

ECOTONES

L.W.G. Higler

ALTERRA, AA Wageningen, The Netherlands

Lapinska M.

University of Lodz, Department of Applied Ecology, Poland

Zalewski M.

International Centre for Ecology, Polish Academy of Sciences, and University of Lodz, Department of Applied Ecology, Poland.

Keywords: ecotones, river ecosystem, selfpurification, watershed management.

Contents

1. Introduction.
2. Typology of ecotones of river ecosystem.
3. Roles of Ecotones of riverine ecosystem.
4. Vertical ecotones.
5. Longitudinal ecotones.
6. Lateral ecotones.

Glossary

Bibliography

Biographical Sketches

Summary

"An ecotone is a zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems" (Holland, 1988).

The term 'ecological systems' makes the definition scale independent and the concept is useful as an abstract framework for organizing the descriptive characteristics and properties of ecotones in general (Risser, 1990).

The boundary between two different ecological systems is seldom an abrupt one, but nearly always a gradual one. Its physical width may differ from centimeters to kilometers, depending on the systems considered, but the mutual influences may reach much further.

In river systems, ecotones can be recognized on the level of discharge areas, the boundary between two river basins, on the level of (hydro)ecoregions, on the level of smaller discharge areas that make up larger discharge areas and on the level of the stream itself.

The ecotone concept is useful for the comprehension of structures and processes in river systems and can be used for landscape management and protection.

1. Introduction

A natural river ecosystem is an open system characterized by a high level of heterogeneity across a range of spatio-temporal scales. Interactive routes along four dimensions can be recognized:

1. Longitudinal dimension: in the flow direction: from sources to river estuary.
2. Lateral dimension: the system of main channel and floodplain.
3. Vertical dimension: the interactions between the river water and the groundwater in the surrounding area.
4. Temporal dimension: processes as succession and rejuvenation.

A typology of riverine ecotones is developed on the basis of this four-dimensional nature of the lotic ecosystem, and encompasses environmental gradients and boundaries as well as distinct transition zones between adjacent patches.

2. Typology of ecotones of river ecosystem

In the context of the four-dimensional nature of the river ecosystem, three types of ecotones might be recognized. These are set out in Table 1.

1. Ecotones along the longitudinal dimension: the entire freshwater course of the river from headwaters to the estuary, with the ecotone being the river continuum (in longitudinal perspective *sensu* Vannote *et al.*, 1980), and the transitions between adjacent, more-or-less discrete, zones (in zonal perspective *sensu* e.g. Illies, 1961; Illies and Botosaneanu, 1963; Statzner and Higler, 1986).
2. Ecotones along the lateral dimension: the lateral extent from riparian vegetation to the floodplain in an unconstrained river (Naiman *et al.*, 1989; Junk *et al.*, 1989;).
3. Ecotones along the vertical dimension: the transition zones between the hypogean and epigeal realms (Ward and Voelz, 1997) or various transitions between ground waters and surface water (Gibert *et al.*, 1990). Exchange between surface water and ground water at river channel boundaries is associated with upwelling/downwelling processes. *Downwelling* zones occur, e.g. where river flows from a constrained canyon reach onto an alluvial floodplain (Stanford and Ward, 1993). *Upwelling* zones occur where, for example, water in the alluvial aquifer upwells into the channel. Upwelling and downwelling zones also exist along the riffle-pool transitions (Hendricks and White, 1991).

ECOTONE	Bounding units	Main gradient	Spatial scale m
Longitudinal dimension			
River continuum	headwater- estuary	Organic resources, temperature	$>10^6$
Zonal transitions		Hydraulics, temperature, oxygen	10^3 - 10^4
River estuary	freshwater- marine	Salinity (surface water)	10^5

Anchialine caves		Salinity (ground water)	10 ⁴
Backwater	parapotamon-channel	Temperature, chemistry	10 ³
Confluence		Current, food resources	10 ²
Erosional/depositional transition	riffle-pool	Current, depth, substrate	10 ² -10 ³
Lateral dimension			
Riparian zone (constrained)	channel-canyon wall	Aquatic-terrestrial (abrupt)	10 ¹
Fringing floodplain	channel-upland	Aquatic-terrestrial (complex)	10 ³ -10 ⁵
Littoral zone (floodplain lake)	pelagic-shore	Macrophyte zonation, depth	10 ¹ -10 ²
Marsh/swamp wetlands	channel-ridge	Substrate, detritus, oxygen	10 ² -10 ⁴
Tributary alluvial fan	upland-floodplain	Slope, substrate, temperature	10 ²
Tributary confluence	channel-tributary	Current, sediment, substrate	10 ² -10 ³
Floodplain springbrook	channel-source	Temperature, chemistry, detritus	10 ²
Vertical dimension			
Downwelling /upwelling zones	aquifer-channel	Nutrients, oxygen, temperature	10 ¹ -10 ²
Sources	aquifer-springbrook	Nutrients, oxygen, temperature	10 ⁰ -10 ¹
Hyporheic zone	aquifer-riverbed	Nutrients, oxygen, temperature	10 ⁰
Psammolittoral zone	aquifer-soil	Water content, oxygen, temperature	10 ⁻¹
Anaerobic sediment layer	aquifer-parapotamon	Redox potential, nutrients	10 ⁰

Table 1. Major ecotones of river ecosystems. Source: Ward and Wiens, 2001, changed.

4. Ecotones along the temporal dimension: the ecotones manifest across a range of temporal scales: daily, seasonal, annual and successional. Examples are given in Table 2.

ECOTONE	Bounding units	Main gradient	Temporal scale
Temporal dimension			
Twilight (crepuscular)	day-night	Light	Minutes
Emergence	larval stage-adult stage	Aquatic-terrestrial	Minutes to days
Dormancy	active stage-quiescent stage	Metabolic rate	Weeks to months
Flood pulse	dry phase-wet phase	Moisture, current	Weeks
Intermittency	wet phase-dry phase	Moisture	Seasonal

Hydrarch succession	aquatic phase-terrestrial phase	Eutrophication	Years to centuries
Alluvial forest succession	pioneer phase-climax phase	Seral stages	Centuries
Disturbance	equilibrium – non-equilibrium	Recovery trajectory	Days to centuries

Table 2. Examples of temporal ecotones associated with riverine ecosystems and aquatic organisms. Source: Ward and Wiens, 2001, changed.

3. Roles of Ecotones of riverine ecosystem

The major roles of river ecosystem ecotones are shown in Table 3.

ECOTONE	ROLE OF ECOTONE
1. Longitudinal dimension	
River continuum	Organic matter - transport and processing Resource partitioning from sources to estuary Biota migration route (drift, potamodromous fish)
Zonal transitions	Species succession/segregation Ecological isolation/speciation
River estuary	Evolutionary invasion pathway Biota longitudinal migration route (diadromous fish) Nursery grounds
Anchialine caves	Evolutionary invasion pathway Biota dispersion route
Parapotamon	Refugium (floods, winter conditions) Spawning and nursery grounds High organic production
Riffle/pool transition	Habitat diversity Habitat segregation
2. Lateral dimension	
Riparian zone (constrained)	Light and temperature control Organic matter - input and retention Habitat structuring
Fringing floodplain	Evolution of flood-dependent flora and fauna Terrestrial production and aquatic production Biota lateral migration pathway High habitat heterogeneity Additionally the roles of floodplain subunits
Littoral zone (floodplain lake)	High organic production Macrophytes - food, cover and habitat space Plant surfaces - substratum for epiphytes
Marsh/swamp wetlands	Foci of biodiversity Regulation of sediment and nutrient flux Inputs of organic matter (leaf litter, wood,

	terrestrial arthropods)
Tributary alluvial fan	Episodic pulses of sediment and woody debris
Tributary confluence	Biota lateral migration pathway Contribution of detritus, sediment, and substrate to main river Reset longitudinal resource gradient of main river channel
Floodplain springbrook	Biota refugium High biota production and biodiversity Fish spawning and rearing habitat
3. Vertical dimension	
Downwelling /upwelling zones	Nutrient cycling Incubation sites for eggs and larvae
Sources	Dispersal route Ecological isolation/speciation
Hyporheic zone	Biota refugium from adverse conditions in surface waters Habitat for eggs and early life stages Protection from large predators
Psammolitoral zone	Ecological isolation/speciation Mineralization of organic matter Microbial loop
Anaerobic sediment layer	Nutrient transformation

Table 3. Major roles of ecotones of riverine ecosystem based on their typology
Source: Ward and Wiens, 2001, changed.

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Biographical Sketches

Bert Higler investigated macroinvertebrate associations in relation to vegetation structure in standing waters and in relation to hydraulics in running waters. His primary research took place in The Netherlands, and the results are being used by water managers.

International activities comprise research and education, both in developed and in developing countries. The latter has resulted in a manual on water quality monitoring for use in developing countries.

He retired as head of the Department of Aquatic Ecology of the Institute for Forestry and Nature Research (now ALTERRA, Research Institute for the Green World), which comprised freshwater and marine research. His present activities as a senior scientist include work for the European Water Framework Directive, nature restoration projects and biodiversity research on macroinvertebrates and fish.

Malgorzata Lapinska

Education: Ph.D 1997 Thesis: Space as a limiting factor for fish communities in lowland and upland river systems. University of Lodz, Poland.

Main Research Areas:

River ecology, biological assessment, fish ecology.

Participation in grants and projects:

2005-2008: AQUA-TNET, Socrates Thematic Network for Aquaculture, Fisheries and Aquatic Resource Management. Network for Education and Training in the Aquaculture Industry 2002-2005:

SOCRATES/ERASMUS New Curriculum Development (CD) European Union Project: Master of Inland Water Quality Assessment – contract no.: 29369-IC-1-2002-1-SE-ERASMUS-PROGUC-1.

2001-2004: Development, Evaluation and Implementation of a Standardized Fish-based Assessment Method for the Ecological Status of European Rivers (A Contribution to the Water Framework Directive) - contract no.: EVK1-CT-2001-00094. Acronym FAME.

1991-1994 Role of land/inland water ecotones in functioning of riverine ecosystem. Provided by Polish Committee of Scientific Researches.

1991-1994 Restoration ecology of two percid fishes. Provided by Agency for International Development (USA).

Maciej Zalewski, Ph.D.1977, D.Sc.1988, Professor Titular 1993.

Main Research Areas:

Application of the Ecohydrology concept for restoration and renaturalisation of river systems and reservoirs, on the basis of analysis of processes from the molecular (enzymatic mechanisms compensating shortage of phosphorus) to the catchment scale, with application of GIS techniques.

Professional experience:

Director of International Centre for Ecology, Polish Academy of Sciences

Director of the European Regional Centre for Ecohydrology (ERCE) under the auspices of UNESCO. PAS, UL, in Lodz, Poland (since May 2006)

Head of the Department of Applied Ecology, University of Lodz

Member of Scientific Council of Regional Bureau for Science for Europe ROSTE (UNESCO), Chairman of the Steering Committee of UNESCO IHP Programme "Ecohydrology", Project 2.3/2.4., Editor of International Journal "Ecohydrology & Hydrobiology", Co-ordinator of Polish Net of International Long Term Ecological Research (ILTER), Representative of UNESCO IHP to Scientific Committee on Water Research (ICSU, SCOWAR).