

Urbanization effects on leaf litter decomposition, foliar nutrient dynamics and aboveground net primary productivity in the subtropics

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Abstract Urbanization can alter nutrient cycling. This research evaluated how urbanization affected nutrient dynamics in the subtropics. We established 17–0.04 ha plots in five different land cover types—slash pine (*Pinus elliottii*) plantations ($n=3$), rural natural pine forests ($n=3$), rural natural oak forests ($n=4$), urban pine forests ($n=3$) and urban oak forests ($n=4$) in the Florida panhandle, a subtropical region that has experienced rapid urbanization. On each plot, we measured the decomposition of mixed species foliar litter, the nutrient release patterns in decomposing litter, foliar litter quality, and forest floor temperatures. Aboveground net primary productivity and soil carbon and nitrogen contents were also measured to characterize the carbon and nitrogen stocks and fluxes in the urban and rural sites. Litter decay rates, litter quality indices and nutrient release patterns in decomposing litter did not differ among urban and rural forests despite differences in forest floor temperatures between urban and rural sites. Urban forest floor temperatures are on average warmer by 0.63 °C in the winter ($p=0.005$) and tend to have a more narrow temperature range than those of the rural forested sites. Foliar mass was measured over an 82 week period that was characterized by drought, which may have masked an urbanization effect. Urban forest land covers had higher aboveground net primary productivity and foliar productivity compared to rural land covers. This increased input of foliar carbon is not reflected in statistically different forest floor or surface soil (0–7.5 cm) carbon contents between urban and rural sites. Understanding how drought interacts with other drivers of change in urban systems may be a necessary component of city specific ecological knowledge.

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Introduction

Soils of the southeastern coastal plain are sandy and nutrient poor and an accumulation of foliar litterfall on the forest floor could immobilize essential nutrients (Gholz et al. 1985). Decomposition rates, along with foliar litterfall production rates, also influence the forest floor depth. A significant difference in forest floor depth between urban and rural forests can impact seedling recruitment, germination, survival and, ultimately, alter long-term patterns of forest regeneration (e.g., Kostel-Hughes et al. 1998).

Few papers have been published that address the impact of urbanization on foliar decomposition by comparing decomposition rates of foliar litter in urban and rural forested sites. Decay rates of urban foliar litter in urban forests were found to be faster (Nikula et al. 2010), slower (Inman and Parker 1978; Cotrufo et al. 1995; Carreiro et al. 1999) or the same (Pouyat and Carreiro 2003) compared to those of rural litter decomposing in rural forests. Two of the aforementioned studies measured site specific, single species foliar litter decomposition in the laboratory under controlled conditions (Cotrufo et al. 1995; Carreiro et al. 1999) and the three others investigated site specific, single species foliar litter decomposition in-situ (Inman and Parker 1978; Nikula et al. 2010; Pouyat and Carreiro 2003). In addition, three studies have measured the in-situ decay of a reference litter in both urban and rural forested sites. Reference litter from rural sites was found to decay faster (Pouyat et al. 1997; Pouyat and Carreiro 2003) and slower (Pavao-Zuckerman and Coleman 2005) in urban forest sites compared to nearby rural forest sites. It is uncertain how urbanization affects decay rates across different cities (Kaye et al. 2006; Pouyat et al. 2007).

The uncertainty associated with the effects of urbanization on decay rates is likely due in part to the large variety of anthropogenic disturbances associated with urbanization and the opposing effects these changes have on the decay process. Urban foliar litter can have a lower litter quality compared to nearby rural litters and can potentially decrease foliar decay rates in urban forests from those in rural areas (Carreiro et al. 1999). In contrast, an increase in urban temperatures, the urban-heat island effect, has been suggested to increase decomposition rates in urban versus rural forested areas (Pouyat and Carreiro 2003). Urban forests can also be subjected to an increased exotic species presence (Zipperer and Guntenspergen 2009). In a reciprocal litterbag experiment, Pouyat and Carreiro (2003) found that rural litter placed in urban sites decomposed faster than rural litter on rural sites due to the higher number of exotic earthworms and increased temperatures found in the urban location. The presence of exotic plants in urban forests could also be expected to increase decomposition rates compared to uninvaded forests areas (see Ehrenfeld 2003) or to minimally invaded urban forests (Trammell et al. 2012).

This research examines how urbanization affects foliar litter decomposition and nutrient cycling in a developing coastal area in the Florida panhandle, a subtropical region. Specifically, we measured foliar litter decomposition rates (decay constants and mass remaining over time) and foliar nutrient immobilization and mineralization patterns in rural and urban forests. For this study, urban forests are defined as unmanaged forest fragments within town boundaries. Rural forests include pine plantation and naturally regenerating forests (hereafter “natural forest”) located outside of town limits. In order to understand the mechanisms behind differences in decay and nutrient cycling across the urban and rural sites, we measured forest floor temperatures and initial foliar litter quality parameters in the urban and rural forest sites. Forest floor and surface mineral soil C and N contents, aboveground plant productivity and

foliar nutrient inputs were also measured in this study to characterize the C and N stocks and fluxes in the urban and rural sites.

Methods

Study area description

The study was conducted within and outside the town limits of Apalachicola and Eastpoint, Franklin County, Florida. In 2010, Apalachicola and Eastpoint had populations of 2242 and 2337 people, respectively, and population densities less than 500 people km⁻² (US Census Bureau 2010). Watersheds that include Apalachicola and Eastpoint have impervious surface percentages that do not exceed 15 % of the watershed land area (Nagy et al. 2012). The five dominant land covers along the mainland coastline in Franklin County are forested wetlands, natural forests, pine plantations, urban lawns, and urban forests (Nagy et al. 2014).

The study area is dominated by topography with very low gradients (slope 0 to 5 %) and elevation changes between adjacent areas are typically small (<4 m). Slight changes in ground elevation result in different soil drainage classes and different plant communities. Moderately well drained soils on summit and shoulder hill slope positions are primarily Resota (thermic, coated Spodic Quartzipsamments) series. Somewhat poorly drained soils on backslope positions are Mandarin (sandy, siliceous, thermic Oxyaquic Alorthods) series. Very poorly and/or poorly drained soils on footslope and toeslope positions include Leon (sandy, siliceous, thermic Aeric Alaquods), Rutlege (sandy, siliceous, thermic Typic Humaquepts) and Scranton (siliceous, thermic, Humaqueptic Psammaquents) series. The soils in the study area are derived from sandy marine sediments (Sasser et al. 1994).

Natural plant communities in the study area include wet and mesic flatwoods, hydric, mesic and xeric hammocks, and sandhill communities (Florida Natural Areas Inventory 1990). The primary overstory tree on wet and mesic flatwood sites is slash pine (*Pinus elliottii* Engelmann). Common overstory trees on the hydric hammock sites include swamp laurel oak (*Quercus laurifolia* Michaux), water oak (*Q. nigra* Linnaeus), and southern magnolia (*Magnolia grandiflora* Linnaeus) with some slash pine. Typically live oak (*Q. virginiana* Miller) and laurel oak (*Q. hemisphaerica* Bartram ex Willdenow) are found on the mesic hardwood sites. The drier sites (xeric hammocks and sandhill communities) are characterized by a mix of live oak, laurel oak, sand live oak (*Q. geminata* Small), myrtle oak (*Q. myrtifolia* Willdenow), southern magnolia, longleaf pine (*P. palustris* Miller) and shortleaf pine (*P. echinata* Miller). Many of the urban forests within Apalachicola and Eastpoint are remnants of these natural plant communities. Camphortree (*Cinnamomum camphora* (L.) J. Presl) is a non-native tree species observed within the urban forests and does not occur within rural counterparts.

Study site selection and history

Previous research defined the common land covers in the region (Nagy et al. 2014) and this study focused on a subset of those land covers: natural forest, pine plantation and urban forest. Urban and natural forest sites were further defined as oak or pine dominated, as hardwood hammocks and pine flatwoods are the two common plant communities along an urbanization gradient in the study area. Seventeen circular plots (0.04 ha) were established in July 2010 in the study area and included urban forest oak dominated ($n=4$), urban forest pine dominated ($n=3$), natural forest oak dominated ($n=4$), natural forest pine dominated ($n=3$) and pine

plantation ($n=3$) land covers. Sites within each land cover were located across a similar range of hill slope positions and soil drainage classifications typical of the area (Sasser et al. 1994; Soil Survey Staff 2008). All seventeen sites exhibited no recent soil disturbance. Urban forests were located within Apalachicola and Eastpoint. Rural forests were located between 8.5 and 10.5 km from the city center and had not been burned in the last 5 years.

Aerial photographs of the study area from 1953 to 2004 were used to track land cover changes for all sites (Florida Department of Environmental Protection 2004; Florida Department of Transportation 2013; US Department of Agriculture 2013). Six of the seven urban forest sites appear to be remnant urban forests, i.e. never been cleared for urban use (Zipperer 2002). The majority of these six sites had an open forest canopy in 1953 that progressed to a closed canopy by 1984. One of the urban forest sites is regenerated (Zipperer 2002) and had a small house on the site in 1953 and by 1969 the house was removed and trees were growing on site. Aerial photos from 1969 to 2004 indicate little change in the vegetation cover for the natural forest sites. The pine plantation sites in this study were 28 to 35 years old (Enloe 2014) and had been unmanaged forest or woodland cover prior to planting.

Forest characteristics, productivity and foliar nutrient analysis

A wedge prism was used to estimate basal area of each of the 17 forested circular plots. All stems within each of the forested plots (0.04 ha) that had diameter at breast height (DBH) greater than 10 cm were identified to species and their DBH measured during the winter of 2011 and 2012. A circular sub-plot (0.0025 ha), located at the center of each plot, was used to identify and measure woody stems whose DBHs were less than 10 cm but greater than or equal to 5 cm. Standing crop biomass was calculated using DBH measurements from winter 2012 in allometric regression equations (Swindel et al. 1979; Clark et al. 1985; Brantley 2008) for total aboveground tree biomass (foliage, bark and wood, Supplementary Table 1). If equations did not exist for a species found in this study, an equation was found for a similar species or species group (i.e. soft hardwoods, white oaks, see Clark et al. 1985).

Aboveground net primary productivity was estimated for the forested sites as the difference between woody biomass in winter 2012 and winter 2011 plus average annual foliar litter productivity. Woody biomass was calculated using DBH measurements from winter 2011 to winter 2012 in allometric regression equations for bark plus wood (Supplementary Table 2). Within each site, litterfall was collected from three 0.25 m² traps suspended above the forest floor on a monthly basis from 2010 to 2012. Litterfall was oven dried at 65 °C and the foliar component was removed and weighed to calculate annual foliar litter productivity (g m⁻² year⁻¹).

A sub-sample from the monthly foliar litterfall collections over an 18 month collection period (April 2010 to August 2012) was finely ground and analyzed for N concentrations using dry combustion on a Perkin Elmer 2400 Series II CHNS/O Analyzer (Perkin Elmer, Waltham, MA). Phosphorus (P) was extracted from the finely ground foliar litterfall subsamples via dry ashing followed by an acid digestion using the vanadomolybdate procedure (Jackson 1958). Extracts were then analyzed for P spectrophotometrically. For each plot, N and P contents (g m⁻² year⁻¹) were estimated by averaging duplicate months and then summing the monthly content values of each element over a 12 month period.

Decomposition and litter quality

A decomposition study using litterbags was conducted from March 2011 to May 2012. From September 2010 to February 2011, foliar litterfall was collected in 0.25 m² traps and tarpaulins

that were suspended 30 and 100 cm above the ground, respectively. Litterfall collected in the traps were also used for annual foliar litter productivity estimates (see above). Leaves were collected each month, air dried, sorted by species and then weighed. Plant species that occupied a dominant proportion of the total litterfall were included in the litterbags. The relative proportions of the dominant plant species composing the litterfall were used to form weighted average mixtures to fill the litterbags (Supplementary Table 3). Twenty litterbags (30.5 by 45.7 cm with 6-mm openings on the upper side and 1-mm openings on the lower side) were filled with 10 g of plot-specific species composition leaves and then placed on the forest floor at each of the 17 forested sites.

Litterbags were collected at 0-, 2-, 4-, 6-, 12-, 18-, 30-, 42-, 60-, and 82-weeks. No litterbags were retrieved from two of the four natural forest oak sites during week-42 and -82 due to destruction of bags from animal activity. The time 0 collection was weighed before deployment and after collection in order to calculate a correction factor for loss on handling. Once litterbags were collected, the foliar litter remaining in the bag was removed, dried at 65 °C, weighed to determine percent mass remaining, and then ground. A subsample was ashed at 550 °C for 12 h to calculate mass remaining on an ash free basis. The decomposition rate constant (k) was calculated from the decay curve over the 82 weeks using the following equation (Swift et al. 1979):

$$\ln(M_0/M_t) = -k \cdot t$$

where, M_0 = mass of litter at time 0, M_t = mass of litter at time t , and t = time of incubation (in years).

Carbon, N, P, and lignin concentrations were measured at time 0 for litter quality analyses and initial content. Nitrogen and P concentrations were measured during the remaining nine collection times. Total N and C were determined using a Perkin Elmer 2400 Series II CHNS/O Analyzer. Phosphorus was extracted and analyzed the same methods used for the foliar litter samples. Lignin was determined using the acid detergent fiber method (Van Soest and Wine 1968). Lignin, C, N and P concentrations estimated at time 0 were used to calculate initial lignin:N, C:N, and C:P ratios. Nitrogen and P concentrations measured during weeks 2 through 82 were converted to a percentage of the initial (time 0) N and P content. This percentage of N and P remaining were used to determine patterns of N and P mineralization and immobilization in the decomposing litter.

Precipitation, temperature and soils

The study area typically receives 143.5 cm of precipitation per year (110 year historical average) and has average summer air temperatures of 27.2 °C and average winter temperatures of 12.4 °C (National Climatic Data Center 2012). Historical precipitation averages (1900–2010) and monthly precipitation amounts (2010–2012) from Apalachicola, Florida, were used to calculate annual precipitation deficits for the study period (National Climatic Data Center 2012). From March 2010 to May 2012, forest floor temperature was monitored on the forested sites by installing one portable temperature recorder (Onset Computer Corporation, Bourne, MA) on the forest floor, under full canopy closure, at each site. Recorded hourly temperatures were averaged within seasons to obtain mean values for fall, winter, spring and summer. Daily minimum and maximum temperatures and their difference (daily temperature range) were also averaged across seasons to obtain seasonal average minimum, maximum and range values.

Two mineral soil and forest floor sub-samples were collected from each of the 17 forested sites during the summer of 2012. The forest floor samples were collected by removing dead organic material within a 0.1 m² frame to the mineral soil surface. The samples were oven dried at 65 °C until their mass did not change. A bucket auger was used to collect mineral soil at four depths (0–7.5 cm, 7.5–30 cm, 30–60 cm, 60–90 cm). Mineral soil samples were air dried and passed through a 2-mm sieve. Finely ground sieved mineral soil samples and forest

floor samples were analyzed for total C and N concentrations using dry combustion on a Perkin Elmer 2400 Series II CHNS/O Analyzer. An intact soil core of a known volume was taken at the surface (0–7.5 cm) and at approximately 19, 45 and 75 cm to estimate the bulk density of the soil within each depth sampled. Bulk density was calculated for the <2 mm mineral soil fraction by accounting for the weight and volume of any coarse fragments (Blake and Hartge 1986). Carbon and N contents (kg m^{-2}) were calculated for each depth (Supplementary Table 4). Statistical comparisons were performed on the C and N contents of the surface soil depth (0–7.5 cm) and for the entire mineral soil sampled (0–90 cm).

Statistical analysis

All data were analyzed by SAS version 9.2 (SAS Institute, Cary, NC). The non-linear (NLIN) procedure was used to calculate k for each of the sites. Treatment effects on forest site characteristics, plant productivity estimates, foliar litterfall nutrient contents, k , the mass and nutrients remaining at week-82, the week-0 litter quality parameters, and the soil C and N content were tested using analysis of variance (ANOVA) with land cover as the primary treatment variable. Contrast statements were used for the following planned comparisons for differences among sites:

- a. Urban forest pine versus natural forest pine
- b. Urban forest oak versus natural forest oak
- c. Natural forest pine versus pine plantation
- d. Urban sites (oak + pine) versus rural sites (natural oak + natural pine + pine plantation)
- e. Pine (urban + natural + plantation) versus oak (urban + natural)

To discern whether N and P percent remaining in the decomposing foliar litter varied over time from the initial content at week 0, paired t-tests (within a land cover) were used to test for differences between week 0 and each of the nine collections. An analysis of variance procedure was used to test for differences in forest floor temperatures between land covers ($n=17$) within each season. When ANOVA results were significant, the contrast statement comparing urban sites versus rural sites (d.) was used to test for an urban heat island effect. The months included in each season were defined as follows: Summer = June, July, August; Fall = September, October, November; and Winter = December, January, February; Spring = March, April, May.

For all tests, differences among means are considered statistically significant at $\alpha \leq 0.05$ and differences with $0.05 \leq \alpha \leq 0.10$ are reported for informational purposes. In select circumstances, the data were natural log transformed to meet the assumption of equality of variance. The model assumption of normality was not violated for the untransformed and transformed data.

Results

Forested site characteristics and aboveground productivity

The urban forested land covers are not statistically different in regard to basal area, stem density, standing crop biomass and foliar litterfall N and P contents to their natural forest counterparts (Table 1). Pine sites have higher stem density compared to oak sites ($p=0.011$, Table 2), yet basal area, standing crop biomass and above ground productivity are statistically similar. Oak sites cycle more N and P in their litterfall on a yearly basis than the pine sites as indicated by the significantly higher N and P content in the foliar litter of oak sites versus pine sites ($p=0.007$ and $p=0.006$, respectively, Table 2).

Urban forest pine sites have a higher woody biomass productivity compared to natural forest pine sites ($p=0.036$) and urban forest oak sites are trending towards a higher foliar productivity compared to natural forest oak sites ($p=0.074$, Table 2). Annual woody growth rates for trees within urban forest pine dominated sites (0.44 ± 0.06 cm yr⁻¹, mean \pm standard error, $n=81$) and oak dominated sites (0.47 ± 0.05 cm yr⁻¹, $n=86$) in this study are similar to those found for trees in urban remnant forests (0.56 ± 0.10 cm yr⁻¹, $n=398$) in Gainesville, Florida (Lawrence et al. 2012). Camphortree is present in the midstory of three of the four urban forest oak sites and one of the three urban forest pine sites. Camphortree has a high annual woody growth rate among urban trees in this study, with rates of 0.69 ± 0.20 cm yr⁻¹ ($n=12$) in urban forest oak forests and rates of 0.99 ± 0.38 cm yr⁻¹ ($n=8$) for urban forest pine forests (Enloe 2014). Slash pine plantations have comparable values for basal area, standing crop biomass, stem density, and aboveground productivity to other slash pine plantations of a similar age (17 to 34 years old) in Florida (Gholz and Fisher 1982; Harding and Jokela 1994; Clark et al. 1999; Shan et al. 2001) and to the natural forest pine dominated sites in this study (Table 1). The absence of significant differences in aboveground productivity between slash pine plantation and natural forest pine sites may be due to their similarities in forest site characteristics and to a lack of fire in both land covers in the last 5 years.

To understand overall trends between urban and rural sites, urban forest sites (pine and oak dominated) are compared to rural forest sites (pine plantation and natural oak and pine dominated forests). Urban forests have higher aboveground NPP compared to rural forests ($p=0.011$). This higher productivity appears to be due to both higher foliar productivity ($p=$

Table 1 Land cover characteristics and productivity values in naturally regenerating forests, urban forests and pine plantation sites in western Florida. Standing crop biomass and stem density includes stems with diameter at breast height greater than 5 cm. Foliar productivity and nutrient content represents mean values from 2010 to 2012. Woody biomass and aboveground net primary productivity (NPP) are from 2012. Standard errors are in parentheses

Response variable	Natural forest oak	Urban forest oak	Natural forest pine	Urban forest pine	Pine plantation
Basal area (m ² ha ⁻¹)	18.94 (3.02)	27.55 (1.33)	37.50 (4.05)	28.32 (2.02)	35.97 (6.67)
Standing crop biomass (g m ⁻²)	22,993 (8076)	23,527 (4256)	32,559 (3375)	31,042 (9516)	15,152 (4703)
Stem density (stems ha ⁻¹)					
Total	500 (49)	494 (61)	675 (38)	650 (109)	917 (183)
Hardwoods	450 (40)	394 (21)	292 (51)	233 (110)	92 (92)
<i>C. camphora</i>	nd ^a	75.0 (27.0) ^b	nd	58.3 (58.3) ^b	nd
Productivity (g m ⁻² year ⁻¹)					
Foliar	523.7 (30.9)	686.4 (81.9)	638.4 (41.8)	779.7 (78.7)	615.1 (66.6)
Woody biomass	535.3 (69.9)	845.1 (109.4)	493.3 (74.8)	1096 (305)	663.9 (202.4)
Aboveground NPP	1059 (57)	1531 (173)	1132 (98)	1876 (383)	1279 (258)
Nutrient content in foliar litterfall (g m ⁻² year ⁻¹)					
N	3.60 (0.16)	5.05 (0.92)	2.23 (0.46)	2.98 (0.90)	2.06 (0.37)
P	0.499 (0.099)	0.666 (0.111)	0.330 (0.066)	0.312 (0.100)	0.266 (0.038)

^a *Cinnamomum camphora* is not detected (nd)

^b *C. camphora* is in three of the four urban forest oak sites and one of the three urban forest pine sites

Table 2 Results of the contrast statements for differences among land covers in site characteristics, aboveground productivity, foliar nutrient contents and soil C and N content. Contrasts with a p -value ≤ 0.10 are reported

Response variable	Contrast	Point estimate	p -value
Total stem density (stems ha ⁻¹)			
	Pine forest—oak forest	250	0.011
Productivity (g m ⁻² year ⁻¹)			
Foliar	UFO—NFO	162.6	0.074
	Urban forest—rural forest	140.6	0.034
Woody biomass	UFP—NFP	602.5	0.036
	Urban forest—rural forest	406.2	0.015
Aboveground NPP	UFO—NFO	472.5	0.069
	UFP—NFP	743.8	0.039
	Urban forest—rural forest	546.8	0.011
Nutrient content in foliar litterfall (g m ⁻² year ⁻¹)			
N	Pine forest—oak forest	-1.90	0.007
P	Pine forest—oak forest	-0.280	0.006
Soil C (kg m ⁻²)			
Forest floor	Pine forest—oak forest	2.22	0.026
Soil N (kg m ⁻²)			
0–7.5 cm	UFO—NFO	0.167	0.017
0–90 cm	UFO—NFO	0.818	0.017

NFO natural forest oak, *NFP* natural forest pine, *UFO* urban forest oak, *UFP* urban forest pine

0.034) and woody productivity ($p=0.015$) in urban versus rural forests. Previous research in the study area found no differences in overstory aboveground NPP between urban forests and rural forests (Nagy et al. 2014). However, Nagy et al. (2014) measured the productivity of overstory trees with $DBH \geq 12.7$ cm and this study included trees with $DBH \geq 5$ cm. In the previous study, foliar productivity was not determined and aboveground productivity was estimated based on differences in above ground tree biomass (using DBH measurements only) over a year period.

Soil carbon and nitrogen content

Soil C contents in the forest floor material, surface mineral soil (0–7.5 cm) and entire mineral soil (0–90 cm) depth are not significantly different between urban forest oak and natural forest oak sites and between urban forest pine and natural forest pine sites (Fig. 1a, Supplementary Table 4). Oak dominated urban forests have significantly higher amounts of N in the upper 7.5 cm ($p=0.017$) and upper 90 cm ($p=0.017$) of mineral soil compared to oak dominated natural forests (Table 2, Fig. 1b). Pine dominated urban forests have a higher mean mineral soil N content compared to natural forest pine sites, however the difference is not significant.

Previous research in the study area indicated that urban forest soils have a higher mean C and N content in the upper 7.5 cm and entire mineral soil depth (0–90 cm) compared to natural forest soils, but the difference was not statistically significant (Nagy et al. 2014). Urban and

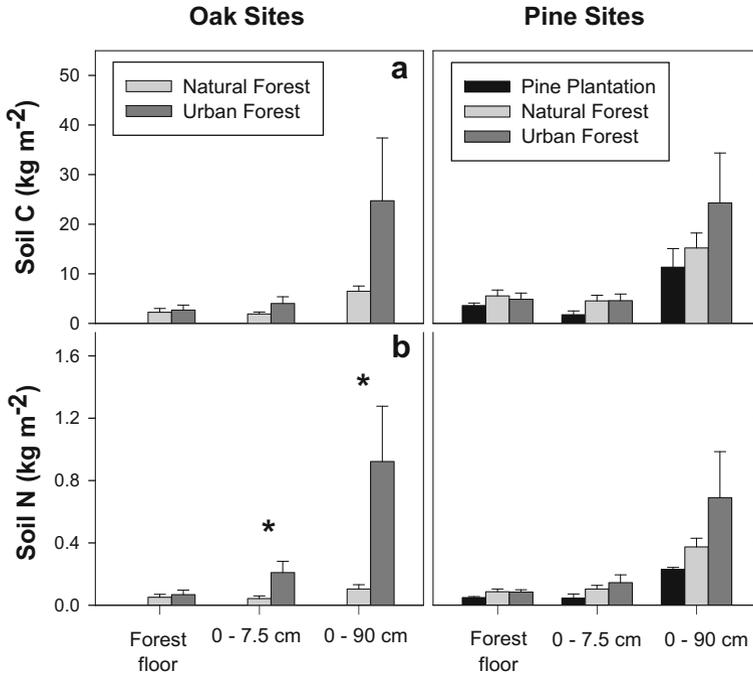


Fig. 1 Soil **a** C and **b** N content (kg m⁻²) for the forest floor and two mineral soil depths (0–7.5 and 0–90 cm) in urban forests, naturally regenerating forests and pine plantation sites in the Florida panhandle. Land covers are clustered to compare urbanization effects within oak and pine dominated sites. Statistically significant differences ($p \leq 0.05$) between land covers are indicated by an asterisk (*)

natural forest land covers in Nagy et al. (2014) included a mix of pine dominated and oak dominated sites. In regards to soil N content, this may have increased the variability within each land cover and decreased the power of the statistical test.

Precipitation and forest floor temperatures

The monthly mean forest floor temperatures averaged across all sites followed a similar pattern as the air temperature in Apalachicola during the study period (Fig. 2a). Seasonal values for the mean, maximum, minimum and range of forest floor temperatures were calculated for the urban (oak and pine dominated) and rural (natural forest and pine plantation) sites. Mean forest floor temperatures for spring, summer and fall are not significantly different between urban and rural sites. However, urban sites are on average warmer by 0.63 ± 0.40 °C than rural sites in the winter ($p=0.005$, Table 3). Urban sites had higher minimum temperatures in the forest floor material across the seasons compared to the rural sites ($p < 0.05$). Heat islands are commonly found to have higher mean and minimum daily air temperatures (see Kaye et al. 2006). For the urban sites in this study, the higher minimum temperatures may have resulted in a more narrow temperature range than the rural sites for spring and fall (Table 3).

The study area underwent a drought from July 2010 to May 2012 and from July 2012 to October 2012 (Fig. 2b, c). Annual precipitation was 41.3 cm below the 110 year historical average from July 2010 to June 2011 and 29.3 cm below the historical average from July 2011 to May 2012. A tropical storm in June 2012 added 32 cm of precipitation to the study area over a 48 h period.

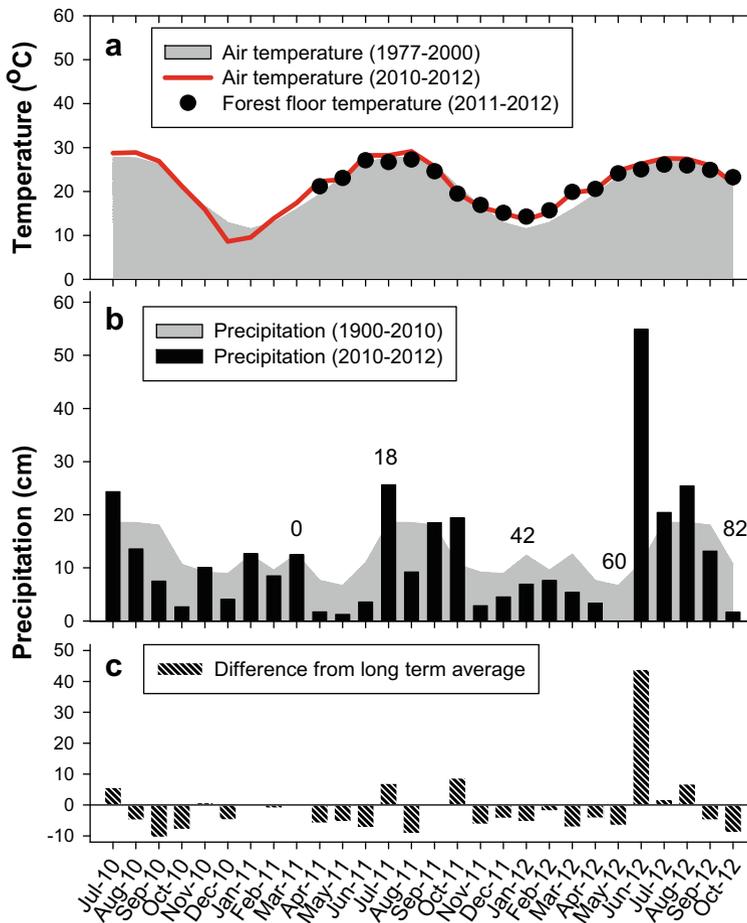


Fig. 2 Monthly mean air temperature and monthly mean precipitation for the study area. Data is reported for **a** mean monthly air and forest floor temperatures, **b** mean monthly precipitation data, and **c** the departure of the monthly precipitation during the study period from the long term monthly mean. Numbers from 0 to 82 above monthly precipitation bars in **(b)** indicate the litterbag collection (week) that took place within that month. Long term mean monthly precipitation and air temperature data were collected from 1977 to 2000 and from 1900 to 2010, respectively, in Apalachicola, Florida (National Climatic Data Center 2012)

Litter quality of mixed foliar species

Urban forests oak and natural forest oak as well as urban forest pine and natural forest pine sites do not have statistically significant differences in regards to initial litter quality N and P concentrations as well as lignin:N, C:N and C:P ratios (Table 4). The only significant difference between urban and rural sites is the lower lignin concentration in the urban forest oak dominated sites compared to the natural forest oak sites ($p < 0.001$, Table 5). No significant differences were found in the lignin concentrations between urban forest pine and natural forest pine sites.

Oak sites have significantly higher litter quality compared to pine sites (Tables 4 and 5). The mixed foliar litter from the pine sites have larger values for the lignin:N ratio ($p < 0.001$), C:N ratio ($p < 0.001$) and C:P ratio ($p < 0.001$) than the mixed foliar litter from the oak sites.

Table 3 Results of the contrast statements for differences among urban and rural land covers for forest floor temperature over an 82 week long litterbag study. Contrasts with a p -value ≤ 0.10 are reported

Contrast	Response variable	Point estimate	p -value
Forest floor temperature (°C)			
Urban forest—rural forest	Mean temperature, fall	0.45	0.097
	Mean temperature, winter	0.63	0.005
	Maximum temperature, spring	-3.14	0.083
	Minimum temperature, spring	1.74	0.001
	Minimum temperature, summer	1.19	<0.001
	Minimum temperature, fall	1.21	0.001
	Minimum temperature, winter	1.28	0.010
	Temperature range, spring	-4.88	0.018
	Temperature range, summer	-2.60	0.062
	Temperature range, fall	-2.81	0.040
	Temperature range, winter	-2.14	0.055

This is primarily due to pine sites having lower initial litter N concentrations ($p < 0.001$) and P concentrations ($p < 0.001$) compared to the oak sites.

Decomposition of foliar litter

No significant differences in k and mass remaining at week-82 are found between the urban forest oak sites and the natural forest oak sites, the urban forest pine sites and the natural forest pine sites, as well as the natural forest pine sites and the pine plantation sites (Table 4, Fig. 3). Gholz et al. (1985) monitored slash pine litter decomposition in a 35 year old slash pine plantation in northern Florida during an unusually dry year and found 85 % of the mass remained at 52 weeks. These results are comparable to this study in that 80 to 81.5 % of the mass remained in slash pine plantations between 42 and 60 weeks of decomposition during a drought period.

Mixed species foliar litter in oak sites have larger k values compared to those of pine sites ($p = 0.002$, Table 5). At week-82, pine sites have on average 19.3 ± 13.5 % ($p = 0.011$) more mass remaining than oak sites. Foliar litter of deciduous species has been found to decompose twice as fast as that of evergreen species during the first year of decomposition (Cornelissen 1996; Prescott et al. 2004).

Across all sites ($n = 17$), k is significantly positively correlated to initial N concentration ($r = 0.807$, $p < 0.001$, Fig. 4a) and to P concentration ($r = 0.695$, $p = 0.002$), but is not related to initial lignin concentration ($r = 0.333$, $p = 0.192$, Fig. 4b). Overall, lignin is not a useful indicator of decay during the 82 weeks of decomposition and this may be a result of the narrow range of lignin values across all sites (147.0 to 178.4 g kg⁻¹). Decomposition rate constants are negatively correlated to the initial C:N ($r = -0.713$, $p = 0.001$, Fig. 4c), lignin:N ($r = -0.687$, $p = 0.002$, Fig. 4d) and C:P ($r = -0.678$, $p = 0.003$) ratios.

Nutrient mineralization and immobilization patterns in decomposing litter

An analysis of the percent N and P remaining at week-82 indicates that urban forest oak and urban forest pine sites are not significantly different from their natural forest counterparts for both nutrients (Table 4, Fig. 5a, b). Pine plantation sites at week-82 had significantly more P remaining in the decomposing litter compared to that in the natural forest pine sites ($p = 0.002$,

Table 4 Initial litter quality indices (week 0) for the mixed species litter placed in litterbags within naturally regenerating forests, urban forests, and pine plantation sites in western Florida. Decomposition rates constants (k) of the mixed species foliar litter were calculated over an 82 week long litterbag study and the mass, N and P remaining of the mixed species foliar litter at week-82 was measured. Standard errors of the means are in parentheses

Land cover	Week 0					Decay constant					Week 82	
	Lignin (g kg^{-1})	N (g kg^{-1})	P (g kg^{-1})	Lignin :N	C:N	C:P	k	Mass remaining (%)	N remaining (%)	P remaining (%)	Mass remaining (%)	P remaining (%)
Natural forest oak	178.4 (2.0)	8.40 (1.19)	1.19 (0.19)	19.2 (1.9)	64.8 (11.7)	472 (89)	0.615 (0.042)	25.4 (1.7)	59.5 (4.4)	48.4 (6.9)	25.4 (1.7)	48.4 (6.9)
Urban forest oak	147.0 (4.5)	7.33 (0.77)	1.20 (0.16)	20.7 (1.9)	71.2 (7.9)	440 (60)	0.555 (0.100)	34.5 (6.8)	44.9 (16.0)	47.9 (12.8)	34.5 (6.8)	47.9 (12.8)
Natural forest pine	157.5 (3.7)	3.43 (0.65)	0.47 (0.16)	49.5 (7.2)	161.9 (26.9)	1445 (404)	0.368 (0.052)	47.1 (6.1)	89.5 (1.4)	83.0 (5.1)	47.1 (6.1)	83.0 (5.1)
Urban forest pine	155.9 (3.4)	4.33 (1.18)	0.36 (0.09)	43.9 (12.2)	143.0 (39.1)	1627 (337)	0.341 (0.084)	49.5 (8.5)	76.9 (13.2)	74.4 (4.3)	49.5 (8.5)	74.4 (4.3)
Pine plantation	156.4 (5.5)	3.12 (0.15)	0.29 (0.04)	50.4 (3.8)	165.1 (7.3)	2051 (332)	0.293 (0.033)	51.2 (3.7)	102.6 (7.5)	148.9 (14.5)	51.2 (3.7)	148.9 (14.5)

Table 5). Pine dominated sites at week-82 have a higher percent N and P remaining compared to oak dominated sites ($p=0.005$ and $p<0.001$, respectively).

Decomposing litter has been observed to have three phases of N (Berg and Staaf 1981) and P (Blair 1988) release: a leaching phase, followed by immobilization, and then finally mineralization. Working within this framework, we used the results from the paired t-tests, C:N and C:P data (Enloe 2014), and information regarding the critical C:N and C:P ratios at which mineralization is thought to occur (Gosz et al. 1973; Saggari et al. 1998; William et al. 2007) to describe the N and P release patterns observed in the decomposing litter (Fig. 5a, b). Rational for determining immobilization and mineralization patterns are described as follows in the methods section. Briefly, we determined nutrient release patterns using the following rational. For each week data was collected, paired t-tests were used to determine if a land cover has a N or P % remaining different from 100 %. Immobilization is in effect if the land cover has a N or P % remaining that is significantly greater than 100 % or not statistically different than 100, regardless of whether the mean percentage is above or below 100. Values significantly below 100 are considered losses due to mineralization if the critical C:N or C:P values have been met and are losses due to leaching if those critical values have not been met.

The natural forest and urban forest pine sites are dominated by immobilization of N and P over the 82 week period, with losses of N occurring via leaching in week-4 and losses of P occurring via leaching in week-18 and possibly week-60. The immobilization trend is strong for pine plantation sites for the duration of the study. For oak sites, both N and P are immobilized over the first 42 weeks of decomposition, with a period of leaching occurring during week-4 for N. Oak sites have P mineralization at week-60 ($p<0.05$) and are trending towards the mineralization of N at week-82 ($0.05\leq p\leq 0.10$). Based on these patterns of immobilization and mineralization, pine sites appear to be more nutrient limited than oak sites regardless of whether they are in an urban or rural setting.

Table 5 Results of the contrast statements for differences among land covers for initial litter quality parameters, decay constants (k) of mixed species litter over the 82-week litterbag study, and mass and nutrients remaining in the litterbags at week-82. Contrasts with a p -value ≤ 0.10 are reported

Contrast	Response variable	Point estimate	p -value
Initial litter quality for litterbags (Week-0)			
UFO—NFO	Lignin (g kg^{-1})	-31.3	<0.001
Pine forest—oak forest	N (g kg^{-1})	-4.24	<0.001
	P (g kg^{-1})	-0.823	<0.001
	Lignin:N	28.0	<0.001
	C:N	88.6	<0.001
	C:P	1252	<0.001
Foliar litter decomposition			
Pine forest—oak forest	k	-0.251	0.002
	Mass remaining (%), week-82	19.3	0.011
Nutrients remaining in litterbags (Week-82)			
Pine forest—oak forest	N remaining (%)	37.5	0.005
	P remaining (%)	53.9	<0.001
NFP—PP	P remaining (%)	-65.9	0.002

NFO natural forest oak, NFP natural forest pine, PP pine plantation, UFO urban forest oak

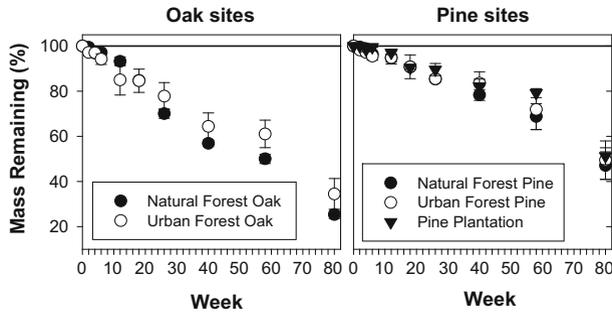


Fig. 3 Percent mass remaining of mixed species foliar litter by either oak or pine dominated land cover during 82 weeks of decomposition (March 2010–October 2012) in the Florida panhandle. Vertical bars represent one standard error from the mean

During the initial leaching phase (week-4) of N observed in this study, the amount of N remaining in the litter dropped on average between 27 and 56 % of the original amount across the different land covers. By week 6, the amount of N remaining in the litter returned to values close to 100 % for all of the land covers. Since very little mass was lost from week-4 to week-6, microorganisms likely accessed N from sources above and below the leaves to convert it

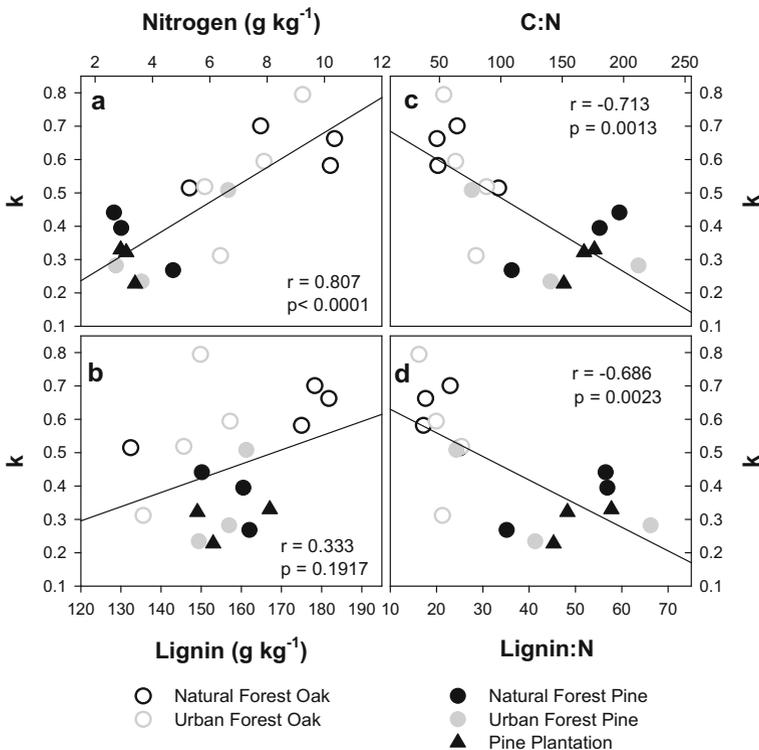


Fig. 4 Pearson's correlation coefficients and associated p-values between the decomposition rate constant (k) and the initial litter quality parameters of **a** nitrogen content (g kg^{-1}), **b** lignin content (g kg^{-1}), **c** C:N ratio, and **d** the lignin:N ratio for the 17 forested sites in the Florida panhandle

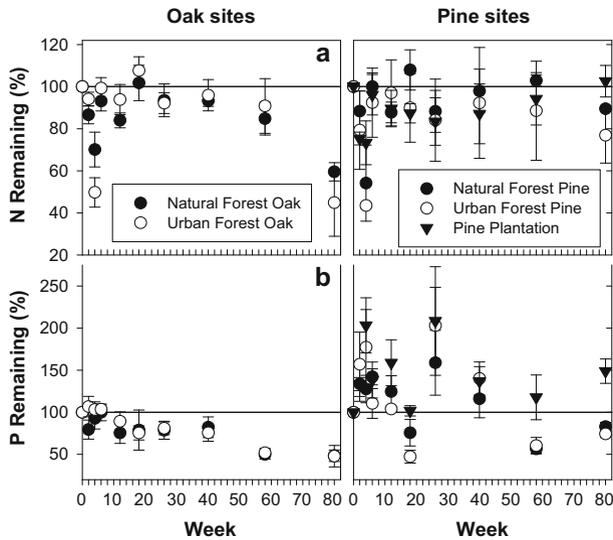


Fig. 5 Percent **a** N and **b** P remaining of mixed species foliar litter by either oak or pine dominated land cover during 82 weeks of decomposition (March 2010–October 2012) in the Florida panhandle. Vertical bars represent one standard error from the mean

into microbial biomass. Nitrogen content in decomposing litter has been observed to increase due to exogenous inputs from the atmosphere (Kochy and Wilson 1997), from fungi translocating soil-derived N to the litter (Hart and Firestone 1991; Frey et al. 2003), and from bacterial transferring N between different sets of leaves (Schimel and Hattenschwiler. 2007).

Discussion

Urbanization does not appear to impact decay rates and N and P immobilization/mineralization patterns of foliar litter in this study. This may indicate that the change in the abiotic and biotic factors that occur from a low population density urban environment do not produce enough of an effect to be detectable above the natural variation associated with decomposition in this region. It is important to note that this research took place during a drought that persisted during the study period (2010–2012). Therefore, low available moisture in the forest floor across all sites may have limited biological activity and masked any effect that urbanization may have had on the forest floor microbial community, and, subsequently, decomposition. Urban sites have higher winter mean temperatures, lower minimum temperatures, and a narrower temperature range compared to rural sites. It appears that this difference in temperatures during a drought period is not reflected in altered decay rates.

The urban environment of a large city has been found to decrease foliar litter quality (Carreiro et al. 1999). In this study, no significant differences were found between N and P concentrations, lignin:N, C:N and C:P ratios between foliar litters collected in rural forests and urban forests of a small city. Whereas Carreiro et al. (1999) studied the impact of urbanization on litter quality of a single species, the litter quality measurements in this study reflect the quality of a mix of foliar litters. Therefore, species composition within the litterbags varied within land covers as well as between land covers. As tree species can vary in their response to pollution, such as N deposition (Aber et al. 2003), changes in tree species composition

between urban and rural forests complicate understanding the role of the urban environment in foliar N concentration (Rao et al. 2013) and overall litter quality.

Soil organic C content is dependent on foliar decomposition rates and on NPP, which reflect additions of organic materials to the soil. No differences between urban and rural sites are observed for foliar decay rates over an 82 week period during a drought. As for aboveground NPP, urban forests have higher foliar productivity rates compared to rural forests. This increased input of foliar C in the urban versus rural sites is not reflected in statistically different forest floor or surface soil (0–7.5 cm) C contents. Furthermore, urbanization does not impact forest floor mass or depth ($p > 0.05$, Enloe 2014). Research along an urban–rural gradient in the New York City Metropolitan area found that forest floor mass and depth increased with increasing distance from the city center and that this change likely influenced seedling species composition (Kostel-Hughes et al. 1998).

Urban vegetation is often suggested to have higher NPP compared to native vegetation (Groffman et al. 2006; Byrne 2007; Lorenz and Lal 2009) or, in general, high productivity. The indirect effects of urbanization, such as higher carbon dioxide production, warmer temperatures (Ziska et al. 2004) and lower ozone concentrations (Gregg et al. 2003), have been found to have a positive impact on a single plant species' productivity in urban versus rural areas. Therefore, the warmer winter forest floor temperatures and higher minimum temperatures found in the urban forests in this study may contribute to the higher above ground productivity in those forests. Furthermore, the conversion of native species to invasive ones (a direct effect of urbanization) would likely alter plant productivity. The contribution of invasive plants to urban forest net C sequestration can be significant (Escobedo et al. 2010) and invasive trees in general have been found to increase productivity of a forest stand compared to a non-invaded stand (Ehrenfeld 2003). Camphortree was observed in four of the seven urban forest sites and exhibited a high annual woody growth rate among urban trees in this study. The results of this paper are relatively consistent with these studies in suggesting that the indirect and direct effects of urbanization can increase urban plant productivity.

The extent to which plant productivity in this study was impacted by drought is unknown. However, the slash pine plantations in this study have comparable values for aboveground productivity as other slash pine plantations in Florida that have similar stand age, basal area, stem density and standing crop biomass (Gholz and Fisher 1982; Harding and Jokela 1994; Clark et al. 1999; Shan et al. 2001). In contrast, microbial activity and decay processes in the forest floor materials are likely impacted by drought. Plants can access the entire soil profile for water and forest soils are protected from moisture loss by the forest floor. Similar to mulch in an agronomic setting, forest floor materials can reduce evaporative water loss from the underlying mineral soil and ameliorate the effect of the drought on soil moisture loss. Although we did not take soil moisture measurements, we hypothesize that the impact of drought on soil moisture was the most severe in the forest floor material compared to the mineral soil and this impacted microbial activity (and decay processes) in the forest floor to a greater extent than plant activity.

Oak and pine dominated forests are two common plant communities within the study area and they have distinct differences in biogeochemical cycling. Oak dominated forest sites have higher foliar N and P contents entering the forest floor on a yearly basis, smaller forest floor C contents, higher litter quality indices (N and P content, Lignin:N, C:N and C:P ratios) and higher decomposition rates compared to pine dominated forest sites. Oak sites may respond differently to the effects of urbanization compared to pine sites through increases in soil N content and they may be more sensitive to invasion by camphortree compared to pine dominated sites. However, other aspects of C and N cycling in these two communities responded similarly to urbanization.

Summary and conclusions

Kaye et al. (2006) suggest that cities have a fundamentally different biogeochemistry than natural systems since "...human actions alter control points, inputs, and outputs in urban ecosystems." In the eastern United States, New York City, Baltimore and Asheville have population sizes that range over three orders of magnitude and "...although all exhibit impacts of urbanization on soil properties, the nature and degree of these impacts vary from city to city" (Pavao-Zuckerman 2008). Therefore, there is a need for city specific ecological knowledge. In conclusion, this study found that urban forests within small cities can have altered biogeochemistry (increased plant productivity) from nearby natural systems. This may have been driven by an urban heat island effect and to some extent from the presence of an invasive tree in urban forests. Furthermore, drought may eliminate the ability to detect the impact of urbanization on biogeochemical processes that are sensitive to soil moisture conditions, such as forest floor decay processes and foliar nutrient immobilization/mineralization patterns. Knowledge of how drought interacts with other drivers of change in urban systems may be a necessary component of city specific ecological knowledge, which is a valuable tool in urban restoration (Pavao-Zuckerman 2008).

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Conflict of interest The authors declare that they have no conflict of interest.

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