

Importance of diversity in the functioning and structure of riverine communities

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Abstract

The natural diversity of biological communities provides many alternative pathways by which nutrients and energy may move through ecosystems. Many different species are capable of performing similar functional roles in nature. When disturbed or polluted, natural systems often become restored first through the activities of species that had not previously been common. Human activities often result in reduction or loss of diversity within ecosystems, particularly through the loss of rare species. Maintenance of diversity is vital because it provides protection against both natural and human-caused catastrophes.

Diversity, in the broadest sense, characterizes and maintains the flexibility of biological communities. Most papers written about diversity have stressed the importance of genotypic diversity for the evolution of species in changing environments. Variations of genotypes within species may be expressed as varieties and subspecies which thrive under differing transient environmental conditions. For example, protein electrophoresis has shown that there are genetic differences between individuals of species of insects living at the extremes of their range and those living where optimum growth conditions permit larger population development (Sweeney et al. 1987).

Patrick (1949) and many others since have quantified species diversity in natural aquatic ecosystems and how various types of pollution alter this diversity. Concern about the importance of diversity of species in nature has grown recently because our accelerated clearing of tropical forests has endangered many native species. Not only are some species destroyed directly but a "border effect" extends for a great distance into the remaining forest and disrupts the

natural community (Lovejoy et al. 1986). The draining of wetlands in industrialized countries, such as the United States, is another example of the large loss of species caused by man's activities.

The reservoir of genetic diversity in extant species is recognized as an economic resource in agriculture, horticulture, medicine, and pollution control. That this diversity has important applications to environmental problems is evidenced in part by the discovery of unusual metabolic pathways that are of value in pollution control, such as the bacterial degradation of trichloroethylene (Fleirmans 1988) or fungal metabolism of heavy metals such as mercury (Brunker and Bott 1974; Brunker 1979).

The total number of species vital to community or ecosystem functions is presently unknown. Dearth of inquiry into the importance of species diversity to mass and material fluxes has particularly plagued the bacteria and fungi, which are important in nutrient and detoxification pathways. Recently Fleirmans (1986) identified over 1,000 physiologically different bacteria at a depth of 250 m near the Savannah River. At issue is not only the present role of the numerous microbial species in all global environments, but also their ability to respond to unplanned or detrimental environmental manipulations, such as increased CO₂ in the atmosphere and the associated problems of increased heat and redistribution of moisture.

The functioning and structure of riverine ecosystems involve invasion and establish-

¹ I have chosen to write this article about diversity in part because the research work of Dr. W. Thomas Edmondson exemplifies the ability of a scholar to work in diverse fields of science. Edmondson's studies range from the life histories and taxonomy of rotifers to the role of nutrient income in eutrophication of Lake Washington. His ability to tackle diverse problems of scientific interest in a scholarly way has made Professor Edmondson one of our most effective and productive limnological scholars.

ment of species as well as the interaction of species with their abiotic environments. The establishment of species in an aquatic community is dependent upon the numbers of species and rate of invasion, as well as on the types of substrates, current patterns, light regime, and nutrient conditions in the stream channel. The nutrients and toxic substances in the sediments also influence the success of the invading species.

Predation has a strong influence on establishment and maintenance of species. The role of refuges from predation became evident when Patrick (1959) established an artificial stream channel complete with typical habitats of the parent stream. When the new stream channel was opened, the black fly, *Simulium vitatum*, rapidly colonized all available habitats because no predators were present (Patrick 1959). In the parent stream these larvae were found only in microhabitat protected from predators.

Prey organisms often survive predation by their prodigious reproduction. As pointed out by Lubchenco (1978), algal species may survive by reproducing faster than the predator can crop them. Predator abundance and foraging behavior also influence the effect of predation. Some stream organisms may prevent predation by production of alleochemicals. Some cyanophytes, in particular, seem to have exploited this strategy of chemical defense. The same may be true of *Cladophora*, which is a very poor food for snails (Patrick et al. 1983). The reason for this may be that *Cladophora glomerata* contains lauric acids, toxic to many invertebrates (Larsen cited by Patrick et al. 1983). Life history variations provide an alternate way to thwart predators. Resistant resting stages provide a means to avoid adverse conditions, both biotic and abiotic.

In order for a large number of species to co-exist, there must be means to prevent monopolization of resources. Rice (1954), Proctor (1957), and Keating (1976) have shown that some algae excrete chemicals that prevent the development of potential competitors. Indeed, suppressing a superior competitor may increase diversity. Other species may reduce competition for a resource by temporal partition of foraging ef-

fort. Vannote and Sweeney (1980) have shown that different stream insects actively exploit algae at different times of the year.

Lawton and Strong (1981) found that factors other than competition were important in maintaining diverse communities of folivorous insects. Density-independent factors and individual species preferences for particular combinations of such factors can reduce competition.

In stream ecosystems the selection by a species for a given pattern of density-independent factors enables it to avoid competition. For example, a rock on a streambed in the flow of the current will have different current patterns and light regimes and be able to support several species. Over the smooth top of the rock there will be a shearing effect and only insects which can withstand strong continuous current can occupy this habitat, such as purse caddis (*Leuctrichia*). The front of the rock that receives the direct force of the current will be the habitat of caddis flies that build stone cases (e.g. *Glossosoma*). The sides of the rock will have a slower, more predictable flow pattern while the area on the back of the rock will have no perceptible current. Each of the areas will be the habitat of different species. In a similar way various species of epiphytes prefer different parts of a plant (e.g. *Zostera*) as habitats.

Fluctuating density-independent environmental factors are as important to diversity-maintenance in stream communities as in the intertidal zone (Connell 1972) and in coral reefs (Watt 1987). Factors such as current direction, velocity, irradiance, and temperature are highly variable, and this variability can cause variance of growth conditions preventing domination by any single species. Extreme current variations can disturb the community and open it to invasion by other species.

These various factors are largely responsible for natural river communities being composed of many species at each trophic level which form different paths for the transfer of nutrients and energy through the system. For example, diatoms produce mainly fats and oils as storage products which are the preferred food of *Daphnia* spp. and enable them to reproduce more

Table 1. Numbers of species within major taxonomic groups identified from different rivers (from Patrick 1984).

	Guadalupe (low flow 1973)		Potomac (low flow 1986)		Savannah (low flow 1968)	
	No.	%	No.	%	No.	%
Algae	53	29.1	87	38.3	44	25.3
Protozoa	66	36.3	49	21.6	40	23.1
Macroinvertebrates	17	9.3	18	8	21	12.1
Insects	29	16.0	41	18.1	41	24
Fish	17	9.3	32	14.0	27	15.5
Total	182		227		173	

successfully (Goulden and Henry 1984). Chlorophyta which store starches and cellulose are the chosen prey of other organisms.

Patrick (1984) has shown in the Savannah, Potomac, and Guadalupe rivers that the numbers of species functioning at each stage of energy and nutrient transfer are quite similar (Table 1). That is, except for invertebrates other than insects, they are within a 33% variation caused by unknown factors that have been found to be characteristic of natural aquatic communities (Patrick 1961). They represent several major groups or phyla of organisms and have different turnover rates. These factors potentially increase the resiliency of the system.

Similarly, when one compares the numbers of species found in structurally analogous sections of hard-water rivers in the tropics, such as the Tulumayo in Peru (Patrick 1964, 1966) with a temperate zone river such as the Potomac in Maryland, one finds that the percentages of the species in the various major groups of organisms forming the community are again somewhat similar (Table 2).

Thus, the numbers of species performing

Table 2. Percentage composition, by species number, of the biological communities identified from structurally similar sections of a tropical and a temperate river.

	Tulumayo (%)	Potomac (%)
Algae	30.38	31.21
Protozoa	13.92	20.61
Other invertebrates (not insects)	2.11	8.18
Insects	42.62	31.52
Fish	10.97	8.48
Total No. of species	237	330

the various important functions in energy and nutrient transfer belong to many different taxonomic groups and have different life cycles. In reaches of rivers with similar habitats and collected in similar ways, the numbers of species are quite similar in different streams in the United States, although the kinds of species in each river are very different (Patrick et al. 1967). Furthermore, the number of species in a community in a tropical stream was found to be similar to that in the temperate zone, but the species were in many cases different. In all riverine communities, some of the species are relatively rare. Rare species are often very significant in the re-establishment and continuance of a community after a severe catastrophe, such as extreme drought or toxic pollution. This function of rare species in a community is similar to that of a rare genome in a species, as discussed by Hutchinson (1981). Continued existence of large natural diversity in biological communities is the best insurance against catastrophic consequences of unplanned ecosystem alterations.

References

- BRUNKER, R. D. 1979. Mercurial toxicity in yeasts and glucose uptake: Glycolytic acid fermentative function remained unimpaired. *Microbios* 26: 147-152.
- , AND T. L. BOTT. 1974. Reduction of mercury to the elemental state by a yeast. *Appl. Microbiol.* 27: 870-873.
- CONNELL, J. H. 1972. Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.* 3: 169-292.
- FLEIRMANS, C. B. 1986. The microbiology of subsurface environments, p. 1-6. *In* Microbiology of subsurface environments, Proc. 2nd Investigators Meeting. U.S. Dep. Energy, Office Health Environ. Res. DOE/ER-0312.
- . 1988. Mineralization of trichloroethylene by

- heterotrophic enrichment cultures. *Appl. Environ. Microbiol.* In press.
- GOULDEN, C. E., AND L. L. HENRY. 1984. Lipid energy reserves and their role in Cladocera, p. 167–185. *In* Trophic interactions within aquatic ecosystems. AAAS Select. Symp. 85. Westview.
- HUTCHINSON, G. E. 1981. Random adaptation and imitation in human evolution. *Am. Sci.* **69**: 161–165.
- KEATING, K. I. 1976. Algal metabolite influence on bloom sequence in eutrophied freshwater ponds. U.S. EPA-600/3-76-081.
- LAWTON, J. H., AND D. R. STRONG, JR. 1981. Community patterns and competition in folivorous insects. *Am. Nat.* **118**: 317–338.
- LOVEJOY, T. E., AND OTHERS. 1986. Edge and other effects of isolation on Amazon forest fragments, p. 257–285. *In* M. E. Soule [ed.], Conservation biology: The science of scarcity and diversity. Sinauer.
- LUBCHENCO, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. *Am. Nat.* **112**: 23–39.
- PATRICK, R. 1949. A proposed biological measure of stream conditions based on a survey of the Conestoga Basin, Lancaster Co., Pa. *Proc. Acad. Nat. Sci. Phila.* **101**: 277–341.
- . 1959. The development of the fauna and flora in a new stream bed, p. 120–136. *In* Proc. Air Water Pollut. Abatement Conf. Water Sewage Works.
- . 1961. A study of the number and kinds of species found in rivers in eastern United States. *Proc. Acad. Nat. Sci. Phila.* **113**: 215–258.
- . 1964. A discussion of the results of the Catherwood Expedition to the Peruvian headwater of the Amazon. *Int. Ver. Theor. Angew. Limnol. Verh.* **15**: 1084–1090.
- . 1966. Introduction and part 1—Limnological observations and discussion of results, p. 1–40. *In* Catherwood Found. Peruvian–Amazon Exped. Monogr. 14. Acad. Nat. Sci. Phila.
- . 1984. Some thoughts concerning the importance of pattern in diverse systems. *Proc. Am. Phil. Soc.* **128**: 48–78.
- , J. CAIRNS, JR., AND S. S. ROBACK. 1967. An ecosystem study of the fauna and flora of the Savannah River. *Proc. Acad. Nat. Sci. Phila.* **118**: 109–407.
- , AND OTHERS. 1983. The potential for biological controls of *Cladophora glomerata* (L.) Kutz. U.S. EPA 600/3-83-065.
- PROCTOR, V. W. 1957. Studies of algal antibiosis using *Hematococcus* and *Chlamydomonas*. *Limnol. Oceanogr.* **2**: 125–139.
- RICE, T. R. 1954. Biotic influences affecting population growth of plankton algae. *Fish. Bull.* **55**: 227–245.
- SWEENEY, B. W., D. H. FUNK, AND R. VANNOTE. 1987. Genetic variation in stream mayflies (Insecta: Ephemeroptera) populations of eastern North America. *Ann. Entomol. Soc. Am.* **80**: 600–613.
- VANNOTE, R. L., AND B. W. SWEENEY. 1980. Analyses of thermal equilibria: Conceptual model for evaluating the effects of natural and thermal regimes on aquatic insect communities. *Am. Nat.* **115**: 667–695.
- WATT, K. E. F. 1987. Deep questions about shallow seas. *Nat. Hist.* **96**(7): 60–65.