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Invasive *Acer platanoides* inhibits native sapling growth in forest understorey communities

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Summary

1. Over three growing seasons, we tested how an invasive tree species (*Acer platanoides*) affected native plant growth in understorey communities of a suburban forest in central New Jersey, USA. We planted similar aged and sized saplings (≥ 0.25 m tall) into experimental plots identified with one of three treatments (0%, 25% and 50% of total stems are invasive species) and hypothesized native species would grow better in communities lacking invasive plants.

2. There was a plant survival rate of 90% for the duration of the experiment, but in treatments where natives competed with *A. platanoides*, growth of native species was significantly less than in the purely native stand. In 2006, the mean height of *A. rubrum* was 110 cm (± 4 SE) in communities with the highest proportion of *A. platanoides*, while it was 149 cm (± 7 SE) in the 0% invasive communities. Conversely, *A. platanoides* grew similarly in treatments where it comprised two different proportions and beneath both canopy types (i.e. invasive and native).

3. Native saplings were 28% shorter beneath an invasive canopy (i.e. *A. platanoides*), compared with a native canopy. A striking interaction existed between community treatment and canopy type, as the invasive canopy had such a strong negative effect on native growth that the presence of invasive saplings was irrelevant. However, beneath a native canopy, the absence of invasive saplings significantly increased growth of native saplings. As the extent and rate of invasive proliferation often makes complete removal unrealistic, this study supports episodic removal (every 2–3 years) of this invasive sapling.

4. *Synthesis*. This experiment showed that native sapling growth was inhibited (i) when growing beneath an invasive canopy and (ii) when competing with *A. platanoides* in forest understorey communities. It appears canopy type is more important, because the negative effects from an invasive canopy were strong enough that the co-occurrence of invasive saplings had no impact on native growth. The capability of *A. platanoides* to inhibit native saplings through understorey competition and overstorey canopy effects, while not affecting conspecifics, may contribute to its success as an invader of North American forests.

Key-words: *Acer platanoides*, *Acer rubrum*, forest canopy, forest understorey communities, interspecific competition, invasive species, Norway maple, *Quercus rubra*, *Ulmus americana*

Introduction

Non-native, exotic plant species that become invasive continue to impact ecological structure and function (Fox & Fox 1986; Mooney & Drake 1986; Luken & Thieret 1997; Mooney & Hobbs 2000). These species are often named as the cause for declines in native biodiversity (McKinney & Lockwood 1999; Wilcove *et al*. 1998) and can complicate ecological restoration efforts (D'Antonio & Meyerson 2002).

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A key concept to address in the greater discussion of invasion and species diversity is 'what exactly is natural?' (McNeely 2000), because many North American communities have become mixtures of native, naturalized and invasive species (Bridgewater 1990; D'Antonio & Meyerson 2002) through human disturbance and introductions over the past four centuries. While it is generally desirable to remove invasive plants through a variety of methods (e.g. by hand, mechanically, or fire), removal may actually increase subsequent invasions (Luken 1997; Webb *et al*. 2001) or destabilize the soil (Wootton *et al*. 2005) or be economically impossible

(Ewel & Putz 2004). In many cases, the most realistic option is not full eradication of the invasive plants (Sauer 1998; Alvarez & Cushman 2002; Daehler 2003), but making the 'most out of a bad situation' while retaining some of the invasives (D'Antonio & Meyerson 2002).

With this reality in mind, understanding how native plant communities are affected by invasive species is of interest. Many invasive plants have been shown to decrease species richness (Martin 1999; Collier *et al.* 2002) and may replace native species as the compositions of natural communities become more homogenized (McKinney & Lockwood 1999), possibly affecting the ability of forests to provide ecological services (Webster *et al.* 2006). The majority of North American studies documenting effects of invasive woody species in forests, such as *Rhamnus* spp. (Fagan & Peart 2004; Knight & Reich 2005), *Acer platanoides* (Martin 1999; Reinhart *et al.* 2005; Webster *et al.* 2005) and *Berberis thunbergii* (Cassidy *et al.* 2004) have all used naturally occurring trees and shrubs, or a design similar to a common garden experiment (Sanford *et al.* 2003).

We used an experimental study in a forest to test how *Acer platanoides* L. (Norway maple) affected the growth of co-occurring planted native tree saplings in understorey communities. *A. platanoides* is a European invasive tree species that was intentionally introduced in North America in 1756 (Nowak & Rowntree 1990), and has continued to spread in eastern (Martin 1999; Webb *et al.* 2000), midwestern (Wangen *et al.* 2006), and western (Reinhart *et al.* 2005) North American forests. The high growth rate (Kloeppel & Abrams 1995), recruitment and persistence of *A. platanoides* in open and closed forests is typically much greater than native trees, which causes concern for the structure and functioning of future forests (Wyckoff & Webb 1996; Martin 1999; Sanford *et al.* 2003).

A recent review found that more than 90% of the studies testing the effects of invasive plants on native community structure were observational, while nearly all the experimental studies investigating effects of invasives on native plants used just one native species (Levine *et al.* 2003). To our knowledge, this temporal study is one of the first to experimentally test the growth of invasive and native saplings in forest understorey communities. We sought to test how varying proportions of a common invasive plant affected the growth and survival of several co-occurring native species. By using these treatments, we tested if there was a population threshold where invasives reduced native sapling growth. We planted all species simultaneously and at the same life-stage to minimize priority effects, which can alter outcomes of species interactions in experiments (Morin 1999), and assembly differences, because late-arriving species may only establish if necessary resources are not consumed by species already present (Tilman 2004).

In this experimental study, we tested how different abundances of an invasive plant affected native species performance (as measured through height, volume and mortality) over three growing seasons. We hypothesized that *A. platanoides* would reduce native plant growth, so that the native trees (*Acer rubrum* L., *Quercus rubra* L., *Ulmus americana* L.) would perform best in treatments where invasive plants were absent.

Methods

This field study evaluated the effect of local invasive sapling (*A. platanoides*) abundance on the survival and growth of native tree saplings in a forest understorey. All saplings (native and invasive) were planted at the same time for this experimental design.

STUDY SITE

We conducted this study in a post-agricultural secondary forest in the Piedmont of central New Jersey (Somerset County, NJ, USA) on the property of Duke Farms (1093 ha total; 40°33.8′ N, 74° 25.4′ W). This forest (0.36 ha = 3600 m^2) had an overstorey canopy (stems > 2.5 cm d.b.h.) dominated by native trees similar to historic descriptions of mixed oak forests in the area (Braun 1950; Monk 1961; Collins & Anderson 1994): *Quercus alba* L. (relative IV = 19.2%), *A. rubrum* (relative IV = 16.9%), *Q. palustris* Muenchh. (relative IV = 14.5%), and *A. platanoides* (relative IV = 11.9%) (S. Galbraith-Kent, unpublished data). The understorey was primarily composed of defined patches of the annual invasive grass, *Microstegium vimineum* Trin. Camus and *B. thunbergii*. The soils in the forest are deep (< 200 cm to fragipan), loamy, and the primary type is Dunellen sandy loam (3–8% slopes), with secondary types of Lamington silt and Penn silt loam (0–2%, 2–6% slopes, respectively) (NRCS 2007).

Between 1971 and 2000, annual mean precipitation for this region of the state was 126.5 cm, with a mean annual temperature of 10.5 °C. During the data collection years of this experiment (2004, 2005 and 2006), precipitation and temperature values were above normal. Illustrating the recent climate variability, the combined months of August and September 2005 had been the warmest and driest on record, while October 2005 was one of the region's wettest months (ONJSC 2007).

DESIGN OF EXPERIMENT

A replacement series experiment using tree community plots was planted in a randomized complete block design to test the effect of varying invasive proportion (0%, 25% and 50% plot treatments) on native and invasive species growth and survival. Three main fixed effects (Time, Treatment, Species) were tested across four sample periods and various plot characteristics were measured to explain species growth patterns over time.

Plot location and construction

In June 2004, locations were selected for 30 experimental woody community plots in the secondary forest at Duke Farms. This forest was part of a 14-ha area that was enclosed by a deer fence, preventing large mammal herbivory. Plots were placed in areas that did not contain *B. thunbergii* and were not in low-lying moist depressions. The absence of *B. thunbergii* was important, so that all plots were initiated in soil chemistry conditions not directly affected by this invasive (Ehrenfeld *et al.* 2001). However, the majority of plots had 100% cover of *M. vimineum*, differing only in density of the grass; these conditions were noted per plot at time of grass removal. All of the grass was removed by hand, with the leaf litter and woody debris remaining.

In July and August 2004, 15 tree community plots were designated, with five plots per treatment type: 0% of the plants are invasive species (i.e. 100% native), 25% invasive, and 50% invasive. Plots were assigned treatment types using a randomized complete block design,

Table 1. Experimental design of the planted tree community plots in the understory of a post-agricultural secondary forest in Somerset County, NJ. The number of plants of each species per plot are shown per treatment (0%, 25%, and 50% invasive). The number of plants per plot (n = 36) was equal for each of the 15 plots

	Plot treatment type (% invasive)*		
Species	0%	25%	50%
Acer platanoides	0	9	18
A. rubrum	12	9	6
Quercus rubra	12	9	6
Ulmus americana	12	9	6
Total number of plants/plot	36	36	36

*Dimensions of each plot were 4 m × 4 m; n = 5 plots per treatment.

which helped spatially balance all three treatments across the forest and control for unwanted variation (Potvin 2001). In each of the five spatial blocks in the forest, one plot of each tree treatment was present. We used a deWit replacement series design and kept the plant density per plot (n = 36 plants per plot) the same, but varied the number of plants per species (Table 1). The density of stems was chosen in response to plant sizes and the experimental constraints of logistics and scale. All plots (4 m × 4 m) were separated by at least 2 m and planted with the same spatial pattern of six plants per six rows with equal plant spacing (0.5 m). Across all plots, there were a total of 540 tree saplings and an equal number of plants per species (n = 180) (Table 1). Based on initial sapling sizes in 2004, the plot size and density were chosen to encourage plant interactions from the beginning of the experiment. When a plant died, it was replaced in October or the following April with a living plant new to the plot. This re-planting allowed the species proportions of treatments to remain consistent through the duration of the experiment.

As stated above, the summer of 2005 set records for high temperatures and a lack of rain. To keep the plants alive during this time, we added 18.5–30 L of water to each plot four to five times per week. For any given week, all 15 plots received the same amount of water to maintain consistency.

Species selection

All native plants selected were regional genotypes that had historical (Monk 1961; Collins & Anderson 1994) or current presence in the area (Handel & Clements 2003) and were donated from Greenbelt Native Plant Nursery (Staten Island, NY, USA). Each tree community plot contained three native species (*A. rubrum*, *Q. rubra*, *Ulmus americana*), with proportions depending on treatment type.

At the study site in 2004, *A. platanoides* was common as a seedling and overstorey canopy tree, but not abundant in the sapling size-class. Therefore, we used saplings transplanted from two sites (Wissahickon Watershed, Philadelphia, PA; Drew University, Madison, NJ), which were then placed into the 25% and 50% invasive tree plots. We chose saplings that were between 0.25 and 0.75 m tall, so that all plants (invasive and native) were mature understorey saplings of similar size and age at the time of planting.

PLOT CHARACTERISTICS

The understorey light environment for each plot was measured using digital photographs from a 36-mm Canon PowerShot S410 Digital Elph (4.0 megapixels; Canon Corporation, Tokyo, Japan). This indirect measure was previously described (Engelbrecht & Herz 2001; Ashton *et al.* 2005) as a good estimate of light when compared with more direct measurements (e.g. leaf area index). On 23 August 2006 (at noon during partly overcast conditions), we took a photograph in the centre of each plot, where the camera was levelled on a small tripod 1.5 m from the ground surface. Photographs were taken with the camera lens facing up towards the canopy and the top of the camera (containing the shutter button) facing magnetic north. For all photos, the lens was at a constant aperture (f = 2.8) and zoom and flash were disabled. The amount of open sky in the field of vision was determined using Adobe Photoshop 5.5 (Adobe Systems, San Jose, CA, USA) as previously described (Engelbrecht & Herz 2001; Ashton *et al.* 2005).

Additionally, for each of the 15 plots, the existing dominant canopy tree species and percentage of its total cover was observed. We also measured the distance to the nearest shrub species (NSS), NSS volume, distance to nearest tree species (NTS), and NTS d.b.h. for each plot. Soil was collected (0–10 cm depth) from each plot on 19 June 2006. Five cores were taken from each plot and combined into one sample for testing. Our samples were analysed for chemical and textural characteristics by the Rutgers Soil Testing Laboratory (Middlesex County, New Jersey, USA).

PLANT DATA COLLECTION

In September 2004 and 2005, June 2006, and September 2006, we measured height, widest width (diameter1), and 90-degrees across widest width (diameter2) on each plant. As these plots will continue to be monitored for several more years, we did not destructively sample the saplings to find biomass. Instead, we approximated whole plant volume by using the geometric shape [right circular cone (cm^3) = 1/3 × pi × height × radius1 × radius2] that best fit the plant form of each species.

DATA ANALYSIS

We evaluated the main effects of plot Treatment type, Species, Time, and Canopy dominant on species growth (mean height and volume) across four sampling periods in the years 2004 (September), 2005 (September) and 2006 (June and September). The data were $\log_{10}$-transformed to increase normality (Underwood 1997) before we did a repeated measures multivariate analysis of variance (MANOVA), which used the four samples as the dependent variables (PROC GLM (general linear model procedure), Pillai's Trace tests). In the overall repeated measures MANOVA, we tested for effects on only the native species to maintain equal sample sizes among all treatments, as the invasive saplings were absent in one of the three treatments (i.e. 0% invasive). For each individual species, we did a repeated measures MANOVA to test growth differences across time. Tukey's multiple comparison tests using least squares means (PDIFF and LSMEANS options) were done to determine differences among samples when a significant trend was detected. Analyses for height and volume were done separately.

Instead of using PROC MIXED (which some current repeated measures studies use), we used PROC GLM for the repeated measures MANOVA with individuals (n = 486 total saplings, n = 363 total native saplings) that survived the duration of the experiment; this eliminated inclusion of missing values. The majority of measurements in our study were taken at evenly spaced intervals (i.e. annually in September), which helped meet the assumption of

Table 2. Statistical results from the Repeated Measures MANOVA (multivariate analysis of variance) evaluating the effects of Time, Treatment, Species, Canopy dominant species, and those interactions, on mean native plant height and volume in tree sapling communities. The dependent variables for each MANOVA were the mean values for each of the four sampling periods (2004, 2005, June 2006, September 2006)

	Mean native tree sapling height (cm)				Mean native tree sapling volume (cm^3)[a]			
Effect	Pillai	d.f.	*F*	*P*	Pillai	d.f.	*F*	*P*
Time	0.6084	3, 343	177.77	**< 0.0001**	0.8033	3, 343	466.81	**< 0.0001**
Canopy dominant[b,c,d]	–	1, 345	21.81	**< 0.0001**	–	1, 345	18.77	**< 0.0001**
Species[b,e]		2, 345	130.73	**< 0.0001**	–	2, 345	66.63	**< 0.0001**
Treatment[b,f]	–	2, 345	4.02	**0.0188**	–	2, 345	3.44	**0.0332**
Canopy dominant × Species[b]	–	2, 345	1.18	0.3098	–	2, 345	1.36	0.2590
Canopy dominant × Treatment[b]	–	2, 345	8.30	**0.0003**	–	2, 345	5.50	**0.0045**
Species × Treatment[b]	–	4, 345	0.37	0.8275	–	4, 345	0.45	0.7757
Canopy dominant × Species × Treatment[b]	–	4, 345	1.70	0.1495	–	4, 345	0.89	0.4702
Time × Canopy dominant	0.1750	3, 343	24.25	**< 0.0001**	0.1437	3, 343	24.25	**< 0.0001**
Time × Species	0.1095	6, 688	6.64	**< 0.0001**	0.3736	6, 688	26.34	**< 0.0001**
Time × Treatment	0.0956	6, 688	5.75	**< 0.0001**	0.0794	6, 688	4.74	**< 0.0001**
Time × Canopy dominant × Species	0.0127	6, 688	0.74	0.6214	0.0083	6, 688	0.48	0.8251
Time × Canopy dominant × Treatment	0.0256	6, 688	1.49	0.1795	0.0294	6, 688	1.71	0.1160
Time × Species × Treatment	0.0307	12, 1035	0.89	0.5536	0.0182	12, 1035	0.53	0.8993
Time × Species × Treatment × Canopy dominant	0.0307	12, 1035	0.89	0.5545	0.0283	12, 1035	0.82	0.6275

[a] Since we did not destructively sample the saplings for biomass, we calculated volume as an approximation by using the geometric formula for a right circular cone (plant volume = 1/3 × pi × h × r1 × r2). This shape is similar to the plant shapes for each species.
[b] Between-subjects effects do not receive a Pillai value.
[c] Canopy dominant and its interactions were treated as random effects. The other three main effects (Time, Species, Treatment) were fixed factors.
[d] Canopy dominant (n = 2) = invasive or native canopy.
[e] Native species (n = 3) = *Acer rubrum*, *Quercus rubra* and *Ulmus americana*.
[f] Plot treatment (n = 3) = 0%, 25% and 50% invasive communities.
Mean values signficant at the $P < 0.05$ level are shown in bold face; 'Pillai' is Pillai's test statistic for MANOVA. n = 363 total native tree saplings.

sphericity of equal covariances between sample times for repeated measures (Gotelli & Ellison 2004). In our mixed effects analysis, we had three independent variables that were fixed effects (Time, Species, Treatment) and one that was random (Canopy dominant and its interactions), which was identified with a RANDOM statement in the PROC GLM program. Two canopy dominant groups (invasive or native canopy) were identified based on the presence or absence of *A. platanoides* as the dominant canopy species above each plot. *A. platanoides* has been shown to drive canopy changes and subsequent reductions in understorey light, which have negatively affected native species (Reinhart *et al*. 2006b), so we evaluated its canopy impact on our sapling communities. After a significant interaction (Treatment × Canopy dominant) was found in the overall MANOVA, we sorted the data by canopy dominant and sapling community type to better identify these trends through analyses of variance (ANOVA). In a separate ANOVA, we tested the effect of Canopy dominant on the percentage of light at the sapling level of each plot. To maintain normality (Shapiro Wilks $P > 0.05$) and homoscedascity, these data were $\log_{10}$-transformed.

Pearson's chi-square and Fisher's exact test (PROC FREQ), with adjusted alpha levels of $P < 0.0125$ to decrease the Type I error rate, were used to examine the differences between survival and mortality of all the original plants (n = 540) among the tree communities.

Using simple linear regressions (PROC REG), we tested the ability of various plot characteristics (light, soil, biotic, and pre-existing conditions) to predict the mean plot plant height in September 2006 (response variable). To increase normality, both response and predictor variables were either $\log_{10}$ or arc-sine transformed.

All mean and standard error values in tables and figures are original (non-transformed) values. All analyses were done with SAS version 9.1 for Windows (SAS Institute, Cary, NC, USA).

Results

We found that the heights and volumes of all native species in the tree communities differed over the sampling Time (from 2004 to 2006), by Treatment type, Species, and Canopy dominant (Table 2). The three significant two-way interactions with Time (Time × Treatment, Time × Species, Time × Canopy dominant) indicated the expected temporal variation of plant growth by each species, treatment and canopy type.

By the last sample period, native plants in communities without *A. platanoides* (i.e. 0% invasive treatment) had significantly greater height and volume than in both treatments where *A. platanoides* was present (Table 3). For example, native saplings were 22% taller and had 40% greater total plant volume in the purely native community (0% invasive) compared with the most invaded community (Table 3). Of the four tree species, heights of *A. rubrum* and *U. americana* were affected by plot Treatment, as both grew significantly better in the 0% invasive treatment than in either of the treatments containing the invasive (i.e. 25%, 50%) (Fig. 1b,d). *A. rubrum* saplings had 26% greater height in the 0% community compared with the 50% community (Fig. 1b), while *A. platanoides* had

Table 3. Statistical results from the Least Squares Means tests evaluating differences of native plant height and volume per treatment type. The dependent variables for each test were the mean values for each of the three treatments (0%, 25% and 50% invasive). Mean values are shown (1 SE)

	Tree sapling community plot treatment (% invasive)		
Sampling period	0% (n = 5 plots)	25% (n = 5 plots)	50% (n = 5 plots)
Mean native tree height (cm)			
2004 September	69.4 (1.81)^{a}	68.0 (2.10)^{a}	67.7 (2.46)^{a}
2005 September	91.2 (2.59)^{a}	83.4 (2.71)^{a,b}	81.2 (2.83)^{b}
2006 June	112.9 (3.39)^{a}	97.5 (3.51)^{b}	91.6 (3.25)^{b}
2006 September	119.7 (3.84)^{a}	101.1 (3.84)^{b}	92.9 (3.25)^{b}
Mean native tree volume (cm^{3})			
2004 September	32,997 (1,933)^{a}	29,982 (2,072)^{a}	32,800 (3,517)^{a}
2005 September	99,952 (6,553)^{a}	75,118 (5,846)^{b}	81,075 (6,908)^{a,b}
2006 June	228,754 (16,393)^{a}	162,835 (18,259)^{b}	156,170 (15,546)^{b}
2006 September	275,741 (23,959)^{a}	177,197 (20,359)^{b}	166,343 (20,856)^{b}

Since we did not destructively sample the saplings for biomass, we calculated volume as an approximation by using the formula for a right circular cone [plant volume (cm^{3}) = 1/3 × pi × h × r1 × r2], which is similar to the plant shapes for each species.
Means per row with the same superscript letter are not significantly different at the $P < 0.05$ level.
Native tree species: *Acer rubrum, Quercus rubra, Ulmus americana*.
n = 363 total native tree saplings.

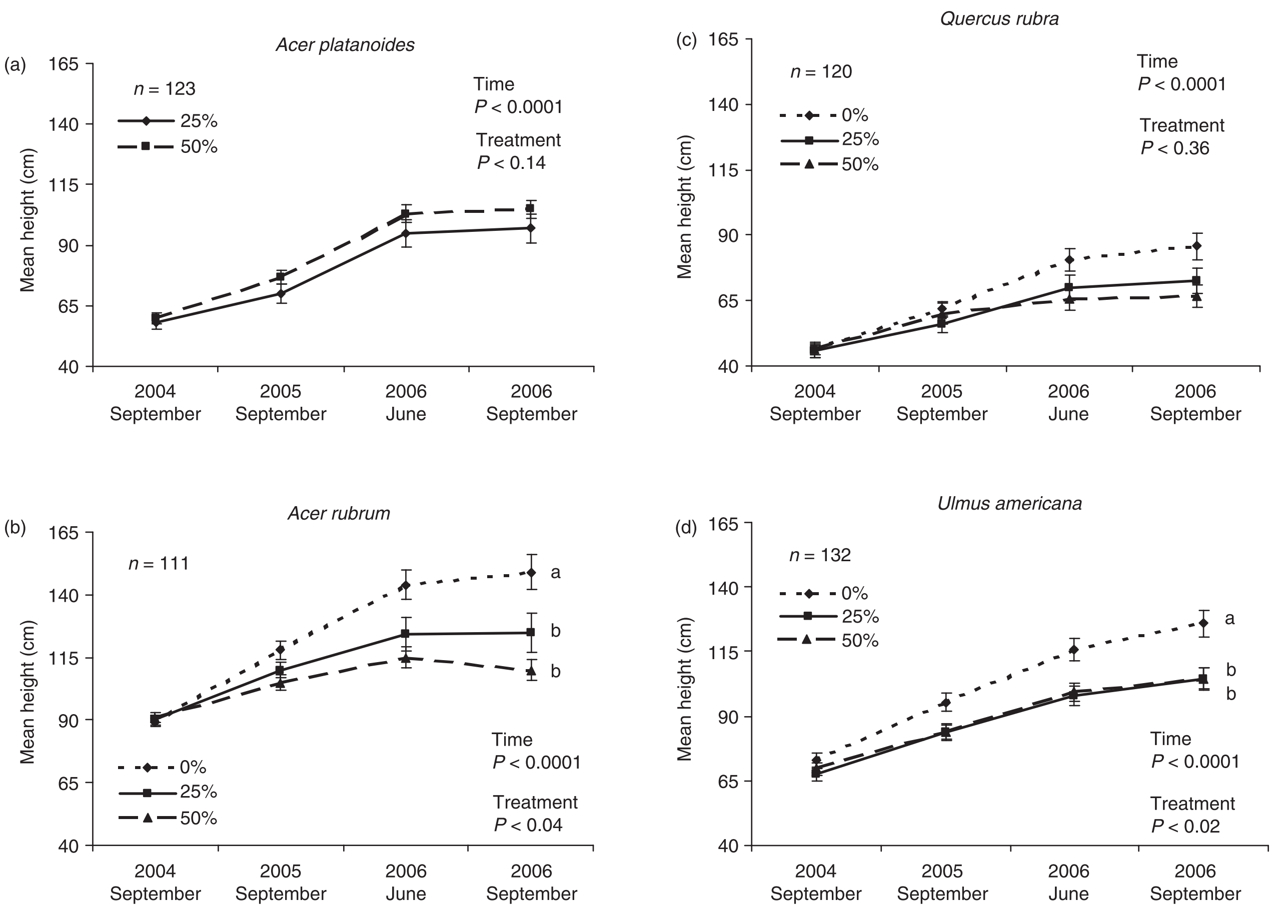

Fig. 1. Statistical analyses evaluating the effect of Time and Treatment on mean species heights ((a) *Acer platanoides*, (b) *A. rubrum*, (c) *Quercus rubra*, (d) *Ulmus americana*) using a repeated measures MANOVA (Pillai's trace test). The dependent variables were the mean heights for each of the sampling years. Treatments are 0%, 25% and 50% invasive species (i.e. *A. platanoides*) abundance per plot (see Table 1 for planting design). Between-treatment comparisons that are significantly different are shown with different letters, as identified through the least squares means tests (Tukey option). Mean values ± 1 SE and sample number are shown per species.

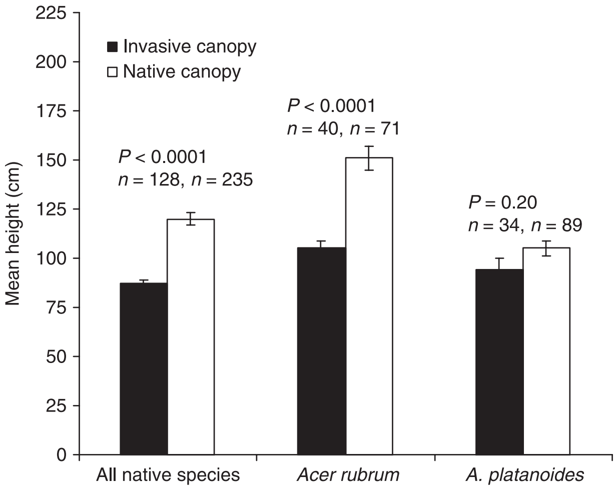

Fig. 2. Analyses of variance evaluating the effect of the existing Canopy dominant species (invasive or native) on mean sapling height (in 2006 September) for all native species (i.e. *Acer rubrum*, *Quercus rubra*, *Ulmus americana*) and both *Acer* species. Saplings beneath an invasive canopy (i.e. *Acer platanoides*) are represented in black bars, while the white bars show saplings with a native species as the canopy dominant (including *A. rubrum*, *Fraxinus americana*, *Quercus alba*, *Q. palustris* and *Pseudotsuga menziesii* (horticultural artifact on forest edge)). Mean values ± 1 SE, level of significance, and the number of saplings per analysis are given.

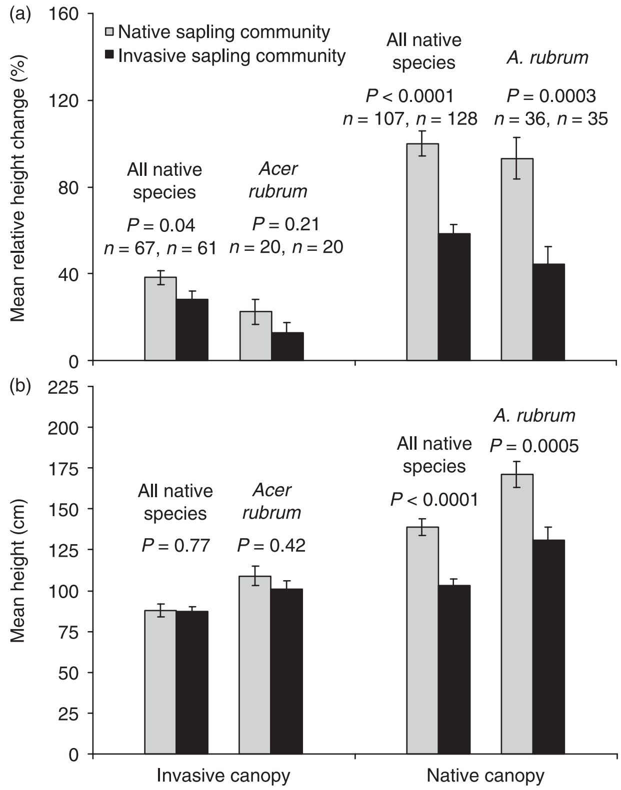

Fig. 3. Statistical analyses evaluating the effect of sapling community Treatment (invasive or native community), within each of the two Canopy dominant types (invasive or native canopy), on (a) mean relative change in height and (b) mean sapling height (in 2006 September). Communities that contain only native saplings (0% invasive) are shown as light bars, while communities with invasive saplings (25% and 50% invasive) are represented as dark bars (see Table 1 for community planting design). The invasive canopy dominant species was *Acer platanoides*, while several native species were canopy dominants, depending on the plot (including *A. rubrum*, *Fraxinus americana*, *Quercus alba*, *Q. palustris* and *Pseudotsuga menziesii* (horticultural artifact on forest edge)). Mean values ± 1 SE, level of significance, and the number of saplings per analysis are given.

equivalent heights in both treatments where it was present (Fig. 1a). In addition to the effect of Treatment on native species growth, the type of Canopy dominant (invasive or native canopy) was also important (Table 2). Grouped together, saplings of the three native species grew 28% taller beneath a native canopy than an invasive, while *A. platanoides* showed no growth difference between canopy types (Fig. 2). While the biotic patterns beneath the canopies were significant, we found that the percentages of light in plots beneath the invasive (11.4 ± 1.0%, $n = 6$) and native canopy (10.2 ± 0.8%, $n = 24$) did not differ ($F_{1,28} = 1.05$, $P = 0.31$).

The only significant interaction in the overall MANOVA, other than the expected two-way interactions with Time, was between Treatment and Canopy dominant (Table 2). This was striking, as *A. rubrum* and the grouped native species had different growth trends in the sapling community treatments depending on the canopy type (Fig. 3). Beneath an invasive canopy, we found that the type of understorey community does not affect native sapling growth, as plants grew similarly in the native (0%) and invasive (25% and 50%) communities. However, when *A. rubrum* saplings grew under a native canopy, they were significantly taller (23%) in the native communities than in the invasive communities (25% and 50% communities) ($F_{1,69} = 13.14$, $P = 0.0005$) (Fig. 3). Overall, it appears that an invasive canopy has such a strong negative effect on native sapling growth that the presence of invasive saplings is irrelevant, while the absence of invasive saplings beneath a native canopy significantly increases native plant growth. Though native species showed a significant interaction between Treatment and Canopy dominant, *A. platanoides* had similar growth patterns in sapling communities beneath each canopy (Fig. 4).

We also found many plot characteristics significantly predicted mean native plant height (Table 4), but most of these relationships were not very strong, as the highest *R*-squared (R^2) value was 0.12 (negative effect of leaf litter depth on sapling height). Other variables (i.e. Treatment, Canopy dominant) were likely to have a greater predictive value for sapling height. However, we did find positive growth when incoming light was high, when existing shrubs and trees were closer to the plot, leaf litter depth was shallow, and the soil had higher concentrations of nitrogenous compounds.

Of the original 540 saplings planted in 2004, 90% survived the duration of the experiment. Compared with treatments where invasive plants were present at proportions of 25% (84% survival) and 50% (83% survival), there was a significantly greater survival of native trees in purely native communities (97% survival) (Pearson's chi-square = 17.33, d.f. = 2, $P = 0.0002$).

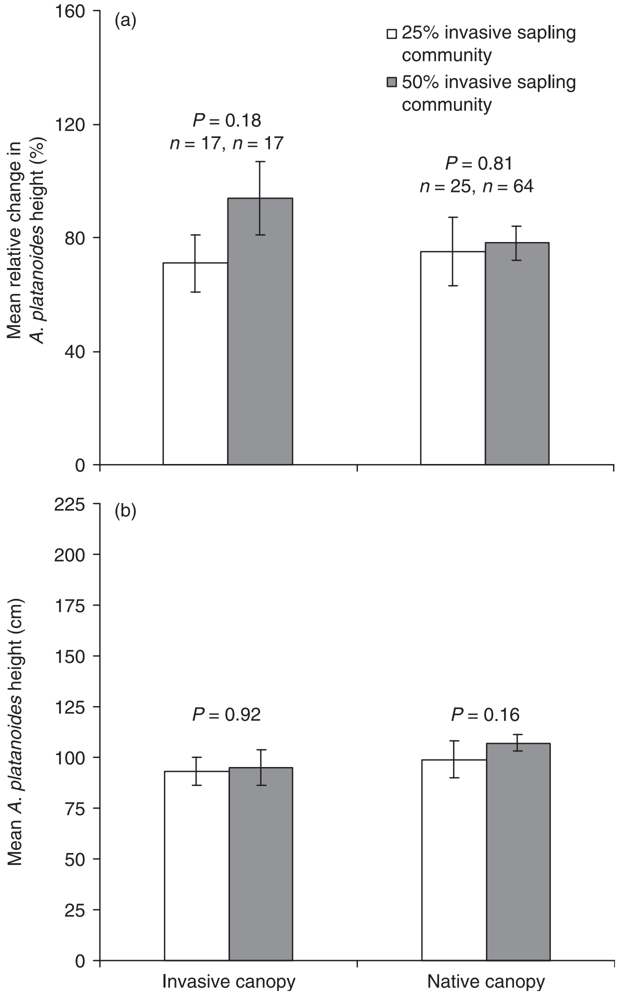

Fig. 4. Statistical analyses evaluating the effect of sapling community type (invasive or native community), within each of the two Canopy dominant types (invasive or native canopy), on (a) mean relative change in *A. platanoides* height and (b) mean *Acer platanoides* sapling height (in 2006 September). Communities with *A. platanoides* comprising 25% of the saplings are shown as white bars, while communities with 50% of the saplings being *A. platanoides* are represented with dark grey bars (see Table 1 for community planting design). The invasive canopy dominant species was *Acer platanoides*, while several native species were canopy dominants, depending on the plot (including *A. rubrum*, *Fraxinus americana*, *Quercus alba*, *Q. palustris* and *Pseudotsuga menziesii* (horticultural artifact on forest edge)). Mean values ± 1 SE, level of significance, and the number of saplings per analysis are given.

Discussion

The impact of non-native invasive species on natural systems continues to be shown through studies investigating interspecific competition (Hamilton *et al*. 1999) and alterations of native plant communities (Wyckoff & Webb 1996; Martin 1999; Von Holle *et al*. 2003) at multiple scales (Pauchard & Shea 2006). In the eastern USA, the majority of forest studies evaluating invasive impacts have been observational (Martin 1999; Webb *et al*. 2000), or experiments with species removals (Gould & Gorchov 2000; Luken & Shea 2000; Webb *et al*. 2001), or additions focusing on a target invasive species (Gorchov & Trisel 2003). This study was one of the first to test the effects of invasive woody species, at varying proportions, on native tree saplings in experimental forest understorey communities.

We found that there were significant effects of all four main factors (Time, Treatment, Species, and Canopy dominant) on heights and volumes of native saplings over the three growing seasons. Due to different life histories of the three species (from three genera), we expected that sapling growth per species would differ. Additionally, temporal variation for each of the main effects was confirmed through the three significant two-way interactions with Time (e.g. Time × Species). All three native species had greater survival and growth in plots where the invasive *Acer platanoides* was absent (0% invasive; Table 1), compared with plots with 25% and 50% of the invasive. The lack of a Treatment × Species interaction effect on both mean height and volume suggests that each native species responded similarly between the treatments of varying invasive proportions.

When *A. rubrum* was growing with *A. platanoides* saplings, its height was significantly less than when the invasive was not present. In the last survey period, *A. rubrum* saplings in the purely native communities (0% invasive) were 16% and 26% taller than *A. rubrum* saplings in plots containing *A. platanoides* at 25% and 50% proportions, respectively. It also appears that *A. rubrum* shoot die-back started in the 50% invasive communities, as its height was decreasing by September 2006. These differences indicate that interspecific competition with *A. platanoides* is likely to inhibit *A. rubrum* growth at the sapling life-stage. However, the mechanisms for the negative effects that we describe are largely unknown. Some have suggested allelopathy may facilitate the success of *A. platanoides* when competing with natives (Wyckoff & Webb 1996; Sauer 1998), but a recent study from the same region as this experimental site indicated allelopathy was unlikely (Rich 2004).

Also, for *Ulmus americana*, it appears that the presence of *A. platanoides* at the sapling community level will inhibit its growth over time, though these saplings had the highest survival of all species and were likely to be too young to be affected by Dutch Elm disease (DED) (Stack *et al*. 1996). We expect that DED will eventually infect these *U. americana* saplings and change the trajectory of the communities where this tree species is present. While similar growth trends for *Quercus rubra* were not statistically significant, they may still be biologically important.

In addition to competitive effects from invasive saplings, the invasive canopy (i.e. *A. platanoides* canopy) negatively affected native plant growth. In the last sample period, native saplings were 28% shorter beneath the invasive canopy compared with a native canopy. It appears that the interaction between sapling communities and canopy type may be important for the trajectory of forest structure. Beneath a native canopy, the absence of invasive saplings significantly increased native growth, but the invasive canopy had such a strong negative effect on growth that the presence of invasives in the understorey had no impact on native saplings. If this trend holds over time, it seems only an absence of *A. platanoides*

Table 4. Linear regression analyses evaluating the ability of each plot variable to significantly predict the response variable. The response (dependent) variable was the mean native sapling height per plot in September 2006 and was $\log_{10}$-transformed to increase normality. Predictor variables were either $\log_{10}$ or arc-sine transformed

Plot predictor variable	R^2	Relationship to mean height	Equation best predicting $\log_{10}$ mean plant height	P
Microstegium vimineum cover[a]	0.0608	+	–0.3523 + 1.197 (arc-sine Micro cover)	**< 0.0001**
Total plant species richness in plot[a]	0.0415	–	2.191 – 0.3167 ($\log_{10}$ plant richness)	**< 0.0001**
Percentage light	0.0947	+	1.629 + 0.3514 (arc-sine light)	**< 0.0001**
Leaf litter depth (December 2006)	0.1152	–	2.6366 – 0.8973 ($\log_{10}$ leaf litter depth)	**< 0.0001**
NSS volume (cm^3)[b]	0.0311	–	2.5683 – 0.0843 ($\log_{10}$ NSS volume)	**0.001**
NSS distance (cm)[b]	0.0715	–	2.2211 – 0.1689 ($\log_{10}$ NSS distance)	**0.005**
NTS distance (cm)[c]	0.0135	–	2.0892 – 0.0924 ($\log_{10}$ NTS distance)	**0.03**
NTS dbh (in)[c]	0.0991	+	1.7627 + 0.1143 ($\log_{10}$ NTS dbh)	**< 0.0001**
pH	0.0001		2.0477 – 0.0754 ($\log_{10}$ pH)	0.88
Phosphorus	0.0101		1.9076 + 0.0588 ($\log_{10}$ Phosphorus)	0.06
Iron	0.0327	+	0.4546 + 0.6614 ($\log_{10}$ Iron)	**0.0005**
Organic matter %	0.0002		1.9842 + 0.0174 (arc-sine Organic matter)	0.79
Nitrate	0.0239	+	1.9527 + 0.0385 ($\log_{10}$ Nitrate)	**0.003**
Ammonium	0.0320	+	1.9114 + 0.0619 ($\log_{10}$ Ammonium)	**0.001**

[a] Prior to planting of plots.
[b] NSS = nearest shrub species.
[c] NTS = nearest tree species.
Native sapling species = *Acer rubrum*, *Quercus rubra*, *Ulmus americana*.
Percentage light = 100 – Percentage canopy cover.

in both the understorey and canopy will provide optimal native sapling growth. However, in a forest with a native canopy, our study has shown that the absence of invasive saplings will increase the growth of natives, which could enhance the presence of native trees in the future canopy. This information could help guide management decisions regarding invasive removal and augmenting native species growth. Nevertheless, the strong competitive effects of *A. platanoides* at the sapling and canopy levels predict that native saplings will be inhibited by the invasive, either through one or both levels.

The capability of an invasive canopy to suppress native understorey growth has been shown (Wyckoff & Webb 1996; Martin 1999) through negative effects of deep shade (Reinhart *et al*. 2006b), and invaded (Howard *et al*. 2000), mesic microenvironments (Howard *et al*. 2000; Bertin *et al*. 2005). While we found that native plants responded positively to higher light percentages at the sapling level (1.5 m from ground), there was no difference in light beneath the invasive and native canopies. Therefore, it is likely that other variables we did not measure, such as light quantity (photosynthetically active radiation) and quality (Red:Far Red light ratio) (Ammer 2003; Reinhart *et al*. 2006b), were important in the negative impact of the invasive canopy.

In a related glasshouse study, *A. rubrum* seedlings had significantly less (32%) above-ground biomass when grown in soil collected from beneath a mature stand of *A. platanoides* (basal area = 48.5 $m^2\ ha^{-1}$) than from a mixed native stand (51.4 $m^2\ ha^{-1}$; S. Galbraith-Kent, unpublished data). Some have suggested that soils already invaded (Howard *et al*. 2000) and with a high moisture content (Howard *et al*. 2000; Reinhart *et al*. 2006a) may increase invasive growth at the expense of native plants. Though we did not measure soil moisture, we found our native saplings responded positively to thinner leaf litter layers, which may have contributed to a drier microenvironment more favourable to native growth.

Converse to the native species, *A. platanoides* grew similarly in treatments where it comprised two different proportions (25%, 50% of saplings) and beneath both canopy types (i.e. invasive (conspecific) and native). The capability of *A. platanoides* to inhibit native saplings through both direct competition and overstorey shade effects, while not affecting conspecifics, may contribute to its success in forests. In other studies, soil from different forest types had no effect on *A. platanoides* seedling growth in the glasshouse (S. Galbraith-Kent, unpublished data) or in the field (Howard *et al*. 2000; Reinhart *et al*. 2006a). It has been shown that when *A. platanoides* is the canopy dominant, soil moisture is increased, which may then promote the understorey success of this invasive species (Reinhart *et al*. 2006a). In our study, the relative homogeneity (e.g. same land-use history, soil type) and proximity of our plots may have contributed to equal *A. platanoides* sapling growth across treatments and canopy type.

In this study, we were solely testing if invasive saplings inhibited the growth of co-occurring native saplings, and if so, at what threshold of invasive proportion is that expressed. We recognize that the trends we observed of these long-lived species were over just three growing seasons and could change over the next several decades. Additionally, asymmetric competition was likely in our study, as the invasive species appeared to have a strong negative effect on the natives, while the natives had little or no negative effect on *A. platanoides*. Nevertheless, the negative effects on native sapling growth by *A. platanoides* (at both the understorey and overstorey canopy levels) cannot be overlooked and should affect future native performance. Even when *A. platanoides* was present in proportions equal to *A. rubrum* and *U. americana* (i.e. 25% invasive treatment; Table 1), both native species grew significantly less than when the invasive was not present.

Many studies have investigated the factors that promote invasive success (Lundgren *et al*. 2004; Aronson *et al*. 2007), but we wanted to gain insight into what happens when the invasive and native species coexist in forest understorey communities. Based on our study, we suggest that management of forests with similar proportions of non-reproductive *A. platanoides* saplings could include episodic removals every 2–3 years. This could give the native saplings opportunities to be released from competition with the invasives and increase in growth. Also, because *A. platanoides* needs several years to mature before reproducing, unlike many herbaceous invasive species (e.g. *Microstegium vimineum*, *Alliaria petiolata*), annual removal may not be essential. High frequencies of *A. platanoides* removals are not only resource (i.e. labour, funds) intensive, but they may promote the spread of the target invasive species, as well as additional invasives (Webb *et al*. 2001). While seedlings can be hand-pulled, saplings must be cut, hacked, and have an application of a systemic herbicide (e.g. glyphosate) with follow-up treatments, because cutting alone is often ineffective (Webster *et al*. 2006). Though our results are based on one invasive tree species, our findings could be applicable to others. We encourage studies that also use an experimental approach to test and quantify competitive effects of invaders on native species.

In conclusion, we have described a study testing interspecific competition between native and invasive saplings in experimental communities within the understorey of an eastern US forest. We found that the presence of *A. platanoides* saplings, at proportions both equal to and greater than native trees, will reduce native species growth. Additionally, native plants grew significantly less under an invasive canopy compared with a native canopy, so it appears that optimal native sapling growth is likely to occur only in the absence of *A. platanoides* in both the understorey and canopy. However, beneath a native canopy, the absence of invasive saplings did facilitate native growth and this information could help guide management decisions in similar forests. Further research combining field experiments and observational studies testing other community effects and mechanisms, such as mycorrhizal relationships (Stinson *et al*. 2006) and shade (Reinhart *et al*. 2006b), would advance our understanding of the interactions between invasive and native species. This knowledge may help make pragmatic and informed improvements in how we should manage an invader in a specific region.

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