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An investigation of water nutrient levels associated with forest vegetation in highly altered landscapes

M.E. Gerken Golay, J.R. Thompson, C.M. Mabry, and R.K. Kolka

Abstract: Stream pollution by nutrient loading is a chronic problem in the Midwest, United States, and greater impacts on water quality are expected as agricultural production and urban areas expand. Remnant riparian forests are critical for maintaining ecosystem functions in this landscape context, allowing water infiltration and capture of nutrients before they are lost from the system. Our objective was to identify linkages between riparian forest plant community composition and water quality in remnant forested headwater streams. We identified watersheds with embedded headwater streams in three land use categories: grazed, urban, and preserved. We assessed plant community composition and nutrient storage. We sampled the forest streams to monitor discharge rates and sediment, nitrogen (N), and phosphorus (P) loads. Herbaceous communities in preserved riparian forests had more native specialist species than urban or grazed sites. Plant N content was higher in preserved forests (17.6 kg ha^{-1} [15.7 lb ac^{-1}]) than grazed (12.5 kg ha^{-1} [11.2 lb ac^{-1}]) or urban forests (10.5 kg ha^{-1} [9.4 lb ac^{-1}]). Conversely, stream water total N delivery was higher in urban watersheds (0.043 kg $ha^{-1}d^{-1}$[0.038 lb $ac^{-1}day^{-1}$]) than preserved (0.026 kg $ha^{-1}d^{-1}$ [0.023 lb $ac^{-1}day^{-1}$]) or grazed watersheds (0.02 kg $ha^{-1}d^{-1}$ [0.018 lb $ac^{-1}day^{-1}$]). Stream water nitrate (NO_3-N) concentration and total P delivery were highest for streams in urban areas. The most pronounced differences for plant composition and stream discharge and pollutant loads were between preserved and urban forests. Seasonal patterns were variable. We detected a weak negative but seasonally important relationship between plant N content and stream water N. We did not detect a similar relationship for P, which may indicate saturation of this nutrient in the watershed system. Detailed knowledge about relationships between land use, plant community composition, and water quality outcomes could be used to target forest restoration efforts in landscapes highly impacted by humans.

Key words: ecosystem function—headwater—herbaceous layer—nutrient storage—water quality

Human land use has had far-reaching effects on natural systems. There is increasingly extensive and intensive pressure for arable land to produce food, fiber, and fuel (Secchi et al. 2008), which are then translocated globally, effectively decoupling natural cycles of water and nutrients. Likewise, the places where people live and work are expanding, with exurban sprawl and pressure intensifying due to growing populations in urban areas. This in turn leads to an increase in the importation and concentration of water and nutrients and disrupts ecosystem processes (Groffman et al. 2003; Bernhardt et al. 2008).

The Cornbelt region of the midwestern United States is an example of a landscape that has been highly altered for both agricultural and urban uses. In the Midwest, and Iowa in particular, increased levels of nutrients, specifically nitrogen (N) and phosphorus (P), which enter the system via application of fertilizers and atmospheric deposition, result in increased nutrient loading in waterways. In such landscapes, hydrological alterations that redirect water quickly off site can exacerbate nutrient loss to streams by reducing on-site storage and processing (Bernhardt et al. 2008).

Because of intense pressure on the land to maximize ecosystem services, "targeted conservation" that can be implemented without sacrificing highly productive land has become a goal for this region (Secchi et al. 2008). Such efforts could rely heavily on conservation of small remnants of natural ecosystems that still exist within this landscape matrix. However, there have been relatively few studies measuring the capacity of remnant systems to provide ecosystem services such as biogeochemical and hydrologic processing in a landscape context. The degree to which these native ecosystem remnants, and specifically, central hardwood forest remnants, still function to preserve biodiversity and maintain cycles of water and nutrients is not known.

In this agriculturally dominated landscape, on-farm woodlands can be important for conserving native plant diversity (Freemark et al. 2002). However, these forests are still part of a working landscape, and many continue to be used for income generation, including firewood harvest, timber production, and livestock grazing (Moser et al. 2009). Cattle grazing in forests can have negative impacts on both overstory and understory vegetation (Brown and Boutin 2009; Mabry 2002). Furthermore, grazing has been shown to alter hydrology and water quality through decreased infiltration, increased runoff, and increased concentration of nutrients in streams (Belsky et al. 1999).

Urban land use and increasingly exurban sprawl also degrade natural ecosystems, resulting in loss of native herbaceous species and an increase in nonnative and woody plants in the understory (DeCandido 2004). Various causes for vegetation changes have been implicated, including increased herbivory from concentrated white-tailed deer populations (Hygnstrom et al. 2011), pollution (Gilliam 2006), trampling (Hamberg et al. 2010), and altered hydrology (Bernhardt et al. 2008). A link between vegetation and

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hydrology also appears to be functionally significant. Changes to hydrology in urban areas include increased impervious surfaces, often leading to lowered water table levels and higher peak discharge events. This in turn leads to lower rates of nutrient accumulation in soil and greater nutrient loss during flashy peak flow events (Bernhardt et al. 2008). Research by investigators at the Baltimore Ecosystem Study site identified a link between lower urban water table levels and plant community composition (Groffman et al. 2002, 2003). These changes in hydrology occur as a result of human effects on vegetation, but it is unclear how this altered vegetation may feed back to exacerbate changes in hydrology.

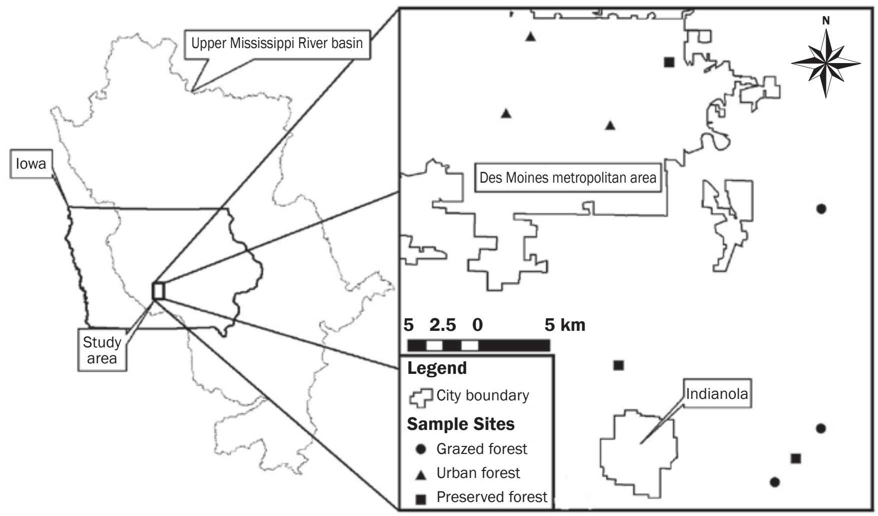
Numerous studies have indicated that shifts in forest community composition and diversity may occur as a result of intense and/or prolonged disturbance such as land use change (Flinn and Vellend 2005; Robinson et al. 1994; Drayton and Primack 1996), which affects the capacity to perform ecosystem services (Hooper et al. 2005). Experimental studies of vegetation diversity have shown that changes to community composition can alter ecosystem processes (Naeem et al. 1995). Specifically, a diverse native forest herbaceous layer can play an important role in seasonal storage of nutrients (Blank et al. 1980; Peterson and Rolfe 1982). Although it represents only a small portion (1%) of forest biomass, the herbaceous layer accounts for 20% of foliar litter, and it is high-quality litter that is cycled quickly (Gilliam 2007) and is thus an important part of seasonal nutrient cycles. Our previous work has shown that intact herbaceous layers in relatively undisturbed forests produce more biomass and are able to store more nutrients in spring than herbaceous layers in heavily disturbed forests (Mabry et al. 2008). This complex relationship between specific land uses, changes in community composition, the resulting temporal changes in nutrient retention, and the potential broader effects on water quality have not yet been documented for forests in the Midwest.

Central hardwood forests in the Midwest are biologically diverse, with a complex herbaceous understory that is important for seasonal nutrient storage (Peterson and Rolfe 1982; Mabry et al. 2008). Headwater streams embedded in these remnant hardwood forests play a critical role in water and nutrient cycling because of the tight coupling of terrestrial and aquatic processes in headwater streams (Gomi et al. 2002). These factors make remnant forested headwater streams an ideal setting for targeted efforts to protect both biodiversity and water quality in the Cornbelt. Quantification of the functional capacity of remnant forests to provide these ecosystem services and an understanding of the effects of intense human land use on their capacity to do so could inform targeted conservation efforts throughout the region.

In this study, we compared three forest land use types—preserved, grazed, and urban—to examine the impacts of land use on plant community composition and water quality in their associated headwater streams. Our study was guided by the following four hypotheses:

1. We expected understory vegetative communities in disturbed (grazed and urban) forests to have more nonnative and weedy generalist species than preserved forests.
2. We also expected understory communities in disturbed forests to have lower plant nutrient content than preserved forests.
3. We concurrently expected headwater streams embedded in disturbed forests to have higher stream nutrient concentrations and delivery.
4. Finally, we expected to find a link between plant community quality, plant nutrient content, and stream water nutrient levels, indicating that forests that retain high levels of nutrients in native herbaceous biomass will exhibit lower nutrient export.

Figure 1
Location of study area and sampling sites.



Materials and Methods

Study Sites. We conducted this study in the Lake Red Rock Watershed in central Iowa (figure 1). The area is dominated by agriculture, with remnant forests concentrated along streams and rivers, and is home to the largest urban area in the state, the Des Moines–West Des Moines metropolitan statistical area (estimated 2010 population of 572,000) (US Census Bureau 2011). The watershed is approximately 21,070 ha (52,043 ac) and is 42% row crop, 8% urban, 33% grassland/pasture/wetland, and 15% forest, as calculated from the National Land Cover Database of 2006 (Fry et al. 2011). Iowa as a whole is approximately 65% row crop, 3% urban, 23% grassland/pasture/wetland, and 8% forest (Fry et al. 2011). Despite recent declines in the practice, about 34% of woodlands in Iowa are grazed (USDA ERS 2012).

Historically, riparian areas with relatively high moisture and greater topographic relief served as refugia from fire for hardwood trees and associated species before settlement and were not appropriate for land use conversion postsettlement. On upland and sloped areas, these forests are characterized as mature oak-hickory forests and range in size from a few hectares in heavily urbanized areas to more than 100 ha (247 ac) in agricultural areas. We did not include bottomland hardwood forests that surround higher-order streams and broader floodplains in this study because they differ in both vegetation and site history of natural and human disturbance.

We identified nine research watersheds as experimental units, three each for urban,

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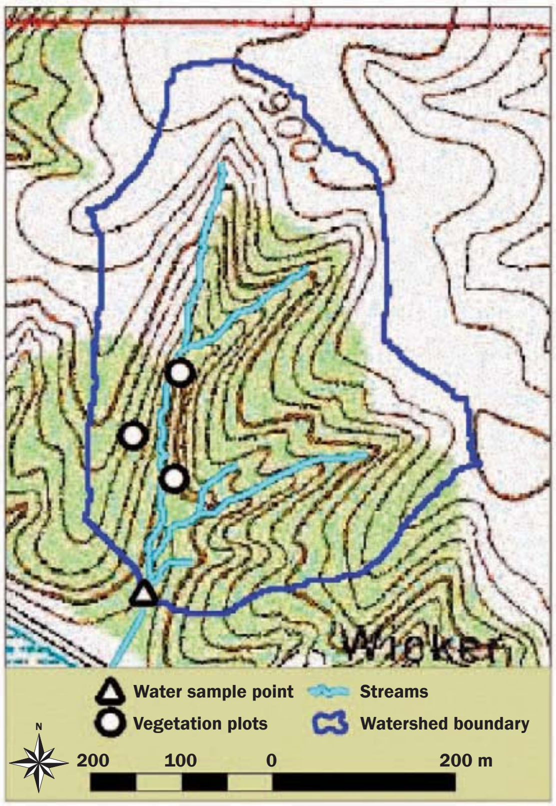
Figure 2

Location of vegetation plots (circles) in relation to the water sampling point (triangle) for one of our research watersheds. Example watershed in grazed land use with predominant forest (green) cover.



grazed, and preserved forest land use (figure 1). Urban forests were within the city matrix, grazed forests were within the agricultural matrix, and preserved forests were in both areas. In each watershed, the headwater stream was embedded in forest. We selected all sites according to the following criteria: the forest remnants were mature oak-hickory communities on uplands and slopes under the designated land uses of urban, grazed, or preserved. There was no harvest or other alteration to the stand for 30 years or more, and there was no discernible tile or artificial drainage in the watershed upstream of the stream sampling point. Sites were further limited to those that fit criteria for the three specific land use types: grazed sites were under current or recent cattle grazing, urban sites were part of the City of Des Moines Parks Department under a common general forest management plan, and preserved sites were all state preserves, with known and minimal disturbance histories as the best proxy available for natural conditions of these forests.

Plant and Soil Sampling. We visited sites in late winter of 2010 to establish a water sampling point on a straight reach of stream free of riffles and pools. To characterize the terrestrial community that drains to our sampling point, we used topographic maps to locate three 20 m^2 (215.3 ft^2) vegetation plots upstream of the water sampling point in the headwater watershed (figure 2) on upland and slope positions (previous work demonstrated the oak-hickory forest type dominates both landscape positions). We surveyed plots once each in spring, summer, and fall between 2010 and 2011 to characterize understory vegetation and herbaceous cover, and to identify trees and quantify canopy cover. These mature, perennial communities were not expected to vary significantly from year to year during the sampling period.

We identified a number of metrics that relate to phenology, species habitat affinity, and conservatism to calculate the contribution that specific life history traits make to overall plant community quality. We coded each species according to these species-quality metrics, as described in Mabry and Fratterigo (2009). The classifications of generalist or conservative species for the Iowa flora (Iowa State University Ada Hayden Herbarium 2004) were used to calculate average Iowa Coefficient of Conservatism for all species present and the average number of conservative herbaceous species in each plot. These metrics quantify habitat specialization (for closed-canopy or moist habitat) and, in conjunction with nativeness, phenology (early flowering), and habitat conservatism (Mabry et al. 2008) of each species, offer a detailed description of the quality of the plant community that can be compared among sites. This more detailed understanding of composition can reveal if certain traits are lost or favored as a result of land use change and thus identify gaps in functional roles, e.g., loss of spring-flowering herbs would indicate decreased nutrient capture early in the growing season (Mabry et al. 2008). Data were collected from three plots at each site to account for variation in vegetation within sites; we averaged these plots to give a single site mean for each metric each season.

After vegetation surveys were completed, we revisited plots to harvest biomass from three 0.25 m^2 (2.7 ft^2) quadrats randomly placed along a diagonal transect in the plot in each of three seasons (spring, summer, and fall). Harvest dates coincided with peak biomass production for suites of species that characterize each season. We identified species present and harvested all aboveground and belowground herbaceous plant material in each quadrat. We stored harvested plants in a cooler for transport and then rinsed them thoroughly with water, separated into roots and stems, and oven dried at 65°C (149°F) for 48 hours. We weighed the dried samples to estimate biomass and then ground them to pass a 20-mesh sieve using a Wiley mill. We analyzed total plant tissue concentration from each quadrat for total N (TN) according to standard combustion procedures using a LECO TruSpec Macro (LECO Corporation, St. Joseph, Michigan). We ashed samples using combustion for P analysis (Alban 1971). All plant nutrient analyses were conducted at the US Forest Service Northern Research Station, Grand Rapids, Minnesota.

We subsampled at the quadrat level to capture variation within plots and averaged the data to determine a mean measurement of biomass, N, and P per plot; data from plots were then averaged to obtain site means (our sampling unit for statistical analysis). We multiplied total plant biomass by the nutrient percentage for N and P, respectively, to calculate plant nutrient content. In this paper, we present combined aboveground and belowground nutrient content after converting to units of kilograms per hectare. Plant community and content variables presented at the site level for the nine watersheds allow for comparison with stream water data.

During harvest (each season), we also collected soil core samples in the center of each vegetation plot. We cold-stored the soil and then oven-dried it at 65°C (149°F) for 48 hours 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 N was determined by combustion using the LECO TruSpec Macro, and soil P was determined according to the Bray and Kurtz P-1 method (Bray and Kurtz 1945) at the US Forest Service Northern Research Station, Grand Rapids, Minnesota.

Stream Sampling. We assessed streams biweekly from April 16, 2010, through October 26, 2010, and from March 21, 2011, through October 16, 2011. We conducted in-stream measurements using a portable Hach HQ40d meter (Hach Company, Loveland, Colorado) to determine pH, dissolved oxygen, conductivity, and temperature, and an Oakton Model T-100 meter (Oakton Instruments, Vernon Hills, Illinois) to measure turbidity. We conducted stream gauging by recording channel width, depth, and flow rates with a Swoffer 2100 current velocity meter (Swoffer Instruments Inc., Seattle, Washington) or FLO-MATE 2000 Water Current and Flowmeter (Marsh-McBirney, Frederick, Maryland) at each sampling event to calculate discharge. Methods for measuring flow followed Rantz (1982). Because streams varied in width throughout the year, we divided them into one to six equally spaced segments during each sampling event and computed discharge based on the sum of areas for each segment multiplied by flow rate.

We collected in-stream grab samples during each sampling event to measure sediment, nitrate (NO_3-N), TN, and total P (TP). We stored samples in a cooler and processed them in the Riparian Management System laboratory in the Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa. Total suspended sediment was determined by filtration (Eaton et al. 2005). Sample processing and spectrophotometric analysis for NO_3-N followed Crumpton et al. (1992). Persulfate digestion of water samples for TN and TP analysis was performed using the method described by Gross and Boyd (1998).

We analyzed and report water sample nutrient concentrations. We also present nutrient delivery, calculated by multiplying concentration by stream discharge (L day^{-1}) and divided by the upstream watershed area (ha). Stream water data were collected over two years and combined to calculate seasonal means that corresponded with vegetation nutrient sampling dates.

Data Analysis. To compare vegetative communities, plant nutrient content, and stream water variables, each watershed was considered an independent sampling unit. Plant variables were subsampled and averaged across space, while stream water subsamples were averaged across time (to account for the variability of plant communities and nutrient content throughout a watershed as well as the variability of water metrics from week to week). Although statistically conservative, the means used to compare watersheds are robust and representative of average conditions. The result was a series of snapshots of each watershed for spring, summer, and fall.

We analyzed plant community data using Analysis of Variance (ANOVA) with land use type as the predictor variable and total species richness, number of nonnative species, average coefficient of conservatism, number of early flowering species, number of habitat specialists for moist or closed-canopy sites, or number of conservative species as the response variables. All analyses were done with JMP Version 9 software (SAS Institute Inc., Cary, North Carolina).

To explore trends in the plant and water nutrient data, we initially conducted principal component analyses (PCA). Variables in the N PCA were land use type, plant N content, soil percentage of N, total watershed area, water TN concentration, percentage forest cover of watershed, total number of species, and total cover of herbaceous plants. Variables in the P PCA were similar, but with P parameters instead of N. The PCA results (not presented) indicated that watershed size was a dominant variable influencing the distribution of sites in ordination space for N, so watershed size was included as a covariate in subsequent analyses. Watershed size was less important for P, but we chose to use comparable analytical models. Other environmental variables, such as slope, aspect, litter depth, and canopy cover, were not included in analyses because they had no effect.

Data exhibited a normal distribution, except when the standard deviation exceeded the mean (for discharge and TP delivery for preserved sites in spring and TP delivery for grazed sites in fall). Variances were equal (according to the Levene test for normally distributed data and the Brown-Forsythe test for nonnormal data) with the following exceptions: water TN concentration in spring and across seasons, TN delivery in fall, and TP delivery in fall and across seasons. We did not transform data because the effect was minimal with our small sample size. We set our accepted p-value as 0.1.

We used an Analysis of Covariance (ANCOVA) to control for the variation caused by watershed size and to allow examination of the effects of land use type; both were fixed effects. Response variables included plant biomass (kg ha^{-1}), plant N content (kg ha^{-1}), plant P content (kg ha^{-1}), soil percentage N, water NO_3-N concentration (mg L^{-1}), water TN concentration (mg L^{-1}), water TN delivery (kg ha^{-1}day^{-1}), soil P (mg kg^{-1}), water TP concentration (μg L^{-1}), water TP delivery (kg ha^{-1}d^{-1}), and sediment, (mg L^{-1}).

We used a second ANCOVA model to examine the link between understory plant characteristics and stream water parameters. We used the model described above, then added plant nutrient content as a predictor of water nutrient levels. The percentage improvement in the r^2 value reflects the influence of this additional predictor variable on each response variable; if this model improves by adding plant nutrients, it suggests a more direct link between plant and water nutrients. By subtracting the effects (the r^2 value) of the original model from this, we isolated the effects of plant nutrients on stream water nutrients. Finally, we examined the slope of the regression line for each of the components of the analytical model to determine if results support our hypothesis that nutrients stored in plant matter are held and not lost to streams. If our hypothesis is supported, we would expect a negative association, i.e., water nutrient concentra-

Table 1
Average number of species surveyed in plots in each of three land use types: urban, grazed, and preserved forests.

	Urban		Grazed		Preserved		Prob > F
Variable	Mean*	sd	Mean	sd	Mean	sd	
Total species	73a	5.8	75a	20.4	72a	6.9	0.8609
Nonnative species	8a	1.7	7a	6.9	3b	1.0	0.0412
Woody nonnative species	5a	1.6	2b	1.3	2b	0.8	<0.0001
Average Iowa Coefficient of Conservatism	4.06a	0.44	3.87a	0.15	4.37b	0.16	0.0036
Herbaceous species only	49a	7.0	56a	19.2	54a	6.2	0.4913
Nonnative herbs	2ab	1.2	5a	5.9	1b	0.3	0.0383
Early flowering herbs	18a	3.5	20a	6.1	22a	2.4	0.1944
Closed-canopy specialist herbs	24a	5.2	22a	4.8	30b	3.7	0.0041
Moist habitat specialist herbs	25a	5.9	28ab	7.6	33b	4.2	0.0312
Conservative herbaceous species	8a	3.2	8a	1.9	11b	1.7	0.0269

* Means with the same letter in a given row do not differ.

tions and delivery decrease linearly as plant nutrient increases.

Results and Discussion

Vegetative Community. Although overstory composition was similar (oak-hickory) for all sites, we detected differences in understory communities between land use types. Land use types did not differ in total plant species richness or in richness of herbaceous plants, however, a greater proportion of plants in grazed and urban sites were nonnative species (table 1). Urban sites had more woody nonnative species such as privet (*Ligustrum vulgare* L.), burning bush (*Euonymus alatus* [Thunb.] Siebold), and winter creeper (*Euonymus fortunei* [Turcz.] Hand.-Maz.) while grazed sites had more herbaceous nonnative species such as orchard grass (*Dactylis glomerata* L.), timothy (*Phleum pratense* L.), and clover (*Melilotus alba* (L.) Lam.; *Trifolium* spp. L.). These species likely reflect invasion by aggressive landscape plants in urban areas and seed introduction by cattle in grazed areas.

The species in grazed and urban forests also had lower average coefficients of conservatism compared to preserved forests (table 1). This metric indicates that there were more weedy species in disturbed forest types, versus more conservative plants in preserved sites. Conversely, plant communities in preserved sites were characterized by more herbaceous species that are habitat specialists for closed-canopy sites and for moist sites. Grazed and urban sites did not differ from each other for these metrics. Based on these metrics of community composition (table 1), preserved sites generally had more consistent community composition (lower standard deviation for each metric), while grazed sites were characterized by greater variability in herbaceous community characteristics. This difference between sites in standard deviation indicates that the impact of grazing is highly site dependent. Further, only one site was being actively grazed during our study, indicating that the practice can have legacy effects on the vegetation (Mabry 2002; Brown and Boutin 2009).

Taken together, these results show that preserved sites had higher floristic quality, as measured by four independent metrics, and more homogeneity within this land use type, as evidenced by low variability among sites. In particular, specialist and conservative species had patchier distributions in grazed sites, with more site-to-site variation. This indicates that land use change does not create a consistent response in forest understory vegetation, and other factors may affect the susceptibility or resiliency of a site. Our results corroborate what others have found related to human disturbance, that weedier and nonnative species may be better adapted to colonize disturbed sites (McIntyre and Lavorel 1994; Brown and Boutin 2009) because seeds are often wind or animal dispersed (McLachlan and Bazely 2001) compared to gravity- or ant-dispersed native herbaceous seeds (Bierzychudek 1982) and that species may be lost gradually over time (Foster 1992). In addition, recovery of herbaceous layer composition after human disturbance may be slow (Flinn and Vellend 2005), due to the limited dispersal of many native forest perennials (Bierzychudek 1982). On the whole, community resistance and resilience to disturbance is related to both the severity of the disturbance and time (Belote et al. 2012).

Plant and Soil Nutrient Content. Plant biomass of combined aboveground and belowground tissue was higher in preserved sites (marginally significant at p = 0.105; table 2). This translated into an average of 55% more plant N content and 46% more plant P content in herbaceous biomass in preserved sites compared to other land use types. In general, urban sites had a trend for lower plant N content in herbaceous biomass for each season (figure 3). Preserved sites consistently averaged 30% or more P content than other sites in each season (data not presented).

Soil N was highest in grazed sites (table 2), indicating that high plant N content on preserved sites was not linked to differences in soil fertility. This overall pattern held for summer and fall, but no differences were detected in spring. This could be due to the effect of animal grazing activity. Soil P was highest in urban sites, but there was no difference between preserved and grazed sites. This was the pattern for spring and summer, but sites did not differ in soil P in the fall. In simple regressions, soil P was predictive of plant P (r^2 = 0.124; p = 0.0712) but not water P (concentration or delivery).

While grazed and urban sites contained some individuals of herbaceous species that accumulate large amounts of biomass (particularly in the spring), the overall contribution of these plants to the nutrient storage capacity of the forest community was lower since they had 35% less biomass than communities in preserved sites (table 2). Thus, total number of species may not be as good an indicator of seasonal nutrient uptake capacity as biomass. It is important to note that preserved sites had higher plant N content

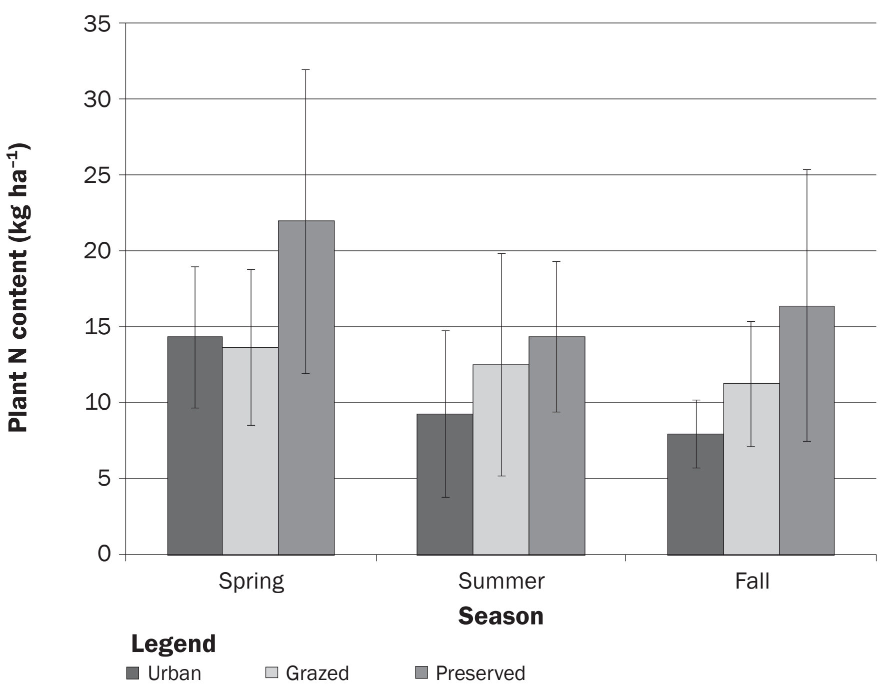
Journal of Soil and Water Conservation 68(5):361-371 www.swcs.org

Table 2
Analysis of covariance (ANCOVA) for test of significant differences among land use types and watershed sizes for nitrogen (N) and phosphorus (P) in herbaceous plants and headwater streams.

	Mean							
Variable	Urban	Grazed	Preserved	Effect	df	Mean square	F-ratio	Prob > F
Plant biomass (kg ha^{-1})	575.0	562.2	778.4	Land use type	2	148,903.3	2.4894	0.1050
				Watershed area	1	33,421.0	0.5587	0.4623
Plant N (kg ha^{-1})	10.5	12.5	17.6	Land use type	2	129.6	4.2783	0.0263
				Watershed area	1	31.6	1.0439	0.3175
Plant P (kg ha^{-1})	2.00	1.74	2.71	Land use type	2	2.33	3.2163	0.0587
				Watershed area	1	0.24	0.3358	0.5679
Soil %N	0.318	0.404	0.338	Land use type	2	0.0118	2.6228	0.0942
				Watershed area	1	0.0030	0.0676	0.7972
Water NO_3-N (mg L^{-1})	1.50	1.19	0.80	Land use type	2	1.80	3.9648	0.0338
				Watershed area	1	5.23	11.5316	0.0026
Water TN (mg L^{-1})	2.08	1.87	1.65	Land use type	2	1.16	2.3398	0.1199
				Watershed area	1	5.00	10.1109	0.0043
Water TN delivery (kg ha^{-1} day^{-1})	0.043	0.020	0.026	Land use type	2	0.0019	4.2576	0.0274
				Watershed area	1	0.0013	2.9690	0.0989
Soil P (mg kg^{-1})	40.49	18.01	26.68	Land use type	2	981.603	10.1320	0.0007
				Watershed area	1	5.890	0.0608	0.8074
Water TP (µg L^{-1})	207.8	174.5	180.4	Land use type	2	1,684.2	0.1819	0.8349
				Watershed area	1	1,733.1	0.1872	0.6695
Water TP delivery (kg ha^{-1} day^{-1})	0.005	0.002	0.003	Land use type	2	0.000019	2.8799	0.0775
				Watershed area	1	0.000000	0.0656	0.8003
Sediment (mg L^{-1})	47.6	33.1	56.4	Land use type	2	669.8	0.3330	0.7202
				Watershed area	1	289.9	0.1441	0.7077

Notes: NO_3-N = nitrate. TN = total N. TP = total P.

Figure 3
Average herbaceous plant total nitrogen (N) content for each land use type across all seasons. Error bars represent 95% confidence interval.



overall (table 2); this pattern was consistent across all seasons (figure 3).

Our previous work on a smaller number of sites also revealed patterns of higher average plant N content in herbaceous plants in spring (34.9 kg ha^{-1}[31.2 lb ac^{-1}]) and summer (24.2 kg ha^{-1}[21.6 lb ac^{-1}]) in preserved sites than disturbed sites in spring (12.2 kg ha^{-1} [10.9 lb ac^{-1}]) and summer (13.8 kg ha^{-1} [12.3 lb ac^{-1}]) (Mabry et al. 2008). Plant P content also followed a similar pattern in our previous study: nearly twice as high on average in preserved (3.75 kg ha^{-1} [3.35 lb ac^{-1}]) versus disturbed (1.80 kg ha^{-1} [1.61lb ac^{-1}]) forest sites (Mabry et al. 2008).

Plant nutrient content is largely driven by the amount of biomass present. In a similar oak-hickory understory in Illinois, nutrient content of spring herbs were 10.6 kg ha^{-1} (9.5 lb ac^{-1}) for N and 1.6 kg ha^{-1} (1.4 lb ac^{-1}) for P, and for summer herbs were 6.3 kg ha^{-1} (5.6 lb ac^{-1}) for N and 0.8 kg ha^{-1} (0.7 lb ac^{-1}) for P (Peterson and Rolfe 1982). In comparison, our nutrient values were higher, with an average of 16.6 kg ha^{-1} (14.8 lb ac^{-1}) for N and 2.2 kg ha^{-1} (2 lb ac^{-1}) for P in spring, and 12 kg ha^{-1} (10.7 lb ac^{-1}) for N and 2.4 kg ha^{-1} (2.1 lb ac^{-1}) for P in summer across land use types. This suggests that the forested areas we studied generally have higher nutrient levels than similar systems reported in the literature. In our study, fall N values were 11.9 kg ha^{-1} (10.6 lb ac^{-1}) and fall P values were 1.8 kg ha^{-1}(1.6 lb ac^{-1}). These values are within the range of, and occasionally exceed, summer nutrient contents (figure 3). This is novel information; in our search of the literature, we did not find reports that included nutrient data for late-season plant communities. Nutrient capture by the herbaceous layer after tree leaf drop in the fall may be critical for retention of N and P in these systems. This is especially evident in preserved sites with an intact herbaceous community, where fall retention is of equal or greater importance than in summer.

Stream Water Nutrient Content. Overall, urban sites had the highest stream NO_3-N and TN concentration (mg L^{-1}; table 2). Total N varied somewhat seasonally, particularly for grazed sites (figure 4a). Urban sites also had the highest TN delivery (kg $ha^{-1}d^{-1}$; table 2) and showed that pattern for each season (figure 4b). In contrast, there were no consistent differences between grazed and preserved sites for TN concentration or delivery (table 2). Watershed area was related to TN concentration (p = 0.0043) and TN delivery (p = 0.0989), but this did not overshadow strong land use effects for these nutrient measures.

Although there were no differences in stream TP concentrations among land use types, urban streams had the highest TP delivery. Sediment concentrations did not differ among land use types (table 2). In contrast with TN, watershed area did not influence TP concentration or delivery. Across land use types, TP fluctuated seasonally. TP concentration was lower in spring (104 μg L^{-1} or ppb) than in summer (227 μg L^{-1} or ppb) and fall (238 μg L^{-1} or ppb), but TP delivery was higher in summer (0.005 kg ha^{-1} d^{-1} [0.004 lb ac^{-1} day^{-1}]) than in fall or spring (0.002 kg ha^{-1} d^{-1} [0.002 lb ac^{-1} day^{-1}]). Using soil P in the ANCOVA instead of watershed size improves the predictability of the model somewhat but not consistently, and it did not result in any changes to the patterns we found.

Our results for overall average TN concentration in stream water for all land use types were below the EPA reference condition for this ecoregion (table 3) (US EPA 2002), although concentrations occasionally exceeded this level during individual sea-

Figure 4

(a) Average stream water total nitrogen (TN) concentration for each land use type across all seasons. Dashed line represents US Environmental Protection Agency criteria for water quality in rivers and streams of 2.18 mg L^{-1}. Error bars represent 95% confidence interval. (b) Average stream water TN delivery for each land use type across all seasons. Error bars represent 95% confidence interval.

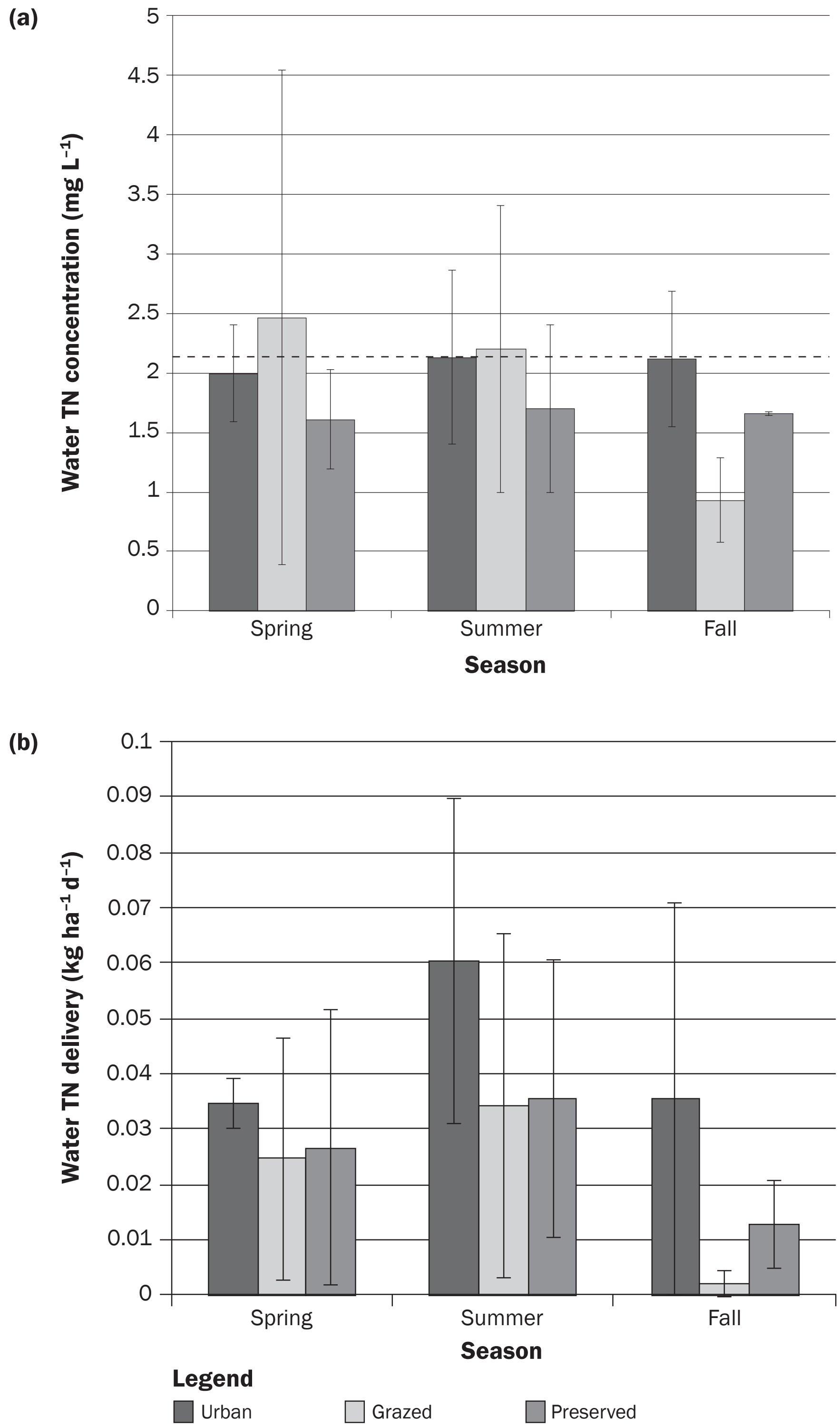


Table 3

Stream water nutrient concentrations and delivery from urban, agricultural (Ag), and reference (Ref) watersheds. Values were converted from published units for comparison or estimated from figures where noted.

	NO_3-N concentration ($mg\ L^{-1}$)			TN concentration ($mg\ L^{-1}$)			TN delivery ($kg\ ha^{-1}\ d^{-1}$)			TP concentration ($\mu g\ L^{-1}$)			TP delivery ($kg\ ha^{-1}\ d^{-1}$)		
Reference	**Urban**	**Ag**	**Ref**	**Urban**	**Ag**	**Ref**	**Urban**	**Ag**	**Ref**	**Urban**	**Ag**	**Ref**	**Urban**	**Ag**	**Ref**
EPA 2002	–	–	–	–	–	2.18	–	–	–	–	–	76.25	–	–	–
Corn Belt and Northern Great Plains Ecoregion VI; reference conditions for rivers and streams															
This study (Means [annual, seasonal])	1.50	1.19	0.80	2.08	1.87	1.65	0.043	0.020	0.026	207.8	174.5	180.4	0.005	0.002	0
9 forested watersheds: 3 each for urban, grazed (Ag), and preserved (Ref.); headwater basin size 4 to 285 ha in Des Moines, Iowa, area				Grazed varies seasonally; spring > summer > fall			Summer > fall or spring			Fall > summer or spring			Summer > fall or spring		
Clark et al. 2000 (Medians [annual])	–	–	0.087	–	–	0.26	–	–	0.0023*	–	–	22*	–	–	0.00023*
National baselines for undeveloped watersheds; Iowa not surveyed; basin size 10 to 270,000* ha															
Coulter et al. 2004 (Means [annual, seasonal])	0.52	1.57	–	–	–	–	–	–	–	340*	440*	–	–	–	–
3 watersheds: 1 each urban, ag (crop, pasture), mixed; totals 2,189* ha in Lexington, Kentucky, area	Spring > fall > summer									Land uses differed in seasonal peaks					
Sonoda et al. 2001† (Means [annual, seasonal])	1.33*	2.33*	–	–	–	–	–	–	–	100*	70*	–	–	–	–
2 watersheds: 1 each urban, ag (crop, nursery, rural); totals 14,200* ha in Portland, Oregon, area	Larger difference in wet season									Variable in wet and dry seasons					
Shields et al. 2008 (N); Duan et al. 2012 (P)† (Means [annual, seasonal])	1.50*	4.40*	0.05*	1.7*	4.8*	0.2*	0.016*	0.062*	0.003*	–	–	–	0.0023*	0.00067*	0.000077*
8 watersheds: multiple urban, 1 each ag (crop), reference (forested); basin size 8 to 16,400 ha in Baltimore, Maryland, area							Seasonal variation not significant						Summer > fall or spring		
Whittaker et al. 1979 (Means [annual])	–	–	–	–	–	–	–	–	0.0063*	–	–	–	–	–	0.000055*
6 watersheds: 1 reference forest approximately 13.3 ha in the Hubbard Brook Experimental Forest, New Hampshire															
Medalie et al. 2012 † (Flow-normalized means [annual])	–	–	–	–	0.9*	0.5*	–	0.011*	0.009*	–	100*	50*	–	0.0014*	0.00068*
18 watersheds; excerpt 1 example each of ag (crop, pasture) and reference (forested); basin size 12,900 to 270,400*ha in the Lake Champlain, Vermont and New York area															

Notes: NO_3-N = nitrate. TN = total nitrogen. TP = total phosphorus.

* Denotes conversion from published units for comparison here

† Values estimated from figures

sons (figure 4a). Concentrations of TP in streams greatly exceeded the EPA reference conditions (table 3). It should be noted that headwater streams, especially those in forested watersheds, may differ from the rivers and streams sampled for development of these criteria because of different in-stream nutrient processing (Ice and Binkley 2003). According to baseline levels established for undeveloped watersheds across the country, concentrations and yields of N and P were highest in parts of the Midwest (Clark et al. 2000). Furthermore, Clark et al. (2000) showed that total nutrients in undeveloped basins rarely exceeded 1 mg L^{-1} (ppm) for TN and 100 µg L^{-1} (ppb) for TP, but that there were a significant portion of impaired streams in basins influenced by urbanization and agriculture. Annual means measured for all land use types, including preserves where the entire watershed is undisturbed forest, exceeded these baselines by 60% to 100%. This may be because all of the watersheds included in our study are embedded in a matrix of very intensive human land use with significant additions of N and P at a landscape scale and over a long period of time.

Studies in other regions have also compared agricultural watersheds (pasture, cropping, and nursery production) with urban sites (table 3). In some studies, urban areas had lower stream NO_3-N concentrations than in agricultural areas (Coulter et al. 2004; Sonoda et al. 2001) or were between the extremes of intensive agriculture and intact reference sites (Shields et al. 2008). Our study shows urban areas had the highest TN concentrations. One explanation for the variability among studies is the obvious differences in type and intensity of agricultural land use and urban development. Baltimore, Maryland (Shields et al. 2008), Lexington, Kentucky (Coulter et al. 2004), and Portland, Oregon (Sonoda et al. 2001) are larger, more heavily urbanized cities than Des Moines, and the agricultural land uses in those studies were more intensive than the cattle grazing in our study. Other factors, such as background levels of nutrients, may be more strongly influenced by natural factors in undeveloped watersheds (e.g., decomposition rates, local N deposition rates) rather than anthropogenic inputs (Clark et al. 2000), leading to variability among different study regions.

We did not find consistent patterns across site types for TP in streams. The reason may be that controls on TP retention and transport can be difficult to tease apart. Contrary to our findings, watershed size was related to TP concentration in Kansas (Banner et al. 2009). TP has been shown to correlate with suspended solids in some cases (Wall et al. 1996) and not in others (Coulter et al. 2004). In a comparison of agricultural, urban, and mixed land use watersheds in Kentucky, researchers did not detect differences in TP among the watersheds (Coulter et al. 2004).

Other studies have found that TP concentrations in streams were higher in urban areas and linked to additional factors. In Oregon, urban land use was linked to higher P input to the stream (Sonoda et al. 2001), and soil chemistry influenced P levels in stream water. These researchers determined that P-saturated soil could not adsorb additional P and it was lost to the stream (Sonoda and Yeakley 2007). In addition to the importance of the source area on P transport to the stream, seasonal fluctuations in flow may mean that P concentrations may lag behind other watershed characteristics because sediment-bound P is deposited and resuspended repeatedly over time (Medalie et al. 2012). Further differences between our findings and those of other studies (table 3) may reflect differential nutrient inputs or land use pressures.

Understory Plant and Stream Water Linkages. In general, the comparison between preserved sites and urban sites suggests a tendency that when nutrient levels were high in plants, those nutrients were low in stream water, and vice versa (figures 3 and 4a). However, our hypothesis that we could identify a direct link between plant nutrient content and stream water nutrient loads did not hold across all land use types and seasons.

Table 4

R-squared values of the analysis of covariance (ANCOVA) with and without plant nutrient content included in the model. Percentage improvement of the model is indicated, with negative associations indicated with negative signs (–) and positive associations indicated with positive signs (+).

ANCOVA model	Land use type, watershed r^2	Land use type, watershed, plant nutrient content r^2	Land use type, watershed, plant nutrient content Improvement (%)
TN (mg L^{-1})			
Spring	0.947	0.947	0
Summer	0.587	0.800	–26.6
Fall	0.766	0.773	+0.8
Overall	0.347	0.351	–1.2
TN delivery			
Spring	0.420	0.675	+37.8
Summer	0.556	0.582	–4.4
Fall	0.465	0.522	–10.9
Overall	0.285	0.286	–0.4
TP(ppb)			
Spring	0.571	0.784	+27.2
Summer	0.137	0.177	+22.8
Fall	0.187	0.501	+62.7
Overall	0.035	0.077	+54.7
TP delivery			
Spring	0.205	0.389	+47.3
Summer	0.453	0.492	+7.9
Fall	0.410	0.497	–17.5
Overall	0.237	0.262	+9.8

Notes: TN = total nitrogen. TP = total phosphorus.

There was a weak but negative association between plant N and stream water TN concentration and delivery overall (table 4). In summer, 27% more of the variation of TN concentration and in fall 11% of TN delivery was explained by plant N content, suggesting a seasonally important link. In contrast, TN delivery in spring was positively associated with plant nutrient content; there was more N in plants, but there were also high levels of N in streamwater. One reason may be that when the system is saturated with nutrients, the ability of plants to absorb additional N reaches capacity and excess N may be lost from the system. Similarly, timing of N inputs may not be concurrent with timing of biomass demands (Sprague et al. 2011) or there may be a time lag in transport or detection of nutrients lost during periods of very low flow because of settling (Medalie et al. 2012).

Phosphorus shows largely positive associations for water concentration and delivery; when plant P was high, water P was high. This did not follow the patterns we expected to see for forest herbaceous plant-stream water relationships, but it supports the hypothesis that P is lost to streams when soils (and plants) are saturated (Sonoda and Yeakley 2007). Few studies have been able to make clear linkages for P with vegetation (Siccama et al. 1970) and land use because soil chemistry (Clark et al. 2000; Sonoda and Yeakley 2007), discharge (Banner et al. 2009), groundwater, and seasonality (Sonoda and Yeakley 2007) may all interact.

Several ecosystem studies have developed budgets for nutrient pools and fluxes as in the Hubbard Brook Experimental Forest (Whittaker et al. 1979) and the Baltimore Ecosystem Study (Groffman et al. 2004), but none have tested the functional role of biomass in relation to water quality. A clear relationship between plant communities and stream metrics for each land use type—preserved, grazed, and urban—in our study was not discernible. In general, we observed a trend for higher N storage rates in herbs concurrent with lower stream nutrient concentrations and delivery. The reverse was also true: when more N was in stream water, less was stored in herbaceous biomass. In contrast, there was increased P in streams when there was more of the nutrient in the system. This may be a result of groundwater conditions (Sonoda et al. 2007), which we did not measure, or a number of other system inputs. Precipitation fluctuations impacting stream flow and a potential threshold at which system response changes may also be factors influencing the trends we see (Banner et al. 2009). This is the case in the urban streams that may have less watershed-level infiltration and experience a greater proportion of their nutrient export during high-flow events in comparison to preserved sites (Shields et al. 2008).

While intact ecosystems are often resilient to naturally occurring fluctuations in nutrient inputs, anthropogenic inputs of N and P may be more than the system can process. For instance, in light-limited understory conditions, shaded herbaceous plants have low nutrient saturation points (Anderson and Eickmeier 1998) and are therefore limited in their ability to absorb excess nutrients. Furthermore, even though intact sites in our study are characterized by early spring-growing species, fall application of fertilizers in the surrounding agricultural landscape is "out of sync" with peak biomass growth (Sprague et al. 2011) and the functional capacity of vegetation to capture N and P. Thus, natural limitations of the system as well as human alterations may explain why we did not find a close coupling of plant and stream water nutrients.

Summary and Conclusions

This study confirms the link between land use, plant community composition, and plant nutrient content across a large number of sites, including urban forests. Sites with more intensive human land use have been associated with fewer herbaceous perennials, suggesting lower nutrient storage and cycling function. The forest herbaceous community plays a vital role in the complex relationships of a functional ecosystem, but its sensitivity to human land use has important implications for hydrologic and nutrient cycling.

While we were able to detect clear land use effects for a number of plant community metrics, plant nutrient content characteristics, and three of four stream-water nutrient metrics, not all metrics followed expected patterns. We were not able to fully explain storage and movement of P in these systems; nor were we able to identify a specific link between herbaceous plant communities and stream water nutrient export. We theorize this may be due to nutrient overenrichment at the landscape scale, especially with respect to P.

Preserved sites were associated with lower stream water nutrient content overall, grazed sites were variable, and urban sites were associated with higher overall stream water nutrient levels. The contrast between preserved and urban sites in terms of vegetation and water quality points to urban areas as an ideal setting for targeted conservation and restoration of native understory plants in areas degraded by intense land use. Increasing understory biomass in depauperate systems could lead to increased storage of nutrients such as N and prevent their loss to stream water.

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