

System-level changes following invasion caused by disruption of functional relationships among plant and soil properties

DANIEL R. TEKIELA† AND JACOB N. BARNEY

Department of Plant Pathology, Physiology, and Weed Science, Virginia Tech, Blacksburg, Virginia 24061 USA

Citation: Tekiela, D. R., and J. N. Barney. 2015. System-level changes following invasion caused by disruption of functional relationships among plant and soil properties. *Ecosphere* 6(12):294. <http://dx.doi.org/10.1890/ES15-00412.1>

Abstract. The ecological impacts of invasive plants have served to justify the cost of their management, which is estimated to exceed \$1 billion annually in the US alone. However, our understanding of the ecological impacts of most invasive plants is extremely limited, and when known, interpretation is confounded with varied measurements and methods. While this can provide important information about specific components of ecosystem function, it limits our understanding of the broader scope of impacts any one species may have. Using Japanese stiltgrass (*Microstegium vimineum*) as a study system, our objectives were to (1) survey a broad suite of 29 important ecological impact metrics (EIMs), (2) identify invader cover-EIM relationships, and (3) test if the comparative reference (uninvaded or invader removal) influences interpretation. Japanese stiltgrass had the strongest effect on the plant community, followed by soil properties, soil nutrients, and other abiotic/biotic factors. Many EIM values differed among reference types, and plant community EIMs were reduced with increasing Japanese stiltgrass abundance. For example, plant biodiversity was lower in the invasion when compared to both removed and uninvaded sites; however, soil organic matter was higher only in the uninvaded site when compared to the invasion. The integrative ecosystem metric $E(c)$ also showed that the system overall was impacted by the Japanese stiltgrass invasion, and this varied among sites. Interestingly, relationships among EIMs were also changed by the presence of Japanese stiltgrass. For example, a strong correlation between pH and soil organic matter disappeared when Japanese stiltgrass was present. Together this suggests that this invaded ecosystem functions in a different way through both individual and correlated alterations to ecosystem properties.

Key words: cover; diversity; ecological impact; invasive species; Japanese stiltgrass; *Microstegium vimineum*; plant invasion.

Received 30 June 2015; **revised** 31 July 2015; **accepted** 4 August 2015; **published** 22 December 2015. Corresponding Editor: M. Perring.

Copyright: © 2015 Tekiela and Barney. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

† **E-mail:** tekiela2@vt.edu

INTRODUCTION

Invasive species can have strong negative impacts on ecosystem function, and are globally ranked as one of the top five threats to biodiversity (Millennium Ecosystem Assessment 2005). Specifically, impacts of invasive plants include alterations to soil nutrient dynamics, plant and animal community assemblages, and

trophic dynamics (Pyšek et al. 2012). These ecological impacts, both known and perceived, serve as the motivation for the research and management of invasive plants (Mack and D'Antonio 1998). Therefore, it stands to reason that the ecological impact of invasive plants is well documented, especially considering that substantial human and economic capital are spent managing exotic plants, estimated at >\$1

billion annually in the US alone (Pimentel et al. 2005). Unfortunately, despite the volume of studies on the ecological impacts of invasive plants, our understanding of these impacts remains surprisingly limited (Hulme et al. 2013).

Of the >14,000 exotic invasive plants estimated to inhabit North America, Europe, Australia, and New Zealand, less than 200 have any quantitative assessments of ecological impact (Hulme et al. 2013). Of these studied species, ~40% include only one ecological impact metric (EIM; e.g., native plant richness, pH), ~35% have only two EIMs, and >95% have had fewer than five EIMs examined (Hulme et al. 2013). Additionally, “the rationale for which response variables [EIMs] have been included in a study does not appear clear and there are no obvious suites of variables that consistently co-occur” (Hulme et al. 2013). Our understanding of the ecological impacts for the vast majority of invasive plant species is limited to a few inconsistent ecological parameters, leaving their broader impact largely unknown (Barney et al. 2013). This shortcoming in our understanding of the broader ecological impacts of invasive plants could have repercussions on management decisions, budget allocations, and regulations intended to limit invader impact (Quinn et al. 2013).

More than once it has been shown that the choice of EIMs can have important implications on our perception of the impact of invasion (Lockwood et al. 2001). For example, while examining the ecological impacts of saltcedar (*Tamarix* spp.), Shafroth and Briggs (2008) concluded saltcedar presence was associated with increased bird density and diversity, but decreased native plant biodiversity. Similarly, Farnsworth and Ellis (2001) concluded that purple loosestrife (*Lythrum salicaria*) presence had no effect on plant richness but a significant negative effect on overall native plant biomass. In both cases, if only one EIM was investigated, it would have greatly misrepresented the broader impact, and perhaps changed the perceived outcome as positive or negative. Single EIM studies may be warranted when a specific hypothesis about a particular species is of interest (Hulme et al. 2014), but often a broader understanding of the overall ecological impact is desired (Barney et al. 2013).

Here we study the effects of Japanese stiltgrass

(*Microstegium vimineum*) on the highland forests of western Virginia. This C₄ shade tolerant annual grass is considered native to most of East Asia and is reported to be one of the top three most prevalent invasive plants in the Eastern United States (Kuppinger 2000). Japanese stiltgrass has spread across much of the forests of the Eastern United States, and now occupies an estimated 260,000 hectares east of the Mississippi River (Kuppinger 2000). With nine EIMs independently studied (Kourtev et al. 1999, 2003, Baiser et al. 2008, Marshall et al. 2009, Marshall and Buckley 2009, Brewer 2010, Simao et al. 2010, Strickland et al. 2010), only cheatgrass (*Bromus tectorum*) and common reed (*Phragmites australis*) are better studied (Hulme et al. 2013). Therefore, one may assume we have a strong understanding of the ecological impact of Japanese stiltgrass.

Unfortunately, the 9 EIMs were studied in separate populations precluding our ability to understand the potential network of interactions and feedbacks among EIMs following invasion (Le Maitre et al. 2011). As Hulme et al. (2013) stated, “response variables should not be assessed in isolation but viewed as inter-related factors of ecosystems that might be directly or indirectly impacted by an alien plant.”

Of additional concern is that some studies have found that impact to EIMs varies with invader abundance (typically measured as percent ground cover; Thiele et al. 2011), but only 18% of invasive plant impact studies consider invader cover (Tekiela and Barney, *unpublished data*). Of those studies, >50% found that impact magnitude varied with invader cover. Of existing studies examining EIMs of Japanese stiltgrass, cover level was never a factor in measuring impact. Thus, the influence of invader cover level for all invasive plants should be further examined because understanding abundance-impact relationships may uncover important thresholds that could be exploited during management or restoration (Barney et al. 2013).

Identifying ecological impacts attributable to invasive plants requires comparing the invaded patch to an alternative patch (often referred to as native or pre-invaded) without the invader (Barney et al. 2015, Kumschick et al. 2015). The two most commonly used references to benchmark invader impacts are (1) a nearby uninvaded site that is assumed to represent the pre-invaded

system or (2) a portion of the invaded patch removed. In the case of Japanese stiltgrass, 66% of studies used observational uninvaded references and 33% used removal references; thus, different methods were used to determine Japanese stiltgrass impacts. Each method has benefits and drawbacks regarding their underlying assumptions (Kumschick et al. 2015), which may affect their utility and interpretation, as well as the magnitude and direction of the resulting impacts.

To obtain a more holistic understanding of the impacts of invasive plants our objectives were to (1) use a multi-metric approach to gain a broader understanding of the consequences of invaders, including EIMs that do not change, (2) determine if EIMs vary with invader cover, and (3) determine if the reference type changes interpretation, all of which have been identified as important, yet understudied components of invader impact (Kumschick et al. 2015).

METHODS

Site selection

We identified Japanese stiltgrass patches within representative habitats of the Virginia section of the Blue Ridge Mountain forest ecosystem that met the following criteria: (1) an invasion patch large enough to contain the study design (see below) with all plots >1m from the invasion front; (2) no clear dispersal boundaries among plots within the invasion (e.g., large felled tree, waterway); (3) Japanese stiltgrass being dominant in the area; and 4) an adjacent uninvaded reference site that is most likely uninvaded due to lack of propagule pressure, not due to inherent abiotic differences (White and Walker 1997, Powell et al. 2013).

The most southern patch was in Pandapas Pond Recreation Area (PAN) located in Montgomery County, Virginia, USA (37.281088° N, 80.475236° W). The forest canopy of this location is primarily red maple (*Acer rubrum*), white oak (*Quercus alba*), and red oak (*Quercus rubra*). The understory community composition is typical of Appalachian forests of Virginia with total richness of 78 species (Brown and Peet 2003). Soils are a Berks-Weikert composition on slopes of 15–25 percent (Web Soil Survey). The reference site was selected beyond a 0.5 m wide ephemeral

creek likely acting as a barrier to dispersal, but was otherwise similar to the invaded sites in canopy composition, soils, and aspect.

The second patch was in Peaks of Otter Recreation Area (POT) in Jefferson National Forest, Bedford County, Virginia (37.442586° N, –79.612103° W). The forest canopy composition is primarily white oak, red oak, and mockernut hickory (*Carya tomentosa*). This location also has a forest understory community typical of the area and similar to PAN. The soils of this location are shallower and rockier than the two other locations, with less than 2 cm of topsoil in some areas. The reference was located adjacent (>5 m) to the Japanese stiltgrass invasion.

The most northern patch, Babbling Springs (BBS) Recreation Area (37.926001° N, –79.605503° W), was located in George Washington National Forest, Rockbridge County, Virginia. The canopy composition of this location is primarily white oak, red oak, and white ash (*Fraxinus americana*). Again, the community of this understory is typical of Virginia Appalachian forests. Soils, similar to PAN, were a Weikert-Berks-Rough complex on moderate slopes (Web Soil Survey). The reference site was defined along the same ephemeral stream where Japanese stiltgrass had not yet invaded. All uninvaded sites were similar in native understory plant composition, soil type, and overstory composition.

Site layout

At each location we established two treatments within the invasion patch, and two within the uninvaded site. Ten replicates of each treatment were placed in PAN and six were placed in both POT and BBS. Within the invasion patch we installed 3.50 × 1.75 m split plots that were randomly assigned to 1.75 × 1.75 m invaded (IN) or invader removal treatments (RE). IN plots were left un-manipulated, while RE plots were managed to remove Japanese stiltgrass by clipping at the soil surface, which imposed minimal disturbance while achieving ~0% cover of Japanese stiltgrass. Removal occurred in mid-May and mid-June while plants were <3 leaf stage. Thus, the Japanese stiltgrass was absent in RE plots for <1 yr, which is a common duration in most existing studies (34% of removal studies; Tekiela and Barney, *unpublished data*). Two independently randomized 1.75 × 1.75 m treat-

ment types were installed in the uninvaded sites. Uninvaded (UN) reference plots were left untouched to act as a reference to the invaded patch. Seeded plots (SE) were sown with Japanese stiltgrass seed at a similar density to the current invasion to ensure the uninvaded reference sites were vulnerable to invasion and were only uninvaded due to a lack of propagules, not due to abiotic differences (Eschtruth and Battles 2011). To determine what density to seed SE plots, average density of Japanese stiltgrass was assessed in the invasion patch to be 1264 plants m^{-2} . Therefore, SE plots were seeded in May 2013 prior to germination by evenly dispersing 3871 seed across the 3.06 m^2 plot using a granular shaker. Thus, seeded plots were only used to assess the quality of the UN reference site and were not considered further during analyses. The outer 0.375 m (2.06 m^2) edge of each plot was designated as a border to reduce edge effects, with only the inner 1 m^2 used for data collection. This dimension was chosen based the average height of Japanese stiltgrass in these habitats.

Selection and method of metric collection

Data collection occurred in late July 2013 during the peak growing season to capture the greatest influence of Japanese stiltgrass. We selected the most commonly measured EIMs that could be practically implemented on a large scale within a brief sampling period, while still representing the primary suite of EIMs present in the literature (Appendix: Table A1). All recorded EIMs represent environmental characteristics implicated in ecosystem function, and were grouped into the general categories of plant community, soil physical property, soil nutrients, or other abiotic/biotic parameters. Using data from multiple impact studies and simulated data, Barney et al. (2013) used a bootstrap method to measure variation in estimated total ecosystem impact, and suggested measuring >15 EIMs to best capture broader invasive plant impacts to the invaded ecosystem regardless of EIM identity. Therefore, by measuring 29 EIMs, we exceeded this minimum and should be capable of making robust conclusions on the ecological impact of Japanese stiltgrass regardless of the selection of EIMs.

Methodology for collecting and analyzing each

EIM was taken from the literature and adapted as needed to our study (Appendix: Table A1). All methodology used was standard except for earthworm extraction and infiltration rate which were combined to reduce disturbance to the plot. In place of water for the infiltration test, mustard powder solution was used to estimate infiltration rate, while simultaneously sampling earthworms.

Data analysis

Similar to the majority of invasive plant impact studies, we performed univariate techniques to test for treatment effects of each EIM independently. For each EIM, we used ANOVA with treatment (UN, RE, IN) and location (PAN, POT, BBS) as fixed effects (Bolker et al. 2009) with post-hoc Tukey's honestly significant difference ($\alpha = 0.05$) for mean separation. To test if Japanese stiltgrass cover influenced individual EIMs, ANCOVA was performed on IN plots using Japanese stiltgrass cover, the quadratic term of Japanese stiltgrass cover (to test for non-linearity), and location as independent variables for each dependent EIM.

To estimate system-level impact we derived the integrated impact value, $E(c)$, according to Barney et al. (2013). $E(c)$ is designed to integrate any number of EIMs as a function of invasive plant cover. A modified version of $E(c)$ was calculated using UN or RE plots independently as references (\bar{n}) to test if different $E(c)$ result from different reference types—in other words, how ecologically different are the uninvaded and removal plots? A Δk was calculated for each EIM as the difference between IN and a reference (UN or RE); which was then integrated into $E(c)$ by determining the geometric mean of Δk s (i.e., $E(c) = \text{geometric mean of } \Delta k$ s). Therefore, $E(c)$ can only be calculated for each IN plot. ANCOVA was then performed separately using UN and RE reference plots on $E(c)$ using Japanese stiltgrass cover and location as independent variables.

We also used a principle component analysis (PCA) to interpret system-level responses (at least within the context of the 29 EIMs we measured) to Japanese stiltgrass invasion and reduce the number of ecological components. PCA was performed using Japanese stiltgrass percent cover and all EIMs listed in Table 1 and

Table 1. Statistical results for independent EIM ANOVA tests based on treatment and location. Significant *P* values (<0.05) are bolded.

Measured EIMs	df	Treatment		Location	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Plant community					
Diversity index (<i>H'</i>)	2	82.23	0.0001	1.82	0.1712
Diversity index w/o invader (<i>H'_i</i>)	2	4.93	0.0103	2.43	0.0964
Richness	2	7.85	0.0009	0.55	0.5795
Native richness	2	9.00	0.0004	0.98	0.3805
Invasive richness	2	12.73	0.0001	24.38	0.0001
Bare ground (%)	2	153.30	0.0001	2.79	0.0695
Other invader cover (%)	2	4.03	0.0227	7.75	0.0010
Native cover (%)	2	6.03	0.0041	0.96	0.3898
Other biotic and abiotic parameters					
Microbial biomass (mg kg ⁻¹)	2	0.16	0.8525	49.75	0.0001
Microbial activity (μg CO ₂ 10 g soil ⁻¹ hr ⁻¹)	2	1.16	0.3195	36.85	0.0001
Light penetration (%)	2	16.23	0.0001	3.36	0.0411
Litter abundance (g m ⁻²)	2	4.47	0.0154	3.95	0.0243
Litter decomposition (%)	2	0.18	0.8386	17.39	0.0001
Earthworms m ⁻²	2	2.47	0.0936	2.45	0.0952
Soil physical properties					
Infiltration rate (cm min ⁻¹)	2	1.94	0.1530	12.3	0.0001
Soil moisture (%)	2	1.36	0.2636	13.03	0.0001
pH	2	8.18	0.0007	14.15	0.0001
Organic matter (%)	2	3.45	0.0381	376.63	0.0001
TOC (ppm)	2	0.15	0.9003	100.64	0.0001
CEC (meq 100 g ⁻¹)	2	0.23	0.7982	3.06	0.0542
Soil nutrients					
N (%)	2	0.17	0.8415	166.62	0.0001
P (ppm)	2	2.40	0.0988	19.35	0.0001
K (ppm)	2	8.99	0.0004	37.37	0.0001
Ca (ppm)	2	6.63	0.0025	12.27	0.0001
Mg (ppm)	2	5.13	0.0087	15.60	0.0001
Zn (ppm)	2	1.26	0.2901	0.60	0.5503
Mn (ppm)	2	7.38	0.0013	3.50	0.0362
Cu (ppm)	2	4.43	0.0160	89.23	0.0001
Fe (ppm)	2	0.15	0.8583	3.12	0.0512
B (ppm)	2	4.38	0.0167	13.92	0.0001

varimax rotated to maximize sums of squared variance for each loading value (Appendix: Fig. 1). The component reduction was performed using a combination of a scree plot, variance explained, and comprehensibility of eigenvector loadings to determine how many components parsimoniously represented the data (Cattell 1966). Five components accounted for 68% of the variation and generally grouped EIMs into the following: component 1 = carbon pools and cycling; component 2 = overall plant diversity and richness; component 3 = pH and cations; component 4 = invasive plant richness and cover; and component 5 = native plant richness and cover (Appendix: Table 2). Additionally, within each component a “flagship” EIM was chosen using the highest loading value. In cases where multiple EIMs loaded strongly and relatively equally to a single component, we chose the EIM based on ecological principles to select a flagship

EIM that best represented the grouping (e.g., pH instead of Ca). Flagship EIMs were as follows: 1 = organic matter; 2 = diversity index; 3 = pH; 4 = invasive richness; and 5 = native cover.

To our knowledge, no study has attempted to determine if an invasive plant modifies interactions among EIMs; the so-called interconnectedness (Hulme et al. 2013). Therefore, we performed a quadratic discriminant analysis, which allows the variation structure among treatments to be independent; allowing the correlation structure within treatment to be driven by changes due to Japanese stiltgrass (Williams 1983). It also allows us to examine the similarities or difference between treatments and if the five components and flagship EIMs are successful at predicting Japanese stiltgrass presence/absence when compared to using the full suite of EIMs. To better understand the correlation structure of EIMs within each treatment and

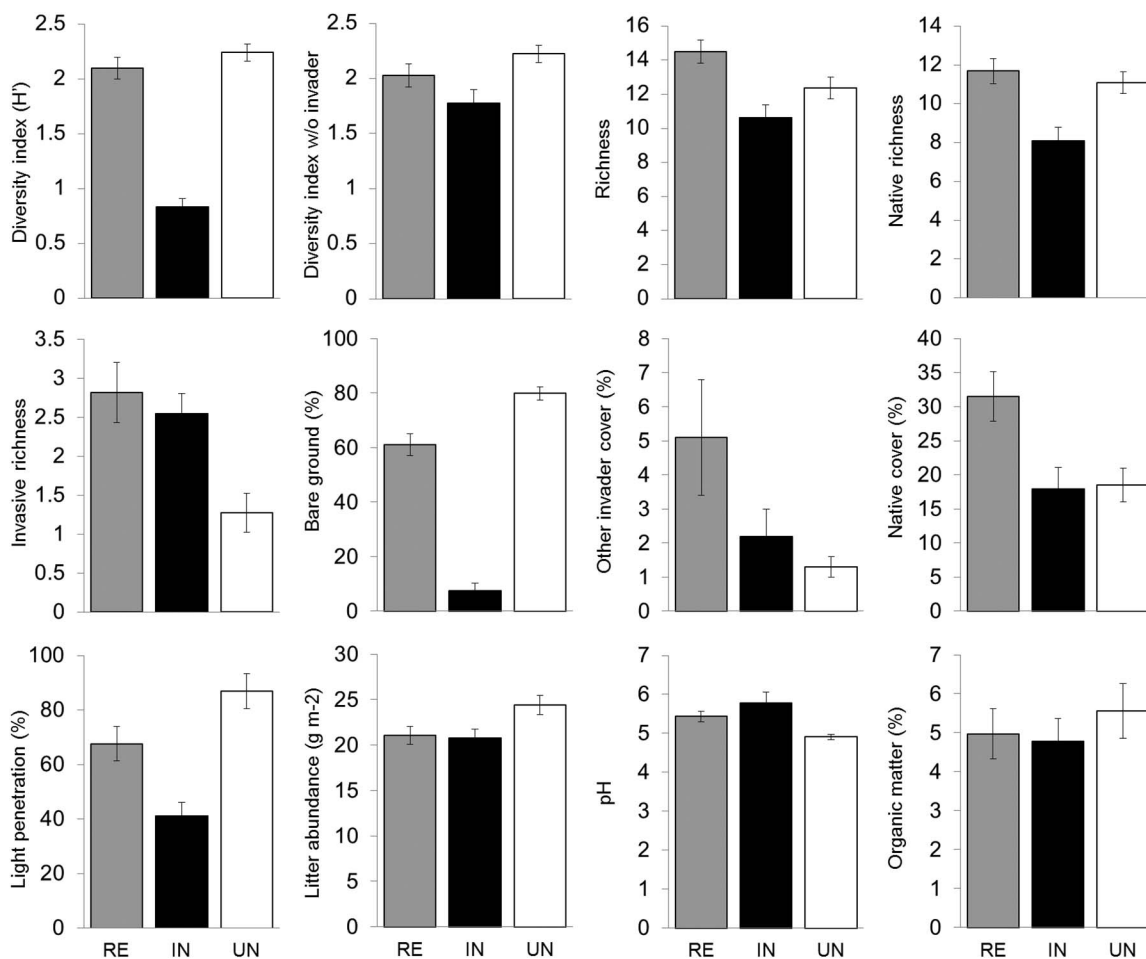


Fig. 1. Univariate plots of significantly different EIMs in plant community metrics, other abiotic/biotic property metrics, and soil physical property metrics; grey bars are RE plots, black bars are IN plots, and white bars are UN plots. For nutrients results see Table 1 and 2.

the predictive quality of EIM's, a quadratic discriminant analysis was performed separately on flagship EIMs, components, and all EIMs using treatment (IN, UN, RE) as the discriminating factor to test how different the correlation structure of treatments were, and if our EIM reduction had similar invasion predictive qualities. Within treatment correlation structure was recorded for each of the three discriminant analyses. To determine if within treatment correlation structure is statistically different, an equality of covariance test was performed on the correlation structure for each group (i.e., flagship EIMs, components, all EIMs). All statistical analyses were run in JMP version 11 (SAS Institute, Cary, North Carolina, USA) except for

the equality of covariance test which was performed in R v.3.1.2 (R Core Team 2013).

RESULTS

By August, Japanese stiltgrass within seeded plots established and began flowering, suggesting uninvaded reference sites were susceptible to invasion by Japanese stiltgrass. During the peak growing season in July, Japanese stiltgrass cover in IN plots averaged $72 \pm 21\%$ (standard deviation), ranged from 18 to 95% and was consistent across sites ($P > 0.05$). Removals reduced Japanese stiltgrass cover in RE plots to $1 \pm 0\%$ with a range of 0–1% in POT and BBS, and $4 \pm 3\%$ with a range 1–10% in PAN.

Table 2. EIM means and standard errors in uninvaded, removed, and invaded plots. Means separated using post-hoc Tukey's honestly significant difference. Means with different letters are statistically different.

Measured EIMs	Uninvaded		Removed		Invaded	
	Mean	SE	Mean	SE	Mean	SE
Plant community						
Diversity index (H')	2.240	0.078a	2.099	0.101a	0.831	0.079b
Diversity index w/o invader	2.224	0.077a	2.027	0.103ab	1.776	0.125b
Richness	12.36	0.636ab	14.50	0.664a	10.63	0.752b
Native richness	11.09	0.569a	11.68	0.643a	8.091	0.705b
Invasive richness	1.273	0.248b	2.818	0.387a	2.545	0.261a
Bare ground (%)	79.9	2.4a	61.1	4.0b	7.5	2.7c
Other invader cover (%)	1.3	0.3a	5.1	1.7b	2.2	0.8ab
Native cover (%)	18.5	2.5b	31.5	3.6a	17.9	3.2b
Other biotic and abiotic parameters						
Microbial biomass (mg kg ⁻¹)	0.249	0.034a	0.242	0.028a	0.233	0.022a
Microbial activity ($\mu\text{g CO}_2$ 10 g soil ⁻¹ hr ⁻¹)	0.0668	0.0054a	0.0684	0.0070a	0.0593	0.0070a
Light penetration (%)	86.90	6.47a	67.63	6.29a	41.15	4.847b
Litter abundance (g m ⁻²)	24.42	1.050a	21.04	0.9855b	20.78	0.9725b
Litter decomposition (%)	14.71	1.33a	15.42	2.46a	16.14	1.55a
Earthworms m ⁻²	10.2	4.65a	6.85	2.60a	0.7616	0.7616a
Soil physical properties						
Infiltration rate (cm min ⁻¹)	3.748	1.132a	1.789	0.8684a	1.962	0.6718a
Soil moisture (%)	30.56	2.066a	34.73	2.016a	32.89	2.228a
pH	4.908	0.0638a	5.435	0.1329a	5.782	0.2807b
Organic matter (%)	5.559	0.7098a	4.968	0.6475b	4.781	0.5798b
TOC (ppm)	2.999	0.3665a	3.129	0.3987a	3.089	0.4820a
CEC (meq 100 g ⁻¹)	5.738	0.6134a	6.049	0.5101a	6.245	0.5355a
Soil nutrients						
N (%)	0.2167	0.0288a	0.2221	0.0260a	0.2131	0.0271a
P (ppm)	2.318	0.1527a	2.045	0.0455a	2.227	0.1127a
K (ppm)	36.32	3.173b	50.14	5.282a	60.18	8.080a
Ca (ppm)	161.6	10.21b	373.0	70.13ab	623.1	166.7a
Mg (ppm)	36.41	3.558b	84.45	21.17ab	165.1	56.18a
Zn (ppm)	1.364	0.062a	1.727	0.188a	6.577	4.454a
Mn (ppm)	9.191	0.880a	10.20	0.834a	14.19	1.262b
Cu (ppm)	0.414	0.039a	0.505	0.060ab	0.527	0.065b
Fe (ppm)	20.40	1.999a	24.00	7.338a	25.64	9.608a
B (ppm)	0.1591	0.0126a	0.2182	0.0333ab	0.3409	0.0839b

Additionally, at all sites UN plots did not have any encroachment of Japanese stiltgrass during the study and remained uninvaded.

The plant community EIMs, plant diversity index (H'), plant diversity index without Japanese stiltgrass (H'_r), native plant richness, invasive plant richness, and bare ground were all reduced by the presence of Japanese stiltgrass when compared to UN plots (Fig. 1, Table 2). Plant diversity index (H'), total plant richness, native plant richness, bare ground and native plant cover were reduced by the presence of Japanese stiltgrass when compared to RE plots (Fig. 1, Table 2). Across all sites, 34 plant species were identified in RE plots that were not present in IN plots (Appendix: Table 3). Other abiotic/biotic EIMs were also impacted by the invasion. For example, light penetration and litter abundance were reduced by the presence of Japanese stiltgrass when compared

to UN plots (Fig. 1, Table 2), while only light penetration was reduced by Japanese stiltgrass when compared to RE plots (Fig. 1, Table 2). Of the soil property EIMs, pH was higher and organic matter was lower in the Japanese stiltgrass invasion, when compared to UN plots (Fig. 1, Table 2). Soil potassium, calcium, magnesium, manganese, copper, and boron were affected by Japanese stiltgrass presence when compared to UN plots (Table 2), but only potassium and manganese were different between IN and RE (Table 2).

Additionally, we compared all EIMs between RE and UN plots to determine the similarities or differences between the two most commonly used reference types. Three of eight plant community EIMs (percent bare ground, percent native cover, percent other invasive cover) were different. The species present in UN but not RE plots were predominately trees, while species

present in RE but not UN plots were predominantly fast growing ruderal species. One of six other abiotic/biotic EIMs (litter abundance) and one of six soil property EIMs (pH), were different between RE and UN (Fig. 1, Table 2).

Plant diversity index (H'), bare ground, and native plant cover decreased linearly with increasing Japanese stiltgrass cover, while total plant richness and native plant richness had a negative quadratic relationship with increasing invasive cover that peaked at 48% and was lowest at maximum Japanese stiltgrass cover (Fig. 2); no other EIMs varied with Japanese stiltgrass cover.

The total ecosystem impact $E(c)$ (the integration of multiple EIMs into a single value sensu Barney et al. [2013]) values varied between the reference types ($P = 0.0053$); therefore, results are reported separately for UN and RE references (Appendix: Table A4). $E(c)$ with UN as the reference was 1.61 ± 0.06 for PAN, 1.85 ± 0.11 for POT, and 1.68 ± 0.06 for BBS. Using RE as reference, $E(c)$ was 1.42 ± 0.04 for PAN, 1.81 ± 0.05 for POT, and 1.51 ± 0.05 for BBS. The similarity in PAN and BBS $E(c)$ values were associated with the overlapping clustering of points in the PCA while the dissimilar POT did not overlap in the PCA (Appendix: Fig. A1). Using UN as reference, $E(c)$ did not vary with Japanese stiltgrass cover ($P = 0.0679$), though $E(c)$ did vary with Japanese stiltgrass cover with RE as a reference ($P = 0.0295$; Appendix: Fig. A2).

Quadratic discriminant analysis with flagship EIM's, components, and all EIM's resulted in successful discrimination of treatment (IN, UN, RE) with Wilks' Lambda test scores of $P < 0.0001$. However, the proportion of misclassified plots after training varied: 13.9% of plots were misclassified using flagship EIM's; 17.5% of plots were misclassified using components; and 0% of plots were misclassified using all EIMs (Fig. 3). With flagship variables, RE plots were most commonly misclassified as UN plots (7.7%) followed by UN plots misclassified as RE plots (3.0%). Components also had RE plots most commonly misclassified as UN (8.8%) but IN plots misclassified as RE plots was the second most common misclassification (5.3%). The within treatment correlation structure was significantly different for all discriminant anal-

yses with all EIMs ($P < 0.0001$), flagship EIMs ($P < 0.0001$), and components ($P < 0.0001$; Fig. 4) suggesting EIMs did not vary similarly within different treatments (Appendix: Table A5).

DISCUSSION

The invasion of Japanese stiltgrass has clear ecological impacts on forests of the Eastern US. Examined individually, plant EIMs were most strongly impacted by Japanese stiltgrass, but all impact categories had at least one EIM altered by the invasion. Multivariate analysis indicated a clear distinction between the invaded site and either reference type, suggesting an ecosystem-level change following invasion that was not immediately alleviated by removing the invader. Additionally, several plant metrics were negatively correlated with increasing Japanese stiltgrass cover, while all other metrics were either unchanged, or changed in a binary (presence/absence of Japanese stiltgrass) fashion—suggesting that ecosystem processes can respond in either a density-dependent or independent fashion, at least given the range of covers observed here. Importantly, our analysis also revealed that removal and uninvaded references are not equitable, which has clear methodological implications for estimating invasive plant impacts.

Proportionally, the plant community exhibited the largest magnitude change following Japanese stiltgrass invasion, suggesting resident plants are most susceptible to forest invaders. The amount of bare ground, native diversity, native cover, and total richness were all reduced in the invaded system, similar to other Japanese stiltgrass invasion studies (Adams and Engelhardt 2009, DeMeester and Richter 2009, Flory 2010). Litter abundance decreased and soil microbial activity and earthworm abundance were unaffected by the invasion, similar to some previous results (Kourtev et al. 1999); however, these similarities existed at only one of two sites studied, suggesting the response of these metrics is site dependent and may not always be driven primarily by Japanese stiltgrass. As has been shown in multiple studies, pH and Mg increased following Japanese stiltgrass invasion (Ehrenfeld et al. 2001, McGrath and Binkley 2009), while

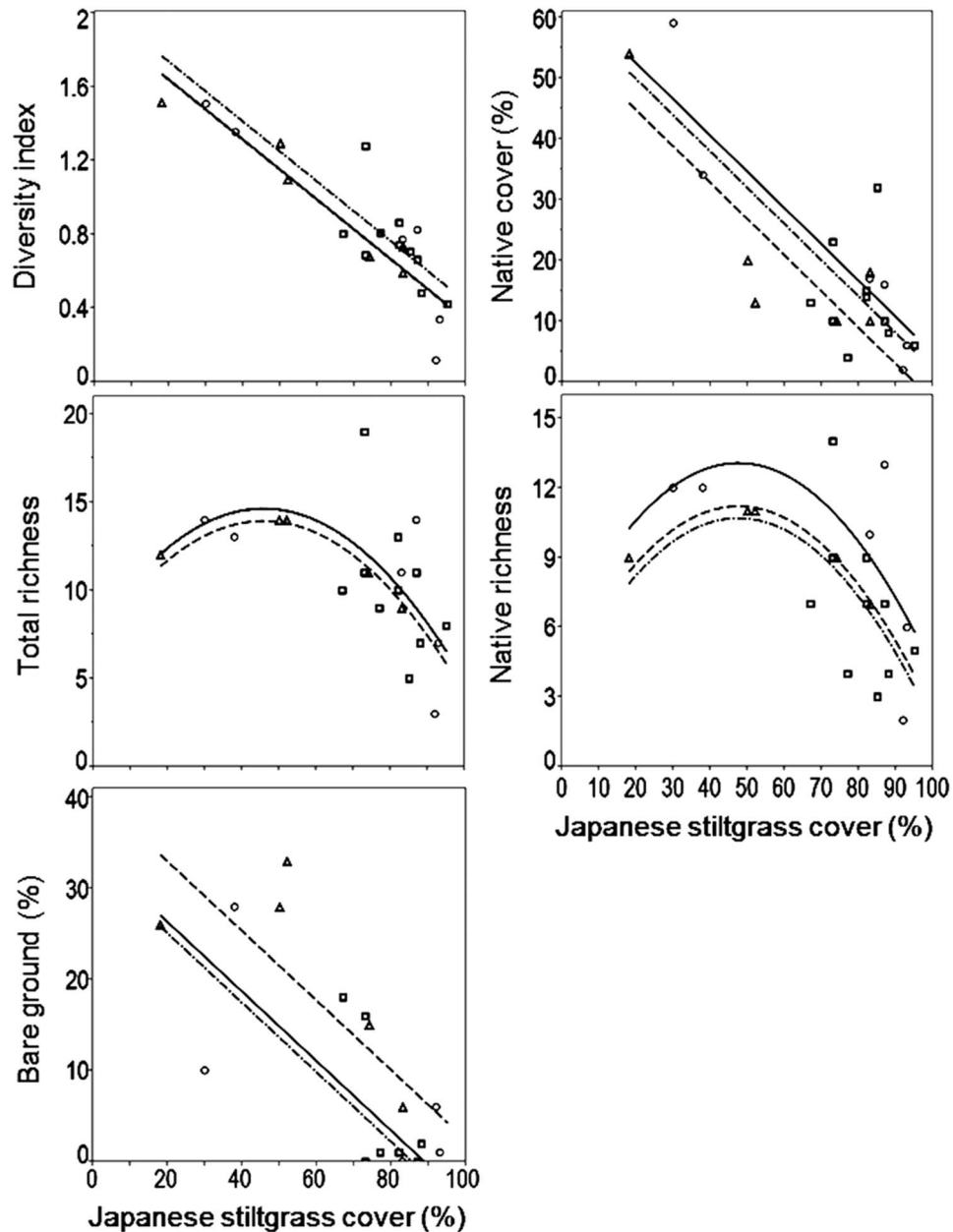


Fig. 2. Significant ANCOVAs for univariate analysis of Japanese stiltgrass cover and EIMs. Circle and solid lines represent BBS, squares and dash-dot lines represent PAN, and triangles and dashed lines represent POT.

TOC, CEC, P, K, Ca, and soil moisture all responded differently in our study compared to others (McGrath and Binkley 2009).

Looking beyond single impact metrics, our multivariate analysis reduced 29 EIMs into five ecologically relevant components: 1 = carbon pools and cycling; 2 = plant community diversity

and richness; 3 = soil pH and cations; 4 = invasive plant richness and cover; and 5 = native plant richness and cover. Additionally, all discriminant analyses differentiated the three treatments (IN, UN, RE), suggesting treatments displayed unique characteristics across all EIMs. Importantly, this analysis revealed that Japanese

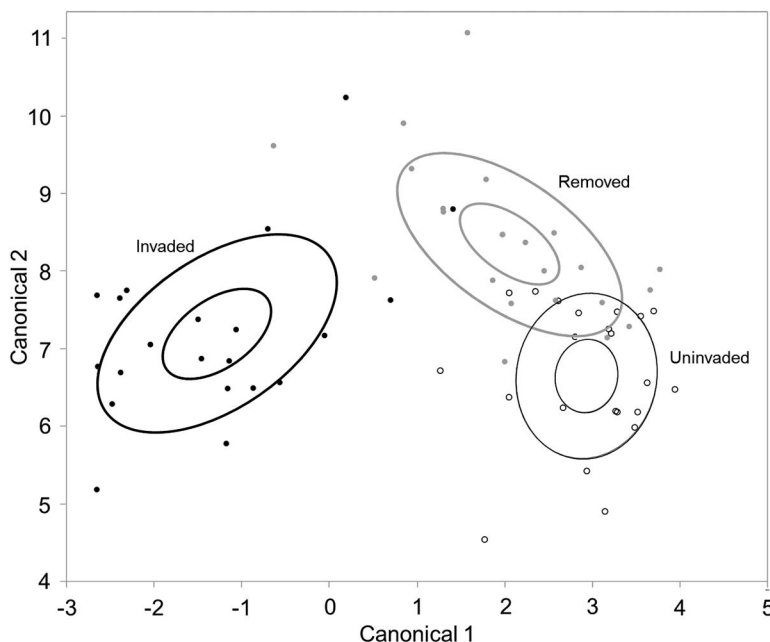


Fig. 3. Quadratic discriminant analysis of flagship EIMs (organic matter, diversity index, pH, invasive richness, native cover) displaying canonical axes one and two. Black circles represent IN plots, grey circles represent RE plots, and white circles represent UN plots. Inner ovals represent 95% confidence of the treatment mean and outer circles represent the area required to account for 50% of points within the treatment group.

stiltgrass invasion altered the broader function of the forest across a range of plant, soil, and other environmental characteristics. Though using the complete suite of EIMs was most successful and led to no errors in discrimination of treatments, use of components or flagship variables was nearly as successful. This suggests an even more limited suite of metrics then was previously suggested (Barney et al. 2013) may effectively represent broad ecological change to an invaded ecosystem. It remains unknown whether these same variables would be ideal indicators of environmental change for other species invading different systems. Although our findings raise the possibility that a small suite of carefully chosen indicator variables could serve to assess broad-scale environmental changes in invaded systems, this should be tested in more species.

The integrated metric $E(c)$ is designed to estimate the total magnitude of impact to an invaded ecosystem (Barney et al. 2013). Integrating the single parameters into $E(c)$ in our study, the first to do so, showed that the locations PAN and BBS had similar $E(c)$ values, both of which were different than POT. Interestingly, the distri-

bution of points showed similar patterns in PCA space: PAN and BBS overlapped, while POT was separate. This suggests that $E(c)$ may allow discrimination of ecosystem-level impact among populations. However, more locations are needed to test this hypothesis, which lends itself to globally distributed experiments (e.g., Barney et al. 2015).

Ecosystems are defined not only by the organisms that inhabit an area and the resources available; but also by the interactions of organisms and resources (O'Neill et al. 1986). All ecosystems have a structure that is defined by the pools and fluxes of energy and matter in the system (Hannon 1973). The addition or removal of any one species or resource from a system can impact the strength of other interactions, especially when that species is a large component of net primary productivity (Wardle and Bonner 1999). Therefore, to better understand the impact of invasive species on an ecosystem, the interactions among EIMs are just as important as their individual changes in magnitude and direction. Not only did we find that invasion changed EIMs using univariate and multivariate analysis, but

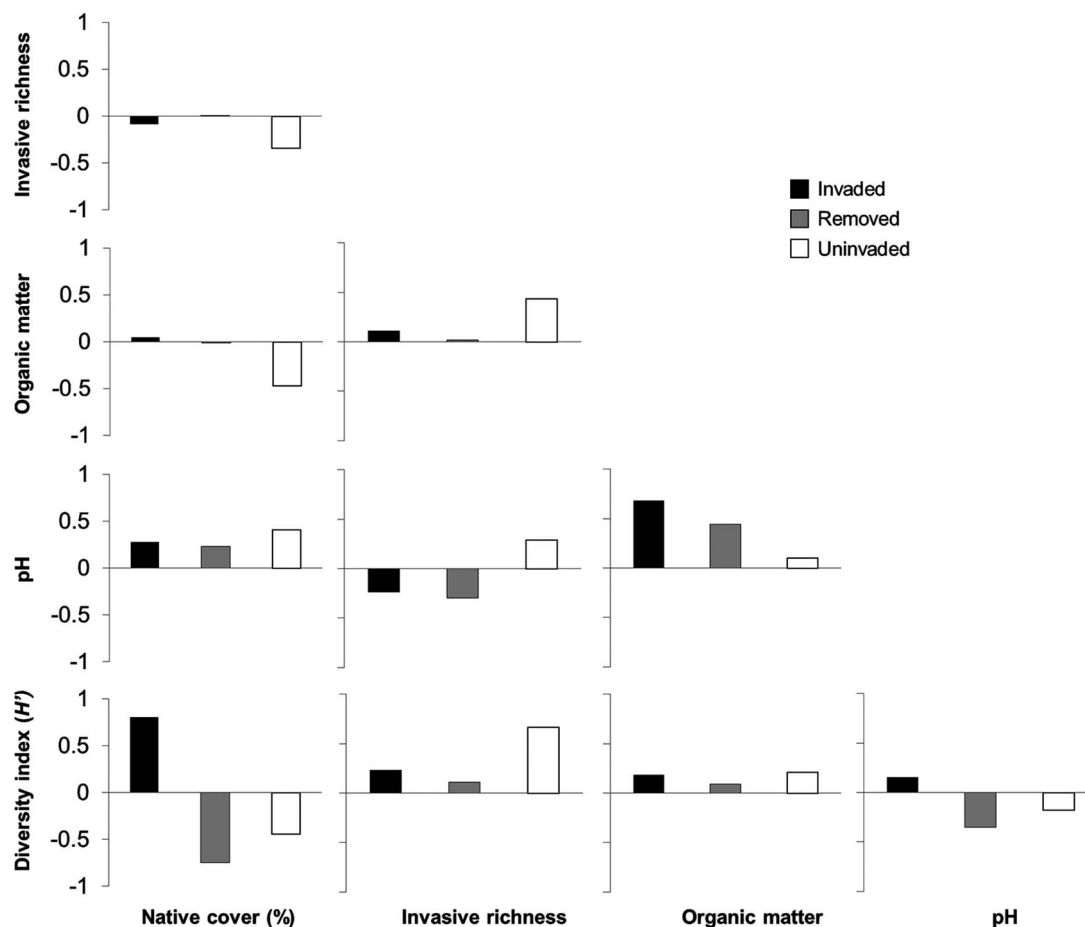


Fig. 4. Correlation structure of flagship EIMs with bars representing correlation strength; black bars are IN plots, grey bars are RE plots, and white bars are UN plots.

we also found that correlations among environmental variables changed in the presence of Japanese stiltgrass. For example, within our flagship EIMs, organic matter and pH were poorly correlated in the uninvaded site, suggesting there was little or no relationship between these two EIMs and they varied independently. However, in the presence of Japanese stiltgrass, organic matter and pH became strongly positively correlated (i.e., plots with increased pH also increased in organic matter) even though organic matter decreased on average in the invasion. Japanese stiltgrass increases soil pH when invading, as found in this study and by others (Kourtev et al. 1999, Ehrenfeld et al. 2001), which is well known to change microbial community composition and litter decomposition rates (Högberg et al. 2007). Because pH

varied less and was more acidic in the uninvaded landscape, the relationship between pH and soil organic matter may have been weaker. However, following the invasion of Japanese stiltgrass and the subsequent less acidic soil pH, soil organic matter was lower; and became coupled. A strong negative correlation between native plant cover and plant diversity (H') in uninvaded sites shifted to a strong positive correlation in invaded sites. When Japanese stiltgrass was present, increased native plant cover indicated decreased exotic plant cover and therefore increased native plant diversity. However, in the absence of invaders, increased native plant cover generally corresponded with dominance of a few species and reductions in diversity. While we cannot identify the mechanism underlying these relationships and are not able to confirm causation,

our data suggest that invaded ecosystems function in a different way than uninvaded systems. Further research should look to understand what role invaders play in the correlation structure of important ecological functions in other systems.

A limited number of studies have demonstrated that some ecosystem processes vary with invader abundance or cover (e.g., Greene and Blossey 2011, Hart and Holmes 2013). The vast majority of existing impact studies do not report invader cover, but the common dichotomous ‘invaded’/‘uninvaded’ comparison may disregard important ecological relationships. For example, Thiele et al. (2011) showed that species richness had a negative non-linear relationship with *Rosa rugosa* cover. In our study system, plant diversity (H'), bare ground, and native plant cover all decreased with increasing Japanese stiltgrass cover and total plant richness and native plant richness had a quadratic relationship with Japanese stiltgrass cover. No other EIM's in any other category responded to increasing cover of Japanese stiltgrass. The plant community-invader cover relationship may be due to the direct competition that occurs between increasing cover of the invader with the resident plant community. Other ecosystem processes (e.g., litter decomposition) are either less labile or are indirectly impacted by Japanese stiltgrass.

The EIM responses to Japanese stiltgrass fall into two categories: (1) density dependent, where the magnitude changes due to increasing invader cover (e.g., native richness); (2) and density-independent (e.g., pH), where the magnitude only changes in the presence of Japanese stiltgrass, regardless of abundance, at least over the surveyed range of covers. Currently, of the 11 studies that explicitly examined the influence of cover level of an invasive species, 91% examined only plant metrics and 90% of those showed a negative relationship of EIMs with increasing cover. Only purple loosestrife cover was shown to not impact plant richness (Farnsworth and Ellis 2001). The one study examining a non-plant EIM studied frog mass with increasing cover of an invasive plant and saw a negative relationship (Maerz et al. 2005). Unfortunately, no other studies examine non-plant metrics in this way so little can be said about the overall influence on non-plant metrics beyond the results of this study. It should be

noted that very few plots had <50% Japanese stiltgrass cover, which could have led to the binary response seen from some metrics (i.e., they did not vary with cover); however, typical Japanese stiltgrass invasions occur at the high levels of cover seen in this study, so our results are representative, but may lack power to test for all cover-impact relationships. Future studies should seek to evaluate broader cover-impact relationships (Barney et al. 2013, Kumschick et al. 2015). Importantly, the potential for density dependent and independent changes to Japanese stiltgrass invasion has important ecological and management implications. First, some metrics change immediately following invasion, while others accrue with increasing invader cover (Levine et al. 2006). Secondly, this can be used to justify management of small low-density incipient populations to mitigate the density-dependent changes before they accumulate larger magnitude changes.

To estimate the impact of an invasive plant, the invaded patch is compared to some benchmark, which most often is an adjacent uninvaded patch or removing the invader (Hulme et al. 2013). Though it is rarely tested, the reference site identity may result in different conclusions on invader impact due to their assumptions and limitations (Kumschick et al. 2015) as has been shown between removal and addition reference sites (Truscott et al. 2008). Although removal and uninvaded references are commonly used to estimate invasive plant impact, our results suggest these two benchmarks are not ecologically equivalent, at least in our timeframe of <1 year. In our study, the discriminant analysis differentiated 84% of UN and RE plots using flagship EIMs and components, and 100% using all EIMs, suggesting a clear distinction between an uninvaded site and one with the invader recently removed. Additionally, $E(c)$ values varied whether removal or uninvaded plots were used as the reference further suggesting the reference types are not equitable. If these reference plots were equitable, the discriminant analysis would not differentiate between them. Removing Japanese stiltgrass did not bring the plot back to the uninvaded state, suggesting that while some components of the ecosystem change immediately following invasion, they do not return following removal of the invader. How-

ever, a longer term study is necessary to fully identify these relationships.

The act of removing a plant species regardless of how carefully performed is itself a disturbance to the system. While reviewing competition studies, Aarssen and Epp (1990) looked at removal methodologies to elucidate competitive relationships, and were concerned that the disturbances associated with removal studies affected results and conclusions. In fact, differing removal methodology may influence the response of the surrounding community (Skurski et al. 2013). Even if the plant can be removed with no physical disturbance, the opening of the canopy itself could have lasting effects. This may partly explain the difference seen in plant EIMs between reference types. Other invasive cover was greater in RE (5.1%) than IN (2.2%) and UN (1.3%), suggesting that other invasive cover increased following removal. We saw a similar pattern in native cover in RE plots, which was nearly twice (31.5%) that of IN and UN (17.9, 18.5%, respectively). Interestingly, the species that increased following removal were generally ruderal fast growing species. In contrast, trees were more common in the UN plots than either IN or RE, suggesting more long-term effects on slow-growing k-selected species, which others have shown following Japanese stiltgrass invasion (Beasley and McCarthy 2011). Skurski et al. (2013) found that the inherent disturbance associated with removal of a grassland herbaceous invasive species only encouraged further invasion of exotic grasses. Therefore, the unavoidable disturbance of removing Japanese stiltgrass may influence the results and their interpretation, and thus the magnitude and interpretation of invader impact if using removal as the benchmark.

Even if disturbance is minimized, removing an invasive plant to represent an uninvaded community may not fully remove the influence of the invader (Corbin and D'Antonio 2012). In our system, removals were performed five months before data was collected, which is a common timeframe in ecological impact studies (Tekiel and Barney, *unpublished data*). However, this presents an obvious temporal limitation and assumes near instant return rates (i.e., invaded changes revert to uninvaded state instantly following invader removal), which may not

occur. Instead, legacy effects, which are the persistent effects of a species even after its removal, disrupt the ability and rate of return of a system to the uninvaded state (Cuddington 2011). Elgersma et al. (2011) showed that the historical presence of Japanese barberry (*Berberis thunbergii*) had lasting effects on the soil microbial community structure even two years after its extirpation from the system. In contrast, we saw no impact to microbial biomass or activity by Japanese stiltgrass in our system. The differences in pH and leaf litter abundance we observed between UN and RE may be explained by legacy effects. For both EIMs, RE values remained similar to IN but distinct from UN. Similar legacies have been reported in leaf litter abundance in common reed (*Phragmites australis*) (Holdredge and Bertness 2010), and similar to our results, Japanese stiltgrass has been previously shown to reduce overall leaf litter depth in forest understory systems (Kourtev et al. 1998). Japanese stiltgrass is also well known to increase pH in soils (Kourtev et al. 1999, Ehrenfeld et al. 2001) as was recorded at our sites (IN = 5.78, RE = 5.44, UN = 4.91). Additionally, McGrath and Binkley (2009) suggest changes in pH are only distinguishable after 6 months of Japanese stiltgrass presence which may explain the lack of difference between invaded and removed treatments. Alternatively, though plant metrics were most greatly impacted by Japanese stiltgrass, they may also have been able to respond within five months of removals and return to a similar state to uninvaded plots in a short period of time due to their lability. DeMeester and Richter (2009) also saw a quick response of native plant cover and bare ground cover after removing Japanese stiltgrass from the plot, further suggesting plant community composition has limited legacy effects when compared to soil and ecosystem EIMs.

Our study suggests that Japanese stiltgrass changes the invaded ecosystem, and that ecosystem pools and fluxes respond in both density dependent and independent patterns. Important for future invasive plant impact studies is to consider the following: (1) a broad suite of relevant ecosystem parameters; (2) identify parameter responses to invader abundance; and (3) thoughtfully consider the reference benchmark.

Enhanced understanding of the ecological impacts of invasive plants allows land managers to more optimally prioritize the utilization of limited resources to focus on highly impactful invasive species, which will therefore lead to more efficacious and cost-effective management.

ACKNOWLEDGMENTS

We would like to thank Carissa Ervine, Elise Benhase, Eugene Dollete, Larissa Smith, Morgan Franke, Rose Peterson, and Ryan Schmitt for help in the field. We thank the National Forest Service for their assistance in obtaining sites. We also thank Dan Atwater for helpful comments on the manuscript. We also acknowledge the Global Invader Impact Network (GIIN) managed by our research group, of which this study is a component.

LITERATURE CITED

- Aarssen, L., and G. Epp. 1990. Neighbour manipulations in natural vegetation: a review. *Journal of Vegetation Science* 1:13–30.
- Adams, S. N., and K. A. M. Engelhardt. 2009. Diversity declines in *Microstegium vimineum* (Japanese stiltgrass) patches. *Biological Conservation* 142:1003–1010.
- Baiser, B., J. L. Lockwood, D. Puma, and M. F. J. Aronson. 2008. A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. *Biological Invasions* 10:785–795.
- Barney, J. N., et al. 2015. Global Invader Impact Network (GIIN): toward standardized evaluation of the ecological impacts of invasive plants. *Ecology and Evolution* 5:2878–2889.
- Barney, J. N., D. R. Tekiela, E. S. Dollete, and B. J. Tomasek. 2013. What is the “real” impact of invasive plant species? *Frontiers in Ecology and the Environment* 11:322–329.
- Beasley, R. R., and B. C. McCarthy. 2011. Effects of *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass) on native hardwood survival and growth: implications for restoration. *Natural Areas Journal* 31:246–255.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127–35.
- Brewer, J. S. 2010. Per capita community-level effects of an invasive grass, *Microstegium vimineum*, on vegetation in mesic forests in northern Mississippi (USA). *Biological Invasions* 13:701–715.
- Brown, R., and R. Peet. 2003. Diversity and invasibility of Southern Appalachian plant communities. *Ecology* 84:32–39.
- Cattell, R. 1966. The scree test for the number of factors. *Multivariate Behavioral Research* 1:245–276.
- Corbin, J. D., and C. M. D’Antonio. 2012. Gone but not forgotten? Invasive plants’ legacies on community and ecosystem properties. *Invasive Plant Science and Management* 5:117–124.
- Cuddington, K. 2011. Legacy effects: the persistent impact of ecological interactions. *Biological Theory* 6:203–210.
- DeMeester, J. E., and D. Richter. 2009. Restoring restoration: removal of the invasive plant *Microstegium vimineum* from a North Carolina wetland. *Biological Invasions* 12:781–793.
- Ehrenfeld, J., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11:1287–1300.
- Elgersma, K. J., J. G. Ehrenfeld, S. Yu, and T. Vor. 2011. Legacy effects overwhelm the short-term effects of exotic plant invasion and restoration on soil microbial community structure, enzyme activities, and nitrogen cycling. *Oecologia* 167:733–45.
- Eschtruth, A., and J. Battles. 2011. The importance of quantifying propagule pressure to understand invasion: an examination of riparian forest invasibility. *Ecology* 92:1314–22.
- Farnsworth, E. J., and D. R. Ellis. 2001. Is purple loosestrife (*Lythrum salicaria*) an invasive threat to freshwater wetlands? Conflicting evidence from several ecological metrics. *Wetlands* 21:199–209.
- Flory, S. L. 2010. Management of *Microstegium vimineum* invasions and recovery of resident plant communities. *Restoration Ecology* 18:1–10.
- Greene, B. T., and B. Blossey. 2011. Lost in the weeds: *Ligustrum sinense* reduces native plant growth and survival. *Biological Invasions* 14:139–150.
- Hannon, B. 1973. The structure of ecosystems. *Journal of Theoretical Biology* 41:535–546.
- Hart, J. L., and B. N. Holmes. 2013. Relationships between *Ligustrum sinense* invasion, biodiversity, and development in a mixed bottomland forest. *Invasive Plant Science and Management* 6:175–186.
- Högberg, M. N., P. Högberg, and D. D. Myrold. 2007. Is microbial community composition in boreal forest soils determined by pH, C-to-N ratio, the trees, or all three? *Oecologia* 150:590–601.
- Holdredge, C., and M. D. Bertness. 2010. Litter legacy increases the competitive advantage of invasive *Phragmites australis* in New England wetlands. *Biological Invasions* 13:423–433.
- Hulme, P. E., P. Pyšek, V. Jarošík, J. Pergl, U. Schaffner, and M. Vilà. 2013. Bias and error in understanding plant invasion impacts. *Trends in Ecology and Evolution* 28:212–8.
- Hulme, P. E., P. Pyšek, J. Pergl, U. Schaffner, and M. Vilà. 2014. Pragmatism required to assess impacts of invasive plants. *Frontiers in Ecology and the*

- Environment 12:153–154.
- Kourtev, P., J. Ehrenfeld, and M. Häggblom. 2003. Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biology and Biochemistry* 35:895–905.
- Kourtev, P., J. Ehrenfeld, and W. Huang. 1998. Effects of exotic plant species on soil properties in hardwood forests of New Jersey. *Water, Air, and Soil Pollution* 105:493–501.
- Kourtev, P., W. Huang, and J. Ehrenfeld. 1999. Differences in earthworm densities and nitrogen dynamics in soils under exotic and native plant species. *Biological Invasions* 1:237–245.
- Kumschick, S., et al. 2015. Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *BioScience* 65:55–63.
- Kuppinger, D. 2000. Management of plant invasions in the southern Appalachians. *Chiquapin* 8:21.
- Levine, J. M., E. Pachepsky, B. E. Kendall, S. G. Yelenik, and J. H. R. Lambers. 2006. Plant-soil feedbacks and invasive spread. *Ecology Letters* 9:1005–1014.
- Lockwood, J. L., D. Simberloff, M. L. McKinney, and B. von Holle. 2001. How many, and which, plants will invade natural areas? *Biological Invasions* 3:1–8.
- Mack, M., and C. D’Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13:195–198.
- Maerz, J. C., B. Blossey, and V. Nuzzo. 2005. Green frogs show reduced foraging success in habitats invaded by Japanese knotweed. *Biodiversity and Conservation* 14:2901–2911.
- Le Maitre, D. C., et al. 2011. Impacts of invasive *Australian acacias*: implications for management and restoration. *Diversity and Distributions* 17:1015–1029.
- Marshall, J. M., and D. S. Buckley. 2009. Influence of *Microstegium vimineum* presence on insect abundance in hardwood forests. *Southeastern Naturalist* 8:515–526.
- Marshall, J. M., D. S. Buckley, and J. A. Franklin. 2009. Competitive interaction between *Microstegium vimineum* and first-year seedlings of three central hardwoods. *Journal of the Torrey Botanical Society* 136:342–349.
- McGrath, D. A., and M. A. Binkley. 2009. *Microstegium vimineum* invasion changes soil chemistry and microarthropod communities in cumberland plateau forests. *Southeastern Naturalist* 8:141–156.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: synthesis*. Island Press, Washington, D.C., USA.
- O’Neill, R. V., D. L. Deangelis, J. B. Waide, and G. E. Allen. 1986. *A hierarchical concept of ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52:273–288.
- Powell, K. I., J. M. Chase, and T. M. Knight. 2013. Invasive plants have scale-dependent effects on diversity by altering species-area relationships. *Science* 339:316–318.
- Pyšek, P., V. Jarošík, P. E. Hulme, J. Pergl, M. Hejda, U. Schaffner, and M. Vilà. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species’ traits and environment. *Global Change Biology* 18:1725–1737.
- Quinn, L., J. N. Barney, J. S. N. McCubbins, and B. Endres. 2013. Navigating the “noxious” and “invasive” regulatory landscape: suggestions for improved regulation. *Bioscience* 63:124–131.
- R Core Team. 2013. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Shafroth, P. B., and M. K. Briggs. 2008. Restoration ecology and invasive riparian plants: an introduction to the special section on *Tamarix* spp. in Western North America. *Restoration Ecology* 16:94–96.
- Simao, M. C. M., S. L. Flory, and J. A. Rudgers. 2010. Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. *Oikos* 119:1553–1562.
- Skurski, T. C., B. D. Maxwell, and L. J. Rew. 2013. Ecological tradeoffs in non-native plant management. *Biological Conservation* 159:292–302.
- Strickland, M. S., J. L. Devore, J. C. Maerz, and M. A. Bradford. 2010. Grass invasion of a hardwood forest is associated with declines in belowground carbon pools. *Global Change Biology* 16:1338–1350.
- Thiele, J., M. Isermann, J. Kollmann, and A. Otte. 2011. Impact scores of invasive plants are biased by disregard of environmental co-variation and non-linearity. *NeoBiota* 10:65.
- Truscott, A. M., S. C. Palmer, C. Soulsby, S. Westaway, and P. E. Hulme. 2008. Consequences of invasion by the alien plant *Mimulus guttatus* on the species composition and soil properties of riparian plant communities in Scotland. *Perspectives in Plant Ecology, Evolution and Systematics* 10:231–240.
- Wardle, D., and K. Bonner. 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs* 69:535–568.
- White, P. S., and J. L. Walker. 1997. Approximating nature’s variation: selecting and using reference information in restoration ecology. *Restoration Ecology* 5:338–349.
- Williams, B. 1983. Some observations of the use of discriminant analysis in ecology. *Ecology* 64:1283–1291.

SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

The Appendix is available online: <http://dx.doi.org/10.1890/ES15-00412.1.sm>