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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 USA. 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. 1998a,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.

1 A central topic of study within the ecology of biological invasions has been the
2 understanding of why plant communities differ in their susceptibility to invasion (i.e. invasibility)
3 (Davis et al. 2000, Richardson and Pysek 2006). Numerous studies have shown that high levels of
4 soil resources promote the invasibility of a site (see Davis et al. 2000 and references therein). On
5 the contrary, only a few studies have explored whether, once established, the impacts of invasive
6 species on ecosystem processes also vary among sites (e.g. Stock et al. 1995, Vilá et al. 2006). If
7 high soil resource availability also increases the intensity of the impact of exotics on ecosystem
8 function, then the effects of invasive species would have a high degree of site-dependency, with
9 the highest impacts occurring in fertile sites due to the generation of feedbacks loops in which
10 invasive themselves increase nutrient availability. Moreover, if this process has a positive
11 feedback on the rate of spread of the invaders, a transformation of ecosystem properties to
12 conditions more favorable to invasive conspecifics would represent a potential mechanistic
13 explanation for the “lag phase” (Hobbs and Humphries 1995, Sax and Brown 2000) common
14 between establishment of exotic species and actual invasion outbreaks.

15 An approach frequently used for the study of species effects on ecosystem processes is the
16 comparison of the average effects of different species at the plot level, typically from common
17 garden studies or comparisons of stands dominated by different species (Binkley and Giardina
18 1998). Although these studies have provided significant contributions to our understanding of
19 plant-soil interactions, their results are not always easy to extrapolate to natural ecosystems, where
20 plants grow intermingled with each other and a unit of soil is affected by multiple species
21 simultaneously (Ehrenfeld et al. 2005). For example, in mixed forests, the dominant ecosystem
22 fluxes driven by canopy trees (e.g. throughfall, litterfall, nutrient uptake) are primarily vertical
23 rather than horizontal, and the tree identities overhead and nearby have distinctive effects on a
24 whole host of ecosystem processes at the “neighborhood” scale [0-25 meters] (Binkley and

Giardina 1998, Finzi et al. 1998a,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 spatial-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 USA - 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 1800's (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 U.S. 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, Inc., 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 x 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 4 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-m² litter traps were placed in each of the six study sites next to a random sub-sample of the 30 points used for soil sampling

(n=120 traps). 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 a 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 2 days. Mean soil moisture for the six sites varied between 18-25%, 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 48h at 60°C and weighed to the nearest 0.1 mg. Ten air-dried leaf sub-samples were selected from the subsample of leaves collected during a 4-day rain-free period in each site and ground in a Kleco Tissue Pulverizer for chemical analyses (n=30 sub-samples per invasive species). 50 mg of each sub-sample were digested in a microwave digester for 1 hour with 9 ml of nitric acid, and the slurry analyzed 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 min, and then allowed to settle for 0.5 h before pH was measured on a Accumet AR20 pH meter (Fisher, Springfield, New Jersey, USA). Exchangeable Ca, Mg and K were extracted using 0.1 mol/L BaCl₂. One hundred milliliters of BaCl₂ were added to 10 g of air-dried sieved soil. The flasks were agitated at 125 revolutions min⁻¹ for 1 h and

1 allowed to settle overnight. Soil slurries were filtered through Whatman Number 41 filter paper
2 and preserved at 4°C until analyses. Concentrations of the three cations were measured using
3 inductively plasma atomic emission spectrometry (Leeman Labs Inductively Couple
4 Plasma/Profile, Hudson, New Hampshire, USA). Standards were prepared from 1000 and 10 000
5 mg/L liquid stock solutions and diluted using 0.1 mol/L BaCl₂. Lower detection limit was 0.1
6 mg/L.

7 Ca mineralization was estimated by comparing the concentration of exchangeable Ca in the
8 initial soils with the concentrations after 6 months of incubation in the laboratory at room
9 temperature (22-23°C). 50-g subsamples of fresh soil were incubated in containers with a plastic
10 cover that allows oxygen exchange but prevents moisture lost. Comparisons of moisture content in
11 the soil subsamples before and after the incubation showed that it did not suffer significant
12 changes throughout the six months of the experiment.

13 Total soil C and N were analyzed on air-dried soils using a Carlo Ebra NA 1500 Analyzer
14 (CE Elantech, Milan, Italy). Samples were combusted at 1020 °C followed by chromatographic
15 analyses of N₂ and CO₂ using 16-20 mg subsamples previously ground in a Kleco Tissue
16 Pulverizer. Acetanilide (C₈H₉N) was used as a standard for both C and N. Analytical error was
17 <5%. For the estimation of inorganic N pools (NH₄⁺ and NO₃⁻), 10-g subsamples of fresh soil were
18 extracted by adding 50 mL of 2M KCl to each sample, shaking the samples at 125 revolutions
19 min⁻¹ for 1 h, and allow settling overnight. The slurry was filtered through Whatman 41 filter
20 papers into 60-mL polyethylene bottles and analyzed using a Lachat QuikChem 8000.

21 Soil microbial biomass was determined using the CHCl₃-fumigation-incubation procedure
22 (Jenkinson and Powlson 1976), a technique that provides a useful measure of microbial-based
23 nutrient pools linked to basic N cycling functions (Bohlen et al. 2001). A 10-g subsample of fresh
24 soil was fumigated for 24h with distilled CHCl₃ 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 CO₂ 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 CO₂ 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 NO₃⁻ 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 (Canham and Bigelow, *unpublished data*). The isotropic lognormal function has the form:

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

where Y_k is the total litter fall (in g/m²) in trap k , DBH_i is the diameter at breast height of $i=1 \dots n$ 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 Eqn. 1, with the mode of the dispersal curve (X_0') modified to take into account wind direction effects:

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

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. %N, C:N ratio, Ca, Mg, K) were analyzed using one-way ANOVAs (JMP Version 4.0.4, SAS Institute 2001), 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

1 native tree species in the neighborhood. Table 1 includes a complete list and initial range values of
 2 all model parameters.

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

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

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

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

12 where X is the combined effect (quantified below) of neighboring trees of the exotic species on
 13 soil property Y and b is the slope of the effect, assumed to be the same for the three sites
 14 (“homogeneous slopes model”). We considered the effect (X_i) of a neighboring individual i of the
 15 exotic tree on a soil property to vary as a direct function of the size of the neighbor, and as an
 16 inverse function of the distance to the neighbor. Then, for $i=1 \dots n$ invasive trees within a radius of
 17 25 m from each sampling point, the combined effect of the invasive species (X) on a given
 18 ecosystem property is defined as:

$$X = \sum_{i=1}^n DBH_i^\alpha \exp(-\gamma \text{distance}_i^\beta) \quad (5)$$

20 where DBH_i is diameter at breast height of the i th exotic tree; distance_i is the distance of i th
 21 individual from the sample point; and α , β and γ are parameters determining the shape of the effect
 22 of the DBH (α) and the distance to the neighbor (β and γ) on X . Instead of setting α and β
 23 arbitrarily, we tested 2 different versions of Eq. 5, fixing α to values 1 or 2 and letting β and γ to

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:

$$Y = a_s + (b + c a_s) X + \varepsilon \quad (6)$$

where the b and c parameters define the shape of the change in Y with X (“heterogeneous slopes model”). 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:

$$Y = c - a_s \exp(-b X) + \varepsilon \quad (7)$$

where c is the asymptote; a_s the mean value of the soil property Y for each of the three study sites; b the slope of the exotic effect; and X 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 (6 sites together) using two different models to describe the species effects (X). The first equation followed an exponential form:

$$X = \sum_{j=1}^s \sum_{i=1}^n \lambda_j DBH_{ji}^{\alpha} \exp\left(-\gamma distance_{ji}^{\beta}\right) \quad (8)$$

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 zero to one 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:

$$X = \sum_{j=1}^s \sum_{i=1}^n \lambda_j DBH_{ji}^{\alpha} \frac{1}{1 + \left(\frac{distance}{X_0} \right)^{X_b}} \quad (9)$$

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 ($Y = a_s$), 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 Corp.). 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 2 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 2-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 degrees (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 ($11.55 \text{ kg}\cdot\text{year}^{-1}$ vs. $5.35 \text{ kg}\cdot\text{year}^{-1}$, 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 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 9 (Norway maple) and 6 (tree of heaven) of the 18 soil variables tested, at least one of the models that considered the effects of the invasive tree species (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, NO₃⁻ pool, net N mineralization, net nitrification and Ca mineralization. Tree of heaven had an effect on pH, exchangeable Ca and K, mass N, NO₃⁻ 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 NO₃⁻ 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) (Appendix B, C). pH and exchangeable cation concentrations declined as a simple negative exponential function of distance ($\beta \sim 1$) from both Norway maple and tree of heaven neighbors (Fig. 2, 3). In contrast, the decline 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. $\beta > 1$) (Appendix B, 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 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; Appendix B, 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 (Fig. 4, 5). In the heterogeneous slopes models, the positive values of c (Appendix B, C) indicate that the magnitude of the effect of the exotic trees was positively related to the mean of the site (Fig. 4, 5). As a consequence, in all cases the maximum impact of the invasive species on a

1 soil property occurred at a neighborhood located in the site with the highest background mean for
 2 that variable (Appendix B, C). Thus, the impact of a standard 30-cm DBH Norway maple on
 3 exchangeable Ca and Mg varied between 2 times the mean (in the site with the lowest mean cation
 4 concentration) and 3 times the mean (in the site with the highest mean), and between no effect and
 5 2 times the mean for exchangeable K and Ca mineralization (Fig. 4). The impact of a 30-cm DBH
 6 tree of heaven was always smaller than the effect of a Norway maple of the similar size, ranging
 7 between null (in the site with the lowest mean) and 1.1-1.4 times the mean (in the site with the
 8 highest mean) for pH, exchangeable Ca, and exchangeable K (Fig. 5). Tree of heaven had an effect
 9 on mass N in the three sites, its magnitude also increasing with the mean of the site (from 1.06 to
 10 1.2 times the mean for a 30-cm DBH tree). The asymptotic slopes model was the most
 11 parsimonious model only for one variable: forest floor depth in Norway maple sites, and predicted
 12 an increase in forest floor depth with distance to Norway maple only in the site with the highest
 13 mean (Fig. 4).

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

15 For 10 of the 18 soil properties analyzed, the basic model that ignored the effects of the
 16 tree species (both natives and invaders) had worse AIC_c scores than at least one of the models
 17 including neighborhood effects of species (i.e. exponential or logistic models) (Table 5).
 18 Neighborhood composition had an effect on forest floor depth, pH, exchangeable Ca and K, mass
 19 N, NO₃⁻, C:N ratio, microbial biomass C and N, and net nitrification. For most of these variables
 20 (7 out of 10), the logistic equation was a better descriptor of the species effects than the
 21 exponential equation (Table 5). The fit of the most parsimonious models for these 10 soil
 22 properties was very good for pH and exchangeable Ca ($R^2 = 0.74-0.77$) and good for the other 9
 23 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 estimate 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 approximately 10 m for forest floor 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 5 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 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 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. 1998a, Ehrenfeld 2003). In fact, the concentrations of Ca, Mg and K in the litter of Norway maple and tree of heaven were 2-4 times higher than values obtained for the six dominant native tree species in the same forests (Canham and 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 (Martin and Canham, *unpublished data*).

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

10 Norway maple and tree of heaven also altered N cycling by increasing cycling rates (i.e.
11 net N mineralization and net nitrification) and the size of ambient N pools. These results mirror
12 previous studies that conclude that increases in inorganic N pool sizes and nitrification rates are
13 one of the most consistent effects of invasive species on nutrient cycling (see Ehrenfeld 2003 and
14 references therein). The stimulation of N cycling under the invasives was at least partially
15 determined by the characteristics of their litter inputs to the soil. High quality litter (i.e. low C:N
16 and lignin:C ratios) and high litter biomass are usually good predictors of positive species effects
17 on nitrogen fluxes (Wedin and Tilman 1990, Scott and Binkley 1997). Both invaders had high
18 quality leaf litter (low C:N ratios and high %N, particularly for tree of heaven) relative to typical
19 leaf litter chemistry for native tree species in temperate forests of northeast US (Scott and Binkley
20 1997, Bohlen et al. 2001, Lovett et al. 2004). For example, C:N ratios for litter of the invaders was
21 half as high (~ 30 vs 60) and %N about twice higher (~ 1.4 vs 0.8) when compared to C and N
22 values reported by Finzi et al. (1998b) for leaf litter of sugar maple and hemlock (*Tsuga*
23 *canadensis*) in forests of the same area (northwestern Connecticut). In contrast, our analyses
24 indicate that litter production in Norway maple (TLP=11.55 kg·year⁻¹ for a 30-cm DBH tree) is in

the same range as estimates obtained using similar methods for the 6 dominant native tree species in the same area (Canham and Bigelow, *unpublished data*), while litter production in tree of heaven is actually lower ($TLP=5.35 \text{ kg-year}^{-1}$ 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. 1998b). 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, 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 and references therein), 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

1 proportional to the size of the canopy (Zinke 1962). However, our results show very different sizes
 2 and shapes of the footprints for different soil properties, and suggest that the spatial patterns of tree
 3 species effects on soils are considerably more complex. For some soil properties, effects extend far
 4 beyond the canopy (i.e. pH, exchangeable Ca), while for others the footprint is restricted to the
 5 first few meters from the trunk (i.e. Mg, NO_3^-). Regarding shape, some footprints were
 6 characterized by an exponential decline with distance (i.e. pH, exchangeable cations) and others by
 7 a “shoulder” followed by a quick decline (i.e. N mineralization, mass N). Therefore, a better
 8 understanding of plant-soil interactions will benefit from spatially-explicit studies that take into
 9 account the relative locations of individual trees and the sampling points where ecosystem
 10 properties are measured.

11 For example, differences in the nature of the footprints were clearly noticeable for the three
 12 cations (Ca, Mg, and K) (Figs. 2, 3), and can be explained by differences in their internal cycling
 13 within these ecosystems. Aboveground cation return to soil takes place by three main pathways:
 14 stemflow, throughfall and litterfall. These processes represent a gradient in spatial extent, from
 15 very localized stemflow (with measurable effects only within 1-2 m around the stem; Levia and
 16 Frost 2003), to throughfall beneath the crown and potentially concentrated around the drip edge
 17 (Levia and Frost 2006), to the effects of litterfall extending well beyond the drip line of the tree
 18 crown (Staelens et al. 2003). The large extent of the impact of the two invasive species on soil Ca
 19 (i.e. measurable impacts within 20-25 m for Norway maple and 15-20 m for tree of heaven)
 20 suggests that the shapes of their footprints for Ca are controlled largely by litterfall, particularly
 21 since the “footprint” of the invasive species effects on soil Ca were similar to their litterfall
 22 dispersal kernels (Fig. 1). Potassium, in contrast, returns to the soil primarily through stemflow
 23 and throughfall, due to its high susceptibility to leaching loss (Tukey 1970). Our analyses show
 24 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 (Canham and 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 (Fig. 4, 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. 1998a). 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 (Appendix B, 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. 1998b, 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 US, 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 and references therein). 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 US, 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 forest 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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REFERENCES

- Aerts, R., and F. S. I. Chapin. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* **30**:1-67.
- Andersson, T. 1991. Influence of stemflow and throughfall from common oak (*Quercus robur*) on soil chemistry and vegetation patterns. *Canadian Journal of Forest Research* **21**:917-924.
- Belnap, J., and S. L. Phillips. 2001. Soil biota in an ungrazed grassland: response to annual grass (*Bromus tectorum*) invasion. *Ecological Applications* **11**:1261-1275.
- Bigelow, S. W., and C. D. Canham. 2002. Community organization of tree species along soil gradients in north-eastern USA forest. *Journal of Ecology* **90**:188-200.
- Binkley, D., and C. Giardina. 1998. Why do tree species affect soils? The Warp and Woof of tree-soil interactions. *Biogeochemistry* **42**:89-106.
- Bohlen, P. J., P. M. Groffman, C. T. Driscoll, T. J. Fahey, and T. G. Siccama. 2001. Plant-soil-microbial interactions in a northern hardwood forest. *Ecology* **82**:965-978.
- Booth, M. S., J. M. Stark, and E. Rastetter. 2005. Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. *Ecological Monographs* **75**:139-157.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, USA.
- Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees.

- 1 Canadian Journal of Forest Research **24**:337-349.
- 2 Canham, C. D., and S. W. Pacala. 1994. Linking tree population dynamics and forest ecosystem
- 3 processes. Pages 84-93 in C. G. Jones and J. H. Lawton, editors. Linking species and
- 4 ecosystems. Chapman and Hall, New York, USA.
- 5 Canham, C. D., and M. Uriarte. 2006. Analysis of neighborhood dynamics of forest ecosystems
- 6 using likelihood methods and modeling. Ecological Applications **16**:62-73.
- 7 Cole, D. W., and M. Rapp. 1981. Elemental cycling in forest ecosystems. Pages 341-409 in D. E.
- 8 Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press,
- 9 London, UK.:341-409.
- 10 Davis, M. A., P. J. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a
- 11 general theory of invasibility. Journal of Ecology **88**:528-534.
- 12 Dijkstra, F. A. 2003. Calcium mineralization in the forest floor and surface soil beneath different
- 13 tree species in the northeastern US. Forest Ecology and Management **175**:185-194.
- 14 Dukes, J. S., and H. A. Mooney. 2004. Disruption of ecosystem processes in western North
- 15 America by invasive species. Revista Chilena de Historia Natural **77**:411-437.
- 16 Edwards, A. W. F. 1992. Likelihood-expanded edition. Johns Hopkins University Press, Baltimore,
- 17 Maryland, USA.
- 18 Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes.
- 19 Ecosystems **6**:503-523.
- 20 Ehrenfeld, J. G., P. S. Kourtev, and W. Z. Huang. 2001. Changes in soil functions following
- 21 invasions of exotic understory plants in deciduous forests. Ecological Applications **11**:1287-
- 22 1300.
- 23 Ehrenfeld, J. G., B. Ravit, and K. Elgersma. 2005. Feedback in the plant-soil system. Annual
- 24 Review of Environmental Resources **30**:75-115.

- 1 Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen
2 dynamics in an arid grassland. *Ecology* **11**:1301-1310.
- 3 Finzi, A. C., and C. D. Canham. 1998. Non-additive effects of litter mixtures on net N
4 mineralization in a southern New England forest. *Forest Ecology and Management* **105**:129-
5 136.
- 6 Finzi, A. C., C. D. Canham, and N. Van Breemen. 1998a. Canopy tree-soil interactions within
7 temperate forests: species effects on pH and cations. *Ecological Applications* **8**:447-454.
- 8 Finzi, A. C., N. Van Breemen, and C. D. Canham. 1998b. Canopy tree-soil interactions within
9 temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications* **8**:440-
10 446.
- 11 Fujinuma, R., J. Bockheim, and N. Balster. 2005. Base-cation cycling by individual tree species in
12 old-growth forests of Upper Michigan, USA. *Biogeochemistry* **74**:357-376.
- 13 Goffe, W. L., G. D. Ferrier, and J. Rogers. 1994. Global optimization of statistical functions with
14 simulated annealing. *Journal of Econometrics* **60**:65-99.
- 15 Greene, D. F., C. D. Canham, K. D. Coates, and P. T. Lepage. 2004. An evaluation of alternative
16 dispersal functions for trees. *Journal of Ecology* **92**:758-766.
- 17 Heisey, R. M. 1996. Identification of an allelopathic compound from *Ailanthus altissima*
18 (Simaroubaceae) and characterization of its herbicidal activity. *American Journal of Botany*
19 **83**:192-200.
- 20 Hill, D. E., E. H. Sautter, and W. N. Gunick. 1980. Soils of Connecticut. Connecticut Agricultural
21 Experiment Station Bulletin Number 787.
- 22 Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management
23 of plant invasions. *Conservation Biology* **9**:761-770.
- 24 Hu, S. Y. 1979. *Ailanthus*. *Arnoldia* **39**:29-50.

- 1 Hughes, R. F., and J. S. Denslow. 2005. Invasion by a N-2-fixing tree alters function and structure
2 in wet lowland forests of Hawaii. *Ecological Applications* **15**:1615-1628.
- 3 Iverson, L. R., and A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate
4 change in the eastern United States. *Ecological Monographs* **68**:465-485.
- 5 Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2003. National-scale biomass
6 estimators for United States tree species. *Forest Science* **49**:12-35.
- 7 Jenkinson, D. S., and D. S. Powlson. 1976. Effects of biocidal treatments on metabolism in soil .V.
8 A method for measuring soil biomass. *Soil Biology and Biochemistry* **8**:209-213.
- 9 Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in*
10 *Ecology and Evolution* **19**:101-108.
- 11 Kloeppel, B. D., and M. D. Abrams. 1995. Ecophysiological attributes of the native *Acer*
12 *saccharum* and the exotic *Acer platanoides* in urban oak forests in Pennsylvania, USA. *Tree*
13 *Physiology* **15**:739-746.
- 14 Knapp, L. B., and C. D. Canham. 2000. Invasion of an old-growth forest in New York by
15 *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. *Journal of the Torrey*
16 *Botanical Society* **127**:307-315.
- 17 Knecht, M. G., and A. Göransson. 2004. Terrestrial plants require nutrients in similar proportions.
18 *Tree Physiology* **24**:447-460.
- 19 Kourtev, P. S., J. G. Ehrenfeld, and M. Häggblom. 2002. Exotic plant species alter the microbial
20 community structure and function in the soil. *Ecology* **83**:3152-3166.
- 21 Kowarik, I. 1995. Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. *Journal*
22 *of Vegetation Science* **6**:853-856.
- 23 Levina, D. F., and E. E. Frost. 2003. A review and evaluation of stemflow literature in the
24 hydrologic and biogeochemical cycles of forested and agricultural ecosystems. *Journal of*

- 1 Hydrology **274**:1-29.
- 2 Levia, D. F., and E. E. Frost. 2006. Variability of throughfall volume and solute inputs in wooded
3 ecosystems. Progress in Physical Geography **30**:605-632.
- 4 Levine, J. M., M. Vilá, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003.
5 Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal
6 Society of London B **270**:775-781.
- 7 Likens, G. E., C. T. Driscoll, and D. C. Buso. 1996. Long-term effects of acid rain: response and
8 recovery of a forest ecosystem. Science **272**:244-246.
- 9 Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest
10 ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience
11 **56**:395-405.
- 12 Lovett, G. M., K. C. Weathers, and M. A. Arthur. 2002. Control of nitrogen loss from forested
13 watersheds by soil carbon: nitrogen ratio and tree species composition. Ecosystems **5**:712-718.
- 14 Lovett, G. M., K. C. Weathers, M. A. Arthur, and J. C. Schultz. 2004. Nitrogen cycling in a
15 northern hardwood forest: do species matter? Biogeochemistry **67**:289-308.
- 16 Martin, P. H. 1999. Norway maple (*Acer platanoides*) invasion of a natural forest stand:
17 understory consequences and regeneration patterns. Biological Invasions **1**:215-222.
- 18 Martin, P. H., and P. L. Marks. 2006. Intact forests provide only weak resistance to a shade-
19 tolerant invasive Norway maple (*Acer platanoides* L.). Journal of Ecology **94**:1070-1079.
- 20 Nowak, D. J., and R. A. Rowntree. 1990. History and range of Norway maple. Journal of
21 Arboriculture **16**:291-296.
- 22 Pastor, J., J. D. Aber, C. A. McLaugherty, and J. M. Melillo. 1984. Aboveground production and
23 N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin.
24 Ecology **65**:256-268.

- 1 Reich, P. B., D. F. Grigal, J. D. Aber, and S. T. Gower. 1997. Nitrogen mineralization and
2 productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* **78**:335-347.
- 3 Reich, P. B., J. Oleksyn, J. Modrzyński, P. Mrozinski, S. E. Hobbie, D. M. Eissenstat, J.
4 Chorover, and others. 2005. Linking litter calcium, earthworms and soil properties: a common
5 garden test with 14 tree species. *Ecology Letters* **8**:811-818.
- 6 Rejmánek, M., D. M. Richardson, S. I. Higgins, M. J. Pitcairn, and E. Grotkopp. 2005. Ecology of
7 invasive plants: state of the art. Pages 104-161 *in* H. A. Mooney, R. N. Mack, J. A. McNeely,
8 L. E. Neville, P. J. Schei, and J. K. Waage, editors. *Invasive alien species. A new synthesis.*
9 SCOPE series. Island Press, Washington, USA.
- 10 Richardson, D. M., and P. Pysek. 2006. Plant invasions: merging the concepts of species
11 invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409-431.
- 12 Santamour, F. S., Jr., and A. J. McArdle. 1982. Checklist of cultivated maples: III. *Acer*
13 *platanoides* L. *Journal of Arboriculture* **8**:241-246.
- 14 Sax, D. F., and J. H. Brown. 2000. The paradox of invasion. *Global Ecology and Biogeography*
15 **9**:363-371.
- 16 Scott, N. A., and D. Binkley. 1997. Foliage litter quality and annual net N mineralization:
17 comparison across North American forest sites. *Oecologia* **111**:151-159.
- 18 Staelens, J., L. Nachtergale, S. Luysaert, and N. Lust. 2003. A model of wind-influenced leaf
19 litterfall in a mixed hardwood forest. *Canadian Journal of Forest Research* **33**:201-209.
- 20 Stock, W. D., K. T. Wienand, and A. C. Baker. 1995. Impacts of invading N₂-fixing *Acacia*
21 species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation
22 studies and 15N natural abundance values. *Oecologia* **101**:375-382.
- 23 Tukey, H. B. J. 1970. The leaching of substances from plants. *Annual Review of Plant Physiology*
24 **21**:305-324.

- 1 Uriarte, M., C. D. Canham, K. Thompson, and J. K. Zimmerman. 2004. A neighborhood analysis
2 of tree growth and survival in a hurricane-driven tropical forest. *Ecological Monographs*
3 **74**:591-614.
- 4 Van Breemen, N., A. C. Finzi, and C. D. Canham. 1997. Canopy tree-soil interactions within
5 temperate forests: effects of soil elemental composition and texture on species distributions.
6 *Canadian Journal of Forest Research* **27**:1110-1116.
- 7 Vilá, M., M. Tessier, C. M. Suehs, G. Brundu, L. Carta, A. Galanidis, P. Lambdon, M. Manca, F.
8 Médail, E. Moragues, A. Traveset, A. Troumbis, and P. E. Hulme. 2006. Local and regional
9 assesment of the impacts of plant invaders on vegetation structure and soil properties of
10 Mediterranean islands. *Journal of Biogeography* **33**:853-861.
- 11 Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of
12 population biology and ecosystem studies. *Oikos* **57**:7-13.
- 13 Wardle, D. A. 2002. *Communities and ecosystems. Linking the aboveground and belowground*
14 *components*. Princeton University Press, New Jersey, USA.
- 15 Wedin, D. A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial
16 grasses. *Oecologia* **84**:433-441.
- 17 Wolfe, B. E., and J. N. Klironomos. 2005. Breaking new ground: soil communities and exotic
18 plant invasion. *Bioscience* **55**:477-487.
- 19 Zinke, P. J. 1962. The pattern of influence of individual forest trees on soil properties. *Ecology*
20 **43**:130-133

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

Parameter	Range	Interpretation
<i>Spatial distribution of leaf litterfall of invasive tree species†</i>		
Normalization constant (η)	0 - 1000	Arcwise integration of the litterfall dispersal kernel
Total litter production (TLP)	0 - 100 kg·year ⁻¹	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
<i>Effects of invasive tree species on soil properties †</i>		
a_s	0 - 1000	Mean of a soil property in each of the 3 sites
b	-1000 to 1000	Slope of the neighborhood effects
c	-1000 to 1000	Together with <i>b</i> determines the slope of the neighborhood effects in the <i>heterogeneous model</i>
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

Parameter	Range	Interpretation
<i>Invasive vs. native species effects on soil properties</i>		
a_s	0 - 1000	Mean of a soil property in each of the 6 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

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

TABLE 2. Summary of leaf litterfall models. The most parsimonious model (indicated in bold) is the one with the lowest AIC_c. Number of parameters (k), R², the normalizer (η) and maximum likelihood parameter estimates and 2-unit support intervals (in brackets) are given for the most parsimonious models.

	<i>Acer platanoides</i>	<i>Ailanthus altissima</i>
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 year ⁻¹)	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]

Note: See the text for description of the parameters

TABLE 3. Mean leaf litter values ($\pm$ SE) of %N, C:N ratio and base cation concentration (Ca, Mg and K, units in $\text{mg}\cdot\text{g}^{-1}$ leaf litterfall) for *Acer platanoides* and *Ailanthus altissima* in each study site (n=5 for %N and C:N, n=10 for Ca, Mg and K). Also reported are F statistics and p values for one-way ANOVAs for differences in nutrient concentration among the three sites invaded by each species.

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

TABLE 4. AIC_c for the 4 models used to analyze the effect of *Acer platanoides* and *Ailanthus altissima* of soil properties. The most parsimonious model (indicated in bold) is the one with the lowest AIC_c. The number of parameters (k) and R² are given for the best model.

	Basic	Homogeneous		Heterogeneous		Asymptotic		k	R ²
Soil property		$\alpha=1$	$\alpha=2$	$\alpha=1$	$\alpha=2$	$\alpha=1$	$\alpha=2$		
<i>Acer platanoides</i>									
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

Soil property	Basic	Homogeneous		Heterogeneous		Asymptotic		k	R ²
		$\alpha=1$	$\alpha=2$	$\alpha=1$	$\alpha=2$	$\alpha=1$	$\alpha=2$		
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
<i>Ailanthus altissima</i>									
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

Soil property	Basic	Homogeneous		Heterogeneous		Asymptotic		k	R ²
		$\alpha=1$	$\alpha=2$	$\alpha=1$	$\alpha=2$	$\alpha=1$	$\alpha=2$		
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

TABLE 5. AIC_c for the 3 models used to analyze the effect of dominant tree species (*Acer platanoides*, *Ailanthus altissima*, *Acer saccharum*, *Fraxinus americana* and *Quercus rubra*) on soil properties. The most parsimonious model (lowest AIC_c) is indicated in bold. The number of parameters (k) and R² are given for the best model.

Soil property	Basic	Exponential	Logistic	k	R ²
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

FIGURE CAPTIONS

- FIG 1. Predicted leaf litterfall biomass (g/m^2) as a function of distance from a 30-cm DBH *Acer platanoides* and *Ailanthus altissima*.
- FIG 2. Footprint of a standard 30-cm DBH *Acer platanoides* on soil properties within a 25-m radius neighborhood. The predicted relative effect at each distance is given by Eq 5 (see *Methods*). The relative effect (X) at distance 0 from the trunk of a 30-cm DBH *Acer platanoides* is only a function of DBH (in m), and has 2 possible values: 0.3 when $\alpha=1$ and 0.09 when $\alpha=2$.
- 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 (X) at distance 0 from the trunk of a 30-cm DBH *Ailanthus altissima* is only a function of DBH (in m), and has 2 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 3 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 3 sites invaded by the species. Soil properties for which the basic model was the best fit (Table 3) are not shown.
- FIG 6. Impact index (λ parameter in Eqs 8 and 9, see *Methods*) for each of the dominant invasive and native tree species. λ ranges between 0 and 1, and allows for relative differences between species in their effects on each of the 18 soil properties analyzed.

FIG 1.

Con formato: Español
(España - alfab. tradicional)

FIG 2.

FIG 3.

FIG 4.

FIG 5.

FIG 6.