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Resource partitioning as determining factor in structuring fish diversity pattern along ecological gradient of River Teesta in Eastern Himalaya

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Abstract

Dietary niche breadth, spatial changes in the diet and analysis of interspecific niche overlap of ninety-two species from four different ecological zones along the longitudinal gradient of River Teesta in West Bengal were studied from December, 2010 to November, 2013. We observed mean niche breadth values to be consistently low (0-0.39) and niche overlap values to be high (0.61-1.0) at most of the zones. High niche overlap tends to reflect intense competition for shared resources which might tend to a strong driving force for fish assemblage pattern and species sorting and survival in nature. However, on analysis of co-occurrence, its low value implied that the fish community is not competitively structured based on their diet intake. Although majority of the species utilize the same resource (aquatic invertebrates), competition apparently did not the main structuring force within the studied fish assemblage in this river which might be attributed to continuous resource replenishment.

Keywords: Eastern Himalaya; Niche breadth; niche overlap; fish diversity; interspecific competition; resource replenishment.

1. Introduction

The Eastern Himalayan Biodiversity Hotspot region and its foothills are very rich in floral and faunal diversity. Especially the piscine diversity and their populations inhabiting these areas are numerous in variety and taxonomically interesting (Allen *et al.* 2010^[1]). Like other Himalayan rivers, Teesta river and its tributaries provide a fair ecological niche for many indigenous and a few exotic fish species. These augmented the study of freshwater fish species and their various ecological implementations towards evaluating their functional traits leading towards assessment of aquatic environment health.

Alterations in water quality or habitat conditions usually lead to variations in the availability of food resources. Fish generally display high diet flexibility and both temporal and spatial variations in their diets (Abelha *et al.* 2001^[2]; Dekar *et al.* 2009^[3]). However, in highly specific and also in disturbed environments, experiencing alterations of water flow and available substrates, these patterns can be altered, and changes like increase in generalist species and reduced numbers of trophic guilds can occur (Casatti *et al.* 2006^[4]; Casatti *et al.* 2009^[5]). Therefore, evaluation in variations in the trophic organization of ichthyofaunal assemblages can be considered to be indicators of changes in the quality and complexity of a habitat (Karr, 1981^[6]). The elucidation of resource utilization patterns has been a topic of considerable interest in community ecology. Habitat, food type, and time (in that order of importance) are the three principal kinds of resource-partitioning differences usually observed (Schoener, 1974^[7], 1986^[8]). However, in the present study, we have combined habitat data and food utilization data into a compound measure of overall niche breadth and niche overlap between species, and then attempted to draw inferences about competition from these overlap measures. Our study is based on the assumptions as to whether species co-existence is dependant or independent of interspecific competition and the role of other factors, if any, in structuring species assemblage. The Teesta river stretch in West Bengal is characterized by a marked variation in altitudinal regime and river bed substratum. Most of the zones are highly characteristic of typical hill streams with the presence of specific fish species along with availability of specific prey resources. As such, the fish fauna is expected to be subject to changes in the food resources

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Related to environmental features. Thus, we focused on the potential differences in the feeding patterns and analyzed species co-occurrence.

2. Material and Methods

2.1 Study Area

The present study area includes the course of the River Teesta within West Bengal divided into ecological zones based on elevation gradient and habitat types. The river stretch was

divided in four zones *viz.* the upper stretch (Rishi khola and Rungpo); middle stretch (Teesta Bazaar); at Sevoke the river hits the plains; lastly the river plains (Gojoldoba, Domohoni and Haldibari). Along the longitudinal stretch of the river in West Bengal covering a distance of 142 km, each site was sampled at regular intervals (pre-monsoon and post-monsoon visits) when flow conditions were the most stable and similar among sites (Table 1; Fig. 1).

Table 1: Habitat types of the sampling zones along longitudinal gradient of River Teesta in West Bengal

Fish Zones	Sampling areas	Elevation	Temperature (°C)		Water velocity (m/sec)	Stream width (ft)	Stream depth (ft)	Habitat guilds
			AT	WT				
High-Mid altitude zone	Rishi Khola	Moderate to high (1093-1000 ft) elevation watersheds dominated by side slopes with gentle slopes and steep slopes.	21-23.7	18.5-21	2.1-2.9	1	1	Primary forest; hilly terrain.
	Rungpo (26°10'21.94" N; 88°31'46.73" E)		21.1-24.5	19.5-21	1.9-2.2	15	31-32.5	Secondary forest.
Mid altitude zone	Teesta Bazaar (26°00'03.97" N; 88°26'31.80" E)	Moderate (628 ft) elevation watersheds dominated by side slopes and gentle slopes.	24-27	20.7-24.9	1.6-1.9	20	23-25	Secondary forest; on going construction work of Teesta Barrage project.
Low altitude-plain zone	Sevoke (26°53'25.37" N; 88°28'22.97" E)	Moderate to low elevation (500 ft) watersheds dominated by gentle slopes with substantial areas of flats and side slopes; river hits the plain at this site.	18.5-25.2	15.4-18.5	1.3-1.6	7.4-21	24-25	Secondary forest
River plains	Gojoldoba (26°45'08.55" N; 88°35'05.04" E)	Low elevation (380-187 ft) dominated by flats, pastured land and urban inhabitation.	30.1-35.5	28.2-31	0.9-1.4	40	25-27	Secondary forest; Urban area; presence of Teesta Barrage
	Domohoni (26°33'47.11" N; 88°45'39.34" E)		34-35.7	30.1-31	0.45-0.9	38	20-22	Agriculture land; Urban area
	Haldibari (26°20'52.00" N; 88°54'16.76" E)		33.7-37.2	29.9-31.1	0.45-0.55	35	20-21	Agriculture land; Urban area

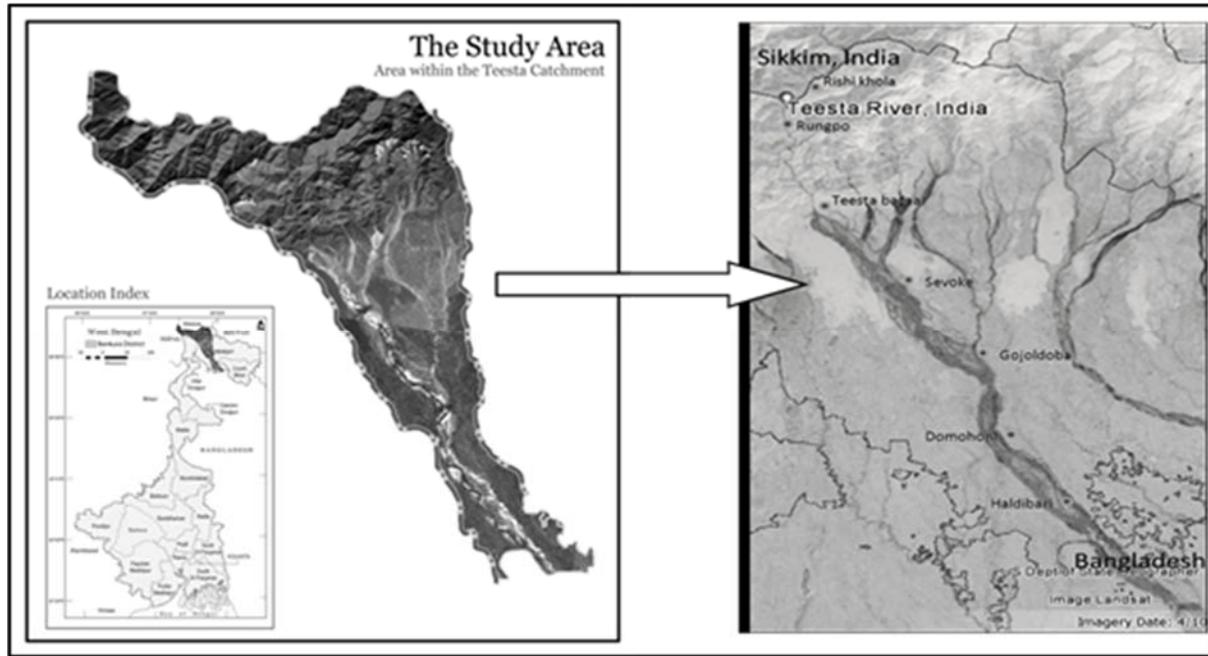


Fig 1: River Teesta Catchment area in West Bengal

2.2 Sampling

Fish sampling was carried out from December, 2010 to November, 2013 at every alternate three months at seven sampling areas (approximately 20-30 km apart) under the four zones covering the longitudinal gradient of River Teesta at Darjeeling and Jalpaiguri districts in West Bengal. Each sampling area was further divided into 4 sampling sites (approx. 1-2 km apart) totaling to 28 sites altogether. All the important freshwater aquatic microhabitats (riffles, pools, cascade, falls, etc.) were sampled using gill nets, cast nets, dragnets, and hooks and lines of varying dimensions. A sample reach of 50m were fished for 2 hours at every sites using above mentioned fish nets as well as electro-fishing method using a single anode electro-fisher (300V, 3-4A, DC) operated by the same person. Captured fish specimens were fixed in 10% formalin solution and, after 48 h, transferred to a 70% Ethyl alcohol solution. Fishes were identified to the lowest taxonomic level (Shaw and Shebbeare, 1937^[9]; Day, 1889^[10]; Talwar and Jhingran, 1991^[11]; Jayaram, 2006^[12], 2010^[13]; Menon, 1987^[14]). All specimens have been deposited in the fish collection repertoire at the Zoological Survey of India, Kolkata.

2.3 Diet Analysis

For 92 of the identified species, sub-samples were used for diet analysis. Stomach contents of two to ten fish specimens were examined in each species (1515 specimens). The standard length and body mass of each preserved specimen was measured to the nearest 0.01 g. Guts were dissected under a binocular microscope and then preserved in 70% ethanol. In species, mostly cyprinids, which do not have a discrete stomach, the anterior third of the intestine was dissected. Specimens in which the stomach (anterior third of intestine in cyprinids) contained no food items were categorized as empty. The contents of each gut were examined under a dissecting microscope using reflected light and each item identified and assigned to broader taxonomic groups (Merona *et al.* 2005^[15]). Each prey item was then allocated to one of a number of taxonomic groups, subsequently referred to as dietary categories. The volume of each food category was measured to calculate the percentage relative volume (V%) to the total volume of stomach contents for each species (Hyslop, 1980^[16]).

The frequency of occurrence of each dietary category in the gut of each fish (% F) was also recorded (Lima-Junior and Goitein, 2001^[17]).

2.4 Trophic Niche Breadth and Niche Overlap

The amplitude of trophic niche was estimated by calculating the diet breadth using volume data in each site to each species following Levin's index (Krebs, 1989^[18]) according to the formula: $B = (\sum p_{ij}^2)^{-1}$, where p_{ij} = proportion of food category j in the diet of species i . Hurlbert's (1978)^[19] formula was applied to standardize the trophic niche measure (ranging from 0 to 1), according to the formula: $B_a = [(\sum_j p_{ij}^2)^{-1} - 1] (n - 1)^{-1}$, where B_a = standardized trophic niche breadth; P_{ij} = proportion of food category j in the diet of species i ; n = total number of food categories.

Niche overlap between species using the same type of resources was calculated through Pianka's (1973)^[20] index and the Czechanowski index (Feinsinger *et al.* 1981^[21]) using the software ECOSIM ver. 7 (Gotelli and Entsminger, 2001^[22]). Both measures are pairwise, meaning that a separate index is calculated for each pair of species in the assemblage. The indices vary from 0 (the species eat only one kind of food) to 1 (the species use many kinds of food and each kind is equally consumed). Both trophic niche breadth and niche overlap was considered low (0 - 0.39), intermediate (0.4 - 0.6) or high (0.61 - 1.0) (Grossman, 1986^[23]; Corrêa *et al.* 2011^[24]).

For species 1 and 2, with resource utilizations P_{1i} and P_{2i} , Pianka's (1973)^[20] overlap index of species 1 on species 2 (O_{12}) is calculated as:

$$O_{12} = O_{21} = \frac{\sum_{i=1}^n p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^n (p_{2i}^2) (p_{1i}^2)}}$$

For species 1 and 2, with resource utilizations P_{1i} and P_{2i} , the Czechanowski index is:

$$O_{12} = O_{21} = 1.0 - 0.5 * \sum_{i=1}^n |p_{1i} - p_{2i}|$$

Moreover, we have also evaluated species co-occurrence where we used the C-score index using the software ECOSIM ver. 7

(Gotelli and Entsminger, 2001 [22]). If a community were structured by competition, we would expect the C-score to be large relative to a randomly assembled community. The number of checkerboard units (CU) for each species pair is calculated as:

$$CU = (r_i - S)(r_j - S)$$

Where S is the number of shared sites (sites containing both species) and r_i and r_j are the row totals for species i and j.

2.5 Data Analysis

Data were grouped considering different ecological zonation along the longitudinal gradient of river Teesta. After testing for normality (Shapiro-Wilk) and homogeneity of variances (Levene), niche breadth means were compared by a one-way ANOVA using the spatial unit as a factor. On the contrary, niche overlap data did not meet the requirements for parametric tests and were therefore compared through a Kruskal-Wallis test. All analyses were performed on the software SPSS 17.0 (SPSS Inc. 2007 [26]).

2.6 Null Models

In the present study, invertivores (mainly aquatic insects) formed the dominant resource available and utilized at all zones of the River Teesta. Hence, niche overlap was mainly estimated for species showing invertivorous feeding habit. Dietary data was distributed into four matrices in order to determine niche

overlap patterns within each of the spatial units. Patterns of niche overlap were calculated and statistically tested against null models using EcoSim 7.0. Null model proposes that niche overlap is statistically lower than expected interpreting that interspecific food partitioning might be occurring when the observed mean overlap values are significantly lower than those expected by chance, whereas similar foraging patterns lead values higher than those expected by chance (Albrecht and Gotelli, 2001 [27]). The algorithm used to test for non-random patterns of resource utilization, as broadly discussed in Winemiller and Pianka (1990) [28] was RA3 (Albrecht and Gotelli, 2001 [27]).

3. Results

A total of 16,703 numbers of fish specimens were collected overall. We have recorded 92 species of fishes belonging to 50 genera and 19 families from the entire longitudinal stretch River Teesta in West Bengal. The gut contents of individual fish species showed that they mainly consumed 10 types of food items (leaves; fruits; higher plants; algae; terrestrial insects; Planktons; crustaceans; aquatic insects; fish; detritus and unidentified food materials). The most consumed types of food items were aquatic insect larvae, especially in high altitude zones (36% of the total resources consumed) followed by algae (23% of the total resources consumed). Aquatic invertebrate comprised mainly of Ephemeropteran, Chironomidae and Hemipteran larvae, annelid and arachnid remains (Fig. 2 a-d).

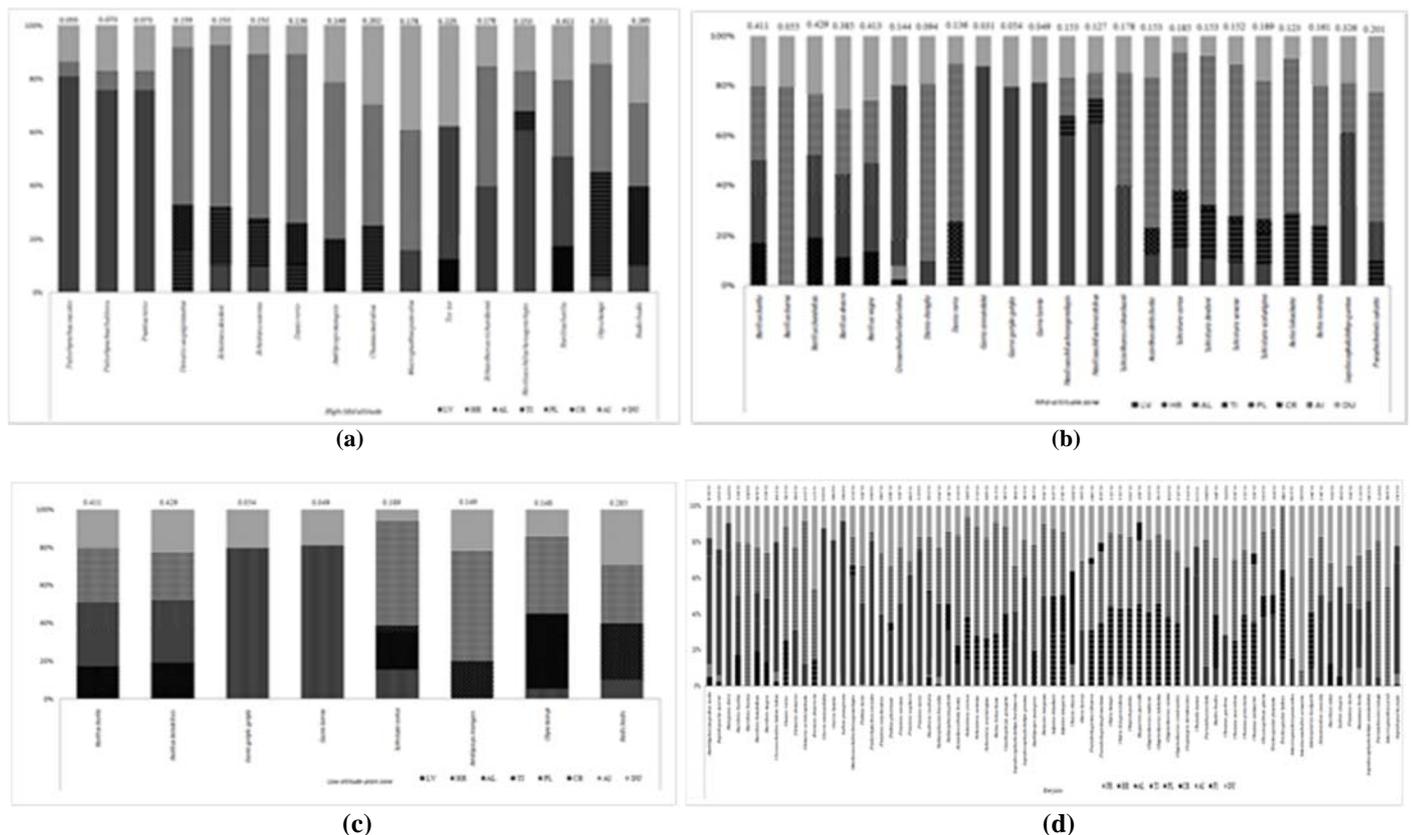


Fig.2 (a-d) Relative Frequency of the diet constituents of the fish species at respective zones. The values above each vertical bars in respective graphs indicate standardized niche breadth (B_n), LV: leaves; FR: fruits; HR: higher plants; AL: Algae; TI: Terrestrial insects; PL: Planktons; CR: crustaceans; AI: aquatic insects; FI: Fish; DU: detritus and unidentified food materials

Relative volumes of the food items and Levin’s Index of trophic niche breadth for all species collected at seven sites (under the four ecological zones) along the longitudinal gradient of river Teesta were calculated in each spatial unit. Niche breadth values for individual species at respective zones have been included in

Fig. 2 (a-d). Overall low values of niche breadth for the fish fauna was observed throughout. Most of the species (>70%) showed low niche breadth values (0-0.39) irrespective of different environmental conditions at respective zones. Intermediate (0.4-0.6) and high values (0.61-1.0) were less

frequent occurring in approximately <30% (cumulative) of the species (Fig. 3). On comparing the niche breadth values across the four zones by one-way anova, obtained mean values at each altitudinal zones were as follows: 0.175 at high-mid altitude

zone; 0.187 at mid altitude zone; 0.222 at low altitude-plain zone and 0.204 at river plains and did not differ significantly ($F=0.572$; $p = 0.634$).

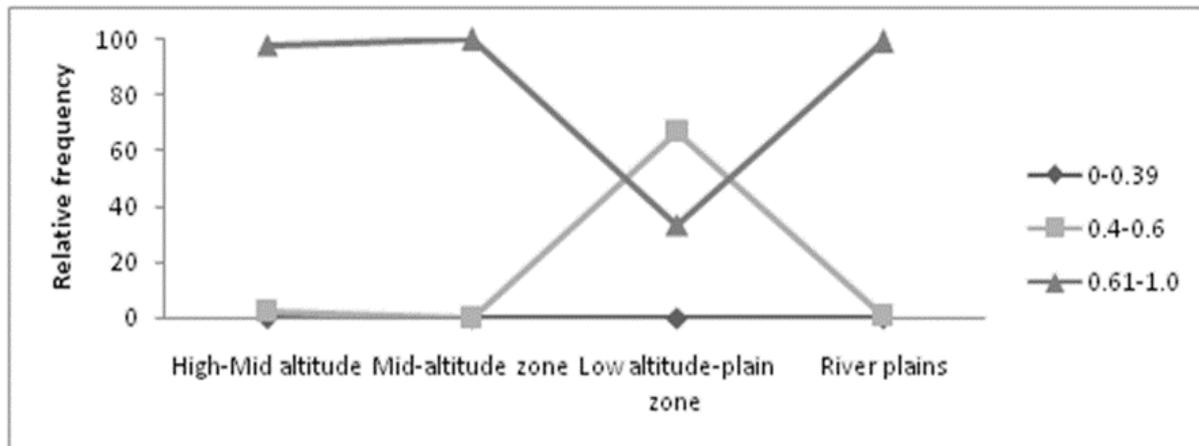


Fig. 3 Relative frequency of Levin's index of trophic niche breadth (B_a) in each spatial unit in the Teesta River, West Bengal, India. Trophic niche breadth was considered low (0-0.39), intermediate (0.4-0.6) or high (0.61-1) (modified of Grossman, 1986)

On analysis of cumulative frequency of the food categories obtained from gut analysis of the individual fish species expressed as percentage at respective altitude zones it was observed that majority of the fish species consumes aquatic invertebrates. Hence, among overall fish species abundance, niche overlap was calculated for species utilizing similar resources viz. invertivores. Niche overlap values were mostly high (0.61-1.0) with >80% of the species falling under this range at all zones except at low altitude –plain zone (Fig.4). However, intermediate and low values were also recorded in frequencies lower than 5%. Majority of the observed values are

significantly higher than those expected by chance (null communities) with the Randomization Algorithm (RA3) showing evidence of significant resource sharing. Kruskal-Wallis test performed on niche overlap values between different zones showed that there was no statistically significant difference between the different zones ($H = 2.00$, $p = 0.368$). Patterns of variance in overlap among fishes accompanied those of niche overlap, with observed values higher than those expected by chance ($p<0.01$) in all spatial units indicating that observed niche overlap is statistically significant than expected niche overlapping (Table 2).

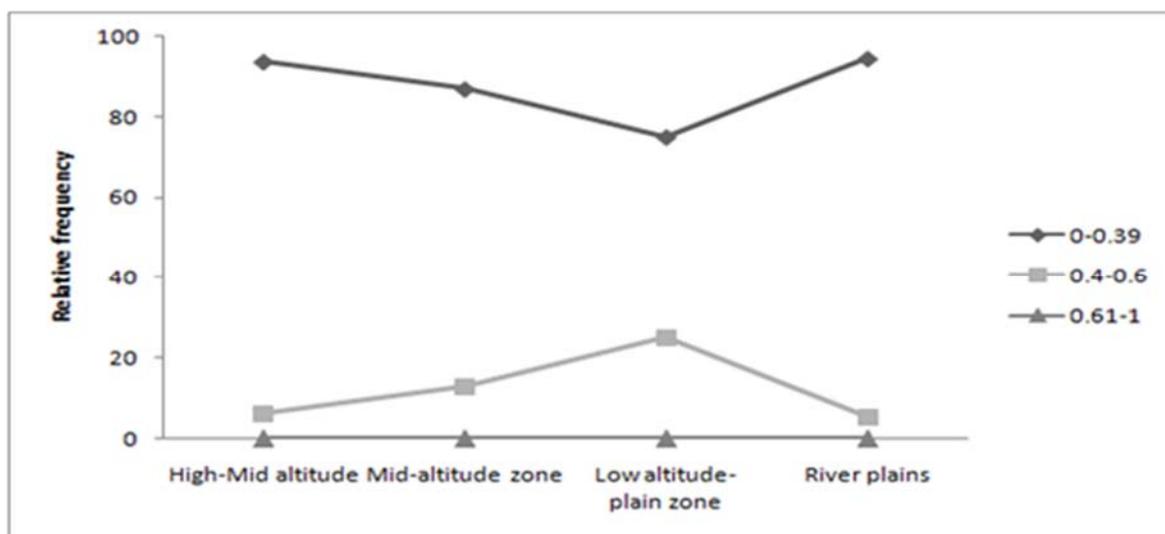


Fig. 4 Relative frequency of the Pianka's index of trophic niche overlap of fish species in each spatial unit in the Teesta River in West Bengal, India. Trophic niche overlap was considered low (0-0.39), intermediate (0.4-0.6) or high (0.61-1) (modified of Grossman, 1986)

We also assessed the fish assemblage structure using Co-occurrence model to evaluate whether competition guides species structure. C-score for the fish matrix was 0.879. In contrast, the average of the 1000 simulated matrices was 0.880, and none of the simulated matrices had a C-score larger than the

observed. So, compared to the simulated universe of random matrices with identical row and column sums, there is much less co-occurrence in the fish matrix than expected by chance ($p = 0.0004$).

Table 2: Mean and variance observed and simulated of the trophic niche overlap of the fish fauna in spatial units, in River Teesta, West Bengal. Algorithms used to test for non-random patterns was “scrambled-zeros” (RA3). *P obs.* = probability that the observed niche overlap mean is higher than the simulated one; *P var* = probability that the observed variance is higher than the simulated one.

zones	Mean observed	Mean Simulated	<i>P obs</i>	Variance observed	Variance simulated	<i>P var</i>
High-mid altitude	0.719	0.454	0.00	0.017	0.071	0.00
Mid altitude	0.814	0.386	0.00	0.012	0.110	0.00
Low-plain	0.666	0.664	0.01	0.083	0.001	0.00
River plain	0.713	0.367	0.00	0.031	0.072	0.00

Values in bold are patterns that were significantly different of the null model

4. Discussion

The simple niche measures can be good estimators of niche breadth and overlap of species. If the system under study is governed by competition for a single resource category, overall niche overlap may bear simple relation to interspecific competition because it summarizes concisely the cluster of dimension required for adequate discrimination of resources used by co-existing consumer populations (Holt, 1987^[29]). If niche overlap is seen as a measure of competition, then demonstrating an overlap in resource use by two species in nature can be evidence either for or against the existence of competition between them. Competition may be operating but exclusion or displacement may be incomplete or even impossible. In this case observed niche overlap is evidence of the existence of competition (Colwell and Futuyma, 1971^[30]). Based on the assumption that niche breadth values are a measure of trophic specialization (Hurlbert, 1978^[19]), the fish fauna of River Teesta can be considered as specialist. Values near zero were obtained for those species that consumed only one type of food item and in the present study, overall dietary niche breadth was analyzed to be low (0-0.39). In the present study, we observed a decrease in niche breadth and an increase in niche overlap (0.61-1.0) among the fish assemblage of Teesta River. It appears that low competition for spaces, predation or environmental conditions would be capable of producing such pattern. As aquatic insects and other invertivores formed the major diet constituent of the majority of the fishes, such diet specificity could lead to minimal microhabitat selection as the prey were restricted to specific microhabitat only. Previous studies of microhabitat use in stream fishes have shown that high interspecific overlap is common. Despite these results, many investigators have concluded that spatial resource Partitioning is an important factor facilitating coexistence (Mendelson, 1975^[31]; Baker and Ross, 1981^[32]). None the less, spatial segregation does promote coexistence in other fish assemblages (Everest and Chapman, 1972^[33]; Cadwallader, 1975^[34]), although in the majority of cases microhabitat segregation was linked to trophic resources (Grossman and Freeman, 1987^[35]). Werner and Hall (1979)^[36] provide excellent documentation of this phenomenon in three species of centrarchid fishes inhabiting artificial ponds. The substratum of the River Teesta is rich in general litter substrates, gravels, sand and silt. The stony substrates and sand substrates become more stable serving as refugia for aquatic insect larvae organisms. The preference for these substrates is related to high availability of dissolved oxygen concentrations, low water temperatures and fairly high velocity of water flow. Hence the sampling offers optimum environment conditions (Baptista *et al.* 2001^[37]) for maximum availability of aquatic invertebrates and algae, which thus form the major dietary constituents of the majority of fish species in this stretch. Thus, despite an overall high value of niche overlap among the fish species, significant resource sharing by the fish assemblage of the river Teesta is evident as all observed values of niche overlap were significantly higher

than those expected by chance. But we were yet to deduce whether a resource sharing has led to competitive existence of the fish faunal community in this stretch of the river.

Various authors have described niche overlap values in view of interspecific competition in an ambiguous way. For example, large overlap values imply shared resource utilization and lack of competition; however, it is also possible that high overlap implies strong competition that has not yet led to segregation in resource use (Gotelli and Graves, 1996^[38]). Therefore, null models can only indicate which direction observed patterns falls. Since, dietary overlap is not sufficient to test for the presence of competition (Colwell and Futuyma, 1971^[29]), we have carried out co-occurrence test to detect the presence of competition, if any, among the fish assemblage of the River Teesta. If a community were structured by the competition, we would expect the C-score to be large relative to a randomly assembled community. Our results imply for less co-occurrence among the species. This implies that the fish community is not competitively structured based on their diet intake. Although majority of the species utilize the same resource (aquatic invertebrates), competition apparently is not the main structuring force within the studied fish assemblage in this river. It was thus observed that the pattern of resource utilization shown by the fish species of the studied region does not reveal high level of interspecific competition in spite of low niche breadth and high niche overlap. This might be possible only when resources replenishment is continuous. However, competition may be predicted in near future from the fact that the C-score is not very much larger compared to the randomly assembled community. High abundance of resources and stochastic processes might promote a relaxation of interspecific competition and facilitate coexistence presently. Concludingly, it may be stated that if the riverine habitat is not conserved on an urgent basis and environmental degradants continue to increase due to anthropogenic activities, competition might lead to severe loss of fish diversity in this region.

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