

Influence of hydrological variability and life history strategy on riverine fish assemblages in the Australian wet-dry tropics

King, Alison J.; Olden, Julian D.; Luiz, Osmar J.; Kennard, Mark J.; Adair, Brendan; Crook, David A.; Douglas, Michael M.; Saunders, Thor M.; Wedd, Dion

Published in:
Ecology of Freshwater Fish

DOI:
[10.1111/eff.12809](https://doi.org/10.1111/eff.12809)

Published: 01/01/2025

Document Version
E-pub ahead of print

[Link to publication](#)

Citation for published version (APA):

King, A. J., Olden, J. D., Luiz, O. J., Kennard, M. J., Adair, B., Crook, D. A., Douglas, M. M., Saunders, T. M., & Wedd, D. (2025). Influence of hydrological variability and life history strategy on riverine fish assemblages in the Australian wet-dry tropics. *Ecology of Freshwater Fish*, 34(1), 1-17. Article e12809. <https://doi.org/10.1111/eff.12809>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.




- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

ORIGINAL ARTICLE

Influence of hydrological variability and life history strategy on riverine fish assemblages in the Australian wet-dry tropics

Alison J. King^{1,2,3}  | Julian D. Olden⁴  | Osmar J. Luiz^{1,5}  | Mark J. Kennard⁶  |
Brendan Adair¹ | David A. Crook^{1,7}  | Michael M. Douglas⁸ | Thor M. Saunders^{7,9} |
Dion Wedd^{1,7} 

¹Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory, Australia

²CSIRO, Environment, Albury, New South Wales, Australia

³Gulbali Institute, Charles Sturt University, Albury, New South Wales, Australia

⁴School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA

⁵CSIRO, Environment, Darwin, Northern Territory, Australia

⁶Australian Rivers Institute, Griffith University, Nathan, Queensland, Australia

⁷NSW Department of Primary Industries, Buckingbong Road, Narrandera, New South Wales, Australia

⁸School of Biological Sciences, School of Agriculture and Environment, The University of Western Australia, Perth, Western Australia, Australia

⁹Department of Primary Industry and Fisheries, Darwin, Northern Territory, Australia

Correspondence

Alison J. King, CSIRO, Charles Sturt University, Albury, New South Wales, 2640, Australia.

Email: alison.king@csiro.au

Funding information

Australian Research Council, Grant/Award Number: LP150100388; Department of Primary Industry and Fisheries, Northern Territory Government

Abstract

Riverine fish assemblages are strongly influenced by attributes of the flow regime. Tropical savannah river systems have distinct and predictable hydrologic seasonality, reflecting the wet-dry climate, but can vary substantially in terms of dry season flow permanency and wet season flow-pulse characteristics. Understanding how flow permanence and variability influence fish assemblages, and whether these factors can be used to predict responses to future hydrological change, are key knowledge gaps that impede effective management. We examined the influence of hydrological variability on the structure and diversity of freshwater fish assemblages across rivers of the wet-dry tropics of northern Australia. We found distinct fish assemblages that varied predictably across three hydrological river types: Intermittent, Perennial Stable and Perennial Flashy flow regimes. This distinction emerged despite a common species pool across the region. Species richness was greatest in rivers with Perennial Stable flow regimes, whereas beta-diversity was greatest in Intermittent rivers. However, life history strategies of constituent species were generally poor predictors of species abundances within each hydrological river type. The distinct fish assemblages evident among hydrological classes may provide some cautious ability to both predict potential fish assemblage changes with future hydrological changes (e.g. if perennial streams became more flashy or intermittent), and to predict fish assemblages expected in unsampled rivers with particular hydrological characteristics. Our findings provide further support for the importance of maintaining regional flow-habitat heterogeneity and the connectivity between hydrological river types, and their essential role for conserving tropical fish species diversity into an uncertain hydrological future.

KEYWORDS

perennial rivers, northern Australia, intermittent rivers, freshwater fish

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Ecology of Freshwater Fish* published by John Wiley & Sons Ltd.

1 | INTRODUCTION

In freshwater systems, the hydrological regime is well recognised as the main driver of biophysical attributes and ecosystem functioning (Naiman et al., 2008; Poff et al., 1997). Critical flow regime characteristics, such as magnitude, frequency, timing and duration of low and high flow events, affect the persistence, abundance and distribution of stream biota. These flow characteristics influence key factors important for biota such as the availability and quality of habitat and food resources, frame biotic interactions, provide connectivity to influence dispersal, and provide cues for critical life events such as breeding and movement (Bunn & Arthington, 2002). Over ecological and evolutionary time scales, the systems' flow regime therefore influences the selection of compatible traits and life histories of aquatic organisms living in it (Lytle & Poff, 2004; Townsend & Hildrew, 1994).

The intrinsic morphological, physiological and behavioural traits of freshwater species are also strongly influenced by flow regimes over evolutionary time scales (Lytle & Poff, 2004). Hence, the species composition of riverine communities is influenced by flow attributes such as magnitude, predictability, variability and intermittency (Craven et al., 2010; McManamay & Frimpong, 2015; Tedesco et al., 2008). For example, flow-mediated habitat connections can influence the spatial variation of riverine assemblages, commonly measured as beta-diversity (Larned et al., 2010; Leigh & Sheldon, 2009; Thomaz et al., 2007); where beta-diversity is defined as the variation in species composition among samples (e.g., habitats or reaches) in a given area (e.g. a river basin) (Anderson et al., 2011; Whittaker, 1972). Beta-diversity is predicted to peak during intermediate connectivity, but to decline both with increases or decreases in connectivity (e.g. Larned et al., 2010; Leigh & Sheldon, 2009). Anthropogenic changes in hydrology due to river regulation, water extraction and climate change may shape patterns of beta-diversity in rivers (Rogosch & Olden, 2019).

The life history continuum model for fish (Winemiller & Rose, 1992), which represents the trade-offs between juvenile survival, fecundity and generation time, has been used to predict the relationship between flow characteristics (e.g. variability, predictability and seasonality) and fish assemblages at various spatial scales (e.g. Mims & Olden, 2012; Olden & Kennard, 2010; Sternberg & Kennard, 2013; Tedesco et al., 2008). For example, in a large-scale analysis of the relationships between flow regime attributes and fish assemblages, Mims and Olden (2012) found strong relationships between specific flow indices and the relative prevalence of fish life history strategies across the entire USA. Opportunistic strategists (early age at maturity, small egg size, high fecundity) were more abundant in streams with high flow variability than in streams with predictable seasonal flows; periodic strategists (late maturity, high fecundity) were more abundant in streams with high flow seasonality and more stable flows; and equilibrium strategists (high parental investment in offspring) were negatively associated with flow variability and positively associated with predictable flows. Similarly, species richness and beta-diversity would be expected to

peak in intermittent river systems with intermediate connectivity, but decline with flow perennality or flow variability (Rogosch & Olden, 2019; Rolls et al., 2012). Conversely, the hydrological regime has been shown in some cases to be a poor predictor of fish assemblages at smaller regional scales, with metrics such as temperature, phylogeography and landscape factors (stream size, gradient) acting as more important drivers of taxonomic composition than local hydrological gradients (e.g. Gido et al., 2013; Pusey et al., 2020; Troia & McManamay, 2020).

Tropical savannah rivers in northern Australia have distinct and predictable hydrologic seasonality, reflecting the wet-dry climate, and can either be permanent or have varying degrees of intermittency (Kennard et al., 2010; King et al., 2015; Warfe et al., 2011). Intermittent flow regimes are the most common hydrological type, with the degree of intermittency varying depending on climate, latitude, and underlying geology, and rivers can cease flowing for several months. Perennial streams and rivers are much less common in the region, and are restricted to areas with strong surface water-groundwater connectivity, such as the Daly and Roper River basins. Tropical savannah rivers of northern Australia are recognised as some of the most hydrologically intact and largest aggregations of free-flowing rivers in the world (Pusey, 2011; Reidy-Liermann et al., 2012), supporting high ecological and cultural values and high freshwater fish diversity (>110 species) (Pusey et al., 2017). However, these rivers are not pristine, with low intensity cattle grazing, forestry, cropping and mining, widespread throughout the region. In recent years, there has been increasing interest in developing both surface and groundwater resources to support expanded agricultural and mining interests (Chan et al., 2012; King et al., 2015; Pusey, 2011).

Factors such as the strong seasonality and interannual variability of the region's tropical flow regime are thought to influence fish distribution and abundance (Pusey et al., 2018, 2020; Stewart-Koster et al., 2011). For example, broad habitat type (creek, wetland), position in catchment and stream flow intermittency were major drivers of fish assemblage composition and species richness in the Daly River catchment (Pusey et al., 2020). However, despite the urgent need to better understand flow-ecology patterns in the region and the likely impacts of flow alteration to the systems' ecology (King et al., 2015; Pusey, 2011), there has been limited quantitative analysis of the influence of hydrology on fish distributions, assemblages and critical ecological life history features (King et al., 2013, 2015; Pusey et al., 2020). Understanding how flow permanence and variability influences fish species distributions and assemblages, and the predictability of these factors with life history strategies, are important considerations for modelling flow-ecology relationships and predicting future impacts of flow alteration (Chan et al., 2012; Chen & Olden, 2018; King et al., 2015; McManamay & Frimpong, 2015; Mims & Olden, 2013).

This study examines the influence of hydrological variability on the structure and diversity of freshwater fish assemblages across rivers of the wet-dry tropics of northern Australia. We sampled fish assemblage composition in contrasting rivers spanning a hydrologic

gradient from intermittent to perennial flow regimes, with analyses revealing three hydrological categories: (1) Intermittent (long periods of zero flow), (2) Perennial Flashy (long low flow periods, flashy floods), (3) Perennial Stable (lower variability within season, long floods). We explored patterns in fish assemblages among rivers with varied hydrological regimes and hydrological seasonality; and tested whether differences in assemblage structure are predictable according to species life history strategy. Next, we disentangled the roles of hydrological variability and species life history strategy in shaping patterns of freshwater fish beta-diversity.

We hypothesised that hydrologic variability in rivers of tropical Australia influences assemblage composition and abundance of species expressing different life history strategies (e.g. Olden & Kennard, 2010; Sternberg & Kennard, 2013; Winemiller, 2005). We predicted that opportunistic species should be more abundant in frequently disturbed habitats (i.e., high hydrologic variability, Intermittent rivers); periodic species abundance should be positively related to productive habitats with flow seasonality and predictability and negatively related to flow variability (Perennial Flashy: perennial rivers with high flow variability); and equilibrium strategists should be more common in localities exhibiting lower flow variability (Perennial Stable: more predictable stable flow rivers). We also predicted that intermittent streams would have higher beta-diversity

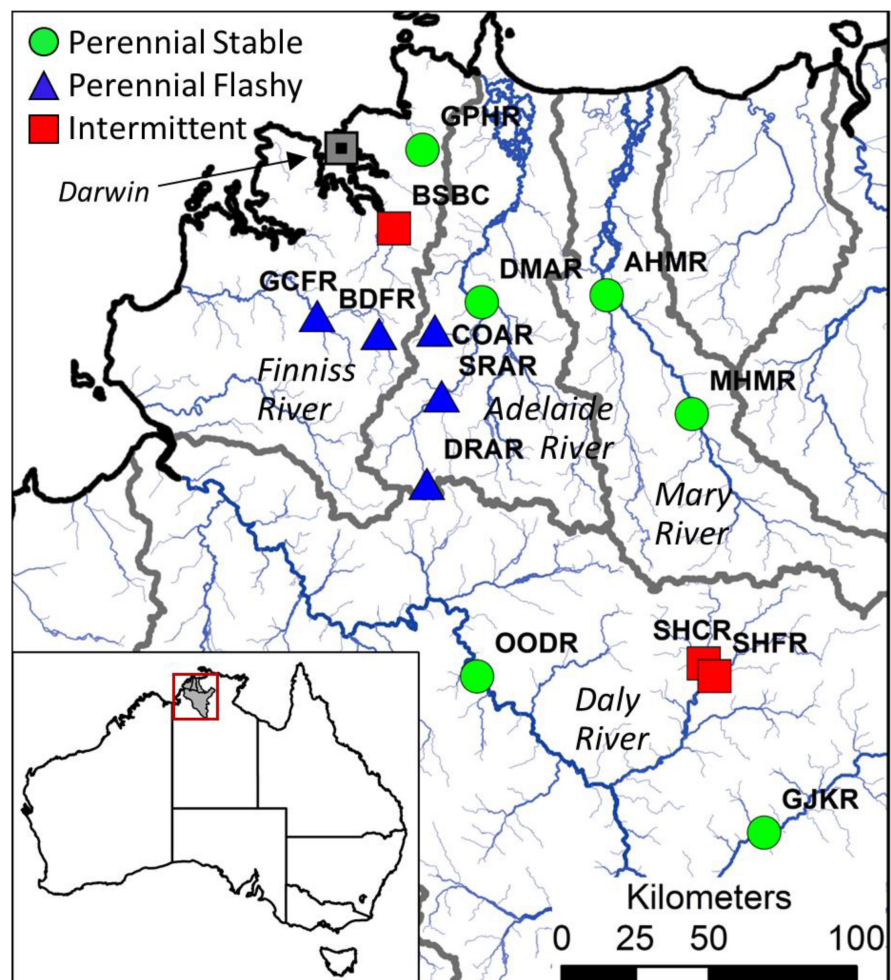
compared to perennial streams by virtue of dynamic flow regimes supporting a diversity of habitats and the persistence of unique fish assemblages (Datry et al., 2016; Pusey et al., 2018; Rogosch & Olden, 2019).

2 | METHODS

2.1 | Fish data collection

Fish assemblages were sampled on four occasions in distinct seasonal periods defined according to rainfall and river hydrology: the late-dry season 2016 (October–November 2016; code: LD2016), early-dry season 2017 (May–June 2017; ED2017), mid-dry season 2017 (August 2017; MD2017) and the late-dry season 2017 (late September–November 2017; LD2017). Wet season fish sampling was not possible due to access limitations. Sampling was conducted in 14 sites across four river basins in the north-western region of the Northern Territory, Australia (Figure 1, Table S1). Fish assemblages were sampled using a boat-mounted (Engineering Technical Services Model MBS-2DHP-SRC; www.etselectrofishing.com) or backpack (Smith Root Model LR20B; www.smith-root.com) electrofishing unit. We selected which electrofishing gear type to use based

FIGURE 1 Location of study region with coloured circles representing sampling sites and hydrological class (red = Intermittent, blue = Perennial Flashy, green = Perennial Stable, see Section 2: Methods for description). Inset map shows location of study region in northern Australia. Grey thinner lines show catchment boundaries. Site codes are: AHMR, Arnhem Highway, Mary River; BDFR, Batchelor Dam, Finnis River; BSBC, Berry Springs, Berry Creek; COAR, Coomalie Creek, Adelaide River; DMAR, Downstream Margaret River, Adelaide River; DRAR, Daly Road, Adelaide River; GCFR, Gitchams Crossing, Finnis River; GJKR, Galloping Jacks, Katherine River; GPHR, Gunn Point, Howard River; MHMR, Mount Harris, Mary River; OODR, Oolloo Crossing, Daly River; SHCR, Stuart Highway, Fergusson River; SHFR, Stuart Highway, Fergusson River; SRAR, Strickland Road, Adelaide River.



on depth and safety considerations as the rivers contain estuarine crocodiles; with deep, slow-flowing habitat sampled by boat electrofishing and shallow, fast-flowing areas sampled by backpack electrofishing. The electrofisher settings were adjusted according to water conductivity levels to maximise capture efficiency, while using the minimum power thresholds required to induce narcosis and capture fishes. At each site, fish were sampled at multiple discrete locations (electrofishing shots) where each electrofishing shot was fixed to 5-min duration (elapsed time). Sites that were totally dry at the time of sampling were recorded as containing zero individuals (see Table S1). Ten electrofishing shots were undertaken at each site to ensure that all available habitat types within the reach were sampled. Fish were identified, counted and measured (standard length in mm) and returned to the water near to where they were originally captured. Catch data was converted to catch per unit effort (CPUE) with the unit effort being defined as a 5-min electrofishing period. Fish sampling was conducted in accordance with the requirements of animal ethics permits (Charles Darwin University) and NT Fisheries S17 Fisheries Act permit.

2.2 | Hydrological classification of sites

Sampling sites were chosen to represent a range of hydrological conditions, from intermittent to perennial, and various flood durations and frequencies of high spells during the wet season (see below and Luiz et al., 2022). All sites were located close to hydrological gauging stations, and were an average of 545 m in length sampled (range: 124–1099 m at a site). To choose sites representing a hydrological gradient, we examined multivariate resemblance in hydrologic regimes across sites using a cluster analysis (Ward's hierarchical algorithm) and principal component analysis (PCA) performed on the standardised Euclidean distances of 22 hydrology metrics (Table S2). Hydrologic metrics described the magnitude, frequency, duration, timing and rate of change in flow events, as well as measures of temporal variability, seasonality and predictability in flow characteristics during an 18-year period (01-01-2000 to 12-31-2017), thus reflecting all major dimensions of the flow regime (Kennard et al., 2010; Olden & Poff, 2003). The number of clusters was determined by the best solution according to an ensemble of 32 clustering indices presented by Milligan and Cooper (1985). Sites showed strong clustering into three hydrological classes (Figure S1, Table S3): (1) Intermittent sites ($n=3$ sites) were characterised by long periods of zero flow (mean 170 ± 14 (SE) days per year), including partial desiccation; (2) Perennial Flashy sites ($n=6$) rarely ceased to flow (mean 2.4 ± 1.6 days per year) in the dry season and were characterised by more frequent high flow spells (mean 5.3 ± 0.1 spells per year) of shorter durations (mean 5.8 ± 0.3 days) during the wet season than sites in other hydrologic classes, with a large variability in the water level; and (3) Perennial Stable sites ($n=5$) were characterised by larger rivers with lower flow variability between the wet-dry seasons than the former two groups, and longer flood periods during the wet season, with less frequent changes in the water level (Table S3).

2.3 | Life history strategy classification

To determine the affinity of the study species to the three-endpoint life history strategies (opportunistic, periodic, or equilibrium) of the Winemiller and Rose (1992) triangular life history strategy model, we examined the life history of 221 Australian freshwater fish species (including those that reproduce in fresh water and diadromous species that spend the majority of their life cycle in fresh waters) using an extensive dataset containing the most current information on their relevant traits (Mark Kennard, unpublished data; Sternberg & Kennard, 2014). We followed a similar methodology to Olden and Kennard et al. (2010) and Mims and Olden (2012), where we established both a 'hard' life history classification and a 'soft' classification according to species' relative affinity towards each strategy. We evaluated all Australian freshwater fish species in the life history continuum model of Winemiller and Rose (1992) and plotted species' positions in relation to three life history axes: (1) \ln age at maturation (2) \ln mean fecundity; and (3) investment per progeny, calculated as $\ln(\text{egg diameter} + 1) + \ln(\text{parental care} + 1)$. Each of our study species was then assigned to one of the three life history strategies by calculating the Euclidean distance in trivariate life history space between the species' position and the strategy endpoints and designating the species to the closest strategy (Figure S2). To enable a distance-weighted measure of proportional affinity to each life history strategy (soft classification) to also be considered, we normalised the Euclidean distances in trivariate life history space between species and each strategy endpoint (i.e., standardised range between 0 and 1 for each distance), and computed the inverse of these values (so that larger values represent a greater 'weight' or affinity of a species towards a life history strategy). There was a large degree of variability between species using this soft classification approach, with some species demonstrating a high level of specificity to a single life history strategy (species close to the triangle vertices, Figure S3), and a large group of species positioned in the centre of the triangle, demonstrating less affinity to any one life history strategy (Figure S3).

2.4 | Analysis

The statistical analysis for our study was conducted in two stages: (1) the evaluation of relationships between species composition, abundance and environmental factors, and (2) the measurement of beta diversity across sites and species.

A multivariate generalised linear modelling approach (Warton et al., 2015) was used to test the relationship between species composition and abundance, and two explanatory variables: hydrological class and seasonal period. We used a latent variable model (LVM) to create an unconstrained ordination to visualise the main trends between sample sites and seasonal period, in terms of their species abundance (Hui et al., 2015). We did not include a row effect to account for differences in abundance between sites (Hui, 2016), meaning that patterns in the ordination are driven by differences

in both abundance and species occurrences between sites. We also evaluated the environmental and residual correlation matrices to explore correlations between species and hydrological classes, season, and residual correlations due to unmeasured variables through correlated response models (CRM; Hui, 2016). Using the CRM model we identified the relative importance of abiotic covariates for each species using Bayesian Markov chain Monte Carlo (MCMC) estimation, with a horizontal line plot showing 95% highest posterior density (HPD) intervals for the column-specific regression coefficients by 'ggboral' package. We identified the ten most influential species as those whose abundance patterns most strongly correlated with the primary latent variables derived from our CRM analysis, thus having the most significant impact on assemblage composition patterns. We further plotted the correlations between species and environmental factors. The role of the latent variables in LVMs and CRMs is to account for unknown or unmeasured variables, and, by inducing correlations between taxa, enable an unconstrained ordination for visualising site and species patterns (Hui, 2016; Warton et al., 2015). We considered both the direction (positive or negative) and the strength of correlations; where stronger correlations were given more weight in our ecological interpretation, regardless of whether their HPD intervals overlapped zero. This approach allows for a more comprehensive understanding of species-environment relationships, considering both effect size and precision, and is more transparent and statistically explicit than classic distance-based approaches (Warton et al., 2015), and improves interpretability of results. LVMs and CRMs were done using the 'boral' package (Hui, 2016) in R.

The strength of the relationships between hydrological classes, seasonal period and species abundance were explored using the 'manyglm' function in the 'mvabund' package (Wang et al., 2012) in R. This analysis fits a specified generalised linear model (GLM) to each species, which are then used to make community-level inferences about the importance of model predictors using resampling-based hypothesis testing (Wang et al., 2012). Species abundance were expressed as counts (summed catch from the 10 electrofishing shots) at each site/season combination. A negative binomial distribution was used and model assumptions were evaluated by examining plots of residuals (Wang et al., 2012). Species for which deviance estimated by the 'manyglm' test was significant were inferred to cause the observed differences in species composition between hydrological classes. Univariate models for each species were used as a post-hoc test to determine the significance of differences of a given species across the hydrological gradients. We then determined the relationships between the proportional affinity of species to a specific life history and their mean abundance across different river types. We expect that species with stronger affinities to a specific life history strategy will also have greater abundances in specific river types as predicted above (see Section 1: Introduction).

Beta diversity can be measured as the total variance in meta-community data, which can subsequently be partitioned into unique variation contributed by individual sites and species within the dissimilarity matrix (Legendre & De Cáceres, 2013). This approach is

advantageous because beta diversity is estimated independent of local (alpha) and regional (gamma) diversity, and thus it is possible to compare estimates across different communities. Prior to beta-diversity calculations for site and species comparisons, we performed the Hellinger transformation on the species abundance matrix. A Hellinger transformation results in a Euclidean distance matrix, making the total variance in community composition range between 0 and 1. This allows estimation of individual site (Local Contributions to Beta Diversity: LCBD) and species (Species Contributions to Beta Diversity: SCBD) contributions to beta-diversity using a relative scale (Legendre & De Cáceres, 2013). We considered the effects of flow variability and season on overall beta-diversity by comparing the unique contribution of sites (LCBD) in different hydrological classes and different seasonal periods, respectively. Next, we compared the unique contributions of species (SCBD) of different life history strategies to overall beta-diversity. Statistical comparisons made between the contributions of hydrological classes, seasonal periods, and life-history strategies to overall beta-diversity were made using Welch's unequal variances *t*-tests (Welch, 1947). Beta-diversity values and LCBD and SCBD contributions were calculated using the 'adespatial' package in software program R (Dray et al., 2017).

We examined the relative roles of species turnover versus nestedness in shaping patterns in beta diversity. Total variance in the Jaccard dissimilarity matrix on presence/absence data was decomposed into complementary components of turnover (i.e. species replacement) and nestedness (i.e. species gain and loss) based on the proportion of shared species across pairwise site comparisons following Legendre (2014). The proportion of total beta diversity accounted for by replacement and richness differences sums to 1. Therefore, these relative indices can be used to determine which of the two processes dominates among sampling sites in a metacommunity. We investigated the proportion of beta diversity variability due to changes in species richness or replacement spatially across all sites according to hydrological class. Turnover and nestedness components of beta diversity were calculated using the 'betapart' package in software program R (Baselga et al., 2021).

3 | RESULTS

In total, 17,096 individuals from 45 species were collected, with 22 species occurring in 50% or more of study sites (Table 1). Seven species were removed from further analysis because they were rarely encountered marine or estuarine vagrants (represented <0.1% of total individuals: *Prionobutis microps*, *Redigobius chryosoma*, *Neoarius midgleyi*, *Ambassis interruptus*, *Scatophagus argus*, *Periophthalmus weberi*, and *Glossogobius* spp.). A higher diversity of species were recorded in Perennial Stable sites ($n=36$), compared to Perennial Flashy ($n=30$) and Intermittent sites ($n=26$) (Table 1). The most abundant species were *Melanotaenia australis*, *Nematolosa erebi*, *M. inornata*, *Glossamia aprion* and *Amniataba percooides* with over 1000 individuals observed of each of these taxa. The most frequently encountered species were *A. percooides* (in 43% of samples), *G. aprion* (39.4%), *Lates*

TABLE 1 Summary of the abundance and frequency of occurrence for species in this study (taxonomy after Bray & Gomon, 2023), grouped according to hard classification of life history association. Intermittent $n = 120$ samples (shots), Perennial Flashy $n = 200$, Perennial Stable $n = 230$.

Species code	Sites occurrence		Major life-history strategy association, species						Frequency (proportion of occurrence in samples)					
	%	Total N	Opportunistic			Abundance (mean number of individuals \pm SD)			Intermittent			PerennStable		
			PerennFlashy	PerennStable	Intermittent	PerennFlashy	PerennStable	Intermittent	PerennFlashy	PerennStable	Intermittent	PerennFlashy	PerennStable	
AMBAGR	42.8	68	Ambassis agrammus	4.83 \pm 4.83	0.35 \pm 0.20	0.13 \pm 0.09	0.01	0.02	0.01	0.01	0.01	0.01	0.01	
AMBMAC	71.4	284	Ambassis macleyi	2.08 \pm 1.99	9.10 \pm 3.11	3.34 \pm 2.08	0.99	0.28	0.99	0.99	0.28	0.08	0.08	
AMBSPP	78.5	205	Ambassis sp.	8.00 \pm 5.41	3.2 \pm 2.05	1.95 \pm 1.15	0.08	0.08	0.08	0.08	0.08	0.06	0.06	
CRASTE	71.4	988	Craterocephalus stercusmuscarum	0	26.35 \pm 11.6	20.04 \pm 12.2	0	0.35	0	0	0.35	0.15	0.15	
CRASTR	35.7	597	Craterocephalus stramineus	0	2.2 \pm 1.00	24.04 \pm 11.25	0	0.04	0	0	0.04	0.19	0.19	
DENBAN	7.1	1	Denariusa bandata	0	0.05 \pm 0.05	0	0	0.005	0	0	0.005	0	0	
GLOAPR	92.8	1188	Glossamia aprion	2.66 \pm 1.42	15.25 \pm 3.62	37.0 \pm 21.39	0.12	0.49	0.12	0.49	0.49	0.44	0.44	
GLOAUR	21.4	6	Glossogobius aureus	0.16 \pm 0.16	0.15 \pm 0.15	0.04 \pm 0.04	0.01	0.01	0.01	0.01	0.01	0.004	0.004	
GLOGIU	7.1	93	Glossogobius giurii	7.75 \pm 7.75	0	0	0.08	0	0	0.08	0	0	0	
HYPCOM	14.3	681	Hypseleotris compressa	0.5 \pm 0.5	0	29.34 \pm 23.74	0.04	0	0.04	0	0	0.06	0.06	
LEIUNI	71.4	757	Leiopotherapon unicolor	50.91 \pm 31.22	0.7 \pm 0.37	5.73 \pm 2.52	0.53	0.04	0.53	0.04	0.04	0.21	0.21	
LEPTRI	7.1	4	Leptachirus triramus	0	0	0.17 \pm 0.17	0	0	0	0	0	0.01	0.01	
MELAUS	64.3	3168	Melanotaenia australis	108.6 \pm 47.65	26.4 \pm 20.29	58.08 \pm 37.88	0.39	0.24	0.39	0.24	0.24	0.24	0.24	
MELEXQ	14.3	59	Melanotaenia exquisita	0.16 \pm 0.11	0	2.47 \pm 1.98	0.01	0	0.01	0	0	0.01	0.01	
MELINO	50	1503	Melanotaenia inornata	4.16 \pm 4.16	58.2 \pm 19.9	12.56 \pm 7.24	0.04	0.39	0.04	0.39	0.39	0.17	0.17	
MELNIG	21.4	226	Melanotaenia nigra	18.5 \pm 17.7	0.1 \pm 0.06	0.08 \pm 0.08	0.09	0.01	0.09	0.01	0.01	0.01	0.01	
MOGMOG	71.4	242	Mogurnda mogurnda	18.91 \pm 9.66	0.45 \pm 0.15	0.26 \pm 0.14	0.33	0.04	0.33	0.04	0.04	0.02	0.02	
PORREN	7.1	1	Porochilus rendahli	0	0	0.04 \pm 0.04	0	0	0	0	0	0.004	0.004	
Periodic														
			Intermittent	PerennFlashy	PerennStable	Intermittent	PerennFlashy	PerennStable	Intermittent	PerennFlashy	PerennStable	Intermittent	PerennFlashy	PerennStable
AMNPER	100	1097	Amniatata percoides	26.16 \pm 12.36	12.95 \pm 2.9	22.78 \pm 5.06	0.03	0.40	0.03	0.40	0.51	0.51	0.51	
HEPFUL	92.8	244	Hephaestus fuliginosus	2.83 \pm 0.99	2.1 \pm 0.5	7.3 \pm 1.4	0.16	0.16	0.16	0.16	0.37	0.37	0.37	
LATCAL	85.7	710	Lates calcarifer	0.16 \pm 0.11	4.9 \pm 1.38	26.52 \pm 5.37	0.01	0.27	0.01	0.27	0.65	0.65	0.65	
LIZORD	57.1	416	Liza ordensis	0	2.15 \pm 0.88	16.21 \pm 6.11	0	0.09	0	0.09	0.31	0.31	0.31	
MEGCYP	85.7	143	Megalops cyprinoides	0.08 \pm 0.08	2 \pm 0.82	4.43 \pm 1.15	0.01	0.09	0.01	0.09	0.14	0.14	0.14	
NEMERE	78.6	1988	Nematalosa erebi	16.75 \pm 9.25	42 \pm 23.24	41.17 \pm 14.65	0.12	0.30	0.12	0.30	0.41	0.41	0.41	
NEOATE	92.8	277	Neosilurus ater	1.91 \pm 1.01	2.2 \pm 0.72	9.13 \pm 1.75	0.14	0.14	0.14	0.14	0.42	0.42	0.42	
NEOHYR	28.6	653	Neosilurus hyrtlilii	54.33 \pm 32.0	0	0.04 \pm 0.04	0.34	0	0.34	0	0.004	0.004	0.004	
OXYLIN	85.7	311	Oxyeleotris lineolata	2.66 \pm 1.52	4.65 \pm 1.03	8.08 \pm 1.51	0.13	0.31	0.13	0.31	0.41	0.41	0.41	
OXYSEL	92.8	101	Oxyeleotris selheimi	2.75 \pm 1.3	0.9 \pm 0.44	2.17 \pm 0.72	0.14	0.07	0.14	0.07	0.16	0.16	0.16	

TABLE 1 (Continued)

			Periodic			Intermittent			PerennFlashy			PerennStable		
			SYNBUT	TOXCHA	TOXLOR	Intermittent	PerennFlashy	PerennStable	Intermittent	PerennFlashy	PerennStable	Intermittent	PerennFlashy	PerennStable
			78.6	78.6	7.1	2.00 ± 1.2	1.2 ± 0.32	10.69 ± 2.53	0.09	0.09	0.32			
			294	348	1	0.66 ± 0.37	4.8 ± 1.99	10.6 ± 2.64	0.20	0.20	0.41			
						0	0	0.04 ± 0.04	0	0	0.004			
Equilibrium														
			28.6	7.1	64.3	0	0	0.73 ± 0.28	0	0.02	0.05			
			23	13	118	0	0	0.56 ± 0.52	0	0	0.01			
						2.66 ± 1.94	0.15 ± 0.08	3.6 ± 0.85	0.04	0.01	0.16			
			28.6	21.4	28.6	0	0.05 ± 0.05	0.39 ± 0.17	0	0.005	0.03			
			10	4	16	0	0.15 ± 0.10	0.04 ± 0.04	0	0.01	0.004			
						0	0.55 ± 0.49	0.21 ± 0.1	0	0.01	0.02			
			71.4	137		0.41 ± 0.25	1.45 ± 0.58	4.47 ± 1.85	0.04	0.11	0.17			

calcarifer (37.8%), *Oxyeleotris lineolata* (31.4%), and *N. erebi* (31.2%); *Amniataba percoides* was the only species encountered across all sites (Table 1).

The unconstrained ordination from the LVM showed that sample clusters based on species abundances were determined more by hydrology class than by seasonal period (Figure 2). The value of the estimated residual covariate matrix decreased from 529.2 to 437.9, when comparing the pure LVM with the correlated response model for hydrology class, and to 528.9, when comparing with the correlated response model for seasonal period. This revealed that hydrology classes alone explained approximately 17.2% of covariations in the composition of riverine fish assemblages. Seasonal period alone explained a negligible 0.05%. We extracted the posterior distribution for hydrological classes and seasonal period levels detailing how each species responded to each variable (Figure 3). There were more positive correlations between each species and the Perennial Stable hydrological class, and more negative correlations between each species and the Intermittent class. The Perennial Flashy class showed similar numbers of positive and negative correlations (Figure 3a). Relationships between species and seasonal periods categories exhibited some strong correlations, but no pattern is visually detected (Figure 3b).

The multivariate GLM analysis showed that hydrological class significantly influenced fish species abundance, while no significant effect of seasonal period was detected (Table 2, note that model with interaction term was $p > .05$ (Table S4)). Overall differences between the three hydrological classes were driven by significant contributions of eight species: *L. calcarifer*, *Mogurnda mogurnda*, *Neosilurus hyrtlilii*, *Leiopotherapon unicolor*, *Craterocephalus stercusmuscarum*, *Liza ordensis*, *Syncomistes butleri*, *Megalops cyprinoides* (Table 1). In the univariate GLM models, seven species were more abundant in Intermittent rivers (*M. australis*, *Melanotaenia nigrans*, *M. mogurnda*, *Glossogobius giurus*, *L. unicolor*, *Oxyeleotris selheimi*, *N. hyrtlilii*); two species (*Ambassis macleayi*, *Melanotaenia inornata*) were more abundant in Perennial Flashy rivers; and 13 species were more abundant and defined the assemblage of Perennial Stable rivers (*Craterocephalus stramineus*, *G. aprion*, *Hypseleotris compressa*, *L. calcarifer*, *L. ordensis*, *Megalops cyprinoides*, *Toxotes chatareus*, *Hephaestus fuliginosus*, *Syncomistes butleri*, *O. lineolata*, *Neosilurus ater*, *Neoarius leptaspis*, *Strongylura krefftii*) (Figure 4, Table 3).

Species abundances demonstrated mixed patterns among life history strategies and hydrological classes (Figure 4, Table 3). The majority of species in each life history strategy, using a hard classification approach, did not show any significant abundance differences between the three hydrological classes (i.e. they were ubiquitous). The prediction that opportunistic species would be more abundant in Intermittent rivers was only partially supported, with only 5 of 18 opportunistic strategists showing greater abundances in Intermittent rivers. Similarly, equilibrium strategists again only partially conformed to our prediction, with only 2 of 7 species showing greater abundance in Perennial Stable rivers. The prediction that periodic strategists would be generally more abundant in Perennial Flashy rivers was not supported. Many periodic and equilibrium

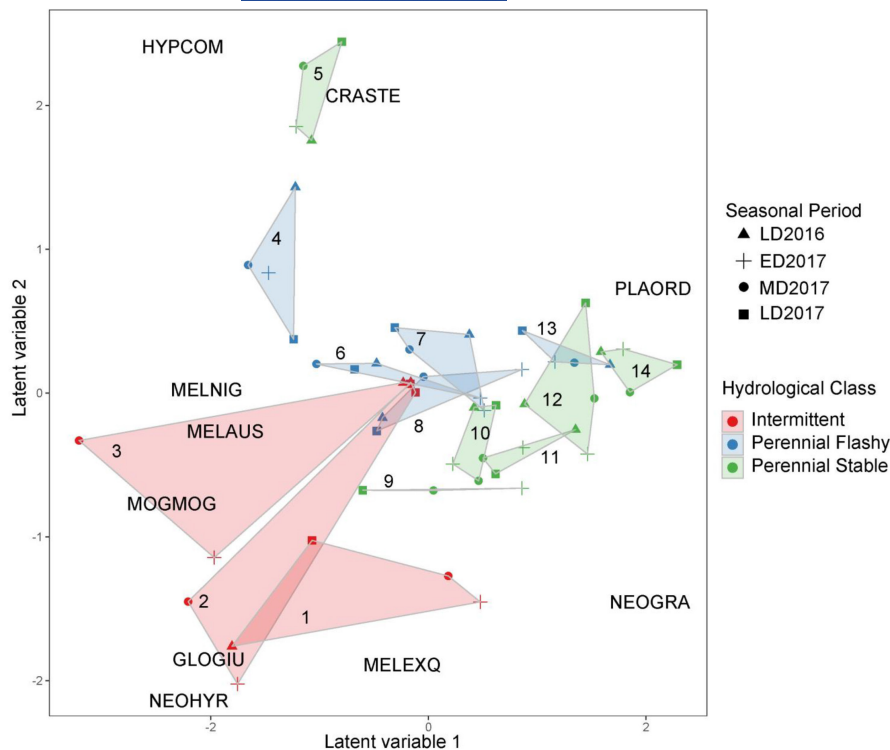


FIGURE 2 Model-based unconstrained ordination biplot based on the posterior median estimates for summed data for each factor combination. The 10 most influential species (i.e. those species with the strongest response to the latent variables identified in our analysis) are shown in black (species code key provided in Table 1). Sites are colour coded corresponding to hydrological class. Different symbols indicate the time period of sampling. Species code as in Table 1. Numbers inside or next to the polygons indicate site identity: 1—SHFR, 2—SHCR, 3—BSBC, 4—DRAR, 5—GPHR, 6—GCFR, 7—COAR, 8—BDFR, 9—MHMR, 10—GJKR, 11—AHMR, 12—OODR, 13—SRAR, 14—DMAR (See Table S1 for details).

classified species were found in higher abundances in perennial rivers (green and blue bars in Figure 4b,c).

These unexpected results can be partly explained by the relative affinity of each species to each life history strategy (soft classification). For example, periodic strategists with heavy partial weight on the periodic strategy (species on the left side, Figure 4b, and see Table 3) conform to the pattern of higher abundances in perennial systems, whereas the exceptions (i.e. periodic species with higher abundances in Intermittent rivers, namely *A. percooides* and *N. hyrtlili*), also have relatively high life history affinities to opportunistic strategies, despite being classified as periodic strategists (Table 3). However, species with stronger affinities to a single strategy endpoint (hard classification, weighting closer to 1) did not show consistent conformity with the hydrological predictions above. For example, *Scleropages jardinii* and *Neoarius graeffei* were both weighted very strongly towards equilibrium affinity, but demonstrated opposite patterns in abundance with *S. jardinii* highest abundances occurring in Perennial Flashy systems, and *N. graeffei* more abundant in Intermittent and Perennial Stable systems.

Hydrological classes of rivers contributed differentially to fish beta-diversity (Figure 5a). Intermittent sites, on average, had greater unique species composition, and thus contributed more to overall beta-diversity, compared to both Perennial Flashy (Welch's *t*-test: $t=1.66$, $df=11.39$, $p=.125$) and Perennial Stable sites ($t=1.61$, $df=12.20$, $p=.134$). However, varying contributions of sites within hydrologic classes meant differences among classes were not statistically significant ($p > .05$). No difference was evident when comparing the contribution of Perennial Flashy and Perennial Stable sites ($t=0.05$, $df=40.84$, $p=.964$). For all hydrological classes, species replacement (turnover) contributed more to total beta-diversity than

differences in species richness (nestedness). These differences were much more pronounced for Perennial flashy ($T=0.93$, $N=0.07$) and Perennial Stable ($T=0.95$, $N=0.05$), compared to Intermittent sites ($T=0.82$, $N=0.18$).

Contributions to overall beta-diversity showed some seasonality that varied according to hydrological class (Figure 5b). For Intermittent (especially) and Perennial Stable sites, contributions to beta-diversity increased from early- to mid-dry seasons and then decreased in the late-dry season. These seasonal trends, however, were variable, and were not evident for Perennial Flashy sites.

Species with different life history strategies showed marked differences in their contribution to overall beta-diversity (Figure 5c). Contributions of opportunistic ($t=2.67$, $df=20.35$, $p=.014$) and periodic strategists ($t=3.17$, $df=14.25$, $p=.007$) were significantly higher than equilibrium strategists. No differences in contributions of opportunistic and periodic strategies were evident ($t=-0.12$, $df=29.97$, $p=.983$). Similarly, contributions of life history strategies to overall beta-diversity did not vary according to hydrological class (results not shown).

4 | DISCUSSION

A river's flow regime is widely recognised to shape its fish populations and species' assemblages via a range of processes (Bunn & Arthington, 2002; Humphries et al., 2020; Poff et al., 1997; Tonkin et al., 2018). Flow characteristics, such as perenniality, and the duration, intensity and frequency of key flow events influence the physical habitat template, strength of biotic interactions, and degree of connectivity and dispersal (Naiman et al., 2008);

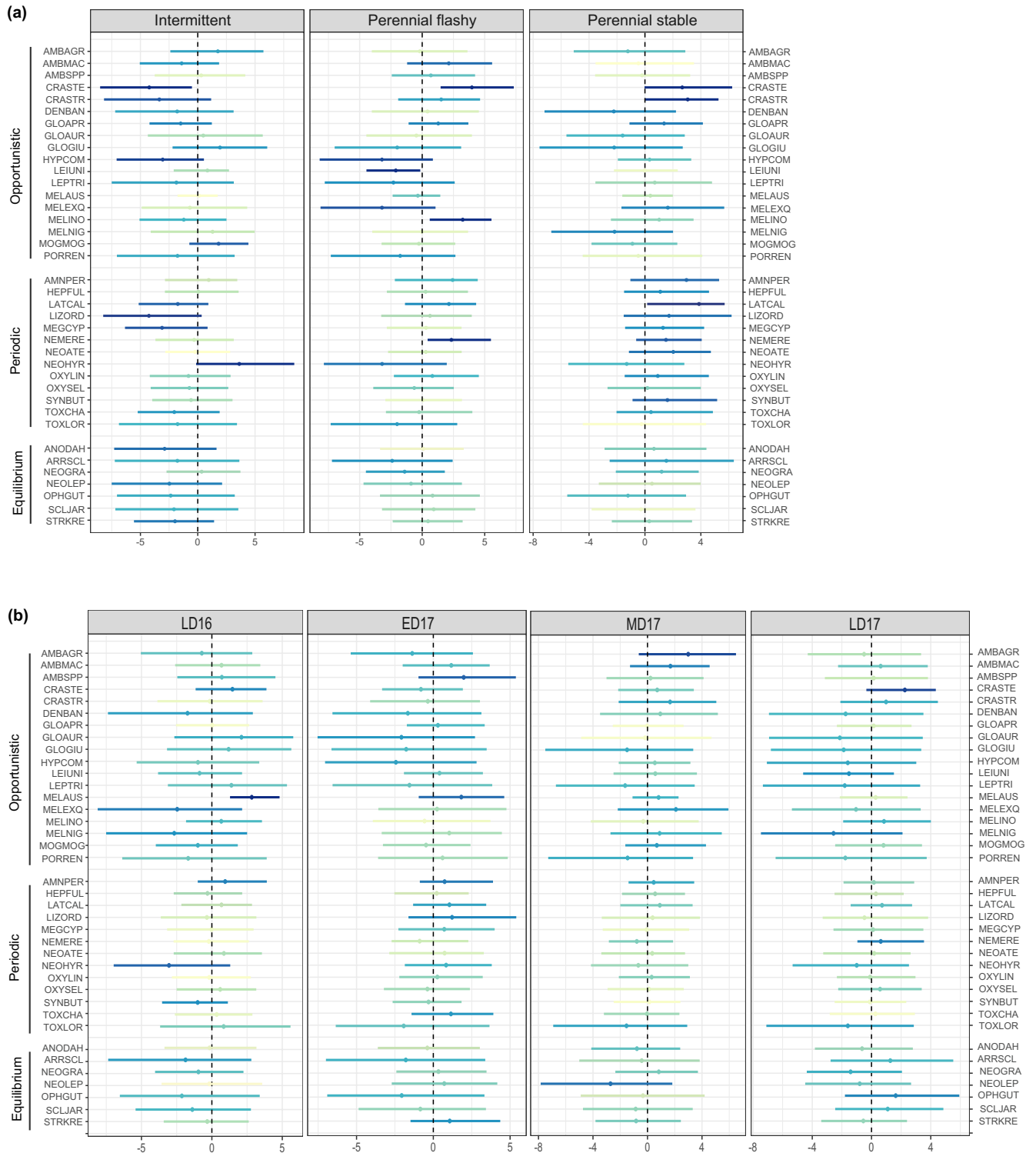


FIGURE 3 Estimated coefficients of covariates hydrological class (a) and seasonal period (b) for riverine fish species in Northern Australia. Points represent the posterior median coefficients, with horizontal lines illustrating the 95% highest posterior density (HPD) intervals. A vertical dotted line denotes the zero value, serving as a reference for effect sizes. HPD intervals are colour-coded based on statistical significance and the effect size: Light green indicates least significant intervals with estimates close to zero and large confidence intervals; a gradient towards dark blue symbolises increasing significance, characterised by larger effect sizes and tighter confidence intervals. Intervals that include zero are coloured towards the lighter end of the spectrum, while those with large effect sizes and HPD diminishing overlap with zero are towards the darker end. This colour coding provides a visual guide to the relative significance and impact of each covariate on riverine fish species in the region. Species code key is provided in [Table 1](#).

TABLE 2 Summary statistics of the overall multivariate generalised linear model for hydrological class and time period effects on fish composition.

	Residual DF	DF	Deviance	p-value	Contribution of significant taxa
Intercept	54				
Hydrological class	52	2	411	0.001	<i>Lates calcarifer</i> (13.9%, $p < .001$) <i>Mogurnda mogurnda</i> (6.3%, $p < .01$) <i>Neosilurus hyrtlili</i> (5.8%, $p < .01$) <i>Leiopotherapon unicolor</i> (5.6%, $p < .01$) <i>Craterocephalus stercusmuscarum</i> (5.0%, $p < .01$) <i>Liza ordensis</i> (4.8%, $p < .05$) <i>Syncomistes butleri</i> (4.1%, $p < .05$) <i>Megalops cyprinoides</i> (4.1%, $p < .05$)
Seasonal period	49	3	153	0.428	NA

Note: Percent contribution of univariate model deviance of significant taxa to the parameter deviance in the multivariate model and the associated p-value shown. See Table S4 for full model results and model with interaction term included.

ultimately leading to the selection of species with life history strategies that are adapted to the prevailing environmental conditions (Bunn & Arthington, 2002; Mims & Olden, 2012; Townsend & Hildrew, 1994). In rivers of Australia's wet-dry tropics, our study found distinct and predictable, fish assemblages across hydrological river types: Intermittent, Perennial Stable and Perennial Flashy flow regimes. This distinction in fish assemblages among hydrological types emerged despite a common species pool across the region, with nearly half of all species (22 of 45 species) being present in over half the sites. Contradicting our predictions based on previous studies, species abundances within each hydrological river type were not well predicted by their affinity to a specific life history strategy, especially when applying an endpoint classification. Hydrological classes also contributed to differences in species diversity with species richness greatest in Perennial Stable rivers, whereas beta-diversity was greatest in Intermittent rivers, where a higher number of unique species were present.

Tropical freshwater fish assemblages are structured by both spatial features (e.g. floodplain-wetland-channel macrohabitats or relative position within the catchment) and strong temporally dynamic features, such as water level variation (Beesley & Prince, 2010; Duarte et al., 2022; Warfe et al., 2011). The majority of studies of fish assemblage structure in the Australian wet-dry tropics describe dry season spatial or structural-habitat affinity, whereas the role of hydrological or seasonal variation has received little consideration (King et al., 2013; Pusey et al., 2020). For example, Keller et al. (2019) used an extensive dataset of fish-habitat associations from the Daly River, and identified four distinct main channel habitat guilds, classifying them largely based on depth, velocity and structural complexity. In the same catchment, Pusey et al. (2020), sampled dry season fish assemblages throughout a wide variety of habitat types, and found fish assemblage composition was mostly related to longitudinal (upstream/downstream) and lateral (river/floodplain) position; however, flow intermittency was also a strong driver of assemblage composition, species richness and body-size distributions. We found striking variability in the role of spatial and temporal hydrologic conditions in explaining fish assemblage composition across rivers in

northern Australia. Hydrological regime at each site was a significant driver of fish assemblages, but was related to changes in the abundance of only eight species. Each hydrological classification type had a distinct assemblage, with 13 species recorded in higher relative abundances in Perennial Stable rivers, seven species more abundant in Intermittent rivers and two species more abundant in Perennial Flashy rivers. While not indicating a preference for a hydrological classification type, these results may help to broadly describe a species' tendency towards certain hydrological conditions across larger spatial scales (Mims & Olden, 2012; Olden & Kennard, 2010; Sternberg & Kennard, 2013).

Previous studies have shown that seasonal variation in water levels may cause strong temporal changes in tropical freshwater fish assemblages (Duarte et al., 2022; Lowe-McConnell, 1987). The annual monsoonal rainfall pattern characterises the wet-dry hydrology cycle of northern Australian rivers (Warfe et al., 2011). The wet season fosters ecosystem productivity, biotic dispersal, connectivity and reproduction, whereas the dry season imposes high resource constraints on many species (King et al., 2015; Tyler et al., 2022; Warfe et al., 2011). Surprisingly, fish assemblages in our study did not vary significantly among hydrological seasons. This result may simply be constrained by our inability to conduct sampling at the peak wet season (water level) conditions, due to site access issues. However, alternatively, analysing various hydrological types together may mask the high seasonal differences evident in the extreme case (Intermittent sites). Assemblage composition and beta-diversity were far more variable across season or sampling time in Intermittent sites, compared to the perennially flowing sites. Intermittent sites exhibited the greatest distance in fish assemblage ordination space among different sample seasons (Figure 2), likely reflecting the most pronounced variability among hydrological conditions. Perennial Flashy and Perennial Stable sites showed relatively smaller distances in ordination space among their seasonal samples, mirroring the more stable hydrological conditions across seasons, and suggesting that fish assemblages in perennial rivers are more influenced by sampling location than by season. This observation underlines the complex interplay between hydrological conditions

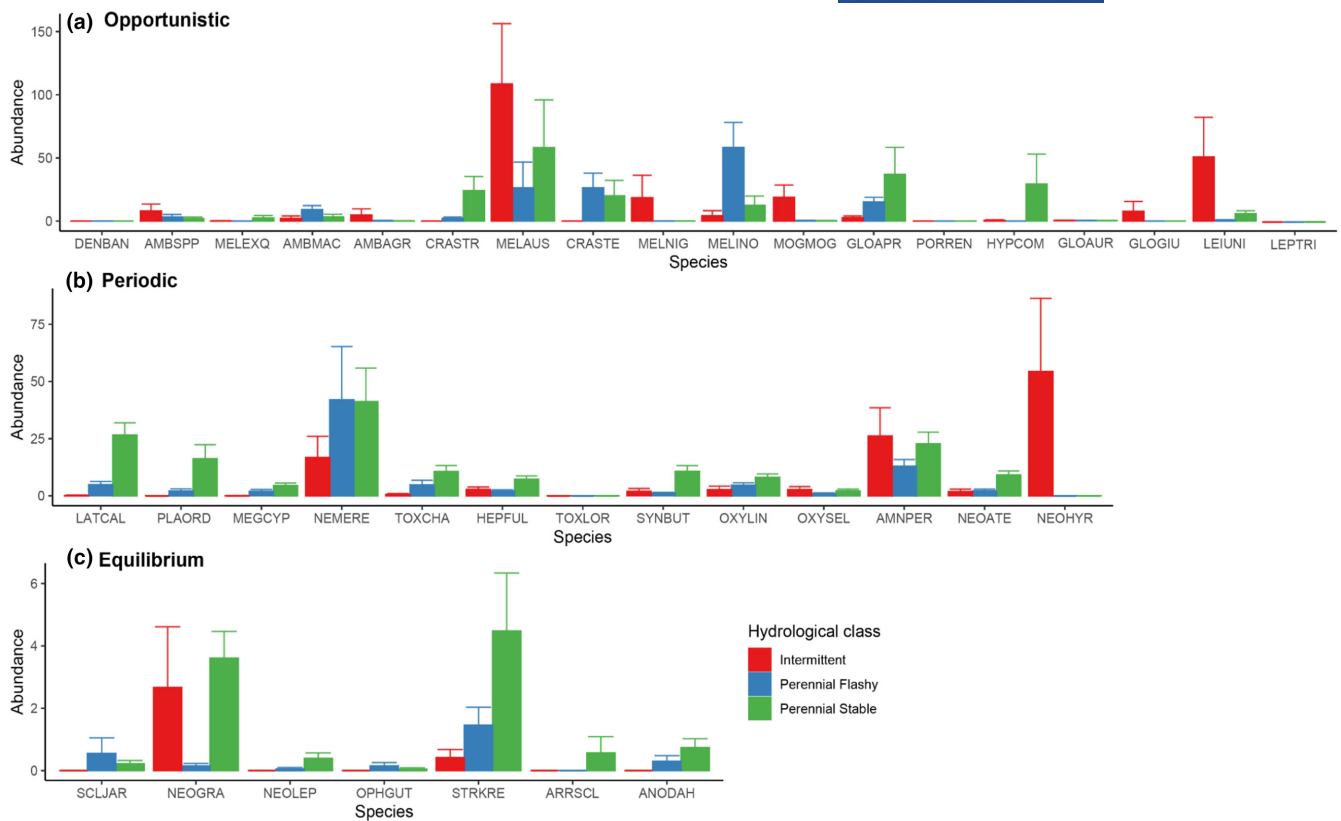


FIGURE 4 Average abundance per shot in sites grouped by river hydrological class. Each panel includes species grouped by their life history strategy (hard classification) weight ((a) Opportunistic, (b) Periodic, (c) Equilibrium) and ordered from left to right according to the weight (specificity, soft classification) of that life history strategy. Species code key is provided in [Table 1](#).

and seasonal variation in shaping fish assemblage structure within these distinct river classes.

Hydrology is a significant factor in determining patterns of freshwater fish beta-diversity (Larned et al., 2010; Leigh & Sheldon, 2009; Thomaz et al., 2007). Reflecting patterns seen previously by Pusey et al. (2020), this study found that perennial sites had a higher number of species present than Intermittent sites. Furthermore, for all hydrological classes, species replacement (turnover) contributed more to total beta-diversity than differences in species richness (nestedness), with this trend more pronounced in Perennial Flashy and Perennial Stable sites. However, despite nearly half of all species being present in over half of the sites, there were pronounced differences in beta-diversity between intermittent and perennial sites. Intermittent streams, in particular, exhibited a more unique species composition, thus contributing to greater beta-diversity compared to perennial sites. Similar findings have also been reported in dryland rivers of the Lower Colorado River Basin, where flow intermittency resulted in greater contributions to fish beta diversity (Rogosch & Olden, 2019).

Intermittent sites exhibit periodic changes in hydrologic connectivity, expanding habitat availability and facilitating dispersal within riverine metacommunities when flowing (Datry et al., 2016, 2022). Seasonal variations in beta-diversity were found to be complex in our study region, particularly in Intermittent sites, where contributions were greatest in the early and mid-dry season periods before

declining by late dry season. This was not observed in Perennial Flashy sites, possibly indicating different underlying mechanisms or resilience to seasonal changes. Our results, together with those of Rogosch and Olden (2019), suggest that the influence of within-year hydrologic conditions are important determinants of spatio-temporal variations in the composition of local fish diversity. Differences were also noted in the contributions to overall beta-diversity among different life history strategies, primarily from opportunistic and periodic compared to equilibrium strategists, although these contributions did not vary according to hydrological class. Overall, our results point to the uniqueness of assemblages in Intermittent sites, driven mostly by strong fluctuations of hydrology patterns. Potential future changes to the hydrology of northern Australian rivers due to water extraction, river regulation or a changing climate, is likely to result in significant implications for fishes in these systems, and further research is required to guide conservation and management (King et al., 2015).

The life history continuum model (Winemiller, 2005; Winemiller & Rose, 1992), which predicts relationships between flow regime variations and life history strategies, has been well supported by many studies (e.g. Mims & Olden, 2012; Olden & Kennard, 2010; Sternberg & Kennard, 2013; Tedesco et al., 2008). Based on these studies, we predicted which life history strategies would be more likely to be dominant in sites across our hydrological gradient. However, although our study identified distinct fish assemblages

TABLE 3 Pairwise post-hoc tests of river type effects on each species observed. Species names are grouped by the life history strategy that they are closely associated by Euclidean distance in the life-history space (hard classification).

Species code	Species	Life history strategy (soft classification affinity)						Deviance (P)			Direction of post-hoc effects
		Life history strategy (soft classification affinity)						Deviance (P)			
		Opp	Per	Equ	I vs. PF	I vs. PS	PF vs. PS				
DENBAN	<i>Denariusus bandata</i>	1.00	0.19	0.05	0.94 (0.42)	0.00 (1.00)	1.53 (0.42)	I = PS = PF			
AMBSPP	<i>Ambassis</i> sp.	1.00	0.17	0.00	1.87 (0.31)	4.39 (0.14)	0.82 (0.40)	I = PS = PF			
MELEXQ	<i>Melanotaenia exilis</i>	0.98	0.15	0.08	3.92 (0.16)	1.85 (0.37)	5.03 (0.13)	I = PF = PS			
AMBMAC	<i>Ambassis macleayi</i>	0.99	0.21	0.01	12.83 (<0.01)	0.424 (0.53)	9.18 (<0.05)	PF > PS = I			
AMBAGR	<i>Ambassis agrammus</i>	0.97	0.22	0.00	2.79 (0.34)	4.26 (0.22)	1.22 (0.35)	I = PS = PF			
CRASTR	<i>Craterocephalus stramineus</i>	0.96	0.13	0.16	8.63 (<0.001)	41.82 (<0.001)	19.10 (<0.001)	PS > PF > I			
MELAUS	<i>Melanotaenia australis</i>	0.93	0.17	0.06	22.08 (<0.001)	6.46 (<0.05)	4.13 (0.07)	I > PF = PS			
CRASTE	<i>Craterocephalus stercusmuscarum</i>	0.93	0.17	0.16	74.66 (<0.001)	32.35 (<0.001)	0.64 (0.53)	PF = PS > I			
MELNIG	<i>Melanotaenia nigrans</i>	0.90	0.21	0.15	24.34 (<0.001)	26.55 (<0.001)	0.02 (0.86)	I > PF = PS			
MELINO	<i>Melanotaenia inornata</i>	0.88	0.22	0.18	18.42 (<0.001)	1.29 (0.20)	22.01 (<0.001)	PF > PS = I			
MOGMOG	<i>Mogurnda mogurnda</i>	0.79	0.22	0.37	93.90 (<0.001)	109.24 (<0.001)	0.99 (0.33)	I > PF = PS			
GLOAPR	<i>Glossamia aprion</i>	0.74	0.21	0.44	41.03 (<0.01)	47.51 (<0.001)	17.57 (<0.01)	PS > PF > I			
PORREN	<i>Porocheilus rendahli</i>	0.71	0.34	0.39	0.00 (1.0)	1.68 (0.28)	2.51 (0.26)	I = PF = PS			
HYPYCOM	<i>Hypseleotris compressa</i>	0.70	0.37	0.20	9.95 (<0.01)	9.11 (<0.01)	20.581 (<0.001)	PS > I > PF			
GLOAUR	<i>Glossogobius aureus</i>	0.69	0.35	0.26	0.01 (0.95)	1.30 (0.73)	0.83 (0.73)	I = PS = PF			
GLOGIU	<i>Glossogobius giurris</i>	0.68	0.35	0.26	20.28 (<0.001)	22.10 (<0.001)	0.00 (1.0)	I > PS = PF			
LEIUNI	<i>Leiopotherapon unicolor</i>	0.62	0.45	0.16	108.28 (<0.001)	58.03 (<0.001)	28.77 (<0.001)	I > PS > PF			
LEPTRI	<i>Leptachirus triramus</i>	0.61	0.46	0.15	0.00 (1.0)	1.68 (0.32)	2.51 (0.25)	I = PF = PS			

TABLE 3 (Continued)

Species code	Life history strategy		Life history strategy (soft affiliation)				Deviance (P)		Direction of post-hoc effects
	Species	Periodic	Opp	Per	Equ	I vs. PS		PF vs. PS	
						I vs. PF	I vs. PS		
LATCAL	<i>Lates calcarifer</i>		0.00	1.00	0.01	45.99 (<0.001)	170.15 (<0.001)	90.84 (<0.001)	PS > PF > I
LIZORD	<i>Liza ordensis</i>		0.25	0.82	0.08	18.73 (<0.001)	71.01 (<0.001)	36.13 (<0.001)	PS > PF > I
MEGCYP	<i>Megalops cyprinoides</i>		0.29	0.80	0.11	13.54 (<0.01)	24.97 (<0.001)	4.26 (<0.05)	PS > PF > I
NEMERE	<i>Nematalosa erebi</i>		0.47	0.66	0.06	3.83 (0.47)	6.15 (0.35)	0.01 (0.97)	I = PF = PS
TOXCHA	<i>Toxotes chatareus</i>		0.51	0.64	0.13	18.25 (<0.001)	63.66 (<0.001)	14.28 (<0.001)	PS > PF > I
HEPFUL	<i>Hephaestus fuliginosus</i>		0.32	0.63	0.48	0.95 (0.35)	14.55 (<0.001)	33.92 (<0.001)	PS > I = PF
TOXLOR	<i>Toxotes lorentzi</i>		0.53	0.63	0.11	0.00 (1.0)	0.83 (0.62)	1.25 (0.62)	I = PF = PS
SYNBUT	<i>Syncomistes butleri</i>		0.47	0.58	0.47	1.38 (0.28)	21.59 (<0.001)	48.86 (<0.001)	PS > PF = I
OXYLIN	<i>Oxyeleotris lineolata</i>		0.30	0.55	0.62	4.40 (<0.05)	20.45 (<0.01)	10.61 (<0.01)	PS > PF > I
OXYSEL	<i>Oxyeleotris selheimi</i>		0.30	0.55	0.62	7.44 (<0.05)	0.57 (0.45)	8.47 (<0.01)	I = PS > PF
AMNPER	<i>Amniataba percoides</i>		0.57	0.52	0.18	6.75 (0.07)	0.33 (0.64)	8.96 (<0.05)	I = PF > PS
NEOATE	<i>Neosilurus ater</i>		0.45	0.52	0.59	0.16 (0.68)	35.10 (<0.001)	42.34 (<0.001)	PS > PF = I
NEOHYR	<i>Neosilurus hyrtlil</i>		0.58	0.46	0.49	90.49 (<0.001)	92.42 (<0.001)	1.25 (0.48)	I > PF = PS
Equilibrium									
SCLJAR	<i>Scleropages jardinii</i>		0.15	0.09	1.00	1.88 (0.54)	4.19 (0.17)	0.79 (0.55)	I = PF = PS
NEOGRA	<i>Neoarius graeffei</i>		0.19	0.00	1.00	8.96 (<0.05)	0.04 (0.87)	34.99 (<0.001)	PS = I > PF
NEOLEP	<i>Neoarius leptaspis</i>		0.15	0.00	0.86	0.94 (0.32)	6.82 (<0.05)	5.55 (<0.05)	PS > I = PF
OPHGUT	<i>Ophistermon gutturale</i>		0.46	0.25	0.71	1.98 (0.55)	0.84 (0.74)	0.83 (0.74)	I = PF = PS
STRKRE	<i>Strongylura krefftii</i>		0.43	0.44	0.71	6.54 (<0.05)	20.24 (<0.001)	11.30 (<0.01)	PS > PF > I
ARRSCL	<i>Arramphus sclerolepis</i>		0.47	0.45	0.59	0.00 (1.0)	2.50 (0.17)	3.77 (0.15)	I = PF = PS
ANODAH	<i>Anodontiglanis dahli</i>		0.41	0.53	0.55	4.75 (0.06)	10.32 (<0.01)	2.52 (0.11)	I = PF < PS

Note: Also shown is the species' relative affinity towards each life-history strategy (soft classification) and the pairwise comparisons across hydrological classes (Deviance (P) and direction of effect). Life history strategy: Opp, opportunistic; Per, periodic; Equ, equilibrium. Hydrology Class: I, intermittent; PF, Perennial Flashy, PS = Perennial Stable. Hydrology classes where the species are significantly more abundant are in bold.

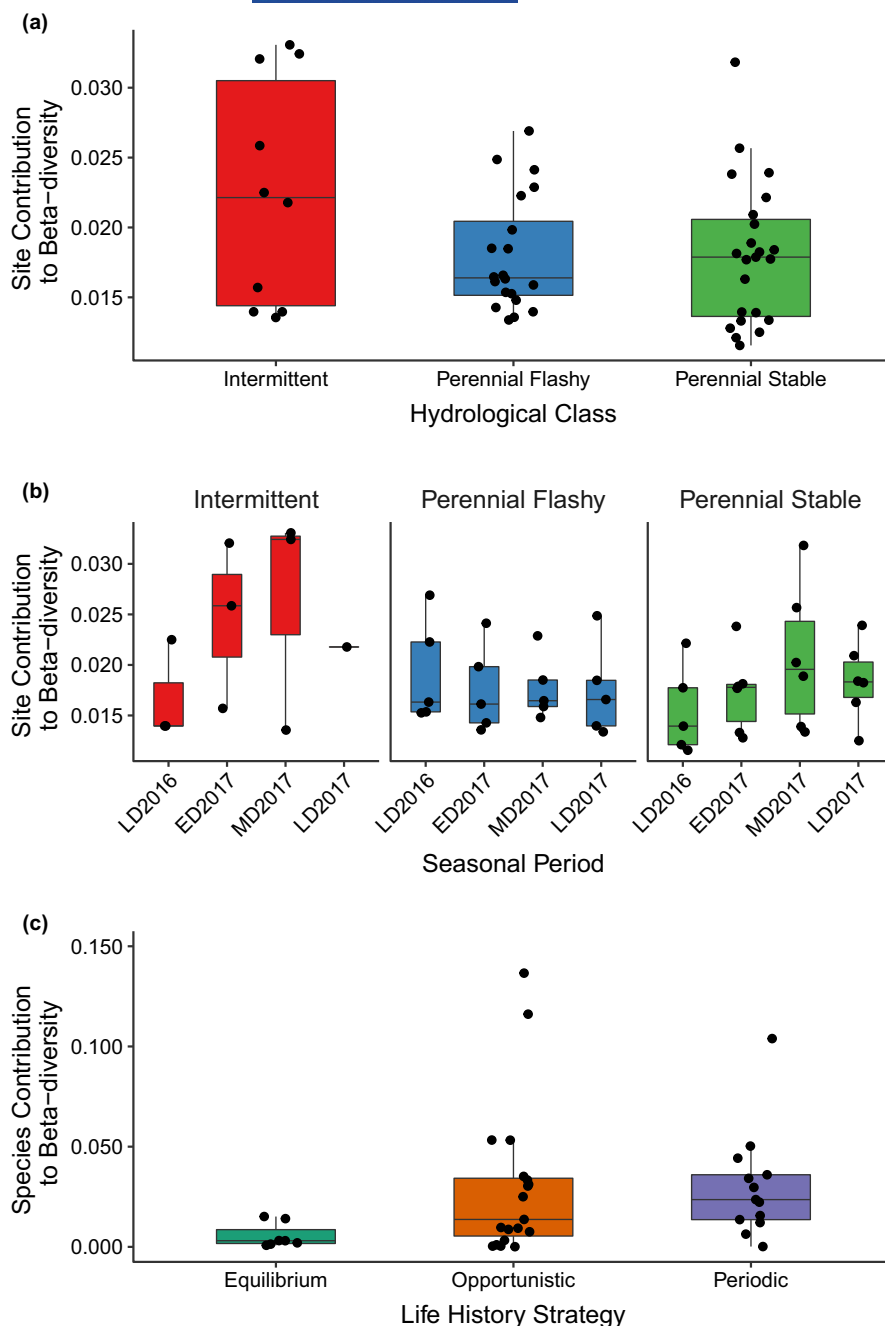


FIGURE 5 Box plots showing patterns of local site (LCBD) and species contributions (SCBD) to beta diversity among (a) hydrological classes, (b) time period and (c) species life-history strategies across all study sites and seasonal periods. Individual sites and samples are indicated with black circles. Vertical lines, boxes and horizontal lines represent respectively, 10th and 90th percentiles, interquartile range and median.

and diversity patterns across hydrological classes, species abundance was not well predicted by an individual species' affinity to a specific life history strategy. For example, our prediction that opportunistic strategists would be more abundant in Intermittent sites was not well supported, with only five of 18 opportunistic strategists showing greater abundances. Similarly, the prediction concerning equilibrium strategists, was not well supported, with only two out of seven equilibrium species displaying greater abundance in Perennial Stable rivers; and the prediction that periodic strategists would be more abundant in Perennial Flashy rivers was also not supported. The more nuanced 'soft' classification approach, which considers a species' relative affinity to all three life history endpoints, helped to explain some of these discrepancies. However, life history classification was not a good predictor of assemblage structure across

the hydrological gradient, irrespective of the approach used. Our findings emphasise the need for caution when considering transferability of predicting species life history affinities to hydrological characteristics and flow-ecology relationships, especially across unsampled rivers (see Chen & Olden, 2018; Kennard et al., 2007).

Rivers of the wet-dry tropics of northern Australia represent some of the most biodiverse and hydrologically intact regions in the world (Pusey, 2011; Woinarski et al., 2007). However, with both the increased utilisation of surface and groundwater resources and the effects of climate change, the region's rivers may be expected to undergo substantial hydrological changes in future years, with potentially negative consequences for the regions' fish fauna (Chan et al., 2012; King et al., 2015; Morrongiello et al., 2011). The distinct fish assemblages evident in different hydrological classes in our

study, may provide some opportunity for cautious prediction about the potential fish assemblage changes likely to occur with future hydrological changes and the potential transferability of these findings to unsampled rivers in the region. However, further research across a wider hydrological gradient, longer time period, and seasonal extremes, would enable stronger predictive capability (see Chen & Olden, 2018). Identifying the factors that affect variation in fish assemblage composition through time will inform effective management and conservation (Angeler, 2013). As climate change and increasing water withdrawals cause perennial sites to become increasingly intermittent, and intermittent rivers to become more ephemeral, the loss of habitat and connectivity is likely to have significant, potentially non-linear, impacts on species diversity and meta-community stability (Thompson et al., 2017; Tonkin et al., 2017). Our findings provide further support for the importance of maintaining regional flow-habitat heterogeneity and the connectivity between hydrological river types, and their essential role for conserving tropical fish species diversity into an uncertain hydrological future (López-Delgado et al., 2019; Pusey et al., 2020).

AUTHOR CONTRIBUTIONS

Conceptualisation and method development: AK, JO, OL, MK, DC, MD, TS, DW. Conducting field research: AK, OL, MK, BA, DW. Data analysis and interpretation: AK, JO, OL, MK. Manuscript preparation and writing: all authors.

ACKNOWLEDGEMENTS

The research team acknowledges the Traditional Owners across our study region and recognise their continuing and unique connection to land and water. We thank K. Keller, D. Loewensteiner, Q. Allsop, W. Baldwin, C. Errity, and N. Crofts for assistance with field sampling, and A. Kirk and D. Loewensteiner for assistance with fish measurement in the laboratory. We also thank two anonymous reviewers for their helpful and insightful comments. Financial support was provided by the Australian Research Council (LP150100388) and the Department of Primary Industry and Fisheries, Northern Territory Government. This research was conducted under the approval of the Charles Darwin University Animal Ethics Committee, permit A16032. The authors declare no conflict of interest with this research. Open access publishing facilitated by Charles Darwin University, as part of the Wiley - Charles Darwin University agreement via the Council of Australian University Librarians.

DATA AVAILABILITY STATEMENT

Data are available from Dryad: <https://doi.org/10.5061/dryad.crjfdn36n>.

ORCID

Alison J. King  <https://orcid.org/0000-0002-0104-2611>

Julian D. Olden  <https://orcid.org/0000-0003-2143-1187>

Osmar J. Luiz  <https://orcid.org/0000-0002-6995-6524>

Mark J. Kennard  <https://orcid.org/0000-0003-4383-4999>

David A. Crook  <https://orcid.org/0000-0003-4035-050X>

Dion Wedd  <https://orcid.org/0000-0003-3170-3078>

REFERENCES

- Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters*, 14, 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>
- Angeler, D. G. (2013). Revealing a conservation challenge through partitioned long-term beta diversity: Increasing turnover and decreasing nestedness of boreal lake metacommunities. *Diversity and Distributions*, 19(7), 772–781. <https://doi.org/10.1111/ddi.12029>
- Baselga, A., Orme, D., Villeger, S., de Bortoli, J., & Leprieux, F. (2021). betapart: Partitioning beta diversity into turnover and nestedness components. [ct.org/package=betapart](https://cran.r-project.org/package=betapart)
- Beesley, L. S., & Prince, J. (2010). Fish community structure in an intermittent river: The importance of environmental stability, landscape factors and within-pool habitat descriptors. *Marine and Freshwater Research*, 61, 605–614. <https://doi.org/10.1111/eff.12325>
- Bray, D. J., & Gomon, M. F. (2023). *Fishes of Australia*. Museums Victoria and OzFishNet. <http://fishesofaustralia.net.au/>
- Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30(4), 492–507. <https://doi.org/10.1007/s00267-002-2737-0>
- Chan, T. U., Hart, B. T., Kennard, M. J., Pusey, B. J., Shenton, W., Douglas, M. M., Valentine, E., & Patel, S. (2012). Bayesian network models for environmental flow decision making in the Daly River, Northern Territory. *Australia. River Research and Applications*, 28(3), 283–301.
- Chen, W., & Olden, J. D. (2018). Evaluating transferability of flow–ecology relationships across space, time and taxonomy. *Freshwater Biology*, 63, 817–830. <https://doi.org/10.1111/fwb.13041>
- Craven, S., Peterson, J., Freeman, M., Kwak, T., & Irwin, E. (2010). Modelling the relations between flow regime components, species traits, and spawning success of fishes in warmwater streams. *Environmental Management*, 46(2), 181–194. <https://doi.org/10.1007/s00267-010-9511-5>
- Datry, T., Fritz, K., & Leigh, C. (2016). Challenges, developments and perspectives in intermittent river ecology. *Freshwater Biology*, 61(8), 1171–1180. <https://doi.org/10.1111/fwb.12789>
- Datry, T., Truchy, A., Olden, J. D., Busch, M. H., Stubbington, R., Dodds, W. K., Zipper, S., Yu, S., Messenger, M. L., Tonkin, J. D., Kaiser, K. E., Hammond, J. C., Moody, E. K., Burrows, R. M., Sarremejane, R., DelVecchia, A. G., Fork, M. L., Little, C. J., Walker, R. H., ... Allen, D. (2022). Causes, responses, and implications of anthropogenic versus natural flow intermittence in river networks. *Bioscience*, 73(1), 9–22. <https://doi.org/10.1093/biosci/biac098>
- Dray, S., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., & Wagner, H. H. (2017). *adespatial: Multivariate multiscale spatial analysis*. <https://cran.r-project.org/package=adespatial>
- Duarte, C., Antão, L. H., Magurran, A. E., & de Deus, C. P. (2022). Shifts in fish community composition and structure linked to seasonality in a tropical river. *Freshwater Biology*, 67(10), 1789–1800. <https://doi.org/10.1111/fwb.13975>
- Gido, K. B., Propst, D. L., Olden, J. D., & Bestgen, K. R. (2013). Multidecadal responses of native and introduced fishes to natural and altered flow regimes in the American southwest. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(4), 554–564. <https://doi.org/10.1139/cjfas-2012-0441>
- Hui, F., Taskinen, S., Pledger, S., Foster, S., & Warton, D. (2015). Model-based approaches to unconstrained ordination. *Methods in Ecology and Evolution*, 6, 399–411. <https://doi.org/10.1111/2041-210X.12236>

- Hui, F. K. C. (2016). Boral – Bayesian ordination and regression analysis of multivariate abundance data in *r*. *Methods in Ecology and Evolution*, 7, 744–750. <https://doi.org/10.1111/2041-210X.12514>
- Humphries, P., King, A. J., McCasker, N., Kopf, R. K., Stoffels, R., Zampatti, B. P., & Price, A. E. (2020). Riverscape recruitment: A conceptual synthesis of drivers of fish recruitment in rivers. *Canadian Journal of Fisheries and Aquatic Sciences*, 77(2), 213–225. <https://doi.org/10.1139/cjfas-2018-0138>
- Keller, K., Allsop, Q., Brim Box, J., Buckle, D., Crook, D. A., Douglas, M. M., Jackson, S., Kennard, M. J., Luiz, O. J., Pusey, B. J., Townsend, S. A., & King, A. J. (2019). Dry season habitat use of fishes in an Australian tropical river. *Scientific Reports*, 9(1), 5677. <https://doi.org/10.1038/s41598-019-41287-x>
- Kennard, M. J., Olden, J. D., Arthington, A. H., Pusey, B. J., & Poff, N. L. (2007). Multiscale effects of flow regime and habitat and their interaction on fish assemblage structure in eastern Australia. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 1346–1359. <https://doi.org/10.1139/f07-108>
- Kennard, M. J., Pusey, B. J., Olden, J. D., Mackay, S. J., Stein, J. L., & Marsh, N. (2010). Classification of natural flow regimes in Australia to support environmental flow management. *Freshwater Biology*, 55, 171–193. <https://doi.org/10.1111/j.1365-2427.2009.02307.x>
- King, A. J., Humphries, P., & McCasker, N. (2013). Reproduction and early life history. In P. Humphries & K. Walker (Eds.), *Ecology of Australian freshwater fish* (pp. 159–193). CSIRO.
- King, A. J., Townsend, S. A., Douglas, M. M., & Kennard, M. (2015). Implications of water extraction on the low-flow hydrology and ecology of tropical savannah rivers: An appraisal for northern Australia. *Freshwater Science*, 34(2), 741–758. <https://doi.org/10.1086/681302>
- Larned, S. T., Datry, T., Arscott, D. B., & Tockner, K. (2010). Emerging concepts in temporary-river ecology. *Freshwater Biology*, 55, 717–738. <https://doi.org/10.1111/j.1365-2427.2009.02322.x>
- Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, 23(11), 1324–1334. <https://doi.org/10.1111/geb.12207>
- Legendre, P., & De Cáceres, M. (2013). Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters*, 16(8), 951–963. <https://doi.org/10.1111/ele.12141>
- Leigh, C., & Sheldon, F. (2009). Hydrological connectivity drives patterns of macroinvertebrate biodiversity in floodplain rivers of the Australian wet/dry tropics. *Freshwater Biology*, 54(3), 549–571. <https://doi.org/10.1111/j.1365-2427.2008.02130.x>
- López-Delgado, E. O., Winemiller, K. O., & Villa-Navarro, F. A. (2019). Do metacommunity theories explain spatial variation in fish assemblage structure in a pristine tropical river? *Freshwater Biology*, 64(2), 367–379. <https://doi.org/10.1111/fwb.13229>
- Lowe-McConnell, R. H. (1987). *Ecological studies in tropical fish communities*. Cambridge University Press.
- Luiz, O. J., Olden, J. D., Kennard, M. J., Crook, D. A., Douglas, M. M., Saunders, T. M., Wedd, D., Adair, B., & King, A. J. (2022). Substantial intraspecific trait variation across a hydrological gradient in northern Australian fishes. *Ecosphere*, 13(7), e4169. <https://doi.org/10.1002/ecs2.4169>
- Lytle, D. A., & Poff, L. N. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, 19(2), 94–100. <https://doi.org/10.1016/j.tree.2003.10.002>
- McManamay, R. A., & Frimpong, E. A. (2015). Hydrologic filtering of fish life history strategies across the United States: Implications for stream flow alteration. *Ecological Applications*, 25, 243–263. <https://doi.org/10.1890/14-0247.1>
- Milligan, G. W., & Cooper, M. C. (1985). An examination of procedures for determining the number of clusters in a data set. *Psychometrika*, 50(2), 159–179. <https://doi.org/10.1007/BF02294245>
- Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology*, 93(1), 35–45. <https://doi.org/10.1890/11-0370.1>
- Mims, M. C., & Olden, J. D. (2013). Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshwater Biology*, 58, 50–62. <https://doi.org/10.1111/fwb.12037>
- Morrongiello, J. R., Beatty, S. J., Bennett, J. C., Crook, D. A., Ikedife, D. N. E. N., Kennard, M. J., Kerezy, A., Lintermans, M., McNeil, D. G., Pusey, B. J., & Rayner, T. (2011). Climate change and its implications for Australia's freshwater fish. *Marine and Freshwater Research*, 62, 1082–1098. <https://doi.org/10.1071/MF10308>
- Naiman, R. J., Latterell, J. J., Pettit, N. E., & Olden, J. D. (2008). Flow variability and the biophysical vitality of river systems. *Comptes Rendus Geoscience*, 340, 629–643. <https://doi.org/10.1016/j.crte.2008.01.002>
- Olden, J. D., & Kennard, M. (2010). Intercontinental comparison of fish life history strategies along a gradient of hydrologic variability. *American Fisheries Society Symposium*, 73, 83–107.
- Olden, J. D., & Poff, N. L. (2003). Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications*, 19, 101–121. <https://doi.org/10.1002/rra.700>
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., Sparks, R. E., & Stromberg, J. C. (1997). The natural flow regime: A paradigm for river conservation and restoration. *Bioscience*, 47(11), 769–784. <https://doi.org/10.2307/1313099>
- Pusey, B. J. (2011). *Aquatic biodiversity in northern Australia: Patterns, threats and future*. Charles Darwin University Press.
- Pusey, B. J., Burrows, D. W., Kennard, M. J., Perna, C. N., Unmack, P. J., Allsop, Q., & Hammer, M. P. (2017). Freshwater fishes of northern Australia. *Zootaxa*, 4253(1), 1–104. <https://doi.org/10.11646/zootaxa.4253.1.1>
- Pusey, B. J., Douglas, M., Olden, J. D., Jackson, S., Allsop, Q., & Kennard, M. J. (2020). Connectivity, habitat, and flow regime influence fish assemblage structure: Implications for environmental water management in a perennial river of the wet-dry tropics of northern Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(7), 1397–1411. <https://doi.org/10.1002/aqc.3347>
- Pusey, B. J., Kennard, M. J., Douglas, M., & Allsop, Q. (2018). Fish assemblage dynamics in an intermittent river of the northern Australian wet-dry tropics. *Ecology of Freshwater Fish*, 27(1), 78–88. <https://doi.org/10.1111/eff.12325>
- Reidy-Liermann, C., Nilsson, C., Robertson, J., & Ng, R. Y. (2012). Implications of dam obstruction for global freshwater fish diversity. *Bioscience*, 62(6), 539–548. <https://doi.org/10.1525/bio.2012.62.6.5>
- Rogosch, J. S., & Olden, J. D. (2019). Dynamic contributions of intermittent and perennial streams to fish beta diversity in dryland rivers. *Journal of Biogeography*, 46(10), 2311–2322. <https://doi.org/10.1111/jbi.13673>
- Rolls, R. J., Leigh, C., & Sheldon, F. (2012). Mechanistic effects of low-flow hydrology on riverine ecosystems: Ecological principles and consequences of alteration. *Freshwater Science*, 31(4), 1163–1186. <https://doi.org/10.1899/12-002.1>
- Sternberg, D., & Kennard, M. J. (2013). Environmental, spatial and phylogenetic determinants of fish life-history traits and functional composition of Australian rivers. *Freshwater Biology*, 58(9), 1767–1778. <https://doi.org/10.1111/fwb.12166>
- Sternberg, D., & Kennard, M. J. (2014). Phylogenetic effects on functional traits and life history strategies of Australian freshwater fish. *Ecography*, 37, 54–64. <https://doi.org/10.1111/j.1600-0587.2013.00362.x>
- Stewart-Koster, B., Olden, J. D., Kennard, M. J., Pusey, B. J., Boone, E. L., Douglas, M., & Jackson, S. (2011). Fish response to the temporal hierarchy of the natural flow regime in the Daly River, northern Australia. *Journal of Fish Biology*, 79(6), 1525–1544. <https://doi.org/10.1111/j.1095-8649.2011.03072.x>

- Tedesco, P. A., Hugueny, B., Oberdorff, T., Dürr, H. H., Méricoux, S., & de Mérona, B. (2008). River hydrological seasonality influences life history strategies of tropical riverine fishes. *Oecologia*, 156(3), 691–702. <https://doi.org/10.1007/s00442-008-1021-2>
- Thomaz, S. M., Bini, L. M., & Bozelli, R. L. (2007). Floods increase similarity among aquatic habitats in river– floodplain systems. *Hydrobiologia*, 579, 1–13. <https://doi.org/10.1007/s10750-006-0285-y>
- Thompson, P. L., Rayfield, B., & Gonzalez, A. (2017). Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*, 40(1), 98–108. <https://doi.org/10.1111/ecog.02558>
- Tonkin, J. D., Altermatt, F., Finn, D. S., Heino, J., Olden, J. D., Pauls, S. U., & Lytle, D. A. (2018). The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshwater Biology*, 63(1), 141–163. <https://doi.org/10.1111/fwb.13037>
- Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., & Lytle, D. A. (2017). Seasonality and predictability shape temporal species diversity. *Ecology*, 98(5), 1201–1216. <https://doi.org/10.1002/ecy.1761>
- Townsend, C. R., & Hildrew, A. G. (1994). Species traits in relation to a habitat template for river systems. *Freshwater Biology*, 31(3), 265–275. <https://doi.org/10.1111/j.1365-2427.1994.tb01740.x>
- Troia, M. J., & McManamay, R. A. (2020). Biogeographic classification of streams using fish community– and trait–environment relationships. *Diversity and Distributions*, 26(1), 108–125. <https://doi.org/10.1111/ddi.13001>
- Tyler, K. J., Wedd, D., Crook, D. A., Kennard, M. J., & King, A. J. (2022). Identifying drivers of tropical riverine larval fish abundance and diversity. *Canadian Journal of Fisheries and Aquatic Sciences*, 79(12), 2160–2178. <https://doi.org/10.1139/cjfas-2021-0233>
- Wang, Y. I., Naumann, U., Wright, S. T., & Warton, D. I. (2012). Mvabund– an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, 3, 471–474. <https://doi.org/10.1111/j.2041-210X.2012.00190.x>
- Warfe, D. M., Pettit, N. E., Davies, P. M., Pusey, B. J., Hamilton, S. K., Kennard, M. J., Townsend, S. A., Bayliss, P., Ward, D. P., Douglas, M. M., Burford, M. A., Finn, M., Bunn, S. E., & Halliday, I. A. (2011). The ‘wet–dry’ in the wet–dry tropics drives river ecosystem structure and processes in northern Australia. *Freshwater Biology*, 56(11), 2169–2195. <https://doi.org/10.1111/j.1365-2427.2011.02660.x>
- Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modelling in community ecology. *Trends in Ecology & Evolution*, 30, 766–779. <https://doi.org/10.1016/j.tree.2015.09.007> **Getrightsand content**
- Welch, B. L. (1947). The generalization of “Student's” problem when several different population variances are involved. *Biometrika*, 34(1–2), 28–35.
- Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21(2/3), 213–251. <https://doi.org/10.2307/1218190>
- Winemiller, K. O. (2005). Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fishery and Aquatic Sciences*, 62, 872–885. <https://doi.org/10.1139/f05-040>
- Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in north American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 2196–2218. <https://doi.org/10.1139/f92-242>
- Woinarski, J., B. Mackey, H. Nix and B. Traill. (2007). *The nature of Northern Australia: Its natural values, ecological processes and future prospects*. ANU Press. <http://doi.org/10.22459/NNA.07.2007>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: King, A. J., Olden, J. D., Luiz, O. J., Kennard, M. J., Adair, B., Crook, D. A., Douglas, M. M., Saunders, T. M., & Wedd, D. (2024). Influence of hydrological variability and life history strategy on riverine fish assemblages in the Australian wet-dry tropics. *Ecology of Freshwater Fish*, 00, e12809. <https://doi.org/10.1111/eff.12809>