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Inferring relationships between native plant diversity and *Lonicera japonica* in upland forests in north Mississippi, USA

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Abstract

Question: Do anthropogenic disturbances interact with local environmental factors to increase the abundance and frequency of invasive species, which in turn exerts a negative effect on native biodiversity?

Location: Mature *Quercus-Carya* and *Quercus-Carya-Pinus* (oak-hickory-pine) forests in north Mississippi, USA.

Methods: We used partial correlation and factor analysis to investigate relationships between native ground cover plant species richness and composition, percent cover of *Lonicera japonica*, and local and landscape-level environmental variables and disturbance patterns in mature upland forests. We directly measured vegetation and environmental variables within 34 sampling subplots and quantified the amount of tree cover surrounding our plots using digital color aerial photography.

Results: Simple bivariate correlations revealed that high species richness and a high proportion of herbs were associated with low *Lonicera japonica* cover, moist and sandy uncompacted soils, low disturbance in the surrounding landscape, and periodic prescribed burning. Partial correlations and factor analysis showed that once we accounted for the environmental factors, *L. japonica* cover was the least important predictor of composition and among the least important predictors of species richness. Hence, much of the negative correlation between native species diversity and this invasive species was explained by soil texture and local and landscape-level land-use practices.

Conclusions: We conclude that negative correlations between the abundance of invasive species and native plant diversity can occur in landscapes with a gradient of human disturbance, regardless of whether there is any negative effect of invasive species on native species.

Keywords: *Carya*; Disturbance; Forest fragmentation; Invasive species; *Pinus echinata*; *Quercus*; Restoration; Species diversity.

Nomenclature: Radford et al. (1968).

Abbreviation: NMS = Non-metric Multidimensional Scaling.

Introduction

Understanding the association between native species diversity and current environmental conditions in forest communities is essential for guiding current restoration and management of ecosystems to preserve biodiversity. Many forest communities currently have low native diversity or declining populations of native species due to degraded environmental conditions, resulting from current or historical land-use practices such as cultivation, clearcutting, fire suppression, and forest fragmentation (Abrams 1992; Waldrop et al. 1992; Cain & Shelton 1994; Duffy & Meier 1992; Matlack 1994; Meier et al. 1995; Sparks et al.1998; Brewer 2001; Bellemare et al. 2002; Heuberger & Putz 2003; Franklin & Kupfer 2004; Flinn & Vellend 2005). Restoration of environmental conditions necessary to preserve biodiversity is becoming an increasingly important component of forest management. Nevertheless, the environmental conditions that promote and maintain biodiversity within forests can be complex and are often not well understood.

As in many fire-suppressed forest communities worldwide, upland forests in Mississippi and elsewhere in eastern North America are currently experiencing declines in populations of shade-intolerant, fire-tolerant plant species (Abrams 1992; Frost 1993; Lorimer 1993; Delcourt & Delcourt 1998; Masters et al. 1998; Brewer 2001; Hutchinson et al. 2005). Historically (i.e. before deforestation), open *Quercus* and *Quercus-Pinus* woodlands once occurred over large portions of the upland landscape in the interior southern United States and were maintained by frequent fires of aboriginal (and possibly lightning) origin (Van Lear & Waldrop 1989; Foti & Glenn 1991; Frost 1998; Brewer 2001; Surrette 2006). Today, the last remaining mature upland forests of this type have experienced a long history of fire suppression and are in danger of losing many fire-dependent species (Arthur et al. 1998; Hutchinson et al. 2005).

Aside from fire suppression, habitat fragmentation and the legacy of disturbances in the past are serious threats to biodiversity in mature upland forests (Wilcox & Murphy 1985; Duffy & Meier 1992; Matlack 1994;

Meier et al. 1995; Bellemare et al. 2002; Yates et al. 2004; Honnay et al. 2005). The last few remaining forests of this type in north Mississippi consist of closed canopy fragments of various sizes, distributed across a range of soil types and land-use histories. In contrast to fire suppression, forest fragmentation and cultivation in the past are thought to favor disturbance dependent species and negatively affect disturbance sensitive species (Alverson et al. 1994; Meier et al. 1995). However, fire dependent, open-habitat species do not generally benefit from the types of disturbances associated with habitat fragmentation or cultivation (Leach & Givnish 1996). Many of the same types of harmful edge effects that occur in small, closed canopy forests (Alverson et al. 1988) can also affect species of more open or disturbed habitats (Simberloff 1993; Donovan & Flather 2002).

One potential side effect of habitat fragmentation and past disturbances is increased contact between native and invasive species. By invasive species, we mean naturalized, non-native species capable of rapid spread and growth. Some invasive species benefit from forest fragmentation (Brothers & Spingarn 1992; Cadenasso & Pickett 2001; Yates et al. 2004). Alleged displacement of native species by invasive species is often inferred from negative correlations between the abundance of invasive species and native diversity (Barden & Matthews 1980; Davison & Forman 1982). Such negative correlations can have a variety of causes that are unrelated to any effects invasive species might have on native species (Levine 2000; Fridley et al. 2004; Gurevitch & Padilla 2004; MacDougall & Turkington 2005). Even when invasive species reduce native species diversity, the mechanism involved may be poor colonization by early-successional species rather than competitive displacement of late-successional species (Yurkonis & Meiners 2004).

This study represents an initial attempt to separate the various environmental factors that potentially affect native plant diversity and species composition in upland hardwood and hardwood-*Pinus* forests in north-central Mississippi. Here, we use a partial correlation approach to examine the relative strengths of relationships among native plant diversity/composition in mature forests and soil variables, canopy density, disturbance in the surrounding landscape, and the percent cover of an invasive vine, *Lonicera japonica*.

Our specific objectives were (1) to determine relationships among ground cover plant diversity/composition within second-growth, upland hardwood and hardwood-*Pinus* forests and soil conditions, position along a slope, recent fire history, canopy density, and the extent of deforestation in the surrounding landscape; (2) to determine the relationship between plant diversity/composition and the percent cover of *L. japonica*, after accounting for its correlation with the aforementioned environmental variables, and (3) to use our results to assess at which sites ecological restoration efforts will be most effective. We hypothesize that: 1. Sites characterized by local environmental factors that favor a mix of open habitat and mesophytic herbaceous species and have minimal disturbance in the surrounding landscape are the most diverse. 2. There is a weak relationship between plant diversity/composition and *L. japonica* cover, when the *L. japonica* disturbance relationship is taken into account. 3. Ideal locations for ecological restoration of fire-dependent plant communities will occur in large forest tracts that contain open habitat species that are not successfully reproducing, and which contain little *L. japonica*.

Methods

Study sites

The upland hardwood and hardwood-*Pinus* forests studied here encompassed a gradient of soil fertility from the relatively rich, northern loess plains (Strawberry Plains, Sardis) to the poorer northern hilly coastal plains of Mississippi Holly Springs National Forest and the Little Tallahatchie Experimental Forest within the Greater Yazoo River Watershed (Fig. 1). Historically, fire-tolerant tree species such as *Quercus velutina*, *Q. marilandica*, *Q. rubra*, and *Q. stellata* dominated the upland landscape within the loess plains, with *Pinus echinata* being an additional dominant component in sandier portions of the northern hilly coastal plains (Nutt 1805 in Jennings 1947; Hilgard 1860; Brewer 2001; Surrette 2006). As a result of fire suppression, tree species that were historically restricted for the most part to floodplains, e.g. *Liquidambar styraciflua*, *Acer rubrum*, *Quercus alba*, and *Nyssa sylvatica*) commonly occur in these upland forests today (Brewer 2001; Surrette 2006).

After cession of north Mississippi by the Chickasaw Nation to the United States in 1832, forests began to be cleared for agricultural production, but the intensity of cultivation varied spatially with respect to soil fertility (Hilgard 1860; Doyle 2001). The fertile, silt-loam soils within Marshall County and central Lafayette County were intensively and extensively cultivated in this region (Hilgard 1860; Doyle 2001). In contrast, the poorer, sandier soils, where *Pinus echinata* was common (e.g. eastern Lafayette County), supported small farms, which focused more on pasture and livestock production (Doyle 2001). Hence, the intensity of soil disturbance was unlikely to have been as great in these areas.

Each of our study's forest locations within north-central Mississippi contained one to six 75 m × 70 m plots for determining tree species composition. All research plots were chosen and positioned to meet the following criteria: (1) located on upland soils (i.e. not floodplains or floodplain terraces); (2) contained mature (90 - 100+ yr old) trees; (3) burned no more than three times since 1978, preceded by a prolonged period (30+ years) of active fire suppression, and (4) contained a ridge and a lower slope or hollow.

Tree composition plots (n = 11) were located in the Little Tallahatchie Experimental Forest and the adjacent ranger district of Holly Springs National Forest in northeastern Lafayette County. This area is mostly dominated by second-growth stands of hardwoods and *Pinus* species (mostly *P. echinata*) that grew back after extensive logging in the early 1900s. The remaining tree composition plots were located in mature upland *Quercus-Carya* forests on property managed by the University of Mississippi in central Lafayette County (Bailey Woods and Jackson Strip), the Strawberry Plains Audubon Center in north-central Marshall County, and the Sardis Lake Recreation area in eastern Panola County (Fig. 1).

Lonicera japonica

The most common invasive species at our sites was *Lonicera japonica*. This species is a semi-evergreen vine that was introduced to the eastern United States some time before 1860 as an ornamental plant (Patterson 1976). It was later widely planted for cattle and wildlife forage (Patterson 1976; Dickson et al. 1978) and is now considered a naturalized, invasive species in upland and lowland forests as well as in forest-edge habitats (Patterson 1976; Westbrooks 1981; Wagner 1981; Cain 1992; Yeiser 1999; Yates et al. 2004). It poses significant problems to commercial forestry, as it has been shown to suppress seedlings of commercially valuable pine species (Cain 1985) and saplings of *Liquidambar styraciflua* (Dillenburg et al. 1993) and reduce colonization of early successional habitats by native species (Yurkonis & Meiners 2004). In addition, *L. japonica* has been implicated in the decline of native forest herbs (Barden & Matthews 1980; Davison & Forman 1982), although direct evidence showing this remains scant (Friedland & Smith 1982).

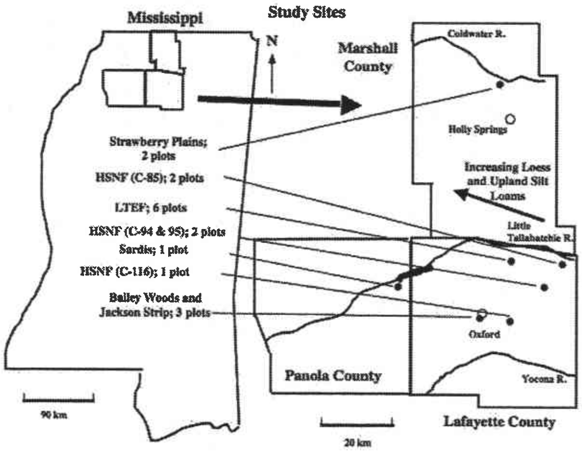

Fig. 1. Location of study sites and associated plots.

Determining ground cover species composition

We determined ground-cover species composition and tabulated species richness in two 10 m × 30 m ground cover subplots within each 75 m × 70 m tree composition plot (17 plots × 2 subplots = 34 subplots). One ground cover subplot was established on the ridge and the other on the slope of each 75 m × 70 m plot. Tree seedling (< 1.5 m height) and herbaceous species abundances were quantified with stem density categories: 0 = absent; 1 = < 5 stems; 2 = 5 to 20 stems; 3 = 21 to 50 stems, and 4 = > 50 stems. We quantified the abundance of each woody vine species, e.g. *Lonicera japonica*, *Vitis rotundifolia*, and *Parthenocissus quinquefolia* with comparable percent cover categories: 0 = absent; 1 = < 1 %, 2 = 1% to 20%; 3 = 21% to 50%, and 4 = > 50%. Cover estimates were made by the first author to be consistent throughout.

Measuring environmental conditions

Local conditions, soil characteristics, fire frequency, topography

We measured local environmental conditions at each site to test the hypothesis that local factors such as soil conditions, recent fire history, canopy closure and/or topography influenced plant species composition and diversity. Canopy closure was quantified with a spherical densitometer at five random points within each subplot during midsummer when canopy expansion was at a maximum (Lemmon 1956).

Soil texture was quantified indirectly by measuring soil compaction to 10 cm depth using a soil penetrometer. Because none of our sites have been exposed to heavy machinery associated with logging operations, we assumed that soil compaction was a reasonably good inverse indicator of particle size (i.e. sandy soils were less compacted than silt or clay soils). In addition, we determined the recent fire history (number of fires between 1979 and 2000, prescribed and not prescribed) within each research plot using land-owner data and records.

The elevation of a subplot below the closest ridge was determined by measuring slope angle and distance between the nearest point on the ridge and the center of the subplot. A clinometer was used to measure the slope angle between a point on the ridge and the center of the subplot. Distances were then measured between these points, and elevation of each subplot below the closest associated ridge was then calculated by taking the product of the sine of the slope angle and the distance.

Landscape disturbance: The amount of non-forested land surrounding each forest plot

We measured the amount of landscape disturbance surrounding each 75 m × 70 m plot to test the hypothesis that the amount of non-forested land surrounding a plot affects its plant species composition. The amount of non-forested land surrounding each plot (hereafter, disturbance in the surrounding landscape) was defined as the proportion of a 10-ha, 30-ha, or 100-ha buffer zone surrounding each research plot that was no longer covered by forest (e.g. agricultural use, urban development, roadsides, and clear-cut forest areas). Remote sensing technology was applied using methods modified from Mast et al. (1997). Digital color aerial photography (taken during the winters of 1995 and 1996) of each 75 m × 70 m tree composition plot and surrounding areas was obtained as Digital Ortho Quarter Quads from the Mississippi Automated Resource Information System (MARIS: http://www.maris.state.ms.us/). These images were then downloaded, geo-rectified, and analysed with ERDAS Imagine® imaging software (http://www.erdas.com). An unsupervised classification then quantified the amount of landscape disturbance (non-tree cover) in each of the three buffer zones surrounding each research plot. After signature classes associated with tree cover and non-tree cover were determined, pixel numbers in each class were tabulated (1 pixel = 1 m^2) and the amount of area representing each 7 m × 70 m tree composition plot was subtracted from the 'tree cover' class and the total area of each image. The total proportion of disturbance represented as 'non-tree cover' surrounding each 75 m × 70 m tree composition plot was then quantified.

Data analysis

Habitat 'affinities' of each species were quantified objectively in the following manner. First, for each species we listed all the habitats in which it occurs regionally using regional flora manuals (Radford et al. 1968; Clewell 1985). We then used Correspondence Analysis (PC-Ord, version 4 for Windows software; McCune & Mefford 1999) to order habitat categories with respect to species co-occurrence. We quantified each species' habitat affinity using axis 1 species scores, which were weighted averages of each species' occurrence in the habitat types in which it occurred. We also interpreted compositional differences among habitat types using axis 1 sample scores.

We quantified differences in groundcover plant species composition among our 34 groundcover subplots using non-metric multidimensional scaling (NMS; Kruskal 1964). The proportion of variation in species composition explained by each axis was quantified 'after the fact' using coefficients of determination (r^2) for the relationships between Sørensen distances among observations (subplots) and axis scores. To interpret the NMS axis scores of a groundcover subplot in terms of habitat type, we weighted the cover value of each species in the subplot with the species score obtained from the correspondence analysis of habitat types (described above), then averaged these weighted values. By examining the simple bivariate correlation between the 34 subplots' NMS axis 1 scores and these weighted averages, we evaluated where each of our 34 ground-cover subplots fell along the habitat gradient identified by axis 1 of the correspondence analysis.

We used simple and partial correlations to examine the relationships among plant species composition, plant species richness, *L. japonica* cover, landscape disturbance variables and local environmental variables. Plant species composition was quantified as axis 1 scores from the NMS analysis described above. Plant species richness was quantified as the number of plant species minus *L. japonica*. In each of the partial correlation analyses, we also included latitude and longitude of the groundcover subplots as spatial co-variables.

Our initial examinations of pairwise correlations among all the environmental variables revealed that subsets of these environmental variables were highly correlated with one another, possibly reflecting one or more underlying latent variables. To examine this more closely, we subjected the measured environmental variables (disturbance in the surrounding landscape, fire frequency, canopy density, soil compaction, and elevation below the ridge) to principle components analysis and subsequent factor rotation of the first three axes (which accounted for 90% of the environmental variation) using JMP (version 5.0.1.2). We then repeated the partial correlation analyses described above, replacing the measured environmental variables with the three factors.

Results

Ground-cover species composition

We identified a total of 192 ground-cover species in closed canopy, second-growth upland forests across Lafayette, Marshall and Panola Counties (App. 1). Of the 192 species found in our ground-cover plots, we were able to obtain habitat information for 163 species from regional flora manuals. We identified a total of 59 distinct habitat types (App. 2) in which these species occurred. Correspondence analysis of habitat types based on presence-absence of each species revealed a solar exposure and moisture gradient, with open and xeric habitat types (e.g. railroad embankments, open woods, prairies, open savannas, pine barrens, sandy fields) having negative axis 1 scores and shady and moist or wet habitat types (e.g. mesic forest slopes, alluvial woods, marshes) having positive axis 1 scores (App. 2). Species associated with open habitats included *Euphorbia corollata*, *Rudbeckia hirta*, *Coreopsis lanceolata*, *Liatris aspera*, *Erianthus giganteus*, and *Pityopsis graminifolia*. Species associated with mesic forested slopes included *Polystichum acrosticoides*, *Osmunda cinnamomea*, and *Heuchera americana*.

Non-metric multidimensional scaling of 34 ground-cover subplots produced a single significant axis (axis 1, r^2= 0.39). Low axis 1 scores were associated with subplots in the Bailey Woods, Jackson Strip, Strawberry Plains, and Sardis sites. High axis 1 scores were largely associated with subplots in the Little Tallahatchie Experimental Forest. Axis 1 appeared to sort subplots according to species' affinities for open vs forested habitats (Fig. 2). This was apparent from a negative correlation between NMS axis 1 scores and weighted averages of species' cover values ($r = -\ 0.54$), wherein the weights were derived from the species scores obtained from the correspondence analysis of habitat affinities. Although statistically significant, the relationship between NMS axis 1 scores and habitat affinity was weakened by the fact that subplots with high NMS axis 1 scores contained a mixture of both open habitat and mesophytic forest species. The difference between these subplots and those with low axis 1 scores is that the latter, for the most part, only contained those species indicative of mesic forests. Furthermore, the mesic forest species found in subplots with low axis 1 scores were also found in subplots with high axis 1 scores. These relationships were also reflected in the strong positive correlation between NMS axis 1 scores and species richness ($r = 0.84$); subplots with low axis 1 scores had lower species richness than subplots with high axis 1 scores.

Relationships between species composition, species richness, and environmental conditions

A high proportion of subplots with open habitat and mesophytic herbs and high species richness were associated with low *Lonicera japonica* cover, low disturbance in the surrounding landscape, high fire frequency, low canopy density, low soil compaction, and the lower portion of the steeper slopes. Simple bivariate correlations revealed strong negative relationships between NMS axis 1 scores and *L. japonica* cover, disturbance in the surrounding landscape, and soil compaction (Table 1). We found a strong positive relationship between axis 1 and elevation below the ridge and fire frequency. Similar relationships were found between species richness and these variables (Table 1).

High *L. japonica* cover was associated with high disturbance in the surrounding landscape, low fire frequency, high canopy density, and high soil compaction, as indicated by significant correlations with these variables.

In contrast to the results of the simple bivariate correlations, partial correlation analyses revealed that the proportion of open habitat and mesophytic herb species (Axis 1 scores) was not significantly correlated with *L. japonica* cover or any of the measured environmental variables (Table 1). Once other variables were taken

Table 1. Simple and (partial) correlations of environmental variables and response variables. Statistically significant ($P < 0.05$) correlations are in bold.

Environmental variables	*Lonicera japonica* cover	NMS Axis 1 (Importance of open-habitat and mesophytic herbs)	Species richness
Lonicera japonica cover		**– 0.62** (-0.005)	**– 0.60** (-0.06)
Disturbance in the surrounding landscape	**0.77** (0.22)	**– 0.65** (0.31)	**– 0.61** (0.04)
Fire frequency	**– 0.71** (0.25)	**0.76** (0.18)	**0.70** (0.26)
Canopy density	**0.41** (0.06)	– 0.35 (0.007)	– 0.31 (0.05)
Soil compaction	**0.69 (0.45)**	**– 0.81** (0.28)	**– 0.73** (0.28)
Elevation below ridge	– 0.16 (0.28)	**0.45** (0.28)	**0.43** (0.24)
Latitude	0.10 (0.12)	0.24 **(0.45)**	0.14 (0.13)
Longitude	0.19 (0.24)	**– 0.50** (0.21)	**– 0.37** (0.05)

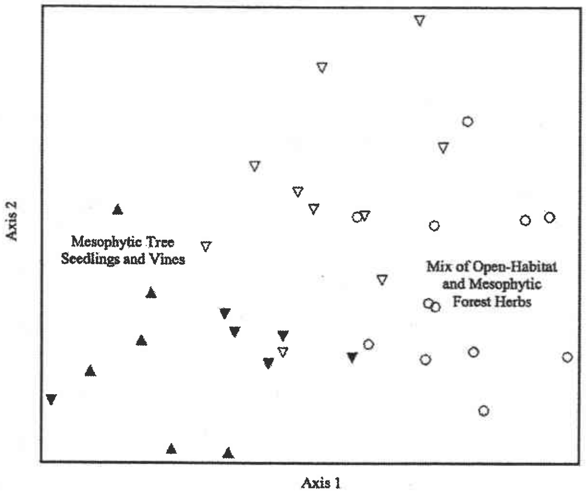

Fig. 2. Non-metric multidimensional scaling of 34 ground-cover subplots in Lafayette, Marshall, and Panola Counties. Bailey Woods and Jackson Strip Subplots (▲); Strawberry Plains and Sardis Subplots (▼); Holly Springs National Forest Subplots (▽); Little Tallahatchie Experimental Forest Subplots (○).

into account, the simple correlation of 0.62 between axis 1 scores and *L. japonica* cover dropped to 0.005 (Table 1). The comparable analysis with species richness produced results similar to axis 1. Once other variables were taken into account, the simple correlation of – 0.60 between species richness and *L. japonica* cover dropped to – 0.06 (Table 1). Partial correlation analysis revealed a significant positive relationship between *L. japonica* cover and soil compaction (Table 2; $r = 0.45$). None of the other partial correlations between *L. japonica* cover and environmental variables were statistically significant (Table 1).

The lack of statistically significant partial correlations between vegetation response variables and measured environmental variables was due in part to correlations among the environmental variables. Correlations among soil compaction, disturbance in the surrounding landscape, and fire frequency were high ($r_{\text{compaction-disturbance}} = 0.64$; $r_{\text{disturbance-fire}} =$ 0.8; $r_{\text{compaction-fire}} =$ 0.68). The high negative correlation between disturbance in the surrounding landscape and fire frequency indicated possible multi-collinearity. Factor analysis revealed that disturbance in the surrounding landscape, fire frequency, and soil compaction all had significant loadings on factor 1, which explained 42% of the environmental variation (Table 2). We named this first factor a soil compaction/ fragmentation factor (Table 2). High factor 1 scores were associated with subplots located on fine-textured soils within agricultural or suburban landscapes. Hence, it is not surprising that high factor 1 scores indicated heavy soils, a high proportion of disturbance in the surrounding landscape, and a low frequency of fire. In contrast, elevation below the nearest ridge was not highly correlated with landscape disturbance, fire frequency, or canopy density (absolute value of $r < 0.33$) but was moderately negatively correlated with soil compaction (0.41), reflecting the sandier soils found at the base of steep slopes. Elevation below the nearest ridge was the only variable that had a high loading on factor 2 (0.98), which explained 21% of the environmental variation (Table 2). We named this factor a slope position factor, with high scores indicating occurrence at the base of steep slopes. High canopy density, which was moderately correlated with disturbance in the surrounding landscape (r

Table 2. Factor loadings of measured environmental variables.

Environmental variables	Factor 1 (Soil compaction / Fragmentation)	Factor 2 (Slope position)	Factor 3 (Canopy openness)
Canopy density	0.22	– 0.03	– 0.95
Landscape disturbance	0.76	– 0.15	– 0.46
Fire frequency	– 0.78	0.09	0.49
Soil compaction	0.90	– 0.24	– 0.03
Elevation below ridge	– 0.20	0.98	0.05

Table 3. Partial correlations of environmental factors, *Lonicera japonica* cover, spatial coordinates, and vegetation response variables. Statistically significant partial correlations are in bold.

Environmental variables	*Lonicera japonica* cover	NMS axis 1 (Importance of open-habitat and mesophytic herbs)	Species richness
Lonicera japonica cover		– 0.002	0.06.
Factor 1 (Soil compaction/ Fragmentation)	**0.83**	**– 0.64**	**– 0.49**
Factor 2 (Slope position)	– 0.03	**0.53**	**0.43**
Factor 3 (Canopy openness)	**– 0.37**	**0.44**	0.26
Latitude	0.13	**0.48**	0.24
Longitude	– 0.27	0.18	– 0.002

$= 0.55$) and fire frequency ($r = \ 0.60$), loaded highly on factor 3, which accounted for 27% of the environmental variation. We named factor 3 a canopy openness factor to reflect the possible effect of higher fire frequencies and limited salvage logging on canopy structure at sites in the National Forest.

Partial correlation analyses of ground-cover composition and richness with variables combined into environmental factors revealed the strongest relationships were with the soil compaction/fragmentation factor. The proportion of open habitat and mesophytic herbs (axis 1 scores) was highest in subplots with uncompacted soils, relatively high fire frequencies, and little disturbance in the surrounding landscape (i.e. low factor 1 scores; Table 3). Likewise, these species were more common at the base of steep slopes (i.e. high factor 2 scores; Table 3). These species were also significantly positively associated with moderate canopy disturbance (i.e. high factor 3 scores; Table 3). Responses of species richness and these factors were similar, except the relationship with the canopy openness factor was not statistically significant (Table 3). *L. japonica* cover was strongly positively correlated with the soil compaction/fragmentation factor, uncorrelated with the slope position factor, and moderately negatively correlated with the canopy disturbance factor (Table 3). As with the partial correlation analysis with environmental variables, the analysis with environmental factors revealed that *L. japonica* cover did not explain a significant amount of variation in composition ($r = 0.002$) or species richness ($r = \ 0.06$).

Discussion

Our findings show that simple correlations between the abundance of invasive species and native plant diversity and composition indicate little about the effect of invasive species on native species or *vice versa.* Despite a strong negative correlation between plant diversity and *L. japonica* cover, we found no relationship between these variables once we accounted for other environmental variables. We found that *L. japonica* cover was greatest within forests with more compacted soils, which may have been more fertile and/or more poorly drained than the sandier soils that favored higher native plant diversity. *L. japonica* was also more abundant in forests with greater disturbance in the surrounding landscape and decreased fire frequency. These same variables may negatively affect native plant diversity directly. Hence, the negative correlation between *L. japonica* cover and plant diversity may simply reflect that the variables that negatively affected *L. japonica* cover positively affected plant diversity and *vice-versa.* Negative correlations between the abundance of invasive species and native plant diversity can be expected in landscapes with a gradient of human disturbance, regardless of whether there is any negative effect of invasive species on native species.

Groundcover species composition differed among mature upland hardwood and hardwood-*Pinus* forests in northern Mississippi that differed in soil texture and perhaps other correlated variables. Although these upland forests currently contain largely closed tree canopies (>80%), groundcover species composition was not entirely indicative of closed canopy conditions. We found that the most diverse sites contained a mixture of open habitat and mesophytic forest herbs. Plant species richness was greatest in sandy, uncompacted soils at the base of steep slopes within forests surrounded by more forest (the same conditions in which *L. japonica* was rare). Many of the open habitat species in these subplots (e.g. *Pityopsis graminifolia*, *Liatris aspera*, *Tephrosia virginiana*) tend to be associated with sandy, nutrient-poor soils, whereas many of the mesophytic species found in these subplots (e.g. *Osmunda cinnamomea*, *Heuchera americana*, *Polystichum acrostichoides*) tend to be associated with moist but light soils. It is possible that the combination of sandy and moist soils associated with seepage areas on lower slopes provided conditions suitable for the coexistence of some open-habitat and mesophytic forest species, at least for the time being.

In contrast to our species-rich samples, the samples with the lowest species richness were represented primarily by animal dispersed seedlings of floodplain or mesophytic trees (e.g. *Liquidambar styraciflua* and *Prunus serotina*) and mesophytic vines [e.g. *Parthenocissus quinquefolia*, *Vitis rotundifolia*, and *L. japonica*]. These samples lacked many of the rarer mesophytic forest herbs (e.g. *Osmunda cinnamomea*, *Heuchera americana*, *Polystichum acrostichoides*) with relatively poor dispersal and virtually all of the open habitat species found in our richer samples. The lack of the mesophytic forest herbs at these sites is consistent with previous findings that poor dispersal limits species diversity in mesic forest fragments or second-growth mesic forests with a history of cultivation (Matlack 1994; Bellemare et al. 2002). This may also partly explain why *L. japonica*, with its efficient means of seed dispersal by animals, is common at these sites. The open habitat species encountered in the current study, many of which are wind-dispersed, simply may not perform well in the relatively heavy, silty soils that characterized these sites.

Our results have important implications for ecological restoration within degraded *Quercus* or *Quercus-Pinus* forests of the interior coastal plain region of the southern USA. We predict that restoration will be most effective in large intact forests with a species-rich native groundcover occurring on well-drained, sandy soils. Many species within these forests are open-habitat species that would likely benefit from opening the forest canopy. If the tree canopy is not opened through selective thinning, we suspect that over time these species will continue to decline because of excess shade, especially considering that very few individuals of open habitat species were observed flowering in this study. We do not know, however, whether the mesophytic forest herbs would respond positively to opening the canopy (Meier et al. 1995). *L. japonica* might also benefit from opening the forest canopy (Yates et al. 2004), but our results show that it is not common at these sites. Forests with silt loam soils are not ideal candidates for restoration, due in part to a relatively low diversity of open habitat species in the interior of fire suppressed forests. Restoration of the forest interior of these sites in a relatively short period of time would require reintroducing native species, which could be costly. On the other hand, restoration of sites with silt loam soils might be successful if thinning and burning were focused at the edges of the forest. Although not encountered in the forest interior subplots on silt loam soils, open habitat species such as *Gentiana villosa*, *Coreopsis tripteris*, and *Andropogon virginicus* are common at the edges of the forest at these sites. These species could respond positively to restoration, provided that competition from *L. japonica* does not intensify with the opening of the tree canopy. Although we found no evidence of a competitive effect of *L. japonica* in our study, this species was common at sites with silt loam soils and has been shown previously to have strong competitive effects at forest edges and in open and disturbed habitats (Cain 1985; Dillenberg et al. 1993; Yurkonis & Meiners 2004). *L. japonica* is likely to preclude restoration in these areas if canopy reduction treatments are not combined with fire or some other means of reducing its abundance.

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For App. 1-2, see JVS/AVS Electronic Archives;
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App. 1. List of species identified to species (excluding *Lonicera japonica*) and associated axis 1 species scores derived from habitat scores from correspondence analysis (App. 2). Nomenclature follows Radford et al. (1968).

Species	Axis 1 score
Acalypha virginica	-84
Acer rubrum	223
Adiantum pedatum	533
Agave virginica	-57
Ailanthus altissima	-260
Albizia julibrissin	-254
Ambrosia artemisiifolia	-229
Amelanchier arborea	97
Ampelopsis arborea	248
Antennaria plantaginifolia	-50
Aralia spinosa	56
Arisaema dracontium	200
Aristolochia serpentaria	-25
Asclepias syriaca	-31
Asplenium platyneuron	-52
Aster drummondii	52
Aster dumosus	-172
Aster linariifolius	-131
Aster patens	-150
Aster pilosus	-148
Aster hemisphericus	-121
Athyrium filix-femina	232
Berchemia scandens	179
Boltonia asteriodes	-134
Botrychium dissectum	34
Callicarpa americana	13
Carex hirsutella	87
Carex muehlenbergii	-125
Carex swanii	150
Carpinus caroliniana	218
Carya glabra	-18
Carya tomentosa	-18
Cassia fasciculata	-189
Chamaelirium luteum	172
Chrysopsis mariana	-152
Clitoria mariana	-150
Commelina erecta	-71
Coreopsis lanceolata	-159
Coreopsis major	-120
Cornus florida	-28
Danthonia spicata	-185
Desmodium nudiflorum	22
Desmodium paniculatum	-124
Desmodium rotundifolium	-54
Dioscorea villosa	134
Diospyros virginiana	-39
Elephantopus tomentosus	-22
Epifagus virginiana	151
Erechtites hieraciifolia	-174
Erianthus giganteus	28
Erigeron pulchellus	534
Euonymus americanus	172
Eupatorium coelestinum	38
Eupatorium fistulosum	129
Eupatorium perfoliatum	96
Euphorbia corollata	-231
Fagus grandifolia	254
Fraxinus americana	175
Galactia macreei	-127
Galium circaezans	152
Galium hispidulum	-165
Galium pilosum	-38
Gentiana villosa	274
Helianthus hirsutus	-406
Heuchera americana	139
Hieracium gronovii	-201
Hydrangea quercifolia	221
Hypericum hypericoides	-27
Hypericum stans	-27
Hypoxis hirsuta	-14
Ilex opaca	131
Impatiens capensis	264
Juniperus virginiana	151
Krigia dandelion	-251
Lactuca canadensis	-177
Leersia virginica	235
Lespedeza capitata	-323
Lespedeza hirta	-323
Lespedeza intermedia	-323
Lespedeza procumbens	-323
Lespedeza repens	-323
Liatris aspera	-260
Ligustrum sinense	-35
Liquidambar styraciflua	109
Liriodendron tulipifera	161
Lobelia inflata	-289
Magnolia grandiflora	153
Malaxis unifolia	60
Microstegium vimineum	227
Mitchella repens	129
Monarda fistulosa	-27
Monotropa uniflora	302
Morus rubra	202
Nandina domestica	15
Nyssa sylvatica	82
Osmunda cinnamomea	208
Osmunda regalis	225
Ostrya virginiana	211
Oxalis violacea	-30
Panicum boscii	-68
Panicum commutatum	44
Panicum dichotomum	-17
Panicum laxiflorum	9
Parthenocissus quinquefolia	36
Passiflora lutea	14
Phlox divaricata	154
Pinus echinata	-109
Pinus taeda	149
Pityopsis graminifolia	-147
Podophyllum peltatum	25
Polygonatum biflorum	220
Polystichum acrostichoides	420
Potentilla simplex	-285
Prunus serotina	9
Psoralia psoralioides	-219
Pteridium aquilinum	-116
Quercus alba	131
Quercus coccinea	-97
Quercus falcata	-31
Quercus marilandica	-80
Quercus nigra	129
Quercus phellos	127
Quercus stellata	-7
Quercus velutina	-77
Rhus copallina	69
Rosa caroliniana	-115
Rubus trivialis	-88
Rudbeckia hirta	-169
Ruellia caroliniana	-6
Salvia lyrata	-112
Sanicula canadensis	39
Sassafras albida	-30

App. 1 & 2. Internet supplement to: Surrette, S.B. & Brewer, J.S.
Inferring relationships between native plant diversity and *Lonicera japonica* in upland forests in north Mississippi, USA
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App. 1, cont.

Species	Axis 1 score
Schizachyrium scoparium	-96
Schrankia microphylla	-194
Scleria pauciflora	-14
Scleria triglomerata	12
Scutellaria elliptica	-196
Scutellaria ovata	368
Silene virginica	37
Smilacina racemosa	215
Smilax bona-nox	-5
Smilax glauca	29
Smilax rotundifolia	129
Solidago caesia	362
Solidago odora	-112
Sorghastrum elliottii	-66
Stylosanthes biflora	-202
Tephrosia virginiana	-268
Thaspium trifoliatum	68
Tipularia discolor	131
Toxicodendron radicans	63
Tradescantia ohiensis	-155
Ulmus alata	188
Ulmus americana	304
Uniola sessiliflora	-12
Vaccinium arboreum	-57
Vaccinium stamineum	-76
Verbesina helianthoides	12
Vernonia gigantea	323
Viola septemloba	-7
Vitis aestivalis	226
Vitis rotundifolia	98
Woodwardia areolata	121

App. 2. Habitats sorted by first axis scores from Correspondence Analysis, which indicate a shade/moisture gradient. These scores were used to interpret how species composition varied among plots.

Habitat	Correspondence Analysis Axis 1 Score
railroad embankments	-300
lawns	-269
open woods	-206
clearings in upland woods	-201
roadsides	-199
clearings/open places	-183
oldfields/fields	-155
cleared floodplains	-154
disturbed/waste ground	-128
pastures	-119
sandy fields	-117
clearings in low woods	-116
woodland borders	-114
pine barrens	-112
prairie	-111
sandhills	-99
rocky woods	-89
wooded roadbanks	-89
sandy woods/woodlands	-71
brushy fields	-61
ruderal	-59
swamp margins/pocosin borders	-56
sandy pinelands	-52
longleaf pinelands	-45
pine-oak-hickory woods	-42
dry bluffs	-37
thickets	-35
scrub	-34
ogs and wet pinelands	-32
condary woods	-29
nd/dry woods	-29
nas	-8
/dunes	2
crops/crevices	2
fencerows	3
coastal hammocks (hardwood forests)	9
meadows/balds	15
mixed deciduous woods	16
flatwoods	28
coastal swales	37
pocosins	43
sinks	45
ditches	62
hammocks (hardwood forests)	91
bayheads	97
bluffs	112
floodplains/alluvial plains	114
low woods	126
alluvial woods	135
calcareous hammocks	139
stream/river banks	144
prairie edges	151
swamps	154
rich or humus-rich woods	159
calcareous swamps	177
marshes	219
stream valleys	225
wooded slopes	334
shady slopes and coves/shady rocky slopes	458

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