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Hydrological connectivity drives patterns of macroinvertebrate biodiversity in floodplain rivers of the Australian wet/dry tropics

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Aquatic macroinvertebrates in floodplain rivers of the wet/dry tropics

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SUMMARY

1. Floodplain rivers in Australia's wet/dry tropics are regarded as being among the most ecologically intact and bio-diverse lotic ecosystems in the world, yet there have been relatively few community-based studies of their aquatic fauna.

2. To investigate relationships between hydrological connectivity and biodiversity in the region, macroinvertebrates were collected from sites within two contrasting floodplain rivers, the 'tropical' Gregory River and 'dryland' Flinders River systems, during the dry season and analysed at various spatial scales. A subset of sites was re-sampled in the following dry season to explore temporal variation. The fauna consisted of 124 morphotaxa, dominated by gatherers and the Insecta.

3. As predicted, hydrological connectivity (the lotic or lentic status of waterbodies) had a major influence on macroinvertebrate assemblage structure and diversity, both in space and time. Assemblages from waterbodies with similar connection histories

were most alike, and beta-diversity between assemblages was greatest between lotic and lentic waterbodies, tending to increase with increasing spatial separation.

4. At smaller spatial scales, a number of within-waterbody, habitat and water quality characteristics were important for explaining variation (61 %) in the taxonomic organisation of assemblages, and characteristics associated with primary productivity and habitat diversity were important for explaining variation (45 %) in the functional organisation of assemblages. However, much of the small-scale environmental variation across the study region appeared to be related to broad-scale variation in hydrological connectivity, which had both direct and indirect effects on macroinvertebrate assemblages.

5. Conservation of the biodiversity in Australia's wet/dry tropics may depend on conserving the natural variation in hydrological connectivity and the unregulated flow of floodplain rivers.

Keywords: beta-diversity, dryland rivers, functional feeding groups, multiple scales, spatiotemporal variation

Introduction

Understanding spatiotemporal variation in patterns of biota and their relationships with the environment is a key theme of riverine ecology (Ward, 1989; Poff, 1997; Ward & Tockner, 2001; Thorp, Thoms & Delong, 2006) including that of floodplain rivers (Ward, Tockner & Schiemer, 1999; Amoros & Bornette, 2002). For example, variation in patterns of biodiversity within unregulated floodplain rivers is related to the complex hydro-geomorphology of such systems and their changing connection and disconnection through space and time (Ward *et al.*, 1999). We can describe this variation in terms of beta-diversity or the turnover in biotic composition (taxonomic or functional) between any two habitats (within or between rivers). Maximum beta-diversity theoretically occurs at some intermediate level of connectivity between habitats (Ward *et al.*, 1999; Ward & Tockner, 2001), as may result from different states of hydrological connection in space and time. However, different types and levels of variation may be associated with different types of river systems.

In dryland rivers with large and active floodplain zones, differentiation among biotic assemblages (beta-diversity) can be explained by the 'connectivity potential' between habitats, a combination of spatial separation and the historical frequency of hydrological disconnection (Marshall *et al.*, 2006). For tropical rivers with active floodplains, however, our understanding of biodiversity patterns stems from concepts developed specifically for, and from, these river types (e.g. Ezcurra De Drago, Marchese & Wantzen, 2004). The most influential of these is the Flood Pulse Concept (Junk, Bayley & Sparks, 1989). This model predicts that biodiversity in floodplain waterbodies is greater than that of main channels due to greater variability within floodplain habitats. In neo-tropical rivers, this has indeed been demonstrated to occur (Ezcurra De Drago *et al.*, 2004). In addition, assemblage structure appears to persist in these systems throughout wet and dry seasons (Melo & Froehlich, 2001). Despite these insights, however, it is uncertain how the interaction between spatial scale (e.g. Boyero & Bailey, 2001) and hydrological connectivity (e.g. Dos Santos & Thomaz, 2007) influences beta-diversity in tropical floodplain systems.

Flow regime plays a major role in structuring patterns of biotic composition and diversity in riverine ecosystems (Poff *et al*., 1997; Puckridge *et al*., 1998). Tropical rivers generally have regular flow regimes (Latrubesse, Stevaux & Sinha, 2005), whereas dryland rivers are characterised by flow variability (Puckridge *et al.*, 1998). Therefore, biodiversity patterns in tropical rivers may not be influenced by variation in hydrological connectivity, and the 'connectivity potential' between habitats, to the same extent as patterns in dryland rivers. This has implications for regions that include both 'tropical' and 'dryland' river types. The wet/dry tropics in northern Australia is one such region: many of the floodplain rivers here have flow regimes that can be described as typically 'tropical' (more permanent with regular flow regimes) or 'dryland' (more ephemeral with greater flow variability) (Leigh & Sheldon, 2008). As such, it is likely that spatiotemporal patterns of variation in the biotic assemblages of these systems will differ between the contrasting river types.

Floodplain river systems in Australia's wet/dry tropics are regarded as among the most ecologically intact and bio-diverse lotic ecosystems in the world (Woinarski *et al*., 2007), yet they have been the focus of relatively few community-based studies (Marchant, 1982; Outridge, 1988; Paltridge *et al*., 1997; Erskine *et al*., 2005). To

increase our understanding of biodiversity patterns and hydrological connectivity within these systems, macroinvertebrates were collected from two contrasting floodplain rivers in the southern Gulf of Carpentaria (the 'tropical' Gregory River and 'dryland' Flinders River systems) across consecutive dry seasons and analysed at various spatial scales. Specifically, we predicted that the two river systems ('tropical' versus 'dryland') would be associated with different patterns of variation in assemblage structure and diversity; that assemblages from waterbodies with different states of hydrological connection (lotic versus lentic waterbodies) would show more differentiation in structure and diversity than those from waterbodies with the same flow status (lotic versus lotic, lentic versus lentic); and that beta-diversity in floodplain habitats ('off-channel' waterbodies) would be much greater than in main channels and would be associated with greater habitat diversity in the floodplain. More generally, we also explored: (a) the effect of spatial scale on beta-diversity; (b) relationships between assemblage structure and environmental conditions at spatial scales smaller than catchment, and; (c) temporal change in assemblage structure between the two dry seasons.

Methods

Study area and design

Australia's wet/dry tropics are located north of the Tropic of Capricorn and are comprised of savannah and dry forest (Fig. 1). Floodplain catchments in this region, including those in the Gulf of Carpentaria drainage division in Australia's northeast, experience an annual cycle of monsoonal rains, high flows and flooding in the wet season (*c*. Nov-Apr) followed by a dry season (*c*. May-Oct) of low flows and virtually no rainfall. Hydrological analysis of rivers here suggests there are two dominant flow patterns—the more regular 'tropical' rivers, and the more ephemeral 'dryland' rivers (Leigh & Sheldon, 2008). During the dry season, flow tends to cease in the 'dryland' rivers, with both channels and floodplains becoming a mosaic of disconnected waterholes. This occurs to a much lesser extent in the floodplains of the 'tropical' rivers. From within these broad groups, we studied two large river systems in the Nicholson (52 300 km^2) and Flinders (109 400 km^2) catchments (Fig. 1), in southern Gulf of Carpentaria. The clear-flowing, perennial and aquifer-fed Gregory River and Beames Brook in the Nicholson catchment are more typically 'tropical', whereas the

turbid Flinders and Cloncurry Rivers in the Flinders catchment are more typically 'dryland'.

Eleven waterbodies were sampled across the lower freshwater sections of the remote Gregory and Flinders river systems during the 2005 dry season (August) (Fig. 1). Waterbodies were classified as either lotic or lentic, representing their hydrological connection or disconnection at the time of sampling (hereafter 'flow status'). Codes were used to represent the catchment (Gregory = G, Flinders = F), river section (downstream = D, mid = M, upstream = U) and lateral position (main channel = m, off-channel = o) of each site (Table 1). Lotic waterbodies tended to have long runs either side of a deep pool, whereas lentic waterbodies were typically reduced to shallow pools. However GDm was a long run, and both GDm and GUm had riffles at their downstream ends. Four of the 11 waterbodies (two in each catchment) were re-sampled in the dry season of 2006 (in September) (Fig. 1). Thus, the study design included one temporal scale (2005 versus 2006 dry season) along with four spatial scales (catchment, waterbody, within waterbody and within habitat) that were described by environmental conditions (see below). Under this design, differences between the Gregory and Flinders river systems could not be attributed to categorical differences between all 'tropical' and 'dryland' river types. However, the design enabled our predictions about patterns of biodiversity and hydrological connectivity in the study region to be explored and allowed us to formulate testable hypotheses about our study systems and about others with similar flow regimes (cf. Hargrove & Pickering, 1992).

Macroinvertebrate assemblages

Macroinvertebrates were sampled from all habitat types present at each waterbody (e.g. bare littoral, snags, leaf litter, aquatic macrophytes) using a (semi-quantitative) patch-weighted composite-habitat protocol (Marshall *et al.*, 2006). The littoral distance covered by each habitat type was estimated and proportional distances for sampling were then allocated to each habitat type. These distances were swept with a 500 µm dip-net and produced samples that represented an entire waterbody, allowing comparison among samples and waterbodies. Three samples were collected at each waterbody, to give 45 samples in total (three samples each from 11 waterbodies in

2005; three samples each from four waterbodies in 2006). Samples were preserved in 70 % aqueous methanol for later identification in the laboratory.

All macroinvertebrates (aquatic invertebrates > 500 µm) were sorted from detritus and sediment under a dissecting microscope, identified according to taxonomic and functional feeding group (FFG) classifications (Cummins & Klug, 1979; Merritt & Cummins, 1996; Hawking, 2000) and counted. Identification was performed to the lowest taxonomic level practicable, given keys, life-history stage and condition. This was most often to genus or species. However, where keys were incomplete or not specific to the study region, or individuals were too small (e.g. tiny Zygoptera) or had lost vital parts (e.g. many mayfly larvae had broken legs and antennae), identification was to a higher taxonomic level (but representative of morphotaxa at lower levels of resolution where practicable). Voucher specimens of all taxa were retained as a reference collection at Griffith University.

Environmental conditions

Hydrographs, produced using mean daily flow data (megalitres per day standardised by upstream catchment area, ML d^{-1} km^{-2}) from gauging stations in and around the study region (DNRM, 2005), were first used to compare flow regimes and likely connection histories among waterbodies and catchments. Although continuous daily flow data were available only until the late 1980s, the purpose was to assess typical patterns in the flow regime (*sensu* Puckridge *et al*., 1998) rather than assess flow records that corresponded directly with macroinvertebrate sampling times.

Secondly, hydro-geomorphological and biophysical measures were used to describe waterbodies at spatial scales smaller than the catchment. These were visually estimated or taken by direct or remote survey and included waterbody (seven variables), within-waterbody (eight variables) and macroinvertebrate habitat (12 variables) scale measures (Appendix S1). Additionally, three replicate samples each of littoral zone sediment and biofilm were collected and analysed for chlorophyll *a* concentration using standard methods (APHA, 1989). Concentrations were converted to median areal values, and these were included in the set of macroinvertebrate habitat variables (14 in total) (Appendix S1).

Water quality characteristics (15 in total) were described using a number of variables (Appendix S1). Conductivity, salinity and pH were measured from a mid-channel location at each waterbody using a multi-parameter sonde (YSI 600XLM in 2005 and YSI 6920 in 2006, Yellow Springs, Ohio, USA). Dissolved oxygen concentration was also recorded but data were unreliable due to a faulty probe. Light irradiance (E, photosynthetic radiation at 400 – 700 nm) was measured as a function of depth (z) with a 2-pi sensor and light meter (Li-cor Li-1400, Lincoln, NE, USA) to determine the euphotic zone depth (equivalent of 1 % of surface irradiance). Light attenuation (*k*) was first determined by fitting a regression to the measured irradiance and depth data, using the exponential equation: $\ln (E_z) = -k(z) + \ln (E_0)$, where E_z is the irradiance at depth z, and E_0 is the irradiance at the surface of the waterbody (Kirk, 2003). The euphotic depth (ED) was then calculated by substituting 1 % of the surface irradiance value for E_z. Three samples of surface water from the mid-channel location were collected and analysed for median concentrations of chlorophyll *a*, total and dissolved nitrogen and phosphorus (N and P), and organic and inorganic fractions of suspended solids using standard methods (APHA, 1989).

Analyses

The approach used in this study was similar to that of previous studies exploring relationships between spatial and temporal patterns of biotic assemblages and environmental factors (e.g. Marshall *et al.*, 2006). Three types of pattern were explored: assemblage composition (based on taxonomic abundances), functional composition (based on the proportionate representation of FFGs calculated from abundance data), and diversity (based on diversity measures calculated from abundance data). For individuals classified by more than one FFG (e.g. elmid beetles were considered both grazers and gatherers), their abundance was shared equally among these groups (e.g. one elmid beetle = 0.5 grazer + 0.5 gatherer) before calculating FFG proportions (Dudgeon, 1994). Diversity measures included richness (S), abundance (N), Margalef's index of richness [$D = (S-1)/\ln N$], the Berger-Parker index of dominance [$BP = N_{max}/N$, where N_{max} = the number of individuals in the most abundant taxon] and a simple measure of beta-diversity [$\beta = (S/S_{av}) - 1$, where S_{av} is the average richness of the sample units used to calculate S]. Margalef's index (D) was used to incorporate evenness and richness into one measure, and the Berger-

Parker index (BP) provided an indication of the unevenness between richness and abundance within a sample (Magurran, 1988). Beta-diversity (β) was calculated within-waterbody (between-sample) and between-waterbodies. Maximum β occurs when no taxa are shared amongst samples, and minimum β (= 0) occurs when all sample units share all the same taxa (McCune, Grace & Urban, 2002).

Multivariate analyses were used to explore patterns of variation in taxonomic and functional composition of assemblages and included analysis of similarities and similarity percentages (ANOSIM and SIMPER), clustering (unweighted pair group method with arithmetic mean, UPMGA), ordination (non-metric multidimensional scaling, MDS) and correlation (BIOENV) techniques in the PRIMER-5 software package (PRIMER-E, 2002). Patterns of variation in diversity were explored using univariate techniques (analysis of variance, ANOVA) in SAS (SAS Institute, 2002).

Spatial patterns were explored using a two-way factorial ANOSIM (with up to 999 permutations) to test for differences in assemblage composition between groups within *a priori*-defined factors ('catchment': Gregory versus Flinders; 'flow status': lotic versus lentic). Groups were based on Bray-Curtis dissimilarity matrices of $\log_{10}x$-transformed data for both taxonomic abundances (x +1) and FFG proportions (x). Patterns of variation among groups were visualised using MDS with default settings and 100 random starts. Ordination solutions were displayed in two dimensions when stress was low (< 0.2) and accompanied by dendrograms produced from agglomerative, hierarchical cluster analyses based on group-averaged Bray-Curtis dissimilarity scores (UPGMA) (McCune *et al.*, 2002). SIMPER was used to identify key taxa contributing to the average dissimilarity between groups that were significantly different (ANOSIM $p < 0.05$).

Analysis of variance (ANOVA) was used to determine the effect of the *a priori*-defined factors on macroinvertebrate diversity measures (S, N, D and BP). All factors were included in each ANOVA model, and non-significant factors were removed stepwise until the most parsimonious and significant model (lowest *P*-value) was achieved. Data were transformed as necessary (e.g. log and arcsine square root transformations) to comply with ANOVA assumptions (normality and homogeneity

of variance) and least squares means were used due to unequal replication among groups within factors. Where multiple comparisons were made between pairs of sample groups or factors (in ANOVA and ANOSIM), their significance was tested using the Bonferonni *t*-test, which controlled the experiment-wise error rate across all paired comparisons (Neter, Wasserman & Kutner, 1985; Montgomery, 2001).

Two issues narrowed the breadth of analyses performed. Firstly, the multivariate interaction effect between catchment and flow status was not tested, as this requires a balanced number of samples within groups. Secondly, nested (hierarchical) designs are common in ecological studies, and for this study, the factor 'lateral position' (main or off-channel waterbody) was nested within catchment. Anderson (2001) provides a method of nonparametric multivariate analysis of variance (NPMANOVA), based on Bray-Curtis dissimilarity scores, that can be used to examine nested designs and effects of main and interaction terms. However, if flow status was found to have a significant effect, this method could not be used due to main and off-channel waterbodies being inconsistently lotic or lentic. Thus, the effect of lateral position could not be partitioned from that of flow status. However, there was enough consistency within the subset of lentic Flinders waterbodies to test for differences between main (FUm and FMm) and off-channel (FUo and FDo) locations in a balanced design using a one-way ANOSIM and SIMPER. Additionally, as ANOVA can cope with unbalanced designs, the effect of lateral position on diversity measures could be tested within lotic waterbodies in the Gregory catchment, as well as lentic waterbodies in the Flinders.

Variation in macroinvertebrate assemblages across a hierarchy of spatial scales (within and between waterbodies, both within and between catchments) was explored using pair-wise Bray-Curtis dissimilarity scores (as a measure of beta-diversity) based on log-transformed abundance and FFG proportion data (Marshall *et al.*, 2006). Sample data were averaged across waterbodies before calculating between-waterbody dissimilarity scores. There is no simple test available to compare Bray-Curtis dissimilarity scores at different scales particularly with low level replication ($n = 3$) at the base level (within-waterbody) (cf. Underwood & Chapman, 1998; Marshall *et al.*, 2006). Thus, differences among scales were interpreted by examining ranges of Bray-Curtis dissimilarity scores with box-plots.

Relationships between assemblages and their environment at spatial scales smaller than catchment (waterbody, within-waterbody, macroinvertebrate habitat, and water quality characteristics) were investigated using generalised Mantel tests with Monte Carlo randomisations (BIOENV). However, as the number of environmental variables within each scale was large (Appendix S1), Spearman's rank correlation coefficients (r_s) were calculated prior to the BIOENV analyses to avoid variable redundancy. Variables with the greatest potential ecological importance acted as surrogates for those variables with which they were highly correlated ($r_s \geq 0.9$) (Clarke & Warwick, 2001). The BIOENV analysis described the association between the assemblage data matrices (log-transformed abundance or proportional FFG data subjected to the Bray-Curtis dissimilarity measure) and environmental matrices (range-standardised variables within each scale, transformed if necessary to reduce skew below 1, and subjected to the normalised Euclidean distance measure) (Clarke & Warwick, 2001). The amount of variation in assemblage patterns explained by combinations of environmental variables was estimated as the square of the BIOENV correlation coefficient (r_s) (cf. Marshall *et al.*, 2006). Additionally, the combinations of variables at each environmental scale that explained the most variation in the biotic datasets (highest BIOENV $r_s > 0.4$) were combined for an overall BIOENV analysis.

Temporal variation was explored by comparing spatial patterns in assemblage composition seen in the 2005 (all waterbodies, and the smaller subset of GUm, GUo, FUm and FUo) and 2006 datasets (GUm, GUo, FUm and FUo), using analyses detailed above. Additionally, 'year' was included as an *a priori*-defined factor (2005 versus 2006) in ANOSIM and ANOVA analyses. Interaction terms were not tested due to insufficient replication within groups, which also affected the ability to test for differences in assemblages between main and off-channel locations across years, particularly in the presence of a significant effect of flow status (see above).

Results

Environmental conditions

The most obvious differences between waterbodies in their environmental characteristics were associated with broad-scale hydro-geomorphology and the

Gregory and Flinders Rivers' flow regimes. Flow records from FDm, the only lotic Flinders waterbody at the time of sampling (also known as Walkers Bend), showed that dry season periods of zero flow are usual at this site and follow a similar pattern as experienced at those immediately upstream of the study region (at the Cloncurry River at Canobie and Flinders River at Etta Plains gauging stations) (Fig. 2). Indeed, the only time in the period of continuous daily flow records from Walkers Bend (1969 – 89) when flow was experienced in the same month as the majority of sampling conducted for this study (August), was in 1988 for 22 days. Although the gauging station at FDm is the only one within the Flinders sampling area, the similarity between flow patterns at this waterbody and the nearby upstream stations suggested that macroinvertebrate assemblages from all the sampled Flinders waterbodies were likely to have experienced a similar connection history (featuring variable lengths of disconnection most dry seasons). Additionally, this history would be in strong contrast to that of the lotic Gregory waterbodies, which permanently connected. In fact, over the same 16 year time period of continuous daily flow records (30/9/72 – 30/9/88), Walkers Bend had zero flow days 59.4 % of the time, Canobie 72.5 % and Etta Plains 69.5 % (Fig. 2). This was in contrast to no zero flow days (0 %) experienced at Gregory River at Gregory Downs, the gauging station immediately upstream of the Gregory sampling area (Fig. 2).

At the waterbody and within-waterbody scales of resolution, a number of variables also appeared related to the broader-scale influence of hydrological connection and disconnection. This included depth, many water quality variables, and macroinvertebrate habitat variables such as macrophyte presence or absence. In general, lotic Gregory waterbodies were deeper and appeared to have lower concentrations of nutrients, suspended solids (but greater % organic solids) and algal biomass in the water column, lower pH, and to have more abundant and diverse vegetation in littoral zones than lentic and Flinders waterbodies, which appeared to have greater proportions of bare sediment and snags. These general trends were observed in the 2005 dry season (as displayed by a number of variables used in the BIOENV analyses below) and in 2006 (Table 2).

Macroinvertebrate assemblages

In total, 48 669 individuals were identified from the 2005 and 2006 dry season samples, representing 124 morphotaxa (Appendix S2). These included a total of 35 664 individuals and 119 morphotaxa from the 33 samples collected from 11 waterbodies in the 2005 dry season. Within these samples, Insecta dominated the abundance (45 %) and richness (79 %). Crustacea made up 38 % of the total abundance, followed by Mollusca (12 %), with these latter two groups comprising 8 and 9 % of the total richness, respectively. Among the Insecta, Diptera were the most abundant (65 %) and Coleoptera the most diverse (33 %); however, most families within Coleoptera were identified to a lower level of taxonomic resolution than Diptera, such that their richness may have been underestimated (Appendix S2). All FFGs were represented, with abundance dominated by gatherers (42 %), and richness by predators (50 %). Shredders were the least abundant (< 1 %) and taxon rich (5 %) FFG.

The twelve 2006 dry season samples (three samples each from GUm, GUo, FUm and FUo) represented 88 morphotaxa, from which 13 005 individuals were identified, compared with 13 053 individuals from 74 morphotaxa from the same waterbodies in 2005 (Appendix S2). Insecta dominated the abundance (43 %) and richness (74 %) of the 2006 samples, which was also the case in 2005 for the same four waterbodies (47 % for abundance and 72 % for richness). All functional feeding groups were represented in samples collected in 2006, showing similar patterns as in 2005.

Spatial variation in taxonomic composition, 2005 dry season

Catchment and flow status both had significant effects on the taxonomic composition of assemblages across the study region (ANOSIM, $P = 0.008$ and 0.004, respectively; Table 3). The effects of these factors were visible on the agglomerative dendrogram and MDS ordination of sample assemblages, with the separation between lotic Gregory waterbodies and all remaining waterbodies, including GUo (the lentic waterbody in the Gregory catchment) clearly evident (Figs 3a & 4a). Additionally, a key group of species were associated with the difference between groups within the factors (SIMPER; Table 3). The abundances of cladocerans (*Simocephalus* sp.), ostracods and bivalves (*Corbicula* sp.) were particularly important in contributing to the difference between catchments (Gregory versus Flinders) and flow states of waterbodies (lotic versus lentic), making up the first 10 % of the difference between

groups within both factors. The abundances of *Simocephalus* sp. and ostracods were higher in samples from the Flinders than from the Gregory. However, *Simocephalus* sp. abundance was greater in samples from lotic waterbodies than lentic, whereas the opposite was the case for ostracods. The abundance of *Corbicula* sp. was greater in samples from Gregory and lotic waterbodies than from Flinders and lentic waterbodies, respectively. This pattern was also the case for *Thiara* (*Plotiopsis*) sp., the fourth most important taxon to contribute to the differences within each factor. Indeed, this taxon was completely absent from both Flinders and lentic waterbodies.

Although catchment and flow status both had significant effects on assemblage structure, differences between main and off-channel waterbodies were not as clear. Within lentic Flinders waterbodies, a weak but significant difference was found between main and off-channel locations (one-way ANOSIM on lateral position, $P = 0.045$; Table 3). This effect was apparent on the dendrogram within groups of the main separation between lotic Gregory waterbodies and all others (Fig. 3a). However, taxa associated with this difference primarily consisted of gatherers, grazers and predators, all of which appeared equally present in both locations (SIMPER, Table 3). The most obvious difference between the two groups of taxa was that main channel assemblages were characterised by greater abundances of two filter feeding taxa (*Simocephalus* sp. and Tanytarsini) (SIMPER, Table 3).

Ranges of pair-wise Bray-Curtis dissimilarity scores within groups of samples at increasing spatial scales of resolution suggested a ‘faunal differentiation by distance’ across the study region (cf. Marshall *et al.*, 2006) (Fig. 5a). Sample assemblages within waterbodies were similar (low pair-wise dissimilarity scores); but, when abundances of taxa were averaged over samples to produce waterbody centroids, pair-wise dissimilarity scores increased (greater between-waterbody variability in assemblages than within-waterbody). Additionally, between-waterbody variation in assemblages was greater (in range and marginally in median score) when catchment boundaries were disregarded (greater between-waterbody variation at the scale of the whole study region than within catchments).

Environmental influences at scales smaller than the broad-scale effects of catchment, flow status and position in the floodplain also related to spatial patterns of assemblage

composition. Multivariate correlations between structural assemblage and environmental variable dissimilarity matrices (BIOENV) indicated relationships at the waterbody and within-waterbody scales, and with habitat and water quality characteristics (Table 4). Combinations of habitat characteristics tended to explain the most variation in assemblage patterns compared with other types of variables, and the proportions of aquatic vegetation (macrophytes plus algae), leaf litter and snags in macroinvertebrate habitats gave the best combination of variables within any one dataset (explaining 39 % of the variation in assemblages). However, the best correlation between environment and assemblage composition (highest r_s) was found using a combination of variables from the within-waterbody scale (presence or absence of macrophytes and undercuts) plus a number of habitat (proportions of aquatic vegetation and leaf litter) and water quality characteristics (concentration of ammonium-N and pH) (61 % of the variation in assemblage patterns explained). Many of these features could be associated with the difference in conditions between lotic Gregory waterbodies and all other waterbodies. In particular, lotic waterbodies in the Gregory catchment were characterised by the presence of undercuts and macrophytes, higher proportions of aquatic vegetation and lower pH (Table 2).

Spatial variation in functional composition, 2005 dry season

In terms of functional feeding groups, a number of general trends in their proportionate representation were observed among waterbodies. Overall, gatherers and filterers tended to dominate the macroinvertebrate FFGs found in samples (Fig. 6). However, shredders were relatively most abundant in Gregory waterbodies, gatherers in lentic waterbodies and filterers in lotic waterbodies. Both grazers and predators appeared to make up at least a quarter of the FFG abundances in most waterbodies, and main channel waterbodies, except for FUm, appeared to have greater proportions of filterers than their corresponding off-channel waterbodies (Fig. 6). Additionally, some waterbodies appeared to have site-specific differences in FGG proportions. Gatherers occurred in comparatively high proportions in assemblages of GUo, FDo, FUm and FUo (waterbody means ≥ 63 %). Grazer proportions were comparatively low at FDm, FUm and FUo (waterbody means ≤ 7 %). FDm had the greatest proportion of predators (29 ± 3 %) and GDo the greatest proportion of shredders (5 ± 1 %).

In addition to these general trends, there were statistically significant differences in the functional composition of assemblages between catchments and states of flow (ANOSIM R = 0.275 and 0.703, *P* = 0.029 and 0.001, respectively). As seen in the taxonomic composition of assemblages, these differences were apparent on the MDS ordination plot based on FFG proportions (Fig. 4c). SIMPER analysis showed that within groups of waterbodies, gatherers made up a greater proportion in lentic and Flinders samples, filterers and grazers in lotic and Gregory samples. Interestingly, flow status had a much stronger influence than catchment (greater R and lower *P*-values) on functional differences between groups within these *a priori*-defined factors, than on taxonomic differences (cf. Table 3). The effect of lateral position on assemblage composition was also different between taxonomic- and functional-based analyses; despite the association of filterers with main channel waterbodies (see above), lateral position did not have a significant effect on variation in the representation of functional feeding groups (one-way ANOSIM between main and off-channel locations for lentic Flinders waterbodies only, R = 0.231, *P* = 0.082). However, faunal differentiation by distance in the functional composition of assemblages was similar to that seen in taxonomic composition, whereby pair-wise variation between assemblages (Bray-Curtis dissimilarity scores and their ranges) increased with spatial scale (Fig. 5b). In contrast to taxonomic composition, however, the variation in functional composition *between waterbodies* was similar at both the within- and across-catchment levels of spatial resolution (Fig. 5).

Within sets of environmental variables at spatial scales smaller than the catchment, relationships between patterns of environmental characteristics and the functional composition of assemblages were strongest for habitat and water quality characteristics (BIOENV, Table 4). However, water quality variables explained a greater amount of the pattern (32 %). In contrast to patterns based on taxonomic composition, within-waterbody scale features were poor at describing functional patterns (≤ 11 % of the variation explained); but combinations of variables across datasets still explained the most variation. The best combination (highest r_s) explained 45 % of the variation in the functional assemblage dataset and included, (i) the number of different macroinvertebrate habitats, (ii) total nitrogen concentration, (iii)

the proportion of organic suspended solids, (iv) the areal amount of chlorophyll *a* and proportion of silt in the littoral-zone sediment, (v) canopy cover, and (vi) waterbody depth (Table 4). Total nitrogen concentration was highly correlated with euphotic depth and concentrations of total phosphorus and suspended solids (redundancy analysis; Spearman's $r_s > 0.9$). Together, the importance of these features suggested a strong influence of primary productivity, along with macroinvertebrate habitat diversity, on the functional organisation of waterbody assemblages.

Spatial variation in diversity, 2005 dry season

Assemblages varied among waterbodies in terms of their calculated measures of diversity (Fig. 7). High abundances of macroinvertebrates were found in FDm, FMm and FUo, probably due to the large numbers of ostracods collected at these waterbodies. Within waterbodies, the variation in abundances between samples was greatest for GMmB (1076 ± 8210); one sample from this site contained a comparatively high number of cladocerans (the filterer, *Simocephalus* sp.). As a result, this site had the highest within-waterbody beta-diversity ($\beta = 0.58$; Fig. 7), which could be seen in the MDS ordinations on the taxonomic and functional compositions of assemblages (Fig. 4). However, beta-diversity scores were low for all waterbodies ($\beta < 1$), which indicated sample assemblages within waterbodies were similar. Richness (S) was highest in GDo (50 ± 3) and lowest in FDo (20 ± 1). In terms of evenness, Margalef's D values suggested that macroinvertebrate assemblages in lotic and Gregory waterbodies were more even (higher means) than in lentic and Flinders waterbodies (lower means) (Fig. 7). Berger-Parker (BP) scores suggested that assemblages from lentic, off-channel waterbodies were more dominated by one taxon than other waterbodies (GUo, FDo, FUo all had mean scores ≥ 0.45 and had large numbers of ostracods compared with abundances of other taxa) (Fig. 7).

Off-channel waterbodies did not appear to have more diverse macroinvertebrate habitats than main channels. Rather, main channel waterbodies tended to have similar or greater numbers of different macroinvertebrate habitats than their corresponding off-channels (within a reach) and as stated above, the greatest within-site beta-diversity (β) was at GMmB, a main channel site (Fig. 7). However, the lowest beta-diversity between waterbodies within a reach was for the two main channel sites,

GMmB and GMmG (β = 0.73), which were both lotic. The highest beta-diversity scores were found between lentic off-channels and lotic-main channels within reaches (GUm and GUo, β = 0.97; FDm and FDo, β = 1.13), and intermediate beta-diversity scores were found between main and off-channel waterbodies that were either lentic (FUm and FUo, β = 0.82) or lotic (GDm and GDo, β = 0.93) (Fig. 7).

Flow status had a statistically significant effect on assemblage richness, evenness and dominance (least squares means ANOVA, $P < 0.05$; Table 5). For evenness (Margalef's D, log-transformed), the effect of flow status interacted with that of catchment ($P < 0.0001$); assemblages in lotic waterbodies in the Gregory catchment were more even than assemblages in the lotic Flinders waterbody (FDm), the lentic Gregory waterbody (GUo) and the lentic waterbodies in the Flinders catchment. For richness and dominance, there was no interaction effect and the only significant main effect ($P < 0.05$) was from flow status (not catchment). Richness (S) was greater in assemblages from lotic waterbodies than lentic, whereas dominance (BP) was greater in lentic waterbodies. Sample abundance (N, log-transformed) and within-waterbody β-diversity were not affected by flow status or catchment ($P > 0.05$), indicating waterbodies from different catchments or states of flow supported similar numbers of biota and had similar levels of within-waterbody variability (despite the comparatively high variation observed among GMmB samples). Within lotic waterbodies in the Gregory catchment only, a significant difference was detected in richness (S) and evenness (D, log-transformed), which were both greater in samples from off-channel waterbodies than from main channels. Within lentic waterbodies in the Flinders catchment only, evenness (D, log-transformed) was greater in samples from main channels than off-channels, and these off-channel samples were less dominated by one taxon, as was indicated by their significantly lower BP scores.

Temporal variation in taxonomic composition

Similar patterns of variation in taxonomic composition of assemblages were seen among all waterbodies sampled in 2005 and those sampled in 2006 (MDS ordination, Fig. 4a,b), supporting the clear separation between assemblages from lotic waterbodies in the Gregory catchment and those from all other waterbodies. However, when patterns of variation in assemblage structure were examined among re-sampled

waterbodies only (GUm, GUo, FUm, FUo in 2005 and 2006 dry seasons), more variation could be attributed to flow status of waterbodies, rather than to other broad-scale factors, such as year or catchment (UPGMA dendrogram, Fig. 3b). This was confirmed by ANOSIM: although year and catchment both had significant effects on assemblage patterns, the effect of flow status was stronger, having higher ANOSIM R and lower *P*-values than other factors (Table 3). Additionally, a similar group of taxa was associated with the difference in assemblage structure between lotic and lentic waterbodies (SIMPER) in both the spatial (11 waterbodies in 2005 only) and the temporal dataset (four waterbodies in both 2005 and 2006) (Table 3). The main difference between these groups of taxa was due to the relative absence of *Simocephalus* sp. from the 2006 samples, such that this species only made an important contribution to the difference between lotic and lentic assemblages within the 2005 dataset.

Temporal variation in assemblage structure between the same two waterbodies appeared greater than spatial variation within waterbodies. This was demonstrated by comparing ranges of pair-wise Bray-Curtis dissimilarity scores between groups of sample assemblages (Fig. 5c). Although dissimilarly increased with distance (between-waterbody greater than within-waterbody) in both 2005 and 2006, the dissimilarity between the same waterbodies across the two dry seasons was much higher than that within waterbodies.

Discussion

Assemblage biodiversity

The diversity of macroinvertebrate fauna collected from the study region (124 taxa in total across 11 locations and two dry seasons) appeared similar to that found elsewhere in Australia's wet/dry tropics, in both numbers and types of taxa present (Marchant, 1982; Outridge, 1988). Different collection methods and levels of taxonomic resolution make comparisons problematic, but diversity in the study region also appeared greater than that found in floodplain-rivers in the neo-tropics (see Ezcurra De Drago *et al.*, 2004) and in dryland Australia (in Cooper Creek; Marshall *et al.*, 2006).

Spatial variation and hydrological connectivity

Hydrological connectivity (the lotic or lentic nature of waterbodies and their connection history) can be considered the key driver of spatial patterns of macroinvertebrate diversity and structural composition (both taxonomic and functional) in the study region. This driver was stronger than catchment in its influence on macroinvertebrates, contributing to major differences between assemblages sampled from lotic Gregory waterbodies and all others (all lentic and Flinders waterbodies). Indeed, a key group of taxa was associated with the difference between lotic and lentic waterbodies. In particular, the gastropod *Thiara* (*Plotiopsis*) sp., which is typically associated with flowing waters in Australian rivers (Hawking & Smith, 1997; Tsyrlin & Gooderham, 2002), was strongly indicative of this split, being found in lotic waterbodies within the Gregory catchment only. Functionally, gatherers tended to be more abundant in lentic and Flinders waterbodies, with filterers and grazers more abundant in lotic and Gregory waterbodies. Additionally, assemblages from lotic waterbodies were more rich and even than those from lentic waterbodies, which were often dominated by a single taxon (although not consistently the same taxon in each waterbody).

Thus, our findings support our prediction that variation in hydrological connectivity has a major influence on macroinvertebrate assemblages in the study region. More specifically, we found greater differentiation between lotic and lentic waterbodies than between waterbodies of the same flow status. In addition, the two river systems (the ‘tropical’ Gregory versus the ‘dryland’ Flinders) were associated with different patterns of variation in assemblage composition and diversity. Indeed, differences in the taxonomic composition of assemblages were more apparent in the ‘tropical’ Gregory catchment, in which lentic waterbodies in the floodplain disconnect from permanently flowing channels each dry season, than in the Flinders, in which waterbodies tend to share similar connection histories.

The effect of hydrological connectivity on assemblages was so strong that the influence of lateral position in the catchment (main versus off-channel location) could not be fully explored, and differences between main and off-channel locations for waterbodies of the same flow status within a catchment were either weak (for taxonomic composition) or non-significant (for proportionate FFG composition). However, differences in diversity were more obvious, and showed opposite trends for

lotic waterbodies in the Gregory compared with lentic waterbodies in the Flinders. Off-channel assemblages were richer and more even than were main channel assemblages within the former group of waterbodies, but were less even within the latter group. This suggests that connection between waterbodies by flow, as found in the Gregory catchment, supported more diverse assemblages in off-channel locations than main channels. Alternatively, lack of flow and disconnection between waterbodies, as found in the Flinders catchment, may have lead to the dominance of assemblages in off-channel locations by particular taxa suited to stable lentic habitats (usually gatherers). Results also suggest that, if a difference in flow status between main and off-channel waterbodies exists, lotic waterbodies would be likely to contain more taxa and be less dominated by particular taxa than lentic waterbodies, regardless of their location (because the strong effect of flow status on assemblage diversity would dominate over that of lateral position).

Our study indicates that concepts of connectivity and biotic diversity developed for dryland rivers (Walker, Sheldon and Puckridge, 1995; Sheldon, Boulton and Puckridge, 2002; 2003; Marshall *et al*., 2006; Sheldon & Thoms, 2006) are well suited to river systems in Australia's wet/dry tropics. In dryland rivers, prolonged flow disconnection among waterbodies (as also occurs in Australia's wet/dry tropics each dry season) is associated with comparatively depauperate assemblages in lentic rather than in lotic waterbodies, regardless of their position in the catchment. Even in Australia's tropical north, a decline in richness over the course of the dry season has been observed for macroinvertebrate assemblages in lentic waterbodies both on and off main channels (Marchant, 1982; Outridge, 1988). In general, these changes in assemblage richness would therefore be expected to affect between-waterbody beta-diversity, such that the greatest beta-diversity would occur between waterbodies of different states of connectivity and thus connectivity potential (*sensu* Marshall *et al.*, 2006; Sheldon & Thoms, 2006). This phenomenon appears to have occurred in the southern Gulf of Carpentaria study region, where the greatest beta-diversity was found within pairs of lotic and lentic waterbodies (as represented by a simple conceptual diagram; Fig. 8). This relates most readily to the modified telescoping ecosystem model of Ward and Tockner (2001) for waterbodies of floodplain rivers, whereby flooding creates uniformity among habitats (maximum connectivity) and drying re-establishes heterogeneity (maximum individually), with maximum diversity

occurring at some intermediate level between these two states (Ward *et al.*, 1999). Although this model was initially developed from temperate floodplain rivers, it is appropriate for describing biodiversity patterns in dryland systems (Sheldon *et al*., 2002; Marshall *et al*., 2006), and, based on our findings, we propose that it also has application in tropical contexts (see also Thomaz, Bini and Bozellii, 2007).

In addition, beta-diversity (as represented by the change in assemblage composition between pairs of samples or waterbodies in the study region) was seen to increase with increasing spatial scale in a similar fashion to the 'faunal differentiation by distance' trend observed for macroinvertebrate assemblages in dryland rivers (Marshall *et al.*, 2006). These authors related spatial proximity between waterbodies to antecedent hydrology, such that waterbodies closest to each other within regions would share the most similar connection histories. For the study region, it was clear that waterbodies within the 'dryland' Flinders catchment (more ephemeral and variable flow regime) share similar connection histories despite differences in flow status at the time of sampling. For the 'tropical' Gregory catchment (more permanent and regular flow regime), however, the lentic waterbody (GUo) clearly has a different connection history to its nearby lotic waterbodies. These lotic waterbodies flow permanently throughout the year whereas GUo becomes disconnected each dry season (personal communication with landholders). Indeed, GUo assemblages were more similar to those in the Flinders sampling region than in the Gregory, a pattern supported by ordination and agglomerative clustering analyses. Therefore, although similar 'differentiation by distance' trends have been observed in both arid-zone, dryland rivers and in the study region, we suggest that for the 'tropical' Gregory river, assemblages in disconnected (lentic) waterbodies may be substantially different from those in connected (lotic) waterbodies, even when these waterbodies are comparatively close together.

At smaller spatial scales, a number of within-waterbody, habitat and water quality characteristics were important for explaining patterns of assemblage structure based on taxonomic composition, particularly those associated with habitat availability and composition. For patterns based on proportions of functional feeding groups, waterbody scale (rather than within-waterbody scale), habitat and water quality characteristics were important, particularly those variables associated with potential

primary productivity and habitat diversity. These patterns were not surprising, as it is well established that small-scale biophysical and chemical variation influences macroinvertebrate composition (Townsend *et al.*, 2003; 2004) and that taxonomic and functional composition may show different relationships with environmental variables (Feld & Hering, 2007; Heino *et al.*, 2007).

However, it is possible that much of the small-scale environmental variation across the study region was a secondary affect of broad-scale variations in hydrological connectivity. For example, many water quality characteristics in the study region appeared to be associated with the flow status of waterbodies. Similarly, the flow status of waterbodies had a major influence on macroinvertebrate assemblages. Thus, water quality characteristics would be expected to explain much of the variation in the biotic datasets, particularly as the influence of local environmental conditions, such as water quality and habitat characteristics, is expected to increase in importance at decreasing spatial scales (Mykra, Heino & Muotka, 2007). However, only 21 to 32 % of the variation in taxonomic abundance and functional feeding group proportion data could be explained by the water quality dataset alone. This suggests that the broader-scale influence of hydrological connectivity, as represented by waterbody flow status, was acting directly on biotic assemblages as well as on water quality; water quality then directly (but secondarily) adds to the variation in biotic assemblages. This may also have been the case for within-waterbody and habitat characteristics of waterbodies, as many of these features, such as the presence of aquatic vegetation, were also associated with hydrological connectivity and waterbody flow status (lotic versus lentic).

Therefore, although natural water quality, habitat and waterbody characteristics at both within- and between-waterbody scales are important for macroinvertebrate structure and diversity in the study region, the broad-scale effect of hydrological connectivity (*sensu* Sheldon & Thoms, 2006) was the main driver, influencing biotic assemblages both directly and indirectly. Despite this, smaller-scale effects are undoubtedly important contributors to assemblage patterns, and environmental factors that act at different spatial scales have been shown to have a combined influence on patterns of variation in aquatic assemblages elsewhere (e.g. in Swedish streams and lakes) (Johnson, Goedkoop & Sandin, 2004). Thus, maintaining the natural

characteristics of waterbodies is likely to be important for their continued function. Of overriding importance for the study region, however, is the maintenance of the key aspects of the natural flow regime (permanence and regularity for 'tropical' rivers; flow variability and ephemerality for 'dryland' rivers; and annual wet/dry seasonality) (Leigh & Sheldon, 2008). This will maintain functional and diverse macroinvertebrate assemblages in Australia's wet/dry tropics, and is a concept well established in riverine ecology (Poff *et al.*, 1997; Benke, 2001).

Temporal variation

Patterns of variation in assemblage structure were generally consistent across the two dry seasons and confirmed the importance of hydrological connectivity on assemblage patterns. Indeed, the effect of flow status was stronger than differences attributable to catchment or year of sampling and a similar group of species was associated with the difference between lotic and lentic waterbodies in both years. In addition, the amount of temporal variation observed in both the 'dryland' Flinders and the 'tropical' Gregory river systems did not appear to have been as great as that observed in dryland rivers, where major changes have been observed through time (Marshall *et al.*, 2006). This may be due to the greater regularity of flow found in rivers in the wet/dry tropics, as a consequence of annual monsoons (Douglas, Bunn & Davies, 2005), in comparison with rivers in arid climates. Monsoonal rainfall produces consistent changes between seasons in both 'dryland' and 'tropical' rivers of Australia's north: each dry season, the number of zero flow days increases in 'dryland' rivers and flow magnitudes decrease in 'tropical' rivers; each wet season, flow magnitudes increase in both river types (Leigh & Sheldon, 2008). Indeed, recolonisation of macroinvertebrates within the lower reaches of Magela Creek, in Australia's wet/dry tropics, has been attributed to downstream drift from its upper reaches each wet season during high flow periods (Paltridge *et al.*, 1997). Such regular cycles would probably assist in the regular and predictable dispersal of invertebrates via aquatic and aerial pathways, so that a similar, but seasonal, fauna persists in these systems through time (Malmqvist, 2002; Robinson, Tockner & Ward, 2002).

Beta-diversity, hydrological connectivity and the Flood Pulse Concept

If the increased diversity often associated with floodplain waterholes (as proposed by the Flood Pulse Concept and demonstrated in the neo-tropics) is due to increased

habitat diversity across the floodplain environment (Junk *et al.*, 1989; Ezcurra De Drago *et al.*, 2004), then increased richness and beta-diversity would be expected within off-channel waterbodies with comparatively high habitat diversity. However, off-channel waterbodies in the study region did not tend to have increased habitat diversity. Although this observation does not refute the contention that increased beta-diversity is related to increased habitat diversity in the floodplain, particularly given the limited number of comparisons involved, it emphasises the more apparent correlation in the study region that was found between beta-diversity and hydrological connectivity (see above), a phenomenon that can act in all directions and across small to large scales.

Synthesis and prospects

Dynamic hydrological connectivity among waterbodies in space and time is important for maintaining high biodiversity and function in large floodplain rivers (Tockner *et al*., 1999; Ward *et al.*, 1999; Ward & Tockner, 2001; Amoros & Bornette, 2002; Robinson *et al.*, 2002; Sheldon *et al.*, 2002; Thorp *et al.*, 2006). In the lower, floodplain reaches of the Gregory and Flinders Rivers in the southern Gulf of Carpentaria, northeast Australia, a close relationship was found between hydrological connectivity and macroinvertebrate assemblage composition and diversity during the dry season. Although differences in biodiversity patterns were apparent between the two river systems, macroinvertebrate assemblages showed similar responses in both: assemblages from waterbodies with similar connection histories were most alike, and beta-diversity between assemblages was greatest between lotic and lentic waterbodies, tending to increase with increasing spatial separation.

The studied rivers systems fall into two major classes of flow regime in Australia's wet/dry tropics ('dryland' and 'tropical'), and the main exception to the above patterns was found in the 'tropical' Gregory River. In this system, lotic and lentic waterbodies may be spatially close but have distinct connection histories (temporally distant), resulting in distinct macroinvertebrate communities. Although, our study can not be used to infer categorical differences between all 'dryland' and 'tropical' rivers across Australia's wet/dry tropics, we propose that this phenomenon may be less likely to occur in the 'dryland' rivers in this region, as these do not have perennially flowing channels, and thus their waterbodies, spatially close or distant, would be more

likely to share a similar connection history. In the wet season, when monsoons produce widespread flooding, particularly in the 'dryland' rivers, we also expect the close relationship between assemblages and hydrological connectivity to remain; maximum beta-diversity would occur between flooded (highly connected) and non-flooded (disconnected) waterbodies within wet seasons, and between lotic (connected) and lentic (disconnected) waterbodies between wet and dry seasons. We recommend the continued study of the Gregory and Flinders river systems, the inclusion of additional sites, greater within-site replication and extension to other 'tropical' and 'dryland' systems in Australia's wet/dry tropics in order to explore the widespread applicability of these proposals.

Like most rivers in Australia's north, the studied Gregory and Flinders systems generally flow unimpeded. However, there is much interest in developing the region, including water resource development options like abstraction and regulation (Woinarski *et al.*, 2007). This will undoubtedly threaten the region's freshwater biodiversity (Pringle, 2001; Dudgeon *et al.*, 2006) including that of aquatic macroinvertebrates (Miller, Wooster & Li, 2007). This study has highlighted the importance of spatiotemporal variation in levels of hydrological connectivity in contributing to the diversity, structure and function of macroinvertebrate communities in two of Australia's northern floodplain rivers. Flow regulation and abstraction reduce variation in connectivity by tending to increase or decrease connection, respectively, in space and for prolonged periods of time (Sheldon & Thoms, 2006; Leigh & Sheldon, 2008). Thus, conservation of the high levels of macroinvertebrate biodiversity in Australia's wet/dry tropics, along with the functional processes in which they take part (e.g. biomass contribution to higher trophic levels, subsidies to terrestrial food webs and resource processing), may depend on conserving the natural variation in hydrological connectivity and the flow regimes that the unregulated floodplain rivers in the region currently possess.

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Table 1: Codes used for waterbodies sampled during the 2005 dry season, with detail of catchment, reach, lateral position in relation to the main channel, and flow status at the time of sampling.

Waterbody code	Catchment	Reach	Lateral position	Flow status
GDm	Gregory	Downstream	Main channel	Lotic
GDo	Gregory	Downstream	Off-channel	Lotic
GMmB	Gregory	Mid	Main channel	Lotic
GMmG	Gregory	Mid	Main channel	Lotic
GUm	Gregory	Upstream	Main channel	Lotic
GUo	Gregory	Upstream	Off-channel	Lentic
FDm	Flinders	Downstream	Main channel	Lotic
FDo	Flinders	Downstream	Off-channel	Lentic
FMm	Flinders	Mid	Main channel	Lentic
FUm	Flinders	Upstream	Main channel	Lentic
FUo	Flinders	Upstream	Off-channel	Lentic

Waterbodies re-sampled during the 2006 dry season are underlined.

Table 2: Environmental conditions of waterbodies in the dry season of 2005, described by variables used in the correlation analyses with macroinvertebrate assemblage data (BIOENV), with water quality data for waterbodies re-sampled in the 2006 dry season.

	GDm 2005	GDo 2005	GMmB 2005	GMmG 2005	GUm 2005	GUm 2006	GUo 2005	GUo 2006	FDm 2005	FDo 2005	FMm 2005	FUm 2005	FUm 2006	FUo 2005	FUm 2006
CW	5	20	30	40	30		40		10	25	30	60		15	
WW	5	15	25	30	15		20		10	15	7	25		12	
LS	80	1125	750	800	450		1500		200	185	25	1000		400	
D	0.8	1.5	5.7	3.9	1.5		0.6		1	0.4	0.4	0.7		0.6	
WV	800	25310	106880	93600	10130		18000		2000	1110	70	17500		2880	
CC	1.00	0.92	0.68	0.77	0.60		0.20		0.62	0.50	0.82	0.01		0.00	
BS	3	1	2	1	1		3		2	1	2	3		1	
MP	0	1	1	1	1		0		0	0	0	0		0	
MA	0	1	1	1	1		0		1	0	1	1		0	
ma	1	0	0	0	1		0		1	0	1	0		1	
UC	1	1	1	1	0		0		0	0	0	0		0	
Hab	4	4	2	5	5		3		6	3	5	4		4	
ChlS	7.1	6.6	1.7	7.1	4.2		4.4		27.0	14.5	3.7	5.8		9.6	
ChlB	23.0	4.4	2.4	13.2	72.4		6.9		27.8	9.9	36.8	37.5		8.9	
%Sn	0.00	0.05	0.00	0.10	0.00		0.10		0.10	0.05	0.20	0.20		0.40	
%LL	0.05	0.35	0.00	0.20	0.10		0.30		0.40	0.85	0.05	0.00		0.05	
%MA	0.00	0.20	0.30	0.20	0.05		0.00		0.10	0.00	0.05	0.05		0.00	
%AV	0.05	0.60	0.80	0.40	0.30		0.00		0.40	0.00	0.05	0.05		0.05	
%Si	0.70	0.70	0.70	0.70	0.15		0.70		0.15	0.70	0.70	0.15		0.15	
pH	8.2	8.3	8.4	8.2	8.3	8.5	8.2	7.6	8.8	8.3	9.0	8.6	8.7	8.8	8.1
TN	0.24	0.20	0.19	0.17	0.12	0.18	0.99	0.63	0.46	0.61	0.69	0.89	0.62	1.10	0.78
NO_x	0.09	0.04	0.01	0.01	0.02	0.02	0.01	0.04	0.03	0.02	0.03	0.03	0.03	0.04	0.07
NH_4	0.05	0.05	0.02	0.02	0.05	0.02	0.02	0.02	0.03	0.02	0.04	0.03	0.03	0.02	0.05
PO_4	0.006	0.007	0.009	0.007	0.010	0.003	0.007	0.003	0.011	0.003	0.005	0.004	0.002	0.005	0.024
N:P	57	34	7	12	10	32	7	45	12	29	34	34	61	29	11
%OSS	0.34	0.40	0.51	0.28	0.39	0.57	0.29	0.52	0.55	0.24	0.26	0.28	0.49	0.22	0.21

Waterbody scale characteristics: CW, channel width (m); WW, wetted width (m); LS, maximum length of straight section (m); D, depth (mid-channel location) (m); WV, wetted volume (m^3); CC, canopy cover (mid-channel location) (0 to 1); BS, bank slope (1, 2 or 3 in increasing levels of steepness). Within-waterbody scale characteristics: MP, macrophytes presence/absence (0 or 1); MA, macroalgae presence/absence (0 or 1); ma, microalgae presence/absence (0 or 1); UC, undercuts presence/absence (0 or 1). Macroinvertebrate habitat characteristics: Hab, number of different macroinvertebrate habitats; ChlS, median biomass chlorophyll *a* in littoral-zone sediment (g m^2); ChlB, median biomass of chlorophyll *a* in littoral-zone biofilm (g m^2); %Sn, proportion snags; %LL, proportion leaf litter; %MP, proportion macrophytes; %AV, proportion all aquatic vegetation; %Si, proportion silt. Water quality characteristics: TN, median total nitrogen concentration (mg N L^{-1}); NO_x, median nitrate/nitrite concentration (mg N L^{-1}); NH_4, median ammonium concentration (mg N L^{-1}); PO_4, median phosphate concentration (mg P L^{-1}); N:P, median dissolved molar N:P ratio; %OSS, median proportion organic suspended solids.

Table 3: Results of ANOSIM on assemblage composition (based on Bray-Curtis dissimilarities using log-transformed abundance data) between groups within *a priori*-defined factors. Results are presented with taxa identified by SIMPER as contributing to more than 50 % of the difference between statistically different groups.

ANOSIM	Factor	Pair-wise comparison	ANOSIM R value (*P*-value)	Significant taxa (SIMPER)
33 samples from 11 waterbodies (2005 dry season only)				
Two-way cross	Catchment	Gregory v. Flinders	0.316 (0.004**)	*Simocephalus* sp., *Corbicula* sp., *Thiara* (*Plotiopsis*) sp.[pa], Baetidae, *Gyraulus* sp., Orthocladinae, *Angrobia* sp., *Caridina* spp., *Tasmanocoenis* sp., Cyclopoida (greater abundances in the Gregory catchment); Ostracoda, *Ferrissia* sp., *Micronecta* spp., Oligochaeta, Tanytarsini, Ceratopogoninae, Nematoda, Hydracarina, Tanypodinae (greater abundances in the Flinders catchment)
	Flow status	Lotic v. Lentic	0.365 (0.008**)	*Simocephalus* sp., *Corbicula* sp., *Thiara* (*Plotiopsis*) sp. [pa], Tanytarsini, Baetidae, Orthocladinae, *Angrobia* sp., *Caridina* spp., *Gyraulus* sp., *Tasmanocoenis* sp., Cyclopoida, Tanypodinae (greater abundances in lotic waterbodies); Ostracoda, *Ferrissia* sp., Oligochaeta, *Micronecta* spp., Nematoda, Ceratopogoninae, Hydracarina, *Hydroglyphus* sp. (greater abundances in lentic waterbodies)
One-way	Lateral position	Main v. off-channel (lentic Flinders waterbodies only)	0.276 (0.045*)	Oligochaeta, *Ferrissia* sp., *Tasmanocoenis* spp., *Simocephalus* sp., *Tanytarsini*, *Wundacaenis* sp. [pa], *Hydroglyphus* sp., Hydrophilidae (indeterminate adult sp.), Tanypodinae (greater abundances in main channel locations); *Micronecta* spp., Hydracarina, Baetidae, *Gyraulus* sp. (greater abundances in off-channels)
24 samples from four waterbodies (2005 and 2006 dry seasons)				
Two-way cross	Catchment	Gregory v. Flinders	0.267 (0.02^{NS})[†]	-
	Flow status	Lotic v. Lentic	0.983 (0.002*)[†]	*Corbicula* sp., *Angrobia* sp., Tanytarsini, *Thiara (Plotiopsis)* sp.[pa], Orthocladinae, *Austrolimnius sp.*, *Gyraulus* sp., Libellulidae (tiny)[pa], *Micronecta* spp., Tanypodinae, Cyclopoida, Economidae (greater abundances in lotic waterbodies); Ostracoda, Oligochaeta, *Austrogomphus* spp. [pa], Nematoda, *Hydroglyphus* sp., *Ferrissia* sp. (greater abundances in lentic waterbodies)
Two-way cross	Year	2005 v. 2006	0.534 (0.001*)[†]	Tanytarsini, *Micronecta* spp., *Hydroglyphus* sp., Tanypodinae, *Corbicula* sp., Baetidae, Hydracarina, Orthocladinae (greater abundances in 2005); Ostracoda, Oligochaeta, Nematoda, *Gyraulus* sp., *Angrobia* sp., *Ferrissia* sp., Cyclopoida, *Neoplea* sp., Ceratopogoninae (greater abundances in 2006)
	Catchment	Gregory v. Flinders	0.362 (0.008*)[†]	*Corbicula* sp. [pa], *Gyraulus* sp. [pa], Tanytarsini, Nematoda, Oligochaeta, *Angrobia* sp. [pa], Cyclopoida, *Hydroglyphus* sp., Orthocladinae, *Cyclestheria* sp. [pa], *Ferrissia* sp., Baetidae, *Triplectides* spp. (greater abundances in the Gregory catchment); Ostracoda, *Micronecta* spp., Tanypodinae, Hydracarina (greater abundances in the Flinders catchment)
Two-way cross	Flow status	Lotic v. Lentic	0.784 (0.001*)[†]	see above
	Year	2005 v. 2006	0.312 (0.003*)[†]	see above

* $P < 0.05$; ** $P < 0.01$; [NS] p is non-significant; [†] Significance of *P*-values adjusted according to the Bonferroni *t*-test, which corrects for the possibility of multiple tests (catchment x flow status; catchment x year; flow status x year) being simultaneously correct. This was used instead of a three-way factorial ANOSIM, and reduced the significance level, α, to 0.017 (0.05/3). [pa] indicates contribution of taxa to the difference between groups is due to presence/absence rather than abundance.

Table 4: Correlations between composition of macroinvertebrate samples (based on taxonomic abundances or functional feeding group proportions, 'function') and combinations of environmental variables (BIOENV results) for the study region during the 2005 dry season.

Environmental variable set	Taxonomic composition: best variable combination (r_s)				Functional composition: best variable combination (r_s)			
	one variable	two variables	three variables	> three variables	one variable	two variables	three variables	> three variables
Waterbodies	D (0.462)	*D, CC (0.473)*	D, CC, WV (0.419)	D, CC, WV, BS (0.367)	CC (0.382)	CC, D *(0.474)*	CC, D, LS (0.368)	CC, D, LS, CW (0.304)
Within-waterbodies	UC (**0.483**)	UC, MP (0.573)	UC, MP, A *(0.584)*	UC, MP, A, MA (0.539)	MP (0.263)	MP, MA (0.290)	MP, MA, A (0.306)	MP, MA, A, UC *(0.307)*
Macroinvertebrate habitats	%AV (0.464)	%AV, %LL (**0.583**)	%AV, %LL, %Sn ***(0.627)***	%AV, %LL, %Sn, %MA (**0.623**)	Hab **(0.485)**	Hab, %AV (0.477)	Hab, ChlS, %AV (0.477)	Hab, ChlS, MA, %Si *(0.496)*
Water Quality	TN (0.419)	TN, NH_4 (0.452)	TN, NH_4, pH *(0.458)*	TN, NH_4, pH, PO_4 (0.437)	TN (0.439)	TN, %OSS ***(0.564)***	TN, %OSS, PO_4 (**0.555**)	TN, %OSS, PO_4, NH_4 **(0.549)**
Combination of variables from each set with r_s > 0.4	UC (0.483)	UC, %LL (0.616)	UC, %LL, %AV (0.699)	**UC, MP, %LL, %AV, NH_4, pH** (0.781)	Hab (0.485)	Hab, TN (0.615)	Hab, TN, %OSS (0.640)	**Hab, TN, %OSS, ChlS, %Si, CC, D** (0.669)

D, depth mid-channel; CC, canopy cover mid-channel; WV, wetted volume of waterbody; BS, bank slope of waterbody; LS, length of straight section of waterbody; CW, channel width. UC, presence or absence of undercuts; MP, presence or absence of macrophytes; A, presence or absence of micro-algae; MA, presence or absence of macro-algae. %AV, proportion of aquatic vegetation (algae + macrophytes); %LL, proportion of leaf litter; %Sn, proportion of snags; %MA, proportion of macroalgae; Hab, number of different macroinvertebrate habitats present; ChlS, chlorophyll *a* on the sediment surface; %Si = proportion of silt. TN, concentration of total particulate nitrogen; NH_4, concentration of ammonium-N; PO_4, concentration of phosphate-P; %OSS, proportion of organic suspended solids. Bold r_s values indicate the highest scores within one, two, three or more than three variable combinations for non-combined environmental sets of variables. Italicised r_s values indicate those combinations within each set of environmental variables with the highest scores. Variable codes in bold indicate the combination with the highest r_s value.

Table 5: Mean values of diversity measures for groups within *a priori*-defined factors with significant differences (ANOVA), based on macroinvertebrate abundance data for samples collected in the study region during the 2005 dry season.

Factor	Diversity measure	Group within factor	Mean (S.E.)	Group within factor	Mean (S.E.)	F statistic (*P*-value)
Catchment x flow status (interaction)	D[ab]					16.66 (<0.0001)****
		Lotic Gregory	6.1 (0.3)	Lotic Flinders	4.3 (0.3)	*t*-test *
		Lotic Gregory	6.1 (0.3)	Lentic Flinders	3.8 (0.3)	*t*-test****
		Lotic Gregory	6.1 (0.3)	Lentic Gregory	3.7 (0.2)	*t*-test**
Flow status	S	Lotic	39 (2)	Lentic	27 (2)	22.10 (<0.0001)****
	BP	Lotic	0.27 (0.03)	Lentic	0.38 (0.03)	6.70 (0.0145)*
Lateral position (lotic Gregory waterbodies only)	S	Main channel	38 (1)	Off-channel	50 (3)	12.70 (0.0035)**
	D [a]	Main channel	5.8 (0.3)	Off-channel	7.5 (0.5)	7.29 (0.0182)*
Lateral position (lentic Flinders waterbodies only)	D [a]	Main channel	4.3 (0.4)	Off-channel	3.3 (0.1)	5.15 (0.0467)*
	BP	Main channel	0.27 (0.02)	Off-channel	0.46 (0.02)	32.28 (0.0002)***

N = abundance; S = richness; D = Margalef's index; BP = Berger-Parker index. [a] D was log-transformed prior to ANOVA to meet test assumptions; [b] *t*-tests for multiple comparisons of group means within interaction terms corrected using the Bonferonni method; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

Figure legends

Fig. 1: The Nicholson and Flinders catchments in the Gulf of Carpentaria drainage division with detail of waterbodies sampled in the lower Gregory and Flinders river systems during the 2005 dry season. Waterbodies re-sampled during the 2006 dry season are underlined. Waterbody abbreviations refer to the catchment (Gregory = G, Flinders = F), river section (downstream = D, mid = M, upstream = U) and lateral position (main channel = m, off-channel = o) of each site (see Table 1 for more detail).

Fig. 2: Historical hydrographs of mean daily flow standardised by upstream catchment area (ML d^{-1} km^{-2}) at gauging stations (□) near waterbodies (●) sampled in the Flinders and Gregory study regions (see map insets). Flinders River at Walkers Bend is at FDm. Flinders River at Etta Plains, Cloncurry River at Canobie, and Gregory River at Gregory Downs stations are approximately 80, 200 and 20 km upstream by middle thread distance from FMm, FUm, and GUm, respectively. Broken arrows indicate direction and ephemerality of flow connection among gauging stations in the Flinders study region. Flows are all > 0 ML d^{-1} km^{-2} between wet season peaks for the Gregory River at Gregory Downs station.

Fig. 3: Agglomerative dendrogram of macroinvertebrate samples collected from the study region in the dry season of 2005 only for 11 waterbodies (a), and in both 2005 and 2006 for the four re-sampled waterbodies only (b), based on group-average linking on Bray-Curtis sample dissimilarities from log-transformed abundance data.

Fig. 4: MDS ordinations on the Bray-Curtis dissimilarity matrix of log-transformed abundance (a and b) and FFG proportion data (c), using the spatial dataset from 2005 alone [33 samples from 11 waterbodies in (a) and (c)] and together with the temporal dataset of four waterbodies from the 2006 dry season [12 additional samples in (b)]. Samples are represented as waterbody centroids (mean ordination co-ordinates for n = 3 samples) with ± 1 standard error bars. Lotic waterbodies are represented by open centroids, lentic by closed.

Fig. 5: Spatial and temporal variation among assemblages at different scales of resolution, measured by pair-wise Bray-Curtis dissimilarities [based on log-transformed abundance data (a and b), and FFG proportion data (c)] within and between waterbodies and between years, for the 11 waterbodies sampled in the 2005 dry season (a and b) and for the four waterbodies sampled in both the 2005 and 2006 dry seasons (c).

Fig. 6: Mean relative abundances of taxa within functional feeding groups for waterbodies sampled in the 2005 dry season (presented with -1 standard error bars).

Fig. 7: Diversity measures (mean +1 standard error bars), based on macroinvertebrate abundance data and habitat types for waterbodies sampled from the study region in the 2005 dry season. N = abundance; S = richness; D = Margalef's index; BP = Berger-Parker index; β = beta-diversity (single value).

Fig. 8: A conceptual diagram of dry season beta-diversity between macroinvertebrate assemblages of waterbodies in the study region, in relationship to the hydrological connectivity potential between any two waterbodies. Developed and modified from ideas presented in previous studies and reviews (Ward *et al*., 1999; Ward & Tockner, 2001; Sheldon *et al*., 2003; Sheldon & Thoms, 2006).