RESEARCH ARTICLE

Comparative assessment of piscine beta diversity profle and key determinant environmental factors in two freshwater rivers of variable spatial scale in Dooars, West Bengal, India

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Abstract

The underlying spatial and environmental processes shape the freshwater fsh assemblage of streams and rivers. Due to dispersal barriers between the river basins, species fltering is associated with longitudinal environmental gradients resulting in distinct assemblages. This study primarily aims to assess the freshwater fsh beta diversity profle inhabiting two rivers of the Upper Brahmaputra basin of Eastern Himalayas, namely River Teesta (large-scale) and Murti (small-scale). The beta profle is further disintegrated into three components, i.e., beta turnover, beta nestedness, and local contribution to beta diversity (LCBD). River Teesta has higher beta diversity and beta turnover values, while River Murti has a higher nestedness in community composition. LCBD is found to be higher in altitudinal extremities, and River Murti seems to have higher values. However, turnover in River Teesta is highly correlated (r>0.5) with 17 environmental factors, while in River Murti, 15 of them seem to be significantly correlated $(r>0.5)$. Similarly, nestedness in River Teesta is correlated with stream slope while with water velocity and river width in River Murti.

Keywords Beta diversity · Beta nestedness · Beta turnover · Eastern Himalayas · LCBD · Stream fshes

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Introduction

According to the current living planet index, the diversity of freshwater species worldwide decreases substantially over time (McRae et al. [2017](#page-10-0); Barrett et al. [2018](#page-8-0)). The largest decline is found in the Neotropical, followed by the Indo-Pacifc realm (Barrett et al. [2018](#page-8-0)). In recent times, such a decline of freshwater fshes is mostly due to habitat degradation and overexploitation, followed by changing climate, increasing pollution, and human footprints (Barrett et al. [2018](#page-8-0)). Fishes are characteristically diferent from other organisms in terms of their sensitivity to the environment of freshwater reaches (Leprieur et al. [2009](#page-10-1), [2011\)](#page-10-2). They are evolved to exploit diferent freshwater habitats (Keast and Webb [1966](#page-9-0); Hynes and Hynes [1970;](#page-9-1) Lowe-McConnell [1975](#page-10-3); Gorman and Karr [1978\)](#page-9-2). Their community structure is modulated by various factors (Zaret and Rand [1971](#page-10-4); Gorman and Karr [1978](#page-9-2)).

Among the three biodiversity hotspots of South-Asia, the Eastern Himalayan biodiversity hotspot is the largest spreading across 524,190 sq. km through central Nepal to northwest Yunnan in China (Allen [2010](#page-8-1); Pathak and Mool [2010](#page-10-5)). It also encompasses Bhutan, the north-eastern states, and northern Bengal hills in India, south-eastern Tibet, and northern Myanmar (Chettri et al. [2010](#page-9-3); Pathak and Mool [2010\)](#page-10-5). Many large and numerous small-scale rivers are fowing downstream through the diverse landscapes of Eastern Himalayas (EH) (Chettri et al. [2010](#page-9-3)). Amongst 1073 freshwater species in total, ichthyofauna dominates with 520 taxa inhabiting these freshwater reaches (Allen [2010](#page-8-1)). Such ichthyofaunal assemblages are distributed in three drainage basins, among which the Ganga-Brahmaputra drainage basin is the most diversifed and so, the most prioritized for conservation (Allen [2010](#page-8-1); Bhatt et al. [2012](#page-8-2)). River Teesta, the most signifcant in northern Bengal, and its tributaries are fowing down through the Upper Brahmaputra basin of EH into the River Brahmaputra (Galy et al. [2008;](#page-9-4) Bhatt et al. [2012;](#page-8-2) Goswami et al. [2012](#page-9-5)). Evidently, the altitudinal gradient and water discharge are the most infuential factors leading to varied local fsh assemblages in this riverine system (Bhatt et al. [2012\)](#page-8-2).

Beta diversity accounts for compositional changes in biotic communities between two given places (Davies et al. [2005\)](#page-9-6). It indicates the turnover/replacement structure in species assemblage while indirectly delineating the formation of biotic regions within the context of regional biota (Davies et al. [2005;](#page-9-6) Legendre and De Cáceres [2013;](#page-9-7) [2014](#page-9-8)). Two additive components, i.e., species turnover and species nestedness (Baselga [2010;](#page-8-3) Baselga and Orme [2012\)](#page-8-4), have been primarily applied to study beta diversity profles of spe-cies assemblages (Koleff et al. [2003](#page-9-9); Anderson et al. [2006](#page-8-5); Baselga [2010;](#page-8-3) Astorga et al. [2014;](#page-8-6) Edge et al. [2017;](#page-9-10) Zbinden and Matthews [2017](#page-10-6); Antiqueira et al. [2018\)](#page-8-7). In freshwater systems, communities have been found to vary along the environmental and spatial gradients (Holyoak et al. [2005](#page-9-11); Heino [2011](#page-9-12)), followed by their dispersal limitation and niche diferences (Hubbell [2001](#page-9-13); Chase and Leibold [2003](#page-9-14); Heino [2011\)](#page-9-12). Therefore, understanding the infuence of environmental variability on beta diversity would explain the underlying species sorting process in freshwater ecosystems.

Several influential research (Chakrabarty and Homechaudhuri [2014](#page-9-15), [2015;](#page-9-16) Debnath [2015](#page-9-17); Dey et al. [2015a](#page-9-18), [b](#page-9-19); Sarkar and Pal [2018](#page-10-7)) previously described different freshwater piscine assemblage of EH. However, a detailed analysis of beta diversity and its relation to environmental variability is still lacking. In Himalayan rivers, rheophilic fsh species are reported to dominate headwaters. In contrast, cold-eurythermal species tend to inhabit the lower meandering zones depending upon the scale of the freshwater reaches (Sehgal [1999;](#page-10-8) Chakrabarty and Homechaudhuri [2013\)](#page-9-20). Large-scale Himalayan rivers also difer signifcantly from other small-scale torrential rivers in their environmental characteristics, resulting in characteristic fsh assemblages (Rudra [2018;](#page-10-9) Chettri et al. [2010;](#page-9-3) Panja et al. [2020\)](#page-10-10). In this study, an account of piscine beta diversity along the longitudinal gradients has been compared between two rivers, representing large (Teesta) and small (Murti) scale freshwater reaches of EH. The underlying processes of fsh replacement and nestedness related to environmental variability have been further assessed for understanding the ecosystem response of these two characteristic freshwater rivers.

Methodology

Study area

River Teesta and Murti typically characterize large and small-scale torrential rivers, respectively, in the riverine landscape of EH. River Teesta, originating from north Sikkim, traverses through Sikkim and northern Bengal and then enters Bangladesh to fnally merge with the River Brahmaputra (Bhatt et al. [2012;](#page-8-2) Chakrabarty and Homechaudhuri [2014](#page-9-15)). This river runs through 309 km with a drainage area of 12540 km^2 (Chakrabarty and Homechaudhuri [2014,](#page-9-15) [2015](#page-9-16)). In contrast, River Murti is comparatively smaller in scale, originating from the Mo forest in the Neora Valley National Park in Darjeeling Himalayas (Chakraborty and Datta [2013;](#page-9-21) Kar et al. [2014](#page-9-22); Kundu et al. [2019](#page-9-23); Panja et al. [2020](#page-10-10)). It traverses 47.5 km before its confuence with a sizeable Himalayan river Jaldhaka near Gorumara National Park (Chakraborty and Datta [2013](#page-9-21); Kar et al. [2014;](#page-9-22) Kundu et al. [2019](#page-9-23)). Both these rivers are replenished by snow-melt water from the mountains of Sikkim and Bhutan (Rudra [2016](#page-10-11)).

As these rivers are torrential bodies, a longitudinal elevational gradient (Bhatt et al. [2012;](#page-8-2) Chakrabarty and Homechaudhuri [2014,](#page-9-15) [2015](#page-9-16)) in both the rivers was considered for selecting sampling stations. River Teesta being a comparatively large river, a range of 1032–67m elevation gradient was covered. In comparison, a range of 597–100m elevation gradient was studied in River Murti. Therefore, seven sites (considering pool and riffle systems) each along the Teesta (Site 1–7) and the Murti (Site 8–14) river were selected for this study (Fig. [1](#page-2-0)). However, sampling stations were set up, avoiding those parts of the rivers draining through the protected areas as reserve forests in the region.

Sampling

Sampling for the environmental variables and fish species from the selected sites were conducted from May 2016–April 2018 during pre-monsoon (March–April), monsoon (July–August), and post-monsoon (November–December) seasons. A 90m (45 m upstream and 45 m downstream) stretch was considered at each site. Environmental variables were sampled at three equal distance (30 m) points within

Fig. 1 Sampling sites in River Teesta and Murti of Dooars ecoregion in West Bengal, India

this stretch. Fish sampling was performed on the entire 90 m stretch at each sampling site. Freshwater fsh abundance was recorded by applying a unifed single-pass electrofshing method by anode type Electro Fisher-Fish Machine Shocker connected to a 300V, DC power system. This event was followed by seining through current nets and gill nets (mesh size 2.5×2.5 cm). The removal method of fish sampling (Bohlin et al. [1989\)](#page-8-8) was applied and achieved through three consecutive efforts at each 90 m stretch for 1 hour. All the immobilized fshes were identifed up to species level following Jhingran and Talwar [\(1991](#page-10-12)) and Fish Base [\(www.](http://www.fishbase.org) [fishbase.org\)](http://www.fishbase.org) (Froese and Pauly [2011\)](#page-9-24) and released as quickly as possible to the same spot. The observed mortality rate for the captured fshes was 7%.

Seventeen environmental variables addressing five categories, i.e., climate, hydrology, landscape, habitat quality, and anthropogenic pressure, were measured following their relevance to freshwater fsh distributions (Edwards and Huryn [1996](#page-9-25); Poiani et al. [2000;](#page-10-13) Hauer and Lamberti [2011](#page-9-26); Pettorelli et al. [2011\)](#page-10-14). Under the category of climate, water temperature (${}^{\circ}$ C) (WT), air temperature (${}^{\circ}$ C) (AT), and annual precipitation (mm) (AP) were measured. Five hydrological variables, namely, water velocity (ms^{-1}) (WV), pH (PH), river width (m) (RW), dissolved oxygen (mgl^{-1}) (DO), turbidity (ppm) (TDS) were assessed. The landscape

attributes viz. stream order (SO), altitude (m) (AL), topographic wetness index (TWI), and slope (°) (SL) of the sampling sites were computed. For habitat diversity, the normalized diference vegetation index (NDVI), substrate coarseness (SC), and qualitat del bosc de ribera (QBR) index were measured. Furthermore, the basin pressure index (BP) and land surface temperature $(^{\circ}C)$ (LST) were quantified to address the anthropogenic pressure of the sampling sites. WT, AT, WV, PH, RW, DO, TD, SC, BP, and QBR index were recorded during in-feld sampling and averaged to obtain fnal values.

OAKTON Multiparameter PCSTestr 35 probe was used to record WT, AT, and TDS. pH and DO were recorded following the standard protocol of Water Ecology Kit, Hach Model AL-36B Kit 180202. WV was measured using a propeller-type water current meter (Lawrence and Mayo), while measuring tape (wherever possible, else in GIS) was used to quantify RW. SC of the stream segment was calculated following the Wentworth scale (Wentworth [1922](#page-10-15)), while QBR Index and BP were calculated following the standard datasheet developed by Colwell [\(2007\)](#page-9-27) and Hermoso et al. [\(2009\)](#page-9-28), respectively. However, AP, NDVI, and LST were obtained from secondary sources, i.e., Indian Meteorological Survey ([www.imd.gov.in/pages/services_](http://www.imd.gov.in/pages/services_hydromet.php) [hydromet.php](http://www.imd.gov.in/pages/services_hydromet.php)), ISRO Bhuvan Database ([https://bhuvan.](https://bhuvan.nrsc.gov.in/bhuvan_links.php) [nrsc.gov.in/bhuvan_links.php\)](https://bhuvan.nrsc.gov.in/bhuvan_links.php), and Climate Engine ([http://](http://climateengine.org/) [climateengine.org/\)](http://climateengine.org/), respectively for each of the sampling sites. SO, AL, TWI, and SL were computed in the QGIS platform (Version: QGIS 3.10 A Coruña) using a digital elevation model from the HydroSHEDS database ([https://](https://www.hydrosheds.org/downloads) [www.hydrosheds.org/downloads\)](https://www.hydrosheds.org/downloads).

Data analysis

The presence and absence of fsh assemblage were used for data analysis. All the multivariate environmental variables were subjected to a log transformation before analysis.

Multivariate homogeneity among groups

The multivariate homogeneity of groups' dispersions (Anderson et al. [2006\)](#page-8-5) between River Teesta and Murti was calculated, followed by an analysis of variance (ANOVA). The results were further projected in principle coordinate (PCoA) analysis to represent distances among the rivers in Euclidean space (Anderson et al. [2006](#page-8-5)).

Computation and partitioning beta diversity

The total beta diversity (BD_{Total}) as the total variance within each river was calculated along with two other components viz. species contributions to beta diversity (SCBD) and local contributions to beta diversity (LCBD) statistics (Legendre and De Cáceres [2013](#page-9-7); Borcard et al. [2018\)](#page-9-29). SCBD values were diferentially plotted for these two rivers to fnd the critical species with a higher contribution in diferential community assemblages (Legendre and Legendre [2012](#page-9-30)). However, LCBD values were mapped for each site to address their comparative evaluation of ecological integrity (Legendre and De Cáceres [2013](#page-9-7); Lopes et al. [2014;](#page-10-16) Szabó et al. [2017](#page-10-17)). In the next step, total beta diversity was partitioned for each river into two components, i.e., the total spatial turnover (Beta_{Sim}) and nestedness (Beta_{Nes}) using Sorensen distances (Baselga [2010](#page-8-3); Baselga and Orme [2012](#page-8-4)). Furthermore, the incidence-based pair-wise dissimilarity matrices were calculated for turnover (replacement) and nestedness following their correlation with the environmental distances (Baselga and Orme [2012\)](#page-8-4).

Identifcation of key environmental parameters

Seventeen environmental variables were used to calculate pair-wise dissimilarity matrices (Clarke and Gorley [2006\)](#page-9-31) for each river. Following dissimilarity, the sites were clustered using group averages for turnover (replacement) and nestedness as well as channeled into non-metric multidimensional plots (nMDS) (Clarke and Gorley [2006\)](#page-9-31). Furthermore, critical variables were identifed (Pearson's correlation

value > 0.5) (Clarke and Gorley [2006](#page-9-31)) and plotted into the same nMDS plot. This analysis would identify the critical environmental factors behind the beta diversity profle of two characteristically diferent rivers belonging to EH.

All the above analyses were computed in the PRIMER V 6.1.15 platform (Clarke and Gorley [2006](#page-9-31)) and R platform (Team [2018](#page-10-18); [2019](#page-10-19)) using packages, namely *vegan, Betapart and adespatial*.

Results

A total of 92 fsh species (See Supporting Information) have been found within two river systems. River Teesta and Murti harbor 75 and 41 fish species, respectively, out of a total of 11,700 individuals collected from River Teesta and 3906 individuals from River Murti (see Appendix Tables). The multivariate homogeneity of groups' dispersions (variances) is prominent and turned out to be signifcant at a 0.05 level of signifcance (See Supporting Information). In the PCoA plot (Fig. [2](#page-3-0)), River Teesta and Murti are distantly plotted with few overlaps. River Teesta has a higher distance from centroid than River Murti (See Supporting Information). The total beta diversity (BD_{Total}) of the River Teesta is 0.8137, more signifcant than the small-scale River Murti, i.e., 0.5271.

For River Teesta, higher SCBD values (Appendix A: Table 1) are found for fsh species, namely *Amblyceps mangois, Olyra kempi, Neolissochilus hexagonolepis, Labeo angra, Schizothorax richardsonii,* and *Mystus bleekeri*. However, in River Murti (Appendix A: Table 2), fish species with higher SCBD values are diferent. They are *Neolissochilus hexagonolepis, Neolissochilus hexastichus, Crossocheilus latius, Devario aequipinnatus, Barilius barila,* and *Psilorhynchus balitora*. Similarly, higher LCBD values (Fig. [3\)](#page-4-0) are observed in sites 1, 2, and 7 for River Teesta.

Fig. 2 Multivariate dispersion of homogeneity based on Sorensen dissimilarities among River Teesta (T) and Murti (M)

Fig. 4 Comparative beta diversity (*BD* beta diversity, *Beta Sim* beta turnover, *Beta Nes* beta nestedness) profle between River Teesta and Murti

Teesta Murti

In contrast, sites 8 and 14 in the River Murti, indicating a diferential degree of ecological uniqueness within the same water reach.

In additive partitioning of beta diversity, the turnover (Beta_{Sim}) component seems to be higher than nestedness (Beta_{Nes}) (Fig. [4](#page-4-1)) in both the rivers, irrespective of their scales. The turnover values are higher (Fig. [4](#page-4-1)) for River Teesta than Murti. However, River Murti seems to have higher nestedness than the large-scale river, Teesta (Fig. [4](#page-4-1)). In the nMDS plot, all the 17 environmental factors are positively correlated with the beta turnover pattern in the River Teesta (Fig. [5](#page-5-0)) and Murti (except TWI and WV) (Fig. [6](#page-5-1)). However, RW and WV seem to be correlated with the high nestedness pattern observed in the River Murti (Fig. [6\)](#page-5-1). SL seems to be the only factor associated with the observed nested pattern in the large-scale river, Teesta (Fig. [5](#page-5-0)). Site 4 and 5 have lower turnover distances in River Teesta (Fig. [5](#page-5-0)), while other sites are distinctly separated due to significant species turnover. In contrast, sites 8–9 and 10–12 are projected with lower turnover distances in River Murti (Fig. [6](#page-5-1)).

Discussion

Detailed analysis of beta diversity provides an understanding of the ecological and evolutionary process of species fltering in natural systems (Davies et al. [2005;](#page-9-6) Legendre et al. [2005](#page-10-20)). It is apparent from the study that the transition

Fig. 5 Non-metric multidimensional plot for beta turnover (left) and nestedness (right) of ichthyofaunal assemblage in River Teesta. *WT* Water temperature, *AT* air temperature, *AP* annual precipitation, *WV* water velocity, *PH* pH, *RW* river width, *DO* dissolved oxygen, *TDS*

turbidity, *SO* stream order, *AL* altitude, *TWI* topographic wetness index, *SL* slope, *NDVI* normalized diference vegetation index, *SC* substrate coarseness, *QBR index* qualitat del bosc de ribera index, *BP* basin pressure index, *LST* land surface temperature

Fig. 6 Non-metric multidimensional plot for beta turnover (left) and nestedness (right) of ichthyofaunal assemblage in River Murti. *WT* Water temperature, *AT* air temperature, *AP* annual precipitation, *WV* water velocity, *PH* pH, *RW* river width, *DO* dissolved oxygen, *TDS*

turbidity, *SO* stream order, *AL* altitude, *TWI* topographic wetness index, *SL* slope, *NDVI* normalized diference vegetation index, *SC* substrate coarseness, *QBR* index qualitat del bosc de ribera index, *BP* basin pressure index, *LST* land surface temperature

of regional biota into localized communities is signifcant (Fig. [2](#page-3-0)) and difers based on the scale of the water reaches. This inference is in agreement with a previous study indicating the presence of signifcant variation within-stream community compositions (Al‐Shami et al. [2013\)](#page-8-9) but contrary to a previous fnding (Zhou et al. [1999](#page-10-21)) where beta diversity has been shown to bear no signifcant diferences in three branches of the same river. Since the freshwater basins impose a substantial dispersal barrier (Cottenie [2005;](#page-9-32) Heino [2011](#page-9-12)), a signifcant diference in beta profle between River Teesta and Murti is justifed from their diference in diversity scale, freshwater connectivity, stream order, and longitudinal gradients. As is known, the elevation is strongly associated

with spatial patterns of species assemblage (Ali et al. [2010](#page-8-10); Bhatt et al. [2012](#page-8-2)). Since both the courses of River Teesta and Murti have varied elevational gradients (Bhatt et al. [2012](#page-8-2); Rudra [2018](#page-10-9); Panja et al. [2020](#page-10-10)), their catchment dynamics must have been infuenced by the hierarchical intertwined processes (Ali et al. [2010\)](#page-8-10). Therefore, watercourse distance is signifcant for stream fshes representing successive levels of scale hierarchy (Ali et al. [2010\)](#page-8-10), which flters the localized species assemblages in the system. This study supports the relative contribution of both the spatial process and environmental gradients contingent upon the underlying process of species sorting (Heino et al. [2015](#page-9-33)).

The total beta diversity value is higher in River Teesta, indicating diferential assemblage of fshes following the drainage basin (Heino [2011;](#page-9-12) Al‐Shami et al. [2013;](#page-8-9) Zbinden and Matthews [2017](#page-10-6)). An inference has been drawn from previous studies that altitudinal gradients and water discharge are the signifcant factors to modulate species richness in these waters (Bhatt et al. [2012](#page-8-2)). Habitat characteristics have also been assessed by computing a surrogate metric, LCBD, which is indicated to contribute towards resultant beta diversity (Legendre [2014](#page-9-8); Lopes et al. [2014;](#page-10-16) Szabó et al. [2017](#page-10-17)). High LCBD values generally put a site away from the mean of the sites in terms of species composition because it might contain unusual or rare species within (Legendre [2014](#page-9-8)). In this study, sites with elevational extremities have comparatively high LCBD values in both the rivers indicating marked diferences in community structure. It also confrms the presence of rare or unique species at two elevational levels, which difer from the other parts of the same water reaches. River Murti has comparatively higher LCBD in sites 8 and 14 (Fig. [3\)](#page-4-0), which call for priority consideration for ecological restoration to conserve the unique and rare assemblage of piscine communities (Legendre and De Cáceres [2013\)](#page-9-7).

According to an earlier study (Goswami et al. [2012](#page-9-5)), fsh species belonging to the genus *Neolissochilus, Garra, Psilorhynchus, Barilius* are highly adaptive species inhabiting freshwater reaches of EH. However, these species have been found to inhibit both these rivers but are assigned higher SCBD values for River Murti. Among them, *Neolissochilus hexagonolepis* is categorized as red-listed by the International Union for Conservation of Nature (IUCN) (IUCN [2020](#page-9-34); Ramirez-Chaves et al. [2015\)](#page-10-22). Therefore, they seem to have delimited distributions and subsequently become habitat specialists in River Murti.

In agreement with the previous studies (Heino [2011](#page-9-12); Al‐ Shami et al. [2013;](#page-8-9) Zbinden and Matthews [2017\)](#page-10-6), the present study indicates the spatial turnover component to be signifcant for the existing beta diversity profle along the longitudinal gradient of these water reaches. The results support the view of a signifcant association of beta turnover with turbidity, stream order, substrate types, altitude, NDVI, and pH in accordance with the previous studies (Al‐Shami et al. [2013](#page-8-9); Zbinden and Matthews [2017\)](#page-10-6). As the headwaters are characterized by varied attitudinal courses followed by merging of anastomosing streams and shift of terrains, the resultant habitat heterogeneity might modulate the turnover of fshes in these torrential waters (Jackson et al. [2001;](#page-9-35) Heino [2011](#page-9-12); [2015](#page-9-33); Zbinden and Matthews [2017](#page-10-6)). As dispersal is limited between freshwater drainage basins (Cottenie [2005;](#page-9-32) Heino [2011](#page-9-12); Laskar et al. [2013](#page-9-36)), such a turnover may directly correspond with the species sorting following resource availability and environmental heterogeneity (Jackson et al. [2001](#page-9-35); Heino et al. [2015](#page-9-33)).

Our findings establish that the nestedness component of beta diversity is weaker than turnover, similar to previous studies on freshwater organisms (Heino [2011](#page-9-12); Zbinden and Matthews [2017](#page-10-6)). Since the replacement is high in River Teesta, a clear nested structure is untenable and indicates a strong infuence of spatial processes. The slope is associated with the observed nestedness, which acts as a proxy for stream dissolved oxygen levels, water fow direction, and accumulation (Austin [2007;](#page-8-11) Kuemmerlen et al. [2014](#page-9-37)). Therefore, the observed nestedness pattern (Fig. [5\)](#page-5-0) might arise based on the adaptability of fshes comprehending the stream slope in River Teesta. However, in River Murti, a prominent correlation of water velocity and river width with beta nestedness has been indicated. Such a higher nestedness might arise due to its smaller scale compared to the large river, Teesta.

Characteristic hill-scapes, undulating valleys, climatic conditions of EH has ensued numerous torrential streams and rivers (Kar et al. [2006](#page-9-38), [2010;](#page-9-39) Allen [2010](#page-8-1); Chettri et al. [2010](#page-9-3); Tse-ring et al. [2010](#page-10-23)) with rich piscine diversity (Goswami et al. [2012;](#page-9-5) Vishwanath [2017a;](#page-10-24) [b\)](#page-10-25). Bhatt et al. ([2012\)](#page-8-2) inferred the diferential impact of drivers modulating richness gradients in terrestrial and aquatic ecosystems of EH. Several relevant studies (Fu et al. [2004](#page-9-40); Bhatt et al. [2012,](#page-8-2) [2016\)](#page-8-12) agree in unison that freshwater fsh diversity decreases gradually with elevation while, on the contrary, the endemic and rare species would show an atypical response. In a longitudinal gradient riverscape, the lateral and vertical ecological attributes for freshwater fsh assemblages are also relevant (Panja et al. [2020\)](#page-10-10). This study synthesizes and explains beta diversity with its potential additive components and ecological variability following such observations. With the understanding of species sorting, this study could formulate a better prioritization schedule and conservation planning of these freshwater reaches (Leprieur et al. [2009,](#page-10-1) [2011;](#page-10-2) Astorga et al. [2014](#page-8-6); Edge et al. [2017](#page-9-10)). The detailed comparison indicates that a fish assemblage of small-scale upland reaches difers from large-scale rivers within the same ecoregion. Small-scale reaches may harbor a signifcant assemblage of characteristics fsh species with habitat specialization, prominent nestedness, and delimited distributions. In contrast, large-scale rivers are more diverse, with beta diversity composition being markedly distinctive as spatial turnover prominently determines the species assemblage.

Conclusion

Hydrological and landscape parameters are contingent on providing a strong flter resulting in a high beta turnover in the fish assemblages of these water reaches. Due to strong spatial structures, large-scale rivers exhibit more heterogeneity through courses and harbors more ecologically fragile sites with unique species assemblages. Therefore, it can be inferred that fshes of torrential waters of EH might exhibit a varied assemblage scale (local to intermediate and regional). As the stream fshes respond to the environmental changes and are highly constrained by dispersal limitation, they are distributed and adapted following the environmental gradients supported by the environmental fltering hypothesis.

Data availability statement

The raw data is not being presently submitted at this moment, so that it cannot be reproduced in any other form before publication of the manuscript. However, it may be shared in the review/revision stage for better analytical clarity during review/ revision.

Appendix A

See Tables [1](#page-7-0) and [2](#page-8-13)

Table 1 Species contributions to beta diversity (SCBD) for fish species inhabiting River Teesta (See Supporting Information for updated nomenclature and global conservation status)

Sl. No	Fish species	SCBD
1	Amblyceps mangois	0.05167
\overline{c}	Olyra kempi	0.05014
3	Neolissochilus hexagonolepis	0.05003
$\overline{4}$	Labeo angra	0.03804
5	Schizothorax richardsonii	0.03804
6	Mystus bleekeri	0.03591
7	Tor tor	0.03511
8	Aspidoparia morar	0.0347
9	Barilius vagra	0.03419
10	Garra gotyla	0.0327
11	Barilius bendelisis	0.03087
12	Garra lamta	0.03087
13	Schistura corica	0.03087
14	Puntius terio	0.02469
15	Schistura savona	0.02469
16	Psilorhynchus sucatio	0.02226
17	Macrognathus pancalus	0.02226
18	Channa gachua	0.02226
19	Devario aequipinnatus	0.02195
20	Psilorhynchus balitora	0.02195
21	Lepidocephalichthys guntea	0.01422
22	Amblypharyngodon mola	0.01009
23	Barilius barna	0.01009
24	Crossocheilus latius	0.01009
25	Devario devario	0.01009

Table 1 (continued)

Table 2 Species contributions to beta diversity (SCBD) for fish species inhabiting River Murti (See Supporting Information for updated nomenclature and global conservation status)

Sl. No	Fish Species	SCBD
1	Neolissochilus hexagonolepis	0.05711
2	Neolissochilus hexactichus	0.04517
3	Crossocheilus latius	0.04305
4	Devario aequipinnatus	0.04305
5	Barilius barila	0.03396
6	Psilorhynchus balitora	0.03104
7	Garra annandalei	0.03027
8	Garra lamta	0.03027
9	Danio rerio	0.02693
10	Balitora brucei	0.02693
11	Esomus danrica	0.02599
12	Chagunius chagunio	0.02508
13	Lepidocephalichthys annandalei	0.02508
14	Barilius vagra	0.02482
15	Labeo gonius	0.02444
16	Puntius chola	0.02444
17	Danio dangila	0.02437
18	Nemacheilus devdevi	0.02437
19	Badis badis	0.02437
20	Lepidocephalichthys guntea	0.02332
21	Macrognathus pancalus	0.02332
22	Mastacembelus armatus	0.02332
23	Barilius barna	0.02316
24	Acanthocobitis botia	0.02316
25	Psilorhynchus sucatio	0.02105
26	Xenentodon cancila	0.02105
27	Schistura savona	0.02045
28	Rita rita	0.02045
29	Glyptothorax indicus	0.02045
30	Hara horai	0.02045
31	Channa orientalis	0.02045
32	Channa stewartii	0.0192
33	Barilius bendelisis	0.0177
34	Puntius conchonius	0.0177
35	Glossogobius giuris	0.01426
36	Garra gotyla	0.0133
37	Botia dario	0.0133
38	Mystus bleekeri	0.0133
39	Heteropneustes fossilis	0.0133
40	Olyra longicaudata	0.0133
41	Schistura multifasciata	0.0133

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Declarations

Conflict of Interest The authors declare that no confict of interest has been raised during the study and published until this report.

Ethical approval statement This study has been conducted by following the ethical guidelines endorsed by the University of Calcutta, University Grant Commission, and Govt. of India. No vertebrate animals have been sampled, which are already forbidden to be captured from the wild. No surveys and sampling procedures were extended to the protected areas and the water bodies within. The authors are with this declaring fulfllment of all ethical commitments subjected to this research work.

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