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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, 2003; 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-García *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

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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-García *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; Naeem *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; Naeem *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 m^2 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

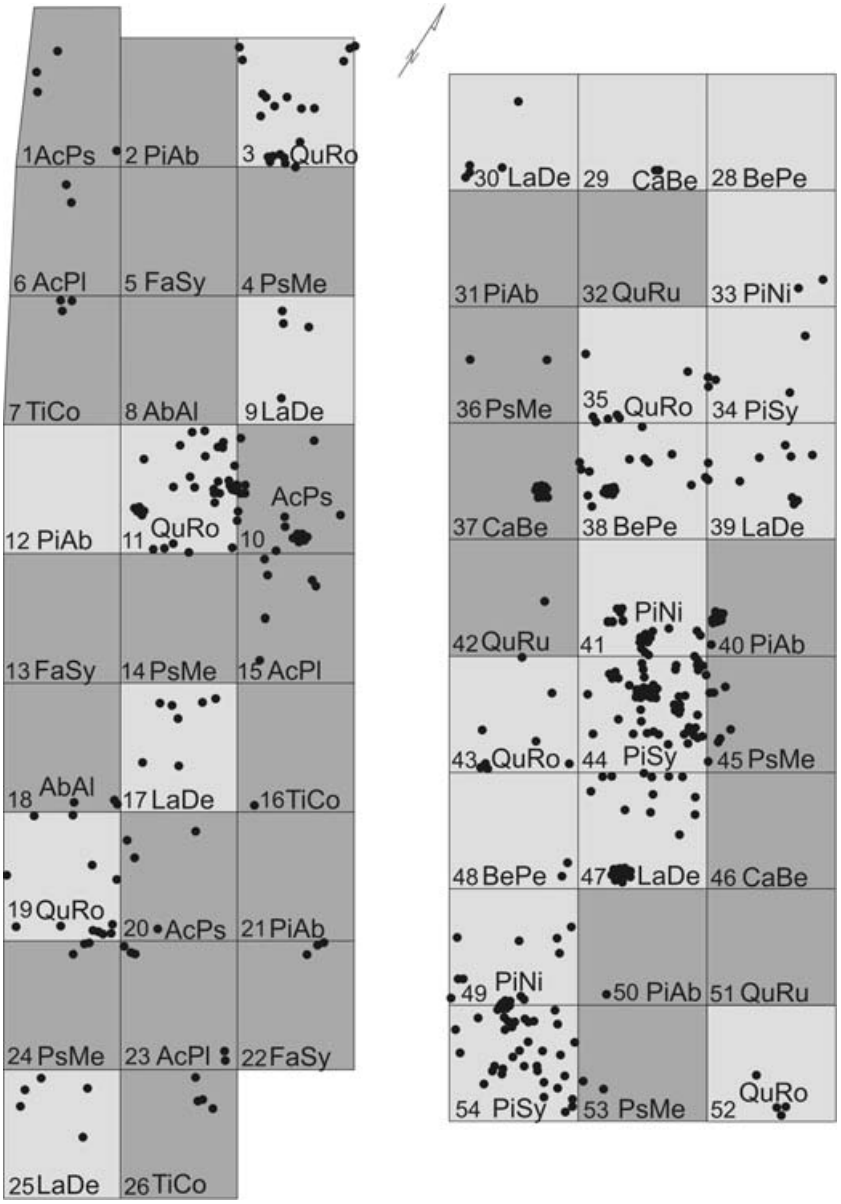

Figure 1 The distribution of *Prunus serotina* Ehrh. seedlings > 1 mm in diameter in the experimental plots. Overstorey tree species names are abbreviated by the first two letters of the genus and specific epithet. Dark grey plots are shadier [average diffuse non-interceptance (DIFN) June – to August = 0.007–0.044], while light grey plots have greater light availability (average DIFN June to August = 0.084–0.22).

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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.) Á. 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 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 ($P = 0.002$, $R^2 = 0.53$) (Fig. 1), diameter ($P = 0.0005$, $R^2 = 0.67$), and height ($P = 0.001$ $R^2 = 0.64$) 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

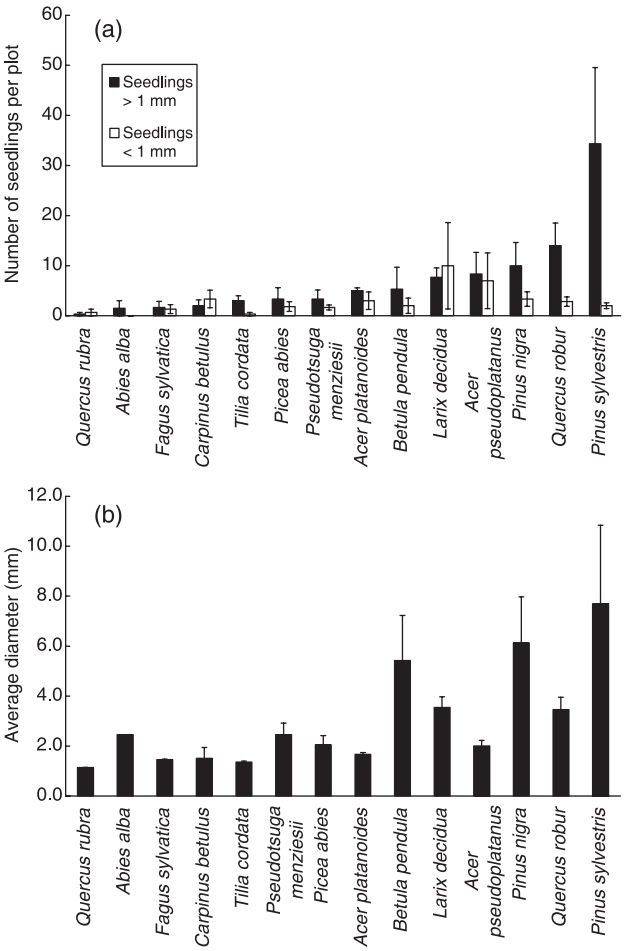

Figure 2 (a) Average number (± 1 standard error) of *Prunus serotina* seedlings per plot for each overstorey tree species (seedlings > 1 mm diameter $P = 0.002$, seedlings < 1 mm diameter $P = 0.86$). (b) Average diameter (± 1 standard error) of *P. serotina* seedlings > 1 mm diameter for each overstorey 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.

Overstorey species	*n*	Number of *P. serotina* Ehrh. > 1 mm/ha	Number of *P. serotina* < 1 mm/ha	Height (cm) > 1 mm *Prunus*	Diameter (mm) > 1 mm *Prunus*	Understorey richness (number of species per plot)	Understorey cover (percentage cover)	DIFN (fraction open sky) June–Aug
Quercus rubra L.	3	8.25b	17.5	6.8ab	1.1abc	4.7c	2.4b	0.035b
Abies alba Mill.	2	37.5b	0	24.3ab	2.5abc	14.0 abc	3.9b	0.008b
Fagus sylvatica L.	3	40b	32.5	8.7ab	1.5bc	9.0bc	0.2b	0.029b
Carpinus betulus L.	3	50b	82.5	5.9b	1.5bc	11.7abc	13.7b	0.048b
Tilia cordata Mill.	3	75b	7.5	13.7ab	1.4c	11.7abc	4.3b	0.032b
Pseudotsuga menziesii Franco	6	82.5b	42.5	17.6ab	2.5abc	9.8c	3.8b	0.025b
Picea abies [L.] Karst	6	82.5ab	45	15.2ab	2.0abc	8.7c	6.1b	0.040b
Acer platanoides L.	3	125ab	75	13.5ab	1.7bc	26.7abc	9.3b	0.019b
Betula pendula Roth.	3	133ab	50	32.5ab	5.4abc	22.0abc	49.7a	0.193a
Larix decidua Mill.	6	193ab	250	25.7ab	3.5abc	16.2abc	17.4b	0.158a
Acer pseudoplatanus L.	3	208ab	175	13.6ab	2.0abc	34.0a	15.9b	0.036b
Pinus nigra Arn.	3	250ab	82.5	37.9a	6.1ab	15.7abc	17.8b	0.147a
Quercus robur L.	6	350ab	70	26.3ab	3.5abc	28.2ab	24.5ab	0.126a
Pinus sylvestris L.	3	850a	50	69.8a	7.7a	22.3abc	30.4ab	0.175a
Overstorey species ANOVA		Square-root transformation		Log transformation	Log transformation			
		$P = 0.002$	$P = 0.86$	$P = 0.001$	$P = 0.0005$	$P = 0.0003$	$P < 0.0001$	$P < 0.0001$
		$R^2 = 0.53$		$R^2 = 0.64$	$R^2 = 0.67$	$R^2 = 0.57$	$R^2 = 0.63$	$R^2 = 0.87$

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. 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. 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. 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. 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. serotina* seedlings > 1 mm ($P < 0.001$), while the cover of understorey species had a negative relationship with *P. serotina* abundance ($P = 0.02$). This indicates that once light and understorey species richness are accounted for, understorey cover is negatively correlated with *P. serotina* abundance. Conversely, once light and understorey cover are accounted for, understorey species richness is positively correlated with increasing *P. serotina* abundance (Fig. 4a). This

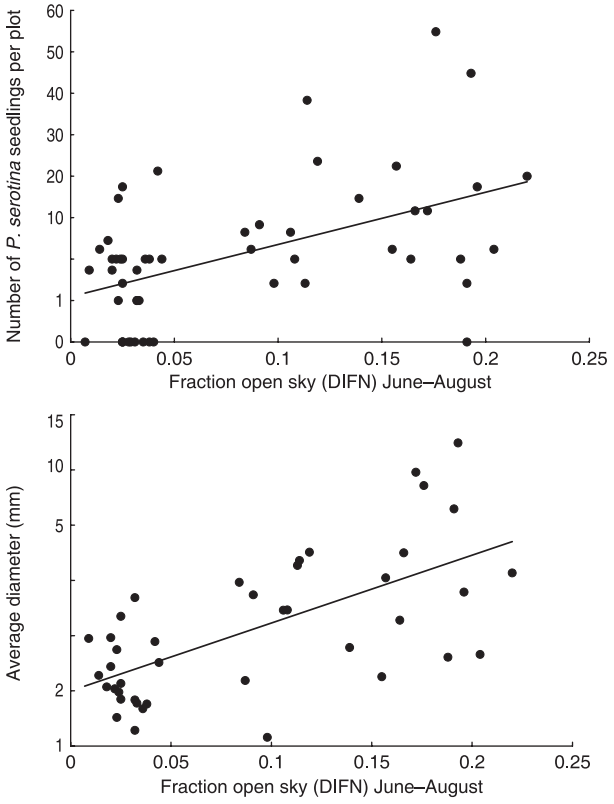

Figure 3 Effect of canopy openness (diffuse non-interceptance) on *Prunus serotina* seedling abundance (number of seedlings per plot on a square root scale) and diameter (plot average diameter of seedlings > 1 mm on a log scale).

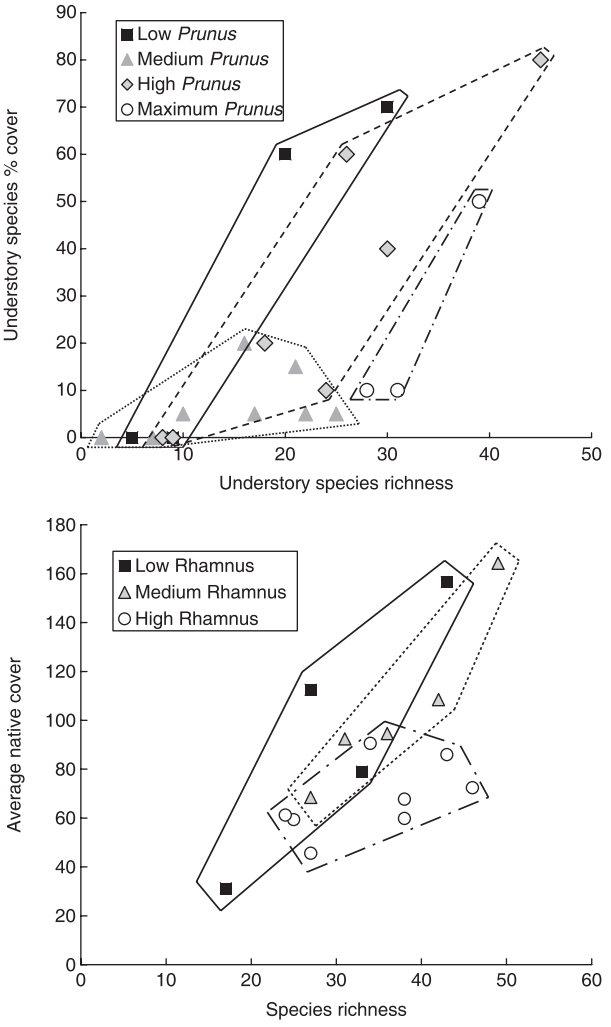

Figure 4 In a multiple regression analysis ($P < 0.0001$, $R^2 = 0.46$), understorey species richness and light were both positively related to *Prunus serotina* seedling abundance ($P < 0.001$), while understorey species cover was negatively related to *P. serotina* abundance ($P = 0.04$). Understorey 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. 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. serotina* seedling abundance. At a fixed herbaceous species richness level, an increase in herbaceous species percentage cover is correlated with a decrease in *P. serotina* seedling abundance. Only high-light plots [average diffuse non-interceptance (DIFN) June to August > 0.08] are shown. These patterns match the patterns found by Knight & Reich (2005) in a survey of *Rhamnus cathartica* L. (lower graph reproduced from Knight & Reich, 2005).

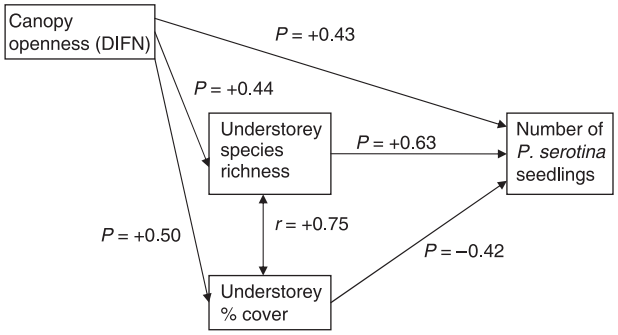

Figure 5 Canopy openness, understorey species richness, and understorey cover have both direct and indirect effects on the abundance of *Prunus serotina* seedlings > 1 mm diameter, as shown by this path diagram. Standardized simple and partial regression coefficients (P) and a simple correlation coefficient (r) show the magnitude and direction of the relationships. All relationships were significant at $P < 0.05$.

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 understorey 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

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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 invasible (Davis, 2005).

The positive relationship between *P. serotina* abundance and understorey 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 overstorey. 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 m^2, 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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