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Stream ecosystem theory

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With 1 figure and 6 tables in the text

Introduction

At one level of resolution all streams and rivers are the same; at another they all differ. The former extreme is rather uninteresting. All contain water and eventually find their way downslope to the next sized tributary, a lake, or the ocean. At the other extreme, recognition that each is different (e. g. no two have exactly the same species composition and abundances), ignores many patterns that transcend streams, watersheds, whole basins, biomes (i. e. with latitude) and even continents (i. e. with longitude). The preoccupation with classification and the economic incentive for management of ecosystems has provided impetus for recognition of patterns and understanding their underlying bases.

Similarities among running waters ecosystems have been recognized for some time (e. g. Thienemann 1925; Leopold et al. 1964; Hynes 1970). Biologically relevant geomorphic similarities result from a limited number of possibilities: channel downcutting and lateral excursion, and sediment transport and deposition. Lotic organisms have adapted, through millions of years of evolution and 10,000 years or more of population acclimatization, to occupy one of several habitat types, broadly classed as either erosional or depositional, and feed on one of the food resource categories available (Table 1). These limited combinations of general physical channel conditions and biotic adaptations are the basis of pattern similarity. The major tenet of this paper is that stream and river-side vegeta-

Table 1. Invertebrate examples of basic adaptations in prototype lotic systems (modified from Cummins 1973, 1974; Cummins & Klug 1979; Merritt & Cummins 1984).

Lotic habitat	Dominant habitat adaptations	Dominant functional feeding groups	Dominant organic food resources
Erosional (riffles, rapids, cascades runs, glides)	Clingers	Scraper	Periphyton
		Filtering collectors	FPOM (sloughed periphyton, transport-suspended and bed-load)
	Swimmers	Gathering collectors	Depositional FPOM
	Burrowers (crevice dwellers)	Gathering collectors	Depositional FPOM
		Shredders	Depositional CPOM macrophytes
Depositional (pools, margins, off channel, side channel)	Sprawlers	Gathering collectors	Depositional FPOM
		Shredders	Leaf packs
	Burrowers	Gathering collectors	Depositional FPOM
		Shredders	Leaf packs, wood
	Climbers	Shredders	Vascular hydrophytes
		Piercers	Macroalgae

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tion, the riparian zone, exerts the primary control over biotic associations. This control is mediated both through physical channel influences (e. g. large woody debris, root bank stabilization, shading, etc.) and the nature of the organic inputs (solutions or particles) from outside the wetted channel (allochthonous) or in-stream plant growth (autochthonous). Such corridors of stream-side vegetation are inseparable from the biology in the channel and constitute a ribbon of continuity responsible for many universally discernable patterns.

Lotic paradigms

Some selected examples of general attempts at classifying patterns in running waters and understanding their underlying controls are summarized in Tables 2 and 3. The riparian zone has not been specifically included as a critical associated component in most runnning water ecosystem paradigms. Geomorphic (especially altitude and gradient) and hydrologic (average and peak flows) associated thermal regimes (with distance along the drainage profile) have been used most frequently in classification schemes. For example, these have been viewed as the major components

Table 2. Examples of control parameters in some exemplary lotic ecosystem paradigms.

Paradigm	Geomorphic (gradient, stream order)	Hydrologic	Thermal	Riparian influence	Temporal perspective	References
Longitudinal zonation	X	X	X			Huet 1954; Schmitz 1955; Botosaneanu 1979
Succession				X	X	Margalef 1960
River Continuum	X	X	X	X	X	Minshall et al. 1983
Spiralling		X				Elwood et al. 1983
Serial discontinuity	X	X	X			Ward & Stanford 1983
Riparian control	X	X		X	X	Cummins et al. 1983

Table 3. Examples of biotic components in some exemplary lotic ecosystem paradigms.

Paradigm	Organic matter processing (budgets)	Primary production, community respiration (P/R)	Species diversity, community structure atributes	Functional organization (groups)	Reference
Longitudinal zonation			+ (fish; invertebrates)		Huet 1954; Schmitz 1955; Illies & Botosaneanu 1963
Succession			+ (primarily algae)		Margalef 1960
River continuum	+	+	+	+	Minshall et al. 1983
Spiralling	+	+		(+)	Elwood et al. 1983
Serial discontinuity	+	+		+	Ward & Stanford 1983
Riparian control	+	+	+	+	Cummins et al. 1983

controlling patterns in fish and invertebrate zonation (Ide 1935; Ruttner 1952; Huet 1954; Schmitz 1955; Illies & Botosaneanu 1963; Botosaneanu 1979). Margalef (1960), relying almost exclusively on algal associations, viewed the succession of pioneer to climax communities as a basic pattern transcending stream size and recognizable on an extra-regional level.

In the last two decades there has been the simple, but important, recognition that running waters differing in expression of the basic geomorphic (e. g. size, gradient), hydrologic (e. g. discharge), and biotic (e. g. community organization) characteristics are linked together in drainage networks (aquatic-aquatic) and functionally are inseparably linked to the stream-side vegetated zone (riparian zone, upper bank, floodplain, etc.) (e. g. Cummins 1974; Hynes 1975; Vannote et al. 1980). The gradual changes along the drainage net have been viewed as a continuum of physical gradients and associated biotic adjustments; organisms become adapted and remain acclimatized to the most probable physical state (quasi-equilibrium; Shumm & Lechty 1956) along such continua (Vannote et al. 1980; Minshall et al. 1983; Cushing et al. 1983).

Paradigms related to the river continuum concept specifically address the transport, processing and storage, and further transport of particulate and dissolved organic matter (POM, DOM) and inorganic nutrients along a sequence of drainage nets (Elwood et al. 1983), and the displacement of functional relationships resulting from impoundment (Ward & Stanford 1983). Spiralling length has been proposed as the length of lotic reach required for one turnover cycle of a given nutrient atom. Thus, higher production rates, as well as slower exchange (greater retention) between water and bottom, decreases spiralling length. As Ward & Stanford (1983) have discussed, impoundment results in a "serial discontinuity" in the continuum as defined by a predictable change in biotic associations along the physical gradient from small streams to large rivers in a drainage basin. Discontinuity distance is the channel length of displacement (towards the head or mouth) of a given biotic functional association.

As proposed above, the characteristics of the streamside vegetation system, the riparian zone, constitute the major organizing function for biotic associations in running waters. This follows logically from the paradigms summarized in Tables 2 and 3. Succession of riparian plant communities following natural disturbances (fire, flood) insured that forested headwater streams returned to predisturbance status of terrestrial-aquatic linkage in aboriginal (prototype) streams and rivers. Both physical and biological conditions described as gradually changing along the continuum of drainage nets are shaped to a major extent by conditions in, and products from, the riparian zone. Spiralling length, i. e. the pattern of storage and processing (turn-over) within, and transport into and out of, a reach is under riparian influence, particularly through the effect of retention. A case in point is the highly retentive nature of very steep gradient streams in the Pacific Northwest (U. S. A.) due largely to breaks in slope attributable to large logs in the channel (Gregory et al. 1984), many of which have been in place for over a century (Swanson & Lienkaemper 1982). This constitutes an example, undoubtedly typical of forested aboriginal running waters, in which extremes in channel roughness are directly related to wood debris, particularly in high gradient streams.

Prototype streams

Presumably most attempts at lotic paradigm building have been intended as models of at least classes of prototype streams. The most probable natural physical state, as enjoined in the river continuum concept, is no longer expressed in most river basins as it was in pre-aboriginal or aboriginal times (Table 4). Pristine conditions are taken as minimally influenced by mechanized man and closely matching the semi-stable (quasi-equilibrium) conditions extant 10,000 years or more ago following the last glacial episodes and general broad scale climatic-terrestrial vegetative biome changes. The extent of human impact on lotic systems can be viewed in three general phases: pre-aboriginal, aboriginal and post-aboriginal (Table 4). The primary impact of aboriginal, and post-aboriginal man has been to increase or decrease the impacts of natural events that change stream ecosystems. Major examples of natural events include flood, drought, fire, effects on banks and sediments by large grazing mammals, alterations in channel structure,

Table 4. Natural disturbance events altering channel form and community functional organization and spatial-temporal alterations attributable to aboriginal and post-aboriginal man.

Pre-aboriginal disturbance	Alterations by aboriginal man	Alterations by post-aboriginal man
Fire	Local increased burning	Regulation – supression and enhancement
Flood (drought)	Small scale effects – tree removal and damming	Regulation – impoundment, dewatering, reduction of peak flows and increase in low flows
Mass movement (mass wasting debris torrents, etc.)	Minor – increased sediment loading at encampments	Acceleration – greatly increased sediment loading (agriculture, logging-road building, draining)
Mammal effects	Locally important – animal drives and harvest	Large scale depletion and extinction (beaver; large grazing mammals, e. g. bison, elephants, hippopotomi)
Organism extinctions and introductions	Minor – increased dispersal by nomadic tribes	Wide scale reductions, extinctions and introduction of exotics 1. Alteration of major plant biomes and associated alteration of riparian zones 2. Over-exploitation of native species 3. Water quality, thermal effects

produced for example by hippopotomi and beaver, and defoliating invertebrate outbreaks (Sedell 1984).

Man often has increased the spatial and/or decreased the temporal scale of these essentially natural events. Human influence on stream blockage is a good example. In aboriginal times, natural blockage, and resulting impoundment, occurred on all sized streams and rivers, produced by mass earth movement and derangement of drainage nets by lakes, such as those formed in glacial depressions. Blockage of smaller channels by trees toppled by wind throw or by animals such as the North American beaver also were undoubtedly common (Sedell 1984). Aboriginal man probably had little effect on these phenomena, although their use of fire, animal drives, or removal of trees from navigable streams may have had local influences. With the advent of mechanized, and more dramatically, industrialized man, the scope of dam construction has increased exponentially. Essentially every major world river system has been impounded to some extent (Ward & Stanford 1979). In some areas, the number of small dams is nearly equal to the number of second to fourth order streams. The wide-scale building of splash dams in streams of the Pacific Northwest (U. S. A.) in the late 1800's to early 1900's is a good case in point (Sedell 1984). In North America the virtual elimination of the beaver from large areas and consequent loss of their dams certainly influenced the existing morphology of small, lower gradient channels. Such headwaters would have been more open, allowing greater primary production (Minshall 1978), and the retention of fine organics in ponds was undoubtedly greater (Sedell 1984).

Within any of these periods of historical importance to stream ecosystems, from pre- to post-aboriginal, a temporal perspective is essential (Cummins et al. 1983). Given the appropriate time and spatial scales, essentially all stream drainage basins with vegetative cover have experienced fire and, with absolute certainty, floods. Periods of annual peak

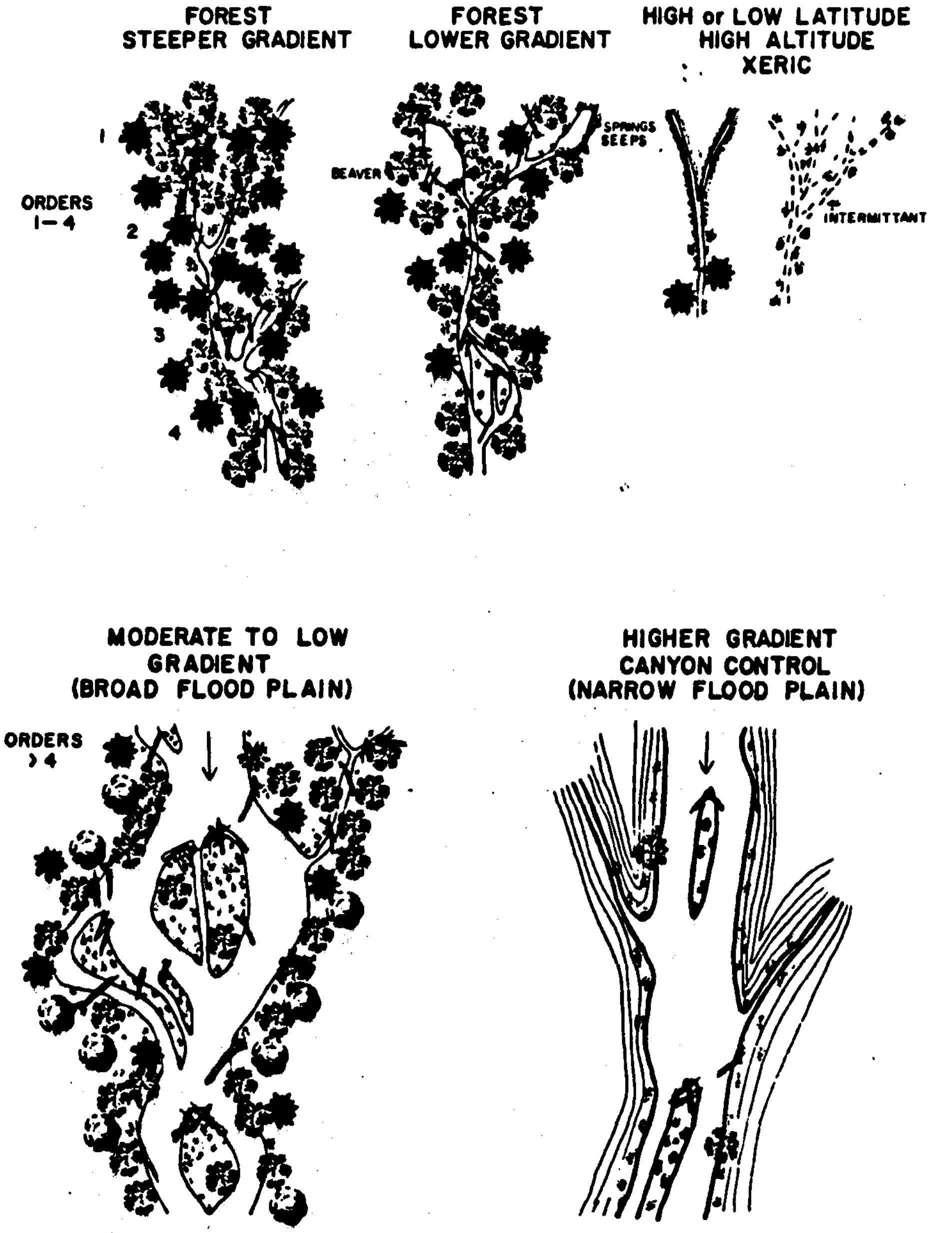

Fig. 1. Comparison of riparian relationships for streams (orders 1–4) and rivers (orders >4) in aboriginal times. Headwater streams in wooded areas shown dominated by large wood debris and stream side vegetation with ponding and springs at lower gradients. At high and low latitudes and at high altitudes and in xeric areas or seasons, streams less controlled by large vegetation. Many channels may be intermittant. Large rivers also influenced by large wood or canyon constricted. All streams and rivers generally more braided and complex than at present, with greater riparian influence.

discharge are a basic characteristic of running waters. The pattern of the runoff cycle (hydrograph) and its relation to the "growing" season, with warm periods at high and low latitudes and high altitudes, wet periods at mid-latitudes, are important to the timing of organic matter inputs, primary production and the life cycles of stream-river organisms (Fig. 1).

Annual peak discharge or drought (drying up of intermittent channels) can be viewed as reset mechanisms; events that confer certain pioneer community characteristics on streams (Cummins et al. 1983). For example, algal communities are scoured or dried in intermittent channels to very low population levels and resting stages, initiating an annual recolonization and sequential community development. Greater than annual or bankful flows have a proportionately larger effect on the physical habitat (depth of sediment scour and fill, size of channel wood debris moved, extent of upperbank, floodplain, captured) and on the lotic biota. Description of each flow year as a recurrance interval (Morisawa 1968) places it in perspective with regard to long-term changes (Cummins et al. 1983).

Functional relationships in running water systems

The extensive use of invertebrates in characterizing various functional relationships in running waters reflects their favorable relative size and abundance, conferring greater ease of sampling and observation. Clearly, most energy and material fluxes are accounted for by microorganisms: algal primary producers and bacterial and fungal consumers. The small size and rapid turnover of the microbes is often restrictive in investigations of community organization (although they lend themselves admirably to measures of community metabolism) while fish, although relatively large, are long-lived, proportionately low in density, and are of negligible importance in community metabolism. The invertebrates constitute a useful link between the quantitatively significant microorganisms and the economically important fish. Individuals are relatively large and numerous, usually have annual or seasonal life cycles, and associations are functionally organized in relation to habitat and nutritional resources (Tables 2 and 3).

Indices based on invertebrate species composition (e. g. diversity, richness, evenness, etc.) are compromised by post-aboriginal disturbance of lotic ecosystems. Invertebrates, particularly in streams and rivers below orders five or six (Strahler 1957) in a given drainage network where insects predominate, have always posed significant taxonomic problems. Separations of immature forms, often the only life stages collected, are difficult. Capability for reasonable taxonomic completeness has come only after extensive cultural expansion and establishment of scientific institutions. In short, by the time species can be separated with certainty, essentially all the stream-river systems have been significantly altered from the aboriginal condition. Thus, only in a few special cases can such indices be taken as reflective of prototype (aboriginal) systems.

Given state-of-the-art limitations in taxonomy together with undetermined loss of taxa, functional categorizations of invertebrate associations have been proposed. For example, functional feeding groups based on morpho-behavioral adaptation of food aquisition (Table 1) emphasize the match between food resource categories (e. g. coarse and fine particulate detritus and attached algae) and feeding methods (Cummins 1973, 1974, 1978; Cummins & Klug 1979; Merritt & Cummins 1984). This functional organization of stream communities also has been incorporated into a process oriented simulation model (McIntire 1983).

As the resource bases have become more fluctuating or permanently changed from the aboriginal state — a condition strongly influenced by the riparian system — the proportion of invertebrate taxa having general feeding strategies probably has increased. The obligate (specialist) or facultative (generalist) adherence of a given invertebrate taxon to a functional category is related both to flexibility of feeding mode and the accompanying assimilation system. The importance of food assimilation systems, especially the role played by microorganisms, both in the food (food biomass, alteration of substrate, acquired enzymes) and as a resident gut flora, is presently one of the most active areas of research in stream ecology (e. g. MERRITT & CUMMINS 1984).

New perspectives

The general concept of running water ecosystems (drainage nets or watersheds in basins) as continuua of adjustments of lotic biota to quasi-equilibrium (high probability) states of the physical systems remains intuitively satisfying. It is well grounded in the earlier literature (e. g. THIENEMANN 1925; HEUT 1954; MARGALEF 1960) and remains a useful conceptual model (CUMMINS 1974; MINSHALL 1978; VANNOTE et al. 1980; MINSHALL et al. 1983), with modifications and elaborations (e. g. ELWOOD et al. 1983; WARD & STANFORD 1983; CUSHING et al. 1983) dealing with special aspects, particularly as applicable to post-aboriginal stream-rivers.

The role of the riparian zone has received increasing attention in emerging lotic ecosystem paradigms. The plant species constituting the streamside vegetation — trees, shrubs, herbaceous plants — differ between watersheds but they represent physical analogues, that have similar impacts on channel structure (shading, retention of allochthonous organic matter, sediment routing, etc.), and biological analogues with regard to the fate of their organic substance once it is entrained in the stream-river network. Critical aspects conferring analogue status to riparian vegetative components are size of trees relative to size of channel (e. g. large or small wood) and rate of biological processing (that is breakdown or turnover, e. g. conversion of leaf litter to DOM, CO_2, biotic biomass, and FPOM, CUMMINS et al. 1980). Thus riparian vegetation species can be classified as fast, medium, or slow with regard to processing rate. The rates are a function of physical nature of the leaf (e. g. cuticle thickness) and biochemical constituents. Thus, given the temperature regime, the rate of processing for a given leaf type is predictable when introduced into a stream along which the species does not occur (e. g. MINSHALL et al. 1983). The basic physical-biochemical differences control the rates of microbial colonization and metabolism of the organic substrates which in turn controls the rate of processing both directly by the microbes (especially aquatic hyphomycete fungi) and indirectly through the action of shredders (a functional group of invertebrates specialized for utilizing coarse particulate organic matter or CPOM).

Examples of the contrasting rates of processing of wood and leaf litter in the conditions encountered from headwaters to mouth (terrestrial to marine) of lotic systems are summarized in Tables 5 and 6. Extensive adaptive radiation of wood-boring, gallery-forming insects and large rot fungi in the terrestrial system and many wood boring marine invertebrates (some with cellulase enzymes) account for the faster processing rates on land and in the estuaries. The slower processing rate of wood in freshwater streams maximizes their role as features shaping channel structure. In contrast the more rapid turnover of leaf litter in streams reflects the preponderance of leaf (CPOM) shredder inver-

Table 5. Comparison of processing of large wood debris in forested, stream and estuarine habitats.

	Forest floor	Stream	Estuary
Processing rate	Fast[1]	Slow[1]	Fast[1]
Microbes (fungi)	Rot fungi diverse and abundant	Aquatic hyphomycetes (rot fungi, virtually absent)	Fungi minor or absent
Invertebrates			
Insects	Diverse and abundant including gallery-forming social insects	Few species (e. g. *Lara*, *Brilla*, Tipulidae), no social insects	Absent
Others	Oligochaeta important in later stages of processing	Absent	Annelida, Mollusca and Crustacea diverse and abundant (some boring forms with cellulase)
Vertebrates	Gallery or destroy wood in search of invertebrate food	Absent	Absent
Environmental controls	Temperature, moisture and oxygen[2]	Temperature and oxygen[2]	Temperature and oxygen[2]

[1] Hardwoods faster than conifers. [2] Lignin decomposed little anaerobically.

Table 6. Comparison of processing of leaf litter in terrestrial, stream and estuarine habitats.

	Terrestrial litter	Stream	Estuary
Sources of litter	General forest or grassland	Riparian zone and macrophyte mortality	Streams, rivers and estuarine marshes
Processing rate	Medium[1]	Fast[1]	Medium[1]
Annual timing of processing	Spring–summer (warm and/or wet)	Fall–winter and spring–summer pulses	Year around
Fungi	Rot fungi diverse and abundant	Aquatic hyphomycetes	Minor role
Invertebrates			
Insects	Some species (Tipulidae, Collembola)	Diverse and abundant (especially Plecoptera, Trichoptera, Tipulidae)	Absent
Others	Abundant (Oligochaeta, Diplopoda, Isopoda)	Few species (Amphipoda, Isopoda, Gastropoda)	Common (Annelida, Gastropoda, Crustacea)
Environmental controls	Temperature and moisture	Temperature and oxygen[2]	Temperature and oxygen[2]

[1] Species differences, e. g. alder fast, oaks and conifers slow.
[2] Little anaerobic lignin decomposition.

tebrates and the presence of aquatic hyphomycete fungi and other microorganisms that can grow at low temperatures.

Even in more xeric regions (e. g. grasslands and savannahs) the maximum development of trees and/or shrubs and large herbaceous species has been along aboriginal stream-river courses. Thus, tree and/or shrub and/or at least herbaceous vegetation (even at high altitudes and high or low latitudes) are essentially universal components of lotic ecosystems. The influences are readily categorized by plant size (physical) and physicalbiochemically controlled biotic processing rates. Thus, inasmuch as these fundamental characteristics of the riparian zone can be recognized or predicted, the associated biotic adjustments should follow.

The final point is that the major shifts from pre-aboriginal and aboriginal conditions have been highly effective in altering the physical characteristics of channels and the associated riparian system. If running water ecosystems are viewed as terrestrial-aquatic inseparably linked components of a single system to which the lotic biota was adapted in aboriginal (prototype) streams, then reconstruction of their most probable condition is essential if the goal is description of prototype stream-rivers.

As shown in Fig. 1, the aboriginal running waters were probably generally characterized by a much greater influence of riparian vegetation further along the drainage network. Records within post-aboriginal historical time indicate that rivers of order six through nine were highly braided, complex channels with greatly expanded opportunity for direct riparian influence. This complexity was maintained, as in the headwaters, by the presence of large amounts of woody debris (Sedell 1984). Further, North American headwater streams of order less than three or four were probably more open as a feature of extensive beaver damming in lower gradient systems.

Thus, it appears that given the river continuum concept, and its more recent corollaries, when adjusted to reflect more acurately aboriginal condition of the lotic-riparian linkages, will go a long way toward improving our conceptual models of prototype running water ecosystems.

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