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Per capita community-level effects of an invasive grass, *Microstegium vimineum*, on vegetation in mesic forests in northern Mississippi (USA)

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Abstract Quantifying per capita impacts of invasive species on resident communities requires integrating regression analyses with experiments under natural conditions. Using multivariate and univariate approaches, I regressed the abundance of 105 resident species of groundcover plants and tree seedlings against the abundance and height of an invasive grass, *Microstegium vimineum*, within 117 plots in four mesic floodplain forests in Mississippi (USA). *Microstegium vimineum* was most productive (i.e., tallest and most abundant) in canopy gaps in floodplains, and a significant amount of variation in resident species composition was directly explained by canopy gaps and stand age. The relatively small (but statistically significant) percentage of variation in resident species composition (1.8%) explained by *M. vimineum* in the multivariate analysis was attributable to significant relationships with a few common species. Most of these were negative relationships with shady mesic forest indicators. Most positive relationships were with infrequent disturbance indicators and with species with growth phenologies that differed from that of *M. vimineum*. Results of field competition experiments with the three most common species to show significant relationships with *M. vimineum* revealed asymmetric competitive effects of *M. vimineum* on *Chasmanthium laxum* and positive responses of *Quercus alba* seedlings and *Leersia virginica* adults to the removal of *M. vimineum* in one growing season. Results of this study suggest that negative per capita community-level effects of *M. vimineum* are likely to be greater in shady forests than in open floodplain forests due to the relative paucity of vulnerable species in the latter.

Keywords Competition · *Chasmanthium laxum* · Disturbance · Facilitation · *Leersia virginica* · Niche complementarity · Phenology · *Quercus alba*

Introduction

The limited availability of resources for the control of invasive species and conservation of biodiversity requires that we measure the impacts of invasive species on biodiversity. We cannot afford to merely assume that an invasive species' impact is proportional to its abundance (Hager and McCoy 1998) and therefore must measure its per capita effect on the recipient community or ecosystem (Parker et al. 1999). Although numerous studies have demonstrated the potential for invasive species to impact communities (e.g., Woods 1993; McCarthy 1997; Meiners et al. 2001; Alvarez and Cushman 2002; Collier et al. 2002; Schooler et al. 2006; Brewer 2008; Adams and Engelhardt 2009), relatively few have examined how the per capita impact of an invader varies along environmental gradients or between habitats

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(Parker et al. 1999; Stachowicz and Tilman 2005). Most invasive species occur primarily in disturbed habitats (Davis et al. 2000), which sometimes support a high diversity of invasive and disturbance-dependent native species due to reduced competition (Huston 2004; Von Holle and Motzkin 2007). Alternatively, the environmental conditions associated with some disturbed habitats favor invasive species but are unsuitable for many native species (Gurevitch and Padilla 2004; MacDougall and Turkington 2005; Surrette and Brewer 2008). Either way, the per capita impact of an invader on the resident plant community may be relatively small in those habitats in which the invader is most abundant.

Investigations of relationships between invasive plants and resident plant communities benefit from taking into account phenology (i.e., seasonal patterns of growth or reproduction; Zavaleta and Hulvey 2004). Negative relationships between an invader and the resident plant community (after accounting for environmental covariables) can either result from competitive displacement by the invader or biotic resistance to invasion by resident plants with similar phenologies to that of the invader (Levine and D'Antonio 1999; Zavaleta and Hulvey 2004). Likewise, positive relationships between an invader and the resident plant community can result from facilitation (Bruno et al. 2005), positively correlated rates of propagule production (Levine 2000; Stachowicz and Tilman 2005), or complementary niches (e.g., complementary phenologies; Zavaleta and Hulvey 2004). Taking into account phenology can help elucidate the mechanisms underlying negative and positive relationships between invaders and residents.

In this study, I examined multivariate partial regressions between the abundance of an invasive grass, *Microstegium vimineum* (Trin.) A. Camus and that of all resident groundcover plant species within 117 plots in four mesic floodplain forests in north Mississippi (USA). I then conducted field competition experiments to determine whether competition was responsible for the negative partial correlations between *M. vimineum* and the three most common native species that showed significant results. I tested four hypotheses: (1) *Microstegium vimineum* invasion alters the composition of resident groundcover communities; (2) The per capita negative effects of *M. vimineum* are greatest within the areas in which *M. vimineum* is least productive; (3) The effects of *M. vimineum* invasion on resident species depend on the resident species' phenologies?, and (4) Low abundance of resident species in invaded areas is the result of competition?

Methods

Description of *Microstegium vimineum*

A native of east Asia, *M. vimineum* was first discovered in Tennessee in 1919 and has since spread throughout most of the eastern United States (Fairbrothers and Gray 1972; Hunt and Zaremba 1992; Redman 1995). It has been described as having greater invasive potential within eastern US deciduous forests than the notorious garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara and Grande; Morrison et al. 2007]. It benefits from disturbances and exhibits high reproductive effort, efficient dispersal, and a short generation time (Gibson et al. 2002; Cheplick 2008; Marshall and Buckley 2008). It can produce very dense stands (>400 rooted stems per m^2), especially in rich, floodplain soils (Barden 1987) and in canopy gaps and areas where the soil has been disturbed and/or litter layer reduced or removed (Cole and Weltzin 2005; Glasgow and Matlack 2007; Marshall and Buckley 2008). It is remarkably shade tolerant for a C4 grass (Winter et al. 1992; Horton and Neufeld 1998), a good competitor under low light conditions (Leicht et al. 2005), and can avoid shade by growing rapidly at the end of the growing season during tree leaf senescence (Cheplick 2008). Despite being an annual plant, it produces a persistent seed bank, which, along with its shade tolerance, allows it to re-establish populations and maintain patches among years in both disturbed areas and in shady forest understory communities (Gibson et al. 2002). Although community-level effects remain poorly understood, previous studies have provided evidence of negative effects on resident plant and animal communities (Belote and Weltzin 2006; Oswalt et al. 2007; Marshall et al. 2009; Adams and Engelhardt 2009; Flory and Clay 2010; Simao et al. 2010).

Description of field sites and sampling design

All work was conducted within forests located on mesic slopes/terraces and floodplains in north-central

Mississippi, USA, corresponding to the Claiborne geologic group, which includes silt loams developed from Pleistocene glacial loess and sandier soils of marine Eocene origin (Surrette and Brewer 2008). In April and October 2008, I visited 117 1-m-radius permanent plots (initially established in 2007; Brewer 2010) in four floodplain and mesic forest stands. Two of the stands were relatively young (<20 years old), and two were mature (greater than 60 years old) stands within the interior of larger tracts of forest. One of the young stands was dominated by sweetgum (*Liquidambar styraciflua* L.) and sycamore (*Platanus occidentalis* L.) and occurred in an impounded floodplain with sandy loam soils (Site 1). The other young stand occurred in a better-drained mesic terrace with silt loam soils and was dominated in the overstory by loblolly pine (*Pinus taeda* L.) and sweetgum (Site 2). One of the mature stands (Site 3) was located on a flat stream terrace within the interior of a large forested area approximately 2 km from sites 1 and 2. It was dominated in both the overstory and understory by white oak (*Quercus alba* L.) and sweetgum, with red maple (*Acer rubrum* L.), winged elm (*Ulmus alata* Michx.), hop hornbeam [*Ostrya virginiana* (Mill.) K. Koch], and blue beech (*Carpinus caroliniana* Walter) limited primarily to the understory. The groundcover vegetation at Site 3 was dominated by the perennial grass, *Chasmanthium laxum* (L.) H. O. Yates. Sites 1, 2, and 3 were located in Oxford, Mississippi in a protected area managed by the University of Mississippi. The other mature stand (Site 4) was located at Strawberry Plains Audubon Center, near Holly Springs, Mississippi. It encompassed a mesic slope with silt loam soils and a floodplain with sandy soils. The mesic slope was dominated by southern red oak (*Quercus falcata*), white oak, and mockernut hickory (*Carya tomentosa*). The floodplain was dominated by white oak, sweetgum, and yellow poplar (*Liriodendron tulipifera*), with scattered bald cypress (*Taxodium distichum*) and boxelder (*Acer negundo*).

The sampling plots were arranged within each stand to encompass as wide a range of gap conditions, soil texture, elevation, and *M. vimineum* densities as possible. To establish the sampling plots in the fall of 2007, random points were located within a population within each hydrologic unit (one per site, with the exception of site 4, which contained a mesic slope and a floodplain). I then found the closest *M. vimineum* stem and made it the center of the sampling plot and then counted all stems within the plots. I ensured a roughly equal number of high density, average density, and low density plots in Fall 2007 by randomly removing some plots from consideration. After exclusion and by 2008 (some flags marking plots were lost to flooding), there were 45 plots at site 1, 16 plots at site 2, 24 plots at site 3, and 32 plots at site 4. These numbers were commensurate with the spatial extent of the populations at each of these sites. Densities of *M. vimineum* ranged from 1 to 1360 stems per 1-m-radius plot in 2008. The following plant measurements were taken at each plot at each census: *M. vimineum* stem density; height of the tallest *M. vimineum* stem; densities of all resident groundcover species [i.e., all herbs and tree seedlings <1.5 m; all shrubs and primocanes (*Rubus* L. spp.) <2 m] and maximum heights of the two tallest native herbs. Production of *M. vimineum* was estimated indirectly by taking the square root of the product of maximum height and log shoot density.

The following environmental measurements were taken at each plot: soil texture (percent sand, silt, and clay), overhead canopy gap fraction (using a concave spherical densiometer), and relative elevation. Stand age was included in regression analyses as a categorical variable. Relative elevation was used to estimate flooding frequency/duration. At each site, plots were grouped into one or more hydrologic units, depending on the primary direction of the slope and thus the prevailing direction of water flow. A point was located 50 m downstream from the plot with the lowest elevation within the hydrologic unit. The elevation of this downslope reference was then divided by the elevation of each plot. The greater the resulting quotient, the greater the presumed frequency/duration of flooding of the plot. Each plot was classified with respect to the age of the stand in which it was located (young, mature).

Regressions between *M. vimineum* and resident groundcover species

I used univariate and multivariate multiple regression approaches to test the hypothesis that *M. vimineum* invasion altered the composition of resident groundcover communities (hypothesis 1). To account for the influence of variables other than *M. vimineum* production on resident species, I first regressed *M. vimineum*

production against all environmental factors and eliminated non-informative predictor variables using a stepwise approach. Second, I used principal coordinates analysis to provide a proxy for species composition (the first principal coordinate axis) and then regressed the axis scores against all environmental factors, eliminating non-informative predictors using stepwise multiple regression. Third, I then regressed *M. vimineum* production against significant predictors of both response variables and used the resulting residual variation in *M. vimineum* production as the sole predictor variable in all subsequent linear, logistic, and multivariate regressions.

I used distance-based multivariate regression (specifically; distance-based redundancy analysis; Legendre and Anderson 1999; McArdle and Anderson 2001) to examine how the plant community as a whole responded to residual *M. vimineum* variation. Univariate partial linear and logistic regressions were used to examine how each common resident species responded to residual variation in *M. vimineum*. These analyses were restricted to those species that occurred in six or more sampling plots (hereafter, common species). All other species were classified as infrequent and were not examined individually using univariate regression. To determine the extent to which the results of the multivariate results reflected the statistically significant negative or positive univariate regressions between *M. vimineum* and common species, I re-ran the distance-based regression after excluding those species.

The relationship between *M. vimineum* and species composition was also assessed by examining the univariate correlation between residual *M. vimineum* production and habitat indication. This approach allowed me to determine the relationship between the pooled abundance of infrequent species and *M. vimineum* production. I calculated the weighted mean fidelity of each sampling plot assemblage to shady mesic forests, wetlands, and anthropogenically disturbed habitats. Habitat indicator scores for all species were obtained from Brewer (2010; the method of calculation of indicator scores is also described in Brewer 2008 and Brewer and Menzel 2009). To determine how infrequent species as a group responded to residual variation in *M. vimineum* production, I examined the correlation between their pooled abundances at each plot and residual *M. vimineum* production.

To test the hypothesis that per capita negative effects of *M. vimineum* were greatest within the areas in which *M. vimineum* was least productive (hypothesis 2), I determined whether the relationships between *M. vimineum* and resident species composition conformed to two conditions of the conceptual model presented in Fig. 1: Condition (1) A significant positive relationship between disturbance (e.g., canopy gap fraction) and the abundance/production of *M. vimineum* (A in Fig. 1), and Condition (2) A significant negative relationship between disturbance and the abundance of those resident species most vulnerable to competition from *M. vimineum* after accounting for the effect of disturbance on *M. vimineum* (B in Fig. 1). Provided these two conditions held, I concluded that the gross negative effect of *M. vimineum* on the resident plant community (C in Fig. 1) did not increase (and possibly decreased) with increasing disturbance (Result 1 in Fig. 1). If so, per capita negative effects of *M. vimineum* on the resident groundcover community (C/A) decreased with increasing disturbance (Result 2 in Fig. 1). A significant positive relationship between *M. vimineum* production and canopy gap fraction and/or flooding was considered evidence in support of condition 1. A significant negative relationship between the abundance of vulnerable resident species and disturbances (gaps or flooding) after accounting for *M. vimineum* production was taken as evidence in support of condition 2.

To test the hypothesis that the effects of *M. vimineum* invasion on resident species depended on resident species phenology (hypothesis 3), I used logistic regression to examine the relationship between the likelihood of occurrence of a resident species that was not fall active (i.e., was not green or flowered in the fall) and the average of the residual variation in *M. vimineum* production weighted by the abundance of the resident species across all plots in which the resident species occurred or:

$$P_i = \frac{\sum a_i p_i}{n}$$

where a_i was the abundance of a given resident species in plot i, p_i was the residual *M. vimineum* production in plot i, and n was the number of plots in which the resident species occurred. Because *M. vimineum* emerges in April and May and reaches peak production and flowering in October, I predicted that resident species that typically died or died back before fall were less likely to compete with *M. vimineum* and therefore would be relatively more positively associated with

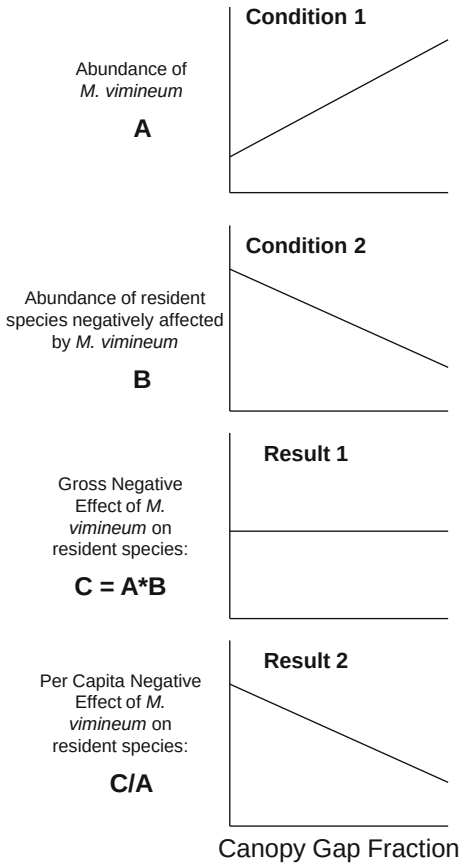

Fig. 1 A conceptual diagram illustrating a hypothetical scenario in which the per capita negative effects of *M. vimineum* on the resident plant community are lowest in areas in which *M. vimineum* is the most productive

M. vimineum than would fall active species. The distance-based multivariate regression was done using Primer 6 + Permanova. All univariate linear and logistic regressions were done using JMP version 5. Abundances of resident species were log transformed to normalize residuals in linear regression analyses.

Field competition experiments

To test the hypothesis that low abundance of resident species in invaded areas was the result of competition from *M. vimineum* (hypothesis 4), I used field experiments to examine the effects of competition from *M. vimineum* on the three most common native species that showed significant partial regression results, *C. laxum*, *Quercus alba*, and *Leersia virginica* Willd. I first transplanted clumps of *C. laxum* into patches of *M. vimineum* and examined reciprocal effects of density. Because *C. laxum* was a perennial bunchgrass that emerged before *M. vimineum*, I predicted that it might affect seedling emergence and growth of *M. vimineum*. I then examined the effect of removing *M. vimineum*, *C. laxum*, or neither on the performance of juvenile transplants of *Q. alba* and *L. virginica*. This experiment was conducted at site 3, a mature shady mesic floodplain forest dominated in the overstory and midstory by *Q. alba*. The groundcover at this site was dominated by *C. laxum*, a perennial bunchgrass. I predicted that *C. laxum* might influence the abundance or survival of *Q. alba* seedlings and *L. virginica*, as well as seedling emergence of *M. vimineum* in the spring following transplantation. Hence, the effect of removing *C. laxum* on *Q. alba* and *L. virginica* was considered a control for the effect of removing *M. vimineum*. To aid in the interpretation of the effect of removing either *M. vimineum* or *C. laxum* on the remaining two species, I regressed the natural abundance of *Q. alba* and *L. virginica* against *C. laxum* (controlling for flooding, gap fraction, and stand age).

I used a regression approach to examine competition between *M. vimineum* and *C. laxum*. A negative response of *C. laxum* to *M. vimineum* density combined with a non-negative response of *M. vimineum* to *C. laxum* density indicated the potential for competitive displacement of *C. laxum* by *M. vimineum*. On June 5, 2008, 48 0.3 × 0.3 m patches containing *M. vimineum* were located. Sixty-four clumps of *C. laxum* (10–15 cm in diameter) were located at the site. Of these, 48 were randomly assigned and transplanted to *M. vimineum* patches and 16 were left as unmanipulated controls. Initial counts of *M. vimineum* density and *C. laxum* were made after transplantation. In addition, I measured the length of the longest leaf of *C. laxum* and the height of the tallest plant of *M. vimineum*. I found that all transplanted clumps were still alive and apparently healthy 1 week after transplantation. On June 12, 2008, one-third of the plots were randomly assigned to the *Microstegium* removal treatment, another was assigned to the *C. laxum* removal treatment, and the remaining third was left unmanipulated (i.e., both species left intact). *Microstegium vimineum* was removed that day, but *C. laxum* removal was delayed until October 12, 2008 to provide sufficient statistical power to examine competitive effects of each species

on one another using the regression approach. There was no difference in growth rate between *C. laxum* clumps in *M. vimineum*-removal plots and the unmanipulated *C. laxum* clumps left intact in areas without *M. vimineum*. Hence, only analyses of transplanted clumps are presented. Overhead tree canopy density (arcsine square-root transformed proportion of sky obscured by foliage and branches), repeated measurements of percent soil moisture (arcsine square-root transformed and averaged), and soil compaction were measured at each plot to serve as covariables in the analysis of density effects on growth of *C. laxum* and *M. vimineum*. Canopy density was measured using a spherical densiometer. Percent soil moisture was measured using an Aquaterr portable soil moisture meter. Relative change in shoot density between May and October 2008 for both *C. laxum* and *M. vimineum* was calculated as ln(shoot density in October)—ln(shoot density in May). In addition, I examined the relative change in average shoot length. Competition intensity was quantified by separately regressing the relative rate of change in shoot density for each the two species against initial log density of *M. vimineum*, initial log density of *C. laxum*, and the three environmental variables. I used backwards stepwise regression to eliminate non-informative environmental covariables.

To examine competitive effects of *M. vimineum* and *C. laxum* on *L. virginica*, I first removed *C. laxum* from the 16 *C. laxum*-removal plots. I then located 48 non-flowering shoots of *L. virginica* on October 12, 2008 and transplanted them at random to the 48 plots. Each transplant was located adjacent to the clump of *C. laxum* (or the spot where it was located before it was removed) and adjacent to individuals of *M. vimineum*. Competitive effects were assessed by measuring relative changes in height, i.e., changes in log-transformed height between May 2009 and October 2009 after correcting for environmental covariables (if significant).

To examine competitive effects of *M. vimineum* and *C. laxum* on *Q. alba* seedlings, I located 48 juveniles (individual shoots < 25 cm with 1–4 primary leaves) of *Q. alba* on May 8, 2009, measured shoot length and root length, and transplanted them at random to the 48 plots. Each transplant was located adjacent to the clump of *C. laxum* (or the spot where it was located before it was removed) and adjacent to individuals of *M. vimineum* (but not adjacent to individuals of *L. virginica*). Survivorship was assessed on July 20, September 3, and October 25, 2009. Because no additional mortality was observed between July and October, analyses were based on survivorship to July 20.

Competitive effects were assessed statistically by examining the association between survivorship and removal treatment using Poisson regression. Two model predictions were tested. One was that survivorship would be greatest in plots in which only *M. vimineum* was removed, lowest in plots in which neither *M. vimineum* nor *C. laxum* was removed, and intermediate in plots in which only *C. laxum* removed. The other model prediction was that survivorship would be greatest in plots in which only *C. laxum* was removed, lowest in plots in which neither *M. vimineum* nor *C. laxum* was removed, and intermediate in plots in which only *M. vimineum* was removed. Prior to the Poisson regression, I used logistic multiple regression to verify that survivorship was not a function of initial size or any of the three environmental variables ($P > 0.26$). Poisson regression was done using Statistix version 8.

Results

Regression analyses

Multiple regression revealed that canopy gap fraction ($r = 0.6$) and flooding ($r = 0.23$) were significant, positive predictors of *M. vimineum* production (Fig. 2a, b), whereas canopy gap fraction ($r = 0.28$) and stand age ($F_{1,113} = 16.32$, $P \ll 0.01$) were significantly important predictors of species composition (Figs. 3a–c; 4a–c). Hence, all univariate and multivariate regressions with *M. vimineum* production were corrected for variation in flooding, canopy gap fraction, and stand age.

Consistent with hypothesis 1, results of the distance-based multivariate regression showed that 1.8% of the variation in species composition among plots could be explained by residual *M. vimineum* production, which, though rather small, was statistically significant ($F = 2.07$; $P = 0.03$; df $= 115$). Much of the variation in species composition explained by *M. vimineum* was attributable to negative and positive relationships with a few common species. The seven common species that showed significant ($P < 0.05$) negative linear or logistic relationships with

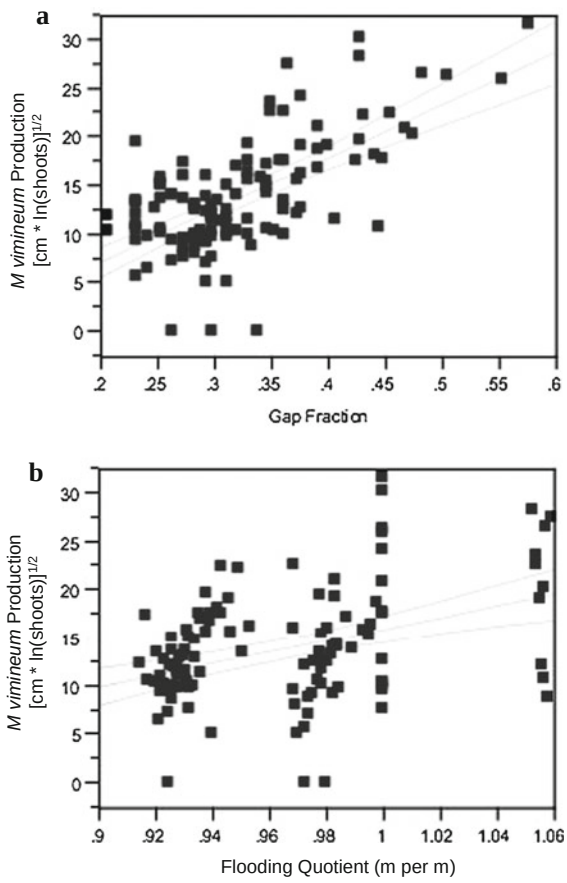

Fig. 2 Scatterplots of *M. vimineum* production versus **a** canopy gap fraction and **b** flooding with regression lines and 95% confidence intervals. *Microstegium vimineum* production was quantified indirectly by taking the square root of the product of log shoot density and height of the tallest shoot in cm

M. vimineum (Appendix) were indicative of shady mesic forests (Brewer 2010). In contrast, the three common species that showed significant positive relationships with *M. vimineum* (Appendix) were not indicative of any particular habitat (Fig. 4a–c). When the ten species that showed significant linear or logistic univariate regression results were removed from the data matrix, distance-based multivariate regression revealed a weaker relationship between *M. vimineum* production and species composition that was not statistically significant ($r^2 < 0.01$; $F = 1.04$; $P = 0.36$). Upon aggregating common and infrequent species with respect to habitat indication, I found a positive relationship between *M. vimineum* production and the abundance or occurrence of species indicative of disturbed habitats. The weighted mean fidelity of plot species composition to disturbed habitats was significantly positively correlated with residual *M. vimineum* production ($r = 0.2$; $P = 0.03$; Table 1). Weighted mean fidelities of plot species composition to shady mesic forests and wetlands were not significant (Table 1).

Consistent with hypothesis 2, the per capita negative effect of *M. vimineum* on the resident plant community appeared to be greatest in areas in which *M. vimineum* was typically unproductive (shady areas). This is because the abundance of *M. vimineum* was lowest in shady areas (Condition 1 in Figs. 1, 2a), whereas vulnerable resident species were largely absent from gaps (Condition 2 in Fig. 1). Examination of Fig. 3 reveals that canopy gap fraction and *M. vimineum* production both increased independently of one another with increasing PCO axis 2 scores, whereas the abundances of the three most common resident species to show negative relationships with *M. vimineum* tended to be greatest in plots with low axis 2 scores (Fig. 3a–c). Hence, these species were negatively correlated with *M. vimineum* production (irrespective of canopy gap fraction) and were negatively correlated with canopy gap fraction (irrespective of *M. vimineum* production). In other words, they were negatively correlated with *M. vimineum* production within shady forests, where the density of *M. vimineum* tended to be relatively low. In contrast, the abundances of the three most common resident species to show positive relationships with *M. vimineum* tended to be greatest in plots with high axis 2 scores (Fig. 4a–c). Hence, these species were abundant in gaps and in plots in which *M. vimineum* was most productive (Fig. 4a–c).

Consistent with hypothesis 3, phenology, especially phenological differences between *M. vimineum* and disturbance indicators that were not fall active, appeared to explain some of the relationship between *M. vimineum* production and species composition. Species that were not fall active were positively associated with high *M. vimineum* production (logistic regression log-odds coefficient = 1.13; Wald chi-square = 6.25; $P = 0.012$). Examples of species that were not fall active and associated with plots with high *M. vimineum* production included *Nothoscordum bivalve* (L.) Britton, *Ophioglossum vulgatum* L., *Krigia dandelion* L. (Nutt.), *Erigeron annuus* (L.) Pers., *E. philadelphicus* L., *Cerastium vulgatum* L., *Trillium recurvatum* L.C. Beck, *Rumex crispus* L., *Stellaria*

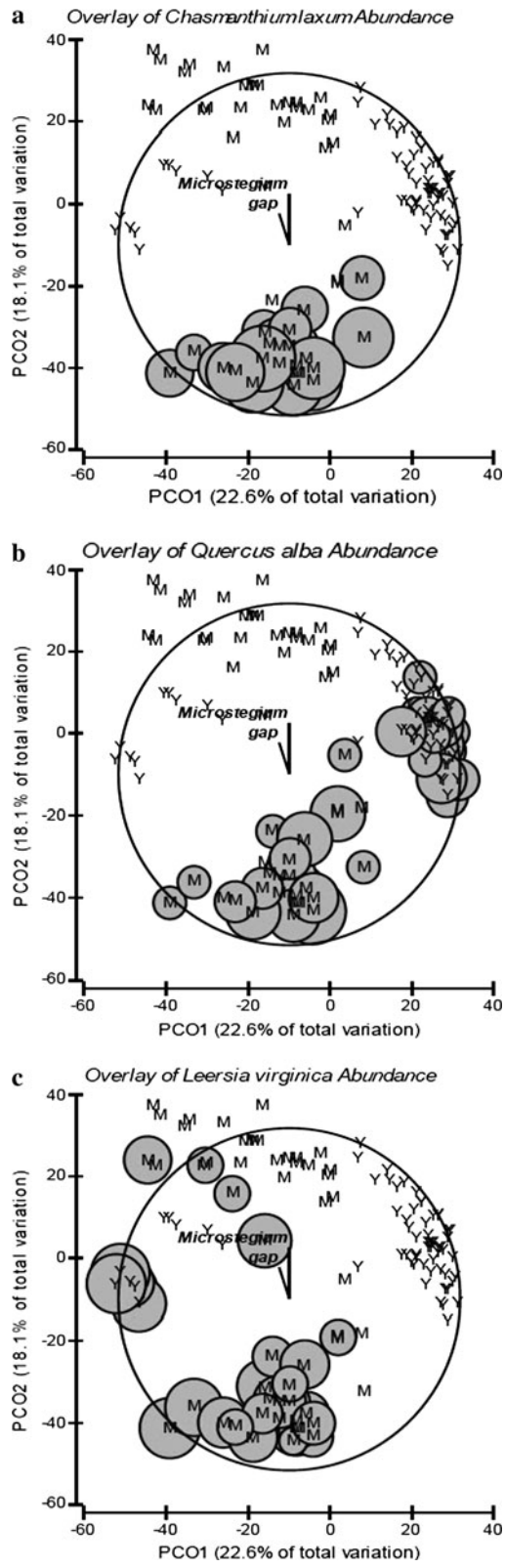

Fig. 3 Principal coordinates analysis ordinations of sampling plots showing vectors derived from partial regression coefficients of canopy gap fraction and *M. vimineum* production, symbols coded according to stand age (M for mature, Y for young), and quantitative bubble overlays of the abundances of the three most common species that were negatively correlated with residual *M. vimineum* production. Larger bubbles indicate greater abundance of the species within the plot. Analysis was performed on the Bray-Curtis distance matrix

pubera Michx., and *Allium vineale* L. Most of these species were indicative of disturbed habitats, but *Ophioglossum vulgatum* and *Trillium recurvatum*, both reliable indicators of shady mesic forests, were notable exceptions (Brewer 2010). Species that were not fall active were positively associated with disturbance indication (logistic regression log-odds coefficient = 2.21; Wald chi-square = 3.8; $P = 0.051$). Rare species that were not fall active were positively associated with high *M. vimineum* production (logistic regression log-odds coefficient = 0.27; Wald chi-square = 5.29; $P = 0.021$; Fig. 5). Otherwise, there was no relationship between the abundance of rare species in general and residual *M. vimineum* production ($r = 0.07$; Table 2).

The positive association of *M. vimineum* with disturbance indicators was not entirely explained by complementary phenologies. After removing nine species that were good disturbance indicators and not fall active, the positive correlation between residual *M. vimineum* production and the weighted mean fidelity of the remaining species to disturbed habitats was still statistically significant ($r = 0.185$, $P = 0.045$).

Field experiment

As predicted by hypothesis 4, *Chasmanthium laxum* appeared to respond negatively to *M. vimineum*, whereas the reverse was not true. Relative change in shoot densities of *C. laxum* in 2008 was negatively correlated with initial *M. vimineum* density, even after accounting for environmental variation and initial *C. laxum* density ($r = -0.38$; $P = 0.03$). The only significant covariable was initial *C. laxum* density ($r = -0.58$; $P < 0.001$). Relative change in *C. laxum* height was not significantly correlated with initial *M. vimineum* density or any covariable ($P > 0.18$). In contrast to *C. laxum*, relative change in shoot density of *M. vimineum* in 2008 was not significantly

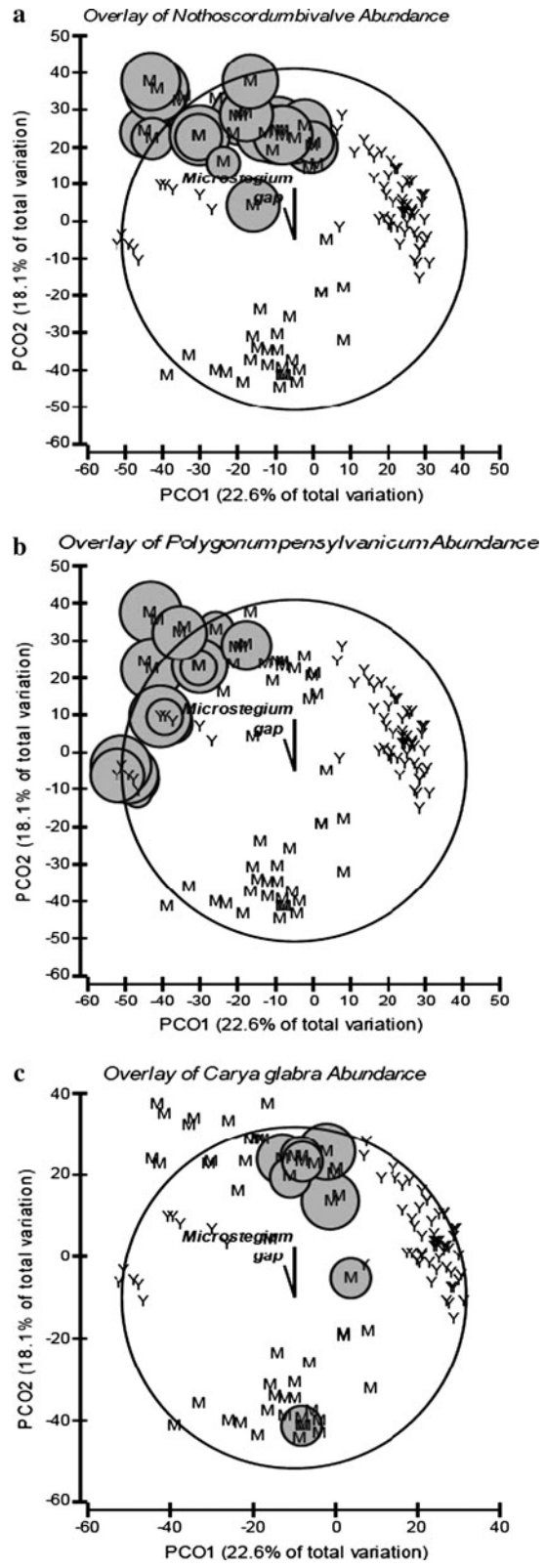

Fig. 4 Principal coordinates analysis ordinations of sampling plots showing vectors derived from partial regression coefficients of canopy gap fraction and *M. vimineum* production, symbols coded according to stand age (M for mature, Y for young), and quantitative overlays of the relative abundances of the three common species that were positively correlated with residual *M. vimineum* production. Analysis was performed on the Bray-Curtis distance matrix

correlated with initial *C. laxum* density ($r = -0.13$; $P = 0.43$). It was, however, significantly negatively correlated with initial *M. vimineum* density ($r = -0.46$; $P < 0.001$). The removal of *C. laxum* also did not significantly affect the relative change in shoot density of *M. vimineum* between June 2008 and May 2009. After correcting for the negative effect of initial *M. vimineum* density, the relative change in *M. vimineum* density was 0.046 ± 0.14 s.e versus 0.049 ± 0.11 s.e. in *C. laxum*-removal and control plots, respectively; $F_{1,28} = 0.27$; $P = 0.61$). For both species, shoot density on October 25, 2009 was highly positively correlated with total dry biomass of excavated shoots/clumps ($r = 0.67$ and 0.61 for *M. vimineum* and *C. laxum*, respectively). Hence, the results based on relative change in shoot density were assumed to apply to biomass as well.

The removal and sustained exclusion of either *M. vimineum* or *C. laxum* had a positive effect on height growth in *L. virginica*. Relative change in *L. virginica* height between May and October 2009 differed significantly among treatments ($F_{2,42} = 3.63$; $P = 0.03$; Fig. 6). Relative height growth (cm per cm per growing season) was significantly greater in *C. laxum*- and *M. vimineum* removal treatments than in the control plots (0.25 and 0.26 versus -0.51, respectively; $t = 2.69$; two-tailed $P = 0.01$) but did not differ between *M. vimineum*- and *C. laxum*-removal treatments ($t = 0.85$; two-tailed $P = 0.4$). Height was highly positively correlated with dry mass ($r = 0.69$, based on sample of 20 discarded plants; $P < 0.01$). Correlations between relative growth rate and October 2008 height and environmental variables were not statistically significant; therefore, none was included as a covariable in the analysis.

Consistent with hypothesis 4, the survival of *Q. alba* seedlings was increased more by the removal of *M. vimineum* than by the removal of *C. laxum* (Fig. 7). Survival (0.5) was low, however, even in the *M. vimineum* removal treatment, suggesting a negative effect of uprooting. This experimental result was

Table 1 Correlations of weighted mean habitat fidelity and rare species abundance with residual *M. vimineum* production

Variable	*r*	*P*
Weighted mean fidelity to Mesic forests	0.03	0.73
Weighted mean fidelity to Wetlands	0.02	0.85
Weighted mean fidelity to disturbed areas	0.2	0.03
Weighted mean fidelity to disturbed areas with nine disturbance indicators that were not fall active excluded	0.18	0.045
Sum of rare species abundance (Unweighted)	0.07	0.44

consistent with the partial regression result that revealed no negative relationship between *C. laxum* and *Q. alba*. In fact, there was a highly significant positive relationship between the abundance of *Q. alba* and that of *C. laxum* ($r = 0.51$; $P \ll 0.01$; df = 112). The Poisson regression model that predicted that survivorship would be greatest when *M. vimineum* was removed and lowest when neither *M. vimineum* nor *C. laxum* was removed better fit the data ($\chi^2 = 0.33$, $P = 0.85$, df = 2) than one that assumed independence between the removal treatment and survivorship ($\chi^2 = 4.94$, $P = 0.18$, df = 3). This difference was statistically significant ($\chi^2 = 4.61$, $P = 0.03$, df = 1). In contrast, the Poisson regression model that predicted that survivorship would be greatest when *C. laxum* was removed ($\chi^2 = 4.88$, $P = 0.09$, df = 2) did not fit the data better than one that assumed independence between removal treatment and survivorship ($\chi^2 = 4.94$). The difference in fit was not statistically significant ($\chi^2 = 0.06$, $P = 0.8$).

Discussion

The current study adds to a growing list of studies examining the effects of *M. vimineum* on plant communities under natural conditions (e.g., Belote and Weltzin 2006; Oswalt et al. 2007; Adams and Engelhardt 2009; Marshall et al. 2009; Flory and Clay 2010). The current study differed from most previous studies in that it used a multivariate regression approach to examine per capita community-level effects of an invader and then addressed the causes of regression results for the most common species using field experiments. I found support for all four hypotheses tested here, which is discussed in greater detail.

Consistent with hypothesis 1, *M. vimineum* production accounted for a small but significant percentage (1.8%) of resident species composition. Stand age was a much more important predictor of composition than was *M. vimineum*. In addition, the low percentage of variation in resident plant species composition accounted for by *M. vimineum* production resulted in part from both being directly influenced by canopy gaps. *Microstegium vimineum* was more productive in gaps (which is consistent with

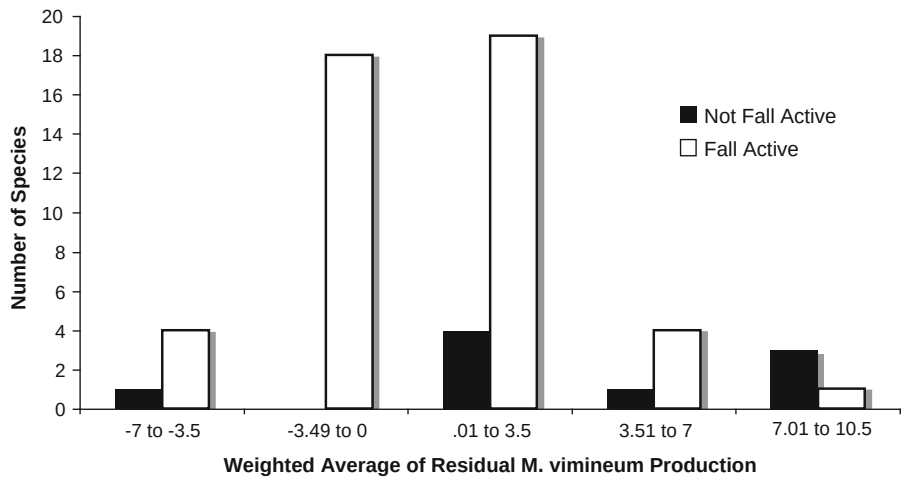

Fig. 5 Frequency distribution of infrequent fall active or not fall active species in relation to residual variation in *M. vimineum* production weighted by the abundance of the resident species in all plots in which each species occurred (see text for a more detailed description and calculation). Because *M. vimineum* production is corrected for gap fraction, flooding, and stand age, half of the resulting residuals were negative, thereby giving rise to negative products of residual *M. vimineum* production and the abundance of the resident species

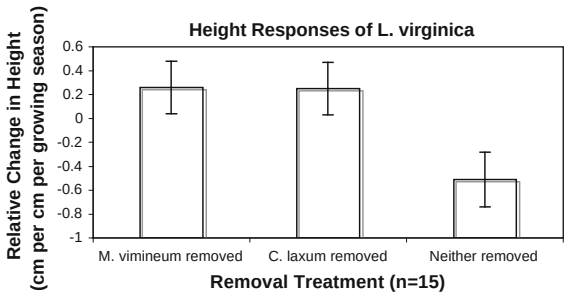

Fig. 6 Relative increase in shoot height of *L. virginica* in response to removal of *M. vimineum*, *C. laxum*, or neither. Values are group means ± 1 standard error. $N = 14$, 16, and 15 for the *M. vimineum* removal, the *C. laxum* removed, and the neither removed treatments, respectively

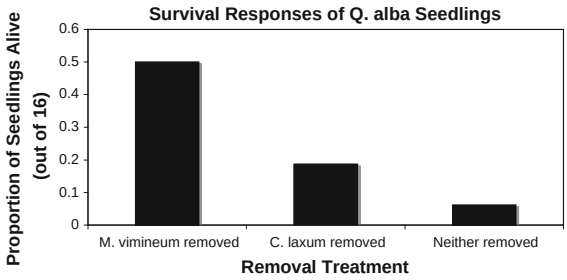

Fig. 7 Survival of *Q. alba* seedlings in response to removal of *M. vimineum*, *C. laxum*, or neither. Survival of seedlings in response to the removal of *M. vimineum* (8 of 16) was not significantly different from that of uprooted and replanted controls (6 of 10; $\chi^2 = 0.25$; $P = 0.62$; df = 1)

findings of other studies; Cole and Weltzin 2005; Glasgow and Matlack 2007; Brewer 2010), whereas gaps appeared to directly favor some resident species but negatively affect others.

The relationship between resident species composition as a whole and *M. vimineum* production was largely driven by negative relationships with seven common mesic forest indicators and positive relationships with three common species that were not indicative of any one habitat. *Chasmanthium laxum*, *Q. alba*, *L. virginica, Dichanthelium boscii* (Poir.) Gould and Clark, *Ulmus americana* L., *Carpinus caroliniana*, and *Symphyotrichum racemosum* (Elliott) G.L. Nesom were significantly negatively correlated/associated with *M. vimineum*. None of these species tended to occur in canopy gaps in this study, even in plots in which *M. vimineum* was sparse or absent. Rather, they were largely restricted to shady mesic forests, where *M. vimineum* was much less productive. This result suggests that shady mesic forests are more likely to contain species that are vulnerable to displacement by *M. vimineum* than are disturbed areas or open floodplain forests.

Consistent with hypothesis 2, the per capita negative effect of *M. vimineum* on the resident plant community appeared to be greatest within shady areas, where it was the least abundant or productive. In contrast, it appeared to either have little effect or was positively associated with species in open floodplains, where it was the most productive. The two conditions necessary to support the hypothesis that per capita negative effects of *M. vimineum* were greater in areas where it relatively unproductive were met (Figs. 1, 3a–c). The abundance and productivity of *M. vimineum* was greater in gaps than away from gaps (Condition 1). The species most vulnerable to competition from *M. vimineum* were more abundant away from gaps than within gaps (Condition 2). In fact, it is possible that the gross competitive effects were also greater in shady areas than in open areas. A previous study of *M. vimineum* effects on the resident plant community revealed more substantial negative effects than observed here (Adams and Engelhardt 2009). In that study, however, all sampling plots were located away from large canopy gaps. Together, the results of that study and the current study suggest that the competitive effects of *M. vimineum* on resident composition might be greatest in shady and relatively unproductive patches of *M. vimineum* within mesic forests.

Consistent with hypothesis 3, phenological complementarity appeared to account for the positive associations between *M. vimineum* production (which peaked in the fall) and one common species *Nothoscordum bivalve* and several infrequent species in the forests studied here. *Nothoscordum bivalve* dies back by the late summer. Most infrequent species that were positively associated with *M. vimineum* were winter annuals or spring ephemerals, and many but not all were indicative of disturbed habitats. Phenological complementarity could partly explain findings of previous studies that showed significant negative partial correlations between *M. vimineum* and species richness late in the growing season but not in the spring (Adams and Engelhardt 2009; Brewer 2010). Even after removing winter annuals and spring ephemerals from the analysis, however, *M. vimineum* production was still positively correlated with the weighted mean fidelity of the remaining species to disturbed habitats, which suggests either facilitation

(Bruno et al. 2005) or positively-correlated propagule production and colonization rates (Levine 2000; Stachowicz and Tilman 2005). It is possible that increases in soil nitrate and/or pH by *M. vimineum* (Ehrenfeld et al. 2001) facilitated some resident disturbance indicators. Alternatively, *M. vimineum* and many resident disturbance indicators might have been the first to colonize localized patchy soil disturbances (Cole and Weltzin 2004; Marshall and Buckley 2008). Positive associations with resident species that were indicative of disturbed areas might contribute to a reduced per capita negative impact in disturbed areas relative to undisturbed areas, given that *M. vimineum* tends to be more abundant in disturbed areas.

Consistent with hypothesis 4, experiments conducted within a generally shady mesic forest (Site 3) showed that competition was most likely responsible for the significant negative relationships between *M. vimineum* and the abundances of two (and possibly all three) of the three most common species. There were asymmetric competitive effects of *M. vimineum* on *C. laxum* and increased *Q. alba* seedling survival and growth of *L. virginica* following the removal of *M. vimineum*. Seedlings of *Q. alba* responded better to *M. vimineum* removal than to *C. laxum* removal, suggesting that invasion by *M. vimineum* could inhibit recruitment of this ecologically and economically important tree species. These results are remarkable when one considers that negative effects were observed in the first growing season (see Marshall et al. 2009 for evidence of first-year effects on other species of tree seedlings) and at a site at which *M. vimineum* was the least productive. Even in the most productive patches at this site (Site 3), the tallest plants of *M. vimineum* were less than 50 cm tall, which is less than half the size of plants observed in canopy gaps in floodplains.

The equally positive responses of *L. virginica* to the removal of either *M. vimineum* or the native groundcover dominant, *C. laxum*, suggest competitive displacement of *L. virginica* by *M. vimineum*, by itself, is not sufficient to account for the negative relationship between these two species. How each of these species responds to disturbance must also be taken into consideration. Unlike *Q. alba*, *L. virginica* was not positively associated with *C. laxum* ($r = -0.04$; $P = 0.67$; df = 112). In fact, it appeared to show a unimodal relationship, which (along with the experimental results) suggests that *L. virginica* may require disturbances in areas of high *C. laxum* density to get established. If so, the propensity for *M. vimineum* to rapidly colonize disturbed patches within mesic forests (where *C. laxum* density is low; Marshall and Buckley 2008) may leave few opportunities for *L. virginica* to get established in either undisturbed or disturbed areas within these forests.

Implications for the management and control of *Microstegium vimineum*

The inverse relationship between productivity of an invader within an area and its per capita negative impact within an area poses a dilemma for managing such invasive species (Parker et al. 1999). On the one hand, productive stands of an invasive species are likely to be the most important seed sources (Cheplick 2008; Huebner 2010). Hence, focusing control efforts on more productive areas will likely be the most effective strategy for limiting further expansion of populations. On the other hand, if a land manager were to focus his/her effort on local eradication of *M. vimineum* in habitats in which it was most productive using non-selective chemical or mechanical treatments, this approach could have unintended, undesirable consequences. It could locally decimate populations of native floodplain and gap specialists that were not responding negatively (or were responding positively) to *M. vimineum*, while disregarding competitive displacement of mesic forest specialists by *M. vimineum* in shady mesic forests. Limiting the impact of invasive plants on native biodiversity requires ranking sites not only in terms of the productivity of an invasive plant, but also ranking community types in terms of their responses to invasive species.

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Appendix

See Table 2.

Table 2 Results of partial linear and logistic regressions of abundance and occurrence of common species versus *M. vimineum* production

Common species	Total # of occurrences	*r*	*P*	Coefficient–log-odds occurrence	SE	Wald χ^2	*P*
Acer negundo	16	0.14	0.12	0.39	0.29	1.75	0.19
Acer rubrum rubrum	15	−0.07	0.46	−0.07	0.27	0.07	0.80
Ageratina altissima	24	−0.06	0.53	−0.17	0.22	0.58	0.45
Agrimonia rostellata	6	0.11	0.26	0.61	0.47	1.67	0.20
Asplenium platyneuron	11	−0.11	0.25	−0.42	0.30	2.05	0.15
Boehmeria cylindrica	7	−0.15	0.10	−0.48	0.35	1.83	0.18
Botrychium virginianum	19	−0.06	0.53	−0.28	0.24	1.33	0.25
Carpinus caroliniana	11	−0.19	0.04	−0.57	0.29	3.80	0.05
Carya glabra	8	0.21	0.02	0.84	0.43	3.76	0.05
Carya tomentosa	14	−0.04	0.67	−0.16	0.28	0.34	0.56
Cercis canadensis	19	−0.02	0.80	−0.09	0.25	0.13	0.72
Chasmanthium latifolium	12	−0.10	0.44	−0.19	0.29	0.42	0.52
Chasmanthium laxum	22	−0.28	0.00	−0.52	0.23	4.88	0.03
Claytonia virginica	11	0.03	0.77	0.09	0.32	0.08	0.78
Clematis virginiana	8	0.05	0.62	0.13	0.38	0.13	0.72
Dichanthelium boscii	10	−0.20	0.03	−0.71	0.31	5.28	0.02
Elephantopus carolinianus	15	−0.06	0.50	−0.36	0.26	1.87	0.17
Erechtites hieraciifolia	13	0.05	0.61	0.17	0.31	0.33	0.57
Fraxinus americana	66	−0.07	0.43	−0.11	0.19	0.36	0.55
Galium aparine	11	0.12	0.19	0.25	0.34	0.55	0.46
Leersia virginica	31	−0.18	0.06	−0.56	0.22	6.40	0.01
Ligustrum sinense	61	−0.05	0.58	−0.14	0.19	0.60	0.44
Liriodendron tulipifera	6	−0.03	0.73	−0.14	0.40	0.12	0.73
Lonicera japonica	79	0.07	0.45	−0.09	0.20	0.22	0.64
Nothoscordum bivalve	19	0.20	0.03	0.53	0.29	3.46	0.06
Nyssa sylvatica	8	0.06	0.52	0.37	0.40	0.86	0.35
Ophioglossum vulgatum	7	0.06	0.53	0.14	0.40	0.12	0.73
Parthenocissus quinquefolia	55	0.03	0.73	−0.04	0.19	0.06	0.81
Podophyllum peltatum	16	−0.08	0.41	−0.14	0.26	0.27	0.60
Polygonum pensylvanicum	17	0.19	0.04	−0.21	0.37	0.33	0.57
Polygonum virginianum	70	0.12	0.20	0.19	0.27	0.47	0.50
Polystichum acrostichoides	7	−0.05	0.58	−0.81	0.58	1.93	0.17
Prunus serotina	36	0.02	0.83	0.16	0.21	0.61	0.43
Quercus alba	39	−0.20	0.03	−0.29	0.20	2.19	0.14
Quercus falcata	27	0.12	0.19	0.24	0.23	1.07	0.30
Quercus nigra	9	−0.02	0.83	−0.10	0.34	0.10	0.76
Rubus argutus	23	−0.15	0.12	−0.39	0.23	2.84	0.09
Rubus trivialis	34	−0.14	0.14	−0.32	0.21	2.47	0.12
Sanicula canadensis	23	0.03	0.73	−0.03	0.23	0.02	0.90
Sanicula trifoliata	13	0.12	0.20	0.30	0.31	0.90	0.34
Sassafras alba	6	−0.04	0.69	−0.17	0.40	0.17	0.68
Smilax bona-nox	8	0.06	0.50	0.39	0.40	0.97	0.33
Smilax glauca	62	−0.07	0.47	−0.22	0.19	1.34	0.25

Table 2 continued

Common species	Total # of occurrences	*r*	*P*	Coefficient–log-odds occurrence	SE	Wald χ^2	*P*
Smilax rotundifolia	30	0.14	0.13	0.29	0.23	1.64	0.20
Symphyotrichum racemosum	6	−0.10	0.20	−0.76	0.37	4.19	0.04
Toxicodendron radicans	42	−0.03	0.73	−0.03	0.19	0.03	0.86
Ulmus alata	16	0.07	0.43	0.20	0.28	0.48	0.49
Ulmus americana	6	−0.21	0.02	−0.71	0.37	3.73	0.05
Viola sororia missouriensis	10	0.04	0.67	0.10	0.34	0.09	0.77
Vitis rotundifolia	40	−0.08	0.37	−0.11	0.19	0.30	0.59

Nomenclature follows Jones (2005)

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