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Beaver pond biogeochemical effects in the Maryland Coastal Plain

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Abstract. The fluxes and concentrations of materials from two contiguous second-order watersheds in the Coastal Plain of Maryland, U.S.A. were measured for six years prior to and six years subsequent to the formation of a 1.25 ha beaver pond near the bottom of one of the watersheds. The watersheds have a clay aquiclude and were equipped with V-notch weirs and continuous volume-integrating water samplers. The beaver pond reduced annual discharge of water, total-N, total-P, dissolved silicate, TOC, and TSS by 8, 18, 21, 32, 28, and 27%, respectively. Most of the total-N reduction was due to increased retention of nitrate in the winter and spring and TON in the winter and summer. Most of the total-P reduction was the result of retention of both TPi and TOP in the winter and summer. Dissolved silicate retention peaked in the spring, while TOC and TSS retention peaked in the winter. Prior to the formation of the beaver pond, concentrations of TON, TPi, TOP, TOC, and TSS had highly significant correlations with stream discharge, especially in the winter, but subsequent to the pond there was little or no relationship between these concentrations and stream discharge. However, concentrations of nitrate in the spring and ammonium in the summer were highly correlated with stream discharge both before and after the formation of the beaver pond and regressions of discharge versus concentrations of these nutrients explained more of the variation in concentrations after the formation of the pond.

Beaver (*Castor canadensis*) were an abundant and important part of the landscape in eastern North America at the time of European settlement in the 15th and 16th centuries, but were extirpated over much of their range for their fur (Naiman et al. 1988). The Coastal Plain of Maryland was among the many regions where beaver populations were extirpated. In the 1970's the U.S. Fish & Wildlife Service reintroduced beaver to the Coastal Plain of southern Maryland and beaver populations have subsequently increased rapidly. What are the biogeochemical effects of this beaver reintroduction on the streams of the Coastal Plain? While the landscape effects of beaver populations on the biogeochemistry of the Minnesota region have been explored in considerable detail (e.g. Johnston & Naiman 1987; Johnston et al. 1995; Naiman et al. 1994), the effects of a renewed beaver population in the Coastal Plain may be somewhat different.

A series of studies of input/output balances for beaver ponds in other parts of North America have yielded results which allow one to make some limited generalizations. Beaver ponds in the Adirondacks of New York, central Ontario, and Wyoming all utilized nitrate (Cirmo & Driscoll 1993, 1996; Devito et al. 1989; Maret et al. 1987). The Adirondacks pond also utilized silicate (Cirmo & Driscoll 1993, 1996) and, during high flows, the Wyoming beaver pond retained total-P, TKN, TSS, and alkali-extractable phosphate (Maret et al. 1987). These results are understandable. Beaver ponds are shallow, sunny places where periphyton and plankton might be expected to take up nitrate, silicate, and phosphate. They are also areas of relatively low water currents where sediments along with their nutrient contents can settle to the bottom.

The beaver pond in the Adirondacks also exported DOC and ammonium (Cirmo & Driscoll 1993, 1996; Smith et al. 1991). One of the two ponds studied in Ontario exported ammonium and both exported TON (Devito et al. 1989). Exports of ammonium and TON could be due to the assimilation of nitrate and releases of reduced forms of nitrogen and DOC exports could be the result of primary production within the pond.

No net retention or export of DOC, total-P, or total-N were detected for the beaver ponds in Ontario (Devito et al. 1989), although they seemed to retain these nutrients in the summer/fall period and release them in the winter/spring period. Also, no net retention or export of DOC or POC were found for a beaver pond in Quebec (Naiman et al. 1986).

These studies may have missed other significant biogeochemical effects of beaver ponds due to; (a) the lack of continuous volume-integrated sampling, (b) inadequate hydrologic data, and (c) failure to measure all forms of the nutrients. In many stream systems the concentrations of nutrients change rapidly, especially during storm events (e.g. Correll et al. 1999d). Most of the beaver pond studies cited above relied upon rather infrequent spot sampling. Most did not continuously measure water discharge. None measured all of the major forms of carbon, nitrogen, and phosphorus, although Naiman et al. (1986) measured both DOC and POC.

When beavers constructed a dam in September, 1990, on one of our long-term Rhode River watershed study sites, it presented an opportunity to document in detail the biogeochemical effects of the beaver pond. Both this watershed (#101) and a contiguous watershed (#102) of similar size, slope, and land use, but with no beavers, have long been equipped with V-notch weirs and volume-integrating flow-proportional water samplers. Both water-

Table 1. Characteristics of Rhode River watersheds.

Watershed	Area[1] (ha)	Mean Slope[2] (%)	Mean Discharge[3] (mm/yr)	Land Use [1](%)				
				Forest	Row Crops	Pasture & Hay Fields	Residential & Roads	Old Fields & Fallow
Beaver Pond	226	7.2	337	49	2	21	14	14
Control	192	6.3	290	52	8	17	13	10

[1] The mean of ground truth surveys in 1990 and 1993.
[2] Correll and Dixon (1980).
[3] Correll et al. (1999b).

sheds have effective aquicludes that allow the sampling of both surface and groundwater discharges at the weirs. Fluxes of a wide range of nutrients have been measured continuously for a period of six years prior to and six years subsequent to the introduction of the beaver pond on watershed 101. This allows us to compare water discharges, and nutrient and sediment discharges on watershed 101 before and after the beaver pond, and to make a paired comparison between watersheds 101 and 102 for the entire 12 years to rule out effects of interannual weather variation (e.g. Correll et al. 1999 a, b, c). Hereafter we will refer to watershed 101 as the beaver pond watershed and watershed 102 as the control watershed or simply the control.

Materials and methods

Research site

The research area (described more fully in Correll et al. 1999a) is located within the Atlantic Coastal Plain of the U.S.A. in Anne Arundel County, Maryland (38°51′ N, 76°32′ W). Annual precipitation averages 1139 mm and temperature 13.2 °C (160 years; Correll et al. 1999b). The watersheds have sedimentary fine sandy loam soils. Bedrock is about 1000 m below the surface, but the Marlboro clay layer forms an effective aquiclude slightly above sea level throughout the area (Chirlin & Shaffner 1977). Therefore, each watershed has a perched aquifer, and overland storm flows, interflow, and groundwater discharges all move to the channel draining each watershed. The two watersheds have similar drainage areas, slopes, and land use (Table 1) and are drained by second order streams.

In the fall of 1990 beavers constructed a dam just above the weir on watershed 101, which created a pond that was maintained until the fall of 1996. The pond was an approximately round shape, with a total area of approximately

1.25 ha and a mean depth of about 0.5 m. The surface dimensions of the pond were determined with an optical range finder.

Sampling

The study period was from September 1984 through August 1996. Discharges of water from each watershed were measured with sharp-crested 120° V-notch weirs, whose foundations were in contact with the Marlboro clay aquiclude (Correll 1981). Each weir had an instrument building and a stilling well. Depths were measured to the nearest 0.3 mm with floats and counterweights and were recorded every 5 minutes for the beaver pond watershed and every 15 minutes for the control watershed.

Stream water samples were composited and volume-integrated for 7-d intervals, then collected and returned to the laboratory. A Stevens, model 61R, flow meter actuated the sampling of an aliquot once every 154 m^3 of flow. The sample water was drawn from the stream channel upstream of the weir and aliquots were deposited into two plastic containers, one pretreated with 20 ml of 18 N sulfuric acid to prevent biological or enzymatic activity during storage. Studies of the acid preservation found no detectable conversion of organic-P, -N, or -C to inorganic forms. After collection, samples were either analyzed immediately or stored at 4 °C.

Sample analysis

Total-P was determined by digestion of acid-preserved samples to orthophosphate with perchloric acid (King 1932). The phosphate in the digestate and in undigested aliquots was analyzed by reaction with stannous chloride and ammonium molybdate (APHA 1989). Total phosphate in the undigested, acid-preserved samples was the sum of dissolved and acid-extractable particulate phosphate. Total organic-P (TOP) was calculated by subtracting total phosphate from total-P. Total Kjeldahl N (TKN) was determined by digestion of acid-preserved samples to ammonium with sulfuric acid, Hengar granules, and hydrogen peroxide (Martin 1972). The ammonium in the digestate was steam distilled and analyzed by Nesslerization (APHA 1989). Ammonium was also determined in undigested aliquots by oxidation to nitrite with alkaline hypochlorite (Strickland & Parsons 1972) and analysis of the nitrite by reaction with sulfanilamide (APHA 1989). Ammonium was the sum of dissolved and acid-extractable particulate ammonium. Total organic-N (TON) was calculated by subtracting ammonium from TKN. The sum of nitrate and nitrite was measured by reducing nitrate to nitrite with cadmium amalgam, and analyzing nitrite by reaction with sulfanilamide (APHA 1989). Unpreserved samples were analyzed for orthosilicate (silicic acid) after filtration through prewashed Millipore 0.45 um filters. Prior to spring of 1991, samples were analyzed for silicate by reaction with ammonium molybdate and colorimetry (Strickland & Parsons 1972). Subsequently, samples were analyzed for silicate by reaction with ammonium molybdate in a Technicon Auto-Analyzer (method 696-82W). The concentration of total suspended solids (TSS) was measured by filtering unpreserved samples through prewashed, preweighed Millipore 0.45 um filters, drying at 60 °C, and reweighing. Total organic-C (TOC) was analyzed by drying samples at 60 °C, followed by reaction with potassium dichromate in 67% sulfuric acid at 100 °C for 3 h (Maciolek 1962). Organic C was calculated from the amount of unreacted dichromate measured colorimetrically (Mackiolek 1962; Gaudy & Ramanathan 1964).

Mass balance calculations

We estimated mean annual (Figure 3) and seasonal (Table 5) mass balances for the beaver pond over the six year period after it was built. Outputs in stream discharge from the beaver dam were measured directly at the watershed weir. Inputs of nitrogen from precipitation were also measured directly at a site on the same watershed, not far from the pond (Correll et al. 1994; Jordan et al. 1995). Inputs of materials into the pond from the watershed were estimated by multiplying control watershed fluxes during the six years subsequent to the beaver pond by linear regressions of weekly fluxes of materials from the beaver pond watershed versus control watershed fluxes during the six years prior to the beaver pond. All regressions were highly significant ($P < 0.00001$).

Results and discussion

Material concentrations

The beaver pond we studied had many significant effects on the nutrient dynamics of the stream draining this watershed. Paired comparisons between the beaver pond and control watersheds show that the water discharge from the beaver pond watershed was five percent higher than from the control watershed before the pond and three percent lower subsequently and both of these differences were highly significant (Table 2). A similar effect was reported by Burns and McDonnell (1998) for a beaver pond in the Adirondack Mountains of New York and was attributed to evaporation from the pond. At our site, average pan evaporation was 11.1, 15.7, and 9.9 mm per season for spring, summer and fall, respectively (Higman & Correll 1982). Simple

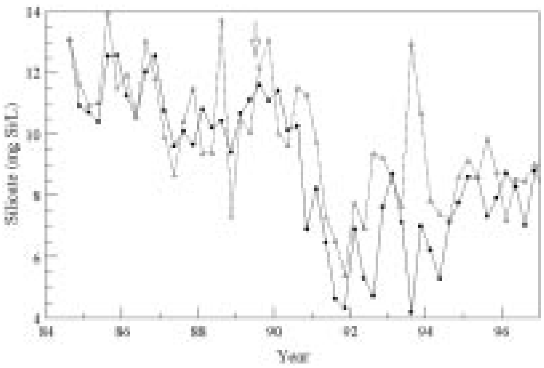

Figure 1. Time series of seasonal volume-weighted mean dissolved silicate concentrations for the beaver pond and control watersheds. An arrow indicates the fall of 1990, when the beaver pond was constructed. Solid circle data points and solid lines are for the beaver pond watershed and triangles and dashed lines are for the control watershed.

evaporation from the beaver pond surface would only account for 0.04, 0.6, and 0.14 percent of average stream flow from this watershed (Correll et al. 1999b). Much of the reduction in flow from the beaver pond may have been due to high evapotranspiration by the riparian forest fringing the pond. Such very high evapotranspiration rates were reported for another riparian forest at a nearby site (Peterjohn & Correll 1986).

Dissolved silicate concentrations from the beaver pond watershed were not significantly different from the control prior to the pond, but were only 69% of those from the control after the pond ($P < 0.0001$, Table 2). Volume-weighted mean seasonal concentrations of dissolved silicate from the beaver pond watershed prior to the pond were sometimes a little higher or lower than from the control (Figure 1). After the construction of the pond dissolved silicate from the beaver pond watershed was lower than from the control watershed almost every season (Figure 1). Cirmo and Driscoll (1993, 1996) reported silicate concentrations leaving a beaver pond in the Adirondacks were only 54% of the concentrations entering the pond. This reduction in dissolved silicate concentration was probably due to the growth of diatoms in the periphyton community of the large shallow beaver pond. The pond was shallow and exposed to full sunlight, an ideal habitat for periphyton growth.

TOC concentrations for the beaver pond watershed were 27% higher ($P = 0.02$) than those of the control watershed before the pond, but not significantly different after the pond, indicating a net consumption of TOC by the pond (Table 2). We presume that much of this reduction in TOC concentrations was due to the deposition of suspended particulates within the beaver pond and these particulates contained organic carbon. In contrast, a beaver pond in Quebec was reported to have no effect on TOC (Naiman et al. 1986), while a

Table 2. Comparisons between the beaver pond and control watersheds for six years of weekly data prior to and six years subsequent to establishment of a beaver pond. Probabilities for comparisons between watersheds prior to and subsequent to the beaver pond are from paired T-tests. Probabilities for whether the beaver pond watershed changed subsequent to the beaver pond are from general T-tests of differences between the watersheds before and after establishment of the pond.

Parameter (units)	Prior to Beaver Pond			Subsequent to Beaver Pond			Was the watershed changed significantly due to Beaver? (*P*)
	Beaver	Control	*P*	Beaver	Control	*P*	
Dischange (mm/wk)	5.26	5.03	0.007	5.44	5.61	0.03	0.0006
Nitrate (ug N/L)	194	395	< 0.0001	113	249	< 0.0001	0.09
Total NH_4 (ug N/L)	191	103	0.0008	406	180	0.04	0.82
TON (ug N/L)	640	563	0.02	601	632	0.92	0.09
TOC (mg C/L)	8.59	6.75	0.02	8.48	8.20	0.30	0.02
Total Pi (ug P/L)	160	169	0.23	201	199	0.74	0.41
TOP (ug P/L)	140	101	0.22	82	101	0.36	0.06
Dis. Silicate (mg Si/L)	10.9	11.1	0.21	7.67	11.1	< 0.0001	< 0.00001
TSS (mg/L)	67.6	47.7	0.03	49.3	56.6	0.25	0.01

beaver pond in the Adirondacks exported DOC (Smith et al. 1991; Cirmo & Driscoll 1996). Two ponds in Ontario retained DOC in the growing season, but exported the rest of the year (Devito et al. 1989).

TSS concentrations from the beaver pond watershed were 42% higher than from the control watershed before the pond (P = 0.03), but not significantly different subsequent to the pond (Table 2), indicating a net retention of TSS by the pond. This was not surprising since the pond was large enough to have a long retention time and very little current velocity. A beaver pond in Wyoming has also been shown to retain TSS, especially during high flows (Maret et al. 1987; Parker 1986).

Beaver pond watershed nitrate concentrations were lower and ammonium concentrations were higher than for the control both prior to and subsequent to the pond (Table 2). Comparisons of mean concentrations from the period before the beaver pond with the period after the pond illustrate the effects of variations in weather, even when the time periods are six years (Table 2).
To test directly for changes in water discharge or materials concentrations due to the beaver pond, we compared differences between weekly values for the beaver pond and control watersheds prior to and subsequent to the pond (Table 2). Overall, average water discharges were significantly reduced as a result of the pond. Nitrate and TON concentrations were lower after the pond, but the change was only marginal statistically (P = 0.09, Table 2) and there was no significant change in ammonium. Cirmo and Driscoll (1996) found a retention of nitrate and release of ammonium. TOC concentrations were significantly lower after the pond (P = 0.02, Table 2). Phosphate concentrations were not significantly different after the pond, but TOP concentrations were lower, although the change was only marginal statistically (P = 0.06, Table 2). Dissolved silicate and TSS concentrations were both significantly reduced (Table 2). The reductions in concentrations of TSS, TOC, TOP, and TON were probably due to sedimentation of suspended particulates along with their carbon, phosphorus, and nitrogen constituents. The small decline in nitrate was probably due to periphyton uptake and denitrification.

Regressions of beaver pond watershed seasonal weekly concentrations versus control watershed concentrations were often informative. Relationships that were significant prior to the beaver pond often either changed or were lost after the pond (e.g. Figure 2). For dissolved silicate there were highly significant linear regressions in the winter, but with different slopes and intercepts (Figure 2). However, in the spring, after the pond there was no significant relationship between silicate concentrations in the two watersheds. The summer and fall silicate concentration patterns were similar to those of the spring. Nitrate concentrations from the beaver pond watershed also had highly significant but different linear regressions versus the control watershed

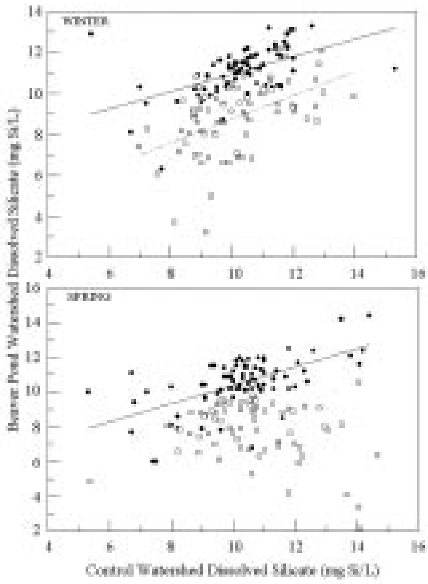

Figure 2. Dissolved silicate weekly concentrations from the beaver pond and control watersheds. Solid circle data points and the solid regression line are from the time prior to the pond and open square data points and dashed regression line are from the time after the pond. Winter regressions for the upper panel: [SiO_4] before beavers = 0.425 [control SiO_4] + 6.68; R^2 = 0.27, $P < 0.0001$. [SiO_4] after beavers = 0.582 [control SiO_4] + 2.92; R^2 = 0.26, $P <$ 0.0001. Spring regressions for the lower panel: [SiO_4] before beavers = 0.525 [control SiO_4] + 5.14; R^2 = 0.37, $P < 0.0001$. [SiO_4] after beavers = -0.161 [control SiO_4] + 9.45; R^2 = 0.03, P = 0.13.

before and after the pond was built in the winter, spring, and fall. However, in the summer there was a high correlation for nitrate concentrations before the pond, but no significant relationship after the pond. This loss of relationship in concentrations between the beaver pond watershed and the control was also observed in the summer for TON, TOP, and TSS and in the fall for TSS. We believe that changes reflect the fact that the dynamics of the beaver pond are those of a small shallow lake, rather than the dynamics of a second order stream.

Material fluxes

Fluxes of nutrients and TSS had a different pattern for the beaver pond watershed than for the control watershed (Table 3). During the six years subsequent to the beaver pond, average annual flux of nitrate from the control watershed was about the same as for the prior time period, but the fluxes of ammonium, dissolved silicate, and TOC were higher, and the fluxes of TON, phosphate,

Table 3. Comparisons of mean annual fluxes between the beaver pond and control watersheds for six years prior to and subsequent to establishment of a beaver pond.

Parameter (units)	Prior to Beaver Pond		Subsequent to Beaver Pond	
	Beaver	Control	Beaver	Control
Discharge (mm/yr)	272	260	282	291
Nitrate (g N/ha yr)	642	917	540	933
TKN (g N/ha yr)	2270	2120	1730	1850
TON (g N/ha yr)	1980	1870	1430	1580
Total NH_4 (g N/ha yr)	285	252	308	285
Total-P (g P/ha yr)	975	1020	565	702
Total-Pi (g P/ha yr)	508	588	377	452
TOP (g P/ha yr)	465	435	188	250
Dis. Silicate (kg Si/ha yr)	28.2	23.1	25.9	27.3
TOC (kg C/ha yr)	26.3	20.8	31.8	36.7
TSS (kg/ha yr)	300	188	111	114

TOP, and TSS were lower (Table 3). However, subsequent to the beaver pond the fluxes of nitrate and dissolved silicate from the beaver pond watershed were reduced, much as found by Cirmo and Driscoll (1993, 1996). While the other material fluxes changed in the same direction as the control watershed, the declines in TOP and TSS fluxes were larger than in the control (Table 3), indicating the net removal of these materials in the beaver pond, similarly to the findings of Maret et al. (1987).

The biogeochemical effects of the beaver pond were seasonal. For example, the beaver pond effect on increased ammonium flux was only significant in the fall (Table 4). Before the pond, fall ammonium fluxes were not significantly different from the control, but after the pond ammonium flux from the beaver pond watershed was 2.7 times higher than the control ($P = 0.02$, Table 4), however, our test for whether the beaver pond caused this change was marginal ($P = 0.09$). One should keep in mind that fall fluxes are low to begin with, due to the low water discharge in the fall. Increased releases of ammonium in the fall were probably due to lower redox potentials in the bottom sediments of the pond. The pond effects on decreased nitrate fluxes were only significant in the winter and spring, but this is when most of the annual nitrate flux occurred. Both nitrate concentrations and water discharge were low in the summer and fall. Beaver pond effects on decreased flux of dissolved silicate were significant in all seasons except the fall (Table 4). In all seasons except spring, nitrate flux was reduced by the pond and in the spring, although nitrate flux increased, it increased much less than for the control watershed 102 (Table 4). One might expect to see a decreased flux of nitrate due, in part, to the opportunity for denitrification within the beaver pond.

The beaver pond retained or volatilized about 30 kg nitrate-N/ha yr, 0.8 kg ammonium-N/ha yr, and 57 kg TON/ha yr, or about 18% of its average total-N inputs (Figure 3). Looked at seasonally, winter was the period of most total-N retention (59 kg/ha, Table 5), with some retention in the spring and summer and no retention in the fall. Nitrogen retention in the winter and summer was dominated by TON (41 and 25 kg N/ha, respectively; Figure 5). There was an equal amount of nitrate retention in the winter and spring (17 kg N/ha; Figure 5). While atmospheric deposition was included in these mass balances, the contribution to the overall budget was small (Figure 3), due to the fact that the surface area of the pond was only 0.5% that of the watershed. However, atmospheric deposition to the watershed was important and contributed to the watershed nitrogen discharges (Correll et al. 1994; Jordan et al. 1995). Our results can be compared to those of Cirmo and Driscoll (1996) who found that a 1.26 ha beaver pond retained 8.33 kg nitrate-N/ha (mostly during the nongrowing season), but released 0.44 kg ammonium-N/ha. Devito et al. (1989) found that two beaver ponds retained 4.6 and 6.1 kg nitrate-N/ha, but exported 3.2 and 7.2 kg TON/ha. One of these ponds retained a trace of ammonium, but the other released 3.2 kg ammonium-N/ha (Devito et al. 1989). A major difference was the fact that our watersheds are more disturbed and discharge much larger amounts of nitrogen.

Our beaver pond retained a little of its phosphate, especially in the winter, and 19 kg/ha yr of its TOP inputs, or about 21% of its average total-P inputs (Figure 3, 5). The seasons of greatest P-retention were the winter and summer and some TPi may have been released in the fall (Table 5; Figure 5). It should be stressed that these mass balances were independently estimated for each season and for the year. This becomes evident when the net seasonal mass balances for total-N and total-P are summed and compared with the annual mass balances, estimated separately. The seasonal total-N retentions sum to 135 kg N/ha yr versus the annual retention of 109 kg N/ha yr. The seasonal total-P retentions sum to 34 kg P/ha yr versus the annual retention of 35 kg P/ha yr. Devito et al. (1989) found that one of their ponds retained 0.1 kg total-P/ha while the other exported 0.3 kg total-P/ha.

Our beaver pond retained 1,680 kg of dissolved silicate-Si/ha yr (Figure 3), or about 32% of inputs, and the highest seasonal retention was 480 kg Si/ha in the spring (Table 5). This corresponds to a retention of 57.8 kg Si/ha yr in a beaver pond in the Adirondacks of New York (Cirmo & Driscoll 1996). Our pond also retained about 2,200 kg TOC/ha yr (Figure 3) or 28%

Table 4. Comparisons among wataershed discharges (mm/season) and seasonal fluxes for the beaver pond and control watersheds for six years before and six years after the construction of a beaver dam. NS = probability $>$ 0.10.

Parameter	Flux or Nutrient Concentration				Probability*		
	Beaver Watershed		Control Watershed		Beaver vs Control		Watershed Changed by Beaver? (P)
	Before	After	Before	After	Before	After	
Winter							
Discharge	91.9	95.4	89.3	103	NS	0.002	0.002
Nitrate (g N/ha)	284	225	355	395	0.0001	$<$ 0.00001	0.03
$NH4^{+}$(g N/ha)	65.1	73.5	52.1	75.1	NS	NS	NS
TON (g N/ha)	480	363	346	444	NS	NS	0.10
TOC (kg C/ha)	7.98	4.91	5.01	6.70	NS	0.006	NS
Total-Pi (g P/ha)	96.3	73.9	76.1	90.3	NS	NS	NS
TOP (g P/ha)	87.1	40.3	67.2	51.4	NS	NS	NS
H_4Si0_4 (kg Si/ha)	9.43	7.80	8.35	8.39	$<$ 0.00001	0.0002	$<$ 0.00001
TSS (kg/ha)	87.1	40.3	67.2	51.4	NS	NS	NS
Spring							
Discharge	104	143	97.9	144	0.05	0.05	NS
Nitrate (g N/ha)	233	256	266	401	NS	$<$ 0.0001	0.01
$NH4^{+}$(g N/ha)	82.9	123	90.6	120	NS	NS	NS
TON (g N/ha)	540	765	512	771	NS	NS	NS
TOC (kg C/ha)	7.05	9.31	6.17	8.89	NS	NS	NS
Total-Pi (g P/ha)	129	192	125	213	NS	NS	NS
TOP (g P/ha)	111	99.5	94.3	119	NS	NS	NS
H_4Si0_4 (kg Si/ha)	10.8	9.53	9.53	11.1	0.0003	0.001	$<$ 0.00001
TSS (kg/ha)	59.6	61.8	33.1	58.9	NS	NS	NS
Summer							
Discharge	48.4	23.2	45.4	23.9	0.08	NS	0.10
Nitrate (g N/ha)	84.4	18.1	197	83.0	0.003	0.0002	0.10
$NH4^{+}$(g N/ha)	102	63.2	76.0	72.0	0.005	NS	NS
TON (g N/ha)	723	179	762	262	NS	0.09	NS
TOC (kg C/ha)	7.96	2.37	6.55	2.92	NS	NS	NS
Total-Pi (g P/ha)	187	63.6	294	117	0.04	NS	NS
TOP (g P/ha)	216	27.3	213	67.2	NS	0.03	NS
H_4Si0_4 (kg Si/ha)	5.46	1.52	5.38	2.02	NS	0.001	0.01
TSS (kg/ha)	144	15.2	114	31.8	NS	0.08	NS

Table 4. Continued.

Parameter	Flux or Nutrient Concentration				Probability*		
	Beaver Watershed		Control Watershed		Beaver vs Control		Watershed
	Before	After	Before	After	Before	After	Changed by Beaver? (P)
Fall							
Discharge	27.9	19.7	27.8	19.7	NS	NS	NS
Nitrate (g N/ha)	40.0	21.9	95.8	114	0.001	0.003	NS
$NH4^+$(g N/ha)	34.9	48.1	32.2	18.0	NS	0.02	0.09
TON (g N/ha)	242	126	244	96.2	NS	NS	NS
TOC (kg C/ha)	3.40	1.67	3.16	1.41	NS	NS	NS
Total-Pi (g P/ha)	95.9	48.0	93.1	31.1	NS	0.002	NS
TOP (g P/ha)	51.0	21.0	59.9	12.3	NS	NS	NS
H_4Si0_4 (kg Si/ha)	3.18	2.18	3.47	4.04	NS	0.01	NS
TSS (kg/ha)	43.4	12.6	23.6	5.58	0.07	0.02	NS

* Paired T-Tests of weekly fluxes or volume-intergrated mean concentrations were used when comparing watersheds for the same time periods, and general T-Tests of weekly data were used to compare differences between watearsheds before and after the establishment of the beaver pond.

of the inputs from the stream to the pond, with the season of greatest retention in the winter, and little or no retention in the spring and fall (Table 5). This corresponds to a net release of 83.8 kg DOC/ha yr from pond in the Adirondacks (Cirmo & Driscoll 1996). Thus, our beaver pond had a net retention of allochthonous TOC inputs from the watershed and autochthonous TOC inputs and was an overall heterotrophic system, as reported for a beaver pond in Alberta (Hodkinson 1975). In contrast, a beaver pond in the Adirondacks released 85 kg DOC/ha yr (Cirmo & Driscoll 1993, 1996), while of two ponds in Ontario, one retained 22 kg DOC/ha yr and one released 70 kg DOC/ha yr (Devito et al. 1989). Our beaver pond also retained about 10 t of TSS/ha yr, or about 27% of inputs, per year and most of this retention was in the winter. It should be noted that summed seasonal mass balances were not close to annual mass balances for TOC or TSS and these values should be viewed with caution.

Effects of variation in stream discharge

The concentrations and fluxes of materials in the stream draining the beaver pond were often modified from what would have been expected based on the behavior of this watershed prior to the beaver pond and the behavior of the

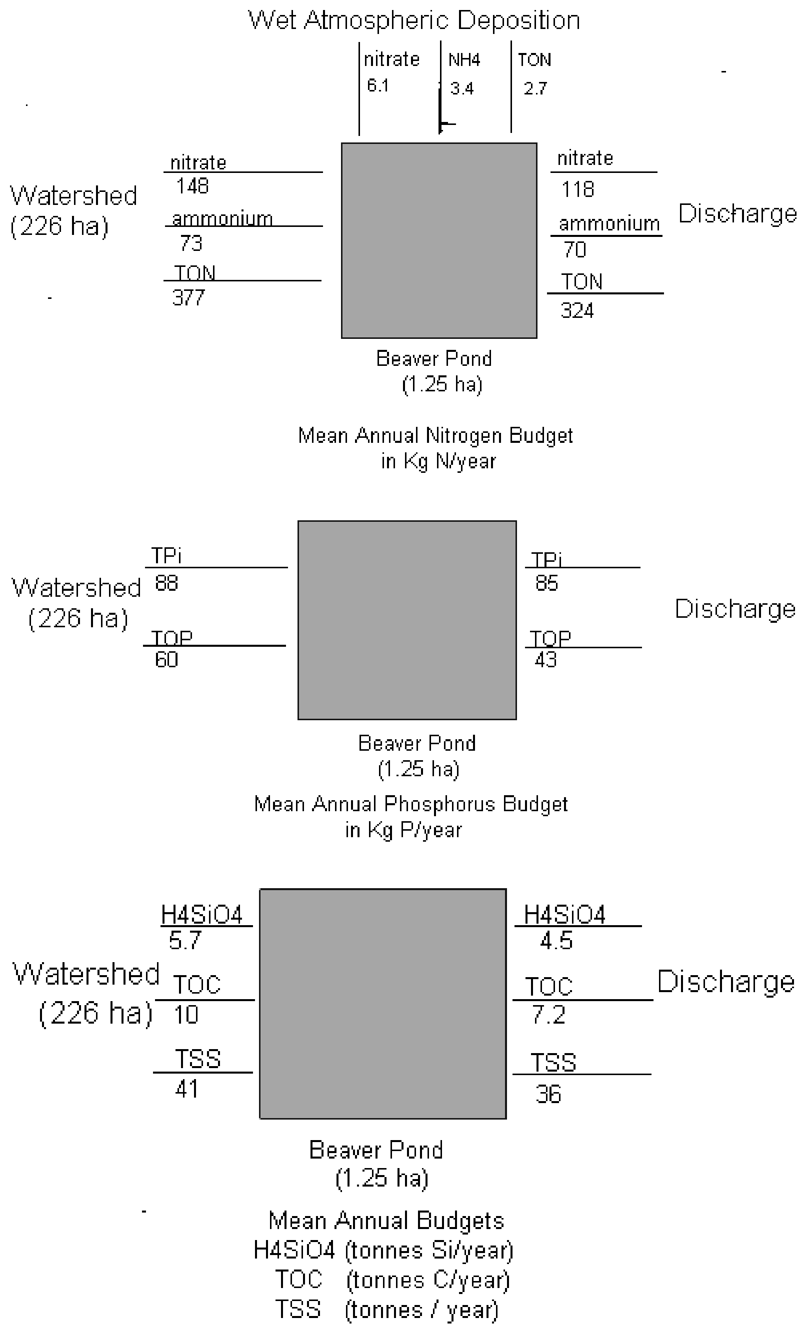

Figure 3. Mean annual mass balances of inputs and outputs from a beaver pond on the Rhode River watershed in the Maryland Coastal Plain for the six years subsequent to the pond formation. Wet deposition fluxes of nitrogen and all discharge fluxes were measured directly. Watershed input fluxes were estimated from control watershed outputs and linear regressions of beaver pond watershed outputs versus control watershed outputs during the six years prior to the beaver pond. All regressions were significant at the $P < 0.00001$ level.

Table 5. Seasonal comparisons of estimated six year mean inputs to a Beaver pond and directly measured outputs as stream discharge. Inputs are the sum of measured atmospheric wet depositon (N only) and mean stream inputs estimated from the control watersheds and linear regressions of fluxes from the beaver pond watershed versus the control during the six years prior to the construction of the Beaver pond.

Parameter	Inputs	Outputs
A. Winter		
Nitrate (kg N/winter)	72	51
Ammonium (kg N/winter)	19	17
TON (kg N/winter)	133	82
Total-N (kg/winter)	224	150
Total Pi (kg P/winter)	28	17
TOP (kg P/winter)	18	9.1
Total-P (kg/winter)	46	26
Dis. Silicic Acid (t Si/winter)	2.2	1.8
TOC (t C/winter)	2.9	1.1
TSS (t/winter)	50	9.1
B. Spring		
Nitrate (kg N/spring)	79	58
Ammonium (kg N/spring)	22	28
TON (kg P/spring)	173	170
Total-N (kg/spring)	270	259
Total Pi (kg P/spring)	42	43
TOP (kg P/spring)	29	22
Total-P (kg/spring)	71	66
Dis. Silicic Acid (t Si/spring)	2.8	2.2
TOC (t C/spring)	2.0	2.1
TSS (t /spring)	22	14

Table 5. Continued.

Parameter	Inputs	Outputs
C. Summer		
Nitrate (kg N/summer)	11	4.1
Ammonium (kg N/summer)	23	14
TON (kg N/summer)	71	40
Total-N (kg/summer)	101	59
Total Pi (kg P/summer)	21	14
TOP (kg P/summer)	17	6.2
Total-P (kg/summer)	38	21
Dis. Silicic Acid (t Si/summer)	0.49	0.34
TOC (t C/summer)	0.99	0.54
TSS (T/summer)	13	3.4
D. Fall		
Nitrate (kg N/fall)	13	4.9
Ammonium (kg N/fall)	6.4	11
TON (kg N/fall)	25	28
Total-N (kg/fall)	42	44
Total pi (kg P/fall)	7.3	11
TOP (kg P/fall)	1.0	4.7
Total-P (kg/fall)	8.3	16
Silicic Acid (t Si/fall)	0.82	0.49
TOC (t C/fall)	0.41	0.38
TSS (t/fall)	1.2	2.8

control watershed for the entire time period. These modifications were also different seasonally. Within a season how did variations in stream discharge affect material retention or export by the pond? In many cases the creation of the beaver pond seemed to uncouple the stream chemistry from short-term variations in discharge. For example, the concentration of TON in the

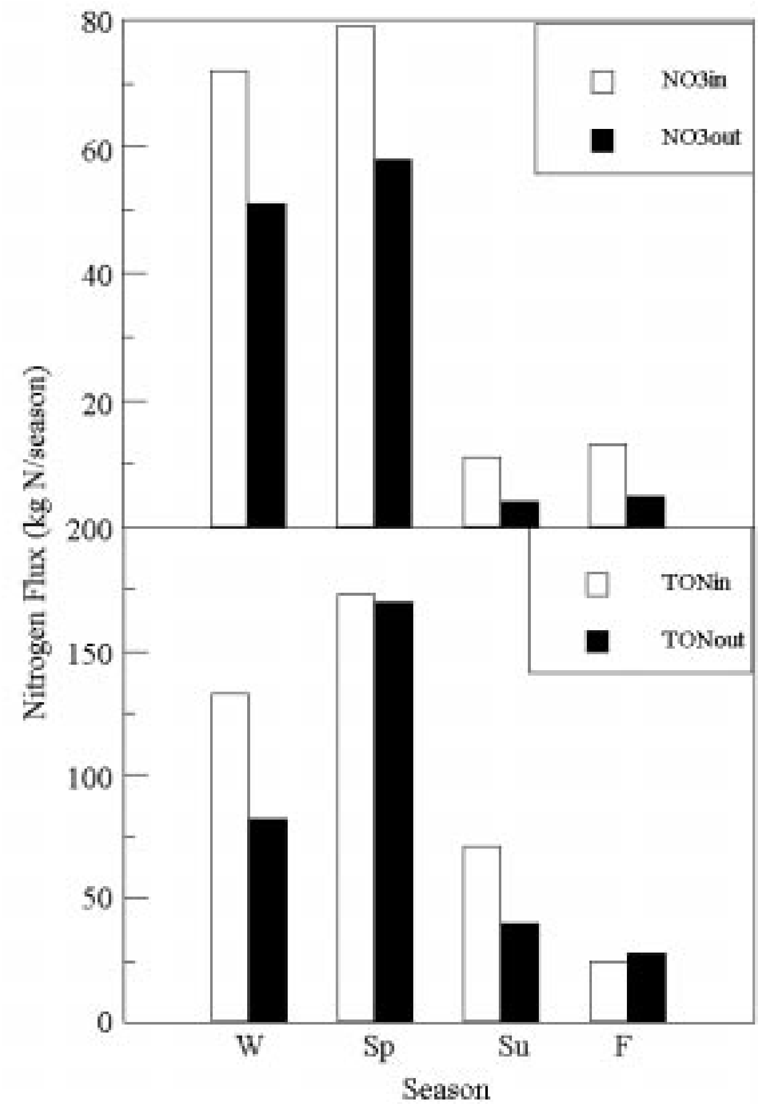

Figure 4. Seasonal mean fluxes of nitrate and TON into and out of the beaver pond. Fluxes into the pond are the sum of direct atmospheric wet deposition and watershed discharges.

winter had a highly significant relationship to stream discharge prior to the pond, but little or no relationship to discharge after the pond (Table 6). This change in winter relationship was similar for concentrations of TOC, TPi, TOP, and TSS (Table 6). A similar change was noted for TOP and TSS in the summer and for TPi in the fall (Table 6). These uncouplings were probably due to the high rates of deposition of particulates along with the nutrients

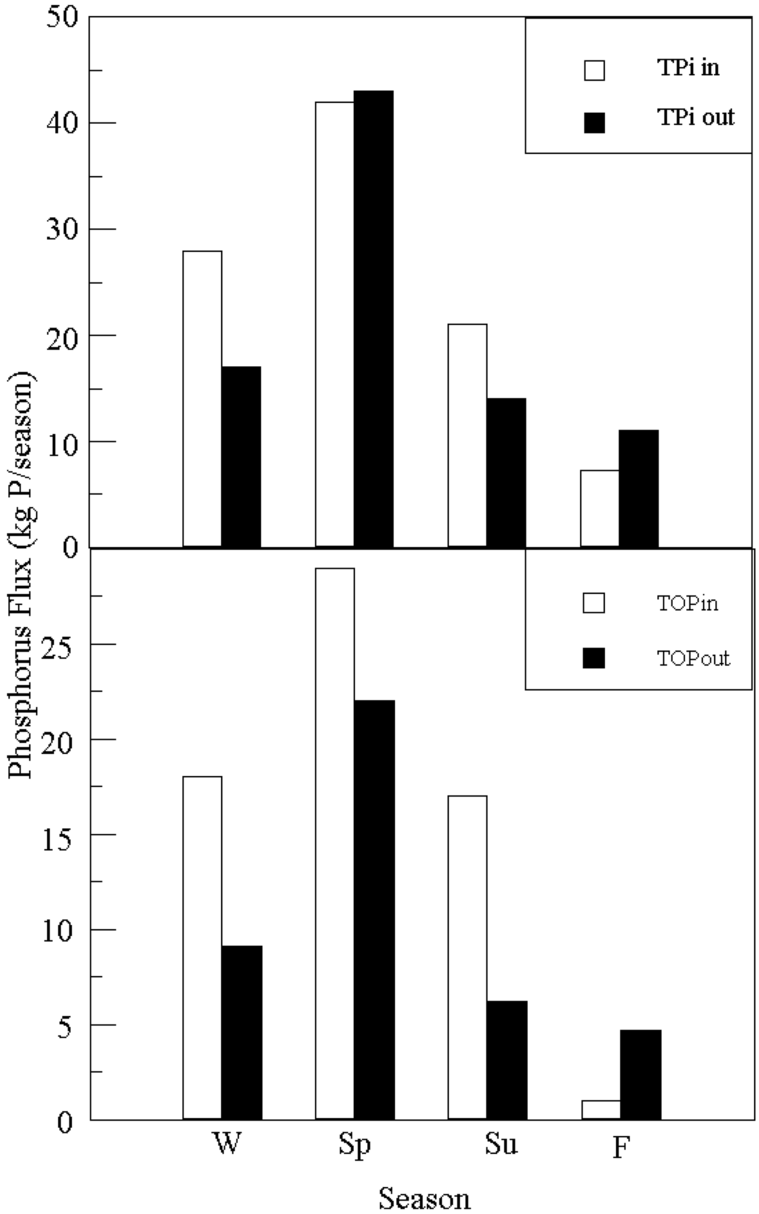

Figure 5. Seasonal mean fluxes of TPi and TOP into and out of the beaver pond.

they contained on the bottom of the pond. The concentrations of suspended particulates increased rapidly as stream discharge increased, but the beaver pond trapped much of the increased load of suspended particulates.

For another group of materials the beaver pond either had no effect or increased the relationship between concentrations and stream discharge. For example, nitrate concentrations had a highly significant correlation with discharge in the spring prior to the pond, but this correlation increased (explained more of the variation in nitrate concentration) subsequent to the formation of the pond (Table 6). Similarly, ammonium concentrations in the summer had a significant negative correlation with discharge before the pond, but a higher correlation with discharge after the pond and this relationship was extended into the fall (Table 6). The higher nitrate and lower ammonium concentrations during periods of high flow may have reflected internal nitrogen processing in the beaver pond. During periods of high flow the pond was more likely to be aerobic and nitrification may have been favored, while during periods of low flow the pond may have been more hypoxic and produced more ammonium. Some of the retained TON (Figure 7) may have been mineralized during the warmer time periods.

Implications and research needs

Landscape managers should pay attention to the impacts of the resurgence of beaver populations both in the Maryland Coastal Plain and World-wide. Beaver have been reintroduced to many habitats in North America and Europe and their populations are increasing rapidly. Their natural predators have been extirpated from much of their natural range, leaving humans as the primary control on their ultimate population. As their populations increase they have both short-term localized effects on stream ecosystems and long-term landscape-level effects on the biogeochemistry of whole regions.

At the short-term, local level beaver remove riparian forest and change the character of streams. In many developed landscapes, such as the Maryland Coastal Plain, most of the remaining forest is riparian and the overall wisdom of allowing beaver to remove much of this forest at a given site is controversial. The ponding and exposure to the sun result in warmer water temperatures and many changes in water quality. Still at the short-term, local level, when the pond is abandoned the resulting beaver meadow undergoes plant succession and the sediments and nutrients that had been trapped in the beaver pond begin to change. The soils of the meadow may become more aerobic and undergo mineralization of organic matter, releasing some of their mineral nutrients.

At the large-scale, long-term level, the landscape becomes a mosaic of current and former beaver sites along stream networks. As a result stream

Table 6. Seasonal regressions of weekly mean material concentrations versus beaver pond watershed water discharge (Q). Only regressions with a $P < 0.10$ are given. Separate regressions are given for the period of six years before the beaver pond was formed and the period of six years after the beaver pond.

Before Beavers	
Winter	Nitrate (ug N/L) = 16.0Q + 135; R^2 = 0.28, P < 0.00001
Spring	Nitrate (ug N/L) = 10.3Q + 90.6; R^2 = 0.21, P = 0.00002
Spring	Ammonium (ug N/L) = 188$Q^{-0.519}$; R^2 = 0.29, P = 0.08
Summer	Ammonium (ug N/L) = 289$Q^{-0.198}$; R^2 = 0.25, P = 0.02
Winter	TON (ug N/L) = 36.4Q + 104; R^2 = 0.12, P = 0.002
Summer	TON (ug N/L) = 6.65Q + 780; R^2 = 0.05, P = 0.09
Winter	TOC (mg C/L) = 8.64Q – 14.5; R^2 = 0.30, P < 0.00001
Winter	TPi (ug P/L) = 9.72Q – 5.62; R^2 = 0.27, P < 0.00001
Summer	TPi (ug P/L0 = 7.14Q + 229; R^2 = 0.04, P = 0.08
Fall	TPi (ug P/L) = 17.9Q + 151; R^2 = 0.08, P = 0.02
Winter	TOP (ug P/L) = 10.8Q – 29.2; R^2 = 0.33, P < 0.00001
Spring	TOP (ug P/L) = 5.81Q + 40.2; R^2 = 0.16, P = 0.0003
Summer	TOP (ug P/L) = 13.6Q + 147; R^2 = 0.13, P = 0.006
Fall	TOP (ug P/L) = 10.6Q + 70.8; R^2 = 0.11, P = 0.02
Winter	TSS (mg/L) = 7.88Q – 32.8; R^2 = 0.32, P < 0.00001
Spring	TSS (mg/L) = 4.25Q + 7.74; R^2 = 0.21, P = 0.00003
Summer	TSS (mg/L) = 8.90Q + 102; R^2 = 0.07, P = 0.05
Fall	TSS (mg/L) = 9.37Q + 51.1; R^2 = 0.12, P = 0.02
After Beavers	
Winter	Nitrate (ug N/L) = 11.3Q + 96.5; R^2 = 0.28, P < 0.00001
Spring	Nitrate (ug N/L) = 7.78Q + 20.1; R^2 = 0.39, P < 0.00001
Summer	Nitrate (ug N/L) = 5.48Q + 31.9; R^2 = 0.06, P = 0.03
Winter	Ammonium (ug N/L) = 112$Q^{-0.251}$; R^2 = 0.07, P = 0.08
Spring	Ammonium (ug N/L) = 238$Q^{-0.516}$; R^2 = 0.22, P = 0.05
Summer	Ammonium (ug N/L) = 409$Q^{-0.368}$; R^2 = 0.63, P = 0.0005
Fall	Ammonium (ug N/L) = 228$Q^{-0.290}$; R^2 = 0.48, P = 0.008
Summer	TOC (mg C/L) = 104$Q^{-0.0819}$; R^2 = 0.18, P = 0.04
Winter	TOP (ug P/L) = 1.22Q + 33.0; R^2 = 0.06, P = 0.03
Spring	TOP (ug P/L) = –1.53Q + 88.8; R^2 = 0.05, P = 0.06
Fall	TOP (ug P/L) = 9.35Q + 56.9; R^2 = 0.08, P = 0.02
Spring	TSS (mg/L) = –1.35Q + 63.3; R^2 = 0.04, P = 0.09
Fall	TSS (mg/L) = 5.63Q + 37.8; R^2 = 0.07, P = 0.02
Spring	Dis. Silicate (mg Si/L) = –0.0350Q + 7.34; R^2 = 0.04, P = 0.09
Summer	Dis Silicate (mg Si/L) = 0.141Q + 5.55; R^2 = 0.05, P = 0.04

corridors are changed from rather narrow, well defined zones in the landscape to much wider, physically more complex, and biologically much more diverse and productive landscape regions. This effect should be most pronounced in very flat terrain, such as many parts of the Coastal Plain. Over time a given region, such as the Maryland Coastal Plain will develop populations of beaver meadows of various ages and sizes. Each of these beaver meadows will be undergoing both plant and soil succession. It will probably take on the order of a century for the stream networks of this landscape with their populations of beaver meadows to approach a new biogeochemical quasi-equilibrium.

Assuming that humans allow beaver populations to remain at moderate to high levels for a long enough time, what will be the implications for the management and health of aquatic ecosystems from headwaters stream corridors to coastal waters? Although the implications will be to some extent regionally specific, some general effects of a resurgent beaver population are clear. The hydrology will be altered by increased evapotranspiration and reduced storm surges. In most settings stream temperatures will be increased during the growing season. A large fraction of the suspended sediments and their nutrient contents will be converted to beaver meadows and much of these sediments and nutrients will remain trapped for the long-term. Riparian vegetation will be extended spatially and greatly increased in diversity. Mineral nutrient fluxes to down-stream systems such as large lakes, estuaries, and coastal waters will be decreased. These implications have thus far been largely overlooked by land managers even though these changes have been under way for decades. There are now thousands of beaver ponds on the Maryland Coastal Plain where there were none a few decades ago. Similar changes are occurring in many parts of North America and Europe.

We believe that our study points to the need for more research of two types on the biogeochemical effects of beavers. More mass balance studies of both active beaver ponds and beaver meadows of various ages are needed to test the generality of our results and the results of others in both the Coastal Plain and in other physiographic regions. More mechanistic studies are also needed to better understand nutrient dynamics within these interesting habitats. Whether the results from a few dozen studies of beaver ponds in more northern latitudes of North America can be transferred to the Maryland Coastal Plain or many other regions of the World is still an open question.

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