



# Scale dependency in fish beta diversity–hydrology linkages in lowland rivers

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## Abstract

**Aim:** A key aspect of biodiversity research is to determine the environmental drivers affecting the degree to which ecological assemblages vary in space (beta diversity). The strength and significance of environmental drivers of beta diversity is, however, influenced by the spatial extent over which beta diversity is assessed. Beta diversity of riverine biota is affected by flow variability. We examined hydrology–beta diversity relationships at two spatial extents (reaches vs. entire systems) within rivers to determine if relationships with hydrological variables are scale dependent or generalisable across spatial scales.

**Location:** Murray–Darling Basin, Australia.

**Taxon:** Freshwater fish.

**Methods:** Fish assemblage data were sourced from two monitoring programmes that sampled sites annually during 2014–2019 and spanned either reaches (<100 km) or the broader ‘system’ extent (>1000 km) of five tributaries. Beta diversity was examined by calculating pairwise (incidence and abundance) dissimilarities for each year to compare temporal trends in beta diversity. Multi-site dissimilarities were modelled against hydrological variables using beta regression.

**Results:** Inter-annual change in assemblage composition was detected only at the extent of river reaches but not at the extent of river systems. Temporal variation in within-river beta diversity showed inconsistent patterns when compared between the two spatial extents. Within-river beta diversity relationships with hydrological gradients were inconsistent among rivers. Overall, statistical models explained much more variation in within-river beta diversity when assessed at the reach extent when compared to broader river system extents.

**Main Conclusions:** Our findings highlight that changes in within-river beta diversity are likely to depend on the spatial extent of sampling. Furthermore, inconsistent beta diversity–hydrology relationships among rivers suggest that both empirical evidence and theoretical predictions adopted in ecohydrology may not be transferable among river systems.

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## KEYWORDS

biotic differentiation, biotic homogenisation, extent, grain, spatial scale

## 1 | INTRODUCTION

Understanding and predicting temporal change in biodiversity across spatial scales is fundamental to conservation ecology and biogeography (McGill et al., 2015; Whittaker & Ladle, 2011). Despite being a simple measure of biodiversity, species richness (e.g. the number of species occurring within a patch, otherwise termed 'alpha diversity') is increasingly recognised as being both (i) an insensitive indicator and (ii) inadequately representative of biodiversity change (Hillebrand et al., 2018; Magurran & Henderson, 2010; Mokany et al., 2022). In contrast to alpha diversity, beta diversity (defined as variability in assemblage composition among sampling units within a given area; Anderson et al., 2006) provides unique information about the distribution of biodiversity across spatial scales and is essential to inform conservation management interventions to prevent biodiversity loss through biotic homogenisation. While the potential effects of spatial scaling on beta diversity (e.g. grain size or the size of the sampling unit, and spatial extent over which sampling units are scattered; sensu Wiens, 1989) are conceptually developed (e.g. Barton et al., 2013), much less is known about how change in beta diversity over time varies when analysed across contrasting spatial scales (e.g. multiple sampling sites spanning small vs. broader spatial extents). Understanding how patterns of beta diversity vary across spatial extents and associations with environmental gradients is necessary because inferences of biodiversity change and underlying environmental drivers at one spatial scale could be inappropriately applied at broader or finer spatial scales (Heino, Melo, Siqueira, et al., 2015; Lansac-Tôha et al., 2021).

Beta diversity quantifies the degree to which ecological assemblages differ in composition and can be measured by the dissimilarity in composition among pairs of (or multiple) samples within a group (Anderson et al., 2011; Baselga, 2013). Changes in spatial beta diversity over time are particularly relevant for guiding environmental management, contributing to conservation planning and tracking biodiversity change (McGill et al., 2015). Decline in beta diversity over time (termed 'biotic homogenisation'; McKinney & Lockwood, 1999; Olden & Rooney, 2006) is particularly meaningful for management. Understanding the process of biotic homogenisation has potential consequences for the resilience of biodiversity to environmental disturbances spanning broad spatial extents (e.g. whole landscapes and regions) (Olden et al., 2018). Also, deciphering how patterns of beta diversity change and underlying ecological drivers vary across spatial extents is especially relevant for theoretical and conservation purposes (McGill et al., 2015). For example, if environmental drivers of beta diversity change are specific to a particular spatial extent (and not consistent across multiple extents), we risk failing to meet expectations of biodiversity responses to environmental change and management interventions if predictions are erroneously extrapolated across spatial scales.

In river–floodplain ecosystems, beta diversity of multiple organism groups is influenced by hydrological variability in space and time (Rolls et al., 2018). Temporal variability in river discharge is predicted to drive significant changes in beta diversity (Larned et al., 2010; Thomaz et al., 2007). For example, beta diversity within rivers typically declines with increasing discharge (e.g. Bower et al., 2019; Bozelli et al., 2015; Sarremejane et al., 2018) as hydrological connectivity increases with flow (Rolls et al., 2018; Thomaz et al., 2007). Following transition to prolonged low flows, beta diversity can also change as organisms are progressively lost from the regional species pool due to loss of habitat heterogeneity (dos Santos Bertoincin et al., 2019; O'Neill, 2016). Such changes in spatial beta diversity are often reported in studies examining change in assemblage composition over time associated with temporal hydrological variability (see Rolls et al., 2018 for review). Understanding the drivers of change in spatial beta diversity over time in riverine systems, particularly the role of hydrology, would be particularly useful for anticipating how natural and anthropogenic hydrological change affect patterns of biodiversity across broad spatial scales.

Developing a strong understanding of the links between hydrology and beta diversity of riverine organisms is hampered primarily by: (1) a lack of analysis of hydrology–beta diversity relationships spanning different spatial extents, (2) an emphasis on beta diversity responses to hydrology in single river systems and (3) unique aspects of assemblage composition that reveal dissimilarity among locations. Relationships between temporal hydrological variation along gradients of flow magnitude are routinely analysed at single spatial extents. For example, change in assemblage composition associated with manipulated floodplain inundation is often analysed by examining beta diversity among locations within a specific spatial extent, such as where sites span across 100–200km of river length (e.g. Rayner et al., 2009). If beta diversity responses to hydrological events (e.g. flooding) are more or less apparent at a particular spatial extent, then this would be useful for decision making about the extent that sampling effort needs to be applied to detect real changes in composition. Furthermore, fish beta diversity–hydrology relationships are almost always examined in single-river studies (e.g. Bower et al., 2019; Dai et al., 2020). Such single-river studies provide useful evidence of beta diversity responses to hydrology (e.g. Rayner et al., 2009), yet are unable to determine if responses are consistent among river systems or show some form of context dependency (Catford et al., 2021; Heino et al., 2012) or 'contingency' (Lawton, 1999). Finally, few studies of hydrology–beta diversity compare how change in dissimilarity varies among incidence (i.e. presence–absence) and abundance aspects of assemblage composition. The limited evidence we have suggests that beta diversity responses to hydrology are variable across different aspects of dissimilarity (e.g. Dai et al., 2020; Taylor et al., 2019). By considering how beta diversity responses to hydrology vary across spatial extents, among

multiple rivers and between different aspects of compositional dissimilarity, we can provide greater insights into our ability to generalise and understand biodiversity change in the context of spatial and temporal changes in hydrology imposed by natural and anthropogenic events.

Australia's Murray–Darling Basin provides a useful context to assess temporal change in spatial beta diversity of fish assemblages across multiple extents. The Basin experiences substantial variation in flow across annual and decadal time spans (Leblanc et al., 2012), such as multi-year droughts punctuated by pronounced flooding. Water management of the Murray–Darling Basin emphasises restoring aspects of hydrological regimes to support species, ecosystem function and biodiversity (e.g. Gawne et al., 2020). Riverine fish are a key focus for the ecological assessment of hydrological alteration and restoration in the Murray–Darling Basin (e.g. Gehrke et al., 1995; Tonkin et al., 2021), yet research has primarily focused on the role of hydrology in population recruitment dynamics (e.g. Tonkin et al., 2021). Beta diversity, in contrast, has had little attention in this context, yet has fundamental research, biodiversity management and societal significance because it emphasises the degree to which assemblages vary in composition from each other.

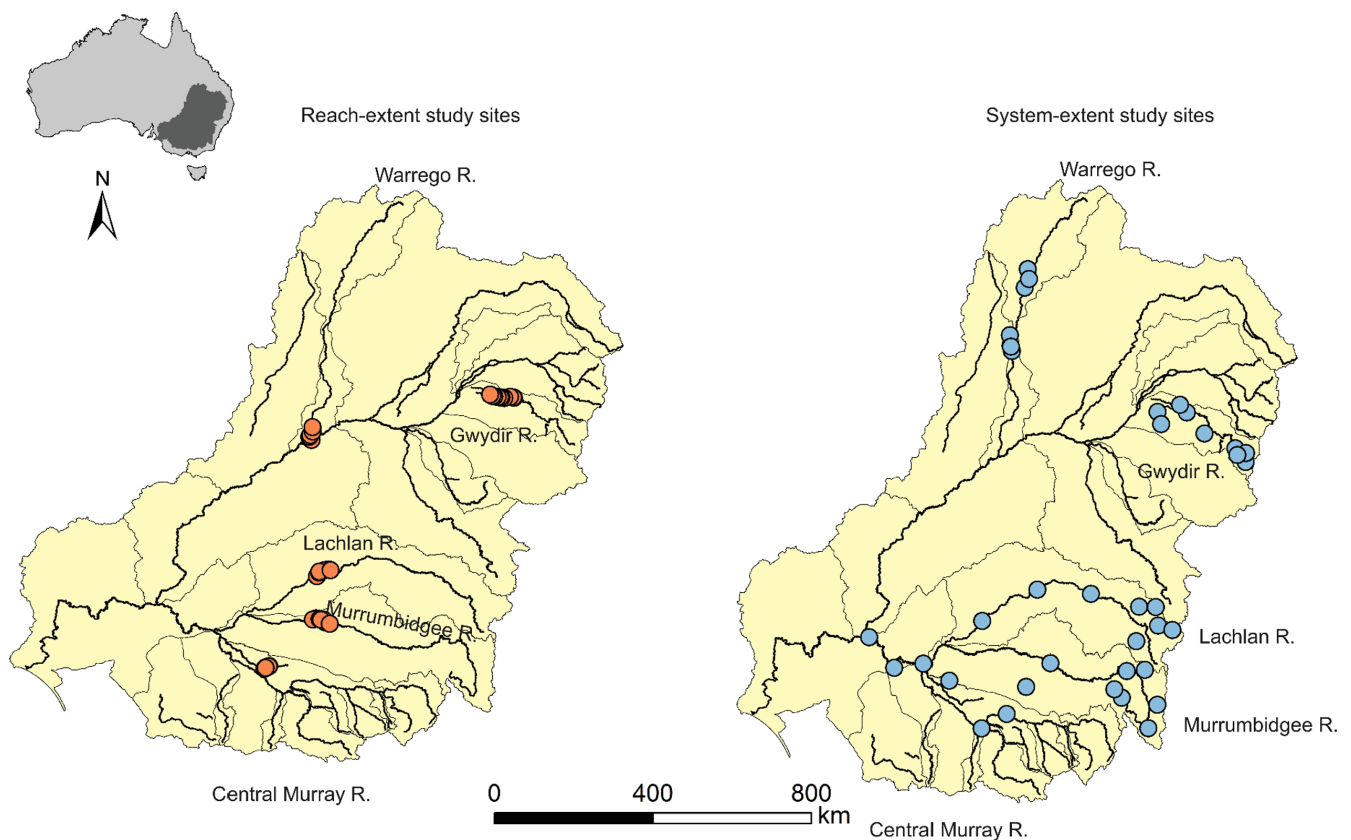
Here, we examined temporal patterns in spatial beta diversity of riverine fish assemblages among five major rivers within the Murray–Darling Basin. We used two fish assemblage datasets

spanning contrasting spatial extents in each river to compare how temporal changes in spatial beta diversity associated with hydrological variability differed between reach and system spatial extents. We began by testing if temporal trends in assemblage composition within rivers were consistent or variable across spatial extents. Second, we examined how temporal trends in spatial beta diversity (within-river dissimilarity) differed when tested across two contrasting spatial extents. Third, we tested if the magnitude of spatial beta diversity was associated with two aspects of hydrology–flooding intensity and antecedent flow variability. Overall, the aim of this study was to better understand how consistent beta diversity responses were to flood history and flow variability across space and time, thereby informing how multi-species biodiversity patterns can be used to assess outcomes of hydrological alteration or restoration efforts.

## 2 | MATERIALS AND METHODS

### 2.1 | Study region

The Murray–Darling Basin is located in south-eastern Australia and is drained by 23 major tributaries (Figure 1). The climate of the western



**FIGURE 1** Map depicting the location of fish sampling sites in five tributary systems of the Murray–Darling Basin (Australia) as part of two separate monitoring programmes spanning two contrasting spatial extents (reach extent vs. system extent). Note that the spread of sampling sites differed considerably between the two monitoring programmes, allowing us to examine potential scale-dependent changes in beta diversity of fish assemblages over time.

basin is semi-arid, whereas in the east it is humid–subtropical in the north transitioning to oceanic in the south. Precipitation seasonality shifts on a longitudinal gradient from summer dominated in the north to late winter and spring dominated in the south. Most of the basin is <400m above sea level and is characterised as lowland plains, with undulating and steeper terrain along the eastern portion. Dryland and irrigated agriculture is the predominant land use of the basin, with smaller portions used for forestry or preserved as national parks.

Hydrological regimes of the Basin's tributary rivers vary substantially (Kennard et al., 2010; MDBC, 2008) due to geographic variation in rainfall, geomorphology and land use. Across the basin, 48% (11,240 GL) of the mean annual surface water (23,417 GL) is diverted to support human needs (agriculture, domestic consumption, mining) (CSIRO, 2008). Generally large dams are located in upland regions, diversion and distribution channels, low-level weirs predominantly in lowland reaches, extraction of water from river channels by pumping and levees and canals for floodplain harvesting. Hydrological alteration is not uniform across the basin, rather the degree of alteration of natural hydrology by water resource development varies substantially among tributary systems (MDBC, 2008).

Our study focused on five tributary systems – the Warrego, Gwydir, Lachlan, Murrumbidgee and Central Murray rivers (Figure 1). These rivers were selected based on availability of suitable and simultaneously collected fish assemblage data. Both the Warrego and Gwydir rivers are situated in the northern portion of the basin and drain into the Darling River, and the Lachlan, Murrumbidgee and Central Murray are in the southern portion of the basin and drain into the Murray River. Each river system has a unique natural hydrology, water resource demands and are currently foci for the delivery of environmental flows, predominantly in the form of controlled floods coordinated by state and federal governments (Gawne et al., 2020).

## 2.2 | Data sources

### 2.2.1 | Fish assemblage datasets

We sourced two datasets generated from monitoring programmes that sampled fish assemblages at multiple sites in the five study rivers. In each monitoring programme, fish assemblages were sampled annually from fixed sites (locations), however, the two monitoring programmes differed in spatial extent over which sample sites were spread throughout each river (Figure 1). Difference in the spatial extent of monitoring allowed us to examine how patterns of fish beta diversity and hydrology–beta diversity relationships were similar or different when considered across two different spatial 'views' of river systems. While there were differences in sampling effort among the two monitoring programmes (which we accept as inevitable when using existing datasets), our interest was primarily

in examining if the same or unique patterns and temporal trends of spatial beta diversity were evident among the two spatial extents. In terms of spatial *grain* (sensu Wiens, 1989), sampling effort at each monitoring site was not notably different between the two monitoring programmes (i.e. the length of river reach sampled at site were similar among monitoring programmes). Therefore, as the spatial spread of monitoring was at an order of magnitude difference between the two programmes, our interest was in questions of differences in spatial extent on beta diversity patterns in river systems.

#### *Data source 1: System-extent dataset*

The Murray–Darling Basin Fish Survey sampled fish assemblages annually from five to eight river channel sites spanning headwater to lowland reaches in each of the basin's 23 tributary systems during 2014–2019 (data source: <https://data.gov.au/data/dataset/murray-darling-basin-fish-and-macroinvertebrate-survey/resource/df01d269-83ce-4894-a1d8-01a792e4f027>). Sampling occurred November–May (austral summer–autumn) during low-to-moderate flow conditions using a standardised protocol of electrofishing and unbaited shrimp traps. Unbaited ( $n=10$ ) shrimp traps were set in shallow (<1m depth) water for ~2h, while electrofishing sampling was done elsewhere in the study site. Electrofishing was done using either boat or backpack (or a combination of the two methods) using a standardised protocol of 8×150second replicates using backpack electrofishing or 12×90second replicates of boat electrofishing. All fish (>15mm total length) captured were measured and released at the completion of sampling (native species) except where state government policies dictated euthanasia (for non-native species) or where voucher specimens were retained to confirm identity.

#### *Data source 2: Reach-extent dataset*

Since 2014, the Commonwealth Environmental Water Office Long-Term Intervention Monitoring programme has monitored riverine fish assemblages and other ecological variables in river and floodplain environments in the five study river systems in the basin (data source: <https://data.gov.au/dataset/ds-dga-641c0396-9703-4dba-8547-65b08a52283e/details?q=CEWO%20fish>). In the Gwydir, Lachlan, Murrumbidgee and Central Murray rivers, fish assemblages were sampled annually (2015–2019) during March–May at 10 study sites spanning 15–53km (as linear distance) in the lowland portion of each river. In these four study rivers, fish were sampled using a standardised combination of boat electrofishing (32×90s of 'power-on' time), 10 unbaited shrimp traps (~3h) and 10 fine-mesh double-wing fykes nets (set overnight). In the Warrego river, fish assemblages were sampled annually from five sites spanning a 30km reach during 2015–2018 using a combination of methods depending on water depth (boat or backpack electrofishing, large and small fyke netting, seine netting). All fish captured or observed during sampling were identified to species, and all captured fish were released. Prior to analysis, the fine-scale fish data were summarised as total counts of each species recorded for each site and year.



## 2.3 | Hydrology

The hydrology of the five rivers is characterised by being highly variable among years due to differences in precipitation, runoff and human water demands (Figure S1). Spatially, the flow regime varies longitudinally in each river (due to tributary inflows, increasing catchment area, etc.) (MDBC, 2008). We used ArcMap 10.6.1 to match each fish sampling site (in both fish datasets) to the nearest streamflow gauging station on the same river reach and sourced the full record of available daily discharge data (as  $\text{ml day}^{-1}$ ) from government water management agencies (WaterNSW; <https://realtimedata.waterrsw.com.au/>). We infilled gaps in flow time series using multiple linear regression as predicted from the nearest streamflow gauging site in the River Analysis Package (Marsh, 2004) to create a complete hydrological dataset for analysis of daily flow discharge from 1980 to 2020. For each fish sampling event, we calculated values for two hydrological variables using the time series discharge data for each paired flow gauging station. These variables were selected because as they were internally standardised by a percentile of the long-term record for each gauge and hence we could test if beta diversity patterns were comparable among our five river systems. These variables were:

1. *Antecedent flood severity*. Ecologically, effects of flooding on riverine biota depend on both the *intensity* (duration) and *history* (time since event). Ceschin et al. (2018) proposed a flood intensity score ('FI') being the duration (days) of the most recent flood event divided by the time (days) since that event and the point of interest (i.e. date of sampling). Therefore, a flood event of 10days duration that occurred 100days prior to sampling ( $\text{FI}=0.1$ ) at one site will have an equal FI value as an event of one day duration that occurred 10days prior to sampling. For consistency across study sites, we set a flood threshold of 0.5 times the mean daily discharge ( $\text{ml day}^{-1}$ ) for each gauge record (calculated from the 1980–2020 dataset). For each study site, we calculated the FI score based on the 12-month period (April–March) from 2014–2019 to match the sampling times (Autumn) of fish sampling.
2. *Antecedent flow variability*. For each year of sampling, we calculate the variability (as coefficient of variation; CV) of daily discharge for each study site based on the preceding 1-year period prior to sampling.

For both hydrological variables, we calculated the mean value for each study year from each hydrological gauging station time series that spanned the extent of river sampled by each monitoring programme. These resulting values were then used as predictor variables in hydrology–beta diversity relationships (detailed below).

## 2.4 | Data analysis

Our primary interest was to examine if temporal change in spatial beta diversity (defined as within-river variation in assemblage composition among sites) was (1) consistent or context dependent among the five study rivers and (2) if temporal patterns of beta diversity differed between the reach and system extents that each dataset spanned (Figure 2). Therefore, our analyses focused heavily on statistical analyses of compositional dissimilarity among samples (Anderson et al., 2011; Cardoso et al., 2015; Legendre & De Cáceres, 2013). Our analyses were done in three components to draw robust understanding of the patterns of beta diversity. Prior to all analyses, fish assemblage composition (as a species  $\times$  sample matrix with data as catch per unit effort) was converted to percentage composition to account for unequal assemblage size (i.e. total counts) among samples and because of the semi-quantitative nature of catch per unit effort data. We recognise that different sampling methods often bias for or against specific species in freshwater systems (Radinger et al., 2019), justifying the use of multiple sampling methods to improve detection of fish species where they occur (as done in both datasets), and assume that fish assemblage composition data (as percentage abundance) reflected the percentage composition of assemblages at each time during sampling.

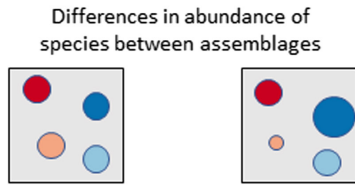
### 2.4.1 | Temporal change in fish assemblage composition among years

We tested how fish assemblage composition in each river varied through time (5 years) and if temporal trajectories in assemblage composition were consistent or unique among the five study rivers using a two-factor (crossed) fixed effects permutational analysis of variance (PERMANOVA; Anderson, 2001) using PRIMER v6 run with 999 permutations and type III sums of squares. Analyses were done using each dissimilarity measure (1: Sørensen's dissimilarity, a 'broad-sense' measure of incidence-based beta diversity and 2: abundance-based percentage-difference dissimilarity) calculated for each of the two fish assemblage datasets. In this set of analyses, our interest was *not* in testing for differences in composition among rivers spanning known distinct biogeographical divides throughout the Basin (Hamilton et al., 2017) but rather to test if temporal variation in assemblage composition was consistent among rivers or if particular rivers had pronounced inter-annual variation in composition compared to others. PERMANOVA tests for *location* differences in multivariate space and aid in interpreting patterns of multivariate dispersions (Anderson et al., 2008). To illustrate temporal changes in assemblage composition among the five study rivers, we used principal coordinates analyses after calculating

**FIGURE 2** Schematic diagram illustrating theoretical aspects of beta diversity (and partitioning in terms of replacement, richness differences and abundance variation among samples), key ecohydrological relationships being tested in this study and the two overarching questions of our study (1, are hydrology–beta diversity relationships consistent among rivers? 2, are hydrology–beta diversity relationships consistent when assessed across contrasting spatial 'views' or extents of rivers?).

**Defining beta diversity and its components**

Beta diversity describes the degree to which ecological assemblages differ from each other. Differences in composition among samples are driven by (a) replacement of species, (b) differences in richness, and (c) variation in species abundances.



**Replacement of species between assemblages**

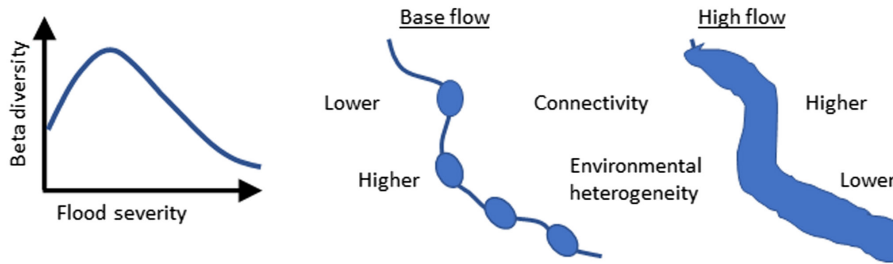


**Differences in richness between assemblages**



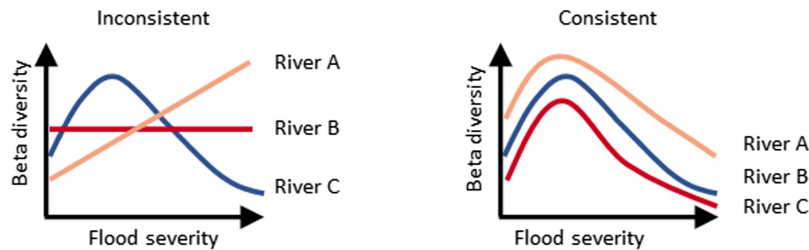
**Ecohydrological concepts of riverine beta diversity**

Ecological theory and empirical evidence highlights that hydrological variability is a key driver of spatial beta diversity. In particular, flood events increase connectivity and reduce environmental dissimilarity among patches, leading to lower beta diversity.



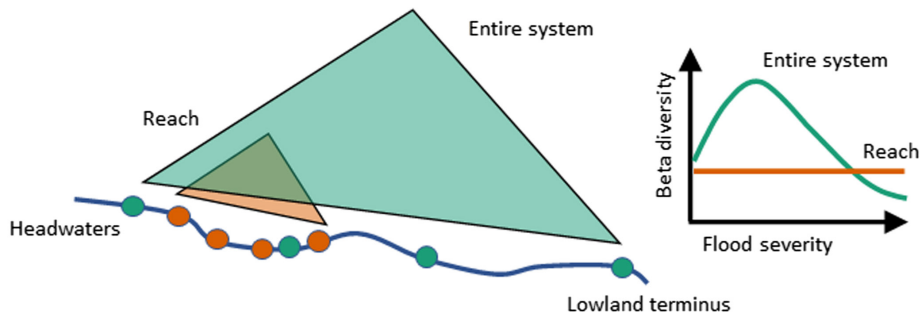
**Consistency or context-dependency of hydrology – beta diversity relationships**

Are hydrology – beta diversity relationships consistent among river systems, or are the effects of hydrological variability on beta diversity unique to specific rivers?



**Scale-dependency of hydrology – beta diversity relationships**

We know of no studies that compare hydrology – beta diversity relationships across different spatial extents. Are hydrology – beta diversity relationships consistent when assessed across contrasting spatial extents? Or is the effect of hydrological variability on beta diversity dependent on our view of river systems?



year  $\times$  river centroids using the *meandist* function with the *VEGAN* package (Oksanen et al., 2019) in R, then ordinating dissimilarities using the *pcoa* function in the *APE* package (Paradis et al., 2019).

## 2.4.2 | Temporal variation in spatial beta diversity across multiple spatial extents

For each dataset (each spanning a different spatial extent), we calculated dissimilarity among pairs of samples using four measures. First, Sørensen's incidence-based dissimilarity (as a 'broad-sense' measure of beta diversity). We decomposed Sørensen's dissimilarity into its (2) replacement and (3) richness difference components using the *beta* function in the *BAT* package in R (Cardoso et al., 2015). Replacement and richness difference dissimilarity measures highlight differences (i.e. variation) in the degree to which species replacements or richness differences among pairs of samples contribute to broad-sense pairwise dissimilarities. Our fourth dissimilarity measure was percentage difference ('Bray-Curtis'), which quantifies pairwise dissimilarity in terms of abundance-based composition. These four dissimilarity measures are suitable for analyses of beta diversity because they are invariant to joint absences (double-zeros) and are invariant to (i) the number of species in a dataset and (ii) measurement units (Anderson et al., 2011; Legendre & De Cáceres, 2013). For each dissimilarity matrix produced from each reach- or system-extent dataset, we tested the null hypothesis of no significant difference in within-group variance among groups using distance-based tests of homogeneity of dispersions (*PERMDISP*; Anderson, 2006; Anderson et al., 2006) using a two-factor (crossed design) of 'river'  $\times$  'year' via the *betadisper* function in the *VEGAN* package (Oksanen et al., 2019). In ecological terms, this test allowed us to determine if within-river beta diversity differed significantly over time (years) and compare if temporal patterns of beta diversity were similar (i) among river systems and (ii) between reach versus system extents. Dissimilarities from group median were graphed as grouped box plots of dissimilarities (y-axis) over time (x-axis) separately for each river system.

## 2.4.3 | Associations between hydrology and multi-site beta diversity

We calculated multi-site beta diversity for each river across each year using the *beta.multi* function in the *BAT* package R. This function calculates the mean 'total' dissimilarity among all pairs of samples (i.e. fish monitoring sites) within a group (i.e. river  $\times$  year combinations separately for each dataset) based on a chosen dissimilarity measure (Cardoso et al., 2015). Here, total beta diversity is an estimate of beta diversity representing both turnover (i.e. replacement) and richness difference (i.e. loss and gain) components of beta diversity. For consistency, multi-site beta diversity values were calculated based on the (1) Sørensen (incidence),

decomposed into (2) replacement and (3) richness-difference dissimilarities and (4) percentage-difference (abundance) dissimilarity metrics.

We plotted values of multi-site beta diversity (as 1, total Sørensen decomposed into 2, replacement and 3, richness-difference and 4, abundance-based dissimilarities) for each river (calculated for each annual period of field monitoring) against values for the flood index (detailed above) and the variability (CV) in discharge separately for each spatial extent of monitoring. We built regression models to test the relationship between our two selected hydrological variables, river (as binary categorical variables) and each measure of beta diversity [total incidence (Sørensen's dissimilarity)], decomposed into both replacement and richness difference dissimilarities and abundance-based beta diversity (percentage difference). Tests were repeated for each spatial extent dataset. We included the interaction between river and each hydrological variable in the model to test if relationships between multi-site beta diversity along hydrological gradients were consistent or context dependent among the five study rivers. As our response variables were scaled between 0 and 1 (i.e. a beta distribution), we built our regression models using beta regression (Douma & Weedon, 2019) in R with the *BETAREG* package (Cribari-Neto & Zeileis, 2010). For all statistical tests, we adopted a significance ( $\alpha$ ) level of  $p \leq 0.05$ . We did not adopt a Bonferroni correction for pairwise tests, because doing so inflates the risk of type 2 errors, which are relevant in ecological studies such as ours where despite substantial sampling effort and costs, monitoring programmes frequently monitor few sampling sites. Instead, we adopted the approach of interpreting our results using 'language of evidence' (Muff et al., 2022).

## 3 | RESULTS

### 3.1 | Fish assemblage summary at two spatial extents

The fish fauna sampled in the five study tributaries comprised 26 species (19 native species, 7 non-native species) (Table S2). In each river, the number of species detected was higher in the system-extent dataset when compared to the reach-extent dataset, despite fewer sampling sites monitored annually. In both datasets, the Murrumbidgee River system and the Warrego River system had the highest and lowest numbers of species compared to the remaining three study rivers respectively.

### 3.2 | Temporal change in fish assemblage composition within river systems

The significance and magnitude of inter-annual change in assemblage composition varied between the two spatial extents of analysis (Table 1, Figure 3). At the reach extent, inter-annual variation in

**TABLE 1** Results of PERMANOVA tests comparing change in assemblage composition among study years among rivers at reach and whole of river system scales in five rivers of the Murray–Darling Basin, Australia.

Source of variation	Reach extent					System extent				
	df	MS	F	p	VC	df	MS	F	p	VC
Sørensen (incidence)										
Year	4	780.0	4.5	<b>0.001</b>	2.7	4	904.7	0.5	0.953	0.0
River	4	15,568.0	89.6	<b>0.001</b>	63.8	4	22,032.0	12.5	<b>0.001</b>	26.8
Year×River	15	351.0	2.0	<b>0.008</b>	3.5	16	895.8	0.5	0.997	0.0
Residual	192	173.7			30.1	135	1768.4			73.2
Percentage difference (abundance)										
Year	4	4441.8	5.7	<b>0.001</b>	3.5	4	1811.3	0.7	0.902	0.0
River	4	55,228.0	70.7	<b>0.001</b>	48.6	4	32,817.0	12.5	<b>0.001</b>	26.8
Year×River	15	5253.0	6.7	<b>0.001</b>	18.8	16	1995.7	0.8	0.975	0.0
Residual	192	781.2			29.2	135	2631.3			73.2

Note: Analyses were repeated for incidence-based (i.e. presence-absence) and abundance-based beta diversity. MS: mean squares, VC: variance component (negative components of variation converted to zero). Significant effects ( $p \leq 0.05$ ) are indicated in bold. Significant interactions highlight inconsistent temporal trajectories among rivers.

fish assemblage composition differed among rivers – both for incidence and abundance-based composition. The highest proportion of variation in assemblage composition was explained by differences among rivers (incidence-based composition: 63.8%, abundance-based composition: 48.6% variation). At the system extent, there was no significant temporal variation in either incidence-based or abundance-based assemblage composition and temporal variation in assemblage composition was similar among rivers (non-significant year×river term with 0% variation explained; Table 1). Both incidence and abundance-based composition differed significantly among rivers when assessed at the system-extent scale (Table 1; all pairwise combinations  $p < 0.05$ , and all rivers showing little to no overlap in ordination space; Figure 3). Despite strong evidence of differences in composition among rivers at both reach and system-extent datasets (Table 1), the proportion of variation explained by the ‘River’ term was substantially lower at the system extent versus the reach extent.

### 3.3 | Temporal variation in within-river beta diversity across spatial extents

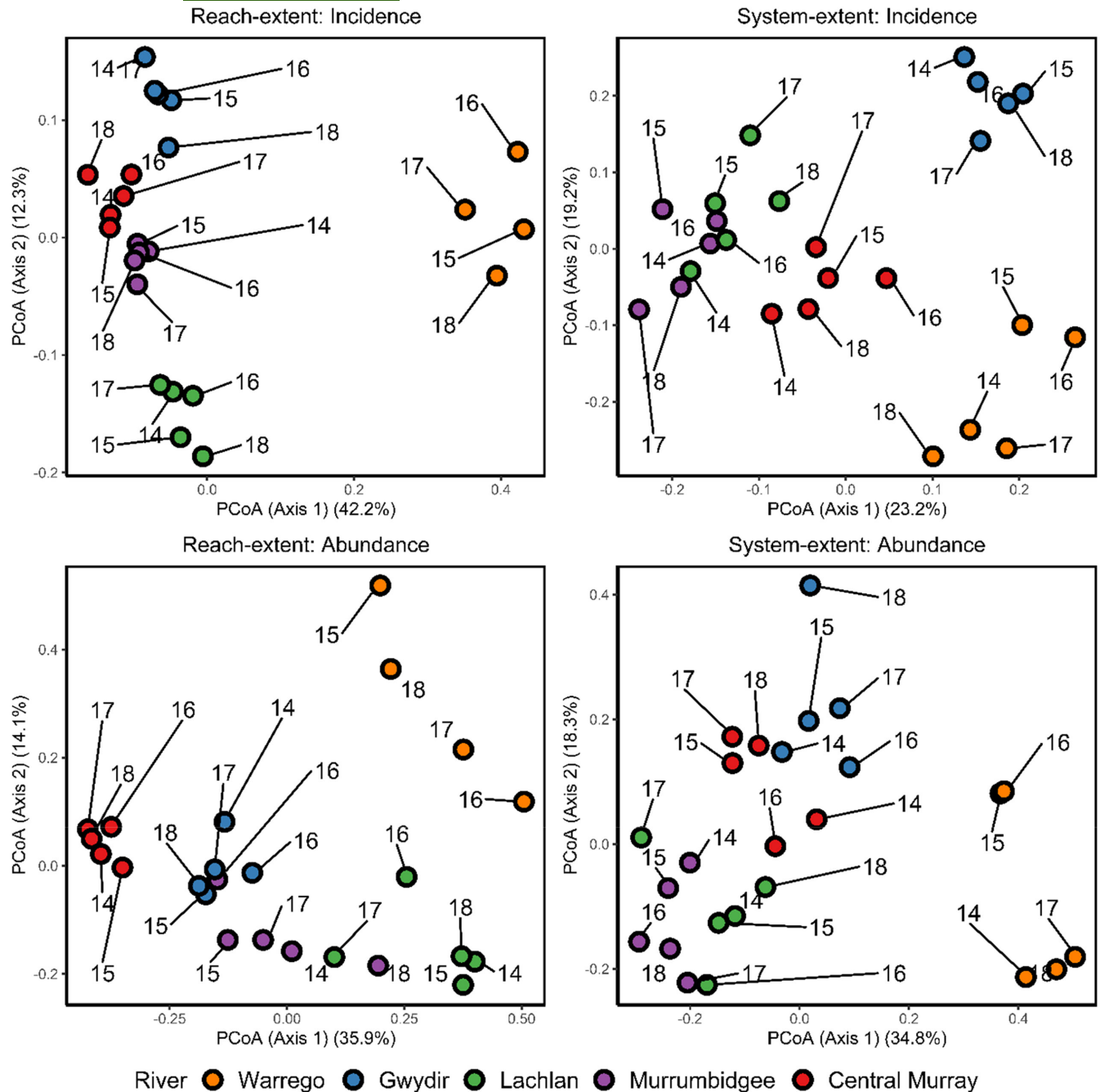
Changes in within-river (incidence-based; Sørensen) beta diversity of fish assemblages through time were both inconsistent when compared among rivers, and between reach and system extents for each river (Table 2). In three rivers (the Gwydir, Murrumbidgee and Central Murray), there was little evidence of apparent change in within-river beta diversity among years at either extent (Figure S2). In the two remaining rivers (Warrego and Lachlan), within-river beta diversity declined significantly in 2017/2018 at the reach extent but did not change significantly in the system-scale extent. Comparisons between reach and system spatial extents revealed apparent inconsistencies in inter-annual changes in

abundance-based beta diversity for each river system (Figure S3). In the Warrego River, abundance-based beta diversity was significantly lower during 2016 and 2017 (compared to 2015 and 2018) at the reach extent, but this pattern was not reflected at the system extent.

Decomposing incidence-based (Sørensen's dissimilarity) beta diversity into replacement and richness difference dissimilarities revealed that the magnitude of either replacement or richness difference components in overall incidence-based beta diversity patterns over time were unique to each river system but inconsistent across spatial extents (Figures S4 and S5). In the Warrego River, variation in the replacement component was the main component of incidence-based beta diversity particular at the reach scale. In the Gwydir River, significantly lower reach-scale beta diversity in 2014/2015 (compared to the subsequent four study years) was associated with lower variation in replacement among samples. However, this pattern was not reflected at the system extent; reduced richness difference component in 2017/2018 was offset by higher replacement among samples. Three study rivers (the Lachlan, Murrumbidgee and Central Murray) had little inter-annual variation in richness difference beta diversity at the reach extent, yet inconsistent trends when analysed at the system extent. In contrast, the replacement component of beta diversity was much more variable through time for the Lachlan and Central Murray rivers at both the reach and system extents.

### 3.4 | Relationships between hydrological variables and beta diversity across multiple spatial extents

Beta regression models consistently explained considerably ( $\geq 2$ ) higher proportions of variation in each aspect of incidence or



**FIGURE 3** Principal coordinate analysis ordinations depicting inter-annual variation (2014–2018) in incidence or abundances-based fish assemblage composition assessed at two spatial extents (reach, system) in five rivers of the Murray–Darling Basin. Years (2014/2015 to 2018/2019 are abbreviated to the last two numbers for clarity). Each point represents the centroid (as mean among-group dissimilarities) of each sampled assemblage across sites in each river for each survey year. Note that for the reach-extent dataset, fish assemblages in each river (i) showed more distinct separation and (ii) variable inter-annual changes in composition than for the system-extent dataset (depicted by the more distinct separation of assemblages among rivers, and differences in the spread of centroids for each river respectively).

abundance-based beta diversity at the reach extent when compared to system extent (Table 3). For overall incidence-based beta diversity, strong evidence of hydrology–beta diversity relationships in the reach-extent dataset were either not evident at the system extent (e.g. positive relationship between flood index and beta diversity) or hydrology–beta diversity relationships were in the opposite direction (e.g. the effect of flood index on beta

diversity in the Murrumbidgee River was negative when assessed at the reach extent, but positive at the system extent). Overall, gradients of flooding (as measured by the flood index) (i) were more strongly associated with incidence-based beta diversity when compared to antecedent flow variability when assessed at either spatial extent and (ii) were inconsistent among river systems (Table 3; Figures 4 and 5). Beta regression models revealed



**TABLE 2** Multivariate dispersions (PERMDISP) examining differences in within-river beta diversity as a Year × River factorial design.

	Reach extent			System extent		
	MS	F	p	MS	F	p
Incidence (Sørensen)	0.04	11.99	0.001	0.05	9.38	0.001
Replacement component	0.03	3.59	0.001	0.04	3.23	0.001
Richness-difference component	0.02	4.41	0.001	0.03	3.45	0.001
Percentage difference	0.05	7.42	0.001	0.04	7.52	0.001

Note: Tests were repeated for each aspect of beta diversity and at reach and system spatial extents. Significant interactions indicate that inter-annual trends in within-river beta diversity differed among rivers.

that overall explained variation was double for richness difference component than the replacement component at the reach extent, but the opposite was found at the system extent (Table 3). For abundance-based dissimilarity, the overall variation explained by the model was almost four times higher when assessed at the reach extent versus the system extent (Table 3). Abundance-based beta diversity was strongly associated with hydrological gradients in only particular rivers and particular spatial extents (e.g. both flooding and variability in the Murrumbidgee River at the system extent, and variability in the Gwydir River at the reach extent).

## 4 | DISCUSSION

In rivers, different ecological relationships are potentially revealed when examined at different spatial scales (Fausch et al., 2002). Yet, despite substantial interest by freshwater ecologists to examine change in freshwater assemblages over time and relationships between patterns of biodiversity along environmental gradients such as hydrology (e.g. Heino, Melo, & Bini, 2015; Larned et al., 2010; Rolls et al., 2018), there is very little evidence to confirm if ecohydrological relationships are consistent when assessed across multiple 'views' (i.e. extents) of river systems. We examined how temporal change in fish assemblage composition and hydrology–beta diversity relationships varied among rivers across two spatial extents – the extent of river reaches (<100km) and the extent of river systems (>1000km). Our analyses revealed inter-annual changes in fish beta diversity and hydrological–beta diversity relationships differ when assemblages were assessed across short portions of rivers ('reaches') versus across broader extents spanning entire river 'systems' (Table 4). By comparing patterns of assemblage change and spatial beta diversity at two spatial extents allows us to identify if ecohydrological gradients were consistent across spatial extents or were extent specific. Overall, such findings are especially relevant for identifying (1) biodiversity change across spatial scales

(sensu McGill et al., 2015) and (2) appropriate spatial scales to monitor biodiversity outcomes to conservation interventions in freshwater ecosystems.

Assessing temporal change in the composition of ecological assemblages is fundamental to interpreting trends in biodiversity and biodiversity responses to anthropogenic environmental change (Czeglédi et al., 2022; McGill et al., 2015). We found that patterns of inter-annual change in fish assemblage composition were inconsistent when compared at the extent of reaches versus broader river systems. At the reach extent, temporal change in fish assemblage composition was inconsistent among rivers, such that assemblage composition (particularly abundance-based composition) changed significantly over time in some rivers and not in others. In contrast, at the system extent, while fish assemblage composition differed significantly among rivers, there was little evidence of change in composition over time. Numerous studies have either shown stable or variable fish assemblage composition among years of monitoring associated with substantial hydrological variability (e.g. Alexandre et al., 2013; Humphries et al., 2008), yet assessments are rarely made beyond one spatial extent. In designing monitoring programmes to assess condition and change in the composition of fish assemblages, researchers frequently focus on the sampling effort required to quantify composition at the site scale (i.e. sampling replicate or spatial grain) (e.g. Kennard et al., 2006). However, even when site-level sampling is robust, different conclusions are potentially drawn when considering temporal change in fish assemblage composition between the extent of river reaches versus the broader river systems (e.g. Crook & Koster, 2006; Pollino et al., 2004, 2006; Taylor et al., 2019).

Numerous empirical studies test for possible relationships between hydrological variables (e.g. flooding, antecedent variability) and beta diversity of riverine fish assemblages (e.g. Benone et al., 2018; Bokhutlo et al., 2021; Cruz et al., 2018). Here, in all beta regression tests done at the reach extent, there was moderate to strong evidence of relationships between hydrological variables (e.g. flooding) and within-river beta diversity. However, the direction of relationships varied among rivers and were associated with different directions of within-river beta diversity. Furthermore, we identified that hydrology–beta diversity relationships can be in the opposite direction when assessed at different spatial extents. For example, within-river (Sørensen's dissimilarity) beta diversity in the Murrumbidgee River had negative and positive relationships with flood intensity when assessed at the reach and river system extents respectively. In the same river, abundance-based dissimilarity was not significantly associated with either flood intensity or antecedent flow variability when assessed at the reach extent, but it was either significantly positively or negatively associated with flood intensity and antecedent variability at the broader system extent. Chase et al. (2018) identified strong scale dependency in measures of change in species richness (alpha diversity), highlighting how scale dependency confounds ability to synthesise biodiversity responses to environmental drivers. Evidence from our study indicates that the same issues occur for beta diversity.

**TABLE 3** Results from beta regression models for multiple components of beta diversity (as multi-sites dissimilarities based on Sørensen dissimilarity, the replacement and richness difference component of Sorensen's distance and abundance-based percentage-difference distance) associated with river, flood index values and antecedent discharge variability (as mean values across the spatial extent of sampling in each monitoring programme).

Predictors	Reach extent				System extent			
	Estimate	SE	Z	p	Estimate	SE	Z	p
<i>Incidence-based dissimilarity (Sorensen's)</i>	Pseudo $R^2=0.923$ ; $p<0.001$				Pseudo $R^2=0.234$ ; $p<0.001$			
<i>Intercept</i>	-1.69	0.16	-10.64	<0.001	1.19	2.03	0.58	0.560
Flood index	0.13	0.04	3.80	<0.001	-0.01	0.02	-0.42	0.674
CV (daily variability, 1 year)	-0.01	<0.01	-3.10	0.002	-0.01	0.01	-0.73	0.465
Gwydir River	1.88	0.35	5.34	<0.001	0.04	2.24	0.02	0.985
Lachlan River	-0.83	0.35	-2.41	0.016	-0.32	2.53	-0.13	0.899
Murrumbidgee River	-1.41	0.47	-3.00	0.003	11.75	2.75	4.28	<0.001
Warrego River	0.16	0.43	0.37	0.712	-2.00	2.26	-0.88	0.377
Flood index × Gwydir	-0.11	0.06	-2.02	0.044	0.10	0.14	0.73	0.465
CV (daily) × Gwydir	0.00	<0.01	0.05	0.959	0.01	0.01	0.55	0.585
Flood index × Lachlan	-0.15	0.05	-3.05	0.002	-0.02	0.08	-0.27	0.787
CV (daily) × Lachlan	0.02	<0.01	4.34	<0.001	0.01	0.02	0.73	0.465
Flood index × Murrumbidgee	-0.14	0.04	-3.77	<0.001	0.08	0.02	3.20	0.001
CV (daily) × Murrumbidgee	0.01	0.01	2.67	0.008	-0.07	0.02	-3.70	<0.001
Flood index × Warrego	0.67	0.29	2.33	0.020	0.03	0.13	0.24	0.810
CV (daily) × Warrego	0.01	<0.01	3.25	0.001	0.01	0.01	0.73	0.463
<i>Replacement dissimilarity</i>	Pseudo $R^2=0.470$ ; $p=0.001$				Pseudo $R^2=0.239$ ; $p<0.001$			
<i>Intercept</i>	-2.59	0.35	-7.35	<0.001	0.05	2.83	0.02	0.987
Flood index	0.18	0.07	2.54	0.011	0.00	0.02	-0.18	0.854
CV (daily variability, 1 year)	-0.01	<0.01	-2.00	0.045	-0.01	0.02	-0.40	0.692
Gwydir	1.48	0.70	2.12	0.034	0.14	3.08	0.05	0.963
Lachlan	-1.36	0.85	-1.61	0.107	0.06	3.36	0.02	0.986
Murrumbidgee	-4.23	1.32	-3.19	0.001	11.75	3.42	3.44	0.001
Warrego	-2.13	1.19	-1.79	0.073	-1.32	3.18	-0.42	0.677
Flood index × Gwydir	-0.18	0.11	-1.65	0.098	0.09	0.17	0.52	0.600
CV (daily) × Gwydir	0.01	0.01	0.85	0.397	0.01	0.02	0.30	0.761
Flood index × Lachlan	-0.29	0.11	-2.60	0.009	-0.04	0.10	-0.37	0.714
CV (daily) × Lachlan	0.02	0.01	2.66	0.008	0.01	0.02	0.38	0.706
Flood index × Murrumbidgee	-0.13	0.08	-1.69	0.092	0.06	0.03	2.04	0.041
CV (daily) × Murrumbidgee	0.03	0.01	2.00	0.046	-0.07	0.02	-2.82	0.005
Flood index × Warrego	4.28	0.90	4.78	<0.001	0.04	0.19	0.21	0.834
CV (daily) × Warrego	0.01	0.01	1.22	0.221	0.01	0.02	0.38	0.704
<i>Richness difference dissimilarity</i>	Pseudo $R^2=0.935$ ; $p<0.001$				Pseudo $R^2=0.087$ ; $p<0.001$			
<i>Intercept</i>	-2.51	0.11	-22.37	<0.001	-0.32	2.01	-0.16	0.872
Flood index	0.07	0.03	2.52	0.012	-0.01	0.02	-0.37	0.710
CV (daily variability, 1 year)	0.00	<0.01	-2.00	0.045	-0.01	0.01	-0.45	0.653
Gwydir	1.61	0.25	6.57	<0.001	-0.93	2.20	-0.42	0.673
Lachlan	-0.54	0.23	-2.29	0.022	-1.30	2.41	-0.54	0.590
Murrumbidgee	-0.89	0.30	-2.94	0.003	0.56	2.36	0.24	0.814
Warrego	1.20	0.26	4.63	<0.001	-1.55	2.28	-0.68	0.495

TABLE 3 (Continued)

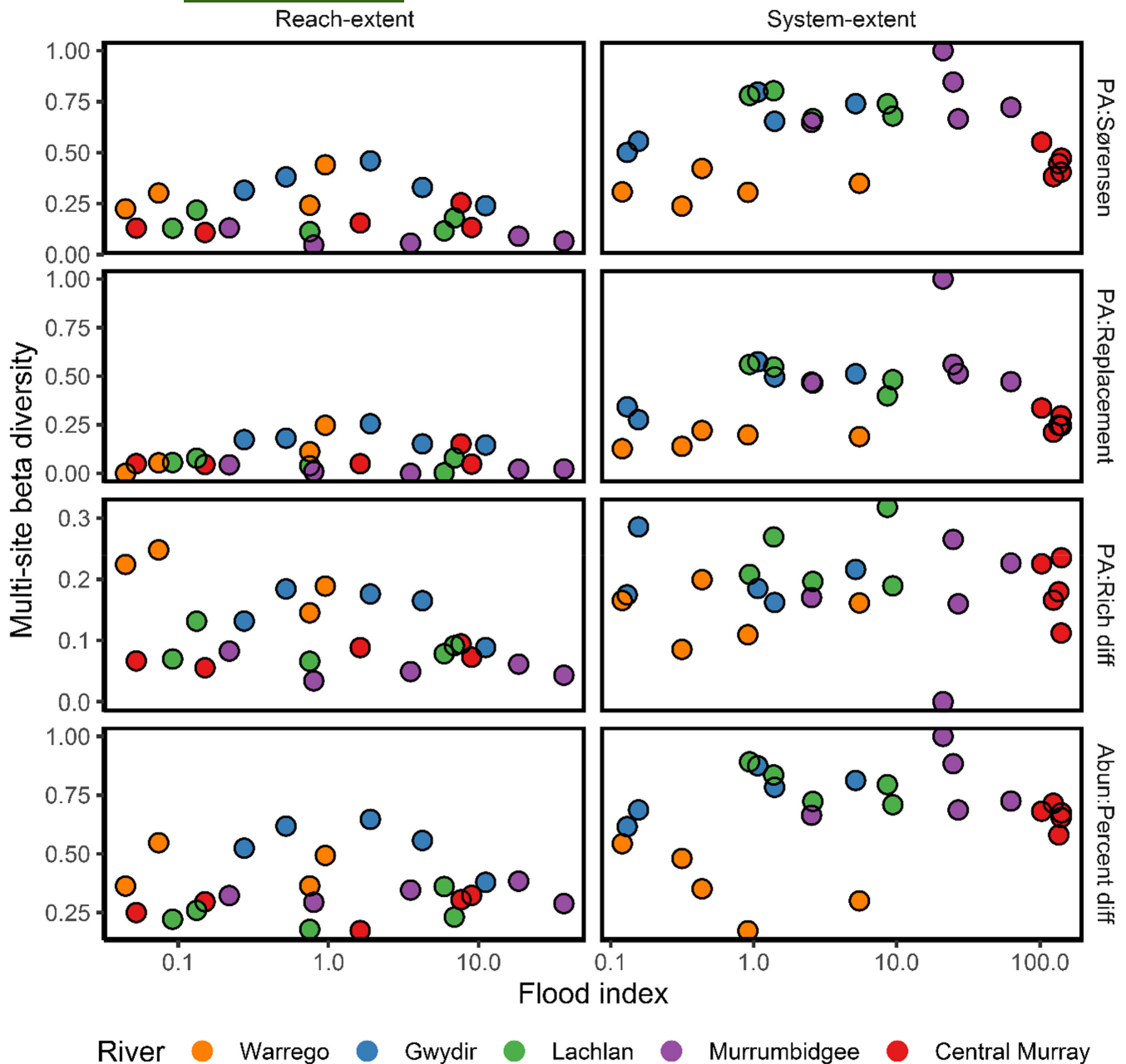
Predictors	Reach extent				System extent			
	Estimate	SE	Z	p	Estimate	SE	Z	p
Flood index × Gwydir	-0.04	0.04	-1.12	0.263	0.00	0.13	0.04	0.970
CV (daily) × Gwydir	0.00	<0.01	-1.33	0.184	0.01	0.01	0.44	0.663
Flood index × Lachlan	-0.08	0.03	-2.43	<b>0.015</b>	0.03	0.07	0.40	0.686
CV (daily) × Lachlan	0.01	<0.01	4.49	<b>&lt;0.001</b>	0.01	0.02	0.55	0.581
Flood index × Murrumbidgee	-0.07	0.03	-2.70	<b>0.007</b>	0.18	0.03	5.92	<b>&lt;0.001</b>
CV (daily) × Murrumbidgee	0.01	<0.01	2.88	<b>0.004</b>	-0.06	0.02	-2.91	<b>0.004</b>
Flood index × Warrego	-0.48	0.17	-2.77	<b>0.006</b>	0.03	0.14	0.22	0.826
CV (daily) × Warrego	0.00	<0.01	2.11	<b>0.035</b>	0.01	0.01	0.47	0.642
Abundance-based dissimilarity (percentage difference)	Pseudo $R^2 = 0.864$ ; $p < 0.001$				Pseudo $R^2 = 0.233$ ; $p < 0.001$			
Intercept	-1.21	0.16	-7.66	<b>&lt;0.001</b>	1.19	2.14	0.56	0.578
Flood index	0.02	0.04	0.48	0.631	-0.01	0.02	-0.33	0.742
CV (daily variability, 1 year)	0.00	<0.01	0.78	0.434	0.00	0.01	0.20	0.839
<i>Gwydir</i>	2.38	0.41	5.76	<b>&lt;0.001</b>	0.77	2.37	0.32	0.746
<i>Lachlan</i>	0.01	0.35	0.03	0.977	0.98	2.72	0.36	0.719
<i>Murrumbidgee</i>	0.07	0.36	0.19	0.848	11.03	2.82	3.91	<b>&lt;0.001</b>
<i>Warrego</i>	1.38	0.48	2.89	<b>0.004</b>	-2.84	2.37	-1.20	0.232
Flood index × Gwydir	-0.01	0.07	-0.09	0.928	0.07	0.15	0.44	0.662
CV (daily) × Gwydir	-0.01	<0.01	-2.08	<b>0.038</b>	-0.01	0.01	-0.41	0.685
Flood index × Lachlan	0.03	0.05	0.64	0.519	-0.08	0.09	-0.87	0.387
CV (daily) × Lachlan	0.00	<0.01	-0.59	0.554	-0.01	0.02	-0.36	0.720
Flood index × Murrumbidgee	-0.02	0.04	-0.54	0.590	0.07	0.02	2.84	<b>0.005</b>
CV (daily) × Murrumbidgee	0.00	<0.01	0.89	0.372	-0.08	0.02	-3.99	<b>&lt;0.001</b>
Flood index × Warrego	-0.25	0.33	-0.75	0.451	-0.17	0.13	-1.28	0.200
CV (daily) × Warrego	0.00	<0.01	-1.09	0.277	0.00	0.01	0.00	0.999

Note: Results are presented for tests done across the reach-scale and system-scale datasets. Significant values ( $p \leq 0.05$ ) are indicated in bold. In these tests, effects of spatial variables (rivers) (indicated in italics) are not of primary interest, but rather the interaction between hydrological variables and each river to determine if beta diversity–hydrology gradients are consistent among rivers or context dependent to rivers (as depicted in Figures 3 and 4).

Hydrology is a key driver of beta diversity within river systems (Larned et al., 2010; Rolls et al., 2018). Mechanistically, increasing discharge increases hydrological connectivity, thereby facilitating the dispersal of organisms in space, contributing to reduced environmental heterogeneity among locations within river systems and causing beta diversity to decline (Penha et al., 2017; Thomaz et al., 2007). Here, we found that inter-annual patterns of within-river beta diversity differed among rivers (at a given spatial extent of assessment), even though major flooding occurred in all study rivers during Spring 2016. For example, incidence-based beta diversity did not differ significantly among years in the Gwydir River at the system extent, whereas it was significantly lower in the Lachlan River in 2016–2017. These inconsistencies in inter-annual changes in beta diversity among rivers were apparent at both survey extents and for each aspect of beta diversity.

Scale-dependent patterns of beta diversity over time can be used to identify drivers of biodiversity change as biotic homogenisation

or biotic differentiation (Chase et al., 2020; Lindholm et al., 2020; Taylor et al., 2019). Our analyses revealed years of contrasting homogenisation and differentiation among fish assemblages within river systems. In both the Lachlan and Warrego rivers, fish assemblages showed significantly higher abundance-based beta diversity at the reach extent during individual years. In the central Murray River, however, we found strong evidence of lower abundance-based beta diversity in 2016/2017. These patterns were not apparent at the system extent for the same study rivers, where overall variation in within-river beta diversity was much less apparent. Changes in incidence-based beta diversity were more muted when compared to abundance-based beta diversity trends. These contrasting patterns of inter-annual beta diversity between incidence-based and abundance-based beta diversity can be hypothesised to occur if hydrological variability (e.g. flooding, drought) does not trigger change in species occurrence (via losses or gains; which would be detected by changes in incidence-based composition) among sites,

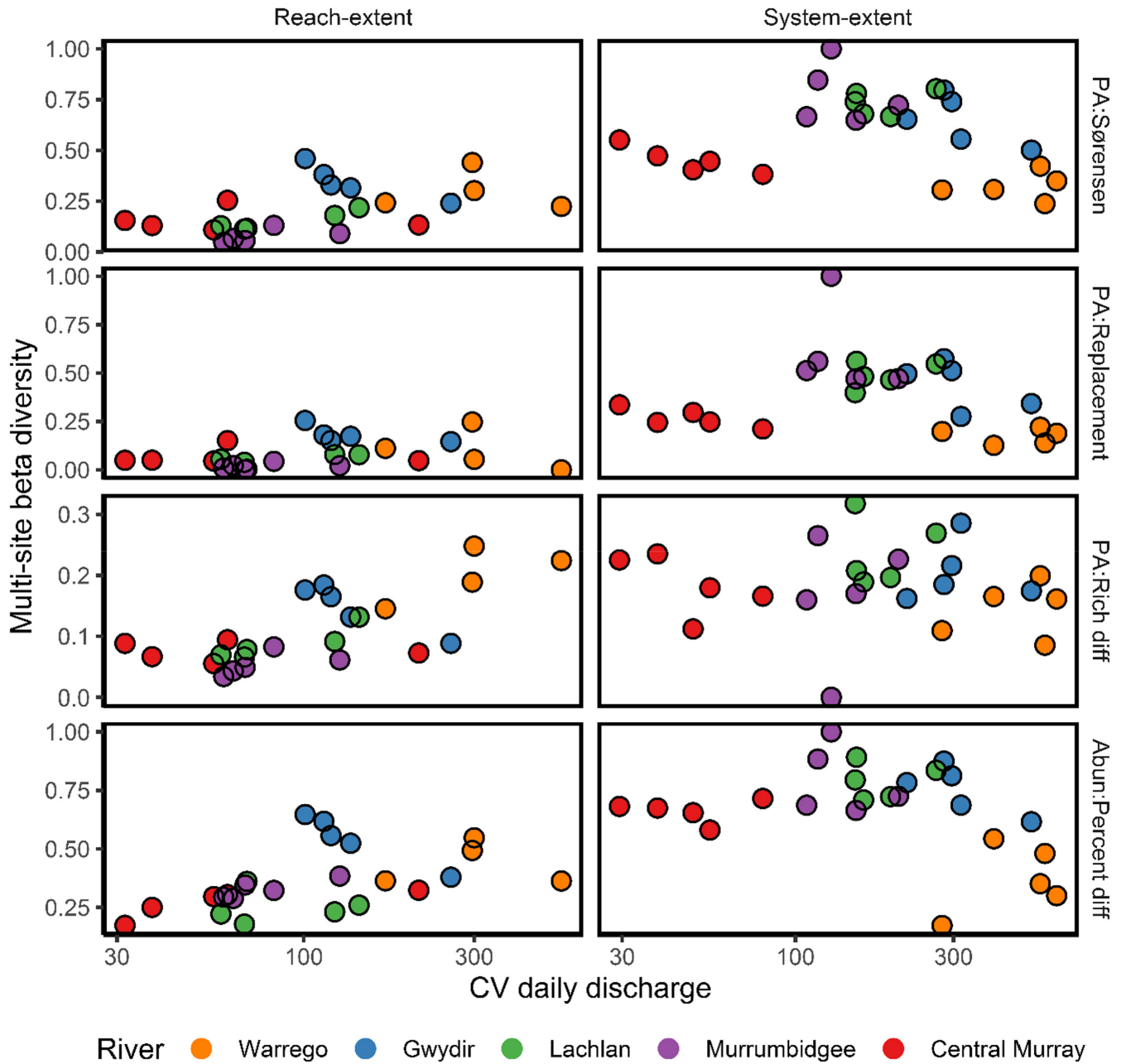


**FIGURE 4** Scatterplots illustrating the relationship between the mean flood index among study sites and multi-site beta diversity (as incidence-based Sørensen dissimilarity, replacement and richness components of incidence-based dissimilarity, and abundance-based 'percentage-difference' dissimilarity) spanning reach or system extents for five rivers of the Murray–Darling Basin. Each point on each plot represents values for each of 5 years of data (2014/2015–2018/2019). The y-axis depicts a gradient of low to high among-site beta diversity; therefore, allowing us to test if increasing flood severity was associated with lower beta diversity within some or all of the five study rivers. Note that relationships between flooding intensity and beta diversity were inconsistent (i) across spatial extents and (ii) among rivers for different aspects of beta diversity.

yet is associated with patchiness in population dynamics associated with hydrological variability that would be reflected in temporal changes in abundance-based beta diversity. In other river systems worldwide, contrasting trends of homogenisation or differentiation have been revealed for fish assemblages when compared at different spatial extents and between incidence- and abundance-based beta diversity (e.g. Taylor et al., 2019). These findings provide strong evidence that conclusions about biodiversity trends (as homogenisation

and differentiation) depend heavily on (i) the spatial extent of analysis and (ii) what aspects of assemblage dissimilarity are used to quantify beta diversity.

The finding that temporal variation in fish assemblage composition and beta diversity varied at different spatial extents has implications for the design of monitoring programmes and interpretation of data resulting from those programmes. We found significant temporal variation in assemblage composition within most rivers when



**FIGURE 5** Scatterplots illustrating the relationship between daily discharge variability (as coefficient of variation) for each year and values for multi-site beta diversity (as incidence-based Sørensen dissimilarity, replacement and richness components of incidence-based dissimilarity and abundance-based ‘percentage-difference’ dissimilarity) for five rivers of the Murray–Darling Basin. Relationships are plotted separately for the ‘reach’ and ‘system’ spatial extent covered by each fish assemblage dataset. The y-axis depicts a gradient of low to high among-site beta diversity; therefore, allowing us to test if increasing antecedent discharge variability was associated with lower beta diversity within some or all of the five study rivers. Note that relationships between flooding intensity and beta diversity were inconsistent (i) across spatial extents and (ii) among rivers for different aspects of beta diversity.

assessed at the reach extent but not at the river system extent, suggesting that interventions applied at relatively fine scales (e.g. river reaches) do not ‘scale up’ to broader extents (e.g. entire river systems). For example, where environmental flows (e.g. hydrological manipulations designed to support ecosystems and biodiversity) are delivered to segments of rivers to address the impacts of hydrological alteration (e.g. King et al., 2009; Thompson et al., 2018). Hydrological alteration itself impacts aquatic ecosystems and the results manifest

throughout entire river networks (Arthington, 2012; Palmer & Ruhi, 2019) meaning that relatively fine-scaled interventions, such as the delivery of environmental flows to lowland portions of river networks, may not lead to change in assemblage composition at broader spatial scales. One hypothesis worthy of examination is that the time scale of assemblage compositional response to hydrological variability may be positively associated with the spatial extent at which assemblages are monitored. If this hypothesis holds true,



**TABLE 4** Summary of the three questions, analytical approaches used and key findings of our study examining scale-dependent changes in spatial beta diversity of fish assemblages and hydrology–beta diversity relationships across five rivers of Australia's Murray–Darling Basin.

Study question	Approach	Key finding
1. Are temporal trends in spatial beta diversity among river systems consistent across spatial extents or scale dependent? (Table 1, Figure 2)	Two-factor (crossed) PERMANOVA design testing for differences in fish assemblage composition among rivers ( $n=5$ ) over time ( $n=5$ years), with tests repeated for datasets spanning river reaches or entire river systems.	Inter-annual variation in assemblage composition was inconsistent among rivers when assessed at the extent of <i>river reaches</i> , especially for abundance-based dissimilarities. At the extent of <i>whole river systems</i> , fish assemblage composition differed significantly among rivers, yet did not show significant change over time (Table 1, Figure 2).
2. Is within-river beta diversity of fish assemblages more pronounced or evident when quantified over particular spatial extents?	Two-factor (crossed) test of homogeneity of dispersions (PERMDISP) testing for differences in spatial variation in fish assemblage composition within rivers ( $n=5$ ) over time ( $n=5$ years), with tests repeated for datasets spanning river reaches or entire river systems.	Incidence-based beta diversity showed significant temporal change among years in two of the five study rivers, with species replacement among sites the primary driver. Inter-annual variation in abundance-based beta diversity was more pronounced at the extent of river reaches (vs. whole river systems), and temporal changes in within-river beta diversity were inconsistent among rivers (Table 2, Tables S3–S6).
3. Are hydrology – beta diversity relationships consistent among river systems and across spatial extents?	Multi-site dissimilarities calculated among fish assemblages within each tributary system ( $n=5$ ) and each year ( $n=5$ ) at either reach or system spatial extents. Beta regression models were then built to test the significance and strength of relationships between within-river beta diversity (as multi-site dissimilarities) and two hydrological variables (1. Coefficient of variation in daily discharge over 1 year prior to sampling, and 2. Flood index, as the duration (days) of the most recent flow event greater than $0.5\times$ the 40-year mean daily discharge, divided by the time (days) since the last flood	Ecohydrological relationships between hydrological gradients and fish beta diversity were stronger when assessed at the extent of river reaches compared to whole river systems. For some rivers, ecohydrological relationships switched direction between reach versus system-extent spatial scales (Table 3, Figures 3 and 4).

then this highlights that monitoring effort over time (frequency and duration) requires careful consideration by researchers and managers to detect true responses to the intervention or event of interest (e.g. flooding).

Spatial scaling (*sensu* Wiens, 1989; Levin, 1992) is fundamental to understanding patterns and drivers of variation in beta diversity, yet paradoxically such concepts appear to have not been explicitly considered in ecohydrology research examining multi-scaled patterns of beta diversity linked with hydrological gradients or hydrological alteration. Consequently, researchers and conservation managers are unable to determine if environmental gradients consistently influence beta diversity across multiple spatial extents, or rather, if a particular environmental driver (e.g. flooding) affects patterns (or temporal variability) of spatial beta diversity at one specific spatial extent (Lansac-Tôha et al., 2021). Despite our findings showing highly variable patterns of beta diversity among five study rivers, our study provides a useful framework for future research aimed at understanding drivers of change in beta diversity across spatial scales, including different spatial grains and extents.

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## CONFLICT OF INTEREST STATEMENT

The authors of this article declare that there is no conflict of interest and that funders had no role in the planning, implementing or reporting the study.

## DATA AVAILABILITY STATEMENT

All data used in this research are publicly available (sources provided in the Methods). The Long-Term Intervention Monitoring dataset were made available from the Commonwealth Environmental Water Office. The Murray–Darling Basin Fish and Macroinvertebrate Survey dataset is available at [www.data.gov.au](http://www.data.gov.au). Streamflow data used here are available from the New South Wales Department of Primary Industries – Water and the Queensland Department of Natural Resources and Mines.

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#### BIOSKETCH

**Robert J. Rolls** is an aquatic ecologist predominantly interested in how hydrology influences riverine biodiversity and ecosystem processes across broad spatial scales, and the translation of ecosystem science into the decision-making related to human impacts to river and estuary systems.

**Author Contributions:** RJR conceived the original research idea, analysed the data and led the writing. All authors contributed to the ideas and writing of the manuscript.

#### SUPPORTING INFORMATION

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

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