Context-Dependent Effects of Monsoon Seasonality on Riverine Fish Assemblages: Case Study From Bharathapuzha River, India

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Abstract: In tropical monsoon rivers, understanding how powerful seasonal hydrology interacts with localized anthropogenic degradation to shape fish assemblages is a central ecological and management challenge. This study investigated fish community dynamics in the Bharathapuzha River, India, using a comprehensive spatio-temporal dataset from 108 sampling events across nine sites and three seasons. Environmental heterogeneity was characterized through hierarchical cluster analysis and principal component analysis, revealing distinct spatial groupings and dominant axes of variation, including flow dynamics (explaining 23.9% of environmental variation) and habitat integrity (explaining 22.8% of environmental variation). Fish community composition showed significant differences based on study site (explaining 33.7% of community variance) and season (explaining 16.4% of community variance), with a crucial and significant interaction between study site and season (explaining 17.6% of community variance). This interaction demonstrated that the monsoon's influence on fish assemblages in the Bharathapuzha River is profoundly context-dependent, varying significantly among sites. Redundancy analysis, explaining 11.6% of adjusted community variance, further identified physical habitat structure as a greater unique driver (5.7%) compared to water quality (3.5%). These findings establish that fish assemblages in the Bharathapuzha River are primarily structured by the intricate interplay between its natural flow regime and site-specific habitat conditions, providing a nuanced understanding essential for localized conservation.

Keywords: River ecology, Fish community, Variance Partitioning, Habitat heterogeneity, Bharathapuzha

1. INTRODUCTION

Riverine ecosystems are globally significant hotspots of biodiversity, yet they are increasingly threatened by a suite of anthropogenic stressors, including flow alteration, habitat degradation, and pollution (Vörösmarty et al., 2010; Reid et al., 2019; Tickner et al., 2020). In tropical regions, which support a disproportionately high share of global freshwater biodiversity, these pressures are often intensified by rapid development and land-use change, leading to profound ecological degradation (Arthington et al., 2018; Albert et al., 2021). This degradation is typically mediated through two primary pathways: the deterioration of water quality and the physical alteration of habitat structure, both acting as critical environmental filters on biological communities (Schippert et al., 2022). A central and ongoing debate in river ecology is to determine the relative influence of these filters in structuring biological communities. While the physical structure of a river—its channel morphology, substrate, and flow heterogeneity—is often considered the primary framework selecting for species with specific traits (Power

et al., 2015), severe pollution can shift this dynamic, making physiological stressors such as hypoxia or chemical toxicity dominant filters shaping community assembly (Palmer et al., 2015; Landman et al., 2022).

This dynamic is further complicated in monsoon-driven rivers, where an annual cycle of extreme floods and droughts imposes a powerful, system-wide disturbance (Datry et al., 2016). This strong seasonality poses a fundamental ecological question: does the monsoon's influence homogenize biological communities across a riverscape, effectively masking the effects of localized degradation? or, conversely, does it interact with local conditions to amplify differences between sites? Resolving this is essential for predicting ecosystem resilience and for developing robust management strategies in these naturally variable systems (Poff, 2018; Tonkin et al., 2018).

The River Bharathapuzha in Kerala, India, serves as a pertinent case study for these complex challenges. As a vital water resource, it is heavily impacted by a mosaic of pressures, including flow regulation, sand mining, and

pollution from urban and agricultural sources (Gopi and Sreepriya, 2018; Remya and Joseph, 2021). Therefore, the overarching objective of this study was to disentangle the complex interplay between powerful seasonal hydrology and localized anthropogenic degradation in shaping fish assemblages within this tropical monsoon river, providing nuanced insights essential for developing effective, localized conservation strategies.

2. MATERIALS AND METHODS

2.1. Study Area and Sampling Design

The study was conducted along the River Bharathapuzha, a 209 km long, monsoon-fed river in Kerala, India (Figure 1). A purposive stratified sampling procedure was used to select nine distinct study sites along the river's longitudinal gradient. This strategic selection aimed to represent the diverse spectrum of geomorphological settings—from high-energy mid-reaches to the low-energy estuarine mouth at Chamravattom—and varying degrees of anthropogenic influences, including agricultural runoff, urban waste, and ritualistic activities (Table 1). Sampling was conducted across two full hydrological years (2023 and 2024), with each site visited during three seasons: Pre-monsoon (February-May), Monsoon (June-September), and Post-monsoon (October-January). This design yielded a total of 108 independent sampling events (9 sites × 3 seasons × 2 years).

2.2. Environmental Data Collection

At each sampling site and event, key physicochemical water quality parameters were quantified, including dissolved oxygen (DO), pH, total suspended solids (TSS), and nitrate concentrations. Physical habitat was characterized using a semi-quantitative protocol (Barbour et al., 1999) where 20 parameters related to channel morphology, flow regime, riparian condition, and human activities were scored on an ordinal scale (0-5) along a representative 100-200m reach. For multivariate analysis, these 20 parameters were aggregated a priori into six functional strata reflecting distinct pressure types (direct pollution/waste, ritualistic activities, channel morphology). This approach was chosen to create predictor variables with direct relevance to specific management actions.

2.3. Fish Community Data Collection

Fish were sampled concurrently with environmental data collection along a standardized 100m reach using a multi-gear approach. The effort included active sampling with a cast net (4.0 m diameter, 10 mm mesh) and passive sampling with a fleet of three gill nets of varying mesh sizes (15, 30, and 50 mm). All captured fish were identified to the species level, counted, and released. For community analysis, raw species abundance data were Hellinger-transformed to down-weigh the influence of rare species (Legendre and Gallagher 2001). Species richness and Shannon diversity were calculated for each sample.

2.4. Statistical Analysis

All statistical procedures were performed in R (v. 4.4.3) using the 'vegan', 'cluster', and 'indicspecies' packages. Prior to analysis, fish abundance data were Hellinger-transformed to down-weigh the influence of rare species, and environmental variables were centered and scaled to ensure comparability.

2.4.1. Environmental heterogeneity: To identify spatial groupings of sites with similar physical characteristics, Hierarchical Cluster Analysis (HCA) was performed on site-averaged, scaled habitat data using Euclidean distance and Ward's linkage. To identify the primary axes of
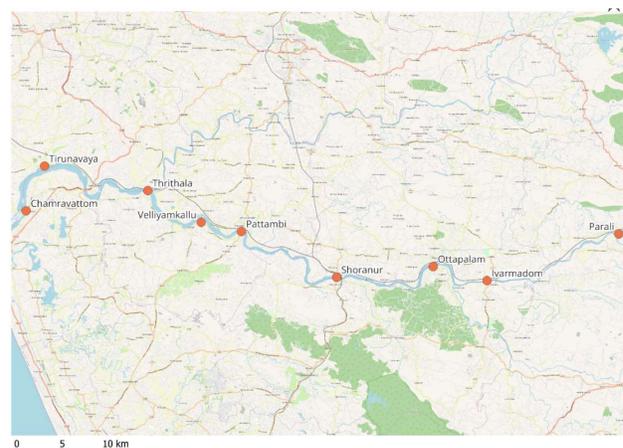

Figure 1. Study area showing the location of the nine sampling sites along the Bharathapuzha river, Kerala

Table 1. Geographic coordinates of the nine sampling sites along the Bharathapuzha river

Site ID	Site name	Latitude (°N)	Longitude (°E)
1	Parali	10.7968	76.5594
2	Ivarmadom	10.7507	76.427
3	Ottapalam	10.7646	76.373
4	Shoranur	10.7541	76.276
5	Pattambi	10.7992	76.1803
6	Velliyamkallu	10.8083	76.1398
7	Thrithala	10.83953	76.0862
8	Tirunavaya	10.8637	75.9825
9	Chamravattom	10.8196	75.963

environmental variation across all 108 sampling events, Principal Component Analysis (PCA) was conducted on the correlation matrix of the habitat variables.

2.4.2. Fish community structure and spatio-temporal variation: To test for differences in fish community composition across sites and seasons, a factorial Permutational Multivariate Analysis of Variance (PERMANOVA) was conducted using a Bray-Curtis dissimilarity matrix (Anderson 2001). The empirical model for PERMANOVA tested the marginal effects of Study Site, Season, and their Interaction as follows:

Distance Matrix ~ Study Site + Season + (Study Site * Season)

The statistical significance was determined using pseudo-F statistics calculated through 999 permutations. To identify specific species significantly associated with particular sites or seasons, Indicator Species Analysis (IndVal) was performed using the multipatt function (Dufrene and Legendre 1997). The Indicator Value (IndVal) was calculated based on the product of specificity (A) and fidelity (B) for each species.

2.4.3. Environment-biotic linkages: The relationship between the fish community and environmental predictors was modeled using Redundancy Analysis (RDA). The empirical model for RDA is defined as:

$$Y = XB + E$$

where Y represents the matrix of Hellinger-transformed species data, X is the matrix of environmental predictors (6 Habitat Strata and 6 Water Quality variables), B is the matrix of regression weights, and E is the residual error. Variance partitioning (Borcard et al., 1992) was subsequently used to decompose the community variance into unique fractions explained by Physical Habitat (fraction [a]) and Water Quality (fraction [b]).

2.4.4. Diversity indices and correlations: Alpha diversity was quantified using Species Richness, Shannon Diversity, Simpson Diversity, and Pielou's Evenness. Relationships between these indices and individual environmental predictors were assessed using Spearman rank correlation coefficients (Spearman 1904). To control for the false discovery rate, p-values were adjusted using the Benjamini-Hochberg (BH) procedure (Benjamini and Hochberg 1995).

3. RESULTS AND DISCUSSION

3.1. Spatio-Temporal Environmental Heterogeneity

All 20 physical habitat parameters showed significant variation among study sites confirming a strong spatial gradient of physical conditions. Seasonally, 14 of the 20 parameters varied significantly, driven primarily by the monsoon.

Hierarchical cluster analysis on site-averaged habitat data identified four distinct groups of sites (Figure 2). Group 1 -Chamravattom, Velliyamkallu was characterized by high scores for Flow Modification and Bank Modification. Group 2 -Ivarmadom, Shoranur) was distinguished by high scores for parameters related to ritualistic activities (cremation, religious use). Group 3 -Thrithala, Thirunavaya exhibited the lowest relative scores for most disturbance parameters. Group 4 -Ottapalam, Parali, Pattambi represented sites with mixed, moderate impacts.

Principal component analysis (PCA) of the 108 samples distilled the environmental variation into three primary axes explaining 62.5% of the total variance (Figure 3). PC1
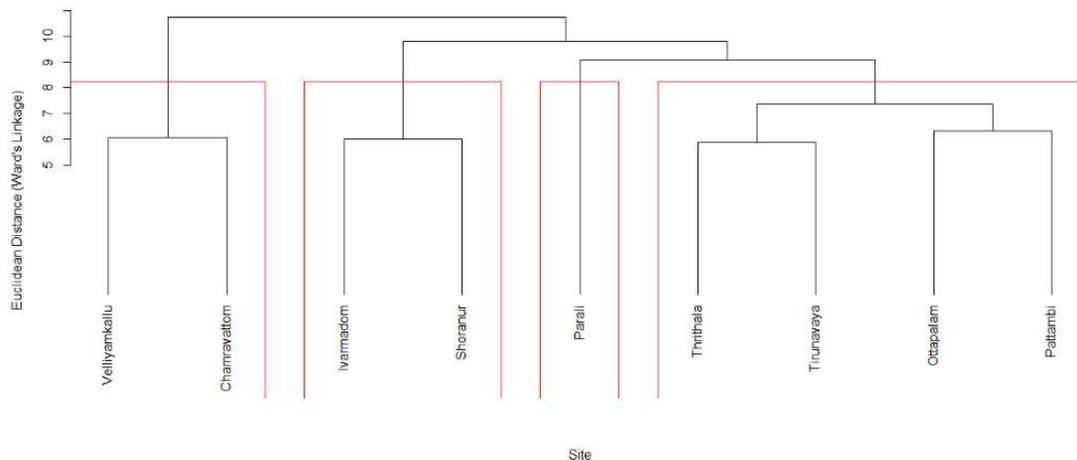

Figure 2. Dendrogram from the hierarchical cluster analysis (HCA) of the nine study sites based on their site-averaged habitat characteristics. The red lines delineate the cluster groupings discussed in the text

(23.9%) represented a 'Flow Dynamics' axis, contrasting high-flow monsoon conditions (high turbidity, flow, width) with low-flow conditions. PC2 (22.8%) represented habitat integrity'axis, separating sites with high tree cover and woody debris from those with high bank modification, trash, and flow obstructions. PC3 (15.9%) separated sites based on specific land uses, contrasting impacts from ritualistic activities with those from agriculture.

3.2. Fish Community Structure

The factorial PERMANOVA revealed significant effects for both study site (F=6.99, R^2=0.337) and season (F=8.53, R^2=0.164) on fish community composition. Crucially, the interaction study site × season was also highly significant (R^2=0.176), indicating that the seasonal trajectory of the fish community differed significantly among the study sites (Table 1).

The environmental analyses provide a mechanistic basis for this interaction. The HCA and PCA results clearly define the distinct physical characteristics of the study sites, grouping them based on dominant pressures such as flow regulation (Group 1) or specific land uses (Group 2). The significant PERMANOVA interaction term can thus be interpreted as evidence that the trajectory of community change—from the pre-monsoon drought to the monsoon flood and subsequent recovery-differs between these site groups. The community response in a highly regulated reach with artificial banks is unlikely to mirror the response in a less-impacted reach with intact riparian zones and natural channel features (Poff et al., 2010).

The study demonstrates that fish assemblages in the River Bharathapuzha are not structured by the monsoon cycle alone, but by a complex interplay between this powerful seasonal pulse and a spatially heterogeneous mosaic of local habitat conditions. The significant site × season interaction is the central finding, rejecting the notion of the monsoon as a uniform, system-wide driver. Instead, it reveals that the ecological response of the fish community to seasonal hydrological shifts is fundamentally context-dependent, filtered through the specific physical template of each river reach.

3.3. Environment- Community Linkages

The RDA model relating environmental predictors to fish community structure was significant with all predictors explaining 11.6% of the adjusted variance. Variance
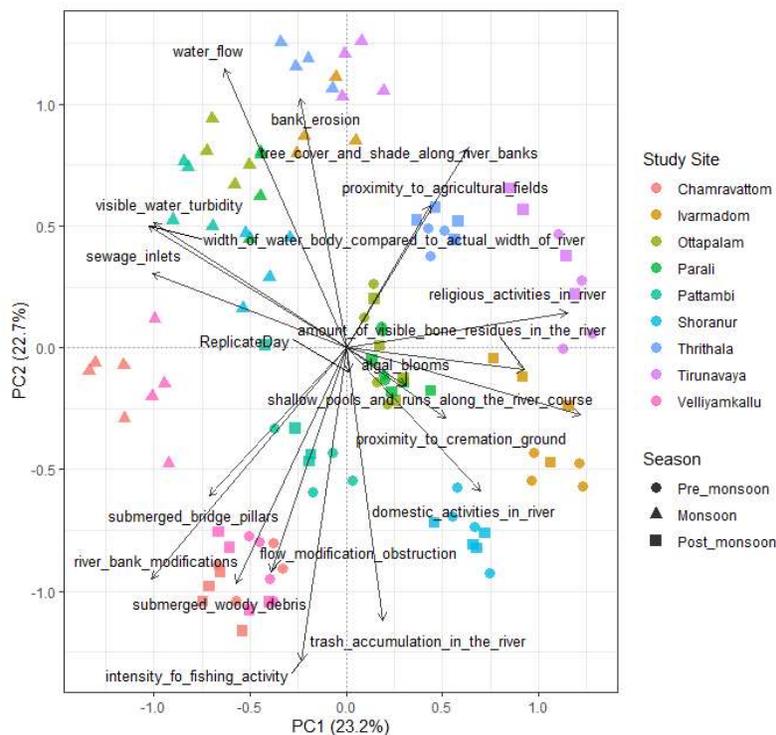

Figure 3. Principal component analysis (PCA) biplot of environmental habitat parameters, showing individual sampling events by site and season. The first two components (PC1: 23.9%, PC2: 22.8%) are displayed

partitioning revealed that the unique fraction of variance explained by the habitat strata (5.7%)was greater than the unique fraction explained by water quality variables (3.5%). The shared variance between the two sets of predictors was 2.5% (Figure 4).

The Spearman rank correlation analysis (Table 3) provided critical insights into the environmental drivers of fish alpha diversity. Statistically, the significant rho values indicate the strength and direction of monotonic relationships between predictors and diversity indices. Two results from Table 3 are particularly significant for the management of the Bharathapuzha River.

First, the significant positive correlation between 'Stratum 1: Pollution and Waste' and both species richness (rho = 0.43) and Shannon diversity (rho = 0.46) suggests a pattern of incidental structural enrichment. In river reaches where the natural habitat has been simplified by sand mining or channelization, the presence of solid waste or moderate nutrient inputs may provide artificial substrate or hydraulic refugia, thereby supporting a higher number of opportunistic or tolerant species. This aligns with the 'Intermediate Disturbance Hypothesis,' where moderate levels of anthropogenic pressure can temporarily increase local richness before reaching a threshold of collapse.

Second, the significant negative correlation between

Dissolved Oxygen (DO) and diversity (rho = -0.36 for both indices) is an indicator of ecological instability. In tropical monsoon rivers like the Bharathapuzha, high daytime DO readings are often a symptom of advanced eutrophication, where nutrient-fueled algal blooms cause daytime supersaturation followed by severe nighttime hypoxia. Therefore, the lower diversity observed at higher DO levels likely reflects a community filtered by these extreme diurnal fluctuations, where only the most resilient species persist. These correlations highlight that simple water quality metrics must be interpreted through the lens of the river's specific ecological context.

Physical habitat structure emerged as a stronger unique predictor of fish community composition than water quality (Figure 4). The influence of physiological stressors like dissolved oxygen is evident, but the greater explanatory power of habitat variables underscores the foundational importance of the physical template in structuring these assemblages. The positive correlation between the stratum1_pollutionwaste metric and fish diversity supports our third hypothesis of non-linear responses. This counter-intuitive result does not imply that waste is beneficial; rather, it suggests a mechanism of incidental structural enrichment. In river reaches that may be otherwise simplified by factors like sand mining or channelization, the physical structure
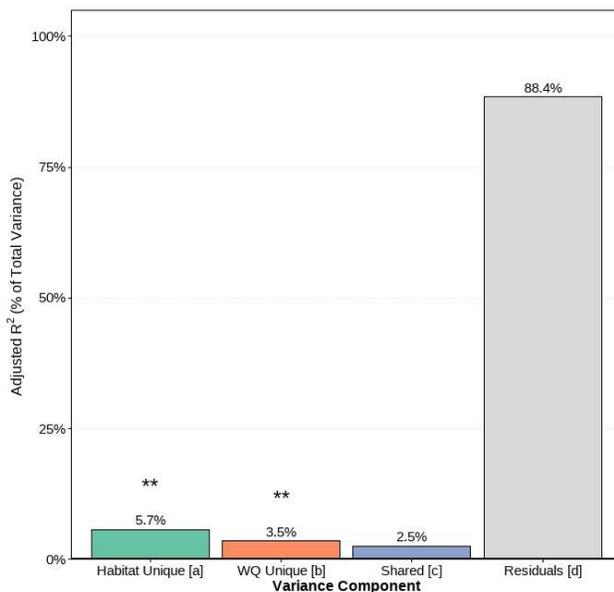

Fig. 4. Partitioning of variance in fish community composition by habitat strata and water quality predictors. Stars indicate statistical significance (*** p < 0.001)

Table 2. Factorial PERMANOVA results showing significant effects of Study Site, Season, and their interaction on fish community composition

Source	R²	F-value	p-value
Study site	0.337	6.999	0.001
Season	0.164	8.531	0.001
Study site: Season	0.176	1.830	0.001
Residuals	0.442		
Total	1.000		

Table 3. Spearman rank correlations between key environmental predictors and fish diversity indices

Predictor	Diversity Index	Rho (ρ)
Stratum1_PollutionWaste	Richness	0.43
Stratum1_PollutionWaste	Shannon	0.46
Dissolved Oxygen (DO)	Richness	-0.36
Dissolved Oxygen (DO)	Shannon	-0.36

provided by solid waste could inadvertently create hydraulic refuges or substrate complexity, a phenomenon observed in other modified aquatic systems (Reis et al., 2017). This highlights that the loss of natural structural elements is a critical, and perhaps primary, component of degradation.

To investigate the mechanism behind the significant site × season interaction and the counter-intuitive negative correlation with DO, the relationship between dissolved oxygen and Shannon diversity was plotted for each site specifically during the pre-monsoon season (Figure 5). The analysis revealed that the nature of the relationship was highly context-dependent. A strong negative linear trend was observed in sites characterized by pollution and/or flow modification (Ivarmadom, Shoranur, Pattambi), whereas a neutral or weakly positive trend was observed in the least-disturbed sites (Thrithala, Thirunavaya).

Similarly, the significant negative correlation between dissolved oxygen and fish diversity is best explained not as a direct effect, but as a statistical signature of advanced eutrophication. As shown in our site-specific analysis for the pre-monsoon season (Figure 5). This negative trend is driven exclusively by the most polluted sites. It is hypothesized that in these reaches, high nutrient loads fuel intense daytime algal photosynthesis, leading to the supersaturated DO levels we recorded and is likely followed by severe nightly hypoxia due to high ecosystem respiration, creating an unstable environment that filters out sensitive species. The absence of this negative trend in cleaner sites like Thrithala (Figure 5) confirms that high daytime DO in this system is a symptom of instability, not health. This finding illustrates why ecological responses are context-dependent and why single-parameter assessments can be misleading.

RDA model explained a modest, though significant, portion of community variance (11.6% Adj. R^2). This low value should not be interpreted as a model deficiency but as a significant ecological finding in itself. The large proportion of unexplained variance is likely a signature of the substantial role of stochastic processes—such as chance colonization, extinction, and dispersal dynamics—which are known to be prominent in disturbance-driven systems like monsoon rivers (Chase 2010; Heino et al., 2015).

The study has direct implications for the conservation and management of the Bharathapuzha and similar tropical rivers. The demonstrated context-dependency of ecological responses means that uniform, basin-wide management policies (e.g., a single environmental flow standard) are likely to be inefficient or even ineffective. Restoration efforts must be tailored to the specific pressures impacting a given reach, as identified by our site groupings. For sites in Group 1, management should prioritize mitigating the effects of hydrological alteration, while for sites in Group 2, efforts might focus on local waste management and stakeholder engagement.
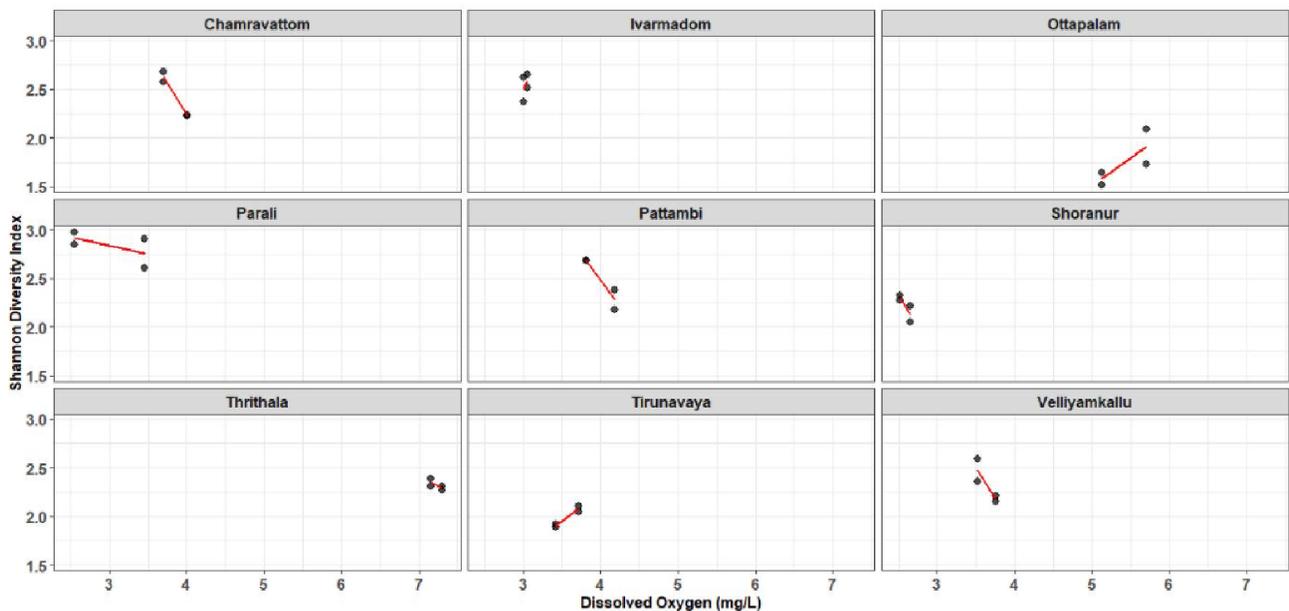

Fig. 5. Site-specific relationships between Dissolved Oxygen and Shannon Diversity Index during the pre-monsoon season

4. CONCLUSION

The structure of fish assemblages in the Bharathapuzha River is governed by a complex interplay of drivers where the regional monsoon cycle is fundamentally mediated by site-specific habitat conditions. Our findings lead to three specific recommendations for the management of this system:

First, because physical habitat structure explained significantly more unique variance (5.7%) in fish community composition than water quality (3.5%), conservation priority should be shifted toward physical habitat restoration—such as bank stabilization and the removal of flow obstructions—rather than focusing solely on chemical water quality monitoring.

Second, the highly significant interaction between study site and season demonstrates that "one-size-fits-all" management is inappropriate for this river. Management actions must be spatially explicit; for instance, reaches like Ivarmadom and Shoranur require targeted mitigation of ritualistic waste, while the Chamravattom and Velliyamkallu reaches require strategies to address the ecological impacts of flow regulation and bank modification.

Finally, our discovery that high daytime dissolved oxygen levels were negatively correlated with fish diversity suggests that standard water quality snapshots can be misleading in eutrophic tropical rivers. We recommend that local environmental agencies adopt the site-specific indicator species identified in this study (e.g., *Silago sihama* for estuarine reaches and *Hypselobarbus dubius* for mid-reaches) as more reliable longitudinal benchmarks for river health than chemical parameters alone.

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Conflicts of Interest

The authors declare they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. The funders had no role in the study design; in the collection, analysis, or interpretation of data; in the writing of the manuscript; or in the decision to submit the manuscript for publication.

Authors' Contributions

Gopika. S. G. Unni: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data Curation, Writing – Original Draft, Visualization. Sreeparvathi. C. K: Conceptualization, Writing – Review & Editing. Remia. K. M: Supervision, Project administration, Writing – Review & Editing. All authors have read and agreed to the published version of the manuscript.

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