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Nomenclature
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Abstract

Question: Herbaceous plant communities in hardwood forests are important for maintaining biodiversity and associated ecosystem services, such as nutrient storage. Are there differences in herbaceous layer nutrient storage for urban park and state preserve forests, and is there seasonal variation?

Location: United States, Midwestern region (Iowa).

Methods: We examined the herbaceous layer in three 20-m^2 plots at six forest sites, in urban parks (city parks with high human visitation) and state preserves (under permanent protection as state preserves). We harvested herbaceous plants from quadrats in each plot in spring, summer and autumn to analyse above- and below-ground tissues for total C, N and P concentrations. Biomass and tissue nutrient concentration data were used to estimate nutrient storage per plot and per hectare. We also collected soil samples at each plot in each season to determine soil C, N and P content.

Results: State preserve and urban park forests did not differ in herbaceous species richness, although state preserve forests were qualitatively distinct. State preserve forests had relatively higher biomass and nutrients than urban park forests. In both forest types, above-ground concentration for N and P were higher in spring than in autumn, whereas below-ground concentration of these nutrients was consistently higher in autumn. In urban parks, total soil N was higher in spring compared to summer and autumn. However, soil nutrient content did not appear to drive differences in plant tissue nutrient content in urban park forests.

Conclusions: Subtle qualitative differences in herbaceous layer composition affected seasonal biomass quantities and nutrient concentrations in urban park and state preserve forests. These differences influenced C, N and P storage and led to consistent trends for relatively higher biomass and nutrient storage in state preserve forests. Above-ground plant tissue provides important storage of N and P in spring, and below-ground plant tissue provides important storage of N and P in autumn. Since spring and autumn are seasons of limited vegetative cover in the regional landscape, with subsequently higher potential for nutrient loss from terrestrial systems, this finding is crucial for provision of ecosystem services.

Introduction

Marked seasonal changes in temperate zone forest vegetation occur for species both in the canopy and in the understorey. Although changes among herbaceous species may appear to be less pronounced than those of canopy trees, a number of studies have demonstrated seasonality in both species composition and percentage cover of the herbaceous layer (e.g. Yorks & Dabydeen 1999; Gilliam et al. 2006; Vymazalová et al. 2012; Murphy & McCarthy 2014). The herbaceous layer also changes in response to a variety of anthropogenic disturbances, such as timber harvest or land-use change, as well as natural disturbances, such as herbivory or canopy openings created by wind damage (Roberts 2004; Baeten et al. 2010). Research has demonstrated that this component of forests is important

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for provision of ecosystem services such as biodiversity (Whigham 2004; Gilliam 2007) and nutrient cycling (Blank et al. 1980; Peterson & Rolfe 1982; Anderson & Eickmeier 2000; Muller 2003). However, even though changes in the role of the herbaceous layer as influenced by land use and across the growing season have implications for variability in the provision of ecosystem services (Murphy & McCarthy 2014; Cameron et al. 2015), these changes have been less well explored.

In general, it is known that forests cycle nutrients tightly among different components of the ecosystem, including the canopy, understorey and forest floor (Whittaker et al. 1979; Yarie 1980; Attiwill & Adams 1993; Muller 2003). Leaves senescing from trees in autumn can release substantial quantities of nutrients that may subsequently be captured by actively growing plants, microbial communities and other organisms on the forest floor (Attiwill & Adams 1993; Aerts 1996). Ret-ranslocation rates for C (23%), N (50–65%) and P (50–65%) among canopy species (Aerts 1996; Vergutz et al. 2012) indicate that the remaining pool of nutrients made available from senesced tree leaves in autumn is considerable. While there are fewer reports in the literature on nutrient storage or resorption rates of the herbaceous layer in the autumn, it is probable that herbaceous plants also release equivalent proportions of nutrients and translocate remaining nutrients into perennial tissues before seasonal senescence. Although total quantities of C and biomass contained in canopy trees are much larger than for the herbaceous layer, the herbaceous layer does play a particularly important role in nutrient retention and may cycle large proportions of the N and P in these systems (Yarie 1980; Gilliam 2007).

In terms of plant community composition, spring ephemerals in the herbaceous layer of temperate forests have been the focus of a number of studies (e.g. Muller & Bormann 1976; Muller 1978, 2003; Meier et al. 1995; Anderson & Eickmeier 2000; Lapointe 2001). The early growth and senescence of spring ephemerals contributes to consistent seasonal changes in community composition, and initiate an annual cycle of species that gain and lose dominance over the growing season (Tremblay & Larocque 2001; Mabry et al. 2008; Lenière & Houle 2009). However, the dynamics of herbaceous layer composition later in the growing season have not been examined as closely. For example, some spring-growing herbaceous plants (e.g. *Hydrophyllum virginianum*) persist longer than the true ephemerals and play a role that extends through spring and into summer and autumn (Lenière & Houle 2009; Gerken et al. 2010) together with a diverse community of aestival species. A number of herbaceous plants may be present and actively growing until after deciduous trees lose their leaves (Tremblay & Larocque 2001). However, compared to spring ephemerals and other spring-growing species, the composition and role of the herbaceous community species that persist after senescence of leaves from trees is less well understood.

Nutrient storage in the herbaceous layer has also been shown to vary seasonally and according to community composition and biomass production (Rothstein & Zak 2001; Muller 2003; Mabry et al. 2008; Gerken et al. 2010). Early research identified spring ephemerals as particularly important for nutrient uptake and storage before canopy leaf-out, when nutrients can readily be leached from soil. This finding led to the 'vernal dam' hypothesis (Muller & Bormann 1976). Over the course of the growing season, different phenological groups, such as aestival species, may also play an important role (Mabry et al. 2008). Floristically diverse native herbaceous plant communities would be most likely to have representatives from these various groups that could contribute to nutrient capture throughout the growing season (Mabry et al. 2008). For example, research to investigate central Iowa hardwood forests under different land uses indicated that higher nutrient capture occurred in herbaceous layer communities in preserved (protected) forests characterized by dense cover of a diverse suite of native specialist herbaceous species, as contrasted with grazed forests characterized by sparse cover comprised of a smaller number of species that were mainly generalists (Mabry et al. 2008). These researchers attributed the differences observed in nutrient capture both to the species present and the biomass produced by those species.

Analogous to herbaceous layer community changes (e.g. fewer species, less biomass production) caused by agricultural activities such as grazing, changes in herbaceous layer composition have been documented for remnant forests affected by urbanization. For the most part, researchers have found declines in species richness and abundance related to increased degree and/or duration of urbanization (Robinson et al. 1994; Drayton & Primack 1996; DeCandido 2004; Moffatt et al. 2004; McKinney 2008; Cameron et al. 2015). Declines in herbaceous species richness have been consistently documented for urban forest areas, and although the mechanisms underlying these declines are less well understood, they are thought to be related to a number of factors including increased herbivory (Hyngstrom et al. 2011), pollution (Gilliam 2006) and trampling (Hamberg et al. 2010). The loss of species in these systems is likely to have ramifications for nutrient capture, although based on a search of the literature we know of no other studies conducted to investigate this phenomenon.

Representative of many landscapes strongly affected by agricultural intensification and urbanization, the landscapes of the Midwest USA (and Iowa in particular) have

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been altered to a large degree by human activities. Land cover in Iowa is approximately 65% row crop agriculture, 3% urban, 23% grassland/pasture/wetland and 8% forest (Fry et al. 2011). Row-crop agriculture in this region, dedicated primarily to production of corn and soybeans, has created a landscape matrix that is minimally vegetated in early spring and late autumn. The remaining areas of perennial vegetation embedded in this landscape, such as forested land, are extremely important for providing ecosystem services, such as water quality protection via nutrient capture, particularly for N and P – two nutrients that are exported from this region via streams and rivers, ultimately contributing to over-enrichment of receiving waters (leading to hypoxia in the Gulf of Mexico; e.g. Scavia et al. 2004). A previous study of forested headwater watersheds embedded in both agricultural and urban landscapes indicated that nutrient delivery rates from urban streams varied seasonally but were generally higher than that of agricultural streams (Gerken Golay et al. 2013). These results point toward the possibility of diminished nutrient capture by herbaceous layer flora in urban forests.

The goal of this study was to examine community-level nutrient storage by the herbaceous layer in a set of forests in urban park and state preserve forest types at three critical points across the growing season. This study builds on previous work in three important ways. First, few studies have considered the role of an entire herbaceous community as opposed to a subset of prominent species (Muller & Bormann 1976; Rothstein & Zak 2001; Gerken et al. 2010). Second, analyses of this type have frequently focused on the flora of one forest site, thereby limiting generalizations based on the results. Third, comparable forest herbaceous layer community studies rarely extend through autumn, after senescence of canopy tree leaves (but see Tremblay & Larocque 2001 for an exception). In our comparison of forest types, we hypothesized that state preserve forests would be characterized by a larger number of native herbaceous species and have higher total biomass production and higher nutrient capture in all seasons compared to urban park forests. In our comparison of seasons, we expected that above-ground plant tissue nutrient concentrations would be highest in spring (contributing to the vernal dam), and that below-ground biomass and nutrient concentrations would be highest in autumn (creating an 'autumnal dam').

Methods

Study sites

We conducted this study in six forest areas in Polk and Warren Counties, in and near the Des Moines metropolitan area in central Iowa (Fig. 1). Overall, this landscape is dominated by intensive row-crop agriculture, with remnant forests embedded in urban landscapes and/or concentrated in areas of relatively steep topography and along streams and rivers. The study area contains the largest urban centre in the state, the Des Moines-West Des Moines metropolitan area, with an estimated 2010 population of 572 000 (US Census Bureau 2011; www.census.gov/popest/data/metro/totals/2011/index.html Accessed 23 May 2016), and was therefore ideal for studying the effects of urban land use on forests. We identified three forest areas each in state preserves (forests under permanent legal protection as state-designated Natural Preserves because they represent outstanding or unique biological features) and urban parks (forests located within parks offering additional amenities such as playgrounds and restroom facilities, characterized by high human visitation and managed as part of an urban park system) forest types. During site selection, we chose forest areas that were as similar as possible with respect to stand age (mature stands > 100 yr old), canopy composition (oak–hickory species) and landscape positions (uplands and slopes). We also limited our selection to sites with no history of silvicultural activity for at least 30 yr. As a final criterion to avoid the known effects of invasive woody shrubs on nutrient dynamics and herbaceous layer composition, we chose forest sites where these plants were absent or only sparsely present.

The three urban park forests ranged in size from 9 to 26 ha (averaging 15.5 ha) and were all under the jurisdiction of the City of Des Moines Parks and Recreation Department. They have all been subject to intense human recreational use and concentrated herbivory (deer density estimates from 60 to 100 deer·km^{-2} according to the Polk County Deer Task Force 2015 report; www.polkcountyiowa.gov/media/196645/14-15%20Deer%20Report.pdf Accessed 23 May 2016) but have not been otherwise manipulated (Julie Hempel, pers. comm.). The three state preserve forest areas ranged in size from 16 to 75 ha (averaging 36 ha). Although one forest preserve site is located within the city limits of Des Moines, none of the state preserve forests offer amenity facilities, and thus regardless of location have been subject to much less human visitation, and deer densities are estimated to be lower (20–50 km^{-2}; according to the Polk County Deer Task Force 2015 report; www.polkcountyiowa.gov/media/196645/14-15%20Deer%20Report.pdf Accessed 23 May 2016). Furthermore, because of their history of legal protection, forest preserves are the best available proxies for natural conditions of the area's forests.

Plant and soil sampling

To characterize the plant community at each forest site, we used topographic maps to place three 20-m^2 vegetation

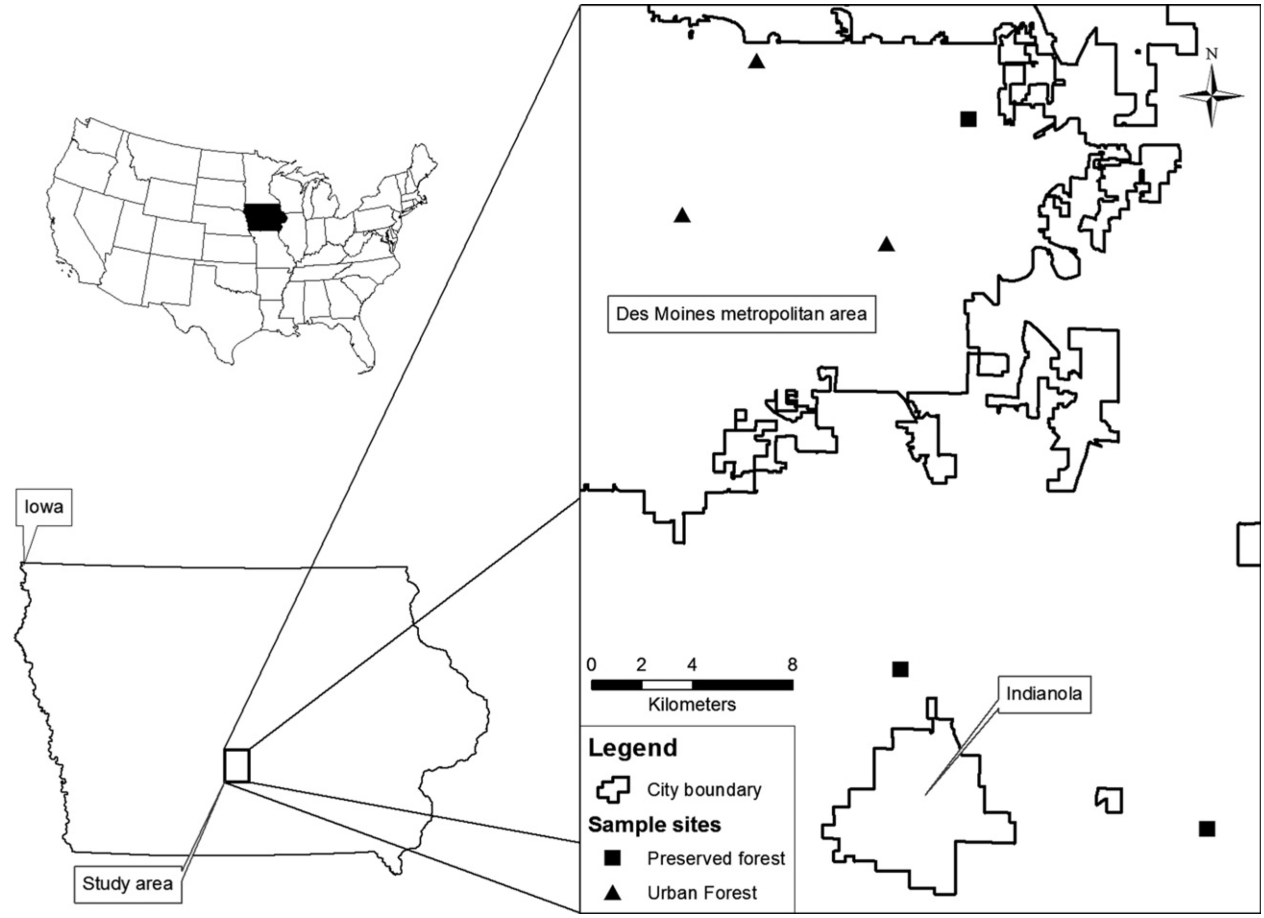

Fig. 1. Location of the six study forests, three state preserves and three urban parks, in and near the Des Moines metropolitan area of central Iowa, US.

plots a minimum of 50 m apart on upland (ridge) and hill slope landscape positions; no bottomland forest plots were included. Previous research (Mabry et al. 2008) indicated no differences in herbaceous layer composition due to upland/slope position or aspect in these systems. We measured slope and aspect variables to verify earlier findings, but plots were not stratified according to these variables. We surveyed plots once each in spring (between 23 Apr and 2 May 2011), summer (18–22 Jun 2010) and autumn (14–22 Oct 2010) to identify herbaceous species present, to identify trees and to quantify canopy cover. Because the herbaceous communities might vary seasonally and from year to year (e.g. Murphy & McCarthy 2014), plots in both forest types were described and harvested within a 1-wk period in the same year.

For each plot, we identified each species present, and documented its Iowa Coefficient of Conservatism (CC). The CC is a metric that describes floristic quality based on ratings for each species as determined by a committee of expert botanists. The ratings are based on a rising 0–10 scale, with higher scores indicating fidelity to undisturbed native habitats (Iowa State University Ada Hayden Herbarium 2004; www.public.iastate.edu/~herbarium Accessed 23 May 2016). We used CC values for all species in each plot to calculate an average CC per plot. We used a published flora for the region to determine the number of native, early flowering and habitat specialist species for closed-canopy and moist, rich sites (Gleason & Cronquist 1991). Nomenclature follows the USDA Plants Database.

After identification of all species in each plot, we excavated three 0.25-m^2 quadrats to harvest above- and below-ground herbaceous biomass along a diagonal transect within each 20-m^2 vegetation plot in each season (spring, summer and autumn). Quadrat locations were randomly selected in each season and were marked to avoid sampling the same location in future harvests. Harvest dates were chosen to coincide with peak above-ground biomass production for the suite of species that characterize each season (Mabry et al. 2008). Additionally, autumn harvest was timed to occur after senescence of tree leaves, which typically occurs in early to mid-Oct in this region.

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When harvesting plant material from each quadrat, we removed litter to prevent mixing with plant samples, and collected all above- and below-ground herbaceous plant tissue. We stored harvested plants in a cooler box for transport and then rinsed them thoroughly with water to remove soil/debris. We separated herbaceous plants into above- and below-ground plant tissue, and oven-dried all samples at 65 °C for 48 h. Dried samples were weighed to estimate biomass and then ground to pass a 20-mesh sieve using a Wiley mill. We determined plant tissue concentration of carbon (C) and total nitrogen (N) by standard combustion procedures using a Leco TruSpec Macro (Leco, St. Joseph, MI, US). We ashed plant tissue samples for phosphorus (P) analysis (Alban 1971).

At the time of plant harvests (each season) we also collected 4-cm deep surface soil core samples (50 cm^3) in the centre of each vegetation plot. Soil samples were cold-stored and then oven-dried at 65 °C for 48 h to prevent loss of N at higher temperatures (Mahaney et al. 2008). We weighed soil before and after drying and divided the dry weight by the volume of the core to determine soil bulk density. Soil C and N were determined by combustion using the Leco TruSpec Macro and soil P was determined according to the Bray and Kurtz P-1 method (Bray & Kurtz 1945). All plant and soil analyses were conducted at the U.S. Forest Service Northern Research Station Chemistry Laboratory in Grand Rapids, MN, US.

Data analyses

For plant tissue, we subsampled at the quadrat level to capture variation within plots, and averaged quadrat-level data to determine plot means. For all other parameters, data from plots were our sampling unit for statistical analysis. We considered all plots independent (n = 18) and we used site as a blocking factor. We used t-tests to compare herbaceous plant composition (e.g. numbers of annual, perennial and native species, habitat specialists, mean CC) between forest types. We used one-way ANOVA (with α = 0.05) to test for relationships between qualitative measures of herbaceous plant community composition (response variables) and environmental parameters (slope, aspect and canopy cover; predictor variables). No relationships were found among community and environmental parameters so no additional tests were performed.

We calculated 95% confidence intervals for plot-level data on biomass, C, N and P concentrations to present baseline information for the herbaceous layer in autumn (e.g. below-ground biomass and nutrient concentration) in a way that would allow comparison among forest types, across seasons and between above- and below-ground plant tissues. Average biomass and nutrient concentration for both above- and below-ground plant tissue for plots was determined as $g \cdot m^{-2}$. To facilitate analysis of data and application of findings at on a per hectare basis, we present tabular data for subsequent statistical comparisons.

We multiplied plant biomass by nutrient concentration for C, N and P, respectively, to calculate total plant nutrient content. We scaled up calculations to estimate total plant biomass and nutrient content in $kg \cdot ha^{-1}$. Soil C, N and P for each plot were determined as concentrations and multiplied by bulk density to determine nutrient content as $g \cdot cm^{-3}$. Plant and soil C:N, N:P and C:P ratios were calculated based on C and nutrient content.

To compare forest types for each season, we used t-tests to examine biomass, C and nutrient content of above- and below-ground plant tissue combined (totals are reported as $kg \cdot ha^{-1}$). To compare seasonal measurements for each forest type, we used ANOVA with season as the predictor variable and plant above-ground biomass and nutrient content, plant below-ground biomass and nutrient content, and soil C and nutrient concentration as the response variables. Post-hoc comparisons among seasons and between types for biomass, nutrient content, soil nutrients and C:N, N:P and C:P ratios were made using Tukey's HSD. Data exhibited normal distribution and variances were equal according to the Levene test for normally distributed data and the Brown-Forsythe test for non-normal data, therefore no transformations were made. All analyses were done with JMP v 9 software (SAS Institute, Cary, NC, US). We declared statistical significance at $P \leq 0.05$.

Results

In spring, understorey species common in these forests included early flowering perennials such as *Asarum canadense, Erythronium albidum* and *Hydrophyllum virginianum.* In summer, the common flowering perennials included *Arisaema triphyllum, Sanicula odorata* and *Maianthemum racemosum*. In autumn, above-ground plant tissue of *A. canadense, H. virginianum, S. odorata* and *Viola* spp. (among others) persisted, and these plants continued to be photosynthetically active after tree canopy leaf senescence. State preserve and urban park forests had similar overall herbaceous species richness, numbers of annual species and mean CC values (Table 1). State preserve forests had higher numbers of perennial species, native species, early flowering species and habitat specialists of closed-canopy and rich, moist sites (Table 1). Environmental variables (% slope, aspect and canopy cover) did not affect these qualitative measures of herbaceous community composition (P = 0.1525–0.8383).

Forest types did not differ significantly for total biomass and nutrients on a per-hectare basis, except that total N was higher in state preserves than urban parks in autumn (Table 2). However, state preserve forests exhibited

Table 1. Mean number of species and mean coefficient of conservatism (CC) for surveys in each of three 20-m^2 plots in three state preserve and three urban park forests (± SD). Surveys were conducted in spring, summer and autumn to generate a complete species list for each plot.

	State Preserve		Urban Park		*P*-Value
	Mean	SD	Mean	SD	
Herbaceous Species	54	6.3	48	6.2	0.0624
Annuals	5	1.3	4	1.9	0.1282
Perennials	46	5.5	40	6.4	0.0378
Native	53	5.7	45	6.7	0.0256
Early Flowering Herbs	22	2.4	18	3.5	0.0137
Closed Canopy Specialist Herbs	30	3.7	24	5	0.0112
Moist Habitat Specialist Herbs	33	4.2	24	5.7	0.0022
Herbaceous Mean CC	4.64	0.19	4.36	0.41	0.0897

consistent trends of: more total herbaceous plant biomass (18–27% more in state preserve forests, depending on season), total C (16–26% more in state preserve forests), total N (24–47% more in state preserve forests) and total P (16–34% more in state preserve forests) compared to urban park forests (Table 2).

Patterns of plant biomass and nutrient allocation allow for general comparisons across seasons and between forest types. Within both state preserve and urban park forests above-ground biomass was higher in summer and lower in autumn (Appendix S1A). However, below-ground biomass was 15–40% higher than above-ground biomass in spring, 10% lower than above-ground in summer and >100% higher than above-ground biomass in autumn (Appendix S1A). Above-ground C concentration mirrored biomass quantities (Appendix S1B). Above-ground N concentration was highest in spring and lowest in autumn for both state preserve and urban park forests (Appendix S1C). Below-ground N concentration was 120% (urban park forests) to 210% (state preserve forests) higher in autumn compared to summer. Total P concentration was highest for above-ground tissue in summer and for below-ground tissue in autumn (Appendix S1D). In autumn, total P concentration in below-ground tissue was 130% (urban park forests) to 190% (state preserve forests) higher compared to above-ground plant tissue.

In state preserve forests above-ground herbaceous plant nutrient concentration did not differ significantly for C and P across seasons. However, percentage N did vary and was highest in spring and lowest in summer (Appendix S2). In urban park forests, above-ground percentage C was highest in autumn, while percentage N and percentage P were highest in spring. For both forest types, below-ground plant tissue concentrations of C, N and P were largest in autumn (Appendix S2). In state preserve forests, soil nutrient concentrations (%) and content (g·cm^{-3}) did not differ across seasons. In urban park forest soils both percentage N and N content were higher in spring and lower in summer (Appendix S2). Soil C and N content did not differ between forest types. Soil P content was higher in urban park than state preserve forests in spring and summer, although there was no difference in autumn (Appendix S2).

Ratios of above- and below-ground plant C:N were generally lower in spring and autumn and highest in summer, with the exception of urban park forests that had similar above-ground plant C:N in summer and autumn (Table 3). For urban park forests soil C:N was also lowest in spring. Conversely, plant above-ground and below-ground N:P ratios were generally highest in spring and autumn and lowest in summer, with the exception of urban park forest above-ground plant tissue, for which there were no differences. Ratios of C:P were only significant for state preserve forests, with highest ratios for below-ground plant parts in summer and lowest ratios in autumn, and in urban parks C:P ratios for above-ground plant material were highest in autumn and lowest in spring. Ratios of C:N were higher in

Table 2. Mean total biomass and nutrient pools of herbaceous material in state preserve and urban park forests harvested in spring, summer and autumn (each mean represents nine plots). Totals include above- and below-ground herbaceous plant material for estimates on a per-hectare basis (kg·ha^{-1}).

	Total Biomass kg·ha^{-1}		Total C kg·ha^{-1}		Total N kg·ha^{-1}		Total P kg·ha^{-1}	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Spring								
State Preserve	810.5	379.7	314.3	150.4	21.00	9.09	2.837	1.415
Urban Park	596.0	295.8	239.5	121.5	13.89	7.09	2.271	1.293
Summer								
State Preserve	832.0	309.9	324.9	116.8	13.52	5.70	2.738	1.232
Urban Park	686.0	382.1	273.8	148.4	10.30	5.78	2.299	1.423
Autumn								
State Preserve	652.5	267.4	268.6	116.3	16.69^{a}	7.94	2.455	1.055
Urban Park	473.3	282.0	197.3	118.2	8.87^{b}	3.63	1.616	1.035

Pairs of means with different letters differ at $P \leq 0.05$ according to Tukey's HSD.

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Table 3. Mean nutrient ratios (± SD) for C:N, N:P and C:P in above-ground herbaceous plant material (Above), below-ground herbaceous plant material (Below) and soil compared across seasons for both state preserve and urban park forests (small letters) and between forests within seasons (large letters).

	State Preserve Forests						Urban Park Forests					
	C:N		N:P		C:P		C:N		N:P		C:P	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Above												
Spring	11.4^{cB}	1.02	8.7^{aA}	0.97	98.1	9.94	13.2^{bA}	0.81	6.9^{B}	0.44	91.2^{b}	5.44
Summer	21.2^{a}	4.00	5.4^{b}	1.30	111.3	26.90	22.6^{a}	2.19	5.1	1.78	112.5^{ab}	36.88
Autumn	16.5^{bB}	3.46	7.5^{a}	2.38	120.2	33.41	27.4^{aA}	8.76	6.4	3.22	160.8^{a}	77.36
Below												
Spring	19.0^{bB}	3.18	6.8^{a}	1.06	126.0^{ab}	10.81	22.9^{bA}	3.68	5.6^{ab}	0.89	128.2	32.44
Summer	30.1^{aB}	5.11	4.8^{b}	1.15	141.8^{a}	28.65	35.0^{aA}	3.77	4.4^{b}	1.00	153.8	43.44
Autumn	16.7^{b}	2.91	6.7^{a}	1.02	110.0^{b}	18.64	19.9^{b}	4.01	6.4^{a}	1.77	125.4	37.63
Soil												
Spring	11.2	1.80	155.4^{A}	80.04	1708.5^{A}	830.04	11.6^{b}	1.02	89.0^{B}	43.78	1010.6^{B}	421.20
Summer	12.3^{B}	0.96	128.1	64.49	1579.7	819.62	14.0^{aA}	1.56	80.1	32.76	1096.8	393.67
Autumn	12.8	1.48	148.7	89.22	1937.4	1297.86	13.3^{a}	1.44	94.0	32.32	1286.2	563.84

Groups of means with different letters differ at $P < 0.05$ according to Tukey's HSD.

urban park forests than state preserve forests for both above- and below-ground vegetation in spring, above-ground vegetation in autumn, below-ground vegetation in summer, and in soils during summer. Conversely, N:P ratios were higher in state preserve forests than urban park forests for above- and below-ground vegetation and soils in spring and for soils in summer. Finally, ratios of C:P were higher in state preserve forests than urban park forests in spring.

Discussion

In our comparison of forest types, our hypotheses that state preserve forests would be characterized by a larger number of native herbaceous species, and have equal or higher total biomass production and nutrient capture in all seasons compared to urban park forests was supported. In our comparison of seasons, we found a more nuanced pattern of nutrient dynamics than expected. For instance, nutrient content of herbaceous plant tissue supports the notion of an autumnal dam in some instances, where storage may equal or exceed levels detected in other seasons and provide an advantage for plants adapted to the seasonal influx of nutrients from senescing tree leaves.

We documented differences in composition between state preserve and urban park forest herbaceous layers in numbers of perennial, native and early flowering species, as well as closed canopy and moist site habitat specialists. The evidence suggests that these qualitative compositional differences were related to seasonal biomass quantities as well as seasonal patterns in nutrient concentration and storage. We found consistent trends of relatively high total biomass and nutrient content for state preserve forests compared to urban park forests across all three seasons. We also generally observed that above-ground plant tissues contained higher concentrations of N and P in spring, and below-ground plant tissues contained higher concentrations of N and P in autumn in state preserve forests compared to urban park forests.

There were subtle yet significant differences in qualitative characteristics of the herbaceous layer between state preserve and urban park forests. State preserve forests had more native perennials and habitat specialists compared to a higher prevalence of non-native species, short-lived species and habitat generalists in urban park forests. In particular, we surmise that native, perennial and early flowering species had a strong influence on the seasonal patterns in biomass quantities and nutrient concentrations of different plant tissues that we observed.

Such differences in community composition could be related to seasonal patterns of growth and nutrient availability, especially in terms of phenological adaptation of native vs non-native plants, as well as resource allocation to above-ground vs below-ground plant components. Since plant nutrient acquisition is related to both plant phenology and nutrient availability (as reviewed by Nord & Lynch 2009), it follows that native habitat specialists may be better adapted to seasonal changes in nutrient availability in deciduous forests. Adaptations among specialist species to closed-canopy conditions may include relatively slow growth rates and low leaf nutrient levels during resource-limited intervals (Muller 2003; Sabatini et al. 2013). Local-scale nutrient fluctuations may not influence the distribution of generalists as strongly, since these plants tolerate a broader range of conditions and habitats than do specialist species (Pandit et al. 2009).

Further research is needed on the seasonality of nutrient capture for both specialist and generalist herbaceous layer species.

Although a large amount of variability among plots/sites within both forest types precluded our ability to distinguish these differences statistically ($\alpha = 0.05$), estimated total biomass, C, N and P were 20–34% higher in spring, 16–24% higher in summer and 27–47% higher in autumn in state preserve forests compared to urban park forests. On a per-hectare basis, estimates for nutrient capture for both the state preserve and urban park forests were comparable to or higher than previous findings for other locations in both spring and summer. Data are generally not available for total nutrient content of the herbaceous layer in autumn. Although our estimates for that season were the lowest values we determined, they are still within the range of values previously reported elsewhere for samples collected earlier in the growing season. For example, our estimates for total N content between 8.9 $kg \cdot ha^{-1}$ (urban park sites in autumn) and 21.0 $kg \cdot ha^{-1}$ (state preserve sites in spring) are comparable to earlier reports for suites of four to six species that contained between 5.5 and 10.6 $kg \cdot ha^{-1}$ in spring (Blank et al. 1980; Peterson & Rolfe 1982; both studies conducted in Indiana). Values we report here are lower than earlier estimates for a different set of forest sites previously studied in Iowa, where estimated total N content was 35 $kg \cdot ha^{-1}$ in spring and 24 $kg \cdot ha^{-1}$ in summer (Mabry et al. 2008). However, the relatively high values determined in that study were attributed to unusual dominance of one site by a spring-growing and persistent species (*H. virginianum*) known to contribute disproportionately to both above- and below-ground biomass production (Mabry et al. 2008). Nutrient capture for that site is the highest we are aware of among previously reported estimates.

Although we found that above-ground biomass was generally lower in autumn (similar to findings of Tremblay & Larocque 2001), below-ground biomass quantities and nutrient concentrations contribute to important nutrient storage by the herbaceous layer at that time. For example, our estimate of 16.7 $kg \cdot ha^{-1}$ for total N content in state preserve forests in autumn is higher than summer means for the same systems and points toward the important role of the herbaceous layer in nutrient capture late in the growing season. Based on our plot surveys, some spring-growing species were still present and produced a second flush of growth in autumn, supporting earlier findings on the potential role of these species (Vymazalová et al. 2012). The significant difference in N storage between state preserve (16.7 $kg \cdot ha^{-1}$) and urban park (8.9 $kg \cdot ha^{-1}$) forests may be related to the qualitative differences we observed in herbaceous layer composition between these forest types, and suggests that there may be opportunities to increase ecosystem services by restoring key species to degraded forest herbaceous communities where they are absent (Mabry et al. 2008; Gerken et al. 2010).

The relative scarcity of previous reports documenting late autumn herbaceous plant community characteristics may be related to the logistical challenges of locating individual plants or species that senesce early (knowing where to dig if above-ground plant parts are absent), and/or being able to identify individual plants if necessary (for single-species studies) by the root structures alone. However, the method we used allowed us to examine biomass, C and nutrient capture for the entire herbaceous community, regardless of late emergence or early senescence, using surveys and harvests of quadrats including both above- and below-ground plant tissue in each season.

Although we detected a decline in soil N concentration and quantity in urban park forests from spring to summer/autumn, this did not appear to be consistently linked to changes in herbaceous plant tissue nutrient storage, supporting the assertion that relationships between soil nutrient availability and plant nutrient concentrations are less obvious under field conditions than in experimental studies (Muller 2003). In addition, although soil P was higher in urban park forests than in state preserve forests in both spring and summer, there was no corresponding significant difference in total herbaceous plant tissue P between these forest types. These systems may be saturated with P, and plants are unable to take up any more available P (Gerken Golay et al. 2013).

Soil and herbaceous plant C and nutrient ratios indicate that seasonal patterns are important to our understanding of nutrient limitations in plants. Generally, our results show lower above- and below-ground C:N and C:P ratios in spring and autumn, this indicates that tissue content is proportionally higher for N and P at those times than it is in summer. Conversely, N:P ratios were generally highest in the spring and autumn. Following senescence, spring and autumn plant tissues would be expected to have higher decomposition rates and promote more rapid cycling of nutrients. The N:P ratios reported here are generally low compared to other studies, and may indicate N limitations to plant growth on both state preserve and urban park sites (Güsewell 2004). We are not aware of other studies that have assessed understorey herbaceous plant above- and below-ground C, N and P across multiple seasons. Urban park forests also had lower soil C:N ratios in spring compared to summer and autumn, possibly a result of more N mineralization during early summer (e.g. Nadelhoffer et al. 1984). In an earlier comparison of C:N ratios in surface soils under young managed and mature mixed oak forests in Ohio, Small & McCarthy (2005) found that spring C:N ratios were lower than summer C:N ratios. This finding is similar to our results for urban park forests. We

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are not aware of other studies for which soil C, N and P were measured multiple times across the growing season for forested sites.

Generally, ratios of C:N were higher in urban park forests for above-ground (spring and autumn) and below-ground (spring and summer) plant materials, indicating higher N in plant tissue relative to C in state preserve forest herbaceous vegetation. Spring N:P ratios were higher in state preserve forests, again indicating a relatively high amount of N in herbaceous vegetation relative to P in those forests. Thus, urban park forests may be more N-limited during spring than are state preserve forests (Güsewell 2004). Similar to patterns observed for vegetation, urban park soils had higher C:N ratios in summer, and lower N:P ratios in spring, indicating that losses of N through mineralization or other means are generally larger in urban park forests. Our soil C:N ratios are slightly less than the mean of 14.5 reported for a recent synthesis of forest studies (Cleveland & Liptzin 2007) but are certainly within the range of variation. We are not aware of other studies that compare urban forest soil elemental ratios to those of preserved or reference forests.

Many of the findings we report here (autumn above- and below-ground herbaceous nutrient levels, seasonal soil comparisons and soil element ratio comparisons across forest types) are novel and as such offer a challenge for comparison to other systems. We acknowledge that individual plants are complex in their phenology and nutrient dynamics and that biogeochemical cycling at the landscape scale for entire plant communities will require additional rigorous study. Further investigations in disturbed and preserved forest systems will likely offer additional insights and context for understanding how plant and surface soil nutrient cycles interact across seasons.

Understanding the composition and function of forest communities that are critical for preservation of biodiversity and provision of nutrient cycling and storage in highly altered landscapes is important to allow development of proactive management and conservation strategies. Furthermore, as landscapes change, it is vital to understand how to mitigate changing conditions such as urbanization and climate change. In particular, our results show the importance of forest herbaceous layers that contain diverse communities of native perennial species for terrestrial nutrient capture throughout the growing season, which is especially important in early spring and late autumn in highly altered landscapes such as those of the agricultural landscapes of the Midwest.

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References

Aerts, R. 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology* 84: 597–608.

Alban, D.H. 1971. *Effect of fertilization on survival and early growth of direct-seeded Red Pine*. United States Department of Agriculture, Forest Service, North Central Forest Experiment Station [Research Note NC-117], St. Paul, MN, US.

Anderson, W.B. & Eickmeier, W.G. 2000. Nutrient resorption in *Claytonia virginica* L.: implications for deciduous forest nutrient cycling. *Canadian Journal of Botany* 78: 832–839.

Attiwill, P.M. & Adams, M.A. 1993. Tansley review No. 50: nutrient cycling in forests. *New Phytologist* 124: 561–582.

Baeten, L., Hermy, M., Van Daele, S. & Verheyen, K. 2010. Unexpected understorey community development after 30 years in ancient and post-agricultural forests. *Journal of Ecology* 98: 1447–1453.

Blank, J.L., Olson, R.K. & Vitousek, P.M. 1980. Nutrient-uptake by a diverse spring ephemeral community. *Oecologia* 47: 96–98.

Bray, R.H. & Kurtz, L.T. 1945. Determination of total, organic and available phosphorus in soil. *Soil Science* 59: 39–45.

Cameron, G.N., Culley, T.M., Kolbe, S.E., Miller, A.I. & Matter, S.F. 2015. Effects of urbanization on herbaceous forest vegetation: the relative impacts of soil, geography, forest composition, human access, and an invasive shrub. *Urban Ecosystems* 18: 1051–1069.

Cleveland, C.C. & Liptzin, D. 2007. C:N: P stoichiometry in soil: is there a "Redfield Ratio" for the microbial biomass. *Biogeochemistry* 85: 235–252.

DeCandido, R. 2004. Recent changes in plant species diversity in urban Pelham Bay Park, 1947–1998. *Biological Conservation* 120: 129–136.

Drayton, B. & Primack, R. 1996. Plant species lost in an isolated conservation area in metropolitan Boston from 1894 to 1993. *Conservation Biology* 10: 30–39.

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N. & Wickham, J. 2011. Completion of the 2006 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering & Remote Sensing* 779: 858–864.

Gerken Golay, M.E., Thompson, J.R., Mabry, C.M. & Kolka, R.K. 2013. An investigation of water nutrient levels associated with forest vegetation in highly altered landscapes. *Journal of Soil and Water Conservation* 68: 361–371.

Gerken, M.E., Thompson, J.R. & Mabry, C.M. 2010. Restoring nutrient capture in forest herbaceous layers of the Midwest. *Ecological Restoration* 28: 14–17.

Gilliam, F.S. 2006. Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology* 94: 1176–1191.

Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57: 845–858.

Gilliam, F.S., Hockenberry, A.W. & Adams, M.B. 2006. Effects of atmospheric nitrogen deposition on the herbaceous layer of a Central Appalachian hardwood forest. *Journal of the Torrey Botanical Society* 133: 240–254.

Gleason, H. & Cronquist, A. 1991. *Manual of the vascular plants of northeastern United States and adjacent Canada*, 2nd edn. The New York Botanical Garden, Bronx, NY, US.

Güsewell, S. 2004. N: P ratios in terrestrial plants: variation, and functional significance. *New Phytologist* 164: 243–266.

Hamberg, L., Malmivaara-Lamsa, M., Lehvavirta, S., O'Hara, R. & Kotze, D. 2010. Quantifying the effects of trampling and habitat edges on forest understory vegetation – a field experiment. *Journal of Environmental Management* 91: 1811–1820.

Hyngstrom, S., Garabrandt, G. & Vercauteren, K. 2011. Fifteen years of urban deer management: the Fontanelle Forest experience. *Wildlife Society Bulletin* 35: 126–136.

Lapointe, L. 2001. How phenology influences physiology in deciduous forest spring ephemerals. *Physiologia Plantarum* 113: 151–157.

Lenière, A. & Houle, G. 2009. Short-term responses of the understory to the removal of plant functional groups in the cold-temperate deciduous forest. *Plant Ecology* 201: 235–245.

Mabry, C.M., Gerken, M.E. & Thompson, J.R. 2008. Seasonal storage of nutrients by perennial herbaceous species in undisturbed and disturbed deciduous hardwood forests. *Applied Vegetation Science* 11: 37–44.

Mahaney, W.M., Smemo, K.A. & Gross, K.L. 2008. Impacts of C_4 grass introductions on soil carbon and nitrogen cycling in C_3-dominated successional systems. *Oecologia* 157: 295–305.

McKinney, M. 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems* 11: 161–176.

Meier, A., Bratton, S. & Duffy, D. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecological Applications* 3: 935–946.

Moffatt, S., McLachlan, S. & Kenkel, N. 2004. Impacts of land use on riparian forest along an urban–rural gradient in southern Manitoba. *Plant Ecology* 174: 119–135.

Muller, R. 1978. The phenology, growth, and ecosystem dynamics of *Erythronium americanum* in the northern hardwood forest. *Ecological Monographs* 48: 1–20.

Muller, R. 2003. Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In: Gilliam, F. & Roberts, M. (eds.) *The herbaceous layer in forests of eastern North America*, pp. 15–37. Oxford University Press, New York, NY, US.

Muller, R.N. & Bormann, F.H. 1976. Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. *Science* 193: 1126–1128.

Murphy, S.J. & McCarthy, B.C. 2014. Temporal change in the herbaceous understory community of an old-growth forest: from seasons to decades. *Plant Ecology* 215: 221–232.

Nadelhoffer, K.J., Aber, J.D. & Melillo, J.M. 1984. Seasonal patterns of ammonium and nitrate uptake in nine temperate forest ecosystems. *Plant and Soil* 80: 321–335.

Nord, E.A. & Lynch, J.P. 2009. Plant phenology: a critical controller of soil resource acquisition. *Journal of Experimental Botany* 60: 1927–1937.

Pandit, S.N., Kolasa, J. & Cottenie, K. 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology* 90: 2253–2262.

Peterson, D.L. & Rolfe, G.L. 1982. Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. *The American Midland Naturalist* 107: 325–339.

Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany* 82: 1273–1283.

Robinson, G.R., Yurlina, M.E. & Handel, S.N. 1994. A Staten Island flora: ecological correlates of species losses and invasions. *Bulletin of the Torrey Botanical Club* 121: 119–129.

Rothstein, D.E. & Zak, D.R. 2001. Relationships between plant nitrogen economy and life history in three deciduous-forest herbs. *Journal of Ecology* 89: 385–394.

Sabatini, F.M., Burton, J.I., Scheller, R.M., Amatangelo, K.L. & Mladenoff, D.J. 2013. Functional diversity of ground-layer plant communities in old-growth and managed northern hardwood forests. *Applied Vegetation Science* 17: 398–407.

Scavia, D., Justic, D. & Bierman, V. 2004. Reducing hypoxia in the Gulf of Mexico: advice from three models. *Estuaries* 27: 419–425.

Small, C.J. & McCarthy, B.C. 2005. Relationship of understory diversity to soil nitrogen, topographic variation and stand age in an eastern oak forest, USA. *Forest Ecology and Management* 217: 229–243.

Tremblay, N.O. & Larocque, G.R. 2001. Seasonal dynamics of understory vegetation in four eastern Canadian forest types. *International Journal of Plant Sciences* 162: 271–286.

Vergutz, L., Manzoni, S., Porporato, A., Novais, R.F. & Jackson, R.B. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecological Monographs* 82: 205–220.

Vymazalová, M., Axmanová, I. & Tichý, L. 2012. Effect of intra-seasonal variability on vegetation data. *Journal of Vegetation Science* 23: 978–984.

Whigham, D.E. 2004. Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology, Evolution, and Systematics* 35: 583–621.

Whittaker, R.H., Likens, G.E., Bormann, F.H., Eaton, J.S. & Siccama, T.G. 1979. Hubbard Brook Ecosystem Study – forest nutrient cycling and element behavior. *Ecology* 60: 203–220.

Yarie, J. 1980. The role of understory vegetation in the nutrient cycle of forested ecosystems in the mountain hemlock biogeoclimatic zone. *Ecology* 61: 1498–1514.

Yorks, T.E. & Dabydeen, S. 1999. Seasonal and successional understory vascular plant diversity in second-growth hardwood clearcuts of western Maryland, USA. *Forest Ecology and Management* 119: 217–230.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Biomass, C, N and P concentration based on above-ground and below-ground herbaceous plant tissue from state preserve and urban park forests in spring, summer and autumn.

Appendix S2. Percentage nutrient content for C, N and P in above-ground and below-ground herbaceous plant material and soil compared across seasons for state preserve and urban park forests.