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Feral pig exclusion fencing provides limited fish conservation value on tropical floodplains

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Running header: Fish occupying tropical wetlands affected by feral pigs

25 **Abstract**

26 Efforts to protect and restore tropical wetlands impacted by feral pigs (*Sus scrofa*) in northern
27 Australia have more recently included exclusion fences, an abatement response proposing
28 fences improve wetland condition by protecting habitat for fish production and water quality.
29 Here we tested: 1) whether the fish assemblage are similar in wetlands with and without
30 fences; and 2) whether specific environmental processes influence fish composition differently
31 between fenced and unfenced wetlands. Twenty-one floodplain and riverine wetlands in the
32 Archer River catchment (Queensland) were surveyed during post-wet (June-August) and late-
33 dry season (November-December) in 2016, 2017 and 2018, using a fyke soaked overnight
34 (~14-15hrs). A total of 6,353 fish representing twenty-six species from 15 families were
35 captured. There were no multivariate differences in fish assemblages between seasons, years
36 and for fenced and unfenced wetlands (PERMANOVA, Pseudo-F <0.58, $P < 0.68$). Late-dry
37 season fish were considerably smaller compared to post-wet season: a strategy presumably to
38 maximise rapid disposal following rain. At each wetland a calibrated Hydrolab was deployed
39 (between 2-4 days, with 20min logging) in the epilimnion (0.2m), and revealed distinct diel
40 water quality cycling of temperature, dissolved oxygen and pH (conductivity represented
41 freshwater wetlands) which was more obvious in the late-dry season survey, because of
42 extreme summer conditions. Water quality varied among wetlands, in terms of the daily
43 amplitude, and extent of daily photosynthesis recovery, which highlights the need to consider
44 local site conditions rather than applying general assumptions around water quality conditions
45 for these types of wetlands examined here. Though many fish access (fenced and unfenced)
46 wetlands during wet season connection, the seasonal effect of reduced water level conditions
47 seems to be more over-improvised compared to whether fences are installed or not, as all
48 wetlands supported few, juvenile, or no fish species because they had dried completely
49 regardless of whether fences were present or not.

50 **Introduction**

51 Wetlands (palustrine and lacustrine) that are located on floodplains away from riverine
52 channels support rich aquatic plant and fauna communities [1-3]. However, some point after
53 peak flood connection, aquatic organisms occupying these wetlands begin to face a moving
54 land-water margin, until connection is broken, at which point the remaining wetland
55 waterbodies typically support a non-random assortment of species, including fish [4, 5]. The
56 duration, timing and frequency that off channel wetlands maintain lateral pulse connection to
57 primary rivers is an important determining factor in broader contribution to coastal fisheries
58 production [6-9]. In addition to connection, environmental conditions become important
59 including water quality [10], access to shelter to escape predation and available food resources
60 [11, 12]. Efforts by managers to restore wetland ecosystem values is increasing, nevertheless
61 access to data establishing success of these programs are limited, which becomes important
62 when attempting to establish biodiversity returns for the funding investment made by
63 government or private investor organisations [13-15].

64
65 After floodplain wetlands begin receding and progressively disconnect from the main river
66 channel, they become smaller and shallower [16] because of water loss via evaporation,
67 groundwater recharge, or consumption by wildlife [17, 18]. In tropical north Australia,
68 seasonal off channel wetlands are more pronounced owing to high evaporation rates, loss to
69 groundwater [19], and in many situations waters quickly retract away from the banks and
70 riparian shade [16]. At that point, it is thought that they become more prone to reduced water
71 quality conditions - most notably reduced water depth [18], and high water temperatures [10,
72 20]. This increases aquatic fauna exposure risks to acute and chronic thresholds [21, 22]. In
73 the late-dry season, fish confined to isolated wetlands on floodplains therefore have very
74 limited avoidance options [10], unlike other fauna such as the freshwater crab also occupying

75 seasonal tropical rivers in northern Australia, that will employ terrestrial re-location and access
76 burrows when confronted with thermoregulation [23]. Fish must exploit available ephemeral
77 aquatic habitats [24, 25], which can be specific to each wetland depending on orientation and
78 location [26], depth and vegetation cover in the landscape [20], in order to survive until
79 monsoonal rain reconnects overbank river networks again.

80
81 Across northern Australia, feral pigs (*Sus scrofa*) contribute wide scale negative impacts on
82 wetland vegetation assemblages, water quality, biological communities and wider ecological
83 processes [27, 28]. Feral pigs utilise an omnivorous diet supported by foraging or digging
84 plant roots, bulbs and other below ground vegetation material over terrestrial or wetland areas
85 [29]. This feeding strategy has a massive impact on wetland aquatic vegetation [30], which
86 gives rise to soil erosion and benthic sediment re-suspension, reduced water clarity and
87 eutrophication which becomes particularly critical late-dry season. The fact that limited data
88 exists on the impact that feral pigs contribute to wetlands [31-34], places a strain on the ability
89 for land managers to quantify the consequences of pig destruction [35]. Conversely, a lack of
90 baseline data means quantifying success following expensive mitigation efforts is difficult.

91
92 Strategies focused on reducing or removing feral pigs from the landscape have been employed
93 since their introduction to Australia [36], including poison baiting, aerial shooting, and
94 trapping using specially constructed mesh cages [37]. Attempts to exclude feral pigs have also
95 included installing exclusion fencing that border the wetland of interest. While advantages of
96 installing fencing around wetlands has been examined only recently in Australia [32], those
97 authors claim fencing might well be less effective particularly in situations where wetlands
98 would normally dry during the dry season. Fencing is expensive to construct and maintain
99 [37], but at the same time may prevent other non-target terrestrial fauna, such as kangaroos,
100 from accessing wetlands which become particularly imperative late-dry season as regional

101 water points [35]. Other terrestrial species including birds, snakes and lizards, for example, are
102 generally able to access wetlands, though access for freshwater turtles might be hindered [38].

103
104 The aims were twofold: first to determine whether the model of non-randomness of fish stands
105 here in wetlands, and secondly whether specific environmental conditions influence fish
106 composition in wetlands with and without fences. These data are important and necessary
107 given increasing government funding investment underway and planned in northern Australia
108 for restoration of wetlands impacted by feral animals (including pigs) [10].

109

110 **Materials and methods**

111 **Ethics Statement**

112 This study was completed in accordance with the Queensland Animal Care and Protection Act
113 2001, and JCU animal ethics permit number A2178.

114

115 **Description of Study System**

116 The Archer River catchment is located on Cape York Peninsula, north Queensland (Fig 1).

117 The head waters of the river rise in the McIlwraith range on the eastern side Cape York, where
118 it flows and then enters Archer Bay on the western side of the Gulf of Carpentaria; along with
119 the Watson and Ward Rivers. The catchment area is approximately 13,820 km², which
120 includes approximately 4% (510 km²) of wetland habitats

121 (<https://wetlandinfo.des.qld.gov.au/wetlands/facts-maps/basin-archer/>), such as estuarine

122 mangroves, salt flats and saltmarshes, wet heath swamps, floodplain grass sedge, herb and tree
123 *Melaleuca* spp. swamps and riverine habitat. The lower region of the catchment includes part

124 of the Directory of Internationally Important Wetland network (i.e. nationally recognised status

125 for conservation and cultural value) that extends along much of the eastern Gulf of Carpentaria,

126 including the Archer Bay Aggregation, Northeast Karumba Plain Aggregation and Northern
127 Holroyd Plain Aggregation. Two national parks are located in the catchment (KULLA
128 (McIlwraith Range) National Park, and Oyala Thumotang National Park). Land use in the
129 catchment is predominately grazing, with some mining activities planned in the next few years
130 on the northern bank of the river (not within the area of this study).

131
132 Rainfall is tropical monsoonal with a strongly seasonal pattern where between 60% and 90% of
133 total annual rain occurs between November and February. Long-term rainfall records for the
134 catchment revealed highest wet season rainfall occurred in 1989/1999 (2515 mm), while the
135 lowest was 1960/1961 (563.5 mm) [39]. Total antecedent rainfall for the wet season prior
136 (Nov 2014 to Feb 2015) to this survey was 1081 mm, which is below the 10th percentile for
137 historical records. The wet seasons experienced through the years prior to this study (2010 to
138 2015) were among the wettest on record, within the 95th percentile of the long-term data
139 records. The low rainfall experienced during this study may have contributed to a short flood
140 duration, and connection between study wetlands and the main Archer River, when compared
141 to average or above average rainfall years (Fig 2).

142
143 Twenty-one wetlands from the Archer River catchment were sampled for this project. These
144 included both floodplain and riverine wetlands that were not on the main flow channels, but
145 rather were on anabranches and flood channels that connect to the main channels only during
146 high flow conditions. All wetlands have been historically damaged by pigs (and cattle to a
147 lesser extent) for up to 160 years [40, 41], until recently, where a small number were fenced to
148 abate feral pig and/or cattle from accessing wetlands, in accordance with the feral animal
149 research and management agenda (to meet the objectives of traditional owners in the region) of
150 both Kalan enterprises and Aak Puul Ngangtam, and their partner.

151 The characteristics of each wetland are summarised in Table S1. Here, sampling focused on
152 two periods: 1) immediately following the wet season after disconnection between the river
153 and wetlands (hereafter referred to as post wet season); and 2) late-dry season (hereafter late-
154 dry) in 2016, 2017 and 2018. Each sampling campaign was completed over 14 days with six
155 campaigns in total (post-wet and late-dry season in 2016, 2017 and 2018).

156

157 **Field Methods**

158 In each wetland, a calibrated high frequency Hydrolab multi-parameter logger (OTT Hydromet
159 USA) was deployed (0.2m depth) for between 2 and 4 days to record epilimnion (0.2m) water
160 temperature, dissolved oxygen (%), electrical conductivity and pH every 20mins; logging at
161 this frequency provides explicit insight into diel changes in environmental water processes [20,
162 22]. Weather conditions were fine with wetlands surveyed on the falling limb of the
163 hydrograph.

164

165 Fish were collected in wetlands using a fyke net (0.8m opening, double 4m wing panels, 1mm
166 stretch mesh) that was soaked overnight (approximately 14:00 to 09:00). Wetlands
167 substantially impacted by feral pigs; secchi disk depth < 0.1m, no submerged or floating
168 aquatic plants exist, while the fenced wetlands were generally deeper (up to 1.5m), and had
169 submerged aquatic vegetation (Fig. 1). Fish were placed in a tub (~150L) temporarily,
170 identified, measured (standard length, mm) and returned to the wetland alive in accordance
171 with Australian laws (except for a small number that were kept food web studies, not shown
172 here, under Australian law).

173

174 **Data Analysis**

175 There are two main biases in the sampling method here: 1) that the sampling technique
176 potentially capture large numbers of schooling fish along the wetland margins; and 2) the fact

177 that predatory aquatic fauna including fish, snakes(macleays watersnakes (*Pseudoferania*
178 *polylepis*), file snakes (*Acrochordus arafurae*)) and freshwater turtles (*Chelodina oblonga*,
179 *Chelodina canni* and *Emydura s. worrelli*), were periodically trapped in the net for hours
180 means that they could consume fish trapped in nets. To overcome these uncertainties, analyses
181 were based on presence/absence of species. Presence/absence provide robust data when
182 relative abundance are of doubtful validity because they treat species with a diversity of
183 behaviours, trophic functions, and spatial distribute in a more equivalent way than fully
184 quantitative techniques [42].

185
186 Multivariate differences were examined using PERMANOVA (Anderson, 2001), using the
187 Bray-Curtis similarities measure [43] with significance determined from 10,000 permutations
188 of presence/absence transformation. Multivariate dispersion were tested using PERMDISP,
189 however, homogeneity of variance could not be stabilized with transformation, and therefore
190 untransformed data were used. Three factors where included: years (fixed), season (fixed); and
191 fenced/unfenced (random). These factors were determined *a-prior* during study design.

192
193 Spatial patterns in multivariate fish assemblage structure and the importance of explanatory
194 data sets were analysed using a multivariate classification and regression tree (mCARTs) [44]
195 package in R (version 3.4.4). Analysis was conducted using presence/absence transformed fish
196 data for the 10 species that occurred in >20% of wetland sites (to remove rare species from this
197 analysis). Selection of the final tree model was conducted using 10-fold cross validation, with
198 a 1-SE tree; the smallest tree with cross validation error within 1 SE of the tree with the
199 minimum cross validation error [45]. The relative importance of the explanatory variables
200 were assessed to determine those with a high overall contribution to tree node split, with the
201 best overall classifier being given a relative importance of 100%.

202

203 Kolmogorov-Smirnov (K-S) two-sample tests determined differences in the overall shape of
204 fish body size distribution using a Bonferroni correction for multiple comparisons. K-S tests
205 take into account differences between the location, skew, and kurtosis of frequency
206 distributions; but do not identify which of these parameters are driving distributional
207 differences. Therefore, we report the following characteristics of each body size distribution to
208 further describe any differences found: mean, standard deviation (sd), minimum value (min),
209 maximum value (max), the range of values, skewness, and kurtosis.

210

211 **Results**

212 **Hydrology and Wetland Water Quality**

213 Wet season rainfall totals in the Archer River catchment were low during the study period
214 compared to the preceding years (Fig. 2), with rainfall within the 10th percentile for historical
215 recordings held by the Australian Bureau of Meteorology. This means that some caution is
216 necessary with interpretation of these data; namely that floodplain connectivity under higher
217 rainfall years is likely to have a longer duration when compared to lower connection duration
218 under the current rainfall conditions.

219

220 A full summary of water quality data are provided in Supplementary files (S1). In summary,
221 water temperatures during the study period were generally about 26°C (Table 1). Minimum
222 water temperature recordings as low as 18°C, while maximum temperatures occurred in
223 November 2016 survey reached above 40°C for several hours of the day in some instances.
224 The water column exhibited pronounced diel temperature periodicity; one or two hours after
225 sunrise each day. Near-surface water temperatures began to rise at an almost linear rate for a
226 period of 8.0 ± 0.5 hours, generally reaching daily maxima during the middle of the afternoon.
227 The mean daily temperature amplitude was 6.2°C (highest daily amplitude 9.6°C, lowest

228 4.4°C). For the remaining 16 hours of each day, near-surface water temperatures gradually
229 declined reaching minimum conditions shortly after sunset.

230
231 The electrical conductivity (EC) was very low (Table S1) during the post wet season surveys,
232 while the late-dry season conductivity was generally higher in wetlands, a consequence of
233 evapo-concentration. The lowest wetland in the catchment (AR08 located on the coastal
234 floodplain) recorded the highest conductivity, suggesting connection with tidal water from the
235 nearby estuary at some stage.

236
237 There was evidence of cyclical daily DO fluctuations supporting the contention that biological
238 diel periodicity processes were probably not significantly inhibited in all wetlands (Fig. 3). Daily
239 minimum DO concentrations were low enough to suggest there was enough respiratory oxygen
240 consumption to measurably affect water quality, particularly so at the pig impacted wetlands, but
241 also during the late-dry season survey in November 2016. Dissolved oxygen (DO) seemed to
242 reach daily minima conditions, well below the asphyxiation thresholds of sensitive fish species,
243 in the early morning hours during all surveys. In the examples shown, after the morning low
244 DO, conditions generally recovered to approximately 50%, but reaching a high of 100-160% in
245 the late afternoon (before sunset).

246
247 pH is also potentially subject to the same kinds of biogenic fluctuations as DO, due to
248 consumption of carbon dioxide (i.e., carbonic acid) by aquatic plants and algae during the day
249 (through photosynthesis), and net production of carbon dioxide at night. If respiratory oxygen
250 consumption is predominant, DO concentrations are low and pH values are generally
251 moderately acidic to neutral, which was the case for wetlands examined here. All
252 photosynthetically active organisms utilise carbon dioxide as a preferred carbon source. Some
253 species (including most green algae) are unable to photosynthesise if carbon dioxide is

254 unavailable, but there are other species (including most cyanobacteria and submerged
255 macrophytes) which can utilise bicarbonate as an alternative carbon source. Carbon dioxide
256 consumption causes pH to rise to values in the order of 8.6 to 8.7 (but that was not the case
257 here during this survey period).

258

259 **Fish Community**

260 A total of 6,353 fish were captured, representing twenty-six species from 15 families (Table 1).
261 The most common species was the freshwater glassfish (*Ambassis sp.*, 51% total catch),
262 delicate blue-eyes (*Pseudomugil tenellus*, 11%), and northern purple-spot gudgeon (*Morgunda*
263 *morgunda*, 9%). A greater number of fish species were caught in the post wet season survey,
264 with a lower number captured during the late-dry season, including the northern purple-spot
265 gudgeon (*Morgunda mogunda*), chequered rainbow fish (*Melanotaenia s. inornata*), and the
266 empire gudgeon (*Hypselostris compressa*). In addition to fish, we captured a freshwater
267 crayfish (*Cherax sp.*), macleays watersnakes (*Pseudoferania polylepis*) and freshwater turtles
268 (*Chelodina oblonga* and *Emydura s. worrelli*) in most wetlands, notably during post wet
269 season. Overall, there was no significant difference between seasons, fenced/unfenced
270 wetlands and among years (PERMANOVA, Pseudo-F <0.58, $P < 0.68$).

271

272 With a reduced list confined to dominant species, occurrence profiles for groups in the terminal
273 branches of the mCART analysis (Fig. 5) show two initial wetland groups based on a split
274 supported by region, with wetlands in the Coen (upper catchment) region separating from those
275 wetlands in the coastal plains. Following the left branch there is inter-annual variation among
276 wetlands, and a second terminal node based on whether wetlands were fenced in 2016, but not
277 so in 2017 and 2018 data. Following the right branch (APN, coastal plains), the first node
278 separates seasons, and following late-dry season wetlands further separate based on mean
279 dissolved oxygen (~3.0%), and then mean temperature (~28.5°C). The post-wet season branch

280 appears to have more separation among data, with a separation based on mean water
281 temperature (~26.5°C), years, and then finally dissolved oxygen (~4%).
282
283 Mean fish body size distributions differed between the three sample years (with fish for each
284 wetland and survey pooled) (KS, $P < 0.001$, Table S2 – S5), with larger fish measured in 2017
285 (50.5mm) compared to 2016 (38.7mm) and 2018 (31.6mm), despite the assemblages having
286 similar size ranges. When comparing the overall fish size distribution by pooling years, post wet
287 season fish were larger (44.9mm) when compared to fish in the late-dry season (39.7mm) (KS,
288 $P < 0.01$). For some fish species such as the chequered rainbow fish (*Melanotaenia s. inornata*),
289 the post wet season (32.5mm) was similar when compared to late-dry season (38.4mm) (KS, P
290 = 0.06, S3). In contrast, the northern purple-spot gudgeon (*Mogurnda mogurnda*) was larger
291 post-wet season (52.8mm) compared to late-dry season (37.1mm) (KS, $P < 0.01$, Figure 5, S4).

292

293 **Discussion**

294 While installation of fences can protect terrestrial ecosystem services from feral impacts [46],
295 however, in the case here abatement fences appear to offer little over-improvised fish
296 additional value compared to those that are not fenced. Many fish indeed access both fenced
297 and unfenced wetlands during wet season connection, however, the seasonal effects of reduced
298 water level conditions and the loss of fish assemblage as the dry season progresses is a pattern
299 that remained regardless of fencing. To this end, installation of expensive exclusion fences
300 might not offer additional protection to fish species occupying these tropical floodplain
301 wetlands. The same conclusion was reported by [32] where those authors surveyed strongly
302 seasonal wetlands (similar to the wetlands here) elsewhere in northern Australia, and
303 concluded that the seasonal dry down of wetlands ultimately prohibits the wetland contribution
304 to future year successful fish recruitment.

305
306 The low species richness in wetlands relative to the main Archer River channel might be a
307 consequence of the frequency and duration of connection between wetlands and the main
308 Archer river channel. The wet season rainfall immediately prior, and during this survey, was
309 within the 10th percentile for historical records. In research elsewhere, a longer connection
310 duration was shown to result in more fish present post wet season, and conceivably more
311 species present late-dry season [6, 47]. Examples exist where longer connection between main
312 river channels and wetlands contributes positively to fish growth rates and higher abundance
313 and diversity of fish [24, 26, 48]. It is also possible that the field methods used here confound
314 our ability to determine the full species composition in wetlands – this could be overcome by
315 using additional survey techniques, including multi-panel gill nets, traps or electrofishing
316 (though we attempted to electrofish these wetlands however, conductivity was too low to
317 effectively use that method).

318
319 An obvious characteristic of the fish data were larger, presumably adult, individuals following
320 the disconnection of wetlands after the wet season compared to small individuals present in the
321 late-dry season. On this basis, it is possible that the wetlands serve as important refugia for
322 successful recruitment of freshwater fish, that adult fish remaining in the wetlands after
323 disconnection are able to complete important life cycle stages. The fact that we did not catch
324 large fish in the late-dry season suggests that adult fish might be lost as the dry season
325 progress, consumed either by larger predators such as estuarine crocodiles (*Crocodylus*
326 *porosus*), or birds feeding in the shallow waters. Wetlands are also popular feeding and
327 roosting locations for birds [2, 49]; we observed a large number of birds at most wetlands in
328 the late-dry season. The value of wetlands to wader birds is limited by the condition of
329 wetlands [50, 51], but wetlands provide an important nutrient subsidy more broadly on
330 seasonal floodplains [52, 53]. Hurd et al. (2017) postulates that differences in fish

331 communities among off channel waters could be more influenced by the presence of
332 piscivorous predators which reduce or eliminate prey species, or even via a function of
333 competitive exclusion may occur within fish guilds as resources diminish in the late-dry
334 season. Examining this point could be achieved by investigating the species niche width [54,
335 55] in drying waters by constructing food webs in individual waters to determine species
336 ranges and changes with fencing treatment and comparing post wet season and late-dry season
337 conditions.

338
339 In the late-dry season for the few fish species present, juveniles dominated the catch regardless
340 whether wetlands were fenced. Having small recruits in the late dry period might be an
341 important strategy in maximising, quick, dispersal after connectivity with the onset of the wet
342 season [56]. Moreover, late season conditions with no flow and warm conditions might favour
343 larval development [57, 58]. *Melanotaeniid* rainbowfish, for example, have a flexible
344 reproductive behaviour that is well adapt to deal with the vagaries of temporal variation in
345 habitat conditions [59]. The same is true for both *Eleotrid gudgeon* species found here, with
346 smaller recruits presumably ready for wide-scape distribution with the onset of seasonal flow.
347 Pusey et al. (2018) provides a case that the reproduction success of freshwater fish in northern
348 Australia could in fact hinge on antecedent flow patterns across the landscape, and that this
349 flexibility ensures population level success [60]. This production strategy might be particularly
350 pertinent given the below average summer rainfall totals witnessed during this survey,
351 particularly when compared to previous years.

352
353 As the dry season takes hold, water quality conditions progressively deteriorate owing mostly
354 to increasing impact from rooting pigs accessing wetland vegetation. Generally, fenced
355 wetlands change little in terms of water conditions (Figure 6). However, it is the late-dry
356 season when water conditions are poorest and therefore most critical to fish. Unfenced

357 wetlands tended to be shallower, highly turbid, and most notably experience water
358 temperatures that exceed acute thermal thresholds for fish [31]. The solubility of dissolved
359 oxygen in water is strongly affected by temperature (i.e. high temperature reduces dissolved
360 oxygen solubility [61]. Data on hypoxia tolerances of local freshwater fish species in northern
361 Queensland is available [62], and while tolerances vary between species and life stages, there
362 were obvious periods in wetlands when these threshold limits are exceeded. During the critical
363 periods, fish must regulate breathing either via increasing ventilation rates [63], or by rising to
364 the surface to utilise aquatic surface respiration and/or air gulping (e.g. tarpon, *Megalops*
365 *cyprinoides*). In any case, the capacity for fish to do that safely depends on the timing of the
366 oxygen sag and antecedent conditions, though notably it appears that most of the hypoxia-
367 induced fish kills is actually due to exposure (e.g., thermal stress and sunburn) resulting from
368 the animals' need to remain at the surface during the heat of the day in order to access available
369 oxygen for respiration. Increasing these risks to fish can have important chronic effects
370 including reducing physical fitness of fish to successfully contribute to future populations [64,
371 65].

372 **Wetlands - A. M. G.**

769 The cultural and ecological value of coastal wetlands means that management intervention is
770 increasingly necessary to ensure they remain productive and viable habitat (Creighton *et al.*,
771 2015). These data support a model that damage to wetlands from pig activities not only
772 contributes to reduced aquatic habitat, through loss of aquatic vegetation communities, but also
773 probably has secondary impacts including water temperature and asphyxiation risks for many
774 hours each day, that are higher than when compared to fenced wetlands (Figure 6). However,
775 fish occupying fenced and unfenced wetlands here were similar, particularly in the late-dry
776 season where those remaining few species were juveniles ready for wet season re-distribution.
777 On this basis, installing fences to both floodplain and riverine wetlands that were not on the
778 main flow channels, but rather were on anabranches and flood channels that connect to the

779 main channels only during high flow conditions, seems to offer little additional habitat value
780 for fish. Where wetlands are largely ephemeral and will dry anyway, or where wetlands remain
781 until the next seasons rain connection; species abundance and/or diversity is not improved by
782 restricting feral pig access. Further research is necessary to examine climate change resilience
783 on permanent wetlands (and managed wetlands) particularly whether they provide a similar
784 level of refugia [66].

785

786 **Acknowledgements**

787 This project builds on a long-term feral animal management and monitoring program
788 developed by Kalan enterprises and Aak Puul Ngangtam (APN) and their partners. Kalan and
789 APN have developed their feral animal research and management agenda to meet the
790 objectives of traditional owners in the region and have invited science organisations (CSIRO,
791 James Cook University and the Department of Science and Environment) to contribute to the
792 outcomes. APN and Kalan have conducted systematic feral pig control and monitoring in the
793 Archer River basin for the past 6 years. We thank the reviewers who improved this manuscript
794 considerably.

795

796 **Author Contributions**

797 NW conceived and designed the study, NW performed the data analysis. NW and JS
798 completed fieldwork and prepared the manuscript.

799

800 **References**

- 801 1. Ambrose RF, Meffert DJ. Fish-assemblage dynamics in Malibu lagoon, a small, hydrologically
802 altered estuary in southern California. *Wetlands*. 1999;19(2):327-40.
803 2. Brandolin PG, Blendinger PG. Effect of habitat and landscape structure on waterbird
804 abundance in wetlands of central Argentina. *Wetlands ecology and management*. 2016;24(1):93-105.

- 805 3. Jiang T-t, Pan J-f, Pu X-M, Wang B, Pan J-J. Current status of coastal wetlands in China:
806 degradation, restoration, and future management. *Estuarine, Coastal and Shelf Science*. 2015;164:265-
807 75.
- 808 4. Arrington DA, Winemiller KO. Habitat affinity, the seasonal flood pulse, and community
809 assembly in the littoral zone of a Neotropical floodplain river. *Journal of the North American*
810 *Benthological Society*. 2006;25(1):126-41.
- 811 5. Pander J, Mueller M, Geist J. Habitat diversity and connectivity govern the conservation value
812 of restored aquatic floodplain habitats. *Biological Conservation*. 2018;217:1-10.
- 813 6. Hurd LE, Sousa RG, Siqueira-Souza FK, Cooper GJ, Kahn JR, Freitas CE. Amazon floodplain
814 fish communities: Habitat connectivity and conservation in a rapidly deteriorating environment.
815 *Biological Conservation*. 2016;195:118-27.
- 816 7. Bennett MG, Kozak JP. Spatial and temporal patterns in fish community structure and
817 abundance in the largest US river swamp, the Atchafalaya River floodplain, Louisiana. *Ecology of*
818 *freshwater fish*. 2016;25(4):577-89.
- 819 8. Galib SM, Lucas MC, Chaki N, Fahad FH, Mohsin A. Is current floodplain management a
820 cause for concern for fish and bird conservation in Bangladesh's largest wetland? *Aquatic Conservation:*
821 *Marine and Freshwater Ecosystems*. 2018.
- 822 9. Górski K, De Leeuw J, Winter H, Khoruzhaya V, Boldyrev V, Vekhov D, et al. The importance
823 of flooded terrestrial habitats for larval fish in a semi-natural large floodplain (Volga, Russian
824 Federation). *Inland Waters*. 2016;6(1):105-10.
- 825 10. Waltham N, Schaffer J. Thermal and asphyxia exposure risk to freshwater fish in
826 feral-pig-damaged tropical wetlands. *Journal of fish biology*. 2018.
- 827 11. Blanchette ML, Davis AM, Jardine TD, Pearson RG. Omnivory and opportunism characterize
828 food webs in a large dry-tropics river system. *Freshwater Science*. 2014;33(1):142-58.
- 829 12. Jardine TD, Pettit NE, Warfe DM, Pusey BJ, Ward DP, Douglas MM, et al. Consumer-resource
830 coupling in wet-dry tropical rivers. *J Anim Ecol*. 2012;81(2):310-22. Epub 2011/11/23. doi:
831 10.1111/j.1365-2656.2011.01925.x. PubMed PMID: 22103689.
- 832 13. Waltham N, Fixler S. Aerial Herbicide Spray to Control Invasive Water Hyacinth (*Eichhornia*
833 *crassipes*): Water Quality Concerns Fronting Fish Occupying a Tropical Floodplain Wetland. *Tropical*
834 *Conservation Science*. 2017;10:1940082917741592.
- 835 14. Weinstein MP, Litvin SY. Macro-Restoration of Tidal Wetlands: A Whole Estuary Approach.
836 *Ecological Restoration*. 2016;34(1):27-38.
- 837 15. Zedler JB. What's New in Adaptive Management and Restoration of Coasts and Estuaries?
838 *Estuaries and Coasts*. 2016:1-21.
- 839 16. Pusey BJ, Arthington AH. Importance of the riparian zone to the conservation and management
840 of freshwater fish: a review. *Marine and Freshwater Research*. 2003;54:1-16.
- 841 17. McJannet D, Marvanek S, Kinsey-Henderson A, Petheram C, Wallace J. Persistence of in-
842 stream waterholes in ephemeral rivers of tropical northern Australia and potential impacts of climate
843 change. *Marine and Freshwater Research*. 2014.
- 844 18. Pettit N, Jardine T, Hamilton S, Sinnamon V, Valdez D, Davies P, et al. Seasonal changes in
845 water quality and macrophytes and the impact of cattle on tropical floodplain waterholes. *Marine and*
846 *Freshwater Research*. 2012;63(9):788-800.
- 847 19. Petheram C, McMahon TA, Peel MC. Flow characteristics of rivers in northern Australia:
848 implications for development. *Journal of Hydrology*. 2008;357(1):93-111.
- 849 20. Wallace J, Waltham N, Burrows D. A comparison of temperature regimes in dry-season
850 waterholes in the Flinders and Gilbert catchments in northern Australia. *Marine and Freshwater*
851 *Research*. 2017;68(4):650-67.
- 852 21. Burrows D, Butler B. Primary studies of temperature regimes and temperature tolerance of
853 aquatic fauna in freshwater habitats of northern Australia. Australian Centre of Tropical Freshwater
854 Research (12/01): James Cook University, Townsville, 2012 Contract No.: 12/01.
- 855 22. Wallace J, Waltham NJ, Burrows DW, McJannet D. The temperature regimes of dry-season
856 waterholes in tropical northern Australia: potential effects on fish refugia. *Freshwater Science*.
857 2015;34(2):663-78.
- 858 23. Waltham NJ. Acute thermal effects in an inland freshwater crab *Austrothelphusa transversa*
859 (von Martens, 1868) occupying seasonal, tropical rivers. *Journal of Crustacean Biology*. 2018.

- 860 24. Love S, Phelps Q, Tripp S, Herzog D. The importance of shallow-low velocity habitats to
861 juvenile fish in the middle Mississippi River. *River Research and Applications*. 2017;33(3):321-7.
- 862 25. Phelps QE, Tripp SJ, Herzog DP, Garvey JE. Temporary connectivity: the relative benefits of
863 large river floodplain inundation in the lower Mississippi River. *Restoration Ecology*. 2015;23(1):53-6.
- 864 26. Schomaker C, Wolter C. The contribution of long-term isolated water bodies to floodplain fish
865 diversity. *Freshwater Biology*. 2011;56(8):1469-80.
- 866 27. Baber DW, Coblenz BE. Density, home range, habitat use, and reproduction in feral pigs on
867 Santa Catalina Island. *Journal of Mammalogy*. 1986;67(3):512-25.
- 868 28. Krull CR, Choquenot D, Burns BR, Stanley MC. Feral pigs in a temperate rainforest
869 ecosystem: disturbance and ecological impacts. *Biological Invasions*. 2013;15(10):2193-204.
- 870 29. Ballari SA, Barrios-Garcia MN. A review of wild boar *Sus scrofa* diet and factors affecting
871 food selection in native and introduced ranges. *Mammal Review*. 2014;44(2):124-34.
- 872 30. Doupe RG, Mitchell J, Knott MJ, Davis AM, Lymbery AJ. Efficacy of exclusion fencing to
873 protect ephemeral floodplain lagoon habitats from feral pigs (*Sus scrofa*). *Wetlands Ecology and*
874 *Management*. 2010;18(1):69-78.
- 875 31. Waltham NJ, Schaffer JR. Thermal and asphyxia exposure risk to freshwater fish in
876 feral-pig-damaged tropical wetlands. *Journal of Fish Biology*. 2018;93(4):723-8.
- 877 32. Doupe RG, Mitchell J, Knott MJ, Davis AM, Lymbery AJ. Efficacy of exclusion fencing to
878 protect ephemeral floodplain lagoon habitats from feral pigs (*Sus scrofa*). *Wetlands Ecology*
879 *Management*. 2010;18:69-78.
- 880 33. Mitchell J, Mayer R. Diggings by feral pigs within the Wet Tropics World Heritage Area of
881 north Queensland. *Wildlife Research*. 1997;24(5):591-601.
- 882 34. Steward AL, Negus P, Marshall JC, Clifford SE, Dent C. Assessing the ecological health of
883 rivers when they are dry. *Ecological Indicators*. 2018;85:537-47.
- 884 35. Australia Co. Threat abatement plan for predation, habitat degradation, competition and disease
885 transmission by feral pigs (*Sus scrofa*) (2017) — Background Document. Canberra: Department of
886 Environment and Energy, 2017.
- 887 36. Fordham D, Georges A, Corey B, Brook BW. Feral pig predation threatens the indigenous
888 harvest and local persistence of snake-necked turtles in northern Australia. *Biological Conservation*.
889 2006;133(3):379-88.
- 890 37. Ross B, Waltham NJ, Schaffer J, Jaffer T, Whyte S, Perry J, et al. Improving biodiversity
891 outcomes and carbon reduction through feral pig abatement. Cairns: Balkanu Cape York Development
892 Corporation Ltd Pty, 2017.
- 893 38. Waltham N, Schaffer J. Continuing aquatic assessment of wetlands with and without feral pig
894 and cattle fence exclusion, Archer River catchment. 2017.
- 895 39. Waltham N, Schaffer J. Continuing aquatic assessment of wetlands with and without feral pig
896 and cattle fence exclusion, Archer River catchment. Townsville Australia: TropWATER James Cook
897 University, 2017 17/04.
- 898 40. Gongora J, Fleming P, Spencer PB, Mason R, Garkavenko O, Meyer J-N, et al. Phylogenetic
899 relationships of Australian and New Zealand feral pigs assessed by mitochondrial control region
900 sequence and nuclear GPIP genotype. *Molecular Phylogenetics and Evolution*. 2004;33(2):339-48.
- 901 41. Lopez J, Hurwood D, Dryden B, Fuller S. Feral pig populations are structured at fine spatial
902 scales in tropical Queensland, Australia. *PloS one*. 2014;9(3):e91657.
- 903 42. Quinn GP, Keough MJ. *Experimental design and data analysis for biologists*: Cambridge
904 University Press; 2002.
- 905 43. Clarke KR. Non-parametric multivariate analyses of changes in community structure.
906 *Australian Journal of Ecology*. 1993;18:117-43.
- 907 44. De'Ath G. Multivariate regression trees: a new technique for modeling species–environment
908 relationships. *Ecology*. 2002;83(4):1105-17.
- 909 45. Sheaves M, Johnston R. Ecological drivers of spatial variability among fish fauna of 21 tropical
910 Australian estuaries. *Marine Ecology Progress Series*. 2009;385:245-60.
- 911 46. Bariyanga JD, Wronski T, Plath M, Apio A. Effectiveness of electro-fencing for restricting the
912 ranging behaviour of wildlife: a case study in the degazetted parts of Akagera National Park. *African*
913 *zoology*. 2016;51(4):183-91.

- 914 47. Arthington AH, Godfrey PC, Pearson RG, Karim F, Wallace J. Biodiversity values of remnant
915 freshwater floodplain lagoons in agricultural catchments: evidence for fish of the Wet Tropics
916 bioregion, northern Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems*.
917 2015;25(3):336-52.
- 918 48. Barko VA, Herzog DP, O'Connell MT. Response of fishes to floodplain connectivity during
919 and following a 500-year flood event in the unimpounded upper Mississippi River. *Wetlands*.
920 2006;26(1):244-57.
- 921 49. Chacin DH, Giery ST, Yeager LA, Layman CA, Langerhans RB. Does hydrological
922 fragmentation affect coastal bird communities? A study from Abaco Island, The Bahamas. *Wetlands*
923 *ecology and management*. 2015;23(3):551-7.
- 924 50. Robertson EP, Fletcher RJ, Austin JD. The Causes of Dispersal and the Cost of Carryover
925 Effects for an Endangered Bird in a Dynamic Wetland Landscape. *Journal of Animal Ecology*. 2017.
- 926 51. Żmihorski M, Pärt T, Gustafson T, Berg Å. Effects of water level and grassland management
927 on alpha and beta diversity of birds in restored wetlands. *Journal of applied ecology*. 2016;53(2):587-
928 95.
- 929 52. Buelow CA, Baker R, Reside AE, Sheaves M. Nutrient subsidy indicators predict the presence
930 of an avian mobile-link species. *Ecological Indicators*. 2018;89:507-15.
- 931 53. Ma Z, Cai Y, Li B, Chen J. Managing wetland habitats for waterbirds: an international
932 perspective. *Wetlands*. 2010;30(1):15-27.
- 933 54. Swanson HK, Lysy M, Power M, Stasko AD, Johnson JD, Reist JD. A new probabilistic
934 method for quantifying n-dimensional ecological niches and niche overlap. *Ecology*. 2015;96(2):318-
935 24.
- 936 55. Jackson AL, Inger R, Parnell AC, Bearhop S. Comparing isotopic niche widths among and
937 within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*.
938 2011;80(3):595-602.
- 939 56. Pusey BJ, Kennard MJ, Douglas M, Allsop Q. Fish assemblage dynamics in an intermittent
940 river of the northern Australian wet-dry tropics. *Ecology of Freshwater Fish*. 2018;27(1):78-88.
- 941 57. King A, Humphries P, Lake P. Fish recruitment on floodplains: the roles of patterns of flooding
942 and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences*. 2003;60(7):773-86.
- 943 58. Godfrey PC, Arthington AH, Pearson RG, Karim F, Wallace J. Fish larvae and recruitment
944 patterns in floodplain lagoons of the Australian Wet Tropics. *Marine and Freshwater Research*. 2016:-.
945 doi: <https://doi.org/10.1071/MF15421>.
- 946 59. Pusey BJ, Bird JR, Close AH, Arthington AH. Reproduction in three species of rainbowfish
947 (*Melanotaeniidae*) in rainforest streams of north-eastern Queensland. *Ecology of Freshwater Fish*.
948 2001;10:75-87.
- 949 60. Stewart-Koster B, Olden J, Kennard M, Pusey B, Boone E, Douglas M, et al. Fish response to
950 the temporal hierarchy of the natural flow regime in the Daly River, northern Australia. *Journal of Fish*
951 *Biology*. 2011;79(6):1525-44.
- 952 61. Diaz RJ, Breitburg DL. The hypoxic environment. *Fish physiology*. 2009;27:1-23.
- 953 62. Butler B, Burrows DW. Dissolved oxygen guidelines for freshwater habitats of northern
954 Australia. . James Cook University, Townsville: Australian Centre for Tropical Freshwater Research
955 (07/31), 2007 Contract No.: 07/31.
- 956 63. Collins GM, Clark TD, Rummer JL, Carton AG. Hypoxia tolerance is conserved across
957 genetically distinct sub-populations of an iconic, tropical Australian teleost (*Lates calcarifer*).
958 *Conservation physiology*. 2013;1(1):cot029.
- 959 64. Flint N, Pearson RG, Crossland MR. Reproduction and embryo viability of a range-limited
960 tropical freshwater fish exposed to fluctuating hypoxia. *Marine and Freshwater Research*.
961 2018;69(2):267-76.
- 962 65. Gilmore KL, Doubleday ZA, Gillanders BM. Testing hypoxia: physiological effects of long-
963 term exposure in two freshwater fishes. *Oecologia*. 2018;186(1):37-47.
- 964 66. James CS, Reside AE, VanDerWal J, Pearson RG, Burrows D, Capon SJ, et al. Sink or swim?
965 Potential for high faunal turnover in Australian rivers under climate change. *Journal of Biogeography*.
966 2017.
- 967 67. Pusey BJ, Burrows DW, Kennard MJ, Perna CN, Unmack PJ, Allsop Q, et al. Freshwater fishes
968 of northern Australia. *Zootaxa*. 2017;4253(1):1-104.

1 List of Figures

2 Fig 1. Location of wetlands in this study: a) location of the Archer River catchment in northern
3 Queensland, Australia and b) wetland sites on the coastal floodplain and mid catchment where
4 feral pig fencing has been completed around wetlands preventing access (yellow circles). The
5 three wetland typologies (C – pig impacted wetlands that are shallow (typically <0.5m deep),
6 without submerged aquatic vegetation, turbid and eutrophic; D – fenced wetland preventing pig
7 access that are deeper (typically <2m deep), clear with submerged aquatic vegetation present)
8 exist across the catchment, and E – permanent wetlands that are deeper (typically <2m deep),
9 steep sides limiting pig access, clear with submerged aquatic vegetation present. Archer River
10 gauge station (red circle).

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11
12 Fig 2. Daily discharge at the Archer River roadhouse gauge (Figure 1) before and during
13 (dashed insert box) this study. Sampling occasions (arrows) are indicated. Data provided by
14 the Queensland Government.

15
16 Fig 3. Examples of the diel dissolved oxygen, pH, water temperature and conductivity cycling
17 in Archer River wetlands. These examples are from KA06 during post-wet season (a), and
18 late-dry season (b) in 2016, and AR01 during post wet season (c) and late-dry season (d) in
19 2016.

20
21 Fig 4. Multivariate regression tree showing the major divisions in the database on assemblage
22 composition. Each of the splits are labelled with the contributing variable, and the division
23 threshold (in the case of electronic conductivity; EC, and dissolved oxygen; DO). The length
24 of the descending branches is proportional to the divergence between groups. Bar plots
25 represent the fish assemblage composition at the corresponding colour code node sharing the

26 same attributes. Values in the bar plots represent the relative frequencies of occurrence of each
27 taxon within a same node.

28

29 Fig 5. Pooled fish length (standard length, mm) frequency comparison of (a) 2016, (b) 2017
30 and (c) 2018. Comparison for *Mogurnda mogurnda* (d) post wet season; and (e) late-dry
31 season (years combined).

32

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33 Fig 6. Conceptual diagram of wetland ecosystem conditions during (a) wet season, and (b)

34 late-dry season. During the wet season, the lateral connection between the Archer River
35 channel and wetlands occurs, during which fish can access wetlands and water quality is
36 generally best because feral pig impact is minimal regardless of fencing. The dry season
37 results in water retracting from the land margins, allowing pigs to access unfenced wetlands.
38 At this stage, water quality conditions are poor in unfenced wetlands with high
39 turbidity/nutrients and temperature, and dissolved oxygen is generally critical for fish. Fenced
40 wetlands become shallower too, through temperature and dissolved oxygen cycling reduced,
41 turbidity is low, while nutrients can be also high. Regardless of fencing, fish community
42 reduced to a few resilient species dominated by juveniles ready for rapid dispersal when wet
43 seasons commences again.

44



D) unfenced wetland



E) fenced wetland

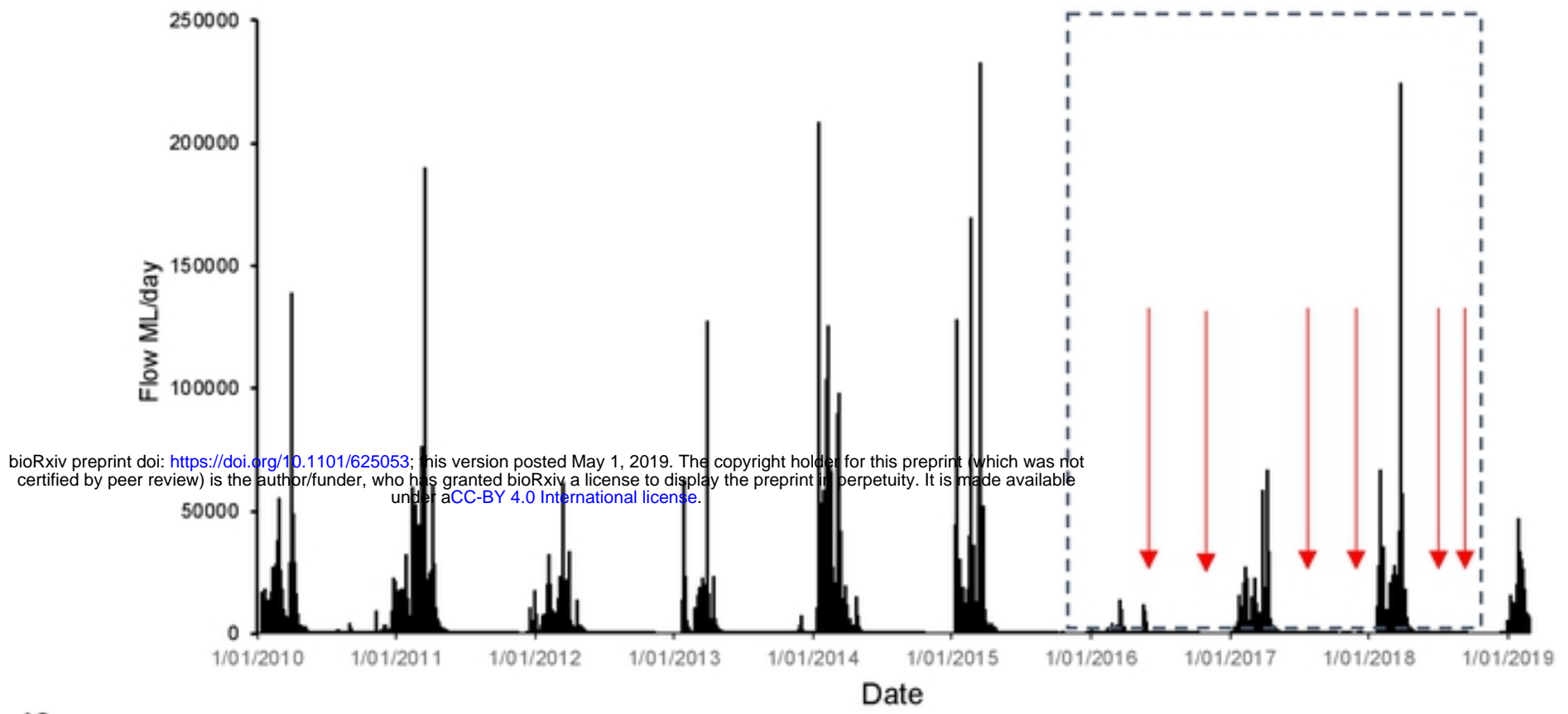


F) persistent wetland



45

46 Fig 1.



48

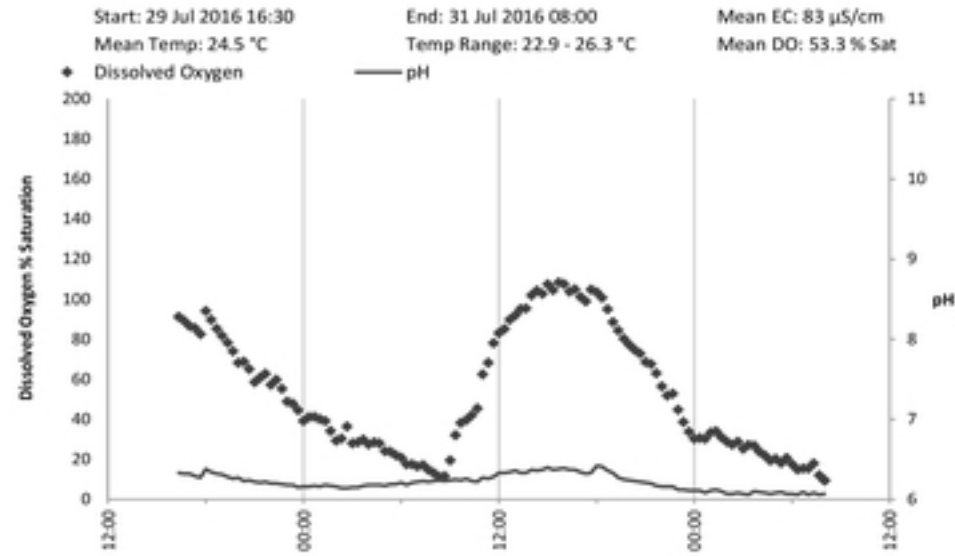
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50 Fig 2

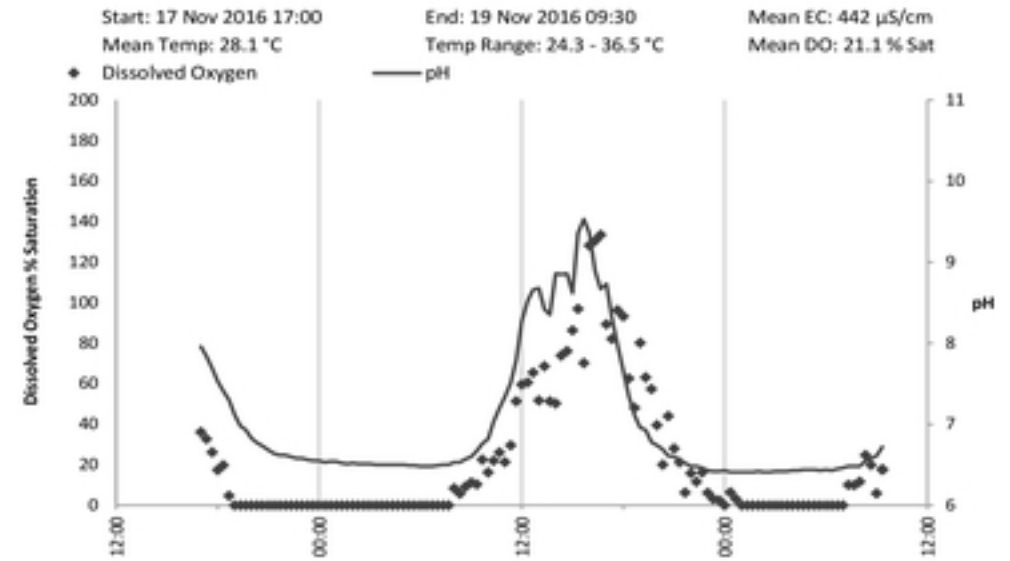
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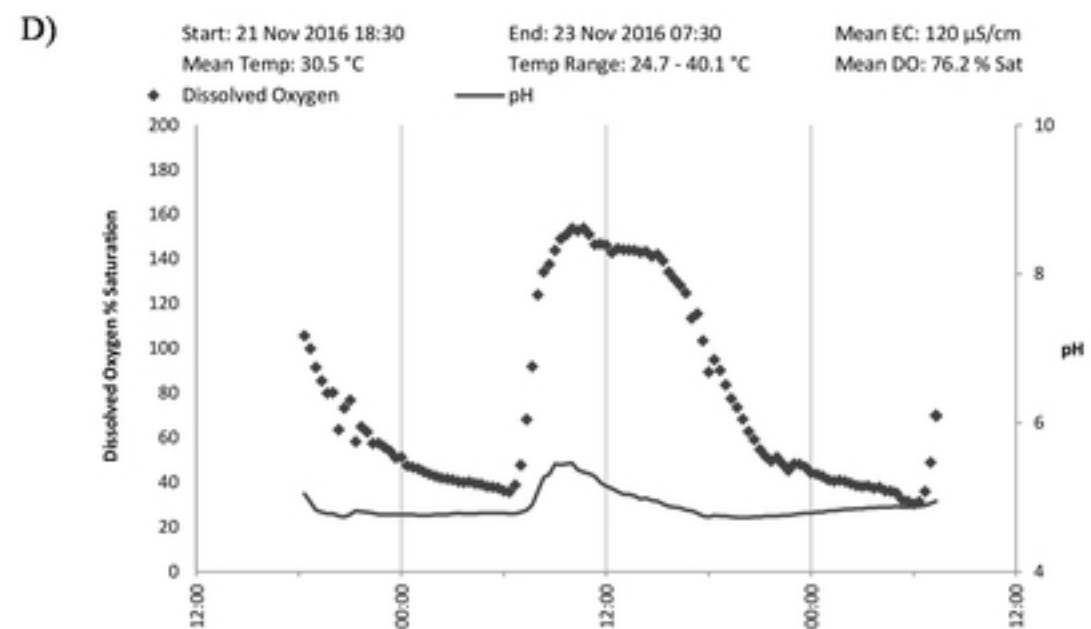
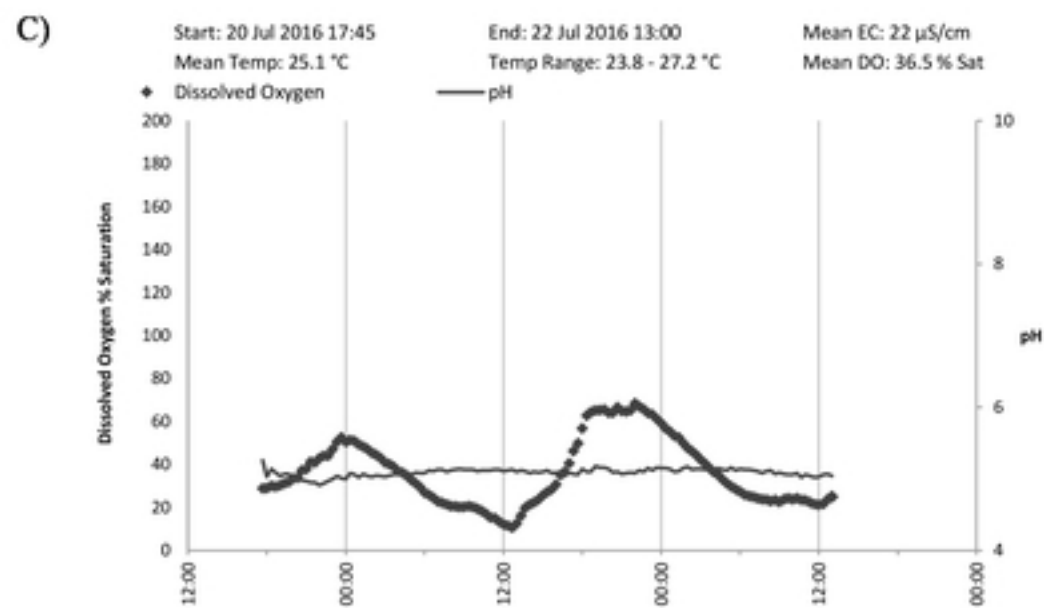
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A)

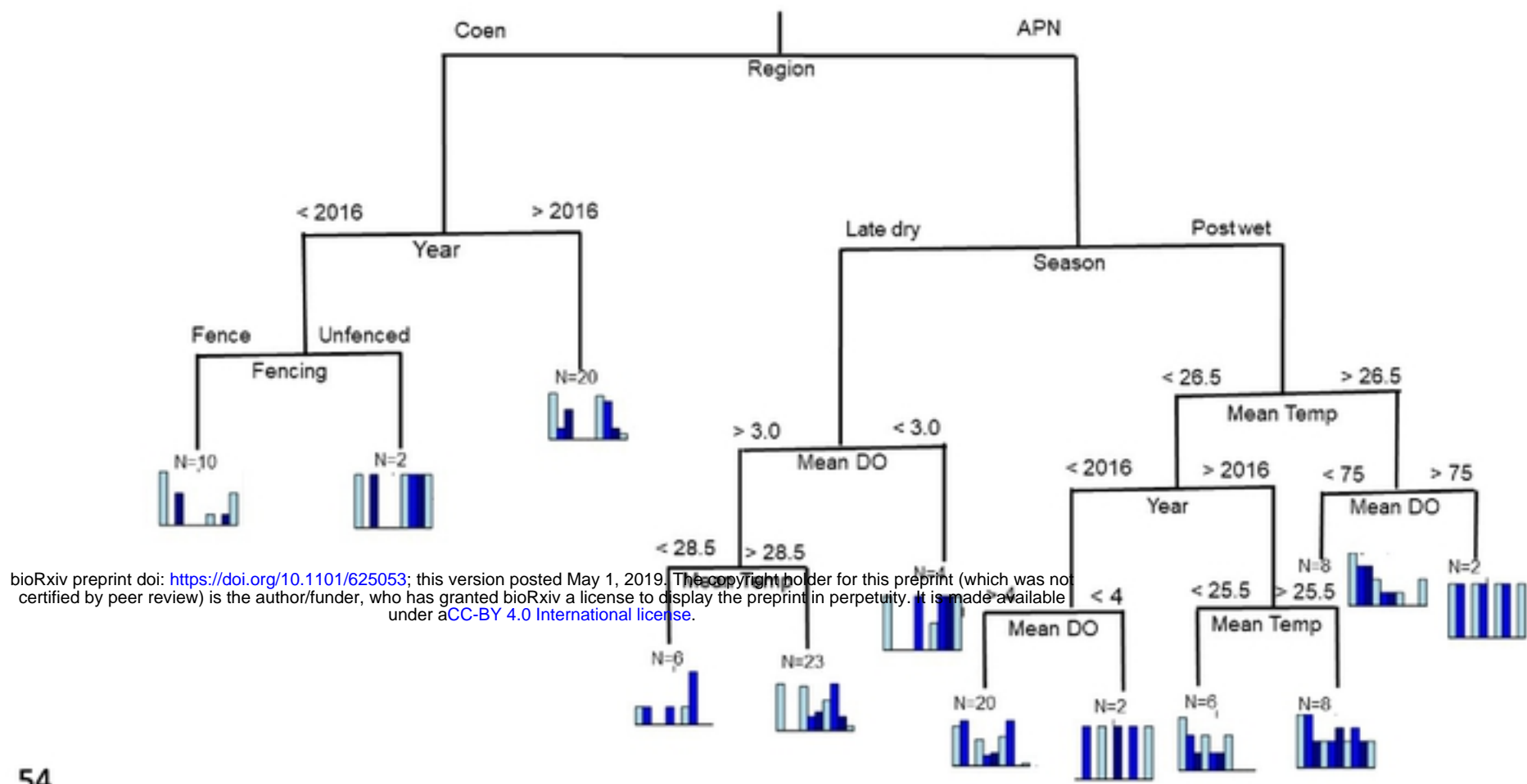


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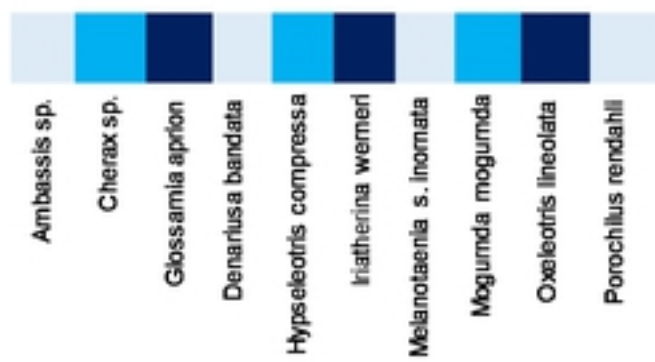




53 Fig 3.



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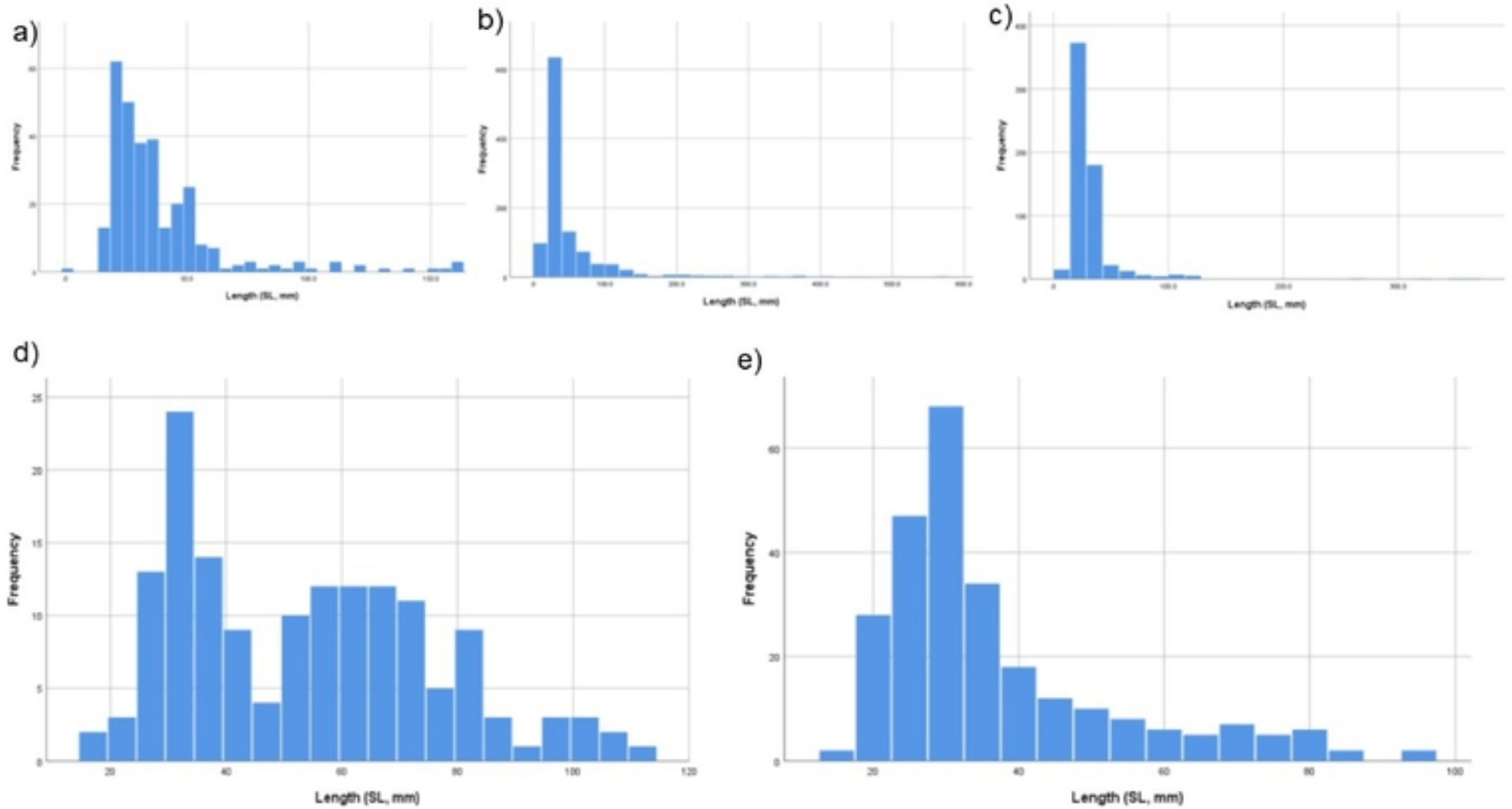
57 Fig 4.

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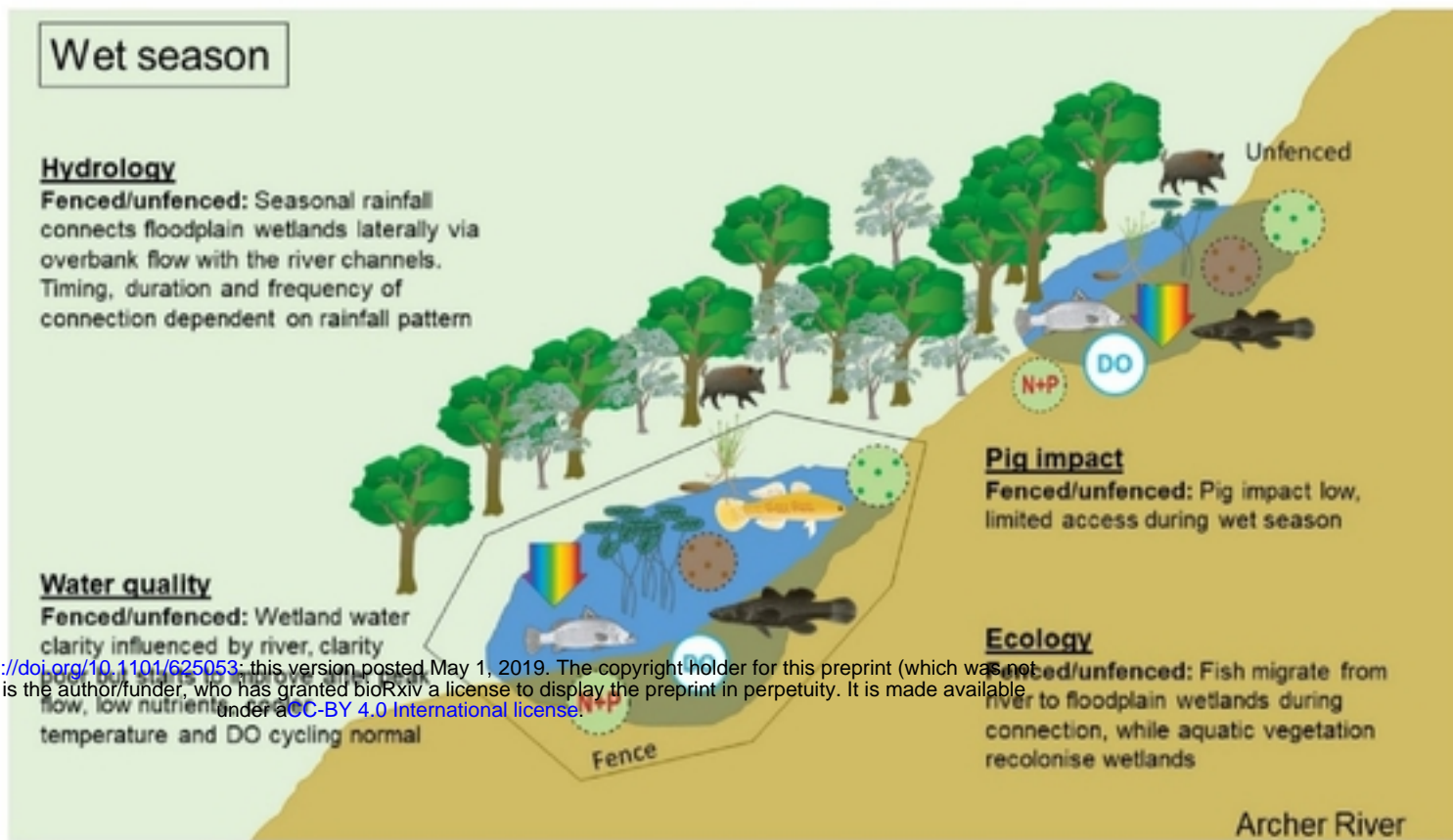


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64 Fig 5.

A)



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B)

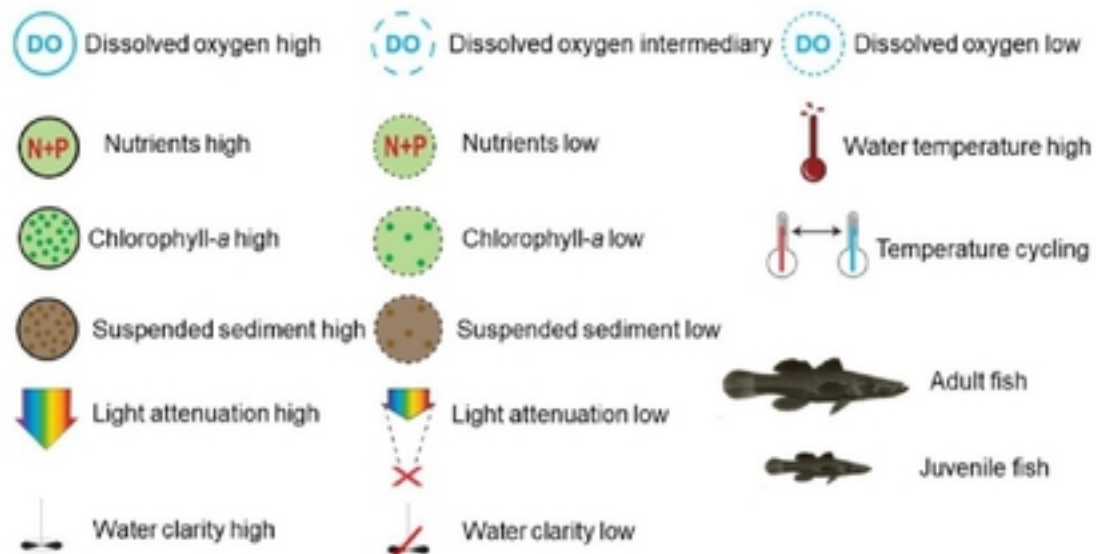
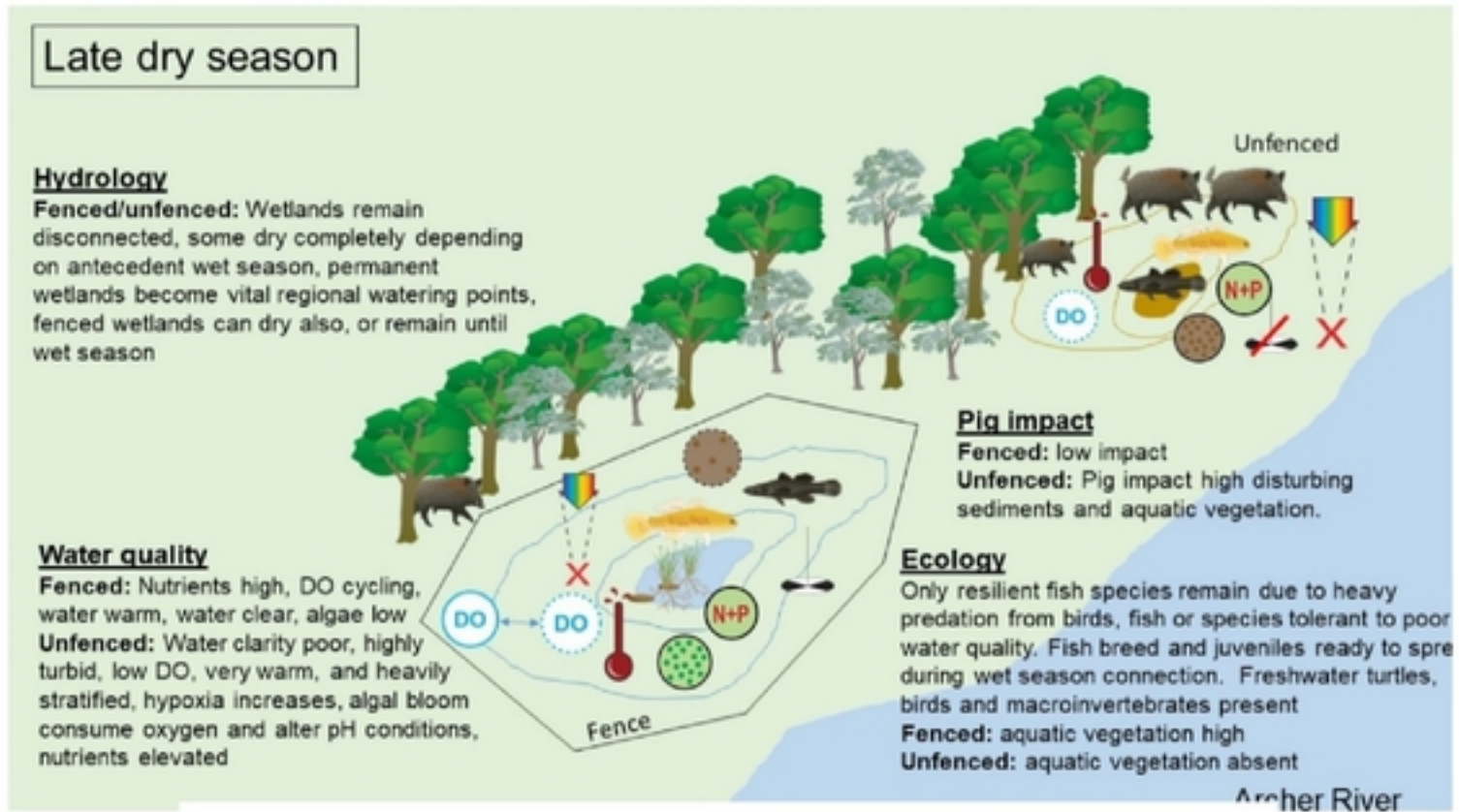


Fig. 6.