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Alteration of North American Streams by Beaver

The structure and dynamics of streams are changing as beaver recolonize their historic habitat

Robert J. Naiman, Carol A. Johnston, and James C. Kelley

Beaver (*Castor canadensis*) provide a striking example of how animals influence ecosystem structure and dynamics in a hierarchical fashion. Initially beaver modify stream morphology and hydrology by cutting wood and building dams. These activities retain sediment and organic matter in the channel, create and maintain wetlands, modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and animal community composition and diversity (Naiman and Melillo 1984, Naiman et al. 1986). In addition to their importance at the ecosystem level, these effects have a significant impact on the landscape and must be interpreted over broad spatial and temporal scales as beaver population dynamics shift in response to disturbance, food supply, disease, and predation.

Although once more prevalent than they are today, beaver-induced alterations to drainage networks are not localized or unusual. Where beaver remain largely free of management or trapping, their activities may influ-

We see a complex pattern that may involve formation of marshes, bogs, and forested wetlands

ence a large proportion of streams in a drainage network; and these alterations may remain as part of the landscape for centuries (Ives 1942, Johnston and Naiman 1987, Rudemann and Schoonmaker 1938).

The objectives of this article are to briefly summarize the history of beaver in North America, then describe some of the ecosystem-level responses of streams to beaver-induced alterations and, finally, to describe beaver-induced changes in the landscape that take place over broad spatial and temporal scales. Our research has been conducted in Quebec, Minnesota, Montana, and Alaska, and it should be representative of northern regions.

History of beaver in North America

Before the arrival of Europeans in North America, the beaver population was estimated to be 60–400 million individuals (Seton 1929), with a geographic range of about 15 million km² (Jenkins and Busher 1979). Beaver were found in nearly all aquatic habitats from the arctic tun-

dra to the deserts of northern Mexico. Historical records provide a chronology of their demise in New England, where nearly every body of water was occupied by beaver prior to European settlement (Rudemann and Schoonmaker 1938). In the early 17th century extensive removal began in North America with more than 10,000 beaver per year taken for the fur trade in Connecticut and Massachusetts between 1620 and 1630 (Moloney 1967). From 1630 to 1640, approximately 80,000 per year were taken from the Hudson River and western New York (Hays 1871). As the eastern beaver population declined, expeditions to the West (1800–1850) often were made solely for the purpose of discovering new trapping areas (Cline 1974). By 1900, continued exploitation left beaver almost extinct in North America (Jenkins and Busher 1979, Johnson and Chance 1974). Concomitantly, since 1834, approximately 195,000–260,000 km² of US wetlands have been converted to dry land (Shaw and Fredine 1971). Undoubtedly, a large proportion of these wetlands was beaver habitat.

Today, with a relative absence of predators, laws regulating trapping, and an abundance of forage and habitat, the beaver population is increasing rapidly. The current population is thought to be between 6 and 12 million individuals. Yet, for most of North America, the present population represents only a small fraction of earlier numbers. Many attributes of stream ecosystems were changed by beaver removal long before mod-

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By building dams, beaver appear to moderate stream discharge regimes.

ern limnological research began. Therefore, much of our understanding of stream ecosystems is derived from sites that lack the influence of this previously abundant and ecologically important herbivore.

Stream channel alterations

Beaver primarily alter the stream channel by impounding water. Their ability to build dams and expand the wetted area increases the amount of

beaver habitat available, often increases their food supply, and offers protection from predators (primarily wolf, *Canis lupus*). This ability comes, in part, from their unique habit of cutting mature trees for food and building material. Although several tree species may be used in construction, beaver prefer aspen (*Populus*) for food.¹

¹C. A. Johnston and R. J. Naiman, 1988, manuscript submitted.

Dam-building changes the annual stream discharge regime, decreases current velocity, gives the channel gradient a stair-step profile, expands the area of flooded soils, and increases the retention of sediment and organic matter (Figure 1). Most dams occur on first- through fourth-order streams, because dams in larger streams are often removed by freshets.

The frequency of dams in first- to fourth-order streams may be substantial, especially if the topography and the beaver food supply are adequate. In Quebec, along the North Shore of the Gulf of St. Lawrence, the dam frequency ranges from 8.6 to 16.0 dams/km and averages 10.6 dams/km (Naiman et al. 1986). On the 294-square-kilometer Kabetogama Peninsula in northern Minnesota the frequency ranges from 2.0 to 3.9 dams/km, with an average of 2.5 dams/km. This frequency of dams is reasonable when one considers that the population density may reach 3 colonies/km², with typical values in favorable habitat ranging between 0.4 and 0.8 colonies/km² (Aleksiuk 1968, Bergerud and Miller 1977, Voigt et al. 1976). Each colony contains, on average, four to eight beaver (Jenkins and Busher 1979).

Every dam has the potential to retain a substantial amount of sediment depending upon its size and geomorphic position in the channel. We have measured several instances where a small dam with 4–18 m³ of wood was able to retain 2000–6500 m³ of sediment (Naiman et al. 1986). We refer to accumulations of water and sediment in the stream channel as patch bodies (Johnston and Naiman 1987); that is, volumetric landscape units that have surficial boundaries with upper and lower strata, and lateral boundaries with adjacent patches within the same stratum (Figure 2). These expanded patch bodies produced by beaver are important because they provide the large reserve of carbon and nutrients needed for ecosystem stability.

Patch bodies created by beaver impoundments include the beaver pond, the aerobic soil beneath the pond, and the underlying anaerobic soil. These patch bodies contain some of the same basic physical structures and processes as patch bodies in the orig-



Figure 1. Beaver build primary dams in locations that will pond a maximum amount of water to insure an abundant food supply. This dam in Voyageurs National Park, Minnesota, is about 80 m long and 2 m high, hydrologically influencing about 1 km².

inal stream channel, but the relative size and, thus, the relative importance of specific processes are different. This can, for instance, be seen in invertebrate community structure, in carbon budgets, and in ecosystem-level efficiencies calculated for streams and ponds in Quebec (McDowell and Naiman 1986, Naiman et al. 1986).

Beaver activities influence invertebrate community structure by replacing running-water taxa by pond taxa (primarily a response to finer sediments and a decrease in current speed). Beaver activities also influence community function by increasing the absolute importance of collectors and predators, while decreasing the relative importance of shredders and scrapers in impounded sites (McDowell and Naiman 1986). Running-water communities that are normally dominated by blackflies, Tanytarsini midges, scraping mayflies, and net

spinning caddisflies are replaced in impoundments by Tanypodinae and Chironomini midges, predaceous dragonflies, tubificid worms, and filtering clams. Total density and biomass in ponds may be two to five times greater than those of riffle sites, ranging from 11,000 to 73,000 organisms/m² and from 1 to 11 g/m², depending upon the season.

Despite these differences, the total number of species in beaver ponds appear to be similar to those in the natural stream channel. Invertebrate communities in beaver impoundments, however, resemble those in slow-water habitats of larger order streams (e.g., the alcoves and pools).² Therefore, invertebrate communities in the beaver impoundments may not be unique within the drainage network but likely represent unparal-

²S. R. Reice and R. J. Naiman, 1988, unpublished data.

leled assemblages in small streams (McDowell and Naiman 1986).

Beaver-induced stream channel alterations also change the way materials flow through streams. Beaver activities substantially change the absolute amounts of carbon inputs, standing stock, and outputs (Table 1). In Beaver Creek, Quebec, riffles received a total carbon input of 220 g C·m⁻²·yr⁻¹ as compared to 65 g C·m⁻²·yr⁻¹ for the beaver pond. Yet, the standing stock (4400 g C/m² versus 12,000 g C/m²) and total carbon output (51 versus 121 g C·m⁻²·yr⁻¹) were much less in the riffle than in the beaver pond. Since, in this case, beaver transformed a one-meter-wide stream into an impoundment averaging 7 m in width, the impact of beaver on the total carbon budget per unit of channel length would be seven times the values given per unit area in Table 1. Thus, total carbon inputs per unit

length of channel were 48% of those in the pond, the standing stock of carbon in the riffle was only 5% of that in the pond, and the total outputs in the riffle were only 6% of those measured in the pond.

Alterations to the carbon budget are also manifested in ecosystem-level efficiency for the retention and processing of organic carbon (Table 2). This efficiency is reflected in the turnover time for carbon, with the standing stock of carbon in the riffle being replaced every 24 years as compared with 161 years for the pond. The stream metabolism index (SMI), a measure of ecosystem efficiency for the utilization or storage of organic inputs, also demonstrates the pond to be more retentive (SMI of 1.63 as compared with 0.30 for the riffle.) Values of more than 1.00 suggest that organic inputs are being accrued or processed; little material, relative to the amount received, is being transported downstream. These increases in retention and processing are caused by the 80–90% decrease in turnover length and rate of downstream movement of organic carbon in the pond compared with the riffle (Table 2). Together, these data on community composition, carbon cycling, and ecosystem processing efficiency indicate that beaver, by changing the hydrologic regime, substantially alter the character of stream channels when compared with unmodified reaches.

Table 1. Comparison of mean annual standing stocks and annual fluxes of carbon in a riffle and pond in Beaver Creek, Quebec. Data are from Naiman et al. 1986.

Component	Carbon		Ratio
	Riffle	Pond	Riffle:Pond
INPUT ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)			
Precipitation and throughfall	16.9	6.9	2.45
Direct allochthonous	123.1	52.6	2.36
Lateral allochthonous	55.8	4.3	12.98
Periphyton production	24.7	1.7	14.53
Total input	220.5	65.1	3.39
STANDING STOCK (g/m^2)			
Water column	2.0	18.0	0.11
Coarse wood	3926.9	3129.2	1.25
CPOM	419.4	5152.0	0.08
FPOM	33.7	3738.8	0.01
Primary producers	0.5	0.1	5.00
Invertebrates	0.4	2.7	0.15
Total standing stock	4382.9	12040.8	0.36
OUTPUTS ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)			
Detritus respiration	22.0	111.5	0.20
Autotrophic respiration	28.0	1.6	17.50
Methane evasion	0.5	7.4	0.07
Insect emergence	0.3	0.4	0.75
Total outputs	50.8	120.9	0.42

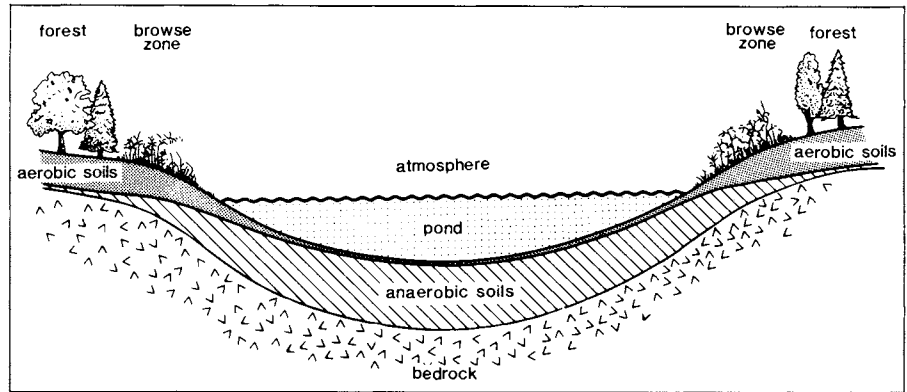


Figure 2. Patch bodies associated with beaver ponds (from Johnston and Naiman 1987). Patch bodies shown are the pond water volume and the volumes of aerobic soils and anaerobic sediments.

Riparian zone alterations

Beaver also have a substantial impact on the structure and productivity of the riparian zone, primarily by cutting trees and shrubs (Jenkins 1980). Beaver are central place foragers (Orians and Pearson 1979) in that they continuously return to their lodge or winter food cache after feeding. In northern regions they annually cut at least a metric ton of wood within approximately 100 m of their pond (Howard 1982, Johnston and Naiman 1987, McGinley and Whitham 1985). Riparian zones dominated by deciduous species preferred by beaver, such as trembling aspen (*Populus tremuloides*), may be virtu-

ally clear-cut. The riparian zone initially becomes more open as shrubs (e.g., alder, *Alnus*, and hazel, *Corylus*) and root suckers of aspen become the dominant growth form. Eventually, nonbrowsed species in the understory, such as black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*), may overtop the shrubs and become the dominant streamside vegetation. Occasionally, selective cutting of the aspen releases understory fir and spruce, and no shrub stage occurs.

By initially reducing vegetation height and then altering biomass partitioning, beaver exert a substantial impact on the structure and function of adjacent terrestrial ecosystems and on terrestrial-aquatic interactions. These alterations influence the amount and character of inputs from the uplands to the stream channel, the amount of light reaching the channel, the development of riparian soils through changes in litter quality returned to the soil, and the availability of nutrients in groundwater moving through the riparian zone to the channel (Naiman et al. 1988, Pringle et al. 1988).

A spatial and temporal mosaic

Changes to the stream channel and the riparian zone become especially important when watersheds are considered. It is first necessary to recognize that the ontogeny of a beaver pond, from its formation to its eventual decay and return to an unaltered stream channel, may range from a year to many centuries, with the

Table 2. Processing efficiencies for carbon are compared for a riffle and adjacent beaver pond in Quebec. Calculations are from Naiman et al. 1986.

Parameter	Riffle	Pond	Riffle:Pond
Turnover time (yr)	24.4	160.7	0.15
Stream metabolism index	0.30	1.63	0.18
Turnover length (km)	8.0	1.2	6.67
Rate of downstream movement (m/d)	0.25	0.03	8.33

pond's physical and chemical characteristics shifting during the aging process. Beaver ponds are a shifting mosaic of environmental conditions, dependent upon pond age and size, successional status, substrate, hydrologic characteristics, and resource inputs.

This shifting mosaic has both spatial and temporal components. Since all ponds along a reach of stream are not identical habitat, the magnitudes or rates of specific ecosystem parameters do not remain spatially constant. The result is a situation where the relative magnitude of an ecosystem parameter varies along the channel (Figure 3a). For example, one pond may be predominantly a bog (due to local hydrology and topography) with one characteristic rate of primary production, another pond may be an emergent marsh with a different rate of primary production, while the connecting riffle has a production rate of the normal second-order stream. Further, since the beaver population will wax and wane (in response to predation, constraints imposed by the food supply, or disease) and ponds will pass through a natural ontogeny (or succession), there will be temporal shifts in the density and diversity of beaver-mediated habitats (Figure 3b). These changes are manifested by alterations to biogeochemical pathways and by alterations to the total watershed budget for specific parameters.

We are currently quantifying the response of a boreal forest landscape to this type of beaver activity on the Kabetogama Peninsula in northern Minnesota. We have been able to document beaver alterations to the hydrology and the vegetation over space and time using eight sets of aerial photographs taken during 46 years (1940–1986), a geographic information system, and information on the number of active colonies since 1958.

Extensive fires and logging after the

turn of the century resulted in a large supply of aspen on the peninsula by 1940. In combination with a low density of predatory wolves and more than 300 km of stream channel available for colonization, beaver increased their habitat use from 71 dams in 1940 to 835 dams in 1986. Less than 1% of the peninsula was impounded by beaver in 1940, as compared with 13% in 1986 (Figure 4). Additionally, 12–15% of the uplands in the riparian zone were altered during the same period by beaver browsing.

As the number of beaver impoundments increased, their spatial distribution changed from scattered individual impoundments to a mosaic of contiguous impoundments along entire valleys. Beaver impoundments in 1940 were widely distributed in the landscape (Figure 5). By 1961, subsequent impoundments had been built in waterways connecting these initial foci. After completely impounding the connecting waterways, by 1986 beaver began building extensions on existing ponds. New beaver ponds created by 1961 were significantly larger than those created after 1961,³ and beaver ponds impounded first tend to have the greatest longevity (Howard and Larson 1985). Altogether, this evidence implies that beaver are selecting optimal pond sites first, then flooding more marginal areas as their population increases and resources are depleted.

A beaver-impounded landscape is thus a mosaic of different vegetation types—due to the dynamic hydrology of beaver ponds, the diversity of pre-impoundment vegetation, and the changes caused by beaver foraging in the riparian zone. Using US Fish and Wildlife Service designations (Cowardin et al. 1979), we mapped 32 different classes of wetland vegetation on the Kabetogama Peninsula. Even

³C. A. Johnston and R. J. Naiman, 1988, unpublished data.

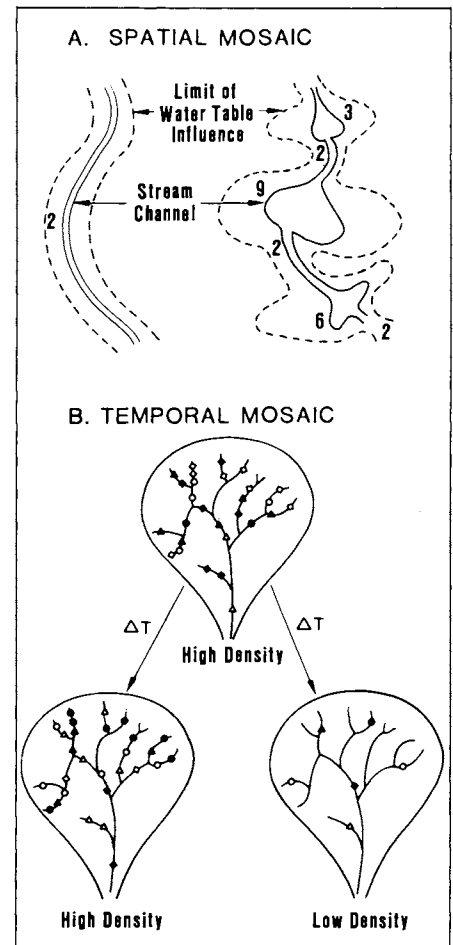


Figure 3. a. The spatial mosaic of beaver-altered habitat changes along stream channels in response to pond age, successional status, and the local environment. In this example, the type of primary production has been shifted from the normal second-order stream to a diversity of habitat types represented by different numbers. b. The spatial mosaic in a will also shift over time. Where beaver density has remained high (left), the number of ponds has remained the same, but the arrangement in the drainage network has changes as ponds undergo succession. Where the beaver population has decreased (right), both the spatial arrangement and the density of ponds in the drainage network have been affected. Symbols refer to beaver ponds in different successional stages.

when generalized to eight different categories, the vegetative pattern is complex (Figure 5). The relative proportion of different vegetation types in beaver impoundments has changed as total impoundment area has increased over time. In 1940, when many of the impoundments appeared to be abandoned, two of the drier vegetation types predominated: bog

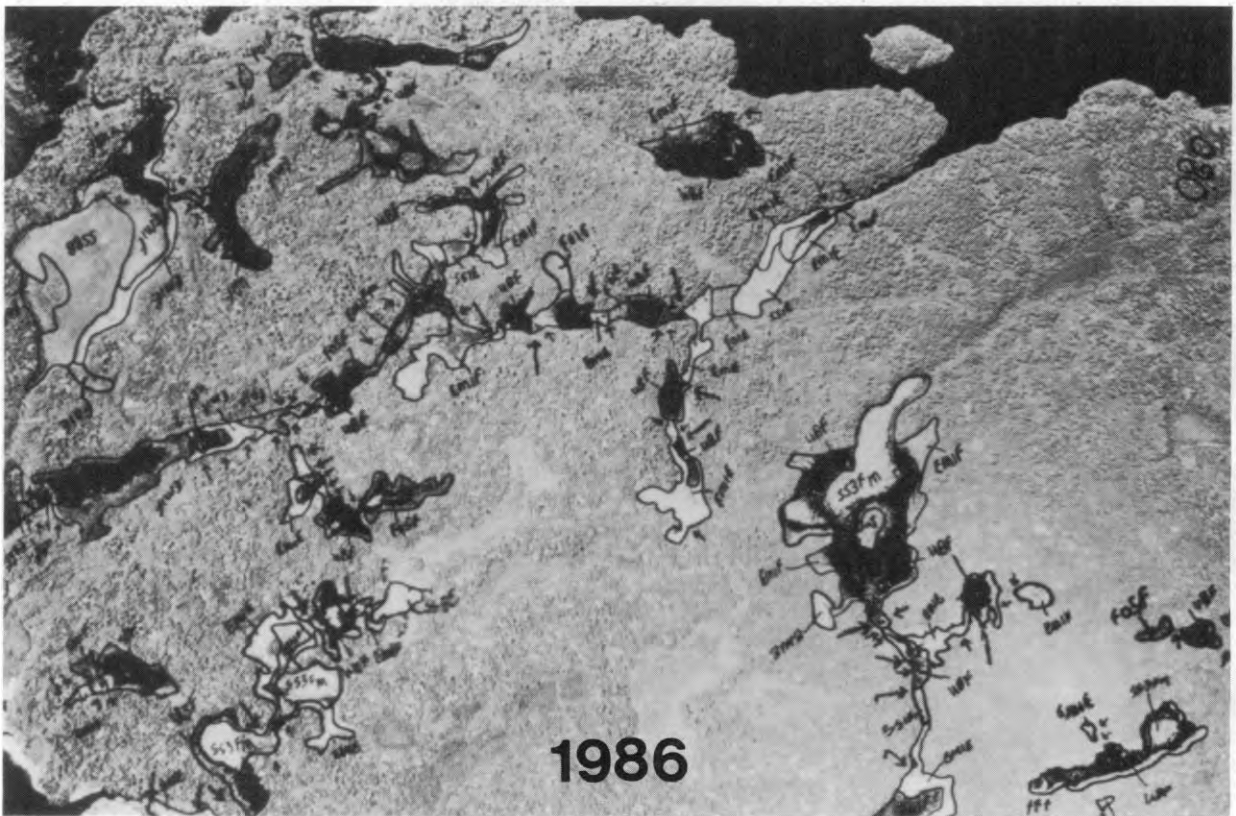
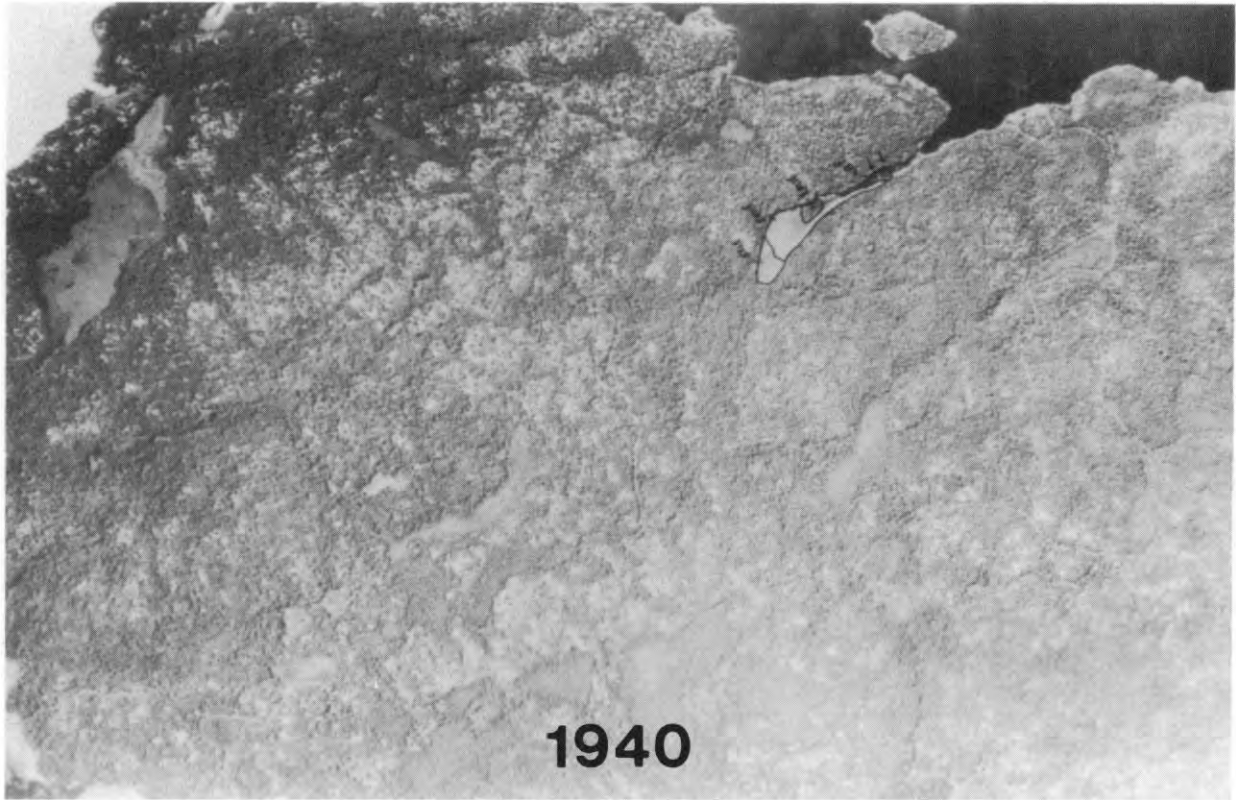


Figure 4. Beaver have had a substantial impact on the drainage network of the Kabetogama Peninsula, Minnesota, between 1940 and 1986. Shown is a representative area. The areas affected by beaver are enclosed by dark lines.

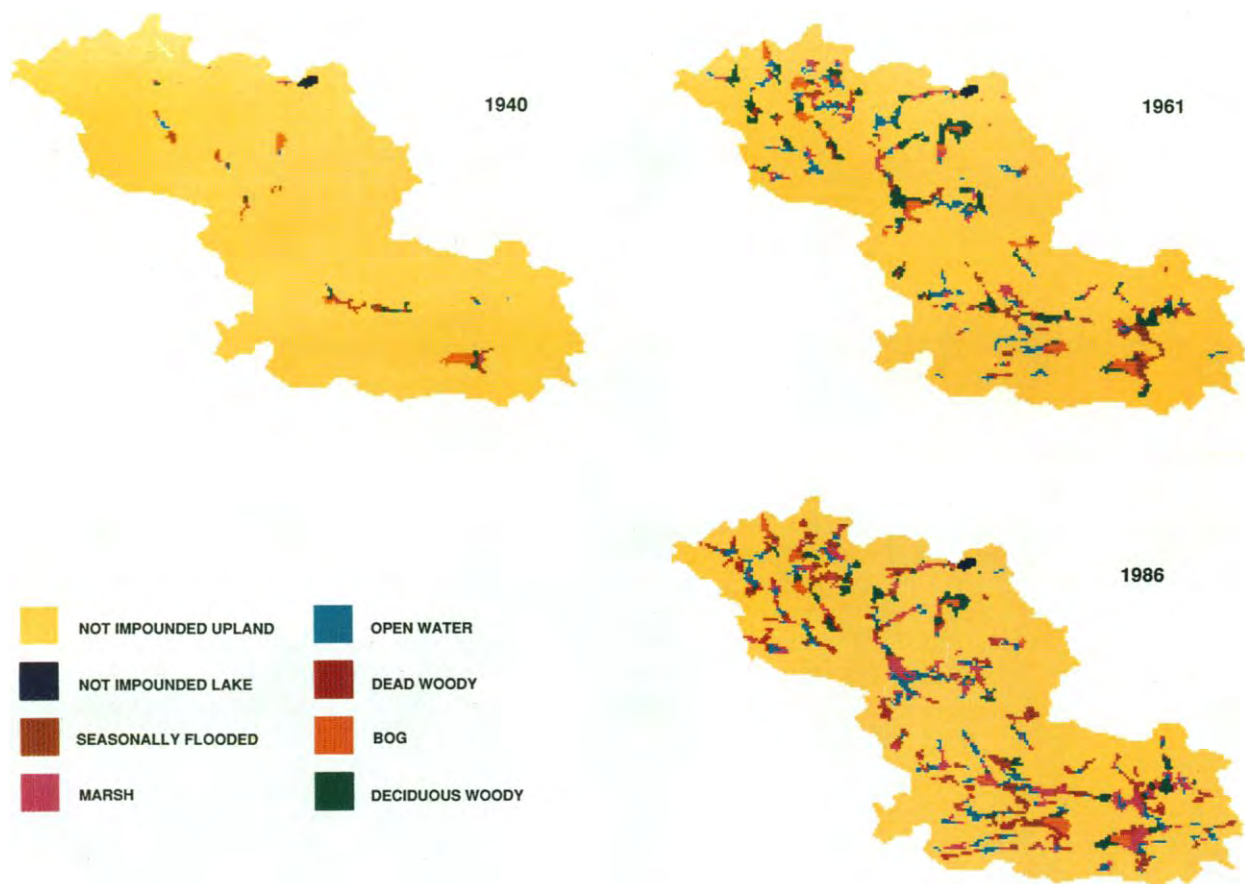


Figure 5. Vegetative change effected by beaver on a 45-square-kilometer watershed on the Kabetogama Peninsula. Colors of individual pixels represent different vegetative community types. Note the increase in dam density between 1940 and 1986, and the shift in vegetative community types over the same period.

and seasonally flooded meadow. By 1986, however, open water was the major impoundment type. The proportion of dead woody vegetation has also increased, because beaver are now flooding more forested areas than they were initially.

Some impoundment types are resistant to change, while others change rapidly as they are flooded and then abandoned by beaver. Bogs impounded by beaver change little over time because of the bog's ability to float up and down with beaver-induced water level changes, so the location and extent of beaver-impounded bog has remained relatively constant since 1961 (Figure 5). The most dynamic categories are open water, marsh, and seasonally flooded meadow, which replace each other in the cycle of beaver-pond abandonment.

The rate of conversion from one impoundment type to another has also changed as the beaver-impounded landscape has matured. In the 1940s, beaver were primarily creating new impoundments rather than altering existing ones. They converted uplands to wet woods, emergent marshes, or ponds (Figure 6). During the 1970s, new impoundments constituted only 9% of the changes, while 25% of the impoundments changed from one vegetation type at

the onset of the decade to another by the end. The majority of the impoundments, however, remained in the same vegetative category over the ten-year period.

Accompanying these vegetative and hydrologic trends are changes in the manner and extent to which nitrogen is cycled. We know, for example, that gradients of soil redox potential (Eh) and pH exist along transects from flooded pond sediments to adjacent upland soils (Table 3). Along this

Table 3. Average redox potential (Eh) and acidity (pH) in 1986 for soil and sediment in the vegetative-hydrologic cover types on the Kabetogama Peninsula, Minnesota.

Cover type	Eh (mv)		pH	
	\bar{x}	S \bar{x}	\bar{x}	S \bar{x}
Forest	638	22.2	3.93	0.27
Moist	587	32.1	4.72	0.28
Wet	-19	38.1	5.80	0.07
Pond	-180	35.7	6.01	0.06

hydrologic gradient, soil Eh increases from reducing values in flooded soils (less than -175 mV) to oxidizing values (more than 500 mV) in well-drained soils. Along the same hydrologic gradient, pH decreases more than two units. These shifts in Eh and pH represent a shift from anaerobic to aerobic conditions and, together with oxygen availability, affect processes controlling the concentrations and cycling of nitrogen in soils and sediments.

Flooding of soil increases the amount of reduced nitrogen (NH₄-N) and available forms of nitrogen in soil solutions. Under flooded conditions oxidized nitrogen species (NO₃-N) are rapidly lost through denitrification if the pond periodically becomes anaerobic.

Two properties of ponds set the stage for anaerobic conditions: their tranquil flow regime, which results in poor aeration, and the abundance of organic matter with its associated high oxygen demand. Flooding creates conditions where accumulations of particulate nitrogen are likely, further increasing the nitrogen content of beaver pond sediments. Our data indicate that plant-available nitrogen (KCl-extractable nitrogen plus dissolved nitrogen in the soil solution) are up to 4.3 times greater under flooded and waterlogged conditions and that beaver activity thus enhances nitrogen availability on the landscape (Table 4).

The relationship between flooding and nitrogen availability, coupled with the dramatic increase in beaver activity on the Kabetogama Peninsula, demonstrates that beaver have had a profound effect on the amount and distribution of nitrogen. During the period from 1940 to 1986, as a result of wetland creation by beaver, we calculate that available forms of nitrogen in pond sediments and the riparian zone has more than doubled (Table 4).

This available nitrogen is strategically situated in or near the aquatic environment where it can undergo substantially different fates than terrestrial nitrogen. For example, decomposition of organic matter in spring and early summer may deplete dissolved oxygen, leading to denitrification in late summer at the aerobic-anaerobic boundary.

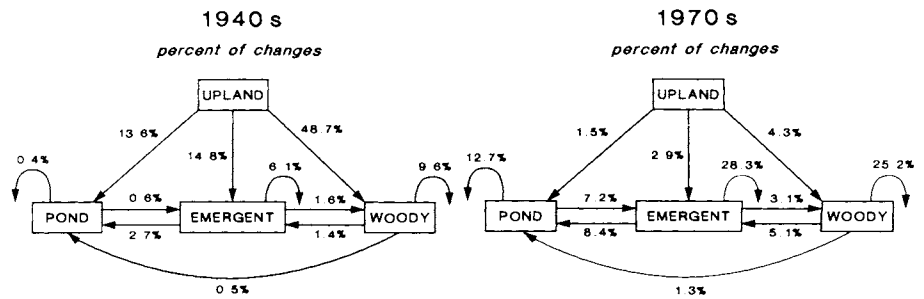


Figure 6. Impoundment conversions, by vegetative type. Expressed as percentage of total area impounded at the end of the decade. New impoundments are indicated by arrows emanating from the upland box. Conversion rates are compared for the 1940s and 1970s for the four-principal community types.

Changing image of stream ecosystems

Collectively, our studies and those of colleagues have produced two conceptual advances concerning stream ecosystems and raise a number of questions for future research. The conceptual advances address the organizational patterns of drainage networks with natural beaver populations and the role of beaver in the complex and dynamic successional pattern of vegetative patches on the landscape.

Drainage networks. Historically, streams throughout North America had different features than they do today (Bakeless 1950, Bartram 1791, Morgan 1868, Sedell and Froggett 1984). Where beaver were present in small streams (i.e., approximate or-

ders 1-4) there were numerous reaches with open canopy, large accumulations of detritus and nutrients, expanded wetted areas (including riparian zones), and substantial shifts to anaerobic biogeochemical cycles (Ford and Naiman 1988, Naiman et al. 1986). In middle-order streams (i.e., orders 5-8), beaver-cut wood from upstream and the immediate riparian zone augmented local allochthonous inputs. Debris accumulations resulted in massive storage of sediment and detritus in the main channel, often forming small islands. In large rivers (i.e., orders greater than 9) beaver utilized floodplains and backwaters, where they constructed dams and canals and cut large amounts of wood. Although these activities diversified stream habitat in the short term, centuries of sediment deposition behind beaver dams may

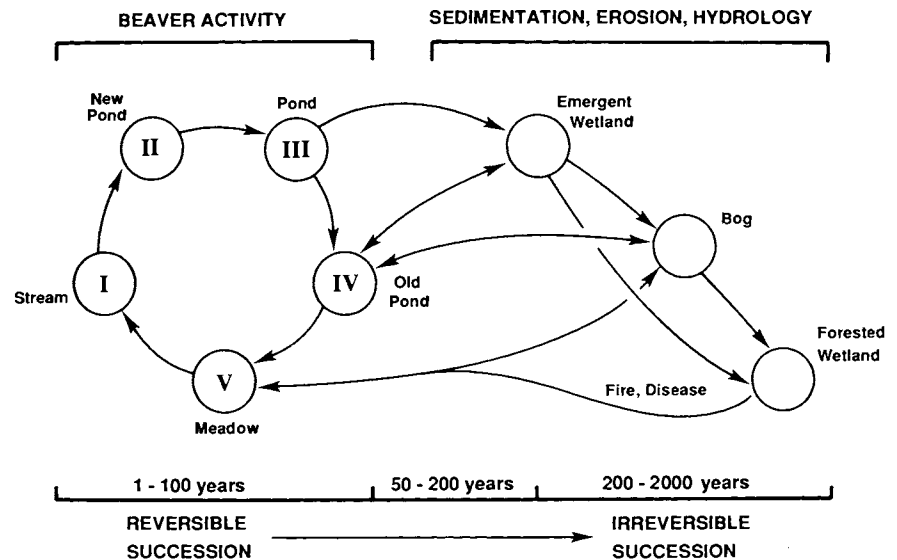


Figure 7. Beaver activity results in multisuccessional pathways, some of which can affect the landscape for centuries. Shown is our concept of how beaver may be affecting the boreal forest landscape of northern Minnesota.

have reduced floodplain complexity (Rutten 1967). The effects of this activity, which can still be seen in the terrestrial vegetation of meadowlands centuries after the extirpation of beaver (Ives 1942, Rudemann and Schoonmaker 1938), is testimony to their widescale influence on the landscape of North America.

These alterations had a substantial effect on the ability of stream ecosystems to resist and recover from disturbance. It has been suggested that modern streams are easily disturbed but have a high resiliency, returning rapidly to a predisturbance condition (Reichle et al. 1975, Webster et al. 1975). A factor contributing to the low resistance is the absence of large stable pools of biomass and nutrients with slow turnover rates to buffer the system from disturbance (e.g., expanded patch bodies). We have suggested that patch bodies associated with beaver ponds function as large-mass, slow-turnover components in stream ecosystems, and that streams with beaver ponds probably have a high resistance to disturbance (Naiman et al. 1986). Beaver also assist in returning the stream to a predisturbance condition, as they rebuild dams that accumulate water and sediment. This concept has been used in Wyoming and Oregon to rehabilitate streams after a long history of abuse.⁴

Vegetative succession. Originally, we envisioned that beaver build dams on a stream and through time the ponds age, are abandoned, meadows form and mature, and eventually a stream is reformed as a new channel is cut and the riparian vegetation matures. In the boreal forests of northern Minnesota, Quebec, and Alaska, however, we see a complex pattern that may involve the formation of emergent marshes, bogs, and forested wetlands, which appear to persist in a somewhat stable condition for centuries (Figure 7). The multisuccessional pathways are complex. Factors responsible for individual successional pathways include existing vegetation, hydrology, topography, fire, disease,

⁴B. Smith and J. R. Sedell, 1987, personal communication. Bureau of Land Management, Rock Springs, WY, and US Forest Service, Forest Sciences Laboratory, Corvallis, OR.

Table 4. Comparison of vegetative-hydrologic cover types, available forms of soil/sediment nitrogen and total nitrogen for 1940 and 1986 on the Kabetogama Peninsula, Minnesota.

Cover type	Area (ha)	Concentrations		Absolute amounts	
		Total nitrogen (kg/ha)	Available nitrogen (kg/ha)	Total nitrogen (kg)	Available nitrogen (kg)
1940:					
Forest	3508	3050	6.8	5.34×10^6	11.92×10^3
Moist	215	3216	7.7	0.35×10^6	0.83×10^3
Wet	28	2912	16.2	0.04×10^6	0.23×10^3
Pond	16	3543	29.8	0.03×10^6	0.24×10^3
Total	3767			5.76×10^6	13.22×10^3
1986:					
Forest*	0	3050	6.8	0	0
Moist	1367	3216	7.7	2.20×10^6	5.26×10^3
Wet	1029	2912	16.2	1.50×10^6	8.33×10^3
Pond	1371	3543	29.8	2.43×10^6	20.41×10^3
Total	3767			6.12×10^6	34.01×10^3

*For 1986 we assume the area affected by beaver is a maximum. Thus, no additional forest area will be affected.

herbivory, and beaver. We are not yet sure how the specific beaver activities interact in this process, but they are an essential component given their ability to influence hydrology and vegetation patterns. Certainly the dynamics of the system would be quite different without beaver. We are currently investigating these complex interactions using the Kabetogama Peninsula as a model, and we hope to be able to provide additional insights in the next few years.

Acknowledgments

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References cited

Aleksiuk, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). *J. Mammal.* 49: 759-762.

Bakeless, J. E. 1950. *The Eyes of Discovery*. J. B. Lippincott, Philadelphia, PA.

Bartram, W. 1791. *The Travels of William Bartram* (1928 ed.). Dover Publ., New York.

Bergerud, A. T., and D. R. Miller. 1977. Population dynamics of Newfoundland beaver. *Can. J. Zool.* 55: 1480-1492.

Cline, G. C. 1974. *Peter Skene Odgen and the Hudson's Bay Company*. University of Oklahoma Press, Norman.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. United States Dept. Interior, Fish and Wildlife Service, Washington, DC FWS/OBS-79/31.

Ford, T. E., and R. J. Naiman. 1988. Alteration of carbon cycling by beaver: methane evasion rates from boreal forest streams and rivers. *Can. J. Zool.* 66: 529-533.

Hays, W. J. 1871. Notes on the range of some of the animals in America at the time of arrival of the whitemen. *Am. Nat.* 5: 25-30.

Howard, R. J. 1982. Beaver habitat classification in Massachusetts, M.S. dissertation, University of Massachusetts, Amherst.

Howard, R. J., and J. S. Larson. 1985. A stream habitat classification for beaver. *J. Wildl. Manage.* 49: 19-25.

Ives, R. L. 1942. The beaver-meadow complex. *J. Geomorphology* 5: 191-203.

Jenkins, S. H. 1980. A size-distance relation in food selection by beavers. *Ecology* 61: 740-746.

Jenkins, S. H., and P. E. Busher. 1979. *Castor canadensis*. *Mamm. Species* 120: 1-9.

Johnson, D. R., and D. H. Chance. 1974. Pre-settlement overharvest of upper Columbia River beaver populations. *Can. J. Zool.* 52: 1519-1521.

Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. *Landscape Ecol.* 1: 47-57.

McDowell, D. M., and R. J. Naiman. 1986. Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia* 68: 481-489.

McGinley, M. A., and T. G. Whitham. 1985. Central place foraging by beavers (*Castor canadensis*): test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). *Oecologia* 66: 558-562.

Moloney, F. X. 1967. *The Fur Trade in New England, 1620-1676*. Archon Books, Ham-

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Morgan, L. H. 1868. *The American Beaver and his Works*. J. B. Lippincott, Philadelphia, PA.

Naiman, R. J., H. Décamps, J. Pastor, and C. A. Johnston. In press. The potential importance of boundaries to fluvial ecosystems. *J. North Am. Benthological Soc.*

Naiman, R. J., and J. M. Melillo. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). *Oecologia* 62: 150-155.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67: 1254-1269.

Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 155-177 in D. J. Horn, G. R. Stairs, and R. D. Mitchell, eds. *Analysis of Ecological Systems*. Ohio State University Press, Columbus.

Pringle, C. M., R. J. Naiman, G. Bretschko, J. Karr, M. Oswood, J. R. Webster, R. Welcomme, and M. J. Winterbourn. In press. Patch dynamics in lotic ecosystems: The stream as a mosaic. *J. North Am. Benthological Soc.*

Reichle, P. E., R. V. O'Neill, and W. F. Harris. 1975. Principles of energy and material exchange in ecosystems. Pages 27-43 in W. H. van Dobben and R. H. Lowe-Connell, eds. *Unifying Concepts in Ecology*. Dr. W. Junk, The Hague, Netherlands.

Rudemann, R., and W. J. Schoonmaker. 1938. Beaver dams as geologic agents. *Science* 88: 523-525.

Rutten, M. G. 1967. Flat bottom glacial valleys, braided rivers and beavers. *Geol. Mijnbouw* 46: 356-360.

Sedell, J. R., and J. L. Froggett. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, USA from its floodplain. *Verh. Int. Verein. Limnol.* 22: 1828-1834.

Seton, J. R. 1929. *Lives of game animals. Vol. 4, Part 2, Rodents, etc.* Doubleday, Doran, Garden City, NY.

Shaw, S. P., and C. G. Fredine. 1971. Wetlands of the United States: Their extent and value to waterfowl and other wildlife. United States Dept. Interior, Fish and Wildlife Service, Circular 39, Washington, DC.

Voigt, D. R., G. B. Kolenosky, and D. H. Pimlott. 1976. Changes in summer food of wolves in central Ontario. *J. Wildl. Manage.* 40: 663-668.

Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient recycling and the stability of ecosystems. Pages 1-27 in F. G. Howell, J. B. Gentry, and H. M. Smith, eds. *Mineral Cycling in Southeastern Ecosystems*. Energy Research and Development Administration Symposium Series CONF-740513, Oak Ridge, TN.