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RESEARCH ARTICLE OPEN ACCESS

Environmental and Biological Drivers of Fish Beta Diversity and Tropical River Conservation in Northern Australia

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ABSTRACT

Aim: This study examines how species traits and landscape features shape beta diversity in Northern Australia's freshwater fish communities, with implications for identifying high-conservation-value river basins.

Location: Northern Australia's freshwater ecosystems, covering 58 river basins draining into the Timor Sea, Arafura Sea, Gulf of Carpentaria, and Coral Sea.

Methods: We analysed four species-level traits—saltwater tolerance, body size, body shape, caudal throttle, and habitat use—to assess their influence on beta diversity at the river basin scale. Additionally, we examined five landscape features—basin area, elevation, terrain slope, ruggedness, and floodplain connectivity—using beta regression analysis to identify significant predictors of beta diversity.

Results: A total of 138 freshwater-associated fish species were recorded, including 76 freshwater-exclusive, 27 freshwater-brackish, and 35 diadromous species. Saltwater tolerance was a key driver of beta-diversity, with diadromous species showing higher Species Contribution to Beta Diversity (SCBD) values, indicating their role in connecting aquatic communities. Freshwater obligates contributed less to SCBD, highlighting their restricted distributions and endemism. Steeper, more rugged basins had higher species turnover, while floodplain connectivity did not homogenise fish communities as expected. Species-rich basins did not necessarily correspond to lower turnover, indicating unique assemblages, while high-nestedness basins were dominated by common species. Sites with intermediate nestedness and high alpha diversity act as biodiversity reservoirs.

Main Conclusions: Species traits and landscape complexity shape fish beta diversity in Northern Australia. Saltwater tolerance and topography strongly influence species distribution, while obligate freshwater species contribute significantly to regional diversity. Conservation strategies should prioritise basins with unique species compositions and biodiversity reservoirs, particularly the Daintree, Victoria, Daly, Finniss, and Roper rivers, to maintain ecological distinctiveness and resilience amid increasing development pressures.

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1 | Introduction

Australia's freshwater fish fauna, shaped by its long geological isolation since separating from Antarctica 45–32 million years ago (Huston et al. 2012), is as distinctive as its unique mammalian fauna. Similar to how geological isolation has resulted in the dominance of marsupials over eutherians in its mammalian fauna, Australia's freshwater fish communities are primarily composed of marine-derived acanthopterygians, unlike other global freshwater systems dominated by ostariophysans (Unmack 2013). Australia's arid climate and unpredictable hydrology have led to a relatively depauperate fish fauna (Allen et al. 2002), yet many species have evolved unique adaptations to persist in these challenging environments. The persistence of populations and species under environmental and climate change is influenced by ecological and demographic processes across their geographic range, as well as their adaptation to local temperature and hydrological regimes (Polechová et al. 2009). Understanding regional and local diversity patterns in freshwater fish provides insights into historical ecological processes and helps predict species responses to environmental change and future climate scenarios.

Northern Australia harbours approximately 60% of the continent's freshwater fish species within only 17% of its land area (Unmack 2001; Pusey et al. 2004), yet research has primarily focused on the Southeast, particularly the Murray-Darling Basin. Most studies in the region have been concentrated around the Darwin Region in the Northern Territory and in Queensland's Wet Tropics, leaving many rivers understudied. These diverse aquatic ecosystems, including floodplain-river systems and deeply incised bedrock rivers in upland plateaus (Pettit et al. 2017), largely remain free-flowing and in good ecological condition due to minimal historical water development (Woinarski et al. 2007; Warfe et al. 2011). However, growing threats such as hydrological alterations, changes in fire regimes, the spread of terrestrial weeds and feral animal pests, poorly managed grazing, land clearing, and invasive fish species are putting pressure on these systems (Douglas et al. 2005; García-Díaz et al. 2018). Increasing interest in water resource development (Hart et al. 2020) further complicates conservation efforts, highlighting the urgent need for a better understanding of Northern Australia's freshwater ecosystems (Pettit et al. 2017).

Biological diversity measures are essential for understanding ecological and evolutionary processes (Magurran and McGill 2011). Diversity is typically assessed through alpha diversity (local species richness) and beta diversity (variation in species composition among sites). While alpha diversity is widely used, its limitations as a biodiversity indicator are increasingly challenged for its insensitivity (Hillebrand et al. 2018), leading to an increased recognition of beta diversity's importance in community ecology (McGill et al. 2015). Beta diversity provides insights into biodiversity determinants (Soininen et al. 2007) and is crucial for informing conservation planning (Socolar et al. 2016), including assessing biodiversity loss (Karp et al. 2012), guiding protected area designation (Gering et al. 2003; Wiersma and Urban 2005), managing invasive species (Powell et al. 2013), and informing

landscape management practices (Gabriel et al. 2006; Edwards et al. 2014). As a result, beta diversity is increasingly valued as a key tool for regional conservation strategies in a changing world (Socolar et al. 2016).

Partitioning beta diversity into turnover and nestedness components offers a nuanced understanding of species distribution patterns, highlighting mechanisms of species replacement and loss (Baselga 2010). Nestedness occurs when species assemblages of sites with fewer species contain subsets of assemblages from richer sites, reflecting either progressive species loss or accumulation across habitats (Baselga 2010). In contrast, turnover represents species substitutions across areas due to environmental or geographical constraints (Baselga and Orme 2012). Decomposing beta diversity into nestedness and turnover components helps identify the processes shaping biodiversity and informs conservation strategies (Monadjem et al. 2023). For instance, distinguishing between nestedness and turnover patterns is essential for biodiversity management because they necessitate opposed conservation strategies (Wright and Reeves 1992). While nestedness suggests prioritising a few species-rich sites for conservation, turnover requires protecting multiple sites to preserve unique species assemblages.

The Species Contributions to Beta Diversity (SCBD) metric indicates the relative importance of individual species to beta diversity, highlighting those that drive community dissimilarity or require conservation attention (Heino and Grönroos 2016; Legendre and De Cáceres 2013). Empirical studies show that SCBD values are typically higher for species with broad but variable distributions (Heino and Grönroos 2016; Legendre and De Cáceres 2013) and may be linked to species' biological traits such as body size, diet, and dispersal capacity. This metric identifies key species shaping beta-diversity patterns, providing insights into the ecological processes underlying community composition (Heino and Grönroos 2016).

The interplay between species dispersal mechanisms and landscape plays a crucial role in shaping beta-biodiversity patterns in freshwater ecosystems (Griffiths 2017). Traits like body size, elongation, caudal fin area, caudal peduncle width, and habitat use enhance swimming speed and long-distance movement (Villéger et al. 2017; Comte and Olden 2018). Furthermore, salinity tolerance in freshwater fishes may influence dispersal across river basins via the sea or coastal waters, as diadromous species with high salt-water tolerance can traverse marine environments to reach isolated freshwater systems (Cano-Barbacid et al. 2022). In many ecosystems, topographic complexity has been shown to modulate species diversity by shaping habitat heterogeneity, dispersal constraints, and species interactions (Thormann et al. 2018). Studies in montane and island environments indicate that fine-scale topographic variation contributes to turnover-driven beta diversity (Schmitt et al. 2021). Applying these concepts to freshwater ecosystems is particularly relevant, as terrain heterogeneity, hydrological connectivity, and species dispersal ability interact to shape fish community structure across river basins. In the monsoonal tropics, wet season flooding connects the floodplains and mouths of many river systems in the Northern Territory, potentially leading

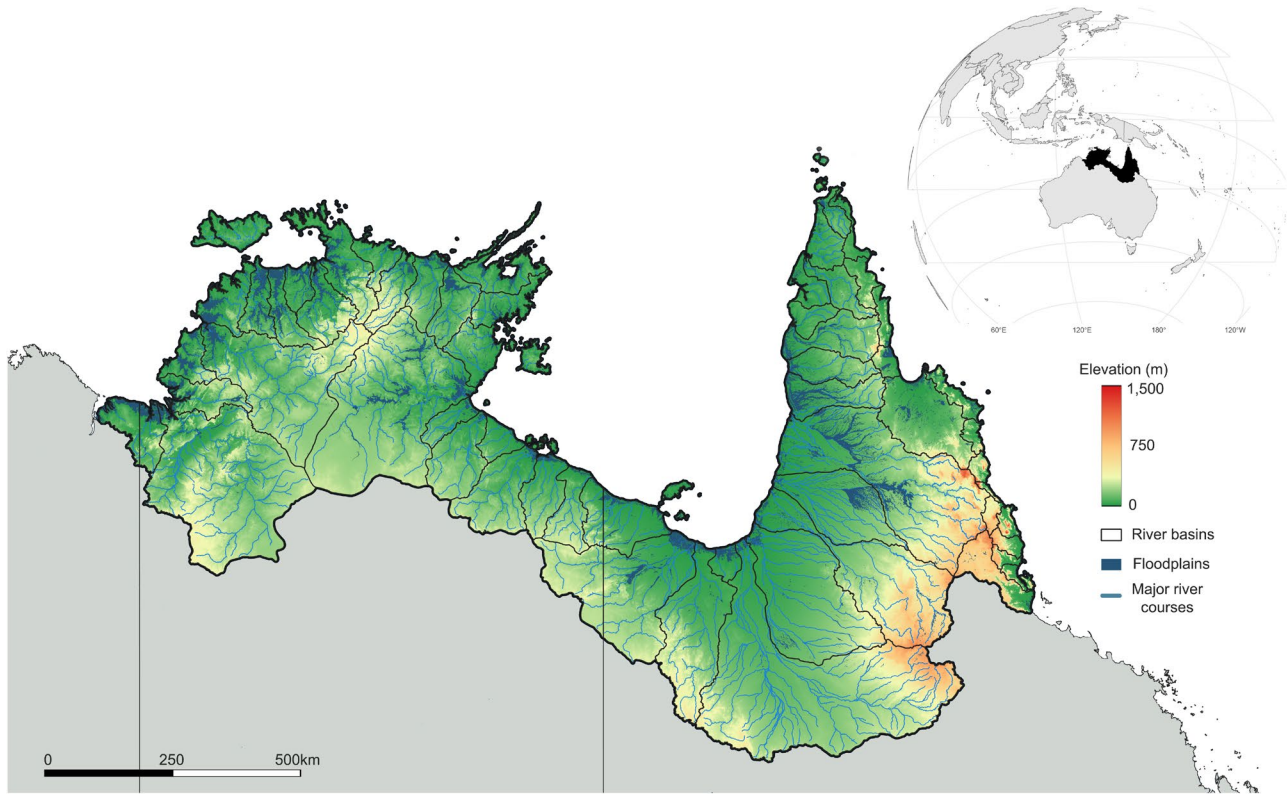


FIGURE 1 | Map of the study region depicting elevation, floodplain areas, and major river courses. Black lines delineate individual river basins.

to greater nestedness values due to easier species movement and the potential for community homogenisation (Lubinski et al. 2008). Conversely, rugged landscapes act as barriers to fish movement, fostering species turnover and endemism (Zbinden and Matthews 2017). Understanding how topographic variation affects fish beta diversity is crucial for conservation planning and management. Conservation strategies should prioritise distinctive habitats in high-relief areas to protect endemic species and maintain longitudinal connectivity in flatter regions to support biodiversity.

Despite its importance for conservation, patterns of beta diversity for freshwater fish in Northern Australia remain largely understudied. This gap is particularly alarming, considering Northern Australia's globally distinctive freshwater fish faunal composition, along with the increasing pressures from water resource development and climate change. This study aims to: (i) Characterise beta diversity patterns of freshwater fish species across river basins in Northern Australia, thereby providing a baseline understanding of species composition and distribution; (ii) Assess how species traits, such as body size, body shape, fin morphology, habitat use and saltwater tolerance, influence beta diversity through dispersal and landscape connectivity; and (iii) Examine the effects of topographic variation, specifically the effects of area, elevation, topographic relief and terrain ruggedness, on species turnover and nestedness. The outcomes of this study will inform conservation planning by identifying biodiversity reservoirs—basins with high species richness and nestedness that can replenish impacted populations—and high-turnover basins that harbour unique, often endemic species requiring targeted protection.

2 | Methods

2.1 | Study Area

For purposes of this study, Northern Australia encompasses the region delineated by 58 river basins that discharge into the Timor Sea and the Arafura Sea, collectively called the Australian Water Resources Council (AWRC) Timor Sea Drainage Division. This area also includes the Gulf of Carpentaria (AWRC Gulf drainage Division) and parts of the Cape York Peninsula rivers that flow into the Coral Sea, which belong to a section of the AWRC North-east Coast drainage Division (Figure 1). The western boundary of our study area is marked by the Keep River, while the eastern boundary is demarcated by the basin formed by the Herbert and Murray Rivers on the eastern side of Cape York Peninsula.

2.2 | Species List and Geographic Distributions

We created species lists for each basin in the area delineated above using species distribution data for the region published by Pusey et al. (2017), which provided approximately 97% of the fish records and complemented them with the Atlas of Living Australia (ALA) records. Each basin was treated as an independent sampling unit in the analysis. Defining a freshwater species in Northern Australia is challenging, not only because approximately one-third of the fauna migrates between freshwaters and estuaries for breeding, but also due to the region's significant tidal range and coastal flatness, which facilitates the ingress of marine and estuarine species into what is often freshwater communities. As a result, many estuarine or near-shore marine

fishes penetrate beyond the estuarine zone into freshwater habitats. Here, we adopted a broad definition of a freshwater fish to include species that can reproduce in freshwater, diadromous species that primarily inhabit freshwaters, and those with marine or estuarine habitats that were observed more than 20 km upstream from a river mouth (Pusey et al. 2017).

2.3 | Species Traits

We collected data on four biological traits influencing fish movement and dispersal ability: saltwater tolerance, maximum body size, body shape (elongation factor), and caudal peduncle throttle. Species with higher saltwater tolerance may circumvent river basin boundaries by moving between river mouths and estuaries via shore waters. Saltwater tolerance levels were inferred from data on the habitat preferences of the studied fish species (Cano-Barbacid et al. 2024). Specifically, information on their utilisation of freshwater, brackish, and marine environments was collected by executing queries via the *species()* and *ecology()* functions within the 'rfishbase' package in R (Boettiger et al. 2012), which allowed for the extraction of habitat usage information. 'rfishbase' is a programmatic interface to [FishBase.com](https://fishbase.org/), a global database that provides extensive information on fish species (Froese and Pauly 2014). The habitat matrix retrieved for the species under study featured three columns (Freshwater, Brackish, and Marine), indicated by 1s and 0s to show a species' presence in those habitats. Species were classified by their saltwater tolerance into (i) exclusive to freshwater environments, (ii) inhabiting both freshwater and brackish waters (estuaries), and (iii) inhabiting both freshwater and marine waters (diadromous). We also used morphological traits that are assumed to influence fish long-distance movement, which affect their dispersal capacity (Villéger et al. 2017), such as body size (maximum body length), body shape (also referred as elongation factor, that is, the ratio between the body height and body length), and caudal peduncle throttle (the ratio between the caudal peduncle depth and the caudal fin height). Morphological trait data were obtained from published databases (Brosse et al. 2021).

2.4 | Topographic Variables

Our study employed digital elevation data to assess topographic heterogeneity across river basins. Specifically, we utilised the Shuttle Radar Topography Mission (SRTM) 1 ArcSecond global digital elevation model, which offers a spatial resolution of 30 m. The vertical accuracy of this dataset is approximately ± 16 m at a 90% confidence level. The raster data, encompassing a size of 1° , were acquired from EarthExplorer, provided by the United States Geological Survey (USGS). Given the large spatial extent of our study area, suitable datasets that offer both high resolution and extensive coverage are limited, making the SRTM data an ideal choice. Using QGIS software (version 3.30), we processed the elevation data to extract four primary topographic variables: basin area, elevation, slope, and terrain ruggedness. Elevation data is a fundamental measure of elevational variation, critical for understanding geographical isolation and its ecological impacts. Slope was computed to determine the angle of inclination across the landscape, reflecting the steepness of the terrain. The

slope calculation used the elevation differences between each cell and its eight surrounding neighbours in a 3×3 grid, corresponding to a 30 m distance. This metric is pivotal in evaluating basin connectivity and potential barriers to species exchange. Terrain Ruggedness Index (TRI) was calculated to quantify the variability in elevation, indicative of the landscape's irregularity. This variable, derived from the elevation data, offers insights into the topographic complexity of each basin. Digital elevation maps were processed with QGIS (ver. 3.30).

In addition to the primary topographic variables, our study incorporated floodplain connectivity as a predictor variable for beta diversity. We measured floodplain connectivity by overlaying a floodplain's shapefile, specifically the Floodplain_250K.shp onto the river basin map. Both the floodplain's and the river basin map—named CatchmentBoundaries_250K.shp—were obtained from Geoscience Australia (Crossman and Li 2015). A visual inspection was performed to determine instances where floodplains intersected basin boundaries. River basins intersected by floodplains were categorised as having overlapping floodplains and were assigned a "yes" designation, whereas basins without overlapping floodplains received a "no" designation. We anticipate that basins with overlapping floodplains will exhibit higher nestedness relative to basins with no overlapping floodplains due to the enhanced habitat connectivity facilitating species presence across adjacent basins.

2.5 | Beta-Diversity and Its Components

To investigate the patterns of species composition across our study area, we first organised the species presence-absence data from each basin into a matrix. This allowed us to determine the species richness for each basin, defined as the number of distinct species identified. Our analysis then extended to assessing the beta diversity among basins, examining all possible pairwise combinations of basins to capture the full spectrum of compositional dissimilarity within the study area. Adopting the framework proposed by Baselga (2010), we decomposed the total beta diversity into two fundamental components: nestedness (β_{nes}) and turnover (β_{sim}). This decomposition is predicated on the calculation of pairwise Sorensen beta diversity (β_{sor}), which measures overall compositional dissimilarity between basin pairs. The relationship among these components is defined by the equation $\beta_{sor} = \beta_{nes} + \beta_{sim}$, illustrating that total beta diversity can be understood as the sum of its nestedness and turnover components. These metrics vary from 0 to 1, where 0 signifies no beta diversity (identical species compositions between basins) and 1 denotes maximum beta diversity (completely dissimilar species compositions). For the computation of these beta diversity metrics, we utilised the 'betapart' package in R (Baselga and Orme 2012), calculating average beta diversity values between site pairs over sampling events for each component.

Further, we quantified the Species Contributions to Beta Diversity (SCBD) to evaluate the extent to which individual species contribute to the overall beta diversity observed across the system. Species with higher SCBD values indicate unique or distinctive species compositions that significantly influence the beta diversity within the ecosystem, offering insights into the relative importance of individual species to the system's overall

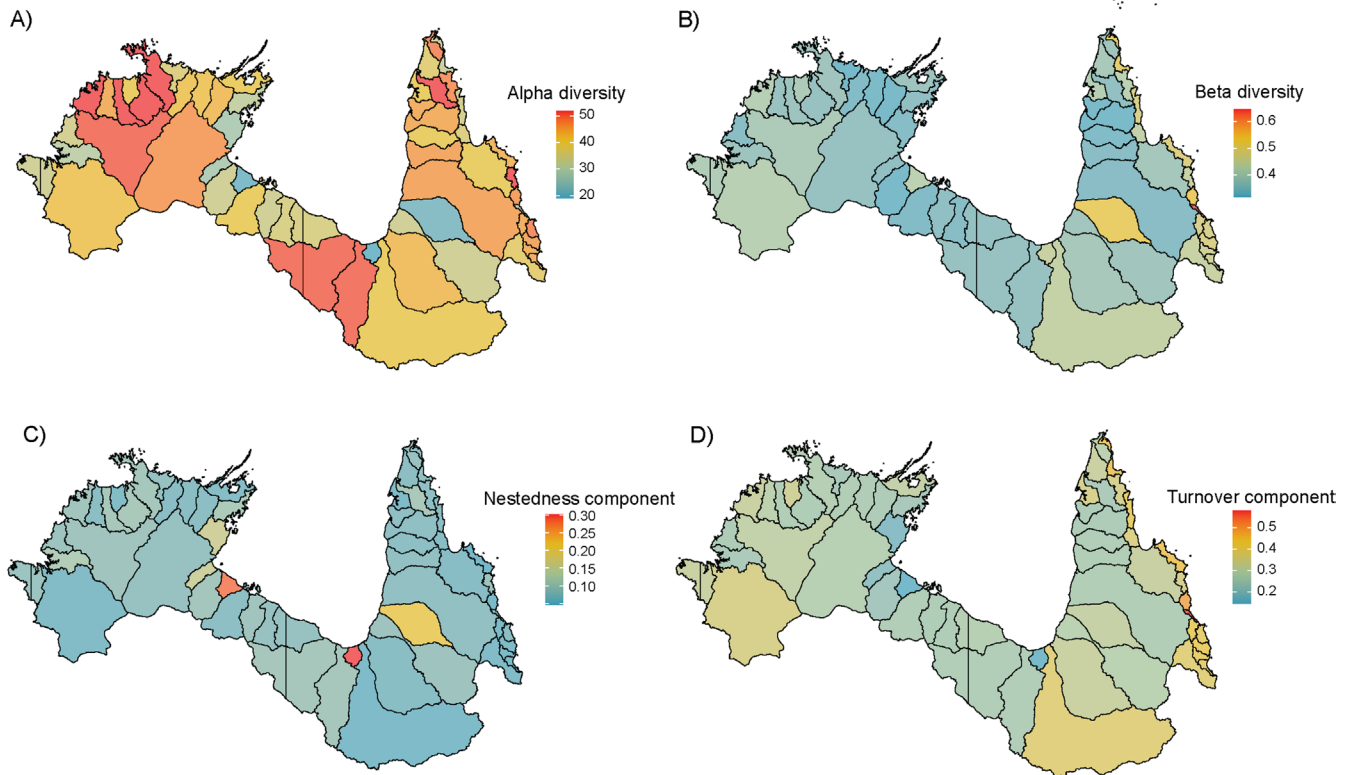


FIGURE 2 | Spatial distribution of diversity components in freshwater fishes across Northern Australia. (A) Alpha diversity, indicated by species richness per basin; (B) Beta diversity, represented by the variation in species composition among basins; (C) The Nestedness component of beta diversity depicts species loss or gain across basins; (D) The Turnover component of beta diversity illustrates species replacement between basins.

beta diversity. SCBD values were calculated using the ‘adespatial’ package in R (Dray et al. 2017).

2.6 | Statistical Modelling

We employed beta regression as our primary modelling method to analyse our response variables (beta diversity turnover/nestedness and SCBD), which varied between 0 and 1. Beta regression is particularly suited for modelling data that are proportions or rates, lying strictly between 0 and 1. We utilised the beta regression with a logit link function for our analyses, following the methodology outlined by Cribari-Neto and Zeileis (2010). We conducted two separate beta regression analyses. Initially, SCBD was related to species traits. Subsequently, we explored the variation in turnover and nestedness across topographic variables through the same analytical approach. These analyses were performed using the *betareg* function from the R package ‘betareg’ (Cribari-Neto and Zeileis 2010). We employed a model-averaging technique to refine our estimation of the model coefficients for each explanatory variable (Anderson 2007). This approach involves averaging models generated from all possible combinations of predictor variables to mitigate model selection uncertainty and account for model variability in the estimation process. Given the potential for multicollinearity, particularly between the topographic variables slope and TRI, which are known to be correlated, we applied a Variance Inflation Factor (VIF) threshold of 5 for excluding models with correlated predictors. This exclusion criterion was implemented to ensure the

robustness and reliability of our model averaging results, preventing the distortion of effect sizes due to multicollinearity (Dormann et al. 2013). For the model-averaging process, we utilised the conditional model averaging approach, which focuses on averaging over models where the predictor variable of interest is present. This method was selected to provide a more accurate estimate of the effect sizes for variables included in the models by considering only the subset of models that contain the variable in question. This process was carried out using the ‘MuMIn’ package in R, which facilitated the exploration of model subsets and the computation of weighted averages of model parameters based on their Akaike information criterion (AIC) values (Burnham and Anderson 2002).

3 | Results

This dataset recorded 138 freshwater-associated fish species from the 58 river basins. Of these, 76 species were classified as freshwater exclusive, 27 as freshwater and brackish, and 35 as diadromous. Alpha diversity (Figure 2A) is highly variable across basins but does not exhibit spatial clustering nor a correlation with basin total area or floodplain extent (Figure S1). Regions with higher species richness are dispersed throughout the study area. Total beta diversity (Figure 2B), in contrast, displays relatively low variability among basins and similarly shows no correlation with basin total area or floodplain extent (Figure S1).

The analysis of species traits demonstrated that saltwater tolerance significantly influenced the SCBD. Specifically,

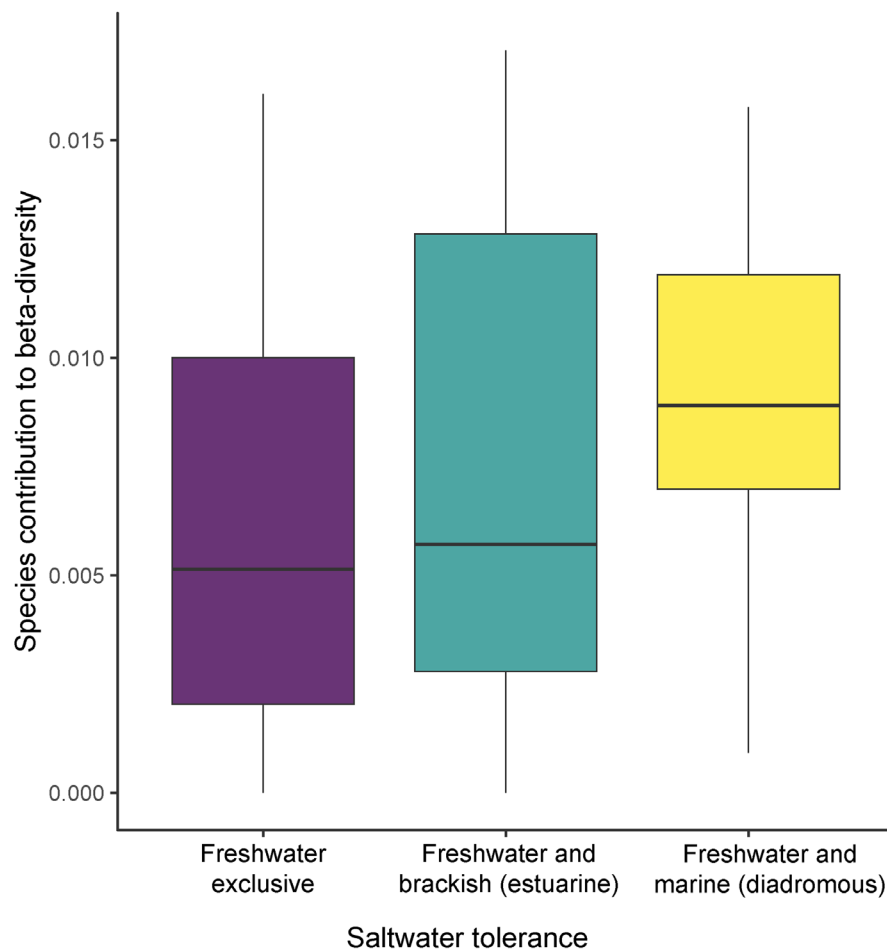


FIGURE 3 | Comparison of SCBD based on saltwater tolerance categories. The boxplots illustrate the SCBD for species exclusively found in freshwater (purple), species inhabiting both freshwater and brackish (estuarine) environments (teal), and diadromous species found in both freshwater and marine environments (yellow). The observed trend suggests that species with greater saltwater tolerance—those capable of dispersing through coastal seas or shoreline habitats—have higher SCBD values. This pattern implies that species associated with marine environments are likely to be more widespread and exhibit greater variability, thereby significantly influencing beta diversity in freshwater ecosystems.

diadromous species, which tolerate both marine and freshwater environments, showed higher SCBD values, indicating a substantial impact on community dissimilarity across sites (Figure 3). Conversely, freshwater obligate species exhibited lower SCBD values, suggesting a tendency towards restricted ranges and endemism to fewer basins. Interestingly, the morphological traits included in the analyses (body size, body shape, and caudal throttle) were not significantly associated with the SCBD (Table 1; Figure 4B; and Figure S2).

The results indicated a significant relationship between the turnover component of beta diversity and topographic variables such as slope and terrain ruggedness (Table 2 and Figure 4A). Basins with steeper slopes and greater terrain ruggedness exhibited higher turnover values, reflecting ecologically distinctive fauna. While elevation and the presence of overlapping floodplains exhibited strong trends in univariate analyses (Figure S3), they were not statistically significant in the multivariate models that included slope or ruggedness (Table 2 and Figure 4A).

Finally, Figure 5 illustrates the relationships between alpha diversity, beta diversity turnover, and nestedness components across the individual river basins. Basins with higher alpha

diversity did not consistently exhibit lower turnover values, indicating that even species-rich areas can vary considerably in species composition between them. Conversely, basins with high nestedness values tended to have lower species richness, suggesting that these areas have fewer species recorded and they are common. Basins with intermediate nestedness values and high alpha diversity contain a large number of species that are common across different sites.

4 | Discussion

This study uncovered patterns of beta diversity among freshwater fish fauna in Northern Australia. We found that a species-specific trait, saltwater tolerance, significantly impacts SCBD. The capacity of diadromous fish to disperse across basins via coastal and estuarine waters enables them to circumvent traditional land barriers to freshwater organisms' dispersal. Our findings also highlight the influence of topographic features on the ecological dynamics of river basins. Terrain slope and ruggedness emerged as determinants of the patterns of turnover and nestedness components of beta diversity. These topographic features likely function as natural barriers that limit freshwater

species dispersal and promote the development of distinct fish communities across different river basins.

The significant influence of saltwater tolerance on the SCBD underscores the adaptive capacity of diadromous species to exploit diverse habitats. The ability of diadromous species to

TABLE 1 | Summary of the averaged beta regression models for species trait predictors of species contributions to beta diversity in freshwater fish of Northern Australia's river basins.

Term	Estimate	Adj. Std. Error	z-value	p-value
(Intercept)	−5.083	0.170	29.869	<0.001
Saltwater tolerance				
<i>brackish (estuarine)</i>	−0.160	0.229	0.733	0.463
<i>marine (diadromous)</i>	0.750	0.219	3.422	<0.001
Max. body size	−0.038	0.081	0.468	0.639
Elongation factor	0.142	0.098	1.450	0.146
Caudal fin throttle	−0.069	0.095	0.732	0.190
Phi	70.250	11.933	5.887	<0.001

Note: The table presents estimates, adjusted standard errors, z-values, and p-values for the trait predictors: Saltwater tolerance (with freshwater exclusivity as the baseline comparison level and categories for brackish and marine habitat use), maximum body size, elongation factor, and caudal fin throttle. The phi coefficient, representing the precision parameter of the beta distribution, is also included. A significant phi coefficient denotes a precise estimation of variability in species contributions to beta diversity. Trait predictors yielding p-values below 0.05 are deemed statistically significant and are denoted in bold.

disperse across river basins using shore waters, circumventing terrestrial barriers typical to freshwater fish, amplifies their role in connecting disparate aquatic communities (Cano-Barbacid et al. 2022) and enables them to maintain populations across varied ecological zones, enhancing their distribution and influence on community dissimilarity. Saltwater tolerance thus not only facilitates widespread dispersal through habitat generalism but also allows these species to bridge ecological gaps between isolated freshwater systems. Conversely, freshwater obligate species exhibited lower average SCBD values, indicating that the majority of these species occupy relatively fewer basins. Their movement is constrained by terrestrial barriers, particularly in rugged terrain, which impedes their ability to traverse across river basins (Dias et al. 2014). This limited dispersal capacity often results in more localised distributions and potentially higher rates of endemism among freshwater obligate species, contributing to distinct community compositions across basins.

A key knowledge gap remains regarding whether diadromous species migrate to the same rivers as their parents, or if their dispersal is more random (Crook et al. 2016). This uncertainty has significant implications for understanding the role of large river basins in maintaining regional fish populations. It is possible that larger river basins, such as the Daly or Flinders rivers, serve as primary sources of colonisers that disperse across smaller river systems, sustaining fish populations and driving regional beta diversity patterns. If true, this would suggest that conservation efforts should prioritise these major rivers as hubs for species dispersal and recruitment. Future research integrating genetic studies and otolith microchemistry analyses could help clarify these movement patterns and assess the extent to which large rivers contribute

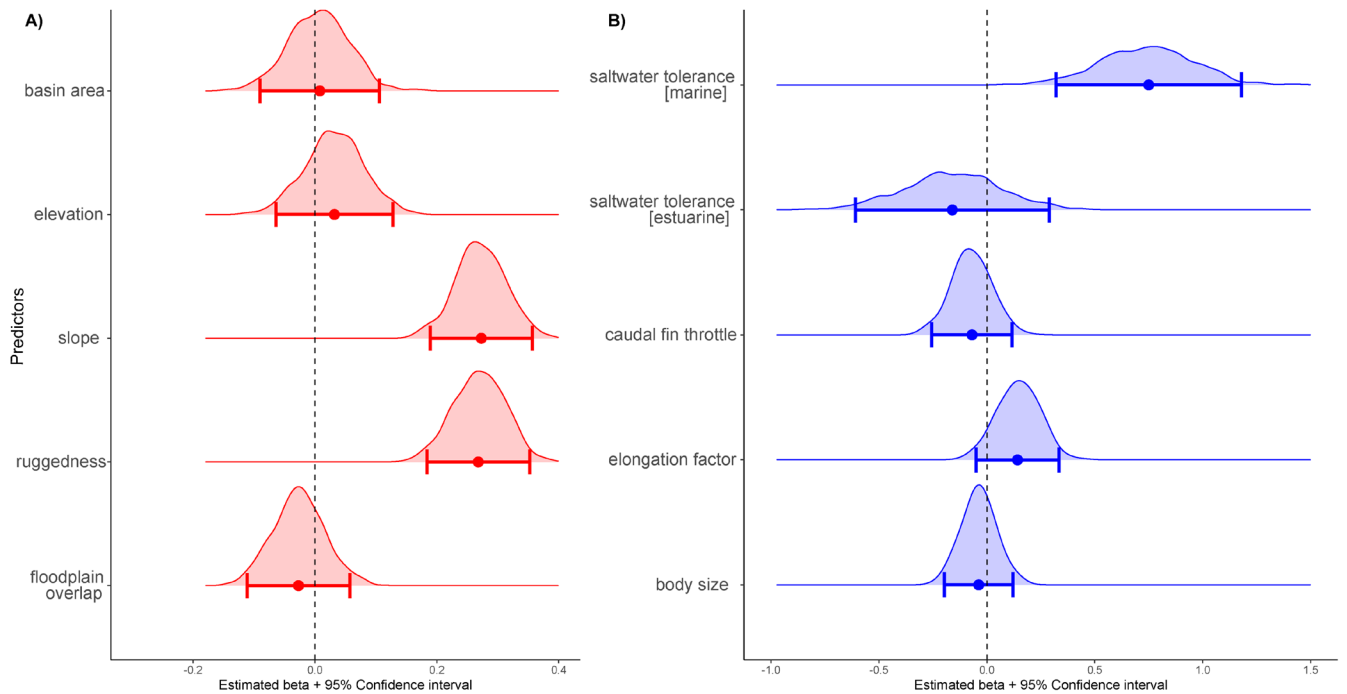


FIGURE 4 | Estimated effects of topographic and species-level trait predictors on beta diversity turnover and species contributions. (A) Topographic variables are shown in red, with the impact on the turnover component of beta diversity across basins; (B) Species-level traits are shown in blue, reflecting their contribution to the overall beta diversity. For saltwater tolerance, the baseline comparison level is freshwater exclusivity. Error bars represent 95% confidence intervals. Predictors are considered statistically significant at the $p < 0.05$ level when their confidence intervals do not intersect the dashed reference line.

TABLE 2 | Summary of the averaged beta regression models for topographical and floodplain connectivity predictors of mean beta turnover values in freshwater fish of Northern Australia's river basins.

Term	Estimate	Adj. Std. Error	z-value	p-value
(Intercept)	−0.810	0.0373	21.793	<0.001
Basin area	0.008	0.0520	0.169	0.865
Elevation	0.031	0.0493	0.644	0.519
Slope	0.274	0.0428	6.401	<0.001
Ruggedness	0.265	0.0429	6.193	<0.001
Floodplain overlap	−0.025	0.0429	0.644	0.520
Phi	62.578	11.916	5.251	<0.001

Note: The table presents estimates, adjusted standard errors, z-values, and p-values for the predictors: Elevation, slope, terrain ruggedness, and the presence of floodplain crossings. The phi coefficient, representing the precision of the beta distribution, is also included. A significant phi coefficient denotes a precise estimation of mean beta turnover values variability. Predictors yielding p-values below 0.05 are deemed statistically significant and are denoted in bold.

to the broader connectivity of freshwater fish populations in Northern Australia.

The absence of significant associations with morphological traits related to species movement, such as body size, shape, and caudal peduncle, in determining beta diversity among freshwater fish across river basins suggests that factors beyond physical locomotion traits may play more critical roles in influencing dispersal and establishment patterns. This could be attributed to the overarching influence of environmental adaptability over morphological traits or the limited variation in these traits within the studied species (Leprieur et al. 2011). The ability of fish to tolerate saltwater, in addition to other non-morphological factors like behavioural and physiological adaptations, may substantially impact dispersal and distribution patterns within the dynamic riverine landscapes of Northern Australia (Unmack 2013). Studies have shown that upper thermal tolerances in fish species are correlated with the temperatures experienced across their ranges, indicating shared selection pressures and limited dispersal from ancestral environments (Comte and Olden 2016). Similar to thermal tolerance, which is shaped by historical exposure to a broader range of experienced temperatures, it would be interesting to investigate whether the

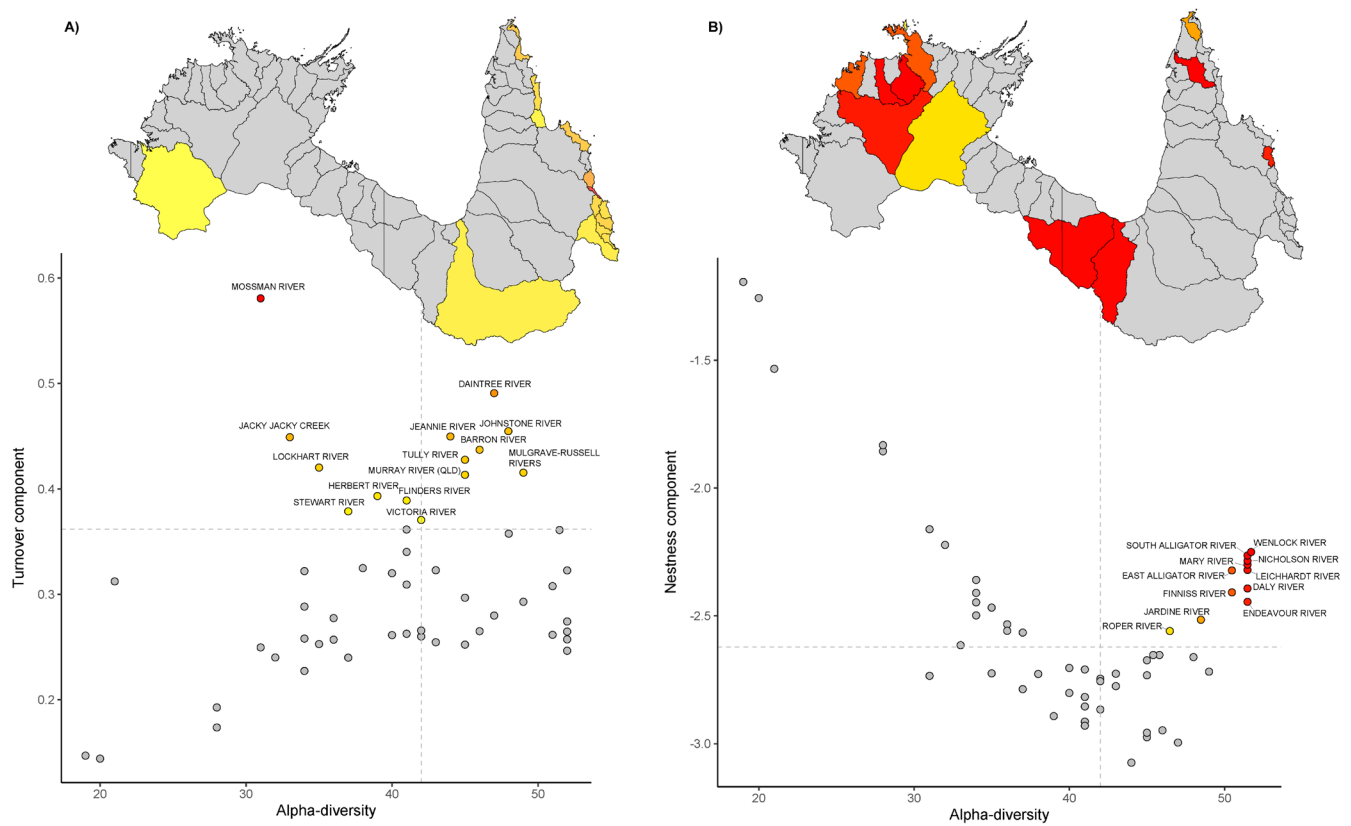


FIGURE 5 | Associations between alpha diversity and beta diversity components across river basins in Northern Australia. (A) Depicts the relationship between alpha diversity and the turnover component of beta diversity, with basins exhibiting a gradient from yellow to red, indicating an increasing quartile of turnover values; this gradient identifies basins with progressively unique species assemblages. The upper right quadrant highlights basins with high turnover and species richness, signifying areas with both unique assemblages and considerable richness. (B) Demonstrates the relationship between alpha diversity and the nestedness component of beta diversity. Unlike turnover, elevated nestedness values are mainly pertinent to basins with higher species richness, which suggests that these basins act as critical reservoirs of diversity. Grey dots and basins in the figure are not important in the context of turnover or nestedness and are included for completeness.

significance of saltwater tolerance to beta diversity is influenced by the predominance of marine clades in the evolutionary history of Australian freshwater fishes or if it is a common feature observed globally.

Another important factor influencing beta diversity is the spatial distance between basins, as distance decay in species composition could play a role in structuring fish communities, particularly for strictly freshwater species with limited dispersal capacity. Future studies incorporating explicit spatial distance metrics, standardised using similar-sized grid areas, along with more comprehensive species sampling across the study area, would help clarify the role of isolation in shaping beta diversity patterns in Northern Australian river basins.

The influence of topographic features, notably slope and terrain ruggedness, on the turnover component of beta diversity among freshwater fish populations across river basins underscores the role of physical landscape structures in shaping ecological connectivity (Dias et al. 2014). Habitat heterogeneity associated with these physical factors has been linked to variations in species turnover and community structure in several taxa and ecosystems (Cáceres et al. 2012). Steep and rugged basins create internal dispersal barriers that not only limit within-basin movement but also reinforce isolation at the basin boundaries, ultimately promoting inter-basin species turnover (Schmitt et al. 2021). Similar patterns have been observed in other systems, where topographic complexity within a basin contributes to regional differentiation by constraining species dispersal across multiple spatial scales (Rodríguez et al. 2015; Thormann et al. 2018). This reinforces the idea that local-scale heterogeneity can scale up to drive inter-basin biodiversity patterns, particularly for species with limited dispersal abilities (Leprieur et al. 2011).

Floodplain connectivity did not have a significant impact in the multivariate model, which was unexpected considering its well-documented importance in facilitating fish movement (Warfe et al. 2011; Pettit et al. 2017; Bogotá-Gregory et al. 2023). This can occur when the predictive power of elevation and floodplain connectivity is absorbed by more dominant variables like slope and ruggedness in the context of a multivariate model. In the presence of stronger predictors, the unique contribution of elevation and floodplain connectivity to the model may be minimised, thus failing to reach statistical significance. Notably, a univariate inspection shows that basins with overlapping floodplains tend to exhibit significantly lower turnover and higher nestedness (Figure S3D). This suggests that the influence of overlapping floodplains in homogenising fish assemblages might have only localised impacts, which could be overshadowed by the more pronounced effects of terrain topography at basin scale. This observation underscores the need for conservation and management strategies to embrace a holistic approach, incorporating a range of landscape and ecological variables to predict and effectively manage biodiversity outcomes accurately.

In addition to the factors we examined, it is well-established in the literature that other drivers, such as hydrological regimes, flow patterns, discharge variability, invasive species, network structure, and connectivity, also play significant roles in shaping beta diversity among freshwater fishes (Lara-Romero

et al. 2019; Rogosch and Olden 2019). Additionally, water quality parameters such as temperature, pH, dissolved oxygen, and nutrient concentrations directly affect the survival and reproduction of fish species, leading to differences in species composition across habitats (Xia et al. 2023). Habitat structure, encompassing the physical complexity of aquatic environments like vegetation, substrate type, and structural features, provides diverse niches that often result in higher beta diversity (Bogotá-Gregory et al. 2023). Furthermore, land use and land cover changes due to anthropogenic activities—such as agriculture, urbanisation, and deforestation—significantly impact freshwater ecosystems by altering runoff patterns, increasing pollution, and modifying habitat structures, thereby affecting species composition and beta diversity (Li et al. 2018). By integrating these additional factors in future studies, our understanding of the multifaceted drivers of beta diversity in freshwater ecosystems becomes more comprehensive, allowing for more effective conservation and management strategies that account for a broader range of ecological variables.

The relationship between species richness and the patterns of turnover and nestedness across river basins provides crucial insights for conservation management. Basins with high turnover values are vital for conservation, irrespective of species richness, as they harbour unique species and assemblages essential for maintaining ecological diversity (Figure 5A). Conversely, basins combining high nestedness and species richness, such as those in the top right quadrant of Figure 5B, are particularly important because they act as biodiversity reservoirs, harbouring a large number of region-wide species. These basins serve as potential sources for replenishing populations in areas where species may be at risk of local extinction. This role underscores the importance of devising conservation strategies that protect these key areas while enhancing ecological connectivity to foster species resilience and stability across the landscape.

In summary, this study highlights the significant role of species traits, especially saltwater tolerance, and landscape features like terrain slope and ruggedness as drivers of freshwater fish beta-diversity patterns in Northern Australia. The distinctive dispersal capabilities of diadromous species, facilitated by their saltwater tolerance, play a pivotal role in shaping the composition of basin assemblages. Our findings align with broader ecological research demonstrating that topographic complexity plays a crucial role in shaping biodiversity patterns across various taxa and ecosystems. Similar to studies on terrestrial species in montane environments and island ecosystems (Cutts et al. 2019; Roell et al. 2021), we found that rugged landscapes promote species turnover by acting as barriers to movement, leading to distinct assemblages across basins. These results reinforce the need to integrate both turnover and nestedness components of beta diversity into conservation planning (Socolar et al. 2016), as protecting only species-rich areas may overlook ecologically distinct communities that contribute to regional biodiversity. Importantly, while floodplain connectivity was expected to facilitate homogenisation, our results suggest that landscape heterogeneity may override the influence of hydrological connectivity. Together, these insights emphasise that conservation strategies must prioritise both biodiversity reservoirs and ecologically distinct basins to maintain freshwater ecosystem resilience in Northern Australia.

4.1 | Conservation Management Implications for Northern Australian River Basins

The findings of this study have significant implications for the conservation management of freshwater ecosystems in Northern Australia. By integrating species traits and landscape features, we can develop more effective strategies for conserving biodiversity across river basins. Our results highlight the importance of saltwater tolerance in shaping fish community compositions. Conservation efforts should consider the role of diadromous species in connecting disparate aquatic communities and maintain connectivity between freshwater and marine environments. It is crucial to look beyond rivers and consider the maintenance of natural functioning estuaries and coastal waters, as these serve as important routes for migratory diadromous fish movement across basins. Additionally, the potential impact of dam construction must be carefully evaluated, as it can fragment the freshwater landscape and impede connectivity for these highly migratory species, potentially altering beta diversity patterns across the region. Simultaneously, special attention should be given to freshwater obligate species, which often have restricted ranges and may be more vulnerable to environmental changes and localised anthropogenic impacts. Topographic features, particularly slope and ruggedness, play a crucial role in maintaining distinct fish communities. Conservation planning should prioritise basins with varied topography to preserve unique assemblages. For instance, the Victoria River in the Northern Territory, The Flinders River in northern Queensland, and several small basins on the east side of the Cape York Peninsula that flow into the Coral Sea exhibited high species turnover, indicating their importance in harbouring distinctive ecological communities.

The relationship between species richness and the patterns of turnover and nestedness across river basins provides crucial insights for conservation management. Basins with high turnover values are vital for conservation, irrespective of species richness, as they harbour species with limited distribution, possibly endemics, and assemblages essential for maintaining ecological diversity (Figure 5A). Conversely, basins combining high nestedness and species richness, such as those in the top right quadrant of Figure 5B, are particularly important because they act as biodiversity reservoirs, harbouring a large number of region-wide species. These basins serve as potential sources for replenishing populations in areas where species may be at risk of local extinction. This role underscores the importance of devising conservation strategies that protect these key areas while enhancing ecological connectivity to foster species resilience and stability across the landscape.

We identified several key river basins for conservation: (1) basins with unique species compositions, such as the above mentioned, are essential for maintaining ecological distinctiveness and should be prioritised for protection; (2) basins acting as biodiversity reservoirs, including the Daly, Finniss, and Roper rivers, are critical for their role in potentially replenishing other areas and should be managed to maintain their diverse fish populations; and (3) already protected basins, such as the Daintree, should continue to receive conservation attention to conserve their ecological integrity.

Development plans should incorporate measures to maintain habitat connectivity and conserve areas of high beta diversity.

Conservation strategies should strike a balance between protecting ecologically distinct areas and safeguarding reservoirs of common species. This approach ensures the conservation of unique assemblages while maintaining population sources that can buffer against localised extinctions. Lastly, our findings on the restricted ranges of many freshwater obligate species underscore the need for targeted conservation efforts. These species may be particularly vulnerable to habitat alterations and require specific protection measures within their limited distributions.

Author Contributions

O.J.L. conceptualized the main ideas of the study and conducted analyses. O.J.L. compiled data. O.J.L., D.S. and R.K.K. interpreted the results and wrote the original draft of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70027>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.