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**RESEARCH ARTICLE**

Connectivity, habitat, and flow regime influence fish assemblage structure: Implications for environmental water management in a perennial river of the wet-dry tropics of northern Australia

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Abstract

1. Environmental water management seeks to balance competing demands between the water needed to sustain human populations and their economic activities and that required to sustain functioning freshwater ecosystems and the species they support. It must be predicated on an understanding of the environmental, hydrological, and biological factors that determine the distribution and abundance of aquatic species.
2. The Daly River of the wet-dry tropics of northern Australia consists of a perennially flowing main stem and large tributaries, as well as many small to large naturally intermittent tributaries, and associated off-channel wetlands. Increased groundwater abstraction to support irrigated agriculture during the dry season threatens to reduce dry-season flows that maintain perenniality and persistence of freshwater fishes.
3. Fish assemblages were surveyed at 55 locations during the dry season over a 2-year period with the goal of establishing the key landscape-scale and local-scale (i.e. habitat) drivers of fish species distribution.
4. Longitudinal (upstream/downstream) and lateral (river/floodplain) gradients in assemblage structure were observed with the latter dependent on the position in the river landscape. Underlying these gradients, stream flow intermittency influenced assemblage composition, species richness, and body size distributions. Natural constraints to dispersal were identified and their influence on assemblage structure was also dependent on position within the catchment.
5. Eight distinct assemblage types were identified, defined by differences in the abundance of species within five groups differing in functional traits describing body size, spawning requirements, and dispersal capacity. These functional groups largely comprised species widely distributed in northern Australia.

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6. The results of the study are discussed with reference to the environmental flow needs of the Daly River and other rivers of northern Australia. The findings may also be applied to environmental flow management in savannah rivers elsewhere.

KEYWORDS

environmental flow management, fish assemblage, flow regime, functional groups, northern Australia, perennial river, savannah

1 | INTRODUCTION

Riverine biota are at risk globally from a range of threats including water abstraction to support irrigated agriculture (Januchowski-Hartley et al., 2016; Reid et al., 2019). This is particularly so for highly seasonal rivers draining catchments typified by savannah-type ecosystems. Such systems often occur in regions of dense human populations and are consequently in poor ecological condition (McClain, 2013; Vörösmarty et al., 2010; Woinarski, Mackey, Nix, & Traill, 2007). The savannah ecosystems of northern Australia, in contrast to other regions of the world, are sparsely populated, and considered to be in good ecological condition with hydrological regimes remaining relatively intact (Pusey et al., 2011; Woinarski et al., 2007). However, increasing demand for water in the region (Joint Select Committee on Northern Australia, 2014) is likely to place increasing pressure on the region's rivers and the biota they sustain.

The Daly River, Northern Territory, is an exemplar of the potential future for the broader region (Douglas, Jackson, Pusey, Kennard, & Burrows, 2011). Expansion of irrigated agriculture in the catchment will depend on groundwater resources, the depletion of which may alter the magnitude and timing of dry season flows and threaten the river's values, including its significant subsistence and recreational fisheries (Erskine et al., 2003; Jackson, Finn, & Scheepers, 2014). Altered flow regimes have the potential to threaten the river's rich freshwater fish fauna (see Table S1) as significant hydro-ecological linkages have been demonstrated for some species in the river (Bayliss, Bartolo, & van Dam, 2008; Chan et al., 2012; Jardine et al., 2012; Keller et al., 2019; Pusey, Kennard, Douglas, & Allsop, 2018; Stewart-Koster et al., 2011; Turschwell et al., 2019). Collectively, this research indicates strong relationships between aspects of the flow regime and the abundance and ecology of several fish species, and raises concern over potential future changes in river hydrology. With the exception of the examples above, however, scant information is available concerning the flow-related ecology of most fish species in the river – a limitation that challenges modelling flow-ecology relationships more broadly (Horne et al., 2019). In addition, information is not available concerning species distributions and habitat requirements, or whether distinctive assemblages or functional groups are present and demonstrate strong flow-dependency – an important precursor to anticipate potential impacts of flow alteration (Anderson et al., 2006; Olden, 2016).

This article addresses these gaps to provide guidance on the environmental water needs of the Daly River. The objectives are to:

(i) describe fish species distributions throughout the catchment; (ii) identify distinctive assemblage types; (iii) quantify environmental factors correlated with assemblage types and diversity; and (iv) determine which habitats are associated with spawning, recruitment, and survival to adulthood. By addressing these objectives, we aim to enhance our understanding of how habitat and critical aspects of the flow regime influence the distribution of fish species and trait complexes and whether insights gained can inform environmental flow management in this and other wet-dry tropical rivers.

2 | METHODS

2.1 | Study area and flow regime

The Daly River is a large (53,000 km²), perennial river supporting significant environmental, economic, and Indigenous cultural values (Hermoso, Cattarino, Linke, & Kennard, 2018; Jackson, 2006; Stoeckl et al., 2013) (Figure 1). Perennial flows along the main stem distinguish it from many other rivers of the region that flow intermittently (Kennard et al., 2010). The river contains a diverse fish fauna of at least 94 species comprising 30 freshwater teleost species, 19 freshwater teleosts requiring access to the estuary for breeding, a further 42 estuarine vagrant teleost species, and three elasmobranch species of conservation significance (Table S1). The majority of the catchment occurs at elevations <100 m above sea level with only the headwaters occurring at >400 m above sea level in the 'stone country' of the Arnhem Land Escarpment. The climate is monsoonal with 90% of rainfall occurring between October and March. Average minimum and maximum air temperatures vary from 13 and 31.7°C, respectively, in July to 22.1 and 36.8°C in October. Three spatially extensive karstic groundwater aquifers (Tindall, Jinduckin, and Ooloo) ensure perennial flow in the main channel and major tributaries (Jolly, 1984).

Discharge in the main stem of the river (Dorisvale gauge G8140067; catchment area = 32,649 km²) during the study was similar to the previous 20-year average although flood flows were large and led to elevated dry season baseflows (Figure 2). The mean annual discharge at this location is 5.072×10^6 ML. Stream flow in tributary systems, even those of large size, is typically naturally intermittent and short-lived unless baseflows are maintained by groundwater. For example, average annual discharge in the Fergusson River (measured at G814008, catchment area 1,685 km²) is 0.527×10^6 ML per annum

FIGURE 1 Map of the study area and fish sampling sites in the Daly River catchment. Sites are numbered according to their fish assemblage type (i.e. group; Figure 3). Places mentioned in the text are indicated with arrows

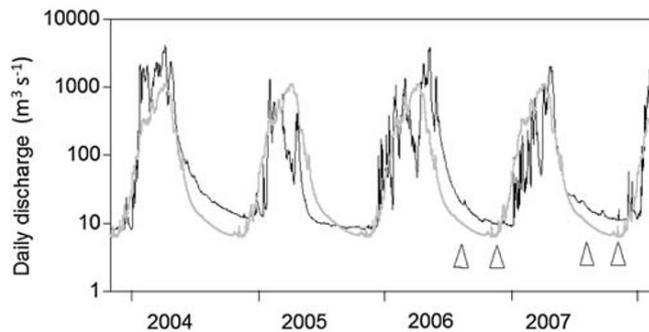
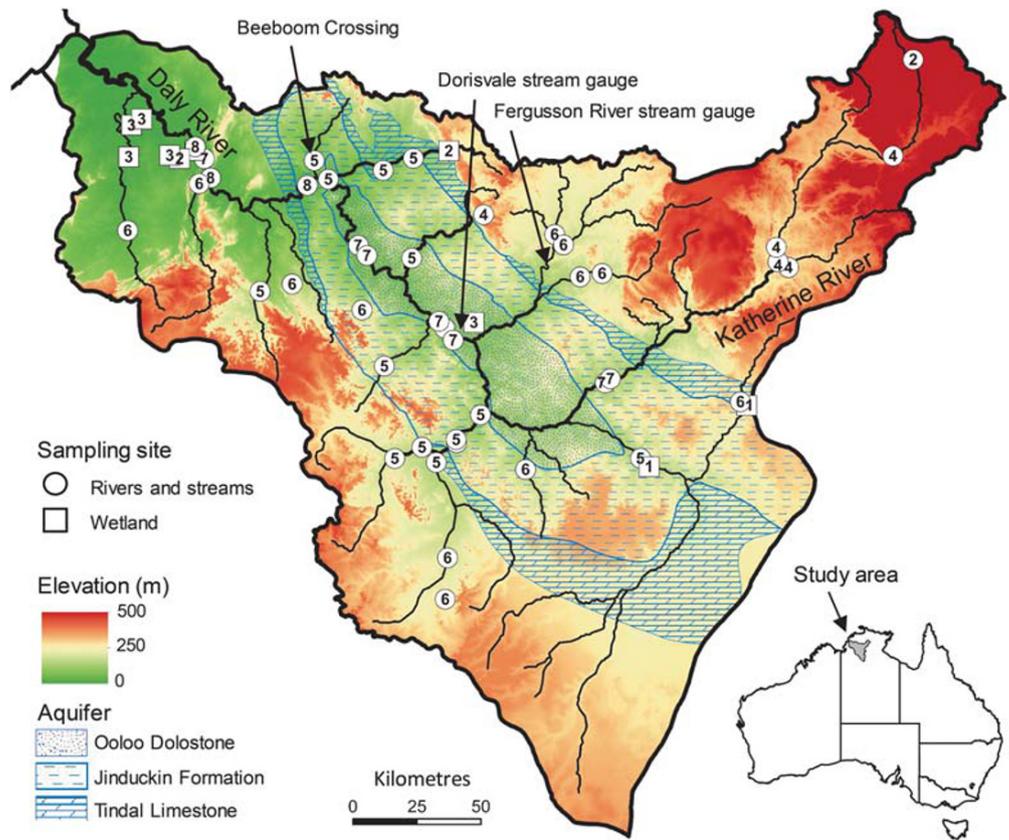


FIGURE 2 Stream flow in the Daly River (at Dorisvale) over the period 2004–2007 (i.e. leading up to and including the present study; solid line). The long-term average based on the period 1987–2007 (grey line) is superimposed across the period. The incidence of the sample occasions is also shown (arrows)

but flow typically ceases between June and August and remains so for 105 days per year on average (Pusey et al., 2018).

2.2 | Sampling of fish assemblages

Fifty-five locations were sampled in the dry season (June–October) of 2006 and 2007. Little change in the condition of the catchment has occurred since this date. Average lineal sampling extent was 352 ± 40 (SE) m. Sampling locations were stratified according to position in the catchment (headwaters, mid-catchment, and

lowlands) and macrohabitat type (main river channel [Daly and Katherine rivers], perennial and intermittent tributary streams, and wetlands [naturally occurring off-channel depressions receiving either direct rainfall or overbank flood flows]). Barriers to fish movement within the main channel are limited to Beeboom Crossing in the lower Daly River, a naturally occurring complex of high-gradient chutes cutting through a bedrock intrusion that restricts dry-season fish movements; and a series of steep gorges and waterfalls located in the upper Katherine River that impose a barrier to upstream movement year-round.

Fish assemblages were sampled using either a boat-mounted (Engineering Technical Services Model MBS-2DHP-SRC; www.etsellectrofishing.com) or backpack (Smith Root Model 12B and LR20B; www.smith-root.com) electrofishing unit, or a combination of both. We selected electrofisher gear based on depth and safety considerations as the river contains estuarine crocodiles. The electrofisher settings were adjusted according to water conductivity levels to maximize capture efficiency, while using the minimum power required to capture fishes (pulsed DC current, $<250 \text{ pulses s}^{-1}$, $<500 \text{ V}$, $<25\%$ duty cycle, maximum 35 A). Within each site, fish were sampled at multiple discrete locations (electrofishing shots) where each electrofishing shot was fixed to 5-min duration (elapsed time) and averaged $42.2 \pm 4.1 \text{ m}$ in length. Environmental conditions determined the choice of sampling method in each shot area, with deep, slow-flowing habitat sampled by boat electrofishing and shallow, fast-flowing areas sampled by backpack electrofishing. Benthic species were sampled effectively by boat electrofishing in deeper

sites because water clarity was generally very good (turbidity usually <5 NTU), and the average maximum depth of sites was 185.5 ± 13.5 cm, which was well within dip-netting range (dip-net poles were ~4 m in length). Thirty sites were sampled exclusively by backpack electrofishing, 13 sites by boat electrofishing, and 12 sites by a mix of both methods. At least 15 electrofishing shots were usually undertaken at each site to ensure that all available habitat types within the reach were sampled. The exception to this was for small isolated off-channel wetlands where the entire water body could be sampled with as few as six electrofishing shots.

Fish were identified (consistent with Pusey et al., 2017), counted and measured (standard length in mm) and returned to the water near to where they were originally captured. Catch data were converted to catch per unit effort (CPUE) with the unit effort being defined as a 5-min electrofishing period. Further details of fish sampling methods are available in Stewart-Koster et al. (2011) and Keller et al. (2019). The sampling effort (i.e. number of electrofishing shots) required to gain accurate and precise estimates of reach-scale fish assemblage structure was evaluated (M.J. Kennard, unpublished data). The analyses indicated that when compared with data obtained from more extensive sampling using up to 25 electrofishing shots, estimates of assemblage structure from 15 electrofishing shots were highly accurate (90% similar to estimates from more extensive sampling) and precise (coefficient of variation = 5%). These analyses indicate that the sampling regime provided quantitative estimates of fish assemblages and that these data were suitable for assessing inter-site variation in fish assemblage attributes. In addition, Turschwell et al. (2019) evaluated the potential effects of different gear types (boat versus backpack electrofishing) on the estimation of site-scale fish assemblage attributes. They found that the total fish abundance (summed CPUE for all species) was significantly higher using backpack compared with boat electrofishing (Tukey HSD; $P < 0.001$). However, abundance (CPUE) of some large-bodied species (e.g. barramundi) was significantly higher using the boat electrofisher, reflecting the preference of deeper pool habitats by these species. The ratio of sampling method type (e.g. 1 = 100% boat; 0.5 = 50% boat and 50% backpack, etc.) was tested as a predictor of total fish abundance using Bayesian hierarchical regression models, but no significant site-level effects of gear type were found, indicating that the possible confounding effects of sampling method were negligible (Turschwell et al., 2019).

Ten commonly collected species (indicated in Table S2) were classified as juvenile or adult and each recorded as a distinct taxon for subsequent analyses. Size used to denote different size classes was 150 mm standard length (SL), except *Lates calcarifer* and *Strongylura krefftii* for which it was 300 mm SL. Catch data for juvenile *Neoarius graeffei* and *Neoarius berneyi* were pooled as it was not possible to distinguish between species at small size. Fish sampling was conducted in accordance with the requirements of animal ethics permits from Griffith University and Charles Darwin University and an NT Fisheries S17 Fisheries Act permit. Indigenous traditional owners from the Wagiman, Wardaman, and Jawoyn language groups participated in accordance with the Human Research Ethics requirements of Charles Darwin University.

2.3 | Quantification of environmental variables at landscape and local scales

The National Environmental Stream Attributes data base for rivers (see Geoscience Australia (2011) and Stein, Hutchinson, and Stein (2014) for details) was used to generate site-specific estimates of environmental variables (climate, topography, geology/lithology, vegetation cover, and hydrology) at the landscape and reach scale (see Table S2 for variables used and their definitions). The areal proportion (%) of the sample reach classed as pool, riffle, or run was apportioned by eye. Five replicate measurements of depth (cm), velocity ($m s^{-1}$), and a single estimate of width (hand-held laser range finder), substratum composition (using a modified Wentworth scale), and microhabitat structure were made for each electrofishing shot. Microhabitat was quantified in terms of the proportion of the sampled area that was covered by filamentous algae, leaf litter, aquatic macrophytes (MAC), submerged terrestrial vegetation, emergent vegetation, overhanging terrestrial vegetation, large wood (>20 cm diameter), or small wood (<20 cm diameter) and the proportional extent of bank length occupied by undercutting or exposed root masses (Pusey, Kennard, & Arthington, 2004).

2.4 | Analysis

Spatial variation in fish assemblages was assessed using classification (UPGMA agglomerative hierarchical clustering) and ordination (non-metric multidimensional scaling) based on site-by-site dissimilarity (Bray–Curtis) matrix measure in the Primer 6.1.1 (2008) package. A combined classification and ordination approach was used to maximize the distinction between assemblage types as this can provide valuable insights into biotically-based river type classifications. Moreover, assemblage types are useful for interpreting and predicting in-stream conditions and are also relevant to water management and conservation policy. A combined classification and ordination approach is better able to explain, justify and communicate management plans and policy (Zorn, Seelbach, & Wiley, 2002).

Assemblages were defined in terms of abundance of individual taxa (mean CPUE; $\log(x + 1)$ transformed). *Neosilurus pseudospinosus*, *Ophisternon gutterale*, and *Arrhamphus sclerolepis* were excluded as each occurred at one site only. Multivariate correlations between habitat (at landscape and local scales) and fish assemblage structure was assessed using the RELATE and BIOENV routines within Primer 6.1.1 (2008). Both are based on non-parametric permutational comparisons of separate dissimilarity matrices: in this case, the first based on fish taxa and a second based on the Euclidean distance and range-standardized habitat variables for different sets of potential environmental correlates (hydrology, geology, climate, geomorphological, and local habitat). For each analysis, only those variables identified as being correlated with the distribution of sampling localities in fish assemblage ordination space were included. A final analysis (BIOENV) was employed with all such variables entered in a step-wise fashion until the optimum solution

(i.e. minimum number of variables for maximum correlation) was achieved.

A second set of multivariate analyses considered fluvial sites only (i.e. no wetland sites). In addition, any high elevation escarpment sites were excluded, reasoning that the factors responsible for determining assemblage structure in these sites will not be affected by water resource use. *Porochilus rendahli*, *N. pseudospinosus*, *O. gutterale*, and *A. sclerolepis* were excluded as in the previous analysis. Analytical procedures followed that outlined above (Figure S1). The final analysis of this reduced data set excluded all species requiring access to the estuary to breed (i.e. it was limited to strictly freshwater species) to determine whether observed spatial structuring of fish assemblages was based on migration needs.

Permutational analysis of variance (PERMANOVA) (Anderson, Gorley, & Clarke, 2008) was used to determine the influence of site group on emergent properties of the fish assemblages, including diversity (taxon, species, and estuarine species richness), abundance (mean CPUE), proportion of total CPUE contributed by species with an estuarine component to their life history, mean CPUE of non-estuarine dependent species, and size structure (mean individual and species lengths). Taxon richness includes species and age/size classes, whereas species richness refers to diversity undifferentiated by length. Mean individual length (across all individuals within all species for each site) and mean species length was estimated for each site, and from these estimates the mean length (\pm SE) of individuals within each group (i.e. site means were within-group replicates) was generated. Spatial variation in species richness related to isolation of the study site from the river mouth (DISTM) and catchment area (CA) above each study location was examined by linear regression for those sites classified as riverine only. In the latter case, both species richness and catchment area were \log_{10} -transformed. PERMANOVA was used to test whether species richness in the site groups identified by classification and ordination differed significantly after accounting for differences due to variation in isolation (i.e. DISTM) and catchment area (i.e. these variables were entered into the models as covariates).

The relationship between local habitat characteristics and assemblage emergent properties and variables describing fish size was further examined by distance-based linear modelling using the DistLM module available within the PERMANOVA + module of Primer 6.1.1. Site-by-site resemblance matrices for each variable were generated based on Euclidean distance. Predictor variables (restricted to local habitat variables only) were selected in a stepwise fashion with the best model (i.e. combination of variables) being selected according to the Akaike information criterion with correction for small sample size. A second set of analyses was undertaken in the same manner but was restricted to fluvial sites only and did not include 'stone country' sites.

3 | RESULTS

In total, 19,822 individuals from 45 species were collected with 11 species occurring in 50% or more of study sites and 25 species occurring in both wetland and river habitats. Abundant species were

often widely distributed within the Daly River catchment (ranked abundance vs frequency of incidence: $r = 0.791$, $P < 0.001$) and were small-bodied; however, a number of small-bodied species restricted to particular habitats (e.g. *Ambassis* sp. in wetlands and *Melanotaenia exquisita* in escarpment streams), and therefore not widely distributed, also achieved high abundance. Species with an estuarine component to their life history were neither widely distributed nor, with the exception of the most downstream locations, abundant (Table S3). Three elasmobranchs of high conservation significance (*Pristis pristis*, *Carcharhinus leucas*, and *Urogymnus dalyensis*; Table S1) were infrequently collected but are not further considered here. No teleost species recorded was of elevated conservation significance.

3.1 | Spatial variation in fish assemblage structure

Clear spatial segregation in fish assemblage structure was evident (Figures 3 and 4). Eight groups of co-occurring species were recognized and further divided into wetland/floodplain habitats (groups 1–3: located positively on axis 2) and stream and river sites (groups 4–8: located negatively on axis 2; Figure 4a). Position on axis 1 was related to location in the river landscape; i.e. a downstream (negative) to upstream (positive) transition for both riverine and many wetland sites.

Group 1 sites consisted of temporary, shallow off-channel wetlands containing 12 species (13 taxa; average species richness = 7.3). This assemblage type was dominated by *Ambassis* sp. (north-west), *Melanotaenia australis*, juvenile *Oxyeleotris selheimi*, and *Porochilus rendahli* (Supplementary Table S3). Group 2 sites consisted of shallow yet perennial swamps. The assemblage was dominated by the same abundant species as in group 1 together with *Mogurnda mogurnda* and *Melanotaenia nigrans*. Group 3 consisted of large perennial, deep floodplain wetlands and was dominated by small-bodied wetland species (*Denariusus bandata*, *Pseudomugil tenellus*, *P. rendahli*, and *Hypseleotris compressa*), a large number of widespread small-bodied species such as *Craterocephalus stercusmuscarum*, *Glossamia aprion*, *Ambassis* sp. (north-west), and *M. australis*, and a large number of widespread large-bodied species such as the plotosid catfishes *Neosilurus hyrtlilii* and *Neosilurus ater*. Most taxa within this group of large wetlands occurred widely throughout the river network of the Daly River, particularly in the main channel (Table S3). Strictly riverine species (see below) were largely absent from all wetland site groups.

The distinctive group 4 contained sites located within the upper Katherine River and Stray Creek (which drains sandstone country) and contained unique upland species such as *Pingalla midgleyi*, *Hypseleotris barrawayi*, and *M. exquisita*. The last two species were the most abundant in this site group. Group 5 comprised naturally intermittent streams, and assemblages therein were dominated by *M. australis*, *Leiopotherapon unicolor*, and *M. mogurnda*. Juvenile *N. hyrtlilii*, *O. selheimi*, *O. lineolata*, *Megalops cyprinoides*, and *Toxotes chatareus* were also abundant in stream sites within this group.

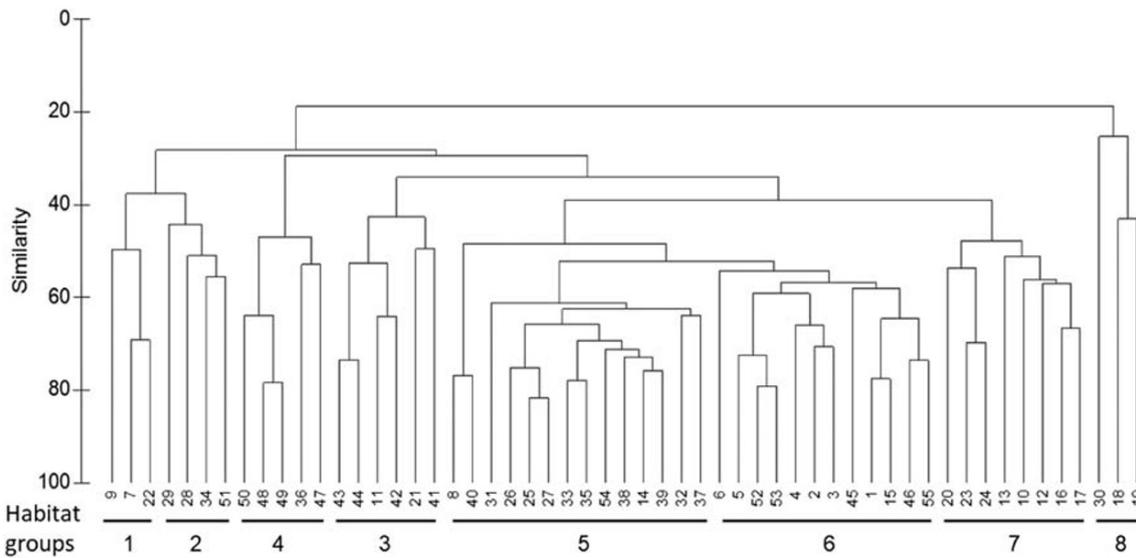


FIGURE 3 Dendrogram showing allocation of sample sites within each of the eight site groups derived from UPGMA cluster analysis of a Bray-Curtis dissimilarity matrix of $\log_{10}(x + 1)$ transformed taxon abundance

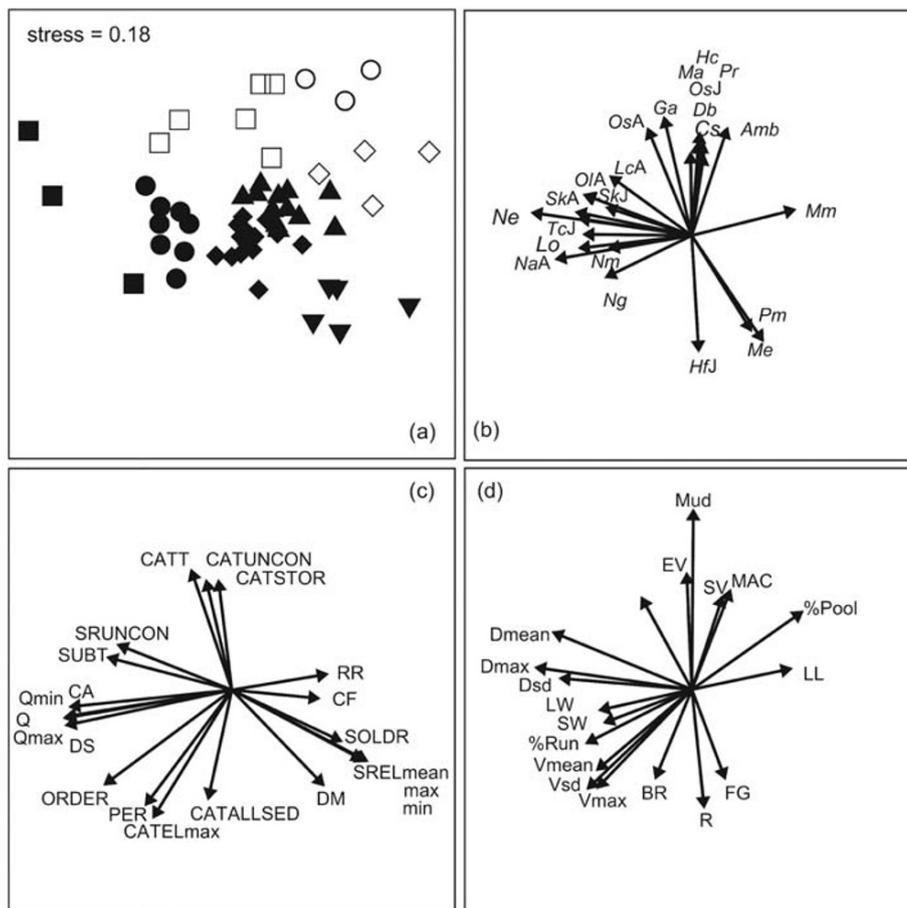


FIGURE 4 Multidimensional ordination biplot showing spatial variation in fish assemblage structure (a). Wetland habitat groups are denoted by: ○ group 1; ◇ group 2; □ group 3; and fluvial habitat groups by ▼ group 4; ▲ group 5; ◆ group 6; ● group 7; and ■ group 8. Significant species vectors are plotted in (b). Species are identified by the first letter of both genus and species and separate age classes are denoted by J = juvenile and A = adult. Significant habitat vectors (at the landscape scale) are plotted in (c). Abbreviations for landscape-scale variables are defined in Table S2. Local scale habitat variables are designated as: M = mud; FG = fine gravel; R = rocks; BR = bedrock; %Pool = proportion of sample reach classified as pool; %Run = proportion of study reach defined as run; Dmean, max, and sd = mean depth, maximum depth, and standard deviation of mean depth, respectively; Vmean, max, and sd = mean velocity, maximum velocity, and standard deviation of mean velocity, respectively; LW = large wood; SW = small wood; LL = leaf litter; MAC = submerged macrophytes; SV = submerged vegetation; and EV = emergent vegetation

Group 6 sites were typically permanent streams or permanent groundwater-maintained habitats within otherwise intermittent streams and contained a similar assemblage to streams in group 5. This group contained six additional species overall and, on average, an additional four species per site (13.9 cf 9.5. species), but which

occurred in low abundance. Species typical of intermittent streams, especially *M. australis*, *L. unicolor*, and *M. mogurnda* were uncommon. The riffle dweller *Craterocephalus stramineus* was much more abundant in permanent stream sites than in intermittent streams (mean CPUE: 5.98 cf. 0.08, respectively). Large predatory species such as

L. calcarifer and *S. krefftii* were present but not abundant in these streams, whereas juvenile forms of many riverine and lowland species were abundant.

An additional increase in mean species and taxon richness was recorded for sites within groups 7 and 8. The mullet *Planiliza ordensis*, sole *Leptachirus triramus*, and ariid catfishes *N. berneyi*, *N. graeffei*, and *Neoarius midgleyorum* were moderately abundant in both site groups (particularly the downstream group 8 in the case of *P. ordensis* and *N. berneyi*). Similarly, the piscivorous *L. calcarifer* and *S. krefftii* were more abundant in main river channel sites than other lotic sites groups although both were abundant in large wetland sites (group 3) also. Conversely, the proportional contribution to mean abundance by small-bodied widespread species was lower in groups 7 and 8 (39.4 and 5.8%, respectively) compared with other lotic site groups. Group 7 sites were located upstream of a natural partial barrier to fish movement (Beeboom Crossing). In total, 17 taxa (16 spp.) exhibited significant differences in abundance upstream and downstream of Beeboom Crossing when the comparison was restricted to perennially flowing sites only and sites were grouped according to their position relative to the Crossing (Table S4). Five species with an estuarine component to their life history (*L. calcarifer* [juveniles], *P. ordensis*, *N. berneyi*, *H. compressa*, and *Scatophagus argus*) were significantly more abundant below the Crossing. A further two strictly freshwater species (*Nematalosa erebi* and *T. chatareus* [juveniles]) were also significantly more abundant downstream of Beeboom Crossing. Nine species, all strictly freshwater in habit, were significantly more abundant upstream of the Crossing.

Taxon richness, species richness, and richness of estuarine-dependent species were significantly greater in lowland wetland and main channel sites, particularly in group 8 sites (Table 1), compared with upland shallow wetlands and permanent and intermittent

tributary stream sites. Species richness in fluvial sites varied significantly with distance from the river mouth (negative) and catchment area (positive; Figure 5). Species richness in intermittent streams (group 5) was significantly less than in perennial streams after accounting for distance from the river mouth (PERMANOVA of fluvial sites: pseudo $F_{1,35} = 6.03$; $P < 0.05$). In addition, among perennial streams, group 6 contained significantly fewer species than perennial groups 7 and 8. Species richness was similarly significantly less in intermittent streams than in perennial streams (6–8) after accounting for catchment area (Pseudo $F_{1,35} = 40.567$; $P < 0.001$).

Spatial variation in abundance (i.e. within-groups) was substantial although within-group variation was high also (Table 1) with only lowland wetland sites (group 3) and lowland river sites (group 8) having significantly elevated CPUE. The proportional contribution by estuarine-dependent species to total CPUE varied significantly in space with these species contributing about 21 and 52% to total CPUE in sites within riverine groups 7 and 8, respectively, but <5% elsewhere. Without these species, the previously detected elevated abundance at group 8 sites was no longer evident. Species with an estuarine life-history component were present (average 2.7 species) at lowland wetland sites but contributed only a small proportion (4.0%) of the total number of fishes collected. Thus, these lowland wetlands (group 3) contained high abundance of entirely freshwater fishes.

The mean body size of individuals and of species within the site groups varied significantly (Table 1). Assemblages in small wetlands (groups 1 and 2) comprised small-bodied species only (see Supplementary Figure S2). Large lowland wetland assemblages were also proportionally dominated by fish <75 mm SL but not to the extent observed in shallow wetland sites (i.e. ~70% cf. ~90% of all individuals being <75 mm SL). Moreover, large lowland wetlands contained many large individuals and species (>200 mm SL); fish of this size were absent

TABLE 1 Differences in emergent properties of fish assemblage between site groups. Values shown are the mean (\pm SE). Also shown are the pseudo-F results of PERMANOVA comparison of group means (** $P < 0.01$; *** $P < 0.001$). Significantly different group values derived from post-hoc comparisons of means are denoted by different superscript values

Group	Wetlands (1–3)			Rivers and streams (4–8)					Pseudo-F
	1	2	3	4	5	6	7	8	
<i>n</i>	3	4	6	5	14	12	8	3	
Mean taxon richness	7.3 (1.7) ^a	6.3 (1.0) ^a	18.8 (1.9) ^{bc}	10.0 (0.8) ^a	10.1 (1.1) ^a	15.5 (1.0) ^a	23.3 (1.4) ^{bc}	23.7 (4.4) ^c	15.434***
Mean species richness	7.3 (1.7) ^a	6.3 (1.0) ^a	16.0 (1.4) ^{cd}	9.2 (0.7) ^a	9.5 (0.9) ^{ab}	13.9 (0.8) ^b	19.5 (1.0) ^{cd}	20.0 (3.0) ^d	15.170***
Mean estuarine species richness	0 (0) ^a	0 (0) ^a	2.7 (0.6) ^c	0 (0) ^a	0.9 (0.3) ^b	0.5 (0.2) ^b	4.6 (0.5) ^d	5.7(0.7) ^d	21.799***
Mean abundance (CPUE)	18.3 (5.6) ^c	23.7 (4.4) ^c	78.3 (16.6) ^a	34.1 (10.2) ^c	27.1 (2.0) ^{bc}	34.0 (4.0) ^c	19.4 (4.7) ^c	50.6 (23.1) ^{ab}	6.05**
Proportion estuarine dependent (%)	0 (0) ^a	0 (0) ^a	4.0 (1.7) ^{ac}	0 (0) ^a	0.8 (0.4) ^{ab}	2.4 (1.7) ^{ab}	20.7 (4.0) ^d	52.3 (22.4) ^d	13.94***
Non-estuarine dependent (CPUE)	18.3 (5.6) ^{ab}	23.7 (4.4) ^{abc}	75.7 (16.7) ^{cd}	34.1 (10.2) ^{cd}	26.9 (2.0) ^{bc}	32.8 (3.6) ^{cd}	15.8 (4.6) ^a	13.8 (4.5) ^a	7.20***
Mean individual length (SL in mm)	39.5 (7.2) ^a	37.8 (4.9) ^a	86.1 (13.2) ^{cd}	54.8 (4.0) ^{ab}	61.1 (3.4) ^{bc}	55.9 (1.7) ^{ab}	134.9 (17.4) ^d	122.8 (11.0) ^d	11.865***
Mean species length (SL in mm)	68.3 (8.1) ^a	43.8 (8.4) ^a	113.3 (10.9) ^d	62.5 (6.5) ^{abc}	84.0 (7.6) ^c	77.5 (5.8) ^b	147.7 (11.2) ^d	124.6 (5.0) ^d	13.891***

Abbreviations: CPUE, catch per unit effort; SL, standard length.

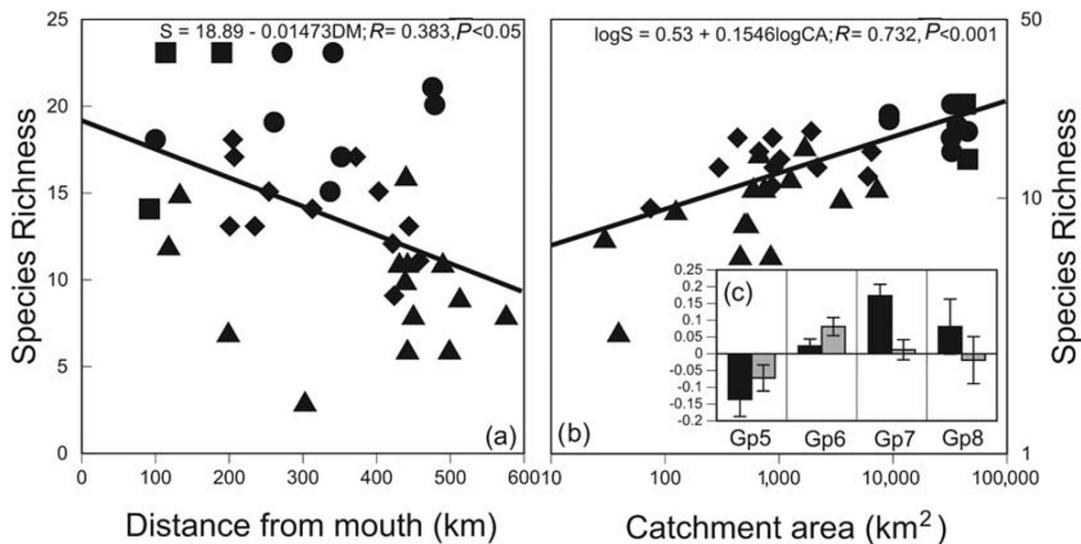


FIGURE 5 Changes in species richness with increasing distance of study sites from the river mouth (a) and increasing catchment size (b). Sites located on off-channel wetlands are not included. Symbols used are based on site groupings revealed by classification (i.e. groups 5–8); ▲ group 5; ◆ group 6; ● group 7; and ■ group 8. The inset (c) shows the mean and SE of the standardized residuals for each ordination group. Closed bars represent residuals from the relationship between richness and distance from river mouth whereas the shaded bars represent residuals from the relationship between richness and catchment area. Note that axes in (b) have been log (10) transformed

from shallow wetlands. A similar progression in individual and species size was observed for fluvial sites. Stone country assemblages (group 4) were dominated by small species and individuals (62 and 58 mm SL, respectively). Large-bodied species were present but not abundant in intermittent (group 5) and permanent tributary streams (group 6; mean species length = 84 and 78 mm, respectively) and assemblages comprised smaller individuals (mean individual length = 61 and 56 mm, respectively; Table 1). Assemblages present at riverine sites (groups 7 and 8) were characterized both by large mean individual size and large species size (135 and 123 mm, and 148 and 125 mm, respectively for groups 7 and 8, respectively).

3.2 | Functional groups

Common fish taxa were apportioned to one of five functional groups based on multiple lines of evidence, including inspection of taxon vectors in ordination space (Figure 4b), frequency of incidence across all study sites (Table S3), assemblage group-related differences in fish size (Table 1), and relative differences in taxon abundance between assemblage groups and habitat types (wetland vs riverine; Table S3). Functional groups were: (1) taxa characteristic of escarpment or 'stone country' sites (site group 4; e.g. *H. barrawayi*, *P. midgleyi*, and *M. exquisita*); (2) small bodied taxa common in wetland habitats (site groups 1, 2 and 3; e.g. *P. rendahli*, *M. nigrans*, *D. bandata*, *P. tenellus*, *H. compressa*, and *Ambassis macleayi*); (3) small-bodied widespread taxa occurring in wetland and river habitats (all site groups; e.g. *C. stercusmuscarum*, *Amniataba percoides*, *G. aprion*, *Ambassis* sp. (north-west), *M. mogurnda*, *L. unicolor*, and *M. australis*); (4) riverine species (site groups 4, 5, 6, 7, 8; e.g. *Glossogobius aureus*, *C. stramineus*, *Hephaestus fuliginosus*,

Syncomistes butleri, *P. ordensis*, and *L. tiramus*); and (5) large-bodied lowland wetland and riverine taxa within the genera *Neosilurus*, *Neorarius*, *Oxyeleotris*, *Toxotes*, *Lates*, *Strongylura*, *Megalops*, *Nematalosa*, and *Scatophagus* (site groups 3, 5, 6, 7, 8).

3.3 | Environmental correlates of fish assemblage structure

Fish assemblage structure was clearly distinct between floodplain wetland and fluvial habitat types. Moreover, species composition varied along an upstream/downstream gradient reflecting differences in lithology, sediment storage, geomorphology, climate, hydrology, and local habitat structure (Figure 4 and Table 2). Lithological differences (i.e. unconsolidated rocks in wetlands, siliciclastic/undifferentiated sedimentary rocks in fluvial catchments and unconsolidated rocks in the stream environs) reflected the different depositional/erosional processes in wetland and fluvial environments which, in turn, influence the nature of the substrate in wetland sites (high proportion of mud in wetlands contrasting with bedrock, rock, and fine gravel in fluvial sites) and physical cover available to fishes (abundant emergent vegetation, submerged terrestrial vegetation, and MAC). The upstream/downstream gradient was correlated with stream reach elevation, confinement ratio and relief ratio (all greater upstream), discharge elements (Q and perenniality) and various local habitat variables such as depth, velocity and wood cover. The model best explaining spatial variation in assemblage structure included the variables Q_{mean} , Mud, confinement ratio, and mean stream reach elevation ($\rho = 0.665$, $P < 0.001$; Table 2). These variables collectively capture the longitudinal gradient from the confined streams of the upland stone country to the large, open, perennial rivers near the river

TABLE 2 Results of BIOENV analyses comparing spatial variation in fish assemblage structure with various sets of environmental predictors (e.g. variables relating to hydrology, geology, climate, landscape, and local habitat structure). The outcomes of BEST analyses are also shown in which variables with the greatest explanatory power from any of the various environmental sets were entered in a stepwise fashion until an optimal solution was reached (i.e. maximum ρ with fewest variables). Analyses were performed for all assemblage groups, for only fluvial sites and for fluvial sites in which estuarine-dependent species were not included. See Figure 4 legend for definitions of abbreviations

Variable set	Variables	ρ	P
All site groups (1–8)			
Hydrology	Per, Q, Q_{\min} , Q_{\max}	0.371	<0.001
Geology	CATTALSED, CATUNCON, SRUNCON	0.158	<0.001
Climate	SUBT, CATT, SOLDR	0.213	<0.001
Landscape	SREL _{meaq, min & max} , RR, CA, ORDER, CATSTOR, DS, DM, CF	0.515	<0.001
Habitat	%Run, %Pool, W, D_{mean} , D_{max} , D_{sd} , V_{mean} , V_{max} , V_{sd} , Mud, FG, R, BR, MAC, SV, EV, LW, SW, LL	0.467	<0.001
BEST	Q + Mud	0.594	<0.001
	Q + Mud + CF	0.652	<0.001
	Q + Mud + CF + SREL _{mean}	0.665	<0.001
Fluvial sites only (Groups 5, 6, 7 & 8)			
Hydrology	Q, Q_{\min} , Q_{\max}	0.750	<0.001
Landscape	RCHEL _{mean} , RCHEL _{max} , CATEL _{max} , RR, CA, ORDER, DS, DM	0.684	<0.001
Habitat	W_{mean} , D_{mean} , D_{max} , D_{sd} , Mud, LL, SV, LW	0.741	<0.001
BEST	Q_{\max} + W_{mean}	0.767	<0.001
Fluvial sites only – no estuarine dependent species			
BEST	Q_{\max} + W_{mean} + CA	0.679	<0.001

mouth and a lateral gradient from stream/river habitats to floodplain wetland habitats.

When only riverine sites were considered (see Figure S1), highly significant multivariate correlations were also observed (Table 2). Two variables (Q_{mean} and W_{av}) provided the best multivariate combination correlated with spatial variation in fish assemblage structure ($\rho = 0.767$; $P < 0.001$). Maximum discharge (Q_{max}), stream width (W_{av}), and CA, comprised the best variable set to explain spatial variation in strictly freshwater fish assemblage structure. That is, despite the abundance of obligate estuarine species being greatest in downstream sites ($R = 0.491, 0.481, \text{ and } 0.481$ for correlations between CPUE and Q_{mean} , CA, and DS, respectively), they did not drive the pattern of spatial variation in total assemblage structure.

3.4 | Local scale habitat correlates of spatial variation in abundance, diversity and fish size

Spatial variation in abundance was most strongly correlated with stream width ($R^2 = 0.32$, $P < 0.001$; Table 3). The addition of velocity, % submerged vegetation and bedrock increased the amount of variation explained but not greatly ($R^2 = 0.449$, $P < 0.001$; Table 3) and described higher abundance in the deeper, wider, wetland and river sites. These same variables plus average

depth accounted for a similar amount of variation in abundance when the analysis was restricted to fluvial sites only ($R^2 = 0.503$, $P < 0.001$). When all sites were considered, spatial variation in taxon richness was strongly correlated with depth ($R^2 = 0.631$, $P < 0.001$), a measure of variability of water velocity (V_{sd}) and leaf litter cover, reflecting an increase in taxon richness in deeper sites (both wetland and riverine) with a diverse flow environment and diverse available cover (Table 3). A similar pattern was recovered for fluvial sites with width, depth and variability in water velocity accounting for two-thirds of the variation in taxon richness (Table 4). These same variables (plus width and MAC in the case of all sites, and large wood and bedrock in the case of fluvial sites) accounted for similar amounts of variation in species richness (Table 3). Thus, spatial variation in diversity was largely related to habitat size (i.e. width and depth), the availability of cover, and diversity of flow environments present.

When all sites were considered, spatial variation in both mean individual size and mean species size were strongly positively related to variation in depth and water velocity (Table 3). In addition, sites with abundant available cover such as undercut banks, large wood aggregations, and leaf litter were also distinguished by larger individuals and larger species. Depth, water velocity, and available cover (wood and undercut banks) were similarly positively related to both measures of fish size when the analysis was restricted to fluvial sites (Table 3).

TABLE 3 Summary of results of distance based linear modelling of assemblage emergent properties and size distribution against local habitat properties (Full presentation of results is given in Table S5). Analyses shown are for all sites and for fluvial sites only ($n = 37$). The order in which separate variables were added is given as 1, 2, 3, etc. All R^2 values are significant at $P < 0.001$

Variable	All sites ($n = 55$)					Fluvial sites ($n = 37$)				
	CPUE	Richness (taxon)	Richness (species)	Mean Length (individual)	Mean Length (species)	CPUE	Richness (taxon)	Richness (species)	Mean Length (individual)	Mean Length (species)
R^2	0.449	0.631	0.667	0.705	0.596	0.503	0.675	0.711	0.852	0.698
Width	1		4			5	1	1		
Depth		1	1	2	1	2	3	3	3	1
Velocity				3	2					2
Depth variability									4	
Velocity variability	2	2	2				2	4		
Mud						1				
Bedrock	4					3		5	5	4
Submerged vegetation	3					4				
Leaf litter		3	3		3					
Large wood				1	4			2	1	3
Undercut banks				4					2	5
Macrophytes			5							

Abbreviation: CPUE, catch per unit effort.

4 | DISCUSSION

This study reflected substantial spatial variation in fish assemblage structure and associated emergent properties within the Daly River catchment, and identified the most important environmental attributes related to these patterns. Fish assemblage composition varied substantially in relation to longitudinal and lateral position of study sites within the river network associated with catchment geomorphology, discharge, and erosional/depositional dynamics. Further spatial variation was related to habitat permanence, barriers to fish movement, the diversity of microhabitats provided by riparian inputs (e.g. wood and leaf litter), macrophytes and variation in depth and water velocity. Although changes in fish assemblage structure were related to location within the river landscape, stream size, and habitat characteristics, differences in assemblage composition were sufficiently pronounced to generate distinct grouping of sites. The overall fish assemblage present within the river was numerically dominated by small-bodied species that are widespread within the Daly River and have broad geographical ranges (Pusey et al., 2017). A distinctive subset of small-bodied wetland specialist species was identified that are similarly prevalent across northern Australia. Mean individual size and mean species size increased with increasing habitat size, in relation to habitat permanence and when instream cover, particularly that provided by wood, was abundant.

4.1 | Functional group and species distribution

It has been suggested that contemporary patterns of species co-occurrence are largely driven by common species-habitat

relationships (Giam & Olden, 2016) to the extent that species may form identifiable functional groups based on habitat use (Hoeinghaus, Winemiller, & Birnbaum, 2007). Five functional groups of taxa were identified based on their distribution and co-occurrence within particular habitat types and by differences in body size. The first, consisting of *H. barrawayi*, *P. midgleyi*, and *M. exquisita*, was characteristic of stream habitats in the 'stone country' of the Arnhem Plateau located above extensive waterfalls and gorges. Although *M. exquisita* and *H. barrawayi* are largely confined to the stone country, *P. midgleyi* also occurs within lowland sections of the East and South Alligator rivers that have their headwaters on the Plateau (Pusey et al., 2017). The terapontids *L. unicolor*, *H. fuliginosus*, and *S. butleri*, eleotrid *M. mogurnda*, and the rainbowfish *M. australis* also occur in stone country streams; thus, although this type of stream habitat could be defined by a functional group of three or perhaps four species, just as many other widespread species also occurred in these upland streams. However, significant phylogeographical differences between stone country populations of three species (herein referred to as *M. mogurnda*, *M. australis*, and *H. fuliginosus*) and populations downstream have been described (see Pusey et al., 2017). The observed distinction of the stone country stream assemblages from other assemblages occurring elsewhere in the catchment may thus be even more substantial, and underscores the role of processes occurring over long temporal scales in influencing the distribution of stream fishes at within-river spatial scales (Olden et al., 2010). Species within the small-bodied wetland group (*P. rendahli*, *D. bandata*, *P. tenellus*, and, to a lesser extent, *A. macleayi*, *H. compressa*, and *M. nigrans*) are characteristic of floodplain wetlands and swamps across much of northern Australia (Pusey et al., 2017). Small size may be advantageous in seasonal wetland habitats as increasing desiccation reduces

water depth in remnant habitats (Winemiller, 1989). The diversity of other species in wetlands of the Daly River was dependent on the location of the wetland within the river landscape (i.e. downstream wetlands contained more such species). Couto, Zuanon, Olden, and Ferraz (2018) similarly document downstream nestedness of floodplain and fluvial fish assemblages dependent on increasing downstream connectedness of both habitats. The riverine species group occurred very infrequently in wetlands. This group was taxonomically diverse and included the terapontids *H. fuliginosus* and *S. butleri*, the juveniles of which are strongly associated with riffle/rapid habitats (Keller et al., 2019). Riverine populations of *C. stramineus* only achieve high abundance in habitats characterized by high water velocity (Keller et al., 2019) and this species appears not to disperse far from such habitats (Jardine et al., 2012). Within the freshwater reaches of the Daly River, *P. ordensis* similarly occurs most abundantly in deep habitats characterized by elevated water velocity (Keller et al., 2019) but contrastingly disperses widely, being estuarine dependent. *Lep-tochirus tiramus*, which recruits upstream from estuarine habitats as a very small juvenile, was limited to lotic habitats of the main river. Similarly, the goby *G. aureus* occurs most abundantly in lotic habitats, whether they occur in tributaries or main river channel. Thus, this functional group is comprised of species for which flowing water habitats are important and are likely to be sensitive to changes in river flow regimes. These species are typically moderately to widely distributed across northern Australia (Pusey et al., 2017). The remaining functional groups (small-bodied widespread and large-bodied lowland riverine and wetland species) were ill-defined other than by size given that these generalist species occurred across a variety of habitat types. Both groups consist of species widely distributed across the region (Pusey et al., 2017). Much of the spatial variation in assemblage structure within the Daly River involved differences in relative abundance of species within these two functional groups. Moreover, differences in the relative abundance of juvenile and adult forms of the large-bodied lowland functional group contributed to the distinction between smaller streams (both intermittent and perennial) and main river (see below for a discussion of the importance of dispersal).

4.2 | The influence of habitat structure

Spatial heterogeneity in fish community composition is often attributed to species-specific sorting along environmental gradients and individual species-habitat relationships with depth, water velocity, substrate composition, and the diversity and nature of microhabitat cover elements (e.g. undercut banks, wood, macrophytes) are well-documented (Giam & Olden, 2016; Heino et al., 2014; Jackson, Peres-Neto, & Olden, 2001). When analyses were restricted to fluvial habitats, associations were detected between fish assemblage structure and habitat elements at the local scale (e.g. depth, velocity, wood); however, these same elements were also correlated with position in catchment and discharge. Discerning the relative importance of these factors is difficult given their relatedness to landscape position, and in the present case landscape-scale factors proved better predictors of

assemblage structure (Stewart-Koster et al., 2011). However, perceived longitudinal, elevational, and total discharge (Q) gradients in rivers function as surrogates for other factors (habitat size and stability, depth, velocity, substrate composition, energy availability, and habitat diversity) that are proximally more influential on patterns of species distribution and abundance (Hitt & Roberts, 2012). Lowland habitats may indeed contain a variety of microhabitats such as macrophyte beds, aggregations of in-stream wood and diverse habitat patches defined by depth, water velocity, and substrate composition and thus contain more species (Pettit et al., 2013). Despite the high richness of species with an estuarine dependence in northern Australian rivers (Pusey et al., 2017), the upstream/downstream gradient in richness detected within the Daly River was not driven by species turnover in this species set alone; rather it was more the result of the nested downstream accumulation of strictly freshwater species.

4.3 | Flow regime and its influence on fish assemblages

Spatial and temporal variation in stream flow regime underlies the manner in which the processes of species sorting, functional organization, extinction dynamics and dispersal influence community assembly (Mims & Olden, 2012; Tonkin, Heino, & Altermatt, 2018). In the Daly River, streams with perennial flow contained more species and more species of larger size, particularly those with a piscivorous habit. Such streams tend to be of large size (width and depth) and contain a greater variety of microhabitats (variability in water velocity and cover elements such as wood aggregations), and consequently are expected to contain more species. The fact that perenniality and stream size are linked in this catchment means that it is difficult to uncouple the relative influences of habitat size and environmental stability (Beesley & Prince, 2010). Assemblages present within perennially habitats, however, even those of small size, were diverse to the extent they resembled those in the main stem of the river with respect to composition and size structure more so than did intermittent streams of large size. Intermittent streams, irrespective of size, contained a reduced number of species and those species present were of small body size. Many species characteristic of such streams are uncommon in sites within the perennial main channel or perennial tributary streams (e.g. *M. mogurnda*, *L. unicolor*, and *M. australis*). Thus, at the landscape level, intermittent streams in this catchment were important in maintaining or contributing to whole-catchment diversity – a result supported in other regions of the world (Rogosch & Olden, 2019). Moreover, as evidenced by the presence of the juvenile forms of many species, these smaller streams provide important spawning and recruitment habitat. Increased primary and secondary production in intermittent and perennial streams, coupled with low predator numbers (this study; Pusey et al., 2018) and depressed production in main-channel habitats during the wet phase may support higher abundance of smaller fishes, including juvenile forms of larger species, compared with perennial main-river channel reaches. The potential for biotic interactions to assume greater importance in structuring stream fish

communities may increase with increasing hydrological stability (Giam & Olden, 2016; Schlosser, 1987). In the Daly River, the increased abundance and incidence of predatory fish species in perennial streams suggests that predation is likely to be important in these streams and this may be one cause of the increase in mean individual and species size (i.e. small forage fish species are selectively removed). Perhaps more importantly, gradients in environmental disturbance regimes (Taylor & Warren, 2001) and access to refugia (Sedell, Reeves, Hauer, Stanford, & Hawkins, 1990) influence species demography through extinction and dispersal with attendant consequences for species persistence, turnover, and assemblage structure (Tonkin, Altermatt, et al., 2018). Downstream reaches are typically more hydrologically stable, especially with regard to seasonal differences in flows in regions within a wet-dry tropical climate (Kennard et al., 2010), and this may allow species to grow to adulthood and larger size.

4.4 | The importance of dispersal

Local to large-scale dispersal is a feature of the ecology of stream fishes in rivers of northern Australia (Bishop, Pidgeon, & Walden, 1995). Such dispersal enables access to habitats for breeding, feeding and growth, and/or dry season refuge (Jardine et al., 2012; Pusey et al., 2018), provides the circumstances in which species sorting along environmental gradients can occur (Tonkin, Altermatt, et al., 2018) and underscores the potential for variation in connectivity to influence community structure at broad spatial scales. Species such as *L. calcarifer* and *P. ordensis* require access to the estuary to complete their life cycle. Many other fish species make use of seasonally available habitats such as intermittent streams and floodplain wetlands, actively and rapidly dispersing over long distances into these habitats from perennial refuges in the main channel at the start of the wet season (Pusey et al., 2004). Access to intermittent streams that provide important spawning habitat for neosilurid catfishes and the grunter *H. fuliginosus*, needs also to be accompanied by later egress back to permanent refugial habitats. Although this was so for the stream habitats examined, connectivity between the main river and floodplain wetlands becomes limited by the early dry season when sampling commenced. At this time, floodplain wetlands had become isolated from the adjacent river (Jardine et al., 2012). Dispersal from wetlands back to river habitats occurs at the end of the wet season (i.e. March to April, locally termed the run-off period); otherwise fish remain in such habitats until the next wet season.

There were marked differences in assemblage structure upstream and downstream of Beeboom Crossing (groups 7 and 8 respectively), a structure that is submerged for extensive periods during the wet season but is likely to pose difficulty for upstream fish passage in the dry season. For example, species more abundant downstream of this barrier included five estuarine-dependent species that disperse upstream during the late wet season and early dry season. Two freshwater species (*N. erebi* and *S. krefftii*) were also more abundant downstream of this barrier. Information on the breeding and movement biology of these two species is limited but, in the former, reproduction

probably occurs in downstream habitats and is followed by an upstream migration (Bishop, Allen, Pollard, & Cook, 2001). Upstream/downstream differences in assemblages may be more pronounced in years of reduced wet-season flow, given that our study occurred over 2 years with large flood flows.

4.5 | Environmental flow management in Daly River

Proposed future increases in water use in the Daly River are likely to be limited to abstraction of groundwater and are unlikely to have impact on wet-season flood flows. Thus, potential hydrological impacts include: (i) a reduction in dry-season flows in perennial reaches and in extreme circumstances, their cessation; (ii) decoupling of wet- and dry-season flows when wet-season flows remain nearly natural but are followed by significantly lower than natural dry-season flows; (iii) altered connection periods between perennial and intermittent habitats and the loss of perennial refugial habitats; and (iv) an extended dry-wet transition period to buffer early wet-season storm runoff (King, Townsend, Douglas, & Kennard, 2015). These same impacts are common to rivers across the wet-dry tropics (e.g. savannah ecosystems) (Naiman, Latterell, Pettit, & Olden, 2008).

With the exception of streams within the stone country of the Arnhem Land Plateau, aquatic habitats within the Daly River are highly connected. Many species are distributed widely, dispersing within the river and its floodplain, and in some cases, using the highly productive intermittent streams as nursery habitats (Pusey et al., 2018). The availability and reliability of spatial food web subsidies from floodplains are likely to be important in sustaining fish biodiversity at the catchment scale (Jardine et al., 2015). The maintenance of within-river continuity to enable access to areas of high production, refugial habitats and spawning habitats is fundamental to maintaining river ecosystem resilience to change (Radinger, Hölker, Horký, Slavík, & Wolter, 2018; Van Looy et al., 2019). Clearly, the maintenance of flows sufficient to maintain high connectivity within the river landscape must be a priority in any consideration of the environmental flow needs of the river. In this regard, existing features that appear to impede fish movement (i.e. Beeboom Crossing) take on additional importance. Changes in flow regime that increase the period in which fish movement is inhibited are likely to have an adverse impact on the distribution of fishes upstream and on predator-prey dynamics (Turschwell et al., 2019). Although landscape-scale changes in fish assemblage composition in the Daly River were not driven by estuarine-dependent species, the fact remains that such species are an important component of the fauna.

Lates calcarifer, for example, is a large apex predator and changes in abundance resulting from reduced connectivity are likely to have profound consequences for other species (Turschwell et al., 2019). Moreover, decoupling of wet-season flows that facilitate recruitment in *L. calcarifer* (Bayliss et al., 2008), from dry-season flows that sustain juvenile production (Stewart-Koster et al., 2011), is likely to reduce the abundance of this economically and culturally important species and may also result in increased predation pressure on forage species

in those stretches it can reach (Turschwell et al., 2019). Small migratory species (e.g. *L. triramus*) or species that migrate upstream as juveniles (e.g. *N. graeffei/berneyi*) would be even less likely to reach upstream habitats when the flood recession period is curtailed (i.e. in the wet-to-dry transition period). Water extraction scenarios that reduce the connectedness of intermittent streams at the end of the wet season (i.e. by shortening the duration of flow) are likely to result in increased mortality of species that use such habitats for reproduction but otherwise migrate back to refugial habitats or the perennial main channel.

Changes in the extent, nature and availability of in-stream habitat have traditionally dominated investigations of the way in which flow regimes affect fishes and the methods used to assess these changes. For example, Chan et al. (2012) demonstrated that some abstraction scenarios for the Daly River increased the risk that the population size of fish species would be depressed. In this case, the mechanisms causing heightened risk differed: changes in the size of riffles were most important for *H. fuliginosus* whereas changes in pool size were most important for *L. calcarifer*. Variation in depth, water velocity, and microhabitat availability (wood aggregations, undercut banks, etc.) were shown in the present study to be correlated with the abundance of a range of species. However, the extent to which changes in habitat diversity and habitat size mediated by flow regime at the local scale under increased water use would translate into catchment-wide changes in fish abundance and diversity is difficult to assess. At a regional scale, the Daly River is distinctive with its perennial flow regime, and it can be argued that it is comparatively species-rich as a result. Perennial rivers within the region contain more species than do comparatively sized intermittent rivers (Pusey et al., 2017). Although the region contains a diverse suite of fishes making use of intermittently available habitats, it is likely that skewing flow regimes towards intermittency will reduce species diversity in the long term.

The distribution and abundance of fish reflect the interaction between gradients of hydrological and environmental variation and species-specific variation in life history traits (Olden & Kennard, 2010). Changes in functional trait composition of fish communities allow greater understanding of the influences of natural (Mims & Olden, 2012) and altered flow regimes (Arantes, Fitzgerald, Hoeinghaus, & Winemiller, 2019). Sternberg and Kennard (2013) found strong relationships between life-history traits and measures of hydrological variation, including a close correlation between maximum size and perenniality. Perennial flow allows fish to grow, mature, and attain large size. We might reasonably expect, therefore, that any water management strategies that shift the flow regime of the Daly River main channel, and of perennial streams, towards intermittency are likely to result in a reduction in the number and abundance of large-bodied species or at least a reduction in growth rates and survivorship. Similarly, increasing intermittency in already intermittent streams is likely to reduce further the number and abundance of species within this stream type, particularly if already limited refugial pools become further reduced in size, longevity, and availability. Moreover, as discussed above, the value of intermittent streams as

nursery habitats for species that as adults reside in downstream perennial habitats, and as habitats supporting a distinct subset of fish species, will be reduced also. Widespread within- and between-river distributions are a feature of the fish species of northern Australia, and the most widely distributed species at both scales tend to be the most abundant (Pusey et al., 2017). Such is also the case in the Daly River. Thus, identification of functional groups, defined by habitat use in the Daly River, may be broadly translatable to other northern river catchments facing demands for increased water use and in the absence of specific information on patterns of habitat use or assemblage structure.

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