ORIGINAL PAPER

Foliar production and decomposition rates in urban forests invaded by the exotic invasive shrub, *Lonicera maackii*

Tara L. E. Trammell · Haylee A. Ralston · Shannon A. Scroggins · Margaret M. Carreiro

Abstract Exotic invasive shrubs can form dense monocultures in forest understories, which can have cascading effects on ecosystem structure and function. Amur honeysuckle, an exotic shrub that forms dense canopies in eastern forests, has the potential to alter plant community structure and ecosystem functions, such as primary production and decomposition. The goal of this study was to examine foliar productivity and leaf litter decomposition in forests invaded by Amur honeysuckle (*Lonicera maackii*) and to determine the extent to which the presence of this dominant exotic species may alter ecosystem function in these forests. We found that forests invaded by Amur honeysuckle had 16 times greater honeysuckle foliar biomass and 1.5 times lower total foliar biomass than forests of equivalent tree basal area, but having few honeysuckle shrubs. This suggests that productivity of native tree and shrub species may be reduced where honeysuckle density is high. Additionally, honeysuckle litter decayed four times faster and released nitrogen more rapidly than sugar maple litter, and sugar maple litter decayed 19% faster in forests invaded by Amur honeysuckle.

These findings suggest that forests invaded by Amur honeysuckle may exhibit lower rates of organic matter accrual and less nitrogen retention in the forest floor. Since honeysuckle leaves develop in early spring before those of other shrubs or trees in the area, the rapid release of nitrogen from honeysuckle litter that we measured in early spring is timed to benefit this invasive species. The temporally coincident phenologies of nitrogen release during decomposition with the foliar growth needs of this shrub indicates that a potential positive feedback loop may exist between these processes that promotes continued growth and dominance of honeysuckle shrubs in these forested systems.

Keywords Amur honeysuckle · *Lonicera maackii* · Decomposition · Productivity · Urban forests · Forest ecosystems

Introduction

Forests in urban environments are subjected to numerous anthropogenic disturbances such as altered temperature and precipitation, elevated pollutant emissions, and increased exotic species presence (Botkin and Beveridge 1997; Gatz 1991; Lovett et al. 2000; Zipperer and Guntenspergen 2009). The introduction of exotic invasive species to forest ecosystems can have cascading impacts on forest structure and function (Lovett et al. 2006; Vitousek et al. 1997)

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since species composition is an important determinant of biodiversity and subsequent ecosystem functioning (Hooper et al. 2005). Exotic shrubs may not only alter the vertical structure of the forest canopy and the productivity of forest ecosystems (Hartman and McCarthy 2007), but also affect soil temperature and moisture conditions and subsequent soil nutrient cycling (Ehrenfeld 2003). Since exotic shrubs can form dense monocultures in the forest understory (Webster et al. 2006), they can be a significant threat to the community structure and ecosystem functioning in forests.

Several exotic shrub species are capable of forming dense monocultures under forest canopies (e.g., *Ligustrum* spp.), but one of the most important exotic shrub species that pose a threat to eastern deciduous forests in the USA is Amur honeysuckle (*Lonicera maackii* (Rupr.) Maxim.; Webster et al. 2006). Amur honeysuckle was introduced to the United States in the late 1800s from Asia as an ornamental species because of its early spring flowers and numerous attractive red berries (Luken and Thieret 1996). Naturalized populations of Amur honeysuckle first appeared in the 1950s, and now are growing and reproducing in 24 states across the eastern United States (Trisel 1997). This woody shrub can reach a height of 7 m and forms dense thickets along edge habitats and under forest canopies. Higher honeysuckle seedling densities have been documented along edge habitats (Luken and Goessling 1995), yet more complex factors than edge habitat alone have been shown to be important in determining honeysuckle spread (Medley 1997). While previous studies have demonstrated decreased native seedling germination and species richness under honeysuckle canopies (Collier et al. 2002; Hutchinson and Vankat 1997; Trammell and Carreiro 2011), the potential impact of this species on ecosystem functioning is not well understood.

We conducted a large research project studying the ecosystem structure, function, and services in forests along urban interstate corridors (Trammell 2010), a forested habitat type understudied in urban environments. Our research demonstrated that the exotic invasive shrub, Amur honeysuckle, was the most important species explaining variation in the composition of woody plant communities in these forests (Trammell and Carreiro 2011). Several studies have documented the relationship between Amur honeysuckle and altered forest community structure

(e.g., Gorchov and Trisel 2003; Hartman and McCarthy 2008; Luken et al. 1997), yet few studies have examined the potential of Amur honeysuckle to alter ecosystem functioning in forest communities (e.g., Hartman and McCarthy 2007). Therefore, the goals of this study were (1) to determine if there was a relationship between density of Amur honeysuckle and foliar production by trees and shrubs in forests; and (2) to compare decomposition rates and nitrogen mineralization dynamics of honeysuckle and sugar maple (*Acer saccharum* Marshall.) leaf litter in forest plots with high versus low densities of honeysuckle.

To assess the effect of Amur honeysuckle (hereafter referred to as honeysuckle) on primary production in these forests, we collected foliar litterfall from woody plants during the autumn. While this is a conservative estimate of annual foliar production, this technique can be used for temperate deciduous forests that lose the majority of annual foliar production in one autumnal pulse (Berg and Laskowski 2006; Chapin et al. 2002). Not surprisingly, we expected foliar litterfall from honeysuckle would be greater in high-density compared to low-density honeysuckle plots. In contrast, where honeysuckle productivity was greater, we expected litterfall from other species to be less based on another study that demonstrated reduced tree growth in forests invaded by honeysuckle (Hartman and McCarthy 2007).

We also measured and compared the processes of decomposition and nitrogen mineralization of leaf litter in these forests colonized at high and low densities with this shrub. High honeysuckle shrub densities in these forests may alter decomposition rates in two ways: (1) by contributing a labile litter to the organic matter pool in the forest floor, and (2) by physically shading the forest floor and altering temperature and moisture conditions there. Therefore, we had two objectives for the litter decomposition study. First, to determine if honeysuckle might alter decomposition rates in forests, we compared litter decay rates of honeysuckle to a native tree species, sugar maple. This tree species was common in these urban forests and was the most frequently found adult and sapling tree species in these forest plots (62% of all adult trees, Trammell and Carreiro 2011). Based on previous work and personal observation (Ashton et al. 2005; Ehrenfeld et al. 2001), we expected honeysuckle foliar litter to be of higher quality compared to sugar maple litter, and therefore, decay

and nitrogen mineralization rates of honeysuckle litter would be faster. Second, to separate the effects of environmental conditions under varying densities of honeysuckle from the effects of decay rates from different litter types, we conducted a decomposition experiment using standardized honeysuckle and sugar maple litters in high-density and low-density honeysuckle plots. By comparing the litter decay rates of the same litter type placed in high-density versus low-density honeysuckle plots, we would be able to detect potential effects of shrub density on litter decay rates. Directionality of the effect of shrub density was not posited.

Methods

Study area

Louisville (38° 15′N, 85° 45′W) is located along the Ohio River in the Interior Low Plateau, Bluegrass Section and in the Eastern Broadleaf Forest biome (The National Atlas of the US 2009). The total population in Louisville, KY is 713,877 with a mean density of 695 persons km^{-2} (US Census Bureau 2008). The mean annual temperature is 13.8°C with a mean minimum temperature in January of −3.9°C and a mean maximum temperature in July of 30.6°C. The mean annual precipitation is 113 cm, which is evenly distributed throughout the year (National Climatic Data Center 2009). The total inorganic nitrogen in wet deposition ranged from 4.6 to 6.2 kg N ha^{-1} from 2006 to 2009 (National Atmospheric Deposition Program 2010).

Louisville forest plots

The Louisville metropolitan area has three interstate highways that extend east (I-64), south (I-65), and northeast (I-71) from the city center. Previous research on woody vegetation composition and soil characteristics was conducted on a total of twenty-six, 100-m^2 (10 × 10 m) forest plots adjacent to I-64, I-65, and I-71. Detailed descriptions of the three interstates and the vegetation and soil data from the study plots are described in Trammell and Carreiro (2011) and Trammell et al. (2011). In summary, across all of our forest plots a large proportion of the tree species were native (94.1%), and the most frequently found adult,

sapling, and seedling trees were native species (*Acer saccharum*, *Acer saccharum*, and *Celtis occidentalis* L., respectively). The tree community was also quite diverse. We found 51 tree species across all forest plots. The Shannon diversity index for all tree species across all three interstates (H' = 3.64) was close to the maximum diversity (H' max = 3.71) and the tree species were equally abundant (J = 0.98).

A subset of the study plots was chosen to address questions related to primary production and decomposition rates in these urban forests. To assess whether differences in ecosystem processes are associated with degree of honeysuckle invasion in urban forests, plots were placed in two categories. High-density honeysuckle plots were defined using an index that combined total honeysuckle stem density (total stem density >80 stems 100 m^2 plot^{-1}) and honeysuckle importance value (IV >90; where honeysuckle IV = [((relative stem density) + (relative stem density >2 m height)) * (100/2)]). All remaining plots were defined as low-density honeysuckle plots (one plot had no honeysuckle shrubs). The foliar production study was conducted in sixteen plots (7 high-density plots, 9 low-density plots) and the decomposition experiment was conducted in fourteen plots (8 high-density plots, 6 low-density plots; Fig. 1). The mean honeysuckle stem densities and the mean importance value (IV) for high-density honeysuckle plots were higher than for the low-density honeysuckle plots in the foliar production study (193 ± 25 vs. 41 ± 12 stems plot^{-1}, IV = 97.0 vs. 55.3, respectively) and in the decomposition study (184 ± 24 vs. 56 ± 14 stems plot^{-1}, IV = 98.2 vs. 68.2, respectively). The mean tree basal area was similar between high-density and low-density honeysuckle plots in the foliar production study (45 ± 9 and 54 ± 6 m^2 ha^{-1}, respectively, P = 0.39) and the decomposition study (44 ± 9 and 54 ± 8 m^2 ha^{-1}, respectively, P = 0.42).

Foliar production

Foliar production was estimated by collecting leaf litterfall during autumn 2006. Four replicate litter traps (each 45 cm diameter, 0.159 m^2) were placed in each 100 m^{-2} plot between October 4 and 5 before the autumnal pulse. Litterfall was collected four times between October 24 and December 15 to minimize nutrient loss due to leaching after precipitation

Fig. 1 Map of Jefferson
county, metro Louisville,
showing location of
forested plots used for both
primary production and
decomposition studies
(*black circles*), additional
plots used for the primary
production study (*gray
circles*), and additional plots
used for the decomposition
study (*white circles*)
alongside I-64, I-65, and
I-71
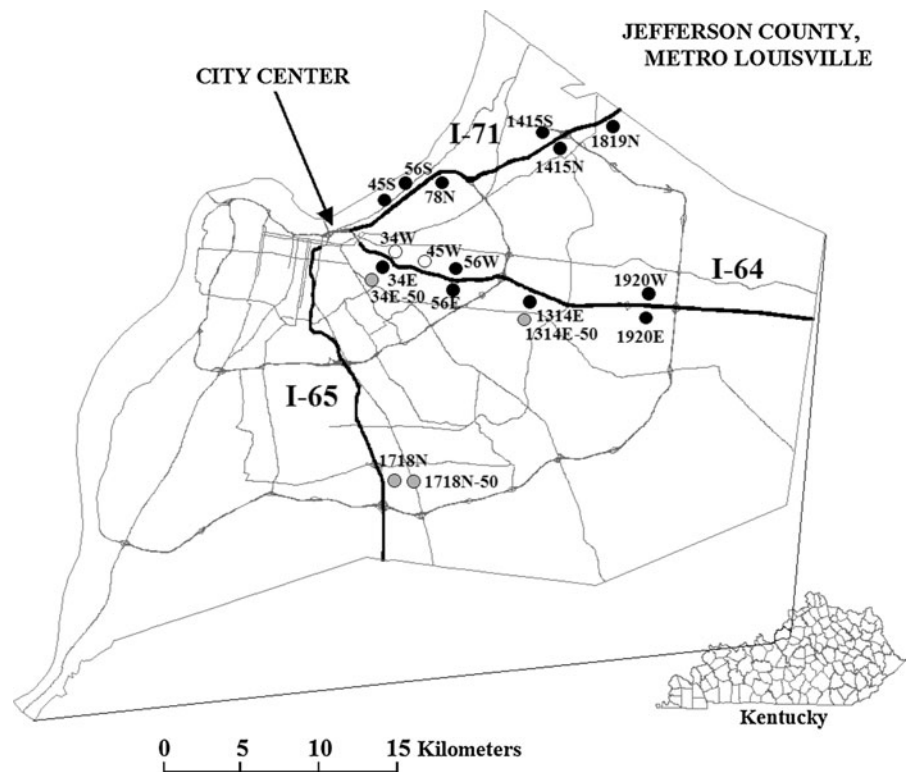
events. Samples were transported to the lab and air-dried. Honeysuckle leaves were separated from leaves of all other species (hereafter referred to as mixed litter) before sample analyses. Fine woody debris (<1 cm diameter) and fruits collected in the litter traps were oven-dried and weighed.

To calculate leaf area index (LAI; m^2 leaves per m^2 of ground area), an index of aboveground primary productivity, the area of foliar samples was measured using a Li-Cor area meter (LI-3100 Area Meter, Lincoln, NE, USA). Subsequently, to obtain productivity measures on a mass basis, leaves were dried at 60°C to obtain their mass. In preparation for chemical analyses, foliar litter samples from each date were combined by litter trap. All litter from each trap was separately ground in a Wiley Mill to pass through a #20 mesh. Subsamples of the milled litter were used to determine carbon (C) and nitrogen (N) content using a Perkin-Elmer 2400 Series II CHNS/O analyzer (Shelton, CT, USA). Molar C:N ratios were calculated from these values. Litterfall lignin content was determined using an ANKOM[200] Fiber Analyzer (Macedon, NY, USA) according to the methods of Van Soest et al. (1991). Following the digestion of

the acid detergent fiber (ADF), acid detergent lignin (ADL) was determined by further digestion in 72% H_2SO_4.

Litter decomposition

Litter decomposition rates and nitrogen dynamics were quantified using the litterbag method. Freshly senesced sugar maple and honeysuckle leaves were collected in litter traps from a single location (Cherokee Park in Louisville, KY). Leaf collection occurred at least once per week throughout autumn 2006 due to the differential timing of sugar maple (October) and honeysuckle (November/December) leaf fall pulses. Prior to litterbag construction, leaves were separated by species, collections from separate dates were pooled and mixed, and air-dried.

Litterbags were constructed from fiberglass window screening with 1.3 mm mesh. Sugar maple litterbags (25 × 40 cm) were filled with 7 ± 0.05 g of leaf litter. Honeysuckle litterbags (15 × 15 cm) were filled with 4 ± 0.03 g of leaf litter. The leaf litter weight differed between honeysuckle and sugar maple litterbags because less honeysuckle litter was

available for collection and a larger amount of sugar maple litter was needed to study its decomposition dynamics over 2 years. Litterbags were constructed to allow for sufficient spread of litter in the bags prior to placement in the field. On January 25 and 26, 2007, litterbags of sugar maple and honeysuckle were placed in the field. Each 10×10 m plot was divided into four quadrats and seven litterbags of each species were placed in species bag pairs (i.e., decomposing side-by-side) randomly within each quadrat, resulting in a total of 28 litterbags species^{-1} plot^{-1}. Sugar maple litterbags were placed in fourteen plots (total = 392 litterbags) whereas honeysuckle litterbags were placed in twelve plots (total = 336 litterbags) due to insufficient litter collection. On the day of bag deployment, seven litterbags of each species were collected immediately and oven-dried at 60°C for 48 h to correct for air-dry to oven-dry mass conversion and any mass loss due to handling. The dried litter was ground in a Wiley Mill to pass through #20 mesh. Subsamples of these initial litterbags were ashed at 500°C for 6 h (Box Muffle Furnace; Asheville, NC, USA) to determine percent ash-free-dry mass (AFDM) and to calculate ash-free-dry mass to oven-dry mass correction factors of the initial litter. Subsamples of the ground litter were also used to determine percent C, N, cellulose, and lignin (see description above for foliar production). Cellulose was determined by subtraction of the ADL from ADF (cellulose + lignin) fractions. The lignocellulose index (LCI) was calculated as the mass ratio of lignin to combined lignin plus cellulose (Melillo et al. 1989).

On each sampling date, one litterbag was collected from each quadrat (4 bags plot^{-1} date^{-1}). Honeysuckle litterbags were collected 28, 55, 82, 105, 124, and 164 days after field placement. Since it was expected that sugar maple leaves would decay more slowly than honeysuckle, sugar maple litterbag collections were spaced at longer intervals and occurred 28, 82, 138, 293, 424, 572, and 759 days after initial placement in the field. The residual litter from each litterbag was oven dried at 60°C for 48 h and weighed to determine mass loss over time. The dried litter was ground and subsamples were ashed and analyzed for C and N as described above for initial litterbags. Soil was sometimes observed in the litterbags, especially in high-density honeysuckle plots, and was carefully removed. However, some soil contamination may have persisted after cleaning visible soil from the litterbags. Therefore, oven-dry and ash-free-dry litter masses and C and N content were corrected for soil contamination using the equations of Blair (1988). These equations are based on the assumptions that the proportion of organic matter in the litter and soil remain constant throughout the decay period, and permits the calculation of the fraction of the litterbag content that is actual litter (vs. soil) based on any reduction in % AFDM of the litter resulting from soil contamination (Blair 1988).

Data and statistical analyses

In the foliar production study, statistical differences in biomass and leaf area index (LAI; m^2 leaves m^{-2} ground area) of the honeysuckle, mixed, and total leaf litter between high-density and low-density honeysuckle plots were determined using the non-parametric Mann–Whitney test because the data did not meet the assumptions of normality and homoscedasticity after data transformations. To assess differences in litterfall phenology between honeysuckle litter and the mixed litter in biomass and LAI on each collection date in high-density honeysuckle plots, we again used the Mann–Whitney test. Potential statistical differences between high- and low-density plots in chemical composition (i.e., %N, C:N, % lignin, and lignin:N) of foliar litterfall were determined using the Mann–Whitney test. Potential differences between high- and low-density honeysuckle plots in fruit and fine woody debris mass were determined using a two-sample t test, after log-transforming the data to meet assumptions of normality and homoscedasticity.

Litter decay rates were calculated from the ovendry (ODM) and ash-free-dry mass (AFDM) remaining using a negative exponential decay model of the form $M_t/M_o = e^{-kt}$, where M_t/M_o is the fraction of mass remaining at time t, t is the time elapsed in days, and k is the daily decay rate constant (Aber and Melillo 1991). Decomposition rate constants (k) were calculated for sugar maple and honeysuckle litter in each plot.

For the decomposition study, statistical differences between initial litter chemistry (%N, C:N, % lignin, lignin:N, % cellulose, and LCI) of honeysuckle and sugar maple leaf litters were determined using two-sample t tests. Differences between decay rates of

sugar maple and honeysuckle litters on an AFDM basis were determined using the Mann–Whitney test. For each litter type, statistically significant differences in the daily decay rate constants (k) between high-density and low-density honeysuckle plots were determined using the Mann–Whitney test. Repeated measures ANOVA was used to determine statistical differences in AFDM remaining, N mass remaining, litter N concentration, and litter C:N for sugar maple and honeysuckle litters decomposing in high- versus low-density honeysuckle plots (i.e., comparison of a single litter type between high-density and low-density honeysuckle plots). In these ANOVA analyses, time was the within-subjects factor and high- versus low-density honeysuckle plots was the between-subjects factor. Prior to conducting the repeated measures ANOVA analyses, we verified that these data met the assumptions of normality and homoscedasticity. Since this study was part of a larger research project on forested interstate verges, we also statistically analyzed the data to determine if other factors may have affected litter decay rates (several soil factors, localized interstate characteristics, and urban-scale factors; see Trammell 2010 for details and results).

To examine patterns of net N uptake (immobilization) and release (mineralization) in sugar maple and honeysuckle litters during decomposition, we measured the N content of the litter in each bag for each collection date by multiplying the N concentration of the litter by the litter mass. The percent of initial N mass remaining was calculated as the product of the mass remaining and the N concentration in the litterbag at time t divided by the initial N content in the litter and multiplying by 100% (% N mass remaining = $((M_t * N_t)/N_o \times 100\%)$ where M_t is the litter mass remaining at time t, N_t is the N concentration at time t, N_o is the initial N content of the litter on day 0, and t is the time elapsed in days). After the initial leaching phase of solubles from litter has occurred, changes in the percent of initial N mass remaining indicate whether growth of microbial decomposers is limited by N. N limitation is characterized by net N accumulation (immobilization) in the litterbag over the initial amount (net N immobilization: % N remaining >100%). Net N release (mineralization) occurs when N exceeds decomposer demand (net N mineralization: % N remaining <100%; Swift et al. 1979).

We evaluated whether relationships existed between litterfall inputs (i.e., litterfall biomass, mixed litter C:N, and mixed litter N concentration) and the peak N immobilization for each litter type. Peak N immobilization provides an indication of the maximum demand for nitrogen required by decomposers in excess of the original N supply in the litter. Relationships between peak N immobilization and the N available in the litter surrounding the litterbag can provide additional information for explaining N dynamics during decomposition of sugar maple and honeysuckle litters in high-density and low-density honeysuckle plots. For each litter type, statistical differences in peak N immobilization, mixed litter biomass, mixed litter C:N, and mixed litter N concentration between high-density and low-density honeysuckle plots were determined using the Mann–Whitney test. All statistical analyses were performed using Systat 10.2 (Richmond, CA).

Results

Foliar production

Autumnal foliar litterfall biomass and leaf area index (LAI) were measured for honeysuckle litter and mixed litter in high-density and low-density honeysuckle plots. As expected, high-density honeysuckle plots produced significantly greater mean honeysuckle leaf biomass (68.9 vs. 4.3 g m^{-2}, $P < 0.001$) and LAI (1.0 vs. 0.1 m^2 m^{-2}, $P < 0.001$) than low-density honeysuckle plots (Fig. 2). On the other hand, mean leaf biomass and LAI of the mixed litter was significantly higher in low-density honeysuckle plots than in high-density honeysuckle plots (biomass: 377 vs. 253 g m^{-2}, $P < 0.01$, respectively; LAI: 4.4 vs. 2.1 m^2 m^{-2}, $P < 0.001$, respectively; Fig. 2). There was a trend for mean total leaf biomass in low-density honeysuckle plots to be greater than that in high-density honeysuckle plots, but the difference was not statistically significant (381 vs. 322 g m^{-2}, respectively; $P = 0.078$). However, the mean total LAI was significantly higher in low-density than in high-density honeysuckle plots (4.5 vs. 3.1 m^2 m^{-2}, respectively; $P = 0.003$).

The temporal patterns of foliar litterfall differed between honeysuckle and the other woody species in the plots. For honeysuckle, mean leaf biomass was
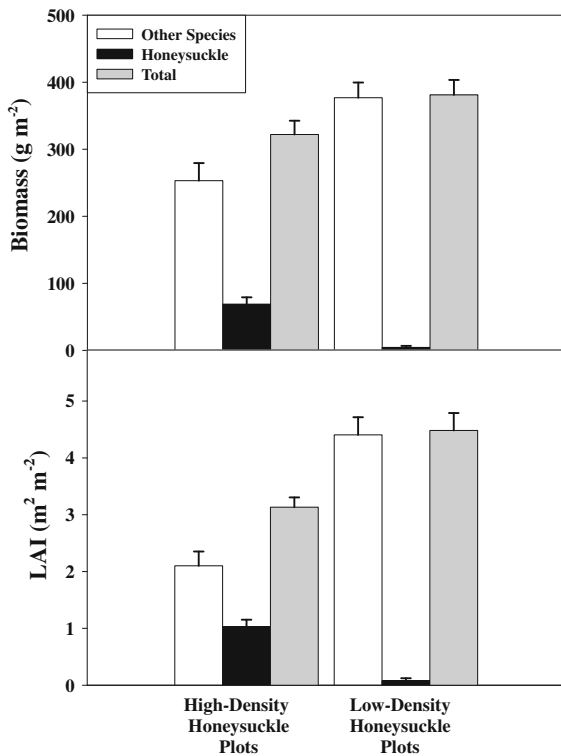
Fig. 2 Honeysuckle (*black bars*), all other species (*white bars*), and the total (*gray bars*) mean leaf biomass (g m^{-2}) and LAI (m^2 m^{-2}) in low-density and high-density honeysuckle plots (±1 SE)

Fig. 3 Mean biomass (g m^{-2}; *top graph*) and LAI (m^2 m^{-2}; *bottom graph*) in high-density honeysuckle plots for each collection date during fall 2006 (±1 SE). Litter traps were installed in the field on October 4 and 5, 2006 and the last collection occurred on December 15, 2006

significantly lower than that of the mixed litter on the first two collections (October 24 and November 3, $P = 0.002$; Fig. 3). By the end of November, inputs of honeysuckle and the mixed litter were similar ($P = 0.277$). However, in the last collection in December honeysuckle litterfall biomass was greater than that of the mixed litter (20.8 vs. 4.2 g m^{-2}, $P = 0.006$; Fig. 3). Litterfall LAI dynamics followed similar patterns to those of the biomass, except on the last November collection when honeysuckle LAI was significantly higher than that of the mixed litter ($P = 0.013$; Fig. 3).

The chemical composition (%N, C:N, %lignin, and lignin:N) of honeysuckle leaves in high-density and low-density honeysuckle plots did not statistically differ (Table 1). However, the chemical composition of the mixed litter between high-density and low-density honeysuckle plots did differ. The %N in the mixed litter was 50% greater in high-density (1.49%) than in low-density honeysuckle plots (0.95%, $P = 0.003$; Table 1). Both C:N and lignin:N
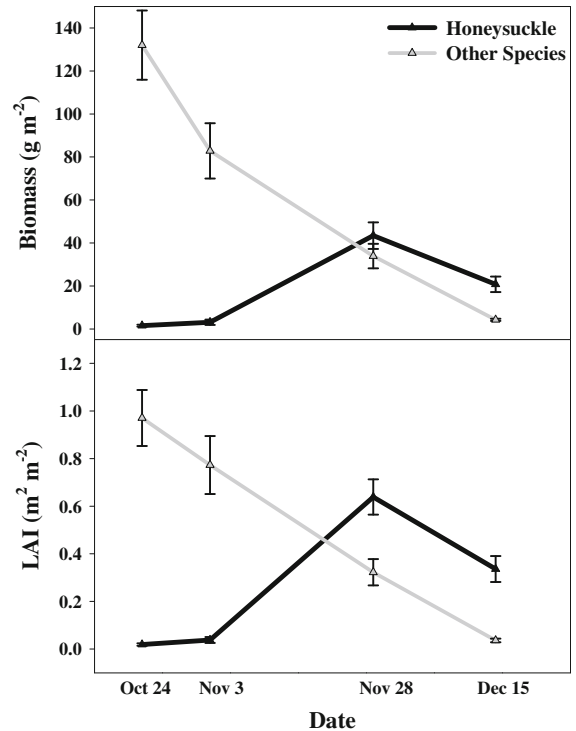
ratios were lower in litterfall collected in high-density than in low-density honeysuckle plots. There was no statistically significant difference in % lignin of mixed litter from high- versus low-density honeysuckle plots (Table 1).

Mean fine woody debris inputs were 3.8 times greater in high-density than in low-density honeysuckle plots (40.1 vs. 10.6 g m^{-2}, $P = 0.001$). While the low-density honeysuckle plots exhibited higher inputs of fruit biomass than high-density plots (26.7 vs. 18.1 g m^{-2}), the difference was not statistically significant due to high variation among plots ($P > 0.10$).

Litter decomposition

As expected, honeysuckle leaf litter was of higher quality than that of sugar maple litter. Honeysuckle litter had higher percent N (1.20% vs. 0.55%), lower C:N (39.87 vs. 87.48), lower percent lignin (7.15% vs. 18.68%), lower lignin:N (6.00 vs. 34.37), lower % cellulose (14.22 vs. 19.02%), and lower LCI (0.33 vs.

Table 1 Chemical composition of honeysuckle leaf litterfall and the combined leaf litterfall of all tree and shrub species (Mixed Litter; excluding honeysuckle litterfall) collected during autumn 2006

		Lignin (%)	N (%)	Lignin:N	Molar C:N
Honeysuckle leaf litterfall	HD mean (SE)	8.66	1.41	6.26	37.36
		(0.450)	(0.058)	(0.468)	(1.654)
	LD mean (SE)	6.90	1.31	6.45	41.13
		(0.632)	(0.105)	(0.344)	(2.838)
Combined tree and shrub leaf litterfall	HD mean (SE)	19.32	**1.49***	**13.28***	**37.52***
		(2.001)	(0.122)	(1.221)	(3.211)
	LD mean (SE)	17.80	**0.95***	**19.16***	**58.69***
		(0.690)	(0.056)	(1.234)	(3.452)

Lignin: N is on a mass basis. *HD* high-density honeysuckle plots, *LD* low-density honeysuckle plots. Statistically significant differences between HD and LD plots for the combined tree and shrub leaf litterfall are shown in bold (* denotes $P < 0.01$). See Trammell 2010 for plot-level data

0.50) than sugar maple leaf litter ($P < 0.002$ for all comparisons). Consequently, honeysuckle and sugar maple litters decomposed at appreciably different rates. Honeysuckle lost 80% of its original AFDM in less than 6 months (164 days) from the start of the experiment whereas sugar maple lost an equivalent mass (81.7%) over a two-year period (759 days). The mean residence time ($1/k$) of honeysuckle litter was 25% that of sugar maple litter (105 vs. 417 days, respectively).

Honeysuckle and sugar maple leaf litters were each placed in high-density and low-density honeysuckle plots to determine if litter decay rates of both species would differ in plots varying in honeysuckle density. We found that honeysuckle litter decomposition rates did not differ between high-density and low-density honeysuckle plots on an AFDM basis (Fig. 4). The mean decay rate constants (k) for honeysuckle litter placed in high-density and low-density honeysuckle plots were 0.892 and 0.831% day^{-1}, respectively, on an AFDM basis ($P > 0.10$). However, sugar maple litter decayed more quickly in high-density ($k = 0.265\%$ day^{-1}) compared to low-density honeysuckle plots ($k = 0.216\%$ day^{-1}) on an AFDM basis ($P < 0.05$; Fig. 4).

Nitrogen dynamics were quite different between the exotic and native litter types throughout the decomposition study. As honeysuckle litter decomposed, patterns of N mass remaining, N concentrations, and ratios of C to N did not differ significantly between high-density and low-density honeysuckle plots (Fig. 5). Little net N was ever immobilized in honeysuckle litter

placed in low-density honeysuckle plots. However, there was a period during the first 80 days of decay when honeysuckle litter immobilized as much as 22% more N than it contained initially in high-density honeysuckle plots (Fig. 5a). N concentrations in honeysuckle litter increased during the decomposition study from 12 mg N g^{-1} litter to as much as 26 mg N g^{-1}, until the last collection date when N concentrations decreased to 19 mg N g^{-1} (Fig. 5b). The C:N ratios of decomposing honeysuckle litter decreased throughout the entire study from 39 to approximately 24 (Fig. 5c).

Sugar maple litter decomposing side-by-side with honeysuckle litter exhibited different nitrogen dynamics. Over the first 572 days of decay, sugar maple litter immobilized N, which peaked to 202% over initial N content on day 138 in the high-density honeysuckle plot and 166% on the same date in the low-density plot. However, after 759 days of decay the net N release phase had begun (74% N mass remaining for litter in high-density plots; Fig. 5d). Sugar maple litter in the high-density honeysuckle plots retained more N early in the study and released more N later in the study than the same litter placed in low-density honeysuckle plots; however, these differences were not statistically significant (repeated measures ANOVA, $P = 0.175$). N concentration in sugar maple litter increased and the C:N ratio decreased throughout the entire decomposition study (Fig. 5e, f). Sugar maple litter in the high-density honeysuckle plots had significantly higher N concentrations and consequently lower C:N ratios than
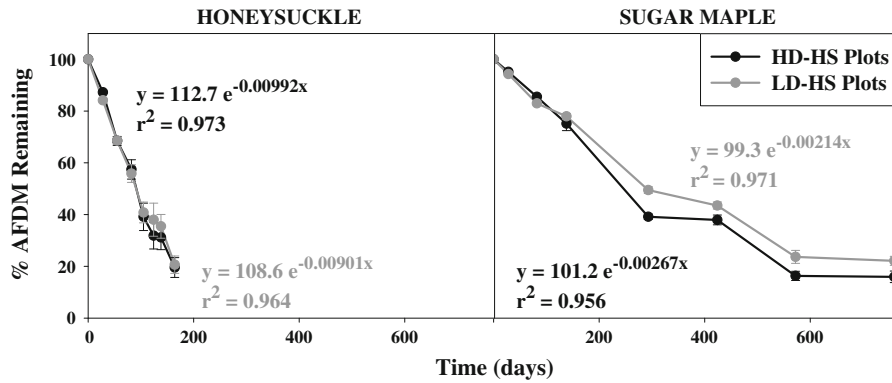
Fig. 4 Ash-free dry mass remaining for honeysuckle and sugar maple litters are shown for low-density (*gray*) and high-density (*black*) honeysuckle plots (±1 SE). The last honeysuckle litter collection occurred after 164 days of decay (July 9, 2007) and the last sugar maple samples were collected after 759 days of decay (February 23, 2009)

Fig. 5 Changes over the time course of decay in nitrogen mass remaining (%), nitrogen concentration (mg N g^{-1}), and C:N for honeysuckle (**a**, **b**, **c**), and sugar maple (**d**, **e**, **f**) litter in low-density (*gray*) and high-density (*black*) honeysuckle plots (±1 SE). *Error bars* not visible are within the radius of plotted *circles*. *Horizontal line* in **a** and **d** represents 100% of initial N in the litter. Note x axes are not the same for honeysuckle versus sugar maple decay periods
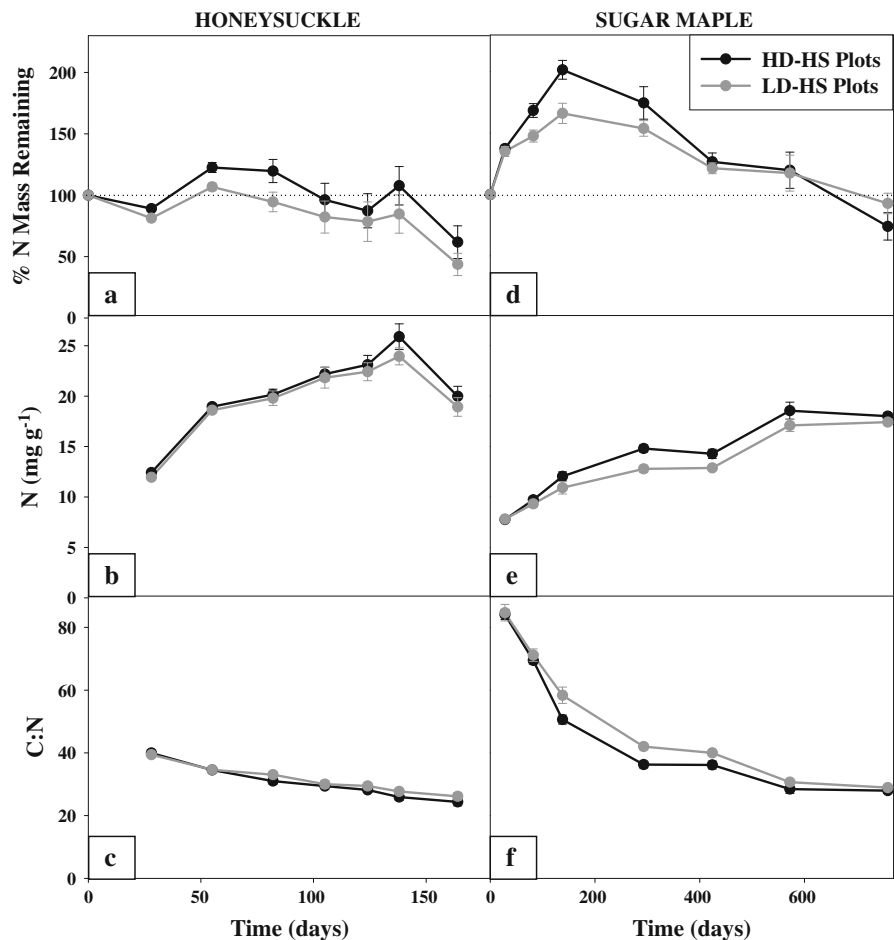
litter in low-density honeysuckle plots (repeated measures ANOVA, $P < 0.01$).

Closer examination of N dynamics with respect to the ODM remaining demonstrates interesting differences between the two litter types over their respective decay periods. As the honeysuckle litter decayed, the N concentration in the litter exhibited a quadratic relationship with the ODM remaining

$(r^2 = 0.740, P < 0.001$; Fig. 6). As litter decayed to about 40% mass remaining, N concentration increased and the relationship between mass remaining and N concentration grew tighter for each collection date (higher r^2 and lower P value up to day 124: $r^2 = 0.75$, $P < 0.001$). However, as litter mass remaining decreased from 40 to 15%, the N concentration decreased and the relationship between them grew weaker compared to day 124 (day 138: $r^2 = 0.56$, $P = 0.005$; day 164: $r^2 = 0.58$, $P = 0.004$). Conversely, for sugar maple litter, the relationship between mass remaining and N concentration was negatively correlated $(r^2 = 0.84, P < 0.001)$ over the entire 759 days of the study when mass remaining averaged 21% (Fig. 6). No strong relationships were found between mass remaining and N concentration within any single collection date except one (day 293). However, as is typical of most decaying litter (e.g., Pavao-Zuckerman and Coleman 2005; Pouyat and Carreiro 2003), honeysuckle and sugar maple litters both showed significant positive relationships between % ODM remaining and C:N ratios throughout the decomposition study (Fig. 6).

Litter N dynamics and litterfall inputs

To provide potential explanations for the different patterns of N dynamics in sugar maple and honeysuckle litters during decomposition, we evaluated relationships between litterfall inputs (i.e., total litterfall biomass, mixed litter C:N, and mixed litter N concentration) and the peak N immobilization for each litter type. Peak N immobilization occurred on day 55 for honeysuckle litter and on day 138 for sugar maple litter placed in both high- and low-density honeysuckle plots (Fig. 5). The peak net N immobilized on day 55 for honeysuckle litter at each plot was negatively correlated with total litterfall inputs in their respective plots $(r^2 = 0.370, P = 0.047)$. However, peak net N immobilized in honeysuckle litter did not exhibit significant relationships with the quality of the mixed litter (all other species exclusive of honeysuckle litter) inputs in each plot (C:N: $r^2 = 0.193$, %N: $r^2 = 0.201$, $P > 0.05$). The net N immobilized by day 138 for sugar maple was also negatively correlated with total litterfall inputs $(r^2 = 0.376, P = 0.034$; Fig. 7). A relationship was
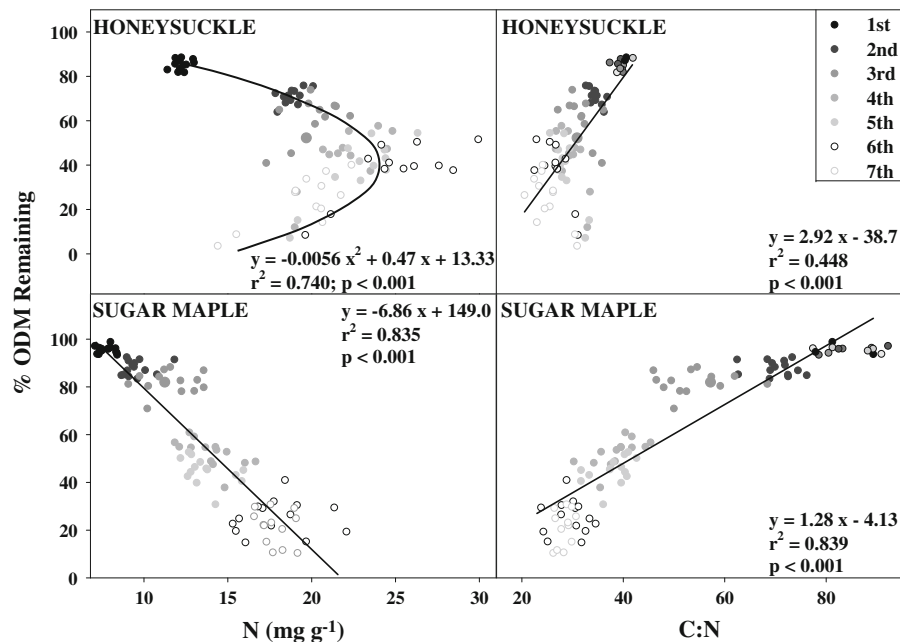

Fig. 6 Relationships between percent oven-dry mass remaining and nitrogen concentration and C:N for honeysuckle and sugar maple litters during decomposition. The symbol color lightens as the number of days since the start of the decomposition period increases (1st, 2nd, 3rd, 4th, 5th, 6th, and 7th collection). The number of days since the start of decomposition differed for honeysuckle (28, 55, 82, 105, 124, 138, and 164 days) and sugar maple litter (28, 82, 138, 293, 424, 572, and 759 days; see "Methods" for details)

also found between peak N immobilized in decaying sugar maple litter and the quality of the mixed litter at each plot. Peak N immobilized in sugar maple litter was negatively correlated with C:N ($r^2 = 0.378$, $P = 0.034$) and positively correlated with % N ($r^2 = 0.361$, $P = 0.039$) of the mixed litter at the site (Fig. 7).

Peak N immobilization and litterfall inputs differed in the high- and low-density honeysuckle plots. In high-density plots, peak N immobilized in honeysuckle litter was 24.3% greater (124.3% N mass remaining) than that in the initial litterbag whereas peak N was only 6.8% greater than that of initial litterbag content for honeysuckle litter placed in low-density honeysuckle plots ($P = 0.028$). For sugar maple in high-density plots, peak N immobilized on day 138 was 103.7% greater than that in the initial litterbag compared to 66.1% greater than initial bag content for litter placed in low-density honeysuckle plots ($P = 0.016$; Table 2). In the decomposition study plots, total litterfall biomass and the C:N of mixed litter (not containing any honeysuckle litter) were 22 and 39% lower, respectively, in high-density than in low-density honeysuckle plots ($P = 0.018$ and $P = 0.037$, respectively; Table 2). The %N of the mixed litter was 1.6 times higher in high-density compared to low-density honeysuckle plots ($P = 0.018$; Table 2).

Discussion

Foliar production

As expected, honeysuckle litterfall biomass and leaf-area index were greater in high-density than in low-density honeysuckle plots (Fig. 2). This corresponded to honeysuckle leaves comprising a larger proportion of the total litterfall biomass (21.4% vs. 1.1%) and leaf-area index (32.9% vs. 1.7%) in the high-density plots. Greater honeysuckle biomass and LAI in high-density honeysuckle plots alter forest physical structure by contributing dense plant biomass and leaf area at lower canopy levels. This altered vertical structure may affect plant and decomposer communities and therefore, seedling recruitment (Collier et al. 2002; Hutchinson and Vankat 1997; Trammell and Carreiro
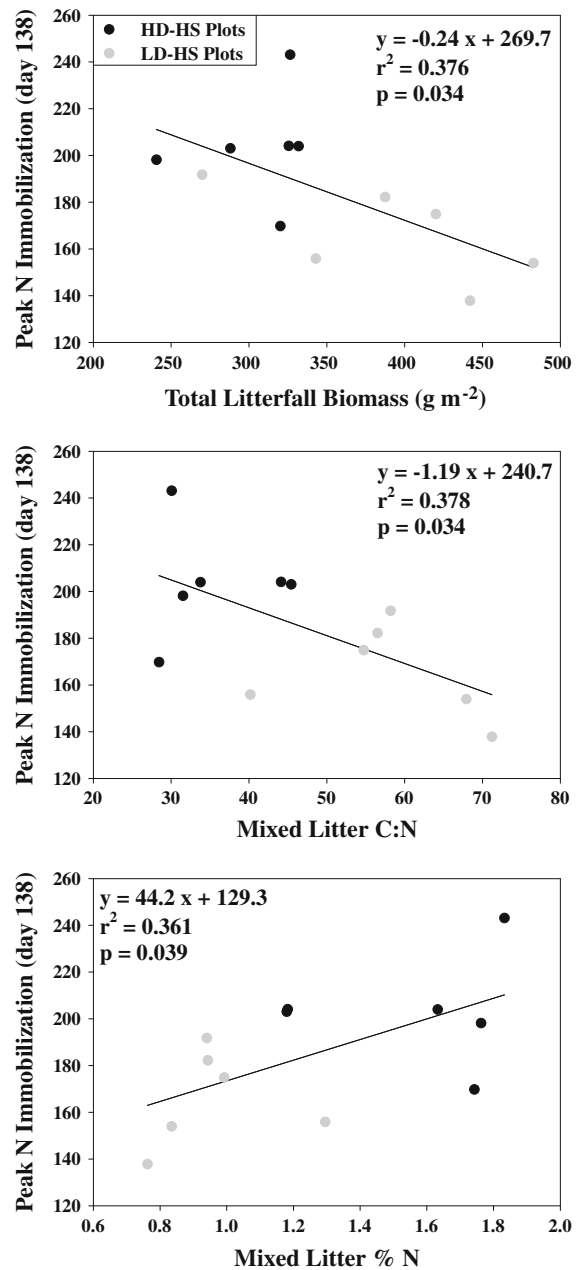

Fig. 7 Relationships between peak nitrogen immobilized (day 138) in decaying sugar maple litter and respective plot-level total litterfall biomass, mixed litter C:N, and mixed litter % N. The mixed litter included all tree and shrub species except honeysuckle. n = 12 plots. Note: high-density honeysuckle plots separate from low-density plots in the above regressions of peak N immobilization versus total litterfall biomass (*left* side of regression), mixed litter C:N (*left* side of regression), and mixed litter %N (*right* side of regression)

Table 2 Mean peak N immobilization (% N mass remaining above original N content) on day 55 for honeysuckle litter and day 138 for sugar maple litter in high-density and low-density honeysuckle plots

	Peak N immobilization honeysuckle litter	Peak N immobilization sugar maple litter	Total biomass (g m^{-2})	Mixed litter C:N	Mixed litter %N
High-density	124.3	203.7	305.4	35.6	1.56
	(4.34)	(9.55)	(14.46)	(3.01)	(0.121)
Low-density	106.8	166.1	390.8	58.1	0.96
	(3.14)	(8.26)	(31.02)	(4.49)	(0.075)

Mean total biomass, mixed litter C:N, and mixed litter %N of litterfall inputs in high-density and low-density honeysuckle plots. Mixed litter does not include honeysuckle litter. Standard error (±) is shown in parentheses below the mean

2011) and decomposition rates (Ehrenfeld et al. 2001) in these forests, by changing the light, temperature, and humidity regime near the ground. As honeysuckle stem density increased, the % light reaching the forest floor decreased exponentially, providing a partial explanation for the decreased tree seedling and sapling densities observed in these forests (Trammell and Carreiro 2011). Honeysuckle was the most abundant plant occupying the lower canopy stratum. Where honeysuckle was not present, few plots had other shrub species that occupied this niche.

Elevated honeysuckle foliar production in high-density honeysuckle plots may also affect the productivity of other plant species occupying higher vertical strata. In these forest plots, the foliar biomass of non-honeysuckle shrubs, vines, and trees was 33% and the LAI 52% lower in high-density honeysuckle plots compared to the low-density honeysuckle plots. This reduction in leaf biomass and LAI of trees and shrubs (other than honeysuckle leaves) occurred despite there being no statistically significant differences in tree basal area between these two categories of forest stands. The fact that total foliar biomass (including honeysuckle shrubs) did not differ significantly between low-density and high-density honeysuckle plots (Fig. 2) suggests that elevated honeysuckle biomass in the shrub layer of the forests may be altering the ability of other plants (in this case, native trees and shrubs) to produce foliar biomass. Another study in hardwood forests of southwestern Ohio, demonstrated reduced growth in tree basal area in sites invaded by honeysuckle shrubs (Hartman and McCarthy 2007). While high-density and low-density honeysuckle plots in our urban forests did not statistically differ in tree basal area, the high-density honeysuckle plots on average were associated with reduced tree basal area, which is consistent with these other findings. We realize that this inverse relationship

between honeysuckle and native tree and shrub foliar biomass may have resulted from honeysuckle invading less productive forests to begin with, taking advantage of an unoccupied niche or increased light to the forest floor. However, whether honeysuckle decreases tree productivity directly or takes advantage of areas with reduced tree growth as an invasion opportunity, results from this study and others suggest that persistent honeysuckle occupation and further invasion may continue to reduce tree growth and foliar productivity in forests.

Shrub honeysuckle exhibits phenological traits that allow it to have a longer growing season than many other native shrubs and trees in the study region. These include longer foliar retention in the fall and earlier bud break in spring (in our area mid-December and first week of March, respectively). This is one potential reason why honeysuckle has an advantage over most native plant species in this region. This study quantified that a higher proportion of the honeysuckle foliar biomass (93%) was collected from November 28 to December 15 compared to the majority of the biomass of the mixed litter, 85% of which fell before November 3. This is similar to other studies that found Amur honeysuckle leaf drop occurring in early-to-mid December in our region (McEwan et al. 2009; Trisel 1997). Another honeysuckle shrub species (*Lonicera X bella*) was shown to comprise up to 47% of its annual carbon gain in understory habitats when native shrub species were leafless (Harrington et al. 1989), suggesting that Amur honeysuckle may also increase carbon gain during their extended spring and fall leaf-on seasons.

Another potential advantage of the extended honeysuckle leaf-on phenology may be to prevent germination of other species. Lab studies of the potential allelopathic effects of honeysuckle found

leachate from honeysuckle leaves prevented germination and survival of native trees (Trisel 1997) and germination of native herbaceous species without preventing self-germination (Dorning and Cipollini 2006). Additionally, an experimental field study found the removal of aboveground Amur honeysuckle shoots enhanced the survival of sugar maple seedlings (Gorchov and Trisel 2003). In our study, 67% of the total fruit biomass of all species fell before November 3rd across all the forested plots. Since honeysuckle leaf fall occurs *after* this seed rain pulse, allelopathic compounds leaching from both its living leaves and perhaps its leaf litter may interact with other factors to decrease seed germination of other species. This would, of course, depend on the activity of these compounds persisting through the winter in the soil. The leaf-on and off phenology of honeysuckle may further enhance the spread of honeysuckle invasion by reducing native species regeneration in early spring, and by enhancing its own carbon reserves both early and late in the growing season.

Total foliar litterfall did not differ greatly in high-density and low-density honeysuckle plots; however, there was a trend toward lower biomass in high-density honeysuckle plots. Over time, decreased foliar biomass of trees and shrubs, as well as reduced seedling recruitment, may entrain a positive feedback loop that continues to reduce primary production in the high-density honeysuckle plots. Such reductions in foliar biomass inputs also affect aboveground carbon and nutrient inputs to decomposers. In forest ecosystems, foliar litter fall represents the largest proportion of primary production that enters soil organic matter pools each year and provides relatively rapid turnover of nutrients to sustain plant growth (Berg and Laskowski 2006). The mixed litter (not including honeysuckle) in the high-density honeysuckle plots had higher %N, lower C:N, and lower lignin:N. Therefore, this difference in chemical composition may alter subsequent soil nutrient cycling process rates and the amount and timing of nutrient availability for plant growth. The high-density honeysuckle plots also produced greater amounts of fine woody debris over the 10-week period of autumnal litter collection. This has implications for changing belowground carbon and nitrogen pools, as well as microbial and invertebrate community composition.

Litter decomposition

Honeysuckle litter decayed almost four times faster than sugar maple litter and reached a level of 4–40% mass remaining within a seven-month period. This rapidly decomposing litter was of higher chemical quality compared to sugar maple litter (e.g., higher % N and lower lignin:N ratio), so it was not surprising that most of the honeysuckle litter decomposed by mid-summer while sugar maple took over 2 years to decompose to similar levels of 21% mass remaining. Other studies have exhibited similar patterns, where exotic species litter of higher quality decayed more rapidly than native species litter (Ashton et al. 2005; Ehrenfeld et al. 2001).

We believe that our ability to detect differences in decay rates between high- versus low-density honeysuckle plots using honeysuckle litter was limited by the rapidity with which this litter broke down. However, by using the longer lasting sugar maple litter, we were able to detect that the decay rate in forested areas densely colonized by this invasive shrub was 1.2 times faster than in areas where honeysuckle was less abundant. Most of this difference in sugar maple decomposition rates between these plot categories was detected in the latter stages of decay and later in the year, after 200 days in the field, when honeysuckle litter had already decomposed and could not be used to assay potential interaction effects like seasonality and honeysuckle shading effects on the decay process.

We are aware that the design of this study does not allow us to distinguish whether decomposition processes that differed by plot type were exclusively and directly caused by differing densities of this shrub. For example, the soils within and between plot types were dissimilar and varied in the extent to which they had been disturbed during highway construction 40 years before this study (Trammell et al. 2011). Tree species composition also varied within and between plots. However, analysis of plot-level variation (e.g., soils and canopy structure variables) did not explain the variation in decay rates for honeysuckle or sugar maple litter (Trammell 2010). Despite differences in soils and overstory species composition, we were nonetheless able to detect changes in litter decay rates and N dynamics in areas colonized differentially by this shrub. This suggests that there is a strong link between the honeysuckle colonization

density and litter decomposition dynamics, since honeysuckle density differences would be a common factor across the plots. Elevated decay rates in high-density honeysuckle plots may be due to direct honeysuckle impacts on decomposition, such as microclimate differences or influences on soil chemistry and decomposers, and/or due to indirect factors that promoted honeysuckle growth in these forests.

Other landscape-scale factors may also have influenced the differential decay rates observed for standardized litters decaying in high- versus low-density honeysuckle plots and cannot be ignored. The faster decomposition rates in high-density honeysuckle plots may be partially explained by their location in the urban landscape. Honeysuckle shrub densities were 5.3 times greater in forest plots close to the city compared to forest plots further from the city center (Trammell and Carreiro 2011). Sugar maple litter decayed 20% faster in high-density honeysuckle plots, and these forest plots were within 10 km of the city. We can suggest at least two possible mechanisms to explain faster decay rates closer to the city center, the urban heat island effect (Oke 1973) and potentially greater N deposition closer to the city (Lovett et al. 2000). One study showed that the maximum urban–rural temperature difference for Louisville (6.5°C in the summer) was among the highest for cities in its region (Matson et al. 1978). Another study performed at ground level showed a maximum urban–rural temperature differential in Louisville of 7.5°C in winter (Westendorf et al. 1989). An earlier study in Louisville found that inorganic N deposition to a forest in the city was 31% greater than to a forest 25 km from the city center and only a few kilometers from interstate 65 (Carreiro et al. 2009). N deposition is known to accelerate the decay rates of labile litter, while decelerating the decomposition rate of litters, like oak, that are high in lignin (Carreiro et al. 2000). Therefore, the faster decay rate of sugar maple litter in high-density honeysuckle plots that are closer to the city center may perhaps be partially explained by the elevated temperatures and N deposition likely to have occurred in the high density honeysuckle plots which were closer to downtown Louisville.

Several urban–rural land-use gradient studies have demonstrated that litter decay rates can vary along urban–rural gradients depending on the interaction between various abiotic (e.g., exotic earthworm density) and biotic (e.g., heavy metals) factors (e.g.,

Cotrufo et al. 1995; Pavao-Zuckerman and Coleman 2005; Pouyat and Carreiro 2003; Pouyat et al. 1997). While our study did not examine the decomposer community, we observed no visible signs of high levels of macroinvertebrate activity in these interstate forest soils. Heavy metals have been shown to have detrimental effects on the abundance and activity of soil microbes (Bååth 1989), but usually at levels much higher than we measured in our plots (Trammell et al. 2011). Other factors besides heavy metal contamination in these forests must be more important in determining decomposition rates because sugar maple litter decayed faster closer to the city despite 40% higher heavy metal concentrations in plot soils within 10 km of the city. Faster decomposition of sugar maple litter closer to the city may be explained by honeysuckle presence since honeysuckle densities were higher closer to the city (Trammell and Carreiro 2011). Dense canopies of honeysuckle shrubs closer to the city may alter sugar maple decay rates directly by increasing moisture availability for soil microbes and potentially decreasing the urban heat island effect on soil temperatures via shading effects on the forest floor, or indirectly by increasing soil nitrogen availability for microbial activity. As honeysuckle litter decomposes, increased nitrogen release from this high N content litter may have helped relieve the microbial N demand in sugar maple litter during decomposition.

Litter N dynamics and litterfall inputs

Sugar maple litter immobilized nitrogen for at least 572 days (% N mass remaining >100%; Fig. 5), suggesting microbes were N-limited while growing on this litter type and that they imported N into the litter from external sources like soil, other litter, and precipitation (Aber and Melillo 1991). This is not surprising considering the low N concentration in the initial sugar maple litter (0.55%), especially compared with that in honeysuckle litter (1.20%). In contrast, honeysuckle litter decomposing in bags placed next to the sugar maple litter, released N quickly as it decomposed. The fact that the two litters were decomposing side by side in the same plots shows that the litter quality difference between these species was a primary driver of N dynamics, and that site factor differences were secondary, but detectable, when within-species comparisons across sites were

made. Nitrogen limitation to soil and litter microbes may help explain the differences observed in sugar maple litter decay rates and N dynamics between high-density and low-density honeysuckle plots, especially when we consider the litter inputs from these forest stands. Sugar maple litter in the high-density honeysuckle plots immobilized more N (204% vs. 166% N mass remaining on day 138; Table 2) and decomposed at a faster rate than the same litter decaying in low-density honeysuckle plots (Fig. 4). Despite lower total litterfall in the high-density honeysuckle plots, the litter quality in the high-density honeysuckle plots was higher and could support rapid microbial growth and hence speed up decomposition over the two-year period of the study. The honeysuckle litter in each of these plot types exhibited similar N dynamics to that of sugar maple litter. At the highest point of nitrogen immobilization for honeysuckle litter (day 55), the high-density honeysuckle plots immobilized significantly more N than the low-density honeysuckle plots, indicating greater N availability to the forest floor in these sites (Table 2). However, there were no relationships between honeysuckle peak immobilization and the quality of the other litter inputs in the plots, most likely because the high initial N concentration of honeysuckle litter itself could support microbial demand over the short decay period.

Honeysuckle litter also exhibited an unusual pattern when examining the relationship between dry mass remaining and nitrogen concentration in the litterbags. Many tree species exhibit a negative linear relationship between these two factors, as did the sugar maple litter in this study (Fig. 6). This relationship occurs when nitrogen is sufficiently low to limit microbial growth (Aber and Melillo 1980). However, for honeysuckle, the relationship between litter dry mass remaining and nitrogen concentration exhibited a quadratic relationship (Fig. 6) over the entire decay period. Furthermore, a more detailed examination of this relationship within each collection date showed that a positive relationship, not a negative one, existed between these two factors. These unusual relationships reinforce the fact that decomposition of honeysuckle litter is not N-limited and organic nitrogen in this litter mineralizes rapidly, at a time of the year when there is low plant and microbial demand (winter and early spring).

The nitrogen released during honeysuckle litter decay occurs when plants are not active enough to take up this nitrogen, and pools of labile nitrogen may then increase in the soil during winter and early spring. As spring temperatures increase, the first plants to leaf-out will have the advantage in acquiring this pool of nitrogen. Leaf development for honeysuckle shrubs occurs in March, weeks before leaf expansion for most other trees and shrubs in forests in our region (McEwan et al. 2009; Trisel 1997; personal observation. in our sites). Thus, assuming this labile nitrogen released in winter and spring remains available in soil, Amur honeysuckle is in an advantageous position to use the early release of inorganic nitrogen from honeysuckle litter decay, creating a positive feedback loop that may promote continued growth and dominance of honeysuckle shrubs in a site. If honeysuckle shrubs are unable to utilize the majority of this nitrogen pulse in late winter-early spring, then nitrogen export from these forests may increase as well. The combined effects of native species dormancy during nitrogen release, low coverage by spring ephemeral herbs under honeysuckle shrubs in our area (M. Carreiro, unpublished data), and the potential increase in nitrogen exports from the system suggests that total nitrogen availability for native shrubs and trees may be reduced in forests invaded by Amur honeysuckle. This potential decrease in nitrogen availability for native trees and shrubs may partially explain reduced production rates observed in these forests and forests in southwestern Ohio invaded by Amur honeysuckle (Hartman and McCarthy 2007). The ability of individual plant species to create positive feedback loops in nutrient cycling is well known (Hobbie 1992), and the ability of an exotic shrub (*Berberis thunbergii*) to promote a positive feedback loop via nitrogen cycling has been previously shown (Ehrenfeld et al. 2001). However, this is the first study to document the potential of Amur honeysuckle to create a positive feedback loop involving nitrogen cycling. Therefore, in addition to other mechanisms such as shading and competition for soil moisture, an increase in nitrogen availability that benefits primarily honeysuckle shrubs may provide an additional mechanism by which honeysuckle can promote its own dominance and simultaneously reduce productivity of other plants in these forests.

Conclusion

The relationships found in this study provide initial evidence that Amur honeysuckle invasion of forests has the potential to alter ecosystem functioning (i.e., primary production, litter decomposition, and timing of net N mineralization from decaying litter). Reductions in foliar biomass of woody species other than honeysuckle were observed in these urban forest plots, which supported high densities of this invasive exotic shrub. This suggests honeysuckle invasion may be detrimental to native tree and shrub productivity, and consequently its structure and species composition into the future. In addition, alterations to ecosystem functioning due to honeysuckle presence in urban forests may be reducing the ability of these forests to provide ecosystem services (i.e., pollutant capture, carbon storage and sequestration) in urban environments. Faster decay rates of honeysuckle litter, as well as faster decay rates of a native species (sugar maple) in high-density honeysuckle plots, suggests the potential for lower rates of soil organic matter accrual and less N retention in forests invaded by honeysuckle. This could create a feedback loop that causes decreased nutrient availability for native plant species and promotes continued dominance of honeysuckle shrubs.

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