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Long-term trends indicate that invasive plants are pervasive and increasing in eastern national parks

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Abstract. While invasive plant distributions are relatively well known in the eastern United States, temporal changes in species distributions and interactions among species have received little attention. Managers are therefore left to make management decisions without knowing which species pose the greatest threats based on their ability to spread, persist and outcompete other invasive species. To fill this gap, we used the U.S. National Park Service's Inventory and Monitoring Program data collected from over 1,400 permanent forest plots spanning 12 yr and covering 39 eastern national parks to analyze invasive plant trends. We analyzed trends in abundance at multiple scales, including plot frequency, quadrat frequency, and average quadrat cover. We examined trends overall, by functional group, and by species. We detected considerably more increasing than decreasing trends in invasive plant abundance. In fact, 80% of the parks in our study had at least one significant increasing trend in invasive abundance over time. Where detected, significant negative trends tended to be herbaceous or graminoid species. However, these declines were often countered by roughly equivalent increases in invasive shrubs over the same time period, and we only detected overall declines in invasive abundance in two parks in our study. Present in over 30% of plots and responsible for the steepest and greatest number of significant increases, Japanese stiltgrass (*Microstegium vimineum*) was the most aggressive invader in our study and is a high management priority. Invasive shrubs, especially Japanese barberry (*Berberis thunbergii*), Japanese honeysuckle (*Lonicera japonica*), multiflora rose (*Rosa multiflora*), and wineberry (*Rubus phoenicolasius*), also increased across multiple parks, and sometimes at the expense of Japanese stiltgrass. Given the added risks to human health from tick-borne diseases, invasive shrubs are a high management priority. While these findings provide critical information to managers for species prioritization, they also demonstrate the incredible management challenge that invasive plants pose in protected areas, particularly since we documented few overall declines in invasive abundance. As parks work to overcome deferred maintenance of infrastructure, our findings suggest that deferred management of natural resources, particularly invasive species, requires similar attention and long-term commitment to reverse these widespread increasing invasive trends.

Key words: exotic plants; invasive plants; invasive shrubs; long-term trends; Microstegium vimineum*; National Park Service Inventory and Monitoring.*

Introduction

Invasive species are a global problem, causing widespread economic and ecological impacts (Vilà et al. 2011). In forest ecosystems alone, invasive species can reduce native diversity (Hartman and McCarthy 2008, Vilà et al. 2011, Waller et al. 2016), alter forest structure (Hartman and McCarthy 2008), suppress tree regeneration (Oswalt et al. 2007, Boyce 2009), alter nutrient cycling (Ehrenfeld et al. 2001), and modify disturbance regimes (D'Antonio and Vitousek 1992). Invasive plants can also negatively impact ecosystem services and human health (Pejchar and Mooney 2009). For example, invasive shrub thickets in the eastern United States have been linked to increased densities of black-legged ticks (*Ixodes scapularis*) and elevated exposure of humans to tick-borne illnesses (Elias et al. 2006, Ward and Williams 2010).

Given the widely documented impacts of invasive plants, it is not surprising that the distributions of invasive plant species are relatively well documented in the

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eastern United States. For example, several online mapping tools, such as the Early Detection and Distribution Mapping System and iNaturalist, have compiled detailed maps of invasive species occurrences across the region (mapping tools *available online*).[8,9] In forests, a number of studies have used the US Forest Service Forest Inventory and Analysis (USFS-FIA) plot data to map the distribution and examine underlying drivers of invasive species occurrences in the eastern United States. Studies include Kurtz (2013), who mapped county-level occurrences for an extensive list of invasive plant species in the USFS Northern Research Station (NRS). Golivets et al. (2019) examined predictors of invasive species occurrence and richness in USFS-FIA plots for the same region. Similarly, Fan et al. (2013) examined regional patterns and modeled probability of occurrence for a variety of invasive plant functional groups in the upper Midwest. While invasive species distributions are relatively well documented in eastern U.S. forests, few studies have examined long-term trends in invasive plant communities over time, particularly at regional scales (Kuebbing et al. 2015). The few regional long-term studies we are aware of typically focused on only a few species (Barney et al. 2008, Rooney and Rogers 2011), or covered a relatively small region (Huebner 2003, Rooney and Rogers 2011, Waller et al. 2016). Given the lack of regional temporal studies on invasive plant communities, we have limited knowledge about which species or functional groups of species are most likely to invade and persist in a given area, are most capable of rapid expansion, and are likely to dominate at the expense of other invasive species.

Adding to the confusion, invasion theory often predicts that, after the initial expansion phase, the impacts of plant invasions may decline over time through stabilizing processes (Strayer et al. 2006, Dostál et al. 2013). This prediction has been supported by several site-based long-term studies that documented reductions in abundance and impacts to native communities over time (Banasiak and Meiners 2009, Flory and Clay 2013), although most studies focused on a single invasive species. For example, in an 8-yr field experiment, Flory et al. (2017) described a pattern of initial dominance by Japanese stiltgrass (*Microstegium vimineum*) and impacts to native species within the first 4 yr of the study, followed by dramatic declines of Japanese stiltgrass and near recovery of native species by the end of the 8-yr study. In another study, the impacts of giant hogweed (*Heracleum mantegazzianum*) on native species were found to be most severe during the initial expansion phase of invasion, with impacts diminishing four to five decades after the initial invasion as a result of stabilizing processes (Dostál et al. 2013). Likewise, the ecological impacts of garlic mustard (*Alliaria petiolata*) were found to decline in older (50+ yr) populations (Lankau et al. 2009). These studies suggest that the invasive plant problems that managers are currently facing could lessen over time, and may not pose the long-term threats to native diversity and forest ecosystems that are generally assumed. Still other long-term studies found evidence of long-term expansion and persistence of invasive forest plants in the absence of management (Fike and Niering 1999, Wangen and Webster 2006, Johnson and Handel 2016). These studies offer conflicting messages about the long-term threats of invasive plants to forest ecosystems, which urgently needs to be resolved.

Invasive plants are a major focus of many land management agencies and managers of protected areas (Hulme 2006, Pearson et al. 2009). However, given the conflicting results of long-term species-level studies and the lack of long-term community-level studies, managers are left to make decisions without fully knowing which species pose the greatest ecological threats and/or are most likely to spread. The National Park Service Inventory and Monitoring Program (NPS I&M), which was established in the late 1990s, was founded in part to provide this type of critical information to managers in U.S. national parks (Fancy et al. 2009). In the eastern United States, NPS I&M is conducting long-term forest monitoring using similar methods in permanent, randomly located plots in more than 50 national parks (Comiskey et al. 2009*a*). Now that at least three rounds of surveys have been conducted in many of these parks, we can examine long-term trends in invasive plant communities to fill this critical gap in the literature and help protected area managers better prioritize invasive management and early detection efforts.

In this study, we combine data from 1,479 permanent forest monitoring plots that span 39 national park units from Virginia to Maine and cover 12 yr (2007–2018) to assess status and temporal trends in invasive plant communities (Fig. 1). Our primary objectives are to identify species or functional groups that consistently achieve and maintain high abundance and/or that exhibit rapid expansion rates across the region. This is the first study we are aware of that assesses long-term trends in invasive plant communities over a broad region.

Methods

Field methods & study sites

The 39 parks included in this study were located across five NPS I&M networks (Fig. 1), with each network responsible for implementing long-term monitoring protocols in their respective parks. Parks in this study ranged in designation type, including National Battlefield (NB), National Battlefield Park (NBP), National Historical Park (NHP), National Historic Site (NHS), National Memorial (NMe), National Military Park (NMP), National Monument (NM), National Park (NP), National Recreation Area (NRA), National River (NR), and National Scenic River (NSR; Fig. 1), but all

[8] EddMaps.org
[9] inaturalist.org

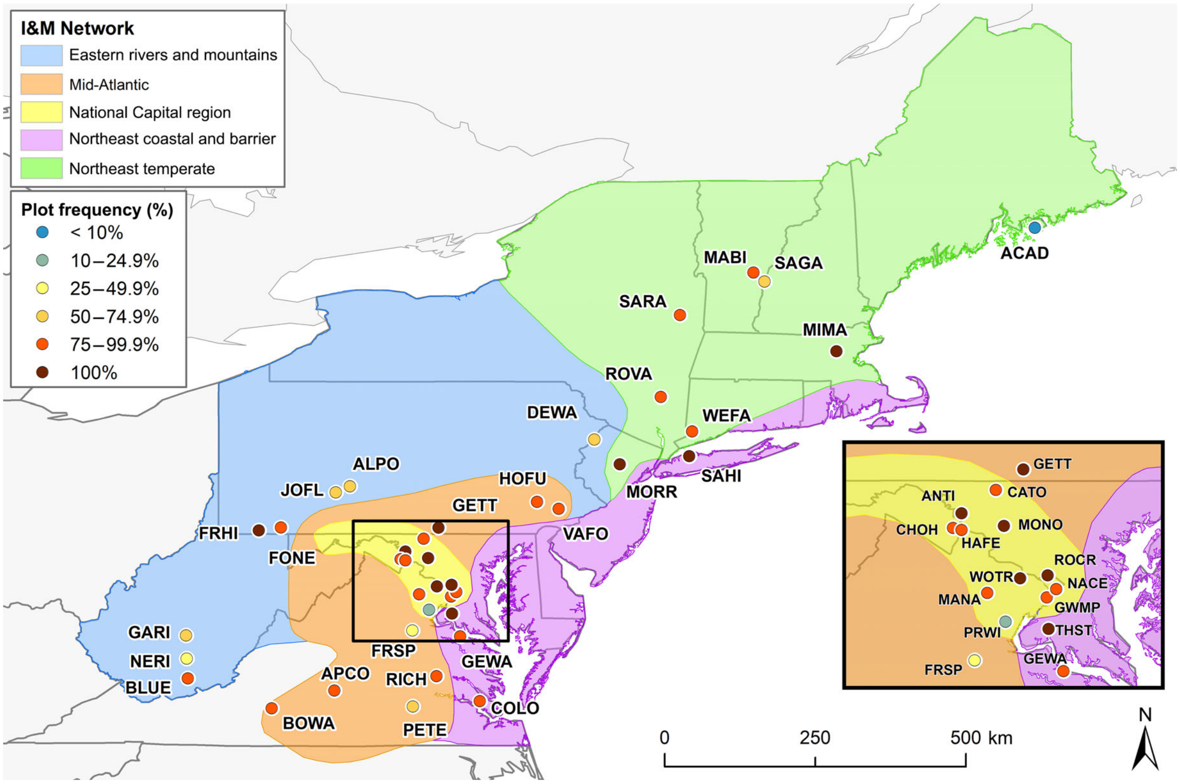

FIG. 1. Map of parks included from the National Park Service Inventory and Monitoring Program (NPS I&M) in this analysis summarized by plot percent frequency, which is the percentage of plots in a park that have at least one invasive species in the most recent survey cycle (2014–2018). See Table 1 for full park names.

parks in the study had significant forest resources that were of management concern. In each park, monitoring plot locations were determined using Generalized Random-Tessellation Stratification (GRTS) to generate a spatially balanced and randomized sample of plot locations across the park's forested area (Stevens and Olsen 2004). Plots were sampled on a 4-yr rotating panel. For this panel design, we sampled one-quarter of the plots every year (i.e., one panel), and each plot was sampled every 4 yr (i.e., one cycle).

In this study, we first summarized the status of invasive species abundance from the most recent cycle of surveys (i.e., 2015–2018) to determine which species or functional groups were most widespread and abundant across the study area. We then conducted a statistical trend analysis of the past three survey cycles where cycle 1 represented survey years 2007–2010, cycle 2 represented survey years 2011–2014, and cycle 3 represented survey years 2015–2018. The majority of plots (88%) included in the trend analysis were monitored for three full cycles. The main exception was Colonial National Historical Park (COLO), which only had two cycles of data because monitoring in COLO did not start until 2011 (Table 1). To maintain consistent year ranges for each cycle across parks (e.g., cycle 2 covers 2011–2014), we set the first survey of COLO plots to start in cycle 2. In addition, Eastern Rivers and Mountains (ERMN) and several Northeast Coastal and Barrier (NCBN) parks completed the fourth panel of cycle 3 in 2019, meaning that panel 4 only had two cycles of data in these parks. However, because of the spatially balanced GRTS algorithm used to determine plot locations, missing panel data (e.g., panel 4 in ERMN and NCBN) were missing at random, and did not contribute bias to statistical analyses.

While protocols and plot designs varied across networks, networks were taking many similar measurements within plots. For example, all trees in each plot that were ≥10 cm diameter at breast height (DBH) were identified to species, measured for DBH, and assessed for status (i.e., live or dead) and condition (Comiskey et al. 2009*b*, Schmit et al. 2009, Perles et al. 2014, Tierney et al. 2017). However, plot sizes varied across networks, with the smallest plot size in Acadia NP, Maine (ACAD) at 225 m^2, and the largest plot size in ERMN and the National Capital Region Network (NCRN) at 706 m^2. Remaining parks/networks had 400-m^2 plots. Live saplings that were >1 and ≤10 cm DBH were all identified to species and measured for DBH in microplots, which were nested within the bigger plots. However, microplot size and number varied, with the Northeast Temperate Network (NETN) sampling three

TABLE 1. Park-level summary of invasive abundance in the most recent 4-yr survey cycle (2015–2018), sorted from high to low abundance.

Network	Park name	Park code	No. plotss	Frequency (%) Plot f	Frequency (%) Quadrat	Cover (%)
NCRN	Antietam National Battlefield	ANTI	7	100.0	97.6	39.6
MIDN	Gettysburg National Military Park	GETT	33	100.0	92.9	21.0
NCRN	Monocacy National Battlefield	MONO	6	100.0	91.7	40.4
ERMN	Friendship Hill National Historic Site	FRHI	20	100.0	85.0	35.3
NCBN	Sagamore Hill National Historic Site	SAHI	4	100.0	83.3	2.1
NETN	Minute Man National Historical Park	MIMA	20	100.0	77.5	17.3
NETN	Morristown National Historical Park	MORR	28	100.0	75.0	35.1
NCBN	Thomas Stone National Historic Site	THST	6	100.0	63.9	11.0
NCRN	Rock Creek Park	ROCR	19	100.0	62.3	14.3
NCRN	Wolf Trap Park for the Performing Arts	WOTR	1	100.0	50.0	12.4
NETN	Saratoga National Historical Park	SARA	32	96.9	78.5	18.2
NETN	Roosevelt-Vanderbilt National Historic Sites	ROVA	40	95.0	49.4	3.2
MIDN	Hopewell Furnace National Historic Site	HOFU	16	93.8	71.4	29.1
NCRN	Chesapeake & Ohio Canal National Historical Park	CHOH	74	91.9	74.3	33.9
NCRN	Harpers Ferry National Historical Park	HAFE	20	90.0	49.6	8.2
NETN	Weir Farm National Historic Site	WEFA	10	90.0	48.8	5.3
ERMN	Fort Necessity National Battlefield	FONE	20	90.0	47.5	15.4
ERMN	Bluestone National Scenic River	BLUE	40	90.0	30.8	3.7
MIDN	Valley Forge National Historical Park	VAFO	28	89.3	69.4	27.2
MIDN	Appomattox Court House National Historical Park	APCO	28	89.3	58.6	7.3
NCRN	Manassas National Battlefield Park	MANA	17	88.2	64.7	21.2
MIDN	Booker T. Washington National Monument	BOWA	8	87.5	66.7	1.8
NETN	Marsh-Billings-Rockefeller National Historical Park	MABI	24	87.5	8.9	0.0
NCRN	National Capital Parks East	NACE	45	86.7	63.0	16.4
NCBN	George Washington Birthplace National Monument	GEWA	6	83.3	51.4	7.1
MIDN	Richmond National Battlefield Park	RICH	32	81.3	40.1	6.9
NCBN	Colonial National Historical Park	COLO	47	80.9	37.4	4.9
NCRN	George Washington Memorial Parkway	GWMP	20	80.0	54.2	22.3
NCRN	Catoctin Mountain Park	CATO	49	79.6	52.9	17.7
ERMN	Delaware Water Gap National Recreation Area	DEWA	102	71.6	42.2	17.3
ERMN	Allegheny Portage Railroad National Historic Site	ALPO	22	63.6	20.8	11.2
ERMN	Johnstown Flood National Memorial	JOFL	12	58.3	22.2	6.1
ERMN	Gauley River National Recreation Area	GARI	43	58.1	13.6	1.6
MIDN	Petersburg National Battlefield	PETE	52	57.7	24.8	6.3
NETN	Saint-Gaudens National Historical Park	SAGA	21	52.4	9.5	1.1
ERMN	New River Gorge National River	NERI	102	45.1	13.3	1.8
MIDN	Fredericksburg & Spotsylvania National Military Park	FRSP	104	35.6	8.7	0.3
NCRN	Prince William Forest Park	PRWI	145	17.9	5.1	0.6
NETN	Acadia National Park	ACAD	176	4.6	0.2	<0.01

Notes: No. plots is the number of forest plots in a given park. Cover is the average percent cover of all invasive species in quadrats averaged across all plots in a given park. Quadrat frequency is the average percentage of quadrats with an invasive species averaged across all plots in a given park. Plot frequency is the percentage of plots in a park with at least one invasive species.

2 m radius microplots, ERMN sampling four 2 m radius microplots, and the Mid-Atlantic Network (MIDN), NCBN, and NCRN all sampling three 3 m radius microplots. Tree seedlings, which were ≥15 cm tall and <1 cm DBH, were tallied by height class, and were measured either in microplots (ERMN and NETN) or in 12 1-m^2 quadrats (MIDN, NCBN, NCRN). ERMN and NETN conducted a timed 15-minute plot search to document all species in a given plot. MIDN and NCBN conducted a timed 15-minute plot search, but only for species on their indicator list. NCRN did not conduct a timed plot search.

Quadrats, 1 m^2 in area, were the most consistently sampled subplot across the networks. In all but NETN, networks monitored 12 1-m^2 quadrats per plot; NETN only monitored eight 1-m^2 quadrats per plot. In ERMN and NETN, all vascular species within 2 m (ERMN) and 1.5 m (NETN) height from the ground were estimated for percent cover within the quadrats. MIDN and NCBN estimated percent cover up to 1.5 m in height for tree seedlings and for a subset of indicator species in the quadrats, and both networks used the same indicator species list. While the MIDN/NCBN indicator list did not cover all invasive and/or exotic species that could potentially occur in network parks, by design they contained the invasive species that are most common and problematic in the region. NCRN's approach was similar to MIDN and NCBN, including having a similar indicator species list as MIDN/NCBN. The main difference was that in NCRN, tree seedlings were tallied by stem counts in quadrats, but their percent cover was not estimated. While the indicator lists were fairly comprehensive for invasive species, the list of native species was much shorter and primarily included native species known to be sensitive to changes in deer density. We were therefore unable to relate trends in invasive plant abundance with changes in native plant abundance in this study.

Data preparation

We defined invasive species similar to the U.S. Executive Order 13112, which defines invasive species as those that are non-native and whose introduction causes or is likely to cause native ecosystem impacts (U.S. Executive Office 1999). We primarily relied on three popular regional reference guides to develop our invasive species list (Mehroff et al. 2003, Miller 2003, Swearingen et al. 2010), although we only included species in our analysis that are invasive in forest habitats (e.g., shade tolerant), and/or that are capable of preventing old fields from succeeding to forest (e.g., exotic shrubs). We also added several species that were not included in the above resources but that we considered invasive or potentially invasive based on collective field experience and park management priorities, including jetbead (*Rhodotypos scandens*), moneywort (*Lysimachia nummularia*), and oriental lady's thumb (*Persicaria longiseta*). We used the same species list across parks and networks with the exception of species that were not on a given network's indicator list. All nomenclature followed the Integrated Taxonomic Information System (ITIS 2019). For the full list of species included in this analysis, refer to Appendix S1: Table S1.

Given the differences between protocols, particularly the variable plot and subplot sizes, we focused most of our analyses on data collected within the 1-m^2 quadrats. The 1-m^2 scale has also been found to be a better scale for detecting interactions among species than larger site-level scales (Waller et al. 2016). To assess the overall status of invasive plants in our region, we summarized the most recent 4-yr cycle of data collected in each park (i.e., cycle 3, 2015–2018). For networks using indicator lists (MIDN, NCBN, NCRN), the status assessment included all species that were on the indicator list at the start of the most recent cycle. For the trend analysis, in contrast, we only included species that have been on indicator lists from the beginning (i.e., 2007) to ensure that we were detecting actual trends in invasives over time rather than species additions to the indicator list.

We were unable to directly measure rates of establishment and expansion of invasives because we could not identify the source populations for each of our plots and could not identify the stage of invasion for each species in every park. However, by using a combination of invasive abundance metrics, we were able to roughly track trends in these phases of invasion in each park. We calculated the following metrics: plot frequency, quadrat frequency, and average cover. Plot frequency was calculated as the percentage of plots within a park and cycle with at least one invasive species, and roughly captured the broader establishment and expansion of invasive species across a park. Quadrat frequency was the percentage of 1-m^2 quadrats per plot containing at least one invasive species, and tracked the local establishment and expansion of invasive species within a plot. Average cover was the percent cover of all invasive species (or functional group or species) estimated in 1-m^2 quadrats, averaged across the quadrats in each plot. Average cover most closely tracked expansion of established invasive species over time. Interpreting the results of each of the metrics for a given functional group or species can also reveal the likely stage of invasion for a given species. For example, a significant increase in plot frequency for a species with otherwise low average cover and quadrat frequency, may indicate a species in the establishment phase. Increasing trends in average cover for a species with relatively high plot frequency is indicative of the expansion phase. These three metrics can also help identify species that have reached the saturation phase of invasion, as indicated by persistently high abundance over the study period. While average cover and quadrat frequency only included species found in quadrats, plot frequency included all species that were observed within a plot (e.g., invasive vines on trees, invasive shrubs in microplots, invasive trees, etc.) and that have been consistently measured over time.

For each of the three invasive metrics, we analyzed three grouping levels: total invasives (all invasive plants monitored in a park), by functional group, and by species. We used the same grouping levels and metrics for both the summary of status and the analysis of temporal trends. We chose these three grouping levels because they answer different management questions, such as: is overall invasive abundance changing, and which species are the most abundant in a given park? These grouping levels also had varying power to detect trends based on prevalence of 0s and number of factor levels in the model. In other words, while the species-level analyses were potentially the most informative, the species-level data also had the most 0s. Species-level analyses may therefore have less power to detect trends than group-level and/or total invasive-level analyses. For taxa that were difficult to consistently identify to species, such as species of exotic bush honeysuckle (*Lonicera* spp.), and privet (*Ligustrum* spp.), we calculated invasive metrics at the genus level. For the functional group analyses, we grouped species into the following life forms: tree, shrub/vine, herbaceous, and graminoid. Graminoids were grasses, sedges, or rushes (families: Poaceae, Cyperaceae, and Juncaceae). Herbaceous species included all non-woody vascular species that were not graminoids. We separated graminoids from the herbaceous group because they have been found to be less sensitive to common eastern forest stressors, such as deer overabundance (Rooney 2009). We combined shrubs and woody vines into one functional group because they often behave similarly in the understory stratum we sample in quadrats (i.e., ground up to 2 m) and were not always easily classified as shrub or vine (e.g., Japanese honeysuckle (*Lonicera japonica*) and multiflora rose (*Rosa multiflora*) exhibit characteristics of both shrubs and vines). We calculated average cover of functional groups by summing the cover of each species within a group per quadrat, and then averaging that sum across all of the quadrats within a plot. Note that because NCRN did not estimate percent cover of tree species in the quadrats, we could not analyze trends in average cover of invasive trees for that network, although we were able to examine trends in plot frequency and quadrat frequency of invasive trees.

Statistical trend analysis

We conducted all statistical analyses in R 3.5.2 (R Core Team 2018) and our code and data are available for download (see Data Availability). To estimate trends over time, we used cycle as a numeric independent variable in our models, with cycle 1 covering survey years 2007–2010, cycle 2 covering survey years 2011–2014, and cycle 3 covering survey years 2015–2018. Models containing functional groups or species were specified as an interaction term with cycle, to allow us to determine change in a functional group or species over time and relative to other functional groups or species. While protocols varied across parks and networks, the sampling protocol within each park has been consistent over time. For the trend analysis, we therefore modeled each park individually, rather than combining multiple parks and networks in the same model. This approach minimized potential biases introduced by differing plot sizes and numbers of quadrats.

We fit linear mixed effects models, with plot as a random intercept, to estimate trends in average cover and quadrat frequency using the lme4 package (Bates et al. 2015). Note that we initially attempted to fit random slope models, but they consistently resulted in singular fits. For the functional group and species-level analyses, we only modeled groups or species that were present in ≥10% of the plots in a given park. To ensure we had sufficient degrees of freedom for the species-level analyses, we also only included one-half as many species as there were plots and selected the most abundant species based on plot frequency. We did this by sorting the species list for each park based on plot frequency and compared the number of species to the number of plots. Parks with more than 1 species per 2 plots were subset to include the most abundant species while maintaining a 1 species to 2 plot ratio. Diagnostics (e.g., residual plots) on these models consistently indicated issues with normality and constant variance. While estimates of coefficients (e.g., slope) are robust to violations of non-normal error, significance testing is not (Maas and Hox 2004, Givens and Hoeting 2012). We therefore used case bootstrapping, a non-parametric bootstrap method, to generate empirical 95% confidence intervals of model coefficients based on 1,000 samples for each model. Case bootstrapping works by randomly sampling plots (i.e., cases) along with the survey data from those plots in the order they were sampled to generate a sampling distribution that maintains the underlying random structure of the dataset (Givens and Hoeting 2012). While case bootstrapping relaxes the assumptions of the underlying error distribution, it also requires a sufficient number of plots to sample because the sampling distribution is derived entirely from resampling the existing data. We therefore had to exclude Sagamore Hill NHS, New York (SAHI) and Wolf Trap Park for the Performing Arts, Virginia (WOTR) from the trend analyses because they had too few plots (i.e., <6 plots) to create a usable sampling distribution. For the quadrat-level trend analyses, we interpreted effect sizes in original metric units (e.g., actual change in percent quadrat frequency over time), rather than percent change over time.

For the plot frequency analysis, we fit generalized mixed effects models to the data in the lme4 package (Bates et al. 2015) with a binomial distribution (i.e., logistic regression) to determine whether plots were significantly more or less likely to be invaded in subsequent cycles. Similar to the quadrat-level models, we modeled each park individually using a random intercept model with plot as the random factor. In this analysis, we only included parks with at least 10% of all combined plot surveys containing an invasive species and no more than 90% of all plot surveys containing an invasive species, to avoid convergence issues. To test for significant trends, we used parametric bootstrapping of 1,000 samples, which is recommended over case bootstrapping for models with a known error distribution (Givens and Hoeting 2012, Bates et al. 2015). We interpreted effect size for plot frequency as the odds ratio for an invasive occurring in a plot each additional cycle, which we calculated by taking the exponent of the slope coefficient.

Results

Status of invasive plants

Invasive species are widespread in the eastern national parks included in this study. In 35 out of the 39 parks in this study, more than one-half of the plots had at least one invasive species in the most recent 4-yr survey, and, in 10 parks, every plot had at least one invasive species present (Table 1, Fig. 1). In 21 (54%) of the parks, invasive quadrat frequency was 50% or greater, meaning that on average one-half of the quadrats in each plot had at least one invasive species. Moreover, cover of invasives averaged over 20% in 10 out of 39 parks.

Parks with the highest invasive abundance tended to be near Washington, D.C., or other densely populated areas, including Minute Man NHP (MIMA) near Boston, Massachusetts, and Sagamore Hill NHS, New York (SAHI) and Morristown NHP, New Jersey (MORR) in the greater New York Metropolitan area (Fig. 1). However, this pattern was not universal, as Friendship Hill NHS (FRHI) in rural southwestern Pennsylvania had consistently high abundance across metrics, and Prince William Forest Park, Virginia (PRWI) near Washington, D.C. was one of the least invaded parks in the study (Table 1; Fig. 1). In addition to PRWI, the overall least invaded parks in this study were Acadia NP, Maine (ACAD), Marsh-Billings-Rockefeller NHP, Vermont (MABI), Fredericksburg and Spotsylvania NMP, Virginia (FRSP)—all averaging <1% invasive cover, and <10% invasive quadrat frequency.

Present in over 75% of parks and at least 25% of all plots in the most recent cycle, Japanese stiltgrass (*Microstegium vimineum*), multiflora rose (*Rosa multiflora*), and Japanese honeysuckle (*Lonicera japonica*) were the most widespread invasive species in our study area (Table 2). Of the 10 most frequently detected species in our plots, seven were shrubs/woody vines, with multiflora rose being the most frequently encountered invasive shrub (found in 28% of plots and 90% of parks). Japanese stiltgrass was found in 34% of plots and was by far the most common invasive graminoid across plots, although the range of Japanese stiltgrass did not extend north of Roosevelt-Vanderbilt NHS, New York (ROVA; Appendix S1: Table S2). The most frequently detected non-graminoid herbaceous species was garlic mustard (*Alliaria petiolata*), which was found in 20% of plots. Unlike Japanese stiltgrass, garlic mustard was found

TABLE 2. Species-level summaries of the 25 most common invasives in the most recent 4-yr survey cycle, based on and sorted by percentage of plots.

Latin name	Common	Func. group	Plots (%)	Parks (%)	Cover (%)	Quad. freq.	Max. cover	Max. freq.
Microstegium vimineum	Japanese stiltgrass	graminoid	33.9	84.6	13.9	42.3	91.2	100.0
Rosa multiflora	multiflora rose	shrub	28.2	89.7	4.9	18.5	61.7	100.0
Lonicera japonica	Japanese honeysuckle	shrub	25.6	82.1	3.3	45.7	52.2	100.0
Alliaria petiolata	garlic mustard	herbaceous	20.3	64.1	2.3	36.6	40.1	100.0
Berberis thunbergii	Japanese barberry	shrub	19.6	76.9	9.1	23.8	86.5	100.0
Celastrus orbiculatus	Asian bittersweet	shrub	16.9	84.6	1.6	27.7	15.9	100.0
Lonicera spp. (Exotic)	exotic bush honeysuckle	shrub	15.4	66.7	7.0	16.7	69.2	100.0
Persicaria longiseta	oriental lady's thumb	herbaceous	14.9	79.5	1.7	21.8	22.6	100.0
Rubus phoenicolasius	wineberry	shrub	12.7	59.0	2.3	21.5	44.2	100.0
Ligustrum spp.	privet	shrub	9.2	66.7	0.9	23.1	14.5	100.0
Ailanthus altissima	tree-of-heaven	tree	8.9	66.7	0.7	12.1	13.3	83.3
Elaeagnus spp.	oleaster	shrub	6.9	51.3	4.7	5.4	36.0	66.7
Euonymus alatus	winged burningbush	shrub	6.7	51.3	0.9	18.8	9.6	75.0
Glechoma hederacea	creeping charlie	gerbaceous	5.3	43.6	5.5	19.9	71.5	100.0
Acer platanoides	Norway maple	tree	4.5	41.0	0.5	27.0	6.0	100.0
Hedera helix	English ivy	shrub	4.1	35.9	5.1	35.3	63.3	100.0
Prunus avium	sweet cherry	tree	3.9	51.3	0.4	12.2	3.4	58.3
Cardamine impatiens	narrowleaf bittercress	herbaceous	3.8	23.1	0.4	22.9	4.8	87.5
Rhamnus cathartica	European buckthorn	shrub	3.4	15.4	1.5	46.5	17.4	100.0
Epipactis helleborine	broadleaf helleborine	herbaceous	3.3	23.1	0.0	12.5	0.0	37.5
Persicaria perfoliata	mile-a-minute	herbaceous	2.2	25.6	2.5	24.0	19.2	83.3
Lysimachia nummularia	moneywort	herbaceous	2.1	28.2	6.1	28.7	29.2	100.0
Robinia pseudoacacia	black locust	tree	1.8	17.9	0.5	14.0	3.1	37.5
Rhamnus frangula	glossy buckthorn	shrub	1.7	7.7	11.1	63.9	35.6	100.0
Euonymus fortunei	climbing euonymus	shrub	1.5	20.5	3.7	35.0	22.8	100.0

Notes: Plots is the percentage of plots (out of 1,479) where a species has been detected. Parks is the percentage of parks (out of 39) where a species has been detected in at least one forest plot. Func. group is the functional group for each species. Cover is the average quadrat cover a species occupies in plots where it is present. Quad. freq. is the average percentage of quadrats a species occurs in on plots where it is present. Max. cover is the highest average cover of a species recorded in a plot. Max. freq. is the highest quadrat frequency of a species recorded in a plot. For the full species list, refer to Appendix S1: Table S3.

throughout the study area (Appendix S1: Table S2). Tree-of-heaven (*Ailanthus altissima*) was the most common invasive tree species, although it was only found in 9% of plots and like Japanese stiltgrass, was not found north of ROVA.

Temporal trends in invasive plants

Overall, we detected considerably more increasing than decreasing trends across all metrics and grouping levels (Table 3, Appendix S2: Figs. S1–S3). For total invasives, only two parks in our analysis, Prince William Forest Park, Virginia (PRWI) and Roosevelt-Vanderbilt NHS, New York (ROVA), had significant negative trends (Table 3). For PRWI, total invasives decreased 0.86% in quadrat frequency per cycle, and in ROVA, average cover of total invasives declined 1.2% per cycle. In contrast, total invasives increased significantly over time in 21 of 37 parks for at least one metric, and in 10 parks, total invasives significantly increased in two of three metrics. In Allegheny Portage Railroad NHS, Pennsylvania (ALPO), Gauley River NRA, West Virginia (GARI), and Petersburg NB, Virginia (PETE), plot frequency, quadrat frequency, and average cover of total invasives all increased significantly over time. Antietam NB, Maryland (ANTI) had the steepest increases, with an estimated increase of 12.5% quadrat frequency per cycle, and an increase in 13.0% average cover per cycle.

Of the invasive functional groups analyzed, graminoids had the most number of significant trends, and were significantly more likely to occur in plots over time in nine parks (Fig. 2, Table S4). Graminoids also increased significantly in quadrat frequency in 15 parks (Fig. 3) and in average cover in 13 parks (Fig. 4). Note that Japanese stiltgrass was the primary species driving the trends in invasive graminoids. Reed canarygrass (*Phalaris arundinacea*), and common reed (*Phragmites australis*) were the only two other invasive graminoid species that were included in the trend analysis, but they were restricted to Minute-Man NHP, Massachusetts (MIMA) and Saratoga NHP, New York (SARA) (Appendix S1: Table S2). Following graminoids, invasive shrubs significantly increased in quadrat frequency in 10 parks and in average cover in six parks. There were only a few significant negative quadrat-level trends in functional group abundance, and all were either herbaceous or graminoid groups (Figs. 3, 4).

At the species level, Japanese stiltgrass demonstrated the greatest potential for expansion across our study area. Japanese stiltgrass was significantly more likely to occur in plots over time in six parks (Fig. 5). Additionally, quadrat frequency and average cover of Japanese stiltgrass both increased significantly in 12 out of the 37 parks that were modeled (Figs. 6, 7). Japanese stiltgrass also increased the fastest of any species in the analysis. Antietam NB, Maryland (ANTI) is the most extreme case, with Japanese stiltgrass increasing 25.6% per cycle in quadrat frequency and increasing 12.9% per cycle in average cover. While no other individual species compared to Japanese stiltgrass in the magnitude of the trend slope or number of parks with significant trends, invasive shrub species, including Japanese barberry

Table 3. Effect sizes for significant park-level trends in total invasives.

Metric	Metric and network	Park code	Effect size
Plot frequency (odds ratio)			
	ERMN	ALPO	6.32
	NCRN	CATO	7.71
	MIDN	FRSP	5.52
	ERMN	GARI	5.00
	MIDN	PETE	2.13
	MIDN	RICH	16.20
Quadrat Frequency (quadrat percent per cycle)			
	ERMN	ALPO	4.48
	NCRN	ANTI	12.50
	NCRN	CATO	4.00
	ERMN	FONE	5.42
	ERMN	FRHI	7.78
	ERMN	GARI	2.16
	MIDN	GETT	4.93
	NCBN	GEWA	9.85
	MIDN	HOFU	4.69
	NETN	MORR	1.79
	ERMN	NERI	1.40
	MIDN	PETE	2.74
	NCRN	PRWI	−0.86
	NETN	SARA	5.22
	MIDN	VAFO	4.17
Cover (average quadrat percent cover per cycle)			
	ERMN	ALPO	4.78
	NCRN	ANTI	13.02
	MIDN	APCO	1.71
	NCRN	CHOH	4.63
	ERMN	FONE	4.26
	ERMN	FRHI	8.31
	ERMN	GARI	0.56
	MIDN	GETT	2.84
	NCBN	GEWA	2.66
	NETN	MORR	3.27
	ERMN	NERI	0.48
	MIDN	PETE	1.44
	MIDN	RICH	1.97
	NETN	ROVA	-1.22
	NETN	SARA	2.63
	NCBN	THST	4.21

Notes: The plot frequency effect size is the odds ratio of an invasive species being present in subsequent cycles, with values >1 indicating that an invasive is more likely to occur on a plot over time. Quadrat frequency and average cover effect sizes represent the change in total invasives in the original metric units. Parks not listed did not have significant trends in total invasives.

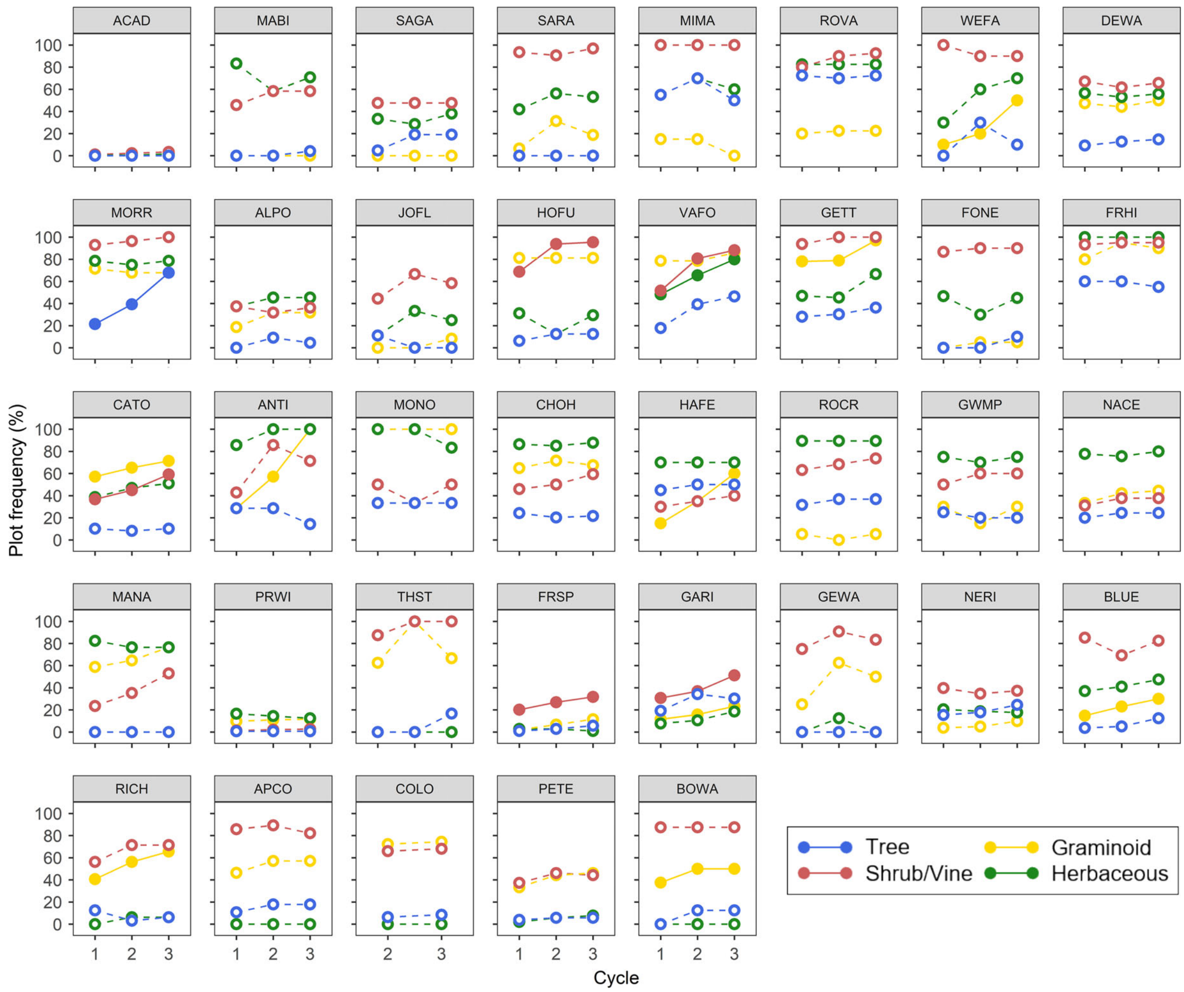

FIG. 2. Percentage of plots with at least one invasive species per functional group by cycle. Cycle 1 spans 2007–2010, cycle 2 spans 2011–2014, and cycle 3 spans 2015–2018. Solid symbols and lines indicate that a given functional group is significantly more or less likely to occur on a plot in subsequent cycles. Appendix S1: Table S4 contains odds ratios for significant models. Parks are ordered by high to low latitude.

(*Berberis thunbergii*), Asian bittersweet (*Celastrus orbiculatus*), Japanese honeysuckle, exotic bush honeysuckles (*Lonicera* spp.), multiflora rose, and wineberry (*Rubus phoenicolasius*) all had significant increasing trends across multiple parks. While a few parks had a significant decline in one of these shrub species, such as quadrat frequency of Japanese honeysuckle in Prince William Forest Park, Virginia (PRWI), the decreases were relatively small compared to the increases of the same species documented in other parks.

Significant declines, while less frequent than increases, were most common among herbaceous and graminoid species. In many cases, declines in herbaceous species and/or Japanese stiltgrass in a given park were met with significant increases of other invasive species, particularly woody species. In Morristown NHP, New Jersey (MORR), for example, quadrat frequency of garlic mustard and narrowleaf bittercress (*Cardamine impatiens*) both decreased by 7.1% and 8.0% per cycle, respectively, while wineberry increased in quadrat frequency by 6.5% per cycle. Also in MORR, Japanese stiltgrass average cover declined by 2.1% and garlic mustard average cover declined by 0.6% per cycle, whereas Japanese barberry average cover increased by 3.2% per cycle. In Roosevelt-Vanderbilt NHS, New York (ROVA), garlic mustard quadrat frequency declined by 3.6% per cycle, whereas Norway maple (*Acer platanoides*) quadrat frequency increased by 3.6% over the same time period. The only exception to this pattern of woody species increasing at the expense of herbaceous or graminoid species was in Appomattox Court House NHP, Virginia (APCO), where Japanese stiltgrass significantly increased in average cover by 2.2% and Japanese honeysuckle significantly decreased in average cover by 0.4% over the same time.

Only two out of 37 parks in our study showed overall declines in invasive plants over time, namely Marsh-Billings-Rockefeller NHP, Vermont (MABI) and Prince

FIG. 3. Percentage of quadrats with at least one invasive species by functional group and cycle based on modeled quadrat frequency. Cycle 1 spans 2007–2010, cycle 2 spans 2011–2014, and cycle 3 spans 2015–2018. Solid symbols and lines indicate a significant trend in quadrat frequency over time. Values are the predicted mean and error bars are 95% empirical confidence intervals. Parks are ordered by high to low latitude.

William Forest Park, Virginia (PRWI). In both parks, we only detected significant negative trends in invasive abundance. MABI and PRWI also had relatively low invasive abundance at the start of the study. Two additional parks maintained relatively low invasive abundance throughout the study period and did not experience any significant increasing trends: Acadia NP, Maine (ACAD), and Saint Gaudens NHP, New Hampshire (SAGA).

Discussion

Our study is one of the first to examine trends in invasive plant communities spanning a broad region and covering over a decade of time. A number of new and key findings emerged from our study, which we summarize below.

Ties to invasion theory: Invasive species continue to establish and expand, even in already heavily invaded forests

Invasive species abundance overwhelmingly increased over time throughout our study area. Unlike several of the long-term studies on invasive impacts (e.g., Banasiak and Meiners 2009, Dostál et al. 2013, Flory et al. 2017), we found little evidence of saturation or declining trends in invasive plants over our 12-yr study period. For example, we would expect the species that were most abundant at the beginning of the study, namely Japanese stiltgrass and invasive shrubs, to be the species most likely to exhibit signs of saturation or decline. In fact, we observed the opposite pattern: Japanese stiltgrass and invasive shrubs were the most likely to invade new plots and to increase in abundance where already well

FIG. 4. Average percent cover of invasive species by functional group and cycle based on modeled percent cover. Cycle 1 spans 2007–2010, cycle 2 spans 2011–2014, and cycle 3 spans 2015–2018. Solid symbols and lines indicate a significant trend in invasive percent cover time. Values are the predicted mean and error bars are 95% empirical confidence intervals. Parks are ordered by high to low latitude.

established. This was true even for parks, like Antietam NB, Maryland (ANTI), Morristown NHP, New Jersey (MORR), and Valley Forge NHP, Pennsylvania (VAFO), which were already heavily invaded at the beginning of monitoring.

Results also suggested multiple phases of invasion playing out in our study area. Based on significant increases over time in plot frequency and relatively low quadrat frequency and average cover, Japanese stiltgrass in Bluestone NSR, West Virginia (BLUE) and wineberry in Gauley River NRA, West Virginia (GARI) may be in the establishment or early expansion phase in these parks. The results in other parks are suggestive of multiple processes of invasion occurring simultaneously within a given park. For example, Japanese stiltgrass significantly increased over time in plot frequency, quadrat frequency and average cover in Harpers Ferry NHP, Maryland/Virginia/West Virginia (HAFE), and Richmond NBP, Virginia (RICH), indicating that this species is firmly established and expanding at multiple spatial scales within these parks. Invasive woody species showed similar trends of establishment and expansion at multiple scales, including oriental bittersweet in Valley Forge NHP, Pennsylvania (VAFO), Japanese barberry in Gettysburg NMP, Pennsylvania (GETT) and Morristown NHP, New Jersey (MORR), multiflora rose in Chesapeake and Ohio Canal NHP Maryland/West Virginia (CHOH), Saratoga NHP, New York (SARA), and VAFO, and wineberry in Hopewell Furnace NHS, Pennsylvania (HOFU), MORR, and VAFO.

Taken together, these findings suggest that the establishment and expansion phases of invasion can occur simultaneously within a given area. There was also little evidence of species reaching saturation or declining over the time period of our study, which is somewhat in conflict with invasion theory (Arim et al. 2006, Dostál et al.

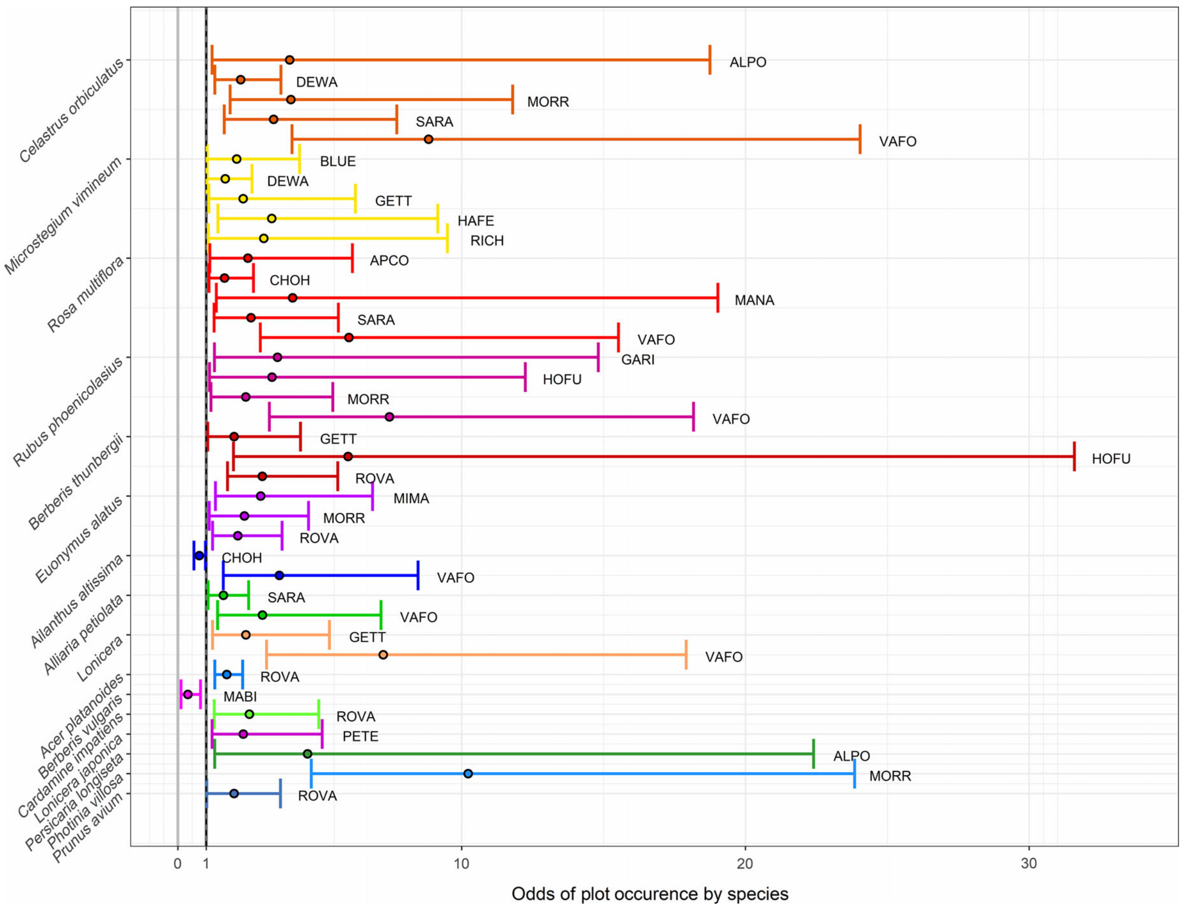

FIG. 5. Species with significant trends by park in plot frequency over time, sorted by total number of significant trends across parks. Circles represent the odds ratio, and error bars are 95% empirical confidence intervals around the odds ratio. Odds greater than 1 indicate a species is more likely to occur in a plot in subsequent cycles. Odds between 0 and 1 indicate species that are less likely to occur in subsequent cycles. Species are color-coded by functional group, such that trees are shades of blue, shrub/vines are shades of red/orange, graminoids are shades of yellow, and herbaceous species are shades of green.

2013). Our multi-species, community-level approach may partially explain why we detected overwhelming increasing trends in invasive plant abundance, compared to other long-term studies that primarily examined trends for an individual species. Moreover, the range of scales in our study, from plots to parks to a broad region, allowed us to examine invasion at multiple scales and phases that few long-term studies have done.

These results also have important management implications. While there is a tendency for invasive species management efforts to focus on less invaded areas of parks, our results suggest that if the heavily invaded areas are ignored, they continue to worsen and will likely function as persistent source populations for less invaded areas.

Antagonistic interactions between invasive species are common

While interactions between invasive and native species have been well studied (e.g., Stinson et al. 2007, Galbraith-Kent and Handel 2008, Adams and Engelhardt 2009, Green and Blossey 2012), interactions, particularly antagonistic interactions, between multiple invasive species have received less attention (Kuebbing et al. 2016). For example, Kuebbing et al. (2015) examined interactions between multiple invasive species, and only found positive interactions between Chinese privet (*Ligustrum sinense*) and two other invasive shrubs, namely Amur honeysuckle (*Lonicera maackii*) and Dahurian buckthorn (*Rhamnus davurica*). Flory and Bauer (2014) documented a positive interaction whereby Japanese stiltgrass facilitated invasion of garlic mustard in a long-term field experiment. Belote and Weltzin (2006) did document an antagonistic interaction, with Japanese stiltgrass outcompeting Japanese honeysuckle in experimental plots. We observed a similar scenario in Appomattox Court House NHP, Virginia (APCO), with average cover of Japanese stiltgrass significantly increasing over time and Japanese honeysuckle significantly decreasing over time. However, invasive shrubs were much more likely to increase at the expense of Japanese

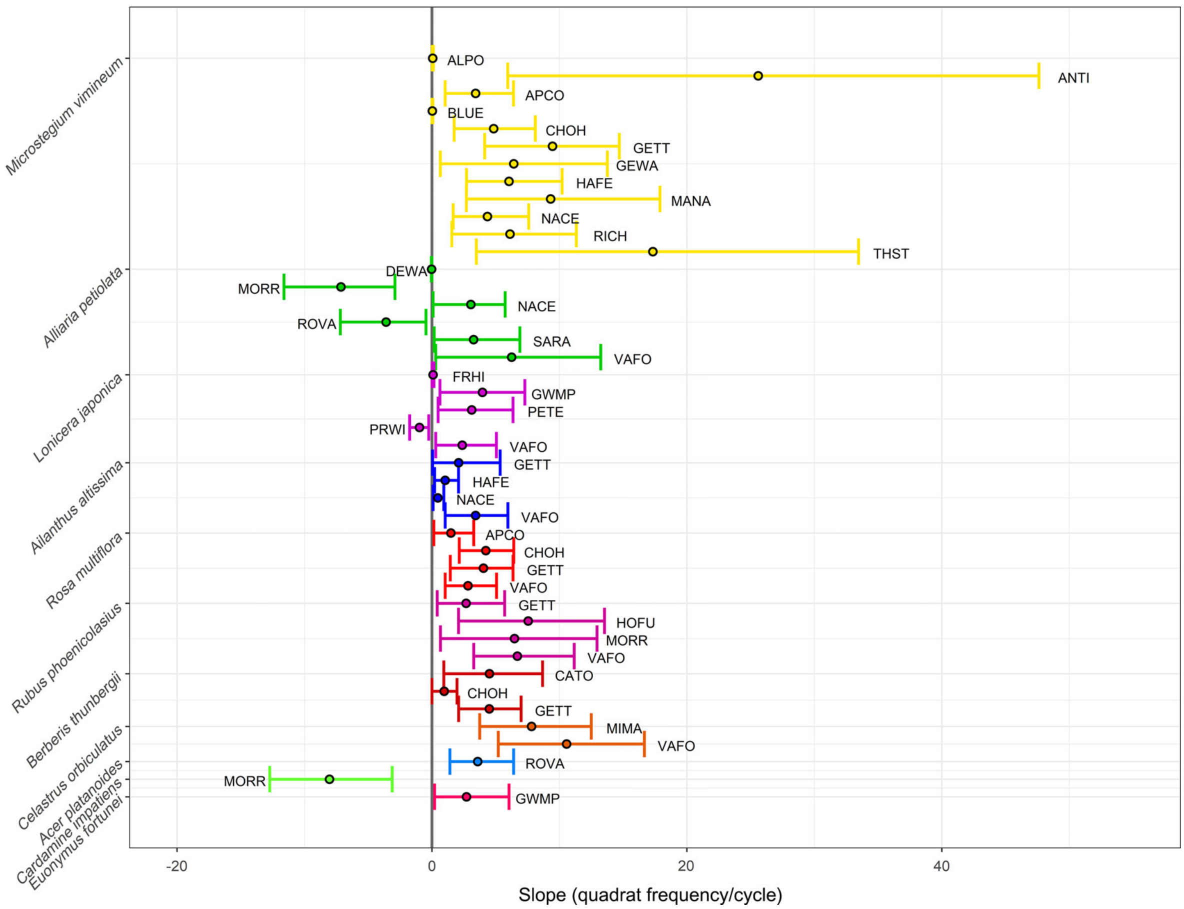

FIG. 6. Species with significant trends by park in quadrat frequency over time, sorted by number of significant trends across parks. Circles represent the change in quadrat frequency per cycle (i.e., the slope), and error bars are 95% empirical confidence intervals around the slope. Species are color-coded by functional group.

stiltgrass and other herbaceous species in our study, and we have not found examples of this type of interaction documented in the literature. Again, our multi-species, community-level approach may explain why we were able to detect antagonistic interactions, compared to other long-term studies that primarily examined trends for an individual species.

Japanese stiltgrass and invasive shrubs are the highest management priorities in eastern forests

The widespread occurrence and rapid expansion rates that we documented for Japanese stiltgrass were concerning. While considerable research has been conducted on Japanese stiltgrass invasion rates, we are unaware of any study that has documented such rapid invasion rates, particularly rates that were sustained over a long time period (12 yr, in our case). For example, Flory et al. (2017) documented a substantial decline in Japanese stiltgrass abundance by the end of an 8-yr field experiment. Estimated expansion rates of Japanese stiltgrass in other studies were typically <1 m per year (Rauschert et al. 2010, Schramm and Ehrenfeld 2012). While we are unable to measure expansion rates in the same distance units, based on the trends we observed, Japanese stiltgrass can expand rapidly (e.g., as high as 13% cover per 4-yr cycle) and maintain high abundance (e.g., >75% plot frequency) for a decade or more.

Next to Japanese stiltgrass, invasive shrubs were the most widespread and frequently increasing invasives in our study area. Additionally, where we detected significant declines in invasive abundance, they were typically Japanese stiltgrass and/or herbaceous species that were often countered by a roughly equivalent increase in abundance of one or more invasive woody species, particularly shrubs.

Japanese stiltgrass and invasive shrubs both have the potential to impact forest ecosystems through suppression of tree regeneration and understory diversity (Hartman and McCarthy 2008, Boyce 2009, Aronson and Handel 2011, Johnson et al. 2015, Link et al. 2018). In addition, invasive shrub thickets pose a threat to human health by supporting higher densities of black-legged ticks (*Ixodes scapularis*) with a higher incidence of Lyme

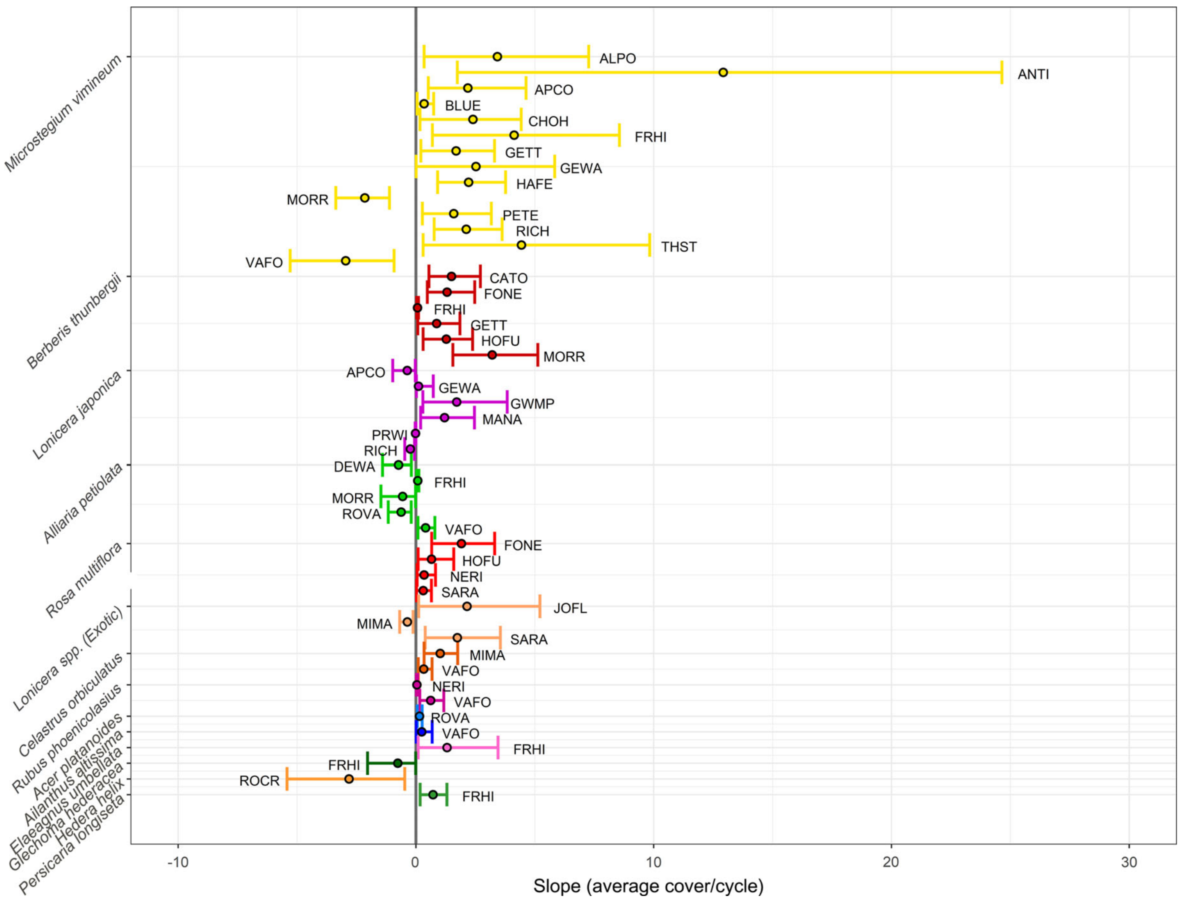

FIG. 7. Species with significant trends by park in average cover over time, sorted by number of significant trends across parks. Circles represent the change in average cover per cycle (i.e., the slope), and error bars are 95% empirical confidence intervals around the slope. Species are color coded by functional group.

disease (Ward and Williams 2010). These species, therefore pose serious threats to eastern forest ecosystems, and should be a top priority for invasive management and early detection efforts.

We need to better understand the drivers and impacts of invasives in eastern forests

The status and trends of invasive plant communities that we documented in this study are an important first step in informing management decisions about invasive species in eastern forests. However, our study did not assess the impacts of invasive trends on native species, and did not examine drivers behind these invasive trends. Overabundant white-tailed (*Odocoileus virginianus*) deer, which are a chronic issue in many of the parks in our study, are especially of interest as drivers of the invasive plant trends we observed. A number of studies have documented associations between overabundant deer, invasive plant species, and impacts to native species (Knight et al. 2009, Aronson and Handel 2011, Frerker et al. 2014, Dávalos et al. 2015, Bourg et al. 2017). Additionally, chronic stressors like deer are often missing from many of the long-term studies that have documented diminishing impacts from invasive plants over time (e.g., Banasiak and Meiners 2009, Dostál et al. 2013, Flory et al. 2017). Japanese stiltgrass abundance and expansion in particular have been associated with high deer densities (Shen et al. 2016, Bourg et al. 2017), and reduction in deer density may lead to a reduction in its abundance (Schmit et al. 2020). Other potential factors or drivers behind the trends we observed may include invasive plant management, latitude, climate change, fragmentation and urbanization. Now that we have identified the species and functional groups with the greatest invasive potential, we will begin examining the underlying drivers to better predict invasive plant abundance and trends in the presence of stressors and to help managers reduce overall threats of invasion.

Our study also did not consider how existing invasive management efforts explain the trends we observed in our parks. This was partially because we were primarily focused on estimating invasive trends in this initial study, with the next steps to focus on drivers. Quantifying management efforts consistently across parks also poses a considerable challenge. This is particularly true for invasive plant management that occurred during the first two cycles of this study, which was largely before national standards existed to track invasive management efforts in parks. For example, in Marsh-Billings-Rockefeller NHP, Vermont (MABI) and Prince William Forest Park, Virginia (PRWI), we know that park managers have actively been treating invasive plants in these parks throughout the period of our study. We suspect management at least partially explains the declining invasive trends in these parks. However, we do not have sufficient data covering the full 12-yr study period to know how many and what type of treatments occurred in or near our plots to confirm whether invasive management or other factors are behind these trends. We also do not know how management efforts compare among parks. That said, now that we know Japanese stiltgrass and invasive shrubs are the most abundant and aggressive invaders and because of the new service-wide reporting standards, we will be able to more easily quantify management efforts for these species in future studies.

Conclusion: invasive plants are a serious problem in eastern parks and there is an urgent need for long-term resources to manage them

The overall high abundance and increasing expansion of invasives that we documented in many eastern parks may be surprising to the broader community of ecologists, as parks are often expected to be in better condition because of their protection status. In fact, we have shown that forests in eastern parks are regionally significant in having older forest structure and higher stand-level tree diversity than surrounding unprotected forests (Miller et al., 2016, 2018). The high and often increasing abundance of invasives that we documented in the majority of the parks in our study poses significant threats to the long-term condition of the forests in these same parks, and is in conflict with the mission of the National Park Service. While many of the parks in our study are actively managing invasives, few parks have access to the long-term resources needed to reduce the persistent, negative impacts of invasive plant species to park resources. Just as the National Park Service is working to overcome a deferred maintenance backlog for buildings, roads and other infrastructure within its parks, we propose that deferred management of natural resources receive equal attention and a sustained commitment to ensure the long-term health of forests in the eastern U.S. national parks.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2239/full

Data Availability

Code and data are available on Zenodo: https://doi.org/10.5281/zenodo.3990574.