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NEIGHBORHOOD MODELS OF THE EFFECTS OF INVASIVE TREE SPECIES ON ECOSYSTEM PROCESSES

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Abstract. Changes in the composition of a community due to the invasion by exotic plant species can lead to modification of ecosystem function that, in turn, produces feedbacks that drive further changes in community composition. The development of predictive models of this process requires an understanding of the spatial extent of the impacts of the exotic species, particularly during early stages of invasion. The main objective of this study was to characterize the neighborhood dynamics of ecosystem transformations by the invasive tree species Norway maple (*Acer platanoides* L.) and tree of heaven (*Ailanthus altissima* Mill.) in temperate forests of the northeastern United States. By using a neighborhood approach in multiple sites, we sought to determine (1) the magnitude and spatial extent of the effects of the two invasive species on soil properties and processes; (2) whether the effects of the invasive species were site dependent; and (3) the differences in the effects of invasive versus native tree species on ecosystem processes.

Our results showed that Norway maple and tree of heaven alter the functioning of temperate forest ecosystems even at relatively low densities by increasing cycling rates (i.e., net N mineralization, net nitrification, Ca mineralization) and nutrient availability (i.e., pH, Ca, Mg, K, N). At the neighborhood scale, the spatial extent of the impact of the two species varied strikingly among soil properties. Moreover, the neighborhood effects of the two invasive species were site dependent, with the magnitude of the impact increasing with soil fertility. At the community level, Norway maple and to a lesser extent tree of heaven had stronger effect on soils than any of the dominant native tree species considered. We conclude that the invasion of northeastern forests by Norway maple and tree of heaven is characterized by predictable, neighborhood-specific acceleration of nutrient cycling rates and localized increases in nutrient pools. These ecosystem alterations have enormous potential for the modification of competitive hierarchies in forest communities. In particular, Norway maple and tree of heaven may change relative abundances within the native community to the benefit of native species that are more competitive on nutrient rich sites.

Key words: Acer platanoides; Ailanthus altissima; *ecosystem processes; exotic species; forest dynamics; neighborhood processes; site dependency; soil properties; spatially explicit models; temperate forests.*

INTRODUCTION

Extensive research has shown that plant effects on soil properties and ecosystem processes are species specific (Zinke 1962, Binkley and Giardina 1998, Finzi et al. 1998*a*, *b*, Ehrenfeld et al. 2001, Lovett et al. 2004, Reich et al. 2005). As a consequence, changes in the composition of a plant community due to natural or anthropogenic causes can lead to modification of ecosystem processes that, in turn, produce feedbacks that drive further changes in community composition (Ehrenfeld et al. 2005). This issue is particularly important in the field of invasion ecology, since the introduction of new species can lead to potentially new, species-specific effects on ecosystem processes (Vitousek 1990, Levine et al. 2003, Dukes and Mooney 2004). In fact, recent research has shown that invasive species have the potential to modify many soil properties, including soil pH and cation availability (Belnap and Phillips 2001, Ehrenfeld et al. 2001), N and C dynamics (Evans et al. 2001, Hughes and Denslow 2005), and microbial community structure and function (Kourtev et al. 2002, Wolfe and Klironomos 2005). An important bias of many of these studies is that they have focused on highly invaded areas, where the invasive species often represent a significant fraction of total plant biomass. In contrast, there is relatively little information on transformation of ecosystem processes during the early stages of invasion, and whether these changes accelerate or retard further invasion.

A central topic of study within the ecology of biological invasions has been the understanding of why plant communities differ in their susceptibility to invasion (i.e., invasibility; Davis et al. 2000, Richardson and Pysek 2006). Numerous studies have shown that

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high levels of soil resources promote the invasibility of a site (see Davis et al. 2000). On the contrary, only a few studies have explored whether, once established, the impacts of invasive species on ecosystem processes also vary among sites (e.g., Stock et al. 1995, Vilá et al. 2006). If high soil resource availability also increases the intensity of the impact of exotics on ecosystem function, then the effects of invasive species would have a high degree of site dependency, with the highest impacts occurring in fertile sites due to the generation of feedbacks loops in which invasives themselves increase nutrient availability. Moreover, if this process has a positive feedback on the rate of spread of the invaders, a transformation of ecosystem properties to conditions more favorable to invasive conspecifics would represent a potential mechanistic explanation for the "lag phase" (Hobbs and Humphries 1995, Sax and Brown 2000) common between establishment of exotic species and actual invasion outbreaks.

An approach frequently used for the study of species effects on ecosystem processes is the comparison of the average effects of different species at the plot level, typically from common garden studies or comparisons of stands dominated by different species (Binkley and Giardina 1998). Although these studies have provided significant contributions to our understanding of plant–soil interactions, their results are not always easy to extrapolate to natural ecosystems, where plants grow intermingled with each other and a unit of soil is affected by multiple species simultaneously (Ehrenfeld et al. 2005). For example, in mixed forests, the dominant ecosystem fluxes driven by canopy trees (e.g., throughfall, litterfall, nutrient uptake) are primarily vertical rather than horizontal, and the tree identities overhead and nearby have distinctive effects on a whole host of ecosystem processes at the "neighborhood" scale (0–25 m; Binkley and Giardina 1998, Finzi et al. 1998*a*, *b*). As a consequence, effects of invasive species on ecosystem processes in mixed forests may be very patchy and highly dependent on the spatial distribution of both native and exotic tree species. Neighborhood models (Canham and Uriarte 2006) offer an approach to the spatially explicit study of the ecosystem effects of invasive tree species in forests. These models have been frequently applied to the study of population dynamics and interactions among sessile organisms, particularly plants (e.g., Uriarte et al. 2004), but there is a wide potential use of this approach for the study of any ecosystem process where the spatial configuration of organisms plays a central role. The approach typically sacrifices mechanistic detail in favor of more phenomenological characterization of the effects of the size and spatial distribution of organisms on ecosystem processes. The simpler structure of these more phenomenological models, in turn, allows a more robust linkage to models of long-term community dynamics (Canham and Pacala 1994).

The main objective of this study was to characterize the neighborhood dynamics of ecosystem transformations by two important invasive tree species in temperate forests of the northeastern United States: Norway maple (*Acer platanoides* L.) and tree of heaven (*Ailanthus altissima* Mill.). Although the abundance of both species has increased steadily since their introduction in the late 1800s (Hu 1979, Nowak and Rowntree 1990), they are rarely dominant in stands outside of urban areas. By using a neighborhood approach in multiple sites, we sought to determine (1) the magnitude and spatial extent of the effects of individuals of each of the two invasive species on an array of soil properties, (2) whether the effects of the invasive tree species were site dependent, and (3) the relative magnitude of the differences in the effects of invasive versus native tree species on forest ecosystem processes.

Material and Methods

Study species and sites

Norway maple was introduced to North America from Europe in 1756 (Nowak and Rowntree 1990). It has a shade tolerance comparable to American beech (*Fagus grandifolia* Ehrh.), prolific seed production, rapid growth, and tolerance of a broad range of environmental stresses (Santamour and McArdle 1982, Kloeppel and Abrams 1995). It is found across a broad climatic spectrum in its native range and occurs over more than half of the United States. It can establish and become abundant not only in open, disturbed areas but also in intact forests, having striking effects on the structure and species richness of the native understory community (Martin 1999).

Tree of heaven was introduced from China in 1784 (Hu 1979). It produces very large numbers of wind-dispersed seeds, grows quickly in high light, and can reproduce asexually via root sprouts (Hu 1979). Its roots, stems, and leaves are rich in secondary compounds (Heisey 1996). Although early studies considered it shade intolerant and unable to invade closed forests, recent studies show that it can establish in intact forests when canopy gaps open (Kowarik 1995, Knapp and Canham 2000). It can reach mature size during a single period of release in a treefall gap, while most native species need several periods (Knapp and Canham 2000).

Our research was conducted at six sites in Litchfield County, northwestern Connecticut, USA, three of which are being invaded by Norway maple and three invaded by tree of heaven. The three Norway maple sites (Sites 1, 2 and 3) are located near the village of Norfolk (42° N, 73°15′ W), roughly 1 km apart from each other. The three tree of heaven sites are about 20 km apart, one located near the village of Amesville (Site 4, 41°58′ N, 73°27′ W), the second located in the Dark Entry Forest near the village of Kent (Site 5, 41°49′ N, 73°23′ W), and the third one located in the village of New Milford (Site 6, 41°36′ N, 73°25′ W). All six sites are at elevations of 300–500 m. Soils at the three Norway maple sites and at one of the tree of heaven sites (Site 5) are Typic Dystrochrepts derived from glacial till over mica–schist bedrocks, whereas soils at the other two tree of heaven sites (Sites 4 and 6) are Dystric Eutrochrepts derived from calcareous glacial outwash over limestone bedrocks (Hill et al. 1980). All sites are in second-growth (80–130 yr) stands 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 northeastern United States and Canada. The main canopy native tree species are sugar maple (*Acer saccharum* L.), white ash (*Fraxinus americana* L.), northern red oak (*Quercus rubra* L.), and black cherry (*Prunus serotina* Ehrh.). The six sites varied in relative basal area of the invasive tree species, ranging between 5.3% and 14.3% for Norway maple and between 8.4% and 32.3% for tree of heaven (Appendix A).

Field and lab methods

We selected 30 sampling locations in each site for measurements of soil properties ($n = 180$). The sampling locations were stratified by the abundance of the invasive tree species (Norway maple or tree of heaven) within the immediate neighborhood. For the characterization of local neighborhoods, we identified and mapped each tree with a diameter at breast height (dbh) $\geq$2 cm within a 25 m radius of each sampling location ($n = 6434$ trees), using a laser rangefinder with a digital compass (Laser Technology, Englewood, Colorado, USA). 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 × 15 cm depth soil core (organic plus mineral soil). We did not sample mineral and organic soils separately because the organic horizon was always relatively thin (i.e., <4 cm), or nonexistent in some cases. The depth of the forest floor was measured in situ as the average of four measurements per sampling location. Samples were obtained using a soil bulk density sampler and brought back to the laboratory in a cooler. All six sites were sampled within the last two weeks of July 2005. In late August, 20 0.5-m^2 litter traps were placed in each of the six study sites next to a random subsample of the 30 points used for soil sampling ($n = 120$ traps; see Plate 1). Traps were emptied every two weeks from September to December. A subset of the leaf litterfall was collected during an interval of four days without rain for analyses of C, N, Ca, Mg, and K.

Soil samples were weighed after being sieved through an 8-mm mesh sieve to remove root material and stones. Soil gravimetric moisture content was measured on 10 g of sieved soil after oven drying at 60°C for two days. Mean soil moisture for the six sites varied between 18% and 25%, and within-site variability was low and of similar magnitude in the six sites (CV < 15% in all cases). Soil moisture was used in the assays for microbial biomass, respiration, and net N mineralization and nitrification.

After collection, leaves of the two invasive species were oven-dried for 48 h at 60°C and weighed to the nearest 0.1 mg. Ten air-dried leaf subsamples were selected from the subsample of leaves collected during a four-day rain-free period in each site and ground in a Kleco Tissue Pulverizer (Kleco, Visalia, California, USA) for chemical analyses ($n = 30$ subsamples per invasive species). We digested 50 mg of each subsample in a microwave digester for one hour with 9 mL of nitric acid and analyzed the slurry for exchangeable Ca, Mg, and K using inductively plasma atomic emission spectrometry (Leeman Labs Inductively Couple Plasma/Profile, Hudson, New Hampshire, USA). Half of the leaf litter samples analyzed for exchangeable cations were also analyzed for C and N using a Carlo Ebra NA 1500 Analyzer (CE Elantech, Milan, Italy). Apple leaves were used as a standard in all cases.

Soil pH was measured in a 2:1 slurry of deionized water and 10 g of sample. All samples were stirred once initially and after 15 minutes, and then allowed to settle for 0.5 h before pH was measured on an Accumet AR20 pH meter (Fisher, Springfield, New Jersey, USA). Exchangeable Ca, Mg, and K were extracted using 0.1 mol/L $BaCl_2$; 100 mL of $BaCl_2$ were added to 10 g of air-dried sieved soil. The flasks were agitated at 125 rpm for 1 h and allowed to settle overnight. Soil slurries were filtered through Whatman Number 41 filter paper and preserved at 4°C until analyses. Concentrations of the three cations were measured using inductively plasma atomic emission spectrometry (Leeman Labs Inductively Couple Plasma/Profile, Hudson, New Hampshire, USA). Standards were prepared from 1000 and 10 000 mg/L liquid stock solutions and diluted using 0.1 mol/L $BaCl_2$. Lower detection limit was 0.1 mg/L.

Ca mineralization was estimated by comparing the concentration of exchangeable Ca in the initial soils with the concentrations after six months of incubation in the laboratory at room temperature (22–23°C). Subsamples of fresh soil (50 g) were incubated in containers with a plastic cover that allows oxygen exchange but prevents moisture lost. Comparisons of moisture content in the soil subsamples before and after the incubation showed that it did not suffer significant changes throughout the six months of the experiment.

Total soil C and N were analyzed on air-dried soils using a Carlo Ebra NA 1500 Analyzer (CE Elantech, Milan, Italy). Samples were combusted at 1020°C followed by chromatographic analyses of N_2 and CO_2 using 16–20-mg subsamples previously ground in a Kleco Tissue Pulverizer. Acetanilide (C_8H_9N) was used as a standard for both C and N. Analytical error was <5%. For the estimation of inorganic N pools (NH_4^+ and NO_3^-), 10-g subsamples of fresh soil were extracted by adding 50 mL of 2 mol/L KCl to each sample, shaking the samples at 125 rpm for 1 h, and allowed to settle overnight. The slurry was filtered through Whatman 41 filter papers into 60-mL polyethylene bottles and analyzed using a Lachat QuikChem 8000 (Lachat Instruments, Milwaukee, Wisconsin, USA).

Soil microbial biomass was determined using the $CHCL_3$-fumigation-incubation procedure (Jenkinson and Powlson 1976), a technique that provides a useful measure of microbial-based nutrient pools linked to basic N cycling functions (Bohlen et al. 2001). A 10-g subsample of fresh soil was fumigated for 24 h with distilled $CHCL_3$ in a humid vacuum desiccator. After fumigation, the samples were inoculated with 0.1 g of fresh soil, placed in 1-L air-tight glass jars, and incubated for 10 days at room temperature (22–23°C). Controls consisting of 10.1-g subsamples of fresh soil were placed in separate jars at the time the fumigated soils were reinoculated, and were incubated alongside the fumigated samples. Accumulation of CO_2 in the headspace of the jars was determined by gas chromatography (Tracor 540 gas chromatograph, thermal conductivity detector, Tracor, Texas, USA). Nitrogen accumulation was determined by extracting incubated samples as previously described. Microbial biomass C was calculated as $B_C = F_C/K_C$, where B_C is biomass C, F_C is the flush of C from fumigated samples, and $K_C = 0.41$. Microbial biomass N was calculated as F_N, or the flush of N from the fumigated samples. Accumulation of CO_2 in the unfumigated controls was used as a measure of soil respiration. Accumulation of inorganic N was used as a measure of potential net N mineralization, and accumulation of NO_3^- was used as a measure of potential net nitrification.

Spatial distribution and chemistry of leaf litterfall

Litter biomass data were fit to isotropic and anisotropic lognormal dispersal functions (Greene et al. 2004). We chose the lognormal function because our previous experience shows that it is a better fit than other functions (e.g., exponential functions) commonly used to model litter dispersal in tree species (C. D. Canham and S. W. Bigelow, *unpublished data*). The isotropic lognormal function has the form

$$Y_k = \mathrm{TLP}\sum_{i=1}^{n}\left(\frac{\mathrm{dbh}_i}{30}\right)^{\alpha}\frac{1}{\eta}\exp -\frac{1}{2}\left[\frac{\ln\left(\frac{\mathrm{distance}_i}{X_0}\right)}{X_b}\right]^2 \quad (1)$$

where Y_k is the total litter fall (in g/m^2) in trap k, dbh$_i$ is the diameter at breast height of $i = 1\ldots n$ trees within a distance of 25 m, distance$_i$ is the distance between the litter trap k and the tree i, η is a normalization constant equal to the arcwise integration of the dispersal kernel, and TLP, α, X_0, and X_b are estimated parameters. TLP is the estimated total litter production of a 30 cm dbh tree. The parameter α scales tree diameter to litter production, X_0 is the distance at which the maximum quantity of litter is dispersed (i.e., the mode of the dispersal kernel), and X_b determines the spread of the dispersal kernel. The anisotropic version of the lognormal function has the same general form as Eq. 1, with the mode of the dispersal curve (X_0') modified to take into account wind direction effects:

$$X_0' = X_0 - [A \times \cos(\mathrm{angle} - \delta)] \quad (2)$$

where X_0 is the mode of the dispersal curve in the isotropic model, A is the amplitude of the displacement of modal dispersal distance downwind, angle is the angle to the trap from a given source tree, and δ is the direction of maximal displacement from a source tree (Staelens et al. 2003). The error terms approximated a normal distribution in all cases. A summary of the parameters included in the litterfall models and their interpretation can be found in Table 1. Differences between sites in litter chemistry (i.e., percentage of N, C:N ratio, Ca, Mg, K) were analyzed using one-way ANOVAs (JMP Version 4.0.4, SAS Institute, Cary, North Carolina, USA), with site as a fixed factor.

Neighborhood models of species effects on ecosystem processes

We used likelihood methods and model selection as an alternative to traditional hypothesis testing (Johnson and Omland 2004, Canham and Uriarte 2006) for analysis of our data. Following the principles of likelihood estimation, we estimated model parameters that maximized the likelihood of observing the soil properties measured in the field, given a suite of alternate neighborhood models. We examined two sets of nested models, one set considering only the distribution and size of the two exotic tree species in the neighborhood (treating the mix of native species as a random background), and the second one considering the effects of both exotic and native tree species in the neighborhood. Table 1 includes a complete list and initial range values of all model parameters.

Effects of invasive tree species on soil properties.—For the first set of models, we conducted separate analyses of the effects on soil properties for each of the two invasive species. Our simplest model estimates soil properties using a single mean for each site, thereby assuming that the spatial distribution of the exotic species has no impact on soil properties. This model has the form

$$Y = a_s + \varepsilon \quad (3)$$

where a_s represents the mean for the soil property Y in each of the three sites, and ε is the error term. The effects of the exotic tree species were incorporated by adding a simple linear term:

$$Y = a_s + (b \times X) + \varepsilon \quad (4)$$

where X is the combined effect (quantified below) of neighboring trees of the exotic species on soil property Y and b is the slope of the effect, assumed to be the same for the three sites (homogeneous-slopes model). We considered the effect (X_i) of a neighboring individual i of the exotic tree on a soil property to vary as a direct

TABLE 1. List and range of parameters included in the models of litter dispersal and neighborhood effects on ecosystem processes.

Parameter	Range	Interpretation
Spatial distribution of leaf litterfall of invasive tree species†		
Normalization constant (η)	0–1000	Arcwise integration of the litterfall dispersal kernel.
Total litter production (TLP)	0–100 kg/yr	Litter production of a 30 cm dbh tree.
α	0–4	Scales tree diameter to litter production.
X_0	0.01–25 m	Mode of the litterfall dispersal kernel in the isotropic model.
X_0'	0.01–25 m	Mode of the litterfall dispersal kernel in the anisotropic model.
X_b	0.01–10	Spread of the litterfall dispersal kernel.
A	0–25 m	Amplitude of the mode displacement downwind.
δ	0–360°	Direction of the mode maximum displacement.
Effects of invasive tree species on soil properties†		
a_s	0–1000	Mean of a soil property in each of the three sites.
b	−1000 to 1000	Slope of the neighborhood effects.
c	−1000 to 1000	Together with b determines the slope of the neighborhood effects in the heterogeneous model.
Neighborhood function (X)		Combined effect of neighboring invasive trees on a soil property.
α	1 or 2	Scales tree diameter to neighborhood effects.
β	1–3	Shape of the decline with distance of the neighborhood effects.
γ	0–5	Steepness of the decline with distance of the neighborhood effects.
Invasive vs. native species effects on soil properties		
a_s	0–1000	Mean of a soil property in each of the six sites.
b	−1000 to 1000	Slope of the neighborhood effects.
Neighborhood function (X)		Combined effect of neighboring trees (both invasive and native) on a soil property.
α	1 or 2	Scales tree diameter to neighborhood effects.
β	1–3	Shape of the decline with distance of the neighborhood effects.
γ	0–5	Steepness of the decline with distance of the neighborhood effects.
λ	0–1	Species-specific impact index.
X_0	0.01–25 m	In the logistic function, distance at which half of the maximum effect occurs.
X_b	0–50	In the logistic function, steepness of the inflection in the curve.

† Separate models were run for *Acer platanoides* and *Ailanthus altissima*.

function of the size of the neighbor, and as an inverse function of the distance to the neighbor. Then, for $i = 1 \ldots . n$ invasive trees within a radius of 25 m from each sampling point, the combined effect of the invasive species (X) on a given ecosystem property is defined as

$$X = \sum_{i=1}^{n} \mathrm{dbh}_i^{\alpha} \exp(-\gamma \times \mathrm{distance}_i^{\beta}) \tag{5}$$

where dbh_i is diameter at breast height of the ith exotic tree; $\mathrm{distance}_i$ is the distance of ith individual from the sample point; and α, β, and γ are parameters determining the shape of the effect of the dbh (α) and the distance to the neighbor (β and γ) on X. Instead of setting α and β arbitrarily, we tested two different versions of Eq. 5, fixing α to values 1 or 2 and letting β and γ vary. We could not let α, β, and γ vary simultaneously due to difficulties in estimation caused by parameter trade-offs. A value of 1 for α implies that the effect of a neighbor is proportional to its dbh and therefore to its crown radius (which is a roughly linear function of dbh; Canham et al. 1994). A value of $\alpha = 2$ implies that the effect of the invasive species scales approximately linearly with plant biomass (Jenkins et al. 2003). If $\beta = 1$, then the decrease of the species effect with distance follows a negative exponential decay. If $\beta > 1$, the function is sigmoidal with an initially slow rate of decline followed by a steeper rate as distance increases. The parameter γ determines the steepness of the decline of the species effect with distance.

We also tested a variant of Eq. 4 in which the effect of the exotic tree species was allowed to vary depending on the site:

$$Y = a_s + (b + c \times a_s)X + \varepsilon \tag{6}$$

where the b and c parameters define the shape of the change in Y with X (heterogeneous-slopes model), and a_s the mean value of the soil property Y for each of the three study sites. We also used an asymptotic functional relationship to describe the effect of exotics on soil properties to reach a plateau at some exotic abundance. The asymptotic model has the form

$$Y = c - a_s \times \exp(-b \times X) + \varepsilon \tag{7}$$

where c is the asymptote; a_s is the mean value of the soil property Y for each of the three study sites; b is the slope of the exotic effect; and X is the magnitude of the exotic effect on soil property Y calculated as in Eq. 5.

Comparison of native vs. invasive species effects on soil properties.—In order to compare the effect of invasive and native tree species on soil properties, we fitted the homogeneous-slopes model defined in Eq. 4 to the whole data set (six sites together) using two different models to describe the species effects (X). The first equation followed an exponential form:

TABLE 2. Summary of leaf litterfall models.

Parameters	*Acer platanoides*	*Ailanthus altissima*
AIC_c		
Isotropic	**543.93**	581.33
Anisotropic	548.26	**571.69**
k	4	6
R^2	0.91	0.75
η	458.12	509.73
TLP (kg/yr)	11.55 [10.85–12.25]	5.35 [4.85–5.86]
α	1.53 [1.40–1.66]	1.84 [1.15–2.51]
X_0 (m)	4.09 [4.03–4.14]	2.28 [1.98–2.69]
X_b	0.68 [0.66–0.70]	0.95 [0.91–0.99]
A (m)		0.97 [0.52–1.42]
δ (°)		115.16 [87.66–142.67]

Notes: The most parsimonious model (indicated in bold) is the one with the lowest AIC_c. The number of parameters (k), R^2, the normalizer (η), and maximum-likelihood parameter estimates and two-unit support intervals (in brackets) are given for the most parsimonious models. Parameter definitions are given in Table 1.

$$X = \sum_{j=1}^{s}\sum_{i=1}^{n} \lambda_j \times \text{dbh}_{ji}^{\alpha}[\exp(-\gamma \times \text{distance}_{ji}^{\beta})] \tag{8}$$

where X was summed over each individual i of species j with dbh_{ji} at a distance_{ji} within a radius of 25 m from a sampling point; λ_j represents a species-specific scalar that ranges from 0 to 1 and allows for differences among species in their effect on soil properties. Five species were considered in this set of "community" models: the two invaders and the three most abundant natives across the six sites (i.e., *Acer saccharum*, *Fraxinus americana*, and *Quercus rubra*; Appendix A). We limited the number of native species included in the model to keep the number of parameters in the model within a reasonable range given the sample size. The remaining parameters in Eq. 8 (α, β, and γ) are as defined for Eq. 5.

The second model used to compare the exotic vs. native species used a logistic function for the effect of different species:

$$X = \sum_{j=1}^{s}\sum_{i=1}^{n} \lambda_j \times \text{dbh}_{ji}^{\alpha} \times \frac{1}{1 + (\text{distance}/X_0)^{X_b}} \tag{9}$$

where X_0 represents the distance at which half of the maximum effect occurs, X_b determines the steepness of the inflection in the curve, and the remaining parameters (α, β, and γ) are as in Eq. 5. The shape of the logistic curve is more flexible than the exponential model. The two "community" models (homogeneous slopes model with exponential or logistic functions) were compared to a basic model of the form described in Eq. 3 ($Y = a_\text{s}$), where the value of each soil property was considered to be only a function of the site, a_s being calculated for each of the six sites. By doing this, we assessed if a model that does not consider any species effects is a better descriptor of the spatial heterogeneity in soil properties than models that consider the neighborhood effects of the main tree species (both invasive and native) in the community.

We used simulated annealing, a global optimization procedure, to determine the most likely parameters (i.e., the parameters that maximize the log likelihood) given our observed data (Goffe et al. 1994). The analyses were done using software written specifically for this study using Delphi for Windows (Version 6, Borland Software, Cupertino, California, USA). Residuals (ε) for the different variables were normal or lognormal distributed, so the error terms were modeled accordingly. The fit of each alternate model was assessed using two metrics: the R^2 of the regression of observed vs. predicted as a measure of goodness of fit, and the slope of the regression as a measure of bias (an unbiased model having a slope of one). Alternate models were compared using the Akaike Information Criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002). We used asymptotic two-unit support intervals to assess the strength of evidence for individual maximum-likelihood parameter estimates (Edwards 1992).

RESULTS

Spatial distribution and chemistry of leaf litterfall

The most parsimonious models were an excellent fit, explaining 75–91% of the spatial variation in leaf litterfall biomass of the two exotic species (Table 2). The modal dispersal distance (X_0) was almost twice as large for Norway maple as for tree of heaven (4.09 m vs. 2.28 m, respectively; Fig. 1). Leaf litterfall was isotropic for Norway maple but there was a distinct directional pattern to litterfall in tree of heaven, with a prevailing litterfall direction (δ) of 115.2° southeast (Table 2). The modal dispersal distance for tree of heaven was located about 1 m (A = 0.97 m) further from the trunk downwind (3.28 m) than upwind (1.28 m). Estimated total litter production (TLP) of a standardized 30 cm dbh tree was two times higher for Norway maple than for tree of heaven (11.55 kg/yr vs. 5.35 kg/yr, respectively). For both species, litter production scaled as approximately a 3/2 power of dbh (i.e., $\alpha \sim 1.5$; Table 2).

The N percentage and C:N ratio in Norway maple leaf litterfall did not vary between sites (Table 3). On the contrary, both variables showed a significant between-site variation in tree of heaven leaf litter (Table 3). Norway maple litter Ca and Mg concentration varied between sites, and was positively related to soil exchangeable Ca and Mg, respectively (Table 3, Appendix B). Tree of heaven showed the same pattern as Norway maple for litter Ca concentration, but not for Mg, which remained relatively constant between sites. Litter K concentration did not show significant between-site variation for either of the two species (Table 3).

The "footprints" of invasive tree species on ecosystem processes

For nine (Norway maple) and six (tree of heaven) of the 18 soil variables tested, at least one of the models that considered the effects of the invasive tree species

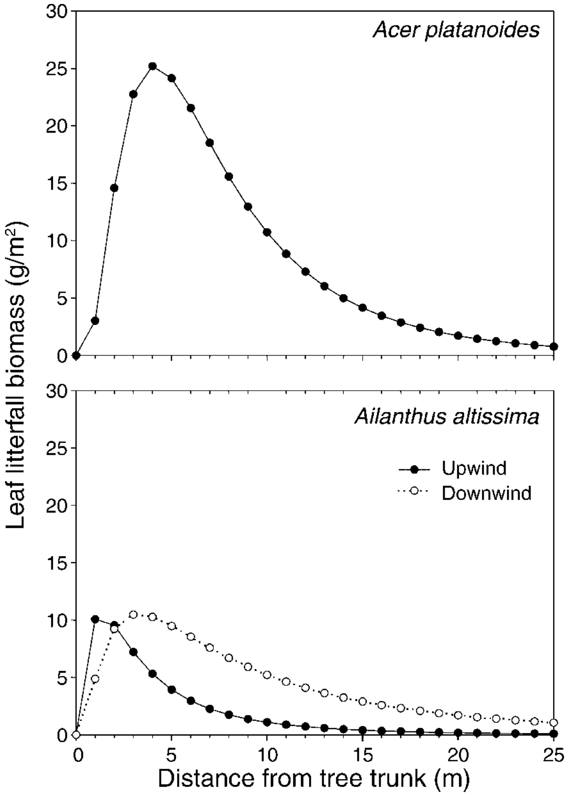

FIG. 1. Predicted leaf litterfall biomass as a function of distance from a single 30 cm dbh tree for each of the two invasive species, *Acer platanoides* and *Ailanthus altissima.*

(i.e., homogeneous slopes, heterogeneous slopes, or asymptotic models) had better AIC_c scores than the basic model that ignored exotic species effects (Table 4). Norway maple had an impact on forest floor depth, pH, exchangeable Ca, Mg, and K, NO_3^- pool, net N mineralization, net nitrification, and Ca mineralization. Tree of heaven had an effect on pH, exchangeable Ca and K, mass N, NO_3^-, and net nitrification (Table 4). The fit of the most parsimonious models for these soil properties ranged from very good for pH and exchangeable Ca ($R^2 = 0.50–0.65$); good for forest floor depth, exchangeable Mg, and exchangeable K ($R^2 = 0.30–0.40$); and relatively low for mass N, net N mineralization, and Ca mineralization ($R^2 = 0.20–0.25$). The fit for NO_3^- and net nitrification was much better for Norway maple ($R^2 = 0.30–0.33$) than for tree of heaven ($R^2 = 0.14–0.20$). All models produced unbiased estimates of soil properties, as indicated by slopes of predicted vs. observed very close to 1.0 (i.e., 0.97–1.02).

The α parameter in Eq. 5 controls the scaling of the effect of invasive tree size on soil properties. Depending on the soil property, the effect of a neighboring invasive tree scaled either linearly with dbh ($\alpha = 1$, i.e., as a function of crown radius), or as a squared function of dbh ($\alpha = 2$, i.e., roughly linearly with the biomass of the neighbor; Appendices B and C). Exchangeable cation concentrations and pH varied as a simple negative exponential function of distance ($\beta \sim 1$) from both Norway maple and tree of heaven neighbors (Figs. 2 and 3). In contrast, the variation in forest floor depth, N-cycling variables (mass N, net N mineralization, and net nitrification), and Ca mineralization as a function of distance from an exotic neighbor was, in most cases, sigmoidal (i.e., $\beta > 1$; Appendices B and C).

The shape of the "footprint" of Norway maple on Mg, NO_3^-, and Ca mineralization was highly localized, with a dramatic decline within 5 m (Fig. 2). Neighborhood effects of Norway maple on forest floor depth, pH, exchangeable Ca, net N mineralization, and net nitrification showed a more gradual decrease that reached background levels within distances of 20–25 m. Exchangeable K showed an intermediate pattern between the two groups of variables, tending to background levels in the first 10 m from the trunk (Fig. 2). The "footprint" of tree of heaven was also very localized for NO_3^- and net nitrification (i.e., sharp decline within 5 m), while the remaining soil properties dropped to background levels more gradually, within a slightly

TABLE 3. Leaf litter values (mean ± SE) of N percentage (%N), C:N ratio, and base cation concentration (Ca, Mg, and K; units in mg/g leaf litterfall) for *Acer platanoides* and *Ailanthus altissima* in each study site ($n = 5$ samples for %N and C:N, $n = 10$ samples for Ca, Mg, and K).

Site	%N	C:N	Ca	Mg	K
Acer platanoides					
Site 1	1.49 ± 0.13	32.32 ± 2.83	15.17 ± 0.57	2.12 ± 0.09	9.11 ± 0.52
Site 2	1.38 ± 0.04	33.18 ± 1.05	20.12 ± 0.77	2.41 ± 0.07	9.78 ± 0.39
Site 3	1.52 ± 0.13	31.54 ± 2.79	16.47 ± 0.56	3.04 ± 0.09	9.54 ± 0.63
F	0.423	0.119	15.96	25.38	0.42
P	ns	ns	<0.0001	<0.0001	ns
Ailanthus altissima					
Site 4	1.81 ± 0.04	24.92 ± 0.59	38.79 ± 1.58	3.98 ± 0.13	9.98 ± 1.16
Site 5	1.35 ± 0.15	33.59 ± 2.04	28.07 ± 1.54	4.16 ± 0.12	10.94 ± 1.22
Site 6	1.24 ± 0.05	36.38 ± 1.78	37.03 ± 1.76	4.39 ± 0.27	8.58 ± 0.47
F	11.92	7.11	11.76	0.84	1.50
P	0.0014	0.007	0.0002	ns	ns

Note: F statistics and *P* values reported are for one-way ANOVAs for differences in nutrient concentration among the three sites invaded by each species; df = 2,12 for %N and C:N, df = 2,27 for Ca, Mg, and K; ns, not significant.

TABLE 4. AIC_c values for the four models used to analyze the effect of *Acer platanoides* and *Ailanthus altissima* on soil properties.

	Model								
		Homogeneous		Heterogeneous		Asymptotic			
Soil property	Basic	$\alpha = 1$	$\alpha = 2$	$\alpha = 1$	$\alpha = 2$	$\alpha = 1$	$\alpha = 2$	k	R^2
Acer platanoides									
Litter depth	**574.71**	581.08	581.12	575.63	577.39	583.67	583.12	4	0.01
Forest floor depth	617.31	617.33	612.73	610.34	610.45	**603.84**	606.26	8	0.38
Bulk density	**290.47**	292.04	292.25	293.30	294.12	306.55	308.36	4	0.09
pH	67.81	**34.27**	42.81	35.63	37.39	36.34	37.67	7	0.50
Exchangeable Ca	888.91	850.62	819.32	855.29	**817.30**	846.84	839.12	8	0.62
Exchangeable Mg	481.02	465.39	463.09	463.40	**460.97**	467.78	464.11	8	0.30
Exchangeable K	423.01	426.63	427.46	**420.16**	427.11	429.77	431.23	8	0.30
Mass C	**253.78**	255.35	259.31	261.42	263.52	256.69	257.53	4	0.28
Mass N	**1004.25**	1048.53	1059.38	1012.48	1012.45	1012.08	1013.11	4	0.32
C:N	**341.23**	348.79	354.61	343.94	345.25	346.21	354.11	4	0.04
NH_4^+	**312.45**	317.44	313.29	321.50	315.08	321.85	319.86	4	0.12
NO_3^-	278.84	**271.26**	273.96	292.14	294.56	272.23	274.89	7	0.33
Microbial biomass C	**1283.03**	1287.73	1287.39	1289.68	1290.96	1290.75	1295.23	4	0.13
Microbial biomass N	**882.14**	883.91	884.66	886.13	887.56	893.08	894.05	4	0.05
Respiration	**546.31**	554.39	552.79	548.64	548.11	553.05	555.23	4	0.13
Net N mineralization	139.99	141.26	**135.57**	147.67	148.38	150.21	151.23	7	0.20
Net nitrification	146.41	142.01	**132.28**	155.72	150.23	141.37	140.25	7	0.30
Ca mineralization	897.69	907.45	899.68	901.15	**890.81**	916.45	911.23	8	0.25
Ailanthus altissima									
Litter depth	**574.71**	581.08	581.12	575.63	596.58	583.67	590.21	4	0.13
Forest floor depth	**582.92**	591.13	590.22	585.51	585.84	594.27	596.23	4	0.29
Bulk density	**246.23**	246.85	247.25	253.52	253.02	247.41	248.36	4	0.12
pH	125.20	127.93	126.12	120.60	**118.19**	129.60	127.25	8	0.63
Exchangeable Ca	1007.94	1010.92	1010.70	**1005.72**	1011.23	1016.84	1022.32	8	0.65
Exchangeable Mg	**699.41**	705.04	705.65	707.86	708.04	707.62	708.66	4	0.41
Exchangeable K	409.29	397.29	397.73	389.39	**387.75**	397.36	395.21	8	0.30
Mass C	**318.29**	322.14	323.1	327.21	328.54	327.10	329.68	4	0.30
Mass N	1035.72	1037.74	1038.24	**1033.51**	1035.69	1044.03	1046.23	8	0.20
C:N	**381.03**	387.28	385.65	388.17	384.86	388.63	389.36	4	0.45
NH_4^+	**290.21**	294.36	294.58	297.16	296.01	299.56	300.21	4	0.08
NO_3^-	340.07	**338.05**	339.99	341.84	340.71	342.33	342.68	7	0.14
Microbial biomass C	**1251.3**	1255.69	1256.48	1258.59	1258.47	1535.74	1510.27	4	0.20
Microbial biomass N	**770.52**	775.08	775.67	778.11	775.74	779.83	178.32	4	0.06
Respiration	**525.45**	531.11	530.80	532.44	531.11	531.47	533.07	4	0.28
Net N mineralization	**41.52**	44.46	43.61	46.43	45.69	47.08	48.25	4	0.04
Net nitrification	20.81	21.13	**18.69**	22.54	21.72	23.46	24.68	7	0.20
Ca mineralization	**630.69**	635.52	632.44	637.60	634.15	638.42	639.53	4	0.19

Notes: The most parsimonious model (indicated in bold) is the one with the lowest AIC_c. The number of parameters (k) and R^2 are given for the best model.

shorter distance than Norway maple (i.e., 15–20 m; Fig. 3).

Site dependency in the impact of invasive tree species

For most of the variables for which an effect of the exotic species was detected, the models that allowed the effect of the exotic species to vary between sites (i.e., the heterogeneous-slopes and asymptotic models) provided a better fit to the data than models assuming similar slopes of the effects in the three sites (i.e., the homogenous-slopes model; Table 4). Only for NO_3^-, net N mineralization, and net nitrification was the homogeneous model a consistently better fit.

In the homogeneous-slopes models, positive values of b (the slope of the regression; Appendices B and C) indicate that the effects of Norway maple and tree of heaven on soil properties were always positive, the magnitude of the soil properties decreasing with distance from the exotic trees (Figs. 4 and 5). In the heterogeneous-slopes models, the positive values of c (Appendices B and C) indicate that the magnitude of the effect of the exotic trees was positively related to the mean of the site (Figs. 4 and 5). As a consequence, in all cases, the maximum impact of the invasive species on a soil property occurred at a neighborhood located in the site with the highest background mean for that variable (Appendices B and C). Thus, the impact of a standard 30 cm dbh Norway maple on exchangeable Ca and Mg varied between two times the mean (in the site with the lowest mean cation concentration) and three times the mean (in the site with the highest mean), and between no effect and two times the mean for exchangeable K and Ca mineralization (Fig. 4). The impact of a 30 cm dbh tree of heaven was always smaller than the effect of a Norway maple of the similar size, ranging between null (in the site with the lowest mean) and 1.1–1.4 times the mean (in the site with the highest mean) for pH, exchangeable Ca, and exchangeable K (Fig. 5). Tree of

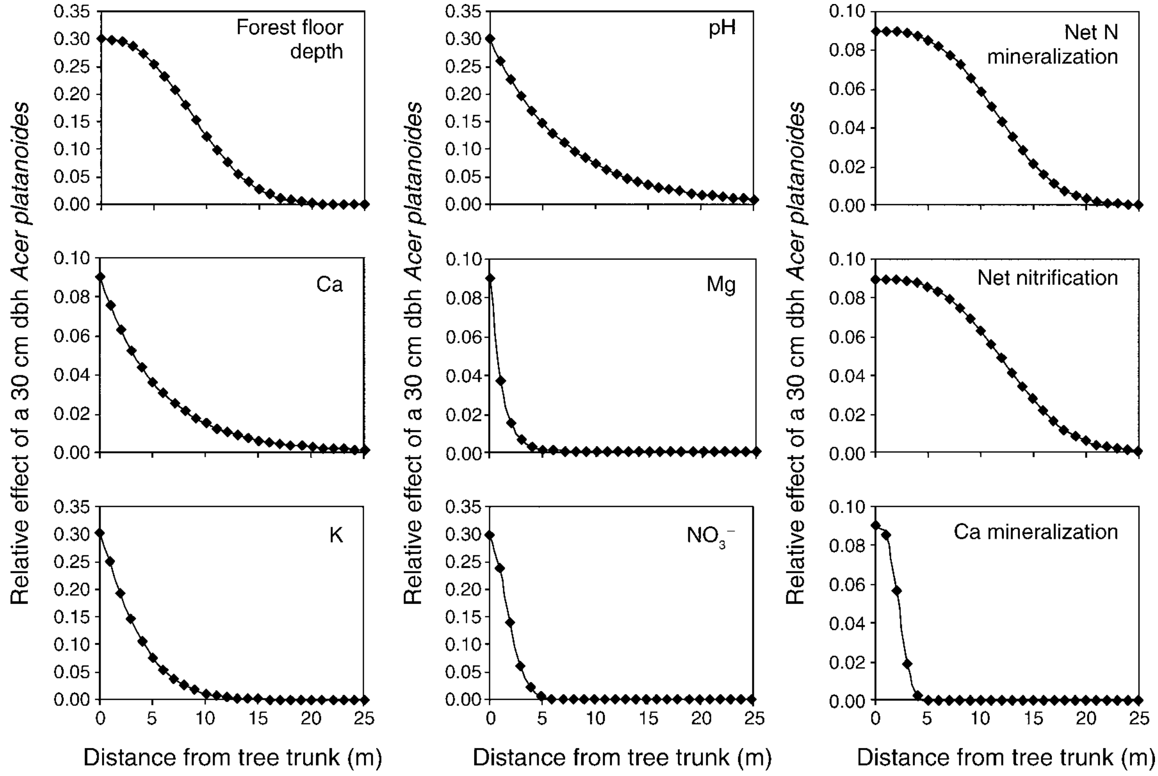

FIG. 2. Footprint of a standard 30 cm dbh *Acer platanoides* on soil properties within a neighborhood of 25 m radius. The predicted relative effect at each distance is given by Eq. 5 (see *Methods*). The relative effect at distance 0 from the trunk of a 30 cm dbh *Acer platanoides* is only a function of dbh (in m), and has two possible values: 0.3 when $\alpha = 1$ and 0.09 when $\alpha = 2$. Parameter α determines the scaling of the effects of neighbor tree size on x: when $\alpha = 1$, the effect of a neighbor is proportional to its dbh and therefore to its crown radius; when $\alpha = 2$, the effect scales approximately linearly with plant biomass.

heaven had an effect on mass N in the three sites, its magnitude also increasing with the mean of the site (from 1.06 to 1.2 times the mean for a 30 cm dbh tree). The asymptotic slopes model was the most parsimonious model only for one variable: forest floor depth in Norway maple sites, and predicted an increase in forest floor depth with distance to Norway maple only in the site with the highest mean (Fig. 4).

Comparison of native vs. invasive tree species impacts on ecosystem processes

For 10 of the 18 soil properties analyzed, the basic model that ignored the effects of the tree species (both natives and invaders) had worse AIC_c scores than at least one of the models including neighborhood effects of species (i.e., exponential or logistic models; Table 5). Neighborhood composition had an effect on forest floor depth, pH, exchangeable Ca and K, mass N, NO_3^-, C:N ratio, microbial biomass C and N, and net nitrification. For most of these variables (seven out of 10), the logistic equation was a better descriptor of the species effects than the exponential equation (Table 5). The fit of the most parsimonious models for these 10 soil properties was very good for pH and exchangeable Ca ($R^2 = 0.74$–0.77) and good for the other nine variables ($R^2 = 0.31$–0.44).

The scaling of the effect of neighboring trees to tree size (α) varied considerably depending on the soil property (Appendix D). Thus, exchangeable K, mass N, C:N ratio, and NO_3^- varied as a linear function of dbh, the estimated value of α for pH was intermediate between 1 and 2, and the estimated value of α for effects on forest floor depth, exchangeable Ca, microbial biomass C and N, and net nitrification was >2, indicating that larger trees have a disproportionately bigger effect on those soil properties. The effect of the distance to the tree species (as controlled by the parameters β and λ in the exponential models and by X_0 and X_b in the logistic models) also varied with the soil property (Appendix D). NO_3^- showed a much steeper decrease with distance than any other variable (i.e., high X_b), the species effect being restricted to the first few meters from the trunk (~0–3 m). Exchangeable K showed the second fastest decrease with distance. The remaining variables showed a "shoulder" in the function (i.e., β and $X_0 > 1$), where the effect initially declines slowly and then drops off exponentially reaching background levels at distances of ~10 m for forest floor

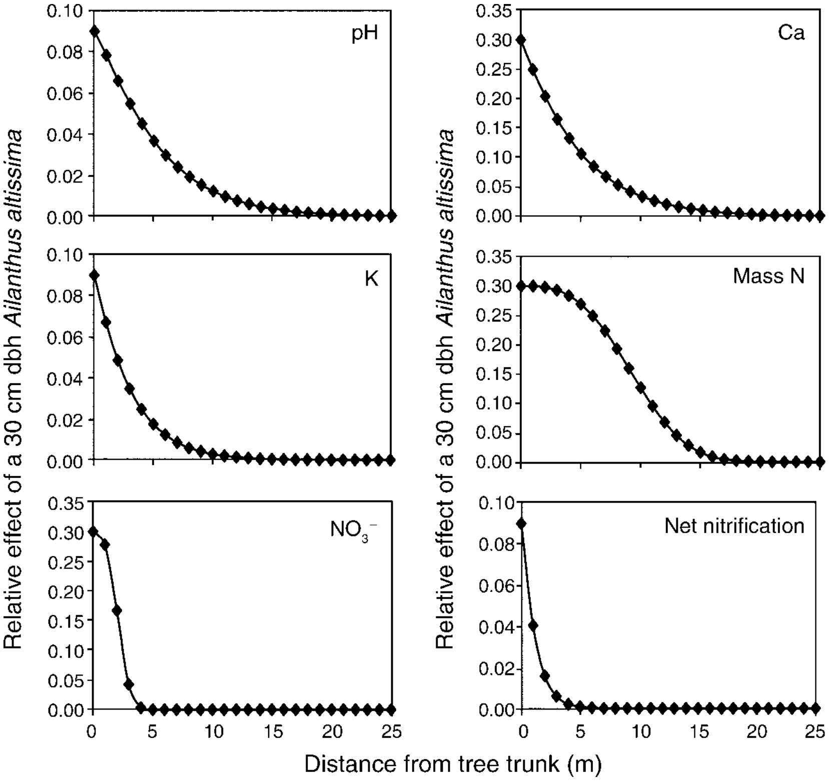

FIG. 3. Footprint of a standard 30 cm dbh *Ailanthus altissima* on soil properties within a neighborhood of 25 m radius. The predicted relative effect at each distance is given by Eq. 5 (see *Methods*). The relative effect at distance 0 from the trunk of a 30 cm dbh *Ailanthus altissima* is only a function of dbh (in m), and has two possible values: 0.3 when $\alpha = 1$ and 0.09 when $\alpha = 2$.

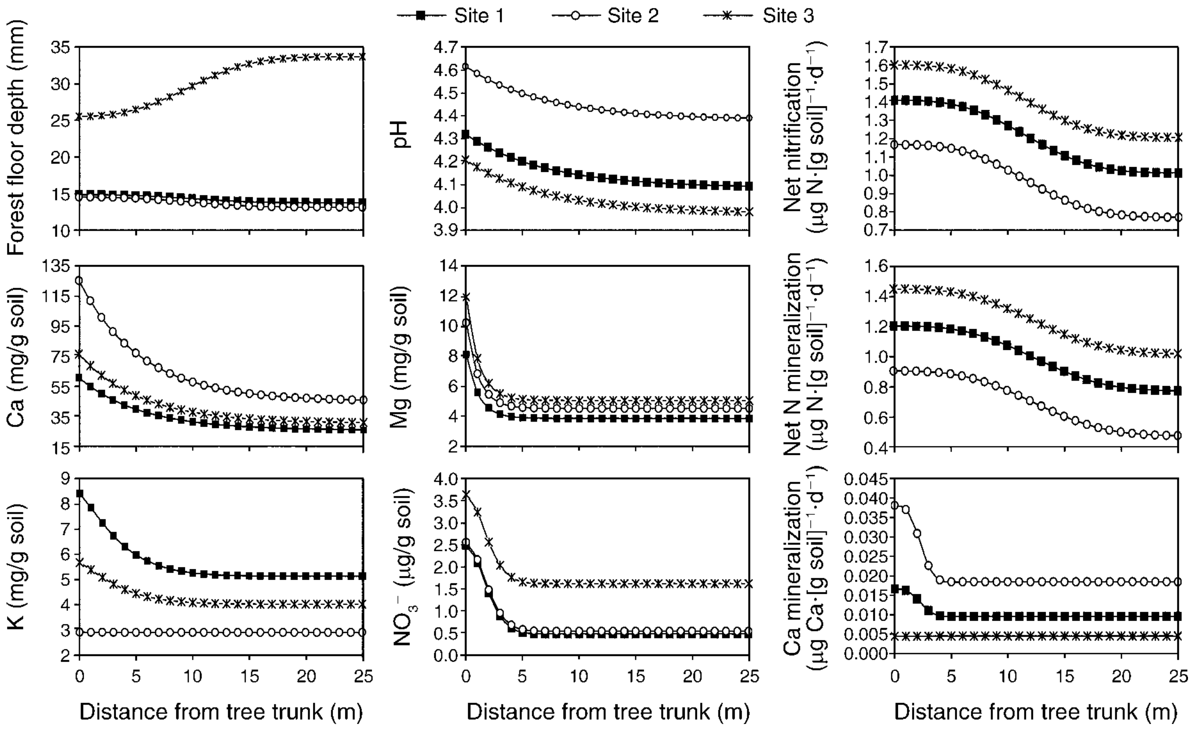

FIG. 4. Predicted values of soil properties as a function of the distance to a standard 30 cm dbh *Acer platanoides* in each of the three sites invaded by the species. Soil properties for which the basic model was the best fit (Table 3) are not shown.

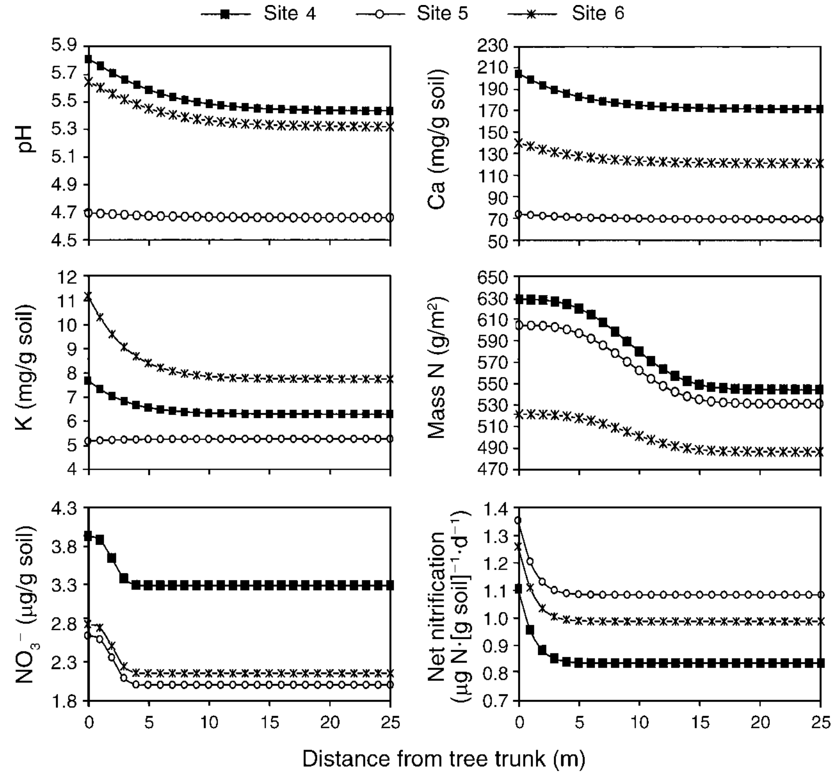

FIG. 5. Predicted values of soil properties as a function of the distance to a standard 30 cm dbh *Ailanthus altissima* in each of the three sites invaded by the species. Soil properties for which the basic model was the best fit (Table 3) are not shown.

depth and further (~15–25 m) for the remaining variables.

The values of the λ parameter, an index of the magnitude of the impact of each tree species on soil properties, varied strikingly between species for the 10 soil properties for which a species effect was detected (Fig. 6, Appendix D). Norway maple was the species with the largest relative per capita effect (λ) for five of the 10 variables (pH, exchangeable Ca and K, NO_3^-, and net nitrification). Tree of heaven had the largest impact on mass N, and the second largest effect on pH, exchangeable Ca and K, and net nitrification. White ash

TABLE 5. AIC_c values for the three models used to analyze the effect of dominant tree species (*Acer platanoides, Ailanthus altissima, Acer saccharum, Fraxinus americana*, and *Quercus rubra*) on soil properties.

Soil property	Model			k	R^2
	Basic	Exponential	Logistic		
Litter depth	**1173.25**	1177.76	1181.91	8	0.08
Forest floor depth	1202.72	1196.99	**1194.93**	16	0.40
Bulk density	**536.60**	562.92	560.51	8	0.10
pH	192.91	182.31	**178.74**	16	0.74
Exchangeable Ca	1914.74	**1910.76**	1919.94	16	0.77
Exchangeable Mg	**1180.33**	1300.23	1298.02	8	0.39
Exchangeable K	832.21	830.88	**830.55**	16	0.38
Mass C	**572.03**	597.37	595.67	8	0.33
Mass N	2038.62	2037.04	**2035.02**	16	0.42
C:N	743.27	742.88	**741.73**	16	0.44
NH_4^+	**602.57**	607.85	606.26	8	0.10
NO_3^-	617.92	631.31	**616.88**	16	0.43
Microbial biomass C	2534.23	**2525.07**	3098.52	16	0.31
Microbial biomass N	1652.56	**1649.91**	1652.25	16	0.34
Respiration	**1103.89**	1120.09	1119.67	8	0.13
Net N mineralization	**181.43**	197.77	196.12	8	0.06
Net nitrification	167.31	169.36	**166.73**	16	0.35
Ca mineralization	**1571.03**	2032.51	2022.77	8	0.05

Notes: The most parsimonious model (lowest AIC_c) is indicated in bold. The number of parameters (k) and R^2 are given for the best model.

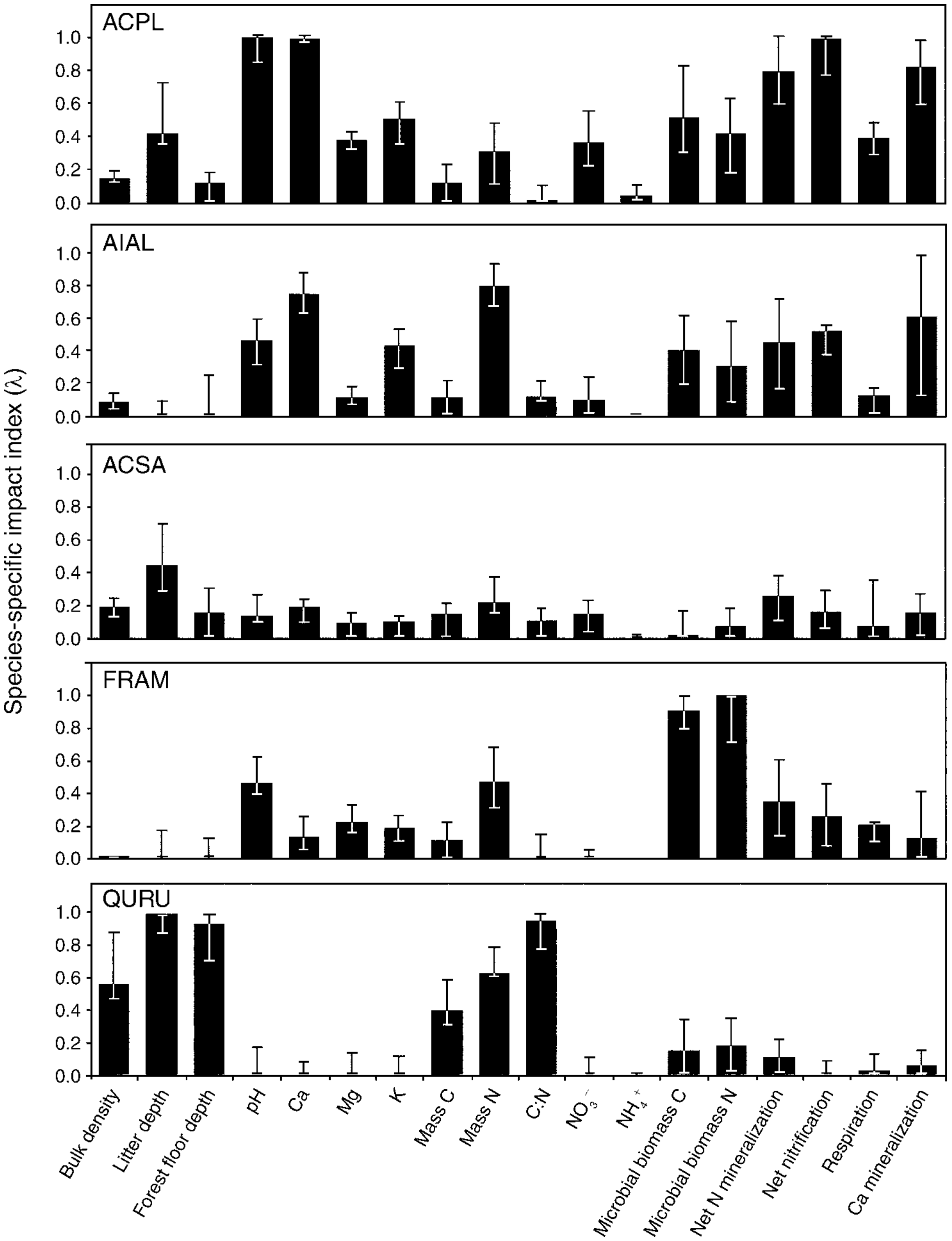

Fig. 6. Impact index (λ parameter in Eqs. 8 and 9, see *Methods*) for each of the dominant invasive and native tree species. The impact index ranges between 0 and 1, and allows for relative differences between species in their effects on each of the 18 soil properties analyzed. Bars represent two-unit support intervals of parameter estimations.

had the largest impact on microbial C and N, red oak had the largest effect on forest floor depth and C:N ratio, and sugar maple did not have large impacts on any soil properties, relative to the other species in the model (Fig. 6).

Discussion

Our research, focused on two exotic tree species that are gradually invading native mixed forests, clearly shows that invasive trees can alter the functioning of temperate forest ecosystems even at relatively low densities by increasing nutrient availability (i.e., pH, Ca, Mg, K, N) and cycling rates (i.e., net N mineralization, net nitrification, Ca mineralization). We recognize that our analyses can not unambiguously ascribe causation to the spatially explicit relationships between the distribution of the exotic species and various soil properties and processes, but the weight of both the empirical evidence presented here, and previous studies documenting the many specific mechanisms by which species differ in their effects on soil properties, strongly suggest that these neighborhood analyses provide a basis

PLATE 1. Litter traps set in a stand with *Acer platanoides* (Norway maple) and native trees in Litchfield County, Connecticut, USA. The white arrow indicates one of the flags marking the locations where soil samples were taken adjacent to the traps. Photo credit: L. Gómez-Aparicio.

for predictive models of the effects of continued spread of these exotic species. This is particularly true in the case of the early stages of invasion of these native forests, where the current distribution of the exotic trees is still largely determined by the distance to seed sources (i.e., roads) rather than by the locations of favorable microsites within a stand. Moreover, the use of neighborhood models to compare species effects at small spatial scales minimizes variance caused by heterogeneity in climate, relief, or parent material.

Modification of soil processes and properties by invasive tree species

Our results show that both Norway maple and tree of heaven are associated with a significant increase in soil pH and availability of the major cations (Ca, Mg, and K). An effect on pH has also been observed for one of the most common invasive shrub species in this region (*Berberis thunbergii*; Ehrenfeld et al. 2001). These effects are usually related to increased base cation concentrations in leaf litter (Finzi et al. 1998*a*, Ehrenfeld 2003). In fact, the concentrations of Ca, Mg, and K in the litter of Norway maple and tree of heaven were two to four times higher than values obtained for the six dominant native tree species in the same forests (C. D. Canham and S. W. Bigelow, *unpublished data*). High litter nutrient content is typically associated with high growth rates (Aerts and Chapin 2000, Reich et al. 2005), and both Norway maple and tree of heaven grow faster than the native tree species across a range of light levels at these sites (P. H. Martin and C. D. Canham, *unpublished data*).

The neighborhood effects of the two invasive species on Ca availability were of much larger magnitude than for K and Mg. In fact, exchangeable Ca was the soil property that was most responsive to the presence of the invaders in the neighborhood. Other studies have shown Ca dynamics to be more plastic and easily influenced by tree species distribution than K or Mg dynamics (Andersson 1991, Fujinuma et al. 2005). Luxury consumption (i.e., nutrient uptake in excess of plant requirements) is much more pronounced for Ca than for K and Mg (Knecht and Göransson 2004), and reabsorption from senescing leaves is typically much lower (Aerts and Chapin 2000). Consequently, species-specific differences in Ca uptake are frequently linked to variability in the magnitude of Ca accumulation in soils under different plant species.

Norway maple and tree of heaven also altered N cycling by increasing cycling rates (i.e., net N mineralization and net nitrification) and the size of ambient N pools. These results mirror previous studies that conclude that increases in inorganic N pool sizes and nitrification rates are one of the most consistent effects of invasive species on nutrient cycling (see Ehrenfeld 2003). The stimulation of N cycling under the invasives was at least partially determined by the characteristics of their litter inputs to the soil. High quality litter (i.e., low C:N and lignin:C ratios) and high litter biomass are usually good predictors of positive species effects on nitrogen fluxes (Wedin and Tilman 1990, Scott and Binkley 1997). Both invaders had high quality leaf litter (low C:N ratios and high N percentage, particularly for tree of heaven) relative to typical leaf litter chemistry for native tree species in temperate forests of northeast United States (Scott and Binkley 1997, Bohlen et al. 2001, Lovett et al. 2004). For example, C:N ratios for litter of the invaders was half as high (~30 vs. 60) and N percentages about twice higher (~1.4 vs. 0.8) when compared to C and N values reported by Finzi et al. (1998*b*) for leaf litter of sugar maple and hemlock (*Tsuga canadensis*) in forests of the same area (northwestern Connecticut). In contrast, our analyses indicate that litter production in Norway maple (TLP = 11.55 kg/yr for a 30 cm dbh tree) is in the same range as estimates obtained using similar methods for the six dominant native tree species in the same area (C. D. Canham and S. W. Bigelow, *unpublished data*), while litter production in tree of heaven is actually lower (TLP = 5.35 kg/yr for a 30 cm dbh tree). Thus, the positive effects of the two exotic species on N cycling were presumably driven by (high) leaf litter quality rather than differences in litter quantity (Scott and Binkley 1997, Finzi et al. 1998*b*). Differences in litter production between the two invasive species, however, are most likely the reason why the per capita impact of Norway maple was of much larger magnitude than the per capita impact of tree of heaven on all soil properties (Figs. 4 and 5).

The neighborhood effects of the exotic species on N cycling were not accompanied by effects on soil C dynamics (i.e., total C, microbial C, respiration). This decoupling between cycles appears to be common in studies of the ecosystem effects of invasive species (Ehrenfeld et al. 2001, Evans et al. 2001). Moreover, the invader impacts on microbial-mediated N transformations were not accompanied by changes in microbial biomass N. This may indicate that our sampling design (i.e., a single point sample in time) was not adequate to assess patterns of variation in microbial biomass due to the high spatial and temporal variability characteristic of soil microorganisms. However, another plausible explanation is that invasive trees may select for a community of soil organisms that facilitates the cycling of their own residues. These species-specific changes in the structure (and not necessarily biomass) of soil communities have been reported for a number of native species in different ecosystems (see Wardle 2002), but their role in determining the impacts of invasive species on nutrient cycling is unknown.

The nature of the footprints of invasive tree species

The spatial patterns of effects of tree species on soil properties have traditionally been envisioned in terms of "influence circles," with individual trees influencing a soil area roughly proportional to the size of the canopy (Zinke 1962). However, our results show very different sizes and shapes of the footprints for different soil properties, and suggest that the spatial patterns of tree species effects on soils are considerably more complex. For some soil properties, effects extend far beyond the canopy (i.e., pH, exchangeable Ca), while for others the footprint is restricted to the first few meters from the trunk (i.e., Mg, NO_3^-). Regarding shape, some footprints were characterized by an exponential decline with distance (i.e., pH, exchangeable cations) and others by a "shoulder" followed by a quick decline (i.e., N mineralization, mass N). Therefore, a better understanding of plant–soil interactions will benefit from spatially explicit studies that take into account the relative locations of individual trees and the sampling points were ecosystem properties are measured.

For example, differences in the nature of the footprints were clearly noticeable for the three cations (Ca, Mg, and K; Figs. 2 and 3), and can be explained by differences in their internal cycling within these ecosystems. Aboveground cation return to soil takes place by three main pathways: stemflow, throughfall and litterfall. These processes represent a gradient in spatial extent, from very localized stemflow (with measurable effects only within 1–2 m around the stem [Levia and Frost 2003]), to throughfall beneath the crown and potentially concentrated around the drip edge (Levia and Frost 2006), to the effects of litterfall extending well beyond the drip line of the tree crown (Staelens et al. 2003). The large extent of the impact of the two invasive species on soil Ca (i.e., measurable impacts within 20–25 m for Norway maple and 15–20 m for tree of heaven) suggests that the shapes of their footprints for Ca are controlled largely by litterfall, particularly since the "footprint" of the invasive species effects on soil Ca were similar to their litterfall dispersal kernels (Fig. 1). Potassium, in contrast, returns to the soil primarily through stemflow and throughfall, due to its high susceptibility to leaching loss (Tukey 1970). Our analyses show that the footprints of the effects of the invaders on K are correspondingly more tightly clustered around the canopies of the invasive tree species. Pathways of Mg return to soil are intermediate between Ca and K, and variable among sites (Cole and Rapp 1981). In addition, differences in litterfall Mg concentration between invasive and native tree species were smaller than for Ca and K (C. D. Canham and S. W. Bigelow, *unpublished data*). Therefore, large quantities of Mg-rich litter biomass are probably necessary for a strong species impact on soil Mg to emerge. This hypothesis is supported by the fact that an impact on soil Mg was only detected for Norway maple, which has much higher litter production than tree of heaven, and that this effect was restricted to the first 4–5 m from the trunk, where most of the litterfall of the species is concentrated (Fig. 1).

The context dependence of the impact of invasive tree species on ecosystems

The neighborhood effects of the exotic species were site dependent for more than half of the soil properties and processes for which the effects were detected. Our results show consistently that the impact of invasive tree species on ecosystem processes was greatest in the sites with the highest background mean for that process (Figs. 4 and 5). In some cases, the effect of the invader was even negligible in sites with the lowest levels of soil fertility. A similar effect has also been found for native species in forests of the area, where differences in exchangeable Ca under different tree species only appear at sites with higher concentrations of Ca in the parent material (Finzi et al. 1998*a*). Context dependency of invader impacts underscores the difficulty inherent in making generalizations about the impacts of invasive species on ecosystems (e.g., Vilá et al. 2006). In particular, it may obscure the relationship between the local abundance of an invader and its impact. For example, for those soil properties for which the homogeneous model was the best fit, the largest impact always occurred in the neighborhood with the highest local density (and basal area) of invaders. However, when the heterogeneous model was the best fit, the neighborhoods with the maximum impact of the invader were always located in the sites with the highest background mean (Appendices B and C). In many cases, these were neighborhoods with much lower local density and biomass of the invader than in sites with a lower background mean. Thus, we suggest that whereas invader density can be a straightforward indicator of invasiveness (i.e., likelihood of species establishment and spread) due to its clear positive relationship with propagule pressure (Rejmánek et al. 2005), it must be interpreted much more cautiously as a basis for predicting the ecosystem impacts of the invader.

Our leaf chemistry data suggest that site dependency in the impact of the invaders was partly mediated by effects of overall site fertility on differences in nutrient uptake and return in litterfall. The concentration of Ca and Mg in Norway maple litter and Ca and N in tree of heaven litterfall was significantly higher at the sites with the highest soil Ca, Mg, and N content respectively. Litterfall nutrient content is thus part of a positive feedback that accentuates inherent differences in site fertility (Pastor et al. 1984, Reich et al. 1997) and generates high-fertility patches associated with the presence of the invaders. The simultaneous variation in litter and soil chemistry also explains the large inter-site variability in the impact of Norway maple on Ca mineralization, with the highest Ca mineralization occurring in the site with the highest soil and litterfall Ca content, presumably due to a higher Ca release through organic matter decomposition (Dijkstra 2003).

Invasive vs. native tree species impacts on ecosystems: how much of a difference?

Our neighborhood approach allowed the calculation of an index (λ) that quantifies the relative magnitude of the neighborhood effects on soil properties of each of the most abundant tree species in the community. Norway maple had the strongest effect on more soil properties than any other tree species considered here (Fig. 6). Tree of heaven had the strongest effect only on one soil property, total N, a result that agrees with the increase in total N recently reported by Vilá et al. (2006) for this species on Mediterranean islands. However, this species was often second to Norway maple in relative impact, and the suite of soil properties influenced by tree of heaven was very similar to those influenced by Norway maple.

The three native species included in the model each had a very different suite of soil properties on which they had significant (if any) neighborhood effects (Fig. 6). The high λ values for microbial biomass C and N for white ash are consistent with the relatively high λ values for respiration and N mineralization. These latter variables are indicative of the labile pools of C and N in the soil, which in turn are known to control microbial biomass (Wardle 2002, Booth et al. 2005). However, other species with high λ values for respiration and N mineralization (e.g., Norway maple) showed much smaller impact on microbial biomass. This suggests that additional factors must be involved in the species-specific effects on microbial biomass. Red oak had the largest effect on forest floor depth, C:N ratios and mass C (although models including species effects for mass C were not a better fit than the basic model). These results agree with previous studies that showed soils under red oak to have relatively high forest floor mass, total C, and C:N ratios as a consequence of the low decomposition rates of its low-quality litter (Finzi and Canham 1998, Lovett et al. 2002). Thus, neighborhoods dominated by red oak are characterized by slower rates of nutrient cycling than neighborhoods dominated by the other main species. We were surprised that sugar maple did not have strong neighborhood effects on any of the soil properties, even though this species is usually considered to exert a strong influence on N cycling (Finzi et al. 1998*b*, Lovett et al. 2004). In fact, when λ values were averaged for the 18 soil properties analyzed, sugar maple showed the lowest mean value (0.07), followed by red oak (0.18), white ash (0.31), tree of heaven (0.35), and Norway maple (0.49).

These findings imply that the consequences for ecosystem function of invasion by exotic tree species will largely depend on the identity of the native species that are displaced by the invaders. One possible consequence of the continued invasion of northeastern forests by these two exotic species is the replacement of sugar maple, one the most dominant and widely distributed tree species in the hardwood forests of the northeastern United States, by its congener Norway maple. Norway maple is as shade tolerant as sugar maple, and has broader tolerance of soil acidity, higher seedling emergence rates and more vigorous response to gaps than sugar maple (Martin and Marks 2006). In fact, Norway maple was the dominant species in the seedling bank at the three Norway maple sites (P. H. Martin, *unpublished data*). Given the differences in the magnitudes of the impacts found here for the two maples on a wide array of soil properties, a change in the composition of late-successional communities from sugar maple dominated to Norway maple dominated could be expected to cause important changes in the main nutrient fluxes and pools of these forest ecosystems.

Implications for forest structure and dynamics

Our results show that the invasion of northeastern forests by Norway maple and tree of heaven is characterized by predictable, neighborhood-specific acceleration of nutrient cycling rates and ecosystem processes, and localized increases in ambient soil nutrient concentrations. The alteration of soil nutrient cycles has enormous potential for the modification of competitive hierarchies among species in a community. A well-known example is the replacement of conservative evergreens by fast-growing deciduous species when nutrient availability in a particular habitat increases. Species with a conservative use of resources (e.g., evergreens) typically have low leaf nutrient concentrations, low carbon assimilation rates and low growth rates, and therefore a low responsiveness to environmental changes. In contrast, fast-growing species (e.g., deciduous) are more plastic in their response to environmental changes and are able to capitalize on increases in resource availability (see Aerts and Chapin 2000). In a similar way, under a scenario of accelerated nutrient cycling, fast-growing species such as Norway maple and tree of heaven are expected to have a competitive advantage over native species with slower growth and nutrient-conserving traits. This process can be expected to create positive feedback loops in which the impacts of the exotic species on ecosystems favor the performance of conspecific seedlings and saplings. Although documentation of these feedbacks is rare (Ehrenfeld et al. 2005), available data suggest that they may be much more common in nature. In fact, one of the largest impacts of Norway maple was the increase in pH and soil cation concentration, what in turn has been shown to benefit survival and growth of Norway maple seedlings (Martin and Marks 2006).

Invasion by the exotic trees can also be expected to alter competitive hierarchies among the native tree species. Among the common early-successional species in temperate forests of the northeastern United States, red oak and red maple (*Acer rubrum*) are characterized by a more conservative nutrient use and lower litter quality than white ash and black cherry. Among the late-successional dominant species, sugar maple is characteristic of richer soils and has a higher quality litter than beech and hemlock (Van Breemen et al. 1997, Bigelow and Canham 2002). These differences in resource use imply that the modification of soil processes and properties by Norway maple and tree of heaven may well change relative abundances within the native community to the benefit of the more competitive species on nutrient rich sites (i.e., white ash, black cherry, sugar maple). Invasion of northeastern forests by tree species should then be considered as one more factor to add to the array of perturbations and stresses (i.e., acid rain [Likens et al. 1996], pests and pathogens [Lovett et al. 2006], climatic change [Iverson and Prasad 1998]) that are already altering the composition and function of these ecosystems.

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APPENDIX A

Basal area, relative basal area, mean dbh, and maximum dbh of trees >2 cm dbh for the main tree species in each of the three *Acer platanoides* and *Ailanthus altissima* study sites (*Ecological Archives* M078-003-A1).

APPENDIX B

Parameter estimates and two-unit support intervals for the most likely models for the 18 soil properties in *Acer platanoides* sites (*Ecological Archives* M078-003-A2).

APPENDIX C

Parameter estimates and two-unit support intervals for the most likely models for the 18 soil properties in *Ailanthus altissima* sites (*Ecological Archives* M078-003-A3).

APPENDIX D

Parameter estimates and two-unit support intervals for the most likely models analyzing the effects of dominant tree species (both invasives and natives) on soil properties (*Ecological Archives* M078-003-A4).