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RESEARCH ARTICLE

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Urbanization and fragmentation have opposing effects on soil nitrogen availability in temperate forest ecosystems

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Abstract

Nitrogen (N) availability relative to plant demand has been declining in recent years in terrestrial ecosystems throughout the world, a phenomenon known as N oligotrophication. The temperate forests of the northeastern U.S. have experienced a particularly steep decline in bioavailable N, which is expected to be exacerbated by climate change. This region has also experienced rapid urban expansion in recent decades that leads to forest fragmentation, and it is unknown whether and how these changes affect N availability and uptake by forest trees. Many studies have examined the impact of either urbanization or forest fragmentation on nitrogen (N) cycling, but none to our knowledge have focused on the combined effects of these co-occurring environmental changes. We examined the effects of urbanization and fragmentation on oak-dominated (*Quercus* spp.) forests along an urban to rural gradient from Boston to central Massachusetts (MA). At eight study sites along the urbanization gradient, plant and soil measurements were made along a 90 m transect from a developed edge to an intact forest interior. Rates of net ammonification, net mineralization, and foliar N concentrations were significantly higher in urban than rural sites, while net nitrification and foliar C:N were not different between urban and rural forests. At urban sites, foliar N and net ammonification and mineralization were higher at forest interiors compared to edges, while net nitrification and foliar C:N were higher at rural forest edges than interiors. These results indicate that urban forests in the northeastern U.S. have greater soil N availability and N uptake by trees compared to rural forests, counteracting the trend for widespread N oligotrophication in temperate forests around the globe. Such increases in available N are diminished at forest edges, however, demonstrating that forest fragmentation has the opposite effect of urbanization on coupled N availability and demand by trees.

KEYWORDS

foliar nitrogen, forest fragmentation, net mineralization, nitrogen, nutrient cycles, temperate forest, urbanization

1 | INTRODUCTION

Nitrogen (N) availability relative to plant N demand is declining in many terrestrial ecosystems around the world, a process known as N oligotrophication (Craine et al., 2018; Mason et al., 2022). Reductions in available N are especially important in temperate forests, where N limits plant productivity (LeBauer & Treseder, 2008). Though N oligotrophication is occurring in terrestrial ecosystems around the globe (Mason et al., 2022), temperate forests in the northeastern U.S. have experienced some of the steepest declines in N availability relative to plant demand in the U.S. (McLauchlan et al., 2017). However, the studies describing decreases in soil N supply relative to plant demand have intentionally focused on non-urban areas, away from confounding sources of local pollution and other disturbances (Craine et al., 2018; Groffman et al., 2018; Luo et al., 2004; Mason et al., 2022). As a result, a significant knowledge gap regarding the sensitivity of urban forests to trends in global N availability has emerged.

More than 55% of the world's population live in cities, including more than 80% of the U.S. population (UN, 2018), causing ongoing expansion of urban development into natural areas, which is projected to double the geographic extent of urban areas in the United States by 2030 relative to 2000 (Seto et al., 2012). In heavily forested regions, such as the northeastern U.S., urbanization leads to increased forest fragmentation and the creation of forest edges, which tend to have higher temperatures and light levels, lower soil moisture levels, stronger winds, and different vegetation composition compared to forest interiors (Magnago et al., 2015). Forest edges can also experience increased rates of N inputs from atmospheric deposition (Spangenberg & Kölling, 2004; Weathers et al., 2001), higher soil N stocks (Wuyts et al., 2011), and greater exposure to airborne pollutants such as sulfate (Weathers et al., 2001). Compared to trees in rural forests, urban trees have both faster growth and higher mortality rates (Smith et al., 2019), higher canopy density, and greater tree species richness (Zhang et al., 2017). Compared to soils in rural forests, urban forest soils may have increased rates of soil N mineralization and nitrification (Reisinger et al., 2016; White & McDonnell, 1988) due to higher rates of local N deposition (Decina et al., 2020; Lovett et al., 2000; Rao et al., 2013; Templer & McCann, 2010).

Nitrogen is often considered to be the limiting element in photosynthesis by terrestrial plants (Evans, 1989; Fleischer, 1935) and net primary productivity of temperate ecosystems (LeBauer & Treseder, 2008). Human activities, such as fossil fuel combustion and agricultural practices, increase rates of N inputs to terrestrial and aquatic ecosystems (Galloway et al., 2008), which can induce N saturation, a syndrome of responses including acidification and eutrophication of soils and streams, as well as nutrient imbalances in vegetation (Aber et al., 1989, 1998; Gilliam et al., 2018; Vitousek et al., 1997). However, recent findings suggest that increased atmospheric carbon dioxide concentrations and longer, warmer growing seasons are increasing demand for N by plants. Increases in N demand, combined with recent declines in atmospheric deposition in many locations (Du et al., 2019; Lloret & Valiela, 2016), leads to N oligotrophication in temperate forest systems where plant demand for N is not met by soil N availability (Craine et al., 2018; Groffman et al., 2018; Luo et al., 2004; Mason et al., 2022). It is possible that forests impacted by both urbanization and fragmentation continue to experience elevated N availability, and hence may not experience N oligotrophication. With higher rates of atmospheric N deposition in urban areas compared to rural areas (Decina et al., 2020; Rao et al., 2013; Templer & McCann, 2010), it is possible that N cycling dynamics in urban forest ecosystems are uncoupled from trends in rural ecosystems. On a regional scale, much of the atmospheric N deposition to the northeastern U.S. can be attributed to agricultural activity and power generation in the Midwest (Driscoll et al., 2003; Ollinger et al., 1993). However, in southern New England, including Boston, MA and Providence, RI, atmospheric N deposition tends to be enhanced compared to rural areas, and is dominated by local sources such as vehicular emissions (Decina et al., 2017, 2020; Joyce et al., 2020). Little is known about how urbanization and forest fragmentation combine to impact soil N availability in temperate forest ecosystems, nor about the ability of trees to take up that N. Trees and their associated mycorrhizal symbionts may shift their nutrient acquisition strategies in response to higher amounts of soil N availability (Ma et al., 2021; Zhao et al., 2022), but whether or how such shifts occur in fragmented, urban forests is not well known. Thus, examining the effects of urbanization and fragmentation on soil N availability and N uptake by trees is crucial to understanding how such forests respond to land use and land cover change, and the extent to which N limits their productivity.

Soil N mineralization and nitrification are critical processes for supplying plant-available N (Aber & Melillo, 2001), particularly in high-N environments (Schimel & Bennett, 2004). Rates of soil net mineralization and N availability were reported to be greater in rural than urban forests in the 1980s (White & McDonnell, 1988), but recent studies indicate that current rates of net mineralization are greater in urban than rural soils (Chen et al., 2010; Enloe et al., 2015; Reisinger et al., 2016; Remy et al., 2018). However, mineralization rates remain lower at forest edges adjacent to agricultural land compared to the forest interior for sugar maple-dominated stands (Masson et al., 2019). Temperate forest trees have also been shown to vary in the amount of ammonium or nitrate they take up, but such preferences are species and substrate dependent (Kalcsits et al., 2015; Schulz et al., 2011; Templer & Dawson, 2004). To our knowledge, the relative magnitude of N uptake by temperate trees has not yet been examined in urban environments. It is possible that urbanization and associated higher rates of N deposition in cities lead to greater rates of soil N cycling and N uptake by plants, but these effects could be offset by other dynamics at the forest edge (e.g., lower soil moisture) that result in reduced rates of N uptake by trees.

Soil N cycling rates are well known to be associated positively with soil properties such as moisture (Guntiñas et al., 2012), pH (Cheng et al., 2013), and organic matter content (Cookson et al., 2007), but negatively associated with soil bulk density (Tan &

Chang, 2007) and electrical conductivity (Green & Cresser, 2008). Among these factors, soil moisture has been shown to be lower in urban forests and at forest edges, including at the forested sites in this study (Garvey et al., 2022), but the combined effects of all these soil properties on soil N cycling are not well quantified in urban and fragmented temperate forests.

Foliar N is often used as a proxy for N uptake by vegetation (Kahmen et al., 2008) and has a strong positive relationship with the photosynthetic capacity of leaves (Evans, 1989). However, the relationship between foliar N concentrations and distance to an urban core is not well known, because while foliar N concentrations are positively correlated with rates of atmospheric N deposition (McNeil et al., 2007; Roth, 2021), they are negatively correlated with urbanization metrics such as percent impervious surface area (% ISA; Rao et al., 2013). Foliar N concentration and N resorption proficiency (i.e., the extent to which trees retain N following leaf senescence and abscission) are higher and foliar carbon to N ratios (C:N) are lower in urban compared to rural temperate forests when urbanization is defined by distance to a city center (Chen et al., 2010; Wei & He, 2020). Results from fragmented tropical forests in both South Africa (Mutanga et al., 2019) and Madagascar (Crowley et al., 2012) show decreasing foliar N with increasing distance from forest edges, possibly due to reduced soil N availability in the forest interior compared to edge. However, foliar N concentrations have also been found to increase with distance from the forest edge in temperate hardwood forests of Canada (Masson et al., 2019), suggesting that local ecosystem dynamics and the particular drivers of fragmentation play a significant role in determining edge effects on foliar N.

Determining the combined effects of urbanization and forest fragmentation on rates of soil N cycling and foliar N will help us better predict the impacts of land use and land cover change on N dynamics in temperate forests in a rapidly urbanizing world. While impacts of global change factors on the N cycle have been heavily studied, it is currently not well known whether the effects of urbanization and fragmentation on N cycling are synergistic, additive, or antagonistic. If effects are additive, we would expect to find similarly enhanced soil N cycling rates and foliar N concentrations in urban forests and at forest edges compared to rural forests and the forest interiors, respectively, with the highest measured rates expected to occur at urban forest edges. If synergistic, however, we would expect to find similarly increased soil N cycling rates and foliar N at urban edges, but a smaller magnitude of difference between rural forests and urban forest edges. If they cancel each other out, we expect urban forests to have higher rates of soil N cycling and foliar N concentrations than rural forests, but for the difference to be eliminated at the forest edge.

In this study, we measured rates of net ammonification, nitrification, and mineralization in soils, as well as foliar N and C:N in oak trees (*Quercus* spp.) and several soil properties in the growing seasons of 2018 and 2019 at eight sites along an urbanization gradient from Boston to central MA. At each site, we established transects that spanned the forest edge to 90 m into the forest interior. We expected soil moisture and soil organic matter (SOM), and pH to be lower, but soil conductivity, and bulk density to be higher in urban than rural forests and at forest edges compared to interiors. Considering these expected patterns in abiotic soil factors, we hypothesized that rates of soil N cycling and foliar N concentrations are higher in urban than rural forests, and higher at forest edges than interiors. We also hypothesized that we would find a synergistic effect, or significant positive interaction, between urbanization and distance from the forest edge, resulting in the highest rates of soil N cycling and foliar N content at urban forest edges.

2 | METHODS

2.1 | Site description and study design

European settlement in what is now the northeastern U.S. included significant forest clearing for farmland and pasture that persisted until the mid-1800s. Agricultural abandonment in the area following that period resulted in a landscape that is once again heavily forested (Pan et al., 2011; Thompson et al., 2013), though a significant amount of forest is cut on an annual basis (Drummond & Loveland, 2010). This region's largely mid-successional mixed temperate forests provide essential ecosystem services, including carbon sequestration, air pollution filtration, and retention of approximately 70% of deposited N (Goodale, 2017; Pan et al., 2011). However, over a fifth of this forested area falls within 30 m of a forest edge caused by agriculture or development (Smith et al., 2018). Massachusetts (MA) alone is currently over 60% forested land, but this area is heavily fragmented due in large part to increasing urban sprawl (Butler, 2018). Moreover, MA is projected to lose an additional 4%–14% of forested area and see a 35%–40% increase in developed land between 2005 and 2050 (Reinmann et al., 2016). It is therefore critical to understand how the interaction of urbanization and fragmentation will influence the ecosystem services and processes, such as N cycling, provided by forests across the region.

Soil and plant samples were collected as part of the Urban New England project with eight sites along a 120 km urban to rural gradient from Boston to central MA. The same sites were used to measure the combined effects urbanization and forest fragmentation on rates of soil respiration and a suite of other properties (Garvey et al., 2022). These sites include a mix of public and privately owned land with at least 200 × 200 m intact forest area. A detailed site map is included in Garvey et al. (2022) and additional topographical and land-use information about the area adjacent to each forest edge is shown in Table 1. All forested sites, including urban and rural forests, were chosen to comply with our minimum threshold of 200 × 200 m size. Elevation ranged from 47 m above sea level at the Arnold Arboretum to 295 m at Harvard Forest 01, with sites further from Boston tending to be higher in elevation than those closer to the city center. Forests were selected with predominately oak species and other mixed hardwoods to represent dominant tree species in MA, with sites being selected to contain as similar tree species composition as possible. The most abundant species throughout the urbanization

TABLE 1 All eight study sites and their distance to Park Street Station in Boston, their % ISA, urbanization designation for each site, and additional topographic information. The two most common tree species at each site are shown in order of abundance. Harvard Forest sites are numbered 1–3 for clarity, differing from the numbering scheme in Garvey et al. (2022).

Site	City or town (MA)	Distance to Boston (km)	Impervious surface area (%)	Urbanization category (distance to Boston)	Urbanization category (% ISA)	Most abundant tree species
Arnold Arboretum	Boston	8.01	26.17	Urban	Urban	*Quercus* spp., *Pinus strobus*
Hammond Woods	Newton	9.63	13.59	Urban	Urban	*Acer rubrum*, *Quercus rubra*
Sutherland Woods	Lexingotn	13.2	27.46	Urban	Urban	*Quercus rubra*, *Carya glabra*
Blue Hills Observatory	Milton	16.34	6.43	Urban	Rural	*Quercus rubra*, *Acer rubrum*
Broad Meadow	Worcester	60.41	25.99	Rural	Urban	*Quercus rubra*, *Betula lenta*
Harvard Forest (1)	Petersham	92.63	4.04	Rural	Rural	*Quercus rubra*, *Tsuga canadensis*
Harvard Forest (2)	Petersham	95.16	0.64	Rural	Rural	*Acer rubrum*, *Acer saccharum*
Harvard Forest (3)	Leverett	119.12	10.74	Rural	Rural	*Acer saccharum*, *Quercus rubra*

Site	Elevation (m)	Edge type	Edge aspect	Edge organic soil depth (cm)	Interior organic soil depth (cm)
Arnold Arboretum	47	Road	NW	5.2 ± 0.91	4.6 ± 0.72
Hammond Woods	59	Road	E	3.49 ± 0.42	2.61 ± 1.21
Sutherland Woods	80	Parking Lot	SW	4.68 ± 0.60	4.53 ± 0.58
Blue Hills Observatory	178	Clearing, ski slope	NE	4.60 ± 0.50	4.74 ± 0.20
Broad Meadow	172	Clearing, powerline	SW	2.75 ± 0.80	3.58 ± 0.61
Harvard Forest (1)	295	Road	SW	3.00 ± 0.49	4.20 ± 0.36
Harvard Forest (2)	239	Open field	E	3.94 ± 0.33	6.35 ± 0.23
Harvard Forest (3)	121	Clearing, residence	W	4.37 ± 0.19	5.70 ± 0.60

gradient include northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), eastern white pine (*Pinus strobus*), and sugar maple (*Acer saccharum*). While understory vegetation was not cataloged at our sites, the most common species in the mixed temperate forests of Massachusetts include northern red oak and red maple saplings, as well as Canada mayflower and starflower (Butler et al., 2011). Each site contains a transect from the forest edge, adjacent to an open field, road, or other human land use, to 90 m into the forest interior. Soil and foliage measurements were taken along the edge to interior gradient at 0, 15, 30, 60, and 90 m into the forest at each site. Soils at all forested sites are inceptisols (USDA NRCS, 2022) with no statistically significant variation across sites in soil organic layer depth with urbanization or distance from the forest edge. Within individual sites, the only site to have significant variation in organic soil depth with distance from the forest edge was Harvard Forest 1 (Table 1).

MA has a temperate climate with mean monthly temperatures of 18.6–21.7°C in the summer, −4.3 to −0.1°C in the winter, with ~1100–1300 mm of precipitation distributed evenly throughout the year (NOAA, 2021). The most abundant tree species in MA forests include red maple, northern red oak, and eastern white pine (Butler, 2018). However, much of this forested area is highly fragmented due to road construction, pastureland and farmland abandonment, and urban sprawl over the last 100 years (Reinmann & Hutyra, 2017a, 2017b).

2.2 | Urbanization

Sites were classified as urban or rural based on % ISA and distance from Boston (Table 1). Park Street Station in Boston represented the urban end of the gradient, and Leverett, MA represented the rural end. Percent ISA for each of the eight sites was classified using 990 × 990 m grid cells using MassGIS data following methods outlined in Raciti et al. (2012). ISA coverage ranged from 1% to 27.5% across the eight sites along the urban to rural gradient. When using distance to Boston as a metric for urbanization, the field site at Blue Hills in Canton, MA is classified as urban and Broad Meadow in Worcester, MA is classified as rural. When urbanization is assigned using % ISA, Blue Hills is classified as rural and Broad Meadow as urban. These two distinct urbanization metrics, % ISA and distance from Boston, were used to examine the impacts of each independently on soil N cycling and foliar N concentrations.

2.3 | Soil collection and analysis: Soil N cycling

Soil net ammonification and net nitrification rates were measured in situ using the “buried bag” method (Durán et al., 2012; Eno, 1960; Hanselman et al., 2004; Westermann & Crothers, 1980). Two adjacent 10 × 10 cm soil samples were taken by removing the litter layer and sampling the full depth of the organic layer at 0, 15, 30, 60, and 90 m from the forest edge. Soil was taken exclusively from the organic layer, as most decomposition of organic material and N mineralization occurs there (McNeill & Unkovich, 2007). The depth of the organic soil layer was determined in the field with a ruler, according to techniques outlined by the Soil Science Society of America (Vero, 2021). Variation in the depth of the soil organic layer was measured and calculated at each plot throughout the edge to interior gradient at each site. For each set of paired samples, one sample was returned to the lab immediately to be analyzed within 24 h of field sampling (T_0; $n = 2$ at each distance from the forest edge), while the remaining sample (T_f; $n = 2$ at each distance from the forest edge) was sealed in a gas-permeable plastic bag and placed back into the hole from which it was taken. The hole was covered with the removed leaf litter, and the bagged T_f sample was left to incubate in situ for 26–35 days. Soils were incubated in the field July 20–August 15 in 2018 and May 23–June 2 and July 17–August 19 in 2019. At the end of the incubation periods, the incubated cores were returned to the laboratory for analysis within 24 h of field collection. The site at Blue Hills in Canton, MA was not sampled in 2018.

After field collection, fresh soils were put through a 2 mm metal sieve to remove roots, rocks, and other large debris and homogenized. 5 g of freshly sieved soils was shaken for 1 h in 60 mL 2 M potassium chloride solution (KCl) to extract ammonium (NH_4^+) and nitrate (NO_3^-) ions for analysis. Each extract solution was then filtered using Whatman Grade 2 filters (8 μm pore size), and the resulting solutions were stored at 4°C until further analysis.

Soil extracts were analyzed colorimetrically for NH_4^+ and NO_3^- concentrations using the microplate method. Soil extracts were pipetted into a 96-well microplate, including ammonium nitrate standards and quality control solutions (ERA Environmental). To quantify ammonium in solution, citrate, sodium nitroprusside, and hypochlorite reagents were added in succession, and the resulting color intensity was measured in a microplate reader (Versa Max tunable microplate reader) at an absorbance wavelength of 667 nm (Ali & Lovatt, 1995). Nitrate in solution was quantified by adding a vanadium chloride solution, incubating for 16 h, and running plates through a microplate reader at an absorbance wavelength of 540 nm. Net rates of ammonification and nitrification were calculated as the respective differences in ammonium and nitrate concentrations between T_f and T_0 samples divided by the duration of the in situ incubation period. Total net mineralization was calculated as the sum of net ammonification and net nitrification.

2.4 | Abiotic soil properties

Soil moisture and SOM content were quantified using a 5-g subsample of fresh, sieved soil from each buried bag soil sample from all three deployment periods ($n = 6$ measurements). Fresh soil was dried in an oven at 65°C, and gravimetric water content was calculated as the difference between wet and dry soil mass, divided by wet mass, and multiplied by 100. SOM was quantified using the loss on ignition method. Each dried subsample used in the moisture analysis was then placed in a muffle furnace at 450°C for 4 h to combust organic matter. The combustion temperature of 450°C was chosen to maximize removal of organic matter while avoiding dehydroxylation of clay minerals in soil samples (Nelson & Sommers, 1996). SOM concentration was calculated as the difference between pre- and post-combustion mass divided by pre-combustion mass of the subsample and multiplied by 100.

Soil samples collected in July 2019 were analyzed for pH, conductivity, and bulk density. Soil pH was determined using a 5-gram subsample of freshly sieved soil from the soil cores collected in July 2019 (T_0 samples). Soils were mixed with 10 mL distilled deionized (DDI) water and shaken to form a slurry, which was then measured with a pH meter (Mettler-Toledo SevenEasy pH). Separate subsamples of the same fresh soil were mixed with DDI water in a 1:5 soil-to-water ratio and shaken for 1 min at 10-min intervals over a period of 30 min for conductivity analysis. Making sure to keep the soil suspended in the water, conductivity (soluble salt content) in each sample was measured with a Hach HQ40D Portable Multi Meter with conductivity probe.

A separate set of soils collected in July 2019 at each transect location at each site were analyzed for bulk density. Samples were collected using a 10 cm depth hammer core (2.4 cm radius), and organic and mineral soil horizons were separated and measured for depth in the field. In the lab, soil samples were homogenized using a 2 mm metal sieve and weighed, dried, and reweighed. Roots, rocks, and other debris were separately weighed for each sample, and rocks were then added to 50 mL of water in a graduated cylinder to measure their volume by displacement. Dry and wet bulk density was then calculated for each sample as soil mass per rock-free volume.

2.5 | Foliar nitrogen and C:N

Foliage from the mid- and upper canopy was sampled from three oak trees (*Quercus* spp.) using a manual pole pruner at each of the transect distances at each site in July 2019, preferentially sampling sun-lit leaves from the mid canopy. Samples were air-dried prior to processing. Leaves were ground using a Wiley mill (40 mesh) and then analyzed for C and N concentration using a NC2500 elemental analyzer (CE Elantech). Foliar N, while it does not consider the nutrient content of belowground plant tissues or microbes, can be used as a proxy for N uptake by trees (Kahmen et al., 2008), and C:N gives a measure of lability of organic tissue.

2.6 | Statistical analysis

Throughout our analyses, distance to the forest edge was treated as a continuous numerical variable, while urban and rural were treated as a categorical binary. Binary urban vs. rural assignments to each site were made according to distance from Boston and ISA using the methods described above. Because urbanization is multidimensional, various definitions of urbanization are applied in different settings and studies, and differing definitions can lead to inconsistent conclusions about urban vs. rural biogeochemistry (Raciti et al., 2012). To examine whether our conclusions are robust to different definitions of urban vs. rural, we conducted parallel analyses using both the ISA-based and distance-based urban–rural site classifications.

Normality of the data was assessed on the residuals of each linear model and using Shapiro–Wilkes tests. When data were verified to be normally distributed, linear mixed-effect (LME) models were used with site as the random effect to account for repeated sampling over time using the *nmle* package (Pinheiro, 2022). LMEs with site as the random effect and abiotic soil factors as well as distance from the forest edge were used to evaluate the relationship between soil properties and soil N cycling variables. Analysis of variance and least squared means regression with pairwise comparisons were used to calculate significant differences in N metrics, abiotic factors, and organic soil depth between distances from the forest edge. Analysis of covariance, commonly used for comparing linear regressions, was used to assess the significance of interactions between site and distance from the forest edge, as well as overall differences between urban and rural sites. When data were non-normally distributed, generalized LME models were used with site as the random effect to account for lack of normality. An alpha value of .05 was used to denote statistical significance. Results of model fitting are displayed within each figure. All statistical analyses were conducted using R version 4.0.2 (R Core Team). All data are available in Caron et al. (2023).

3 | RESULTS

3.1 | Soil N cycling rates

Net ammonification and net mineralization had significant relationships with distance to Boston (p = .039 and .0047, respectively), but only net mineralization had a significant relationship with % ISA ($p<.001$). When urbanization is defined by distance to Boston, rates of net ammonification and net mineralization were higher in urban than rural forests (p = .0051 and .0047, respectively; Figure 1a,e). Within urban forests, net ammonification and net mineralization were both higher in the forest interior than near edges and showed a significant relationship with distance from the edge ($p<.01$ for both; Figure 1a,e). Net nitrification rates were very low across sites, though varied significantly with distance from the forest edge ($p=.016$; Figure 1c,d). There were no significant differences in rates of net nitrification between urban and rural forests, regardless of urbanization metric used ($p=.69$ and .14 for urbanization defined as distance to Boston and percent ISA, respectively; Figure 1c,d). When urbanization is defined by percent ISA, rates of net ammonification and net mineralization did not differ significantly between urban and rural forests (p = .42 and .36, respectively; Figure 1b,f). The patterns of soil N cycling rates averaged over 2 years (Figure 1) are similar to those observed individually within each of the 2 years of field sampling (Figure S1). Patterns of net ammonification, nitrification, and mineralization measured per mass of SOM were similar to those per mass of dried soil (Figure S2).

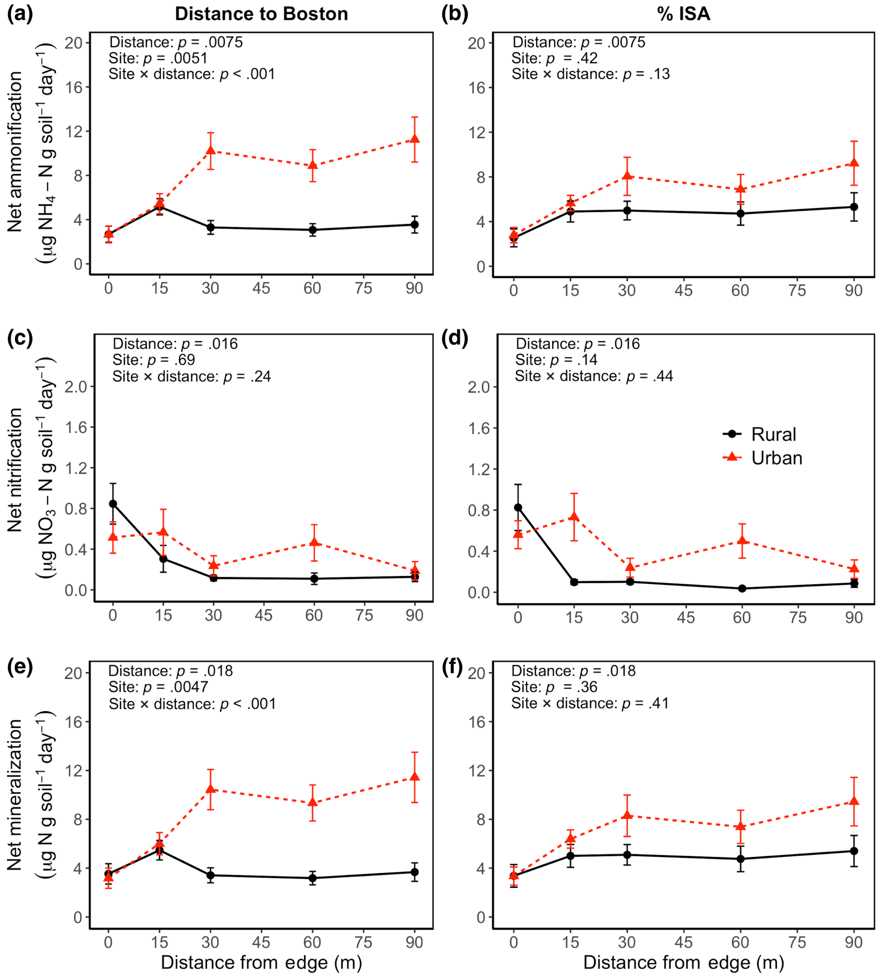


FIGURE 1 Spatial patterns in rates of net ammonification (a, b), net nitrification (c, d), and net mineralization (e, f) at each distance from forest edge (0, 15, 30, 60, and 90 m) at four urban (red triangles) and four rural (black circles) sites. Points represent the average rates over three measurement periods during the 2018 and 2019 growing seasons, with error bars representing ± one standard error. In panels a, c, and e (left), urban is defined by distance to Boston. In panels b, d, and f (right), urban is defined by percent impervious surface area (% ISA). *p*-Values are shown for results of a linear mixed effects model describing the relationship between soil N cycling and distance from the forest edge, and an analysis of covariance examining site (urban vs. rural) and the interaction between site and distance from the forest edge.

3.2 | Foliar N

Foliar N concentrations were significantly higher in urban than rural forests, but only when urbanization was defined as distance to Boston ($p = .0017$; Figure 2a). When urbanization was defined by percent ISA, there was no difference in foliar N between forest types ($p = .23$; Figure 2b). Foliar C:N ratio did not differ between urban and rural sites regardless of the urbanization metric used ($p = .093$ and .29, respectively; Figure 2c,d). Neither foliar percent N nor C:N had statistically significant relationships with soil pH, conductivity, bulk density, or any of our measured N cycling rates (all $p > .05$).

3.3 | Abiotic soil factors

Soil conductivity and organic matter were both significantly higher in urban than rural forests when urbanization is defined as distance to Boston ($p = .01$ and <.001, respectively; Figure 3a,e). Soil bulk density was higher in rural than urban forests when urbanization is defined by distance to Boston ($p < .001$; Figure 3c). When urbanization is defined by percent ISA, none of the measured abiotic soil factors or percent SOM were significantly different between urban and rural forests (Figure 3b,d,f; $p > .05$ for all). Across all sites, there were no statistically significant relationships between urbanization or distance from the forest edge with soil organic layer depth ($p > .05$). Aside from the Blue Hills Observatory site, which has rockier soils and a shallow organic soil layer (2.94 cm), average depth of the organic soil layer ranged from 3.81 cm at Harvard Forest Site 3 to 4.96 cm at the Arnold Arboretum (Table 1). The only site that had a statistically significant difference in organic soil horizon depth between the forest edge and interior difference was Harvard Forest site 1, where the organic soil layer was 1.21 cm deeper at the forest interior compared to the edge ($p < .05$).

Net ammonification and mineralization were both negatively related to soil pH and soil bulk density in both urban and rural (defined by distance to Boston) forests ($p < .05$; Figure 4a,c,g,i), but were not related significantly to soil moisture (Figure 5b,f). Net ammonification and mineralization were both positively related to soil conductivity, but in urban sites only ($p < .001$; Figure 4b,h). Net ammonification and net mineralization had significant positive relationships with percent SOM in both urban and rural sites ($p < .001$; Figure 5a,e). Net nitrification was positively related to soil pH in both urban and rural forests ($p = .040$ and .001, Figure 4d), but negatively to soil moisture in rural forests only ($p = .034$, Figure 5d).

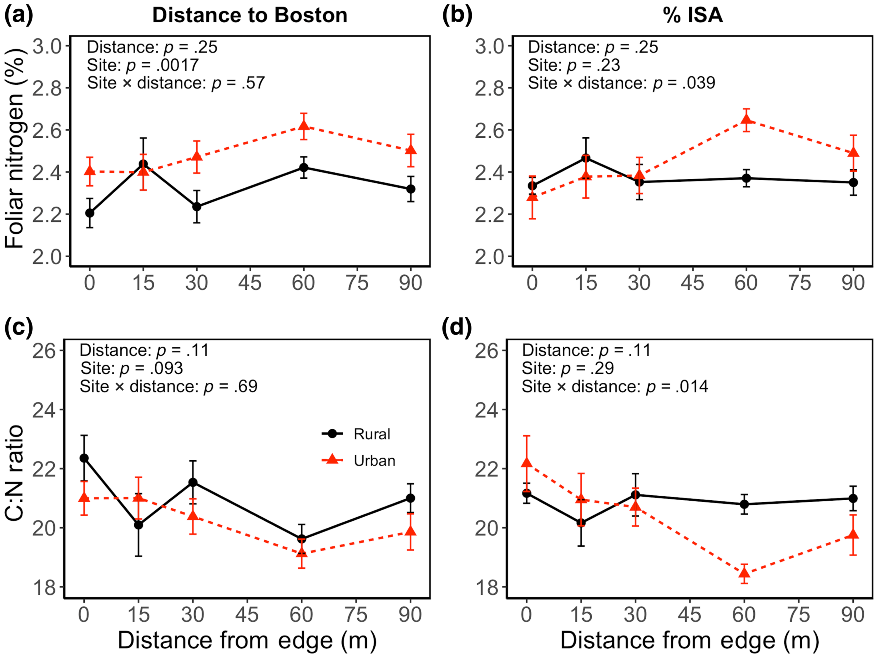


FIGURE 2 Spatial patterns in foliar nitrogen concentration (a, b) and C:N ratio (c, d). Points represent the averages at each distance from the forest edge (0, 15, 30, 60, and 90 m) during 2019 growing season, with error bars representing ± one standard error. Red triangles show the average at four urban sites, and black circles represent averages at four rural sites. In panels a and c (left), urban is defined by distance to Boston. In panels b and d (right), urban is defined by percent impervious surface area (% ISA). *p*-values are shown for results of a linear mixed effects model describing the relationship between soil N cycling and distance from the forest edge, and an analysis of covariance examining site (urban vs. rural) and the interaction between site and distance from the forest edge.

4 | DISCUSSION

This study shows that the urban forests of the Greater Boston Area experience greater rates of soil net ammonification and mineralization and higher foliar N concentrations than rural forests, but that the increases in soil N cycling rates in urban forests disappear at the forest edge. These findings confirm our first hypothesis with rates of net ammonification and mineralization (both per mass soil and SOM) and foliar N being significantly higher in urban than rural forests, when urbanization is defined as distance to Boston. However, rates of soil net nitrification and foliar C:N ratios showed no statistical difference between urban and rural forest types, regardless of how urbanization is defined. Our second hypothesis that soil N cycling rates and foliar N concentration are higher at forest edges than interiors was only partially supported by our findings; net nitrification rates were fourfold to fivefold higher at rural forest edges than interiors, but this pattern was not present in urban forests regardless of the urbanization metric used. In contrast to our expectation, rates of net ammonification and mineralization, as well as foliar N concentration, were significantly lower at forest edges compared to the forest interior in both urban and rural sites. While some caution should be used in interpreting the results of a short-term study like this one, the consistency we observed across both years and sites in soil N cycling rates and foliar N patterns demonstrate that we likely observed larger trends. These results also highlight the complex relationship between urbanization and forest fragmentation and demonstrate that future ecological research in human-influenced environments should continue to consider the interconnected nature of anthropogenic impacts to natural systems. Taken together, our results demonstrate that soil N availability is greater in urban than rural temperate forests, supporting our conclusion that urban forests are not as susceptible to the phenomena of N oligotrophication as rural forests; however, forest fragmentation and the introduction of edge environments counteract the benefits of urbanization for N supply to temperate forest trees.

4.1 | Urbanization metric

In general, we found more significant differences between urban and rural sites when urbanization was defined as distance to Boston rather than percent ISA, as well as stronger relationships between distance to Boston and all soil N cycling variables, suggesting that regional factors like atmospheric deposition may be more important than local factors like pavement or human activity in areas adjacent to forests for controlling patterns of soil N cycling and plant N uptake. The fact that distance to Boston appears to be the urbanization metric that more strongly relates to soil N cycling rates is not surprising, as Rao et al. (2013) found that percent ISA was not a strong predictor of soil or foliar N across a similar urban to rural transect to that used in our study. Raciti et al. (2012), on the other hand, found ISA to be the best metric to describe the impact of urbanization on soil and vegetation C and N stocks in Massachusetts, but recommended using a variety of indicators of urban intensity in future

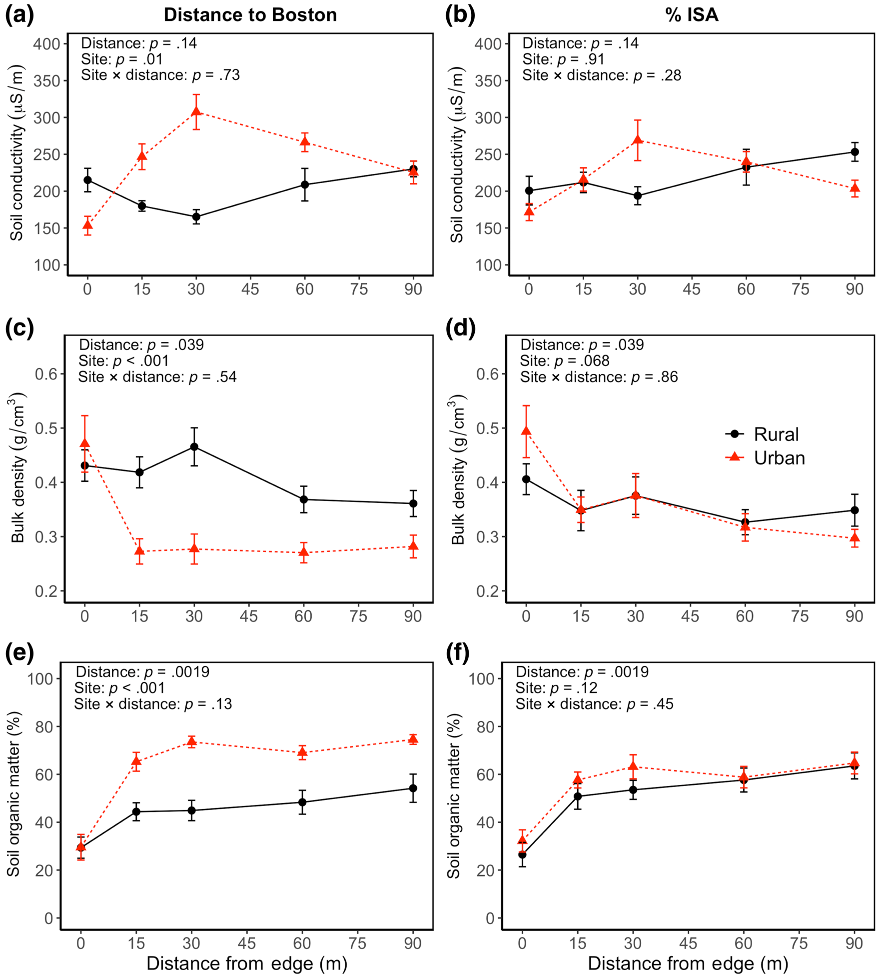


FIGURE 3 Spatial patterns in soil properties: soil conductivity (a, b), bulk density (c, d), and percent soil organic matter (e, f) in urban (red triangle) and rural (black circle) sites at each distance from the forest edge (0, 15, 30, 60, and 90 m). Points represent averages with standard error over three measurement periods during the 2018 and 2019 growing seasons. In panels a, c, and e (left), urban is defined by distance to Boston. In panels b, d, and f (right), urban is defined by percent impervious surface area (% ISA). p-values are shown for results of a linear mixed effects model describing the relationship between soil N cycling and distance from the forest edge, and an analysis of covariance examining site (urban vs. rural) and the interaction between site and distance from the forest edge.

research to capture the heterogeneity of urban landscapes. That said, soil chemistry has been shown to vary significantly with distance from an urban core in addition to with more detailed metrics such as ISA, demonstrating that impacts of urban areas on nutrient cycling are more complex than can be explained by local conditions alone (Pouyat et al., 2008). Soil N content and C:N ratios were also shown to be affected by distance to the city center of Baltimore, MD, where both were found to be highest in suburban forests compared to urban and rural sites (Yesilonis et al., 2022). This lack of consistency in the literature regarding which aspects of urbanization most strongly affect nutrient cycles is likely due to the heterogeneity of urban environments. Garvey et al. (2022), for example, found variation in soil respiration at the same eight study sites was more strongly related to %ISA than to distance to Boston. As such, we conclude that it is important to consider multiple metrics of urbanization, and how they interact with each other, when assessing the impacts of cities on nearby forests.

4.2 | Soil net ammonification and mineralization

The higher rates of net ammonification and mineralization in urban than rural sites when urbanization is defined as distance from Boston may be due to in part to previously reported higher rates of atmospheric deposition in urban compared to rural areas (Decina et al., 2018; Rao et al., 2014; Templer & McCann, 2010; Weathers et al., 1995), as well as measured lower bulk density, and higher soil conductivity and SOM at the urban than rural sites found in this study. Higher bulk density, as we observed in rural sites, has been shown to be associated with reduced SOM (Pouyat et al., 2002) and lower net N mineralization rates (Tan & Chang, 2007), which is consistent with our findings. In addition, past research shows that rates of atmospheric N deposition are elevated in cities around the globe (Decina et al., 2020), including Boston (Decina et al., 2018; Rao et al., 2014). A similar MA study along this urbanization gradient shows distance to the urban core of Boston to be positively correlated with atmospheric ammonium and total inorganic N inputs to forested areas (Rao et al., 2014). Though site-level throughfall inputs are not reported here, the previously described patterns of N deposition and our measured soil properties may explain the higher rates of net ammonification and mineralization in the urban forests of greater Boston compared to nearby rural forests.

While there were pronounced differences in net ammonification and net mineralization rates between urban and rural (defined by distance to Boston) forest interiors, these soil N cycling rates were nearly identical at urban and rural forest edges. Soil pH, bulk

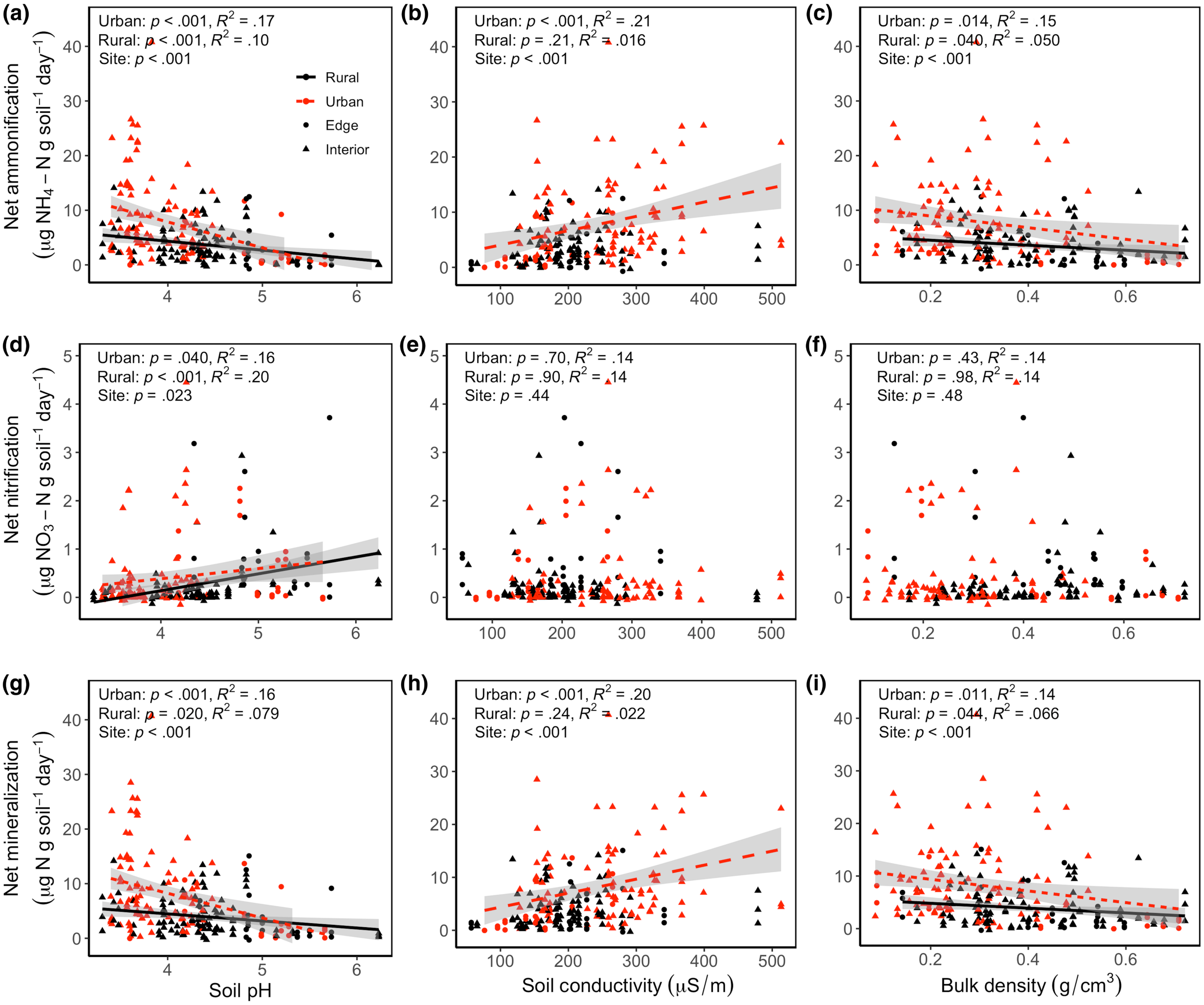
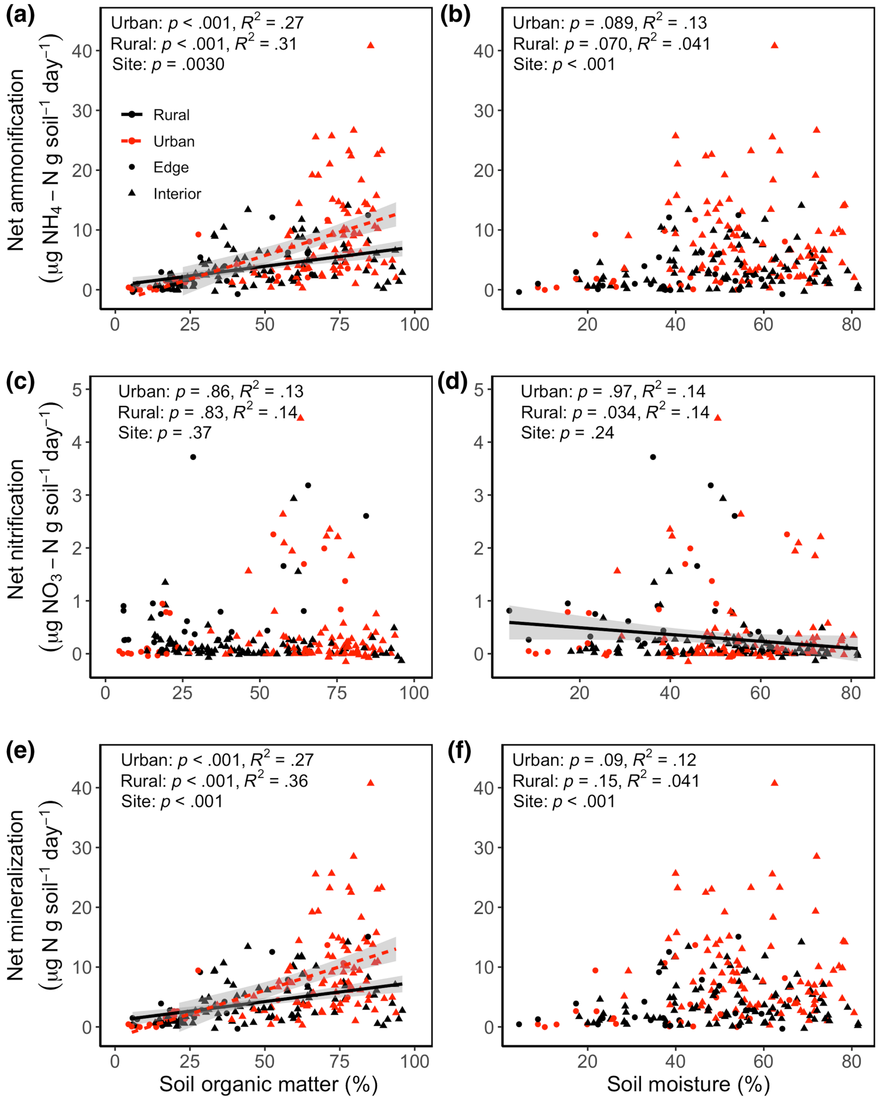


FIGURE 4 Relationships between rates of net ammonification, net nitrification, and overall net mineralization with soil pH (a, d, g), conductivity (b, e, h), and bulk density (c, f, i). Points represent the average rates over three measurement periods during the 2018 and 2019 growing seasons, with urban sites in red and rural sites in black. Urbanization is defined by distance to Boston. Forest edge plots are represented by circles (0 m) and forest interior points (15–90 m) are triangles. Best fit lines with a shaded 95% confidence interval are shown when relationships are statistically significant.

density, and SOM were also very similar between urban and rural forest edges, which likely led to the convergence of N cycling rates at these sites. However, Garvey et al. (2022), another study using the same sites as our study, found soil temperature to be higher and soil moisture to be lower at urban compared to rural forest edges when defined by % ISA. Soil moisture has been shown to correlate positively with rates of net N mineralization (Guntiñas et al., 2012), likely due to the stimulation of microbial activity. In our study, while there was a positive relationship between rates of net ammonification and net mineralization with soil moisture, these relationships were not significant. Bulk density decreased nearly twofold from 0 to 15 m from the forest edge at our urban sites and remained low further into the forest interior. Rural sites had a slight decrease in bulk density after 30 m from the forest edge, but soils remained denser at forests further from Boston throughout the edge to interior transect, while there was little difference between sites when using % ISA as an urbanization metric. Greater bulk density in rural sites and at the urban edge than interior likely contributed to lower soil N cycling rates as compacted soils have been shown to suppress microbial processes that drive net N mineralization (Tan & Chang, 2007). It is possible that the unexpected higher bulk density at rural sites is not due to compaction, but due to variation in organic soil depth. However, our results show that organic soil depth did not vary with urbanization ($p = .38$). Only one site showed a significant relationship between organic soil depth and distance from the forest edge (Harvard Forest 1, $p < .05$; remaining sites, $p > .05$). The similarities we found in soil pH, SOM, and bulk density at forest edges across urban and rural forest sites may have been sufficient to offset other environmental differences, such soil moisture and atmospheric N

FIGURE 5 Relationships between rates of net ammonification, net nitrification, and overall net mineralization with soil organic matter (a, c, e) and gravimetric soil moisture (b, d, f). Points represent the average rates over three measurement periods during the 2018 and 2019 growing seasons, with urban sites in red and rural sites in black. Urbanization is defined by distance to Boston. Forest edge plots are represented by circles (0 m) and forest interior points (15–90 m) are triangles. Best fit lines with a shaded 95% confidence interval are shown when relationships are statistically significant.



deposition, that would otherwise have likely lead to differences in N cycling rates between urban and rural forest edges.

Overall, it appears that much of the observed enhancement of net ammonification and mineralization in urban forest interiors compared to urban edges and rural forests can be attributed to patterns in soil properties along our urbanization and edge to interior gradients. The higher rates of net ammonification and mineralization in the forest interior than edge of urban sites were surprising but may be due to greater amounts of SOM and lower soil pH in the forest interior sites. SOM has been found to correlate positively with rates of net N mineralization (Cookson et al., 2007), but soil pH can have mixed effects on rates of ammonification and net N mineralization (Cheng et al., 2013). Higher soil pH may decrease net ammonification rates at urban forest edges compared to interiors, though determining the exact mechanism responsible for the patterns we observed in soil pH was beyond the scope of this work. Similar to our study, rates of net mineralization were lower with higher pH after calcium was added to northern hardwood forest soils in New Hampshire to increase pH to pre-industrial levels (Groffman et al., 2006). Higher pH has also been associated with increased ammonium immobilization by microbes and decreased rates of net N mineralization in aspen dominated forests of central Canada (Cheng et al., 2013). It is likely that anthropogenic forces associated with urbanization and fragmentation are driving the observed differences in soil conditions. Assessing these drivers was outside the scope of our project, but warrants further study.

The positive relationships between soil conductivity and both net ammonification and mineralization rates found in this study are similar to the results found by Green and Cresser (2008) in temperate grassland ecosystems, but in contrast to the patterns reported by Duan et al. (2018) and Irshad et al. (2005) in temperate and boreal ecosystems, where higher rates of net mineralization in soils were associated with lower levels of conductivity. It should be noted that our soil measurements were taken in mid-summer, well removed from seasonal applications of road salt. Despite this, the positive relationship we found in our study between net ammonification and mineralization with soil conductivity suggests that conductivity may have played a role, albeit an unexpected one, in contributing to the higher observed rates of N cycling in urban than rural forests.

Rates of net ammonification and mineralization per unit SOM remained generally higher in urban than rural forests and at urban forest interiors compared to edges. These higher rates of net ammonification and mineralization per gram SOM in urban compared to rural forests suggest the presence of higher quality (i.e., more labile) organic matter in urban than rural sites (Booth et al., 2005). Data from temperate forests of China also reveal greater SOM accumulation in urban than rural soils, suggesting the SOM dynamics we observed may be occurring in other temperate systems (Zhai et al., 2017). SOM quantity and quality have been shown to be play a critical role in regulating soil N cycling processes (Cookson et al., 2007; Schimel & Bennett, 2004), with larger and more labile SOM pools being associated with higher rates of net ammonification and mineralization in forest soils (Booth et al., 2005). Our results demonstrate that the distribution of SOM along the urbanization and forest edge to interior gradients, as well as patterns of abiotic soil properties, may explain much of the observed patterns in net ammonification and mineralization. While the activity and community composition of the soil microbes responsible for mineralizing organic N are not described here, the statistically significant positive relationships between percent SOM and both net ammonification and mineralization, as well as the consistent edge to interior patterns displayed by SOM and soil N cycling, highlight the importance of considering the combined impacts of urbanization and the creation of forest edges on organic soil and N dynamics.

4.3 | Net nitrification

The relatively low rates of net nitrification in all our sites likely contributed to the lack of observed difference in rates of this process between urban and rural sites. Nitrification rates are variable within temperate systems (Attiwill & Adams, 1993; Schmidt, 1982) and are often controlled by soil pH, moisture, organic matter quality, and tree species composition (Cookson et al., 2007; Lovett et al., 2004; Schmidt, 1982; Templer & Dawson, 2004). Other studies have found net nitrification rates in forest soils as low as ours (Remy et al., 2018; Verchot et al., 2001; Zhu & Carreiro, 1999), which has been attributed to tree species composition, as well as low soil pH (Aber et al., 1991; Hobbie, 2015; Templer, 2003; Venterea et al., 2003). In our study, we selected all sites to be dominated by oaks (*Quercus* spp.). Red oaks (*Quercus rubra*), which are the dominant tree species at all eight sites along our urbanization gradient, are associated with lower net nitrification rates compared to other dominant tree species in the Northeastern U.S. such as sugar maple (Lovett et al., 2004; Templer, 2003). The dominance of oak trees and consistency of species composition across sites may have been more influential in determining patterns of net nitrification between urban and rural forests than differences in atmospheric deposition, soil properties, and/or microclimatic conditions between sites due to urbanization.

Soil properties that varied between forest edges and interior may explain patterns in net nitrification we observed, though the impact of these properties on the nitrifying bacteria responsible for the transformation of ammonium to nitrate in soil are not quantified here. Soil pH, which has been shown to positively correlate with soil nitrification (Cookson et al., 2007; Schmidt, 1982) was highest at rural forest edges, likely contributing to the higher net nitrification rates compared to the forest interior. Urban forest edges also had higher soil pH than interiors, but did not show the same net nitrification edge enhancement observed in rural forests. The difference in net nitrification dynamics at rural compared to urban forest edges, despite both having similar soil pH, may indicate that soil acidity was not the dominant influencing factor on nitrification rates. We were surprised by the higher rates of net nitrification in rural forest edges than interiors given their lower soil moisture (Garvey et al., 2022) and because soil moisture is typically positively related to net nitrification rates (Schmidt, 1982). However, in our sites gravimetric soil moisture did not appear to be a major predictor of net nitrification at rural edges despite the significant relationship between nitrification and moisture at rural sites across the edge to interior gradient.

4.4 | Foliar nitrogen

The pattern of higher foliar N concentrations in forests closer to Boston mirrored observed patterns in soil N cycling rates for net ammonification and mineralization, suggesting that greater N availability from soil microbial processes in urban sites contributed to greater N uptake by trees compared to rural sites. Atmospheric N deposition, while still high in urban areas throughout the world (Decina et al., 2020) and in the Greater Boston area (Decina et al., 2018; Rao et al., 2014), has been declining across the United States, including substantial decreases in the northeastern U.S. in recent decades (Ackerman et al., 2019; Lloret & Valiela, 2016). Such a decline, coupled with increasing plant demand for N caused by warming temperatures, has contributed to N oligotrophication in rural forests throughout this region (Goodale et al., 2003; Groffman et al., 2018; McLauchlan et al., 2017) and elsewhere around the globe (Craine et al., 2018; Elmore et al., 2016; Mason et al., 2022). However, higher concentrations of foliar N in urban forests of our study suggest that trees in urban forests may be less limited by N than their rural counterparts. Fine root biomass of trees has been shown to decrease, and root functional traits and mycorrhizal strategies tend to shift away from prioritizing N acquisition, under elevated N deposition (Ma et al., 2021; Zhao et al., 2022). These plant and fungal responses, in addition to reported perturbations in litter decomposition dynamics in urban forests (Pouyat & Carreiro, 2003), likely also influenced the foliar N patterns we measured, but were outside the scope of our study.

Foliar N concentrations did not vary significantly with distance from the forest edge at urban nor rural sites, suggesting that the impacts of urbanization on foliar N per unit leaf area act on a larger spatial scale than was captured in our forest edge to interior gradient. Trees at the forest edge in Massachusetts have been shown to grow faster and sequester more carbon than interior trees (Reinmann & Hutyra, 2017a, 2017b; Smith et al., 2018). Although studies in Europe have attributed the forest edge growth enhancement to increased N availability (Meeussen et al., 2021; Remy et al., 2016), lower rates of atmospheric deposition and a lack of difference in foliar N between edge and interior trees suggest this is not the primary driving variable in eastern U.S. forests (Reinmann et al., 2020; Reinmann & Hutyra, 2017b). Other studies evaluating the effects of forest fragmentation similarly showed no statistically significant variation in foliar N with distance from the forest edge, despite finding significant relationships with soil N pools (Duquesnay et al., 2000; Rao et al., 2013; Remy et al., 2016).

5 | CONCLUSIONS

Taken together, these results indicate that urban forests in the northeastern U.S. generally have increased soil N availability for plant uptake compared to rural forests, but soil properties and other dynamics at the forest edge cancel out this increase. Foliar N concentrations in trees show similar urban enhancement, suggesting that the urban forests of the northeastern U.S. may not be as strongly impacted by the trend of N oligotrophication observed in rural temperate forests around the globe. While future work should be done to examine the biological mechanisms which drive the terrestrial N cycle, our findings reveal that urban forests and forest edges have considerably different N cycling dynamics than intact rural forests, underscoring the importance of accounting for urban ecosystems and forest fragmentation in global change research.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at the Environmental Data Initiative: [edirepository.org] at [https://doi.org/10.6073/pasta/e031d09b306ca4e49c699e81e378d87d].

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