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Research Article

Using Invasional Meltdown Theory to Understand Patterns of Invasive Richness and Abundance in Forests of the Northeastern USA

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ABSTRACT

Invasional meltdown hypothesizes that invasive species facilitate the establishment of subsequent invaders, with cascading consequences for ecosystem structure and function, including the extirpation of native species. However, meltdown has rarely been tested empirically with large regional data sets, leading to somewhat equivocal support. Recently, the USDA Forest Service initiated sampling of nonnative plants within a subset of their Forest Inventory and Analysis (FIA) plots, presenting an ideal dataset to evaluate meltdown and its consequences across large geographies. We used FIA data from 963 plots across 11 northeastern states to test the predictions of invasional meltdown and to examine the mechanism through which invasion impacts native tree seedling richness. Remeasured plots showed a significant increase in the number and cover of invasive species over time. We provide support for invasional meltdown, finding a pattern of accelerating invasive species richness over 4–5 y in plots with higher initial invasive species richness. Also, we found that plots with higher levels of invasive abundance corresponded to decreased native tree species richness at one point in time and that the magnitude of the relationship appeared to be stronger after 4–5 y. Our results suggest that evidence of invasional meltdown is more clearly evident when examining invasive plant species richness over time; further, invader abundance (measured as cover) is a better predictor of impacts than invader richness, which supports growing evidence that invasive abundance is an important driver of ecological impact.

Index terms: biological invasions; FIA data; forest ecology; invasive species; native plant decline; nonnative plants

INTRODUCTION

In 1999, Simberloff and Von Holle called upon ecologists researching biological invasions to focus on facilitation among invasive species as a mechanism for successful establishment of multiple nonindigenous species at the expense of native biota. The authors developed the concept of invasional meltdown, which they defined as "the process by which a group of nonindigenous species facilitate one another's invasion in various ways, increasing the likelihood of survival and/or ecological impact, and possibly the magnitude of impact" (Simberloff and Von Holle 1999). What followed was a shift in the way ecologists thought about biological invasions, and a change in the methods used to quantify species interactions during the establishment of other nonnative invasive species. Researchers began to identify and document invasional meltdown across a wide variety of ecosystems including lacustrine (Ricciardi 2001), coastal (Grosholz 2005), and oceanic island (O'Dowd et al. 2003) communities. Although Shea and Chesson (2002) suggested that invasional meltdown may be more applicable to plants than animals because plants are sessile and therefore unable to escape environmental conditions modified by invasive species, researchers continued to identify examples of invasional meltdown in mammals, birds, insects, fungi, and fish (Ricciardi 2001; Blackburn et al. 2005; Heimpel et al. 2010). The enthusiastic reception of the concept caused Simberloff (2006) to publish a follow-up piece reemphasizing that there were two components to invasional meltdown: (1) invasive species beget invasive species, and (2) a population-level acceleration in the number of invasive species causes negative impacts on native species.

As research on invasional meltdown nears two decades, support for the concept remains strong, with 77% of studies providing empirical support for the hypothesis across a wide variety of ecosystems and taxa (Jeschke et al. 2012). One challenge with providing empirical evidence of invasional meltdown is that the hypothesis involves quantifying the interactions among multiple species. However, a majority of studies have examined a single invasive species and its impacts within a single ecosystem (Kuebbing et al. 2013). Studies involving multiple invasive species have found negative, neutral, and positive interactions in how invasive species interact with other invasive species (Kuebbing and Nuñez 2015). In a neutral response, each invasive species maintains the same level of impact on native species and the environment regardless of whether the invasive species establish individually or concurrently (Tekiela and Barney 2017). In a negative impact, when one invasive species successfully establishes and then a second one invades, there was no additional impact on the native ecosystem because the invasion of the first species negated the other's impact (Cushman and Gaffney 2010). In a positive impact, two or more invasive species establish concurrently and their impact on native species and the environment is synergistic or more than additive (Rivett et al. 2018). According to the invasional meltdown hypothesis, the facilitation among invasive species should trigger acceleration in the rate of increase of invasive species richness. Differentiating among positive, neutral, or negative interactions is important in refining the invasional meltdown hypothesis and invasive impacts.

Concurrent with the large volume of work on invasional meltdown is extensive literature on the impact of single invasive species in communities. Studies that experimentally manipulate abundance of a wide variety of invasives including vertebrates, invertebrates, forbs (Stinson et al. 2007), shrubs (Peebles-Spencer et al. 2017), and grasses (Flory and Clay 2010), suggest that invasives impacts are driven by mechanisms associated with the abundance of the invasive. In these studies, invasive abundance was identified as causing changes in native species despite other drivers such as apparent competition or disturbance that may be occurring at these sites. When invasive species become very abundant they have more impact on native species through their alteration of ecosystem properties and functions (Ehrenfeld 2010; Gaertner et al. 2014). At low abundances, invasive species may effect no discernable impact on native species (Bradley et al. 2019). A majority of single–invasive species studies were conducted over relatively small spatial extents and over short time periods (Stricker et al. 2015). Whether the same mechanisms also operate across large spatial extents is largely untested. Also understudied is directly comparing how invasive species richness and invasive species abundance directly impact native species; thus, evaluating the premise of invasional meltdown and the findings of many single-invasive studies together. Understanding large-scale patterns of multiple invasive species would elucidate its relative importance as a driver on native species dynamics.

In this study, we employ native tree seedling and invasive plant species data collected by the USDA Forest Service's Forest Inventory and Analysis program to examine invasional meltdown in eastern deciduous forests. Specifically, we examined (1) whether sites with higher numbers of invasive species experienced higher increases in invasive species richness over time (invasives beget invasives), (2) whether areas with higher invasive species richness experienced a greater decline in native tree seedling richness over time (level of invasion predicts level of impact), and (3) whether invasive species richness or abundance, measured as cover, was a better predictor of impact on native tree seedling richness. As the world becomes increasingly invaded by exotic species, elucidating these interactions will be important in management and conservation decisions.

METHODS

Data Source

The USDA Forest Service's Forest Inventory and Analysis (FIA) Program monitors the forest resources of the United States to accurately measure the extent of existing forest land and timber resources and predict future growth of forests. Sampling teams conduct continuous vegetation inventories on permanent plots located on public and private land with a stratified grid of one plot occurring within every 4428 ha. As part of the sampling procedures for FIA's Phase 2, a subset of plots was included for sampling of invasive plants. Sampling for invasive species was limited to forested FIA plots. The USDA Forest Service Northern Research Station identified 40 vascular, nonnative plants to be included in FIA invasive species surveys in the northeastern region of the United States (Table 1). In FIA plots where invasive species were sampled, invasive species were identified and their associated percent cover was estimated to the closest percent cover within four subplots totaling 0.07 ha (USDA Forest Service 2018). For this study, we limited our data set to the period from 2007 to 2014, completely forested plots, and the geographic region to 11 contiguous northeastern states because sampling protocols over this time and geographic region were uniform for invasive species monitoring. Thus, the subset of FIA data we evaluated included 963 FIA plots, where invasive species had been identified within the subplots (42 in Connecticut, 30 in Delaware, 39 in Massachusetts, 56 in Maryland, 71 in Maine, 16 in New Hampshire, 32 in New Jersey, 271 in New York, 361 in Pennsylvania, 13 in Rhode Island, and 32 in Vermont). Of these 963 plots, 119 plots were sampled twice and this allowed a comparison of invasive species richness and percent cover across two time periods (spaced 4 or 5 y apart).

The FIA plots also included tree seedling data, which were sampled in 0.0013 ha microplots located within each of the four subplots. Tree seedlings were recorded in two categories depending on sampling protocols: (1) Regeneration, sampled from 2007 to 2014, was defined as tree species seedlings as least 15.2 cm tall for conifers and 30.5 cm tall for angiosperms and less than 2.5 cm in diameter at breast height (1.4 m above the root collar), and (2) Advanced Tree Seedling Regeneration (ATSR), sampled on plots from 2012 to 2014, was defined as hardwood or conifer tree seedlings that were at least 5.1 cm tall and less than 2.5 cm in diameter at breast height. Regeneration was sampled on 917 of the 963 plots for which we had invasive species records and within this dataset, 453 of these plots were sampled two times during this time period (spaced 4 or 5 y apart); this allowed us to examine how both tree seedling richness and invasive species abundance and richness changed over time. Of the 963 plots with invasive species data, a subset of 353 had ATSR data, none of which had been sampled more than once. For both datasets, we summed the total number of unique tree seedling species across the four microplots for total tree seedling richness per plot.

Data Analysis

Characterization of Invasive Species: Invasive plant richness was identified for each FIA plot by summing the number of unique invasive species recorded across the four subplots. Plot-level invasive species cover was calculated as the mean total cover across the four subplots. Spearman rank correlation and Pearson's correlation coefficients were used to quantify the strength of linear or nonlinear relationship between invasive species richness and percent cover of invasive species with data from 963 FIA plots.

Table 1.—Invasive species and their abundances in 963 FIA plots in 11 northeastern states.

Scientific name	Common name	Growth habit	*N* of plots	Percent cover Mean (St Dev)
Rosa multiflora	multiflora rose	SHRUB	543	20.8 (38.0)
Berberis thunbergii	Japanese barberry	SHRUB	245	12.9 (27.4)
Alliaria petiolata	garlic mustard	HERB	241	27.3 (42.4)
Lonicera morrowii	Morrow's honeysuckle	SHRUB	228	20.9 (34.1
Microstegium vimineum	Japanese stiltgrass	GRASS	159	26.9 (39.6)
Celastrus orbiculatus	Oriental bittersweet	VINE	132	23.7 (47.0)
Rhamnus cathartica	common buckthorn	SHRUB	127	28.6 (51.7)
Robinia pseudoacacia	black locust	TREE	123	23.1 (29.4)
Lonicera tatarica	Tatarian honeysuckle	SHRUB	116	18.5 (37.6)
Lonicera japonica	Japanese honeysuckle	VINE	113	28.8 (41.1)
Elaeagnus umbellata	autumn olive	SHRUB	104	22.1 (41.8)
Frangula alnus	glossy buckthorn	SHRUB	67	26.0 (52.5)
Ligustrum vulgare	European privet	SHRUB	61	13.3 (31.7)
Phalaris arundinacea	reed canary grass	GRASS	59	16.8 (31.4)
Ailanthus altissima	tree of heaven	TREE	53	21.4 (29.7)
Lonicera maackii	Amur honeysuckle	SHRUB	44	24.3 (37.9)
Lysimachia nummularia	creeping jenny	HERB	44	26.4 (37.6)
Acer platanoides	Norway maple	TREE	40	23.4 (36.5)
Cirsium vulgare	bull thistle	HERB	29	1.8 (1.7)
Berberis vulgaris	common barberry	SHRUB	23	4.3 (2.9)
Cirsium arvense	Canada thistle	HERB	23	2.1 (1.3
Lonicera × *bella*	showy fly honeysuckle	SHRUB	19	17.4 (23.7)
Phragmites australis	common reed	GRASS	16	77.5 (113.9)
Polygonum sachalinense	giant knotweed	HERB	16	16.2 (33.8)
Hesperis matronalis	dames rocket	HERB	15	7.1 (7.1)
Lonicera spp.	nonnative bush honeysuckles	SHRUB	11	24.1 (31.6)
Centaurea stoebe	spotted knapweed	HERB	5	39.8 (54.0)
Hedera helix	English ivy	VINE	5	5.8 (9.1)
Paulownia tomentosa	princesstree	TREE	5	32.2 (30.9)
Elaeagnus angustifolia	Russian olive	TREE	4	5.3 (7.8)
Lythrum salicaria	purple loosestrife	HERB	3	1.3 (0.6)
Cynanchum louiseae	Louis' swallow-wort	HERB	2	2.5 (2.1)
Euphorbia esula	leafy spurge	HERB	2	9.5 (7.8)
Polygonum × *bohemicum*	Japanese/giant knotweed hybrid	HERB	2	35.5 (38.9)
Spiraea japonica	Japanese meadowsweet	SHRUB	2	1.5 (0.7)
Viburnum opulus	European cranberrybush	SHRUB	2	1.0 (0.0)
Cynanchum rossicum	European swallow-wort	HERB	1	4.0
Melia azedarach	Chinaberrytree	TREE	1	1.0
Polygonum cuspidatum	Japanese knotweed	HERB	1	6.0
Ulmus pumila	Siberian elm	TREE	1	1.0

Invasives Beget Invasives: We tested whether invasive species richness and/or cover had changed over time, using paired *t*-tests for the plots that were measured twice, during 2007–2009 and again during 2011–2014 inventory periods ($N = 119$). To evaluate whether sites with higher initial levels of invasive species (richness or cover) experienced greater increases in invasion between sampling periods, we used Poisson regression when invasive species richness was the response variable. When invasive percent cover was the response we fitted a nonlinear regression model $Y = aX^b$ with Y denoting invasive percent cover 2011–2014 and X denoting invasive percent cover 2007–2009. The nonlinear modeling approach was chosen instead of a log–log transformed linear regression to avoid potential problems with transformation bias (Clifford et al. 2013). A chi-square test for overdispersion was used to test whether a quasi-Poisson regression was needed in place of Poisson regression. Zero inflation was not a problem in Poisson regression since all plots included at least one invasive plant species. Moran's I was tested for nonzero values to indicate whether a generalized linear or nonlinear mixed modeling approach was needed to account for spatial autocorrelation in model residuals.

Level of Invasion Predicts Level of Impact: To evaluate the impact of invasive species on native tree seedlings we used a paired *t*-test across the two sampling periods for native tree seedling richness (453 plots). Further, we examined if there were differences in the relationships between invasive percent cover in 2007–2009 and tree seedling richness in either the same time (2007–2009) or 4–5 y later (2011–2014). We did this using a generalized linear mixed modeling (GLMM) approach to account for spatial autocorrelation in Poisson regression involving $Y =$ Tree seedling richness 2007–2009 and $X =$ Invasive percent cover 2007–2009. Since the GLMM algorithm in R package *glmmTMB* (Brooks et al. 2017) failed to converge on model parameters for the full data set ($n = 289$), a slightly reduced-size data set ($n = 275$) of randomly selected observations was used in place of the full data set. For comparison of

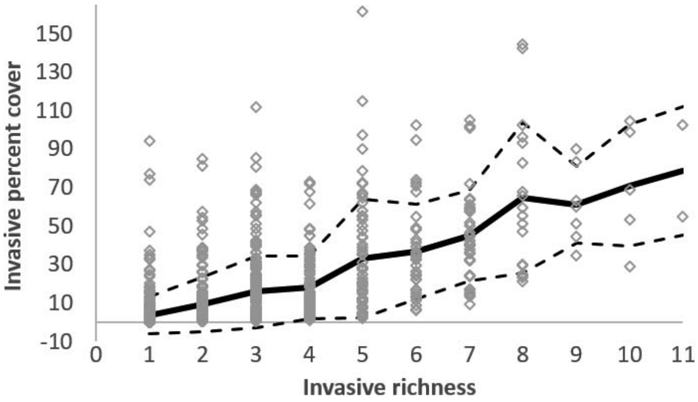

Figure 1.—Correlation between invasive species richness and invasive percent cover (Spearman's $r = 0.738$ and Pearson's $r = 0.636$, $P < 0.001$ on both; $N = 963$ plots). Mean cover at each level of richness (black line) increases as does standard deviation (dashed line).

parameter estimates and statistical significance the full data set was used to fit Y vs. X by quasi-Poisson regression in a generalized linear model (GLM) without accounting for spatial autocorrelation. The quasi-Poisson approach was chosen over Poisson regression in the GLM based on results of a chi-square test for overdispersion.

Predicting Invasional Meltdown: Richness vs. Cover: To evaluate whether invasive species richness or cover was a better predictor of impact on native species richness, we used least squares regression using both the Regeneration dataset (917 plots) and the ATSR dataset (353 plots). In both cases, tree seedling richness was natural log transformed to improve the fit of the model. We analyzed the data with two different approaches: (1) all invasive species were combined into variables for total invasive cover or total invasive richness, and (2) invasive species were separated into life form categories (shrubs, grasses, herbs, trees, or vines) and invasive species richness and cover were evaluated as separate variables by life form.

We used JMP Pro 11 (SAS Institute, Inc., Cary, North Carolina, USA) and R (R Core Team 2018) on all analyses.

RESULTS

Characterization of Invasive Species

All 40 possible invasive species identified by the USDA Forest Service Northern Research Station were found within the 963 FIA plots in this study (Table 1). Across all plots, mean invasive species cover was 15% (± 22% standard deviation, range 0.25–161.5%) and mean invasive richness was 2.79 (± 2.00 standard deviation, range 1–11 species). The most common invasive species were multiflora rose (*Rosa multiflora*, occurred in 543 plots), Japanese barberry (*Berberis thunbergii*, 245 plots), garlic mustard (*Alliaria petiolata*, 241 plots), and Japanese stiltgrass (*Microstegium vimineum*, 159 plots). Shrub honeysuckle (*Lonicera* spp.) was not always classified into separate species groups; therefore, we combined all *Lonicera* into a single category, which made this a very common (388 plots) and abundant invasive plant (6% cover ± 9% standard deviation). Invasive plant cover was moderately and positively correlated with invasive species richness (Spearman $r = 0.738$, $P < 0.001$; Pearson's $r = 0.636$, $P < 0.001$; 963 plots; Figure 1). Invasive cover varied less at low levels than at higher levels of invasive richness. Attempts to account for the nonlinear trend and increasing variance of the relationship (e.g., logarithmic transformation, Poisson or negative binomial regression) were ineffective in satisfying the assumptions of regression analysis, so those results are not shown.

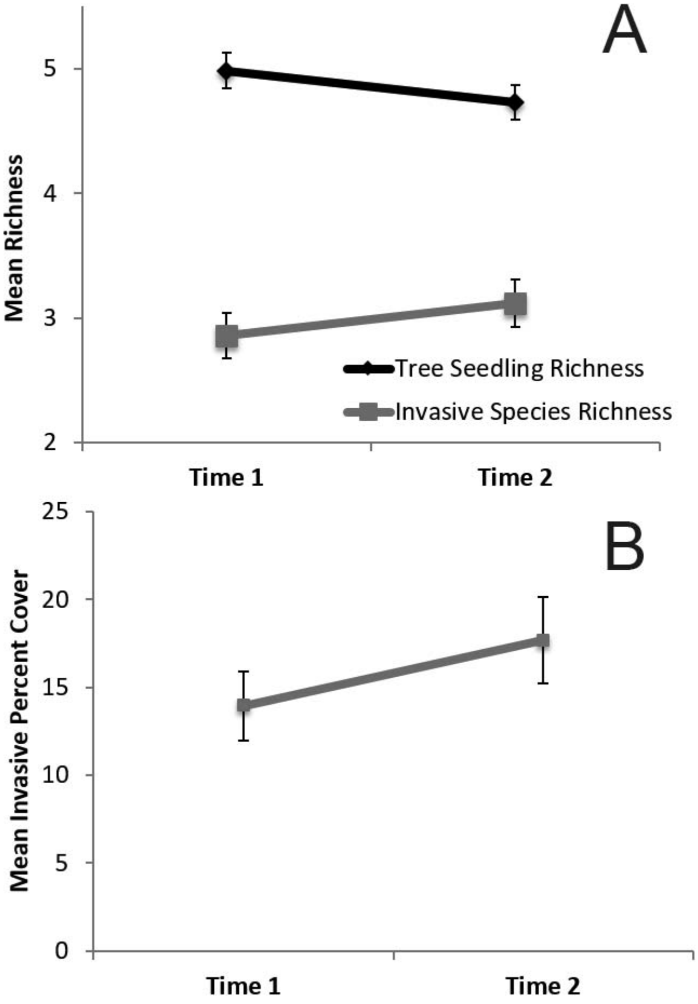

Figure 2.—Mean (± SE) change in richness of tree seedlings and invasive species (A) and invasive percent cover (B) over a 4–5 y remeasurement interval. Invasive species richness and percent cover significantly increased (paired *t*-tests: for richness $\delta = 0.26$, $t = 2.08$, $P = 0.040$, df = 118 and for percent cover $\delta = 3.74$, $t = 2.31$, $P = 0.023$, df = 118). Tree seedling richness significantly decreased by about one-fourth of one species (paired *t*-test: $\delta = -0.26$, $t = -2.66$, $P = 0.008$, df = 452). Only plots measured twice were used, with time 1 measurements made from 2007–2009 and time 2 measurements from 2011–2014.

Invasives Beget Invasives

The remeasurement of FIA plots allowed us to characterize vegetation change over time. Both invasive species richness (paired *t*-test: $t = 2.08$, $P = 0.040$, df = 118; Figure 2A) and invasive species cover (paired *t*-test: $t = 2.31$, $P = 0.023$, df = 118; Figure 2B) significantly increased over the sampling period. The mean change over time (δ) in invasive species richness was $\delta =$

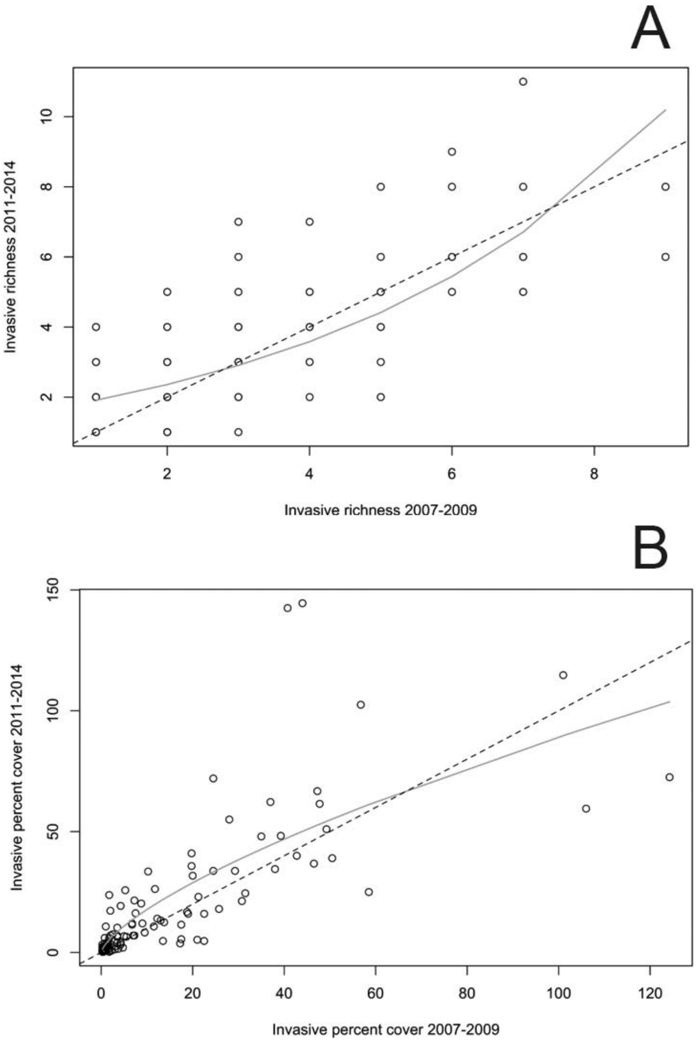

Figure 3.—Effect of invasive richness in 2007–2009 on invasive richness 2011–2014 (A) and effect of invasive percent cover in 2007–2009 on invasive percent cover 2011–2014 (B). Invasive species richness increases accelerated at higher initial invasive species richness (A: Poisson regression ($Y = 1.55 \times 1.233^X$), $Y =$ plots sampled in 2011–2014, $X =$ plots sampled in 2007–2009). Invasive percent cover also increase in plots with higher initial invasive percent cover but with a decelerating pattern (B: Nonlinear regression ($Y = 3.53X^{0.701}$), $Y =$ plots sampled in 2011–2014, $X =$ plots sampled in 2007–2009). Solid line is regression and dotted line is the 1:1 line for comparison.

0.26, which represents an increase of about ¼ additional invasive species observed per plot on FIA plots over the 4–5 y sampling period. The mean increase in invasive percent cover was $\delta = 3.74\%$.

Increases in invasive species richness between measurements were largest at sites with the highest initial invasive species richness (Figure 3A). Poisson regression for $X =$ Invasive Richness 2007–2009 and $Y =$ Invasive Richness 2011–2014 showed no evidence ($P > 0.99$) of overdispersion based on χ^2 (residual deviance = 68.7, df = 117). An observed Moran's $I = -0.027$ showed no evidence of spatial autocorrelation in model residuals ($P = 0.19$). The resulting Poisson regression had an estimated slope coefficient of 1.233 and 95% confidence interval [1.18, 1.28], characteristic of an accelerating rate of increase in Y with X and indicative of invasional meltdown over the range of species richness observed in FIA field plots.

In a somewhat contrasting pattern, the nonlinear trend in $Y =$ invasive percent cover observed in 2011–2014 over $X =$ initial invasive percent cover in 2007–2009 showed an increasing pattern but without the same positive acceleration noted in invasive species richness (Figure 3B). The exponent on X in the nonlinear regression was estimated as 0.70 with 95% confidence interval [0.58, 0.83], i.e., a value <1 as would be expected in a relationship exhibiting saturation.

Level of Invasion Predicts Level of Impact

Native tree seedling richness decreased from 4.98 to 4.72, an average of about –0.26 (paired *t*-test: $t = -2.66$, $P = 0.008$, df = 452; Figure 2A) across the two sampling periods at the same time that invasive species richness and cover increased (Figure 2). Evidence of a nonzero Moran's I as a test for spatial autocorrelation was somewhat weak ($P = 0.055$) and regression results did not support the accounting for spatial autocorrelation in the full data set of $n = 289$ plots where both invasive plants and native tree seedlings were measured at the initial inventory period 2007–2009. Nonetheless, regression results were consistent in both GLMM Poisson and GLM quasi-Poisson models, with slope coefficients on $X =$ Invasive percent cover estimated as –0.00568 and –0.00537, respectively, for the response variable $Y =$ tree seedling richness 2007–2009 (Figure 4A). These coefficient estimates corresponded to decreases of either 41.5% or 43.3% in tree seedling species richness as invasive plant cover increases from zero to 100% in FIA plots across the northeastern United States. Using the quasi-Poisson model fitted to all plots ($N = 289$) to illustrate the magnitude of decrease, the model predicted mean tree seedling richness of 5.2 species at 0% invasive cover decreased to less than 3.1 species at 100% cover (quasi-Poisson regression coefficients $b_0 = 1.651$, $b_1 = -0.005365$, $P < 0.01$; Figure 4A).

Tree seedling species richness observed on the same vegetation plots revisited between 2011 and 2014 showed a steeper decrease with initial invasive percent cover (Figure 4B). Here, tree seedling richness decreased 58% as invasive plant cover increased from zero to 100%, from a predicted mean of 4.45 tree seedling species at 0% invasive cover to 1.87 tree seedling species per plot at 100% invasive cover (GLMM Poisson regression, $b_o = 1.494$, $b_1 = -0.0087$, $P < 0.001$; Figure 4B).

Predicting Invasional Meltdown: Richness vs. Cover

In both the Regeneration dataset and the ATSR dataset, native tree seedling richness declined as a function of invasive species cover, but not richness (Table 2). The pattern of invasive species cover being a better predictor of native tree seedling richness than invasive species richness also carried through to the life form analysis for shrubs, grasses, and forbs in the Regeneration data set and for shrubs in the ATSR dataset (Table 2).

DISCUSSION

Using FIA data to test predictions of invasional meltdown and impact of invasive abundance is a powerful tool, but has

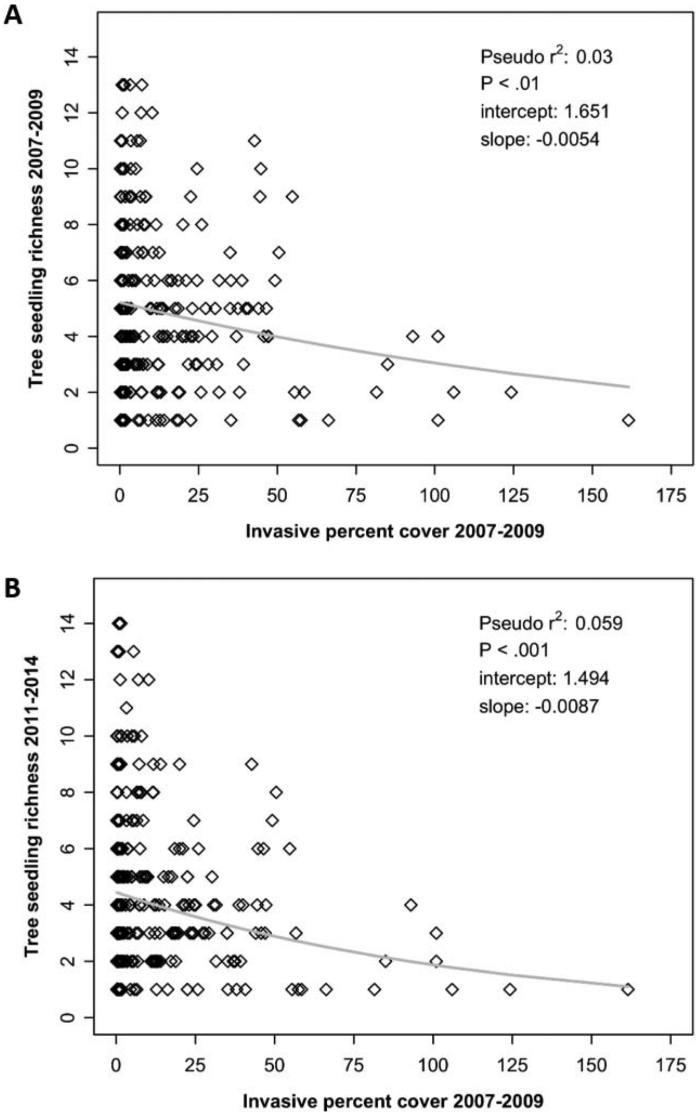

Figure 4.—Tree seedling richness in 2007–2009 (A) and in 2011–2014 (B) as a function of invasive percent cover 2007–2009. Invasive species cover in 2007–2009 was more strongly and negatively correlated with tree seedling richness in 2011–2014 than in 2007–2009 (Poisson regression: pseudo $r^2 = 0.029$, $P < 0.01$ and pseudo $r^2 = 0.059$, $P < 0.001$, respectively; $N = 289$ plots for both).

limitations. Large-scale observational studies can reveal whether patterns identified in small-scale experiments are present across broader spatial scales (Stricker et al. 2015). FIA data represent arguably the largest dataset employing consistent methods with repeat measures of the same plots across private and public lands in the United States, and they can be used to investigate and test hypotheses related to emergent patterns of invasive species richness, abundance, and impacts (Oswalt et al. 2015). One limitation of FIA data sets is that they may underestimate invasive impact because only nonnatives that were judged to have significant ecological or economic impacts were recorded (Riitters et al. 2018). Another limitation is that patterns reported in this study represent sites across substantial gradients in productivity, climate, disturbance, and white-tailed deer (*Odocoileus virginianus*) herbivory. Thus, this study cannot stand alone to identify driving mechanisms of tree seedling richness. Greatly debated in the literature is whether invasive species are a driver, passenger, or backseat driver of native species dynamics (Bauer 2012). Nonetheless, invasive species abundance has been shown to directly reduce native species richness (Bradley et al. 2019) even if it is unclear whether invasive abundance was the proximate or ultimate cause (Didham et al. 2005).

Eastern deciduous forests are complex ecosystems with high biodiversity, many life forms, substantial structural diversity, and a wide variety of invasive species. As such, they are important ecosystems to evaluate the invasional meltdown hypothesis. The USDA Forest Service's FIA data provided a unique opportunity to test the prediction that invasion begets invasion, followed by a subsequent and proportional increase in ecological impact (e.g., a decrease in native species). We also identified the importance of cover as a predictor of invasive impacts, supporting observations of other researchers (Ehrenfeld 2010).

The founding tenet of invasional meltdown is that invasives beget invasives (Simberloff and Von Holle 1999). Overall, the results observed here illustrated this tenet for forested lands in the U.S. Northeast. Plots with higher invasive richness gained disproportionally more invasive species over time. Invasive cover, on the other hand, appears to be reaching a saturation point in these FIA data (Figure 3), likely due to resource competition (Levine et al 2003). Globally, invasive richness does not appear to have reached a saturation point in the establishment of invasive species across continents (Seebens et al. 2017), whereas global patterns of invasive percent cover are less well studied. It is unclear whether invasive species richness has reached a saturation point in these FIA data. The statistical model developed here does show an accelerating pattern of invasive richness over the range of data observed, but extrapolation beyond roughly 8–10 invasive plant species in a 0.07 ha field plot is outside of the scope of the data at present (Figure 3A).

Shrubs were the most common life form for invasive species with *R. multiflora*, *B. thunbergii*, and *Lonicera* spp. especially prevalent. In the case of *R. multiflora*, the invasive shrub is able to tolerate a wider range in soil fertility than native shrubs (Huebner et al. 2014) and therefore its frequency across the landscape reflects its ability to grow in a wider range of environmental conditions. *Berberis thunbergii* reduces the density of native tree seedlings by shading the understory (Link et al. 2018) and *Lonicera maackii* (Amur honeysuckle) retains its leaves longer during the growing season than native shrubs, affording a competitive advantage (Caplan et al. 2018). The mechanisms facilitating invasion meltdown are unclear, but may result from a combination of invasive plant niche complementarity, advantageous edaphic and soil microbial changes (Levine et al. 2006; Gaertner et al. 2014), and plant–animal interactions (Clause et al. 2015). Elucidating the mechanisms and processes facilitating meltdown, and the subsequent community saturation, remain important objectives for the future.

A second important tenet of invasional meltdown is that higher invasive richness results in higher levels of impact

Table 2.—Least square regression with LN tree seedling richness for the ATSR data set ($N = 343$ plots) and the Regeneration data set ($N = 917$ plots) as the response variables and independent variables of invasive richness and percent cover in the whole community (a) and for each life form separately (b–f). Invasive species richness was never a significant predictor of tree seedling richness. For the specific life form regressions, plots with zeros were removed reducing the sample size.

	Advance Tree Seedling Regeneration				Regeneration			
Independent variables	*P*	Partial coefficients	R^2	*N*	*P*	Partial coefficients	R^2	*N*
(a)								
Intercept	<0.001	1.939	0.12	353	<0.001	1.404	0.06	917
Total invasive richness	0.168	−0.03			0.473	−0.011		
Total invasive % cover	**<0.001**	−0.01			**<0.001**	−0.008		
(b)								
Intercept	<0.001	1.789	0.13	295	<0.001	1.259	0.03	763
Invasive shrub richness	0.074	0.065			0.1831	0.042		
Invasive shrub % cover	**<0.001**	−0.015			**<0.001**	−0.008		
(c)								
Intercept	n.s		0.03	86	<0.001	1.498	0.06	213
Invasive grass richness					0.103	−0.152		
Invasive grass % cover					**0.007**	−0.016		
(d)								
Intercept	n.s.		0.01	137	<0.001	1.211	0.05	305
Invasive herb richness					0.710	0.020		
Invasive herb % cover					**<0.001**	−0.016		
(e)								
Intercept	n.s		0.04	78	n.s		0.02	179
Invasive tree richness								
Invasive tree % cover								
(f)								
Intercept	n.s.		0.02	72	n.s.		0.02	193
Invasive vine richness								
Invasive vine % cover								

(Simberloff and Von Holle 1999). We found invasive species cover served well as an explanatory variable in characterizing the impact of invasion on native tree seedling richness. When examining the pattern of tree seedling richness over a wide range of invasive abundance, we found that in plots where invasive species cover was near 100% there were an average of two fewer native tree seedlings species observed than where invasive cover was 0%. An even higher impact (58% decrease compared to 41%) was observed examining tree seedling richness after 4 or 5 y given the same range of initial invasive plant cover.

In other ecosystems, abundance, measured either as invasive species cover or number of individuals, appears to be more important as a measure of impact on native species than invasive species richness (Jackson et al. 2014; Tekiela and Barney 2017). This suggests that invasive species identity matters less than their total abundance. This has important implications for how invasive species are managed, which to date has largely been single species–focused (Kuebbing et al. 2013). Given that management to remove one invasive species is nearly always followed by reinvasion (Pearson et al. 2016), perhaps conservation goals focused on reducing overall invasive plant abundance would be more successful.

As humans continue to homogenize the world's biota, and climate change reshuffles communities, we urgently need to understand the forces shaping communities. Invasive species facilitation of invasion, or meltdown, may serve as an accelerant of ecological change and the deterioration of native diversity. We found evidence of meltdown in northeastern forests in that invasives beget invasives, and we found support for further examination of invasive species cover as a driver of ecological impact. Our results provide important evidence that strongly supports early detection and rapid response to nascent invasion (Bradley et al. 2019), as well as managing invasive plant abundance to limit their impact after establishment.

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