

A Potential Conflict between Preserving Regional Plant Diversity and Biotic Resistance to an Invasive Grass, *Microstegium vimineum*

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ABSTRACT: The relevance of diversity-biotic resistance studies to conservation of biodiversity could be improved by simultaneously examining the drivers of regional diversity and their effects on local species diversity and invasion. Using path analysis, I examined direct and indirect effects of various abiotic factors (i.e., flooding, treefall gaps, soil texture, proximity to roads, and stand age) on plant species richness, floristic quality (a proxy for regional plant diversity), and the abundance of a non-native invasive grass, *Microstegium vimineum*, in 117 3.14-m² plots within four stands of mesic floodplain forests in northern Mississippi. Results of this study showed a significant negative effect of species richness on *M. vimineum* abundance in year two. However, species richness varied in response to flooding and gaps, and the positive indirect effects of flooding and gaps on *M. vimineum* abundance mediated through reductions in species richness in fall 2008 were not nearly as great as the positive direct effects of these disturbances on *M. vimineum* abundance. In contrast to species richness, floristic quality (weighted mean fidelity to mesic forests or wetlands minus fidelity to anthropogenically disturbed areas) responded positively to gaps in flooded areas and was not affected by *M. vimineum*. Altogether, these results suggest that the same factors that reduce biotic resistance have even greater direct positive effects on the abundance of an invasive grass and native floodplain specialists. Control of *M. vimineum* in mature floodplain forest ecosystems should be done selectively to avoid collateral damage of native floodplain specialists.

Index terms: competition, disturbance, floodplain, floristic quality, habitat specialists, mesic forest, *Microstegium vimineum*, path analysis, wetlands

INTRODUCTION

The resistance of diverse assemblages to invasions, as hypothesized by Elton (1958), has been a focus of much recent research and controversy (Robinson et al. 1995; Levine 2000; Stohlgren et al. 2001; Sax et al. 2002; Zavaleta and Hulvey 2004; Stachowicz and Tilman 2005). All else being equal, if species losses make communities more invulnerable, then management practices aimed at preserving species diversity could have the added side benefit of reducing the impact of non-native species on natural communities (Elton 1958; Levine 2000). Therefore, experiments of diversity/invasibility relationships inform not only patterns of community assembly but, potentially, also land management decisions.

Diversity-invasibility relationships will be most relevant to efforts at conserving biodiversity when (1) diversity-mediated effects on invasion have realistic causes and that these causes of diversity are not already recognized to have strong direct effects on invasion; (2) the environmental factors that reduce species diversity locally also reduce habitat specialists and thus regional biodiversity; and (3) increased abundance of non-native species reduces habitat specialists. Conservation biologists and ecologists have disputed one or more of these assumptions (Alverson et al. 1994; Schwartz et al. 2000; Davis 2003; Gurevitch and Padilla 2004; Weiher et al.

2004; Gagnon and Platt 2008). Alternative approaches are, therefore, needed to examine diversity-invasion relationships, which include a multivariate approach to examining direct and indirect effects of drivers of diversity on invasion, a regional perspective on biodiversity conservation, and an examination of the actual impacts of invasive species.

Drivers of species diversity that can be altered by management decisions may have both direct and indirect effects on invasion. Most land managers are aware of the direct effects of some environmental factors on both diversity and invasions, even if they are not aware of the effects of these same factors on diversity-mediated biotic resistance to invasions. For example, although disturbances may indirectly promote invasions by reducing resident species diversity (Zavaleta and Hulvey 2004), the more common and widely recognized mechanism by which disturbances promote invasions is by directly providing safe sites for establishment (Hobbs and Huenneke 1992; Burke and Grime 1996). Hence, experimentally demonstrating an indirect positive effect of disturbances on invasion mediated through a reduction in local species diversity would be superfluous for management decisions if the direct effects of these disturbances on invasion were even greater.

Although most diversity-invasibility experiments focus on the effects of local

species diversity, fidelity of local assemblages to regionally rare habitats is more relevant to biodiversity conservation than is the preservation of local species diversity (Alverson et al. 1994; Rosen et al. 2008). Regional biodiversity is more likely to be affected by local extirpation of species that specialize in regionally rare or declining habitats than by local extirpation of widespread generalists. Most species vulnerable to extinction tend to be local endemics and habitat specialists (Cody 1986; Lawton and May 1995; Farnsworth 2007). These species need not be locally rare or sparse (Rabinowitz et al. 1989; Walker 1993), nor would their local abundance necessarily be positively correlated with local species diversity (Whittaker 1972; Alverson et al. 1994). Local species richness and the abundance of habitat specialists may respond to some environmental factors or management practices in opposite ways. For example, in some situations, anthropogenic disturbances such as the clearing of forests can result in a short-term local increase in species richness of widespread weeds but reduce metapopulation viability of forest specialists within forest fragments due to a regional loss or degradation of suitable forest habitat (Nee and May 1992; Alverson et al. 1994). In contrast, some natural disturbances may directly benefit native habitat specialists that are adapted to the disturbances while filtering out and reducing the local richness of non-tolerant generalist species (Collins et al. 1995; Brewer et al. 1998; Gagnon and Platt 2008). Such disturbances could increase regional diversity or wildlife habitat quality without increasing local species diversity (Noss et al. 1995; Gagnon and Platt 2008).

Conservationists are most concerned by invasive species that have demonstrably negative effects on species of significant conservation concern, including habitat specialists. Invasive species are defined here as those that acquire a competitive advantage (*sensu lato*) following the removal of natural obstacles to dispersal among ecosystems, which enables them to spread rapidly and dominate areas within recipient ecosystems (Valéry et al. 2008). It is impossible to prove that an invasive species has no undesirable impact on the resident ecosystem. Hence, efforts at control may

be worthwhile, even if the invader has not been shown to have a measurable effect on native habitat specialists. Nevertheless, the lack of an effect on native habitat specialists should impel land managers to opt for selective over non-selective methods of control.

Path analysis presents a potentially powerful alternative to manipulative experiments for examining not only diversity-invasibility relationships, but also their relevance to natural field conditions and land management decisions. Although manipulative experiments, when feasible, remain the best approach for testing biotic resistance to invasion, they do not actually quantify the importance of biotic resistance relative to that of other causes of invasion in the field (Levine 2000). Furthermore, diversity-invasibility experiments typically examine only the initial invasion and not the subsequent impact of the invaders on the abundance of species of potential conservation concern, such as habitat specialists. By simultaneously examining multiple response variables, path analysis is an appropriate technique for identifying important drivers of diversity and their direct and indirect impacts on invasion, as well as the direct effects of the drivers of diversity and invaders on habitat specialists.

This study used path analysis to test three specific hypotheses (Table 1) that, if correct, call into question the relevance of species richness-mediated biotic resistance to conservation: (1) natural disturbances (such as flooding and canopy gaps) increase the abundance of a non-native invasive grass, *Microstegium vimineum* (Trin.) A. Camus, by reducing local species richness of the groundcover flora of forests in northern Mississippi, but such indirect effects are not as great as the direct positive effects of these disturbances on the abundance of *M. vimineum*; (2) the factors that reduce local plant species richness (e.g., canopy gaps) simultaneously increase floristic quality (weighted mean fidelity of local plant assemblages to regionally rare or threatened habitats minus fidelity to anthropogenically disturbed habitats); and (3) *M. vimineum* has little effect on floristic quality.

METHODS

Description of *Microstegium vimineum*

A native of East Asia, *Microstegium vimineum* was 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 benefits from disturbance 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 m²), 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 (Glasgow and Matlack 2007; Marshall and Buckley 2008). *M. vimineum* has also been shown to competitively suppress native perennial grasses and forbs in additive competition experiments under controlled garden conditions (Flory et al. 2007) and may benefit from reduced competition following deer herbivory (Knight et al. 2009). It also alters soil microbial communities and associated ecosystem processes (Kourtev et al. 2003). It is remarkably shade-tolerant for a C4 grass (Winter et al. 1992; Horton and Neufeld 1998) 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). The ability of this species to persist in shaded forests potentially enables it to respond rapidly to severe disturbances of these forests and produce productive stands immediately following these disturbances (Oswalt et al. 2007).

Description of Field Sites and Sampling Design

All work was conducted within forests located on mesic slopes/terraces and floodplains in north-central Mississippi, corresponding to the Pleistocene loess

Table 1. Hypotheses tested during this study (H1 to H3) and associated path analyses.

General Hypothesis	Specific Hypothesis	Associated Path Analysis
H1: Direct effects of disturbances on invasion are greater than biotic resistance.	H1: Disturbances (flooding, canopy gaps) increase the abundance of <i>Microstegium vimineum</i> by reducing local species richness of the fall flora, but such indirect effects are not as great as the direct positive effects of these disturbances on the abundance of <i>M. vimineum</i> .	Using path models 1a (fall data) and 1b (spring and fall data), show that the direct effect of gap and the sum of the direct effect of flooding and the indirect effect of flooding via gap on <i>M. vimineum</i> is greater than sum of these indirect effects of these disturbances on <i>M. vimineum</i> via fall richness.
H2: Increasing biotic resistance conflicts with maintaining floristic quality.	H2: The factors that reduce local plant species richness (e.g., flooding, gaps) simultaneously increase floristic quality.	Using path model 2, show that at least one of the factors that significantly decreases local species richness significantly increases floristic quality.
H3: Invaders do not reduce floristic quality.	H3: <i>Microstegium vimineum</i> production has little effect on floristic quality.	Using path model 3, show that the path lead to floristic quality from <i>M. vimineum</i> is not statistically significant.

plains region and the adjacent loess/sandy loam transition into the Eocene hills region (Surrette and Brewer 2008). In fall 2007, I established 125 1-m-radius plots in each of four floodplain and mesic forest stands. Two of the stands were relatively young (< 20 years old) and located close to disturbed roads or powerline clearings (average distance = 45 m, S.D. = 22 m; minimum = 23 m, maximum = 128 m), and two were mature (> 60 years old) stands within the interior of larger tracts of forest (average distance = 539 m, S.D. = 149 m; minimum = 338 m, maximum = 724 m). One of the young stands was dominated by sweetgum (*Liquidambar styraciflua*) and sycamore (*Platanus occidentalis*) and occurred in an impounded floodplain with sandy loam soils (Site 1). See Appendix 1 for taxonomic authorities. 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*) 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*) and sweetgum, with red maple (*Acer rubrum*), winged elm (*Ulmus alata*), hop hornbeam (*Ostrya virginiana*),

and blue beech (*Carpinus caroliniana*) limited primarily to the understory. 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*).

Sampling plots were arranged within each stand to encompass as wide a range of gap conditions, soil texture, elevation, and *Microstegium vimineum* densities as possible. Every plot contained at least one rooted stem or branch of *M. vimineum* in fall 2007. Densities ranged from 1 to 996 stems in 2007. Censusing of the plots began in fall 2007, with two additional census seasons in April 2008 and throughout the fall of 2008. Densities of *M. vimineum* ranged from 1 to 1360 stems in 2008. Between December 2007 and April 2008, flags of eight plots (all in floodplains) were washed away by

floodwaters and could not be recovered. Hence, analyses of 2008 data were based on 117 plots instead of 125 plots.

The following plant measurements were taken at each plot at each census: *Microstegium 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* spp.) < 2 m] and maximum heights of the two tallest native herbs.

The following environmental measurements were taken at each plot in the fall of 2007: soil texture (percent sand, silt, and clay), overhead canopy density (using a concave spherical densiometer), relative elevation, and distance to the nearest road or powerline. 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. Distance to the nearest road or powerline was considered a general inverse proxy for anthropogenic disturbance, which incorporated both the lack of disturbance in the surrounding landscape and time since the forest was cleared. Plots in younger stands were on average located closer to roads or powerlines, so distance confounded edge effects with stand age.

Characterization of Indicative Habitats of Each Species and Floristic Quality of Samples

I used the method described in Brewer and Menzel (2009) to quantify habitat associations for each vascular plant species and floristic quality of samples. I first generated a binary habitat x species matrix for all species encountered and obtained names of habitats and their associated descriptions from two regional flora manuals (Godfrey and Wooten 1979a,b; Jones 2005). The community similarity between each of the tabulated habitats and three focal habitat categories (wetlands, shady mesic forests, and disturbed habitats) was quantified by calculating Sorensen's quotient of similarity [Sorensen (1948) in Brower et al. 1998]. The calculated similarity scores for all identified habitats are included in Appendix 2. The disturbed habitat type included anthropogenically disturbed habitats described by Jones (2005) and Godfrey and Wooten (1979a; b). These included "disturbed areas", "waste places", "weedy areas", "fencerows", "ditches", "fallow fields", and "roadbanks". The resulting community similarity scores ranged from 1 (a community that shared all species with the focal habitat) to 0 (a community that shared no species with the focal habitat).

To determine the degree to which each species was restricted to each of the three focal habitat categories, I inserted the similarity scores into the species x habitat matrix (replacing the 1s) and then for each species calculated the average of the similarity scores for all the habitats in which it occurred (hereafter, the species' indicator score for a given focal habitat). A list of the 113 identified species and their associated habitat indicator scores is pro-

vided in Appendix 1. Values ranged from 0 (absent from the focal habitat or any other habitat that shared species with the focal habitat) to 1 (occurring exclusively in the focal habitat). For example, a species that occurred in floodplain forests (a type of wetland) and no other habitat would have a wetland indicator score of 1. Its indicator scores for the other two focal habitat categories would depend on the proportion of species floodplain forests shared with habitats in these categories.

I describe samples dominated by species with high wetland indication and/or mesic forest indication averages and low disturbance indication averages as having high floristic quality. I assumed that plots with the highest floristic quality contributed the most to regional plant diversity for two reasons: (1) anthropogenically disturbed habitats have increased in the past and/or are continuing to increase at the expense of mesic forests and wetlands as a result of past or ongoing development and timber operations within the region; and (2) logistic regressions showed the likelihood of a species having a widespread distribution (i.e., throughout Kentucky and the southeastern United States) or being frequent or abundant (as determined by Jones 2005) was positively associated with its indication of anthropogenically disturbed habitats (estimate = 8.29; $\chi^2 = 5.5$; $P = 0.019$) and moderately negatively associated with its indication of mesic forests (estimate = -1.87; $\chi^2 = 3.02$; $P = 0.08$). The degree to which a sampling plot was dominated by species indicative of a particular habitat was quantified by calculating weighted averages of log-transformed abundances of all species (other than *Microstegium vimineum*) present within the sampling plot at a given census. The weight was the species' indicator score for a given focal habitat. Specifically, floristic quality of a given sample was quantified as:

$$\text{floristic quality} = wa_{\text{wetland}} + wa_{\text{mesic forest}} - wa_{\text{disturbed}}$$

When calculating weighted averages (wa) of wetland indicator and mesic forest indicator abundance (wa_{wetland} ; $wa_{\text{mesic forest}}$), I assigned all non-native species a value of 0 for wetland and mesic forest indication (instead of the values derived from com-

munity similarities). Doing so allowed me to adjust floristic quality downward for samples with a significant number of non-native species. If *M. vimineum* displaced wetland and mesic forest indicators but favored disturbance indicators or non-native species, this would result in a reduction of floristic quality but not necessarily a reduction in species richness.

Hypothesized Path Models

Exploratory Analysis and Model Development

Data from the 2007 census were used to investigate separately relationships of richness, floristic quality, and *Microstegium vimineum* production, with the abiotic variables using backward stepwise multiple regression. The results of these regressions were then used to generate three path models corresponding to the three a priori competition-based hypotheses listed in Table 1 and were evaluated with data from the 2008 censuses. These path models included the environmental variables that were significant in 2007 as well as various hypothesized relationships among the biotic variables. The models also assumed that canopy gap fraction was potentially affected by flooding disturbance.

Path Model Evaluation and Hypothesis Testing

Hypothesis 1 (Table 1) was tested by evaluating the goodness-of-fit of path model 1 to fall 2008 species data and by quantifying the direct and indirect effects of flooding and canopy gap fraction on *Microstegium vimineum* (Figure 1a). Three parts were evaluated: (1) flooding and canopy gaps directly influenced both biotic response variables; (2) flooding and canopy gaps indirectly increased *M. vimineum* production by reducing species richness (biotic resistance); and (3) flooding indirectly increased *M. vimineum* and decreased richness by increasing canopy gap fraction. Each of these parts of hypothesis 1 was evaluated by examining the magnitude of the standardized path coefficient and its statistical significance. Because *M. vimineum* does not emerge until mid-

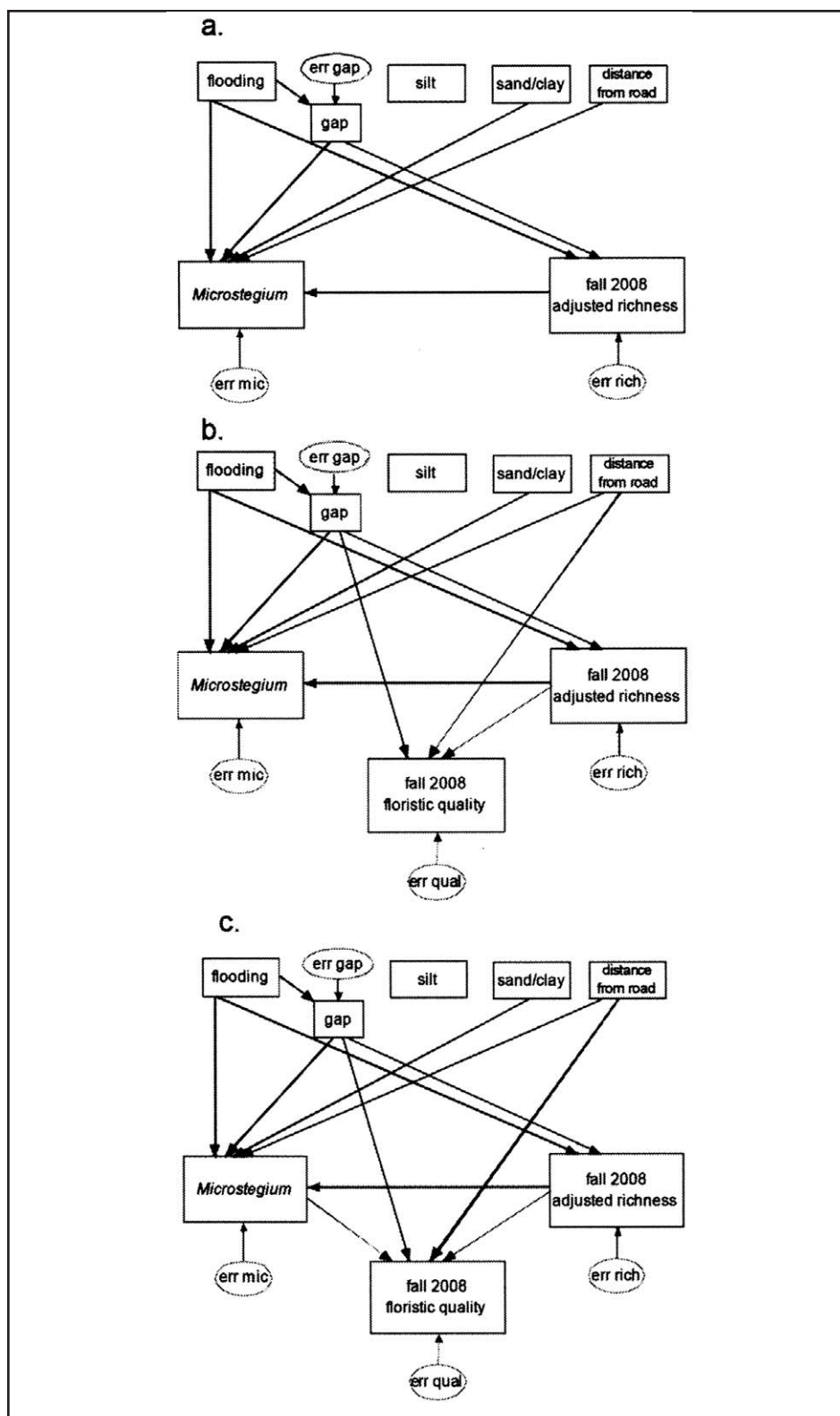


Figure 1. The refined hypothesized path models for a) biotic resistance in fall 2008 (Hypothesis 1); b) contrasting effects of disturbances on richness and floristic quality in fall 2008 (Hypothesis 2); and c) effect of *Microstegium vimineum* on floristic quality in fall 2008 (Hypothesis 3). Specified covariance paths among abiotic variables (and between the error associated with gap and silt, sand/clay, and distance from road) were removed from the diagram to highlight the hypothesized direct and indirect effects. Error ("err") terms associated with endogenous (dependent) variables (i.e., gaps, *Microstegium vimineum*, richness, and floristic quality) are represented by ellipses.

spring and reaches maximum production in the fall, I assumed that the inclusion of spring ephemerals and winter annuals in the calculation of species richness would weaken the relationship between species richness and *M. vimineum* production. This assumption is tested here by running a separate path analysis using spring and fall 2008 data and comparing the results to those based on fall data.

Hypothesis 2 (Table 1) was tested by evaluating the goodness-of-fit of path model 2 to fall 2008 species data (Figure 1b). This path model included all the paths specified in path model 1 plus a path between gap and floristic quality, between distance from the nearest road and floristic quality, and between richness and floristic quality. After path model refinement, I found that only one variable (canopy gap fraction) significantly and directly influenced both species richness and floristic quality in fall 2008. Three parts were evaluated: (1) canopy gaps directly decreased species richness and increased floristic quality; (2) canopy gaps indirectly reduced floristic quality by reducing species richness; and (3) flooding indirectly increased floristic quality and decreased richness by increasing canopy gap fraction. Each of these parts of hypothesis 2 was evaluated by examining the magnitude of the standardized path coefficient and its statistical significance.

Hypothesis 3 (Table 1) was tested by evaluating the goodness-of-fit of path model 3 to fall 2008 species data (Figure 1c). This path model included all the paths specified in path model 2 plus a path between *Microstegium vimineum* and floristic quality. The effect of *M. vimineum* on floristic quality was tested by examining the magnitude of the standardized path coefficient and its statistical significance.

Measurements of abiotic variables done in 2007 were used for the analysis of the 2008 responses, with the exception of canopy gap fraction and soil texture. Canopy gap fraction had changed significantly near three plots at site 3 (the Strawberry Plains site) due to a large treefall gap that formed during February 2008. Hence, canopy gap fraction at site 3 was based on summer 2008 measurements. In addition, soil tex-

ture was re-sampled within the floodplains in fall 2008 to account for sedimentation associated with spring 2008 floods.

Data Analysis

Following transformations (natural log or fourth-root) to normalize residuals, all pair-wise relationships were linear, with the exception of the relationships of richness and *Microstegium vimineum* with distance from the nearest road. After accounting for gap fraction, however, these relationships were linear as well. Soil texture was subjected to a principal component analysis (using JMP version 5), yielding a first principal component highly correlated with silt and a second highly correlated with sand-to-clay ratio. These principal components were used in the regression and path model analyses. All path model analyses were performed using Amos version 6 (Amos Development Corporation, Spring House, PA, and SPSS, Chicago, IL). The goodness-of-fit of each hypothesized path model to the observed covariances was assessed by calculating a minimum discrepancy or chi-square value using a maximum likelihood approach. The most parsimonious refined model was assessed by adjusting the chi-square values using the Akaike Information Criterion (AIC), which applied a penalty for model complexity ($AIC = \chi^2 + 2 \times \text{number of paths estimated}$). To refine the path models, abiotic variables with poor explanatory power were removed

by examining the effect of their removal on the AIC. A variable whose removal reduced the AIC was permanently omitted from the model. This procedure was continued until no further reduction in AIC occurred. Path coefficients and associated P-values, indirect effects, multiple squared correlation coefficients, and indirect effects were calculated for each of the hypothesized models and compared.

RESULTS

Simple Correlations Among Variables in 2008

Examination of all pair-wise simple correlations for 2008 data revealed that density-adjusted species richness in fall 2008 was highly negatively correlated with *Microstegium vimineum* production ($r = -0.49$; $P < 0.001$). In this instance, production was estimated indirectly from height and density (square root of the product of maximum height per plot and log density per plot). The addition of the spring species composition data weakened this relationship somewhat, but the simple correlation was still statistically significant ($r = -0.4$; $P < 0.001$). In contrast, none of the simple correlations between floristic quality and *M. vimineum* production or species richness was statistically significant (Table 2).

Hypothesis 1: Direct Effects of Disturbances on Invasion are Greater than Biotic Resistance.

Path model 1 fit the fall 2008 data well. The AIC adjusted chi-square was 49.51 with 5 df (unadjusted chi-square = 3.5, $P = 0.622$) and the model explained 17%, 49%, and 50% of the variation in canopy gap fraction, *Microstegium vimineum* production, and species richness, respectively (Figure 2a). Inspection of the path coefficients and the associated P-values revealed that species richness was significantly and directly negatively affected by flooding ($r = -0.54$; $P < 0.001$) and gaps (-0.28 ; $P < 0.01$). The indirect effect of flooding on species richness (mediated through gaps) was -0.12 . Species richness in the fall of 2008 appeared to significantly reduce *M. vimineum* production ($r = -0.19$; $P = 0.048$), whereas the path analysis that included spring 2008 species data did not reveal a significant effect of richness on *M. vimineum* ($r = -0.09$; $P = 0.32$). Together, these results are consistent with biotic resistance. However, the positive indirect effects of flooding and gap on *M. vimineum* mediated through reductions in species richness in fall 2008 (0.12 and 0.053, respectively) were not nearly as great as the positive direct effect of gaps on *M. vimineum* ($r = 0.55$; $P < 0.001$) or the combined direct effects of flooding and indirect effects of flooding mediated through gaps ($0.12 + 0.23 = 0.35$). All standardized indirect effects are presented in Table 3.

Table 2. Simple Pearson correlation coefficients among all variables measured in 2008. Bold values indicate two-tailed statistical significance at $P < 0.05$.

	1	2	3	4	5	6	7	8	9	10
<i>Microstegium</i> -1	1									
fall 2008 adjusted richness-2	-0.49	1								
fall 2008 floristic quality-3	0.10	-0.15	1							
spring/fall 2008 adjusted richness-4	-0.40	0.93	-0.03	1						
spring/fall 2008 floristic quality-5	0.01	-0.05	0.89	0.03	1					
flooding-6	0.40	-0.68	0.34	-0.63	0.27	1				
gap-7	0.66	-0.48	0.21	-0.41	0.20	0.42	1			
silt-8	0.13	-0.03	0.24	0.00	0.29	0.06	0.14	1		
sand/clay ratio-9	-0.11	0.16	0.09	0.23	0.01	-0.19	-0.28	0.00	1	
distance from nearest road-10	0.01	-0.28	0.62	-0.16	0.59	0.48	0.04	0.35	0.02	1

Hypothesis 2: Increasing Biotic Resistance Conflicts with Maintaining Floristic Quality.

Path model 2 fit the fall 2008 data well. The AIC adjusted chi-square was 62.15 with 9 df (unadjusted chi-square = 8.15, $p = 0.519$) and the model explained 43% of the variation in floristic quality (Figure 2b). Inspection of the path coefficients for path model 2 (Figure 2b) revealed that gaps influenced floristic quality and species richness in roughly equal but opposite ways ($r = 0.28$ and -0.28 , respectively; $P < 0.001$). Floristic quality was moderately but significantly positively related to species richness ($r = 0.18$; $P = 0.041$). As a result, the direct positive effect of gaps on floristic quality ($r = 0.28$; $P < 0.01$) was greater than the total indirect effects of gaps on floristic quality mediated through reductions in species richness ($r = -0.049$). Floristic quality was most strongly influenced by distance from the nearest road ($r = 0.65$; $P < 0.001$). In contrast, species richness in fall 2008 was most strongly affected by flooding ($r = -0.54$; $P < 0.001$).

Hypothesis 3: Invader Does Not Reduce Floristic Quality.

Path model 3 fit the fall 2008 data well. The AIC adjusted chi-square was 64.15 with 8 df (unadjusted chi-square = 8.15, $P = 0.419$) and the model explained 43% of the variation in floristic quality (Figure 2c). The effect of *Microstegium vimineum* on floristic quality was not significant ($r < 0.01$; $P = 0.97$). As a result, path model 3 did not fit the data any better than path model 2 (which lacked the path between *M. vimineum* and floristic quality).

DISCUSSION

In this study, path analysis revealed the potential for realistic diversity-mediated biotic resistance of forest groundcover plant communities to invasion by *Microstegium vimineum*. Plant species richness was reduced significantly by flooding and canopy gaps and had a significantly negative direct effect on *M. vimineum* production. Hence, flooding and canopy gaps may have indirectly increased *M. vimineum*

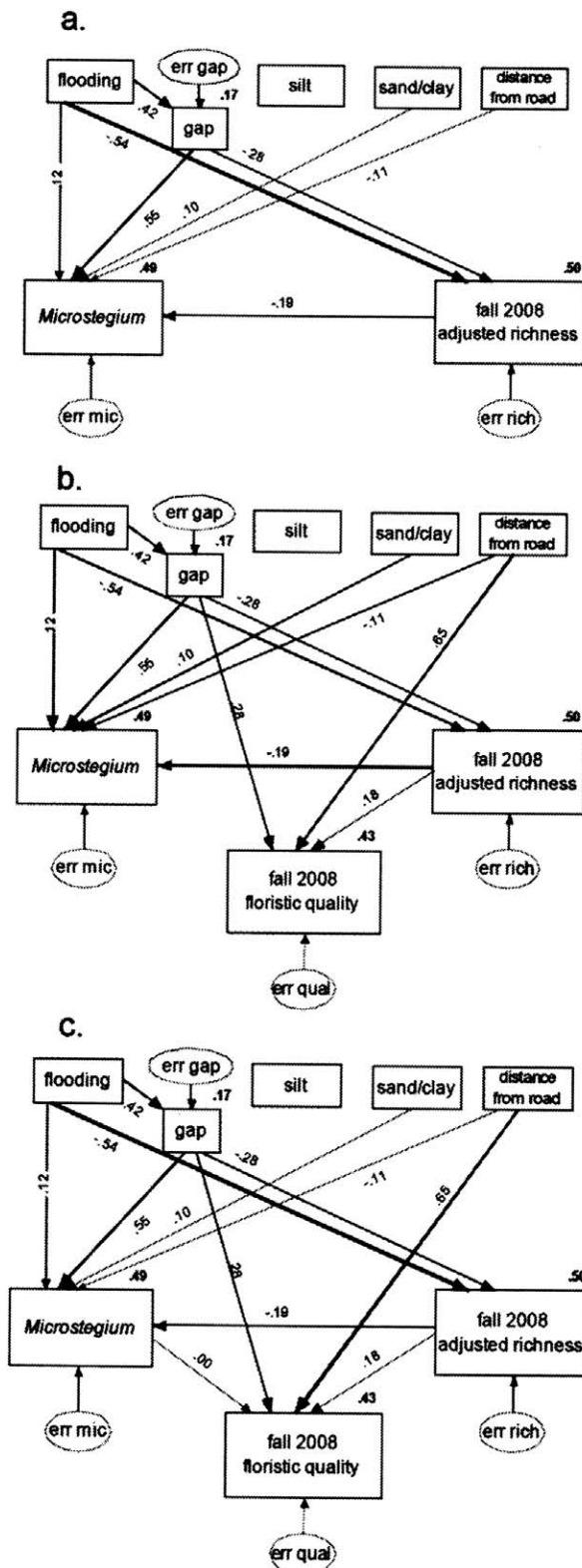


Figure 2. Path models and path coefficients for a) hypothesis 1; b) hypothesis 2; and c) hypothesis 3. Bold type coefficients are multiple squared correlation coefficients. Regular type coefficients are standardized partial correlation (path) coefficients. Specified covariance paths among abiotic variables were removed from the diagram to highlight the hypothesized direct and indirect effects. Error ("err") terms associated with endogenous (dependent) variables are represented by ellipses.

Table 3. Standardized indirect effects for path model 3 (inclusive of the indirect effects in path models 1 and 2).

Endogenous (Response) Variables	Exogenous (Predictor) Variables		
	Flooding	Gap	Fall 2008 Adjusted Richness
Fall 2008 Adjusted Richness	-0.12	0	0
Microstegium	0.35	0.052	0
Floristic Quality	-0.001	-0.049	-0.001

production by reducing plant species richness. One caveat to the conclusion of biotic resistance in the current study, however, is that I cannot rule out the possibility that the negative relationship was caused by competitive displacement of resident species by *M. vimineum*. A separate path analysis (results not shown) revealed that switching the path direction between *M. vimineum* and richness produced a nearly identical path coefficient (-0.18) and a model that fit the data equally well. In theory, both resistance and displacement can be driven by the same mechanism (i.e., interspecific competition combined with stochastic species loss; Case 1990). The fact that the negative relationship was stronger for the fall 2008 species data than for the pooled spring and fall data strongly suggests that competition was intense between *M. vimineum* and resident species with a similar growth phenology (*M. vimineum* emerges from seed in late April and May and reaches its maximum production in the fall). Path analysis, therefore, provided results comparable to those of a previous experimental study on the effects of realistic reductions in species richness on invasion in California, in which the mechanism of resistance was primarily phenological niche overlap (Zavaleta and Hulvey 2004).

Despite the apparent existence of diversity-mediated resistance to invasion in this system, the relevance of this finding to the conservation of plant diversity is uncertain because the factors that indirectly promoted invasion by reducing plant species richness (flooding, canopy gaps) had even greater direct positive effects on invasion

by *Microstegium vimineum*. Hence, demonstrating an indirect diversity-mediated effect of disturbances on invasion is likely to have no bearing on current management decisions in this system because the more widely appreciated direct effects of these disturbances on local species richness and invasion were even greater. This situation is probably not limited to the system studied here. Disturbances are widely recognized for their ability to promote invasions directly by creating safe sites for establishment (Hobbs and Huenneke 1992). It is also widely recognized that, given a high enough frequency or intensity, disturbances can also reduce species diversity (Connell 1978). Hence, to be relevant to conservation management decisions, it is not sufficient to simply demonstrate that realistic reductions in species diversity promote invasions. Researchers must also show that diversity-mediated reductions in invasion are caused by factors for which land managers have had little appreciation or concern.

Another reason why diversity-mediated resistance to invasion might not be relevant to conservation in this study is that the same factor(s) responsible for reducing local species richness increased floristic quality and thus might increase regional plant diversity. Canopy gaps increased the relative abundance of native plants indicative of threatened habitats but not increasingly common habitats (i.e., anthropogenically disturbed areas). In fact, the positive effect of canopy gaps on floristic quality far exceeded the indirect effects of gaps on biotic resistance. The potential for a conflict to arise between preserving

regional plant diversity and reducing opportunities for invasive species is most likely to occur when selective agents simultaneously favor native habitat specialists and non-native species, but reduce the native species pool. Such a conflict appears likely to arise when considering management options in floodplain forests in northern Mississippi. Most of the native species that benefited from gaps in these forests were wetland/floodplain specialists. The two best examples of species associated with regionally rare habitats that also benefited from gaps in this study were *Chasmanthium latifolium* (river oats) and *Rosa palustris* (swamp rose). The former is a good indicator of mesic forests and wetlands, and the latter is an obligate wetland indicator. The abundance of rare species (i.e., those present in < 5% of all plots in fall 2008, including *C. latifolium* and *R. palustris*) was positively correlated with flooding; partial $r = 0.44$; $P < 0.001$). In contrast, the majority of species that were not associated with gaps in floodplains were widespread generalists, disturbance indicators, or mesic forest specialists. Similar to *C. latifolium* and *R. palustris* and several locally rare species, *Microstegium vimineum* benefited greatly from canopy gaps in floodplains. If one were to implement flood control measures to reduce these disturbances, *M. vimineum* production would likely decrease. At the same time, species richness could very well increase, but at the expense of floristic quality and locally rare species, as numerous common opportunistic mesophytic and generalist species colonized the floodplain. Flood control measures could cause a net loss of regional plant diversity and locally rare species, not to mention a major disruption of a natural ecosystem process.

A third reason why diversity-mediated resistance to invasion by *Microstegium vimineum* might have limited relevance to conservation is that *M. vimineum* apparently had no effect on floristic quality of the resident community (partial $r < 0.01$; $P = 0.97$) or the abundance of locally rare plant species (partial $r = 0.07$; $P = 0.45$) in this study. Although this may come as a surprise to some, given the notoriety of this species (it has a NatureServe I-rank of high/medium), it is important to bear in

mind that the most productive patches of this species occurred in disturbed areas. In general, disturbances tend to reduce the intensity of competition (Burke and Grime 1996) and thus potentially the competitive effects of invaders. Also, the annual life history of *M. vimineum* might reduce its competitive impact on a resident groundcover flora dominated by perennials. It is impossible to prove and premature to conclude, however, that *M. vimineum* had no negative impact on the resident habitat specialists. Recent studies have shown that competitive effects of *M. vimineum* on resident vegetation could be masked or overridden by deer herbivory (Webster et al. 2008; Knight et al. 2009). In addition, partial correlations between *M. vimineum* production and the abundance of some mesic forest specialists (e.g., *Chasmanthium laxum*, *Quercus alba*, *Leersia virginica*, *Dichanthelium boscii*) were significantly negative (J.S. Brewer, unpubl. data).

The lack of a negative impact of *Microstegium vimineum* on floristic quality does not mean that land managers need not be concerned with this species. This species affects soil biota and associated ecosystem processes (Kourtev et al. 2003) and potentially suppresses seedlings of commercially valuable trees (e.g., *Quercus*

alba; Oswalt et al. 2007; Webster et al. 2008; J.S. Brewer, unpubl. data). The issue is not whether to control this species, but how. Non-selective chemical or mechanical methods of control could have dramatically negative effects on floristic quality. "Spraying and walking away" would likely do little more than replace native wetland specialists and *M. vimineum* with weeds. In contrast, the demonstrably negative impact of long-lived perennial invasives such as *Imperata cylindrica* on floristic quality of the resident vegetation in longleaf pine savannas warrants the use of intensive control measures followed by community restoration (Brewer 2008).

The results of the current study are relevant to interpretations of experimental studies that focus on local species diversity and the role that niches play in invasions (Robinson et al. 1995; Levine 2000; Zavaleta and Hulvey 2004). Experimental studies of diversity-mediated biotic resistance provide interesting demonstrations of the role that competition plays in community assembly and species coexistence. It remains to be seen, however, whether increasing biotic resistance by preventing reductions in local species diversity will prove important for preserving diversity at a regional scale, the scale arguably most relevant to biodiversity

conservation (Rosen et al. 2008). Reducing anthropogenic disturbances (deforestation, forest fragmentation) and restoring natural disturbance regimes (flooding), notwithstanding their effects on *Microstegium vimineum*, appear to be the most important priorities for preserving plant diversity in forests in northern Mississippi.

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Appendix 1. Calculated habitat indicator scores for each of 113 taxa identified to species. Nomenclature follows Jones (2005) except when missing. Otherwise follows Godfrey and Wooten 1979a, b, or Lelong, M.G. 1986.

species	shady mesic forests indicator score	wetlands indicator score	anthropogenic disturbance indicator score
<i>Acalypha rhomboidea</i>	0.26	0.31	0.32
<i>Acer negundo</i>	0.42	0.52	0.38
<i>Acer rubrum rubrum</i>	0.65	0.36	0.14
<i>Aesculus pavia</i>	0.53	0.81	0.24
<i>Ageratina altissima</i>	0.69	0.44	0.22
<i>Agrimonia rostellata</i>	0.69	0.63	0.24
<i>Allium vineale</i> ¹	0 (0.13)	0 (0.16)	1.00
<i>Ambrosia artemisiifolia</i>	0.17	0.22	1.00
<i>Ambrosia trifida</i>	0.21	0.54	0.53
<i>Arisaema dracontium</i>	0.47	0.55	0.24
<i>Aristolochia serpentaria</i>	0.31	0.28	0.14
<i>Asplenium platyneuron</i>	0.26	0.13	0.30
<i>Baccharis halimifolia</i> ²	0.13	0.44	0.35
<i>Bidens frondosa</i>	0.14	0.49	0.37
<i>Boehmeria cylindrica</i>	0.29	1.00	0.33
<i>Botrychium dissectum</i>	0.69	0.63	0.21
<i>Botrychium virginianum</i>	0.49	0.42	0.21
<i>Carpinus caroliniana</i>	0.72	0.81	0.29
<i>Carya glabra</i>	0.27	0.29	0.18
<i>Carya tomentosa</i>	0.35	0.27	0.14
<i>Cercis canadensis</i>	1.00	0.62	0.30
<i>Cerastium vulgatum</i>	0.18	0.23	1.00
<i>Chaerophyllum procumbens</i>	0.36	0.46	0.26
<i>Chasmanthium latifolium</i>	0.51	0.41	0.19
<i>Chasmanthium laxum</i>	0.29	0.50	0.28
<i>Claytonia virginica</i>	0.53	0.34	0.38
<i>Clematis virginiana</i>	0.39	0.43	0.22
<i>Collinsonia canadensis</i>	0.69	0.38	0.17
<i>Commelina virginica</i>	0.45	1.00	0.27
<i>Conoclinium coelestinum</i>	0.26	0.40	0.32
<i>Dichanthelium boscii</i>	0.52	0.32	0.17
<i>Dioscorea villosa</i>	0.28	0.29	0.31
<i>Diospyros virginiana</i>	0.45	0.46	0.20
<i>Elephantopus carolinianus</i>	0.34	0.40	0.29
<i>Elymus virginicus</i>	0.24	0.39	0.32
<i>Erechtites hieraciifolia</i>	0.21	0.26	0.65
<i>Erigeron annuus</i>	0.21	0.27	0.69
<i>Erigeron philadelphicus</i>	0.27	0.37	0.33
<i>Euonymus americanus</i>	1.00	0.81	0.35
<i>Eupatorium serotinum</i>	0.22	0.38	0.32
<i>Fraxinus americana</i>	0.69	0.44	0.22

Continued

Appendix 1. Continued

species	shady mesic forests indicator score	wetlands indicator score	anthropogenic disturbance indicator score
<i>Fraxinus pennsylvanica</i>	0.44	0.81	0.25
<i>Galium aparine</i>	0.27	0.37	0.34
<i>Galium circaezans</i>	0.56	0.40	0.25
<i>Gelsemium sempervirens</i> ²	0.32	0.37	0.15
<i>Gentiana villosa</i>	0.20	0.19	0.17
<i>Hedera helix</i> ¹	0 (0.19)	0 (0.27)	1.00
<i>Ilex opaca</i>	0.49	0.81	0.29
<i>Impatiens capensis</i>	0.51	1.00	0.27
<i>Ipomoea purpurea</i> ¹	0 (0.19)	0 (0.27)	1.00
<i>Juncus effusus</i>	0.10	0.68	0.29
<i>Krigia dandelion</i>	0.14	0.25	0.33
<i>Leersia oryzoides</i>	0.15	1.00	0.32
<i>Leersia virginica</i>	0.45	0.57	0.23
<i>Lespedeza cuneata</i> ¹	0 (0.19)	0 (0.24)	1.00
<i>Ligustrum sinense</i> ¹	0 (0.31)	0 (0.35)	0.35
<i>Liquidambar styraciflua</i>	0.47	0.56	0.41
<i>Liriodendron tulipifera</i>	0.65	0.57	0.14
<i>Lobelia cardinalis</i>	0.31	0.60	0.20
<i>Lobelia puberula</i>	0.34	0.44	0.37
<i>Lonicera japonica</i> ¹	0 (0.22)	0 (0.25)	0.47
<i>Maianthemum racemosum</i>	1.00	0.62	0.30
<i>Morus rubra</i>	0.65	0.65	0.34
<i>Nandina domestica</i> ¹	0 (0.26)	0 (0.27)	0.30
<i>Nothoscordum bivalve</i>	0.35	0.30	0.53
<i>Nyssa sylvatica</i>	0.44	0.47	0.22
<i>Ophioglossum vulgatum</i>	0.56	0.58	0.19
<i>Panicum dichotomum ramulosum</i> ³	0.37	0.60	0.21
<i>Parthenocissus quinquefolia</i>	0.33	0.40	0.26
<i>Paspalum laeve</i>	0.19	0.27	1.00
<i>Podophyllum peltatum</i>	0.43	0.50	0.36
<i>Polygonum virginianum</i>	0.39	0.46	0.21
<i>Polygonum pensylvanicum</i>	0.34	0.46	0.42
<i>Polystichum acrostichoides</i>	0.38	0.46	0.22
<i>Potentilla simplex</i>	0.32	0.27	0.36
<i>Prunus serotina</i>	0.59	0.45	0.65
<i>Quercus alba</i>	0.69	0.17	0.08
<i>Quercus falcata</i>	0.51	0.32	0.13
<i>Quercus michauxii</i>	0.48	0.41	0.22
<i>Quercus nigra</i>	0.39	0.45	0.35
<i>Quercus stellata</i>	0.47	0.29	0.14
<i>Rhus copallinum</i>	0.13	0.17	0.59

Continued

Appendix 1. Continued

species	shady mesic forests indicator score	wetlands indicator score	anthropogenic disturbance indicator score
<i>Rosa palustris</i>	0.16	1.00	0.19
<i>Rubus argutus</i>	0.23	0.35	0.29
<i>Ruellia caroliniensis</i>	0.27	0.22	0.16
<i>Rumex crispus</i> ¹	0 (0.14)	0 (0.45)	0.45
<i>Saccharum giganteum</i>	0.40	0.45	0.25
<i>Salix nigra</i>	0.30	0.54	0.35
<i>Sambucus canadensis</i>	0.32	0.43	0.36
<i>Sanicula canadensis</i>	0.36	0.29	0.40
<i>Sanicula trifoliata</i>	1.00	0.62	0.30
<i>Sassafras alba</i>	0.13	0.15	0.31
<i>Silphium perfoliatum</i>	0.39	0.56	0.24
<i>Smilax bona-nox</i>	0.38	0.41	0.33
<i>Smilax glauca</i>	0.35	0.38	0.31
<i>Smilax rotundifolia</i>	0.30	0.36	0.17
<i>Solidago canadensis</i>	0.16	0.16	0.35
<i>Stellaria pubera</i>	1.00	0.44	0.20
<i>Symphyotrichum dumosum</i>	0.13	0.24	0.22
<i>Symphyotrichum pilosum</i>	0.19	0.16	0.54
<i>Symphyotrichum racemosum</i>	0.30	0.40	0.35
<i>Symphoricarpos orbiculatus</i>	0.51	0.41	0.41
<i>Tipularia discolor</i>	0.51	0.48	0.23
<i>Toxicodendron radicans</i>	0.18	0.20	0.52
<i>Trillium recurvatum</i>	1.00	0.24	0.12
<i>Ulmus alata</i>	0.48	0.48	0.21
<i>Ulmus americana</i>	1.00	0.49	0.22
<i>Vaccinium elliotii</i>	0.40	0.47	0.25
<i>Valerianella radiata</i>	0.22	0.22	0.45
<i>Vernonia altissima</i>	0.40	0.37	0.34
<i>Viola sororia missouriensis</i> ⁴	0.72	0.58	0.19
<i>Vitis rotundifolia</i>	0.37	0.41	0.21
<i>Woodwardia areolata</i>	0.37	1.00	0.15

1 - exotic; values in parentheses are calculated mesic forest and wetland indicator scores; zeroes were used in the calculation of floristic quality.

2 - Habitat described by Godfrey and Wooten, 1979a, b

3 - Habitat described by Lelong, M.G., 1986.

4 - Assumed synonymous with *V. affinis* in Godfrey and Wooten

Twelve other species were encountered that have not yet been identified to species, including four species of *Carex*. These were included in calculations of species richness but not floristic quality.

Appendix 2. List of all habitats (as named and described in Jones 2005 or Godfrey and Wooten 1979a, b) in which at least one species from Appendix 1 occurred.

habitat	shady mesic forests similarity score	wetlands similarity score	anthropogenically disturbed similarity score
acid woods	0.03	0.03	0
banks of marshes	0.03	1.00	0.12
barrens	0.00	0.03	0.08
basic circumneutral upland woods	1.00	0.03	0.04
bogs	0.05	1.00	0.00
clearings	0.05	0.09	0.12
clearings in or edges of bottomland forests and low woodlands	0.12	1.00	0.22
clearings in pine savannas	0.03	1.00	0.04
cut-over areas	0.03	0.03	1.00
cypress-gum ponds depressions	0.03	1.00	0.04
depressions in bogs	0.03	1.00	0.04
disturbed sites, waste places, cultivated & fallow fields	0.19	0.28	1.00
ditches	0.10	1.00	1.00
dry woods	0.39	0.28	0.14
edges of rich woods	0.03	0.03	0.04
fence rows and hedgerows	0.17	0.16	0.29
fields and oldfields	0.27	0.37	1.00
floodplain and bottomland forests	1.00	1.00	0.39
forested river bluffs	1.00	0.03	0.04
glades	0.00	0.03	0.04
lawns	0.08	0.06	1.00
lowland woods	1.00	0.40	0.12
low-lying areas	0.05	0.06	0.00
marshes	0.10	1.00	0.11
meadows	0.21	0.29	0.31
moist clearings	0.13	0.17	0.19
moist hammocks, woodlands, forests	1.00	0.61	0.29
moist open woodlands	0.14	0.16	0.18
moist road banks	0.03	0.03	0.00
moist thickets	0.15	0.17	0.08
old stabilized dunes	0.03	0.03	0.00
open stream banks	0.08	1.00	0.16
open woods	0.03	0.06	0.19
pastures	0.12	0.16	1.00
pine flatwoods	0.13	0.14	0.04
pine-oak scrub	0.03	0.03	0.00
pond edges	0.10	1.00	0.15
poorly-drained pinelands and pine savannas	0.10	1.00	0.08
prairies	0.00	0.03	0.04
ravine bottoms and slopes	1.00	0.03	0.00
rich or loamy woods	1.00	0.28	0.10

Continued

Appendix 2. Continued

habitat	shady mesic forests similarity score	wetlands similarity score	anthropogenically disturbed similarity score
ridgetop woodlands	0.03	0.03	0.00
river banks	0.19	1.00	0.25
roadsides	0.09	0.08	0.49
rocky soils	0.00	0.00	0.00
rocky woods	0.00	0.03	0.04
seasonally wet places	0.00	0.03	0.08
seepage areas in woodlands	1.00	1.00	0.04
semi-open dry woods	0.05	0.03	0.04
shady and mesic slopes	1.00	0.09	0.04
shores and marshy shores	0.10	1.00	0.29
sloughs	0.05	1.00	0.08
stream banks and edges	0.43	1.00	0.30
swales	0.08	0.12	0.16
swamp margins	0.08	1.00	0.12
swamps	0.31	1.00	0.23
thickets	0.27	0.28	0.30
upland woods and forests	0.33	0.29	0.16
well drained	0.24	0.27	0.14
wet clearings and wet open woods	0.23	1.00	0.37
wet fields and cut-over areas	0.03	1.00	1.00
wet hammocks, woodlands, forests	1.00	1.00	0.28
wet limestone hammocks	1.00	1.00	0.00
wet meadows	0.05	1.00	0.12
wet thickets	0.28	1.00	0.24
wooded river banks	1.00	1.00	0.00
wooded stream banks	1.00	1.00	0.00
woodland borders and margins	0.12	0.16	0.25
woodlands	0.24	0.25	0.25

1 - Habitats with a similarity score of 1 for a given focal habitat category were included in that habitat category.

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