

Nonnative vegetation dynamics in the understory of a fragmented temperate forest¹

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Abstract. Although the conditions that render forests likely to support nonnative plants are well documented, there are surprisingly few data on the long-term dynamics of nonnative invasive species in eastern temperate forests. We examined 11 years of compositional and structural change in a small (60 ha) forest preserve in Connecticut with abundant invasive plants, a diverse land use history, and varied edaphic characteristics. We quantified the extent to which vegetation composition changed at the species, life form, and community scales and then assessed the possible factors driving these changes. Fifty-four plots were sampled in 2004, 2009, and 2015; these plots spanned two major forest types, (a) *Acer rubrum* L.-*Fraxinus americana* L and (b) *Quercus montana* Willd.-*Quercus coccinea* Muenchh. Significant changes in composition occurred over time with a greater magnitude of change in the *Acer-Fraxinus* forest than in the *Quercus* forest at all scales of analysis. Large increases in the abundance of the invasive *Microstegium vimineum* (Trin.) A. Camus (+1760%), *Berberis thunbergii* DC. (+180%), and *Rosa multiflora* Thunb. ex Murr (+1790%), along with a surprisingly large decline in the dominant *Alliaria petiolata* (Bieb.) Cavara & Grande (−86%) occurred in the *Acer-Fraxinus* forest. Native shrub and herb life forms growing alongside these invasive species remained unchanged or increased in abundance. Soil moisture predicted change in abundance of *R. multiflora* and *B. thunbergii*. Our results suggest that *A. petiolata* may be less persistent over time than previously believed and underscore the difficulties of generalizing about invasive species dynamics and relationships with native plants.

Key words: *Alliaria petiolata*, deer, invasive, long-term forest monitoring, temperate forest

Introduction. Long-term forest monitoring has increasingly shown that understories of many intact temperate forests have little stability in species composition over time (Davison and Forman 1982; Taverna *et al.* 2005; Thiemann *et al.* 2009; Woods *et al.* 2012). An important

contributor to this lack of compositional stability is the colonization and establishment of nonnative species (Taverna *et al.* 2005). Forest understories with nonnative species are often prevalent in fragmented landscapes with abundant edge effects, high deer populations, propagule pressure from nonforest sources, and altered soil and drainage due to land-use (Baiser *et al.* 2008, Hobbs *et al.* 2014, Oswald *et al.* 2014). Additionally, soil nutrient levels and the extent to which a forest was formerly cleared for agriculture are important predictors of the presence of nonnative species (Lundgren *et al.* 2004, DeGasperis and Motzkin 2007, Von Holle and Motzkin 2007).

In addition to the factors determining the invasibility of a particular forest, much research has focused over the past 10–15 years in the eastern United States on the impacts of nonnative invasive plant species on native plant communi-

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ties; for example, *Alliaria petiolata* (Bieb.) Cavara & Grande (Stinson *et al.* 2007; Davis *et al.* 2015), *Berberis thunbergii* DC. (Flinn *et al.* 2014), *Microstegium vimineum* (Trin.) A. Camus (Oswalt *et al.* 2007; Adams and Engelhardt 2009), *Rosa multiflora* Thunb. ex Murr (Meiners 2007), and *Celastrus orbiculatus* Thunb. (Browder 2011). Yet, there are surprisingly little data on the long-term dynamics of many invasive species in eastern North America and what may be driving these dynamics (but see Banasiak and Meiners 2009; Murphy and McCarthy 2014). Similarly, there are limited data on the long-term trajectories of many of the dominant native shrub species (*e.g.*, *Kalmia latifolia* L.) in eastern forests. As species colonize new areas, they generally exhibit a predictable sequence of colonization and growth that includes an “expansion phase”—a period of exponential population growth and expansion before saturation of a particular habitat or area occurs (Arim *et al.* 2006; Webster *et al.* 2006). However, we know much less about the dynamics of individual invasive species after they have long been present in a forest.

Here we examine 11 years of change to the structure and composition of a small forest preserve in a fragmented landscape of southwestern Connecticut (CT). We posed the following questions: (a) What were the most important changes in community, life form, and individual species composition in the shrub and herb layer across the forested preserve? (b) How did the dynamics of invasive plant species, in particular, reflect their different life histories and arrival times? and (c) How did environmental setting, recent disturbance, and contemporary and historical land use correlate with vegetation patterns?

Materials and Methods. **STUDY AREA.** The study was conducted at Highstead, a 60-ha woodland preserve in southwestern Connecticut (41.325, -73.388). The preserve is located along the margins of an 80-ha core forest block mostly to the west. A golf course abuts the preserve to the south, extensive hay meadows (mowed once a year) with tree and shrub-dominated hedgerows occur to the east, and residential development to the north. The climate consists of cold winters and warm summers with average temperatures of -2.9 °C in January and 23.3 °C in July, and average annual precipitation of 132.4 cm (Northeast Regional Climate Center 2013). The landscape

has two contrasting geomorphological features: a bedrock ridge on the west side and a glacial drumlin on the east. The soils on and around the bedrock ridge are relatively shallow and strongly acidic, and are generally well-drained to excessively well-drained, with limited areas of moderately well-drained soils on the lower slopes (Faber 2008).

Xeric forest (≥ 100 years old) with an ericaceous shrub layer and sparse herb layer characterizes the 23 ha of vegetation on the west side of the property (Faison *et al.* unpublished data). This forest was never cleared for agriculture, although some isolated strands of barbed wire on some smaller trees suggest some previous woodland grazing. Aerial photos from 1934 and the abundance of multiple-stemmed trees suggest that this forest was cut heavily, and likely repeatedly, in the past for firewood and timber.

On the east side of the preserve, at the base of the drumlin, is mixed mesic forest, which spans about 10 ha. The topography is gently sloping and the soils are relatively deep, acidic and moderately well drained to poorly drained (Faber 2008). Historical aerial photographs and the presence of stone walls indicate that the entire forest was previously agricultural fields that reverted back to forest by the mid-to-late twentieth century. Tree cores indicate that the forest ranges from 50–90 years old. Forest pests and pathogens affecting this mesic forest in recent decades include the ash yellows fungus (*Candidatus fraxinii*; ash decline complex) and the very early stages of the emerald ash borer (*Agrilus planipennis*).

Distinct browse lines from *Odocoileus virginianus* Zimmerman (hereafter, deer) have been noted for the past few decades in this landscape (Faison *et al.* 2016). After reaching peak densities in the early 2000s in CT, deer densities declined from approximately 23 km⁻² prior in 2009 to about 15 km⁻² in 2015 in the town of Redding (Kilpatrick 2009; Williams *et al.* 2015; A. Labonte, personal communication). Between fall 2011 and fall 2012, three major storms struck Redding, CT, resulting in significant windthrow and tree breakage in Highstead’s forests: Tropical Storm Irene in August 2011, the Halloween Blizzard in 2011, and Tropical Storm Sandy in 2012.

VEGETATION SAMPLING. In 2004, a systematic grid of 75 permanent forest plots, 20 × 20 m in size, was established and permanently marked across

the approximately 40 ha of upland forest. In each plot, we measured and identified all trees ≥ 2.5 cm DBH to species; we also identified all herb and shrub species and estimated the percent cover abundance of each using the following cover classes (1 = $<1\%$, 2 = 1–3%, 3 = 3–5%; 4 = 6–15%, 5 = 16–25%; 6 = 26–50%, 7 = 51–75%, 8 = 76–100%; Motzkin *et al.* 1999; Eberhardt *et al.* 2003). Cover of individual species often overlapped with other species, and therefore total percent cover could, and often did, exceed 100% in a plot. Because the plots were sampled in June, July, and early August, we undoubtedly missed detecting some spring ephemeral herb species.

At each plot we also collected soil samples (0–15 cm), using a cylindrical steel corer, at four locations. Sub samples were aggregated into a single sample, air dried, sieved (<2 mm), and analyzed for texture and extractable nutrients (calcium, magnesium, nitrogen, phosphorus, and potassium concentrations; percentage of organic matter; and pH (1:1 in water) by Brookside Labs, Inc. (New Knoxville, OH, USA). We also recorded landscape position and other topographical characteristics (*e.g.*, slope, aspect).

We resampled the plots in 2009 and again in 2015. Some plots could not be relocated, some were determined to occur outside the Preserve boundaries, and some were positioned too close to one another to be independent. Fifty-four common plots were sampled in each of the three sampling periods, and all plots were located at least 35 m apart. Nomenclature followed Haines (2011).

DATA ANALYSIS. To standardize herb and shrub identification across different sampling years and observers, we combined several genera that included many similar, and easy to confuse, species. Such groups included *Carex* spp., *Solidago* spp., *Symphotrichum* spp. and *Viola* spp. We also lumped *Vaccinium pallidum* and *V. angustifolium* into one low *Vaccinium* spp. taxon and *Rubus flagellaris* and *R. hispida* into a single low *Rubus* spp.

We analyzed all data using R statistical software. We first performed an agglomerative hierarchical cluster analysis (Wards) on the 54 plots to identify forest types using tree species that occurred in at least 5% of the plots (McCune *et al.* 2002; Sanders and Kirschbaum 2015). This analysis used the importance value—the sum of the relative density and relative basal area—of each species-plot combination into the cluster

analysis (Sanders and Kirschbaum 2015). We also performed cluster analyses with just basal area and tree density and achieved the same groupings of the plots into two major forest types.

We tested for differences in species composition among sampling years (2004, 2009, 2015) and between forest types—identified by the cluster analysis—with permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis distance (1,000 permutations) with the Adonis function of vegan (Oksanen *et al.* 2015). We used shrub and herb taxon abundances (percent cover midpoints; *e.g.*, cover class 1 = 0.5%, cover class 2 = 2%, cover class 3 = 4%, etc.) into the multivariate test (Motzkin *et al.* 1999), and removed rare taxa that occurred in less than 5% of the plots prior to analysis (McCune *et al.* 2002). We also removed the following undifferentiated genera from the analysis: *Carex* spp., *Symphotrichum* spp., and *Solidago* spp.

We then used nonmetric multidimensional scaling (NMS) to visualize differences in species composition among plots over time. Community abundance data were first square root transformed, followed by Wisconsin double transformation (species divided by their maxima and plots standardized to equal totals). We assessed compositional dissimilarity using the Bray-Curtis dissimilarity measure. Appropriate dimensionality of the ordination was determined by evaluating stress measures for ordinations of 1–4 dimensions. For each dimensionality, we tried several random starts until we found two configurations with similar minimum stress and low residual differences. The analysis of two dimensions did not converge to a single solution because residual differences between lowest stress solutions did not meet the criteria, even after 3,000 random starts. Other dimensionalities did converge to a single solution (after 20–38 random starts), and we report the three-dimensional solution because it had substantially lower stress than the one-dimensional solution, while the four-dimensional solution was much less of an improvement. The final solution was rotated so that the largest variance of site scores was on the first axis.

We also ran an indicator species analysis using the *multipatt* function within the package *indic-species* (De Cáceres and Legendre 2009). We considered species as good indicators for a vegetation type if they had specificity, sensitivity, and stat scores greater than 0.7.

Table 1. Indicator species for 2004, 2009, and 2015 in the shrub and herb layer in the two vegetation types ranked in descending order of importance.

Forest type	Taxon	
<i>Quercus</i>	<i>Kalmia latifolia</i>	
	Low <i>Vaccinium</i> spp.	
	<i>Gaylussacia baccata</i>	
	<i>Hamamelis virginiana</i>	
	<i>Maianthemum canadense</i>	
	<i>Acer-Fraxinus</i>	<i>Berberis thunbergii</i>
		<i>Lindera benzoin</i>
		<i>Celastrus orbiculatus</i>
		<i>Arisaema triphyllum</i>
		<i>Rosa multiflora</i>
<i>Galium</i> spp.		
<i>Vitis</i> spp.		
<i>Oxalis stricta</i>		
<i>Ilex verticillata</i>		
<i>Euonymus alatus</i>		
<i>Leersia virginica</i>		
<i>Solidago</i> spp.		
<i>Circaea canadensis</i>		
<i>Glyceria striata</i>		
<i>Toxicodendron radicans</i>		
<i>Parthenocissus quinquefolia</i>		
<i>Carex</i> spp.		

We examined change in mean abundance of life forms (*i.e.*, ferns, forbs, graminoids, shrubs) and individual dominant species among sampling years with repeated measures ANOVA (rmANOVA). We examined the residuals of both log-transformed and untransformed models for each response variable to determine the best fit, which we then used for the rmANOVA. Tukey's *post hoc* tests were used to determine significant differences between sampling periods.

For species and life form groups that were significant in the rmANOVAs, we then examined change in abundance between 2004 and 2015 in relation to three predictor variables: (a) *Change in canopy stem density* (stems ≥ 25 cm DBH) from 2004–2015 as a surrogate for change in canopy cover, (b) *soil moisture-holding class*, and (3) *core or edge forest* as a measure of the influence of fragmentation on the vegetation. We identified four soil moisture classes from a detailed soil map of the property: poorly drained, moderately well drained, well drained, and excessively well drained as defined by Faber (2008). We determined core or edge forest from the University of Connecticut's Forest Fragmentation and Analysis data layer (Center for Land Use Education and Research [CLEAR] 2006). Core forest is greater than 91 meters from a non-forest edge in any direction,

whereas edge forest is less than or equal to 91 meters from a non-forest edge in any direction (CLEAR 2006). We examined the three predictor variables for multicollinearity and determined all correlation coefficients to be < 0.19 , increasing the reliability of the results (Graham 2003). Additionally, we examined the relationship between two dominant invasive herb species—*A. petiolata* and *M. vimineum*—that were undergoing opposing trajectories during the study period.

Results. VEGETATION VARIATION. We identified two dominant vegetation types from the hierarchical cluster analysis:

- Acer rubrum-Fraxinus americana* L. with *A. rubrum* dominant and *F. americana* and *Liriodendron tulipifera* L. as sub-dominants. *Berberis thunbergii*, *Lindera benzoin* (L.) Blume, and *C. orbiculatus* were the best indicator species in the shrub layer and *Arisaema triphyllum* and *Gallium* spp. the best indicators in the herb layer (Table 1).
- Quercus montana* Willd.-*Quercus coccinea* Muenchh. with *Q. montana* dominant and *Q. coccinea* and *Quercus rubra* L. common in the overstory and *Betula lenta* L. and *A. rubrum* very common in the subcanopy. *Kalmia latifolia* L. and *Vaccinium* spp. were the best indicator species in the shrub layer and *Maianthemum canadense* the only indicator species in the herb layer (Table 1).

CHANGES IN OVERSTORY STRUCTURE AND COMPOSITION. In the *Quercus* forest, overstory basal area increased over time ($P = 0.011$; Table 2). Basal area increased between 2004 and 2009, but leveled off between 2009 and 2015. Stem densities did not differ among sampling years ($P = 0.5$; Table 2), and there were no significant changes in basal area or stem densities of individual major taxa (*Q. rubra*, *Q. coccinea*, *Q. montana*, *B. lenta*, and *A. rubrum*). In the *Acer-Fraxinus* forest, neither overstory basal area ($P = 0.40$) nor stem density ($P = 0.84$) differed overall (Table 2) or among major taxa (*A. rubrum*, *F. americana*, *L. tulipifera*) among sampling periods.

CHANGES IN HERBACEOUS AND SHRUB COMPOSITION. Community composition changed significantly among sampling years (Adonis $F_{1,158} = 3.47$, $R^2 = 0.01$; $P = 0.01$) and by forest type (Adonis $F_{1,158} = 105.0$; $R^2 = 0.39$; $P = 0.001$).

Table 2. Forest structural characteristics from three sampling years in the two major vegetation types. Values are means with standard errors in parentheses. Significant differences ($P \leq 0.05$) as determined by rmANOVA are in bold. Sampling years with different superscript letters differ significantly from one another.

Forest type	N	Variable	2004	2009	2015	F	d.f.	P
<i>Quercus</i>	38	Basal area (m ² /ha)	24.3 (0.9) ^a	28.0 (1.0) ^b	27.8 (1.1) ^b	4.7	2,111	0.01
		Tree density (no. stems/400m ²)	35.1 (2.9)	35.6 (2.7)	31.4 (2.1)	0.7	2,111	0.50
<i>Acer-Fraxinus</i>	16	Basal area (m ² /ha)	31.5 (2.3)	36.5 (2.8)	34.0 (2.7)	0.9	2,45	0.40
		Tree density (no. stems/400m ²)	22.6 (4.0)	22.0 (3.3)	19.8 (3.0)	0.2	2,45	0.84

There was also a significant interaction between forest type and sampling year (Adonis $F_{1,158} = 5.1$; $R^2 = 0.02$; $P = 0.002$). The best NMS solution with three dimensions had a stress of 0.11, and an R^2 between the observed dissimilarity and ordination distance of 0.987. The first axis separated plots in the *Quercus* forest from those in the *Acer-Fraxinus* forest, while the second axis differentiated plots through time (Fig. 1). The third axis showed no obvious association with observed environmental variables and is not shown. Compositional changes over time were stronger from 2004 to 2009 than from 2009 to 2015 and stronger in the *Acer-Fraxinus* forest than in the *Quercus* forest.

Among life forms, shrub cover increased by 105% in the *Acer-Fraxinus* forest and declined by a relatively modest 21% in the *Quercus* forest (Table 3). Nonnative shrub cover increased by over 270% in the *Acer-Fraxinus* forest ($F_{2,45} = 10.7$; $P < 0.001$) and far surpassed native shrub cover, which changed little in abundance over time ($F_{2,45} = 0.03$; $P = 0.97$; Fig. 2). Herb cover increased in both forest types (Table 3). Graminoids increased

by almost 300% in the *Acer-Fraxinus* forest, while forbs exhibited a small upward trend (Table 3). In the *Quercus* forest, both forbs and graminoids showed significant but moderate increases (Table 3).

Significant changes to individual species in the *Acer-Fraxinus* forest included very large increases in the invasive *R. multiflora*, *M. vimineum*, and *B. thunbergii* and the native *Carex* spp. and a notable decline in *A. petiolata* (Table 3; Fig. 3). In the *Quercus* forest, significant but proportionately smaller changes occurred to *K. latifolia*, *Carex* spp., and *M. canadense* Desf; Table 3; Fig. 3).

FACTORS RELATED TO CHANGES IN SPECIES AND PLANT GROUP ABUNDANCES. In the *Acer-Fraxinus* forest, *R. multiflora* abundance increased in areas with wetter soils (abundance = 21.3%; $SE = 6.8$) than in drier soils (abundance = 3.4%; $SE = 2.6$; Est. = 17.9 $SE = 7.47$; $t = -2.4$; $P = 0.03$) and marginally with a decline in canopy tree density (Est. = -2.9; $SE = 1.4$; $t = -2.04$; $P = 0.06$). *Berberis thunbergii* abundance increased on drier soils (abundance = 34.7%; $SE = 6.6$) compared to wetter soils (abundance = 11.2%; $SE = 5.8$; Est. = 23.9; $SE = 9.28$; $t = 2.57$; $P = 0.024$). No other change in species or plant group abundance was related to soil moisture, edge effects, or change in canopy tree density. Change in *A. petiolata* abundance was unrelated to change in *M. vimineum* abundance.

Discussion. Our results revealed large changes in community composition, individual species, and life form abundance in a small forest preserve over an 11-year period. Magnitude of vegetation changes varied sharply by forest type, with changes generally larger and in a direction toward greater invasive species dominance in the *Acer-Fraxinus* forest and generally smaller and consisting of differences in abundance of a few native species in the *Quercus* forest. Our results revealed both expected and surprising dynamics of invasive species common to the Northeastern United States.

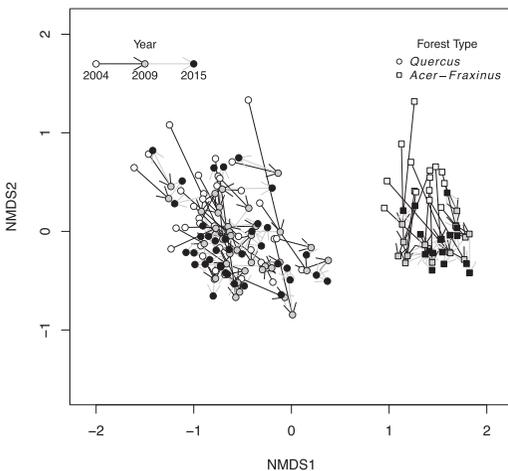


FIG. 1. Nonmetric multidimensional scaling (NMS) ordination with vectors showing how plots moved in species space over time.

Table 3. Mean abundance (% cover) of dominant shrub and herb taxa and life form groups in three sampling years in the two forest types. Standard errors are in parentheses. Significant differences ($P \leq 0.05$) as determined by rmANOVA are in bold. Sampling years with different superscript letters differ significantly from one another. $N = 16$ plots for *Acer-Fraxinus* forest and $N = 38$ plots for *Quercus* forest.

Forest type		2004	2009	2015	<i>F</i>	d.f.	<i>P</i>
<i>Acer-Fraxinus</i>	Life form						
	Ferns	1.6 (0.5)	2.6 (0.5)	2.8 (0.5)	1.5	2,45	0.24
	Forbs	10.1 (1.8) ^a	14.6 (1.7) ^b	14.1 (2.8) ^{ab}	3.3	2,45	0.05
	Graminoids	5.5 (2.3) ^a	16.6 (3.6) ^b	21.6 (5.4) ^b	13.6	2,45	<0.001
	Shrubs	36.4 (6.1) ^a	38.3 (6.2) ^a	74.6 (8.9) ^b	9.0	2,45	<0.001
	Species						
	<i>Alliaria petiolata</i>	2.2 (1.2) ^a	1.2 (0.6) ^{ab}	0.3 (0.1) ^b	4.5	2,45	0.02
	<i>Berberis thunbergii</i>	11.9 (4.6) ^a	14.5 (3.8) ^{ab}	33.6 (6.7) ^b	3.7	2,45	0.03
	<i>Carex</i> spp.	1.6 (0.4) ^a	5.1 (0.8) ^b	7.9 (2.5) ^b	17.0	2,45	<0.001
	<i>Lindera benzoin</i>	15.1 (5.0)	9.3 (3.0)	12.2 (3.6)	0.2	2,45	0.80
	<i>Microstegium vimineum</i>	0 (0) ^a	0.59 (0.2) ^a	11.0 (4.5) ^b	23.8	2,45	<0.001
	<i>Rosa multiflora</i>	0.75 (0.2) ^a	1.2 (0.3) ^a	14.2 (4.6) ^b	13.9	2,45	<0.001
	<i>Quercus</i>	Life form					
Ferns		0.8 (0.3)	1.5 (0.6)	1.7 (0.75)	0.15	2,111	0.86
Forbs		1.7 (0.2) ^a	2.9 (0.3) ^b	2.6 (0.3) ^b	5.8	2,111	0.004
Graminoids		0.51 (0.1) ^a	0.9 (0.2) ^{ab}	1.1 (0.2) ^b	4.6	2,111	0.01
Shrubs		52.6 (4.6) ^a	38.5 (3.7) ^b	41.5 (4.0) ^{ab}	3.2	2,111	0.04
Species							
<i>Kalmia latifolia</i>		40.1 (4.2) ^a	27.5 (3.6) ^b	26.8 (3.3) ^b	4.1	2,111	0.02
<i>Maianthemum canadense</i>		0.4 (0.03) ^a	0.5 (0.1) ^{ab}	0.7 (0.1) ^b	3.1	2,111	0.05

Several shrub and herb species exhibited explosive growth in the *Acer-Fraxinus* forest during the study period (2004–2015). Increases in abundance of the invasive annual grass, *M. vimineum*; the shrubs, *R. multiflora* and *B. thunbergii*; and the native sedge species *Carex* spp. were all much larger than any change that occurred in the *Quercus* forest.

Microstegium vimineum was first detected anecdotally after the 2004 sampling and increased by over 1,700% between 2009 and 2015, becoming the new dominant herb species in the forest.

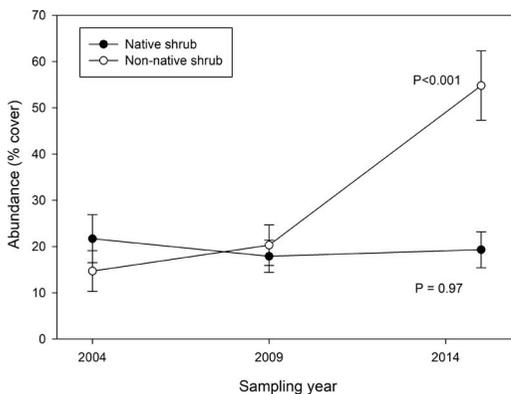


FIG. 2. Comparison of native and nonnative shrub cover in the *Acer-Fraxinus* forest from 2004 to 2015. $N = 16$. Bars = mean \pm SE.

Microstegium vimineum is readily dispersed by deer and appeared to take advantage of open midstory conditions and a lack of competition from a sparse tall shrub and small tree layer caused by decades of deer browsing (cf. Baiser *et al.*

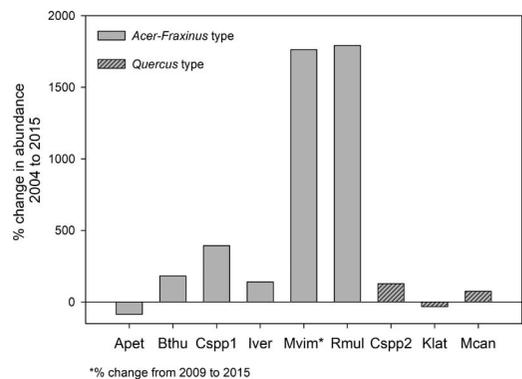


FIG. 3. Percentage change of dominant shrub and herb species in two vegetation types from 2004 to 2015. Only individual taxa that differed significantly in abundance over time are depicted (see Table 3). Note the much larger changes in the *Acer-Fraxinus* forest. Key: Apet = *Alliaria petiolata*, Bthu = *Berberis thunbergii*, Cssp1 = *Carex* spp. in *Acer-Fraxinus* forest, Cssp2 = *Carex* spp. in *Quercus* forest, Iver = *Ilex verticillata*, Klat = *Kalmia latifolia*, Mcan = *Maianthemum canadense*, Mvim = *Microstegium vimineum*, Rmul = *Rosa multiflora*.

2008). Indeed, *M. vimineum* was largely absent from a large (0.4 ha) 17-year-old deer enclosure (located in the same *Acer-Fraxinus* forest) with a dense tall shrub layer, but was abundant just outside of it (Faison *et al.* 2016).

Interestingly, native herb cover increased sharply with the arrival of *M. vimineum* between 2004 and 2009; however, the upward trend of native herbs leveled off by 2015. Other long-term studies in temperate forests have documented similar large increases in herb cover (Davison and Forman 1982; Baeten *et al.* 2010; Woods *et al.* 2012, but see Murphy and McCarthy 2014). The almost 400% rise in the native *Carex* spp. was likely facilitated by deer herbivory (*cf.* Waller 2014), as *Carex* abundance was unrelated to soil moisture, edge effect, or change in canopy tree density, but was 28 times lower inside the aforementioned deer enclosure compared to outside (Faison *et al.* 2016). Graminoids are generally more resistant to herbivory than are forbs because of their less accessible basal meristems (Waller 2014). The combined rise in *M. vimineum* and *Carex* spp. resulted in a shift in cover from forb to graminoid-dominated, resulting in a wood pasture-like physiognomy of the forest (*cf.*, Rooney 2009). In the process of simplifying the vertical structure of the forest, deer and other ungulates are often assumed to be reducing forest diversity, when in fact the opposite is often true in the herbaceous layer (Webster *et al.* 2016; Boulanger *et al.* 2018; Haffey and Gorchov 2019).

In the shrub layer, the dramatic rise of *R. multiflora* and *B. thunbergii* between 2009 and 2015 resulted in a transition from a native-dominated shrub layer in 2004 to a nonnative-dominated layer in 2015 (Fig. 2). Interestingly, no loss in absolute native shrub cover occurred with the increase in invasive shrub cover. Perhaps a contributing factor to this coexistence is the relatively short stature of *B. thunbergii*, which enables this species to develop beneath the taller mature *L. benzoin* and *Ilex verticillata*, without competing with these native shrubs for light.

Berberis thunbergii has likely been a component of the *Acer-Fraxinus* forest since agricultural abandonment 50–90 years ago; *B. thunbergii*'s first occurrence in central Fairfield County, CT dates back to the 1920s (Silander and Klepeis 1999). In our study area, this species replaced the native *L. benzoin* as the dominant shrub species after 2004. *Berberis thunbergii* increased on soils

of moderate drainage compared to poorly drained soils, reflecting its general intolerance of extremely wet conditions (Silander and Klepeis 1999). It also likely benefited from persistent deer herbivory on other woody plants via competitive release. As one of the few species avoided by deer, *B. thunbergii* often occurs in greater abundances in browsed areas relative to enclosures in the eastern US (Eschtruth and Battles 2009; Faison *et al.* 2016; Shen *et al.* 2016).

Canopy thinning appeared to play a possible role ($P = 0.06$) in the dramatic rise of the shade intolerant *R. multiflora* between 2009 and 2015. The combination of tree loss from three major wind/ice storms in 2011–2012 and ash mortality from the ash decline resulted in almost a third of the plots in the *Acer-Fraxinus* forest losing canopy trees. In these plots, the increase in *Rosa multiflora* was four times higher than in the plots that did not lose canopy trees. *Rosa multiflora* also increased significantly on wetter soils and was the dominant shrub species on poorly drained soils. Water availability promotes greater seed production and overwinter survival of *R. multiflora* when it is associated with canopy gaps (Banasiak and Meiners 2009). With the recent arrival of *Agrilus planipennis* (emerald ash borer) to the preserve in 2016, *R. multiflora* could further expand in cover in subsequent years, as *F. americana* comprised about 15% of the basal area in the *Acer-Fraxinus* forest in 2015. However, the eastward expansion of rose rosette disease could potentially offset the expansion of *R. multiflora*.

An unexpected result was the 86% decline of the dominant invasive herb, *A. petiolata* in the *Acer-Fraxinus* forest. Although the decline in *A. petiolata* coincided with the rise in *M. vimineum*, the change in abundance of the two species was unrelated in our analysis. Few previous studies have reported a decline in *A. petiolata* in unmanaged forests; however, Boyce (2015) reported that *A. petiolata* increased initially after the removal of a dense *Lonicera* shrub layer and then declined sharply 4–5 years later. Older populations of *A. petiolata* produce less glucosinolate and have decreased allelopathic effects on trees and arbuscular mycorrhizal fungal communities (Evans *et al.* 2016), perhaps reducing the herbivory resistance and competitive ability of this species over time. Another possible mechanism in the species' decline is the development of soil microbial

communities over time that inhibit *A. petiolata* (B. Blosssey, unpublished data).

Changes at the individual species, life form, and community scale were notably smaller in the *Quercus* forest compared to the *Acer-Fraxinus* forest. The decline in the dominant shrub species, *K. latifolia* from over 40% cover in 2004 to <28% cover in 2009 and 2015 was nonetheless an important change, continuing a trend that we had observed anecdotally for decades in these forests. *Kalmia latifolia* exhibits declines in vigor or cover in maturing and heavily browsed forests (Hemond *et al.* 1983; League 2005; Levri *et al.* 2009); thus, the increase in tree basal area (and presumably a reduction in understory light) from 2004 to 2009 may have contributed to the shrub's ongoing decline (*cf.* Chastain and Townsend 2008). The lack of additional decline of *K. latifolia* from 2009 to 2015 may be related to the three major canopy disturbances in 2011–2012 that created gaps in the canopy; however, we did not detect any relationship between change in *K. latifolia* abundance and change in canopy tree density.

We also observed a moderate increase in total abundance of forbs (including *M. canadense*) and graminoids (mostly *Carex* spp.) in the *Quercus* forest. Reduced competition and increased ground-level light from the declining shrub layer may have aided specific herbs (*e.g.*, Baker and Van Lear 1998). Long-term increases in the abundance of *M. canadense* have been noted in other regions despite this herb's palatability to deer (Frerker *et al.* 2014).

Conclusions. The explosive growth of several invasive species in this long-term study reveal how rapidly novel ecosystems are developing in landscapes of the northeastern United States that occur within areas of high human population and activities (Hobbs *et al.* 2014, Oswalt *et al.* 2014). At the same time, the lack of change or increase in abundance of native shrub and herb life forms growing alongside these invasive species underscores the difficulties of generalizing about invasive species impacts on native floras. Additionally, the dramatic decline of *A. petiolata* over the 11-year study is largely undocumented in unmanaged forests of the Northeastern US. Given that *A. petiolata* was recently reported to have few, if any, limitations in achieving dominance in the understories of eastern forests (Rodgers *et al.*

2008), this result suggests the species may be more vulnerable to environmental constraints and less persistent over time than previously believed (*e.g.*, Merow *et al.* 2017).

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Nonnative vegetation dynamics in the understory of a fragmented temperate forest¹

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