COMPARATIVE STUDIES ON THE STRUCTURE OF AN UPLAND AFRICAN STREAM ECOSYSTEM

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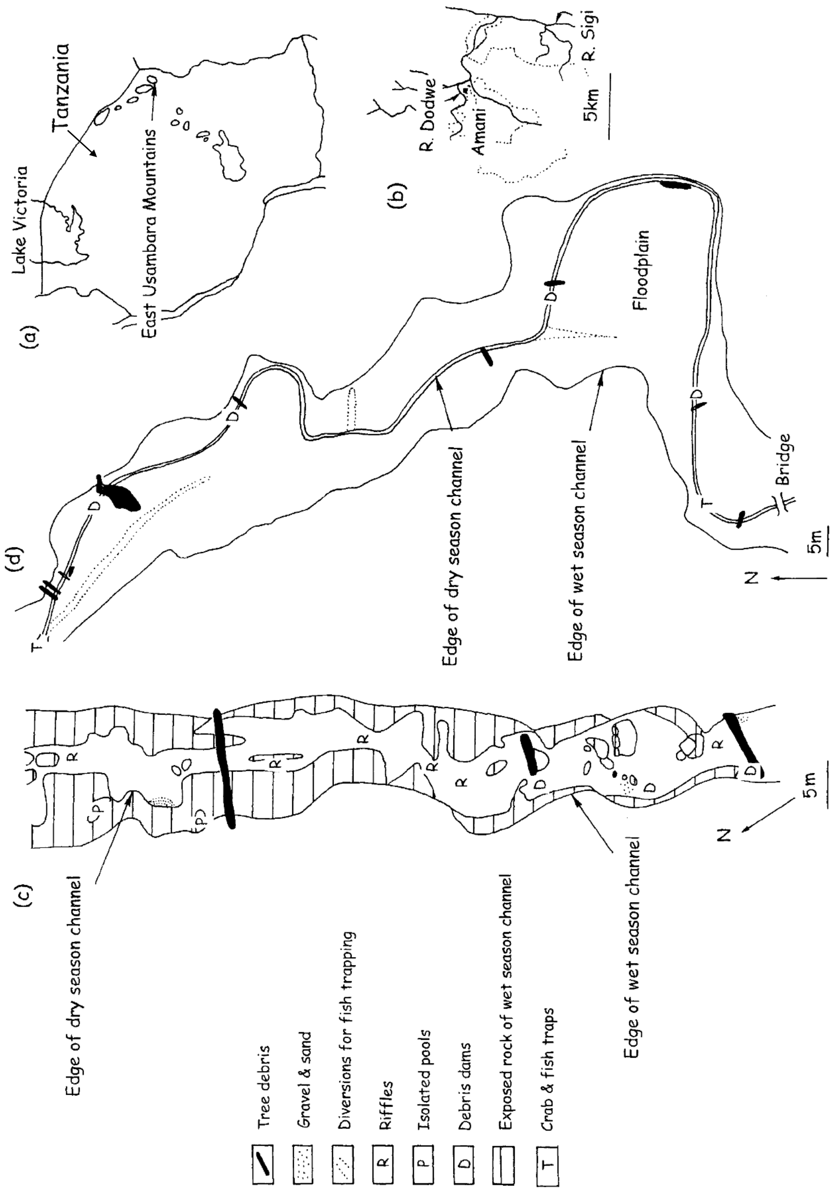
Introduction

Upland stream systems have been extensively investigated in Europe, North America and Australasia and many of the central ideas concerning their function are based on these systems. One central paradigm, the river continuum concept (Vannote et al. 1980) is ultimately derived from those North American streams whose catchments remain forested with native vegetation.

In this model, the main source of energy for upland stream systems is allochthonous material, derived from the surrounding forest. In the shaded stream bed, primary production is limited or absent and invertebrate shredders feed on leaves and woody material conditioned by hyphomycete fungi and other microorganisms. Fine particles, produced as by-products of the shredding and washed in from the forest soils, are similarly conditioned. They are then fed upon by filter-collectors in the main current, and deposit feeders where these particles settle in pools and at the edges. In the upper reaches, community respiration (R) exceeds in-situ photosynthesis (P). As the river widens, more *in situ* photosynthesis is possible and the P:R ratio increases. In the floodplain sections, the situation becomes more complex, but production in the emergent swamps of the floodplain must increase the P:R ratio of the wet-season system, whilst in the dry season, the channel, loaded with organic matter from upstream and washed in from the floodplain vegetation, may have very low P:R ratios.

Australasian workers have challenged the river continuum concept. Australian catchments are naturally very different (sometimes very arid or otherwise not overhung by forest vegetation). Likewise in many European



rivers, deforestation for agriculture or grazing, replanting with exotic conifers, river engineering and nutrient, organic and toxic pollution have rendered application of the river continuum and other such concepts largely irrelevant. But there seems good reason to expect that it would have applied to pristine rivers of the north-temperate zone, at least.

Streams of the tropics may or may not fit the model. They have been little studied. The tropical world is increasingly influenced by the problems of temperate systems as populations increase and land is sought for cultivation (Dudgeon 2000; Malmquist & Rundle 2002). However, there remain some upland areas where, despite past exploitation of many areas for forestry, establishment of national parks or nature reserves has preserved largely intact systems. Other than in limited areas of Central America, there has, however, been little detailed description of these systems, let alone comprehensive studies of functioning. Despite much interest in East African lakes (Beadle 1981; Talling & Lemoalle 1998; Crisman et al. 2003) and large African floodplain systems (Tockner & Stanford 2002), little (Dobson et al. 2002) has been published on the upland stream systems.

The Amani Nature Reserve in the East Usambara Mountains of north-eastern Tanzania offers an opportunity to bring these naturally forested systems to the attention of the ecological community. This article describes a comparison made between two lengths of the River Dodwe in this area. One stretch was a typical erosive section, with turbulent water, a rocky bed and overhanging tropical rain forest; the other was a bijou floodplain stretch. It was created by the damming of the stream in the early 20th century by German colonists to create a small lake, which has now nearly filled in. The work was carried out by a group of postgraduate students from eighteen European and African countries with advice from five staff members, as part of a course organised by the Tropical Biology Association. Rigorous efforts were made to standardise techniques, in a situation where equipment and laboratory facilities were very basic, through a management structure and deliberate allocation of work to specialists in each area.

The East Usambara Mountains and the River Dodwe

The 1300 km^2 of the East Usambara Mountains (Fig. 1a) (Hamilton & Bensted-Smith 1989) are part of a chain, the Eastern Arc, of very ancient, igneous Precambrian rocks (gneisses, granulites and amphibolites). It extends

FIG. 1 *(opposite)*. Location of the East Usambara mountains (a), the River Dodwe (b) and plan maps (c, d) of the study stretches.

from the Kenyan border southwards through Tanzania in a broad curve of mountains isolated among lowland forest and savannah. The East Usambara was aggressively logged until the 1980s when it was realised that it contained a very high proportion of endemic tree, herb (including the wild ancestors of African violets, *Saintpaulia* spp.), amphibian and invertebrate species (Burgess et al. 1998; Lovett 1998). Logging was stopped and about 235 km^2 of closed montane forest, largely on steep, inaccessible slopes, remain with a further 178 km^2 of modified but still intact forest. A preservationist policy has since prevailed, resulting in the establishment of the Amani Nature Reserve in 1996.

The River Dodwe (5°6'S, 38°38'E, 910 m above sea level) (Fig. 1b) is a second order tributary of the Sigi River, whose water quality and hydrology have been examined by Litterick (1989) because of the importance of this river for water supply to the coastal town of Tanga. Soil erosion, caused by past logging, was considered a major problem. The Dodwe was dammed about one hundred years ago and this created a section of standing water, which has filled with detritus and now bears a meandering stream in a floodplain 15–50 m wide and about 2 km long, which is inundated in the wet season. The stream rises in native forest, flows through this plain (Fig. 1d), which is surrounded by a patchwork of forest remnants and cleared areas, and ends at Amani pond, now very shallow (< 50 cm) and almost completely covered with the introduced *Myriophyllum aquaticum*. Beyond the pond dam, the river plunges into a rocky, erosive stretch (Fig. 1c) surrounded by largely intact natural forest for several kilometres before joining another tributary and eventually the main stem of the Sigi. Two sub-stretches of the floodplain and erosive sections were plan-mapped in detail using tapes and compasses (Fig 1c, d) as a basis for the study. Figs 2 and 3 show photographs of the two contrasted stretches.

The climate is wet, with rain in every month, but heaviest in March–May and October–November. Annual rainfall averaged 1,918 mm at Amani over a 66-year record, with a mean annual temperature of 20.6°C (mean maximum 24.8, mean minimum 16.3) (Hamilton 1989). There is evidence that rainfall has declined with changes in local weather, associated with 20th century deforestation (Hamilton & MacFadyen 1989). The work described in this article was carried out in September 2003.

The study was a teaching exercise in which, following some lectures on the basics of river ecology, it was decided to examine physico-chemical characteristics (insofar as equipment allowed), stocks of allochthonous material and *in situ* primary producers, and the invertebrate community. Some simple meters for light, oxygen, conductivity and redox potential were available, together with high quality pH papers and a Chemetric C-6095 nitrate test kit (Galgo, UK Ltd). We had pond nets and two Surber

FIG. 2. The erosive stretch. *Above:* Overhanging forest and the major items of tree debris in the stream. *Below:* Sampling invertebrates.

FIG. 3. The floodplain stretch. (a) *Above:* Forest with cultivation (banana trees) on slopes whilst the stream flows through its flat grassy floodplain. (b) *Below: Sagittaria montevidensis* (an exotic species) lines the banks with native ferns and cyperaceans. Stumps mark position in which the crab trap (upended on bank) is positioned.

Table 1. Comparative physical and chemical conditions in two stretches of an East African stream, the River Dodwe. Values are means ± 1 standard deviation (n = 7).

	Light (klux)	Temp °C	Current (cm s^{-1})	Discharge (m^3 s^{-1})	Conductivity (µS cm^{-1})	pH (log units)	NO_3-N (mgl^{-1})	DissO_2 (mg l^{-1}) [% satn]	Redox (mv)
Erosive	6.6±2.3	19.9	0.6±0.4	0.17±0.27	59±2	5.3	<0.1	7.7±1.0 [87±12]	159±52
Floodplain	34±11	19.2	0.2±0.14	0.15±0.1	57±2	5.3	<0.1	5.4±0.1 [64±1]	66±13
(P)	<0.001	ns	ns	ns	ns	ns	ns	<0.001	0.009

samplers with a mesh size of about 100 µm. Much improvisation took place, with quadrats constructed from bamboo and sticky tape, current measured by floating sticks, and surveying carried out with tapes and compasses. There were no ovens so animals and detritus were weighed after sun-drying in the open air. Decisions about what to sample and how were made by appropriate groups and agreed at plenary meetings. Staff gave guidance but tried not to make decisions. In this way comparable data were obtained in forms chosen by the students and an interesting picture began to emerge.

Physico-chemical environment

Table 1 shows data for physical and chemical variables. Not unexpectedly, significantly more light was received in the dry season channel of the floodplain section than in that of the erosive section, by a factor of five, but water temperatures were not significantly different. Current speeds were not significantly different either but there was greater variance ($F_{6,6}$ = 8.95, $P < 0.001$) in the erosive channel. Discharge remained constant, there being no notable tributary flows entering the two adjacent stretches. Conductivity was low, less than 60 µS cm^{-1}, as was pH (5.3) and there were no significant differences between stretches. The pH of rainfall, determined directly from the fall during storms was consistently 4.7. This may have been due to acidification from nitrogen oxides produced by vegetation burning in the savannahs surrounding the mountains. Nitrate was undetectable (< 0.05 mg N l^{-1}) in either stretch, whilst oxygen concentrations, saturation and redox potentials of the water were significantly lower in the floodplain section. This was expected from the sedimentary nature of the bed.

In situ photosynthetic energy sources

Biofilms in the erosive section were dominated (about 66%) by non-algal material. The main algae were diatoms (92 ± SD7 % of cell numbers and mostly *Synedra,* with *Pinnularia*, *Gomphonema, Eunotia, Nitzschia* and *Navicula*). Chlorophytes (5 ± 6 %) were also present (*Chlamydomonas, Cladophora, Oedogonium, Coleochaete*) with occasional cyanophytes (*Oscillatoria)* and cryptophytes (*Rhodomonas*). Coverage of bryophytes in the erosive section was 27 ± 38 % of the rock surface of the wet-season channel, with about two thirds mosses and one third thalloid liverworts. Vascular plants rooted in the wet season channel included a variety of forest saplings, shrubs and herbs, including *Clidemia hirta* (an introduced South American species*), Eriocaulon schimperi, Leptaspis cochleata, Lantana camera* (also exotic), *Pennisetum perperum, Hypserodelphis scandens, Ageratum conyzaeoides, Datura candida, Alchornea hirtella, Eleusine indica* and species of *Impatiens, Pteris, Dracaena, Euphorbia, Bambusa, Momordica* and *Vernonia*.

The floodplain section included very few algae in the water. There were some epipelic cells on the sediments but these were not examined in detail. The dry season channel had a thalloid green alga, not unlike *Enteromorpha,* but more robust and attached to woody detritus. Its dry biomass averaged 28 ± SD82 g m^{-2}. Clumps of *Sagittaria montevidensis* were common (Fig. 3b). The floodplain itself (the wet season channel) was a lawn of grasses, small cyperaceans and small herbs, including *Cyperus, Spilanthes mauritiana, Ageratum conyzaeoides, Arundinaria* sp., *Lobelia flaccida* and *Clidemia hirta.* There was evidence, from the severed leaves of the grasses and sedges, and from direct observation, that the area was extensively cut to feed cattle housed in shade in a nearby shamba (small farm). Elsewhere on the floodplain was a taller vegetation of large *Cyperus* species, *Typha capensis* and ferns. Yams (*Colocasia esculentum*) were present in the cut lawn, but upstream of the studied section they grew much taller and had evidently been planted originally and were now harvested for subsistence and sale.

Allochthonous energy sources

In the erosive section, about 900 m^2 in area, were three large fallen trees (Fig. 1c), one recently fallen, the others well rotted. Their volume was estimated as 10.5 m^3, giving a mass of hardwood of about 12.6 tonnes (averaging 14 kg m^{-2} of wet season channel for the section). Smaller detritus amounted to 545 ± 295 g m^{-2}. It was noticeable that although leaf material was abundant, together with twigs on the dry rocks of the wet season channel, only twigs persisted in the then submerged dry season channel. It later became clear that leaf material falling into the water was very rapidly shredded and removed. The total amount of plant detritus (trunk, twig and leaf) for the erosive section was about 14.5 kg m^{-2}.

In the floodplain, small debris accounted for 810 ± SD684 g m^{-2} of the dry season channel and there were ten major logs of wood within the channel. These amounted to about 5.1 m^3 and averaged 32.5 kg m^{-2} of the dry season channel, giving a total of 33.3 kg m^{-2}. However, the comparison should be made with the wet season channel, in which case, the floodplain (3,180 m^2) had 1.96 kg m^{-2} – still a substantial stock of material.

Invertebrates

Invertebrate populations in the erosive stretch were recorded by stratified random sampling. Rocks were systematically rubbed by hand into the Surber sampler net from the designated area. Riffles and debris (n = 10) were separately sampled from pools (n = 10). Surface dwellers on pools (largely gyrinids) and frog tadpoles (honorary invertebrates for the present purposes!) were counted on individual pools. In the floodplain stretch, stratified random sampling of open sediment (n = 9) and debris dams (n = 10) was carried out using a pond net dragged through a known area of sediment or kick sampling of an estimated area in debris dams. A total of 39 samples was taken and processed in all. Samples were sorted live and preserved in 50% alcohol for storage prior to biomass determination, large predators having been separately transported to the laboratory. Sorted animals were identified to family level using a standard key (Davis & Day 1998) to maintain consistency. Different individuals cross-checked identifications. Following counting, the samples were transferred to weighed weighing boats, air-dried over three days and weighed. Crabs and tadpoles were weighed separately from other animals. Animals were classified into feeding guilds using information in Davis & Day (1998). Sampling was designed for testing by t-tests and one-way analysis of variance.

A summary of the animal communities in the dry season channels is given in Table 2. Animals of the floodplain lawns were not studied but included numerous Orthoptera; frogs and snakes were also seen. Table 2 shows numbers m^{-2} (dry season channels in all cases) and feeding guild. Fig. 4 shows the proportions of the major groups in the four habitats sampled, and Table 3, the proportions by numbers and feeding guild. Finally Fig. 5 shows the percentage contributions of crabs to the total biomass in the habitats sampled and in the dry season channels in total.

Forty-three families of invertebrates were recorded, most of them insects (Table 2, Fig. 4). Numbers were generally low with fewer than one thousand animals m^{-2} in any sub-habitat. Other than hydracarinids, numbers in non-insect families were also very low. Notable absences were bivalve molluscs (gastropods were also very scarce), stoneflies (though one

Table 2 Composition of animal communities in four sub-habitats of two contrasted stretches of an upland East African stream system, the River Dodwe. Values are numbers per m^2, with SD (n = 9 or 10) in parentheses. Feeding guilds are P, predators, Sc, scrapers, Sh, shredders, D, deposit feeders, and C, filter collectors.

Group	Family	Guild	Erosive riffles	Erosive pools	Floodplain sediment	Floodplain debris dams
Platyhelminthes	*Planariae*	P	-	-	-	1.6(5.1)
Annelida	*Lumbriculidae*	D	-	-	3.2(2.4)	17.6(50.2)
	Tubificidae	D	-	2(6)	1.6(5.1)	68.8(218)
Gastropoda	*Planorbidae*	Sc	-	-	-	1.6(5.1)
Crustacea	*Brachyura*	Sh/P	6.4(2.4)	1.6(5.0)	1.6(5.1)	48(42.7)
Acarina	*Hydracarina*	P	114(107)	5.7(4.9)	-	-
	Arachnida	P	-	-	-	4.8(10.2
Insecta						
Anisoptera	*Cordulidae*	P	-	3.8(12)	-	1.6(5.1)
	Gomphidae	P	3.2(0.8)	3.8(8.0)	20.8(20)	64(52.8)
Zygoptera	*Chlorolestidae*	P	-	2.0(2.00)	1.6(5.1)	6.4(15.5)
	Lestidae	P	-	-	1.6(5.1)	-
	Platycnemidae	P	-	-	1.6(5.1)	3.2(6.7)
	Calypterygidae	P	-	-	-	3.2(10.1)
Hemiptera	*Corixidae*	P	150(146)	506(636)	1.6(5.1)	3.2(6.7)
	Veliidae	P	-	2.0(6.0)	4.8(10.7)	-
	Hydrometridae	P	-	10.8(14.6)	-	3.2(6.7)
	Gerridae	P	-	-	-	3.2(6.7)
Diptera	*Ceratopogonidae*	D	1.6(6.0)	3.8(12.0)	1.6(5.1)	4.8(10.7)
	Chironomidae	D	78(78)	47(30)	41.6(44.80	106(99)
	Dolichopodidae	P	1.6(6.0)	-	-	-
	Simuliidae	C	-	-	8(17.3)	24(33.9)
	Anthericidae	P	9.6(17.2)	-	-	4.8(10.7)
	Tipulidae	Sh	-	-	-	1.6(5.1)
	Tabanidae	P	-	-	-	1.6(5.1)
Trichoptera	*Ecnomidae*	C/P	-	3.8(3.8)	11.2(30.2)	19.2(27)
	Hydropsychidae	C/P	43(86)	3.8(3.8)	1.6(5.10	4.8(7.7)
	Polycentropidae	P	1.6(6.0)	-	-	1.6(5.1)
	Leptoceridae	?	-	-	3.2(6.7)	1.6(5.1)
	Sericosomatidae	Sc	-	-	1.6(5.1)	-
Ephemeroptera	*Baetidae*	Sc	14 (35)	25(34)	9.6(15.5)	9.6(11.2)
	Caenidae	D	1.6(6.0)	39(173)	11.2(21.4)	12.8(18.2)
	Heptageniidae	Sc	-	15(48)	-	-
	Trichohythridae	D/C	1.6(6.0)	7.6(18.4)	-	3.2(10.1)
	Oligonuridae	C	-	3.8(12)	-	-
	Leptophlebiidae	Sc	75(120)	-	-	4.8(10.7)
	Ephemeridae	D	-	-	1.6(5.1)	4.8(15.2)

continued opposite...

Table 2, continued...

Group	Family	Guild	Erosive riffles	Erosive pools	Floodplain sediment	Floodplain debris dams
Coleoptera	*Gyrinidae*	P	-	1.9(2.1)	4.8(10.7)	9.6(13.4)
	Elmidae	Sc	11.2(18.4)	-	1.6(5.1)	1.6(5.1)
	Dytiscidae	P	-	-	-	1.6(5.1)
	Hydrophilidae	Sc/P	-	-	-	1.6(5.1)
	Noteridae	Sc	12.8(36)	-	-	-
Amphibia	*Ranidae*	Sc	3.2(12)	24(39)	-	-
Osteichthes	*Siluridae*	P	1.6(6.0)			
			-	-	-	-
TOTAL			534(404)	712(676)	136(95)	446(342)

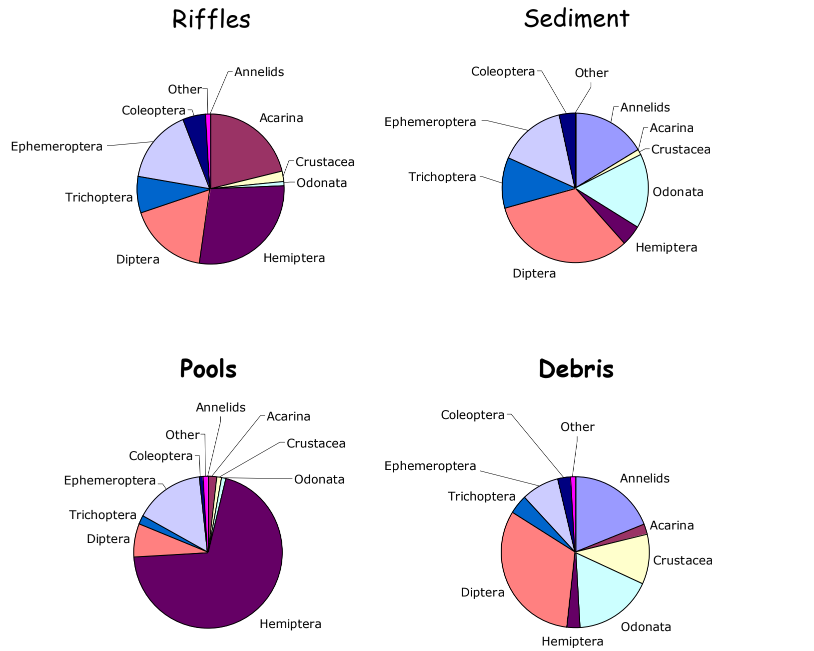


FIG. 4. Distribution, by numerical percentage, of major invertebrate groups among the communities in four sub-habitats in two contrasted sections of an upland East African stream, the River Dodwe.

Table 3. Feeding guild structure (by number) of the invertebrate communities in four sub-habitats of two contrasted stretches of an upland African stream, the River Dodwe. Values are percentages and derived from the data in Table 2.

	Erosive, riffle	Erosive, pool	Floodplain, sediment	Floodplain, debris dams
Scrapers	22	8.6	9.5	4.3
Shredders	1.2	0.3	1.2	11.2
Collectors	8.1	1.5	10.6	8.7
Deposit feeders	15.7	15.9	44.7	48.6
Predators	55.1	75	31.8	27.8

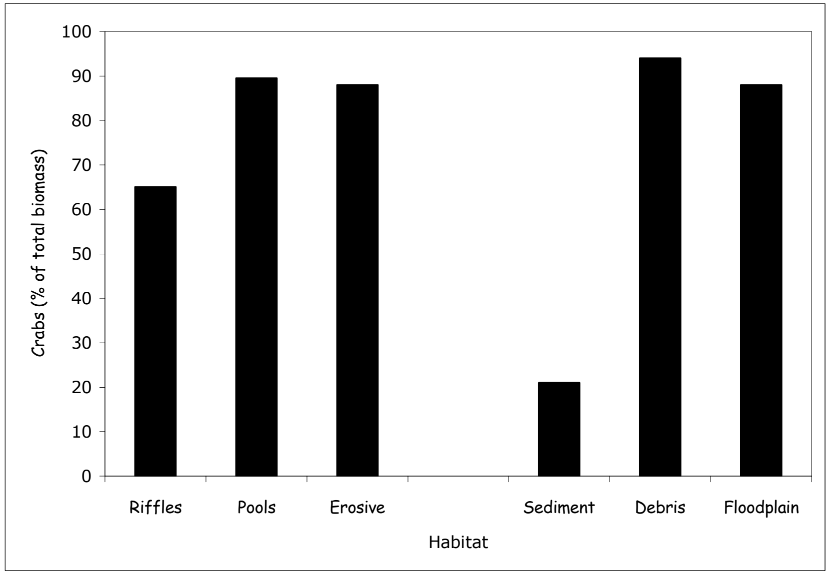


FIG. 5. Contribution of crabs to total invertebrate biomass of biomass in four sub-habitats of two contrasted sections of an upland East African stream, the River Dodwe. Riffles and pools (left) were in the erosive section, sediment and debris dams (right) in the floodplain section.

specimen was found in a different stream), leeches and crustaceans other than crabs. There was no significant difference in invertebrate family richness between the erosive site (5.0 ± SD2.4) and the floodplain site (6.1 ± 3.2), nor between the pools and riffles in the erosive section (4.6 ± 2.0; 5.4 ± 2.7), but the debris dams in the floodplain had greater richness (7.6 ± 3.4) than the sediment (4.3 ± 2.0) ($P < 0.02$). The same pattern of significant differences was found with total numbers of invertebrates.

Significance testing among the families with more than very small numbers showed that crabs were significantly more abundant in the riffles than the pools of the erosive section ($P < 0.02$), in the debris dams compared with the sediment in the floodplain section ($P < 0.01$) and in the floodplain as a whole compared with the erosive section ($P < 0.01$). Hydracarinids were significantly more abundant in the erosive section but were equally abundant in the riffles compared with the pools. Dragonfly nymphs of the burrowing family Gomphidae were significantly more abundant in the floodplain section ($P < 0.01$) and in the debris dams compared with the sediment of the floodplain ($P < 0.05$). Chironomid larvae and tubificids were more abundant in the floodplain compared with the erosive reach ($P < 0.05$) whilst the reverse applied to the corixids ($P < 0.01$). Gyrinids were also more abundant in the floodplain stream ($P < 0.05$).

The distribution of animals among feeding guilds (Table 3) showed some expected features and some unexpected. Scrapers occupied a greater proportion in the erosive stream than in the floodplain and vice versa for deposit feeders. Filter-collectors were relatively scarce (maximally only 10.6%) and shredders (tipulids and crabs) had very low percentages, except in the debris dams of the floodplain. Separate experiments (B. Moss, unpublished data) showed crabs to be vigorous shredders. Predators were relatively abundant, minimally 27.8%, maximally 75% of total numbers).

The picture changed markedly when biomass was considered (Table 4, Fig. 5, Fig. 6). Crabs dominated the biomass in all habitats except the floodplain sediment, comprising, on average, 88% of the biomass in both the floodplain and erosive sections and accounting for 94% in the debris dams. Per unit area, there was significantly more total biomass ($P < 0.05$), crab biomass ($P < 0.02$) and biomass of other animals ($P < 0.02$) in the floodplain than in the erosive stretch and crabs had significantly greater biomass ($P < 0.05$) in the debris dams than in the sediments of the floodplain.

How the system might function

Very few studies have been made of African upland streams as systems. The present study thus suggests, tentatively, some of the mechanisms which might underlie the functioning of such habitats. Previous studies

Table 4. Biomass (sun-dried weight, g m^{-2}, ± SD) of crabs and invertebrates other than crabs in four sub-habitats of two contrasted stretches of an upland African stream, the River Dodwe. Total values also include anuran tadpoles, whose biomass was extremely small. Values sharing a superscript letter are significantly different at $P < 0.05$.

	Erosive			Floodplain		
	Riffles	*Pools*	*Both habitats*	*Sediment*	*Debris dams*	*Both habitats*
Crabs	0.065±0.154	1.14±3.52	0.6±2.5^{b}	0.42±0.75^{d}	22.6±28.2^{d}	11.5±22.3^{b}
Other	0.04±0.03	0.08±0.11	0.06±0.08^{c}	1.6±2.0	1.39±2.4	1.49±2.14^{c}
Total	0.1±0.15	1.26±3.5	0.68±2.5^{a}	2.02±1.84	24.0±27.9	13.0±21.1^{a}

(Raybould et al. 1978; Williams & Hynes 1971) have been made of the relationship of crabs with *Simulium neavei*, a carrier of onchocerciasis in the Usambaras, but none has examined more than specialist aspects of the invertebrate fauna. Dobson et al. (2002) propose that shredders are very scarce in Kenyan streams but speculate that this niche may be occupied by crabs missed by their sampling methods. This study and supplementary experiments to be reported elsewhere suggest that crabs are not only vigorous and rapid shredders but exercise their omnivory in two other guilds also.

The water was nutrient poor, with low pH and conductivity, and nitrate was undetectable. A separate stream also showed a pH of 5.3 and up to 0.3 mg NO_3-N l^{-1}, still a very low value, and consistent with the general presumption of nitrogen limitation of production in tropical African waters (Talling & Lemoalle 1998). This infertility perhaps explains the rather low numbers of animals in the stream but opens the question of the high crab biomass, and indeed sufficient abundance in the floodplain section for crabs to be regularly caught as human food. We ate them ourselves! There was a crab trap along the floodplain section and local information was that fish ('tilapia' and a small catfish) were also caught.

The floodplain has received large quantities of soil as a result of erosion. Soil profiles had a thin dark organic rich layer of a few centimetres, underlain by 15–20 cm of reddish lateritic soil, eroded from the hillsides following deforestation in the mid-late 20th century. Below this were up to 40 cm of grey clay, presumably laid down in the early part of the 20th century when the present floodplain was a lake. Eroded soil will have brought in a stock of nutrients and the waterlogged conditions will favour nitrogen fixation by soil bacteria. Woody debris is still entering the floodplain from the forests at its edges. The higher invertebrate biomass of

FIG. 6. Samples of invertebrates being dried for biomass determinations. The predominance of crabs is obvious. Other large invertebrates included nymphs of Gomphidae.

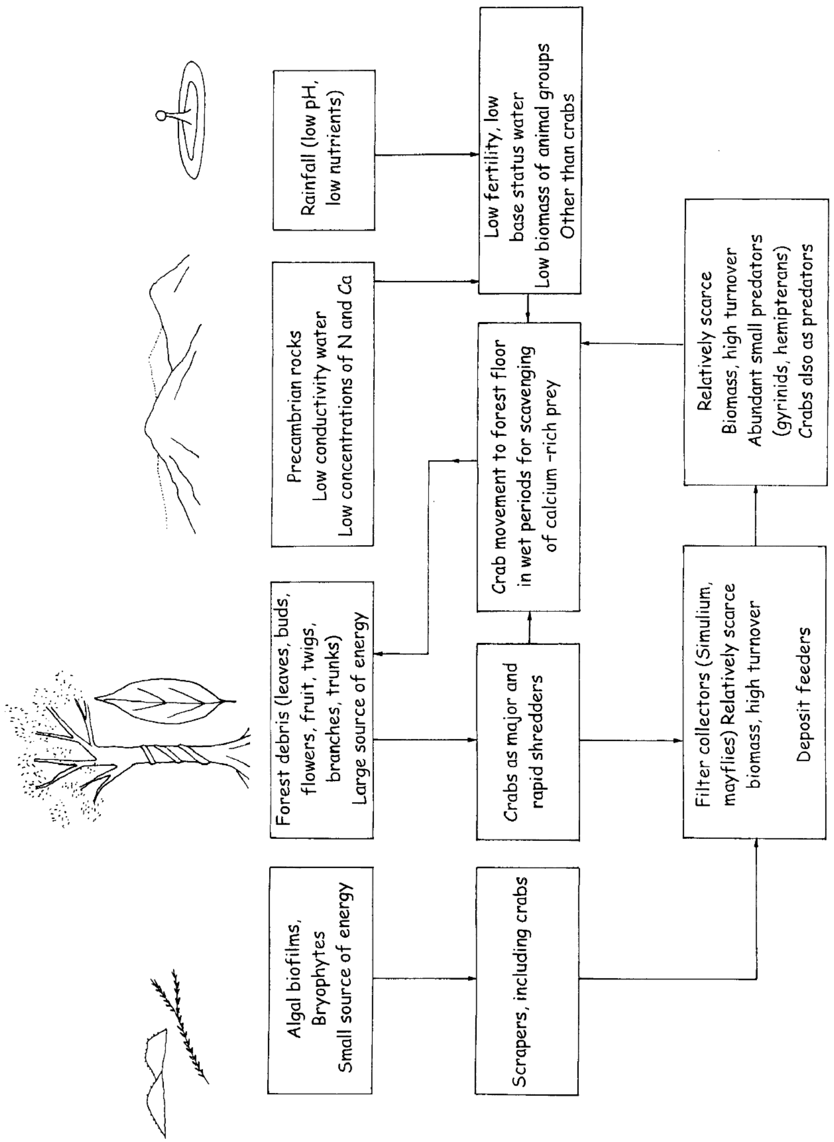
FIG. 7. Some results of a litter bag experiment conducted over one week. Ten leaves of *Ficus mucoso* that had been enclosed in coarse (top) and fine (middle) mesh bags show no damage. Ten leaves that had been exposed in the water show considerable damage. The bundle on the left has been completely stripped and only the stalks, bound with twine, remain. The other five leaves are from the exposed bundle that had suffered *least* damage over a week.

the floodplain will thus have benefited from these additional nutrient sources.

The eroded section clearly received substantial quantities of tree debris. It was overhung by forest, whose shading nonetheless did not prevent development of *in situ* primary producers (algae and bryophytes) but these sources were almost certainly eclipsed by the input of allochthonous material. Tree leaves drifted continually into the system (between 5 and 20 g m^{-2} each day) and bigger debris must move in during the rainy season. The eroded section epitomised the classic picture of upland forested stream reaches visualised in the river continuum concept. The near absence of shredder groups typical of temperate streams, such as amphipods and isopods, and of the prawns common in Asian and South American streams, is interesting but they are replaced by crabs as shredders in this system. Experiments showed virtually no loss of material from litter bags with 20 µm or 3 mm mesh but losses of 33% per day from leaf bundles exposed to the larger fauna, which constituted entirely crabs (Fig. 7, B. Moss, unpublished data). The high ratio of numbers of predators to potential prey is also notable and may reflect a high turnover of organisms in these warm waters.

The floodplain system may also receive a lot of forest detritus, but the vegetation must contribute a lot of material, made available on flooding in the wet season. Detritus dams were the foci of both family richness and biomass compared with the channel sediments. Like the swamps of large floodplains, the vegetation of the floodplain was apparently very productive, sustaining continued cutting for cattle fodder, which had converted a tall, *Cyperus*- and *Typha*-dominated vegetation to a low lawn, rich in orthopteran grazers. Estimates of biomass and cutting rates suggested a very high turnover, perhaps ten or more times per year. The floodplain was also especially rich in crabs.

Crabs, accounting for nearly nine tenths of the biomass, seem likely to be key organisms in both of these stream sections. Their abundance in the floodplain section may be explained by the greater nutrient sources or stocks available, but they dominated the biomass even in the erosive stretch and were similarly predominant in other erosive streams in the area examined in less detail. Crabs appear to be omnivorous. They were shown to take leaf detritus and the existence of skeletonised leaves in the streams suggests the activity of shredders, for which crabs are the only likely candidates. Occasional tipulid larvae were found but no other notable shredders. Crab traps in the floodplain were baited with plant material (chopped cassava). Crabs were also observed to scrape mosses and larger ones, at least, proved efficient predators when confined with other invertebrates, such as zygopteran nymphs.



Crabs require much calcium for their carapaces and it is difficult to see how this can be obtained from waters with conductivities as low as those recorded. The near absence of molluscs is consistent with this. However, crabs are highly mobile and in wet weather were noted on the surrounding forest floor. One Usambaran crab, hitherto unnamed, lives in water-filled, acid tree-bole holes, but survives by hunting forest molluscs and neutralising its habitat water with the shells that it brings back to the holes (Bayliss 2002). Such a mechanism is unlikely in flowing streams where the ratio of water to mollusc would be very high, but it is not impossible that crabs acquire the necessary calcium from eating small molluscs, shell and contents, hunted in the forest and that this is essential if they are to grow to large size. Some are as much as 14 cm across the carapace.

Fig. 8 shows a hypothetical conceptual model of the erosive system and if supported by more detailed work, adds to the increasing appreciation of the close interlinks between freshwaters and their catchments (Naiman et al. 2002). The boundary to freshwater systems is in no way the wetted perimeter.

Acknowledgements

The Tropical Biology Association is a charity whose function is to hold multinationally taught and received courses in Africa for senior undergraduate and postgraduate students from Africa and the developed world. It is grateful to the European Union, the British Ecological Society, individual University subscriptions and BAT Biodiversity Partnership for sponsorship of Course 02/03 held at the IUCN Hostel, Amani, Tanzania.

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FIG. 8 *(opposite)*. Conceptual model of the functioning of upland erosive streams in the East Usambaran Mountains of Tanzania.

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