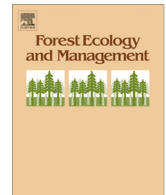




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## Effects of co-occurring non-native invasive plant species on old-field succession

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## ABSTRACT

Old fields are diverse forb-dominated ecosystems transitioning into woody-dominated forested ecosystems. However, the susceptibility of old fields to high levels of plant invasion can lead to the co-occurrence of multiple non-native invasive plant species at the fine-scale of plant neighborhoods, which can alter native species co-occurrence patterns and successional trajectories into forest communities. Community disassembly by invasive species occurs when the presence of one or more invaders shifts co-occurrence patterns of native species from structured to random. Disassembly can imply a loss of existing co-evolved interactions among native species, which has ramifications for community dynamics and trajectories of invaded ecosystems. Here, we quantify relationships among multiple invasive plant species and two indicators of community succession in old-field plant communities in East Tennessee: co-occurrence patterns of native and non-native species and successional trajectories. First, we examine how biotic and abiotic factors shape the abundance of invasive species, as well as native and invasive functional groups across old fields. Second, we ask whether invasive species influence co-occurrence patterns among native species and whether invasive species are associated with altered herbaceous:woody foliar cover ratios. We found that biotic and abiotic predictors associated with invasive species were not consistent in identity or direction of association, indicating that predicting which sites or suite of biotic and abiotic variables are associated with invasive species will be challenging. Importantly, as the number of invasive plants increased in 1-m<sup>2</sup> plots, native species co-occurrence patterns shifted from structured to random, whereas invasive species co-occurrence patterns remained random irrespective of the number of invasive species. Plots containing three or more invaders had significant changes in native and invasive herbaceous:woody foliar cover ratios. The herbaceous:woody foliar cover ratio of native species was 4× lower and of invasive species was 2× greater compared to plots with one or two invaders, and this shift was in part explained by an increase in foliar cover of non-native woody species. Our data suggest that increased number of invasive species in old fields alters both native species interactions and the trajectories of old-field communities, which could influence the developing understory community as old fields transition into forests. We recommend that management of fields during succession should focus on decreasing the total number of invasive species to restore species co-occurrence patterns and prevent altered successional trajectories, including accelerated succession of non-native woody species.

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## 1. Introduction

Old-field communities are successional ecosystems in transition from herbaceous-dominated abandoned agricultural land into woody-dominated forests. In the eastern United States,

approximately one-third of pre-European settlement forests were cleared for cultivation (Smith et al., 2003) and approximately 50 million acres of once forested agricultural lands have been abandoned and are reverting back to forest (Cramer et al., 2008; Hobbs and Cramer, 2007). Agricultural abandonment creates local- and landscape-scale legacies, which include the creation of post-agricultural soil conditions that can select for a different suite of understory species (Dupouey et al., 2002; Koerner et al., 1997; Motzkin et al., 1996; Verheyen et al., 1999) or a fragmented landscape that prevents dispersal of some forest herbs (Bellemare et al., 2002; Dyer, 2010; Matlack, 1994; Singleton et al., 2001). Additionally, old-field species, both native and non-native, that

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establish in post-agricultural areas can directly impact the understories of future forests. Old-field species may persist in forest understories after canopy closure (Bazzaz, 1968; Dyer, 2010; Motzkin et al., 1996) or they may interact with newly colonizing understory herbs to influence final understory forest composition (Endels et al., 2004). Understanding how these disturbance legacies might alter transitions from field to forest is important for predicting the understory plant composition of future forests (Flinn and Vellend, 2005).

Old-field ecosystems harbor many native and non-native species (Bazzaz, 1996; Fridley et al., 2007; Souza et al., 2011a). The legacy of cultivation—alteration of plant biomass, tillage, and fertilization—can decrease seeds of native species in the soil seed banks and lead to higher probability of invasion by non-native species (Cramer et al., 2008). Similarly, disturbances like periodic mowing in old-field ecosystems could influence the establishment and growth of non-native species (Davis et al., 2000; MacDougall and Turkington, 2005), but the effects of disturbance in old-field plant communities tend to be species specific (Averill et al., 2010; Brandon et al., 2004; Renne et al., 2006). In a survey of 250 1-m<sup>2</sup> quadrats across 17 old fields, Souza et al. (2011a) did not find a single plot without non-native species and 90% of surveyed plots had non-native invasive species. Of those plots containing non-native invasive plants, ~47% had two or more non-native invasive species. Because non-native, invasive plant species can modify community structure and composition across a wide variety of ecosystems (Vilà et al., 2011), it is also important to study them in the context of succession from old field to forest.

Non-native invasive species can directly affect native communities by altering species richness, evenness, or diversity in recipient communities (Vilà et al., 2011; Wardle et al., 2011). Some invasive species, however, might have more subtle effects on community structure, such as altering co-occurrence patterns among species, which may not necessarily coincide with short-term declines in richness, evenness, or diversity (Sanders et al., 2003). This change in species co-occurrence patterns is termed “community disassembly” and occurs when a non-native invasive species causes association patterns of native species to shift from non-random (i.e., segregated or aggregated) to random (Sanders et al., 2003). Disassembly has been documented in ant and plant communities, where highly segregated or aggregated communities lose their structure after the arrival of a non-native invasive species (Gotelli and Arnett, 2000; Sanders et al., 2003; Santoro et al., 2012).

The presence of one or more invasive species in old fields could influence co-occurrence patterns among native species and successional dynamics of old fields in two ways. First, if invasive plants are associated with disassembly of old-field native plant species, this could suggest an alteration of interspecific interactions among native species (Sanders et al., 2003). Plant community organization can be strongly influenced by interspecific interactions (Brooker et al., 2008; Callaway and Walker, 1997; Freckleton et al., 2009; Goldberg and Barton, 1992), particularly during old-field succession (Connell and Slatyer, 1977; Fortner and Weltzin, 2007; Huston and Smith, 1987; Jensen et al., 2012; Li and Wilson, 1998). The alteration of interactions at early successional stages could lead to unpredictable paths of forest succession or, alternatively, to an ecosystem where succession is arrested and dominated by non-native grasses or shrubs (Cramer et al., 2008; Tognetti et al., 2010). Additionally, if a particular invasive species occurs in both old-field and forest ecosystems (Belote et al., 2003; Cole and Weltzin, 2005; Souza et al., 2010) and if these species persist in secondary forest understories they could negatively affect colonization by forest herbs (McLane et al., 2012; Meiners, 2007; Myster and Pickett, 1992). Second, old field to forest succession can be measured as the change in woody:herbaceous ratios through time (i.e., increasing proportion of woody plants as old fields age; Wright and Fridley,

2010). If the presence of invasive plants is associated with differences in herbaceous:woody cover ratios, this could indicate that invaders might alter the rate at which fields transition to forests.

Though the impacts of individual invaders in old-field ecosystems have been intensively studied (Brandon et al., 2004; Dickson et al., 2010; Emery and Gross, 2006; Knapp, 1996), studies on the effects of multiple invasive species on the co-occurrence patterns of old-field species are less common (Powell et al., 2013). Here, we use a multifaceted approach to explore how invasive species might affect the trajectories of old-field communities as they transition into forests. First, we examine the patterns of occurrence of invasive plants in old-field ecosystems by asking (1) What abiotic and biotic factors shape the abundance of non-native invasive species and invasive and native functional groups? Predictive models, such as these, could assist managers in targeting areas that have a higher likelihood of invasion by multiple species. Next, to understand how nonnative invasive species affect assembly patterns and successional dynamics in old-field communities we address the following two questions: (2) How do multiple invasive species alter co-occurrence patterns of native and non-native invasive species? and (3) How do multiple invasive species alter successional trajectories (herbaceous:woody foliar cover ratios) in old fields?

## 2. Materials and methods

### 2.1. Study site and plant surveys

In the summer of 2006, we located 17 fields across the Three Bend Scenic and Wildlife Management Refuge, which is part of the Oak Ridge National Environmental Research Park near Oak Ridge, TN (35–58°N, 84–17°W). Old-field communities were agricultural fields until ca. 1943 following abandonment and are maintained by periodic mowing for early-successional wildlife species. Management regimes among fields varied in mowing frequency: monthly mowing, annual mowing, biannual mowing (half of the field in the spring and other half of the field in the fall), or biennial mowing. Soils at the sites are characterized as Typic Hapludult with a silty clay loam texture (Phillips et al., 2001). Mean monthly temperatures range from approximately 3 °C in the winter to 31 °C in the summer and mean annual rainfall is 1322 mm.

We chose fields based on the presence of well-defined boundaries such as forests or roads. Within each field, we randomly placed two to six 50-m transects (depending on field area, which ranged from ca. 2000 m<sup>2</sup> to 50,000 m<sup>2</sup>). We placed five 1-m<sup>2</sup> plots 10 m apart starting 10 m from the origin of each transect. In each 1-m<sup>2</sup> plot, we identified and estimated percent foliar cover of all native and non-native vascular plant species during the peak of the growing season. We estimated species-specific foliar cover using a modified Braun-Blanquet cover class scale (Braun-Blanquet, 1932). The modified Braun-Blanquet scale included six categories: 1 = <1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–100%.

For the purpose of our study, we considered a species to be non-native if humans transported it across fundamental geographic barriers (Richardson et al., 2011). We also distinguish between “naturalized” non-native species (hereinafter, non-native)—those that are remnants of old-field agricultural but do not spread far from the source of introduction—and “invasive” non-native species (hereinafter, invasive)—those that have spread far from their original source of introduction and therefore are considered rank one invasive species (for a full list of species see [Supplementary Information Table 1](#)). We consider this to be an important distinction because while non-native and native species tend to follow similar successional patterns from old field to forest (i.e., decrease in herbaceous cover and increase woody cover) invasive plants do

not (i.e., dominant during all stages of succession, regardless of functional characteristics; [McLane et al., 2012](#); [Meiners, 2007](#); [Tognetti et al., 2010](#)).

## 2.2. What abiotic and biotic factors shape the abundance of non-native invasive species and invasive and native functional groups?

To determine the relationships between abiotic and biotic factors associated with the abundance of each invasive plant species (*Allium vineale* L., *Cirsium vulgare* (Savi) Ten., *Coronilla varia* L., *Daucus carota* L., *Elaeagnus umbellata* Thunb., *Lespedeza cuneata* (Dum. Cours.) G. Don, *Lonicera japonica* Thunb., *Microstegium vimineum* (Trin.) A. Camus, *Senna obtusifolia* (L.) Irwin & Barneby, *Sorghum halepense* (L.) Pers., and *Verbascum thapsus* L.), as well as with the abundance of native and invasive functional groups (e.g., graminoids, nitrogen fixers, forbs, and woody plants) at the 1-m<sup>2</sup> plot level, we conducted variable selection procedures using all possible variable selection approach. All abiotic and biotic variables were measured at the 1-m<sup>2</sup> plot level (see [Souza et al. \(2011b\)](#) for more information). Prior to performing variable selection, we tested for multicollinearity among the biotic (non-native richness, native richness, non-native foliar cover, nitrogen-fixer biomass, total biomass) and abiotic (light availability – photosynthetically active radiation, soil moisture – percent volumetric water content, soil nitrogen – potential nitrogen mineralization, soil bulk density, soil texture – percent clay and sand, litter mass, mowing frequency) predictors by constructing a correlation matrix using Pearson's correlation coefficients. Predictor variables with significant correlation coefficients ( $-0.75 > r > 0.75$ ) were excluded from variable selection procedure ([Kumar et al., 2006](#)). We also tested for spatial autocorrelation of dependent variables, prior to variable selection, with Moran's I correlogram plots in SAM v4.0 software ([Rangel et al., 2010](#)). We accounted for spatial autocorrelation in variables by running spatial models. If spatial autocorrelation was detected, we performed variable selection procedure on the detrended response variables (i.e., residuals of multiple regression of dependent variables and X and Y coordinate predictor variables; [Borcard and Legendre, 2002](#); [Borcard et al., 2004](#)).

During variable selection, we generated several linear and multiple regression models to determine the best single or best combination of explanatory variables associated with each invasive plant species and native or invasive functional groups. To evaluate the best multiple regression model predicting the abundance of each invasive plant species, we used the Akaike Information Criterion adjusted for small sample size (AIC<sub>c</sub>; [Burnham and Anderson, 2004](#)). All regression analyses were performed using SAS 9.1.3 (SAS Institute, Inc., Cary, NC) from which we obtained partial regression coefficient (<sup>2</sup>), partial *P*-value for each contributing predictor variable, and full model *P* and *R*<sup>2</sup> values.

## 2.3. How do multiple invasive species alter co-occurrence patterns of native and non-native invasive species?

We used [Stone and Roberts \(1990\)](#) C-score index to examine patterns of co-occurrence for native and invasive species across 1-m<sup>2</sup> plots that varied in the number of invasive plant species present. We calculated C-scores as  $(R_i - S)(R_j - S)$ , where  $R_i$  is the number of occurrences for species  $i$ ,  $R_j$  is the number of species occurrences for species  $j$ , and  $S$  is the number of sample plots in which both species occur. To determine C-scores, we created 10 separate presence-absence submatrices from plant survey data (2 species categories [native (107 species) or invasive (11 species)] × 5 plot richness values [0 (25 plots), 1 (120 plots), 2 (82 plots), 3 (19 plots) or 4 (4 plots) invasive plant species]). Because C-score analyses on larger matrices have higher statistical power, we used ANCOVA models with matrix size (number of

species × number of plots) as a covariate to test whether number of invaders in a plot was still a significant factor in predicting co-occurrence patterns ([Gotelli and McCabe, 2002](#)).

To compare C-scores, we calculated the standardized effect size (SES) of each C-score by measuring the number of standard deviations the observed index is above or below the mean index of simulated communities. We calculated the SES as  $(I_o - I_s)/S_s$  where  $I_o$  is the index value of a given matrix and  $I_s$  is the mean index value and  $S_s$  the standard deviation of 5000 simulated communities. For each simulated “null” community, we randomly shuffled row and column values within a matrix but constrained null matrices to fixed column and fixed row totals ([Gotelli and McCabe, 2002](#)), which has low Type I error rates ([Gotelli, 2000](#)). When a C-score index is significantly higher than its null model index, then species pairs are co-occurring less frequently than expected (i.e., segregated), which could be a result of competition among species or subtle differences in habitat requirements. Alternatively, a significantly lower C-score value indicates that species pairs are co-occurring more frequently than expected by chance (i.e., aggregated), which could imply facilitative interactions or similarities in habitat requirements. Thus, when an invasive species causes communities to shift from nonrandom to random, the implication is that former interspecific interactions shaping that community no longer exist. For C-score analyses, we used EcoSim software v.7 ([Gotelli and Entsminger, 2011](#)).

## 2.4. How do multiple invasive species alter successional trajectories in old fields?

As old fields transition to young forests the ratio of herbaceous to woody cover shifts from herbaceous dominated to woody dominated ([Inouye et al., 1987](#); [Meiners et al., 2002](#)). We therefore compared the herbaceous:woody ratios of plots with varying levels of invasion to determine if the number of invasive plant species in 1-m<sup>2</sup> plots was associated with differences in successional trajectories. We calculated the herbaceous to woody plant cover ratios for total, native, and invasive species in 1-m<sup>2</sup> plots. We ran one-way analysis of variance (ANOVA) with number of invasive species as the main effect (fixed) and herbaceous:woody foliar cover as the response variable. To determine which invader treatment level influenced our response variables, we used Student's *T*-test at  $\alpha = 0.05$ . The one-way ANOVA and Student's *T*-tests were performed using JMP 10.0 (SAS Institute, Inc., Cary NC).

## 3. Results

### 3.1. What abiotic and biotic factors shape the abundance of non-native invasive species and invasive and native functional groups?

There were no consistent predictors (in number, identity, or direction of association) explaining the variation in the abundance of most old-field invasive species ([Table 1](#)). Model *R*<sup>2</sup> values ranged from very low predictive ability (*V. thapsus*,  $N = 250$ ,  $P = 0.04$ ,  $R^2 = 0.02$ ; [SI Table 2](#)) to a moderate predictive ability (*C. varia*,  $N = 250$ ,  $P < 0.0001$ ,  $R^2 = 0.44$ ; [SI Table 2](#)). For three of the eleven invaders, we were unable to find significant regression models (*D. carota*, *E. umbellata*, *S. obtusifolia*;  $P > 0.05$ ; [SI Table 2](#)). Two of the 11 invasive species, *L. japonica* and *M. vimineum*, are of potential concern to forest managers because they are common in both old fields and forests. Multiple regression models for both species had moderate explanatory power (*L. japonica*,  $N = 249$ ,  $P < 0.0001$ ,  $R^2 = 0.28$ ; *M. vimineum*,  $N = 250$ ,  $P < 0.0001$ ,  $R^2 = 0.20$ ; [SI Table 2](#)). *L. japonica* cover increased positively with other non-native species cover (partial  $R^2 = 0.21$ ,  $P < 0.0001$ ; [SI Table 2](#)). In contrast, *M. vimineum* abundance was associated with variation in the

**Table 1**

There was little consistency between abiotic or biotic predictors that explained the variation in foliar cover of eleven non-native invasive plant species and native and non-native invasive species functional groups in multivariate regression models. The “+” and “-” symbols indicate the direction of the relationship between each predictor to the abundance of each species or functional group. The two most important predictors (those with highest partial  $R^2$  values) are represented in black, all other predictors in gray. Asterisks (\*) represent models accounting for spatial autocorrelation.

	Abiotic variables									Biotic Variables				
	Bulk Density	Light Availability	Litter Mass	Mowing	Soil Clay (%)	Soil Moisture	Soil Nitrogen	Soil pH	Soil Sand (%)	Native Richness	Nitrogen Fixer Mass	Non-native Cover	Non-native Richness	Total Mass
<b>Invasive Species</b>														
* <i>Allium vineale</i>			+	+	+			-			+		+	
<i>Cirsium vulgare</i>		+						+						
* <i>Coronilla varia</i>			-		-			-			+	+	-	-
<i>Daucus carota</i>								-						
<i>Eleaagnus umbellata</i>										+				
* <i>Lespedeza cuneata</i>	-	+		+				-			-	+	-	+
* <i>Lonicera japonica</i>			+	+	-						-	+	-	
* <i>Microstegium vimineum</i>						+		+	+			+		
* <i>Senna obtusifolia</i>					-									
* <i>Sorghum halepense</i>	+				-							+		
<i>Verbascum thapsus</i>														+
<b>Functional Groups</b>														
*Native Forb	-	-			+	+					-	-	+	+
Invasive Forb		+												
*Native Graminoid		+	-							+			-	+
Invasive Graminoid					-	+		+			+			
*Native N-fixer										+				
*Invasive N-fixer		+		+						+	+	+	-	
*Native Woody												-		
*Invasive Woody	-			+		+					-	+	-	+

abiotic predictors soil pH (partial  $R^2 = 0.08$ ,  $P < 0.0001$ ) and soil moisture (partial  $R^2 = 0.03$ ,  $P = 0.002$ ), which explained over 80% of the total model variation (e.g., full model  $R^2$ ; SI Table 2).

Abiotic and biotic variables were also highly variable in their predictive power of the abundances of native and invasive functional groups (SI Table 2) and models predicting the total abundance for native and invasive functional groups rarely shared predictor variables in common. For example, we did not find a significant model that explained the abundances of native nitrogen fixers across plots ( $N = 250$ ,  $P = 0.45$ ,  $R^2 < 0.01$ ) but found a highly significant model that explained 41% of the variation of invasive nitrogen fixers ( $N = 249$ ,  $P < 0.0001$ ,  $R^2 = 0.41$ ; SI Table 2). Overall, total variation of invasive functional group abundance explained by the models ranged from 2% to 61% (forbs,  $N = 250$ ,  $P = 0.02$ ,  $R^2 = 0.02$ ; graminoids,  $N = 250$ ,  $P < 0.001$ ,  $R^2 = 0.10$ ; nitrogen-fixers,  $N = 249$ ,  $P < 0.0001$ ,  $R^2 = 0.41$ ; woody,  $N = 249$ ,  $P < 0.0001$ ,  $R^2 = 0.61$ ; SI Table 2). Total variation of native functional group abundance explain by the models ranged from 2% to 19% (forbs,  $N = 249$ ,  $P < 0.0001$ ,  $R^2 = 0.19$ ; graminoids,  $N = 249$ ,  $P < 0.0001$ ,  $R^2 = 0.13$ ; woody,  $N = 250$ ,  $P = 0.03$ ,  $R^2 = 0.02$ ; SI Table 2).

### 3.2. How do multiple invasive species alter co-occurrence patterns of native and non-native invasive species?

Native species co-occurrence patterns shifted from non-random to random as the number of invasive plants increased in 1-m<sup>2</sup> plots

across old-field communities. The standardized effect sizes for native species decreased by almost 90% as the number of invasive plant species increased in plots (Fig. 1). Native species found in plots with less than two invasive plants were strongly segregated (i.e., high C-score values ranging from 3.7 to 10.2) but in plots with greater than three invasive species, native species co-occurrence patterns became indistinguishable from random (i.e., low C-score values close to 0). This pattern remained statistically significant after taking matrix size into account (SI Table 3). Co-occurrence patterns of invasive species, in contrast, were always indistinguishable from random no matter how many invasive species were present (i.e., C-score values were all near 0).

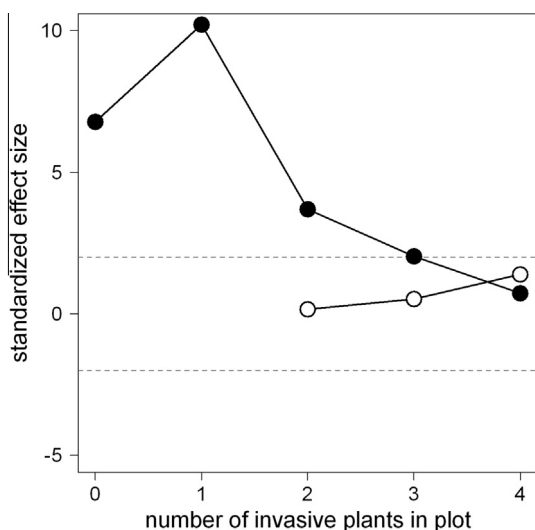
### 3.3. How do multiple invasive species alter successional trajectories in old fields?

The co-occurrence of multiple invasive plant species in old-field communities was associated with lower ratios of herbaceous:woody foliar cover for native and invasive species. Higher number of invasive plants were linked with lower herbaceous:woody foliar cover ratios for total species and native species (Fig. 2). Plots with three or four invasive plants had approximately 6× lower herbaceous:woody foliar cover for total species and 4× lower herbaceous:woody cover for native species. However, this pattern was opposite for invasive species. The herbaceous:woody foliar cover in plots with three or four invasive plants

was 2× greater than in plots with only two invaders (Fig. 2). The change in total and native herbaceous:woody cover ratios was primarily driven by a decline in the abundance of the most dominant native herbaceous species, *Solidago altissima* L., and an increase in the three most dominant woody species, the native shrubs *Rubus argutus* Link and *R. flagellaris* Willd., and the invasive woody vine *L. japonica*. The dominant herbaceous species, *S. altissima*, had less than half of its average biomass in heavily invaded ( $\geq 3$  invasive plant species) plots compared to less invaded plots ( $< 3$  invasive plant species). Alternatively, biomass of the native shrubs *R. argutus* and *R. flagellaris* nearly doubled and the non-native vine *L. japonica* biomass increased nearly 2.5× in heavily invaded plots ( $\geq 3$  invasive plant species) when compared to less invaded plots ( $< 3$  invasive plant species; Table 2). The herbaceous:woody foliar cover ratio for invasive species increased due to the 2× increase in the two invaders *C. varia* and *S. halepense*, which offset the increase in the woody invader *L. japonica*.

#### 4. Discussion

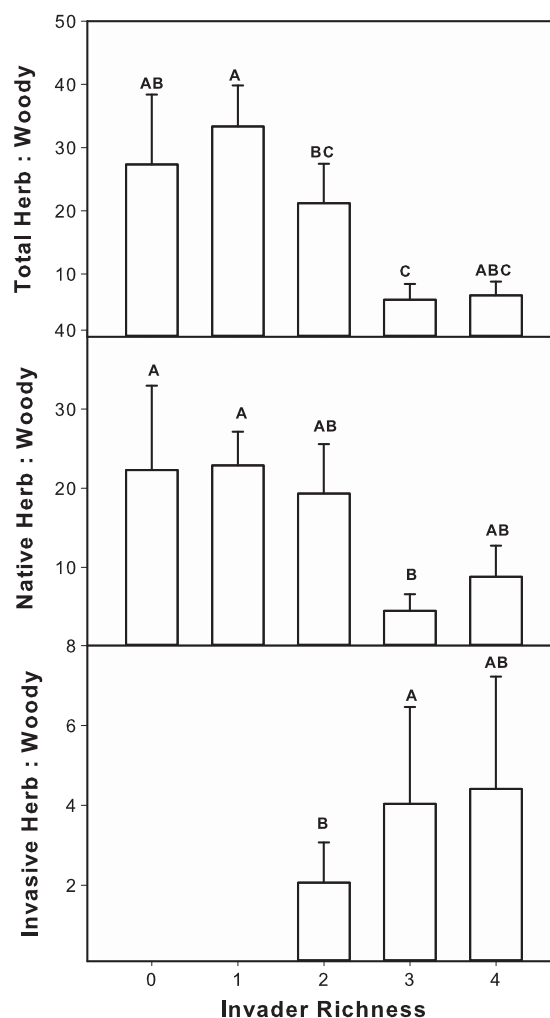
We found that an increasing number of invasive plant species was associated with changes in co-occurrence patterns of native plant species and alterations of successional trajectories of old-field communities. Our results suggest that an increasing level of invasion (in terms of the number of different invasive species) in old fields could alter interactions among native plant species, leading to an alteration of community successional trajectories by lowering the herbaceous:woody foliar cover ratio. As old fields transition into forests, high levels of invasion might be problematic and managers may consider decreasing the total number of co-occurring invasive species in these transitional ecosystems. However, characterizing old fields that are the most prone to high levels of invasion might be a challenge. We found that models predicting the abundance of invasive plant species or invasive plant functional groups had low explanatory power and high inconsistency in the identity of abiotic and biotic predictors, even using a wide suite of biotic and abiotic variables.



**Fig. 1.** An increasing number of invasive plant species in 1-m<sup>2</sup> plots in old-field communities changed native plant species (black circles) organization from highly segregated to random. Non-native invasive plant species (white circles) had random assembly patterns across plots. Standardized effect sizes are measures of the extent species co-occur more or less frequently than expected by chance and larger C-scores indicate species are co-occurring less than expected. The dashed lines represent 1.96 standard deviations, which is an approximation for statistical significance.

#### 4.1. What abiotic and biotic factors shape the abundance of non-native invasive species and invasive and native functional groups?

The abundance of individual invasive species and invasive and native functional groups were generally poorly predicted by abiotic and biotic variables. Though previous studies have shown positive relationships between native and non-native species richness in old fields (Souza et al., 2011a), our results indicate that the underlying mechanisms explaining the abundances of species might not track those of richness. Differential responses of native and non-native species to environmental drivers has been reported for other early successional forested ecosystems (Parker et al., 2010) and this may be because in this ecosystem, historical and ecological processes govern the abundance of invasive species rather than the environmental traits we measured. The introduction history and initial propagule pressure (i.e., planting history) of the invaders might better explain the overall abundance of invasive species in these fields. For example, we failed to find a model explaining *E. umbellata* abundance, which was originally widely planted for erosion control and wildlife habitat (Orr et al., 2005). It is possible that the introduction history of this species might better explain its abundance in these fields (Lockwood et al., 2009). Interestingly, we did not find a strong effect of periodic disturbance, the mowing of



**Fig. 2.** The ratio of herbaceous to woody plant cover decreased for all species and native species as the number of invasive plants increased in 1-m<sup>2</sup> plots in old field ecosystems. The herbaceous:woody cover ratio for invasive plants increased as the number of invasive plants increased. Letters above the bars represent differences at  $\alpha = 0.05$ .

fields, on the abundance of native or non-natives species, although disturbances can promote non-native species in other ecosystems (Davis et al., 2000; MacDougall and Turkington, 2005). Mowing frequency was sporadically included as an important variable in the best models and had low predictive power in the models in which it was included. Our findings corroborate recent reviews that suggest disturbance may not be as important predictor of invasion as once thought (Moles et al., 2012). Overall, our results show that for these old fields, there may be no single explanation for the abundance or occurrence of invasive plants and that manipulation of environmental conditions (i.e., increased mowing frequency or planting to increase native species richness) will not necessarily result in an overall decrease of the number of non-native invasive species.

Of the 11 invasive plant species present in the old fields we studied, two should be of particular concern for forest conservation. Both the woody vine *L. japonica* and the annual grass *M. vimineum* are highly invasive in forested ecosystems in the southeastern United States (Rudis et al., 2006) and their presence in forest understories is associated with decreased native plant richness and abundance (Dillenburg et al., 1993; Marshall et al., 2009; Oswalt et al., 2007). Thus, if these species persist as old fields transition into forests, their continued presence might prevent the successful establishment of recolonizing understory forest herbs (Flinn and Vellend, 2005; Flory and Clay, 2010).

#### 4.2. How do multiple invasive species alter co-occurrence patterns of native and non-native invasive species?

An increase in the number of invasive plant species was associated with the disassembly of native plant communities in old fields. Native plants in 1-m<sup>2</sup> plots with lower levels of invasion showed segregated assembly patterns. As the number of invasive species increased above three, native plant co-occurrence patterns became indistinguishable from random. Segregated co-occurrence patterns are common in plant communities (Gotelli and McCabe, 2002) and could be a consequence of two mechanisms: species interactions or environmental filtering. Environmental filtering includes species selection of preferred habitat types (i.e., habitat filtering), differences in species dispersal abilities, or historical disturbances that might preclude species from tolerating certain habitats. Although, the C-score analysis describes patterns and cannot determine the underlying mechanism, we argue that loss of interactions among native species is more likely the cause of disassembly in these old fields. If habitat filtering affected species co-occurrence patterns, we would expect to find that changes in invader richness correlated with abiotic changes across 1-m<sup>2</sup> plots in old-field communities. This was not the case for any of the abiotic variables we measured ( $P > 0.1$ ). Likewise, our use of fine-scale data within a single habitat type reduces the possibility that disturbance or dispersal limitations might affect co-occurrence patterns, because our plots were located in fields with similar

types of disturbance and species-specific dispersal limitations should be random across plots. Finally, we found that in heavily invaded plots the average biomass of the most dominant native species, *Solidago altissima*, was nearly two times lower than when compared to less heavily invaded plots (Table 2). Previous studies show that removing *S. altissima* from old fields resulted in increases of subdominant species biomass, evenness, and diversity, which indicates that this species suppresses the abundance of many species in old fields (Souza et al., 2011c). The decrease in biomass of this competitively-dominant species further supports a decrease in competitive interactions within heavily invaded plots leading to random patterns of associations among native plant species.

Community disassembly by invasive species can have important repercussions when disassembly is caused by loss of interactions among native species (Rodriguez-Cabal et al., 2013; Sanders et al., 2003). For example, the invasive succulent ice-plant, *Carpobrotus acinaciformis* (L.) L. Bolus, causes community disassembly in coastal dune systems (Santoro et al., 2012). Backdune plant communities have segregated assembly patterns in the absence of *C. acinaciformis* and random assembly patterns in the invaders' presence. As in our study, the presence of *C. acinaciformis* is associated with a decrease in the foliar cover of the dominant species in coastal dunes. Again, a decrease in dominant species biomass could be associated with a decrease in antagonistic interactions between the shrub and other back dune plant species. The loss of competitive interactions, in dune system and in the old fields in our study, could imply changes in successional trajectories of these plant communities (Santoro et al., 2012). Theory and empirical evidence suggest that competition, primarily for soil nutrients and light, is a critical mechanistic component predicting plant population dynamics during old-field succession (Tilman, 1990). Thus, loss of these competitive interactions could ultimately reduce native diversity and alter future trajectories of community development (e.g., successional dynamics).

Interestingly, invasive species had random assembly patterns along the invasive richness gradient. A meta-analysis of studies on native plant assembly patterns indicates native plant communities are frequently highly structured (Gotelli and McCabe, 2002), which is consistent with empirical evidence that shows competitive and facilitative interactions are important components structuring plant community dynamics (Bengtsson et al., 1994; Brooker et al., 2008; Keddy and Shipley, 1989; Tilman, 1990). However, much less is known about interactions among invasive plant species and how these interactions might shape plant community assembly. It might be expected that strong interactions among native plants are fostered by their shared co-evolutionary histories (Cavender-Bares et al., 2009; Johnson and Stinchcombe, 2007) and that invasive species may be less likely to share evolutionary histories and thus less likely to have strong interactions with one another. Of the limited studies on

**Table 2**

The number of invasive plants found in 1-m<sup>2</sup> plots was associated with differences in the herbaceous:woody foliar cover ratios in old-field plant communities. The shift was due to large (>50%) changes in the average cover of dominant herbaceous (h) and woody (w) species between plots with less than three or three or more invasive plant species. Rank represents the species ranking based on average percent cover across 1-m<sup>2</sup> plots and asterisks (\*) denote non-native invasive species.

Plots with <3 invasive plants			Plots with ≥3 invasive plants		
Species	Cover (%)	Rank	Species	Cover (%)	Rank
<i>Solidago altissima</i> (h)	15.8	1	<i>Verbesina occidentalis</i> (h)	16.0	1
<i>Verbesina occidentalis</i> (h)	10.8	2	<i>Rubus argutus</i> (w)	15.8	2
<i>Rubus argutus</i> (w)	7.8	5	<i>Lonicera japonica</i> (w)*	8.9	3
<i>Lonicera japonica</i> (w)*	3.8	8	<i>Solidago altissima</i> (h)	6.9	5
<i>Rubus flagellaris</i> (w)	3.4	9	<i>Rubus flagellaris</i> (w)	6.3	7

invasive plant-plant interactions, there are reports of invaders with overlapping native ranges having strongly competitive (Belote and Weltzin, 2006; Besaw et al., 2011; Metlen et al., 2013) or facilitative (Cushman et al., 2011; Tecco et al., 2006) interactions in their non-native range, although these studies do not explicitly test whether a shared co-evolutionary history of the species is responsible for these interactions.

#### 4.3. How do multiple invasive species alter successional trajectories in old fields?

Increases in invader richness may increase rates of community succession by significantly lowering herbaceous:woody cover ratios of native species. As old-fields succeed to forested ecosystems, herbaceous:woody cover ratios should decrease as woody trees and shrubs become more dominant (Inouye et al., 1987; Meiners et al., 2002). We studied fields of the same age and disturbance history and found that plots with higher invasive plant richness were associated with significantly lower herbaceous:woody cover ratios of native plant species. The change in herbaceous:woody cover ratio occurred once the number of invasive plant species reached 3 species per 1-m<sup>2</sup> plot, which coincides with our finding that native plant species assembly patterns became random in plots with 3 or 4 invaders.

As with our finding on community co-occurrence patterns, the herbaceous:woody foliar cover ratios of invasive species did not follow the same trend as native species. As the number of invasive plants increased in plots the herbaceous:woody cover ratio of invaders increased as well, meaning that more heavily invaded plots were associated with a higher proportion of herbaceous invasive cover than less invaded plots. Species sampling was not likely the cause of this difference because the proportion of herbaceous species in the total native or invasive species pool were similar (75% and 81%, respectively). In contrast to our findings, previous old field successional studies show that native and non-native functional groups have similar population dynamics throughout succession in old fields (Meiners, 2007; Meiners et al., 2002; Tognetti et al., 2010), suggesting that abundances of native and non-native functional groups are governed by similar ecological constraints and trade-offs (Davis et al., 2000; Thompson et al., 1995). Studies in other successional ecosystems have found non-native and native woody species do not have similar population dynamics (McLane et al., 2012) and that some invasive species can persist and increase in cover during succession (Tognetti et al., 2010). In our study, we do not find similar dynamics between native and non-native invasive species, which could be due to the fact that we limited our analysis to the subset non-native invasive species, which by their very definition behave differently than other non-native species (Ortega and Pearson, 2005).

Overall, the total herbaceous:woody cover ratio for all species decreased in plots with 3 or 4 invasive plants, which indicates that increased invasive species richness is 'speeding up' succession by increasing the proportion of native woody species in plots with more invaders. If disassembly of native plants is due to the loss of competitive interactions among co-occurring natives, this might explain the change in herbaceous:woody cover ratios. Typically, herbaceous plants with greater nutrient-acquisition abilities are more dominant in younger fields such as the ones we studied (these fields, though abandoned for more than 50 years, are mowed frequently to maintain an early successional stage), while older fields favor woody species that are more competitive in light-capturing ability. The decrease in biomass of the competitively dominant native herbaceous species, *Solidago altissima*, coincided with the increase in biomass of the three most dominant woody species in heavily invaded plots (i.e., three or more invasive plant species), which explains the overall decrease in

herbaceous:woody cover ratios in these plots. Again, if competitive interactions among native species (predominantly herbaceous) are lost in plots with more than three invaders, then this might explain the greater ability of woody species, both native and invasive, to increase in biomass in heavily invaded plots.

## 5. Conclusions

Old-field communities are transitional ecosystems that if left unmanaged will succeed into forest ecosystems. However, old-field ecosystems are commonly invaded by numerous invasive plant species, which could alter successional dynamics and affect the characteristics of young forests derived from invaded old fields. Here, we show that the number of invasive species in a plant neighborhood can simultaneously disassemble native plant communities, indicating a loss of interactions among native plants, and decrease herbaceous:woody cover ratios, indicating a change in successional dynamics. Because increasing the number of plant invaders has potentially dramatic impacts on old-field successional patterns, we suggest that managers should attempt to keep total invasive plant richness low in old-fields if forest restoration is the ultimate goal for old-field ecosystems. Because environmental variables generally did a poor job predicting abundances of invasive plants and invasive plant functional groups in old-fields, there may be limited "silver bullet" options for management of multiple invasive species in old-fields. Instead, managers may include targeted management of specific invasive species to keep overall invasive richness low. This may include direct management of woody invaders to prevent accelerated succession to non-native woody communities or direct management of non-native plants that are most likely to persist under similar environmental conditions in both old fields and young forests. Finally, determining how continued anthropogenic disturbances, including field-scale disturbances like mowing or landscape-scale disturbances like nitrogen deposition and climate change, might assist or impede non-native species management in old fields could be a fruitful area of future research.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.10.031>.

## References

- Averill, K.M., DiTommaso, A., Mohler, C.L., Milbrath, L.R., 2010. Establishment of the invasive perennial *Vincetoxicum rossicum* across a disturbance gradient in New York State, USA. *Plant Ecol.* 211, 65–77.
- Bazzaz, F.A., 1968. Succession on abandoned fields in the Shawnee Hills, southern Illinois. *Ecology* 49, 924–936.
- Bazzaz, F.A., 1996. *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge University Press, Cambridge, United Kingdom.
- Bellemare, J., Motzkin, G., Foster, D.R., 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *J. Biogeogr.* 29, 1401–1420.
- Belote, R.T., Weltzin, J.F., 2006. Interactions between two co-dominant, invasive plants in the understory of a temperate deciduous forest. *Biol. Invasions* 8, 1629–1641.
- Belote, R.T., Weltzin, J.F., Norby, R.J., 2003. Response of an understory plant community to elevated [CO<sub>2</sub>] depends on differential responses of dominant

- invasive species and is mediated by soil water availability. *New Phytol.* 161, 827–835.
- Bengtsson, J., Fagerström, T., Rydin, H., 1994. Competition and coexistence in plant communities. *Trends Ecol. Evol.* 9, 246–250.
- Besaw, L.M., Thelen, G.C., Sutherland, S., Metlen, K., Callaway, R.M., 2011. Disturbance, resource pulses and invasion: short-term shifts in competitive effects, not growth responses, favour exotic annuals. *J. Appl. Ecol.* 48, 998–1006.
- Borcard, D., Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Model.* 153, 51–68.
- Borcard, D., Legendre, P., Avois-Jacquet, C., Tuomisto, H., 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85, 1826–1832.
- Brandon, A.L., Gibson, D.J., Middleton, B.A., 2004. Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. *Biol. Invasions* 6, 483–493.
- Braun-Blanquet, J., 1932. *Plant sociology. The Study of Plant Communities.* McGraw-Hill Book Co., New York.
- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffrers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: the past, the present, and the future. *J. Ecol.* 96, 18–34.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference understanding AIC and BIC in model selection. *Sociol. Method Res.* 33, 261–304.
- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett.* 12, 693–715.
- Cole, P.G., Weltzin, J.F., 2005. Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests. *Biol. Invasions* 7, 477–488.
- Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111, 1119–1144.
- Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields? land abandonment and ecosystem assembly. *Trends Ecol. Evol.* 23, 104–112.
- Cushman, J.H., Lortie, C.J., Christian, C.E., 2011. Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. *J. Ecol.* 99, 524–531.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88, 528–534.
- Dickson, T.L., Wilsey, B.J., Busby, R.R., Gebhart, D.L., 2010. *Melilotus officinalis* (yellow sweetclover) causes large changes in community and ecosystem processes in both the presence and absence of a cover crop. *Biol. Invasions* 12, 65–76.
- Dillenburg, L.R., Whigham, D.F., Teramura, A.H., Forseth, I.N., 1993. Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. *Oecologia* 93, 48–54.
- Dupouey, J., Dambrine, E., Laffite, J., Moares, C., 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83, 2978–2984.
- Dyer, J.M., 2010. Land-use legacies in a central Appalachian forest: differential response of trees and herbs to historic agricultural practices. *Appl. Veg. Sci.* 13, 195–206.
- Emery, S.M., Gross, K.L., 2006. Dominant species identity regulates invasibility of old-field plant communities. *Oikos* 115, 549–558.
- Endels, P., Adriaens, D., Verheyen, K., Hermy, M., 2004. Population structure and adult plant performance of forest herbs in three contrasting habitats. *Ecography* 27, 225–241.
- Flinn, K.M., Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. *Front. Ecol. Environ.* 3, 243–250.
- Flory, S.L., Clay, K., 2010. Non-native grass invasion suppresses forest succession. *Oecologia* 164, 1029–1038.
- Fortner, A.M., Weltzin, J.F., 2007. Competitive hierarchy for four common old-field plant species depends on resource identity and availability. *J. Torrey Bot. Soc.* 134, 166–176.
- Freckleton, R.P., Watkinson, A.R., Rees, M., 2009. Measuring the importance of competition in plant communities. *J. Ecol.* 97, 379–384.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D., Von Holle, B., 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88, 3–17.
- Goldberg, D.E., Barton, A.M., 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am. Nat.* 139, 771–801.
- Gotelli, N.J., 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81, 2606–2621.
- Gotelli, N.J., Arnett, A.E., 2000. Biogeographic effects of red fire ant invasion. *Ecol. Lett.* 3, 257–261.
- Gotelli, N.J., Entsminger, G.L., 2011. EocSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. <<http://www.garyentsminger.com/ecosim.htm>>.
- Gotelli, N.J., McCabe, D.J., 2002. Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology* 83, 2091–2096.
- Hobbs, R.J., Cramer, V.A., 2007. Why old fields? socioeconomic and ecological causes and consequences of land abandonment. In: Cramer, V.A., Hobbs, R.J. (Eds.), *Old Fields: Dynamics and Restoration of Abandoned Farmland.* Island Press, Washington, D.C., pp. 1–14.
- Huston, M., Smith, T., 1987. Plant succession: life history and competition. *Am. Nat.* 130, 168–198.
- Inouye, R.S., Huntly, N.J., Tilman, D., Tester, J.R., Stillwell, M., Zinnel, K.C., 1987. Old-field succession on a Minnesota sand plain. *Ecology* 68, 12–26.
- Jensen, A.M., Löf, M., Witzell, J., 2012. Effects of competition and indirect facilitation by shrubs on *Quercus robur* saplings. *Plant Ecol.* 213, 535–543.
- Johnson, M.T., Stinchcombe, J.R., 2007. An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.* 22, 250–257.
- Keddy, P.A., Shipley, B., 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54, 234–241.
- Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert: history, persistence, and influences to human activities. *Global Environ. Change* 6, 37–52.
- Koerner, W., Dupouey, J., Dambrine, E., Benoît, M., 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. *J. Ecol.* 85, 351–358.
- Kumar, S., Stohlgren, T.J., Chong, G.W., 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87, 3186–3199.
- Li, X.D., Wilson, S.D., 1998. Facilitation among woody plants establishing in an old field. *Ecology* 79, 2694–2705.
- Lockwood, J.L., Cassey, P., Blackburn, T.M., 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Divers. Distribut.* 15, 904–910.
- MacDougall, A.S., Turkington, R., 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86, 42–55.
- Marshall, J.M., Buckley, D.S., Franklin, J.A., 2009. Competitive interaction between *Microstegium vimineum* and first-year seedlings of three central hardwoods. *J. Torrey Bot. Soc.* 136, 342–349.
- Matlack, G.R., 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75, 1491–1502.
- McLane, C.R., Battaglia, L.L., Gibson, D.J., Groninger, J.W., 2012. Succession of exotic and native species assemblages within restored floodplain forests: a test of the parallel dynamics hypothesis. *Restor. Ecol.* 20, 202–210.
- Meiners, S.J., 2007. Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88, 1098–1104.
- Meiners, S.J., Pickett, S.T.A., Cadenasso, M.L., 2002. Exotic plant invasions over 40 years of old field successions: community patterns and associations. *Ecography* 25, 215–223.
- Metlen, K., Aschehoug, E.T., Callaway, R.M., 2013. Competitive outcomes between two exotic invaders are modified by direct and indirect effects of a native conifer. *Oikos* 122, 632–640.
- Moles, A.T., Flores-Moreno, H., Bonser, S.P., Warton, D.I., Helm, A., Warman, L., Eldridge, D.J., Jurado, E., Hemmings, F.A., Reich, P.B., Cavender-Bares, J., Seabloom, E.W., Mayfield, M.M., Sheil, D., Djietror, J.C., Peri, P.L., Enrico, L., Cabido, M.R., Setterfield, S.A., Lehmann, C.E.R., Thomson, F.J., 2012. Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *J. Ecol.* 100, 116–127.
- Motzkin, G., Foster, D., Allen, A., Harrod, J., Boone, R., 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. *Ecol. Monogr.* 66, 345–365.
- Myster, R.W., Pickett, S.T.A., 1992. Dynamics of associations between plants in ten old fields during 31 years of succession. *J. Ecol.* 80, 291–302.
- Orr, S.P., Rudgers, J.A., Clay, K., 2005. Invasive plants can inhibit native tree seedlings: testing potential allelopathic mechanisms. *Plant Ecol.* 181, 153–165.
- Ortega, Y.K., Pearson, D.E., 2005. Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecol. Appl.* 15, 651–661.
- Oswalt, C.M., Oswalt, S.N., Clatterbuck, W.K., 2007. Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. *For. Ecol. Manage.* 242, 727–732.
- Parker, J.D., Richie, L.J., Lind, E.M., Maloney, K.O., 2010. Land use history alters the relationship between native and exotic plants: the rich don't always get richer. *Biol. Invasions* 12, 1557–1571.
- Phillips, D., Foss, J., Stiles, C., Trettin, C.C., Luxmoore, R., 2001. Soil–landscape relationships at the lower reaches of a watershed at Bear Creek near Oak Ridge, Catena. 44, pp. 205–222.
- Powell, K.I., Chase, J.M., Knight, T.M., 2013. Invasive plants have scale-dependent effects on diversity by altering species–area relationships. *Science* 339, 316–318.
- Rangel, T.F., Diniz-Filho, J.A.F., Bini, L.M., 2010. SAM: a comprehensive application for spatial analysis in macroecology. *Ecography* 33, 46–50.
- Renne, I.J., Tracy, B.F., Colonna, I.A., 2006. Shifts in grassland invasibility: effects of soil resources, disturbance, composition, and invader size. *Ecology* 87, 2264–2277.
- Richardson, D.M., Pyšek, P., Carlton, J.T., 2011. A compendium of essential concepts and terminology in invasion ecology. In: Richardson, D.M. (Ed.), *Fifty Years of Invasion Ecology: The Legacy of Charles Elton.* Blackwell Publishing LTD., West Sussex, UK, pp. 409–420.
- Rodriguez-Cabal, M., Barrios-Garcia, M., Amico, G., Aizen, M., Sanders, N., 2013. Node-by-node disassembly of a mutualistic network driven by species introductions. *P. Natl. Acad. Sci. – Biol.* 110, 16503–16507.
- Rudis, V.A., Gray, A., McWilliams, W., O'Brien, R., Olson, C., Oswalt, S., Schulz, B., 2006. Regional monitoring of nonnative plant invasions with the Forest Inventory and Analysis program. In: McRoberts, R., Reams, G., Van Duesen, P., McWilliams, W. (Eds.), *Proceedings of the 6th Annual FIA Symposium.* USDA For. Serv. Gen. Tech. Rep. WO-70. Washington, DC, pp. 49–64.



- Sanders, N.J., Gotelli, N.J., Heller, N.E., Gordon, D.M., 2003. Community disassembly by an invasive species. *P. Natl. Acad. Sci – Biol.* 100, 2474–2477.
- Santoro, R., Jucker, T., Carboni, M., Acosta, A.T.R., 2012. Patterns of plant community assembly in invaded and non-invaded communities along a natural environmental gradient. *J. Veg. Sci.* 23, 483–494.
- Singleton, R., Gardescu, S., Marks, P.L., Geber, M.A., 2001. Forest herb colonization of postagricultural forests in central New York State, USA. *J. Ecol.* 89, 325–338.
- Smith, B.W., Miles, P.D., Vissage, J.S., Pugh, S.A., 2003. Forest Resources of the United States, 2002. Gen. Tech. Rep. NC-241. St. Paul, MN: US Department of Agriculture, Forest Service, North Central Research Station. 137 p.
- Souza, L., Belote, R.T., Kardol, P., Weltzin, J.F., Norby, R.J., 2010. CO<sub>2</sub> enrichment accelerates successional development of an understory plant community. *J. Plant Ecol.* 3, 33–39.
- Souza, L., Bunn, W.A., Simberloff, D., Lawton, R.M., Sanders, N.J., 2011a. Biotic and abiotic influences on native and nonnative richness relationship across spatial scales: favourable environments for native species are highly invulnerable. *Funct. Ecol.* 25, 1106–1112.
- Souza, L., Bunn, W.A., Weltzin, J.F., Sanders, N.J., 2011b. Similar biotic factors affect early establishment and abundance of an invasive plant species across spatial scales. *Biol. Invasions* 13, 255–267.
- Souza, L., Weltzin, J.F., Sanders, N.J., 2011c. Differential effects of two dominant plant species on community structure and invasibility in an old-field ecosystem. *J. Plant Ecol.* 4, 123–131.
- Stone, L., Roberts, A., 1990. The checkerboard score and species distributions. *Oecologia*, 85, pp. 74–79.
- Tecco, P.A., Gurvich, D.E., Díaz, S., Pérez-Harguindeguy, N.P., Cabido, M., 2006. Positive interaction between invasive plants: the influence of *Pyracantha angustifolia* on the recruitment of native and exotic woody species. *Austral. Ecol.* 31, 293–300.
- Thompson, K., Hodgson, J.G., Rich, T.C., 1995. Native and alien invasive plants: more of the same? *Ecography* 18, 390–402.
- Tilman, D., 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58, 3–15.
- Tognetti, P.M., Chaneton, E.J., Omacini, M., Trebino, H.J., León, R.J.C., 2010. Exotic vs. native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina. *Biol. Conserv.* 143, 2494–2503.
- Verheyen, K., Bossuyt, B., Hermy, M., Tack, G., 1999. The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *J. Biogeogr.* 26, 1115–1128.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14, 702–708.
- Wardle, D.A., Bardgett, R.D., Callaway, R.M., Van der Putten, W.H., 2011. Terrestrial ecosystem responses to species gains and losses. *Science* 332, 1273–1277.
- Wright, J.P., Fridley, J.D., 2010. Biogeographic synthesis of secondary succession rates in eastern North America. *J. Biogeogr.* 37, 1584–1596.