Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invasibility

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ABSTRACT

The North American woody species, Prunus serotina Ehrh., is an aggressive invader of forest understories in Europe. To better understand the plant invasion process, we assessed understorey plants and Prunus serotina seedlings that have colonized a 35-year-old replicated common-garden experiment of 14 tree species in south-western Poland. The density and size of established (> 1 year old) P. serotina seedlings varied among overstorey species and were related to variation in light availability and attributes of the understorey layer. In a multiple regression analysis, the density of established P. serotina seedlings was positively correlated with light availability and understorey species richness and negatively correlated with understorey species cover. These results suggest that woody invader success is adversely affected by overstorey shading and understorey competition for resources. Simultaneously, however, invader success may generally be positively associated with understorey species richness because both native and invasive plant colonization respond similarly to environmental conditions, including those influenced by overstorey tree species. Identification of characteristics of forests that increase their susceptibility to invasion may allow managers to target efforts to detect invasives and to restore forests to states that may be less invasible.

Keywords

Biological invasions, competition, diversity, invasibility, light, Prunus serotina, species richness.

INTRODUCTION

Invasibility has been defined as the susceptibility of an ecosystem to invasion by one or more non-resident species (Lonsdale, 1999; Davis, 2005). While many recent studies have shown relationships between invasibility and resident diversity, the existence and direction of these relationships, as well as the mechanisms leading to these patterns, are in debate. Most experiments involving manipulations of diversity have shown negative relationships between diversity and invasibility, which have been largely attributed to competition (Tilman, 1997; Knops et al., 1999; Levine, 2000; Dukes, 2001; Hector et al., 2001; Kennedy et al., 2002; Stachowicz et al., 2002; Troumbis et al., 2002; Brown & Fridley, 2004; Pfisterer et al., 2004; but see Von Holle, 2005). In contrast, seed addition experiments across natural diversity gradients (Foster et al., 2002) and surveys of larger areas (Stohlgren et al., 1998, 1999, 2005, 2006; Lonsdale, 1999; Levine, 2000; McKinney, 2002; Sax, 2002; Brown & Peet, 2003; Cleland et al., 2004; Espinosa-Garcia et al., 2004; Davies et al., 2005; Gilbert & Lechowicz, 2005; Richardson et al., 2005; but see Stachowicz et al., 2002) have shown positive relationships between diversity and invader (non-resident species) richness. Relationships between diversity and invasion may depend on the size and resolution of the area examined, with a few recent studies showing negative relationships in small habitat patches and positive relationships across larger areas (Brown & Peet, 2003; Davies et al., 2005; Knight & Reich, 2005). Additionally, when native cover and native diversity are examined simultaneously, they may have opposite effects on invasibility (Knight & Reich, 2005).

Many potential mechanisms have been proposed to explain large-scale positive relationships between native diversity and
invasibility. Propagule pressure of exotic species may be greater in areas with greater native diversity (Lonsdale, 1999; Levine, 2000; Rejmánek, 2003). Characteristics of the surveyed areas such as size (Lonsdale, 1999; McKinney, 2002), heterogeneity (Huston & DeAngelis, 1994; Lonsdale, 1999; McKinney, 2002; Espinosa-Garcia et al., 2004; Davies et al., 2005; Richardson et al., 2005; Richardson & Pyšek, 2006), gross resource levels (Shea & Chesson, 2002; Huebner & Tobin, 2006), climate (Richardson et al., 2005), identity of dominant species (Emery & Gross, 2006), or unidentified environmental factors (Sax, 2002; Cleland et al., 2004; Gilbert & Lechowicz, 2005; Knight & Reich, 2005) may affect native and exotic plants in the same way, leading to positive relationships between native diversity and invasibility: Identification of the mechanisms responsible for the positive association of invasibility and diversity may have important implications for both community ecology theory and the management of invasive species.

Invasibility has been measured as the species richness of non-native species ( Tilman, 1997; Stohlgren et al., 1998, 1999; Knops et al., 1999; Lonsdale, 1999; Levine, 2000; Hector et al., 2001; Foster et al., 2002; Kennedy et al., 2002; McKinney, 2002; Troumbis et al., 2002; Brown & Peet, 2003; Pfisterer et al., 2004), the total biomass of the invaders ( Knops et al., 1999; Hector et al., 2001; Kennedy et al., 2002; Troumbis et al., 2002), and the presence, abundance, cover, or success of individual invasive species (Levine, 2000; Naem et al., 2000; Dukes, 2001; Knight & Reich, 2005). Examining the response of one invasive species, rather than the richness of invasive species, to biotic or abiotic factors is a bottom-up approach that may facilitate the identification of mechanisms underlying patterns of invasibility. The response of a single invasive species may also be a particularly relevant measure of invasibility in environments where invasive richness is low and that invader is particularly important (e.g. Levine, 2000; Naem et al., 2000; Dukes, 2001; Knight & Reich, 2005).

To better understand factors that control plant invasion, we assessed the relationship between overstorey tree species, understorey plant communities and resources, and the abundance and size of P. serotina Ehrh. seedlings in a well-replicated 35-year-old common-garden experiment of 14 tree species. In this experiment at the Siemianice Experimental Forest in south-western Poland, P. serotina is one of the most common of 111 non-planted species (M.K., unpublished data). The present experiment relates the size and density of invading P. serotina seedlings to biotic and abiotic understorey conditions created by different overstorey tree species.

**Study species**

*Prunus serotina* is a tree native to eastern North America and invasive in Poland and other areas of Europe. It was introduced for timber in the early 1800s, and widely planted in the understories of European conifer plantations from the 1930s to the 1950s (Muys et al., 1993). *Prunus serotina* commonly invades hedgerows in agricultural landscapes (Deckers et al., 2005), urban forest patches (Honnay et al., 1999), and forests with overstories dominated by *Pinus sylvestris* (Muys et al., 1993). It is abundant in forests dominated by *Quercus petraea*, *Q. robur*, *P. sylvestris*, and *Betula pendula*, where it was formerly planted (Starfinger et al., 2003). *Prunus serotina* can tolerate a wide range of environmental conditions (Auclair & Cottam, 1971). Although seedlings may persist in shady conditions (Burns & Honkala, 1990; Closset-Kopp et al., 2007), saplings are intolerant of deep shade, with poor growth (Auclair & Cottam, 1971; Kobe et al., 1995; Tripler et al., 2002; Closset-Kopp et al., 2007) and survival (Kobe et al., 1995; Lei et al., 2002) in low-light conditions and rapid height growth in gaps (Closset-Kopp et al., 2007). *Prunus serotina* may begin to reproduce at the age of 10 years, but maximum reproduction usually occurs after the age of 30 years, with production of large seed crops occurring every 1–5 years (Burns & Honkala, 1990). Seeds are bird-dispersed (Smith, 1975).

**Methods**

A long-term replicated tree species common garden experiment at the Siemianice Experimental Forest near Biadaszki, Poland, (51°14.87′N, 18°06.35′E, elevation 150 m, mean annual temperature 8.2 °C) provided an ideal setting to examine relationships between invasion and native diversity across plots differing in dominant overstorey tree species, but with similar soil parent material, climate, and site history. Monospecific plots (400 m² each, most of them 20 × 20 m) of *P. sylvestris* L. (Scots pine), *B. pendula* Roth. (silver birch), *Carpinus betulus* L. (European hornbeam), *Pinus nigra* Arn. (Austrian black pine), *Quercus rubra* L. (red oak), *Abies alba* Mill. (silver fir), *Fagus sylvatica* L. (European beech), *Acer pseudoplatanus* L. (sycamore), *Acer platanoides* L. (Norway maple), *Tilia cordata* Mill. (small leafed lime), *Picea abies* [L.] Karst. (Norway spruce), *Larix decidua* Mill. (European larch), *Pseudotsuga menziesii* Franco (Douglas fir), and *Quercus robur* L. (English oak) were established in 1970 and 1971 in two blocks (nine species per block, three replicates per species) with four species (*Picea, Larix, Pseudotsuga*, and *Q. robur*) grown in both blocks (Reich et al., 2005). Because of poor survival of *Abies* seedlings, only two of its replicate plots survived. Many characteristics of the experimental plots, including plant, litter, and soil attributes, and earthworm diversity and abundances (Reich et al., 2005; Hobbie et al., 2006, 2007), root and leaf lifespan (Withington et al., 2006), fine root biomass (J.O., unpublished data), overstorey light interception (A.M.J., unpublished data), and understorey plant composition (M.K., unpublished data) have been found to vary among overstorey species.

Reproductive *P. serotina* trees growing in Scots pine forest existed to the north, north-east, west, and south-west of the experimental blocks, at distances of 50–200 m. While many *P. serotina* seeds may fall beneath the parent tree, birds disperse approximately 25% of the seed crop to distances greater than 25 m from the parent tree (Smith, 1975). It is likely that birds consumed *P. serotina* drupes and dispersed the seeds into the experimental plots. While differences in propagule pressure among plots, possibly due to suitability of roosting trees or distance from reproductive trees, were not measured, there was
no difference in the abundance of newly germinated *P. serotina* seedlings in plots dominated by different tree species.

*Prunus serotina* seedlings, defined here as young or small individuals that have not reached reproductive maturity, were surveyed in all experimental plots to determine associations between seedling success (abundance and size) and characteristics of the plots. Although the edges of some plots were probably influenced by the dominant tree species in the neighbouring plots or adjacent areas (M.K., unpublished data), we surveyed *P. serotina* seedlings in the entire plot as a conservative estimate of overstorey species effects.

To assess juvenile success in relation to overstorey tree effects, we needed to account for and distinguish among potential differences in propagule availability, initial seedling establishment, and established juvenile populations. We used observations over 2 years in a subset (*n* = 15) of the plots to develop a system to characterize seedlings by size into newly emerged (current-year) and established (second-year or older) classes. All seedlings that were not present in the first year, but appeared in the second year, were considered to be newly germinated seedlings less than 1 year old. The diameter distributions of seedlings classed as either greater than 1 year or less than 1 year old were compared to determine a cut-off diameter to use in all plots to distinguish these two classes of seedlings.

During the summer of 2004, all *P. serotina* seedlings in the first consecutive 15 (by plot number, Fig. 1) of the 53 plots were counted and tagged. During the summer of 2005, all *P. serotina* seedlings in the 53 plots were measured and mapped. Height and diameter 1 cm above the ground were measured. Seedlings with tags from 2004 were noted. In the first 15 plots in 2005, 56 seedlings were found without tags (38 of these were < 1 mm

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**Figure 1** The distribution of *Prunus serotina* Ehrh. seedlings > 1 mm in diameter in the experimental plots. Overstorey tree species names are abbreviated by the first two letters of the genus and specific epithet. Dark grey plots are shadier [average diffuse non-interceptance (DIFN) June–to August = 0.007–0.044], while light grey plots have greater light availability (average DIFN June to August = 0.084–0.22).
diameter) and 91 were found with tags (80 of these were > 1 mm), so 78% of seedlings < 1 mm (38 of 49) were < 1 year old, and 82% of seedlings > 1 mm (80 of 98) were older than 1 year. Therefore, 1 mm diameter was chosen as a cut-off point to distinguish current-year from second-year or older seedlings on all 53 plots, because it balanced the error for each category.

Understorey plant species were surveyed three times per year (in spring, summer, and autumn) in 2004 and 2005. Understorey vegetation of the study area (53 plots) was divided into smaller units with homogenous floristic structure and cover which were subsequently mapped. For each plot and unit, a list of vascular plants with cover data for each species and total cover of the herb layer was created. In all plots we identified a total of 111 species of vascular plants, including 45 specific only for Block 1 (plots 1–26), and 17 specific for Block 2 (plots 28–54). Understorey plant communities varied dramatically among overstorey tree species, with their species richness varying from three to 47 species, and cover ranging from < 1% to 70%. Besides the cultivated experimental tree species, only five exotic species were observed in the experimental plots: Lactuca serriola L., Fallopia convolvulus (L.) A. Löve, Impatiens parviflora DC., Prunus serotina Ehrh., and Conyza canadensis (L.) Cronquist. Other than P. serotina, these species usually exhibited low cover (<1%) and were found in only a few plots. Of the cultivated exotic tree species (P. menziesii, P. nigra, and Q. rubra), only Q. rubra seedlings were encountered frequently.

An index of canopy openness (diffuse non-interceptance, DIFN) was measured monthly during 2005 using a pair of LAI-2000 plant canopy analysers (Li-Cor Inc., Lincoln, NE, USA) following the methods in Machado & Reich (1999). The above-canopy sensor, monitoring changes in sky conditions every 15 s automatically, was located in a clearing close to the site, and the below-canopy sensor was used in the sampling plots. Because plots were relatively small, a 90° view cap was used, and readings were made at six points near the centre of each plot. DIFN values for June, July, and August were averaged to produce a proxy for light availability throughout the growing season (Machado & Reich, 1999), which was used in the analyses. The average light level across the growing season (June–August) is appropriate for June, July, and August were averaged to produce a proxy for light availability throughout the growing season (Machado & Reich, 1999), which was used in the analyses. The average light level across the growing season (June–August) is appropriate because P. serotina employs a continuous growth strategy, growing throughout the growing season (Canham et al., 1999).

Transformations were used to approximate normality for response variables. The square root of the abundance of seedlings, and the log of the diameter and height of seedlings were used in all of the following analyses (Quinn & Keough, 2003). ANOVA (JMP 5.0.1a statistical software, SAS Institute Inc., Chicago, IL, USA) was used to determine the effect of overstorey species on the abundance of P. serotina seedlings < 1 mm in diameter and > 1 mm in diameter, as well as the average diameter and height of seedlings > 1 mm. Multiple regression analyses were used to determine the relationships among light, native species richness, native species cover, and abundance and diameter of P. serotina seedlings. Multiple regression analyses of standardized z-scores were used to obtain standardized partial regression coefficients, which were used to construct a path diagram (Pedhazur, 1997) to elucidate relationships among these factors.

Other biotic and abiotic characteristics of the plots were tested for relationships with P. serotina seedling abundance and diameter with regression analysis.

RESULTS

The identity of overstorey tree species had no significant effect on the abundance of P. serotina seedlings < 1 mm in diameter (P = 0.91), however, abundance (P = 0.002, R² = 0.53) (Fig. 1), diameter (P = 0.0005, R² = 0.67), and height (P = 0.001 R² = 0.64) of P. serotina seedlings > 1 mm in diameter were strongly influenced by overstorey species (Table 1 and Fig. 2). Given that seedlings < 1 mm in diameter were largely current year, whereas those > 1 mm were largely older, these results suggest that propagule pressure and germination of P. serotina seeds do not differ among plots, but successful establishment and growth of P. serotina seedlings depends on the conditions created by the overstorey tree species.

The effects of overstorey tree species on survival and growth of P. serotina may occur through their effects on the biotic and abiotic

![Figure 2](image-url)

**Figure 2** (a) Average number (± 1 standard error) of Prunus serotina seedlings per plot for each overstorey tree species (seedlings < 1 mm diameter P = 0.002, seedlings < 1 mm diameter P = 0.86). (b) Average diameter (± 1 standard error) of P. serotina seedlings > 1 mm diameter for each overstorey tree species (P = 0.0005).
Table 1  Average plot values for each overstorey species and results of ANOVA for each response against overstorey species with response transformations as labelled. There are three replicates for all species, except *Abies alba* Mill., which has two replicates, and *Picea abies* [L.] Mill., *Larix decidua* Karst., *Pseudotsuga menziesii* Franco, and *Quercus robur* L., which each have six replicates. The letters (a, b, c) represent statistical differences as determined by a Tukey post hoc test.

<table>
<thead>
<tr>
<th>Overstorey species</th>
<th>Number of <em>P. serotina</em> Ehrh. &gt; 1 mm/ha</th>
<th>Number of <em>P. serotina</em> &lt; 1 mm/ha</th>
<th>Height (cm) &gt; 1 mm <em>Prunus</em></th>
<th>Diameter (mm) &gt; 1 mm <em>Prunus</em></th>
<th>Understorey richness (number of species per plot)</th>
<th>Understorey cover (percentage cover)</th>
<th>DIFN (fraction open sky) June–Aug</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Quercus rubra</em> L.</td>
<td>3 8.25b</td>
<td>17.5</td>
<td>6.8ab</td>
<td>1.1abc</td>
<td>4.7c</td>
<td>2.4b</td>
<td>0.035b</td>
</tr>
<tr>
<td><em>Abies alba</em> Mill.</td>
<td>2 37.5b</td>
<td>0</td>
<td>24.3ab</td>
<td>2.5abc</td>
<td>14.0 abc</td>
<td>3.9b</td>
<td>0.008b</td>
</tr>
<tr>
<td><em>Fagus sylvatica</em> L.</td>
<td>3 40b</td>
<td>32.5</td>
<td>8.7ab</td>
<td>1.3bc</td>
<td>9.0bc</td>
<td>0.2b</td>
<td>0.029b</td>
</tr>
<tr>
<td><em>Carpinus betulus</em> L.</td>
<td>3 50b</td>
<td>82.5</td>
<td>5.9b</td>
<td>1.3bc</td>
<td>11.7abc</td>
<td>13.7b</td>
<td>0.048b</td>
</tr>
<tr>
<td><em>Tilia cordata</em> Mill.</td>
<td>3 75b</td>
<td>7.5</td>
<td>13.7ab</td>
<td>1.4c</td>
<td>11.7abc</td>
<td>4.3b</td>
<td>0.032b</td>
</tr>
<tr>
<td><em>Pseudotsuga menziesii</em> Franco</td>
<td>6 82.5b</td>
<td>42.5</td>
<td>17.6ab</td>
<td>2.5abc</td>
<td>9.8c</td>
<td>3.8b</td>
<td>0.025b</td>
</tr>
<tr>
<td><em>Picea abies</em> [L.] Karst</td>
<td>6 82.5ab</td>
<td>45</td>
<td>15.2ab</td>
<td>2.0abc</td>
<td>8.7c</td>
<td>6.1b</td>
<td>0.040b</td>
</tr>
<tr>
<td><em>Acer platanoides</em> L.</td>
<td>3 125ab</td>
<td>75</td>
<td>13.5ab</td>
<td>1.7bc</td>
<td>26.7abc</td>
<td>9.3b</td>
<td>0.019b</td>
</tr>
<tr>
<td><em>Betula pendula</em> Roth.</td>
<td>3 133ab</td>
<td>50</td>
<td>32.5ab</td>
<td>5.4abc</td>
<td>22.0abc</td>
<td>49.7a</td>
<td>0.193a</td>
</tr>
<tr>
<td><em>Larix decidua</em> Mill.</td>
<td>6 193ab</td>
<td>250</td>
<td>25.7ab</td>
<td>3.5abc</td>
<td>16.2abc</td>
<td>17.4b</td>
<td>0.158a</td>
</tr>
<tr>
<td><em>Acer pseudoplatanus</em> L.</td>
<td>3 208ab</td>
<td>175</td>
<td>13.6ab</td>
<td>2.0abc</td>
<td>34.0a</td>
<td>15.9b</td>
<td>0.036b</td>
</tr>
<tr>
<td><em>Pinus nigra</em> Arn.</td>
<td>3 250ab</td>
<td>82.5</td>
<td>37.9a</td>
<td>6.1ab</td>
<td>15.7abc</td>
<td>17.8b</td>
<td>0.147a</td>
</tr>
<tr>
<td><em>Quercus robur</em> L.</td>
<td>6 350ab</td>
<td>70</td>
<td>26.3ab</td>
<td>3.5abc</td>
<td>28.2ab</td>
<td>24.5ab</td>
<td>0.126a</td>
</tr>
<tr>
<td><em>Pinus sylvestris</em> L.</td>
<td>3 850a</td>
<td>50</td>
<td>69.8a</td>
<td>7.7a</td>
<td>22.3abc</td>
<td>30.4ab</td>
<td>0.175a</td>
</tr>
</tbody>
</table>

DIFN, diffuse non-interceptance.
environmental conditions in the understorey. In this study, different overstorey species created different average understorey light environments ($P < 0.0001$), which, in turn, were related to the abundance ($P = 0.0001, R^2 = 0.25$), diameter ($P < 0.0001, R^2 = 0.42$), and height ($P < 0.0001, R^2 = 0.31$) of $P. \text{serotina}$ seedlings $> 1$ mm in diameter (Fig. 3). This is in agreement with other studies that have found greater growth (Auclair & Cottam, 1971; Kobe et al., 1995; Tripler et al., 2002; Closset-Kopp et al., 2007), survival (Smith, 1975; Kobe et al., 1995; Lei et al., 2002), and emergence (Harrington & Bluhm, 2001) of $P. \text{serotina}$, as well as greater abundance of other forest invaders (Hutchinson & Vankat, 1997; Knight & Reich, 2005), in higher light conditions. Light conditions had a small effect on the abundance of $P. \text{serotina}$ seedlings $< 1$ mm ($P = 0.04, R^2 = 0.08$). However, when one plot, an outlier with 53 newly germinated seedlings, the majority (50) of which were in three unusually prolific clumps, was excluded, light had no significant effect ($P = 0.83, R^2 = 0.00$). This contrasts with the findings of another study, where more newly germinated $P. \text{serotina}$ seedlings were found in shady conditions (Closset-Kopp et al., 2007).

In multiple regression analysis ($P < 0.0001, R^2 = 0.42$), understorey species richness and light both had positive relationships with abundance of $P. \text{serotina}$ seedlings $> 1$ mm ($P < 0.001$), while the cover of understorey species had a negative relationship with $P. \text{serotina}$ abundance ($P = 0.02$). This indicates that once light and understorey species richness are accounted for, understorey cover is negatively correlated with $P. \text{serotina}$ abundance. Conversely, once light and understorey cover are accounted for, understorey species richness is positively correlated with increasing $P. \text{serotina}$ abundance (Fig. 4a). This

**Figure 3** Effect of canopy openness (diffuse non-interception) on $Prunus \text{serotina}$ seedling abundance (number of seedlings per plot on a square root scale) and diameter (plot average diameter of seedlings $> 1$ mm on a log scale).

**Figure 4** In a multiple regression analysis ($P < 0.0001, R^2 = 0.46$), understorey species richness and light were both positively related to $Prunus \text{serotina}$ seedling abundance ($P < 0.001$), while understorey species cover was negatively related to $P. \text{serotina}$ abundance ($P = 0.04$). Understorey species richness and understorey cover are positively related ($P < 0.0001, R^2 = 0.57$ for all plots). The shapes denote the abundance of $P. \text{serotina}$ seedlings $> 1$ mm in diameter per plot. 'Low Prunus' = 0–50 seedlings/ha; 'Medium Prunus' = 100–200 seedlings/ha; 'High Prunus' = 250–500 seedlings/ha; and 'Maximum Prunus' = 850–1400 seedlings/ha. Lines surround groups of points with the same abundance category. When herbaceous species cover is held constant, an increase in herbaceous species richness coincides with an increase in $P. \text{serotina}$ seedling abundance. At a fixed herbaceous species richness level, an increase in herbaceous species percentage cover is correlated with a decrease in $P. \text{serotina}$ seedling abundance. Only high-light plots [average diffuse non-interception (DIFN) June to August $> 0.08$] are shown. These patterns match the patterns found by Knight & Reich (2005) in a survey of $Rhamnus \text{cathartica}$ L. (lower graph reproduced from Knight & Reich, 2005).
positive correlation probably results from associations between understorey species richness and factors that affect colonization. Light, understorey species richness, and understorey cover have both direct and indirect relationships with P. serotina abundance (Fig. 5).

A second multiple regression analysis \( (P = 0.0001, R^2 = 0.44) \) with the same predictors showed that the diameter of P. serotina seedlings \( > 1 \) mm was positively related to light \( (P < 0.0001) \), but was not related to the species richness \( (P = 0.35) \) or cover \( (P = 0.91) \) of understorey plants. In a similar multiple regression analysis \( (P = 0.55, R^2 = 0.02 \) with the outlier plot removed as before), the abundance of P. serotina seedlings \( < 1 \) mm was not related to light, understorey cover, or understorey species richness. These analyses suggest that different factors may be important for different life stages and processes.

**DISCUSSION**

The results of our study indicate that different overstorey tree species create different understorey environments, which affect both components of the herbaceous flora: native species and exotic invaders. In turn, the native understorey species may themselves reduce the success of invading plants through greater competition in areas with greater native cover. Understorey species richness per se, however, did not seem to have a negative effect on invading plants. To the contrary, if the understorey environment was conducive to colonization by a large number of native species, it was also likely to be conducive to invasion by exotic species. Understorey species richness is probably a surrogate for many factors that affect colonization. Relationships among overstorey tree species, understorey richness, and invasibility found in the present study reflect those found in old-field communities among dominant species identity, native richness, and invasibility (Emery & Gross, 2006).

Multiple regression analysis revealed a negative relationship between understorey cover and P. serotina abundance, a positive relationship between understorey richness and P. serotina abundance, and a positive relationship between understory light availability (DIFN) and P. serotina abundance. Several examples illustrate the seemingly complex patterns. For example, plots dominated by B. pendula had high understorey light availability and high species richness similar to P. sylvestris plots (Table 1). However, the understorey cover in the B. pendula plots was greater than in P. sylvestris plots, and the abundance of P. serotina seedlings in these plots was only one-sixth of the abundance in P. sylvestris plots. In another example, plots dominated by A. pseudoplatanus had low light availability similar to Q. rubra and T. cordata. However, the A. pseudoplatanus plots had much higher species richness, and much greater abundance of P. serotina.

What mechanisms control the relationships between P. serotina invasion and resident richness and cover? Understorey cover may have a direct negative effect on P. serotina success via competitive interactions. The positive relationship between P. serotina success and understorey species richness, however, may arise due to correlations between species richness and a variety of factors that affect colonization. Soil texture, land-use history, climate, precipitation, and proximity to seed sources were similar for all plots, so these factors are probably not mechanisms that lead to the relationship observed in this study. Heterogeneity, which has been invoked as the mechanism behind positive relationships between native species richness and invasive species richness (Lonsdale, 1999; Espinosa-García et al., 2004; Davies et al., 2005; Richardson et al., 2005; Richardson & Pyšek, 2006), was probably not responsible for the positive relationship between species richness and P. serotina success seen in this study. While the richness of both invasive and native species may peak in heterogeneous areas, the success of one invasive species should peak in homogeneous areas with conditions in which the invader is the competitively superior species (Pacala & Tilman, 1994). The abundance of a resource, rather than the heterogeneity of the resource, can positively influence both species richness and abundance (Stevens & Carson, 2002) or invasion (Jiang & Morin, 2004) of individual species. It seems most likely that the biotic and abiotic plot environment, created by the overstorey tree species and affecting resources available to both native and exotic plants, was responsible for the observed relationships.

Light was one important component of the plot environment, and had significant positive effects on P. serotina abundance and size, as well as understorey species richness and cover (data not shown). However, the relationships between P. serotina and understorey species richness and cover were present even after effects of light availability were accounted for in the multiple regression model, so factors besides light were involved in these relationships. Other potentially important characteristics that may affect both native and exotic plants include soil moisture, fertility, leaf litter, and root competition from overstorey trees; however, these were not significant in this study when included with light in statistical models (data not shown). Other factors which have not been measured may play a role in creating the observed relationships. It is possible that even if all potential environmental factors were measured, species richness would
continue to be a better proxy for invasibility than any environmental factor because it integrates the effects of many factors. Indeed, if all species currently in the plots have ‘invaded’ over time (i.e. colonized), then the more species-rich plots are by definition more invisible (Davis, 2005).

The positive relationship between P. serotina abundance and understory species richness found in this study contrasts with the results of three surveys of forests in Europe, which showed negative (Honnay et al., 1999; Godefroid et al., 2005) or few (Chabrerie et al., 2008) relationships between native plant species richness and P. serotina abundance. However, none of those studies took native plant cover into account in their analyses of these relationships.

Forest fragments in the study by Honnay et al. (1999) varied in size, with larger patches having greater native species richness and less P. serotina. The authors suggest that smaller fragments may be more easily invaded by P. serotina, which may ultimately reduce the abundance of native plants. Perhaps some characteristics, like forest size, affect native and invasive plants in opposite ways, while other environmental characteristics have similar effects on native and invasive plants. Alternatively, the negative relationship between native richness and P. serotina abundance they reported could reflect competition and be entirely or in part due to the abundance rather than the richness of the native community.

The studies by Godefroid et al. (2005) and Chabrerie et al. (2008) each used plots within one forest. Godefroid et al. (2005) found a negative correlation between herbaceous species richness and P. serotina in the shrub layer. However, there was no correlation between herbaceous species richness and P. serotina in the herb layer. Godefroid et al. (2005) suggest that a dense P. serotina shrub layer may have negative impacts on herbaceous species. Chabrerie et al. (2008) found no differences in diversity of the tree, shrub, and herb layers in paired plots with and without P. serotina in the overstory. However, diversity of the undershrub layer increased in invaded plots. Our study did not distinguish between the herb and the shrub layer for P. serotina, however, most of the P. serotina seedlings in the present study were small (average height = 23 cm), and therefore may not be affecting herbaceous species at the present time.

The patterns found in our study extend the results of a survey of the invasion of another bird-dispersed exotic woody invader of forest understories, Rhamnus cathartica L., in forests in Minnesota, USA (Knight & Reich, 2005). The patterns we found were similar (Fig. 4), despite the differences between the forests in the respective studies. The forest patches in that study were 10,000 m², over 25 times as large as the patches in the present study, and were located across a 50 km area. The forest patches in that study were selected to have similar, Quercus-dominated, overstories but varied in unknown ways in site history, soil properties, and native and exotic propagule pressure. However, the same results emerged: a positive relationship between invader abundance (measured as percentage cover of R. cathartica seedlings in that study and P. serotina seedling density in the present study) and native species richness, and a negative relationship between invader abundance and native species cover. The fact that these two studies, an ocean apart, with different invaders and different forest types, revealed the same patterns suggests that these relationships, and the mechanisms underlying them, may be generalizable to other situations. As our understanding of these relationships develops further, it could assist in land management decisions by identifying sites with relatively high native diversity and low native cover as more susceptible to invasion by exotic species.

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