

Impacts of Soil Nitrogen and Carbon Additions on Forest Understory Communities with a Long Nitrogen Deposition History

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ABSTRACT

Rates of nitrogen (N) deposition have been historically high throughout much of the northeastern United States; thus, understanding the legacy of these high N loads is important for maintaining forest productivity and resilience. Though many studies have documented plant invasions due to N deposition and associated impacts on ecosystems, less is known about whether invasive plants will continue to increase in dominance with further shifting nutrient regimes. Using soil N and carbon additions, we examined the impact of both increasing and decreasing soil N on native and invasive understory plant dynamics over 4 years in a northeastern deciduous forest with a long history of N deposition. Despite applying large quantities of N, we found no difference in soil nitrate (NO_3^-) or ammonium (NH_4^+) pools in N addition plots over the course of the study. Indicative of the potential N saturation in these forest soils, resin-available

NO_3^- and NH_4^+ showed evidence that the added N was rapidly moving out of the soil in N addition plots. Accordingly, we also found that adding N to soil altered neither invasive nor native plant abundance, though adding N temporally increased invasive plant richness. Carbon additions decreased soil N availability seasonally, but did not alter the total percent cover of invasive or native plants. Rather than being suppressed by excess N availability, native plant species in this ecosystem are primarily inhibited by the invasive species, which now dominate this site. In conclusion, understory plant communities in this potentially N-saturated ecosystem may be buffered to future alterations in N availability.

Key words: invasive species; plant community; nitrogen deposition; nitrate; understory; carbon additions; deciduous forest.

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INTRODUCTION

Chronic resource alterations are occurring worldwide and can cause large changes in ecological

dynamics (Smith and others 2009). For example, changes in soil nitrogen (N) availability due to N deposition can alter plant and microbial community structure (Huenneke and others 1990; Dighton and others 2004; Frey and others 2004; Waldrop and others 2004; Stevens and others 2004; van Diepen and others 2010). Increasing soil N availability, in particular, has been predicted to encourage invasive plant species (Davis and others 2000). Indeed, increasing soil N availability above background rates has been correlated with the abundance of invasive plant species in contrasting ecosystems (Burke and Grime 1996; Brooks 2003; Fenn and others 2003; Magill and others 2004; Allen and others 2009; Pardo and others 2011), likely because many invasive plant species are nitrophilic and faster-growing than native species (Theoharides and Dukes 2007; Funk 2008). Understanding how deposition-mediated N availability alters plant community composition is important to understanding future ecosystem structure and productivity (Ehrenfeld 2003).

Rates of N deposition are heterogeneous across the landscape and can interact with background soil N to alter N availability in soils (Bobbink and others 2010). Deposition can occur as either inorganic N, which can be immediately taken up by many plants and microbes, or as organic N, which can be accessed by only specific plants or is processed by microbes (Lipson and Nasholm 2001; Bardgett and others 2003; Chapman and others 2006). Europe has experienced high rates of inorganic N deposition for decades and impacts of this deposition on ecosystems have been investigated thoroughly (for example, Gundersen and others 1998). In some areas of the United States, particularly the northeast, deposition rates of both inorganic and organic N have been relatively high for many decades, leading to high levels of soil N availability and even N saturation (Aber and others 1989; Ollinger and others 1993; Lovett 1994; Lovett and others 2000). In these systems, of which many are likely still N-limited, plant communities likely shifted upon initial exposure to increased N availability, but these changes may have occurred in the absence of scientific documentation (Bobbink and others 2010). Ecosystems where N deposition has been historically high may provide good opportunities to examine how plant communities respond to increased N availability over the long term.

Carbon (C) additions to soils have been shown to decrease N availability in soil, at least temporarily, leading to lower non-native plant abundance (Ridenour and Callaway 2001; Sanders and others

2007; Perry and others 2010; Steers and others 2011; Kulmatiski 2011). Microbial immobilization following C additions decreases availability of nitrate (NO_3^-) and ammonium (NH_4^+) to plants. Such decreases, however, are often followed by a release of N due to turnover of microbial biomass (Perry and others 2010). Though use of C additions to decrease invasive plant abundance has been attempted in many systems, it is rarely employed in deciduous forest understories, particularly those of semi-urban areas with long histories of N deposition.

Herbaceous understory plants are often the largest reservoir of diversity in deciduous forests and can contribute significantly to total forest net primary productivity (NPP) (Gilliam 2007, 2014). These communities are traditionally co-limited by light and N availability (Cole and Weltzin 2005; Verheyen and others 2012). Invasive plants are abundant in the understory of some northeastern United States deciduous forests (for example, Ehrenfeld and others 2001; Ashton and others 2005), which have had historically high N deposition rates (National Atmospheric Deposition Program National Trends Network). The N-rich, diverse, and invaded understory plant communities in these forests present an opportunity to examine how long-term increased N availability can alter plant community dynamics (Gilliam 2006). Responses of understory vegetation to N additions have been varied in the literature (Gilliam 2006), with some studies finding declines in diversity (Strengbom and others 2001) and biomass (Mäkipää 1998), and others finding no impact of N amendments (Gilliam and others 2006). The nitrogen homogeneity hypothesis posits that a loss in spatial heterogeneity of N, which can occur with chronic N deposition, causes declines in forest biodiversity, particularly for understory vegetation (Gilliam 2006). Here, we examine whether additional nitrogen can further alter understory vegetation biodiversity in a system that has experienced such chronic deposition.

In this study, we aim to understand how short-term increases in soil nutrients alter plant communities in an environment that has already been subject to several decades of elevated N deposition. In a previous study, in a deciduous forest with historically elevated N deposition rates ($6\text{--}8 \text{ kg ha}^{-1} \text{ y}^{-1}$ N over the past few decades), we found that native understory plant species richness was negatively correlated with higher soil inorganic N and that organic soil N additions decreased native understory plant richness (Jones and Chapman 2011). However, this relatively low-level soil N

enrichment ($6.5 \text{ kg ha}^{-1} \text{ y}^{-1}$) did not alter native plant abundance or invasive plant abundance. In this four-year study in the same forest, we examined how understory plant community composition changes across a larger gradient of N manipulations, both increased and decreased (via C additions). The novelty of our study arises from our experimental manipulation of a forest understory where both invasive plant species and soil N (particularly NO_3^-) are abundant. Relative to Europe, wherein NH_4^+ typically predominates N deposition, deposition of N in eastern North America is predominantly as NO_3^- , a form of N that is more favorable to invasive plants (Fargione and Tilman 2005; Gilliam 2006). We hypothesized that soil N additions would increase invasive understory plant diversity and abundance and decrease native understory plant species diversity and abundance due to increased soil N availability. We also hypothesized that decreasing soil N availability via C additions would increase native plant species abundance and diversity. After finding that soil N pools were not changing drastically due to treatments, we examined integrated soil N availability using ion exchange resins. We hypothesized that N additions would increase resin NO_3^- and NH_4^+ and that carbon addition would decrease resin NO_3^- and NH_4^+ .

METHODS

Site Description

Ridley Creek State Park comprises 1054 ha 20 km west of Philadelphia in Delaware County, Pennsylvania ($39^\circ 57' \text{N}$, $75^\circ 26' \text{W}$). The ecosystems in this park are predominantly secondary oak forests, a common ecotype in the northeastern United States. Due to proximity to urban areas and a history of farming (back into the 17th century), Ridley Creek State Park has experienced substantial N deposition for several decades (current rates are $6.5 \text{ kg N ha}^{-1} \text{ y}^{-1}$; <http://nadp.sws.uiuc.edu>). Dominant forest trees include *Quercus rubra*, *Acer rubrum*, *Fagus grandifolia*, *Liriodendrum tulipifera*, and *Carya* spp. Many non-native invasive plant species inhabit the understory of these forests, including but not limited to *Alliaria petiolata*, *Celastrus orbiculatus*, *Glechoma hederacea*, *Microstegium vimineum*, *Persicaria perfoliata*, *Rosa multiflora*, and *Rubus phoenicolasius*. Common native understory species at Ridley Creek State Park include *Celastrus scandens*, *Crataegus* spp., *Parthenocissus quinquefolia*, *Lindera benzoin*, *Toxicodendron radicans*, *Caulophyllum thalictroides*, *Fraxinus* spp. seedlings, *Menispermum canadense*, *Trifolium* spp., as well as many species of ferns. Soils are predominately

well draining, weathered mica schist comprising silt loam (<http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx>).

Experimental Design

We randomly chose 10 sets of four 0.5-m^2 plots within a 1-ha site which was characteristic of the forest interior. Each set of four plots initially had similar species composition and plant density and were chosen to not include trees larger than 2–3 cm in diameter to ensure that understory plants comprised the dominant cover. Each set of four plots comprised a block, which was at least 5 m away from any other block, and to which four treatments were applied (10 blocks of 4 plots—40 total plots). These treatments include control, low N addition ($100 \text{ kg ha}^{-1} \text{ y}^{-1}$ N as NH_4NO_3 added, +N), high N addition ($200 \text{ kg ha}^{-1} \text{ y}^{-1}$ N as NH_4NO_3 added, ++N), and carbon addition ($7000 \text{ kg ha}^{-1} \text{ y}^{-1}$ sucrose added, +C). These rates of N addition were chosen (1) to substantially increase the inorganic N deposition rates simulated by the Jones and Chapman study (2011; $6.5 \text{ kg N ha}^{-1} \text{ y}^{-1}$), which showed no impact, and (2) to simulate 15 times and 30 times the current deposition rates (which are $6.5 \text{ kg N ha}^{-1} \text{ y}^{-1}$). Though these rates are high, we are using them as a proxy for long-term deposition, rather than rates indicating a future predicted N deposition regime. The C addition rates and form of C (that is, sucrose) employed were chosen based on previous C addition studies (for example, Vinton and Goergen 2003) and on the suggestion that high rates of C addition are necessary to induce N immobilization (Blumenthal and others 2003). Specifically, we doubled the rates used by Vinton and Goergen (2003) because soil NO_3^- at our study site is high.

Treatments were applied by dissolving half of the added N or C in 0.9 L deionized water and dispensing over the surface of the plot in both June and September of 2010, 2011, 2012, and 2013 (that is, the treatment was divided into two applications). Control plots received an equal volume of deionized water. Treatments were applied over the course of the year in order to be present at the peak of the growing season (June addition) and in the soil with initial emergence (over winter- September addition).

Soil Sampling and Nutrient Analyses

We sampled soil cores at each plot in early June (pre-treatment), late June (post-treatment), July, and August of 2010 and June (pre-treatment), July

(post-treatment) and September (pre-treatment) of 2011, 2012, and 2013 using a 15-cm hammer corer (AMS Sampling Equipment, American Falls, ID) with a diameter of 3.5 cm. The timing of sampling was adjusted after the first year to better capture phenology of all understory plant species. In all 4 years, we removed large roots and rocks from within all of the samples and homogenized the soil using a 2-mm soil sieve. Approximately, 5 g of each sample was weighed fresh, oven-dried at 105°C for 24 h, and then reweighed to determine soil moisture. Four grams of each soil sample was extracted in the lab using 20 mL of 2 M KCl and concentrations of NH_4^+ and NO_3^- in the resulting extracts were measured on a Lachat QuikChem 8500 Series 2 flow-injection autoanalyzer (Quikchem® Method 12-107-06-1-A for NH_4^+ and Quikchem® Method 12-107-04-1-F for NO_3^-). Total soil N, C, and C:N were assessed by drying subsamples of 15 cm cores that were taken in July at 105°C for 24 h, and analyzing them on a TruSpec C:N analyzer (LECO, MI).

A relative index of available soil N was determined using mixed ionic bed resins (Unibest International, Washington, USA). Resins were deployed as small mesh bags containing beads that have been charged with H^+ and OH^- ions, which are replaced by NO_3^- and NH_4^+ present in the soil solution over time. Mixed-bed ionic resins were placed at 10 cm below the soil surface in the center of each plot. Resins were deployed in all plots (10 per treatment; 4 treatments) for 3 weeks at the peak of the growing season in June 2013. Resin deployment occurred within the same week as nitrogen availability treatment application and was chosen to coincide with peak understory plant biomass. Resins were extracted with three successive 20 min baths of 25 ml 2 M KCl which were pooled and analyzed on a Lachat QuikChem 8500 Series 2 flow-injection analyzer (Quikchem® Method 12-107-06-1-A for NH_4^+ and Quikchem® Method 12-107-04-1-F for NO_3^-). Measurements for resins are reported in $\mu\text{mol N-NO}_3^-$ or NH_4^+ per gram of resin per day deployed.

Soil pH was assessed in June 2013 when peak nitrification would be likely. Soil pH was determined by creating a slurry of 10 mL of DI water and 5 g of air-dried soil. Soil slurries were shaken every 10 min for half an hour and then were left to settle for 1 hour before being measured with a pH meter.

Plant Abundance and Nutrient Analyses

We assessed native and non-native plant species abundances by visually determining the percent

cover of each species within a 0.5 quadrat placed over each plot. Native and invasive plant species richness were also determined at this time. We assessed plant abundance and richness in June, July, August, and September of 2010 and June, July, and September of 2011–2013. These months correspond with the primary growing season for understory plants at our site.

Throughout the course of the study, we performed herbivory assessments of vegetation to determine if nitrogen treatments impacted the relatively low rates of herbivory in this system (data not shown). Specifically, we estimated percent leaf damage for each species in each plot. Herbivory did not vary due to nitrogen treatments and, therefore, would not differentially impact vegetation abundance in plots.

To determine N concentrations in plant tissue, we gathered whole-plant samples from each species (native and invasive) from plots where they were present in August of 2012. We bulked all samples of each plant species by treatment (that is, combining across plots prior to analyses) because individual plant species were not found in a sufficient number of plots. Plant tissue N was assessed by drying plant samples at 65°C for 24 h, grinding samples using a Wiley Mill (Thomas Scientific, PA), and analyzing them on a TruSpec C:N analyzer (LECO, MI).

Light Availability

Plot light levels were assessed in order to determine any differences in plant light availability across the four treatments. We measured light availability using a light meter held over each plot at breast height during peak overstory canopy cover in July of 2012 and again in September of 2013.

Statistical Analyses

We examined how carbon and nitrogen treatments (also referred to as “nutrient treatments” here) impacted plot soil NO_3^- and NH_4^+ using a repeated measure ANOVA with block, nutrient treatment, and time as factors. When block was an insignificant factor it was excluded from the analysis. Soil NO_3^- and NH_4^+ values were log-transformed due to non-normality. We also assessed how nutrient treatments impacted soil NO_3^- and NH_4^+ pools for each of the 4 years using repeated measures ANOVA's with block, nutrient treatment, and time (here, 3 sampling dates/year) as factors. Total soil %N and C:N were analyzed using a one-way ANOVA with nutrient treatment as the independent variable. When appropriate, we used post hoc contrasts to

determine the differences in soil N pools, total N, soil C:N, and percent cover among nutrient treatments. Differences across treatments for soil nitrogen pools on individual sampling dates and for soil N, C, and C:N were examined using ANOVAs.

Total native and invasive plant cover were determined by adding the percent cover of each individual plant species (sorted into either native or invasive) in each plot. We examined how carbon and nitrogen treatments impacted plot percent cover of native and invasive plant species (individually) and total plot percent cover (invasive + native) using repeated measures ANOVA's with block, nutrient treatment, and time as factors. When block was an insignificant factor it was excluded from the analysis.

Plant richness varied throughout the growing season due to the differing phenologies of individual species. To obtain an integrated view of the impact of nutrient treatments on plant richness throughout the year, we quantified annual species richness as the total number of species that appear in each plot during the three to four sampling dates each year (that is, how many species were present during a given summer). We analyzed invasive and native richness with repeated measures ANOVA's with nutrient treatment and time as factors. We also employed a one-way ANOVA for each year with nutrient treatment as a factor, followed by post hoc Tukey's tests to examine the treatment influences on plant richness in each year. Individual plant species exhibited high inter-annual variation in percent cover, likely due to the predominance of annual plant species in the understory. Thus, individual species percent cover responses to nutrient treatments were analyzed using repeated measures ANOVA analyses for each year, with block, nutrient treatment, and time as factors. We again used post hoc contrasts to determine the differences in individual species % cover among nutrient treatments. Principal component analyses were employed to test plant community composition differences between soil treatments.

To examine differences in plant N between control and treated plots, we performed matched pairs analyses, pairing plant N in each treatment plot type (+N, ++N, +C) with plant N from control plots (leading to 3 separate analyses). Replicates were individual plant species. We also compared native plant %N changes to invasive plant %N changes using the above-mentioned matched pair analyses with plant type as an added factor. Alpha was set at $p = 0.05$ for all analyses. Statistical analyses were performed using JMP Pro 11.0 (SAS Institute, Cary, NC).

RESULTS

Light Availability

There were no differences in light availability across the four types of treatment plots in 2012 or 2013.

Soil Responses

Soil treatments did not generate significantly different soil NO_3^- pools over the course of the experiment (Figure 1A; model $p = 0.76$, time $p < 0.0001$, time \times treatment $p = 0.93$). In 2011, soil nutrient treatments altered soil NO_3^- pools (Figure 1A; model $p < 0.01$, treatment $p = 0.056$, block $p = 0.01$ and time $p < 0.001$). *Post hoc* contrasts showed that soils in +C plots had lower NO_3^- than +N plots but were not different than controls and ++N plots. When differences in NO_3^- pools were assessed individually by month, carbon additions were most impactful on soil NO_3^- pools

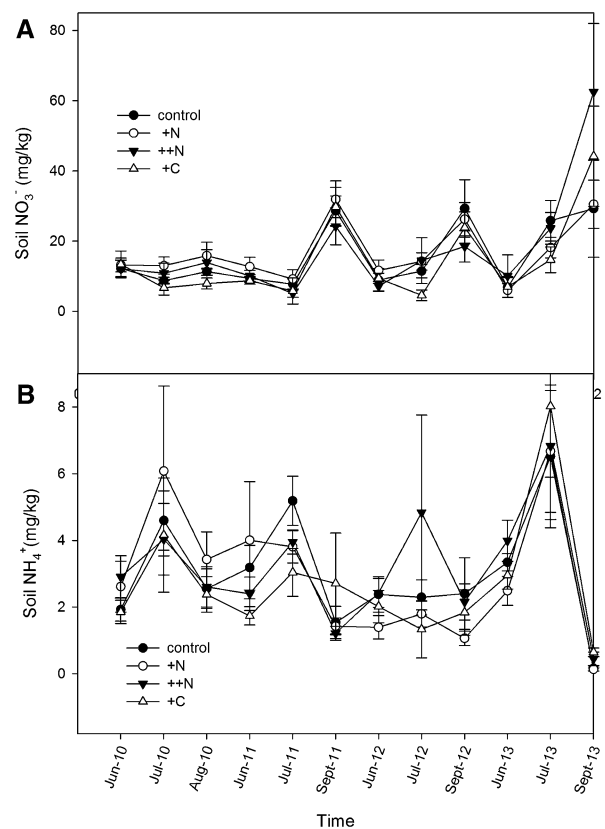


Figure 1. Mineral soil N pools over 4 years. Soil N pools did not respond to soil N (+N and ++N) and carbon (+C) additions over the course of the experiment. Soil nitrate (A) was significantly lower in carbon addition plots than in low nitrogen addition plots in 2012. Soil ammonium (B) did not differ significantly over the course of the experiment. Error bars represent standard errors.

in July, the month after C was added. Specifically in July of 2010 and July of 2012, C addition plots had lower and marginally lower different NO_3^- than other plots (Figure 1A, 2010; $p = 0.09$, 2012 $p = 0.0004$). Soil nutrient treatments did not impact soil NH_4^+ pools over the course of the experiment (Figure 1B; model $p = 0.63$, time $p < 0.0001$, time \times treatment $p = 0.71$). However, in July 2011, +C plots had lower soil NH_4^+ than ++N and control plots (Figure 1B; model $p = 0.03$).

Soil %N, %C, or C:N did not vary due to nitrogen or carbon addition treatments. Average soil %N was 0.25% ($\pm 0.02\%$ SE). Average soil %C was 2.76% ($\pm 0.19\%$). Average soil C:N was 11.33 (± 0.30).

Resin-available N as NO_3^- and NH_4^+ differed dramatically due to nitrogen additions ($p < 0.0001$, Figure 2). Post hoc tests showed that both the +N and ++N treatments showed increased resin N as NO_3^- (6 \times and 8 \times higher than control plots, respectively; $p < 0.0001$), indicating that the fertilization treatments increased N in the soil solution ($p < 0.0001$). Post hoc tests showed that N as NH_4^+ was also substantially increased by the N addition treatments (4 \times and 5 \times higher above the control plots respectively, $p < 0.0001$). The C addition plots were equivalent to the control plots for both NO_3^- and NH_4^+ . There was no significant difference in soil pH among the treated plots. Average soil pH was 5.5 across all treatments.

Plant Responses

Changes in plant abundance due to nutrient treatments were assessed by examining invasive and native cover, total percent cover, and percent cover of individual species. Native and invasive plant percent cover did not change due to nutrient

treatments over the course of the experiment (Figure 3; native $p = 0.37$, time $p < 0.0001$, time \times treatment $p = 0.62$; invasive $p = 0.53$, time $p < 0.0001$, time \times treatment $p = 0.62$). Total percent cover also did not change due to soil treatments over the course of the experiment (data not shown; $p = 0.10$, time $p < 0.0001$, time \times treatment $p = 0.17$). Individual plant species responses are reported below.

Invasive plant species richness was not altered by nutrient treatments over the entire course of the experiment ($p = 0.06$, time \times treatment $p = 0.44$) but was impacted in certain years. Specifically, invasive species richness was increased in 2010 (Figure 3, $F = 4.73$, $p < 0.01$), and 2011 (Figure 4, $F = 3.53$, $p = 0.03$) due to soil nutrient treatment. Post hoc student's t test showed that in 2010 +N plots had higher invasive species richness than either ++N or control plots. In 2011, the +N and ++N plots had higher invasive species richness than control plots. Native plant species richness did not significantly differ due to soil treatment over the course of the experiment or within any year of the experiment.

Individual native plant species did not shift in percent cover in response to any nutrient treatments (Tables 1, 2). Conversely, some of the dominant invasive plant species did increase in response to +C treatments but only in the early years of the study (Table 1). After 2 years of treatment (2011), garlic mustard (*A. petiolata*) had higher percent cover in +C plots than in +N and ++N plots (Table 2). In both 2010 and 2011, Asian bittersweet (*C. orbiculatus*) had higher percent cover in control plots (and in 2010 in +C plots) than in +N plots (and than ++N plots in 2011; Tables 1, 2). There were no significant shifts in community

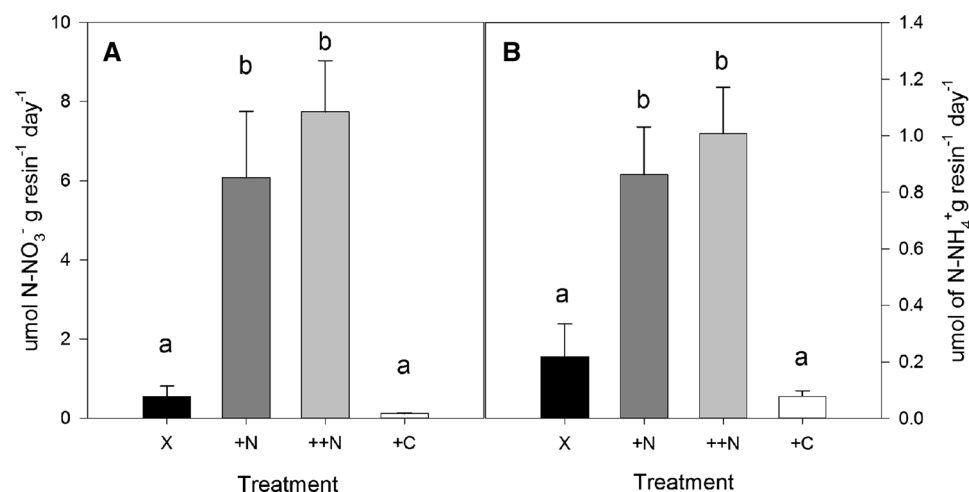


Figure 2. Resin-available NO_3^- (left panel) and NH_4^+ (B) change due to soil treatments in 2013. Nitrogen additions (+N and ++N) increased resin-available NO_3^- and NH_4^+ as compared to control (X) and C additions (+C). Lower case letters indicate significant differences between treatments as indicated by a student's t post hoc test. Error bars represent standard errors.

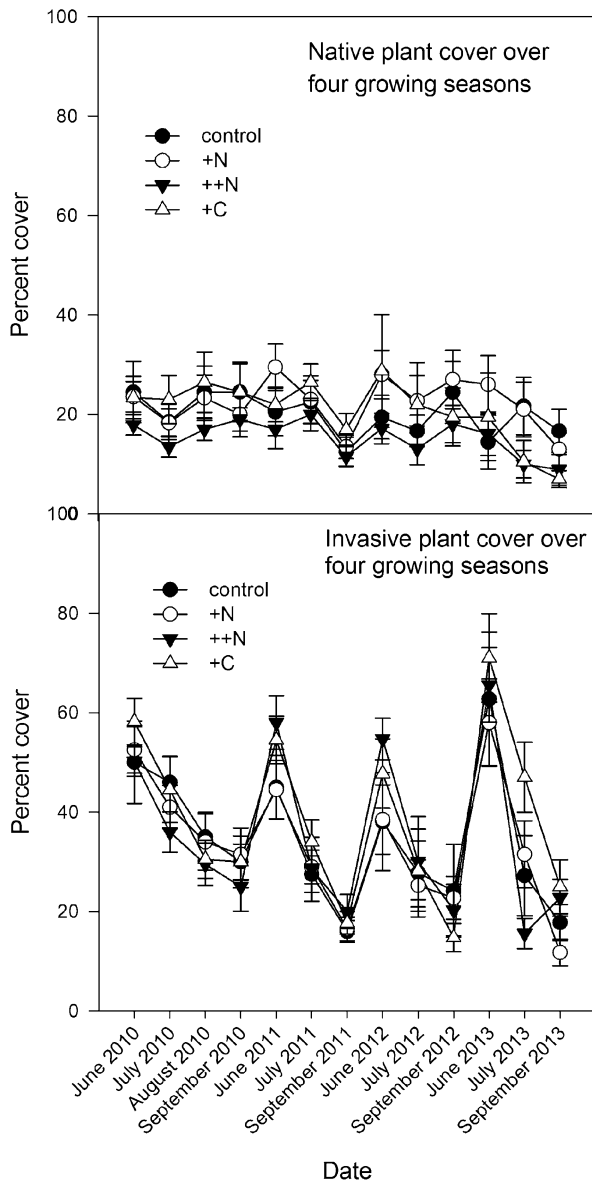


Figure 3. Total plant percent cover for native (*top panel*) and invasive plants (*bottom panel*) over the course of the four-year study. Invasive plant abundance is greater than native plant abundance throughout the 4 years of the study. Plant percent cover did not differ due to nitrogen additions or carbon additions over the 4 years of the experiment. Error bars represent standard errors.

composition due to soil nutrient treatments, as indicated by principal component analyses.

Plant tissue %N was not different in control versus +N plots ($t = 0.341$, $p > |t| = 0.7433$) nor was it different when plant type was included as a factor ($p > |t| = 0.379$). Plant tissue % N also did not differ between control and ++N plots ($t = 1.36$, $p > |t| = 0.211$) or between control and +C plots ($t = 0.856$, $p > |t| = 0.856$, even when plant type was included as a factor.

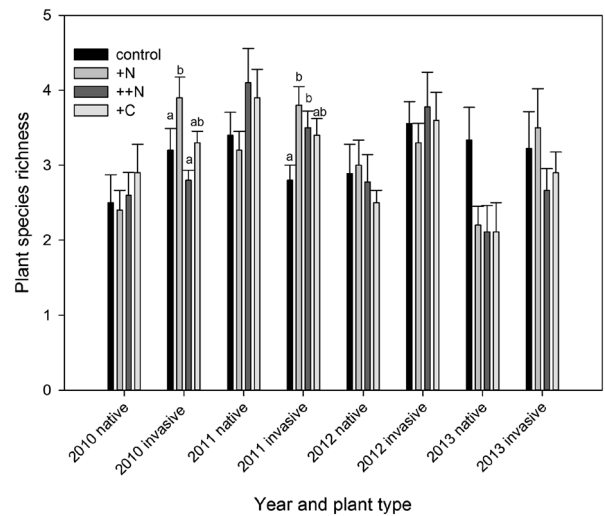


Figure 4. Richness of native and invasive plants for each year of the study. Invasive plant richness varied due to nitrogen and carbon soil additions, though only in 2 of the 4 years. Specifically, nitrogen additions (+N in 2010, and +N and ++N in 2011) increased invasive plant richness as compared to controls. Carbon additions (+C) did not impact native or invasive plant richness. Error bars represent standard errors. Letters indicate differences according to post hoc tests in 2010 and 2011 when nutrient treatments impacted richness.

DISCUSSION

Our study site, typical of many ecosystems impacted by long-term N deposition, has relatively high soil N availability, particularly NO_3^- availability, which ranges between 15–30 mg N kg^{-1} of soil. The high NO_3^- values we measured mimic high NO_3^- values seen in a recent study in nitrogen-fixing plant-dominated stands in eastern Connecticut forests (Dreiss and Volin 2013) and exceed those documented for a N-saturated forest in the tropics (Lu and others 2010). In the Ridley Creek forests, high NO_3^- availability may result from both long-term N deposition and from high rates of nitrification (Lu and others 2014). Interestingly, soil pH, which often declines with increasing NO_3^- , did not change in the high and low N addition plots (Lu and others 2014). Regardless, vegetation dynamics in this high- NO_3^- system can yield insight into the future of other ecosystems, which are not yet as high in soil N.

In this heavily N-impacted system, we hypothesized that increasing soil N availability further would increase invasive plant diversity and abundance and decrease native plant diversity and abundance. However, we found that large additions of N did not significantly increase soil pools of either NO_3^- or NH_4^+ , nor did it increase total soil N,

Table 1. Responses of Selected Dominant Plant Species to Soil Carbon and Nitrogen Additions Varied by Species, Year, and Plant Status (Invasive or Native)

Species name	Native/invasive	2010 response	2011 response	2012 response	2013 response
<i>Celastrus scandens</i>	Native	No significant effect of treatment	No significant effect of treatment	No significant effect of treatment	No significant effect of treatment
American Bittersweet					
<i>Parthenocissus quinquefolia</i>	Native	No significant effect of treatment	No significant effect of treatment	No significant effect of treatment	No significant effect of treatment
Virginia Creeper					
<i>Crataegus</i> spp.	Native	No significant effect of treatment effects	No significant effect of treatment	No significant effect of treatment	No significant effect of treatment
Hawthorn spp.					
<i>Alliaria petiolata</i>	Invasive	No significant effect of treatment	Higher percent cover in + C plots than in control, +N and ++N plots ($p = 0.01$)	No significant effect of treatment	No significant effect of treatment
Garlic Mustard					
<i>Celastrus orbiculatus</i>	Invasive	Higher percent cover in control and +C plots than in +N plots ($p = 0.01$)	Higher percent cover in control plots than in +N and ++N plots ($p = 0.05$)	No significant effect of treatment	No significant effect of treatment
Asian Bittersweet					
<i>Rosa multiflora</i>	Invasive	No significant effect of treatment	No significant effect of treatment	No significant effect of treatment	No significant effect of treatment
Multiflora Rose					

No native plants showed responses to addition treatments and differences were only seen in the first 2 years of the experiment. Both scientific and common names of the three most dominant native and invasive plant species are provided. When repeated measures ANOVA's yielded a significant effect of treatment, post hoc contrasts were employed to determine differences between treatments. We report the results of these contrasts below the ANOVA results when applicable.

Table 2. Mean Percent Cover of the Eight Most Dominant Plant Species in June (Peak Cover) 2010–2014 Across All Treatments

	2010					2011					2012					2013																										
	X	+N	++N	+C		X	+N	++N	+C		X	+N	++N	+C		X	+N	++N	+C		X	+N	++N	+C																		
<i>Celastrus scandens</i>	8.33 (4.41)	10 (2.89)	10 (0)	11.75 (1.18)		6.11 (2.86)	6.67 (3.44)	2.22 (1.21)			6.25 (2.06)	5.94 (2.5)	7.5 (4.61)	5 (2.58)		4.38 (1.99)	6.88 (2.3)	6.67 (4.94)			6.25 (2.06)	1.88 (0.91)	4.17 (2.39)	4.17 (2.2)	4.29 (2.3)		4.38 (1.99)	6.88 (2.3)	6.67 (4.94)			6.25 (2.06)	1.88 (0.91)	4.17 (2.39)	4.17 (2.2)	4.29 (2.3)		4.38 (1.99)	6.88 (2.3)	6.67 (4.94)		
<i>Alliaria petiolata</i>	6.25 (1.25)	7 (1.22)	15 (5)	8.33 (3.33)		7.5 (2.83)	10 (1.86)	10 (2.76)			14.38 (8.25)	9.44 (2.94)	11.43 (3.57)	18.75 (4.3)		13.13 (2.98)	6.67 (1.05)	10 (5.77)			14.38 (8.25)	9.44 (2.94)	11.43 (3.57)	18.75 (4.3)		13.13 (2.98)	6.67 (1.05)	10 (5.77)			14.38 (8.25)	9.44 (2.94)	11.43 (3.57)	18.75 (4.3)		13.13 (2.98)	6.67 (1.05)	10 (5.77)				
<i>Alliaria petiolata rosette</i>	17.22 (4.09)	15.5 (2.73)	15.56 (2.69)	18.56 (2.56)		2.5 (1.71)	4 (3.06)	2.78 (2.78)			30 (14.05)	22.5 (6.2)	30.63 (8.73)	21.11 (7.85)		5.63 (3.95)	6.11 (4.39)	4.29 (2.97)			30 (14.05)	22.5 (6.2)	30.63 (8.73)	21.11 (7.85)		5.63 (3.95)	6.11 (4.39)	4.29 (2.97)			30 (14.05)	22.5 (6.2)	30.63 (8.73)	21.11 (7.85)		5.63 (3.95)	6.11 (4.39)	4.29 (2.97)				
<i>Rosa multiflora</i>	16.67 (5.43)	16.25 (6.25)	21.67 (4.01)	19.29 (4.81)		28.33 (7.49)	15 (6.41)	35 (8.78)			2.5 (1.12)	5 (0)	21.25 (10.08)	2.5 (2.5)		57 (15.7)	31.88 (10.48)	53.75 (12.6)			2.5 (1.12)	5 (0)	21.25 (10.08)	2.5 (2.5)		57 (15.7)	31.88 (10.48)	53.75 (12.6)			2.5 (1.12)	5 (0)	21.25 (10.08)	2.5 (2.5)		57 (15.7)	31.88 (10.48)	53.75 (12.6)				
<i>Celastrus orbiculatus</i>	19 (3.79)	11.67 (2.36)	19.2 (3.35)	23 (3.35)		19.5 (3.83)	10 (3.5)	10.5 (1.74)			2.5 (1.67)	8.75 (1.25)	4.5 (2)	20.42 (10.69)		2 (2)	0	0			2.5 (1.67)	8.75 (1.25)	4.5 (2)	20.42 (10.69)		2 (2)	0			2.5 (1.67)	8.75 (1.25)	4.5 (2)	20.42 (10.69)		2 (2)	0						
<i>Parthenocissus quinquefolia</i>	11.25 (4.73)	6.43 (1.8)	7.75 (1.06)	8.56 (2.08)		4 (4)	7.86 (2.14)	5 (2.76)			1.67 (1.67)	18.13 (5.66)	7.78 (1.88)	10.5 (5.02)		4.29 (2.77)	14.38 (5.46)	6.11 (3.2)			1.67 (1.67)	18.13 (5.66)	7.78 (1.88)	10.5 (5.02)		4.29 (2.77)	14.38 (5.46)	6.11 (3.2)			1.67 (1.67)	18.13 (5.66)	7.78 (1.88)	10.5 (5.02)		4.29 (2.77)	14.38 (5.46)	6.11 (3.2)				
<i>Crataegus spp</i>	11.43 (2.1)	12.5 (3.1)	8 (2.55)	6.25 (1.25)		6.25 (1.57)	9.44 (2.56)	5 (1.97)			0 (0)	25 (25)	0	7.5 (7.5)		0	0	0			0 (0)	25 (25)	0	7.5 (7.5)		0	0			0 (0)	25 (25)	0	7.5 (7.5)		0	0						
<i>Rubus phoenicolasius</i>	12.5 (12.5)	25 (0)	10 (0)	5 (5)		0	15 (5.4)	25 (0)			0 (0)	25 (25)	0	7.5 (7.5)		0	0	0			0 (0)	25 (25)	0	7.5 (7.5)		0	0			0 (0)	25 (25)	0	7.5 (7.5)		0	0						

Letters at the top of the columns under each year refer to control (X), soil N (+N and ++N), and carbon (+C) plots where the species cover is measured. Average percent cover is provided in each cell with standard errors indicated in parentheses.

thereby potentially negating any strong influence on plant dynamics. In fact, the background intra-annual variability in mineral N pools at Ridley Creek State Park greatly exceeded the magnitude of N and C treatment effects where they occurred.

Several reasons may explain lack of increased soil total N or N pools with added N fertilizer. In a conceptual model of N saturation, Lovett and Goodale (2011) provide a list of multiple, potentially simultaneous fates of added N in a forest ecosystem. They predict that added N can be 1) incorporated into vegetation, 2) incorporated into detritus and soil organic matter, 3) lost via leaching, or 4) lost via gaseous emissions. We address each of these possible fates for N here. Understory plant uptake of N in this system is likely high during the growing season, as indicated by the spikes in soil NO_3^- in September of 2011, 2012, and 2013, when sampling was performed after most understory plants had senesced, yet overstory trees had not senesced. It is possible that the uptake rates of understory plants in our N fertilized plots could have exceeded those in unfertilized plots, thus masking the soil treatment effects. However, N of invasive and native plants in fertilized plots did not increase compared to unfertilized plots. It is important to note that we did not sample adjacent tree foliage N concentrations. The N we added could have been incorporated into detritus but we also did not measure this pool. It is unlikely that added N was incorporated into soil organic matter because total soil N and C:N did not differ between treated and untreated plots. Losses through denitrification are unlikely due to the soil aeration by abundant earthworms at this site (Chapman, personal observation). Considering the lack of support for these other three fates, we suspect that added N may be leaching from these soils.

As we hypothesized, resin-available N, assessed shortly after fertilization, was much higher in nitrogen addition plots, likely indicating that this nitrogen is soluble and mobile in these soils. We did not measure leaching directly (that is, using lysimeters) over the course of this study. However, measurements of ion resin N provide a good assessment of the soil solution and thus mobility of N, particularly in soils with high nitrification potential, such as ours (Binkley 1984). To confirm that this system is N saturated we need to track the fate of added N. Regardless of the fate of our N additions, fertilization did not alter soil N pools, potentially indicating high outputs to adjacent waterways.

Despite the lack of a significant change in soil N pools in response to our N additions, we did find

partial support for our hypothesis regarding plant diversity. Similar to the findings in Jones and Chapman (2011), we found that the low N addition treatment increased the diversity of invasive plant species in 2010 and both the low and high N addition treatments increased invasive species diversity in 2011 (Figure 4). However, these changes were not maintained over the course of the experiment and disappeared after 2 years of fertilization. Other studies have shown increases in invasive plant richness following N fertilization (Huenneke and others 1990; Weiss 1999; Kochy and Wilson 2001; Ostertag and Verville 2002; Rickey and Anderson 2004; Gurevitch and others 2008). Nitrophilic invasive plant species have been shown to take advantage of these increases more than native plant species (Theoharides and Dukes 2007; Pfeifer-Meister and others 2008). Thus, it is possible that more invasive plant species could be supported by the N we added to a given amended plot, though we suspect this to be a transient response in these already high- NO_3^- soils. Native species richness did not decline in the N addition plots, thus these additional invasive species did not seem to displace the extant plants. Similarly, overall plant community structure was not changed due to N treatment.

Though plant richness sometimes shifted among N treatments, plant abundances were unchanged due to any soil N addition or removal (Figure 3). In contrast, other studies have found that N additions decreased abundance of native tree seedlings and understory plants (Talhelm and others 2013) and native mosses (Mäkipää 1998). The total cover in the plots varied by season but not by N treatment, suggesting an additional factor is limiting plant cover (Figure 3). Though light availability varied little across plots during one time of year, the seasonal differences in cover suggest light is limiting across this site, considering that understory plant cover decreases from June to August, a time of maximum overstory canopy development. Interestingly, native plant cover seems to stay stable throughout the growing season while a pronounced decrease occurs for invasive plant species when the overstory canopy fills in. Similar to findings for richness, invasive plant species exhibited annual dynamic changes in cover at Ridley Creek but native plant species maintain consistent percent cover as compared to invasive plant species.

We hypothesized that decreasing soil N availability via C additions would increase native abundance and diversity. Other studies have found C additions to be an effective way to decrease soil N

availability and invasive plant abundance (Jonasson and others 1996; Morgan and Seastadt 1999; Paschke and others 2000; Mazzola and others 2010). Though we did decrease NO_3^- in 2011 and 2012 and NH_4^+ pools in July of 2011 via C additions, we did not find consistent decreases in invasive plant abundance and richness or increases in native plant abundance and richness in +C plots. As suggested in other studies (for example, Steers and others 2011), N immobilization in microbial biomass can be followed by pulses of N availability during turnover of microbial biomass. Although the soil data do not illustrate N pulses in the +C plots, some of this may have resulted because the soil pool measurements were done on a coarse time scale. It is possible that the decreases in N availability we observed were followed by micro-pulses of N that retained high N in soil, or that the ephemeral decreases in N availability we saw were insufficient for decreasing nitrophilic invasive plant percent cover. Interestingly, at least two invasive plant species *C. orbiculatus* and *A. petiolata* actually showed increased percent cover in C addition plots as compared to N addition plots in the first 2 years of the study, suggesting that high N levels may be detrimental to some invasive plant species.

In conclusion, our four-year study provides evidence that this deciduous forest understory plant community composition appears stable in the face of further increases in N availability. Rather than being impacted by excess N, native understory plant richness and abundance may be controlled by the dominance of invasive species at this site and these invasive species may promote the high rate of N cycling (Dornbush and Hahn 2013). Gilliam (2006) proposed that herbaceous understories impacted by N deposition would progress through predictable stages starting with an increase in cover, progressing through decline in species richness and evenness, and ending with a decline in forest biodiversity. This ecosystem likely progressed through these stages in previous decades, when N deposition levels initially increased and generated high abundances of invasive plant species that concomitantly reduced the abundance of native plants. Since that time, the long history of high deposition that has occurred at this site may have produced a novel community, dominated by invasive plant species and populated by a consistent and stable contingent of native plant species. This invasive-dominated community may be an important sink for NO_3^- during the growing season (approximately 6 g/m^2 at this site) and thus may play a role in buffering NO_3^- outputs into nearby

waterways. Because N deposition in this area is currently on the decline, we suggest that these plant communities, although altered, are somewhat resilient in their provisioning of understory productivity. However, if future increases in N deposition were to occur, we cannot predict the stability of this plant productivity. Invasive plants may be the new dominant understory species in N-rich forested ecosystems, systems that are widespread in the United States. Finally, in N-saturated systems, other factors such as climate change may hold greater importance in controlling ecosystem processes than future increases in N deposition.

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