

Neighbourhood models of the effects of the invasive *Acer platanoides* on tree seedling dynamics: linking impacts on communities and ecosystems

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Summary

1. Effects of invasive species on ecosystem processes are often thought to underlie the effects of invaders on community dynamics. Specifically, positive feedbacks in which invasive species alter ecosystem function in ways that favour their own growth have been suggested as an important mechanism contributing to the success of invasion.

2. In this study, we analysed the impacts of the invasive exotic tree *Acer platanoides* on survival and growth of conspecific and native tree seedlings, and explored whether these impacts can be explained by the ecosystem effects of the invader. Seedlings of *Acer platanoides*, *Acer saccharum*, *Fraxinus americana* and *Prunus serotina* were monitored in quadrats in three forest stands in north-western Connecticut. Soil resources and light levels were quantified in the same quadrats.

3. Maximum-likelihood methods were used to predict seedling survival and growth as a function of the size and spatial configuration of *A. platanoides* trees in the immediate neighbourhood (0–25 m).

4. The abundance of *A. platanoides* in the neighbourhood had moderate negative effects on survival of first-year conspecific seedlings, but did not affect survival of older conspecific or native seedlings. These negative effects on conspecifics were not correlated with soil nutrients or light levels, but were presumably related to Janzen-Connell effects. In contrast, *A. platanoides* had strong positive effects on the growth of seedlings of all four species. These positive effects appear to be related to the positive impacts of the invader on soil fertility.

5. Our results support the importance of canopy-seedling feedbacks as a mechanism regulating the rate of invasion in forests. However, they also indicate that the net consequences of feedbacks on the process of invasion are probably determined by the balance of positive and negative feedbacks acting at the same time on different aspects of regeneration (i.e. survival vs. growth).

6. *Synthesis.* Because the species with the highest inherent growth rates were the most responsive to the ‘fertilizing’ effect of *A. platanoides*, we conclude that the invasion of north-eastern forests by this exotic tree may facilitate canopy dominance by fast-growing native and exotic species associated with fertile soils.

Key-words: *Acer platanoides*, invasive species, neighbourhood index, plant-soil feedbacks, seedling survival and growth, spatially explicit models, soil fertility, temperate forests

Introduction

Invasive species have fundamentally changed the structure and function of natural communities and ecosystems worldwide (Williamson 1996; Vitousek *et al.* 1997; Mack *et al.* 2000). From the perspective of community structure and composition, invasive plant species are usually reported to cause declines in local biodiversity and native abundance

(Vivrette & Muller 1977; Hutchinson & Vankat 1997; Meiners *et al.* 2001; Alvarez & Cushman 2002; Badano & Pugnaire 2004). Invaders have also been shown to alter ecosystem processes, including nutrient cycling (Vitousek *et al.* 1987; Ehrenfeld 2003), light regimes (Dyer & Rice 1999; Reinhart *et al.* 2006), hydrology (Zavaleta 2000; Gerlach 2004), and fire cycles (D’Antonio & Vitousek 1992). For many invasive species, however, it is poorly understood to what extent changes in ecosystem processes actually translate into changes in community composition and dynamics (Levine *et al.* 2003).

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Disentangling community responses to the ecosystem impacts of invasive species should contribute to a better understanding of the mechanisms of invasion. It has been suggested that invasive species can alter ecosystem function in ways that favour their own growth and spread, creating positive feedback loops that enhance subsequent invasion (Ehrenfeld 2003). However, evidence for this is still very limited (Levine *et al.* 2003; Ehrenfeld *et al.* 2005) and even contradictory (i.e. Hager 2004; Vinton & Goergen 2006). Moreover, even if positive feedbacks exist within the invader population, the consequences of those feedbacks for invasion rates and community dynamics will be modulated by how the native species respond to the same ecosystem changes. For example, facilitation of native species by invaders is much more common than previously recognized (Bruno *et al.* 2005; Rodríguez 2006). As a result, growth and spread of invasive species could be reduced if the performance and therefore competitive ability of native species also improves as a result of the presence of the invader. Multi-species studies that quantify the differential impacts of an invasive species on both conspecifics and native species are necessary to gain insights into the role that positive feedbacks play in the success of invasive species.

Acer platanoides L. (Norway maple) is one of the most common invasive tree species in temperate forests of the north-eastern USA (Webster *et al.* 2006). It is also a common invader of riparian and montane forests of the northern Rocky Mountains (Reinhart *et al.* 2005, 2006). *Acer platanoides* is very shade tolerant (Niinemets 1997), characterized by prolific seed production, rapid growth, widespread horticultural use, and tolerance of a broad range of environmental stresses (Santamour & McArdle 1982; Kloeppe & Abrams 1995). It can establish and become abundant not only in open, disturbed areas (Anderson 1999) but also in intact forests (Webb & Kaunzinger 1993; Webb *et al.* 2000; Martin & Marks 2006). Observational studies have reported lower native species richness and abundance under *A. platanoides* canopies than under native tree species in north-eastern forests (Wyckoff & Webb 1996; Martin 1999; Fang 2005), although the mechanisms have not been fully explored.

Neighbourhood models indicate that *A. platanoides* alters the functioning of temperate forest ecosystems, even at relatively low densities, by increasing nutrient availability (i.e. Ca, Mg, K, N) and cycling rates (i.e. net N mineralization, net nitrification, Ca mineralization; Gómez-Aparicio & Canham 2008). Increases in soil resources have the potential to drastically alter the growth and competitive interactions among invasive and native species. For example, N fertilization treatments in invaded grasslands usually cause decreases in abundance and/or competitive ability of native species, presumably because native grasses are well adapted to low soil N availability and have a lower ability to capitalize on resources than invasive species (Wedin & Tilman 1996; Vinton & Goergen 2006). In north-eastern forests, however, increases in soil fertility due to *A. platanoides* invasion might translate into positive effects on the native community, because these systems are traditionally considered N-limited (Vitousek &

Howarth 1991) and may experience deficits in Ca and other base cations (Juice *et al.* 2006). Moreover, fertilization experiments have shown that nutrient additions improve growth and survival of many native species in these forests (Kobe *et al.* 2002; Tripler *et al.* 2002; Bigelow & Canham 2007). This possibility of a positive impact of *A. platanoides* on performance of native plants is at odds with previous studies suggesting negative impacts on community structure (e.g. Wyckoff & Webb 1996), and illustrates how a thorough understanding of the impacts of invasion requires studies that link the community and ecosystem effects of invasive species.

The objective of this paper was twofold: (i) analyse the impacts of *A. platanoides* trees on survival and growth of conspecific and native tree seedlings; and (ii) analyse whether the community impacts of *A. platanoides* can be explained on the basis of its impacts on ecosystem processes, specifically on soil resources and light levels. By doing so, we hope to gain insights into the coupling of ecosystem and community impacts of invasive species, the existence of feedback mechanisms during the process of invasion, and the implications for the dynamics of invaded forests.

Methods

STUDY SITES

The study was conducted in three forest stands located in Litchfield county, north-western Connecticut, USA (42° N, 73°15' W). These stands are the same as those used by Gómez-Aparicio & Canham (2008) to analyse the impacts of *A. platanoides* on soil processes. The three sites are located on private lands about 1 km apart from each other, at elevations of 300–500 m. Soils are Typic Dystrochrepts derived from glacial till over mica-schist bedrock (Hill *et al.* 1980). The canopy is second-growth (80–130 years), with a history of logging but no history of agriculture. The species composition of these stands included elements of the oak forests of southern New England and the northern hardwood forests of the north-eastern United States and Canada. The main canopy tree species are *Acer platanoides* L. (Norway maple), *Acer saccharum* Marsh (sugar maple), *Fraxinus americana* L. (white ash), *Prunus serotina* Ehrh. (black cherry) and *Quercus rubra* L. (northern red oak).

SEEDLING MEASUREMENTS

In June 2004, 30 1-m² permanent seedling quadrats were set up at each of the three study sites for monitoring of seedling survival and growth. Our analytical methods (likelihood estimation and neighbourhood models) do not require systematic or random sampling of distances away from *A. platanoides* trees, but require that sampling points represent a range of variation in the numbers, sizes and distances to *A. platanoides* in their neighbourhoods. Therefore, the location of the permanent quadrats was chosen according to this requisite. Within a 25-m radius circle around each of the 90 seedling quadrats, we identified and mapped every tree with a diameter at breast height (d.b.h.) ≥ 2 cm ($n = 3620$ trees), using a laser range-finder with a digital compass (Laser Technology, Inc., Englewood, CO, USA). Relative basal area of *A. platanoides* in the 25-m radius neighbourhoods varied between 0% and 51%. The variation in the relative basal area of the dominant native tree species in the

neighbourhood of the quadrats was: 0–73% for *Acer saccharum*; 0–52% for *Fraxinus americana*; and 0–42% for *Prunus serotina*.

The number of seedlings (both exotic and native) per quadrat was counted in early June each year from 2004 to 2006. We chose this date to ensure that most seedlings had emerged. For each individual seedling, species and age (estimated using annual bud scars) were recorded. In 2004, only new seedlings (i.e. seedlings germinated that spring) were recorded, whereas in 2005 and 2006 all seedlings ≤ 50 cm height (i.e. new to c. 12 years old) were enumerated. This sampling scheme allows the estimation, for each quadrat, of the probability of first-year seedling survival in two years (2004 and 2005) and the probability of older seedling (> 1 year old) survival in one year (2005). First-year and older seedlings were analysed separately because first-year seedling survival is usually much lower than older seedling survival, and therefore the two groups might have different responses to the presence of *A. platanoides*. Seedlings of four tree species (*A. platanoides*, *A. saccharum*, *F. americana* and *P. serotina*) constituted $> 95\%$ of the seedling bank in any of the years, and therefore they were the only species considered for growth measurements (see below) and statistical analyses.

In September 2006, we measured the annual stem extension growth (G), total stem height (H) and basal diameter (D) of every older (> 1 year old) seedling of the four study species in the 90 permanent quadrats. Growth measurements were also taken in 15 additional quadrats per site established that autumn to increase sample size ($n = 135$ quadrats, 1764 seedlings total). We also recorded whether seedlings had suffered browsing and/or died back in the past. Field measurements (G, H and D) were used to calculate three response variables: (i) *relative growth*, estimated as G/H^b ; (ii) *relative height*, estimated as H/A^b ; and (iii) *relative diameter*, estimated as D/A^b , where A is the age of the seedling. The exponent b was estimated, for each species, by fitting the data to a power function (i.e. $G = aH^b$), and corrects for the fact that differences among quadrats in relative growth, height or diameter could be influenced by differences in seedling size or age, especially if growth does not increase linearly with size or age (i.e. $b > 1$ or $b < 1$). The variables *relative height* and *relative diameter* represent estimations of the growth rates experienced by seedlings throughout their life, and therefore compensate for the fact that *relative growth* was measured in only one year. The three power functions, the values of the b exponents, and the R^2 of the regressions are shown for each seedling species in Fig. 1.

ECOSYSTEM MEASUREMENTS

Soil samples were taken next to each of the 90 permanent seedling quadrats during the last week of July 2005. At each sampling location, we measured the depth of the litter layer by inserting a metal ruler down to the soil surface. Litter was then removed to obtain a 5 cm diameter \times 15 cm depth soil core (organic plus mineral soil) using a soil bulk density sampler. The depth of the forest floor was measured *in situ* as the average of four measurements per sampling location. All samples were brought to the laboratory within 2 h of sampling. Detailed methods for the laboratory analyses are reported in Gómez-Aparicio & Canham (2008). In brief, soil gravimetric moisture content was measured on 10 g of sieved soil after oven drying at 60 °C for 2 days. Soil pH was measured in a 2 : 1 slurry of deionized water and 10 g of sample using a Accumet AR20 pH meter (Fisher, Springfield, New Jersey, USA). Exchangeable Ca, Mg and K were extracted using 0.1 mol L⁻¹ BaCl₂ and concentrations of the three cations were measured using inductively plasma atomic emission spectrometry (Leeman Laboratories Inductively Couple Plasma/Profile, Hudson, New Hampshire, USA). Ca

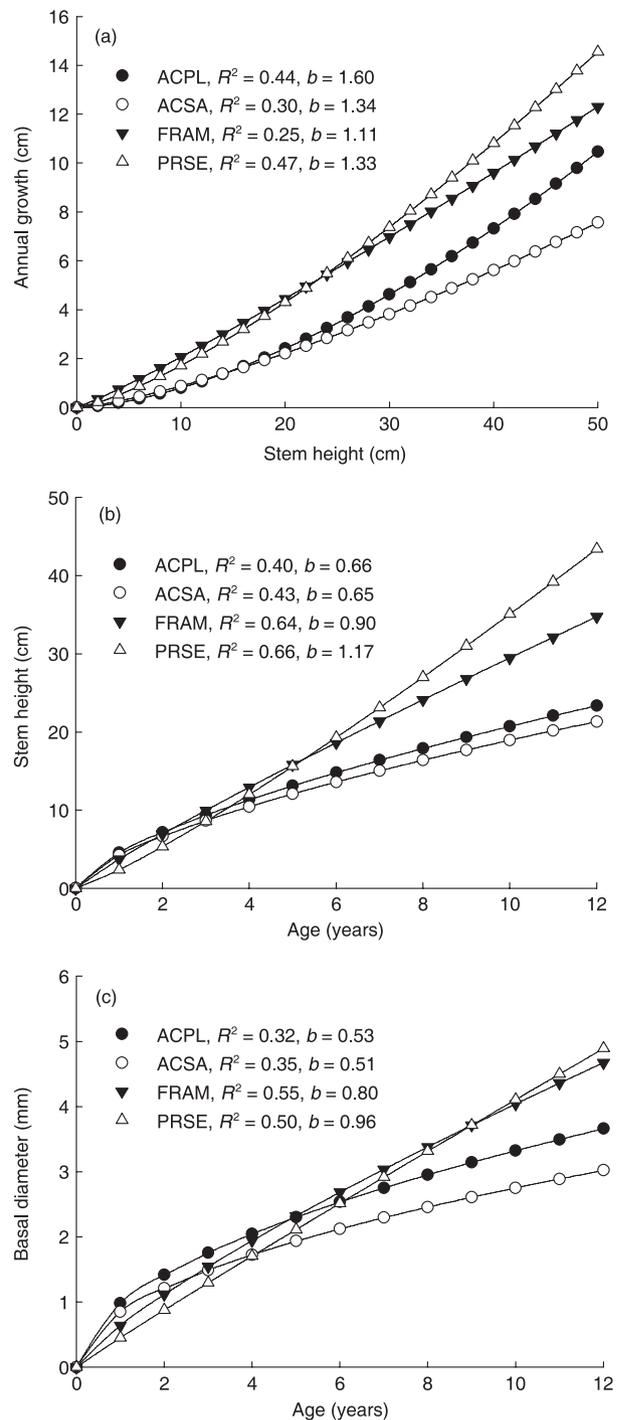


Fig. 1. Power functions showing the predicted relationship between (a) total stem height and annual growth, (b) seedling age and total stem height, and (c) seedling age and basal diameter. The parameter b is the exponent of the power functions, and R^2 gives the goodness of fit of the regressions. ACPL, *Acer platanoides*; ACSA, *Acer saccharum*; FRAM, *Fraxinus americana*; PRSE, *Prunus serotina*.

mineralization was estimated by comparing the concentration of exchangeable Ca in the initial soils with the concentrations after 6 months of incubation in the laboratory at room temperature (22–23 °C). Total soil C and N were analysed on air-dried soils using a Carlo Ebra NA 1500 Analyser (CE Elantech, Milan, Italy). Inorganic N pools (NH_4^+ and NO_3^-) were extracted with 2 mol L⁻¹

KCl and concentrations measured in a Lachat QuikChem 8000. Soil microbial biomass was determined using the CHCL₃-fumigation-incubation procedure (Jenkinson & Powlson 1976), which provides measurements of microbial biomass C, microbial biomass N, soil respiration, potential net N mineralization, and potential net nitrification.

Understorey light levels were measured using fisheye photography to estimate a gap light index (GLI, Canham 1988) for each of the 90 permanent seedling quadrats. GLI is the percentage of 'gap' light (i.e. photosynthetically active radiation transmitted through discrete openings in the canopy) that reaches a point in the understorey over the course of a defined growing season. Photographs were taken in the middle of each quadrat by placing the camera (with a fisheye lens) at approximately 30 cm above the ground. All pictures were taken on cloudy days during August 2005.

MAXIMUM LIKELIHOOD ANALYSES OF SEEDLING SURVIVAL AND GROWTH

We used maximum-likelihood methods to predict mean seedling survival and growth in each quadrat as a function of two components: (i) the potential seedling survival/growth at each of the three study sites in the absence of specific effects of neighbouring trees (i.e. site effects); and (ii) the identity, size and spatial distribution of the trees in the neighbourhood (i.e. neighbourhood effects). We examined two sets of models, one set considering only the distribution and size of *A. platanoides* in the neighbourhood (treating the mix of native species as a random background effect), and a second set of models considering the effects of both the invasive and different native tree species in the immediate neighbourhood.

Effects of *Acer platanoides* on seedling survival and growth

We used three competing models that tested a wide range of possible responses to describe the effect of *A. platanoides* on either seedling survival or growth (Y):

$$\text{Linear model } Y = A_{\text{Site}} + a \left(\frac{\text{NI}_i}{\text{NI}_{\text{max}}} \right) + \varepsilon \quad \text{eqn 1}$$

$$\text{Logistic model } Y = A_{\text{Site}} + \left[\frac{D}{1 + \left(\frac{\text{NI}_i/\text{NI}_{\text{max}}}{a} \right)^b} \right] + \varepsilon \quad \text{eqn 2}$$

$$\text{Exponential model } Y = A_{\text{Site}} * \exp a \left(\frac{\text{NI}_i}{\text{NI}_{\text{max}}} \right)^b + \varepsilon \quad \text{eqn 3}$$

The first term in the models, A_{Site} , represents the potential seedling survival/growth in each of the three study sites in the absence of distinct effects of neighbouring trees. The second term in each equation accounts for the neighbourhood effects of *A. platanoides* on seedling performance, and is calculated as a function of a *neighbourhood index* (NI). NI_i is the neighbourhood index for seedling i of the target species (equations below), and NI_{max} is the maximum value of NI for all seedlings of the target species. The use of NI_{max} standardizes the neighbourhood effect term ($0 < \text{NI}_i/\text{NI}_{\text{max}} < 1$) and facilitates comparisons across seedling species. In the *linear model* (eqn 1), the neighbourhood effects of *A. platanoides* vary as a linear function of NI with slope given by the parameter a . In the *logistic model* (eqn 2), the neighbourhood effects of *A. platanoides* vary following

a logistic function of NI, where the parameter a represents the value of NI at which half the maximum effect is achieved, the parameter b controls the shape of the function, and the parameter D defines the asymptote (or maximum value) for the neighbourhood effects. In the *exponential model* (eqn 3), the neighbourhood effects vary exponentially as a function of NI, with the parameter a defining the steepness of the variation in performance due to an increment in NI and the parameter b determining whether there is a threshold at which the variation in performance takes effect.

Two different functional forms were tested to calculate the *neighbourhood index* (NI): a Weibull function and a lognormal function. In the two cases, the net effect of a neighbouring *A. platanoides* tree on seedling survival/growth is assumed to vary as a direct function of the size of the neighbour, and as an inverse function of the distance to the neighbour. Then, for $i = 1 \dots n$ *A. platanoides* in the neighbourhood, the *neighbourhood index* (NI) is defined as:

$$\text{Weibull } \text{NI} = \sum_{i=1}^n \text{DBH}_i^\alpha \exp(-\gamma \text{distance}_i^\beta) \quad \text{eqn 4}$$

$$\text{Lognormal } \text{NI} = \sum_{i=1}^n \text{DBH}_i^\alpha \exp\left(-\frac{1}{2}\right) \left[\frac{\ln(\text{distance}_i/\beta)}{\gamma} \right]^2 \quad \text{eqn 5}$$

where DBH_i is the diameter at breast height of the i th *A. platanoides*; distance_i is the distance of i th *A. platanoides* from the seedling quadrat, and α , β and γ are parameters determining the shape of the effect of the d.b.h. (α) and the distance to the *A. platanoides* trees (β and γ) on NI. The Weibull function assumes that the neighbourhood effects decline monotonically with distance to a neighbouring *A. platanoides*, whereas the lognormal function allows for the effect of *A. platanoides* to reach a maximum at some distance β from *A. platanoides* trees.

We explored the relationship between light levels (i.e. GLI) and the neighbourhood effects of *A. platanoides* (i.e. neighbourhood index) by conducting regressions of GLI vs. NI. As these regressions did not show any pattern of variation in light regimes as a consequence of the presence of *A. platanoides* in the neighbourhood, we decided not to include light as an additional term in the models. In fact, understorey light levels were relatively homogeneous and low at all quadrats (mean GLI (Q10%–Q90%) = 4.86 (4.00–6.21)).

In order to test whether the effects of *A. platanoides* varied among sites, we also tried a variation of the linear model (eqn 1) in which the slope of the regression (i.e. parameter a) was allowed to vary among sites (*Site-specific model*). However, this model was never the best fit for either survival or growth (results not shown for simplicity). These results imply that the neighbourhood effects of *A. platanoides* on seedling performance were consistent across sites.

The three models described in equations 1–3 were compared with a fourth model (the *null model*), which assumes no effect of *A. platanoides* on seedlings. In this model, seedling survival and growth vary solely as a function of the site (i.e. setting to zero the second term in equations 1–2 and to one in equation 3). All models were fitted individually for each of the four seedling species. Quadrat means of survival and growth were analysed in the models (instead of individual seedling data) to avoid issues of pseudoreplication. For survival, the response variable differed among species due to differences in natural availability of seedlings. Thus, for *A. platanoides* and *P. serotina*, survival models were fitted to first-year seedling survival (2004) and older seedling survival. For *A. saccharum*, survival models were fitted only to older seedling survival, and for *F. americana*, survival models were fitted only to first-year seedling survival (2005). In the case of growth, the same response variables were used for each of the four species (i.e. relative growth, relative height, and relative diameter of

older seedlings). However, because the results of the models for relative growth and relative height were similar and to some extent redundant, only the results for relative height (which integrates growth over a longer period of time) are shown. The relationships between ecosystem variables (i.e. soil processes and light levels) and seedling survival and growth were explored using Spearman rank correlations and Pearson product-moment correlations, respectively.

Comparison of *Acer platanoides* vs. native species effects on seedling survival and growth

In order to compare the effect of *A. platanoides* trees on seedling survival and growth with the effects of canopy trees of the three native tree species studied, we fit the *linear model* (Eqn 1) to the data using a modified version of the neighbourhood functions (Eqn 4 and 5):

$$\text{Weibull NI} = \sum_{j=1}^s \sum_{i=1}^n \lambda_j \text{DBH}_{ji}^{\alpha} \exp(-\gamma \text{distance}_{ji}^{\beta}) \quad \text{eqn 6}$$

$$\text{Lognormal NI} = \sum_{j=1}^s \sum_{i=1}^n \lambda_j \text{DBH}_{ji}^{\alpha} \exp\left(-\frac{1}{2} \left[\frac{\ln(\text{distance}_{ji}/\beta)}{\gamma} \right]^2\right) \quad \text{eqn 7}$$

The neighbourhood index (NI) here is summed over all trees of the $j = 1 \dots 4$ species (s). The parameters in eqns 6 and 7 are the same as in eqns 4 and 5 (respectively), with the only exception of the addition of a new parameter, λ_j , which represents a species-specific scalar that ranges from -1 to 1 and allows for differences among the four species in their effect (positive or negative) on seedling survival and growth.

PARAMETER ESTIMATION AND MODEL COMPARISON

We solved for the maximum likelihood parameter values using simulated annealing (Goffe *et al.* 1994), a global optimization procedure. The error terms (ϵ) for the survival data were modelled using a binomial distribution, whereas the error terms for the growth data were normally distributed and modelled accordingly. Alternate models were compared using the Akaike information criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson 2002). The absolute magnitude of the differences in AIC_c between alternate models provides an objective measure of the strength of empirical support for the competing models (Burnham & Anderson 2002). Models with a difference in $AIC_c < 2$ units are considered to have equivalent empirical support. When the difference in AIC_c between two models is > 2 , the model with the lowest AIC_c is considered to have larger empirical support. We used asymptotic 2-unit support intervals to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards 1992). The R^2 of the regression of observed vs. predicted was used as a measure of goodness of fit of each alternate model. All analyses were done using software written specifically for this study using Delphi for Windows (Version 6, Borland Software Corp., Austin, TX, USA) (see Appendix S3 in Supplementary Material for the executable programs and source code).

Results

EFFECTS OF ACER PLATANOIDES ON SEEDLING SURVIVAL

Models that included the neighbourhood effects of *A. platanoides* on seedling survival were a better fit to the data than the *null model* for seedlings of *A. platanoides*, *A. saccharum*

Table 1. Comparison of alternate models analysing the effect of *Acer platanoides* trees on survival of first-year and older seedlings of the four study species. The most parsimonious model (indicated in bold) is the one with the lowest AIC_c . NP = number of parameters. NI indicates the functional form of the neighbourhood index that provided the best fit for each model (WBL, Weibull; LGN, lognormal). The goodness of fit (R^2) is given for the best model. ACPL, *Acer platanoides*; ACSA, *Acer saccharum*; FRAM, *Fraxinus americana*; PRSE, *Prunus serotina*. $n = 64$ for ACPL_{First-year}, $n = 77$ for ACPL_{Older}, $n = 54$ for ACSA_{Older}, $n = 76$ for FRAM_{First-year}, $n = 53$ for PRSE_{First-year}, and $n = 57$ for PRSE_{Older}

Variable	Model	NP	NI	AIC_c	R^2
ACPL _{First-year}	Null	3		232.84	0.08
	Linear	7	WBL	224.09	
	Logistic	9	LGN	230.62	
	Exponential	8	LGN	229.73	
ACPL _{Older}	Null	3		307.29	0.20
	Linear	7	LGN	304.96	
	Logistic	9	LGN	316.37	
	Exponential	8	WBL	305.96	
ACSA _{Older}	Null	3		187.58	0.18
	Linear	7	LGN	187.24	
	Logistic	9	WBL	186.56	
	Exponential	8	LGN	185.99	
FRAM _{First-year}	Null	3		174.81	0.10
	Linear	7	WBL	173.07	
	Logistic	9	LGN	174.98	
	Exponential	8	LGN	173.34	
PRSE _{First-year}	Null	3		121.96	0.09
	Linear	7	LGN	124.68	
	Logistic	9	LGN	124.35	
	Exponential	8	LGN	127.24	
PRSE _{Older}	Null	3		167.14	0.07
	Linear	7	LGN	169.01	
	Logistic	9	LGN	169.34	
	Exponential	8	LGN	168.46	

and *F. americana*, but not for *P. serotina* (Table 1). The R^2 of the models was low (i.e. 0.07–0.20; Table 1), in part because of the low number of seedlings in many of the quadrats. As a result, the response variable (the observed proportion of seedlings surviving) was often either 0 or 1. In the case of older seedlings of *A. platanoides* and *A. saccharum*, and first-year seedlings of *F. americana*, the differences in AIC_c with the *null model* were < 2 units, and therefore do not provide strong support for an effect of *A. platanoides* trees on the survival of these species and age classes. For survival of first-year *A. platanoides* seedlings, however, the neighbourhood effects of conspecific adults were strongly negative (negative value of the parameter a in the *linear model*; see Appendix S1), with the survival of first-year *A. platanoides* seedlings decreasing by 35–40% at the highest levels of the neighbourhood index (NI) (Fig. 2a).

The Weibull function (eqn 4) provided a better description than the lognormal function of the neighbourhood effects of *A. platanoides* on the survival of first-year conspecific seedlings (Table 1). The value of the α parameter in the Weibull function was close to two (Appendix S1), indicating that neighbourhood effects scaled roughly with canopy tree

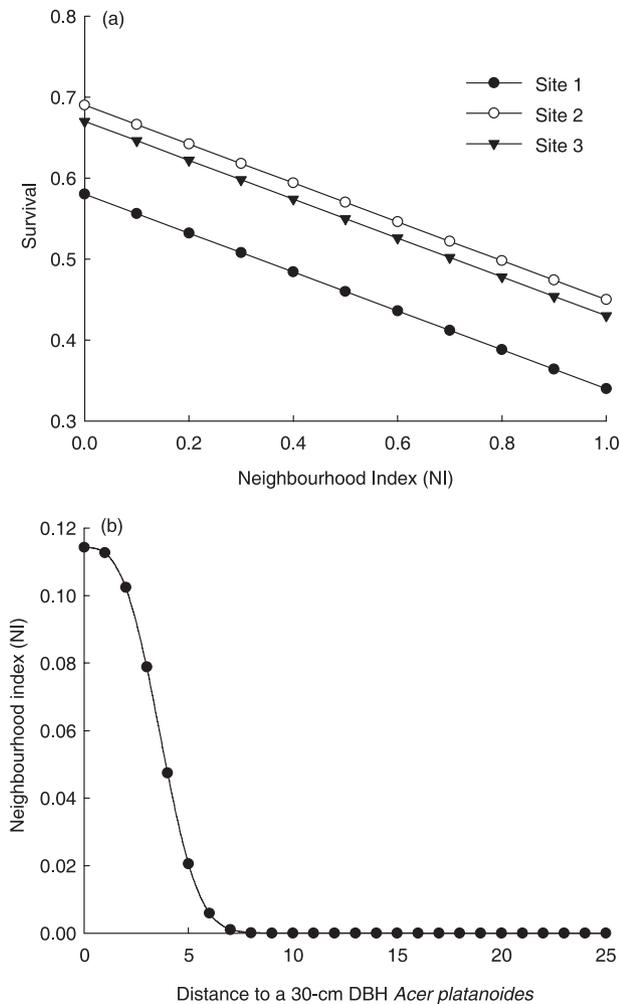


Fig. 2. (a) Predicted survival of first-year *Acer platanoides* seedlings as a function of the neighbourhood index (NI) using the most parsimonious model and parameters given in Appendix S1. Values of the neighbourhood index of 1 represent the neighbourhoods in the data set with the highest observed value of NI. (b) Predicted change in the neighbourhood index (NI) for survival of first-year *Acer platanoides* seedlings as a function of the distance to a 30-cm d.b.h. *Acer platanoides* using the most parsimonious model and parameters given in Appendix S1.

biomass (i.e. DBH^2). The parameters β and γ control the magnitude of the decline in effect of an *A. platanoides* neighbour with distance from a seedling quadrat. The ‘footprint’ of the effect of *A. platanoides* canopy trees on survival of first-year conspecific seedlings was strongly sigmoidal (i.e. $\beta > 1$; Appendix S1) and highly localized (Fig. 2b). For example, for a 30-cm d.b.h. *A. platanoides*, neighbourhood effects on first-year conspecific seedling survival were restricted to the first 5 m from the trunk (Fig. 2b).

EFFECTS OF ACER PLATANOIDES ON SEEDLING GROWTH

For the four seedling species, the *null model* ignoring the effect of *A. platanoides* on seedling relative height and diameter had

much poorer AIC_c scores than at least one of the models that included neighbourhood effects of the invader (Table 2). The most parsimonious model was in all cases the *linear model*, providing reasonably good fits for most analyses ($R^2 = 0.24\text{--}0.49$; Table 2). The neighbourhood effects of *A. platanoides* on seedling relative height and diameter were always positive for all four species, as indicated by positive values of the parameter a (slope of the regression in the linear model; see Appendix S2). Thus, seedling relative height increased linearly with the increasing value of the NI for all four seedling species (Fig. 3a). The predicted increase for relative height at the maximum NI was greatest for *F. americana* (93–111%), followed by *P. serotina* (73–89%), *A. platanoides* (53–60%), and *A. saccharum* (32–26%). When the among-species comparison was based on relative diameter, *P. serotina* benefited the most from the presence of *A. platanoides* (90–130% increase), followed by *F. americana* (71–80% increase) and *A. platanoides* (60–68% increase). *A. saccharum* again showed the smallest response to abundance of *A. platanoides* in the immediate neighbourhood (45–53% increase; Fig. 3b).

The *lognormal function* (Eqn 5) provided the best fit of the effect of neighbouring *A. platanoides* trees on seedling relative height of the two maples, whereas the *Weibull function* (Eqn 4) provided a better fit for *F. americana* and *P. serotina* seedlings (Table 2). The exponent α had values *c.* 2 for *A. platanoides*, *A. saccharum* and *F. americana*, indicating that the effect of *A. platanoides* on seedling relative height scaled with biomass of the neighbouring canopy trees (Appendix S2). For *P. serotina*, α was considerably > 2 , indicating that larger *A. platanoides* trees had disproportionately bigger effects on seedling height. The decrease with distance of the effect of *A. platanoides* on seedling relative height declined much more gradually for *F. americana* and *P. serotina* (i.e. within 20–25 m) than for *A. platanoides* (i.e. within 10–15 m) and particularly for *A. saccharum* (i.e. within 5–10 m; Fig. 4a). Moreover, for *F. americana* and *P. serotina* seedlings, the shape of the footprint had a shoulder (i.e. $\beta > 1$ in the *Weibull function*; Appendix S2) within the first 5 m from the trunk, whereas for the two maples the footprint had a peak within 1 m from the trunk (i.e. $\beta < 1$ in the *lognormal function*; Appendix S2) and decreased very steeply with distance. The *lognormal* was also the functional form that best described the neighbourhood effects of *A. platanoides* on the relative diameter of conspecific seedlings, whereas the *Weibull function* provided a better fit for the three native species (Table 2). The footprint of the effects of *A. platanoides* trees on relative diameter mirrored the footprint on relative height: rapid decrease with distance for *A. saccharum*, intermediate decline with distance for *A. platanoides*, and much slower declines with distance for *F. americana* and *P. serotina* (Fig. 4b).

COMPARISON OF ACER PLATANOIDES VS. NATIVE SPECIES EFFECTS ON SEEDLING SURVIVAL AND GROWTH

Our approach allowed us to calculate a matrix of species-specific indexes (λ_s) to compare the effects of *A. platanoides*

Table 2. Comparison of alternate models analysing the effect of *Acer platanoides* trees on the relative height and diameter of older seedlings of the four study species. The most parsimonious model (indicated in bold) is the one with the lowest AIC_c. NP = number of parameters. NI indicates the functional form of the neighbourhood index that provided the best fit for each model (WBL, Weibull; LGN, lognormal). The goodness of fit (R^2) is given for the best model. ACPL, *Acer platanoides*; ACSA, *Acer saccharum*; FRAM, *Fraxinus americana*; PRSE, *Prunus serotina*. $n = 132$ for ACPL, $n = 103$ for ACSA, $n = 81$ for FRAM, and $n = 98$ for PRSE

Species	Model	NP	Relative height			Relative diameter		
			NI	AIC _c	R^2	NI	AIC _c	R^2
ACPL	Null	4		335.91			511.61	
	Linear	8	LGN	319.61	0.26	LGN	481.97	0.40
	Logistic	10	WBL	320.68		WBL	489.31	
	Exponential	9	LGN	323.76		WBL	492.17	
ACSA	Null	4		269.88			375.76	
	Linear	8	LGN	247.71	0.34	WBL	368.05	0.38
	Logistic	10	LGN	251.60		LGN	369.98	
	Exponential	9	LGN	250.45		LGN	370.49	
FRAM	Null	4		168.40			281.79	
	Linear	8	WBL	134.05	0.49	WBL	259.66	0.44
	Logistic	10	WBL	137.38		LGN	265.78	
	Exponential	9	WBL	134.97		WBL	264.39	
PRSE	Null	4		213.33			319.30	
	Linear	8	WBL	206.88	0.24	WBL	307.45	0.38
	Logistic	10	LGN	212.29		LGN	328.02	
	Exponential	9	LGN	207.73		LGN	308.58	

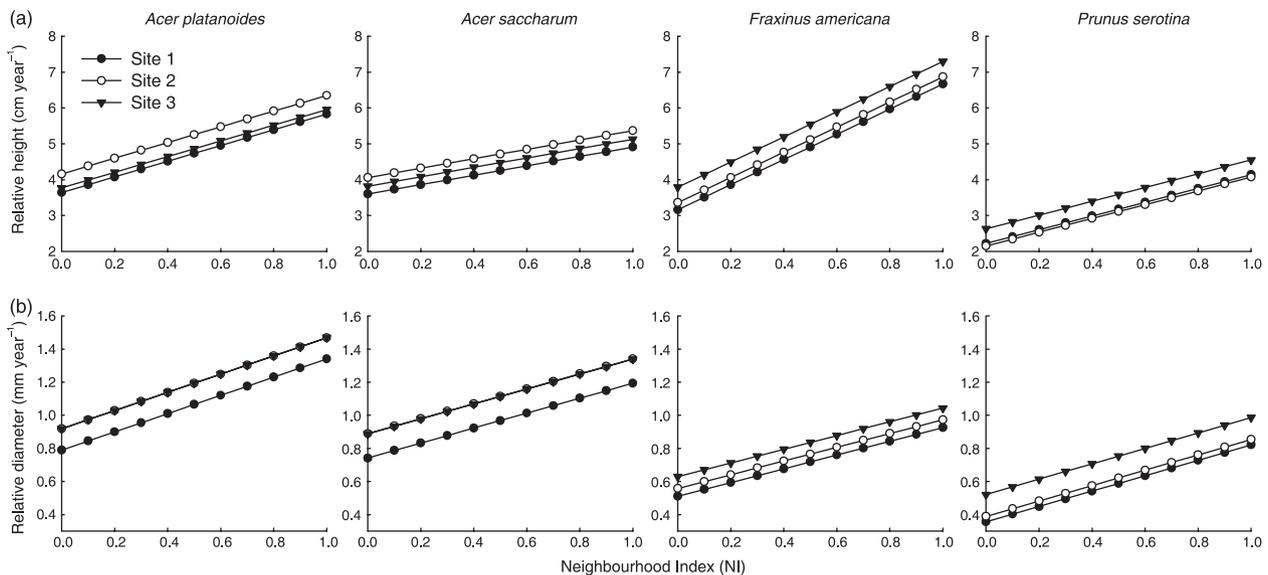


Fig. 3. Predicted (a) seedling relative height and (b) seedling relative diameter as a function of the neighbourhood index (NI) using the most parsimonious models and parameters given in Appendix S2. Values of the neighbourhood index of 1 represent the neighbourhoods in the data set with the highest observed value of NI.

trees on seedling survival and growth with the effects of the three native tree species. *A. platanoides* had negative λ values for survival of conspecific seedlings (both first-year and older seedlings), whereas the three native tree species had positive λ for *A. platanoides* seedling survival (Table 3). All three native species also had negative λ values on conspecific seedling survival. For seedling relative height and diameter, *A. platanoides*

was the species with the largest λ in all cases but one (i.e. relative height of conspecific seedlings; Table 3), indicating a stronger effect on seedling growth than any of the natives. The λ values for *A. platanoides* effects on seedling growth were positive for both conspecific and native seedlings. Among the three native species, *A. saccharum* was in most cases the species with the lowest λ values.

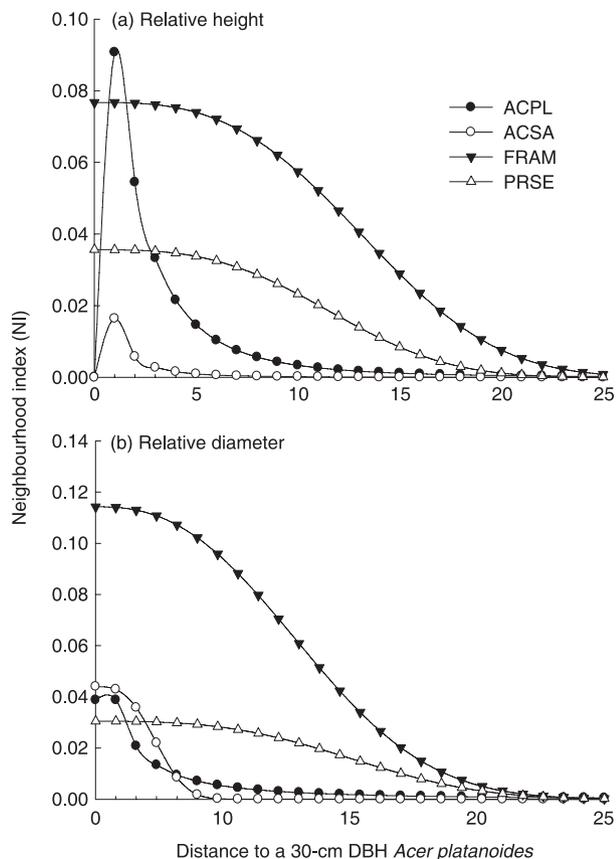


Fig. 4. Predicted variation in the neighbourhood index (NI) for (a) seedling relative height and (b) seedling relative diameter as a function of the distance to a 30-cm d.b.h. *Acer platanoides* using the most parsimonious models and parameters given in Appendix S2. ACPL, *Acer platanoides*; ACSA, *Acer saccharum*; FRAM, *Fraxinus americana*; PRSE, *Prunus serotina*.

RELATIONSHIPS AMONG SEEDLING PERFORMANCE AND ECOSYSTEM PROPERTIES

No significant correlations were found between ecosystem properties (i.e. soil properties and light levels) and seedling survival for any tree species ($P > 0.05$ in all cases, Spearman rank correlations). In contrast, very significant correlations were found between several soil properties and seedling relative height and diameter (Table 4). The strongest positive correlations for growth measurements (for all four species) were with soil exchangeable Ca ($r = 0.42\text{--}0.60$), followed by nitrification ($r = 0.25\text{--}0.41$), NO_3^- ($r = 0.21\text{--}0.41$), and exchangeable Mg ($r = 0.25\text{--}0.39$). pH was also positively correlated with seedling relative height and diameter in most cases (Table 4). The remainder of the soil properties only showed significant correlations with seedling growth in limited cases. When significant, the correlations were positive for forest floor depth, litter depth, microbial N, N mineralization, and Ca mineralization, but negative for total C and C:N ratios (Table 4). Light levels (i.e. GLI) were never correlated with relative height, and only weakly correlated with relative diameter for *A. platanoides* and *A. saccharum* (Table 4).

Discussion

EFFECTS OF *ACER PLATANOIDES* ON SEEDLING SURVIVAL AND GROWTH

Our results show that the invasive tree *A. platanoides* has distinctive effects on survival and growth of both conspecific and native tree seedlings in north-eastern forests, with the sign of the effects varying from negative to strongly positive. Whereas the presence of *A. platanoides* trees in the immediate neighbourhood (0–25 m) decreased survival of 1-year-old conspecific seedlings, it consistently increased seedling growth (in height and diameter) of both conspecific and native seedlings. Moreover, the fact that the linear model provided in all cases the most parsimonious fit for these effects suggests an absence of density thresholds for the appearance of invasive impacts, with even low *A. platanoides* abundance having detectable effects on the demography of tree seedlings at our study sites. We recognize that our comparative approach is essentially based on correlations, and does not have the power of an experimental manipulation in unambiguously demonstrating a mechanistic link between the distribution of invasive species and seedling demography. However, it has the strength of providing a simple framework that integrates the myriad ways that native and introduced species interact under natural conditions, improving our understanding of the net effects of invasive species on community dynamics.

The negative effects of *A. platanoides* trees on first-year conspecific seedling survival were of intermediate magnitude (i.e. maximum decrease of 35–40%), and are unlikely to have an abiotic explanation. The lack of correlation between *A. platanoides* seedling survival and soil variables, and the fact that water is rarely an important limiting factor in these forests (Kobe 1996; Caspersen *et al.* 1999), argues against modification of soil resources as the underlying mechanism of survival patterns. Similarly, the lack of correlation between GLI and *A. platanoides* seedling survival and between GLI and the neighbourhood index (NI), together with the fact that *A. platanoides* seedlings are very shade tolerant (Martin & Marks 2006; Reinhart *et al.* 2006), suggests that the alteration of understorey light levels cannot explain the negative effects on conspecific survival. However, the fact that first-year conspecific seedlings were negatively affected by *A. platanoides* trees (i.e. $\lambda < 0$; Table 3) but not by any native species (i.e. $\lambda \geq 0$) could indicate the existence of negative distance- and/or density-dependent processes from conspecifics due to host-specialized herbivores, parasites or pathogens (e.g. Janzen-Connell effects; Janzen 1970; Connell 1971). This hypothesis is supported by the results of Reinhart & Callaway (2004), who found that biomass of 1-year-old *A. platanoides* seedlings was greater when seedlings grew in sterilized soils collected under conspecific trees than when grown in non-sterilized conspecific soils, suggesting the accumulation of inhibitory soil biota under *A. platanoides* adults. The weaker support for a negative effect of *A. platanoides* on older conspecific seedling survival than on 1-year-old seedling survival could result from an increase in the resistance to species-specific enemies

Table 3. Species-specific effects index (λ_{ji} parameter in eqns 6 and 7) representing the relative effects of neighbouring trees of the species j on survival and growth of seedlings of the species i . Two-unit support intervals are also reported, in parentheses. ACPL, *Acer platanoides*; ACSA, *Acer saccharum*; FRAM, *Fraxinus americana*; PRSE, *Prunus serotina*

Variable	On ...	Effect of ...			
		ACPL	ACSA	FRAM	PRSE
Survival	ACPL _{First-year}	-0.18 (-0.33 to -0.05)	0.10 (-0.14 to 0.19)	0.11 (-0.15 to 0.22)	0.49 (0.30 to 1)
	ACPL _{Older}	-0.10 (-0.33 to 0.15)	0.05 (-0.17 to 0.09)	1 (0.72 to 1)	0.70 (0.32 to 1)
	ACSA _{Older}	0.46 (0.26 to 1)	-1 (-1 to -0.60)	-0.22 (-0.45 to -0.04)	-0.90 (-1 to -0.82)
	FRAM _{First-year}	1 (0.45 to 1)	-0.04 (-0.06 to 0.01)	-1 (-1 to -0.68)	-0.85 (-1 to -0.58)
	PRSE _{First-year}	0.41 (0.24 to 0.62)	0.24 (0.12 to 0.38)	1 (0.81 to 1)	-1 (-1 to -0.82)
	PRSE _{Older}	-0.03 (-0.23 to 0.11)	-0.07 (-0.15 to 0.10)	1 (0.72 to 1)	-0.75 (-0.96 to -0.53)
Relative height	ACPL	0.48 (0.24 to 0.56)	-0.36 (-0.39 to -0.33)	0.72 (0.57 to 0.88)	1 (0.82 to 1)
	ACSA	1 (0.76 to 1)	0.19 (0.01 to 0.41)	0.32 (0.12 to 0.54)	0.46 (0.17 to 0.74)
	FRAM	1 (0.61 to 1)	0.05 (-0.06 to 0.12)	0.24 (0.18 to 0.31)	0.30 (0.21 to 0.35)
	PRSE	1 (0.74 to 1)	0.39 (0.21 to 0.47)	0.48 (0.34 to 0.62)	0.65 (0.60 to 0.71)
Relative diameter	ACPL	1 (0.57 to 1)	-1 (-1 to -0.67)	-0.06 (-0.35 to 0.22)	0.01 (-0.38 to 0.37)
	ACSA	0.95 (0.55 to 1)	0.06 (-0.35 to 0.28)	0.19 (0.04 to 0.42)	-0.11 (-0.24 to 0.16)
	FRAM	1 (0.66 to 1)	-0.34 (-0.52 to -0.16)	-0.09 (-0.12 to 0.16)	0.15 (0.03 to 0.27)
	PRSE	1 (0.75 to 1)	0.36 (0.15 to 0.59)	0.47 (0.24 to 0.78)	0.49 (0.23 to 0.80)

Table 4. Pearson product-moment correlation coefficients for the relationships among ecosystem properties and seedling relative height and diameter. Significant correlations are shown in bold. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

	ACPL		ACSA		FRAM		PRSE	
	Height	Diameter	Height	Diameter	Height	Diameter	Height	Diameter
Soil properties								
Moisture	-0.06	-0.09	-0.02	-0.04	0.06	-0.14	0.26*	0.32**
Bulk density	-0.06	0.09	-0.09	0.01	-0.01	0.21	-0.18	-0.22
Forest floor depth	-0.11	0.12	-0.03	0.34**	0.04	0.08	0.31**	0.44***
Litter depth	-0.01	0.18	0.16	0.10	0.09	0.25	0.40***	0.19
pH	0.49****	0.26**	0.46****	0.16	0.31*	0.32*	0.19	0.14
Extractable Ca	0.52****	0.42****	0.60****	0.42***	0.59****	0.43***	0.45***	0.45***
Extractable Mg	0.38***	0.35***	0.39***	0.29**	0.33**	0.25*	0.39**	0.38**
Extractable K	0.04	0.14	0.01	0.06	0.11	0.08	0.17	0.15
Ca Mineralization	0.07	0.17	0.19	0.14	0.23	0.34**	0.17	0.19
Total C	-0.24*	-0.24*	-0.25*	-0.14	-0.17	-0.17	-0.05	-0.02
Total N	-0.09	-0.23	-0.07	-0.15	-0.10	-0.19	-0.02	-0.03
C:N ratio	-0.33***	-0.04	-0.44***	-0.10	-0.17	0.01	-0.03	0.03
NO ₃ ⁻	0.21*	0.36***	0.32**	0.39***	0.41***	0.35**	0.40***	0.34**
NH ₄ ⁺	0.13	-0.03	0.07	-0.04	0.01	-0.14	-0.01	-0.01
Microbial C	0.05	-0.03	0.10	0.02	0.02	-0.20	0.13	0.11
Microbial N	0.21*	0.01	0.22*	0.17	0.02	0.12	0.14	0.23
N _{min}	0.35***	0.36***	0.17	0.14	0.07	0.03	0.14	0.34**
Nitrification	0.35***	0.25*	0.40***	0.33**	0.41***	0.27*	0.40***	0.39**
Respiration	0.02	-0.03	0.08	-0.06	0.02	-0.16	0.11	0.23
Light	0.14	0.28*	0.10	0.27*	0.13	0.06	-0.02	0.12

through ontogeny (i.e. Packer & Clay 2003). Interestingly, trees of the three native species also had stronger negative effects on conspecific seedling survival than heterospecific trees (as indicated by $\lambda = -1$; Table 3). These results affirm the seminal studies conducted with *P. serotina* (e.g. Packer & Clay 2000, 2003; Reinhart *et al.* 2003) in suggesting that Janzen-Connell effects could be more important in temperate forests than previously thought.

Acer platanoides had a consistently positive effect on seedling growth of all four species, because all seedlings grew faster (both in diameter and height) in neighbourhoods with *A. platanoides* than in neighbourhoods containing only native species. Moreover, the highly significant correlations between seedling relative height and diameter and soil resources suggest that the positive effect of *A. platanoides* on growth could be to a large extent the consequence of the increases in soil fertility caused by the invader (Gómez-Aparicio & Canham 2008). In fact, the strongest correlations between relative height and diameter and soil properties were with Ca, nitrate and nitrification, followed by Mg and pH; these are the same soil properties identified by Gómez-Aparicio & Canham (2008) as the most strongly affected by the presence of *A. platanoides* trees. Even though light is probably the key limiting resource in the understorey of temperate forests (Canham 1988; Kobe *et al.* 1995; Pacala *et al.* 1996), fertilization experiments have shown that soil nutrients, especially Ca and N, can also limit seedling and sapling growth in these systems (Kobe *et al.* 2002; Juice *et al.* 2006; Bigelow & Canham 2007). Observational studies point in the same direction. For example, Walters & Reich (1996) found that soil N mineralization and especially nitrification were strongly positively correlated with growth of *A. saccharum* seedlings, concluding that low nitrate along with light may limit *A. saccharum* growth in forest understoreys of northern Wisconsin. The results of this study, together with those reported previously by Gómez-Aparicio & Canham (2008), indicate that *A. platanoides* trees modify ecosystem processes by increasing soil fertility, and that these ecosystem transformations translate into increased growth rates of tree seedlings at the neighbourhood scale. Interestingly, although the impacts of *A. platanoides* trees on several soil properties (e.g. Ca, Mg, K) have been shown to vary among sites and to increase with soil fertility (Gómez-Aparicio & Canham 2008), site-dependent effects on seedling growth were not detected in this study. This result is presumably influenced by the fact that seedling growth was not affected by a single soil property but by several nutrients (e.g. N, Ca) that vary independently from one another across the study area (Bigelow & Canham 2002).

The positive effects of *A. platanoides* on the native seedling community reported here seem to be at odds with the negative effects reported in previous studies (Martin 1999; Fang 2005). Such discrepancies among studies could be influenced by differences in site characteristics, stages of invasion, or community composition. In addition, a further explanation may be the fact that previous studies were based on observations of seedling richness and abundance, rather than seedling performance and demography. Patterns of seedling abundance

can provide useful insights into the nature of interactions between invasive and native species, but they can also be affected by confounding factors (e.g. seed availability and the spatial distribution of adults of the native species) and should be interpreted cautiously. For example, even in the absence of any kind of interaction between *A. platanoides* trees and native seedlings, lower richness and/or abundance of native seedlings could be expected in neighbourhoods dominated by *A. platanoides* simply because of spatial constraints inherent to closed-canopy forests. That is, as the abundance of *A. platanoides* increases in a neighbourhood, the local abundance of native canopy trees necessarily declines. As a result, there may be less seed input of native species due to the limited dispersal that characterizes native tree species in these forests (Ribbens *et al.* 1994). As pointed out by Fridley *et al.* (2004), failure to consider the patterns produced by null models (e.g. absence of interaction) can lead to mistakenly interpreting neutral processes as reflections of species interactions or other ecological processes.

POSITIVE AND NEGATIVE FEEDBACKS DURING THE PROCESS OF INVASION

Positive feedbacks in which the impacts of exotic species on ecosystem processes favour the performance of conspecific seedlings and saplings have been suggested as a mechanism contributing to the success of invasive species (Ehrenfeld 2003). Our measurements of seedling growth support this hypothesis. When the effect of *A. platanoides* and native trees on the growth of *A. platanoides* seedlings was compared using the species-specific index (i.e. λ parameter; Table 3), the invader had by far the largest positive values, indicating that *A. platanoides* seedlings grow better under conspecific than under heterospecific trees. This result agrees with the fact that *A. platanoides* has been shown to have a larger positive effect on soil fertility than dominant native species (Gómez-Aparicio & Canham 2008), with its seedlings benefiting from the differential ability of conspecific trees to increase soil nutrient pools and turnover rates.

However, the fact that survival of 1-year-old *A. platanoides* seedlings was negatively influenced by the presence of conspecific trees indicates that negative feedbacks can also operate during the process of invasion. In the case of *A. platanoides*, there are reasons to believe that the positive feedbacks on seedling growth will outweigh the negative feedbacks on first-year seedling survival. Growth early in life is an important driver of successional dynamics in these forests (Pacala *et al.* 1996), because it represents an integrated measure of whole-plant carbon balance, which ultimately determines survival (Kobe *et al.* 1995). Under the influence of *A. platanoides* trees, conspecific seedlings had heights and diameters 50–70% larger than conspecific seedlings in native neighbourhoods. This positive effect could confer on surviving *A. platanoides* seedlings in conspecific neighbourhoods a greater ability to outgrow competitors and reach the canopy level, closing a feedback loop in which more adults will benefit future seedlings. Furthermore, given the abundant seed production of

the species and the extraordinarily high densities of older seedlings found at our study sites (i.e. 100 seedlings m⁻²), it is unlikely that moderate mortality levels of first-year seedlings due to negative feedbacks limit *A. platanooides* population growth. In fact, older seedling density of *A. platanooides* exceeded that of *A. saccharum* by 3-fold, of *F. americana* by 4.5-fold, and of *P. serotina* by 6-fold. Moreover, the negative feedback on survival was much more localized than the positive feedback on growth, being mainly restricted to the area below the canopy of adult trees (i.e. first 4–5 m from the trunk), where the highest densities of 1-year-old *A. platanooides* seedlings occurred. As a proviso, we note that survival data must be interpreted cautiously, because they were collected during a short period of time (2004–06) and therefore may not be representative of longer-term dynamics. Overall, our results support the importance of canopy-seedling feedbacks as a mechanism regulating the rate of invasion in native forests. However, they also indicate that the net consequences of the feedbacks for the process of invasion might be determined by the balance of positive and negative feedbacks acting at the same time on different aspects of regeneration (i.e. survival vs. growth).

IMPLICATIONS FOR THE COMPOSITION AND DYNAMICS OF INVADED FORESTS

Our study sites constitute examples of northern hardwood forests in North America where late-successional communities are often dominated by *A. saccharum*. Therefore, understanding the mechanisms by which the invasion by the shade-tolerant *A. platanooides* could ultimately change patterns of dominance in these forests requires comparing the differential effects of the invader on regeneration dynamics of the two congeners. Our results indicate that although *A. saccharum* seedlings benefited from the presence of *A. platanooides* trees, presumably due to its effects on soil fertility, the magnitude of the positive effect was much lower than for *A. platanooides* seedlings. When we add this result to the fact that *A. platanooides* had higher inherent growth rates and higher seedling densities than *A. saccharum*, we predict that positive feedbacks (in which *A. platanooides* trees promote conspecific seedling growth to a greater degree than *A. saccharum* growth) will accelerate rates of invasion, by magnifying differences in competitive ability between the invader and the native. This type of positive feedback in forests invaded by *A. platanooides* has been previously reported in the western USA (Reinhart *et al.* 2005, 2006), but with a different mechanistic basis. Whereas in the western USA, with a comparatively shade-intolerant flora, disparities in light requirements mediated the differential response of native and invasive species to the presence of *A. platanooides*, differences in the use of soil resources seem to underlie the species-specific responses observed in our study. These results indicate that the impact of invasive species and the mechanisms of invasion can be highly context-specific.

An important result of this study is that the strongest positive effects of *A. platanooides* trees on seedling growth were not on either of the two maple species, but on the early succes-

sional species *F. americana* and *P. serotina*. The strong response of *F. americana* and *P. serotina* to the presence of *A. platanooides* is reflected not only in the larger magnitude of neighbourhood effects, but also by its greater spatial extent. Thus, whereas the effect of a 30-cm d.b.h. *A. platanooides* on seedling growth of the two maples had a peak close to the trunk and decreased steeply with distance within 15 m, the effect on *F. americana* and *P. serotina* seedlings had a shoulder in the first 5 m from the trunk and decreased slowly, tending to zero in 20–25 m. Fast-growing species are usually considered to be more plastic in their response to environmental changes and more able to capitalize on increases in resource availability than comparatively slow-growing species (Grime 1979; Aerts & Chapin 2000). This may explain why *F. americana* and *P. serotina*, the two species with the highest inherent growth rates, showed the largest responsiveness to the ‘fertilizing’ effect of *A. platanooides*. This result has important implications for the alteration of the competitive hierarchy of the native community. It implies that the invasion of north-eastern forests by *A. platanooides* may well benefit the native species that are more competitive under nutrient-rich conditions. Thus, *F. americana* and *P. serotina* may be favoured at the expense of *Quercus rubra* and *Acer rubrum* within the early successional species, and *A. saccharum* may be favoured at the expense of *Fagus americana* and *Tsuga canadensis* within the late-successional community. Moreover, the few available studies on the impacts of other invasive woody species in temperate forests (i.e. *Berberis thunbergii*, Ehrenfeld *et al.* 2001; *Ailanthus altissima*, Gómez-Aparicio & Canham 2008) suggest that increases in soil fertility could be a common consequence of invasion in these systems. Whether this leads, in the long term, to canopy dominance by native and introduced species associated with fertile soils remains to be seen.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Parameter estimates and support intervals for the most likely survival models.

Appendix S2. Parameter estimates and support intervals for the most likely growth models.

Appendix S3. Executable programs and source code used for fitting models for growth and survival.

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