Occurrence of Non-native Species Deep in Natural Areas of the Shawnee National Forest, Southern Illinois, U.S.A.

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ABSTRACT: Biological invasion is a leading threat to the ecological integrity of forest ecosystems around the world. The objective of our study was to examine the relationship between the abundance of non-native species in the vegetation and the seed bank to abiotic factors and distance from the nearest forest edge. We identified and estimated the abundance of plant species in sixty-two 0.4 ha permanent plots in natural areas across the Shawnee National Forest in southern Illinois in late spring and summer 2002. The distance of each plot to the closest forest edge was determined using GIS. A 550 cm3 soil core was extracted from five random points within each of the plots in August 2002 to allow measurement of soil nutrient levels and estimates of the abundance of exotic and native species in the soil seed bank. Soils from these cores were placed in trays in a greenhouse on 10 January 2003. Seedlings emerging from the soil cores were identified and tallied every two weeks until no further seed germination was observed. The plots were located deep in the forest interior (up to 730 m), yet forest edge effects predominate. Distance from forest edges was negatively related to density of both native and non-native species in the seed bank. The largest numbers of non-natives in the seed bank were present in those plots closest to the forest edge. None of the nine important abiotic factors (K, Ca, P, Mg, pH, CEC, % silt, canopy opening) measured in this study was related to the seed bank density of the native and non-native species. Potassium was negatively and calcium was positively related to richness of understory native species and distance from forest edge. Phosphorus, Mg, pH, CEC, % silt, OM, and canopy opening were not related to the richness of native species and distance. Commelina communis, Lonicer a japonica, Microstegium vimineum, and Rosa multiflora were non-native species present in the understory vegetation while Cardamine hirsuta, Lactuca serriola, Lespedeza cuneata, M. vimineum, Mollugo verticillata, and Stellaria media were non-native species present in the seed bank. The discordance between non-native species richness in the seed bank and vegetation community indicates that management of invasive species must extend beyond eradication of non-natives in the aboveground vegetation. Land and forest managers should eradicate seedlings of non-native species before they reach seed production stage to decrease their accumulation in the seed bank even at sites located at a great distance from the forest edge.

Index terms: abiotic factors, biological invasions, forest edges, natural areas, non-native species, seed bank

INTRODUCTION

Natural areas and reserves are established to preserve biological diversity, rare species, and important ecological habitats and geological features (Cain 1947). However, studies from around the world have shown that these natural areas and reserves are susceptible to invasion by non-native species (Evans 1984; Macdonald and Frame 1988; Honu and Dang 2002; Weber 2004). Non-native species are those species, often referred to as exotic species, that have been introduced accidentally or intentionally into a new environment (Richardson et al. 2000).

A forest edge represents a junction between two landscape elements (e.g., a forest stand and a crop field) (Ambrose and Bratton 1990; Honu and Gibson 2006) and may act as a filter restricting the movement of agricultural weeds into the forest interior (Devlaeminck et al. 2005). In addition, a forest edge can serve as an entry point for non-native species where they can establish and reproduce producing propagules for dispersal into the forest interior (Brothers and Spingarn 1992; Matlack 1994). Forest edges have a habitat gradient that generally supports an abundance of plant species compared with the forest interior (Fraver 1994; Matlack 1994). The general change of biotic (e.g., species richness) and abiotic factors (e.g., canopy openness) from the forest edge into the interior is known as the edge effect (Leopold 1933; Brothers and Spingarn 1992).

Abiotic factors such as canopy openness or light (Parendes and Jones 2000; Honu and Gibson 2006), disturbance (Huebner and Tobin 2006), and altitude (Macdonald et al. 1988) have been shown to be related to the distribution of non-native species. These studies suggest that understanding the relationship between abiotic factors and non-native species is critical in the management of these species. However, the relationship between variation of levels of abiotic factors and the abundance of non-native species present in the forest interior is poorly understood (Hester and Hobbs 2000; Underwood et al. 2004).
Additionally, non-native species have been observed to occur in the interior of forest stands (Evans 1984; Mooney and Drake 1984; Macdonald et al. 1986; Cox 1999), suggesting the importance of the relationship between long dispersal and abundance of non-native species (MacArthur and Wilson 1963; Fang 2005; Piessens et al. 2005). However, previous studies are mostly limited to 100 m from the forest edge (e.g., Matlack 1994; Underwood et al. 2004; Honu and Gibson 2006; Honu and Gibson 2008). Seed bank studies in our study region of southern Illinois showed that several non-native species can have a persistent seed bank (Gibson et al. 2002; Honu 2004); the distribution of non-native species is related to abiotic factors such as canopy openness (Honu and Gibson 2006). Both of these factors may allow non-native species to disperse and spread into the forest interior.

In this study, we address the issue of whether non-native species can penetrate the forest interior at distances greater than the 100 m usually considered to represent the depth of the forest edge (Murcia 1995). Specifically we address the question, does distance from forest edges into the interior and abiotic factors relate to the abundance of non-native species in (1) the understory vegetation and (2) the soil seed bank? We hypothesized that the abundance of non-native species in the understory vegetation (H1) and the soil seed bank (H2) would decrease with increasing distance into the forest interior; (H3) abiotic factors will be related to the distribution of the non-native species in the understory vegetation and seed bank, and (H4) the non-native species will develop a persistent seed bank (i.e., we expect more non-native species to be in the seed bank than in the understory vegetation) (Abrahamson 1984; Greenberg et al. 2001; Honu and Gibson 2008).

**METHODS**

**Study Sites**

The study took place in eight Research Natural Areas (RNAs) in the Shawnee National Forest (SNF) in southern Illinois (Table 1). The RNAs were established by the United States Forest Service over a period of three years and Table 1 provides a description of the RNAs. The RNAs represent relatively undisturbed protected areas (Hutchison et al. 1988). Three hundred and seventy-eight 0.1-0.4-ha permanent plots across the eight RNAs were established and sampled between 1995 and 1998 (Chandy et al. 2006). The plots were established according to a stratified random design by landform under areas of visually homogeneous topography.

**Understory Vegetation Assessment**

To test hypotheses H1 and H3 we resampled 62 out of 378 permanent plots across the eight RNAs using a stratified random pattern (Table 1). The stratification was based on a Nonmetric Multidimensional Scaling (NMDS) ordination (Minchin 1991) of tree basal area from previous studies (1996-1998) (Chandy et al. 2006). Two ordination axes adequately summarized the vegetation data (Chandy 2007), and the scatter diagram from a plot of these axes was divided into 16 quadrants, and five plots were selected randomly from each quadrant. Plots were randomly chosen from each quadrant and where plots were absent from a quadrant, outliers were chosen. The ordination provided an objective means of selecting the most representative plots to sample from across the Shawnee without bias. The tree layer was the most stable and the number of plots sampled captured 99% of the species, which is good. The distance to the closest forest edge of each of the 62 selected plots was determined from GPS coordinates of the plots using aerial photographs and field reconnaissance (see understory vegetation assessment) (Chandy 2002). The distance of the plots to the closest forest edge ranged from 10 to 730 m with 55% of the plots at distances > 100 m (Table 2). In the field, the plots were divided into four quadrants by the four cardinal points. Four 0.25 m² subplots were randomly established within each of the four quadrants, totaling 16 subplots. The subplots were located by random selection of distances along the four cardinal directions followed by perpendicular distances from the cardinal directions into the quadrant. All the herba-

**Seed Bank Density Assessment**

To test hypotheses H2 and H4, we randomly selected one of the four subplots per quadrant (see understory vegetation assessment) and extracted a 550 cm³ soil core from the top six cm of the A-horizon in August 2002 (d = 5.4 cm and h = 6 cm). An additional soil core was extracted from the center of one of the remaining randomly selected subplots, totaling five soil cores. We mixed the five soil cores thoroughly and 1/5 separated for soil analysis (Table 2). The seed bank samples (4/5ths of remaining soil cores) were kept in cold storage at 4 °C for four months in the Department of Plant Biology (DPLB), Southern Illinois University at Carbondale (SIUC) to break the dormancy of the seeds (Baskin and Baskin 1998). A germination experiment was set up in the DPLB greenhouse on 10 January 2003. Each seed bank sample was spread on a mixed base of vermiculite and potting soil (50:50) to increase the rooting medium in a free-draining plastic germination tray (30 cm x 48 cm). Twenty trays containing only vermiculite and potting soil were located among the seed bank trays to serve as controls for seed contamination. Samples were watered daily. Emerging seedlings were identified and tallied every two weeks until no further seed germination was observed. The identified seedlings were removed at each stage of the sampling. Seedlings that could not be identified were transplanted individually into large pots and allowed to grow until flowering stage. In order to maximize randomization of the samples to avoid microenvironmental
<table>
<thead>
<tr>
<th>RNA</th>
<th>Atwood Ridge</th>
<th>Baker Bluff</th>
<th>Burke Branch</th>
<th>Dennison Hollow</th>
<th>Panther Hollow</th>
<th>La Rue Pine Hills</th>
<th>Ozark Hill Prairies</th>
<th>Whoopie Cat Mountain</th>
</tr>
</thead>
<tbody>
<tr>
<td>County</td>
<td>Union County</td>
<td>Hardin County</td>
<td>Pope County</td>
<td>Saline County</td>
<td>Hardin County</td>
<td>Union County</td>
<td>Alexander County</td>
<td>Hardin County</td>
</tr>
<tr>
<td>Area (ha)</td>
<td>369</td>
<td>24</td>
<td>83</td>
<td>83</td>
<td>73</td>
<td>105</td>
<td>217</td>
<td>7</td>
</tr>
<tr>
<td># of plots surveyed.</td>
<td>6</td>
<td>4</td>
<td>10</td>
<td>3</td>
<td>8</td>
<td>15</td>
<td>12</td>
<td>4</td>
</tr>
<tr>
<td>Landscape elements</td>
<td>Roads</td>
<td>Crop &amp; hay fields</td>
<td>Road, trail, &amp; riparian corridors</td>
<td>Roads</td>
<td>Road &amp; riparian corridors</td>
<td>Roads</td>
<td>Trail &amp; wildlife openings</td>
<td>Roads</td>
</tr>
<tr>
<td>bordering the forest</td>
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</tr>
<tr>
<td>Relief</td>
<td>Barrens, sandstone glades, cliffs</td>
<td>Glade &amp; forest complex</td>
<td>Juncture of Mississippi Embayment/Shawnee Hills</td>
<td>Sandstone glades &amp; cliffs</td>
<td>Sandstone hollow &amp; cliffs</td>
<td>Bottomland forest ponds, swamps, bluffs, &amp; upland forests</td>
<td>Bluff ridge &amp; steep sided canyons</td>
<td>Limestone cedar glades</td>
</tr>
<tr>
<td>Mean Elevation (m)</td>
<td>850</td>
<td>544</td>
<td>130</td>
<td>760</td>
<td>460</td>
<td>200</td>
<td>225</td>
<td>140</td>
</tr>
<tr>
<td>Forest cover types</td>
<td>40, 44, 52, 60</td>
<td>40</td>
<td>40, 52, 53, 59</td>
<td>40, 52, 53, 110</td>
<td>40, 52, 60</td>
<td>40, 52, 53, 59, 60, 62</td>
<td>40, 52, 59, 60, 62, 65, 76, 87, 93, 110</td>
<td>52</td>
</tr>
</tbody>
</table>

effects of position in the greenhouse, the
plastic trays were rearranged twice during
the germination studies (Gibson 2002). The
soils in the germination trays were stirred
on 24 June 2003 after the primary flush of
emerging seedlings had ended to expose
any ungerminated seeds. No emerging
seedlings were observed after the soils
were stirred. The experiment was termi-
nated in September 2003. The emerging
seedlings provided an approximation of
the germinable seed bank (Gibson 2002).
Oxalis stricta was the only species found
in the control germination trays and was
eliminated from the analysis. Additionally,
one species that could not be identified was
eliminated from the analysis.

Abiotic Factor Assessment

One-fifth of the soil in each soil core
from each of the 62 permanent plots was
analyzed for available phosphorus (P),
potassium (K), calcium (Ca), magnesium
(Mg), pH, cation exchange capacity (CEC),
and percent organic matter. An atomic ab-
sorption method was used to measure Ca
and Mg while flame emission was used to
measure K. A molybdate blue calorimetric
procedure was used to extract P. Mehlich
(1984) provides a detailed analytical pro-
cedure for the extraction of the cations,
Dahnke (1975) for the estimation of the
pH, and Donald (1996) for the percent
organic matter.

Determination of soil texture (% sand,
clay, and, silt) was based on dispersion
and settlement of particles in water (Ball
1986).

We took hemispherical fish eye photo-
graphs for the examination of canopy
openness over the permanent plots (Frazer
et al. 1999). The fish eye photographs were
taken at 76 cm above the ground level on
overcast days in August 2004. The Gap
Light Analyzer (version 2.0) software was
used to determine the canopy openness
(Frazer et al. 1999).

DATA ANALYSIS

Multiple linear regression (backward se-
lection) (SAS 1990) was used to examine
the relationship between species richness
and diversity of the understory vegetation
and seed bank (dependent variables) and
the independent variables (distance and the
nine abiotic factors) from forest edges. Of
the potential independent variables, Spear-
man correlation analysis showed that %
sand, clay, and silt were correlated with
each another. Percent silt was retained in
the analysis but % sand and % clay were
eliminated from the analysis. Percent silt
was retained because it generally affects
vegetation dynamics more than sand and
clay. The relationship between log spe-
cies richness of exotic and native species
distance from nearest forest edge was
investigated with linear regression. A com-
parison of the slope and y-axis intercept of
these two regression lines was conducted
using a Student’s t-test (Zar 1984).

RESULTS

Understory Vegetation

Four non-native species (Commelina com-
munis, Lonicera japonica, Microstegium
vimineum, and Rosa multiflora) occurred
in the understory vegetation of four out of
the eight RNAs (Table 3). Burke Branch
RNA was invaded by more non-native
species than any of the other eight RNAs
and had the highest Relative Index of
Invasion (RII) (Table 3). Relative Index
of Invasion is defined as total number of
exotic species divided by number of exotic
and native species combined multiplied
by 100 (Macdonald et al. 1988). Relative
frequencies (RF) of the non-native species
among the RNAs ranged from 10% to 70%.
Lonicera japonica was the most abundant
non-native species in the understory veg-
etation (Table 3). Relative frequency is
defined here as number of occurrences
divided by the number of plots sampled
multiplied by 100.

A total of 175 native understory species
were present in the understory vegetation
across the RNAs. Amphicarpa bracteata,
Botrychium virginianum, Ditrichum pal-

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>Std Dev</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot distance from nearest edge (m)</td>
<td>176.9</td>
<td>166.4</td>
<td>10.0</td>
<td>730.0</td>
</tr>
<tr>
<td>Species richness/plot</td>
<td>16.1</td>
<td>6.2</td>
<td>4.0</td>
<td>38.0</td>
</tr>
<tr>
<td>Total seed bank density/m²</td>
<td>1729.0</td>
<td>1206.0</td>
<td>217.0</td>
<td>5978.0</td>
</tr>
<tr>
<td>Seed bank density of native species/m²</td>
<td>1494.0</td>
<td>1057.0</td>
<td>217.0</td>
<td>5652.0</td>
</tr>
<tr>
<td>Seed bank density of non-native species/m²/plot</td>
<td>234.9</td>
<td>367.7</td>
<td>0.0</td>
<td>1413.0</td>
</tr>
<tr>
<td>pH</td>
<td>5.3</td>
<td>0.8</td>
<td>4.2</td>
<td>7.8</td>
</tr>
<tr>
<td>phosphorus (P µg g⁻¹)</td>
<td>19.2</td>
<td>12.0</td>
<td>4.0</td>
<td>64.0</td>
</tr>
<tr>
<td>potassium (K µg g⁻¹)</td>
<td>86.6</td>
<td>36.3</td>
<td>36.0</td>
<td>202.0</td>
</tr>
<tr>
<td>calcium (Ca µg g⁻¹)</td>
<td>1148.0</td>
<td>1365.0</td>
<td>126.0</td>
<td>8961.0</td>
</tr>
<tr>
<td>magnesium (Mg µg g⁻¹)</td>
<td>116.9</td>
<td>77.0</td>
<td>21.0</td>
<td>380.0</td>
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<td>Organic matter (% OM)</td>
<td>3.2</td>
<td>0.7</td>
<td>1.1</td>
<td>4.5</td>
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<tr>
<td>Sand (%)</td>
<td>20.3</td>
<td>0.1</td>
<td>20.1</td>
<td>20.5</td>
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<tr>
<td>Clay (%)</td>
<td>20.2</td>
<td>0.1</td>
<td>20.1</td>
<td>20.4</td>
</tr>
<tr>
<td>Silt (%)</td>
<td>59.5</td>
<td>0.1</td>
<td>59.2</td>
<td>59.8</td>
</tr>
<tr>
<td>Canopy openness (%)</td>
<td>14.4</td>
<td>3.4</td>
<td>10.0</td>
<td>31.9</td>
</tr>
</tbody>
</table>

Table 2. Range of variation of species richness, seed bank density, and abiotic variables including
distance from nearest edge in plots surveyed across the Shawnee National Forest, southern Illinois,
n = 62.
**Seed Bank Density**

Seven non-native species were present in the seed bank and unlike in the understory vegetation, non-native species germinated from soil cores from all eight RNAs (Table 3). The relative frequency of the non-native species varied between 7% and 40% (Table 3). *Lactuca serriola* and *Stellaria media* were the most frequent non-native species across the RNAs (Table 3). The seed bank density of the non-native species per plot ranged from 109 to 965 seeds m$^{-2}$ (Table 4). *Lactuca serriola* germinated from the plots deepest in the forest – 730 m from the nearest edge. The abundance of non-native species in the seed bank decreased with increasing distance from the nearest forest edge ($H_2$; Table 4, Figure 1).

*Microstegium vimineum* was the only non-native species present in both the understory vegetation and the seed bank (Table 3). The RII of the seed banks was higher than those of the understory vegetation across the SNF (Table 3).

A total of 46 native species were present as emergents from the seed bank across the eight RNAs (Table 5). *Carex cimphibola*, *Carex digitalis*, *Carex grisea*, *Eupatorium rugosum*, *Juncus tenuis*, and *Panicum boscii* were the most widespread species across the RNAs (Table 5). The total seed bank density of the native species per plot was negatively related to distance to nearest forest edge (Table 4, Figure 1). The rate of decline in the seed bank density of non-native and native species from the forest edge to the interior was essentially the same (slope = −0.0029 and −0.0024, respectively) even though the total seed bank density was higher for native species than for non-native species (Figure 1). In other words, the two fitted regression lines do not have a significantly different slope ($t_{0.05(2), 276} = 1.16, p > 0.05$), but have significantly different y-axis intercepts ($t_{0.05(2), 277} = 3.28, p < 0.002$).

**Abiotic Variables**

A multiple regression analysis showed a significant relationship between the levels of soil potassium and calcium and native species richness (Table 4). Potassium was negatively and calcium was positively related to species richness and distance from forest edge. The amount of variability explained ($R^2$) by the additive effect of the potassium and the calcium was 27%. Species diversity was not related to any of the nine independent variables examined (Table 4).
DISCUSSION

Our study documents the occurrence of non-native species deep in the interior (up to 730 m from the nearest edge) of native-species dominated forests in southern Illinois. More species were found in the soil seed bank than in the herbaceous understory vegetation, suggesting that the seed bank acts as a reserve for non-native species. We discuss below the implications of these findings for understanding and managing non-native species in forest systems.

Table 4. Multiple Linear Regression Models (Backward Selection) of non-native and native species present in the vegetation and the soil seed bank across natural areas in the Shawnee National Forest, southern Illinois.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Parameter Estimate</th>
<th>Standard Error</th>
<th>Type II SS</th>
<th>F Value</th>
<th>Pr &gt; F</th>
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</thead>
<tbody>
<tr>
<td>Vegetation</td>
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</tr>
<tr>
<td>Non-native species</td>
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</tr>
<tr>
<td>Species richness</td>
<td>No analysis because of too few species per plot</td>
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<td></td>
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</tr>
<tr>
<td>Species diversity (H')</td>
<td>No analysis because of too few species per plot</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>Native species</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species richness</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>19.30022</td>
<td>1.87714</td>
<td>3051.899</td>
<td>105.71</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Potassium</td>
<td>-0.08253</td>
<td>0.02648</td>
<td>280.4198</td>
<td>9.71</td>
<td>0.0028</td>
</tr>
<tr>
<td>Calcium</td>
<td>0.00343</td>
<td>0.000731</td>
<td>635.056</td>
<td>22</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Species diversity (H')</td>
<td>No relationship</td>
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<td>Seed bank density</td>
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<tr>
<td>Non-native species</td>
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<td>By individual species</td>
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<tr>
<td>Intercept</td>
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<td>17.46</td>
<td>6994465</td>
<td>1534.72</td>
<td>&lt;.0001</td>
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<td>Distance from forest edge</td>
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<td>700914</td>
<td>153.79</td>
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<tr>
<td>By plots</td>
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<td></td>
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</tr>
<tr>
<td>Intercept</td>
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<td>64.0493</td>
<td>9072959</td>
<td>185.99</td>
<td>&lt;.0001</td>
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<tr>
<td>Distance from forest edge</td>
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<td>1422925</td>
<td>29.17</td>
<td>&lt;.0001</td>
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<td>Native species</td>
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</tr>
<tr>
<td>By individual species</td>
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<td>184.8531</td>
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<td>9057456</td>
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</table>

DISCUSSION

Our study documents the occurrence of non-native species deep in the interior (up to 730 m from the nearest edge) of native-species dominated forests in southern Illinois. More species were found in the soil seed bank than in the herbaceous understory vegetation, suggesting that the seed bank acts as a reserve for non-native species. We discuss below the implications of these findings for understanding and managing non-native species in forest systems.

Understory Vegetation

Non-native plant species are an increasing problem in the forests of eastern North America (Cox 1999) including the southern Illinois region studied here (Ebinger 1993; Spyreas et al. 2004). Nevertheless, we document only four non-native plant taxa (Commelina communis, Lonicera japonica, Microstegium vimineum, and Rosa multiflora) in the herbaceous vegetation from a survey of 62 forest interior plots across eight Research Natural Areas. In our region, non-native species are more commonly associated with forest edges and trails than with the forest interior (Campbell and Gibson 2001; Honu and Gibson 2008). However, while the general restriction of many non-natives to forest edges is encouraging from a natural areas preservation perspective, the occurrence of non-natives in the seed bank of the forest interior up to 730 m from the nearest forest edge indicates the potential for recruitment into the vegetation of non-natives in the future. Some non-natives such as Elaeagnus umbellata (not found in our survey, but locally common invading young, secondary forest) and Cardamine hirsuta appear edge insensitive in our region, making them of particular concern (Yates et al. 2004; Honu and Gibson 2006).

The most abundant non-native species ob-
served in the understory vegetation in the forest interior (i.e., *Lonicera japonica*) has been shown to be abundant at forest edges (Yates et al. 2004; Honu and Gibson 2008) yet still occurs within the forest interior (Brothers and Spingarn 1992). Non-native species reproduce within their microhabitat and disperse their propagules to other parts of the forest by dispersal agents such as frugivores and wind (Estrada and Fleming 1986; Brothers and Spingarn 1992). Few studies compare the reproductive strategies of non-native species in forest edges and the interior. However, field observations have shown that *L. japonica* may be spread vegetatively rather than via seed dispersal in the forest interior (Yates et al. 2004; Honu and Gibson 2008). The presence of *Microstegium vimineum* in the floodplain at Burke Branch RNA emphasized the importance of riparian pathways in the invasion of exotics (Barden 1987; Parendes and Jones 2000; Gibson et al. 2002; Thomas et al. 2006). The severe invasion of Burke Branch RNA by non-native species may be due to the high variability of forest edge types there compared with the other RNAs (Table 1). *Lonicera japonica* has been a problem at Burke Branch (overgrowing barrens in the absence of fire since at least 1968) (Anderson and Schwegman 1971), and *M. vimineum* has been reported since 1992 (Anderson et al. 2000). We show that elevation (Macdonald et al. 1988), soil resources (Hobbs 2000), and canopy openness (Honu and Gibson 2006) are not the only factors that affect the distribution of non-native species; distance from forest edges is also important (Table 4, Figure 1). Forest edges serve as a seed source for non-native species, and closeness to a rich seed source increases forest invasibility (Hutchinson and Vankat 1997; Cadenasso and Pickett 2001). Our study differed from other edge studies because the plots were a long way from the nearest edge (≤ 730 m), yet forest edge effects predominate. The two soil nutrients (K and Ca) we found to be related to species richness of native species have been shown to be important in the distribution of plant species (Gates et al. 1956; Freligh et al. 2003). The decreasing levels of soil potassium from the edge into the forest interior were expected, while the increasing levels of calcium were not. Soil nutrient levels may decrease from the forest edge into the forest interior because of decreasing accumulation and deposition of debris at the forest edge compared to the forest interior (Matlack 1993; Hester and Hobbs 2000). The increasing levels of calcium from the edge into the forest interior may be due to increasing abundance of limestone rocks from the edge into the forest interior (Honu, pers. observation).

**Seed Bank Density and Richness**

Distance from forest edge rather than abiotic factors was most strongly related to seed bank density of the exotics, reflecting the need to take a regional landscape perspective for understanding non-native species distribution patterns (Thomas et al. 2006; Predick and Turner 2008). The number of non-native species present in the understory vegetation was less than those present in the seed bank (vegetation = 3; seed bank = 6; vegetation and seed bank = 1; Table 3). The relatively large number of non-native species found in the seed bank but absent in the understory vegetation supports the seed bank persistence of invasive species (Table 3) (Abrahamson 1984; Greenberg et al. 2001). We found a large number of non-native species in the seed bank in the natural areas, but only a limited number were present in the understory vegetation. Similarly, Honu (2004) found non-native species to be abundant across forest edges in the Shawnee National Forest, southern Illinois, but only a few were present in the understory vegetation. Seeds of non-native species are generally capable of remaining dormant in the seed bank for a long period waiting for a disturbance event that would allow them to establish in the vegetation (Cousens and Mortimer 1995; Baskin and Baskin 1998; Piessens et al. 2005). A disturbance event can range from a single to several fallen trees (Bormann and Likens 1979; Runkle and Yetter 1987) or from fire or animal activity (Heinselman 1973). When canopy closure increases, these species disappear from the above ground vegetation and strategically remain in the seed bank waiting for a disturbance event that may open the canopy for favorable conditions (Usher et al. 1998). In a similar survey restricted to within 50 m of forest edges at three southern Illinois RNAs, non-native species abundance in the understory vegetation was related to overhead canopy cover (Honu and Gibson 2006).

The number of native species present in the understory vegetation was more than the number present in only the seed bank, supporting the idea that non-native species we observed in this study have high seed bank persistence compared with the native species (vegetation = 139 species,
<table>
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<tr>
<th>Species</th>
<th>AR (n = 6)</th>
<th>BB (n = 4)</th>
<th>BU (n = 10)</th>
<th>DH (n = 4)</th>
<th>OZ (n = 12)</th>
<th>PH (n = 8)</th>
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Table 5. Seed bank density (no. m⁻²) of native species present across the Shawnee National Forest, southern Illinois. AR = Atwood Ridge, BB = Baker Bluff, BU = Burke Branch, DH = Dennison Hollow, OZ = Ozark Hills, PH = Panther Hollow, PHL = LaRue Pine Hills, and WC = Whoopie Cat Mountain Research Natural Areas. Numbers in parentheses are % relative frequencies (# of occurrence/n *100). * = species also present in the vegetation.
seed bank = 13, present in both vegetation and seed bank = 33; Table 5). Matlack and Good (1990) found that 25% of native species in the seed bank were not present in forest stands, comparable to the 28% of the native species we observed in the seed bank that were not present in the forest stands (Table 5). Devlaeminck (2005) found the similarity between the vegetation and seed bank to decrease with distance from forest edge and interior up to 3 m from the edge. Those species represented in the seed bank that were not present in the understory vegetation may have arrived at the site recently through seed dispersal agents or may have been in the soil seed bank for a long period of time without receiving an appropriate germination cue.

**CONCLUSIONS AND MANAGEMENT IMPLICATIONS**

This study confirmed the susceptibility of natural areas to invasion by non-native species even at distances up to 730 m deep into the natural area. The abundance of non-native species in the seed bank decrease with distance from forest edges. We found more non-native species in the seed bank than in the understory vegetation, suggesting that non-native species are likely to remain dormant in the seed bank for a period of time waiting for suitable environmental conditions for germination and establishment (Cousens and Mortimer 1995; Baskin and Baskin 1998; Piessens et al. 2005). Distance from forest edge was the most important factor of those tested related to the seed bank density of non-native species. Potassium and calcium are essential soil nutrients that were related to richness of native species. The results of this study are important in making forest managers aware of the presence of non-native species as seed below ground in the soil that may not be growing in the understory vegetation. Reduction in accumulation of non-native species in the seed bank may be achieved by land and forest managers by the eradication of seedlings of non-native species before they reach seed production stage.
We thank Sedonia Sipes, Charles Ruffner, Andrew Carver, and Dale Vitt for their helpful comments on many aspects dealt with in this manuscript; Allen Dzurney for assistance with the field work; Mark Basinger and Michael Mibb for assistance with the species’ identification; the SIUC greenhouse staff for watering the soil seed bank, and Kevin Davie for assisting in the determination of plot distances to seed bank, and Kevin Davie for assisting in the determination of plot distances to forest edge. Partial funding was provided by the U.S. Forest Service, North Central Research Station, James E. Ozment Achievement Award, and a Southern Illinois University at Carbondale Dissertation Research Award received by Yohanes A.K. Honu.

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