COM) for IN and UN treatments was calculated independently for each year by each site in multivariate space by averaging the plots in each treatment (i.e., IN or UN) across each component (6 or 10 respective to site). Then, Euclidean distances were calculated to measure the distance between individual plots and the COM (i.e., correct removal year and site) of each treatment within multivariate space for plant community composition and ecosystem properties separately. This means, for example, when comparing the COM of IN to IN plots, the average distance describes the variation within the treatment. ANOVA was performed on the log-transformed Euclidean distance of each treatment to the COM of IN and UN plots, because these two are the "original state" references using removal year, treatment, and site as main effects and the interactions treatment by removal year. Means were separated using post hoc Tukey's HSD.

Results

For metrics evaluated independently, a significant treatment by year interaction term would mean the relationship among treatments changed from year to year, which is what we predicted. While there were no significant interactions for any of the abiotic metrics, there were treatment differences for all abiotic metrics except CEC, P, Fe, and soil infiltration (Table 1). Of the metrics that varied among treatments, pH, K, Zn, Cu, and soil moisture did not show a significant difference between IN and RE plots, while Ca, Mg, Mn, B, and light penetration did show a significant difference between IN and RE plots (Figure 1). Only Zn showed a difference between IN and SE plots (Figure 1).

For all measurements of plant richness, treatment effects did not change over the course of the experiment (Table 1). RE plots had the greatest total plant richness, and IN plots had fewer species than UN plots (Table 1; Figure 2). RE and UN plots had greater native richness compared with SE and IN plots (Table 1; Figure 2), and RE and IN plots had the greatest invasive richness, while UN had lowest invasive richness (Table 1; Figure 2).

When the abiotic metrics were integrated and their distances measured to the COM of the reference UN and IN plots, it was found that their relationships did not change over the course of the experiment (Table 2). IN plots were least similar to the COM of UN plots, while SE plots were most similar to the COM of UN across all years (Table 2; Figure 3). UN and SE plots were equally dissimilar to the COM of IN, and RE plots were not significantly different from IN plots (Figure 1).

As with the abiotic metrics, the integrated plant communities showed no treatment variation over the course of the

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Table 1. Statistics from ANOVA of individual metrics.[a]

	Year			Treatment			Treatment × year		
	df	*F*-value	P-value	df	*F*-value	P-value	df	*F*-value	P-value
Total richness	2	0.70	0.4989	3	22.99	0.0001	6	0.31	0.9203
Native richness	2	0.63	0.5362	3	24.62	0.0001	6	0.47	0.8280
Invasive richness	2	0.43	0.8267	3	26.59	0.0001	6	0.27	0.9497
pH	2	1.86	0.1586	3	28.04	0.0001	6	0.54	0.7804
CEC	2	6.78	0.0014	3	0.87	0.4577	6	0.41	0.8754
P	2	1.80	0.1683	3	6.66	0.4577	6	0.83	0.8754
K	2	8.11	0.0004	3	15.38	0.0001	6	1.28	0.2657
Ca	2	0.415	0.6605	3	23.07	0.0001	6	0.26	0.9571
Mg	2	0.55	0.5788	3	17.44	0.0001	6	0.13	0.9920
Zn	2	2.78	0.0640	3	7.07	0.0001	6	0.62	0.7065
Mn	2	2.59	0.0771	3	8.37	0.0001	6	1.35	0.2374
Cu	2	22.30	0.0001	3	12.68	0.0001	6	0.66	0.6817
Fe	2	0.72	0.4869	3	1.66	0.1766	6	0.35	0.9069
B	2	0.14	0.8659	3	12.32	0.0001	6	0.09	0.9971
Soil infiltration	2	4.15	0.0168	3	0.19	0.9065	6	0.48	0.8235
Soil moisture	2	172.37	0.0001	3	5.29	0.0015	6	0.71	0.6413
Light penetration	2	0.93	0.3961	3	20.65	0.0001	6	2.00	0.0654

[a] See Figure 1 for means.

experiment (Table 2). Additionally, there was no difference among SE, UN, and IN plot richness in relation to the COM of UN; only RE plots were different (Figure 3). IN plots were most similar to the COM of IN; however, SE plots were more similar to the COM of IN than RA plots (Figure 3).

Discussion

Consistent with other studies on the ecological impacts of *M. vimineum* to forest understories (e.g., Ehrenfeld et al. 2001; Kourtev et al. 1998, 2003; McGrath and Binkley 2009; Tekiela and Barney 2015), we found that most metrics were different in the invaded patch compared with the uninvaded forest. However, few studies have investigated the temporal dynamics of invader impacts. In our 3-yr study, the differences between the invaded and uninvaded plots remained stable. While the age of the populations we studied is unknown, the stability we observed suggests the invasions are mature (i.e., not increasing or decreasing in local density or impacts). This impact stability provides an important baseline for gauging temporal trends following invader removal and establishment.

Following annual invader removal, where *M. vimineum* was assumed to make no contribution to observed impacts, greater than 50% of the individual abiotic parameters remained close to invaded levels. However, although those metrics that did change shifted within the first year toward those of the uninvaded plots, the predicted gradual return to an uninvaded state was not seen (Cuddington 2011). Similar to the abiotic variables, plant community richness changed immediately and dramatically following invader removal. Removal plots gained four to five more species than invaded plots, and two to three more than uninvaded plots. This may have resulted from either the small disturbance imposed by the removal of *M. vimineum* or a competitive release. Skurski et al. (2013) found that different removal methods lead to different disturbances, which themselves may affect observations. Not only does the removal create a minor soil disturbance, but it also modifies soil surface light exposure, which has been shown to affect germination (Baskin and Baskin 1998). Many of the species that emerged in removal plots were weedy species themselves (e.g., ladysthumb [*Polygonum persicaria* L.] and clearweed [*Pilea pumila* (L.) Gray]) that may have taken advantage of the disturbance. We cannot parse whether the additional recruitment in the removal plots was a result of reduced competition from *M. vimineum*, increased light availability and soil moisture, or the disturbance from management. Nevertheless, these new species clearly either recruited from a suppressed seedbank that was "released" or from surrounding vegetation following invader removal.

Contrary to our expectations, there was little evidence for temporal variation in abiotic impacts following the establishment of *M. vimineum*. In fact, abiotic factor levels in the seeded plots remained similar to uninvaded levels, suggesting these edaphic factors have both slow turnover rates and that the differences between invaded and uninvaded plots

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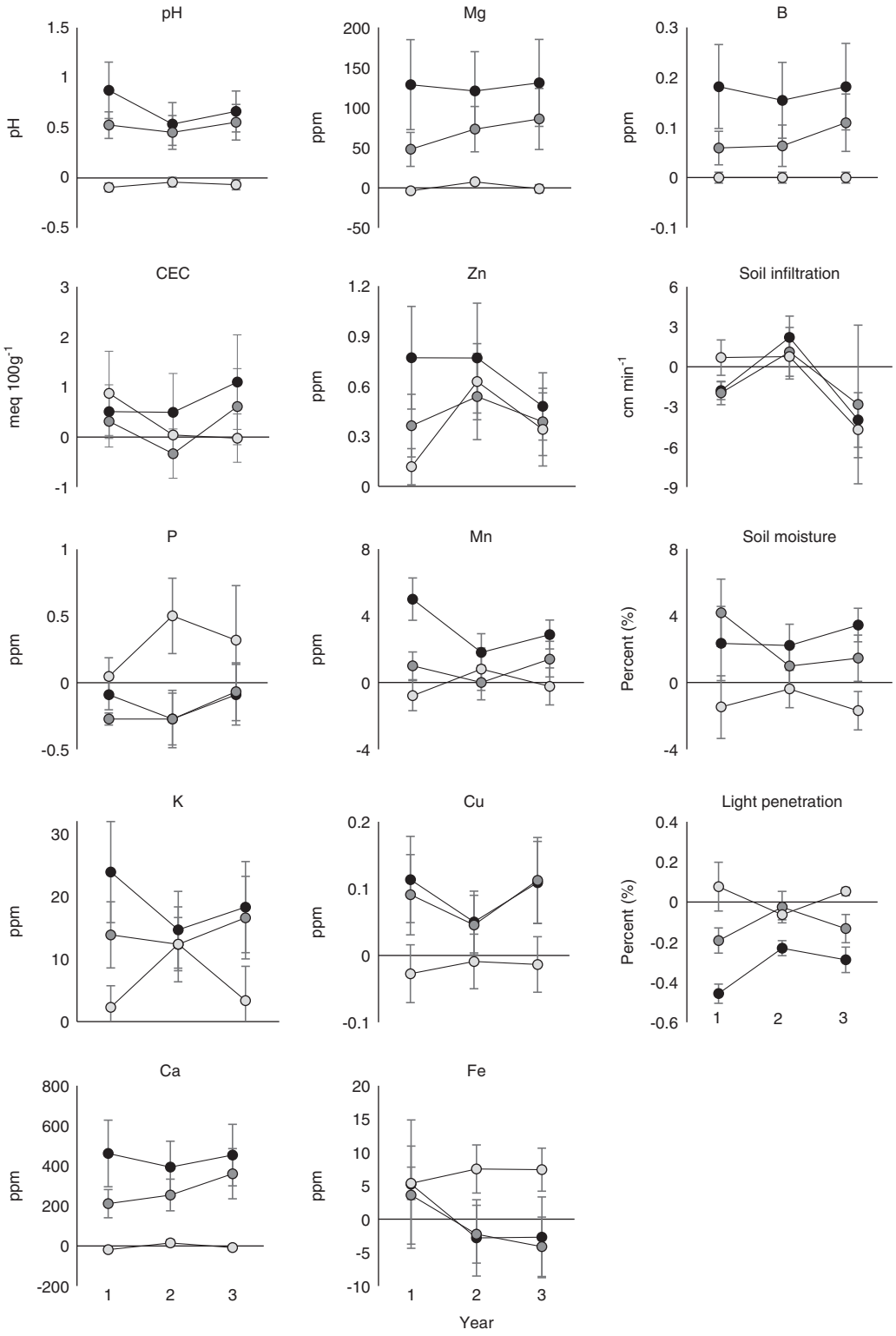

Figure 1. Difference between individual abiotic metrics of invaded (IN, black circles), removed (RE, dark gray circles), and seeded (SE, light gray circles) plots compared with uninvaded (UN) plots for each year after initial removal and seeding.

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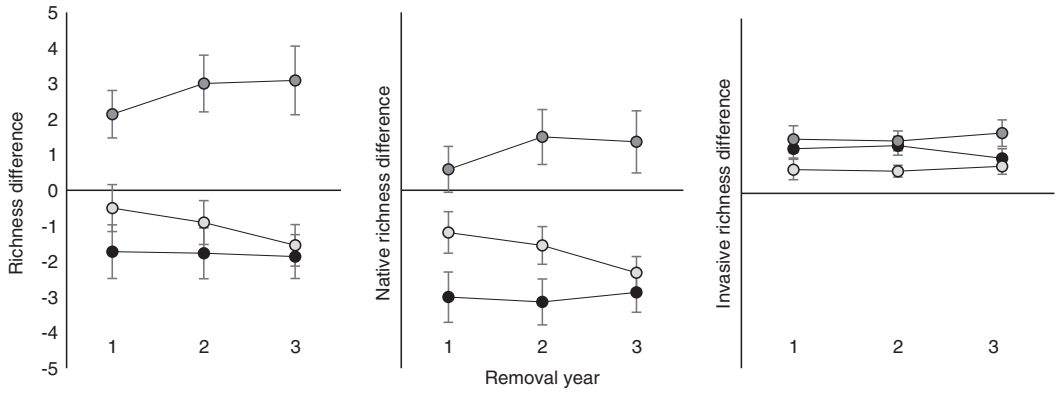

Figure 2. Difference between total richness, native richness, and invasive richness of invaded (IN, black circles), removed (RE, dark gray circles), and seeded (SE, light gray circles) plots compared with uninvaded (UN) plot richness for each year after initial removal and seeding.

accrued over many years or at least in a greater time span than our study. Additionally, *M. vimineum* cover in the seeded plots remained at very low density for years 1 and 2 (~1%) and only began to become established in the 3rd year (20%). For many invasive plants, the impact magnitude has been shown to scale with invader cover. Various linear and nonlinear relationships have been identified in many species (Pearson et al. 2015; Tekiela and Barney 2015; Thiele et al. 2011). In fact, *M. vimineum* has been shown to have a potential impact threshold for many factors at ~40% cover. In other words, impacts were not observed until 40% invader cover was reached, which was not achieved in the seeded plots within the first 3 yr (Tekiela and Barney 2015). Thus, the small changes we observed for most factors could also be explained by the very low *M. vimineum* cover.

However, when abiotic factors were integrated using multivariate techniques, much of the individual metric noise was reduced and a clear pattern emerged. Removal plots became more similar to uninvaded plots, while becoming less similar to invaded plots. Similarly, seeded plots became more similar to invaded plots. In short, removing the invader made the abiotic characteristics become more associated with an uninvaded state, while seeding an uninvaded area made it look more similar to an invaded state. Surprisingly, these shifts happened within the first year, with no additional change over the next 2 yr. This immediate change followed by persistent legacy effects has also been observed in Scotch broom [*Cytisus scoparius* (L.) Link] and was suggested to be due to the nitrogen pulse left by the carcasses of this nitrogen-fixing invader (Grove et al. 2015). However, in our study, *M. vimineum* was hand managed at the seedling stage, and carcasses were removed; thus, these dramatic legacy litter effects were not possible. Although we did not examine the soil microbial community, long-lasting legacies in the microbial community (see Elgersma et al. 2011; König et al. 2016) could have changed the nutrient-cycling characteristics of this system and been responsible for the soil legacies that did not appear to change in 3 yr.

The resident plant community showed minor compositional changes due to the presence of *M. vimineum*. In fact, removing *M. vimineum* may have done more harm than good and further distanced the resident plant community from an

Table 2. Statistics from ANOVA of the integrated plant community and abiotic metrics comparing distance of plots to multidimensional center of mass (COM) of invaded (IN) and uninvaded (UN) plots.[a]

	Year			Treatment			Treatment × year		
	DF	*F*-value	P-value	DF	*F*-value	P-value	DF	*F*-value	P-value
To IN COM									
Plant community	2	9.44	0.0001	3	23.75	0.0001	6	0.70	0.6506
Abiotic metrics	2	12.64	0.0001	3	15.16	0.0001	6	0.83	0.2294
To UN COM									
Plant community	2	9.03	0.0002	3	14.25	0.0001	6	0.86	0.5232
Abiotic metrics	2	0.63	0.5344	3	46.35	0.0001	6	0.13	0.3304

[a] See Figure 2 for distance to COM means.

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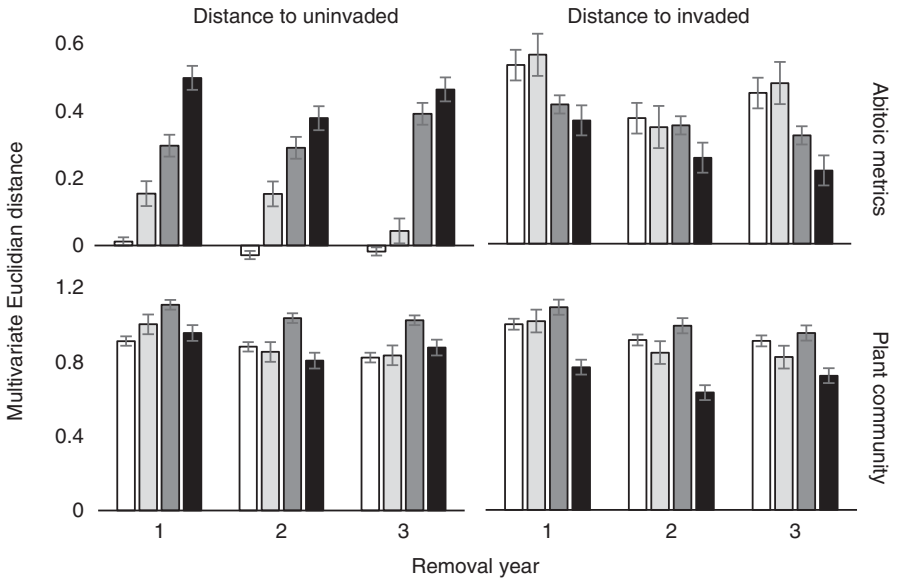

Figure 3. The Euclidean distances to the multidimensional center of mass (COM) for the plant community and abiotic metrics of both uninvaded (UN) and invaded (IN) plots for each year. UN plots are white, seeded (SE) plots are light gray, removal (RE) plots are dark gray, and IN plots are black. Greater distances suggest less similarity to the respective COM.

uninvaded or invaded landscape. The plant community—incorporating richness, identity, and abundance—became entirely novel with respect to both reference communities. In this case, other ruderal weedy species that were not well represented in either invaded or uninvaded plots now dominate where invader removals occurred. In the context of legacy effects, this is a worst-case scenario, as the legacy in fact makes the new plant community even less like the uninvaded landscape. One invader was replaced by a variety of additional weedy species, an occurrence that has been described as the "bane of weed management" (Pearson et al. 2016). This negative response to management is often seen in the systems of the western United States, where the removal of invasive perennial forbs does little to restore the native plant community and instead encourages establishment of new invasive annual grasses (Skurski et al. 2013). This is additionally concerning for *M. vimineum* invasions, because re-establishment of this primary invader is likely, potentially leaving an even poorer-quality community when management is terminated (DeMeester and Richter 2009). If a return to an uninvaded state is desirable, active restoration involving reseeding of desirable species may be the only viable option, although many species of the desired native community may not have readily available commercial seed stocks.

In contrast, seeding an uninvaded area with *M. vimineum* did not change the resident plant community in 3 yr. It remained similar to the uninvaded resident plant community and dissimilar to the invaded plant community. This may not be surprising, considering the *M. vimineum* cover was so low and its residence time short. Dostál et al. (2013) showed that newly established giant hogweed (*Heracleum mantegazzianum* Sommier & Levier) imposed greater reductions in species richness early in the invasion process, but those authors' time frame was much longer, and *H. mantegazzianum* had much higher cover early in the invasion, further suggesting this is likely a function of cover not time. Thus, we would expect the plant community to begin to shift in the nascent invasion as *M. vimineum* expanded and became denser.

Here we have shown that important temporal effects do exist following both removal and establishment of *M. vimineum*—a dominant forest understory invader in the eastern United States. Importantly, the accrual and loss of changes differed between biotic and abiotic components and occurred at different timescales. Many responses occurred immediately after our interventions and will now either persist in a different state in perpetuity or are shifting to the new state at too slow a rate to identify within 3 yr. Most concerning from a management perspective is the shift of the resident plant community to a novel condition not seen in either the invaded or uninvaded states. If management efforts only replace a problematic invader with other weedy species, the cost of management may outweigh its gains. Temporal dynamics in relation to density of invasions is an important factor to consider when elucidating invader impacts and designing management plans.

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