

# Predicting native fish diversity in river Bharathapuzha: Non-linear responses to environmental drivers revealed by Generalised Additive Models

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## Abstract

Predicting how biodiversity responds to environmental changes is crucial for effective conservation; however, the functional relationships underpinning diversity metrics often remain obscure. In this study, we developed a robust predictive model for Shannon diversity in fish in the Bharathapuzha River, Kerala, India, a system experiencing significant anthropogenic pressure. Utilising a comprehensive dataset (N=108), we applied Generalised Additive Models (GAMs) to predict Shannon diversity in native fish, a metric chosen for its sensitivity to community evenness in a system impacted by dominant invasive species. Our final model demonstrated an Adjusted  $R^2$  of 0.171, a deviance explained by 20.7%, and was validated using 10-fold cross-validation ( $CV-R^2 = 0.138$ ). Focusing on native species diversity, the model revealed a complex bimodal response to environmental drivers. Native fish diversity exhibited a significant nonlinear relationship with dissolved oxygen and nitrate, reflecting a fundamental longitudinal phase shift from sensitive upstream specialists to tolerant downstream generalists. These findings provide critical management insights; while habitat restoration offers direct, proportional gains in diversity, water quality management requires targeting specific ecological optima to maximise biodiversity benefits. This study underscores the utility of GAMs for developing mechanistically informative predictive models that are essential for guiding effective river restoration and conservation.

## Introduction

The escalating degradation of freshwater ecosystems globally poses a severe threat to aquatic biodiversity and the critical services these systems provide (Vörösmarty *et al.*, 2010; Albert *et al.*, 2020). Effective management and restoration of these ecosystems depend on our ability to identify stressors and predict how biological communities respond to changes in environmental conditions. Fish assemblages are exceptional indicators of riverine health, integrating the cumulative impacts of stressors, such as pollution, habitat loss, and hydrological alteration over time (Karr, 1981; Brosse *et al.*, 2021). Consequently, understanding and predicting the patterns of fish diversity is a cornerstone of aquatic conservation..

However, ecological relationships are rarely linear. The response of a diversity metric, such as the Shannon index ( $H'$ ), to an environmental gradient can be complex, exhibiting thresholds, ceilings, or unimodal (hump-shaped) patterns (Dodson *et al.*, 2000). For example, a slight increase in nutrient availability in an oligotrophic system may boost diversity; however, further enrichment can lead to eutrophication and a subsequent diversity crash. While many ecological studies have identified general environmental drivers of fish communities, the precise functional forms of these relationships, especially distinguishing between linear and non-linear responses, are often assumed or oversimplified. This oversight can lead to inefficient or even counterproductive management strategies, as interventions optimised for linear responses



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may fail when faced with ecological thresholds or optima. Traditional linear models are ill-equipped to capture these subtleties, potentially obscuring critical ecological dynamics and leading to suboptimal management strategies (Guisan *et al.*, 2002). In systems dominated by invasive generalists, focusing exclusively on native diversity ( $H'_{\text{native}}$ ) is essential to reveal the true environmental requirements of indigenous species, which are often masked by the broad tolerances of non-native taxa.

Generalised Additive Models (GAMs) provide a powerful data-driven framework to overcome this limitation. By fitting flexible smooth functions to predictor variables, GAMs can uncover the true shape of ecological relationships without forcing them into preconceived linear or polynomial forms (Wood, 2017). This approach is increasingly vital in applied ecology to build more realistic and predictive models that can directly inform decision making (Elith and Leathwick, 2009).

This study focuses on the Bharathapuzha River, the second longest river in Kerala, India, and a vital lifeline for the region's ecology, agriculture, and culture. The river basin is not only a critical water source for several districts but also harbours a remarkable ichthyofauna, with 117 recorded species, a high degree of Western Ghats endemism, and several threatened species (Bijukumar *et al.*, 2013). However, this socio-ecological system is under severe and escalating anthropogenic stress. Key pressures include unregulated sand mining, which degrades channel morphology, widespread land-use changes, and impaired water quality from domestic sewage and agricultural runoff (Anto *et al.*, 2021; Kannan and Joseph, 2022). Furthermore, extensive hydrological alterations from numerous dams and regulators disrupt the natural flow regimes (Raj and Azeez, 2009). The river also experiences unique cultural pressures, including large-scale ritualistic activities, such as the deposition of crematorial ashes at significant religious sites, the ecological impacts of which are not well understood. Consequently, Bharathapuzha serves as a critical

yet representative case study to understand how fish communities in anthropogenically modified tropical rivers respond to a complex suite of environmental gradients. We investigated an 85 km stretch from Parali to Chamravattom, a reach that encapsulates this pronounced gradient of human impacts, including several of these key religious centres. The objective of this study was to move from explanation to prediction and we aimed to develop a robust GAM to predict fish Shannon diversity using key habitat and water quality variables; characterise the functional form (linear or non-linear) of these predictor-response relationships; as well as to validate the model's predictive performance on an independent dataset, thereby assessing its utility as a tool for forecasting the outcomes of management interventions.

## Methods

### Study area and sampling design

The study was conducted along the Bharathapuzha River, Kerala, India, focusing on an 85 km stretch from Parali to Chamravattom. Nine sampling sites (Fig. 1) were strategically selected to capture a diverse gradient of anthropogenic conditions and habitat characteristics, ranging from relatively undisturbed areas to areas affected by urban effluent, religious activities, agricultural runoff, and hydrological modifications from regulator-cum-bridges.

Sampling was rigorously conducted over two consecutive years (2023–2024), and data were collected during three distinct hydrological seasons to capture seasonal variation in fish assemblages and environmental conditions: pre-monsoon (low flow; March-May), monsoon (high flow; June-September), and post-monsoon (receding flow; October-January). This seasonal approach is critical for understanding fish responses in highly dynamic tropical river systems, where flow regimes and water

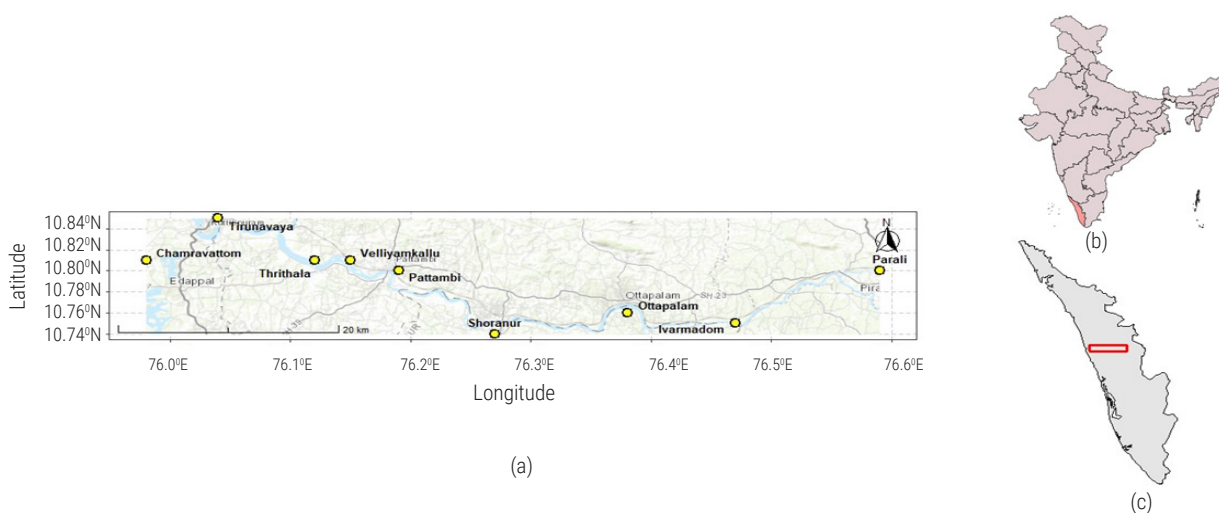


Fig. 1. Map of the study area along the Bharathapuzha River, Kerala, India. (a) Detailed view of the 85 km study reach showing the nine sampling sites (yellow circles); (b) Location of Kerala State within India; (c) The specific study reach (indicated by the red box) within the state of Kerala.

quality can vary drastically. To ensure robust data collection and account for within-site variability, two replicate sampling events were performed per site per season, yielding a comprehensive dataset of 108 sampling events.

## Environmental predictors: Habitat and water quality

The environmental conditions at each sampling event were characterised by two main types of predictors: physical habitat strata and water quality parameters. Habitat quality at each site was quantitatively assessed using a semi-quantitative Rapid Bioassessment Protocol (RBP) adapted from Barbour *et al.* (1999) for wadable tropical rivers. Our adaptation involved scoring 20 specific habitat parameters across the sampled reach. Each parameter was assigned an integer score ranging from 0 to 5, based on visual assessment. The interpretation of this scale depends on the ecological impact of the parameter. For parameters representing positive habitat attributes, such as tree cover (H4) or the presence of diverse pool/run habitats (H19), a higher score indicated an optimal near-natural state. Conversely, for parameters representing habitat degradation, such as trash accumulation (H6), bank erosion (H9), and the intensity of sewage inlets (H5), a higher score indicated the worst-case condition. To ensure a consistent interpretation across all metrics, scores for these negative-impact parameters were reversed (*i.e.*, a score of 5 became 0; 4 became 1... *etc.*) prior to the analysis. Following this standardisation, the individual scores were averaged (unweighted) to create six ecologically relevant composite strata that served as predictors in our models. This process ensures that for all final composite strata used in the GAM, a higher score consistently represents a better overall ecological condition.

- Direct pollution sources: Scores reflect the presence and intensity of visible human-derived pollutants (*e.g.*, solid waste, sewage outfalls and foam).
- Ritualistic impacts: Scores assess the direct impacts of religious activities, such as the deposition of crematorial ashes or flower offerings.
- Adjacent land use: Characterises the type and intensity of land use immediately adjacent to the river (*e.g.*, natural vegetation, agriculture, and urban development).
- Channel and bank morphology: Evaluates the physical structure of the river channel and banks (*e.g.*, substrate diversity, bank stability, presence of large woody debris, and sinuosity).
- Flow obstruction: Assesses the presence and degree of structures or natural features that impede natural water flow (*e.g.*, instream construction and significant debris dams).
- Riparian and biotic integrity: Scores for the quality and extent of riparian vegetation, canopy cover, and indicators of biological health (*e.g.*, presence of diverse aquatic macrophytes and absence of invasive plant species).

From a broader suite of physicochemical parameters, six key water quality variables were selected based on their ecological relevance to fish and to minimise multicollinearity (all retained variables had a Variance Inflation Factor (VIF) <5, confirming minimal shared variance between predictors): Total suspended solids (TSS), Salinity, Dissolved oxygen (DO), Nitrate (as  $\text{NO}_3^-$ -N), pH, and Total hardness.

All water quality parameters were measured concurrently with fish sampling. Dissolved oxygen (DO), pH, and salinity were measured *in situ* using a calibrated YSI ProPlus multiparameter probe (YSI Inc., Yellow Springs, OH, USA). Water samples for laboratory analysis (TSS, Nitrate, Total hardness) were collected in sterile acid-washed bottles, stored on ice, and transported immediately to the laboratory. Total suspended solids were determined gravimetrically after filtration. Nitrate (as  $\text{NO}_3^-$ -N) was analysed spectrophotometrically using the cadmium reduction method (APHA, 2017). The total hardness was determined using the EDTA titrimetric method (APHA, 2017).

## Fish community data

Fish sampling was standardised across all sites and seasons. At each site, a 100 m river reach was demarcated. Fish were collected using a multi-gear approach to maximise the species capture efficiency across different habitats and fish sizes.

Cast net: A cast net (4.0 m diameter, 10 mm mesh size) was deployed a minimum of 10 times per 100 m reach by experienced local fishers or trained field personnel to effectively sample shallow, open-water areas.

Gill nets: A fleet of three monofilament gill nets of varying mesh sizes (15, 30 and 50 mm bar mesh) was deployed overnight (approximately 12 h soak time) along the banks and across various instream habitats within the 100 m reach. The three nets were set in a staggered manner to cover the different microhabitats present at each site.

All captured fish were identified to the species level using standard taxonomic keys for freshwater fishes of peninsular India (Talwar and Jhingran, 1991), counted, and promptly returned alive to the river at the point of capture to minimise stress. A minimum number of voucher specimens, essential for definitive taxonomic verification, were ethically collected, humanely euthanised following accepted ichthyological methods, and deposited in the reference collection of the Department of Zoology, MES Mampad College. Abundance data from all gears were pooled for each sampling event to represent the total fish assemblage.

## Response variable: Native Shannon Diversity ( $H'_{\text{native}}$ )

The response variable for our predictive model was the Native Shannon Diversity Index ( $H'_{\text{native}}$ ), calculated for the fish assemblage at each of the 108 sampling events. This metric was deliberately prioritised over simpler indices, such as species richness, owing to the specific composition of fish assemblages in the Bharathapuzha River. The system is characterised by the presence of highly abundant invasive species (*e.g.*, *Pterygoplichthys disjunctivus*. and *Oreochromis niloticus*) and intentionally stocked carps, often introduced through government programs. In this context, species richness alone can be a deceptive indicator of ecological health; a site might retain a high number of species, but be numerically dominated by a few tolerant, non-native taxa, masking the decline of sensitive native species. The Shannon Index, which integrates both the richness and evenness of species abundance, is highly

sensitive to shifts in community structure. It effectively penalises communities skewed by hyperabundant species, thereby providing a more robust and realistic assessment of biotic integrity in this disturbed river system. Crucially, individuals of invasive or exotic species were excluded from this calculation to reveal the underlying environmental responses of the indigenous community. Therefore,  $H'_{\text{native}}$  was selected as the most appropriate single metric to capture the overall community response to the measured environmental drivers. It was calculated using the formula  $H'_{\text{native}} = -\sum (\pi_i * \ln(\pi_i))$ , where  $\pi_i$  is the proportion of individuals belonging to the  $i^{\text{th}}$  species.

Predictive modeling was performed in R (v4.3.1; R Core Team, 2023) using the mgcv package (Wood, 2017) for Generalized Additive Models. The modeling process was designed to first identify the most influential environmental drivers and then rigorously assess the predictive power of the final model. An initial full model was constructed using the entire dataset (N=108), including the smooth terms for all 10 environmental predictors (six habitat strata and four water quality parameters). To balance flexibility and prevent overfitting, the basis dimension for each smoothing term was explicitly set to  $k=3$ . The model used a Gaussian error distribution with an identity link function, which was supported by an approximately symmetrical distribution of the Shannon index. Smoothness selection was optimised using Restricted Maximum Likelihood (REML), which is preferred because of its stability and performance with smaller sample sizes.

To derive the final parsimonious model, a backward selection process was employed on this full model. Predictors were sequentially removed if their smooth terms exhibited p-values greater than 0.1, aiming for a balance between the model fit and simplicity. The final model resulting from this selection process, which was fitted to all available data, was used for inferential purposes, including interpreting the functional relationships of the predictors. The overall explanatory power was assessed using the Adjusted  $R^2$  and Deviance explained. The predictive performance and generalisation ability of the final model were then rigorously assessed using a 10-fold cross-validation procedure. The entire dataset was randomly partitioned into ten equal-sized folds. In ten successive iterations, one fold was held out as a test set, while the remaining nine folds were used to train the model. The trained model was then used to predict the hold-out fold values. This process was repeated until each observation was used in the test set. The aggregated predictions from all folds were then compared against the observed values to calculate the cross-validated R-squared (CV- $R^2$ ), Root Mean Squared Error (RMSE), and Mean Absolute Error (MAE), providing a robust estimate of the model's performance on unseen data. The statistical validity of the final model (fit of all data) was confirmed by inspecting diagnostic plots and the sufficiency of the basis dimensions ( $k$ ) was confirmed using standard diagnostic checks (Wood, 2017).

## Results

### Seasonal patterns in fish diversity

To assess the influence of seasonality, we tested for differences in Shannon diversity across three sampling seasons (Pre-monsoon, Monsoon, and Post-monsoon). The Kruskal-Wallis test showed no significant variation in fish diversity among the seasons ( $\chi^2 = 3.29$ ,  $df = 2$ ,  $p = 0.193$ ). This suggests

that the measured habitat and water quality variables were stronger drivers of community structure than season alone. Therefore, data from all seasons were pooled for the primary predictive modeling analysis.

### Model performance and diagnostics

Diagnostic plots (Fig. 2) confirmed that the model assumptions were met with residuals exhibiting an approximately normal distribution and no evidence of heteroscedasticity. The assessment of the basis dimensions further indicated their sufficiency for all smooth terms, confirming that the chosen level of model complexity was appropriate and did not lead to underfitting.

### Key predictors and their functional relationships

The final GAM focused on native fish diversity ( $H'_{\text{native}}$ ) revealed highly significant environmental drivers with complex, non-linear functional forms (Table 1 and Fig. 3).

**Habitat quality:** Native diversity showed a stable response across the gradient of cumulative habitat quality ( $\$p = 0.441\$$ ), suggesting that water quality stressors may be the immediate drivers of community structure.

**Water quality (Nitrate and DO):** Dissolved oxygen exhibited a highly significant bimodal (U-shaped) response ( $p < 0.001$ ), while nitrate showed a similar bimodal trend ( $p = 0.070$ ). The peak at high DO (7–8  $\text{mg l}^{-1}$ ) represents a sensitive specialist assemblage (e.g., *Garra* spp., *Tor* spp.) characteristic of healthy upstream reaches. Conversely, the high diversity at lower DO levels (2–4  $\text{mg l}^{-1}$ ) represents the high abundance of tolerant native generalists (e.g., *Channa striata*) and estuarine/migratory species (e.g., *Megalops cyprinoides*) that accumulate in larger downstream reaches. This bimodal pattern highlights a community transition along the longitudinal river gradient that was previously masked by invasive species 'noise'

### Predictive validation

The predictive performance of the native diversity model was rigorously assessed using 10-fold cross-validation (Table 2). The model demonstrated a stable generalisation ability, explaining 13.8% of the variance in native Shannon diversity on unseen data (CV-  $R^2 = 0.138$ ). A Root Mean Squared Error (RMSE) of 0.337 and Mean Absolute Error (MAE) of 0.278 indicate a reasonable level of predictive accuracy for the indigenous community. The close proximity between the Adjusted  $R^2$  (0.171) and CV- $R^2$  (0.138)

Table 1. Summary of the final, parsimonious GAM for predicting fish Shannon diversity ( $H'_{\text{native}}$ ).

Predictor variable	Type	Edf	F-statistic	p-value	Significance
Smooth terms					
s(Habitat quality)	Habitat	1.000	0.598	0.441	ns
s(Nitrate)	Water	1.847	2.883	0.070	.
s(Dissolved oxygen)	Water	1.909	7.546	< 0.001	***
Model fit metrics					
Adjusted $R^2$		0.171			
Deviance explained		20.7%			

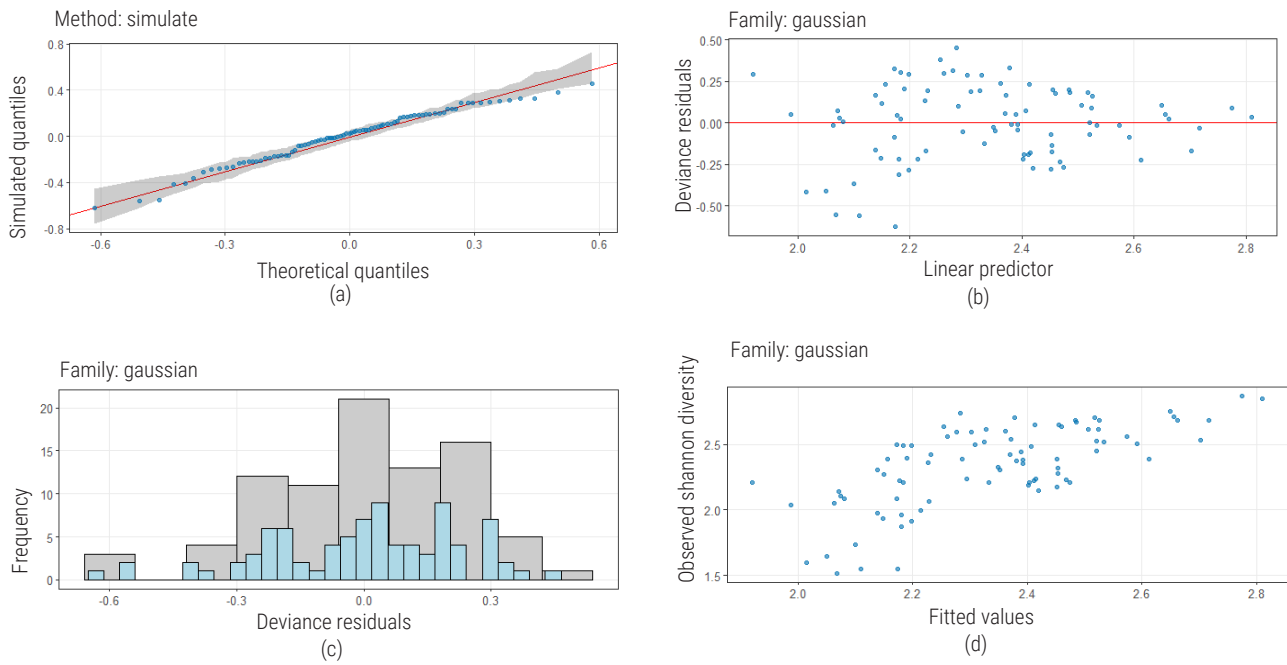


Fig. 2. Diagnostic plots for the final GAM predicting fish Shannon diversity. (a) Q-Q plot of residuals: Compares the quantiles of the model's residuals against the theoretical quantiles of a normal distribution. The points fall closely along the 1:1 line, indicating that the residuals are approximately normally distributed; (b) Residuals vs. linear predictor: Plots the model residuals against the fitted values. The random scatter of points around the zero line suggests that the variance of the residuals is constant (homoscedasticity) and there are no unmodeled patterns; (c) Histogram of residuals: Provides a visual check of the distribution of model residuals, which conforms to a roughly normal (Gaussian) distribution; (d) Response vs. fitted values: Plots the observed Shannon diversity values against the values predicted by the model. The positive correlation indicates the model's overall explanatory power

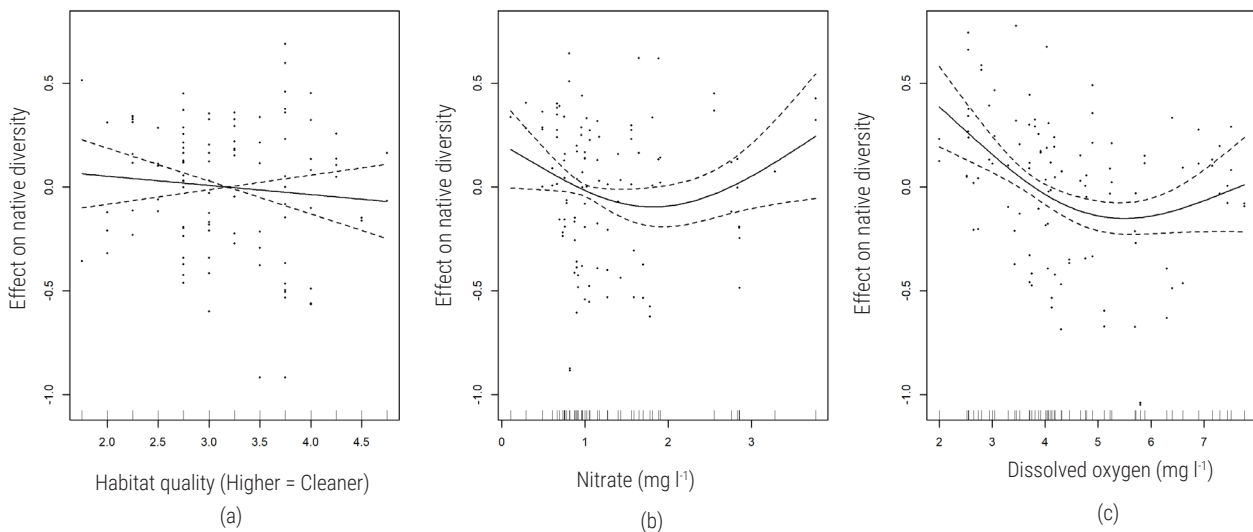


Fig. 3. Partial effect plots from the final GAM predicting fish diversity. (a) Quality response; (b) Nitrate response; (c) Oxygen response

suggests that the model is robust and not overfitted to the training data. Fig. 4. shows the correlation between the observed and predicted values, confirming the utility of the model in forecasting native assemblage responses to water quality thresholds.

Table 2. Cross-validated predictive performance of the final GAM for native fish diversity (n=108, k=10 folds).

Metric	Value	Units
Cross-validated R <sup>2</sup> (CV-R <sup>2</sup> )	0.138	Proportion
Root mean squared error (RMSE)	0.337	Shannon units
Mean absolute error (MAE)	0.278	Shannon units

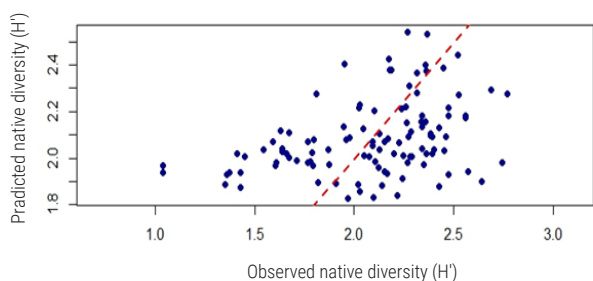


Fig. 4. Cross-validated predictive performance of the final GAM, plotting observed vs. predicted Shannon diversity (N=108). The dashed line indicates a perfect 1:1 relationship.

## Discussion

The 'masking effect' of invasive species on diversity metrics is the primary challenge in the bioassessment of tropical rivers. In Bharathapuzha, the initial high explanatory power of our total diversity model (Adj. R<sup>2</sup>=0.41) was partially driven by the predictable dominance of invasive generalists such as *O. niloticus* and *Pterygoplichthys* spp. By refining our model to focus exclusively on native species diversity ( $H'_{\text{native}}$ ), we obtained a more nuanced and biologically honest Adj. R<sup>2</sup> of 0.17. This shift indicates that, while invasive species respond predictably to simple degradation gradients, the native community is governed by a more complex hierarchy of physiological and environmental filters.

### The hierarchy of stressors: Water quality as the primary bottleneck

A noteworthy finding of our final model was the non-significance of broader habitat features, such as channel morphology and riparian integrity, for native diversity. These factors are recognized as critical for river health and have been cited as major threats to the ichthyofauna of Bharathapuzha in previous comprehensive surveys (e.g., Biju Kumar *et al.*, 2013). However, our results support the 'hierarchy of stressors' hypothesis (Pusey and Arthington, 2003; Allan, 2004), suggesting that immediate physiological pressures, specifically dissolved oxygen instability ( $p < 0.001$ ), currently act as the primary bottleneck for native fish. This aligns with previous assessments of rivers that have documented severe pollution

from urban and agricultural sources (Anto *et al.*, 2021; Kannan and Joseph, 2022). In this scenario, acute water quality stressors likely mask the subtler and chronic effects of structural habitat degradation.

### Linear gains vs. Ecological optima: A tale of two responses

The highly significant bimodal relationship with DO identified a critical 'environmental tolerance window' for native assemblages. A decline in diversity under unstable oxygen regimes is a classic symptom of eutrophication, in which oxygen instability is detrimental to aquatic life (Paerl and Huisman, 2009). However, the observed bimodal peak also reflects a longitudinal community phase shift. Higher native diversity at the upper end of the DO gradient represents sensitive endemics requiring high oxygen (Pollock *et al.*, 2007), whereas the peak at the lower end reflects the accumulation of tolerant generalists in larger downstream reaches. This distinction remains a vital tool for evidence-based management, allowing endangered specialists to prioritise oxygen-rich 'refugia.'

### Management implications: A tailored strategy for the Bharathapuzha

Our findings will allow for the development of a prioritised action plan that complements ongoing hydrological and pollution assessment work in the basin (Anto *et al.*, 2021; Kannan and Joseph, 2022). The clear hierarchy of stressors suggests that, for restoration to be effective, remediating water quality and abating point-source pollution must be the critical first steps, without which broader habitat restoration efforts may fail to yield the desired native biodiversity outcomes.

**Targeted abatement for pollution hotspots:** The significant impact of cumulative human stress calls for targeted interventions. For culturally significant sites such as Ivarmadom and Thirunavaya, where crematorial and ritualistic waste is concentrated, management should focus on engineering solutions, such as designated, contained ghats, and rapid waste removal systems. For urban centres, the Kerala State Pollution Control Board (KSPCB) must prioritise the modernisation and expansion of sewage treatment plants, which is strongly supported by previous pollution studies (Anto *et al.*, 2021).

**Bio-informed "E-Flow" management:** The bimodal oxygen response identified by our model provides a concrete, data-driven biological target for managing the river's regulator-cum-bridges at Velliyamkallu and Chamravattom. We recommend that the Kerala Irrigation Department move beyond purely hydrological targets to incorporate "bio-informed" ecological flows aimed at protecting sensitive endemic refugia. This would involve scheduling periodic, high-volume releases specifically designed to maintain dissolved oxygen levels within the identified optimal range for endemics ( $>7 \text{ mg l}^{-1}$ ), disrupting thermal stratification, increasing aeration, and flushing pollutants, thereby actively managing the downstream river chemistry to stay within the optimal physiological range for native fish.

Although our model provides a robust framework for native community response, the unexplained variance (Adj. R<sup>2</sup> = 0.17)

highlights other influential factors beyond water and habitat quality. A primary driver is likely the pervasive impact of invasive species, particularly suckermouth sailfin catfish (*Pterygoplichthys* spp.), which is a major concern in Kerala's rivers (Bijukumar *et al.*, 2013). Although our modeling approach explicitly focused on native diversity ( $H'_{\text{native}}$ ) to mitigate the masking effect of these taxa, their physical role as ecosystem engineers causing benthic habitat disturbance and direct competition with native fauna, remains a significant unmeasured pressure (Cucherousset and Olden, 2011). Future predictive models could be greatly enhanced by incorporating the biomass or density of key invasive species as a covariate to further disentangle the competitive effects of environmental drivers. Additionally, targeted analysis of agricultural pesticides and micro-habitat flow velocity, which were not captured in this reach-scale assessment, represents a critical next step for refining biodiversity forecasts in Bharathapuzha.

In conclusion, this study moves beyond simple correlations to rigorously model the complex and functional impacts of environmental stressors on native fish diversity in the Bharathapuzha River. Our findings revealed a clear hierarchy of stressors, where acute dissolved oxygen instability ( $p < 0.001$ ) currently overrides the effects of chronic habitat degradation, acting as the primary physiological bottleneck for native fish survival. While the native community model captures a more modest portion of the total variance (17.1%) compared to the total diversity metrics, it provides a biologically more accurate and honest foundation for river restoration. Our results provide a concrete blueprint for evidence-based management, identifying oxygen-rich upstream 'refugia' ( $>7 \text{ mg l}^{-1}$ ) as critical conservation targets for endemics in Western Ghats. By distinguishing between linear drivers of direct pollution and the non-linear optimality-driven influence of water quality, this study provides a nuanced and powerful tool for prioritising restoration efforts.

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