Community Structure and Phenology of the Intermittent Treed Swamps of the Paroo, Semi-Arid Inland NSW, Australia.

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Research Article

Keywords: Branchiopod crustaceans, insects, diversity, hydroperiod, habitat heterogeneity.

DOI: https://doi.org/10.21203/rs.3.rs-441295/v1

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Abstract

The middle Paroo lowlands in semi-arid western New South Wales support numerous intermittent wetlands of various types. Differences between them are promoted by three ecological drivers: salinity, turbidity and hydroperiod. Community structure and phenology of the two most common types, saline lakes and claypans, and also creek pools are known, but similar ecologies are lacking for the third most common wetland, the treed swamps. These are of six subtypes distinguished by dominant tree species, geomorphology and hydroperiod, all with similar community structure and phenology, but with differing diversities. Summed diversity is not as high as in local creek pools, the shorter hydroperiods and simpler geomorphology of the treed swamps being restrictive so that there is almost no replacement of species during the early dominance of branchiopods and later of insects. Such treed swamps are uncommon in the semi-arid zone, but much more speciose treed swamps are known under similar and seasonally dry Mediterranean climes of the Western Australian Wheatbelt where hydroperiods more stable.

Introduction

Of all the intermittent wetlands of the world, most is known on those of Mediterranean lands (Boix et al., 2016) including of the two Mediterranean climate zones in Australia: southwest Western Australia and southeast South Australia- western Victoria (e.g. Bayly and Williams 1966, Davis et.al. 1993, Horwitz et al. 2009 and Pinder et al. 2004). The major environmental control in these is seasonal drying, which is shared with the dryland wetlands of the semiarid climes, though more intensely and less seasonally predictable. Adaptations to survive intermittent drying are similar in each (Williams, 1985). Introductions to Australia’s arid/semiarid wetlands are provided by Davis et al. 2013, 2016 and Timms and Boulton 2001.

In the Australian semi-arid zone, the middle and lower Paroo of north-western New South Wales contains many and varied wetlands, almost all unreliably filled (Goodrick 1984; Timms and Boulton 2001). Most notable because of their size and human visitation are a series of episodic terminal lakes and also permanent waterholes on the main river channel. Besides these, there are many saline lakes and samphires, innumerable shallow claypans, many varieties of vegetated swamps and marshes, and a few temporary creek pools, small grassy pools, and shallow flood outs. Prominent and common among the swamps are those dominated by lignum or surrounding trees, the two types differing in hydrology, dominant plants and invertebrates (Timms 1997a). Diversity is further enhanced by the different faunas in the waterholes, claypans, salinas, small pools, etc. as outlined in Timms 1997b. The chief ecological drivers separating the wetland types are salinity, turbidity and hydrology (Timms and Boulton 2001).

The characteristics of many of these wetlands have now been elucidated. Foremost are the saline lakes (Timms 1993,1998a,2018), followed by claypans (Hancock &Timms 2002; Timms 2002), creek pools (Timms 2001), with less known of the large episodic terminal lakes, smaller intermittent freshwater lakes and permanent riverine waterholes (Timms and Boulton 2001). Least is known of the fauna, phenology
and ecological drivers of the vegetated temporary lakes/swamps surrounded by trees or supporting trees within — the treed swamps.

These wetlands are superficially similar to lignum (*Muehlenbeckia cunninghamii*) and Yapunyah (*Eucalyptus ochrophloia*) swamps of the adjacent Bulloo, Paroo and Warrego River systems, all being dominated by Eucalypt trees. Lignum Swamps, which generally have an overstorey of Black Box trees (*E. largiflorens*), and Yapunyah Swamps receive riverine floodwater, with lignum swamps generally being inundated episodically for many months and Yapunyah swamps only briefly (Maher 1991; Timms 1995). By contrast Black Box Swamps and Poplar/Bimble Box (*E. populnea*) Flats (Figs. 1a,b) have no association with the river, filling entirely by local rain waters. Also, trees tend to be mainly littoral though there may be a few internally. Generally, Black Box Swamps and Poplar Box Flats are relatively small (< 10 ha) shallow (< 1 m) with short hydrological periods (< 6 months, often much less). Many questions arise, including if these two treed wetlands are just variants of a distinctive type of wetland, if there are distinctive and major phenological and diversity differences between these and other Paroo wetlands, and are the ecological drivers in these temporary freshwater wetlands similar to most Australian arid-zone wetlands (Davis et al. 2017) and indeed the wider arid-zone or can they be explained within those already known for other Paroo wetlands, ie. salinity, turbidity and hydrology.

**Methods**

This study is based mainly on a major fill on March 3–5, 2020 resulting from 261 mm rainfall and very little afterwards. Eighteen swamps were subsequently monitored monthly for six months (but missed twice due to covid-19 travel restrictions), however some data were collected from a more average fill in May 2019, but it could only be followed for 6 weeks at fortnightly intervals. Also, comparative collections were taken from a claypan, a freshwater lake and two saline lakes. Comments on overall filling frequency are based on field experience 1987–2020. In the main study, water samples from 18 sites were collected regularly and conductivity measured with an Oakton ECTestr11 meter, pH with a Hanna pHeP meter and turbidity with a Secchi disc tube. Inundated area of each site was estimated from Google Earth maps and depth from a marker installed at full level and when dry the difference to the deepest area established with a dumpy level. Habitat heterogeneity was subjectively measured equally by extent of bottom irregularity, the area occupied by vegetation, and the amount of inundated woody detritus across the floor of the swamp.

All biological sampling was done from the swamp edge, as it was dangerous to wander too far out due to unpredictable location of unconsolidated sediments. So, while every effort was made to make the samples representative, this was not strictly possible; thus, all samples were taken from different physical sites as each swamp dried. Zooplankton was collected with a net of 159 μm mesh and opening 25 x 15 cm and trawled for 2 minutes in each swamp on each visit. Littoral invertebrates were collected with a D-shaped pond net (25 x 23 cm) of mesh 1mm trawled for 10 minutes altogether at 3 different sites in each swamp on each visit. The zooplankton collection was preserved in total in alcohol, but the littoral invertebrates were sorted in a tray and only representatives of each species retained in alcohol.
Abundances were estimated on a log scale (1–2 individuals = 0.1; 3–5 = 0.3; 6–8 = 0.7; 9–20 = 1; 21–50 = 1.3, etc)

The correlation coefficient was used to test a possible relationship between alpha diversity and hydroperiod and habitat heterogeneity. To test questions of faunal relationships between the six groups of swamps/flats, multivariate analyses were calculated using PRIMER (v5) (Clarke & Gorley 2001). Data on a freshwater lake, a claypan and two saline lakes were added to ascertain their relationships to the freshwater swamps/flats.

**Results**

The treed sites, all ephemeral, varied greatly in size with the Poplar Box Flats generally larger than the Black Box Swamps (Table 1). This is an artefact as most of the large Black Box Swamps on Bloodwood Station have dams sunk deep within them thus making them unsuitable for study. Poplar Box Flats generally were almost flat in profile, perhaps with a distinctly deeper channel accounting for much (>60%) of their recorded maximum depth, whereas the Black Box Swamps typically were saucer shape, often again with a distinct channel but contributing less (<40%) to their maximum depth. In the swamps/flats studied, those with channels were larger than those without (Table 1). In Black Box Swamps a further irregularity was provided by randomly arranged humps of unstructured sediments, perhaps the result of deltaic sedimentation in the past. Particularly small sites of both types were considered separately as their hydroperiods were distinctly shorter (Table 1).

Water in all sites was fresh (< 250 µS/cm), with the larger, deeper swamps/flats concentrating more over time than the smaller/shallower sites (Table 1, Appendix 1). Also, pH varied though the hydroperiod, commencing about neutral and moving quickly to being moderately alkaline (i.e. ca 7.0 to ca. 8.3) (Table 1, Appendix 1). Water turbidities were low, always below 70 NTU and often < 30 NTU (Table 1, Appendix 1). The Black Box Swamps cleared somewhat during their hydroperiod, but the Poplar Box Flats increased in turbidity with time (Table 1). This is not natural as stock had access only to the Poplar Box Flats on Muella Station.

Eighty-two taxa of invertebrates were encountered overall (Appendix 2), though 25 of these were collected fewer than three times (marked ‘u’ in Appendix 2). Almost none were unique to any one site or type of site, though *Eulimnadia hansonii, Eocyclus phytophyllus, Asplanchna* spp. and *Laninularia racemovata* were restricted to Poplar Box Flats. Black Box sites with channels were the most speciose, followed by Poplar Box Flats with channels, then Black Box sites without channels, Poplar Box sites without channels and the short hydroperiod sites last (Table 2). The channels add to habitat complexity and hence species diversity. This contrast in diversity patterns was evident also temporal patterns in momentary alpha diversity between the deepest sites with channels in which diversity increased with time and the shallowest nearly flat Poplar Box sites without channels in which diversity slowly decreased as they became shallower (Fig 2a,2b). Alpha diversity was significantly higher the longer the hydroperiod (r^2 =
0.7921, P<0.01) and also was significantly influenced by habitat heterogeneity ($r^2 = 0.7583, P<0.01$). Beta and gamma diversities were also higher the longer the hydroperiod, but these were not tested statistically.

There was a major change in communities with aging of sites (Table 3), with all sites dominated initially by large branchiopods then insects and changing slightly as species matured according to their life cycle characteristics. Zooplankton usually was dominated early and briefly by *Moina australiensis* then communities were dominated by either or both *Boeckella triarticulata* and *Daphnia carinata* s.l. Larger littoral invertebrates were sparse initially though *Triops australiensis*, larger clam shrimps (*Limnadopsis birchii*, *L. tatei* and *L. parvispinus*) soon were obvious as well as *Micronecta* sp. After two months these had largely disappeared to be replaced by various juvenile insects. These matured over the ensuing months, with almost no addition or replacement of species. Both the larger invertebrates and smaller planktonic invertebrates had many species considered uncommon (noted as u in Appendix 2) or in low numbers and not always present in one particular site or group of similar sites (marked as x in Appendix 2). In the main study of 2020, most branchiopods were restricted to the first sampling soon after filling and were not present at 2 months, but in 2019, when the sampling frequency was fortnightly, many persisted for 6 weeks. *Ozestheria packardi* was unusual for a branchiopod, persisting right through the hydroperiod in some sites.

No data were collected on diets of the invertebrates, though from generalised information, most initial branchiopod colonizers were filter feeders on algae, and were replaced by more filter feeders in the form of copepods and cladocerans. Ostracods also ate algae, but by scraping or collecting them from plants and sediments. *Triops* was an early omnivore in most sites and *Eretes* larvae a prominent early carnivore in some sites. Interestingly their presence was patchy, varying in different fills (in some sites the 2019 populations were different from that in 2020). Detritus and partial omnivorous feeders were represented by *Micronecta*, *Agraptocorixa* and various beetle adults. Prominent carnivores towards drying were *Anisops* spp and odonates. Strict vegetarians were uncommon, represented by limited and patchy populations of snails, though the periphyton on the plants (mainly *Chara*, also *Myriophyllum*) supported *Cloeon*, many ostracods and probably *Micronecta*.

An ordination of the 18 ephemeral treed swamps plus an episodic freshwater lake, a claypan, and two saline lakes as outgroups, all based on Bray Curtis similarities of average abundances over their hydroperiods, is shown in Fig 3. It suggests a close relationship between the three channelled Black Box Swamps, the three non-channelled Black Box Swamps, the three channelled Poplar Box Flats and the four non-channelled Poplar Box Flats. Thus, these four wetland types can be considered as one, the treed swamps. The smaller Black Box Swamps are not far removed from this cluster, with the four small Poplar Box Flats further removed. Surprisingly the one episodic freshwater lake included in the analysis lies close to the cluster of temporary sites, with the claypan showing some similarity but the two saline sites are well removed.

**Discussion**
Over 34 years of casual monitoring at Bloodwood, the 2020 filling was the greatest ever observed, while the 2019 filling, though not measured, was more ‘average’ at about half the inundated area measured in 2020. The great filling of 2020 filling was akin to that in 1974-76 (D. Leigo, pers. com.) and going back to 1885 in the wider Paroo, of great fillings of Lake Wyara in 1890, 1959-50 and 1974-76 (A. McGrath pers. com; Timms, 1998b) indicating a return interval of about 44 years.

In general, Black Box Swamps wetted every 2-3 years, always in a La Nina climatic year and perhaps weakly two or rarely three times in between and/or two years in succession if La Nina events lasted two years. Smaller Black Box Swamps such as Marsilea Swamp filled to a maximum ca 30 cm depth only in La Nina years, with other wettings 5 - 10 cm deep and lasting only a few days to weeks. Poplar Box Swamps filled a little less frequently at about 3-5 year intervals, again in the same temporal pattern. In strong El Nino years, all swamps remain dry for years, perhaps up to 6 years, as in the Millennium drought of 2001-2006.

There is a vast difference in habitat characteristics and faunal composition between these treed swamps and salt lakes and claypans, the other common wetlands of the Paroo (Fig 3, Table 4; Timms and Boulton 2001). On the other hand, there are many similarities in habitat and fauna between these treed swamps and episodic freshwater lakes and creek pools (Fig 3, Table 4; Timms and Boulton 2001). The ecological drivers suggested for all Paroo wetlands also apply specifically to these Treed Swamps, namely water fresh (EC< 250 uS/cm) (as against saline waters of the salt lakes and samphires), water turbidity low (<50 NTU) (as against high turbidity in claypans and crystal-clear saline waters and somewhat turbid waters of other freshwaters), and relatively short hydroperiods (< 6 months) (applies to many Paroo habitat types but some are permanent or episodic persisting a year or more).

In a more comprehensive study of freshwater aquatic habitats across the Australian arid and semiarid zones but excluding any sites in the Murray Darling basin, Davis et al. (2014, 2016) noted 10 types of habitats and major ecological drivers of latitude, connectivity, hydroperiod and biogeographic history, ie relic fauna in some isolated sites. Each of the drivers varied in importance with habitat type: latitude applied to most, connectivity to the riverine systems and isolation to desert rockholes, some waters were permanent and hydrologically stable, others temporary and variable. These authors did not look at the influence of water chemistry/properties, but had they done so, then (a) salinity as an ecological driver would have featured, as it does in the Paroo, (b) turbidity featured only for the uncommon claypan sites across the arid inland whereas in the Paroo these are common and there are minor variations in water clarity in other Paroo habitat types, and (c) hydrological variability is arguably the most important driver everywhere.

The factor of hydrological variability is shared with Mediterranean wetlands, though in these there is seasonal reliability (Boix et al. 2016), important for at least some niche separation of species, and hence increased diversity. Paroo treed swamps are not as speciose as local freshwater lakes (Timms and Boulton 2001) and creek pools (Timms 2001). Diversity in the Paroo is artificially low because some groups have hardly been studied (rotifers) or have probably been incompletely collected (e.g
chironomids). However, this is not enough to account for the lower species richness in the Paroo treed pools when compared to the generally speciose Mediterranean pools or the temporary wetland ponds of temperate regions — gamma diversity >100 species (Boix et al. 2016; Lake et al. 1989; Pinder et al. 2004; Jeffries et al. 2016). The reason is probably largely due to the unreliable filling of the semiarid Paroo treed swamps, but short hydroperiods and simpler habitat structure may contribute (Florencio et al. 2014a, 2014b). These factors probably also contribute to the lack of any detailed seasonal succession, except those determined by phylogenetic characteristics (e.g., branchiopods early in succession, predatory insects including odonatans maturing late).

Treed swamps also occur in the wheatbelt of Western Australia, including Southern Yate (Eucalyptus occidentalis) and Melaleuca spp. swamps. Such generally have abundant vegetation of sedges and a greater diversity of invertebrate assemblages (Pinder et al. 2004) but fewer branchiopods (author unpublished data) compared with Paroo treed swamps. Gross differences could be explained by lower vegetation density and greater environmental harshness of the Paroo treed swamps. Phenology of the western swamps is unknown.

Perhaps the most similar study of a treed swamp in a semiarid climate is by Lahr et al. (1999) of a sahelian temporary pond in Senegal. It had an eight-month hydroperiod and similar fluctuations over time in conductivity, turbidity and pH as in Paroo treed swamps. Its fauna was dominated early by crustaceans, mainly branchiopods, then later by insects, particularly hemipterans and dytiscids, but with some specific separation in abundances perhaps explained by its longer hydroperiod. Striking similarities include the early dominance of the zooplankter Moina, the early abundance of two species of Anostraca, and the later dominance of the insects Micronecta and Anisops and Eretes. Significant differences include the variety of clam shrimps and ostracods in the Paroo sites in keeping with their high diversity in inland Australia (Schwentner et al. 2015; De Deckker 1983; Halse and Martens 2019), and the greater importance of some lesser insect groups (odonatans, ephemopterans and tricopterans) in Paroo sites.

Management

These treed swamps are unmanaged on Bloodwood/Muella as elsewhere in the Paroo, though some larger Black Box Swamps have long been much modified ecologically by the sinking of dams in them. Many decades of sheep grazing are believed not to have affected them as sheep keep out water, but same cannot be said for more recent cattle grazing as cattle pug the wet surfaces. The ecological effect of this is unknown, but thought to be minor.

Declarations

Acknowledgements

I am indebted to the Hansons of Bloodwood and the Batys of Muella for access to their properties and for various other kind logistic help over the years, also to David Leigo of Dungsarvon and Allan McGrath of Booroora for long term rainfall records. I thank Jason Morton for the multivariate analysis, Stuart Halse
for the identification of ostracods, Russ Shiel for identification of many cladocerans, cyclopoids and rotifers, and Adrian Pinder and Joan Powling for constructive criticism of the manuscript.

This research was funded by the author

There are no conflicts of interest

The detailed datasets generated during this study, besides that reported in the paper and appendices, are available from the author on a reasonable request.

No ethics approval was necessary to study invertebrates in the jurisdiction of the field sites.

As noted in the acknowledgements I had permission from the owners to study the treed swamps on their lands.

As a retiree under my own auspices I do not need consent for publication.

References

1. Bayly IAEB, Williams WD (1966) Chemical and biological studies on some saline lakes of south-east Australia. Aust J Mar Freshwat Res 17(2):177-228.

2. Boix D et al. (2016) Invertebrates of Freshwater Temporary Ponds in Mediterranean Climates. In: Baxter D, Boix D (eds) Invertebrates in Freshwater Wetlands. Springer Switzerland pp 141-189. https://doi.org/10.1007/978-3-319-24978-0_5.

3. Clarke KR, Gorley RN (2001) Primer v5: user manual/ tutorial. PRIMER-E. Plymouth Marine Laboratory, Plymouth.

4. Davis JA et al. (1993) Wetlands Classification on the Basis of Water Quality and Invertebrate Community Data Vol 6 Wetlands of the Swan Coastal Plain. Water Authority of Western Australia, Perth.

5. Davis JA et al. (2013) Building the Climate Resilience of Arid Zone Freshwater Biota. National Climate Change Adaptation Research Facility, Monash University, Melbourne.

6. Davis JA et al., 2018. Patterns and drivers of aquatic invertebrate diversity across an arid biome. Ecography December 2016; https://doi.org/10.1111/ecog.02334.

7. De Deckker P (1983) Australian salt lakes and their history, chemistry and biota — a review. Hydrobiologia 105: 231-244.

8. Florencio M et al. (2009) Inter- and intra-annual variations of macroinvertebrate assemblages are related to the hydroperiod in Mediterranean temporary ponds. Hydrobiologia 634: 167-183; https://doi:10.1007/s10750-009-9897-3

9. Florencio M et al. (2014a) Biodiversity patterns in a macroinvertebrate community of a temporary pond network. Insect Conservation and Diversity 7: 4-21; https://doi:10.1111/icad.12029
10. Florencio M et al. (2014b) The influence of geomorphology on the composition of aquatic flora and fauna within a temporary pond network. Limnetica 33(2): 327-340.

11. Goodrick GN (1984) Wetlands of north-western New South Wales. NSW National Parks and Wildlife Service Occasional Paper No. 6.

12. Halse S, Martens K (2019) Four new genera and five new species of 'Heterocypris' from Western Australia (Crustacea, Ostracoda, Cyprinotinae). European Journal of Taxonomy 493: 1-35; https://doi:10.5852/ejt.2019.493

13. Hancock MA, Timms BV (2002) Ecology of four turbid claypans during a filling-drying cycle in the Paroo, semi-arid Australia. Hydrobiologia 479: 95-107.

14. Horwitz P et al. (2009) Wetland invertebrate richness and endemism on the Swan Coastal Plain, Western Australia. Marine and Freshwater Research. 60: 1006-1020; https://doi.org/10.1071/MFO8204

15. Jeffries MJ et al. (2016) Invertebrates in Temporary Wetland Ponds of the Temperate Biomes. In: Baxter D, Boix D (eds) Invertebrates in Freshwater Wetlands. Springer, Switzerland pp. 105-139; doi.10.1007/978-3-319-24978-0_4

16. Lahr J et al. (1999) Phenology of invertebrates living in a sahelian temporary pond. Hydrobiologia 405: 189-205.

17. Lake PS, Bayly IAE, Morton DW (1989) The phenology of a temporary pond in western Victoria, Australia, with special reference to invertebrates. Archiv für Hydrobiologie 115(2): 171-202.

18. Maher MT (1991) Waterbirds back o’ Bourke, an inland perspective on the conservation of waterbirds. Ph D Thesis, University of New England.

19. Meintjes S (1996) Seasonal changes in the invertebrate community of small shallow ephemeral pans at Bain’s Vlei, South Africa. Hydrobiologia 317: 51-64.

20. Pinder A et al. (2004) Aquatic invertebrate assemblages of wetlands and rivers in the Wheatbelt region of Western Australia. Records of the Western Australian Museum Supplement 67: 7-37.

21. Schwentner M et al. (2015) Spinicaudata (Branchiopoda: Diplostraca) in Australia’s arid zone: unparalleled diversity at regional scales and within water bodies. Journal of Crustacean Biology 35 (3): 366-378; doi.10.1163/1937240X-00002339

22. Timms BV 1993. Saline lakes of the Paroo, inland New South Wales, Australia. Hydrobiologia 267: 269-280.

23. Timms BV (1997a) A Study of the Wetlands of Currawinya National Park. A report to the Queensland Department of Environment, Toowoomba.

24. Timms BV (1997b) A comparison between saline and freshwater wetlands on Bloodwood Station, the Paroo, Australia, with special reference to their use by waterbirds. International Journal of Salt Lake Research 5: 287-313.

25. Timms BV (1998a) Further studies on the saline lakes of the eastern Paroo, New South Wales, Australia. Hydrobiologia 381: 31-42.
26. Timms BV (1998b) A study of lake Wyara, an episodically filled saline lake in southwest Queensland, Australia. International Journal of Salt Lake Research 7: 113-132.

27. Timms BV (2001) Limnology of the intermittent pools of Bells Creek, Paroo, arid Australia, with special reference to biodiversity of invertebrates and succession. Proceedings of the Linnean Society of New South Wales 123: 193-213.

28. Timms BV (2002) Limnology of the claypans of the Paroo, arid-zone Australia. Verh. Internat. Verein. Limnol. 28: 130-133.

29. Timms BV (2018) On the influence of season and salinity on the phenology of invertebrates in Australian saline lakes, with special reference to those of the Paroo in the semi-arid inland. Journal of Oceanology and Limnology 36 (6): 1907-1918 https://doi.org/10.1007/s00343-018-7308-1

30. Timms BV, Boulton AJ (2001) Typology of arid-zone oodplain wetlands of the Paroo River (inland Australia) and the influence of water regime, Turbidity and salinity on their aquatic invertebrate assemblages. Archiv für Hydrobiologie 153(1): 1-27.

31. Williams, W.D. 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. Hydrobiologia 125: 85-110.

Tables

Table 1 Physicochemical features of six types of treed swamps on Bloodwood and Muella Stations

| Sites                        | No. | Mean ± SE Area (ha) | Mean ± SE maximum depths (cm) | Mean Cond. first-final (µS/cm) | Mean pH first-final | Mean Turbidity first-final (NTU) |
|------------------------------|-----|---------------------|--------------------------------|-------------------------------|--------------------|----------------------------------|
| Black Box swamp with channels | 3   | 2.7 ± 0.4           | 90.0 ± 9.8                     | 57 – 250                      | 7.1 – 8.7          | 22 – 5                           |
| Black Box swamps no channels | 3   | 1.2 ± 0.2           | 74.3 ± 14.2                    | 73 – 173                      | 7.1 – 8.2          | 34 – 14                          |
| Black Box swamps small       | 2   | 0.3 ± 0.1           | 28.5 ± 3.5                     | 55 – 70                       | 6.8 – 8.4          | 25 – 10                          |
| Poplar Box flats with channels | 3   | 7.1 ± 2.1           | 64.7 ± 11.2                    | 32 – 77                       | 7.4 – 8.3          | 45 – 58                          |
| Poplar Box flats no channels | 4   | 6.3 ± 4.8           | 26.7 ± 4.3                     | 35 – 95                       | 7.0 – 8.4          | 39 – 68                          |
| Poplar Box flats small       | 3   | 0.3 ± 0.1           | 23.8 ± 6.0                     | 73                            | 7.2                | 10                               |

Table 2 Diversity in six types of treed swamps on Bloodwood and Muella Stations
| Sites                         | number | Alpha Diversity mean ± SE | Beta Diversity mean ± SE | Gamma Diversity |
|------------------------------|--------|---------------------------|--------------------------|-----------------|
| Black Box swamps with channels | 3      | 27.7 ± 1.3                | 43.3 ± 0.5               | 54              |
| Black Box swamps no channels  | 3      | 19.4 ± 0.7                | 36.3 ± 2.5               | 49              |
| Black Box swamps small       | 2      | 16.0 ± 0.9                | 25.5 ± 1.2               | 32              |
| Poplar Box flats with channels | 3      | 21.9 ± 1.4                | 33.7 ± 1.8               | 44              |
| Poplar Box flats no channels  | 4      | 14.1 ± 0.7                | 26.2 ± 1.5               | 40              |
| Poplar Box flats very small  | 3      | 6.3 ± 0.3                 |                          | 13              |

Table 3 Phenology of dominant invertebrates in treed swamps on Bloodwood and Muella.
## Table 4 Prominent invertebrates in five wetland types in the Paroo

|                     | Two weeks | Two months | Four to six months |
|---------------------|-----------|------------|--------------------|
| **A. Poplar Box Flats** |           |            |                    |
| **Open waters**     |           |            |                    |
| *Moina australiensis* | maybe cyclopoid | maybe cyclopoid |            |
| *Branchinello spp.*  | maybe *Daphnia carinata* | maybe rotifers |            |
| *Paralimnadia or Euimnadia* | | |            |
| **Littoral** |           |            |                    |
| *Micronecta sp.*    | Anisops juv. | Anisops adults |             |
| *mayoe Eretes larvae* | Agraptocorixa juv. | Agraptocorixa adults |   |
| *mayoe Triops australiensis* | Odonata juv. | mature Odonata |            |
| *mayoe Berosus/Steronoprisus* | *mayoe Cloeon larvae* | maybe few adult dytiscids | |
| *mayoe mosquito*     | | |            |

| **A. Black Box Swamps** |           |            |                    |
| **Open waters**     |           |            |                    |
| *Moina australiensis* | Boeckella triarticulata | Boeckella triarticulata |            |
| *Branchinello spp.*  | *Daphnia carinata* | *maybe Calamoecia lucasi* |             |
| *Limnadiopsis spp.*  | various ostracods | *Daphnia carinata* |            |
| *mayoe Paralimnadia, Ozestheria* | *maybe Ozestheria* | *maybe Ozestheria* | |
| *mayoe Daphanosoma*  | *maybe other cladocera* | *maybe other cladocera* | |
| *mayoe cyclopoid*    | | |            |

| **Littoral** |           |            |                    |
| *Triops australiensis* | Anisops juv. | Anisops adults | |
| *Micronecta sp.*    | Agraptocorixa juv. | Agraptocorixa adults | |
| *clam shrimps as above* | Cloeon larvae | mature Cloeon larve | |
| *Eretes larvae*     | Triplectides larvae | mature Triplectides larve | |
| *mayoe Berosus/Steronoprisus* | dytiscid larvae and adults | dytiscid adults | |
|                     | chironomid larvae | chironomid larvae | |
|                     | odenata larve | mature odenata larve | |
|                     | | water mites | |

Table 4 Prominent invertebrates in five wetland types in the Paroo
| Treed swamps<sup>1</sup> | Salt lakes<sup>2</sup> | Claypans<sup>3</sup> | Episodic freshwaters<sup>4</sup> | Creek Pools<sup>5</sup> |
|------------------------|----------------------|---------------------|--------------------------|---------------------|
| Branchinella frondosa  | Parartemia minuta    | Branchinella lyrifera| Branchinella australiensis| Branchinella australiensis |
| Limnodopsis spp.       | Daphniopsis queenslandicus | Branchinella affinis | Paralimnadia spp.       | Limnodopsis spp.       |
| Boeckella triarticulata| Trigonocypris globulosus | Ozestheria lutaria  | Ozestheria parkardi     | Boeckella triarticulata |
| Daphnia carinata       | Cyprinotus edwardsi  | Ozestheria packardi | Boeckella triarticulata | Ozestheria packardi   |
| Micronecta sp.         | Diacypris spp.       | Micronecta sp.      | Daphnia carinata        | Micronecta sp.        |
| Anisops spp.           | Micronecta sp.       | Anisops stali       | Anisops spp.            | Anisops spp.          |
| odonates               | Anisops spp.         | Eretes australis    | Dytiscid beetles        | Dytiscid beetles      |
| Dytiscid beetles       | Tanytarsus barbitarsus | Other dytiscids    | Physa acuta             | Physa acuta           |

<sup>1</sup> Appendix 1; <sup>2</sup> Timms, 1993, 1998, 2018; <sup>3</sup> Hancock and Timms, 2002, Timms, 2002; <sup>4</sup> Timms, 1997, 2001b; <sup>5</sup> Timms, 2001.

**Figures**
These wetlands are superficially similar to lignum (Muehlenbeckia cunninghamii) and Yapunyah (Eucalyptus ochrophloia) swamps of the adjacent Bulloo, Paroo and Warrego River systems, all being dominated by Eucalypt trees. Lignum Swamps, which generally have an overstorey of Black Box trees (E. largiflorens), and Yapunyah Swamps receive riverine floodwater, with lignum swamps generally being inundated episodically for many months and Yapunyah swamps only briefly (Maher 1991; Timms 1995).
By contrast Black Box Swamps and Poplar/Bimble Box (E. populnea) Flats (Figs. 1a,b) have no association with the river, filling entirely by local rain waters.

Figure 2

Alpha diversity was significantly higher the longer the hydroperiod ($r^2 = 0.7921$, $P<0.01$) and also was significantly influenced by habitat heterogeneity ($r^2= 0.7583$, $P<0.01$). Beta and gamma diversities were also higher the longer the hydroperiod, but these were not tested statistically.
Figure 3

An ordination of the 18 ephemeral treed swamps plus an episodic freshwater lake, a claypan, and two saline lakes as outgroups, all based on Bray Curtis similarities of average abundances over their hydroperiods, is shown in Fig 3.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Appendix1Somecharacteristics.docx
- Appendix2SpeciesList.docx