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RESEARCH PAPER

Longitudinal variation of benthic macroinvertebrate communities in two contrasting tropical streams in Sri Lanka

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The benthic macroinvertebrate fauna and main abiotic parameters were studied to understand the patterns of diversity and structure along the temporal and longitudinal gradients in two tropical lotic ecosystems in the wet and dry zones of Sri Lanka. Invertebrate abundance (annual means) was in the same magnitude in the two streams (2,520 ind. m^{-2} in the wet zone stream and 2,940 ind. m^{-2} in the dry zone stream). Both streams had similar annual mean diversity levels measured as Shannon diversity (Eswathu Oya (wet zone) = 2.11; Yan Oya (dry zone) = 2.07), with a mean annual evenness (Pielou evenness) of 0.56 ± 0.14 for Eswathu Oya and 0.60 ± 0.09 for Yan Oya. Along the longitudinal gradient, abundance and taxa richness increased toward the lower reaches in the wet zone stream but decreased in the dry zone stream. Composition of functional feeding groups was greatly influenced by abiotic factors in the temporal gradient than in the longitudinal gradient. This was possibly due to the seasonal patterns of flow regimes, and allochthonous nutrient inputs into the streams. Hence, resource management and conservation as well as attempts of ecological assessment in tropical streams should be based not only on the in-stream characteristics but also on the catchment properties.

KEYWORDS
benthic animals, functional feeding groups, lotic ecosystems, particulate organic matter

1 | INTRODUCTION

Benthic macroinvertebrates are an important component of biodiversity in lotic systems (Merritt & Cummins, 1996). They play significant roles in energy fluxes, nutrient cycling, as consumers of dead and living organic material, as prey for aquatic insects and fishes (Muñoz & Ojeda, 1997; Wong, Williams, McQueen, Demeres, & Ramcharan, 1998) and their adults for insectivorous birds (Ward, Holmes, & José, 1995). Although Koperski (2011) pointed out that diversity of freshwater benthic macroinvertebrates would not be a strong metric for biological assessment, generally, benthic macroinvertebrates are widely used in biological monitoring (de Villiers & Thiart, 2007; Nyenje, Foppen, Uhlenbrook, Kulabako, & Muwanga, 2010; Sandin & Hering, 2004), especially in tropical streams, where environmental degradation is commonplace (Boyero & Bailey, 2001).

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Benthic macroinvertebrate communities in streams are structured by abiotic and biotic factors that interact over a range of spatial and temporal scales (Carter, Fend, & Kennelly, 1996; Richards, Haro, Johnson, & Host, 1997). Major abiotic factors include flow regimes (Brown & Brussock, 1991; Statzner, Gore, & Resh, 1988; Ward, 1992), geomorphology of the stream bed (Wallace & Webster, 1996), land use patterns in the riparian zones (Resh et al., 1988), and presence of large wood and debris (Benke, Henry, Gillespie, & Hunter, 1985). Benthic invertebrate abundance is also related to substrate quality (Buss, Baptista, Nessimian, & Elger, 2004; Death, 1995) and biological interactions (Kohler, 1992).

In streams, leaf litter is readily leached, colonized, and decomposed by microorganisms, and consumed by macroinvertebrate shredders (Graça, 2001). These processes lead to production of particulate organic matter (POM), which is consumed by a suite of gathering and filtering collector organisms. Shredders and collectors are thus the major primary consumers in forest streams, providing the main link between organic inputs and the predatory invertebrates and vertebrates (Cheshire, Boyero, & Pearson, 2005; Graça et al., 2015; Walpola, Leichtfried, Amarasinghe, & Füreder, 2011).

Tropical streams and rivers support rich invertebrate and vertebrate communities, but information about benthic macroinvertebrates is, to a great extent, incomplete (Dudgeon, 2000; Tomanowa, Goitia, & Helešic, 2006). Although the structure and function of tropical streams have been studied in several regions (Jacobsen, Schultz, & Encalada, 1997; Matagi, 1996; Pringle & Ramírez, 1988), little information is available about tropical streams of south and south-east Asia; especially of Sri Lanka. Hydrological changes are known to affect the temporal variation in macroinvertebrate communities in streams (Townsend, Dolédec, & Scarsbrook, 1997; Weatherley & Ormerod, 1990). In tropical lotic systems, monsoonal floods cause disturbances to instream communities (Miller & Golladay, 1996). Minshall (1988), Arunachalam, Nair, Vijverberg, Kortmulder, & Suriyanarayanan (1991), and Flecker and Feifarek (1994) have shown the importance of investigating the monsoon affected flood regimes on streams communities.

In the present study, two monsoon-driven tropical streams were investigated to understand the temporal and longitudinal gradients of benthic macroinvertebrates (i) in terms of distribution and abundance; (ii) in relation to abiotic factors; and (iii) according to the pattern of functional feeding groups.

2 | MATERIALS AND METHODS

2.1 | Study area

Eswathu Oya (hereafter EO-WZ) is a low order wet-zone stream, begins at 6°53′ 15″ N, 80°11′ 38″ E (203 m a.s.l.), flows through a cascading landscape and drains into the second largest river in Sri Lanka; the Kelani Ganga (Figure 1a and b). Its catchment receives rainfall by convectional rains during south-west monsoon (April to August) and EO-WZ flows throughout the year with frequent flashy floods. The canopy cover above the stretch was about 80%.

Along the longitudinal gradient (Figure 1b), there were home gardens and rubber plantations but the high plant diversity was due to riparian vegetation. A high frequency of pool–riffle combinations was a characteristic feature. Washing of clothes and bathing were the major human activities that took place here. This EO-WZ was not connected to any lentic water bodies such as reservoirs.

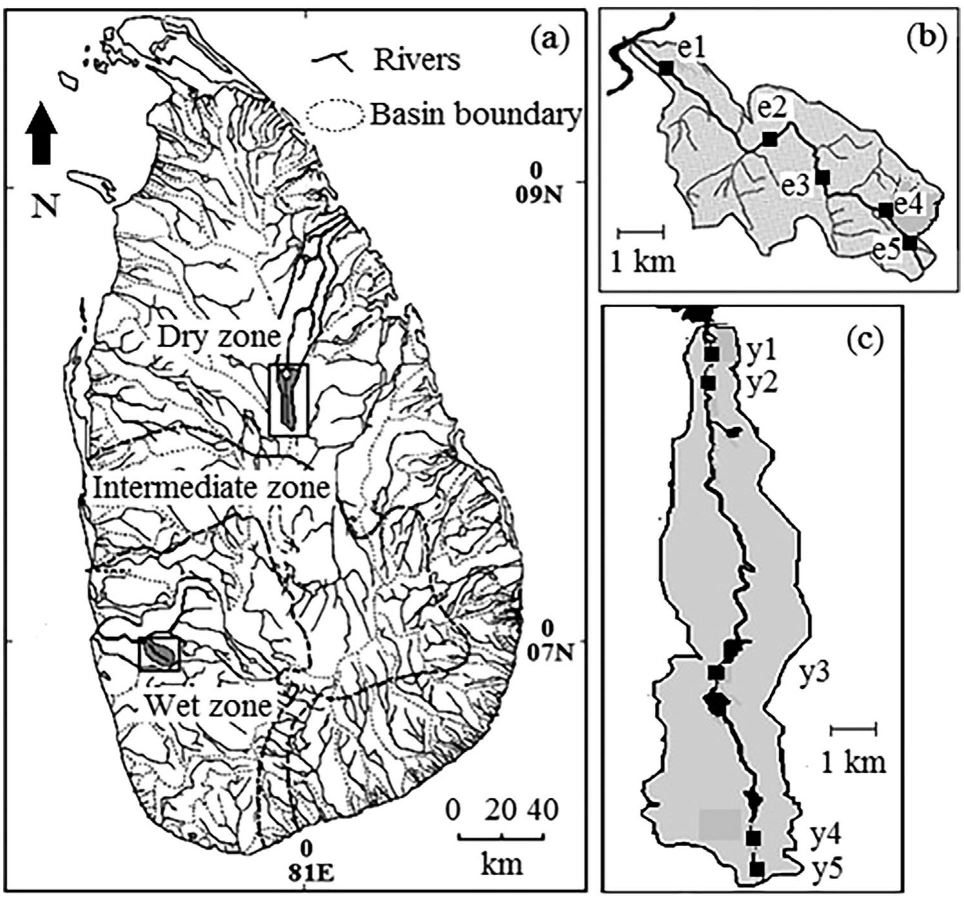

FIGURE 1 (a) Map of Sri Lanka showing 103 river catchments. Framed areas enclose the catchment of (b) Eswathu Oya in the wet zone (EO-WZ) and sampling stretches; e1–e5; (c) Yan Oya in the dry zone (YO-DZ) and sampling stretches; y1–y5

Yan Oya (hereafter YO–DZ) is a low order dry-zone stream, starting at 7°5 6′ 77″ N, 80°45′ 42″ E (186 m a.s.l.), flows through the flat terrain and reaches the Indian Ocean as a fourth order stream (Figure 1a and c). YO-DZ receives precipitation during the northeast monsoon (November to February). The canopy cover over this stretch was almost 100% being *Terminalia arjuna* (Roxb. ex DC.) Wight & Arn., 1834 the most dominant riparian tree species. Three small reservoirs were located between y2 and y3 (Figure 1c). The catchment has rice and other agricultural crop farming which possibly brings fertilizer and other agrochemicals into the stream. Washing of clothes and bathing were the other major human activities that took place here.

Although there is a potential threat of agrochemical pollution, no sign of pollution was observed or reported in both streams, which were running through rural areas.

2.2 | Sampling

Sampling was designed to study the patterns of abiotic and biotic parameters in two streams along temporal and longitudinal gradients. Five stretches in EO-WZ (e1–e5; Figure 1b) were selected to study the longitudinal pattern while the temporal gradient was studied in e2 stretch (Figure 1b). The e2 stretch was a riffle–pool combination, gneiss bed rock formed the bottom on which sand, silt and leaf litter were found. In YO-DZ, a longitudinal gradient was studied in stretches y1–y5, while the temporal gradient was studied in y5 (Figure 1c). The y5 stretch was characterized by the absence of riffles or pools and the dominating bottom sediment was sand with leaf litter packs. To study the temporal gradient, a stretch of 25 m in each stream (e2 in EO-WZ and y5 in YO-DZ) was sampled from September 2004 to March 2006. There were 10 sampling visits to each stream during the study period. During each field visit, ten replicates were taken from randomly selected sites within e2 and y5. To study the longitudinal pattern, sampling was done during February–March 2006 in both streams in the 10 stretches (5 stretches in each stream) shown in Figure 1b and c, and from each stretch, five replicates were taken. For clarity, in the analysis of data, sampling sites for longitudinal gradients were coded as eL1–eL5 in EO-WZ and yL1–yL5 in YO-DZ. Similarly, sampling occasions for studying temporal gradients were coded as eT1–eT10 in EO-WZ and yT1–yT10 in YO-DZ.

Sampling included (i) measuring daily water level; (ii) determining monthly values of abiotic parameters (temperature, pH, conductivity, depth, and flow velocity of each sampling site); (iii) measuring velocity profile across each stretch; and (iv) collecting sediments for coarse particulate organic matter (CPOM, organic matter >100 μm) and fine particulate organic matter (FPOM, organic matter <100 μm). These sediment samples were also used to separate benthic macroinvertebrates.

Sediments from a 10 cm depth were obtained with two methods; a modified Hess sampler (20 cm in diameter, 50 cm in height) with a 100 μm mesh and a core sampler of 5 cm diameter. Sediments from Hess sampler were used to obtain CPOM and those from core sampler were used to obtain FPOM. All sediment samples were preserved in 4% formalin in situ.

Daily water level data were collected in EO-WZ and YO-DZ separately using temporarily fixed and permanent gauges in each stream. Abiotic factors were measured during each sampling replicate before taking sediment samples.

After taking all samples for determination of abiotic factors, velocity depth profile was measured during each visit at a depth of 60% from left to right bank in a 0.5 m distance and discharge was calculated (Gordon, McMahon, Finlayson, Gippel, & Nathan, 2004) from the flow rate measured using a flow meter (FLO-MATE 2000, Marsh – McBirney, Inc., Flo-Mate, USA).

2.3 | Sample and data analysis

In the laboratory, CPOM samples were washed through 1000, 500, and 100 μm sieves and each fraction was treated separately. FPOM samples were fractionated passing through a 100 μm sieve. Altogether four fractions of sediment samples were separately dried at 80 °C for 24 hr and weighed to the nearest 0.01 mg. The three CPOM fractions were muffled at 500 °C for 2 hr, weighed to the nearest 0.01 mg and ash free dry mass (AFDM) of organic matter was determined per m^2. Mean value was obtained for each visit. The dry mass of the FPOM fractions was calculated per m^2, and mean dry mass was calculated for each visit. The mean values of all the abiotic parameters were determined for each visit and each stretch.

Animals >500 μm were defined as benthic macroinvertebrates in this study. They were separated from 500 and 1000 μm sieves and identified to the lowest feasible taxonomic level using taxonomic key in Merritt and Cummins (1996), Dudgeon (1999), and Fernando and Weerawardhane (2002). Functional feeding groups (FFGs) were assigned to each taxon following Merritt and Cummins (1996). The composition of FFGs (shredders, gathering collectors, filtering collectors, scrapers, piercer herbivores, and predators) was determined. Each benthic macroinvertebrate community per sampling stretch was described as density (ind. m^{-2}), richness (total number of taxa found in each stretch), diversity (Shannon, 1948), and evenness (Pielou, 1975).

To investigate underlying patterns of multivariate datasets of abiotic factors and abundance of FFGs in the two streams, principal component analysis (PCA) was performed for abiotic factors and FFGs separately using MINITAB (Version 14) statistical software package. Here, PCA was performed for data sets of temporal gradients and longitudinal gradients separately. Prior to PCA, data were ln $(x + 1)$ transformed to reduce non-normality in the data set. Also, to detect which abiotic parameters influenced the distribution of FFGs along the temporal and longitudinal gradients, principal component scores of abiotic factors and those of FFGs were related using linear regression analysis.

3 | RESULTS

3.1 | Temporal gradient in the two streams

The regular sampling stretch (e2) in EO-WZ flooded during April–May 2005 due to convectional rains. Altogether 10 field visits were successfully made. The water level showed three distinct phases as high, low and peaks during high water level (Table 1). The highest water level recorded was 60 cm, during which channel width expanded to 7.5 m. With the onset of the dry season, gradual drying started since

TABLE 1 Abiotic parameters (mean ± SE) of the 10 sampling months in the Eswathu Oya wet zone stream (EO-WZ)

Month	No.	pH	Conductivity (µS cm^{-1})	Water temperature (°C)	Depth (cm)	Velocity (m s^{-1})	Discharge (m^3 s^{-1})	FPOM (g DW m^{-2})	CPOM (g AFDW m^{-2})		
								<100	>100	>500	>1000
Sep '04	1	6.58 ± 0.08	25.70 ± 0.26	28.14 ± 0.57	17.95 ± 11.05	0.00 ± 0.00	0.47 ± 0.03	0.00 ± 0.00	12.11 ± 6.92	5.09 ± 4.88	200.46 ± 241.41
Jan '05	2	6.56 ± 0.40	23.06 ± 0.22	24.06 ± 1.06	23.70 ± 11.24	0.11 ± 0.11	0.15 ± 0.02	24.40 ± 27.85	892.21 ± 1894.34	26.63 ± 28.15	992.59 ± 1345.60
Feb '05	3	6.63 ± 0.22	24.20 ± 0.94	25.15 ± 0.61	21.00 ± 13.35	0.05 ± 0.05	0.01 ± 0.00	82.89 ± 56.51	37.35 ± 27.15	10.06 ± 10.01	289.24 ± 169.04
May '05	4	6.18 ± 0.13	22.43 ± 0.46	26.86 ± 0.35	27.25 ± 11.48	0.05 ± 0.05	0.03 ± 0.00	117.66 ± 59.27	54.32 ± 56.13	61.30 ± 57.66	545.51 ± 667.77
Jun '05	5	6.79 ± 0.62	23.18 ± 1.16	26.27 ± 0.12	21.90 ± 9.99	0.07 ± 0.07	0.01 ± 0.00	146.17 ± 80.33	65.30 ± 44.80	17.60 ± 10.24	612.61 ± 273.61
Aug '05	6	5.69 ± 0.14	24.92 ± 0.91	26.32 ± 0.67	19.50 ± 10.04	0.06 ± 0.04	0.00 ± 0.00	2636.47 ± 5685.98	43.40 ± 31.55	31.02 ± 51	897.95 ± 325.59
Oct '05	7	6.11 ± 0.47	24.38 ± 0.35	25.72 ± 0.32	21.90 ± 10.30	0.15 ± 0.19	1.05 ± 0.07	132.24 ± 52.79	38.28 ± 29.38	26.53 ± 24.07	555.40 ± 420.84
Nov '05	8	5.73 ± 0.19	21.91 ± 1.05	25.73 ± 0.40	25.00 ± 10.23	0.13 ± 0.18	0.79 ± 0.04	304.05 ± 266.96	141.31 ± 203.44	18.65 ± 28.28	484.84 ± 443.67
Jan '06	9	5.84 ± 0.10	24.56 ± 1.22	25.51 ± 0.54	27.70 ± 9.19	0.04 ± 0.08	0.12 ± 0.03	127.90 ± 88.00	55.15 ± 29.55	19.62 ± 11.55	396.30 ± 338.96
Mar '06	10	5.84 ± 0.10	24.56 ± 1.22	25.51 ± 0.54	27.70 ± 9.19	0.04 ± 0.08	0.02 ± 0.01	94.75 ± 67.64	62.45 ± 30.47	15.48 ± 7.24	231.67 ± 179.62

CPOM: Coarse Particulate Organic Matter; FPOM: Fine Particulate Organic Matter; gDWm^{-2}: g dry weight m^{-2}; g AFDW m^{-2}: g ash-free dry weight m^{-2}.

May 2005, when water level declined to 10 cm and main channel narrowed down to 1.5 m. Monsoon started in August 2005 and water level rose to 50 cm. During this wet period with convectional rainfall, many flashy floods occurred. However, flow velocity remained low as <0.5 m per second during both dry and wet periods (Table 1). The discharge was low throughout but fluxed during October and November 2005 due to monsoonal rains (Table 1).

In the e2 stretch, water temperature varied between 24 and 27 °C. The highest temperature occurred during the seasons of low water level. The pH ranged from 5.9 to 6.8, conductivity ranged between 22 and 25 µS cm^{-1}. The average depth of sampling sites varied from 17.9 cm in September 2004 to 27.7 cm in January–March 2006 (Table 1).

The amount of organic matter found in e2 stretch varied between 217 g m^{-2} and 3.6 kg m^{-2} during the study period. The FPOM showed a greater abundance in August 2005 when water level was gradually rising. The amount of CPOM of >1000 µm was in a steady supply throughout the sampling period ranging from 200 to 992 g m^{-2} (Table 1). The vegetation cover over this stretch remained 80% throughout the 10-month sampling period.

A total of 945 individuals from 51 taxa of benthic macroinvertebrates belonging to 43 families were found in the e2 during the study period. Coleoptera (471 individuals) and Diptera (316 ind.) represented 83% of the benthic macroinvertebrates, while Trichoptera (7%), Ephemeroptera (5%), Odonata (5%), and Plecoptera (0.004%) formed the rest. Elmidae and Psephenidae were the most abundant coleopterans among 18 families. Chironomidae and Psychodidae represented the majority among 11 dipteran families. Trichopteran abundance and richness was low and dominated by Hydropsychidae and Leptoceridae. The most dominant ephemeropterans were Caenidae and Baetidae.

The highest abundance of benthic macroinvertebrates (5300 and 5245 ind. m^{-2}) was reported during low discharge in January, February and August 2005. The lowest abundance of benthic macroinvertebrates (649 ind. m^{-2}) was reported during the highest discharge (October to November 2005) (Figure 2a). The highest evenness was recorded during low discharge while lowest evenness was recorded in high discharge. The diversity also showed a relationship to evenness (Figure 2b). Richness and abundance showed a corresponding relationship (Figure 2a).

The water level of the regular sampling stretch (y5) of YO-DZ reached the bank level in February and December in 2005 and February in 2006 (Table 2). Ten sampling visits were successfully conducted in this stretch. The highest water level (3 m) recorded was from November 2005 to February 2006 during when the width of the channel reached 14 m. The vegetation cover over this stretch was almost 100%. Discharge had two peaks in February and October 2005 (Table 2).

The highest abundance of benthic macroinvertebrates was reported during the lowering of the water level (March and July 2005) and vice versa (Figure 3a). The richness showed a pattern related to abundance. The evenness and diversity showed similar pattern (Figure 3b). Lowest evenness and diversity was from high discharge and vice versa (Figure 3b and Table 2).

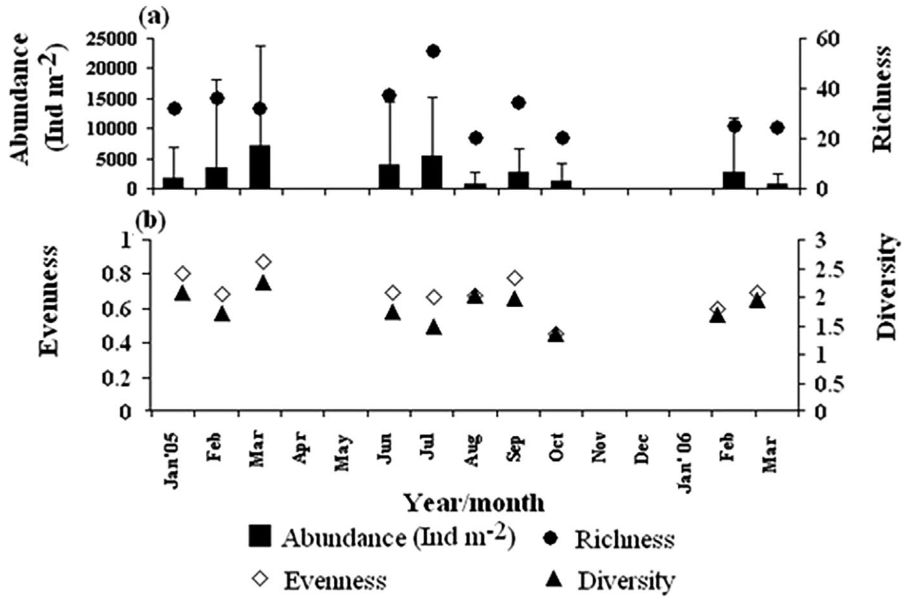

FIGURE 2 (a) Mean abundance (ind. m^{-2}), taxa richness, and (b) Shannon diversity index and evenness for the 10 sampling occasions in the EO-WZ. Number of replicates was 10

In YO-DZ, due to gradual drying from May 2005, pools started to isolate and by the end of November 2005 most of the bottom was exposed. During the 5 months long dry period, the channel narrowed down to 2 m in width and flow velocity fluxed to the highest (2.89 m s^{-1}) in July 2005 (Table 2). Water was turbid during high water level and clearer during low water level. The average depth of sampling in the regular sampling stretch varied between 17 and 36 cm. Water temperature ranged from 25 to 28 °C, pH varied between 7.1 and 7.85 and the conductivity varied from 138 to 721 µS cm^{-1}. Higher conductivity was corresponding to low water level and vice versa.

All four fractions of POM were found in the regular stretch of YO-DZ throughout the 10 sampling occasions, but their amounts and compositions varied (Table 2). The FPOM showed a corresponding decrease with the lowering of water level. The highest amount of total POM (1.5 kg m^{-2}) was found in January 2005 when the highest water level was registered, and with gradual drying, the amount of POM decreased. The least amount of total POM (387 g m^{-2}) was found during the dry month of August 2005 (Table 2).

A total of 895 individuals from 42 taxa belonging to 29 families were collected in the regular sampling stretch in YO-DZ throughout the 10 sampling occasions. Dipterans dominated and contributed 62% of the total individuals recovered, followed by Ephemeroptera (16%), Trichoptera (7%), Mollusca (4%), Coleoptera (3%), Cladocera (3%), and Hemiptera (2%). Other taxa like Odonata, Plecoptera, Hydrachnida, Copepoda, and Turbellaria were also found <1%.

Among dipterans Chironomidae, Ceratopogonidae, and Tanypodinae were dominating. Ephemeropterans were represented by Caenidae, Baetidae, and Leptophlebiidae among 13 taxa. Among 15 taxa of Trichoptera, Hydropsychidae, and Leptoceridae dominated. Coleopterans were less abundant but there were 12 taxa from which Elmidae dominated.

3.2 | Temporal gradient of FFGs in the two streams

All FFGs were found among the benthic macroinvertebrates in e2 stretch of EO-WZ (Figure 4a). Shredders were found only during dry period, which were represented by one taxon from Calamoceratidae. Among the collectors, gathering collectors were more dominant. Gathering collectors were represented by 9 taxa. Filtering collectors were less and inconsistent, and were represented by 2 taxa from Hydropsychidae and Simuliidae families. Scrapers were a dominant FFG in e2 stretch, which were represented by 15 taxa from Elmidae, Psephenidae, Glossosomatidae, Helicopsychidae, and Heptageniidae. Abundance of scrapers was small during low-water level, but high after the monsoon. March 2006 was an extraordinary month for FFGs, and the scraper population rose above 90% perhaps indicating the presence of biofilms in the stretch.

Predator population was less and fluctuated. More predators were found during low water in the dry season. Predators were represented by 16 taxa from 12 families. Piercer herbivores were found at the onset of the monsoon in August 2005, which were represented by three taxa from family Hydroptilidae.

Although all the six FFGs were found in the regular sampling stretch of y5 in YO-DZ, their abundance and composition varied seasonally (Figure 4b). Shredders were very low and inconspicuous, and were represented by one taxon from family Calamoceratidae. They were found only during the dry periods (July, August 2005 and March 2006), which were the major leaf fall seasons.

The most dominant FFG in this regular sampling stretch in YO-DZ was gathering collectors. They were represented by 27 taxa from 11 families. Filtering collectors were less abundant and represented by 10 taxa from 6 families. Scrapers were few, and were represented by 14 taxa from six families. A single taxon of piercer herbivore was represented by family Hydrophilidae. Predators were the second most

TABLE 2 Abiotic parameters (mean ± SE) of the 10 sampling months in the Yan Oya dry zone stream (YO-DZ)

Month	No.	pH	Conductivity ($\mu S\,cm^{-1}$)	Water temperature (°C)	Depth (cm)	Velocity ($m\,s^{-1}$)	Discharge ($m^3\,s^{-1}$)	FPOM ($g\,DW\,m^{-2}$) <100	CPOM ($AFDW\,m^{-2}$) >100	>500	>1000
Jan '05	1	7.80 ± 0.00	374.00 ± 18.07	25.90 ± 0.26	36.30 ± 11.80	0.34 ± 0.14	na	1126.31 ± 1334.75	316.93 ± 680.93	14.96 ± 7.42	122.32 ± 166.49
Feb '05	2	7.85 ± 0.24	357.40 ± 6.95	27.17 ± 0.94	26.60 ± 13.04	0.24 ± 0.18	1.52 ± 0.04	736.84 ± 764.35	40.72 ± 32.13	8.98 ± 5.72	128.94 ± 110.72
May '05	3	7.54 ± 0.12	721.00 ± 13.34	28.23 ± 0.11	23.20 ± 10.91	0.19 ± 0.25	0.08 ± 0.01	592.51 ± 365.33	22.33 ± 16.21	3.16 ± 1.96	128.02 ± 173.03
Jun '05	4	7.58 ± 0.12	664.30 ± 26.85	26.66 ± 0.35	18.20 ± 10.96	0.17 ± 0.20	0.03 ± 0.01	353.76 ± 346.01	51.90 ± 22.23	7.48 ± 3.20	375.85 ± 537.69
Jul '05	5	7.67 ± 0.07	671.40 ± 19.59	25.37 ± 0.80	17.30 ± 12.45	2.89 ± 5.86	0.02 ± 0.01	331.66 ± 137.39	52.48 ± 59.76	7.40 ± 8.49	70.44 ± 65.57
Aug '05	6	7.56 ± 0.05	418.67 ± 1.50	26.82 ± 0.41	20.00 ± 11.25	0.23 ± 0.11	0.09 ± 0.01	147.18 ± 65.22	26.37 ± 19.17	5.17 ± 2.62	182.63 ± 241.38
Oct '05	7	7.22 ± 0.08	145.80 ± 15.06	26.95 ± 0.92	17.60 ± 6.42	0.12 ± 0.13	0.18 ± 0.01	472.75 ± 529.83	45.67 ± 59.67	14.51 ± 23.18	231.22 ± 439.52
Nov '05	8	7.33 ± 0.09	138.40 ± 1.71	26.10 ± 0.12	21.40 ± 12.29	0.24 ± 0.17	1.30 ± 0.05	605.30 ± 830.81	55.02 ± 50.42	21.04 ± 35.28	140.80 ± 214.96
Jan '06	9	7.23 ± 0.08	541.60 ± 12.22	26.37 ± 0.24	22.80 ± 12.61	0.20 ± 0.19	0.48 ± 0.03	646.06 ± 725.50	58.33 ± 126.38	7.31 ± 6.97	160.67 ± 344.05
Mar '06	10	7.10 ± 0.00	323.00 ± 0.00	27.80 ± 0.00	30.00 ± 9.07	0.10 ± 0.06	0.49 ± 0.03	347.58 ± 320.68	407.03 ± 1204.93	7.21 ± 5.38	238.82 ± 351.74

CPOM: Coarse Particulate Organic Matter; FPOM: Fine Particulate Organic Matter; $gDWm^{-2}$: g dry weight m^{-2}; g AFDW m^{-2}: g ash-free dry weight m^{-2}.

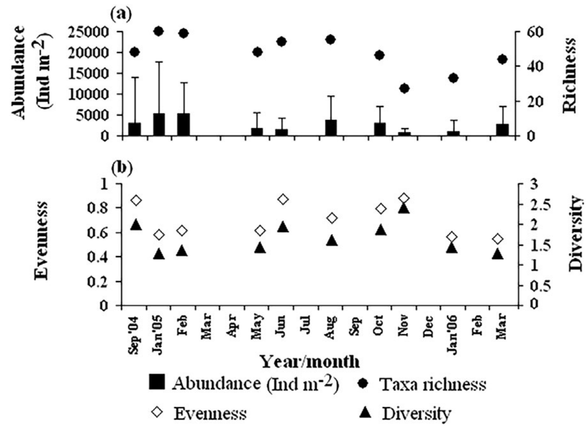

FIGURE 3 (a) Mean abundance (ind. m^{-2}), taxa richness, and (b) Shannon diversity index and evenness for the in 10 sampling occasions in YO-DZ. Number of replicates was 10

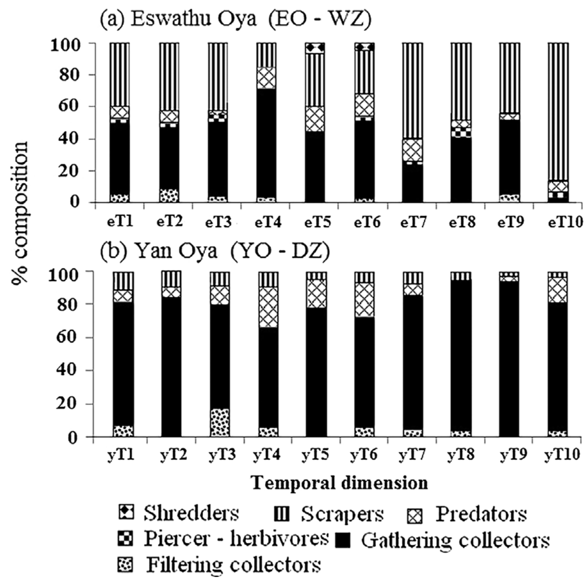

FIGURE 4 Temporal gradient of percentage composition of functional feeding groups (FFGs) found in the regular stretch in (a) Eswathu Oya (EO-WZ) (eT1–eT10) and (b) Yan Oya (YO-DZ) (yT1–yT10)

abundant FFG, which was composed of 16 taxa from 14 families and their populations changed seasonally.

3.3 | Longitudinal gradient of abiotic factors in the two streams

The five stretches (e1, e2, e3, e4, and e5) selected for longitudinal gradient covered a total channel area of 11 km in EO-WZ (Figure 1b). In general riffle–pool combination was more frequent within the first four stretches (e1–e4) where hard bedrocks were imminent as outcrops. The e5 stretch flows through a flat area. The vegetation cover over e1–e3 was almost 100%. In e4 and e5 stretches, vegetation cover was about 10%. Water was clear in all stretches and temperature ranged from 25 to 28 °C with an increment towards downstream reaches (Table 3). The pH varied from 5.5 to 6.1 and conductivity varied between 24 and 41 µS cm^{-1}. A slight increment in conductivity was seen from e2 to e5. The average depth of the sampling sites along the longitudinal gradient had increased. Flow velocity also increased along the gradient from e1 to e5. All four fractions of POM were found in the sediments along the five stretches but with varied amounts and compositions. CPOM of >1000 µm were more abundant throughout the five sites followed by >100 µm, >500 µm, and FPOM. The FPOM were inconsistent and least abundant.

The five stretches (y1, y2, y3, y4, and y5) selected for longitudinal gradient covered a total channel length of 20 km in YO-DZ (Figure 1c). The selected five stretches flow through a flat landscape and riffle–pool combination was rare. The discharge was low (0.5 $m^3 s^{-1}$) in all five stretches (Table 3). Temperature ranged from 26.5 to 28 °C with clear flux in the stretch y3. The pH also showed a slight decrease in y3, but fluctuated between 6 and 7. Conductivity was high and showed clear downfall in y3, but generally fluctuated between 323 and 507 µS cm^{-1}. The average depth of the sampling sites increased from 17 to 35 cm from y1 to y5. The flow velocity varied between 0.1 and 0.5 cm s^{-1}. The highest velocity was found in y4. The vegetation cover over y1 stretch was about 50% and in other four sites, it was about 80%.

All four fractions of POM were found throughout the longitudinal gradient. CPOM of >1000 µm were the most abundant and consistent in all the five stretches followed by >500 µm. FPOM were slightly higher in y1 and y2. Also, y3, y4, and y5 seem to be similar in composition of POM (Table 3).

3.4 | Longitudinal gradient of FFGs in the two streams

Gathering collectors, predators and scrapers were the dominant FFGs in all five stretches in EO-WZ (Figure 5a). Filtering collectors and shredders were less abundant. Although the composition of FFGs in e1 and e5 was similar, the taxonomic composition was different.

All FFGs were present but gathering collectors were the most dominant followed by filtering collectors and predators in YO-DZ (Figure 5b). Scrapers and piercer herbivores were less conspicuous and inconsistent. The composition of benthic macroinvertebrates along the gradient varied much. For example, y3 had over 90% of gathering collectors but in y1 their abundance was <20%.

3.5 | Longitudinal gradient of taxa in two stream

Sixty-five taxa from 46 families were recorded along the longitudinal gradient in EO-WZ. The e1 stretch was recorded with 24 taxa from 21 families. The e2 stretch had 30 taxa belonging to 22 families. The highest richness of 38 taxa belonging to 29 families occurred in the e4 stretch. The abundance and richness of those taxa increased from e1 to e4 and decreased in e5 (Figure 6a). Diversity and evenness decreased from e1 to e4 but increased again in e5 (Figure 6a).

A total of 53 taxa were recorded from 35 families within five stretches in YO-DZ. The y5 stretch had 39 taxa belonging to 27 families and y4 stretch had 15 taxa belonging to 12 families. Their

TABLE 3 Abiotic parameters of the five sites in the longitudinal gradient in Eswathu Oya wet zone stream (EO-WZ) and Yan Oya dry zone stream (YO-DZ)

Site	pH	Conductivity (µS cm^{-1})	Water temperature (°C)	Depth (cm)	Velocity (m s^{-1})	Discharge ($m^3 s^{-1}$)	FPOM (g DW m^{-2})	CPOM (g AFDW m^{-2})		
							<100	>100	>500	>1000
Wet zone stream (EO-WZ)										
1	5.44 ± 0.21	32.14 ± 9.68	25.30 ± 0.41	14.70 ± 10.05	0.07 ± 0.06	0.00	32.05 ± 17.11	40.43 ± 29.68	10.26 ± 11.27	2098.95 ± 4434.25
2	5.84 ± 0.11	23.76 ± 1.22	25.22 ± 0.67	29.40 ± 8.32	0.03 ± 0.05	0.02	139.54 ± 108.62	72.06 ± 38.52	32.10 ± 23.54	420.51 ± 129.61
3	6.20 ± 0.31	28.58 ± 0.34	25.94 ± 0.42	23.50 ± 11.47	0.05 ± 0.05	0.02	181.04 ± 120.63	64.44 ± 67.26	19.74 ± 16.70	439.34 ± 281.53
4	6.8 ± 0.07	28.00 ± 0.00	25.90 ± 0.00	40.40 ± 5.59	0.09 ± 0.20	2.53	95.36 ± 48.45	29.72 ± 0.02	5.69 ± 2.16	434.52 ± 467.35
5	6.12 ± 0.13	41.42 ± 0.18	27.80 ± 0.00	23.80 ± 15.35	0.39 ± 0.35	0.65	62.1 ± 37.09	145.70 ± 85.09	130.11 ± 44.91	461.39 ± 390.05
Dry zone stream (YO-DZ)										
1	7.30 ± 0.12	325.20 ± 1.30	26.48 ± 0.11	17.00 ± 10.63	0.10 ± 0.12	0.00	165.53 ± 76.74	6.34 ± 5.29	3.67 ± 3.85	150.95 ± 134.64
2	7.50 ± 0.00	507.80 ± 2.49	26.60 ± 0.00	16.80 ± 8.29	0.19 ± 0.19	0.07	478.17 ± 551.84	16.42 ± 5.30	20.37 ± 40.86	85.13 ± 57.27
3	7.10 ± 0.00	323.00 ± 0.00	27.80 ± 0.00	30.00 ± 9.62	0.10 ± 0.06	0.41	128.99 ± 64.15	790.22 ± 1678.43	16.99 ± 7.50	201.57 ± 219.70
4	7.10 ± 0.00	323.00 ± 0.00	27.80 ± 0.00	30.00 ± 9.62	0.10 ± 0.06	0.44	298.14 ± 101.68	35.07 ± 25.04	3.53 ± 5.29	74.90 ± 103.57
5	7.10 ± 0.00	323.00 ± 0.00	27.80 ± 0.00	30.00 ± 9.62	0.10 ± 0.06	0.42	129.30 ± 104.58	43.00 ± 69.10	2.42 ± 1.66	66.29 ± 116.21

CPOM: Coarse Particulate Organic Matter; FPOM: Fine Particulate Organic Matter; gDWm^{-2}: g dry weight m^{-2}; g AFDW m^{-2}: g ash-free dry weight m^{-2}.

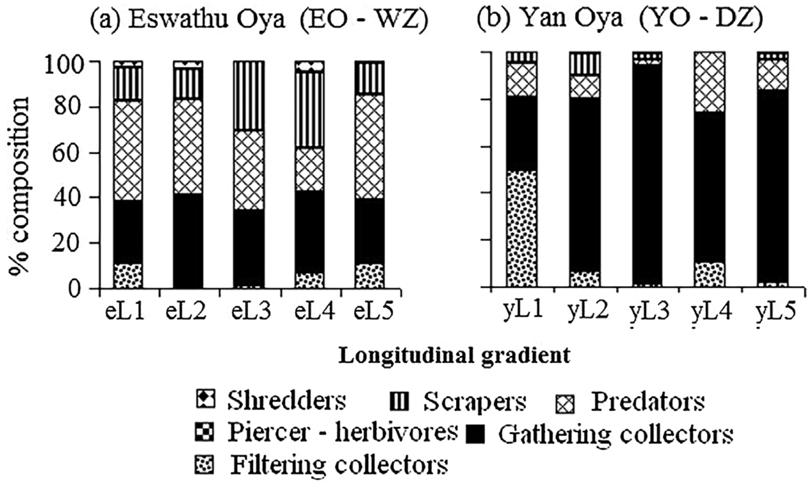

FIGURE 5 Percentage composition of functional feeding groups (FFG) in the 5 stretches along the longitudinal gradients in (a) EO-WZ (eL1–eL5) and (b) YO-DZ (yL1–yL5)

abundance and richness decreased from y1, and accordingly evenness and diversity changed (Figure 6b).

3.6 | Underlying patterns of temporal gradients of FFGs and abiotic factors of two streams

The first two axes of the PCA of functional feeding groups (PC1 and PC2) based on the monthly abundance of FFGs in both stream explained 73% of the cumulative variance (Table 4a). PC1 (eigenvalue = 2.516) and PC2 (eigenvalue = 1.918) accounted for 41 and 32% of the variance, respectively. The positive loading in PC1 of FEGs was due to higher abundance of predators and scrapers as well as presence of shredders. The negative score loading in PC1 was influenced by higher number of gathering and filtering collectors as well as presence of piercer herbivores.

In the second PC axis (PC2) of functional feeding groups, positive score loading was influenced by higher abundance of gathering collectors, and lower amount of filtering collectors as well as presence of scrapers. None of the FFGs was responsible for negative loading in PC2 (Table 4a).

The first two axes of the PCA (PC1 and PC2) of abiotic factors explained 55% of the total variation (Table 4b). In PC1 (eigenvalue = 3.584, variance explained = 35.8%), positive loading was characterized by higher values of conductivity, pH, velocity, temperature, and FPOM. The negative loading in the PC1 was by higher amounts of CPOM of >100, >500, and >1000 µm.

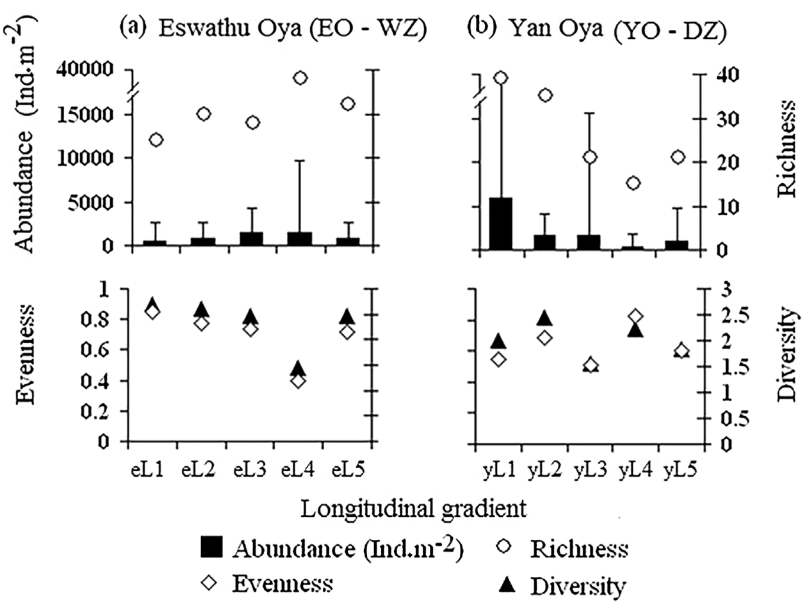

FIGURE 6 Mean abundance (ind. m^{-2}), taxa richness, Shannon diversity and evenness in five stretches along the longitudinal gradient in (a) EO-WZ (eL1–eL5) and (b) YO-DZ (yL1–yL5)

TABLE 4 Eigenvalues, percentage variance explained, and coefficients of the principal component analysis of the temporal gradients of (a) the abundance of six functional feeding groups (FFGs) and (b) the abiotic factors during the 10 sampling occasions in the two streams studied

	PC 1	PC 2
(a) FEGs		
Eigenvalue	2.516	1.918
Proportion	0.419	0.320
Cumulative variance explained	0.419	0.739
Variables		
Filtering collectors	−0.327	0.497
Gathering collectors	−0.072	0.637
Piercer – herbivore	−0.484	0.234
Predators	0.570	0.134
Scrapers	0.393	0.514
Shredders	0.417	0.104
(b) Abiotic factors		
Eigenvalue	3.584	1.916
Proportion	0.358	0.192
Cumulative variance explained	0.358	0.550
Variables		
pH	0.474	−0.110
Conductivity (μS cm^{-1})	0.481	−0.179
Water temperature (°C)	0.186	0.364
Depth (cm)	−0.084	−0.429
Velocity (m s^{-1})	0.280	−0.083
Discharge (m^3 s^{-1})	0.028	−0.421
<100 (g DW m^{-2})	0.126	−0.536
>100 (g AFDW m^{-2})	−0.163	−0.366
>500 (g AFDW m^{-2})	−0.431	−0.185
>1000 (g AFDW m^{-2})	−0.441	0.007

eT1–eT10: Sampling occasions in Eswathu Oya, wet zone (EO-WZ); yT1–yT10: Sampling occasions in Yan Oya, dry zone (YO-DZ).

TABLE 5 Eigenvalues, percentage variance explained, coefficients of (a) the abundance of six functional feeding groups (FEGs) and (b) the abiotic factors for 5 sites along the longitudinal gradients in the two streams studied

	PC1	PC2
(a) FEGs		
Eigenvalue	1.943	1.625
Proportion explained	0.324	0.271
Cumulative variance explained	0.324	0.595
Variables		
Filtering collectors	−0.199	−0.510
Gathering collectors	−0.201	−0.481
Piercer – herbivores	−0.422	0.336
Predators	−0.523	−0.154
Scrapers	−0.643	−0.007
Shredders	−0.233	−0.609
(b) Abiotic factors		
Eigenvalue	4.054	2.245
Proportion explained	0.405	0.225
Cumulative variance explained	0.405	0.630
Variables		
pH	0.475	−0.022
Conductivity (μS cm^{-1})	0.450	−0.075
Water temperature (°C)	0.331	−0.394
Depth (cm)	0.080	−0.412
Velocity (m s^{-1})	0.050	−0.391
Discharge (m^3 s^{-1})	0.038	−0.423
<100 (g DW m^{-2})	0.383	0.148
>100 (g AFDW m^{-2})	−0.115	−0.473
>500 (g AFDW m^{-2})	−0.247	−0.300
>1000 (g AFDW m^{-2})	−0.481	0.018

eL1–eL5: Stretches in Eswathu Oya, wet zone (EO-WZ); yL1–yL5: Stretches in Yan Oya, dry zone (YO-DZ).

PC2 of abiotic factors explained 19.2% of the variance (eigenvalue = 1.916). Its positive scores were influenced by higher values of temperature and CPOM of >1000 µm. The negative loading of PC2 was influenced by FPOM, higher values of discharge, and CPOM of >100 µm.

3.7 | Underlying patterns of abiotic factors and FFGs along the longitudinal gradient

First two axes of PCA (PC1 and PC2) of FFGs of the 10 stretches along the longitudinal gradient in two streams explained 59.4% of the cumulative variance (Table 5a). PC1 (eigenvalue = 1.943) accounted for 32.4% of the variance, and its positive score loading was influenced by low abundance of predators, shredders, and scrapers. The negative scores of PC1 was due to low abundance of piercer herbivore and filtering collectors. PC2 (eigenvalue = 1.625) explained 27% of the variance, and was positively influenced by the presence of piercer herbivores, and the negatively by higher abundance of filtering collectors and gathering collectors.

First two PCA axes (PC1 and PC2) based on abiotic parameters of 10 stretches from two streams explained 63% of the total variation (Table 5b). The positive factor loading of PC1 (eigenvalue = 4.054, variance explained = 40.56%) was by higher values of pH, conductivity, FPOM, and lower value of temperature. The negative loading of PC1 was due to CPOM of >1000, >500 and >100 µm.

PC2 (eigenvalue = 2.245) explained 22.5% of the variance and loaded positively by higher values of FPOM and CPOM of >1000 µm. Negative loading was influenced by CPOM of >100 µm, discharge, depth, temperature, and flow velocity.

3.8 | Influence of abiotic factors on FFGs

Strong negative correlation (r = −0.555; p < 0.02) between PC1 scores of FEG and those of abiotic factors in the temporal gradient indicates that in both streams, sampling occasions which recorded higher values of conductivity, pH, velocity, temperature, and FPOM (positive loadings of PC1 scores of abiotic factors) were dominated by gathering and filtering collectors as well as presence of piercer herbivores (negative loadings of PC1 scores of FEGs). On the other hand, when the amounts of CPOM (negatively loaded PC1 of abiotic factors) were higher, higher abundance of predators and scrapers as well as presence of shredders (positive loading of PC1 of FEGs) occurred.

Although not significant ($r = 0.359$; $p > 0.05$), there was a positive correlation between PC1 of abiotic factors and PC1 of FEGs along the longitudinal gradients in both streams. This indicates that in the stretches with positive loading in PC1 of abiotic factors, which were caused by higher values of pH, conductivity, FPOM, and lower value of temperature, there was less abundance of piercer herbivore and filtering collectors. Also, negative PC1 of abiotic factors due to CPOM of >1000, >500, and >100 µm was related to less abundance of predators, shredders, and scrapers.

However, stronger correlation of PC1 of abiotic factors and FEGs in temporal gradient than in longitudinal gradient indicates that influence of abiotic factors in the temporal gradient is more prominent than in longitudinal gradient.

4 | DISCUSSION

4.1 | Population structure

High diversity indices of macroinvertebrates were evident from the two streams studied. Dominance of some species groups appears to be due to differences in water quality between the two streams. For example, the presence of coleopterans along with Ephemeroptera, Plecoptera, Trichoptera, and Odonata has been observed to reflect clean water conditions (Miserendino & Pizzolon, 2003). A study done by Gunarathna, Kumari, Nirmanee, and Jayasinghe (2016) also indicated that water quality in Yan Oya river basin is acceptable and had minimal impact from land uses.

Compared to other tropical streams, where benthic macroinvertebrate densities vary between 1400 and 5500 ind. m^{-2} (Cressa, 1994), mean densities of benthic macroinvertebrates in both streams (Figures 2 and 3) were very low. Some families and subfamilies (e.g., Eubrinae, Gyrinidae, Blephariceridae, Ephemereliidae, Hebridae, Naucoridae, Amphipterygidae, Libellulidae, and Polycentropodidae) were found only in EO-WZ, which is an indication of higher richness in EO-WZ than in YO-DZ. Between the two streams, EO-WZ had the most diverse benthic macroinvertebrate assemblage, as indicated by higher values of diversity indices (EO-WZ: diversity = 2.11 and YO-DZ: diversity = 2.07). Higher taxa richness in EO-WZ can be related to the habitat heterogeneity. The higher values of diversity indicated presence of clean or unpolluted habitat thus showing the importance of macroinvertebrate diversity for monitoring organic pollution (Lenat & Penrose, 1996). The difference in evenness (higher evenness in YO-DZ than in EO-WZ) is a result of changing relative abundance of a particular taxon. Variable abundance of certain taxa were observed in the months with lower evenness (Figures 2 and 3).

4.2 | Eswathu Oya—wet zone

The southwest monsoon brings a considerable amount of water to the EO-WZ during when the stream swells, but drains faster in its cascading landscape. Therefore, stream returns to its original size sooner. Although monsoons retreat, the stream runs for about nine months from the water trapped in the ground in the catchment. Therefore, throughout the year water level remained high (around 50 cm) but decreased for 4 months during dry season from May to August 2005. The amplitude of water level fluctuations was about 40 cm. During low water level, factors such as flow velocity and discharge also reduced (Table 1). The flashy floods during the wet season elevated the water level and discharge, which toppled the substratum and removed litter packs as described by Pearson (2005). The flashy floods flush a greater portion of FPOM downstream.

The low conductivity in this stream may be attributed to the presence of gneissic bedrock in the underlying geology. Lower temperature may attribute to its higher altitude (203–151 m a.s.l.). In this stream, coarse detritus were consumed by few shredders. Gathering collectors (Chironomidae, Caenidae, Psychodidae, Leptoceridae, and Baetidae) were abundant and they consumed particulate organic matter deposited on the substrate. Scrapers were abundant and according to Rosenberg and Resh (1993), they feed on the epilithic layer that grows on the submerged substrates. Piercer herbivores (Hydrophilidae and Hydroptilidae) were present in very low abundance. Predators were the ultimate consumers among macroinvertebrates and were abundant. In cascading, EO-WZ upstream migration was not seen, but it accommodates nearly 15 fish species (Weliange, Amarasinghe, Vijverberg, Leichtfried, & Füreder, 2017).

4.3 | Yan Oya—dry zone

The dry period lasted for five months during which pools could be seen. Water was turbid throughout the wet period and harbored 18 fish species (Weliange et al., 2017). In this stream, heterogeneity is low and homogenous sandy bottom can be observed throughout the year. Gathering collectors (Chironomidae, Caenidae, Baetidae, and Leptophlebiidae) were abundant throughout the temporal and longitudinal gradients. Predators and scrapers also were abundant. Predator populations appeared to vary according to the water level fluctuations; during high water level less predators were seen and vice versa. Fish also migrate upstream during high water levels. Carnivorous fishes may directly impact on the density of predators as described by Greathouse and Pringle (2006). Shredders, filtering collectors and piercer herbivores were less. According to Shieh and Yang (2000), higher sedimentation may lead to a decrease in the densities of scrapers, shredders, and predators. The turbid water and higher amount of FPOM result in increased sedimentation process, which possibly would have brought about lower populations of scrapers and shredders. Scanty piercer herbivores were represented by Hydrophilidae (Coleoptera) and Hydroptilidae (Trichoptera).

4.4 | Shredders

Shredders were very low in both streams, and represented by one taxon belonging to Calamoceratidae (Trichoptera). During the lowest water level when major leaf fall occurred, higher abundances of shredders were observed in both streams. However, shredders are known to be scarce in tropical streams (Dobson, Magana, Mathooko, & Ndegwa, 2002; Dudgeon & Wu, 1999), and leaves are processed by microbes (Graça, 2001). High concentration of toxic compounds in leaves also favours their faster decomposition (Wantzen, Wagner, Suetfeld, & Junk, 2002).

4.5 | Collectors

Gathering collectors were the most dominant FFG in both streams throughout temporal and longitudinal gradients. They feed on detritus found on leaf packs in unstable streams (Death, 1995). Population sizes of gathering collectors are known to increase with food supply (Suren & McMurtrie, 2005), especially when there are high allochthonous inputs (Bispo, Oliveira, Bini, & Sausa, 2006). High-bacterial decomposition also increases the populations of gathering collectors (Dobson, Mathooko, Ndegwa, & M'Erimba, 2003; Mathuriau & Chauvet, 2002). The dominance of gathering collectors and filtering collectors reflect organic enrichment of freshwaters (Rosenberg & Resh, 1993).

Low densities of filtering collectors in both streams may be attributed to by and large, sandy and silted nature of the two streams. It is reported that sandy and heavily silted streams have reduced densities and diversity of filtering collectors (Reger & Kevern, 1981).

4.6 | Vegetation cover

Vegetation cover along the riparian zone helped maintain low water temperatures and provided diverse habitats for a variety of macroinvertebrates, leading to increased diversity in both streams. During low water level, major leaf fall was observed in both streams. Under shaded conditions, periphytic algae grow on leaf litter (Delong & Brusven, 1993). This organic matter can alter the nutrient flow (Gregory, Swanson, McKee, & Cummins, 1991), eventually changing the quality of food (Elliott, Naiman, & Bisson, 2004). Other than predators, all FFGs directly depend on the organic matter. As such, allochthonous organic matter, mainly leaves from riparian vegetation, is a major energy source for streams and rivers (Benfield, 1997).

4.7 | Longitudinal variation

According to river continuum concept (RCC; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980), the shredders may dominate in the shaded head waters, gathering collectors, filtering collectors and scrapers may stay similar or increase downstream, and predators may stay similar along the gradient. However, in the two streams studied, shredders were not dominant in the head waters. Gathering collectors, filtering collectors, and scrapers did not increase their abundance along the gradient. Predators also did not stay similar along the gradient. Variations along the gradient in the two streams implied that the energy input in each stretch was dissimilar. The decreasing taxa richness in some stretches along the longitudinal gradient could be attributed to the low habitat heterogeneity as described by Vannote et al. (1980) and Vinson and Hawkins (1998) for streams and rivers.

4.8 | Effect of abiotic factors on FFGs

As evident from the present analysis, effect of abiotic factors on FFGs of benthic macroinvertebrates in the two streams studied was more prominent in the temporal gradient than in the longitudinal gradient. The low influence of abiotic factors on FFGs along the longitudinal gradient might be due to the reason that in both streams, the stretches selected for the study (11 km in EO-WZ and 20 km in YO-DZ), were perhaps not long enough to reflect characteristics of RCC as described by Vannote et al. (1980).

On the other hand, influence of abiotic factors on FFGs was high in the temporal gradient and as such, it can be postulated that seasonal patterns of flood regimes might govern abiotic factors in the two streams, which in turn influence the abundance and composition of various FFGs.

5 | CONCLUSION

In this study, we provided fundamental knowledge to understand the structure and functions of streams, which flow in the two major eco-climatic zones of Sri Lanka. The study demonstrated a strong seasonality in the composition and abundance of FFGs of benthic macroinvertebrate communities in the two streams which are relating to the flow regime, caused by weather pattern. Seasonality and duration of water level fluctuations in the two streams were contrasting, which defined EO-WZ as a perennial and YO-DZ as a seasonal stream. Resource management activities that attempt to conserve the aquatic diversity as well as attempts of ecological assessment in lotic habitats should therefore be based on their seasonal flood regimes. Further, biodiversity conservation in streams should be based not only on the in-stream characteristics but also on the catchment properties and riparian vegetation, as they strongly interact to produce a system-specific fauna with peculiar functional interactions and adaptations.

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CONFLICTS OF INTEREST

The authors have declared no conflict of interest.

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