Impacts of Invasive Woody Vines on Carbon and Nitrogen Dynamics in Forested Urban Natural Areas: Implications for Ecology and Management

Hixon Fellowship Report
December 2017

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Introduction

Urbanization is a dominant pattern of land use that alters ecosystem structure and function in different biomes around the world (Grimm et al. 2008, Pickett et al. 2011). As the global population and urban centers grow, natural areas will face increasing pressure as a result of human settlement (White et al. 2009). Potential impacts include fragmentation (Luck & Wu 2002), soil disturbance (Pavao-Zuckerman 2008), and invasion by non-native species (Kowarik 2011). These changes have the potential to alter ecosystem processes, including carbon (C), water, and nutrient cycling (Alberti 2005, Pickett et al. 2011). In an effort to counter these impacts, cities worldwide are investing in restoration projects that enhance the social and ecological value of their natural areas (Pataki et al. 2011, Oldfield et al. 2013). One of the most common and costly restoration measures in urban environments is invasive species removal (Vidra et al. 2007, Daniels et al. 2016).

Urban natural areas face frequent and sustained pressures from plant invasions due to high levels of fragmentation, heavy recreational use, and dispersal of non-native plant propagules (Williams et al. 2009, Cadotte et al. 2017). Once established, invasive plants can have significant and prolonged impacts on the function and diversity of native communities (Levine et al. 2003, Simberloff et al. 2013). Previous work has also demonstrated that non-native species can alter soil processes, such as C and nitrogen (N) availability, through changes in leaf litter quantity and quality, root exudates, and communities of associated soil microorganisms (Ehrenfeld et al. 2003, Corbin and D’Antonio 2004, Liao et al. 2008, Castro-Diaz et al. 2014, Suseela et al. 2016).

Invasive woody vines (lianas) pose a particularly significant threat to native forests in cities (Green Seattle Partnership 2004, Bounds et al. 2014, Leicht-Young and Pavlovic 2015). Lianas are disturbance-adapted plants that thrive in urban systems due to high levels of fragmentation, elevated temperatures, and increased carbon dioxide concentrations (Brice et al. 2014). Recent work also suggests that the abundance of lianas is increasing worldwide in response to drivers of global change (Phillips et al. 2002, Schnitzer and Bongers 2011, Laurance et al. 2014). In New York City’s (NYC) forested parklands, native and non-native vines are the most abundant understory species (Pregitzer et al. In prep). While canopy trees in NYC are predominantly native, the proportion of non-native species increases in the midstory and herbaceous layers, suggesting that the composition of New York’s forests may shift as canopy trees age and die (Pregitzer et al. In prep). Woody vines have the potential to accelerate this process by increasing tree mortality and turnover and reducing regeneration (Ladwig and Meiners 2010, Matthews et al. 2016).

In addition to altering tree performance and forest structure, lianas can also impact belowground processes (Leicht-Young et al. 2009, Powers 2015, van der Heijden et al. 2015). Woody vines invest in large canopies with high leaf areas, and their foliage is often more nutrient rich than leaves from trees (Asner and Martin 2012, Powers 2015). Lianas may therefore increase local N availability through large inputs of high quality leaf litter, and these changes may persist as legacy effects following the removal of invasive vines during restoration (Ehrenfeld et al. 2003, Kuebbing et al. 2015, Suseela et al. 2016). Elevated inorganic N levels may also give fast-growing, invasive plants a competitive advantage over native species, resulting in positive feedbacks that facilitate further invasion (Ehrenfeld et al. 2003, Suding et al. 2004).
Despite management concerns regarding the impacts of woody vines on forest dynamics, there is limited knowledge on the ecological role of native and non-native lianas in temperate systems (Londre and Schnitzer 2006, Ladwig and Meiners 2015, Matthews et al. 2016). Studies gauging the effectiveness of restoration treatments in urban areas are also scarce (Ruiz-Jaén and Aide 2005), and the research that does exist focuses on changes in plant community composition rather than the impacts of restoration on soil processes (Pavao-Zuckerman 2008). If invasive woody vines create soil legacies by building inorganic N pools, successful reestablishment of diverse, native communities may require additional site treatments beyond the removal of target species. An improved understanding of the impacts of lianas on soil nutrient cycling as well as any legacy effects following invasive vine removal is therefore critical to the long-term success of future urban forest restoration efforts.

This study aims to advance knowledge of the impacts of lianas on soil processes by examining the relationship between woody vine abundance and C and N availability in invaded, un-invaded, and restored forest plots in NYC’s forested natural areas. Specifically, this study addresses the following questions:

1. To what extent do woody vines influence C and N availability in forested urban natural areas?
2. Do native and non-native vines have similar impacts on C and N dynamics?
3. To what extent do the impacts of invasive vines on soil processes persist following their removal?

**Methods**

*Study Area and Site Selection*

With more than 8.5 million residents, New York City (NYC, 40.7127°N, 74.0059°W) is the most populous city in the United States (U.S. Census Bureau 2016), and historically it harbored a rich diversity of ecological communities (DeCandido 2004, Kiviat and Johnson 2013). Situated at the confluence of the Hudson River and the Atlantic Ocean, NYC’s five boroughs straddle three distinct physiographic provinces—New England Upland to the north, the Atlantic Coastal Plain to the southeast, and the Piedmont to the southwest (USGS 2003, NRCS 2005). NYC has a moist, temperate climate, with an average winter temperature of 2°C, an average summer temperature of 23.9°C, and a mean annual precipitation of 118.4 cm (NOAA 2010). While humans have altered much of the city’s native ecosystems, NYC still contains over 16,000 hectares of public parklands, which amounts to 21.2% of the city’s land area (Trust for Public Land 2017). Thirty-five percent of NYC’s parks are designated natural areas, and this includes 5,280 hectares of forests, half of which are classified as oak-hickory (Quercus-Carya) (Forgione et al. 2016).

Oak-hickory forests typically occur on well-drained ridge tops and south- and west-facing slopes (New York City Department of Parks and Recreation 1995). Soils are primarily of glacial origin and include deep, well-drained ablation till (Charlton, Chatfield, and Hollis Series), mesic, fertile basal till of drumlins (Paxton, Montauk, and Woodbridge Series), moderately well-drained......
glacial outwash (Sutton Series), and poorly drained glaciolacustrine deposits (Tonawanda Series, NRCS 2017, see Table 1). Oak-hickory forests in NYC are also commonly underlain by human-transported materials derived from locally excavated upland loams (Greenbelt Series, NRCS 2017). Common overstory species include red, black, and white oaks (Quercus rubra, Q. velutina, and Q. alba, respectively), shagbark, bitternut, and mockernut hickories (Carya ovata, C. cordiformis, and C. tomentosa, respectively), and American beech (Fagus grandifolia, New York City Department of Parks and Recreation 1995). The understory and shrub layers commonly include mapleleaf viburnum (Viburnum acerifolium), lowbush blueberry (Vaccinium angustifolium), and flowering dogwood (Cornus florida, New York City Department of Parks and Recreation 1995).

We conducted this study in a subset of the Natural Areas Conservancy’s (NAC) citywide Ecological Assessment (EA) plots, which were established in 2013 to provide a baseline assessment of NYC’s natural areas. Ecologists at NAC selected the locations of these plots in ArcGIS by randomly generating points within parklands designated as natural areas by the New York City Department of Parks and Recreation (NYC DPR) at a density of one point per two-hectares (Pregitzer et al. In prep). PLOTS with greater than 50% impervious surfaces, landscaping, or tidal areas were excluded from the study (Pregitzer et al. In prep). From May-October in 2013-2014, ecologists from NAC collected forest assessment data for 1,124 10-meter radius forest plots in more than 50 parks (Forgione et al. 2016). The team surveyed overstory, midstory, and understory vegetation as well as canopy transparency, site disturbance, tree recruitment, vine growth, and soil properties (Forgione et al. 2016, Pregitzer et al. In Prep). The plots were then assigned vegetation associations using the U.S. National Vegetation Classification (Edinger et al. 2016). In total, the study classified 157 plots as oak-hickory forests (Pregitzer et al. In prep).

Using NAC’s 2013-2014 field data, we selected 54 oak-hickory forest plots in six parks that captured a range of native and non-native woody vine abundance in the understory (Figures 1 and 2). We excluded sites completely underlain by anthropogenic soils as well as sites located on Staten Island due to the heavy influence of deer browse on understory plant communities. We classified the remaining 109 oak-hickory plots into three vine abundance categories. Low vine abundance plots had less than 12.5% total woody vine cover, intermediate plots had greater than 12.5% total woody vine cover but less than 12.5% non-native woody vine cover, and high invasive plots had greater than 12.5% non-native woody vine cover (Figure 1). The final six parks we selected— Alley Pond, Cunningham, Forest, Inwood Hill, Pelham Bay, and Van Cortlandt— contained at least one plot within each vine abundance category (Table 1). After verifying the understory vine cover through site visits, we selected 18 plots from each vine cover class (Figure 2).

In addition to studying the impacts of woody vine abundance on C and N cycling, we also examined the effects of invasive vine management practices on the restoration of soil processes. Using NYC DPR’s management tracking database, we identified treated sites where three invasive woody vines—porcelainberry (Ampelopsis brevipedunculata), oriental bittersweet (Celastrus orbiculatus), and Japanese honeysuckle (Lonicera japonica)— had been targeted for removal through cutting and herbicide application within the past seven years. Overall, NYC DPR managed 15 of the 54 sites included in this study through invasive vine eradication.
### Table 1 – Site Descriptions for the Six NYC Parks Sampled in this Study

<table>
<thead>
<tr>
<th>Park</th>
<th>Borough</th>
<th>Location</th>
<th>Soil Types (NRCS 2017)</th>
<th>Park Size (Ha)</th>
<th>Woodland Area (Ha)</th>
<th>Plots</th>
<th>Area Sampled (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alley Pond</td>
<td>Queens</td>
<td>40.7424° N, 73.7384° W</td>
<td>Charlton Loam, Montauk Loam</td>
<td>248</td>
<td>120</td>
<td>3</td>
<td>942</td>
</tr>
<tr>
<td>Cunningham</td>
<td>Queens</td>
<td>40.7291° N, 73.7742° W</td>
<td>Charlton Fine Sandy Loam</td>
<td>153</td>
<td>103</td>
<td>8</td>
<td>2513</td>
</tr>
<tr>
<td>Forest</td>
<td>Queens</td>
<td>40.7000° N, 73.8566° W</td>
<td>Charlton Fine Sandy Loam</td>
<td>203</td>
<td>146</td>
<td>7</td>
<td>2199</td>
</tr>
<tr>
<td>Inwood Hill</td>
<td>Manhattan</td>
<td>40.8723° N, 73.9244° W</td>
<td>Charlton-Chatfield-Hollis Complex, Chatfield-Hollis-Rock Outcrop Complex</td>
<td>79</td>
<td>50</td>
<td>4</td>
<td>1257</td>
</tr>
<tr>
<td>Pelham Bay</td>
<td>Bronx</td>
<td>40.8506° N, 73.8210° W</td>
<td>Charlton Fine Sandy Loam, Charlton-Chatfield-Hollis Complex, Chatfield-Charlton Complex, Chatfield-Hollis-Greenbelt, Chatfield-Charlton-Hollis-Rock Complex, Chatfield-Greenbelt-Hollis-Rock Outcrop Complex, Paxton Loam, Woodbridge Loam</td>
<td>1084</td>
<td>313</td>
<td>14</td>
<td>4398</td>
</tr>
<tr>
<td>Van Cortlandt</td>
<td>Bronx</td>
<td>40.8979° N, 73.8860° W</td>
<td>Chatfield-Hollis-Rock Outcrop Complex, Chatfield-Carlton Complex, Woodbridge Loam, Tonawanda Silt Loam, Paxton Loam</td>
<td>436</td>
<td>262</td>
<td>18</td>
<td>5655</td>
</tr>
</tbody>
</table>

Soil types obtained from NRCS 2017. Park size and woodland area obtained from NAC 2017.
Figure 1 – Examples of forest plots from each vine cover class. All photographs were taken June-July 2017. (a) Low vine cover plot in Pelham Bay Park. Understory is dominated by *Vaccinium angustifolium* and *Quercus rubra* and *Quercus alba* regeneration (b) Intermediate vine cover plot in Forest Park. Understory consisted of *Eurybia divaricata, Toxicodendron radicans, Viburnum acerifolium,* and small amounts of *Celastrus orbiculatus.* (c) High vine cover plot in Van Cortlandt Park. Understory dominated by *Celastrus orbiculatus* and *Rubus* brambles. (d) Managed forest plot with removed *Celastrus orbiculatus* in Van Cortlandt Park.
Figure 2 — Locations of the 54 plots and six parks sampled in this study. Green polygons are the park boundaries and red points are the forest plots.

**Vegetation, Soil, and Leaf Litter Sampling**

For consistency, we used methods modified from NAC’s Upland Forest Assessment Field Protocol (2016) to survey overstory, midstory, and understory vegetation (Pregitzer et al. *In prep*). Within each 10-meter radius plot, we identified the species of all living and standing dead trees greater than 2 cm diameter at breast height (DBH, breast height is defined as 1.37 m). We also recorded the species and growth stage of all woody vines attached to midstory (2-10 cm DBH) and overstory (>10 cm DBH) trees using the following classes: (1) vine attached below DBH, (2) vine attached above DBH but below crown, (3) vine attached within the crown. We identified species to the highest taxonomic precision possible; however, we could often only describe dead or dying trees as hardwood or softwood.

For overstory trees, we recorded DBH to the nearest 0.1 cm using standard DBH tape and performed a visual canopy health assessment. Health metrics included crown dieback (percentage of dieback the live crown area), crown leaf discoloration (percentage of abnormal changes in leaf tissue color within the live crown area), leaf defoliation (percentage of total leaf defoliation resulting from insect, disease, or drought), and overall crown vigor. We estimated crown dieback and leaf discoloration to the nearest 5% and leaf defoliation using the following bins: (0) none to trace defoliated, (1) trace to 30% defoliated, (2) 31 to 60% defoliated, (3)
greater than 60% defoliated. Finally, we classified overall crown vigor according to the following definitions (NAC 2016):

1. Healthy: Tree appears to be in reasonably good health. No major branch mortality; crown is reasonably normal within the stand situation (dominant co-dominant, intermediate, suppressed); less than 10% branch and twig mortality, defoliation or discoloration present.
2. Slight Decline: Branch mortality, dieback, or discoloration in 10-25% of the crown branches; broken branches/crown area missing is less than 26%.
3. Moderate Decline: Branch mortality, dieback, or discoloration in 26-50% of the crown branches; broken branches/crown area missing is less than 50%.
4. Severe decline: Branch mortality, dieback, or discoloration in 51-100% of the crown branches; broken branches/crown area missing is 51-100%.

We also assigned ectomycorrhizal (ECM) and arbuscular mycorrhizal (AM) fungal associations for each tree species using the supplemental data file in Phillips et al. (2013). Basal area of each species was then used to determine ECM- or AM-dominance for each site (Phillips et al. 2013).

Within each forest plot, we placed eight nested 1-m² quadrats to estimate aerial and understory vegetation cover, count and measure tree seedlings (<2cm DBH), collect soil and leaf litter samples, and measure soil moisture and temperature (Figure 3). We stratified understory sampling by vine cover to capture the range of conditions present within each larger plot. To determine the number of subplots per vine class, we first estimated the total percent cover of four vine abundance bins across the larger plot: (0) None to trace, (1) 1-30%, (2) 31-60%, and (3) >60% woody vine cover. We then allocated one subplot for every 12.5% of the plot covered by a particular vine abundance bin with a minimum of two subplots per bin. To arrange the quadrats, we placed four subplots 5m from plot center in each cardinal direction and four plots 7m northeast, southeast, southwest, and northwest from plot center (Figure 3). If this arrangement did not result in one subplot per 12.5% cover of each vine class, we shifted one plot clockwise until we reached the predefined number of subplots for each vine abundance bin.
Within each nested subplot, we estimated the percent cover of each understory species to the nearest 1%. We also counted native tree seedlings (<2cm DBH) and categorized their height according to the following classes: (1) <10cm, (2) 10-30cm, (3) 30-100cm, (4) 100-200cm, (5) >200cm. We estimated aerial cover of vegetation, coarse woody debris (CWD), fine woody debris (FWD), leaf litter, impervious surface, bare soil, live wood, rock, and trash expressed as a percentage of the total subplot area looking down from 1m. We defined CWD as material greater than 10cm in diameter and 1m in length and FWD as less than 10cm diameter and 1m in length. We collected 2-cm diameter, 10-cm deep soil cores from the four corners and center of each quadrat for a total of five cores per subplot, and we collected one 0.25m\(^2\) litter patch from the center of each subplot (Figure 3). We pooled soil and leaf litter samples by vine cover class within each larger plot, so each of the 54 plots could contain up to four distinct soil and leaf litter samples depending on the number of vine cover classes present in the plot. Finally, we measured volumetric soil moisture to a depth of 12cm within the four corners of each subplot using an HS2 HydroSense Soil Moisture Probe (Campbell Scientific, Logan, UT, USA) and soil temperature to a depth of 30cm within the center of each quadrat using an HI 145 T-Shaped Soil Thermometer (Hanna Instruments, Inc., Woonsocket, RI, USA, Figure 3). We also recorded time of day along with each soil temperature measurement.

**Lab Analyses**

In total, we collected 94 soil samples and 93 leaf litter samples (one plot had no litter layer) from the 54 forest plots sampled in this study. We measured the mass of leaf litter mass by drying each sample to constant mass at 65 °C and weighing it. We homogenized and sieved each soil sample to 2 mm to measure pH, gravimetric moisture content, water holding capacity (WHC), microbial biomass, labile C, soil organic matter (SOM) and potential rates of net N mineralization and nitrification. For pH, we mixed each sample with water in a 1-to-1 volumetric ratio and measured the pH of the soil water after 10 minutes using a benchtop meter (VWR...
sympHony Sb70p, Allen 1989). We determined gravimetric moisture by weighing and oven drying each soil sample to constant mass at 105°C and then recording the dry weight. We determined water-holding capacity by saturating the soil and allowing it to drain for exactly 2 hours then weighing and drying each sample. For active microbial biomass, we used a modified substrate-induced respiration (SIR) method that measures rates of CO₂ efflux over a 4-hour incubation period using an Infra-Red Gas Analyzer (IRGA, Li-COR model Li-7000, West and Sparling 1986, Bradford et al. 2008a, Oldfield et al. 2014). Since measurement of respiration provides a coarse estimate of microbially available C concentrations (Bradford et al. 2008b), we measured labile C using a C mineralization assay that determines potential CO₂ production rates over a 28-day incubation period at 20°C (Fierer et al. 2005, Bradford et al. 2008b, Oldfield et al. 2014, Keiser et al. 2016). Labile C is then calculated as the cumulative CO₂ efflux over the course of the incubation period. To determine potential rates of net N mineralization, we used the 28-day N mineralization assay described in Robertson et al. (1999), Fraterrigo et al. (2005), and Keiser et al. (2016). We estimated SOM through loss on ignition (LOI) by determining mass loss of soils heated at 375°C for 18 hours in a muffle furnace. Finally, the soil texture measurements were collected by NAC during the initial ecological assessment using a hydrometer (Day 1965).

**Data Analysis**

We used linear mixed models (LMMs) to analyze the impacts of native and non-native vine cover on C and N availability across the 54 forest plots. Using the LMMs, we tested the relative effect sizes of different vegetation cover types on net potential nitrogen mineralization, net potential nitrification, and labile carbon. The understory vegetation types tested were the percent cover of all native species, all non-native species, all woody vines, all non-native woody vines, and all native vines.

We classified native status and growth form using the USDA PLANTS Database (USDA 2017). We included all species designated as “vine”, “vine/subshrub”, “vine/shrub”, or a combination of these terms as woody vines in our analysis (see Table 2). We then excluded herbaceous vines (classified as “Forbs/herbs”) from the woody vine cover types. We normalized the percent cover of each of these vegetation types by the total vegetated area in the understory to avoid results based solely on changes in total vegetation cover. We calculated relative abundance and abundance rank by dividing the combined cover of each species across all plots by the sum the cover of all species observed throughout the 54 plots (Tables 2, 3, 4). Finally, we calculated the frequency of each species by dividing the number of plots where each species was observed by the total number of plots sampled (Tables 2, 3, 4).

Other fixed effects tested in our models include overstory and midstory vegetation measurements, soil variables, and percent aerial cover (e.g. CWD, FWD). By specifying plot and park as random effects, we accounted for likely spatial associations between nearby sites. We tested all independent variables for collinearity using a variance inflation factor (VIF) test and only included variables when the square root of the VIF was less than 2. We estimated variance explained by these variables by calculating r² values for the LMMs using the methods described in Nakagawa and Schielzeth (2013). We fit the models using a Gaussian error distribution and ran all analyses with the ‘lme4’ package in R (R Development Core Team 2013).
Table 2 – Species, abundance, and frequency of all woody vines observed in the understory.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Native Status</th>
<th>Abundance Rank</th>
<th>Frequency (% of Plots)</th>
<th>Relative Abundance (% of Total Species Cover)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Toxicodendron radicans</em></td>
<td>Eastern Poison Ivy</td>
<td>Native</td>
<td>1</td>
<td>91</td>
<td>17.2</td>
</tr>
<tr>
<td><em>Parthenocissus quinquefolia</em></td>
<td>Virginia Creeper</td>
<td>Native</td>
<td>2</td>
<td>94</td>
<td>13.3</td>
</tr>
<tr>
<td><em>Celastrus orbiculatus</em></td>
<td>Oriental Bittersweet</td>
<td>Introduced</td>
<td>3</td>
<td>72</td>
<td>7.7</td>
</tr>
<tr>
<td><em>Rosa multiflora</em></td>
<td>Multiflora Rose</td>
<td>Introduced</td>
<td>5</td>
<td>41</td>
<td>4.9</td>
</tr>
<tr>
<td><em>Lonicera japonica</em></td>
<td>Japanese Honeysuckle</td>
<td>Introduced</td>
<td>6</td>
<td>35</td>
<td>4.6</td>
</tr>
<tr>
<td><em>Ampelopsis brevipedunculata</em></td>
<td>Porcelainberry</td>
<td>Introduced</td>
<td>8</td>
<td>41</td>
<td>3.4</td>
</tr>
<tr>
<td><em>Vitis spp.</em></td>
<td>Grape Species</td>
<td>Native</td>
<td>15</td>
<td>17</td>
<td>1.3</td>
</tr>
<tr>
<td><em>Wisteria sinensis</em></td>
<td>Chinese Wisteria</td>
<td>Introduced</td>
<td>19</td>
<td>2</td>
<td>1.2</td>
</tr>
<tr>
<td><em>Smilax spp.</em></td>
<td>Greenbrier Species</td>
<td>Native</td>
<td>22</td>
<td>20</td>
<td>1.0</td>
</tr>
<tr>
<td><em>Hedera helix</em></td>
<td>English Ivy</td>
<td>Introduced</td>
<td>25</td>
<td>11</td>
<td>0.8</td>
</tr>
<tr>
<td><em>Menispermum canadense</em></td>
<td>Common Moonseed</td>
<td>Native</td>
<td>79</td>
<td>2</td>
<td>0.06</td>
</tr>
<tr>
<td><em>Solanum dulcamara</em></td>
<td>Climbing Nightshade</td>
<td>Introduced</td>
<td>82</td>
<td>4</td>
<td>0.04</td>
</tr>
<tr>
<td><em>Parthenocissus tricuspidata</em></td>
<td>Boston ivy</td>
<td>Introduced</td>
<td>91</td>
<td>2</td>
<td>0.03</td>
</tr>
</tbody>
</table>

We combined all species in Vitis and Smilax since some observations were only identified to their genera. Identified Smilax species include S. rotundifolia (9.3% of observations) and S. glauca (8.6% of observations). Vitis species include V. labrusca (48% of observations), V. aestivalis, and V. riparia. In total, we observed 142 understory species over the course of our study. Asterix (*) indicates a nitrogen fixing species.
Table 3 – Species, abundance, and frequency of top five non-native, non-vine species present in the understory

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Abundance Rank</th>
<th>Frequency</th>
<th>Relative Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alliaria petiolata</em></td>
<td>Garlic Mustard</td>
<td>11</td>
<td>65</td>
<td>2.2</td>
</tr>
<tr>
<td><em>Lonicera maackii</em></td>
<td>Amur Honeysuckle</td>
<td>16</td>
<td>7</td>
<td>1.3</td>
</tr>
<tr>
<td><em>Euonymus alatus</em></td>
<td>Burningbush</td>
<td>17</td>
<td>17</td>
<td>1.2</td>
</tr>
<tr>
<td><em>Rubus phoenicolasius</em></td>
<td>Japanese Wineberry</td>
<td>26</td>
<td>24</td>
<td>0.8</td>
</tr>
<tr>
<td><em>Artemisia vulgaris</em></td>
<td>Mugwort</td>
<td>27</td>
<td>6</td>
<td>0.7</td>
</tr>
</tbody>
</table>

Table 4 – Species, abundance, and frequency of top five native, non-vine species present in the understory

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Abundance Rank</th>
<th>Frequency</th>
<th>Relative Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Rubus spp.</em></td>
<td>Blackberry Species</td>
<td>4</td>
<td>59</td>
<td>5.2</td>
</tr>
<tr>
<td><em>Eurybia divaricata</em></td>
<td>White Wood Aster</td>
<td>5</td>
<td>50</td>
<td>4.9</td>
</tr>
<tr>
<td><em>Polygonum virginianum</em></td>
<td>Jumpseed</td>
<td>9</td>
<td>37</td>
<td>2.8</td>
</tr>
<tr>
<td><em>Circaea lutetiana</em></td>
<td>Broadleaf Enchanter's Nightshade</td>
<td>10</td>
<td>54</td>
<td>2.7</td>
</tr>
<tr>
<td><em>Viburnum acerifolium</em></td>
<td>Mapleleaf Viburnum</td>
<td>12</td>
<td>20</td>
<td>1.9</td>
</tr>
</tbody>
</table>

We combined all non-native Rubus species observed in this study since some of the species were only identified to genera. Native Rubus species include *R. flagellaris*, *R. pensilvanicus*, *R. canadensis*, and *R. allegheniensis*.

Due to collinearity in our dataset, we were unable to include all soil variables in the LMMs. Therefore, we supplemented our analysis with a second statistical approach to further investigate our results. We ran a principal component analysis on all the soil variables measured and extracted the primary and secondary components from the analysis (Figure 6). We then included these components in models with and without the different vegetation cover types and tested whether the addition of each vegetation group significantly improved the fit of the model using ANOVA.

**Results and Discussion**

*Impacts of Native and Non-native Woody Vines on Nitrogen Availability*

We found a positive relationship between the relative abundance of non-native species cover and net nitrification rates (Figures 4 and 5). In contrast, we found no relationship between native species cover and net nitrification (Figures 4 and 5). This held true for all non-native species (Figure 5) as well as non-native woody vines (Figure 4).
Figure 4 – Relationship between native and non-native woody vines and nitrogen availability across the study area. (a) and (b) illustrate the relationship between native and non-native woody vines and net potential nitrification rates. The percent cover in these figures is expressed as a proportion of vegetated area in the understory, so values could exceed 1 due to multiple layers of vegetation. (c) and (d) depict the linear relationship between net potential nitrogen mineralization and net potential nitrification. Colors in (c) and (d) indicate the relative abundance of non-native (c, red) and native (d, green) woody vines in the understory. While there is a loose positive relationship between non-native woody vine abundance and net potential nitrification rates (a), there is no such relationship between native vines and nitrification rates (b). Similarly, sites with high non-native vine cover (orange, red) are clustered higher along the net nitrification/net N mineralization curve (c) whereas sites with high native vine cover (dark green) occur at sites that span the gradient of nitrogen availability.
The proportion of introduced species was calculated as non-native species cover divided by the sum of non-native and native species cover. This relationship is significant ($p < 0.05$).

The average net nitrification rate across all sites was $0.844 \pm 0.052 \, \mu g \, N \, g^{-1} \, d^{-1}$, and this rate increased in conjunction with non-native vine cover. Sites with trace amounts of non-native vines ($< 10\%$) had an average nitrification rate of $0.748 \pm 0.078 \, \mu g \, N \, g^{-1} \, d^{-1}$ whereas sites with low (10-33\%), intermediate (34-66\%) and high (>66\%) abundances of non-native vines had rates of $0.906 \pm 0.096$, $0.975 \pm 0.127$, and $0.935 \pm 0.149 \, \mu g \, N \, g^{-1} \, d^{-1}$, respectively. In contrast, net nitrification rates did not vary across plots with different native vine cover classes. Sites with a high abundance of native vines had an average nitrification rate of $0.874 \pm 0.115 \, \mu g \, N \, g^{-1} \, d^{-1}$, intermediate sites had an average of $0.747 \pm 0.115 \, \mu g \, N \, g^{-1} \, d^{-1}$, low sites had an average of $0.914 \pm 0.084 \, \mu g \, N \, g^{-1} \, d^{-1}$, and trace sites had an average of $0.864 \pm 0.089 \, \mu g \, N \, g^{-1} \, d^{-1}$.

In the full mixed effects models, we found a significant relationship between non-native species cover and net nitrification ($p < 0.05$) and a marginally significant relationship between non-native woody vines and net nitrification rates ($p < 0.1$). The adjusted $r^2$ of the model was 0.81. Fixed effects included the vegetation cover type, net nitrogen mineralization ($p < 0.001$), labile carbon ($p < 0.01$), volumetric soil moisture, leaf litter mass, pH and soil temperature. Random
effects included plot and park. The interaction between labile C and N mineralization was also significant ($p < 0.001$).

We found similar results when we modeled nitrification as function of vegetation cover type and the two principal components of all soil measurements (Table 5, Figure 6). Woody vines, non-native woody vines, and all non-native species had significant impacts on net nitrification, but there was no significant relationship between native woody vines and nitrification.

Figure 6 – Principal components of all soil variables measured in this study. Strong factor loadings on principal component 1 relate to carbon availability (C mineralization, soil organic matter, and water holding capacity). Strong factor loadings on principal component 2 include net potential mineralization, pH and volumetric soil moisture.
There was a strong linear relationship between net potential mineralization and net nitrification across our sites (Figure 4). However, the relationship between non-native species cover and net potential mineralization was not significant. We also found no significant relationship between woody vines and net potential mineralization. This finding suggests that microbial activity in the majority of the sites is limited by C rather than N availability (Keiser et al. 2015). Nitrification rates reflect plant N availability better than N mineralization rates due to competition between nitrifiers and heterotrophic microbes for ammonium (\(\text{NH}_4^+\)) under N-limiting (high C) conditions (Hart et al. 1994). Therefore, the tight association between net mineralization and net nitrification suggests that N availability across our plots is sufficiently high to promote the conversion of \(\text{NH}_4^+\) to \(\text{NO}_3^-\) by nitrifying bacteria. Similar coupling of nitrification and net mineralization was observed in disturbed forested watersheds at the Coweeta Hydrologic Laboratory in North Carolina (Keiser et al. 2015), indicating that disturbance may a driver of C and N dynamics in New York City’s forests.

This finding is consistent with numerous other studies that have found elevated nitrogen mineralization and nitrification rates in urban areas relative to non-urban reference sites (Pouyat et al. 1997, Pouyat and Turechek, 2001; Pavao-Zuckerman and Coleman 2005, Groffman et al. 2006, Szlavecz et al. 2006, Chenetal. 2010, Enloe et al. 2015). In studies conducted in oak forests along an urban-rural gradient in New York, this trend was primarily driven by exotic earthworm activity (Pouyat et al. 1997, Pouyat and Turechek, 2001, Szlavecz et al. 2006, Zhu and Carreiro 2004). While comparisons between urban and rural sites are useful tools for

### Table 5 – Standardized coefficients and p-values for linear mixed effects models of net nitrification as a function of different understory vegetation cover types and principal components of soil variables

<table>
<thead>
<tr>
<th>Independent Variable</th>
<th>Standardized Coefficient</th>
<th>P - value</th>
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<tbody>
<tr>
<td><strong>Model 1:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>* All Woody Vine Cover</td>
<td>0.17 ± 0.082</td>
<td>0.045</td>
</tr>
<tr>
<td>PC1</td>
<td>0.063 ± 0.022</td>
<td>0.0058</td>
</tr>
<tr>
<td>PC2</td>
<td>0.18 ± 0.025</td>
<td>1.36E-10</td>
</tr>
<tr>
<td>Overall R(^2): 0.40</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Model 2:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>* Introduced Vine Cover</td>
<td>0.18 ± 0.082</td>
<td>0.033</td>
</tr>
<tr>
<td>PC1</td>
<td>0.070 ± 0.022</td>
<td>0.0028</td>
</tr>
<tr>
<td>PC2</td>
<td>0.17 ± 0.025</td>
<td>6.15E-10</td>
</tr>
<tr>
<td>Overall R(^2): 0.41</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Model 3:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>All Introduced Species Cover</strong></td>
<td>0.24 ± 0.080</td>
<td>0.0041</td>
</tr>
<tr>
<td>PC1</td>
<td>0.063 ± 0.022</td>
<td>0.00461</td>
</tr>
<tr>
<td>PC2</td>
<td>0.17 ± 0.025</td>
<td>2.52E-10</td>
</tr>
<tr>
<td>Overall R(^2): 0.43</td>
<td></td>
<td></td>
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<tr>
<td><strong>Model 4:</strong></td>
<td></td>
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</tr>
<tr>
<td>Native Woody Vine Cover n.s.</td>
<td>0.046 ± 0.086</td>
<td>0.59</td>
</tr>
<tr>
<td>PC1</td>
<td>0.064 ± 0.023</td>
<td>0.0065</td>
</tr>
<tr>
<td>PC2</td>
<td>0.18 ± 0.026</td>
<td>6.09E-10</td>
</tr>
<tr>
<td>Overall R(^2): 0.38</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Bold font indicates significance (p < 0.05). Asterix (*) indicates a p-value of less than 0.05 and two asterix (**) indicate a p-value less than 0.01*
understanding changes in biogeochemical processes associated with urbanization, our study demonstrates that a range of nitrification and net mineralization rates also exist along a gradient of invasive species abundance within urban settings. Net nitrification and net mineralization rates observed in this study range from negative values (-0.422 and -0.4663 µg N g soil\(^{-1}\) d\(^{-1}\) for nitrification and mineralization, respectively) indicating net N immobilization to very high positive values (1.8641 and 1.9522 µg N g soil\(^{-1}\) d\(^{-1}\) for nitrification and mineralization, respectively) indicating high N availability. While the sites sampled in our study did, on average, have higher nitrification and mineralization rates than literature values from forested ecosystems (Keiser et al. 2015), the wide range of N transformation rates measured in oak-hickory forests across New York City illustrates the heterogeneous nature of urban soil conditions. Comparisons of soil processes in forested natural areas within cities may therefore be more useful for management than studies spanning urban-rural gradients.

The higher net potential nitrification rates observed in invaded plots in this study are also consistent with previous work on the impacts of non-native, invasive species on nitrogen dynamics (Ehrenfeld et al. 2003, Hawkes et al. 2005, Heneghan et al. 2006, Leicht-Young et al. 2009). However, due to the observational nature of this study, we cannot definitively determine the directionality of these effects. In other words, rather than directly increasing nitrogen availability, non-native species may be more likely to occupy systems already rich in nitrogen. Deciduous forests in the northeastern U.S. are historically N-limited systems (Aber et al. 1983; Melillo et al. 1983), and elevated N levels in cities may favor the growth of non-native species. Regardless of the directionality of the effects, the association between non-native plants and nitrification rates observed in this study suggests that urban forest management should include measures to limit nitrification rates to reduce the likelihood of plant invasions.

Impacts of Native and Non-native Woody Vines on Carbon Availability

While we hypothesized that vine abundance would reduce C availability across our sites, we found no significant relationships between woody vines and labile C. Soil microbial communities drive C and N cycling (van der Heijden et al. 2008), and under conditions of low C availability, soil microbes become energy limited, resulting in increased rates of nitrification (van der Heijden et al. 2008). However, other mechanisms may confound the tight relationship between C and N availability. While results from this study found that sites with high introduced vine abundance are more likely to have high levels of inorganic N, non-native vines also commonly occupy tree fall gaps. C inputs from the decomposition of coarse- and fine- woody material may therefore cause periodic spikes in soil C levels in invaded sites. These opposing mechanisms may partially explain the limited relationship between C and N availability across our study area.

Impacts of Invasive Vine Removal on the Soil Processes

Finally, we hypothesized that sites with removed invasive vines would have lower N availability than heavily invaded sites but higher N levels compared to uninvaded sites due to legacy effects. However, we observed no clear trends between forest management practices and C and N availability. Sites that were managed for invasive vine species often showed no evidence of treatment, and sites where we observed cut vines were often not listed in the database (Figure 7).
Therefore, our findings may reflect poor records rather lack of an effect. Further investigations of the impacts of invasive vine removal on C and N dynamics, such as experimental removal treatments, are therefore required to understand the effects of invasive vine management on soil processes.

![Comparison of Management Database and Field Observations](image)

**Figure 7** – Comparison of invasive vine removal in management tracking database and field observations.

**Management Implications**

This study found that woody vines can have an impact on net nitrification rates in forested urban natural areas, and these results are driven by non-native species, rather than natives. However, additional work is required to understand the relationship between invasive woody vines and C availability as well as the impacts of restoration on soil processes. Moving forward, findings from this study support two changes to current management practices.

First, land managers may need to supplement invasive species removal and plantings with soil treatments that reduce N availability. Findings that support the association between the abundance of invasive plants and elevated N availability are now widespread, and managers should incorporate this knowledge in future restoration treatments by testing ways to reduce nitrification rates in forested urban natural areas. Potential measures include applications of locally-sourced woody materials from tree removals to increase soil C levels. A second recommendation that emerged from this study is the need for improved monitoring of forest management practices to inform future urban forest restoration efforts.
References Cited


