

Seasonal and spatial hydrological variability drives aquatic biodiversity in a flood-pulsed, sub-tropical wetland

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3 1 Seasonal and spatial hydrological variability drives aquatic biodiversity in a
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36 16 Keywords

38 17 Flood-pulsed wetlands, biodiversity, fresh waters, climate change, macroinvertebrates, diatoms, Okavango
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22 Summary

23 1. Flood-pulsed wetlands make vital contributions to local and global biodiversity. However, the
24 patterns and controls of spatial and temporal variation in aquatic biodiversity in flood-pulsed
25 wetlands are not well understood. We analysed the relationship between variation in hydrological
26 regime and the patterns of aquatic biodiversity in a large pristine flood-pulsed wetland, the
27 Okavango Delta, Botswana.

28
29 2. Surveys of water chemistry, diatoms and macroinvertebrates were conducted over the seasonal
30 phases of the flood pulse. Hydrological variables of flood frequency and hydroperiod class were
31 collated from 16 years of satellite images. Multivariate regression trees and generalised least
32 squares regression were used to determine the chief controls of community composition and taxon
33 richness

34
35 3. Hydroperiod class, phase of the flood and conductivity explained 32% and 43% of the variation
36 in diatom and invertebrate taxon richness respectively. There was a negative relationship between
37 hydroperiod class and invertebrate taxon richness on the rising, peak and receding flood, whereas at
38 low flood there was no significant relationship. Multivariate regression tree analysis revealed
39 hydroperiod class, phase of the flood and conductivity as the dominant forces shaping invertebrate
40 and diatom community composition.

41
42 4. Seasonal and spatial variation in hydrological conditions are the principal drivers of variation in
43 aquatic biodiversity in flood-pulsed wetlands. In pristine flood-pulsed wetlands increased
44 productivity caused by the arrival of the flood waters appears to override disturbance and
45 connectivity in shaping taxon richness and community composition. Thus, these data suggest that
46 the maintenance of a rich mosaic of habitats covering a broad range of hydroperiod is the key to

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47 preserving aquatic biodiversity and natural ecosystem function in flood-pulsed wetlands.

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Copy for Review

49 INTRODUCTION

50 Wetlands provide multiple ecosystem services, including important contributions to biological
51 diversity (Keddy *et al.*, 2009). Flood-pulsed wetlands (Junk, Bayley & Sparks, 1989) occur where
52 there is a pronounced seasonal variation in water availability. The flood pulse integrates aquatic and
53 terrestrial habitats, and the seasonally flooded areas are of particular importance as the cyclical
54 wetting and drying results in the enhanced productivity of both phases (Bayley, 1995; Ramberg *et*
55 *al.*, 2006; Høberg *et al.*, 2002; Lindholm *et al.*, 2007; Kobayashi *et al.*, 2009; Bonyongo,
56 Bredenkamp & Veenendaal, 2000). Seasonal inundation is typical of many flood-pulsed wetlands
57 but there may be considerable variation, at a range of temporal scales, in the size and duration of the
58 flood pulse (Hamilton, Sippel & Melack, 2002; Milzow *et al.*, 2009). This variability in water
59 supply combines with a number of successional processes (hydrological, geomorphological,
60 biological and biogeochemical) to result in a dynamic mosaic of land and water of extraordinary
61 habitat richness (e.g. Ramberg *et al.*, 2006) which, notwithstanding a low incidence of endemism,
62 contributes to local, regional and, through the provision of resources to migratory species, global
63 biodiversity (Junk *et al.*, 2006).

64
65 The relationship between climate and the hydrological regime of wetlands is relatively well
66 understood (Hamilton *et al.*, 2002). Flood-pulsed wetlands are ecosystems where hydrology and, on
67 a longer timescale, geomorphology combine with a number of ecosystem processes to shape habitat
68 diversity (Wolski & Murray-Hudson, 2006; Ramberg *et al.*, 2006). Wetland vegetation is shaped by
69 moisture availability, in particular duration and depth of flooding (Casanova & Brock, 2000).

70 Furthermore, hydroperiod has a strong influence on biological community composition (Mackay *et*
71 *al.*, 2011b; Batzer, 1996; Douglas, Bunn & Davies, 2005) and productivity (Lindholm *et al.*, 2007)
72 with aquatic invertebrate species richness generally increasing as disturbance decreases with a
73 longer hydroperiod (Wissinger, 1999). Connectivity also affects species richness and community

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3 74 heterogeneity, as the heterogeneity of less connected sites is reduced when a flood arrives and
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5 75 increases connectivity (Thomaz, Bini & Bozelli, 2006), generally increasing site richness but
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7 76 perhaps reducing beta and gamma diversity. How these forces interact to shape spatial and temporal
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10 77 patterns of aquatic biodiversity and community composition in flood-pulsed wetland is not well
11
12 78 understood (Dallas & Mosepele, 2007). Flood plains have been identified as hotspots of
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14 79 biodiversity (Tockner, Malard & Ward, 2000), in part as they are ecotones supporting both
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16 80 terrestrial and aquatic taxa (Junk *et al.*, 1989). These short hydroperiod, seasonally flooded sites are
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18 81 areas of high disturbance and large temporal variation in connectivity and productivity. The
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20 82 quantification of hydroperiod class, which is a summariser of disturbance, connectivity, water
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22 83 chemistry and productivity, provides the opportunity to analyse not just the patterns but also the
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24 84 drivers of biodiversity in space and time and thus provides a link between patterns and the
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26 85 processes which shape them.
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34 87 The last 100 years has seen a dramatic decline in the biodiversity of inland waters largely due to
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36 88 habitat change and excessive nutrient loading. In the next 100 years climate change is likely to
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38 89 exacerbate these problems, with wetlands influenced by inter-tropical convergence zone (ICTZ)
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40 90 especially vulnerable (Mitsch *et al.*, 2010). Whilst there is uncertainty concerning how water
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42 91 availability, particularly in sub-tropical regions, will change as a result of climate change (Hughes,
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44 92 Kingston & Todd, 2010), rising temperatures are sure to increase evapotranspiration and therefore it
45
46 93 is likely that water availability will decline (IPCC, 2007). It is, therefore, important to gain a better
47
48 94 understanding of the relationship between climate, hydrology and biodiversity in order to predict
49
50 95 how flood-pulsed wetlands may be affected by various climate change and development scenarios.
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52 96 Here we sought to identify the patterns and controls of the diversity and community composition of
53
54 97 diatoms and macroinvertebrates in the Okavango Delta, one of the world's most important sub-
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56 98 tropical flood-pulsed wetlands. The near-pristine state of the Delta with few confounding influences
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3 99 (e.g. nutrient enrichment or technological management of water level regime) provides a rare
4
5 100 opportunity to investigate patterns in aquatic biodiversity in a system largely unaltered by human
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7 101 activity.
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11 12 13 103 **METHODS**

14 15 16 104 **The Okavango Delta**

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18 105 The Okavango Delta is a low-gradient alluvial fan lying in the lowest region of the Kalahari Basin
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20 106 (Fig. 1). The origins of the flood waters are chiefly the Okavango River (c. $9 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$), with a
21
22 107 significant, highly variable, input from local summer rainfall (c. $6 \times 10^9 \text{ m}^3 \text{ yr}^{-1}$) (McCarthy *et al.*,
23
24 108 2003). The Delta is the most biodiverse region in Botswana and its spatial extent is greatest during
25
26 109 the dry winter, due to the slow moving flood pulse (Ramberg *et al.*, 2006). It differs from other
27
28 110 wetlands as it supports very high biological productivity and a mammalian biomass, estimated to
29
30 111 reach 12 t km^{-2} (Junk *et al.*, 2006). The Delta is vital to the conservation of regional biodiversity,
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32 112 and represents, for many Zambebian species, their southernmost limit. Globally, the Delta also
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34 113 supports the largest breeding populations of several Red Data bird species.
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41 115 Patterns in the aquatic biodiversity and variation in the biological assemblages across the Delta
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43 116 have been identified for some aquatic organisms (Ramberg *et al.*, 2006; Mackay *et al.*, 2011b).

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45 117 Botanical studies have identified distinct plant communities related to a gradient of water
46
47 118 availability. However, there are few systematic studies of other primary producers, such as plankton
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49 119 or attached algae (Mackay *et al.*, 2011b). Aquatic macroinvertebrates show variation in space that
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51 120 has been attributed to habitat, but the drivers of change are less clear (Dallas & Mosepele, 2007).

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53 121 Recent developments in the hydrological modelling and mapping of the Delta (Wolski *et al.*, 2006)
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55 122 have made possible the location-specific quantification of the frequency and duration of inundation
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3 123 based on 16 years of flood pattern data in the delta (see methods). This, combined with extensive
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5 124 field survey, provides the opportunity to analyse and quantify the influence of hydroperiod on the
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7 125 aquatic biodiversity at a range of scales.
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11 12 13 127 **Site selection**

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15 128 Sites were selected from a number of regions, designed to maximise hydrological and chemical
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17 129 gradients across the Okavango Delta which are likely to have an impact on aquatic biodiversity
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19 130 (Fig. 1). The upper and lower Panhandle regions (UPH & LPH) are dominated by riverine habitat
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21 131 which is generally permanently flooded and experiences large variation in water levels. Below the
22
23 132 LPH the Okavango River divides into a number of distributaries (Wolski & Murray-Hudson, 2006).
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25 133 The main channel running to the north of Chief's Island is the Maunachira/Khwai system which
26
27 134 flows through a region of diverse habitats, including channels, lagoons and seasonally-inundated
28
29 135 floodplains (XAK). The main channel and lagoons in the XAK region typically show little variation
30
31 136 in water levels. South of Chief's Island other distributaries sampled were the Jao/Boro river system
32
33 137 (BOR) and the Santantadibe (SAN) (Fig. 1). Seasonally flooded habitats are more common in these
34
35 138 distal regions. The location of each site was geo-referenced using a hand-held GPS. When sampling
36
37 139 invertebrates and diatoms of a site, the location was divided into up to three sub-sites characterised
38
39 140 by different vegetation and coded a, b and c. For example UPH5 is divided into UPH5a dominated
40
41 141 by the water-lily (*Nymphaea nouchali* var. *caerulea* Sav.), UPH5b dominated by Hippo grass
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43 142 (*Vossia cuspidate* Roxb.) and UPH5c dominated by papyrus (*Cyperus papyrus* L.).
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51 144 Here we report on data collected during a complete flood cycle, encompassing periods of both high
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53 145 and low flood, and flood expansion and flood 'recession' (Table 1).
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3 147 **Collation of physicochemical variables**
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5 148 Detailed water chemistry variables are available for selected sites during trips 2 to 5 (6 December, 7
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7 149 May, 8 July and 8 October; Table 1). Dissolved Oxygen (DO), pH and conductivity were measured
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9 150 at sub-sites using portable YSI 550 & Fisher Scientific accumet AP85 meters respectively (n=211).
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11 151 The more detailed water chemistry was carried out on water samples collected in the field for each
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13 152 of the main sites and was: 1) filtered, 2) preserved with nitric acid or 3) unfiltered dependent on the
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15 153 analysis to be conducted. Samples were stored in a cool box before being transported back to
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17 154 laboratories in Maun and analysed for a range of parameters (Table 2); full details of the methods
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19 155 used can be found in Mackay *et al.* (2011a).
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24 156 **Collation of hydrological variables**
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26 157 Flood frequency and hydroperiod (HP) class were determined from a set of 16 inundation maps
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28 158 depicting maximum annual inundation extent during years 1989-2006 (excluding 1991 and 2003)
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30 159 obtained from Landsat (5 and ETM) images, and using a classification procedure involving spectral
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32 160 clustering and contextual classification. The number of years of inundation was calculated for the
33
34 161 entire Delta on a pixel-by-pixel basis by stacking individual maps. The variable Flood Frequency
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36 162 was then obtained by dividing years with inundation by the total number of flood maps. The
37
38 163 relationship between the amplitude of annual water level fluctuations and flood frequency varies for
39
40 164 different regions of the Delta. Hydrometric data are insufficient to formalise these relationships in
41
42 165 strict mathematical form; instead a set of seven HP amplitude classes for each site sampled were
43
44 166 defined (Table 3). The classification was based on flood frequency maps, data from hydrometric
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46 167 stations in the vicinity of sampling points, and on expert assessment of hydrological conditions at
47
48 168 the sampling points (Mackay *et al.*, 2011a). For example, Class 7 included permanently flooded
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50 169 sites with low amplitude (under 0.3 m) while Class 1 included sites which were only seasonally
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52 170 flooded, with a short period of inundation. Classes 6 and 5 were also permanently flooded regions,
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54 171 but flood amplitude varied between 0.3-1.0m and 1.0-3.0m respectively. Sampling points allocated
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3 172 to class 4 and 3 have, since 2004, been flooded every year, but over the longer term (16 years) were
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5 173 classified as seasonally flooded with the period of inundation longer in class 4 than 3 (Table 3).
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10 175 **Collation of biological variables**

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13 176 Diatom samples from 53 sites were investigated. A 5 cm section of dominant macrophyte species at
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15 177 each site was cut c. 20 cm below the water surface (avoiding dead stems, new shoots and recently
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17 178 wetter sections resulting from rising water level) and fixed with ethanol. Diatoms were prepared for
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19 179 counting using standard techniques (Battarbee *et al.*, 2001). At least 350-400 valves were counted
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21 180 for each sample, with taxa identified with the assistance of several flora (e.g. Krammer & Lange-
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23 181 Bertalot, 1999; Lange-Bertalot, 2001); see Mackay *et al.* (2011b) for full details.
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29 183 Aquatic macroinvertebrates were semi-quantitatively sampled by sweeping a reinforced pond net
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31 184 (30 cm x 30 cm net square frame, 500 µm mesh) for exactly 2 minutes in the selected aquatic
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33 185 vegetation. A preliminary assessment of the families collected was conducted in the field and
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35 186 abundance estimates made according to the following ranks: 1=1 individual, A= 2-9 individuals, B=
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37 187 10-99 individuals, C= 100- 1000 individuals and D= over 1000 individuals (Dallas & Mosepele,
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39 188 2007) and then the samples were preserved in 70% ethanol. Organisms were identified to family
40
41 189 level in the laboratory using a Carl Zeiss dissecting microscope and a number of identification keys
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43 190 (de Moor, Day & de Moor, 2003; Day, Harrison & de Moor, 2003; Day *et al.*, 1999; Day *et al.*,
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45 191 2001).
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50 51 52 193 **Statistical methods**

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54 194 Significant differences and the controls of taxon richness were explored using generalised least
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56 195 squares (GLS) which can allow for heterogeneity of variance in the response data. Models were
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3 196 compared using Akaike information criteria (AIC) with the minimum adequate model chosen by
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5 197 backward selection. The homogeneity of the model residuals was examined following common
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7 198 protocols (e.g. Zuur, Ieno & Elphick, 2010). Model residuals were checked for spatial patterns (both
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9 199 visually and statistically using a variogram) to assess independence. GLS does not produce a
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11 200 coefficient of determination, so the square of a correlation coefficient of observed versus predicted
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13 201 values was used instead as an estimate of percentage variance explained by the optimal model. All
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15 202 univariate analyses were carried out using the package nlme (Pinheiro *et al.*, 2011) R 2.0.0 (R,
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17 203 2007).

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23 205 Patterns in water chemistry data were explored using principal components analysis (PCA) and the
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25 206 significance of the axes determined using broken stick (Jolliffe, 1986). Relationships between
26
27 207 biological assemblages and potential drivers were explored using multivariate regression tree
28
29 208 (MRT) analyses (Breiman *et al.*, 1984). The diatom data were Hellinger transformed (Legendre &
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31 209 Gallagher, 2001) prior to the application of the regression tree analysis as this is an effective
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33 210 transformation for relative abundance data where Euclidean distance, as is used in MRT, is the
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35 211 measure of between-site differences (Legendre & Gallagher, 2001). A distance-based MRT using
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37 212 Bray-Curtis dissimilarity, a non-symmetric measure of dissimilarity (Legendre & Legendre, 1998),
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39 213 was used for the invertebrate abundance data as the distribution of data was such, containing a large
40
41 214 number of zeros, that a non-symmetric distance measure was more appropriate. Multivariate
42
43 215 regression trees rank sites by the explanatory variables and split them into groups so as to minimise
44
45 216 the sum of squared distance (SSD) in the resultant groups. The amount of variance explained by the
46
47 217 final MRT model is calculated by the proportion of the sum of squared distances (SSD) from the
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49 218 entire data set that remains in the final MRT 'leaves'. This analysis is an appropriate tool for
50
51 219 modelling the data presented here, having the facility to handle complex ecological data, with both
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53 220 continuous and categorical predictors and a mix of linear and non-linear responses to the underlying
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3 221 change and high-order interactions (Breiman *et al.*, 1984; De'ath & Fabricius, 2000). Cross
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5 222 validation was applied to determine the optimal number of splits in the tree (Breiman *et al.*, 1984).
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7 223 De'ath & Fabricius (2000) state that it is appropriate to select either the model with the minimum
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9 224 cross-validated error or the most complex tree within one standard error of the best predictive tree ;
10
11 225 here the tree with the minimum cross validated error was selected. Indicator species analysis was
12
13 226 used to determine any significant associations between taxa and the final regression tree groups
14
15 227 (Dufréne & Legendre, 1997). All MRT analysis was carried out using the mvpart library (version
16
17 228 1.4) (De'ath & Fabricius, 2000)and indicator species analysis using labdsv (version 1.4) in R 2.0.0
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19 229 (R, 2007).
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26 231 **RESULTS**

29 232 **Water chemistry and hydroperiod**

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32 233 The first three axes of the PCA of water chemistry data (Fig. 2a and 2b) were significant and
33
34 234 explained 69% of the variation in the data. The main gradient in the data was strongly associated
35
36 235 with ionic strength, i.e. conductivity along with silicate and bicarbonate concentrations. This main
37
38 236 axis correlated with HP class, negative axis 1 scores having HP class > 4 and positive axis 1 a HP
39
40 237 class of < 4 (Fig. 2a). Thus, sites where inundation was less frequent and shorter were characterised
41
42 238 by higher conductivity, K⁺ and bicarbonate. The second axis was associated with pH, sulphate and
43
44 239 total nitrogen. There was a marked seasonality evident in the water chemistry, with less
45
46 240 heterogeneity amongst sites at lower water levels (December 2006 and October 2007) compared to
47
48 241 the periods of flood expansion and peak flood (April and July 2007) (Fig. 2b). The mid and high
49
50 242 water periods had higher TN and Mg²⁺ irrespective of the HP class, whereas conductivity was
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52 243 elevated only at lower HP class sites.
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245 **Taxon richness and diversity**

246 The generalised least squares regression (GLS) showed that diatom taxon richness was best
247 predicted by conductivity, HP class and season ($P < 0.001$); these three variables explained 32% of
248 the variance (proxy r^2 0.32) in the diatom richness data. HP class 5 had a significantly different
249 taxon richness ($p < 0.05$) (Fig. 3). In addition diatom taxon richness was positively related to
250 conductivity. The range of richness was similar across the seasons apart from peak flood when it
251 was significantly lower.

252

253 Aquatic macroinvertebrate taxon richness and abundance showed clear responses to HP class (Fig.
254 4). The optimal model produced by GLS regression predicting taxon richness contained HP class,
255 season and conductivity and explained 43% of the variance (p -value < 0.0001 , proxy r^2 of 0.43).

256 This is supported by the clear patterns in the relationship between total abundance and taxon
257 richness (Fig. 5a & 5b) which demonstrates that low HP class sites were richer and more abundant
258 in aquatic invertebrates, but also that samples collected on the rising, peak and receding flood tend
259 to be richer and more abundant (Fig. 5a & 5b). At low flood, low HP class sites had similar taxon
260 richness and abundance compared with higher HP class sites, with the exception of an isolated
261 floodplain with an HP class of 2 (XAK7; Fig 4). There was a reversal of this pattern with the first
262 influence of flood expansion in April/May 2007 as the abundance and richness rose at all sites, with
263 low HP class having the highest richness and abundance. At the peak flood the abundance of
264 invertebrates was much higher across all the HP classes but the patterns in richness remained the
265 same, with low HP classes being more taxon rich. Similarly, as the flood receded the abundances
266 and richness fell but the higher richness persisted in low HP classes (Fig. 4).

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3 268 **Community composition**
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5 269 Diatom community composition was shaped by a number of factors and the multivariate regression
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7 270 tree with five leaves explained 36.9% of the variance in the diatom data (Fig. 6). Sites sampled
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9 271 during flood expansion were initially split from all other sites, and these flood expansion sites were
10
11 272 then separated into two groups based on the conductivity value of $54 \mu\text{S cm}^{-1}$. Above $54 \mu\text{S cm}^{-1}$
12
13 273 low profile and low adhesive taxa characterised the distal sites (Group E). Group D sites had a
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15 274 conductivity below $54 \mu\text{S cm}^{-1}$, were in the UPH and were characterised by both low and high
16
17 275 profile guild diatoms. *Encyonema* species, which are able to tolerate high flow velocities by
18
19 276 growing in mucilaginous communities, dominate the low profile diatom flora. High profile growth
20
21 277 diatoms are dominated by *Eunotia* species, which grow best in low alkalinity waters (Van Dam &
22
23 278 Mertens, 1994). The samples from the other seasons were split by HP class and conductivity. Group
24
25 279 A has sites with HP class of 3 and 4, while the other branch of the tree combined low and high HP
26
27 280 classes 1, 2, 5, 6 and 7. This group was then split according to whether conductivity was above
28
29 281 (Group B) or below (Group C) $49.5 \mu\text{S cm}^{-1}$ (Fig 6). Group B combines low and high HP classes in
30
31 282 sites mainly sampled during low flood. Diatom indicator species had high growth profiles, able to
32
33 283 compete for resources effectively when flow and grazing pressures are low (Passy, 2007). In
34
35 284 contrast, Group C sites are all from the Panhandle, sampled during either low or peak flood, and
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37 285 indicator species are mainly of low profile growth forms and therefore able to tolerate some
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39 286 disturbance, but occur in well aerated, highly oxygenated waters.
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48 288 The regression tree of the invertebrate community demonstrates that assemblage composition is
49
50 289 strongly influenced by seasonality and HP class. The seven-leaved tree presented here explained
51
52 290 11.9 % of the variance in the invertebrate data. The first split reflects the difference in community
53
54 291 composition at low flood from that at the other periods (Fig. 7). The 59 sites sampled at low flood
55
56 292 were split at conductivity of $42.4 \mu\text{S cm}^{-1}$ into groups E & F on one side and group G on the other.
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3 293 Sites E and F were split by HP class, group F containing the lowest and highest HP classes and
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5 294 having 3 indicator taxa, whereas the other groups on this branch (groups E and G) had no indicator
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7 295 taxa. The 124 sites on the other main branch were split into seasonally flooded sites, HP class 1, 2,
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9 296 3 & 4 (55 sites) and permanently flooded sites with HP class 5,6 & 7 (69 sites). The higher HP class
10
11 297 sites were then split at K^+ concentrations of 1.1 mg L^{-1} ; Group A had values $< 1.1 \text{ mg L}^{-1}$ and
12
13 298 contained sites from UPH and LPH from the rising and high flood period (Fig. 7). The indicator
14
15 299 taxa from this group included Velidae, Hydracarina, and Geridae which are either free swimming or
16
17 300 neustonic taxa reflecting the presence of open water, pelagic habitat. Group B sites, with $K > 1.1$
18
19 301 mg L^{-1} , contained sites from the LPH from the period of receding flood and XAK sites of HP class
20
21 302 6 & 7, with indicator taxa of Atyidae and Heptageniidae. Groups C and D contained low HP class
22
23 303 sites and the model splits the two at SiO_2 of 20.5 mg L^{-1} . Group C was distinct from D, the latter
24
25 304 containing sites from the BORO region on the rising flood, with HP class of 3 and 4, whereas
26
27 305 Group C had HP class 1 to 4 and these sites were sampled almost exclusively at peak and receding
28
29 306 flood (Fig. 7) The sites in groups C & D had the richest and most diverse assemblages with a large
30
31 307 number of indicator taxa. The indicator taxa are generally benthic and represent a number of trophic
32
33 308 levels from grazers and collectors such as Baetidae, Ostracoda and a number of gastropods, to
34
35 309 predatory taxa, such as Libellulidae. The MRT and indicator species analysis revealed that several
36
37 310 taxa are associated with low HP class during flood expansion and peak flood. In particular
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39 311 Dytiscidae (adult and larvae), Notonectidae, Hydrophiloidea, and Pleidae are associated with
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41 312 shorter hydroperiod and higher water levels, whereas Velidae, Hydracarina, Caenidae and Atyidae
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43 313 are associated with longer hydroperiod and the higher water phases of the flood cycle.
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53 315 **DISCUSSION**

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55 316 The models describing taxon richness and the multivariate analyses (MRT for biology and PCA for
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57 317 water chemistry) revealed significant variation in water chemistry and in diatom and invertebrate
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3 318 assemblages in the Delta that could be separated into two main gradients. The first was a spatial HP
4
5 319 class gradient running from permanently inundated sites with little variation in water level to
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7 320 infrequently flooded sites, via sites with longer periods of inundation but greater variation in water
8
9 321 level. The second gradient was temporal and linked to the seasonal phase of the flood. There were
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11 322 interactions between the spatial and temporal gradients in the data. At low water there was no
12
13 323 significant relationship between HP class and invertebrate taxon richness, with homogeneous
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15 324 assemblages with few indicator taxa (Fig 7), in agreement with other investigations of invertebrate
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17 325 community composition at low water (Dallas & Mosepele, 2007). However, temporal variation, in
18
19 326 the form of the arrival of floodwaters, changed the relationship in the spatial gradient as the effects
20
21 327 of HP class and conductivity (associated with lower HP class and the arrival of the flood) start to
22
23 328 become apparent on the macroinvertebrate community. The spatial gradient of HP class results
24
25 329 from the accretion of decades of variation in the size of the flood pulse combined with both plant
26
27 330 and geomorphological successional processes (Ramberg *et al.*, 2006). The determination of site-
28
29 331 specific HP required 16 years of data (Mackay *et al.*, 2011a) and has been crucial to disentangling
30
31 332 the spatial and temporal patterns of aquatic biodiversity. For example, both diatom and invertebrate
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33 333 taxon richness responded to increased conductivity at low HP class and at peak flood, when
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35 334 conductivity was increased as a result of the arrival of the flood pulse and the increased flooded
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37 335 area (Mackay *et al.*, 2011a). The increased conductivity was strongly associated with HP class and
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39 336 season (Fig. 2). Detection of such a spatially and temporally discrete response would have been
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41 337 impossible without HP class as a predictor.
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49 339 Species or taxon richness generally reflects a balance between productivity (Chase & Leibold,
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51 340 2002), disturbance (Connell, 1978), connectivity (Thomaz *et al.*, 2006) and trophic interactions
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53 341 (Worm & Duffy, 2003). There is, however, some debate over the shape of the relationship (Kadmon
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55 342 & Benjamini, 2006) and how these drivers interact (Cardinale *et al.*, 2005). Invertebrate taxon
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3 343 richness and abundance at low HP class rose with increasing disturbance, which is in direct contrast
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5 344 to observations from non-flood-pulsed wetlands sampled along a hydroperiod gradient (Wissinger,
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7 345 1999; Tarr, Baber & Babbitt, 2005). Furthermore, flood events connecting isolated areas are
8
9 346 reported to homogenise community composition (Thomaz *et al.*, 2006), whereas here the period of
10
11 347 greatest connection with the arrival of the flood pulse increased heterogeneity in water chemistry
12
13 348 and invertebrate richness and community composition. The arrival of a flood pulse precipitates a
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15 349 burst of primary productivity fuelling the aquatic food-web (Bayley, 1995; Høberg *et al.*, 2002;
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17 350 Bunn, Davies & Winning, 2003; Lindholm *et al.*, 2007; Ramberg *et al.*, 2010), influences water
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19 351 chemistry (Mackay *et al.*, 2011a), detritus processing and the presence of vertebrate predators
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21 352 (Mosepele *et al.*, 2009), and therefore has both a direct and indirect influence on the invertebrate
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23 353 communities. The abundance and diversity of invertebrates were highest on the rising and peak
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25 354 flood, generally, but not exclusively, at low HP class sites. The MRT analysis identified distinct
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27 355 groups (C and D, Fig 7) which were low HP class and had greater within-group heterogeneity and
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29 356 many benthic indicator taxa. Group D was associated with the rising flood and group C with the
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31 357 peak and falling flood. Thus, there is seasonal variation in the spatial patterns in invertebrate
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33 358 richness, abundance and community composition linked to the phase of the flood, with the effects
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35 359 most evident at high water and at low HP class sites. The strong relationship between invertebrate
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37 360 abundance and richness (Fig. 5) and the large increase in invertebrate abundance suggests that
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39 361 elevated productivity is the root cause (Yee & Juliano, 2007). It seems likely, therefore, that the
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41 362 effects of increased productivity associated with the arrival of the flood pulse confound the effects
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43 363 of both disturbance and connectivity in controlling the richness, abundance and composition of the
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45 364 invertebrate fauna.
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54 366 Diatom taxon richness followed an inverse seasonal pattern to invertebrates, being highest during
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56 367 the low flood when invertebrate taxon richness and abundance were lowest. Moreover, diatom
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3 368 community composition at low flood was characterised by high growth forms (MRT group B, Fig.
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5 369 6), which are the most susceptible to invertebrate grazing (Passy, 2007). As the flood-waters
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7 370 arrived, invertebrate richness and abundance rose dramatically, whereas diatom taxon richness fell
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9 371 markedly at the height of the flood and the higher growth forms most susceptible to grazing were
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11 372 absent. This highlights the crucial role of trophic interactions on patterns in aquatic biodiversity
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13 373 (Worm & Duffy, 2003), as whilst richness for invertebrates and diatoms had the same drivers,
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15 374 linked to the arrival of the flood-pulse and HP class, the seasonal patterns were mirror images as a
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17 375 result of the trophic interactions taking place between the two groups. Furthermore, the invertebrate
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19 376 assemblages are subject to both bottom-up productivity linked and top-down predation linked
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21 377 control. Predation by fish and birds can strongly affect community structure, abundance and
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23 378 biodiversity (Hanson & Riggs, 1995; Wissinger, 1999). The very low invertebrate abundance and
24
25 379 distinct community composition at the minimum extent of the wetted area may result from a
26
27 380 combination of reduced primary production as available nutrients are depleted, and increased
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29 381 predation as fish and invertebrate-feeding birds reach higher densities as the flooded area is reduced
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31 382 (Mosepele *et al.*, 2009).
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384 The data presented here suggest that in flood pulsed wetlands there is a strong link between
385 hydrological variation and aquatic biodiversity with pronounced spatial and temporal heterogeneity.
386 There are many theories about what leads to species-rich communities and their importance to
387 ecosystem stability, resistance, resilience and function (Hillebrand, Bennett & Cadotte, 2008). This
388 study suggests that for flood-pulsed wetlands, particularly pristine, nutrient-limited systems, HP
389 class and phase of flood combine to be a good predictor of richness, abundance and community
390 composition and thus serve as the best integrators of a number of direct and indirect forces shaping
391 the biotic communities, of which productivity and trophic interactions are perhaps the most
392 important.

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5 394 The linking of hydrological and ecological investigation has increased our understanding of how6
7 395 and why water chemistry and aquatic biodiversity vary in space and time in a flood-pulsed wetland.8
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10 396 The patterns of diversity suggest links between productivity influenced by trophic interactions11
12 397 (Worm & Duffy, 2003), which perhaps accounts for the variety of productivity-diversity13
14 398 relationships observed in the past (Waide *et al.*, 1999). The data suggest that very short hydroperiod15
16 399 sites are asymmetrically important to the functioning and overall productivity of flood-pulsed17
18 400 wetlands supporting directly and indirectly, through subsidisation of the food web of other areas,19
20 401 both the aquatic terrestrial flora and fauna of the system. The existence of these short hydroperiod21
22 402 areas is the result of the natural variability in the size of the flood pulse at a range of temporal23
24 403 scales, inter-annual and decadal. Establishing these relationships is a key step towards being able to25
26 404 predict better the impacts of future climate change on the aquatic ecology of flood pulsed wetlands.27
28 405 The investigation of a pristine system allowed the determination of the role of the flood pulse to be29
30 406 clarified in the absence of confounding factors such as organic pollution or hydrological31
32 407 modification. Further work is required to investigate directly spatial and temporal patterns of33
34 408 productivity and how they relate to biodiversity across the cycle of flood pulse and the role of fish35
36 409 and other vertebrates as integrators of the spatially and temporally discrete productivity. However,37
38 410 establishing such a strong link between hydrology and the aquatic ecology of these systems39
40 411 represents significant progress towards being able to extend predictions of the impact of climate41
42 412 change and development scenarios beyond the hydrology of flood-pulsed wetlands (Murray-43
44 413 Hudson, Wolski & Ringrose, 2006) to the potential impacts on aquatic biodiversity and45
46 414 productivity.47
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585 **Table Legends**

586 Table 1. Details of sample period, numbers of sites and sub-sites visited.

Trip	flood phase	Date	number of sites	number of sub-sites
1	High	01/09 – 14/09 2006	19	33
2	Low	28/11 – 10/12 2006	28	59
3	Expansion	23/4 – 6/5 2007	23	42
4	High	24/7 – 7/8 2007	26	47
5	Recession	2/10 – 12/10 2007	21	38

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588 Table 2. Details of physical and chemical parameters sampled at each site.

	Min	Max	Mean
Depth (m)	0.00	5.00	1.43
Velocity (M S ⁻¹)	0.00	1.56	0.15
pH (pH units)	4.97	7.89	6.64
Temperature (°C)	13.60	35.00	23.47
DO (mg L ⁻¹)	0.39	10.37	3.49
Conductivity (µS cm ⁻¹)	19.30	119.10	61.72
TSS (mg L ⁻¹)	0.00	10.00	2.34
DOC (mg L ⁻¹)	2.73	23.62	8.03
Alkalinity (mg L ⁻¹)	3.50	168.30	57.30
K ⁺ (mg L ⁻¹)	0.33	6.90	2.28
Na ⁺ (mg L ⁻¹)	0.10	7.19	2.01
SiO ₂ (mg L ⁻¹)	3.00	32.34	11.35
Cl ⁻ (mg L ⁻¹)	0.11	4.24	0.66
TP (mg L ⁻¹)	0.00	0.25	0.04
TN (mg L ⁻¹)	0.08	1.94	0.62
NO ₃ ⁻ - N (mg L ⁻¹)	0.00	0.71	0.20
SO ₄ ²⁻ (mg L ⁻¹)	0.01	2.58	0.35
Mg ²⁺ (mg L ⁻¹)	0.14	2.00	0.92
Ca ²⁺ (mg L ⁻¹)	3.20	15.46	7.68

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3 591 Table 3. Details of hydroperiod class characteristics. The current hydrological state of the Delta is
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5 592 wetter in the context of the past 20 years, hence Hydroperiod classes 4 and 1 are designated
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7 593 seasonal and dry respectively, but in the context of the last 20 years have experienced 12 month and
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10 594 seasonal inundation respectively.

Hydroperiod class	Flood frequency since 2004	Flood duration	Flood amplitude	Long-term (20 years) flood conditions
7	every year	12 months	10-30 cm	permanent
6	every year	12 months	30-100 cm	permanent
5	every year	12 months	100-300 cm	permanent
4	every year	12 months	50-100 cm	seasonal
3	every year	6-11 months	50-100 cm	seasonal
2	3/4 or less	3-6 months	10-50 cm	seasonal
1	3/4 or less	3-6 months	10-50 cm	dry

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3 597 **Figure Legends**
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7 599 Figure 1. Map of the Okavango Delta with sample areas highlighted: UPH - Upper Pan Handle;
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9 LPH – Lower Pan Handle; BORO – The Jao/Boro river system, XAK – Xakanaxa region and SAN
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11 – Santantadibe river.
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16 603 Figure 2. Principal Components Analysis (PCA) biplots of water chemistry variables with sites
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18 coded by a) hydroperiod class (HP) in which sites with longer HP tend fall on the left of axis 1 and
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20 those with shorter HP tend to fall the right and b) phase of the flood cycle. Chemical variables
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22 included were DO (mg L^{-1}), pH, Conductivity (mS cm^{-1}), HCO_3^- (mg L^{-1}), SiO_2 (mg L^{-1}), K^+ (mg L^{-1}),
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24 TN (mg L^{-1}), SO_4^{2-} (mg L^{-1}), Mg^{2+} (mg L^{-1}).
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30 609 Figure 3. Diatom taxon richness plotted against hydroperiod class.
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34 611 Figure 4. Invertebrate taxon richness and abundance plotted against hydroperiod class at each phase
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36 of the flood.
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40 614 Figure 5. Relation between invertebrate taxon richness and abundance classified a) by hydroperiod
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42 class (1-7) and b) by phase of the flood.
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47 617 Figure 6. Multivariate Regression tree of diatom assemblage constrained by the environmental
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49 variables that result in the most distinct groups. The sites in each group are listed at each 'leaf' and
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51 the indicator species for each group is also defined (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$)
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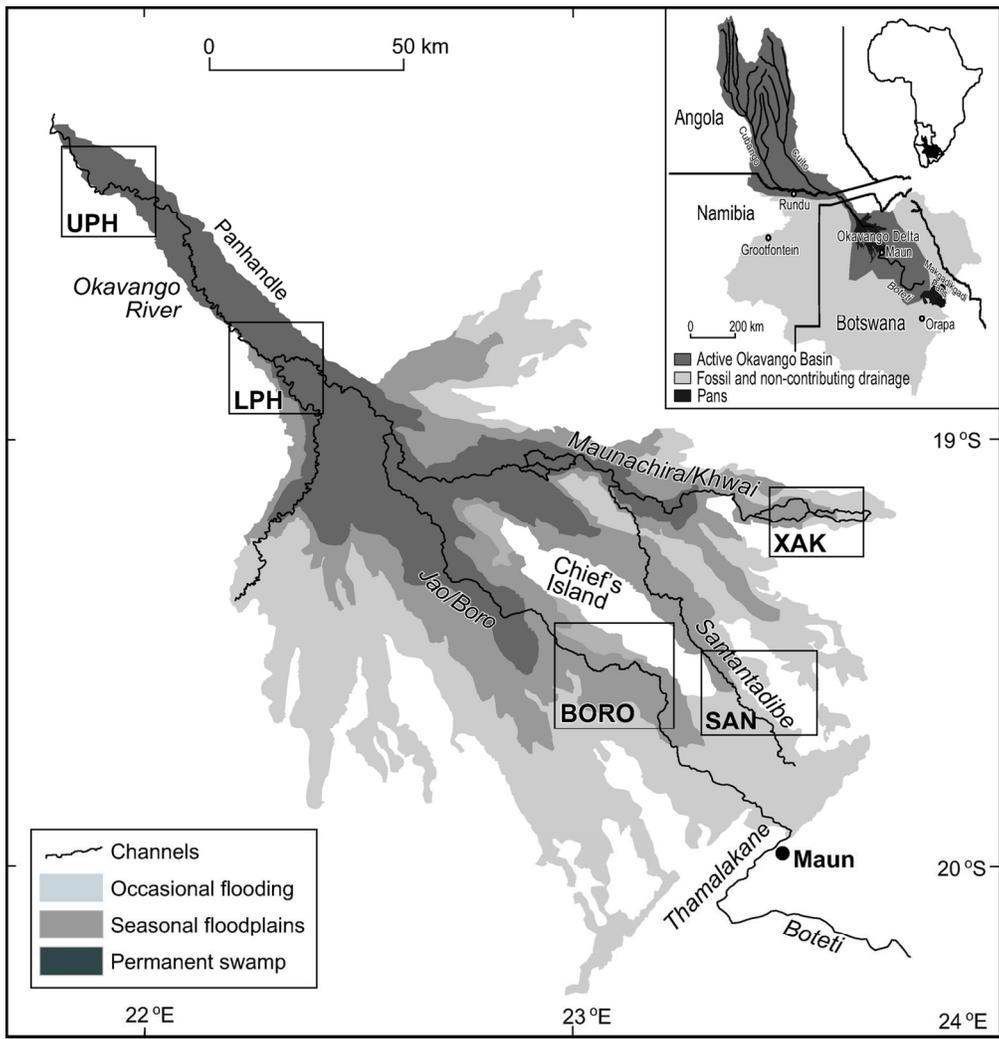
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3 621 Figure 7. Multivariate Regression tree of invertebrate assemblage constrained by the environmental
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5 622 variables that result in the most distinct groups. The sites in each group are summarised at each
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7 623 'leaf' and the indicator species for each group is also defined (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

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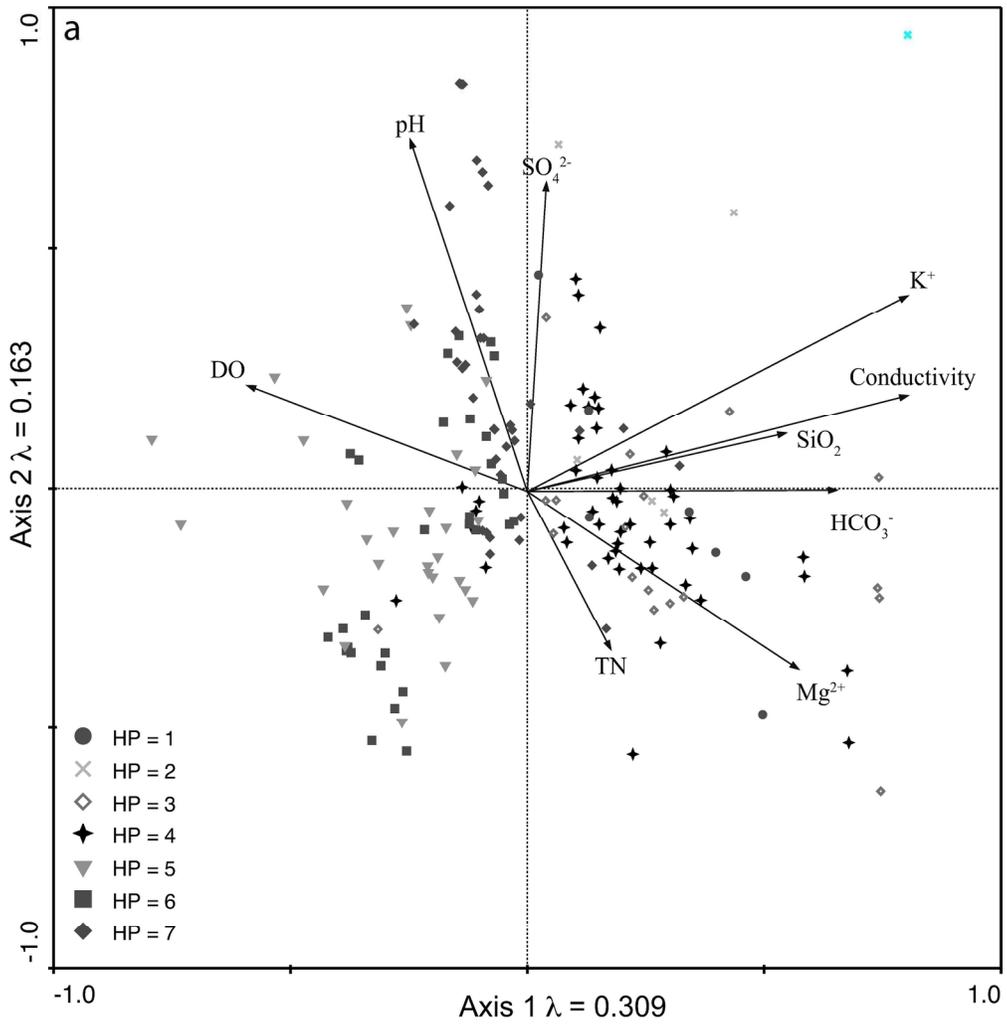
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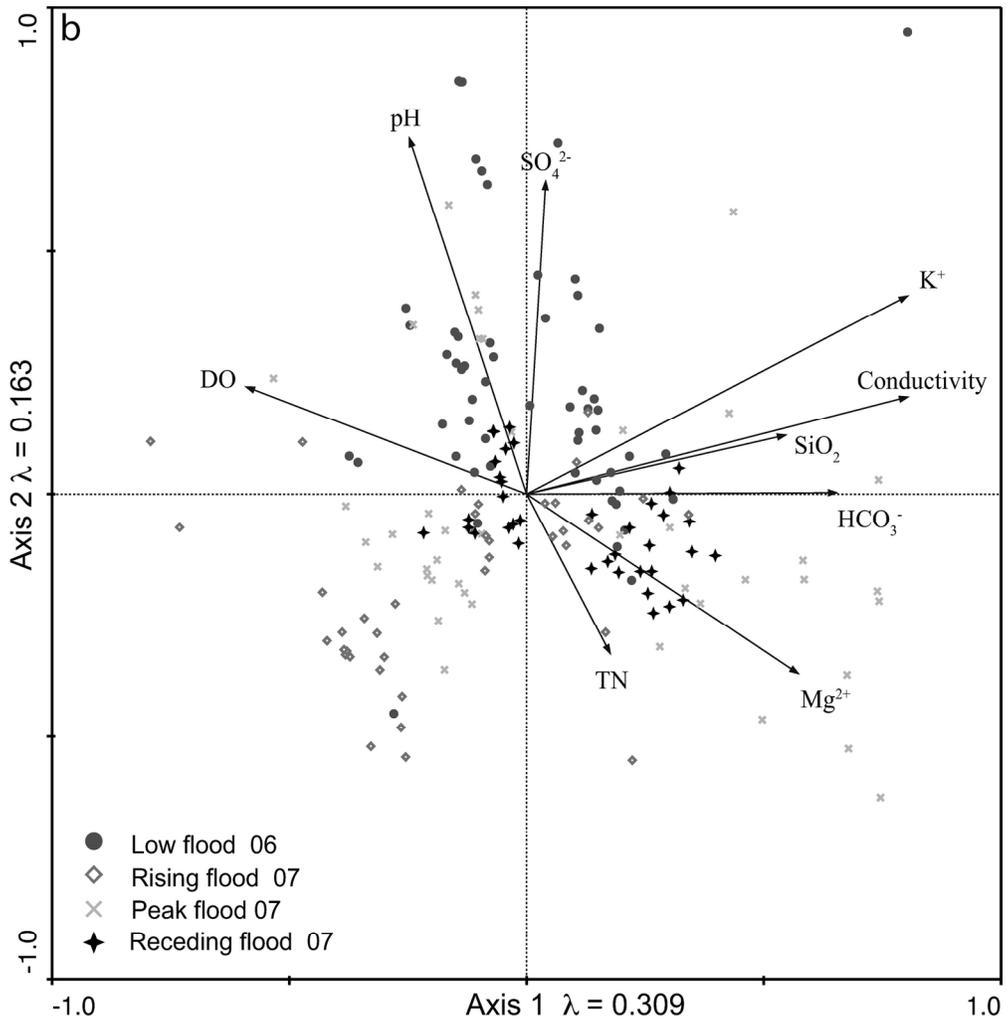
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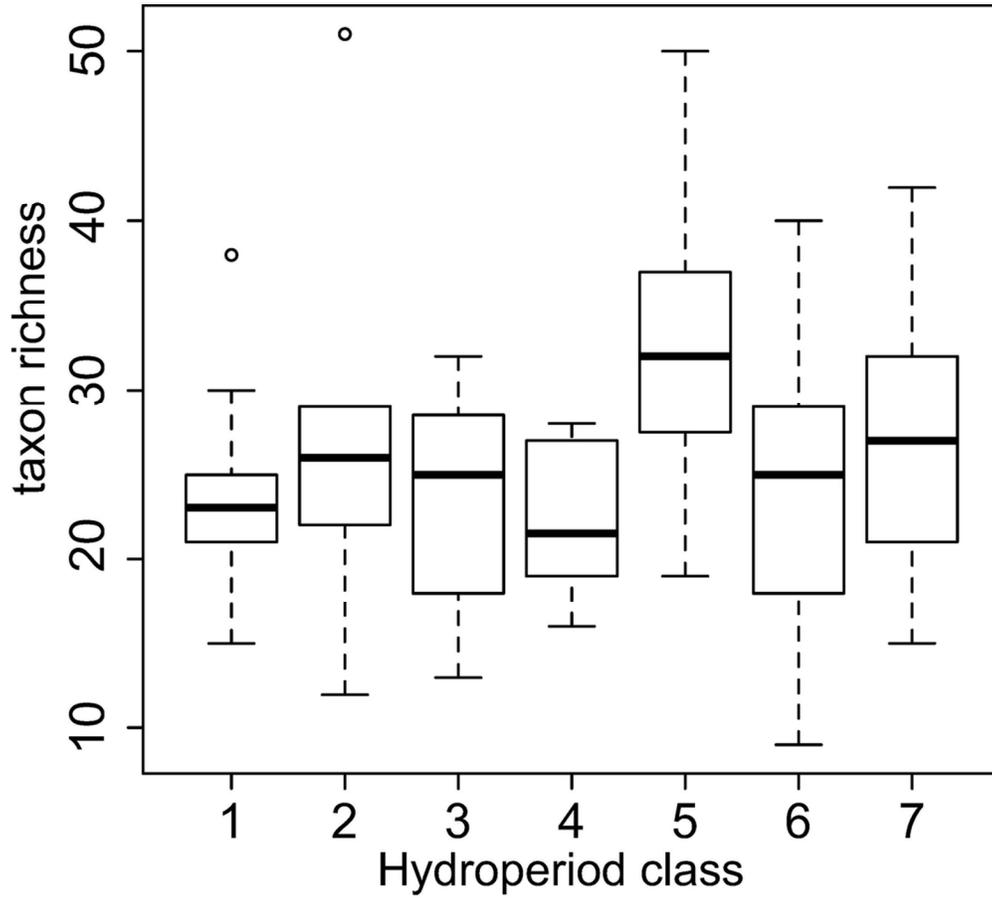
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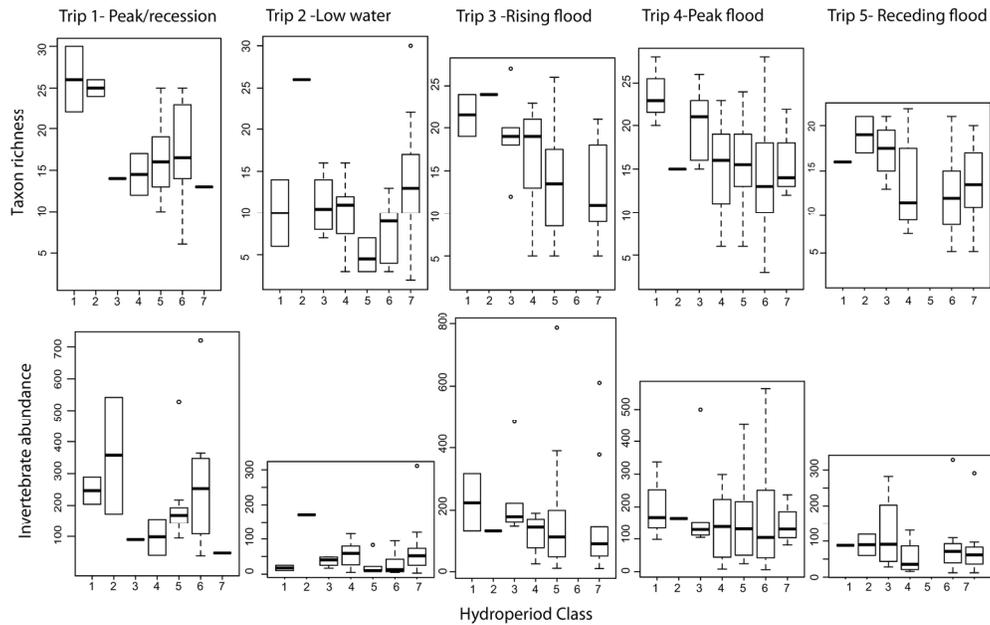
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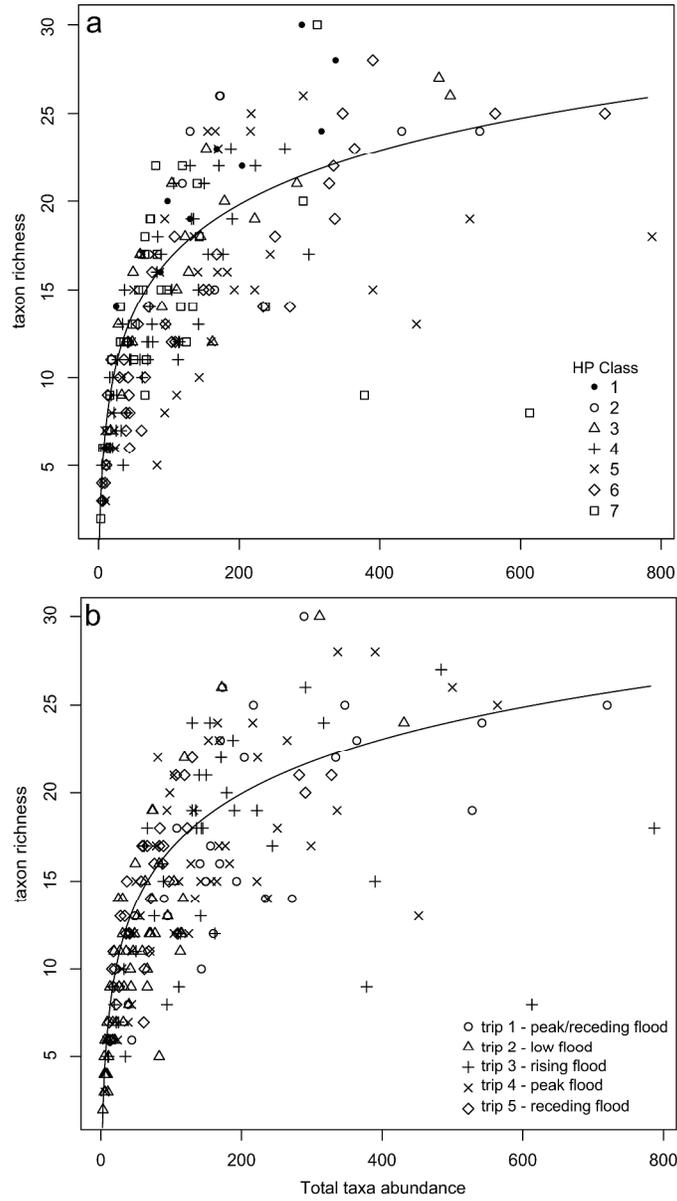
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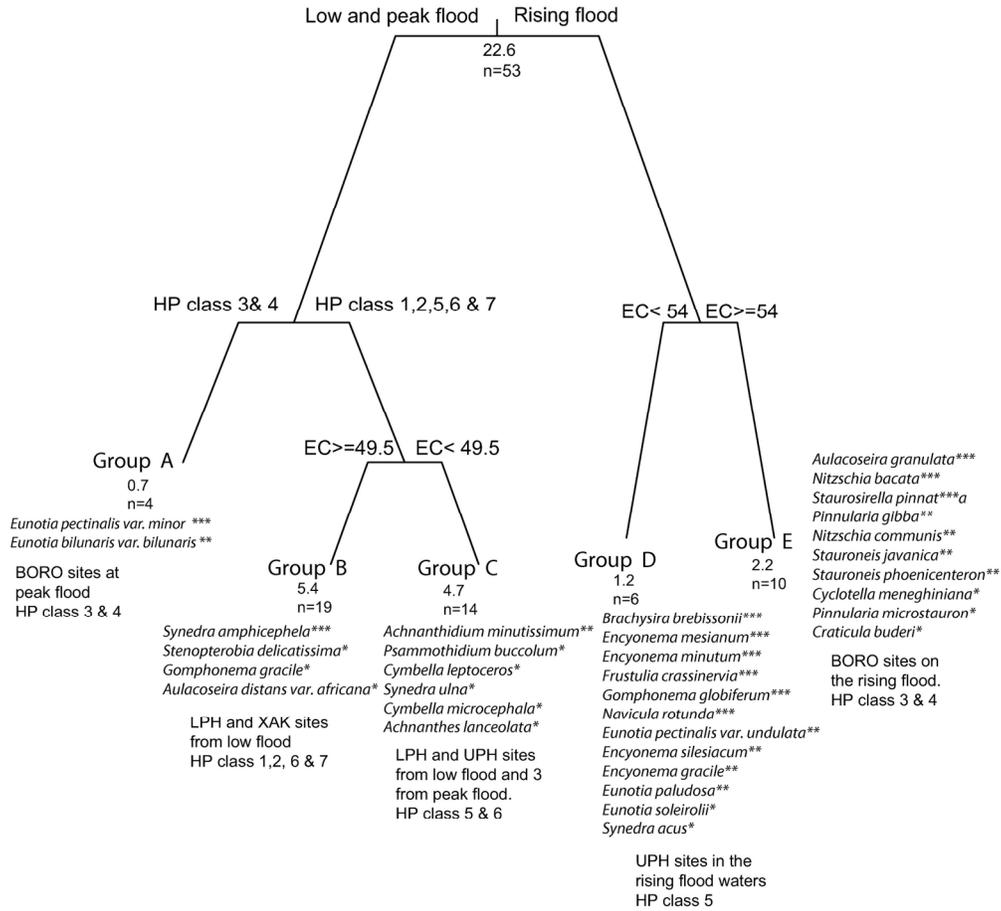
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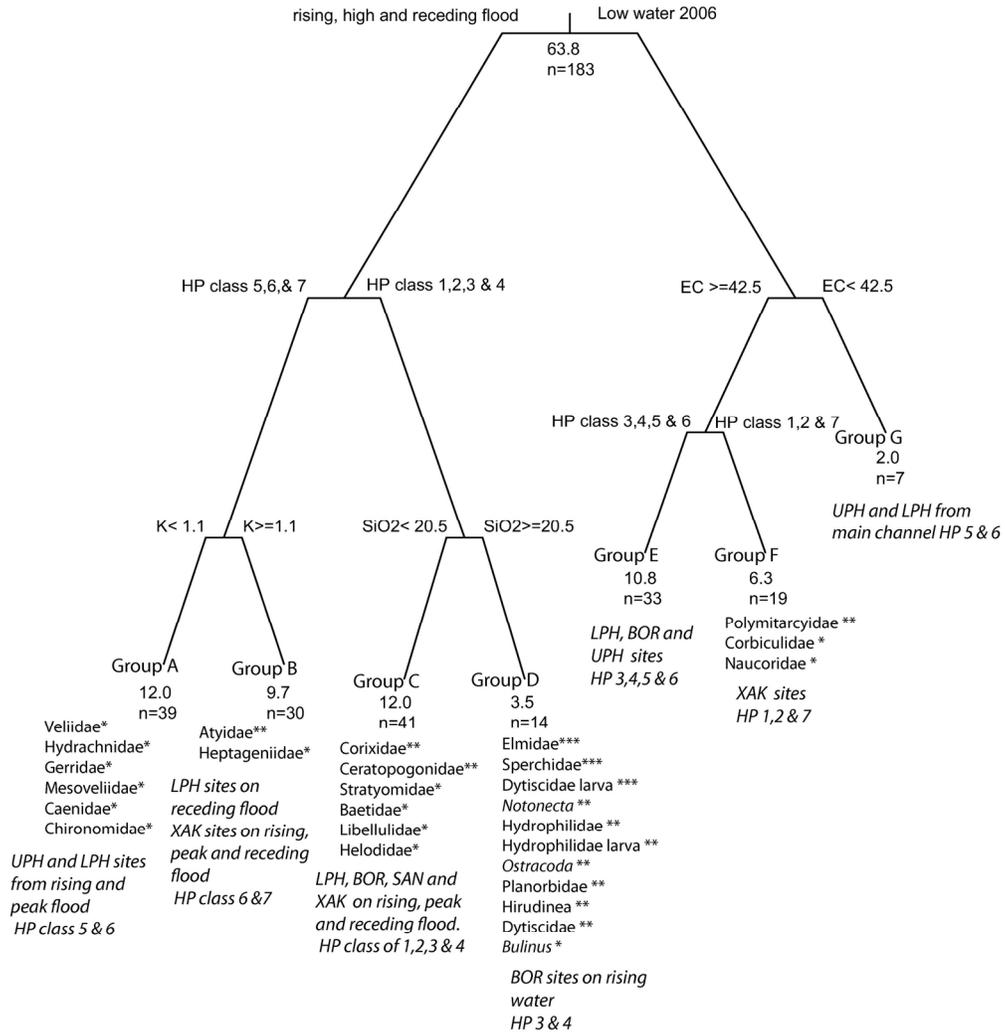


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