Effect of *Lonicera maackii* on Soil Carbon and Nitrogen in Southwestern Ohio Forests

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Introduced plants threaten biodiversity and ecosystem processes, including carbon (C) and nitrogen (N) cycles, but little is known about the threshold at which such effects occur. We examined the impact of the invasive shrub Amur honeysuckle on soil organic carbon (SOC) and N density at study sites that varied in invasion history. In plots with and without honeysuckle, we measured honeysuckle abundance and size (basal area) and extracted soil cores. SOC and N densities were highest at the site with the longest invasion history and highest invasion intensity (i.e., greatest abundance and basal area of honeysuckle). Basal area of honeysuckle positively affected SOC and N densities likely because of increased litter decomposition and altered microbial communities. Because honeysuckle increases forest net primary productivity (NPP) and SOC, it also may play a role in C sequestration. Our results demonstrate the need to consider the influence of invasion history and intensity when evaluating the potential impact of invasive species.
Nomenclature: Amur honeysuckle; *Lonicera maackii* (Rupr.) Herder LOMA6.
Key words: Amur honeysuckle, deciduous forest, invasion history, invasion intensity, invasive plants, soil nutrients.

Invasions by exotic plant species can profoundly alter the biodiversity and stability of ecosystems (e.g., Gaertner et al. 2009; Pyšek et al. 2012; Vilà et al. 2011). While the effects of plant invasions on native community composition and structure are widely documented, comparatively little is understood about the effects of specific plant invasions on ecosystem function and processes (Ehrenfeld 2003; Liao et al. 2008; Vitousek et al. 1997), although these may be common (Simberloff 2011). For example, nonnative plant species may alter natural biogeochemical cycles of C and N (Ehrenfeld 2003, 2010; Liao et al. 2008; Weidenhamer and Callaway 2012), sometimes making environments more hospitable to other invasive species (Ehrenfeld 2003; Kuebbing et al. 2014, 2015; Liao 2008).

Once established in an area, invasive plant species can influence multiple components of C and N cycles. They can increase aboveground biomass and NPP of invaded ecosystems (Ehrenfeld 2010; Lett et al. 2004), even as overall species diversity declines (Vilà et al. 2011). Differences in leaf and litter quality between invasive and native species can alter litter decomposition rates (Allison and Vitousek 2004; Grout et al. 1997) and litter C : N ratios (Blank and

Young 1997; Evans et al. 2001). Plant invasions also may alter N-fixation and mineralization rates; N availability is frequently higher in invaded than in uninvaded ecosystems, particularly in N-limited systems (Ehrenfeld et al. 2001; Iannone et al. 2015; Liao et al. 2008; Vitousek and Walker 1989 and references therein) although there is variability among these results (Ehrenfeld 2003; Windam and Ehrenfeld 2003).

Worldwide, invasions by woody plants are increasing rapidly (Rejmánek 2014; Richardson and Rejmánek 2011) and, due in part to their perennial nature, these plants can be drivers of ecosystem change including changes to C and N cycles (Liao et al. 2008). One such species, Amur honeysuckle [*Lonicera maackii* (Rupr.) Herder, hereafter honeysuckle], is prolific in forests, open areas, and urban-fringe landscapes of eastern and midwestern North America (Luken and Thieret 1996; USDA NRCS 2014). A native of eastern Asia, this species is a multi-stemmed, deciduous shrub that can reach heights > 5 m (> 16 ft) and densities > 20,000 individuals ha^{-1} (> 7,800 individuals ac^{-1}) (Hartman and McCarthy 2004; Luken and Mattimiro 1991; Luken and Thieret 1996; Luken et al. 1995). Its extended leaf phenology, with leaf-out early in spring and leaf retention into late autumn and an ability to resprout after cutting, as well as its use as an ornamental, have contributed to its invasion in many habitats (Fridley 2012; Luken and Thieret 1996; McEwan et al. 2009). Numerous studies have documented the negative effects of honeysuckle on understory herb and tree seedling abundance and

Management Implications

Amur honeysuckle, an invasive shrub in the eastern United States and Canada, forms dense thickets that negatively affect tree seedlings and ground herbaceous vegetation in eastern deciduous forests. Honeysuckle also is allelopathic but other belowground dynamics remain largely unknown, such as whether the shrub affects C and N cycles, which can in turn affect forest productivity. Unfortunately, little is known about how invasion history (e.g., time since invasion) or invasion intensity (e.g., abundance and size of honeysuckle) affects these processes. We established plots with and without honeysuckle at four study sites that varied in invasion history and measured honeysuckle abundance and size as well as SOC and N density within each plot. SOC, N, and abundance and size (basal area) of honeysuckle were highest in plots invaded by honeysuckle at the site with the longest time since invasion. Basal area of honeysuckle positively affected SOC and N densities at this site and likely contributed to increased soil pH. These effects likely were related to increased decomposition of litter and alteration of microbial communities under honeysuckle. Because the effect of honeysuckle on SOC and N density was greatest in stands with the highest basal area, the alteration in density of SOC and N and in the C : N ratio also could positively or negatively affect native herbs or could intensify invasion by other nonnative herbaceous or woody plants. In addition, because honeysuckle affects soil chemistry and increases forest NPP, it may play a role in C sequestration. Resource managers should be attuned to these effects in areas with high abundance of large honeysuckle shrubs (i.e., those with large basal area) and the longest time since invasion. To maximize the limited resources often available for invasive plant control and to reduce ecosystem-level effects, management intervention should be directed toward stands with those characteristics. Our results demonstrate that knowledge of the history and intensity of invasion are important to fully understand the impact of Amur honeysuckle in native forests, especially with respect to belowground dynamics.

richness, presumably related to competition for light, moisture, and soil resources (Collier et al. 2002; Gorchov and Trisel 2003; Hartman and McCarthy 2008; Hutchinson and Vankat 1997; Miller and Gorchov 2004). While belowground impacts of honeysuckle formerly had received comparatively little attention, recent studies find that secretion of allelochemics by honeysuckle may negatively affect native vegetation (Cipollini and Dorning 2008; Cipollini et al. 2012; Dorning and Cipollini 2006), presence of honeysuckle alters soil nutrient availability (Arthur et al. 2012; McEwan et al. 2012; Poulette and Arthur 2012; Trammell et al. 2012), and secretion of an enzyme by honeysuckle breaks down cellulose which may aid in decomposition of forest litter (Kuebbing et al. 2014). Others have demonstrated that honeysuckle grows better in soil conditioned by another nonnative shrub (Kuebbing et al. 2015) and reduces mycorrhizal fungi of native roots (Shannon et al. 2014). Changes to NPP in honeysuckle-invaded habitats also imply changes to soil C and nutrient availability (Luken 1988). For example, NPP of open-grown honeysuckle thickets approaches values of entire woodland communities (Luken 1988).

The direction and magnitude of response of C and N cycles can vary depending on the invader, and may be linked to specific ecophysiological traits (Liao et al. 2008). Effects of a particular invasive species also may differ by site, suggesting that differences in environmental factors among sites or in the composition, density, and degree of dominance of the invaded community may strongly influence ecosystem-level impacts (Ehrenfeld 2003). Few studies assess invasion intensity with respect to changes in soil nutrient cycles, so little is known about the threshold at which an invasive species will begin to alter ecosystem processes (Ehrenfeld 2003). As such, a major gap remains in our understanding of the relationship between invasive plant abundance and ecosystem impacts (Ehrenfeld 2010; Vilà et al. 2011). Hence, our overall goals were to examine the effect that honeysuckle may have on soil SOC and N density, and to determine whether there is a threshold of this effect related to time since invasion. Our specific objectives were to (1) determine the presence and magnitude of differences in SOC and N density between sites invaded by honeysuckle and sites without honeysuckle and (2) assess the relationship of soil SOC and N density to invasion intensity, including abundance, size, and time since introduction of honeysuckle.

Materials and Methods

Site Description. We selected four forest sites in southwestern Ohio dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), hickory (*Carya* sp.), American elm (*Ulmus americana* L.), slippery elm (*Ulmus rubra* Muhl.), and oak (*Quercus* sp.) (Figure 1). The climate in this area is temperate with warm, humid summers and mild winters. Soils in the region are mesic alfisols, most commonly typic hapludalfs and aquic fragiudalfs (Soil Survey Staff 2011). Study sites were selected to minimize potential differences in soil type, meteorological conditions, nitrogen deposition, and other environmental factors, and to capture variation in honeysuckle invasion history. Mount Airy Forest (MAF; 39°10′06.11″N, 84°34′09.28″ W) is a protected urban forest in Cincinnati, near the epicenter of honeysuckle introduction in southwestern Ohio. Honeysuckle has been present in this forest since at least 1941, when it was planted to prevent erosion (Stradling 2011). Miami Whitewater Forest (MWW; 30°15′42.17″ N, 84°44′21.81″W) and Benedict Nature Preserve (BEN; 39°15′50.34″N, 84°21′16.08″W) are located on the suburban to exurban fringes of Cincinnati, where honeysuckle introduction occurred following its escape from cultivation in the late 1950s to early 1960s (Braun 1961; Luken and Thieret 1996). East Fork State Park (EF; 39°01′06.81″N, 84°07′48.96″W) is located in a rural setting that has been invaded by honeysuckle only within the last few decades.

1 = Miami Whitewater Forest
2 = Mt. Airy Forest
3 = Benedict Nature Preserve
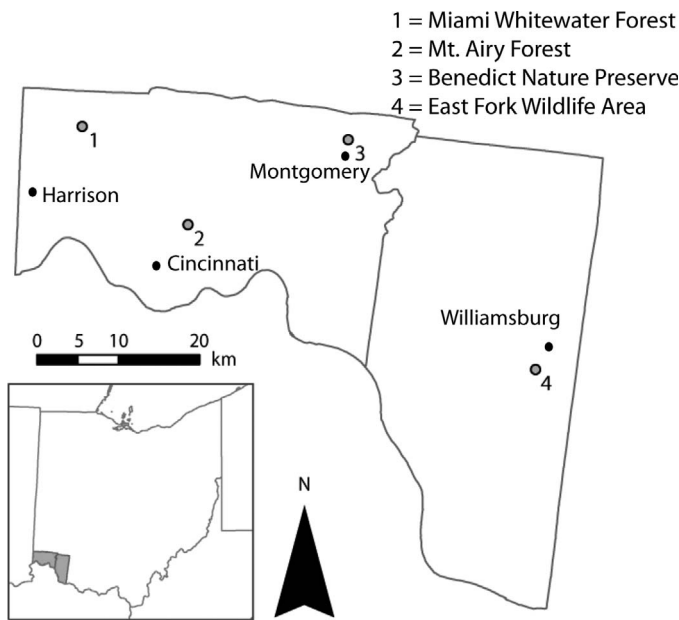4 = East Fork Wildlife Area

Figure 1. Location of study sites (open circles) and nearby cities/towns (closed circles) in southwestern Ohio.

Honeysuckle Censusing. Within each study site, we established 16 30- by 30-m plots, eight in areas without honeysuckle and eight in areas containing honeysuckle. Plots were selected to minimize variation in forest composition, slope, aspect, and soil type. Although there was some variation in each of these parameters, it was relatively low (mean slope = 8 ± 6%, dominantly west and northwest aspects with typic hapludalf soils). We censused honeysuckle at BEN and EF during July to October 2008, and at MWW and MAF in September and October 2009. To measure abundance of honeysuckle, we established three transect lines in each plot; one transect line was centered on a 30-m side of a plot and two additional lines were placed parallel to the first, and 7.5 m away on either side. Along each of these transect lines, we counted any honeysuckle whose canopy intersected a transect line, and, for each individual shrub, we recorded the number of stems and the diameter of the largest (primary) stem. To incorporate both abundance and size data into an estimate of invasion intensity, we computed an approximation of basal area by summing the total cross-sectional diameter of primary honeysuckle stems in each plot.

Soil Sample Collection. We sampled soil in each plot during 2 wk from late July to early August 2011. At each of the four study sites, we collected one soil core from the center of each sampling plot (i.e., 16 soil cores, 8 each from areas invaded and uninvaded by honeysuckle at each study site). We extracted the undisturbed soil cores to depths ranging from 15 to 35 cm (6 to 14 in) using a 2.5-cm diam AMS soil recovery probe (AMS Inc., American Falls, ID); variation

in depth reflected the degree of ground penetrability. We enclosed soil cores in plastic sleeves with end-caps and immediately transported them to the laboratory, where they were stored at 4 C (39 F) until processed (see below).

Efforts to eradicate honeysuckle in southwestern Ohio have been ongoing for more than 25 yr (Luken and Mattimiro 1991). MAF and MWW have active eradication programs that employ a combination of repeated clipping and stem and foliar application of glyphosate (Roundup®, Monsanto Company, St. Louis, MO). Whenever possible, we selected plots outside of the target areas for honeysuckle treatment and removal. However, two of eight of our nominally honeysuckle-free plots at MAF fell within a treatment zone. Three of eight plots in honeysuckle areas at MWW were in the target zone for foliar application of glyphosate. The soil characteristics of these plots were similar to those of the untreated plots, consistent with evidence from previous studies that glyphosate does not have a significant impact on nutrient cycling in forests (Stratton and Stewart 1991).

Soil Sample Processing. We subdivided soil cores into 5-cm depth increments, and sieved each subsample to remove coarse material (> 2 mm) (> 0.08 in), including rocks and roots. Both fractions were dried at 70 C and weighed. For each 5-cm subsample, we calculated bulk density as (total dry mass − rock mass)/(total volume − rock volume). We determined rock volume based on the mass of the coarse fraction and an assumed coarse-fraction density of 2.7 g cm^{-3} (0.98 lb in^{-3}) (following Raciti et al. 2011 and Townsend-Small and Czimczik 2010), and total volume based on the diameter of the core sleeve and the length of the increment (5 cm). After removal of the coarse fraction, we homogenized each 5-cm subsample of each core and then measured pH on these increments separately using the slurry method (Watson and Brown 1998) with a glass electrode pH meter (Mettler-Toledo InLab® Expert Pro, Mettler-Toledo LLC, Columbus, OH). We acidified a portion of each subsample to remove inorganic C (carbonates); acidified samples were used to determine SOC concentration, and unacidified samples were used to determine total N concentration. SOC and N concentrations were determined for each 5-cm subsample by flash-combustion/oxidation using a Thermo CE Elantech Flash EA 1200 elemental analyzer (0.06% C and 0.01% N detection limits; CE Elantech, Inc., Lakewood, NJ). We calculated the density of SOC and N per square meter for each subsample as $D = M_f BD(1 - \delta_{2mm})V$, where D is C or N density, δ_{2mm} is the fraction of material larger than 2 mm diam, BD is bulk density, M_f is the fraction by mass of SOC or N, and V is the volume of the soil core (Post et al. 1982).

Statistical Analyses. We then used two-tailed Wilcoxon rank sum tests (W) and t tests to assess differences in

whole-core SOC and N density (kg m^{-2}) between invaded and uninvaded areas at each site. For total core comparisons, we used SOC and N densities only from the top 15 cm because these depths were available across all cores; depths > 15 cm were missing for multiple cores because of the limits of ground penetration. We used ANOVA to separately test for differences among sites in honeysuckle abundance, size, basal area, and pH, and followed this with Tukey's honestly significant difference (HSD) tests to determine the nature of the differences among sites. We used linear mixed models to determine the relationship between honeysuckle basal area and abundance and SOC and N while accounting for differences among sites by treating site as a random effects variable. We log (base 10) transformed these variables to meet the assumptions of equality of variance and linearity. To examine the relationship between honeysuckle and soil chemistry, we compared a full model to a null model containing only the random effects (slope and intercept). For example, a full model determined the effect of a fixed effect (e.g., basal area) on the dependent variable (e.g., SOC). Full and null models were compared with likelihood ratio tests and a chi-square test determined whether the full model containing the fixed effect contributed significantly to explaining variation in the dependent variable. We used t tests to analyze differences in pH between invaded and uninvaded areas. All statistical analyses were performed using R (versions 2.9.2 and 3.0.2R, Development Core Team 2009, R Foundation for Statistical Computing, Vienna, Austria).

Results and Discussion

Differences in Soil C and N Density. Aggregate profiles based on average values for all invaded and uninvaded plots indicated that SOC and N density decreased with depth across all sites. SOC and N density was slightly higher in plots where honeysuckle was present, particularly in the shallow subsurface soil (5 to 20 cm; SOC: $W = 506$, P = 0.942, N: $W = 416$, P = 0.201; Figure 2). In addition, SOC and N density varied considerably among study sites, with no consistent difference between invaded and uninvaded areas (Figure 3). When values were considered at each study site individually, SOC and N were higher in invaded areas than uninvaded areas only at MAF (SOC: $t_7 = -2.60$, P = 0.022, N: $t_7 = -2.77$, P = 0.015; Figure 3). The overall difference in total SOC and N density observed across all study sites was largely driven by the magnitude of the difference at MAF, the site with the longest history of honeysuckle invasion and the largest honeysuckle plants (see Honeysuckle Density and Basal Area, below). At this site, SOC and N densities were 26 and 30% higher in invaded areas, respectively, exceeding values of SOC and N reported by Liao et al. (2008), where plant invasions, on average, increased soil pools of SOC and N by 7 and 19%, respectively.
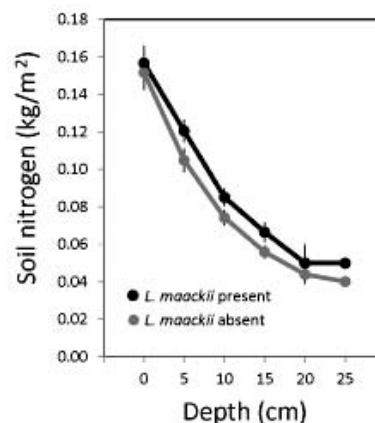

A. Total organic carbon
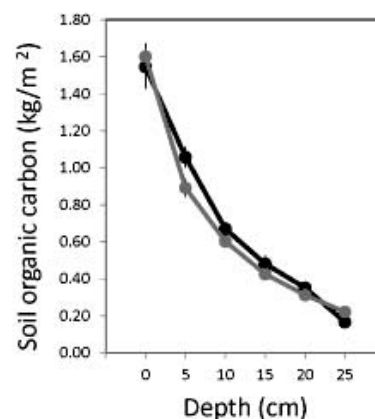
B. Total nitrogen

Figure 2. Aggregate soil profiles for total (A) soil organic carbon and (B) nitrogen for areas invaded and uninvaded by Amur honeysuckle based on average values at each depth across all sites. Error bars represent one standard error of the mean values at a given depth.

Increases in SOC and N densities in invaded areas at the site with the longest time since introduction (MAF) may impact ecosystem processes such as N and C cycling. A similar increase elsewhere in total soil C and N by the exotic weed *Hieracium* also suggested alteration in ecosystem processes (Scott et al. 2001). Honeysuckle may increase SOC density by producing recalcitrant, decomposition-resistant woody debris; by elevating leaf-litter inputs; or by altering the soil microbial community that mediates components of the C cycle. Honeysuckle allocates a large amount of C to physical support structures, which have a high rate of mortality and form dense, resistant debris (De Deyn et al. 2008; Luken 1988) that degrades slowly, and can be an important component of C storage in forest ecosystems (Asner et al. 2003; Sitch et al. 2003). Changes in soil microbial communities that could impact the C cycle have been
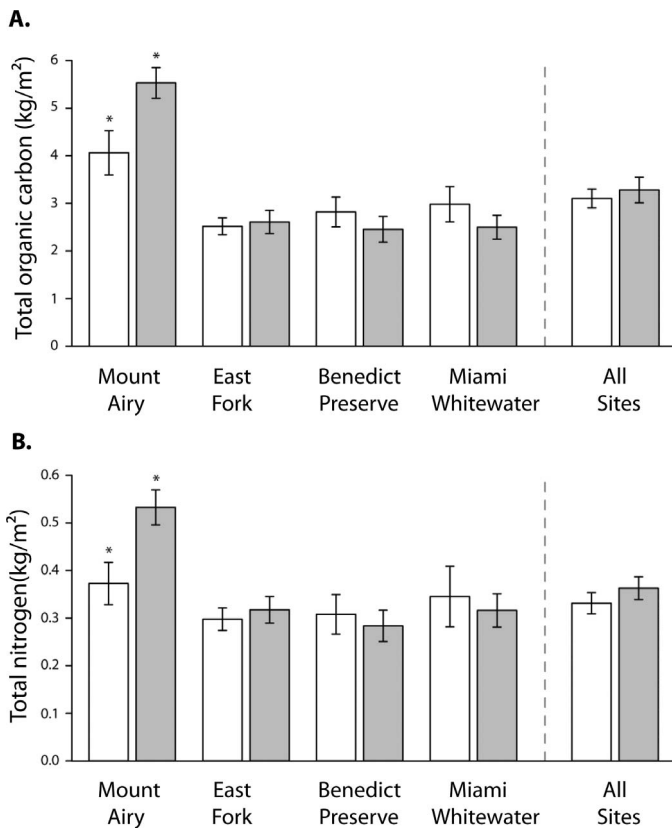
A.

B.

Figure 3. Total (A) soil organic carbon and (B) nitrogen in top 0 to 15 cm of soil at each site in areas uninvaded (white bars) and invaded (gray bars) by Amur honeysuckle. Age of honeysuckle invasion was oldest at Mount Airy, intermediate at Benedict and Miami Whitewater, and youngest at East Fork. Error bars represent one standard deviation of mean values. * P < 0.05.

related to the rapid decay of leaf litter from honeysuckle as well as litter from native plants intermixed with honeysuckle litter (Arthur et al. 2012) and to alteration of soil enzymes (Kuebbing et al. 2014). However, the relationship between litter decomposition rates and soil C pools is complex; an increase in litter decomposition rates does not always lead to an increase in soil C content. Generally, high rates of litter decomposition increase soil C density by increasing C inputs to soil or by increasing the rate of soil C cycling, but in other cases, an elevated rate of decomposition can stimulate C mineralization, causing soil C pools to decline (De Deyn et al. 2008).

Higher density of N in soil at MAF also can be related to increased litter decomposition or alteration in microbial communities under stands of honeysuckle, processes that may be linked. For example, increases in soil N can occur in response to enhanced organic matter input to soils, which contains N and can stimulate biological N fixation by providing microbes with more carbohydrates (Knops et al. 2002; Luo et al. 2006). Furthermore, changes in the

community structure of soil microbes can stimulate N accumulation (Hawkes et al. 2005; Knops et al. 2002; van der Heijden et al. 2008), a process that could explain higher N at MAF because honeysuckle can alter soil microbial communities (Arthur et al. 2012; Kuebbing et al. 2014).

Introduced species are commonly associated with increases in litter decomposition and transfer of N from litter to soil, even in the absence of differences in litter quality (Ashton et al. 2005). In fact, comparison of litter decomposition rates of honeysuckle and native tree species common in our study area demonstrated that honeysuckle leaf litter decomposed and lost N to soil more rapidly than native species in forest environments (Arthur et al. 2012; Blair and Stowasser 2009; Poulette and Arthur 2012; Trammell et al. 2012). Furthermore, in honeysuckle-invaded forests, litter decomposition rates of all species (native and invasive) tended to be higher (Blair and Stowasser 2009; Trammell et al. 2012; but see Arthur et al. 2012). These results suggest that leaf litter from honeysuckle may be more palatable to decomposers, allowing them to maintain higher populations where this leaf litter is present (Blair and Stowasser 2009). Because many native species are dormant during the interval when honeysuckle litter decomposition is at its peak and cannot immediately utilize N released to the soil during litter decay, Trammell et al. (2012) suggested that invaded forests may experience increased N export, ultimately decreasing N availability in the ecosystem. However, we found no evidence of a decrease in soil N content in invaded areas.

The effects of elevated litter decomposition on N pools are variable. For example, high N fluxes from rapidly decomposing litter can increase the potential for N to be lost from the system during disturbance (Hättenschwiler et al. 2005), but more commonly, high fluxes of N from litter to soil increase nutrient cycling rates, and thereby increase soil N availability (Allison and Vitousek 2004; Liao et al. 2008). This latter pattern is consistent with our observation of higher soil N in invaded plots, where honeysuckle inputs to leaf litter increase overall decomposition rates and N density, likely by altering soil microbial community structure (Arthur et al. 2012; Kuebbing et al. 2014).

Honeysuckle Density and Basal Area. Comparison of the average number of honeysuckle individuals observed in invaded plots indicated differences among the four study sites (Figure 4A; $F_{3,28}$ = 9.67, P < 0.001). MAF and MWW had more honeysuckle per plot than BEN or EF (Tukey's HSD, P < 0.05 between groups). Multiflora rose *(Rosa multiflora* Thunb.), spicebush *(Lindera benzoin* (L.) Blume), and blackberry *(Rubus* sp.) also were censused in the plots. However, the total density of all nonhoneysuckle shrubs observed along transect lines was low (< 2.5 individuals plot^{-1}) compared to honeysuckle.
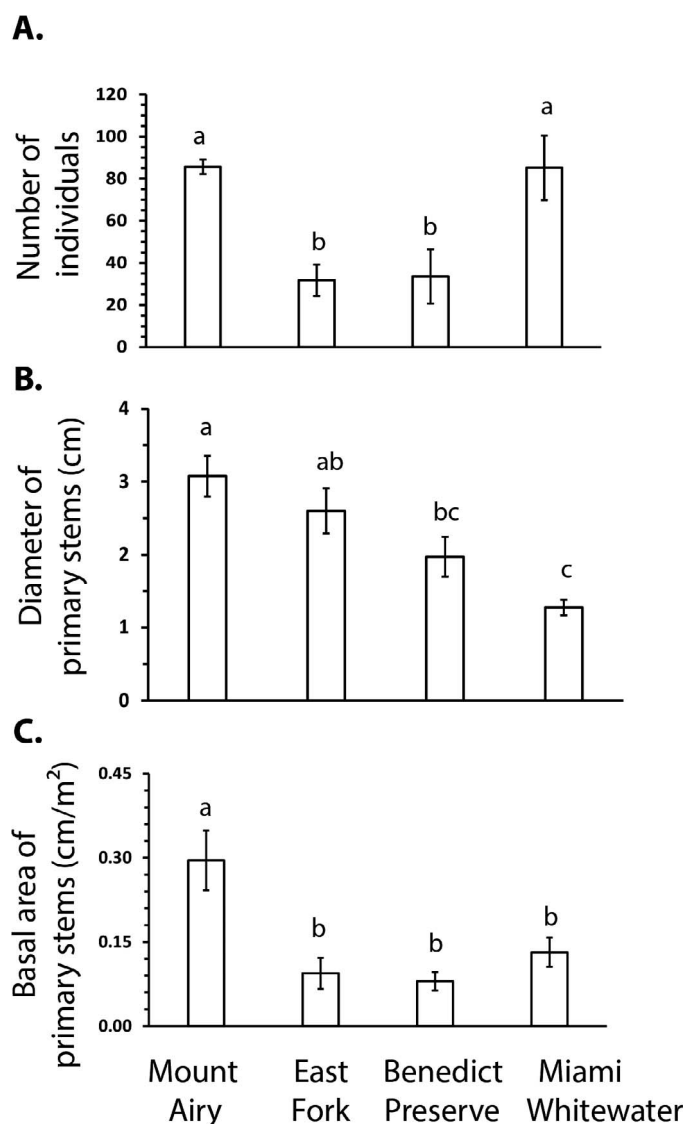
Figure 4. (A) Mean number of Amur honeysuckle individuals per plot, (B) mean diameter of primary honeysuckle stems per plot, and (C) mean basal area computed as sum of diameter of primary honeysuckle stems per plot. Age of honeysuckle invasion was oldest at Mount Airy, intermediate at Benedict and Miami Whitewater, and youngest at East Fork. Error bars represent one standard error and different letters above bars indicate statistically significant differences (P < 0.05) among sites.

The average size of honeysuckle individuals, based on the diameter of each individual's largest (primary) stem, also differed among study sites (Figure 4B; $F_{3,28} = 10.57$, P < 0.001). Average stem diameters were largest at MAF, and were smaller at BEN and MWW (Tukey's HSD, P < 0.05).

Likewise, relative basal area of honeysuckle differed among sites (Figure 4C; $F_{3,28} = 5.68$, P < 0.005). Relative basal area was highest at MAF, and was lower at all other sites (Tukey's HSD, P < 0.05). There were no differences in relative basal area among EF, BEN, and MWW (Tukey's HSD, P > 0.90).

Although the mean number of individuals at MWW was comparable to that at MAF (Figure 4A), the mean basal area and primary stem diameter were much smaller (Figures 4B and 4C). It might therefore not be surprising that there was little difference at MWW in soil C and N density observed in invaded vs. uninvaded sites (Figure 3).

Effect of Invasion History and Intensity. Density of N (χ^2 = 5.71, P < 0.01; SD intercept = 0.27, SD slope = 0.15, SD residual = 0.12) and SOC (χ^2 = 2.81, P = 0.09, SD intercept = 0.43; SD slope = 0.21, SD residual = 0.11) increased with basal area of honeysuckle (Figures 5A and 5B). However, there was no effect of abundance of honeysuckle on N (χ^2 = 2.31, P = 0.13; SD intercept = 0.53, SD slope = 0.34, SD residual = 0.13) or SOC (SOC (χ^2 = 1.91, P = 0.17, SD intercept = 0.64; SD slope = 0.37, SD residual = 0.10; d.f. = 1 for all tests; Figures 5C and 5D).

Invaded areas at MAF had higher densities of SOC and N than uninvaded areas; MAF also has the longest history of honeysuckle presence and the highest invasion intensity (e.g., the greatest number of individuals and highest relative basal area). These results are consistent with the mass ratio hypothesis, which predicts that the extent of impact of a plant species on a given ecosystem function is closely related to its contribution to the total plant biomass of the community (Grime 1998). Larger, more abundant individuals will have a greater ecosystem impact than smaller, sparser individuals, which at least partially explains differences in SOC and N density among our study sites.

Because basal area of honeysuckle is more closely related to biomass than other measures of invasion intensity such as number or size of individuals (Hartman and McCarthy 2004; Luken 1988), the higher basal area of honeysuckle at MAF reflects a higher biomass that contributes to greater densities of SOC and N. Hartman and McCarthy (2008) found that nearly all honeysuckle impacts on native seedlings and herbaceous vegetation were greater at sites with a longer history of honeysuckle invasion, and the same appears to be true for SOC and N densities. Such ecosystem impacts of an invasive species can be cumulative and slow, and may take decades to be fully expressed (Crooks 2005; Simberloff 2011; Strayer et al. 2006). This is the case at MAF, where honeysuckle has been present since at least 1941. At our other sites, honeysuckle individuals may be too small, too few, or too recently introduced to produce a strong effect on SOC and N density (McEwan et al. 2012). Trammell and Carreiro (2011) also reported that size of honeysuckle was larger toward the center of Louisville, KY, compared to areas away from the urban center.
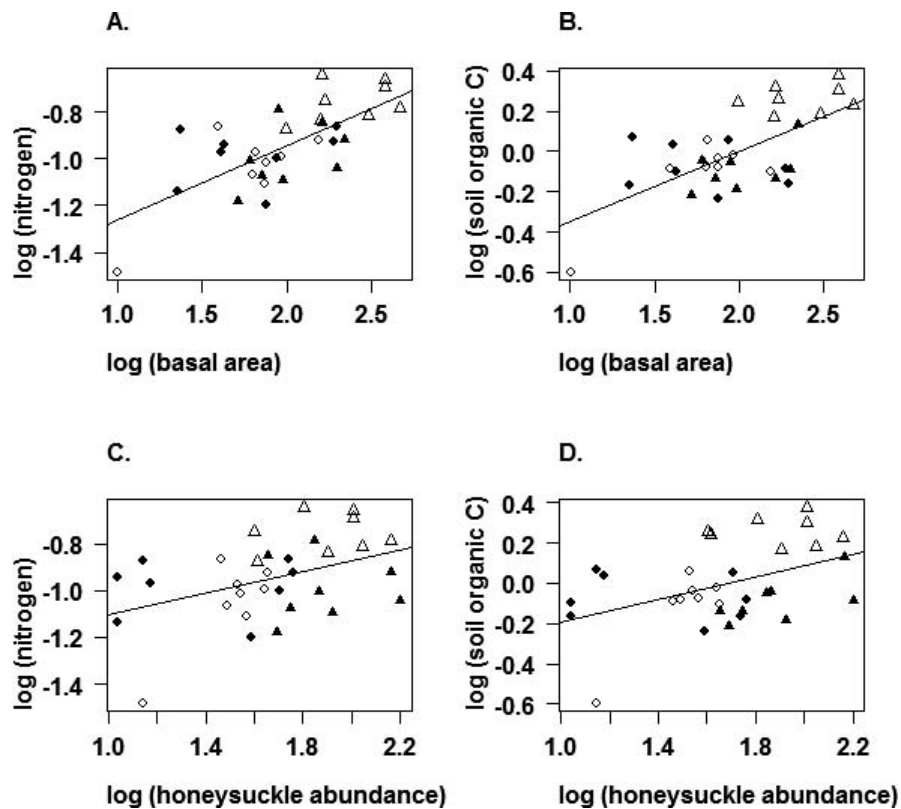
Figure 5. Scatterplots and regression line that shows the mean effect across all sites (i.e., not including random effects variation) of (A, C) total nitrogen (kg m^{-2}) and (B, D) total soil organic carbon (kg m^{-2}) with Amur honeysuckle abundance and basal area. Symbols represent different study sites: open circle = Benedict Preserve, filled circle = East Fork, open triangle = Mount Airy, closed triangle = Miami Whitewater.

Most likely, as in our study, honeysuckle near the urban center that they studied was established prior to expansion away from the urban center. These results demonstrate that the increases in soil SOC and N are determined by thresholds of honeysuckle size and time since introduction.

Honeysuckle basal area ($t_7 = 3.16$, $r_{30} = 0.507$, P = 0.004) and abundance ($t_7 = 2.21$, $r_{30} = 0.380$, P = 0.035) were positively related to soil pH. This is consistent with previous documentation of a positive correlation between honeysuckle density and soil pH (Trammell et al. 2011), although the direction of causality between honeysuckle density and higher pH is not clear. While the difference between plots with and without honeysuckle across the study area as a whole was not significant (mean $\pm$ SE, invaded areas pH 5.6 $\pm$ 0.14, uninvaded areas pH 5.4 $\pm$ 0.13, $t_{61} = -1.03$, P = 0.31), soil pH at MAF was higher than pH at the other study sites (mean $\pm$ SE; BEN, pH 5.5 $\pm$ 0.13; EF, pH 5.1 $\pm$ 0.11; MAF, pH 6.2 $\pm$ 0.20; MWW, pH 5.3 $\pm$ 0.16; $F_{3,60} = 11.64$, P < 0.01). Additionally, pH was higher in invaded plots at MAF (pH 6.7 $\pm$ 0.15) than in uninvaded plots at MAF (pH 5.8 $\pm$ 0.30, $t_7 = -2.68$, P = 0.022). Iannone et al. (2015) also found

higher pH in soil invaded by common buckthorn (*Rhamnus cathartica* L.), but concluded that this difference was related to preexisting conditions. Supporting the idea that honeysuckle was responsible for increased soil pH, Schradin and Cipollini (2012) determined that honeysuckle increased soil pH in greenhouse experiments.

By altering ecosystem processes, honeysuckle and other invasive plants can accelerate their own invasiveness, or, by changing ecosystem processes, they can provide an environment hospitable to other invasive plants. For example, feedbacks from enhanced SOC and N in soil resulting from invasive plants can stabilize or accelerate such invasions resulting in their rapid spread (Liao et al. 2008). Additionally, by altering soil nutrient pools and microbial functions, invasive plants can enhance their invasiveness and likely provide hospitable habitats for new invasions (Ehrenfeld 2003; Ehrenfeld et al. 2001). Kuebbing et al. (2014) found that plots with honeysuckle and Chinese privet (*Ligustrum sinense* Lour.), another invasive shrub, contained more invasive plant species than plots with each shrub alone. In addition, Kuebbing et al. (2015) determined that two invasive shrubs, honeysuckle and Dahurian buckthorn (*Rhamnus*

davurica Pall.), each altered forest soil, improving the performance of the other shrub. This effect indicated a positive feedback among co-occurring shrubs that promoted continued invasion.

Our results demonstrate that long-term invasion by honeysuckle increases SOC and N density in soils and likely also soil pH, and thereby demonstrate the need to consider the complex influence of invasive species when evaluating the potential for forests to serve as C sinks. Previous research and policy development on C sequestration has largely focused on forest ecosystems because of their relatively high primary production and their role as an important global C stock (Peltzer et al. 2010). Despite extensive evidence that plant invasions can dramatically affect these ecosystems through above- and belowground impacts (Ehrenfeld 2003, 2010), the potential impacts of invaders on short- and long-term C sequestration remain poorly understood (Peltzer et al. 2010). Short-term alterations to C sequestration may result from changes in NPP, decomposition, or nutrient fluxes, whereas changes in community composition and structure can produce longer-term effects (Bunker et al. 2005). In relatively productive temperate forest environments, primary productivity is expected to be the principal driver of soil C sequestration (De Deyn et al. 2008). Liao et al. (2008) determined that positive effects by invasive plants, such as honeysuckle, on C and N cycles could stimulate fixation of atmospheric CO_2. Given evidence that honeysuckle significantly increases aboveground NPP in forests (Luken 1988), an increase in soil C density is predicted in invaded forest settings, which is verified by our results. We also show that honeysuckle invasions increase soil N density, which may be useful in immobilizing excess N in urban and suburban environments. Our findings indicate that while such increases are observed in some cases, the presence or absence alone of honeysuckle is not necessarily a good predictor of soil C and N densities. Variations in time since invasion and invasion intensity play significant roles in the impact of honeysuckle on C and N density in deciduous forests.

Acknowledgments

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