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Spatial variability of aquatic macroinvertebrate assemblages in the Okavango Delta, Botswana: considerations for developing a rapid bioassessment tool

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Spatial variability in macroinvertebrate assemblages of the Okavango Delta, Botswana, was examined to evaluate differences in assemblages at a regional and habitat scale. Sampling was undertaken six times during a one-year cycle from 2005 to 2006, with 228 macroinvertebrates samples collected from different aquatic habitats in 22 sites in four study areas. Sixty-four taxa, mainly families, and >30 000 individuals were recorded. Multivariate analysis of aquatic macroinvertebrates revealed that the distribution of macroinvertebrate fauna is relatively homogenous among study regions, with some variation in number of taxa. Differences were observed in the macroinvertebrate assemblages associated with different aquatic habitats, with fauna from deltaic habitats (floating vegetation, inundated floodplain and marginal vegetation) different from non-deltaic habitats (isolated, seasonally flooded pools and isolated, temporary, rain-filled pools). Within the deltaic habitats, there were no significant differences among the habitats in terms of number of taxa and abundance, although assemblages and frequency of occurrence of taxa differed among habitats, providing evidence of habitat preferences for certain taxa. Future development of a macroinvertebrate-based bioassessment tool should account for aquatic habitat, although the tool does not need to be region specific. Temporal variability of macroinvertebrate assemblages should be examined to evaluate potential hydrological effects on the tool.

Keywords: aquatic habitat, biodiversity, bioassessment, flood-pulsed wetland, seasonal floodplain, southern Africa

Introduction

The Okavango Delta is a highly variable and complex inland delta, largely structured by the climatic regime, physical and chemical environment, and the biological interactions that occur within it (Gronberg 1995; Gronberg 1996). The delta is not only an area of immense ecological importance, but is also one of extreme socio-economic importance. Local communities are highly dependent on freshwater and natural resources of the delta (Okavango Delta Management Plan 2008; Mendelsohn 2010), whereas ecotourism in the region ranks high on the global scale. About 17% of the country is designated as National Parks and Game Reserves and an additional 20% as Wildlife Management Areas (Tawana Land Board 2009). The necessity to conserve and manage the delta in a sustainable manner, based on reliable scientific knowledge, is thus critically important.

Aspects such as the hydrology, physico-chemistry, geology, geomorphology and vegetation of the delta have been well studied (e.g. Sawula and Martins 1991; Ellery 1993; Hart 1997; McCarthy and Ellery 1998; McCarthy 1998; McCarthy 2000; Masamba and Muzila 2005; Wolski 2005). Several studies have also been undertaken on fish (e.g. Merron 1993; Merron and Bruton 1995; Mosepele and Mosepele 2005; Mosepele 2009; Mosepele 2017), terrestrial invertebrates, including dragonflies (Pinhey 1967, 1976a; Kipping 2006) and, butterflies (Pinhey 1968, 1971, 1974, 1976b). Aquatic invertebrate studies have largely focused on microinvertebrates (Hart 1997; Masundire 1998; Hart 2003; Lindholm 2009; Siziba 2011; 2012; 2013; West 2016), coleopterans (Bilardo and Rocchi 1987) and molluscs (Appleton 1979; Curtis and Appleton 1987; Brown 1992; Curtis 1997), with two general assessments (Alonso and Nordin 2003; Dallas and Mosepele 2007), and two studies relating aquatic biodiversity to spatial and seasonal hydrological variability (Davidson 2012; Mackay 2012).

Aquatic macroinvertebrates are ubiquitous, important primary and secondary consumers, and routinely included in bioassessment protocols for lotic environments in southern Africa and elsewhere (e.g. Dickens and Graham 2002; Ollis 2006; Kaaya 2015; Dallas 2018). In comparison, bioassessment of lentic environments using macroinvertebrates is relatively new (Bird 2013, 2014). In lotic systems, macroinvertebrates typically have a patchy distribution, with patchiness resulting from a range of factors at the regional scale, such as geology or climate (Richards 1997; Dallas 2004); reach scale, such as channel type or riparian canopy cover; and site or habitat scale, such as the relative abundance of different biotopes (Dallas and Day 2007), substratum (Collier 1999), hydraulics (Padmore 1998), water depth and water velocity (Poff and Ward 1990). Bioassessment tools and indices have been developed and reliably used to evaluate ecological condition in lotic systems, as long as they are applied within a spatial context, thereby ensuring that intrinsic spatial variability is considered. Spatial heterogeneity is often accounted for by partitioning areas into relatively homogeneous regions, i.e. regional classification and geomorphological zonation, and by undertaking biotope-specific sampling (Dallas and Day 2007). In comparison, studies examining the utility of macroinvertebrates for bioassessment in lentic environments report mixed reliability of the indices, with some considered effective within regions (e.g. Chessman 2002; Uzarski 2004; Davis 2006), whereas others have concluded that the use of macroinvertebrate indices to determine wetland condition is not a feasible option (e.g. Cooper 2007; Bird 2013).

The Okavango Delta is a flood-pulsed wetland (Davidson 2012) where lentic and lotic conditions alternate in a temporal dimension, with temporal and spatial variation in hydrological conditions the principal drivers of variation in aquatic biodiversity (Davidson 2012). To date, no macroinvertebrate-based bioassessment tools exist for flood-pulsed wetlands, even though these wetlands make vital contributions to local and global biodiversity (Davidson 2012). The temporal transition between a lentic and lotic environment adds complexity for developing appropriate bioassessment tools, with careful consideration required in terms of aquatic habitats sampled, connectivity and hydrological phase. An understanding of the spatial variability of aquatic macroinvertebrate assemblages, at both a regional and habitat scale, as well as temporal variability, is thus required before any bioassessment tools can be developed for the delta.

The focus of the current study was thus to investigate the spatial variability of aquatic macroinvertebrate assemblages in the Okavango Delta, with the aim of evaluating inherent heterogeneity in these assemblages at different spatial (region and habitat) scales. It was hypothesised that aquatic macroinvertebrate assemblages of the Okavango Delta would vary spatially by region and between aquatic habitat types. An additional hypothesis was that aquatic macroinvertebrates would demonstrate habitat preference.

Methods

Study area

The Okavango Delta is divided into three major biomes; the permanent swamp, the seasonal swamp and the drainage rivers (Ramberg 2006), which create a mosaic of aquatic habitats for the associated biota. The delta floods annually, fed by water originating upstream in the source rivers of Angola, with the flood peak reaching the Upper Panhandle between February and April, and moving through the delta to reach the distal end of the delta in July. Another localised wet period is caused by rains occurring in December to March, and the delta thus has two fairly predictable wet periods (Ramberg 2006). The flooding is vital for the survival of the Okavango Delta ecosystem, which is in flood when the surrounding Kalahari Desert is at its driest, thereby providing a crucial source of water to its occupants.

Site selection

Aquatic macroinvertebrates were sampled at 22 sites in four study areas spread across the Okavango Delta, namely Upper Panhandle (Shakawe), Lower Panhandle (Guma), Moremi Game Reserve (Xakanaka) and Chief's Island (Nxaraga) (Figure 1). The Upper and Lower Panhandle regions are dominated by riverine habitat that is generally permanently flooded and experiences large variation in water levels (Davidson 2012). Below the Lower Panhandle, the Okavango River divides into a number of distributaries (Wolski and Murray-Hudson 2006), with a main channel flowing east towards the Moremi Game Reserve and one flowing south-east towards Chief's Island. These distal regions have diverse habitats, including channels, lagoons, seasonally inundated floodplains, with seasonally flooded habitats generally more common in these distal regions. Sites were distinguished as deltaic sites, which are connected and inundated by the main river channels, and non-deltaic sites, which are not connected to the main river channels. At each site up to three different aquatic habitats were sampled, including marginal vegetation, floating vegetation, seasonally inundated floodplains for deltaic sites, and seasonally flooded and temporary, rain-filled pools for non-deltaic sites (Table 1). Based on the wetland classification of Ollis et al. (2015), aquatic habitats comprising marginal vegetation and floating vegetation are best classified as floodplain depressions, although additional refinement of the classification is recommended to accommodate these wetland types (pers. comm. DJ Ollis, Freshwater Research Centre).

Deltaic sites with seasonally inundated floodplains typically comprise a mosaic of floodplain flats and depressions (Ollis 2015). Non-deltaic sites are classified as endorheic depressions, with channelled inflow (seasonally flooded pools) and endorheic depressions, without channelled inflow (temporary, rain-filled pools). It is acknowledged that deltaic and non-deltaic sites are fundamentally different, however, from the perspective of future development of rapid bioassessment tools, both were included in the current study to enable a broad understanding of aquatic macroinvertebrate assemblages typically associated with each aquatic habitat. Although the distribution of sites represents a relatively limited spatial distribution within the Okavango Delta, they are representative of areas in the permanent and seasonal swamp and include permanent channels and lagoons, and thus represent different types of broad habitat within the delta.

Aquatic macroinvertebrate sampling

Sampling was conducted six times during a one-year cycle as follows: February, April, July, September, November 2005 and January 2006. Every effort was made to sample each habitat during each sampling month, but availability varied with time of year and thus not all were sampled each month. Details of the study areas, sites and sample numbers giving latitude, longitude and habitat type is provided in Appendix 1. In addition, as a result of extensive rain and flooding in January 2006, access to Nxaraga was not possible and thus sites in the current study area could not be sampled. In the deltaic areas, 39 samples included

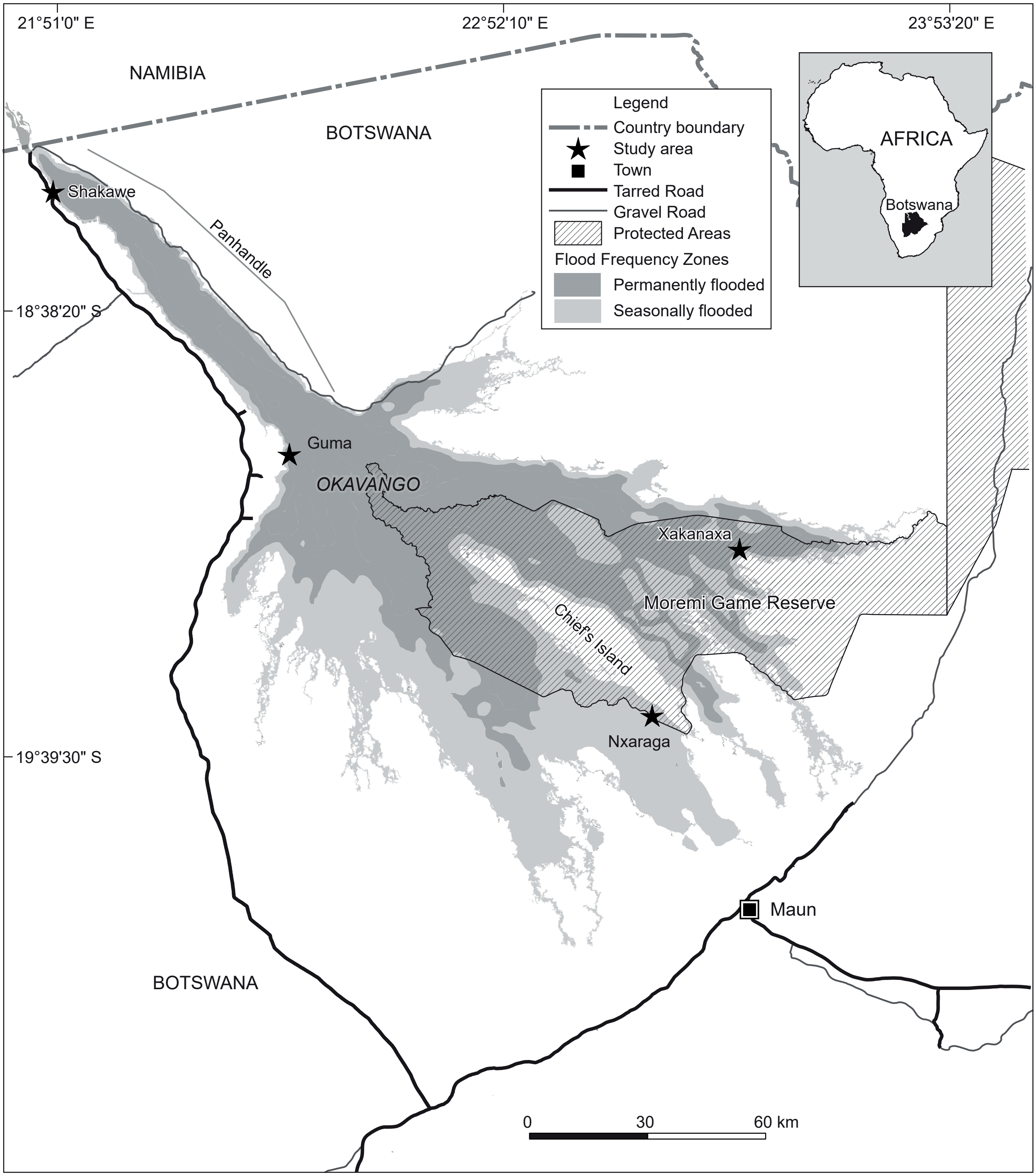

Figure 1: The Okavango Delta, Botswana, showing four study areas

marginal vegetation, floating vegetation and seasonally inundated floodplains. Marginal vegetation in Shakawe and Guma, was dominated by *Cyperus papyrus*, *Vossia cuspidata* and *Phragmites* spp. In Nxaraga, marginal vegetation sampled was primarily *V. cuspidata*. Species changed in Xakanaka to a mosaic of aquatic, semiaquatic and terrestrial species, with marginal vegetation and inundated floodplain dominated by *Miscanthus junceaus,* with different proportions of *Phragmites australis*, *C. papyrus*, grasses (including *V. cuspidata*,

Table 1: The number of sites and samples collected in four study areas of the Okavango Delta: Upper Panhandle (Shakawe), Lower Panhandle (Guma), Moremi Game Reserve (Xakanaka) and Chief's Island (Nxaraga)

	Study area	Upper Panhandle (Shakawe)	Lower Panhandle (Guma)	Moremi Game Reserve (Xakanaka)	Chief's Island (Nxaraga)
	Number of sites per study area	4	6	6	6
		Number of samples in each aquatic habitat at each site			
Permanent swamp/Channel	Marginal vegetation	6	4	1	1
Permanent swamp/Lagoon	Marginal vegetation		4	2	1
Permanent swamp/Channel	Floating vegetation	3	1		1
Permanent swamp/Lagoon	Floating vegetation		2	2	1
Seasonal swamp	Seasonally inundated floodplain	3	2	2	3
Seasonal swamp	Seasonally flooded pool		1	1	3
Seasonal swamp	Temporary, rain-filled pool			2	

Pycreus mundii, *Echinochloe pyramidalis*, *Panicum repens*) present. Floating vegetation was largely *Nymphea nouchalii* and *Trapa natans.* In the non-deltaic areas, seven samples were taken, either isolated, seasonally flooded pools or isolated temporary, rain-filled pools, with the latter only in Xakanaka.

Semiquantitative sampling of aquatic macroinvertebrate assemblages from each aquatic habitat was undertaken using a sweep net (30 × 30 cm square frame, 950 µm mesh). One person intensively sampled each habitat for two minutes by sweeping the net through the vegetation, sediment and/or water. Given the variation in habitat type and accessibility to different habitats, sampling was standardised as sampling effort, i.e. time sampled. This period of time was deemed sufficient to collect the variety of aquatic taxa associated with a particular habitat (Dallas and Mosepele 2007). The collected sample was sorted on site using large sorting trays and the abundance of each taxon was estimated using the following scale: one individual, 2–10 individuals, 11–100 individuals, 101–1 000 individuals and >1 000 individuals. Taxa were first identified in the field, mostly to family level, and recorded on a datasheet. The entire sample was then collected, preserved in 70% ethanol, and checked in the laboratory for any additional specimens. Identifications were verified using available identification guides and the number of individuals in each taxon was counted. Most taxa were identified to family, with the exception of Oligochaeta, Hirudinea, which were identified to class, Acarina, which were identified to order, and certain Coleopteran families (Dytiscidae, Haliplidae, Hydrophillidae, Noteridae, Sperchidae and Elmidae), which were combined. The latter was necessitated by the richness of coleopteran families and taxonomic uncertainties for deltaic species.

Data analysis

Data analysis was undertaken using Statistica (Version 13) for the univariate analysis and Primer (Version 7) for the multivariate analysis. Data were checked for normality (Shapiro–Wilk *W* test) and found to be non-normally distributed and thus the non-parametric Kruskal–Wallis ANOVA was used to test the significance of differences in number of taxa and abundance among study areas and aquatic habitats. Cluster analysis and non-metric multidimensional scaling (nMDS) were used to examine similarities among study areas and aquatic habitats, based on macroinvertebrate assemblage composition (Clarke and Warwick 2001). The data were fourth root transformed and the Bray–Curtis coefficient was used on the data. Hierarchical agglomerative clustering, using group-average linking, was used on the data matrix, to produce a dendrogram. Ordination of samples by MDS was undertaken, and stress values used to assess the reliability of the MDS ordination. Because the focus of the current study was on investigating the spatial variation in macroinvertebrate assemblages among study areas and habitats; analyses were based on data generated from macroinvertebrates collected in all six sampling periods. Classification of sites based on two or three seasons (or months) rather than one season (or month) is recommended for evaluation of spatial variability, because it is considered a more robust means of classifying sites, because temporal variation is reduced (Turak 1999).

To determine whether certain taxa showed a preference for a particular aquatic habitat, the relative frequency of occurrence of each taxon within each of the three deltaic habitats was calculated. This was done by counting the number of times a taxon was recorded in a particular habitat, divided by the number of times the habitat was sampled (*n*), expressed as a percentage. For example, Hirudinea were recorded in 25 of the 112 marginal vegetation samples (22%), 10 of the 38 inundated floodplain samples (26%), and six of the 54 floating vegetation samples (11%). These percentages are then summed to get 60% and then rescaled to 100%, so (22/60) × 100 = 37% for marginal vegetation samples. When each of these percentages is expressed relative to each other habitat, then the relative frequency of occurrence for Hirudinea is 37%, 44% and 19% for marginal vegetation, inundated floodplain and floating vegetation, respectively (Table 3). The frequency of occurrence for a specific taxon demonstrates which habitat a taxon is more often present, relative to other habitats. The total number of times each taxon was recorded across all habitats is given as the count. To determine whether certain taxa associated with floating vegetation showed a preference for a particular floating vegetation type, namely *Nymphea* spp. and *T. natans*, relative frequencies were also calculated for each floating vegetation type. Relative frequencies were not calculated for non-deltaic habitats (seasonally flooded and temporary, rain-filled pools), because the sampling frequency for each habitat was too low (15 and 9, respectively), although taxa present in deltaic habitats, but absent from non-deltaic habitats were noted.

Results

Variation in macroinvertebrate assemblages among study areas

Approximately 64 taxa, mainly families, and >30 000 individuals were recorded in the current study, although this is likely to be an underestimate of the total number of taxa, because certain groups were not identified beyond class, order or were combined at family level. The total number of taxa and total abundance per study area (i.e. data combined from all samples and months) was highest at Guma (number of taxa = 57, abundance = 11 200), followed by Xakanaka (number of taxa = 54, abundance = 8 500), Shakawe (number of taxa = 49, abundance = 7 300) and Nxaraga (number of taxa = 49, abundance = 6 500) (Table 2). Because Nxaraga was not sampled in January 2006 total numbers for the current study area may be lower than expected. Mean number of taxa per sample (Figure 2) was significantly different among study areas, primarily, because of the significantly higher mean number of taxa at Xakanaka (mean number of taxa = 18.3, compared with 12.2, 15.0 and 13.8 for Shakawe, Guma and Nxaraga, respectively) (Kruskal–Wallis test: $H = 28.70915$, $p < 0.01$). Mean abundance per sample was not significantly different among study areas (Figure 2). Cluster and ordination of macroinvertebrate assemblages recorded in each study area revealed that study areas were between 79% and 84% similar (Figure 3).

Table 2: Total number of taxa and total abundance recorded per study area (habitats and sites combined) and per habitat (sites combined)

Study area	Number of taxa	Abundance
Upper Panhandle (Shakawe)	49	7 300
Lower Panhandle (Guma)	57	11 200
Moremi Game Reserve (Xakanaka)	54	8 500
Chief's Island (Nxaraga)	49	6 500
Habitat	**Number of taxa**	**Abundance**
Marginal vegetation	59	12 605
Floating vegetation	55	8 035
Seasonally inundated floodplains	54	6 725
Seasonally flooded pools	36	3 155
Temporary, rain-filled pools	37	3 714

Variation in macroinvertebrate assemblages among habitats

The total number of taxa and total abundance per aquatic habitat (i.e. data combined from all sites and months) was highest in marginal vegetation (Number of Taxa = 59, Abundance = 12 605), followed by floating vegetation (Number of Taxa = 55, Abundance = 8 035), and seasonally inundated floodplains (Number of Taxa = 54, Abundance = 6 725). Both total number of taxa and total abundance were lowest in the seasonally flooded pools (Number of Taxa = 36, Abundance = 3 155) and temporary, rain-filled pools (Number of Taxa = 37, Abundance = 3 714) (Table 2). When macroinvertebrate assemblages among aquatic habitats were compared, regardless of study area, neither the mean number of taxa nor abundance per sample were significantly different among habitats (Figure 4). When both study area and habitat were considered, only mean number of taxa per sample were significant different, primarily, because of richness in the marginal vegetation habitat at Xakanaka, thus largely reflecting differences in study areas (Number of Taxa: Kruskal–Wallis test: $H = 50.14\,917$, $p < 0.01$). Mean number of taxa in floating vegetation was highest at Guma (15) and Xakanaka (15.5) and lowest at Shakawe (11) (Figure 4). Mean abundance of macroinvertebrates in floating vegetation was highest and most variable at Guma (263), and lowest in Shakawe (72) and Nxaraga (78). In Shakawe and Nxaraga, floating vegetation was primarily *Nymphea* spp., whereas in Guma and Xakanaka it was *T. natans*. The very high abundance at Guma was recorded in August in the lagoon (1 375). Mean number of taxa in inundated floodplain

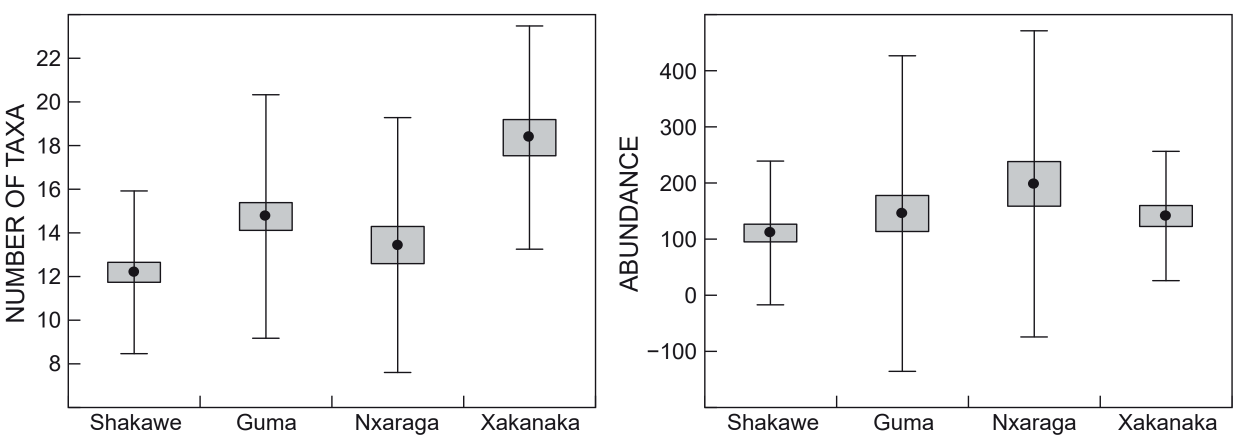

Figure 2: Mean, ± Standard Error (box) and ± Standard Deviation (lines) number of taxa and abundance per sample for each study area: Shakawe (S), Guma (G), Nxaraga (N) and Xakanaka (X)

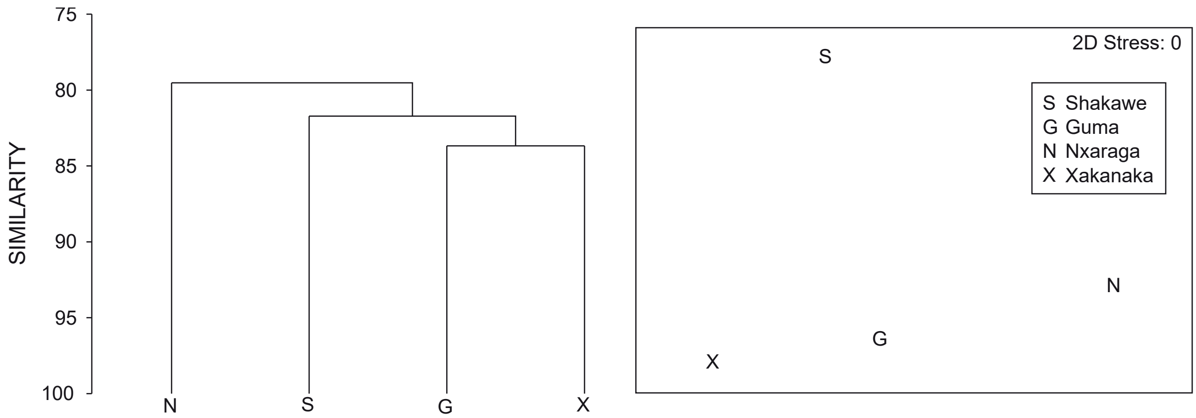

Figure 3: Cluster and non-metric multidimensional scaling ordination plots for macroinvertebrate family assemblages in each study area: Shakawe (S), Guma (G), Nxaraga (N) and Xakanaka (X)

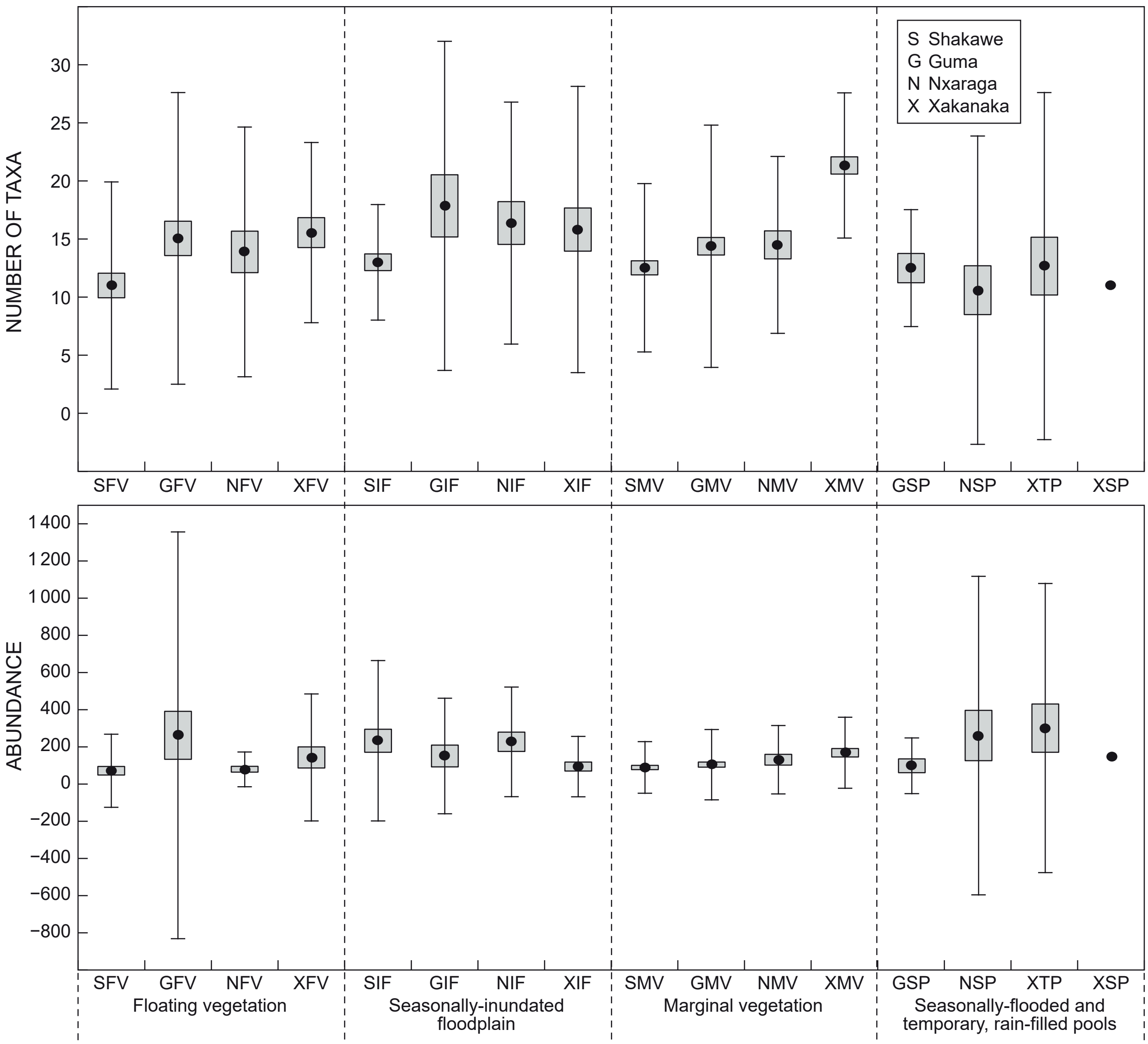

Figure 4: Mean, ± Standard Error (box) and ± Standard Deviation (lines) number of taxa per habitat type per study area. Study areas: Shakawe (S), Guma (G), Nxaraga (N) and Xakanaka (X); and habitats: floating vegetation (FV), seasonally inundated floodplain (IF), marginal vegetation (MV), seasonally flooded pools (SP) and temporary, rain-filled pools (TP)

was highest and most variable in Guma (18), and lowest and least variable at Shakawe (13). Mean abundance of macroinvertebrates in seasonally inundated floodplains was highest in Shakawe (233) and Nxaraga (228), and lowest and least variable in Xakanaka (95). Mean number of taxa in marginal vegetation was highest in Xakanaka (21), where the vegetation sampled was *M. junceaus*, as opposed to *Cyperus* spp., *V. cuspidata* or *Phragmites* spp., and lowest in Shakawe (13). Mean abundance of macroinvertebrates in marginal vegetation was highest in Xakanaka (167), lowest in Shakawe (89) and generally less variable than other habitats. Mean number of taxa in seasonally flooded pools and temporary, rain-filled pools varied from 10 to 12 and mean abundance was highest in the temporary, rain-filled pool at Xakanaka (302) and lowest at the seasonally flooded pools in Guma (99).

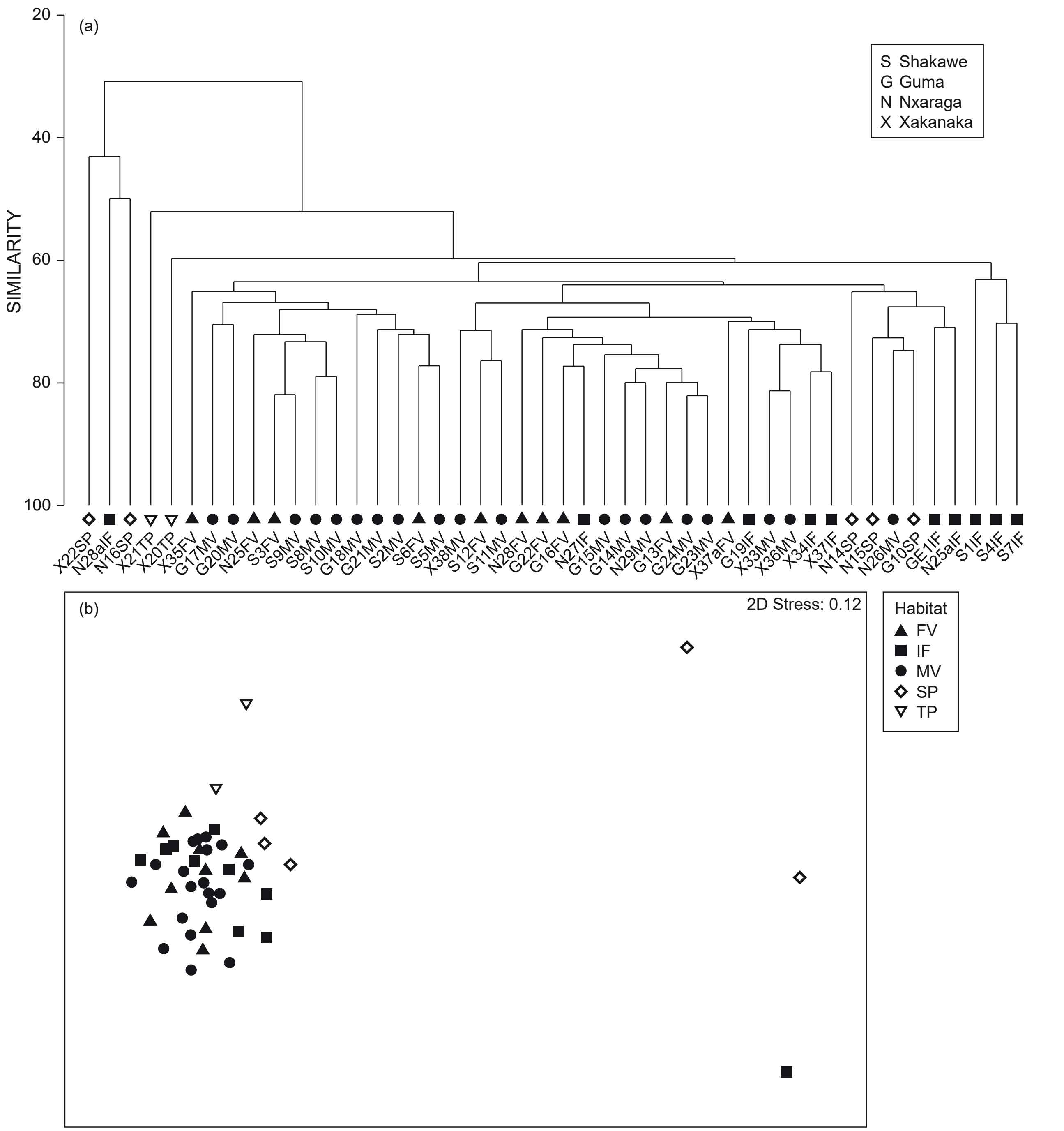

Figure 5: Cluster and non-metric multidimensional scaling ordination plots for macroinvertebrate family assemblages in each aquatic habitat. Sites are coded by study area: Shakawe (S), Guma (G), Nxaraga (N) and Xakanaka (X) and habitat: floating vegetation (FV), seasonally inundated floodplain (IF), marginal vegetation (MV), isolated, seasonally flooded pool (SP) and isolated, temporary rain-filled pool (TP)

Cluster and ordination of macroinvertebrate assemblages recorded in each aquatic habitat in each study area (i.e. taxa combined for all months) revealed that faunal samples did not group based on study area, although there was some differentiation based on habitat (Figure 5, stress = 0.12). Three sites (two seasonally flooded pools and one inundated floodplain) were 30% dissimilar from all other sites, largely, because of their low taxon richness (7, 8 and 11). The two temporary, rain-filled pools sites, although having relatively high taxon richness (29 and 30), were the only sites to have fairy shrimps (Anostraca), an order typical of temporary systems. Three seasonally inundated floodplain samples from Shakawe were 40% dissimilar to the primary group of sites, which included all the floating vegetation and marginal vegetation samples, and three seasonally flooded pools samples. There was also some additional differentiation on the basis of whether the site was a channel (with flowing water) or a lagoon (without flowing water). Macroinvertebrate assemblages from floating vegetation and marginal vegetation were at least 60% similar.

Multivariate analysis run for each deltaic habitat separately showed that macroinvertebrate assemblages within each deltaic habitat were approximately 60% similar, and although there was some separation into groups within each habitat, this was not based on study area, with the exception of seasonally inundated floodplain habitats in Shakawe (Figure 6). Multivariate analysis of pool samples did not show any clear separation on the basis of either study area or pool type (Figure 7), although two sites (NX16 and XA22), both seasonally flooded pools, formed a distinct group. Examination of the fauna associated with each site revealed that both sites had substantially fewer taxa (n = 7 and 11, respectively), compared with other sites (n ranged from 22 to 29 taxa), crustaceans and molluscs were absent, and odonates and dipterans were scarce.

Frequency of occurrence of macroinvertebrate taxa among deltaic habitats

The relative frequency of occurrence of each taxon within each of the three deltaic habitats is tabulated in Table 3. Many taxa were recorded with equal frequency among all three deltaic habitats. Five taxa were more common in marginal vegetation, including mayflies (Heptageniidae, Leptophlebiidae, Polymitarcyidae), bugs (Nepidae) and flies (Simuliidae). Ten taxa were more common in seasonally inundated floodplains, including bugs (Naucoridae), beetles (Scirtidae), flies (Stratiomyidae, Syrphidae, Tabanidae) and snails (Bithyniidae, Hydrobiidae, Thiaridae, Viviparidae and Sphaeridae). No taxa were more frequently recorded in floating vegetation, although when *Nymphea* spp. and *T. natans* were considered separately, several taxa showed a preference for one or the other floating vegetation type, with nine taxa were more frequently recorded in *Nymphea* spp. and 23 taxa were more common in *T. natans* (Table 3).

In addition, 21 families recorded in deltaic habitats were absent from non-deltaic habitats, including shrimps (Atyidae), crabs (Potamonautidae), mayflies (Heptageniidae,

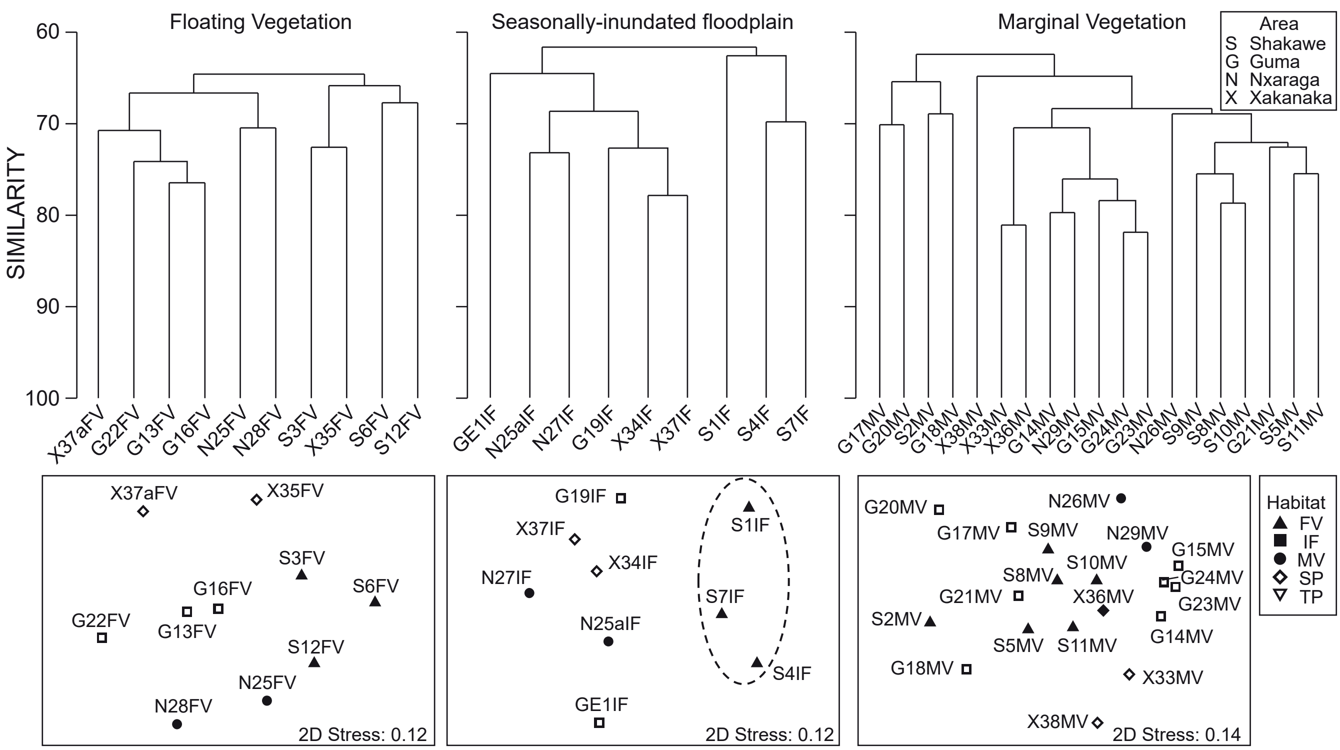

Figure 6: Cluster and non-metric multidimensional scaling ordination plots for macroinvertebrate assemblages in each deltaic habitat: floating vegetation (FV), seasonally inundated floodplain (IF) and marginal vegetation (MV). Coded by study area: Shakawe (S), Guma (G), Nxaraga (N) and Xakanaka (X)

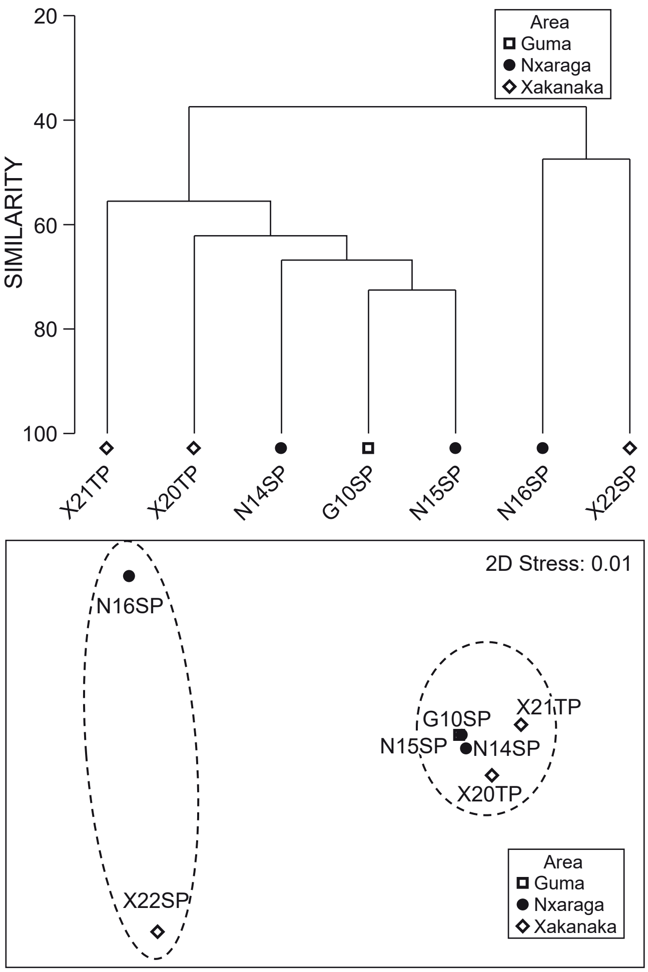

Figure 7: Cluster and non-metric multidimensional scaling ordination plots for macroinvertebrate assemblages in each non-deltaic habitat: seasonally flooded pools (SP) and temporary, rain-filled pools (TP). Coded by study area: Guma (G), Nxaraga (N) and Xakanaka (X)

Leptophlebiidae, Polymitarcyidae and Tricorythidae), damselflies (Synlestidae and Platycnemididae), caddisflies (Hydropsychidae, Philopotamidae), beetles (Scirtidae), flies (Empididae, Sciomyzidae, Simuliidae and Tipulidae) and snails (Ampullariidae, Bithyniidae, Hydrobiidae, Thiaridae, Viviparidae and Corbiculidae). Taxa present in > 50% of the seasonally flooded pools included mayflies (Baetidae, and Caenidae), dragonflies (Libellulidae), damselflies (Coenagrionidae), bugs (Belostomatidae, Corixidae, Notonectidae and Pleidae), beetles (Coleoptera − combined) and flies (Ceratopogonidae and Chironomidae). Taxa present in > 50% of the temporary, rain-filled pools included mayflies (Baetidae, and Caenidae), dragonflies (Libellulidae), damselflies (Coenagrionidae), bugs (Corixidae, Nepidae, Notonectidae and Pleidae), beetles (Coleoptera − combined) and flies (Ceratopogonidae, Chronomidae and Culicidae). In addition, fairy shrimps (Anostraca), which were absent in deltaic habitats and seasonally flooded pools, were recorded in the temporary, rain-filled pools.

Discussion

The current study, which examined spatial variability of aquatic macroinvertebrate assemblages at regional and habitat spatial scales, revealed that assemblages are relatively homogenous among study areas (> 79% similar), with some variation in number of taxa. Similarly, Dallas and Mosepele (2007), noted a 71% similarity in macroinvertebrate assemblages among study areas, even though this was based on a once-off assessment during the low-flow period. In comparison, and perhaps unsurprisingly, aquatic macroinvertebrate assemblages differed substantially between deltaic (floodplain depressions and flats) and non-deltaic (endorheic depressions) habitats, with deltaic sites having higher taxon richness (54 to 59 taxa) than non-deltaic sites (36 to 37 taxa) and abundances in deltaic habitats generally double those in non-deltaic habitats. Twenty-one families that were common in deltaic sites were absent from non-deltaic sites, whereas one order, the Anostraca, was exclusive to temporary, rain-filled pools. The absence of these 21 families from non-deltaic sites relates to perenniality of the habitat and the seasonality of the inundation of pools, with these taxa requiring more perennial habitats for completion of their life cycle. In comparison, crustaceans tend to dominate in ephemeral habitats, because of their short life cycles and desiccation-resistant eggs, with many species hatching within 24 hours (Allan 1995). McInerney et al. (2017) observed similar differences when comparing ephemeral and permanent wetlands in the Murray–Darling Basin in Australia. Mackay et al. (2012) observed a significant difference between diatom species inhabiting temporary, seasonally flooded pools and seasonally inundated floodplains in the Okavango Delta, and those diatom species inhabiting permanently inundated deltaic sites. These isolated, seasonally flooded pools and isolated temporary, rain-filled pools were only inundated once the flood waters had reached them, or adequate rainfall had fallen. Furthermore, more intensive additional sampling over the three-month inundation period of these isolated, seasonally flooded pools and isolated temporary, rain-filled pools habitats is recommended in order to gain greater understanding of the macroinvertebrate dynamics within these non-deltaic habitats.

Assemblages also differed among deltaic habitats, specifically in response to changes in hydrology, with permanently inundated deltaic habitats (marginal and floating vegetation) distinct from seasonally inundated floodplains. Seasonally inundated floodplains are transient habitats that become available for aquatic macroinvertebrates when the flood peak arrives. Although the waters of the delta are oligotrophic (Cronberg 1995, 1996), flooding increases the concentration of nutrients to high levels, especially in lagoons and off-channel areas, such as seasonal floodplains (Mosepele 2009). The flood pulses mobilise latent terrestrial energy sources within floodplain wetlands and support a rapid increase in aquatic invertebrate biomass, with important implications for both terrestrial and aquatic food webs (McInerney 2017). During these high-water periods, the production of

Table 3: Relative frequency of occurrence (as a percentage) of each taxon in each deltaic habitat, together with separation into genera/species for floating vegetation. The total number of samples per habitat is given as *N*, and the total number of times each taxon was recorded (in all habitats) is given as the count. Taxa with a frequency >50% and count >3 are highlighted in bold for the three habitats: marginal vegetation (MV), seasonally inundated floodplain (IF) and floating vegetation (FV). Taxa with ≤3 counts are not considered reliable and are indicated with *

	Habitat		MV	IF	FV		Nymphea	Trapa natans
		N	112	38	54	*N*	27	27
Group	Taxon	Count (MV + IF + FV)				Count (FV only)		
Annelida	Hirudinea	41	37	44	19	6	67	33
	Oligochaeta	55	27	39	34	16	44	56
Crustacea	Atyidae	91	42	34	24	16	50	50
	Cladocera	16	33	44	23	3*	33	67
	Conchostraca	125	40	25	36	33	42	58
	Ostracoda	32	29	32	38	10	20	80
	Potamonautidae	3*	17	49	34	1*	100	0
Arachnida	Hydracarina	72	37	36	27	15	47	53
Ephemeroptera	Baetidae	179	35	31	34	48	44	56
	Caenidae	142	39	32	30	32	59	41
	Heptageniidae	19	62	12	26	3*	100	0
	Leptophlebiidae	4	100	0	0	0	0	0
	Polymitarcyidae	40	51	11	38	10	60	40
	Tricorythidae	3*	100	0	0	0	0	0
Odonata	Aeshnidae	16	28	42	30	4	0	100
	Corduliidae	23	30	44	26	5	40	60
	Gomphidae	18	33	39	28	4	100	0
	Libellulidae	93	29	42	29	23	52	48
Zygoptera	Synlestidae	3*	17	49	34	1*	0	100
	Coenagrionidae	158	36	26	38	46	50	50
	Lestidae	25	31	28	40	8	38	63
	Platycnemididae	1*	100	0	0	0	0	0
Lepidoptera	Crambidae	70	23	28	48	29	24	76
Hemiptera	Belostomatidae	113	32	36	33	30	47	53
	Corixidae	107	28	36	36	32	44	56
	Gerridae	70	31	30	39	22	41	59
	Hydrometridae	11	33	33	34	3*	0	100
	Mesoveliidae	57	38	30	32	14	71	29
	Naucoridae	52	27	58	15	7	29	71
	Nepidae	85	56	26	18	10	50	50
	Notonectidae	67	42	32	26	13	54	46
	Pleidae	84	29	25	46	31	35	65
	Veliidae	70	47	18	35	17	35	65
Trichoptera	Ecnomidae	20	37	37	26	4	50	50
	Hydropsychidae	10	40	19	41	3*	67	33
	Hydroptilidae	25	16	47	37	9	11	89
	Leptoceridae	55	36	33	30	13	38	62
	Philopotamidae	11	43	18	38	3*	0	100
Coleoptera	Combined	180	33	35	32	46	46	54
	Gyrinidae	25	47	24	29	5	80	20
	Scirtidae	32	22	65	13	4	50	50
Diptera	Ceratopogonidae	112	33	33	34	30	40	60
	Chironomidae	173	33	34	33	46	46	54
	Culicidae	50	30	41	29	12	25	75
	Empididae	1*	0	100	0	0	0	0
	Muscidae	5	37	37	26	1*	0	100
	Sciomyzidae	3	49	0	51	1*	100	0
	Simuliidae	11	68	0	32	2*	100	0
	Stratiomyidae	8	0	91	9	1*	0	100
	Syrphidae	5	34	66	0	0	0	0
	Tabanidae	12	21	62	17	2*	0	100
	Tipulidae	1*	100	0	0	0	0	0
Gastropoda	Ampullariidae	3*	17	49	34	1*	0	100
	Bithyniidae	17	13	76	11	2*	100	0
	Hydrobiidae	10	13	78	9	1*	0	100
	Lymnaeidae	85	35	44	21	14	14	86
	Planorbidae	142	32	37	30	35	49	51
	Thiaridae	14	12	81	6	1*	0	100
	Viviparidae	6	27	54	19	1*	0	100
Pelecypoda	Corbiculidae	1*	100	0	0	0	0	0
	Sphaeriidae	27	29	54	17	4	75	25
	Unionidae	1*	0	0	100	1*	100	0

ostracods, copepods and cladocerans can be extremely high temporarily, making zooplankton on seasonal floodplains a crucial link in the aquatic food web (Høgberg 2002; Siziba 2011, 2013). These seasonally inundated floodplains also support substantial populations of cichlid juveniles (Mendelsohn 2010; Siziba 2013). Ramberg et al. (2006) noted that of the three different zooplankton habitats distinguished in the delta, namely permanent lagoons, seasonal floodplains (equivalent to seasonally inundated floodplains in our study) and isolated temporary rain pools; seasonal floodplains offered the most diverse zooplankton fauna. Davidson et al. (2012) showed that patterns of both diatom and invertebrate diversity in the Okavango Delta were related to hydroperiod class, phase of the flood and conductivity. The seasonal flooding of the delta is, therefore, crucial for the maintenance of seasonally inundated floodplains, which are a highly productive and diverse habitat utilised seasonally by a great diversity of zooplankton, aquatic macroinvertebrates and fish communities.

Within the marginal vegetation habitat, there appeared to be additional differentiation of macroinvertebrate assemblages into channel sites and lagoon sites, where most channel sites had flowing water, compared with lagoon sites, which resembled a lentic environment. The importance of flow in influencing the distribution of aquatic macroinvertebrates on stony substrates in perennial rivers is well documented (e.g. Bunn and Arthington 2002; Masikini 2018), however, few studies have examined the influence of current velocity on other habitats, such as wood or vegetation. Schoen et al. (2013) showed that macroinvertebrate abundance and richness on wood surfaces in sandy bottomed streams increased with current velocity. This increased current velocity concentrates nutrients for benthic algae (Biggs 1998), which serve as food for macroinvertebrate grazers, and provide particulate food for filter-feeders (Lancaster and Downes 2010). Additional investigation of the potential influence of flow on macroinvertebrates is recommended to validate this finding for aquatic macroinvertebrates inhabiting marginal vegetation habitats in channels and lagoons of the Okavango Delta.

Non-deltaic habitats, which are seasonally inundated by either flood water or filled during rain events, were more common in the distal end of the delta. Even though they had fewer taxa than deltaic habitats, and less than half the total abundance, they are nonetheless important aquatic habitats. Indeed, Siziba et al. (2011, 2013) showed that soon after inundation of the floodplains, highest densities of microinvertebrates developed in areas that were rarely flooded, such as these seasonally flooded pools in the current study, compared with more frequently flooded primary floodplains. These rarely flooded wetlands are important nursery habitats for cichlids, and these small fishes dominate the temporary wetland habitats feeding predominantly on microcrustaceans (Siziba 2013). Siziba et al. (2013) emphasised the importance of incorporating these temporary wetlands, including the rarely inundated terrestrial patches, in management and conservation plans for the delta, given their importance for microcrustaceans and production of small fishes.

The current study, which builds on previous work by Dallas and Mosepele (2007), shows that aquatic macroinvertebrate assemblages do not vary significantly among study areas and that greatest spatial variability is evident in relation to aquatic habitat, with certain taxa demonstrating habitat preferences. Each of the three deltaic habitats supported relatively high diversity and abundances of aquatic macroinvertebrates. In comparison, non-deltaic habitats supporting lower diversity and abundances. However, the presence of unique taxa, such as Anostracans, together with evidence from other studies, makes these aquatic habitats equally important for conservation. The maintenance of a diversity of aquatic habitats in all study areas is thus critical for the conservation of the long-term diversity of aquatic macroinvertebrates in the Okavango Delta.

Whilst the focus of this paper is spatial variability of macroinvertebrate assemblages, it is likely that hydrological phase is an important driver of variability of macroinvertebrate assemblages, reflecting the temporal transition between lentic and lotic states, which is typical of flood-pulse wetlands, such as the Okavango Delta. The temporal variability of aquatic macroinvertebrate assemblages at deltaic habitats will be examined in a follow-on paper to evaluate intrinsic temporal variability of this hydrologically dynamic ecosystem. Typically, high intrinsic variability (spatial and temporal) reduces the efficacy of bioassessment tools.

From the perspective of the development of a macroinvertebrate-based rapid bioassessment tool in the future, the current study has shown that the bioassessment tool must account for aquatic habitat, although the tool does not have to be area specific. In addition, temporal variability of macroinvertebrate assemblages should be examined to evaluate potential hydrological effects on the tool. Our study additionally suggests that, given the distinctiveness of the biota inhabiting endorheic depression wetlands, such as the seasonally flooded and temporary rain-filled pools in the current study, a separate bioassessment tool that includes taxa typical to these wetland types may have to be the developed, and additional research is thus recommended.

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Appendix 1: Study areas, sites and sample numbers giving latitude, longitude and habitat type

Site_Sample Code	Focal area	Latitude S	Longitude E	Aquatic habitat
1_INV01	Upper Panhandle (Shakawe)	18°20’27.2”	21°50’09.4”	Seasonally inundated floodplain
1_INV02	Upper Panhandle (Shakawe)	18°20’25.6”	21°50’09.7”	Marginal vegetation
1_INV03	Upper Panhandle (Shakawe)	18°20’20.5”	21°50’12.7”	Floating vegetation
2_INV04	Upper Panhandle (Shakawe)	18°24’39.1”	21°52’44.3”	Seasonally inundated floodplain
2_INV05	Upper Panhandle (Shakawe)	18°24’40.0”	21°52’51.3”	Marginal vegetation
2_INV06	Upper Panhandle (Shakawe)	18°24’40.6”	21°52’51.8”	Floating vegetation
3_INV07	Upper Panhandle (Shakawe)	18°24’20.9”	21°53’08.9”	Seasonally inundated floodplain
3_INV08	Upper Panhandle (Shakawe)	18°24’20.6”	21°53’07.7”	Marginal vegetation
3_INV09	Upper Panhandle (Shakawe)	18°24’19.5”	21°53’04.1”	Marginal vegetation
4_INV10	Upper Panhandle (Shakawe)	18°26’22.1”	21°54’41.0”	Marginal vegetation
4_INV11	Upper Panhandle (Shakawe)	18°26’22.8”	21°54’41.6”	Marginal vegetation
4_INV12	Upper Panhandle (Shakawe)	18°26’22.8”	21°54’41.6”	Floating vegetation
5_INV13	Lower Panhandle (Guma Lagoon)	18°57’24.1”	22°22’38.1”	Floating vegetation
5_INV14	Lower Panhandle (Guma Lagoon)	18°57’21.8”	22°22’38.2”	Marginal vegetation
5_INV15	Lower Panhandle (Guma Lagoon)	18°57’19.4”	22°22’35.0”	Marginal vegetation
6_INV16	Lower Panhandle (Guma Lagoon)	18°50’32.3”	22°24’13.0”	Floating vegetation
6_INV17	Lower Panhandle (Guma Lagoon)	18°50’34.2”	22°24’16.1”	Marginal vegetation
6_INV18	Lower Panhandle (Guma Lagoon)	18°50’34.2”	22°24’16.1”	Marginal vegetation
7_INV19	Lower Panhandle (Guma Lagoon)	18°52’44.8”	22°23’28.3”	Seasonally inundated floodplain
7_INV20	Lower Panhandle (Guma Lagoon)	18°52’44.8”	22°23’28.3”	Marginal vegetation
7_INV21	Lower Panhandle (Guma Lagoon)	18°52’44.5”	22°23’27.8”	Marginal vegetation
8_INV22	Lower Panhandle (Guma Lagoon)	18°57’37.3”	22°23’0.16”	Floating vegetation
8_INV23	Lower Panhandle (Guma Lagoon)	18°57’33.6”	22°22’57.8”	Marginal vegetation
8_INV24	Lower Panhandle (Guma Lagoon)	18°57’38.4”	22°22’57.9”	Marginal vegetation
9_INVGE1	Lower Panhandle (Guma Lagoon)	18°57’14.2”	22°22’12.2”	Seasonally inundated floodplain
10_INVGE2 + 3	Lower Panhandle (Guma Lagoon)	18°57’14.2”	22°22’12.2”	Seasonally flooded pool
11_INV25	Chiefs Island (Nxaraga)	19°32’57.3”	23°10’38.3”	Floating vegetation
11_INV25A	Chiefs Island (Nxaraga)	19°32’57.3”	23°10’38.3”	Seasonally inundated floodplain
11_INV26	Chiefs Island (Nxaraga)	19°32’57.3”	23°10’38.3”	Marginal vegetation
12_INV27	Chiefs Island (Nxaraga)	19°32’20.6”	23°11’02.3”	Seasonally inundated floodplain
13_INV28	Chiefs Island (Nxaraga)	19°33’00.5”	23°12’02.7”	Floating vegetation
13_INV28A	Chiefs Island (Nxaraga)	19°33’00.5”	23°12’02.7”	Seasonally inundated floodplain
13_INV29	Chiefs Island (Nxaraga)	19°33’00.5”	23°12’02.7”	Marginal vegetation
14_INV30	Chiefs Island (Nxaraga)	19°32’10.6”	23°11’36.8”	Seasonally flooded pool
15_INV31	Chiefs Island (Nxaraga)	19°31’53.6”	23°10’57.5”	Seasonally flooded pool
16_INV32	Chiefs Island (Nxaraga)	19°31’08.1”	23°10’21.4”	Seasonally flooded pool
17_INV33	Moremi Game Reserve (Xakanana)	19°10’03.3”	23°23’34.3”	Marginal vegetation
17_INV34	Moremi Game Reserve (Xakanana)	19°10’03.3”	23°23’34.3”	Seasonally inundated floodplain
17_INV35	Moremi Game Reserve (Xakanana)	19°10’03.3”	23°23’34.3”	Floating vegetation
18_INV36	Moremi Game Reserve (Xakanana)	19°11’26.1”	23°23’46.5”	Marginal vegetation
18_INV37	Moremi Game Reserve (Xakanana)	19°11’25.0”	23°23’43.6”	Seasonally inundated floodplain
18_INV37A	Moremi Game Reserve (Xakanana)	19°11’20.9”	23°23’42.7”	Floating vegetation
19_INV38	Moremi Game Reserve (Xakanana)	19°11’17.1”	23°26’01.2”	Marginal vegetation
20_INV40A, INV40B	Moremi Game Reserve (Xakanana)	19°12’06.9”	23°27’38.5”	Temporary, rain-filled pool
21_INV41A, INV41B	Moremi Game Reserve (Xakanana)	19°12’48.0”	23°25’15.0”	Temporary, rain-filled pool
22_INV42, INV43	Moremi Game Reserve (Xakanana)	19°12’35.6”	23°24’05.0”	Seasonally flooded pool