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Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology

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Abstract

Beaver *(Castor canadensis)* impoundments are used to illustrate the effect of large animals on the boundary dynamics of 'patch bodies', volumetric landscape units which have surficial boundaries with upper and lower strata, and lateral boundaries with adjacent patches within the same stratum. Patch bodies created by beaver impoundments include the beaver pond, the aerobic soil beneath the pond, and the underlying anaerobic soil. Beaver herbivory in the riparian zone creates an additional patch body concentric to the pond. Beaver and water are the primary biotic and abiotic vectors mediating fluxes across lateral patch body boundaries; vegetation and microbes are the primary biotic vectors mediating fluxes across surficial patch body boundaries. Basin geomorphology affects the permeability of pond boundaries *(i.e.*, their ability to transmit, energy and materials) by affecting the kinetic energy of water, the surface-to-volume ratio of the impoundment, and the movement of beaver between the pond and the riparian foraging zone. We suggest that: (1) permeability of lateral boundaries to abiotic vectors is a function of kinetic energy; (2) within-patch retention of particulate matter transferred by abiotic vectors across lateral boundaries is maximized by a decrease in kinetic energy; (3) lateral patch boundaries between safe refuge and a resource used by an animal vector are most permeable when they are narrow; and (4) total amount of energy and materials transferred across surficial boundaries is maximized by increasing surface area.

Introduction: Patch bodies and their boundaries

Most discussions of spatial patterning portray patches as two-dimensional areas pieced together on the surface of the landscape (Levin and Paine 1974, White and Pickett 1985, Forman and Godron 1986). While this two-dimensional view of patches is appropriate for ecosystems where the substrate is a surface plane (e.g. rocks providing holdfast surfaces for intertidal organisms; Paine and Levin 1981, Sousa 1985), it is less appropriate for ecosystems with vertically-stratified resources. For example, although lakes are surficially homogeneous, their vertical stratification into epilimnion and hypolimnion has an important effect on resource distribution (Hutchinson 1957). Each layer is analogous to an environmental resource patch (Forman and Godron 1986): organisms and processes differ between adjacent layers because of differing environmental conditions and resources.

We use the phrase *patch body* to describe volumetric landscape units which have boundaries with upper and lower strata, in addition to boundaries with adjacent patches. This use is analogous to the concept of water body or soil body (Buol *et al.*

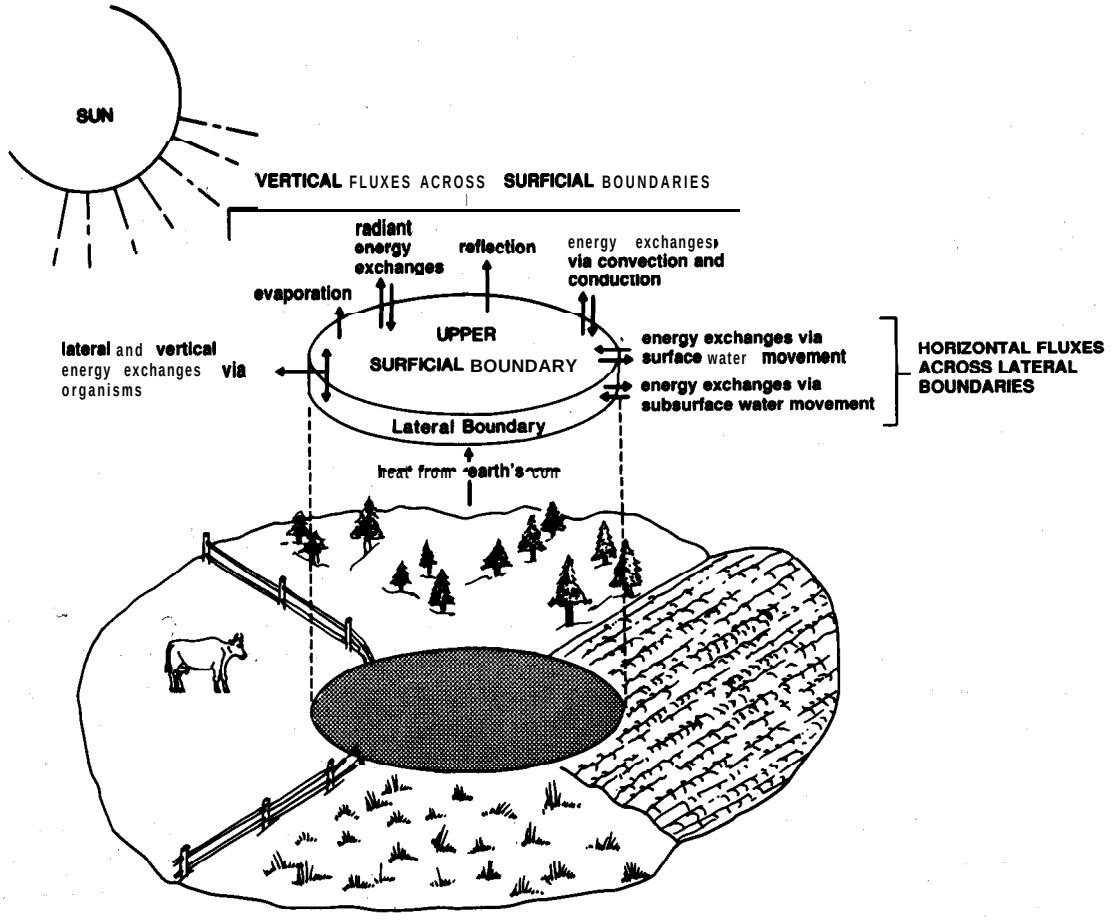

Fig. 1. A patch body extracted from a landscape mosaic, with associated energy fluxes (after Buol *et al.* 1973).

1973). ***Surficial boundaries*** separate overlying patch bodies, while ***lateral boundaries*** separate adjacent patch bodies on the same plane (Fig. 1). Transfers across surficial boundaries have a vertical direction while transfers across lateral boundaries are primarily horizontal.

Large animals can play a significant role in the development of some patch bodies, as well as the movement of energy and materials across their boundaries. Animals alter patch bodies through herbivory (Botkin *et al.* 1981, McNaughton 1985, Hatton and Smart 1984), translocation of nutrients and biomass (Kitchell *et al.* 1979, Wiens 1985) and physical perturbation of the environment (Bratton 1974, 1975; Turner 1985). Previous studies of animal-landscape interactions have focused primarily on aboveground patch disturbances, ignoring the effects of those disturbances within the soil and water bodies below the surface. We have chosen beaver ***(Castor canadensis)*** to illustrate how large animals affect entire patch bodies and landscape processes associated with the patches.

Beaver have the ability to alter their physical environment more than any other animal, creating a layered assemblage of patch bodies, each with varying dimensions and characteristics. A beaver pond and associated riparian zone include the following patch bodies: the bedrock, the anaerobic soil, the aerobic soil, the pond, the browse zone concentric to the pond, and the overlying atmosphere (Fig. 2). Although at a higher perceptual scale each of these patch bodies could be considered as layers in the stratified structure of a composite patch body, we treat them as individual patch bodies because they possess different resources, processes, and biota.

Each patch body has lateral boundaries with

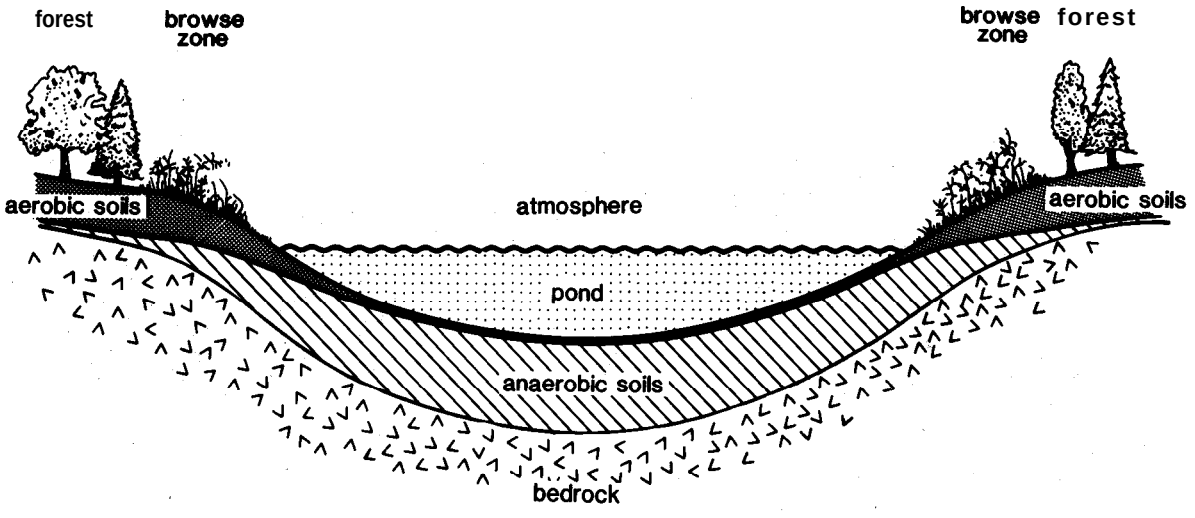

Fig. 2. Patch bodies associated with beaver ponds.

other patch bodies on the same stratum (e.g., the boundary between the pond and the browse zone), and surficial boundaries with patch bodies in upper or lower strata (e.g., the boundary between the pond and the atmosphere). Beaver affect fluxes of materials and energy across these boundaries directly by foraging, and indirectly by altering physical, chemical, and biotic conditions within patch bodies. The magnitude of beaver-mediated fluxes across lateral vs. surficial boundaries is modified by the geomorphology of areas they impound.

The specific objectives of this paper are to: (1) describe patch bodies and boundaries which are associated with beaver impoundments; (2) discuss the diffusive and vector-mediated transfer of materials and energy across those boundaries; and (3) discuss how cross-boundary transfers are moderated by impoundment topography.

Creation of patch bodies by beaver

Beaver are a keystone species (sensu Paine 1966), which affect ecosystem structure and dynamics far beyond their immediate requirements for food and space (Naiman and Melillo 1984). Beaver dams and canals modify edaphic conditions by altering water flow. Where before there was only a narrow stream corridor among the forest matrix, a beaver dam creates a patch of water with very different properties than the stream and forest it replaced. In natural landscapes, beaver ponds may be thought of as spot disturbance patches in a matrix of upland forest (Forman and Godron 1981, Remillard *et al.* 1987).

As beaver harvest trees and shrubs in the riparian zone surrounding their pond, a second patch develops concentric to the first. Beaver are central place foragers (Orians and Pearson 1979), so their feeding activities are confined to the riparian zone within about 100 m of their pond (McGinley and Whitham 1985, Jenkins 1980, Hodgon and Hunt 1953, McDonald 1956). Riparian zones dominated by the deciduous species preferred by beaver, such as aspen (*Populus tremuloides*), may be virtually clear-cut (Fig. 3). The stand becomes more open, and shrubs and root suckers become the dominant growth form. By reducing vegetation height and altering biomass partitioning, beaver cause vertical as well as horizontal stratification when creating these patches.

Where beaver raise the water table in soils adjacent to the pond, they create an important subterranean patch body. Anaerobic conditions within this patch body limit the biota to organisms which can either use compounds other than oxygen for respiration, or can import oxygen from overlying aerobic strata. Beaver impoundments which flood wetlands may also cause a floating mat of peat and

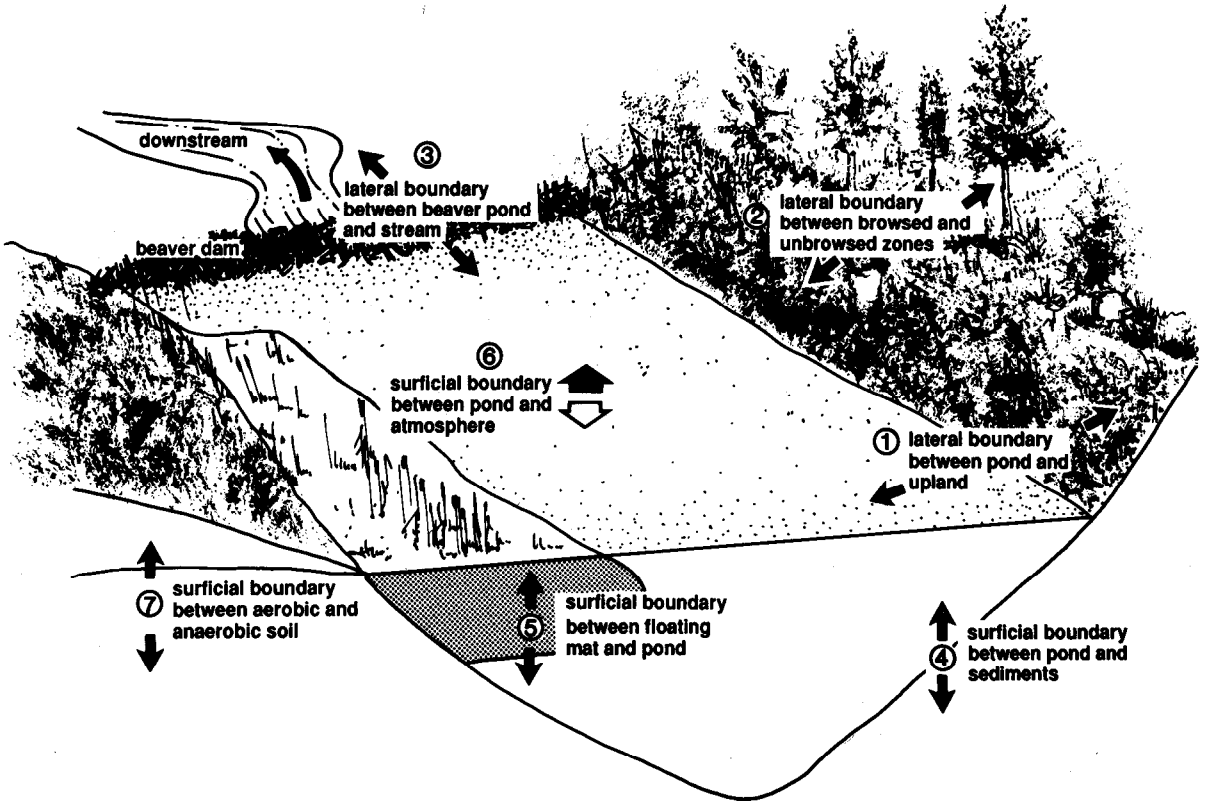

Fig. 3. Selected boundaries of patch bodies associated with beaver impoundments.

vegetation to separate from the mineral substrate (Rebertus 1985), creating a new patch body at the pond surface.

The boundaries of beaver pond patch bodies coincide with spatial discontinuities in soil, water, and/or vegetation properties (Fig. 3). Lateral boundaries occur between (1) the pond and the riparian zone, (2) the foraged and unforaged riparian zones, and (3) the pond and the stream. Surficial boundaries occur between the (4) pond and its sediments, (5) the floating mat and the pond, (6) the pond and the atmosphere, and (7) the aerobic and anaerobic soil strata. In some instances these boundaries are sharp (e.g., the pond/stream juncture at the beaver dam); in others they are gradual (e.g., the pond/stream juncture at the upstream end of the pond).

Fluxes across impoundment boundaries

Boundaries differ in permeability, their ability to transmit energy and materials. The pond surface is more permeable to light than is the soil surface, for example. Like a semipermeable membrane, some forms of energy and materials pass more readily through these boundaries than others. The pond surface transmits some light wavelengths better than others, so the spectral distribution of underwater light differs from that of light transmitted through the atmosphere.

Fluxes of energy and materials across patch body boundaries may be increased by abiotic vectors (i.e., physical forces) or biotic vectors (i.e., organisms) that actively move materials or energy in the system (Forman 1981). As used by Wiens *et al.* (1985), wind and moving water are abiotic vectors, but fluxes caused by resource concentration gradients and passive diffusion are not. Vectors can increase the permeability of a boundary by actively transporting materials between two patch bodies. For example, although the boundary between a beaver pond and the atmosphere is normally not permeable to fish, an osprey (*Pandion haliaetus*)

Table 1. Characteristics of boundaries associated with beaver ponds. Boundary numbers are shown in Fig. 3

Boundary number	Description	Boundary type	Primary vector(s)	Primary material(s) transported across boundary
1	pond/riparian zone	lateral	beaver wind water	wood plant litter dissolved nutrients
2	browsed riparian/ unbrowsed riparian	lateral	wind	plant litter
3	pond/stream (dam) pond/stream (upstream)	lateral lateral	water water	dissolved nutrients sediment, organic matter, nutrients
4	pond/bottom	surficial	water	sediment, organic matter
5	peat mat/pond	surficial	water	organic matter, nutrients
6	pond/atmosphere	surficial	wind	gases
7	aerobic/anaerobic soil	surficial	microbes, vegetation	gases, nutrients, organic matter

makes it permeable by transporting fish from the pond to its nest.

Previous use of the term vector excluded plants and other immobile organisms, presumably because they have little effect on fluxes across the lateral boundaries which separate adjacent patches. However, sessile organisms can have a pronounced effect on transfers across surficial boundaries. Rooted plants actively transfer gases down and nutrients and water up across the soil surficial boundary (Dacey 1981). Microorganisms which fix or release gaseous compounds increase gaseous fluxes across surficial boundaries by altering concentration gradients (Reddy *et al.* 1976). We consider any organism which alters the exchange of materials across a patch body boundary to be a biotic vector.

Beaver are important biotic vectors, affecting fluxes of materials and energy across boundaries in two major ways: (1) they actively transport materials across the riparian/pond boundary, and (2) they alter the action of other biotic and abiotic vectors by changing the physical environment (Table 1).

Material transport by beaver

An individual beaver cuts about a metric ton-of wood for growth and maintenance annually (Howard 1982, Howard and Larson 1985), which results in substantial inputs of organic matter and nutrients to ponds. Naiman and Melillo (1984) calculated that the feeding activities of a colony of six beaver could contribute as much as 10.3 g $N/m^2/yr$ to a beaver pond in Quebec, potentially increasing nitrogen inputs by 145%. Fallen wood from dead trees in new beaver impoundments and wood transported into the pond for dam and lodge construction augment this input.

The temporal distribution of material transport by beaver varies because of seasonal changes in beaver foraging. Upland foraging in northern latitudes is most intense during the fall and early spring (Jenkins 1979), so interpatch transfers of biomass and nutrients would be at a maximum. Beaver rarely cross the pond boundary over winter, and during summer they largely forage within their ponds for herbaceous and aquatic vegetation (Bradt 1938, Hall 1960, Svendsen 1980, Northcott 1971). At

these times, there is little beaver-mediated transport of organic matter and nutrients into the pond.

Although beaver can actively move materials both with and against. the physical gradient, the predominant direction of movement is downslope from the riparian zone into the pond, especially in the fall when beaver stockpile woody stems in underwater food caches. During the summer, net movement of nutrients would be upslope if beaver defecate on land after feeding on pond vegetation. If the beaver both feed and defecate on land, however, there would be no net movement of nutrients. Buech (1984) has observed that both feeding and defecation in captive beaver were most intense during the early evening, a time when they are most likely to be found in riparian zones.

Indirect effects of beaver on cross-boundary fluxes

Beaver dams indirectly affect fluxes of materials across boundaries by increasing water body dimensions. Increased water depth decreases the transmittance of solar energy to the bottom, which may contribute to the decrease in periphyton production *(i.e.,* microfloral growth on bottom materials) documented by Naiman *et al.* (1986). Increased water surface increases riparian inputs to the pond by increasing the collecting area for plant litter (Fig. 3, boundary 1: Naiman *et al.* 1986).

Beaver-induced alterations to the water table cause substantial changes in the type and magnitude of microbially-mediated fluxes across the lower surficial boundary of the pond (Fig. 3, boundary 4). The substrate conditions created by beaver ponds increase nitrogen fixation (Francis *et al.* 1985), methane flux to the atmosphere (Ford and Naiman, unpublished data), and probably denitrification (Keeney 1973, Engler and Patrick 1974) and H_2S emissions (Connell and Patrick 1969). These processes rely on the molecular diffusion of gases (i.e., N_2, methane, H_2S) and ions *(i.e.,* NO_3^-), which may control their rates. For example, the upward diffusion of ammonium from the anaerobic soil body limits the rate of nitrification in the aerobic soil body, and the downward diffusion of nitrate limits denitrification (Reddy et *al.* 1976).

Beaver dam construction and foraging also indirectly affect fluxes across boundaries by influencing the kinetic energy of abiotic vectors. When beaver dams decrease water velocity, the transporting capacity of the water is reduced (Hjulstrom 1939) resulting in sedimentation (Fig. 3, boundary 4). Likewise, an abrupt change in canopy height between the browsed and unbrowsed zones would alter wind direction and force, affecting snow deposition (Van Eimern *et al.* 1964, Geiger 1965, Grace 1977).

Geomorphic controls on boundary properties in beaver impounded uplands and wetlands

Streams flowing through uplands tend to have V-shaped valleys, so new beaver ponds created by flooding uplands have steeply sloping bottoms with closely spaced elevational contours (Fig. 4). As a result, upland ponds are generally small and there is little change in surface area as the water level fluctuates. The boundary between pond and upland is abrupt, and the perimeter-to-surface area ratio is low because of the relatively straight boundary. There is little or no zonation of wetland vegetation around the pond since edaphic conditions change abruptly from aquatic to terrestrial with little transition zone between them.

In contrast, wetlands have extensive floodplains (Johnston 1982), such that a low beaver dam can impound a relatively large surface area. The pond is broadly U-shaped in cross section, and water depth is shallower and more uniform throughout (Fig. 4). The pond boundary is wide and diffuse because the land flooded has a small elevational gradient. Small variations in microtopography, such as those created by sedge tussocks *(Carex stricta, Carex aquatilis),* increase boundary sinousity and result in a high perimeter-to-surface area ratio. These boundaries are often made even more sinuous by the beavers themselves, who dig canals to create better access to riparian food reserves (Fig. 4).

Due to these basic differences in basin geomorphology, beaver impoundments appear to cause less alteration of ecosystem level processes in wet-

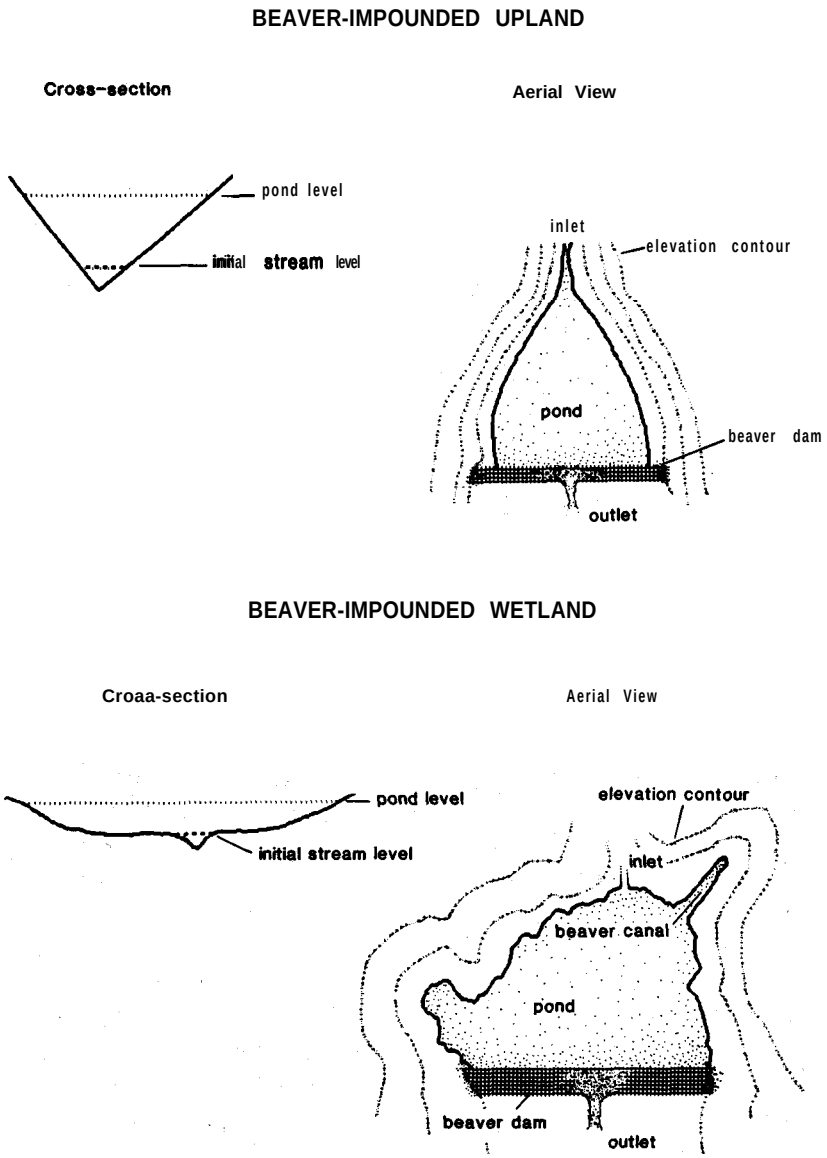

Fig. 4. Cross-sectional and plan views of a hypothetical beaver pond created by flooding an upland vs. a wetland.

lands than in uplands because wetland soils and vegetation were already under saturated conditions before impoundment (Kelley *et al.*, unpublished data). Anaerobic soil processes (e.g., methanogenesis) predominate in both wetlands (Gambrel1 and Patrick 1978, Ponnamperuma 1984) and beaver ponds (Ford and Naiman, unpublished data), whereas aerobic processes (e.g., carbon dioxide evolution) predominate in uplands. Both wetlands and beaver ponds retain substantial carbon (Armentano *et a/.* 1984, Naiman *et al.* 1986) and sediments (Johnston *et al.* 1984, Ives 1942).

Beaver dams which flood uplands reduce the kinetic energy of the stream more than those which flood wetlands. The gradient of the inlet stream imparts substantial kinetic energy to the water vector, so the upstream pond boundary is very permeable. The downstream pond boundary (the beaver dam in Fig. 3) is much less permeable to water, and the net results is storage of water and particles in the beaver pond. Quiescent conditions within the pond promote the flux of particulate organic matter and

nutrients from the incoming water to the underlying substrate (Fig. 3). This is substantiated by the work of Ives (1942), who observed maximum sedimentation at the upstream end of beaver ponds, and Naiman et *al.* (1986) and Naiman and Melillo (1984), who documented large standing stocks of carbon and nitrogen in the substrate of beaver ponds

The high surface-to-volume ratio of patch bodies in beaver-flooded wetlands promotes the exchange of energy and materials across surficial boundaries (Fig. 3). Fluxes which are directly proportional to surface area, such as solar radiation and evaporation, are maximized. Plant biomass is-optimized by the large rooting area and high light availability per unit volume of pond water: Gaseous (oxygen, evapo-transpiration) and energy (photosynthesis) exchanges between the rooting zone and the atmosphere are increased by the large surface area of emergent plants, which act as extensions of the pond/sediment boundary. Total fluxes of compounds involved in microbal transformations at or near the aerobic/anaerobic interface (e.g., methanogenesis, denitrification, H_2S emission) are increased by the larger total surface area of the anaerobic soil body, assuming that other environmental conditions remain the same. If the microbial environment is improved as well (e.g., more and/or better quality organic matter, increased temperature), total fluxes would increase even more.

Some spatial configurations of organic matter in many beaver-flooded wetlands further increase the surface-to-volume ratio of the aerobic soil body by modifying its surface morphology. For example, tussock sedges form cylindrical mounds of organic matter up to 1 .O m high at densities of up to five tussocks per m^2 (Costello 1936). The large area of this hummocky surface maximizes exchanges across the aerobic/anaerobic boundary.

The morphology of lateral pond boundaries affects their permeability to beaver as biotic vectors. Beaver are more susceptible to predation on land than in water, so quick access to deep water is important for survival when foraging on the upland (McGinley and Whitham 1985). The relatively steep sides and straight boundary of flooded uplands provide good access completely around the pond, allowing beaver to forage uniformly throughout the riparian zone. In contrast, the broad riparian/pond boundary around wetland ponds forces beaver to travel much farther to reach the safety of deep water, and riparian foraging is restricted to trails leading from canals and other extensions of the wetland pond boundary. This results in scattered riparian browse patches, rather than the unbroken concentric patch typical of upland ponds. Thus, a lateral boundary between a safe refuge (i.e., the pond) and a resource used by the beaver (i.e., the riparian forest) is most permeable where it is narrow.

The effect of pond geomorphology on foraging patterns is demonstrated by data in Table 2. Foraging occurred in 83% of sample plots randomly located within 20 m of a flooded upland pond, but only 33% of plots within the same distance of a flooded wetland pond downstream. Even though the area subject to browsing is nearly identical at both ponds (about 12,900 m^2) riparian foraging was less evenly distributed around the flooded wetland pond. Biotic (e.g., wood transfer) and abiotic (e.g., trail erosion) vector transfers at the wetland pond. were concentrated along specific radii.

Conclusions

Beaver create patch bodies through browsing pressure, an ability which they share with many other large animals. Like other animals, beaver affect the

Table 2. Comparison of beaver foraging patterns in the riparian zones around a flooded wetland and a flooded upland pond near Duluth, Minnesota

Characteristic	Wetland pond	Upland pond
1. Perimeter of upland riparian zone, meters	800	500
2. Mean maximum foraging radius, meters (± S.D.)	16.1 ± 10.9	25.8 ± 12.7
3. Area of riparian foraging, sq. meters (row 1 * row 2)	12,880	12,900
4. Foraging occurrence within 20 m of pond (% of plots browsed)	33%	83%

spatial distribution of landscape resources by transporting materials across patch body boundaries. Unlike most other animals, however, beaver can also create patch bodies by modifying their physical environment, which indirectly affects other fluxes of energy and materials across lateral and surficial boundaries.

The impoundment of water by beaver creates or modifies the following patch bodies: the beaver pond, the aerobic soil beneath the pond, and the underlying anaerobic soil. Beaver herbivory in the riparian zone creates an additional patch body concentric to the pond. Beaver and water are the primary biotic and abiotic vectors mediating fluxes across lateral patch body boundaries; vegetation and microbes are the primary vectors mediating fluxes across surficial patch body boundaries.

Basin geomorphology affects the magnitude of these fluxes because of its relationship to the kinetic energy and surface-to-volume ratio of ponded water, and should be taken into consideration when discussing ecological structure and function of beaver-created patch bodies. The high surface-to-volume ratio of patch bodies in beaver-impounded wetlands maximizes exchanges across surficial boundaries (e.g., insolation, gaseous diffusion). Emergent vegetation and special configurations of organic matter accumulation in wetlands (i.e., peat mats, sedge tussocks) increase fluxes across surficial boundaries by further increasing surface area. The broad lateral boundary reduces the effect of beaver-mediated transfers between the riparian foraging zone and the pond by restricting beaver movements to widely-spaced nodes in the boundary.

The steeper slope of upland surfaces decreases the surface-to-volume ratio of pond bodies and anaerobic soil bodies associated with beaver-impounded uplands, but increases fluxes across lateral boundaries. Fluxes mediated by water and beaver are favored by the kinetic energy and protection from predation provided to these respective vectors. The uniform permeability of the riparian/pond boundary around upland ponds affects the spatial configuration of beaver foraging, which in turn affects the geometry of the boundary between browsed and unbrowsed riparian zones.

Several generalities regarding landscape boundary dynamics can be derived from-the spatial and temporal heterogeneity of beaver-created patch bodies and their associated fluxes: (1) The permeability of a lateral boundary to abiotic vectors is a function of the kinetic energy of the vector. Both wind and water have higher transporting capacities at higher velocities. (2) Within-patch retention of particulate matter transferred by abiotic vectors across lateral boundaries is maximized by a decrease in kinetic energy. For waterborne transfers, this would occur where the patch boundary coincides with a decrease in slope, such as the boundary between an upland stream and a beaver impoundment. For wind-borne transfers a decrease in kinetic energy would occur where there is a change in vertical structure, such as a row of trees. (3) A lateral patch boundary between safe refuge and a resource used by an animal vector is most permeable when it is narrow. We have used the example of beaver foraging adjacent to upland vs. wetland ponds, but believe that the principle holds for other animals (e.g., ungulate foraging movements between a field and forest edge). (4) The total amount of energy and materials transferred across surficial boundaries is maximized by increasing patch body surface area. Most vertical transfers which are not vector mediated (e.g., evaporation, insolation) and many vertical transfers mediated by biotic vectors (e.g., denitrification, rooting zone aeration) are proportional to surface area. Factors which increase surface area, such as emergent leaf surface and microtopography, maximize these total fluxes.

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