Zoodiversity, **55**(6): 439–450, 2021
DOI 10.15407/zoo2021.06.439

UDC 594.3(94)

ON THE BIODIVERSITY HOTSPOT OF LARGE BRANCHIOPODS (CRUSTACEA, BRANCHIOPODA) IN THE CENTRAL PAROO IN SEMIARID AUSTRALIA

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On the Biodiversity Hotspot of Large Branchiopods (Crustacea, Branchiopoda) in the Central Paroo in Semi-Arid Australia. Timms, B. V., Schwentner, M., Rogers, D. C. — Biodiversity is central to the structure and functioning of communities including those of temporary water bodies. Worldwide the large branchiopod component commonly consists up to about six species instantaneously per site and twice that number across the surrounding district. Where these figures reach eight to ten species per site and about twice that number per district, the term diversity hotspot is sometimes used. In eastern Australia, biogeographical factors have facilitated a rich large branchiopod fauna ca 80 species and locally within 500 km^2 of the central Paroo in northwestern New South Wales where a rarely diverse and abundant array of habitats supports at least 38 species, though the maximum per site syntopically is still near 10 species.
Key words: fairy shrimps, shield shrimps and clam shrimps, alpha diversity, habitat heterogeneity.

Large Branchiopoda (Anostraca, Notostraca, Laevicaudata, Spinicaudata and Cyclestherida) are an important and charismatic faunal component of temporary water bodies. Although the large Branchiopoda is not a monophyletic group as are the water fleas (Cladocera) nested within the wider Branchiopoda (Schwentner et al., 2018), they are commonly grouped together in ecological studies due to their overall life history similarities. Reports abound on alpha diversity (species richness) of the large branchiopod fauna of the world (e. g. Brendonck et al., 2008; Rogers, 2009), of continents (e. g. Anostraca of North America, Rogers, 2014; Branchiopods of South America, Rogers et al., 2021; Spinicaudata of Australia; Schwentner et al., 2015 a), large parts of continents (e. g. Anostraca in Southern Africa, Hamer and Brendonck, 1997), large countries (e. g. Large branchiopods of India, Rogers and Padhye, 2015), smaller countries (e. g. Anostraca of Botswana, Brendonck and Riddoch, 1997), districts (e. g. large branchiopods of the Chaouia Plain of western Morocco, Thiery, 1991), small groups of wetlands (e. g. Galapagos Islands, Brendonck et al., 1990) and even single wetlands (e.g. Hamer and Appleton, 1991; Wang et al., 2010). Such reports may not necessarily be complete due to further discoveries or taxonomic revisions after their publication, but are essential in comparative diversity studies of regional or global patterns of diversity. In some cases, there appears to be a particularly high number of the species per unit area in which case the term 'hotspot' may be used. This has been applied continentally (e. g. Spinicaudata in

Australia, Schwentner et al., 2015 a), by country or district and even to individual sites (e. g. Bovin et al, 2018 for a district; Weise, 1964 for a single site). There is no rule as to how to apply this term, e. g. no defined number of species per unit of area, and indeed in many cases use of the term appears to be overrated when compared to diversity in other areas.

In the Australian context, the region with the most large branchiopod species is the Paroo catchment (area 73,600 km^2) in northwestern New South Wales (NSW) (Timms and Sanders, 2002; Timms and Richter 2002; Schwentner et al., 2015 a). This can be narrowed down to a much smaller segment without much loss of diversity to about 500 km^2 in the central parts of the Paroo catchment.

Here we detail this fauna, to consider why it should be so diverse and to consider how best to define a biodiversity 'hotspot'.

Material and methods

The area of study is three privately owned adjacent station properties, Bloodwood, Tredega and Muella in the central Paroo, 130 km northwest of Bourke in northwestern New South Wales (NSW) (fig. 1). These stations (combined area about 500 km^2) are vegetated with semiarid scrub on a dune field on the southern and western half and subdued ridges of brown earths on the eastern half (Hazelton and Johnson, 1973). The overall landscape contains many temporary lakes plus other depressions of various sizes, depth, and hydroperiod. Following significant rainfall some to all of these partially or completely fill to form a variety of seasonally astatic aquatic habitats (table 1; fig. 2) characterized by differing salinity, turbidity and hydroperiod as well as sizes, pH and the presence/absence and type of submerged vegetation. These dryland wetlands are a significant feature of the Paroo catchment and adjacent Bulloo and Warrego systems (combined area 210,000 km^2), with some areas especially rich in large lakes and claypans as in the Currawinya National Park, a Ramsar site (Timms, 1999; 2008). While wetlands may be densest at Currawinya, a limited area of ca 500 km^2 on Bloodwood, Tredega and Muella in NSW arguably has greatest variety of wetlands within these semi-arid catchments.

Following significant rainfall events, many wetlands on these stations were sampled for large branchiopods with D-shaped pond nets with mesh sizes 1 to 2 mm. Usually the net was swept randomly through littoral areas, but in some sites notably Gidgee Lake, the fairy shrimp, *Branchinella buchananensis* actively avoided nets, so a search and quick snatch method was needed. Generally branchiopod populations reached a maximum 1–2 months after wetland filling, so that collections taken within this period were used for assessment of species richness. However in some wetlands, particularly in grassy pools and some other small sites, population development was quicker so that signature collections were made two to four weeks after site filling. Collections made earlier than these windows were full of immature specimens difficult to identify, or if later, missing some quickly developing species. One frustrating aspect of collecting was access after rainfall events. This was partly due to station tracks being impassable sometimes for weeks, but also contributed to by public unsealed roads being closed after rains.

Samples were taken from the wetlands over a 35-year period, 1987–2021 inclusive. However not all types of wetlands were studied simultaneously, so that there was specialization on various wetland types over the years (see table 1). Some wetlands were studied more intensely, which may have biased the data, and of course

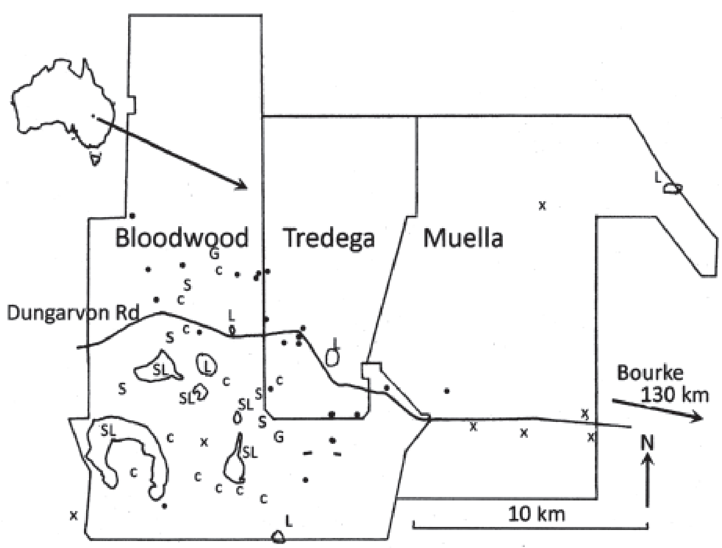

Fig. 1. Map of Bloodwood, Tregeda, and Muella Stations, central Paroo, northwestern NSW. Code to symbols: SL — Salt Lake; L — Freshwater Lake; C — Claypan; G — Grassy swamp; S — Samphire swamp; X — Poplar Box flat; short line, creek pool; dot — Black Box swamp.

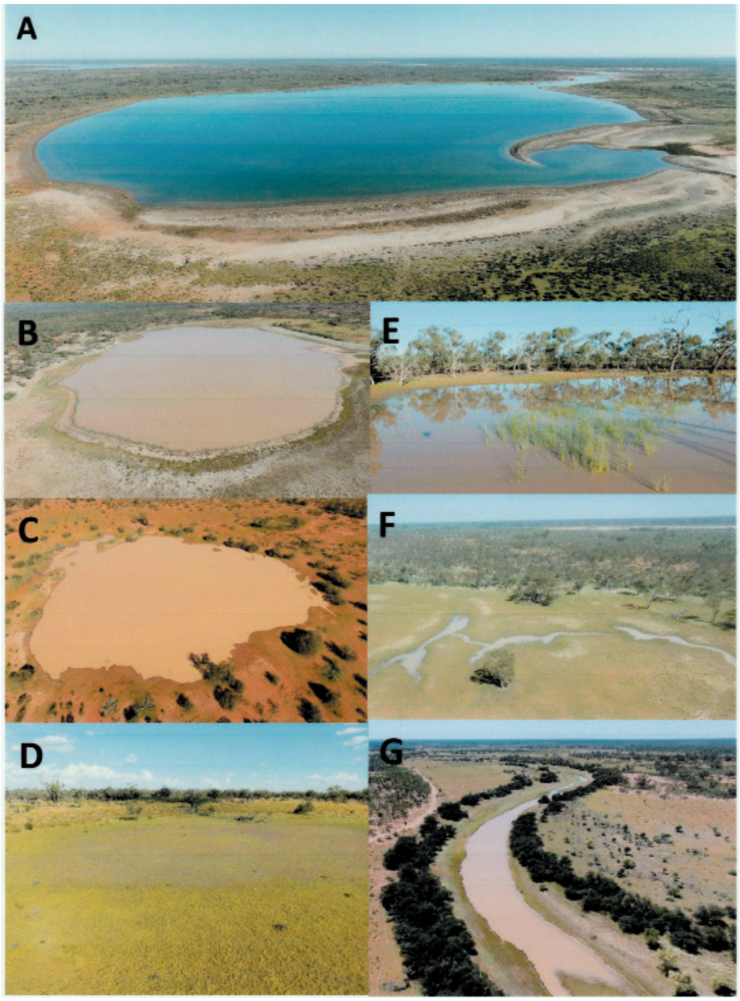

Fig. 2. Images of seven types of wetlands in the central Paroo., northwestern New South Wales: A — Gidgee Salt Lake; B — Ski Freshwater Lake; C — Melaleuca claypan; D — Beverley's grassy pool (dry); E — Reedy Black Box swamp; F — Utah Poplar Box flat; G — Lower Crescent creek pool. Not to scale.

there were differing numbers of each wetland type as dictated by the landscape. So no claim is made for the exact internal comparability of the data. However, the long study period is sufficient to encounter all extant species in the 500 km^2 study area and for common combinations of species instantaneously present to be recorded at least for the most numerous wetland types.

Species were identified using early working versions of Timms (2012, 2015 b, 2018) with representatives of the major groups illustrated in fig 3. In addition molecular analyses was conducted once for many species of *Eulimnadia* (Schwentner et al., 2015 a) *Eocyzicus* (Schwentner et al., 2014; Tippelt and Schwentner, 2018), *Ozestheria* (Schwentner et al., 2015 b; Schwentner et al., 2020) and *Triops* (Meusel and Schwentner, 2017). In our count of species, we distinguish between formally described species and species known and delimited only genetically. Of the latter, we only included those species that were genetically unambiguously delimited from all other species of the respective genus. In a few cases, additional rather divergent lineages whose status is questionable were identified within some species, (e. g., *Ozestheria* sp. Q1–Q5; Schwentner et al., 2020); these were not included in the species count so as not to artificially inflate the observed diversity. Three commonly encountered species — *Triops australiensis*, *Ozestheria packardi* and *Ozestheria berneyi* — were genetically shown recently to comprise more than one species each (Schwentner et al., 2015 b; Schwentner et al., 2020; Meusel and Schwentner, 2017). Although we attempted to treat each of these species separately whenever possible, for some summary statistics (e. g. species co-occurrences) we had to lump them each under one taxon, as they cannot be retrospectively separated. Because it is likely that the "true" *Triops australiensis* and *Ozestheria packardi* do not occur in the middle Paroo, but morphologically similar species do, we have counted these two species as "undescribed".

Table 1. Wetland Types in the central Paroo, northwestern New South Wales

Wetland	No.	Hydrology	Turbidity	Conductivity	Reference
Treed Swamps	ca 50	Two physical types. Black Box Swamps fill every 2–3 years, Poplar Box Flats every 3–5 years. Persist 3–6 mths.	50–300 NTU	50–500 mS/cm	Timms, in press
Claypans	ca 40	Fill every 2–3 years, more in La Nina years. Persist 3–6 months, more in La Nina years.	1000–5000 NTU	100–1000 mS/cm	Hancock and Timms, 2002
Grassy pools/swamps	5	Fill rarely, mainly in strong La Nina years. Persist only a few weeks.	< 50 NTU	< 100 mS/cm	Timms, 1997
Creek Pools	8	Fill most years, sometimes 2–3 times. Persist 3–36 mths.	50–500 NTU	100–10000 mS/cm	Timms, 2001
Salt Lakes	6	Of various salinity ranges. Persist 3–30 mths, mainly in La Nina years. Often dry for years in El Nino conditions.	10–100 NTU	1000–250000 mS/cm	Timms, 1993,1998, 2018
Samphire Swamps	5	Fill every 3–5 years, certainly in La Nina years. Persist 3–6 months.	< 100 NTU	200–5000 mS/cm	Schwentner et al .,2012
Freshwater Lakes	5	Episodic, lasting 6–24 mths, Ski L fills every 2–3 yrs, Wirrania every 2–4 years, L. Muella every 5–8 yrs	Ski 200–500 NTU, others 20–100 NTU	All 100–750 mS/cm	Timms, 1997
Table drains	many	Occasionally support branchiopods. Persist only a few weeks in very wet conditions.	< 100 NTU	< 100 mS/cm	
Farm dams	many	Most are permanent and sunk into Black Box Swamps. Some dug out on slopes. These persist for a few mths.	turbid	fresh	

Note. NTU — Nephrometric Turbidity Unit.

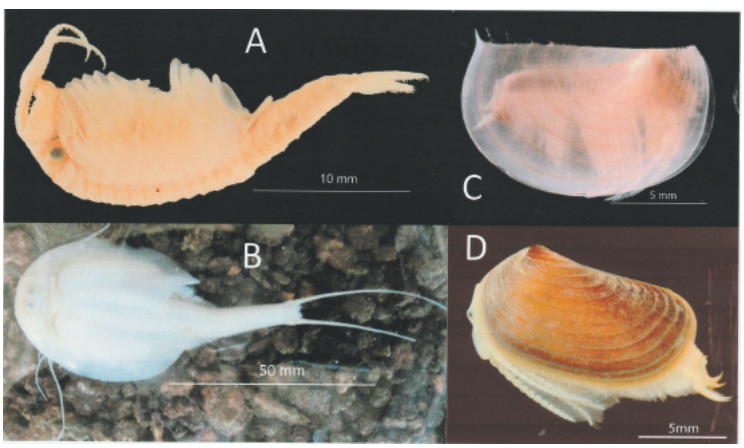

Fig. 3. Four representative branchiopods from the central Paroo. A — Anostracan *Branchinella australiensis*; B — Notostracan *Triops* sp.; C — Spinicaudatan *Limnadopsis tatei*; D — Spinicaudatan *Ozestheria lutraria*.

Results

The species encountered are listed in tables 2 to 5, together with data on their relative abundance and habitat preferences. The total is 38 species. This includes 16 species of Anostraca, dominated by 13 species of *Branchinella*, one species each of Laevicaudata and of Cyclestherida, and 20 species of Spinicaudata (in the seven spinicudatan genera there are multiple species of *Eocyzicus* (six) and *Limnadopsis* (five)) (tables 2, 3, 4). However, a number of still undescribed species greatly increase the number of species recorded for Spinicaudata (total of 33 described and undescribed species) and *Triops* (total of six undescribed species) (table 7). Most of the undescribed Spinicaudata are *Ozestheria* species (Schwentner et al.,

Table 2. Fairy shrimps (Anostraca) of the central Paroo, northwestern New South Wales

Species	Spread in central Paroo	Distribution beyond central Paroo	Regularity of appearance	Habitat range
Australobranchipus parooensis Rogers et al., 2007	< 5 sites	SW Qld and West NSW	Rare	Fresh waters, mainly clear
Branchinella affinis Linder, 1941	> 25 sites	Australia wide	Most fillings	Fresh waters, mainly intermediate clarity
Branchinella angelica Timms, 2016	1 site	Western NSW	Rare	Fresh waters, mainly intermediate clarity
Branchinella arborea Geddes, 1981	> 50 sites	Central eastern inland	All fillings	Fresh waters, mainly clear
Branchinella australiensis (Richters, 1876)	> 50 sites	Australia wide	All fillings	Fresh waters, mainly intermediate clarity
Branchinella buchananensis Geddes, 1981	< 5 sites	North and central eastern inland	Some fillings	Hypo and mesosaline waters
Branchinella budjiti Timms, 2001	> 50 sites	Central eastern inland	Most fillings	Fresh waters, mainly turbid
Branchinella campbelli Timms, 2001	< 5 sites	Central eastern inland	Some fillings	Clear fresh waters,
Branchinella frondosa Henry, 1924	< 10 sites	North and central Aust.	Some fillings	Freshwaters, mainly of intermediate clarity
Branchinellla lyrifera Linder, 1941	> 50 sites	Australia wide	All fillings	Turbid to extremely turbid waters
Branchinella occidentalis Dakin, 1914	< 50 sites	Australia wide	All fillings	Turbid to extremely turbid waters
Branchinella pinnata Geddes, 1981	< 25 sites	North and central Aust.	Most fillings	Fresh waters, mainly intermediate clarity
Branchinella proboscida Henry, 1924	< 50 sites	Australia wide	Most fillings	Mainly turbid waters
Branchinella wellardi Milner, 1929	< 5 sites	North and central Aust.	Some fillings	Clear fresh waters
Parartemia minuta Geddes, 1973	< 5 sites	Eastern inland	Most fillings	Saline waters
Streptocephalus archeri Sars, 1896	< 5 sites	Australia wide	Some fillings	Fresh waters, mainly intermediate clarity

2015 b). Syntopic occurrences are common within *Branchinella, Eulimnadia, Limnadopsis, Eocyzicus, Ozestheria* and *Triops*. The grand total is at least 56 species of large branchiopods within the study area.

Not all of the wetlands within the central Paroo were equally speciose (table 5). High diversity in Black Box swamps and claypans is well supported with many sites studied and many samples (tables 1, 5). Poplar Box flats, another variety of treed swamps unique to inland eastern Australia, are also speciose, despite their generally shorter hydroperiods

Table 3. Shield shrimps (Notostraca) of the central Paroo, northwestern New South Wales*

Species	Wetland types with records	Distribution beyond middle Paroo	Examples
Triops sp. A	Black Box swamps	within 500 km	Marsilea Pan
Triops sp. B	Black Box swamps, Poplar Box flats, Claypans	within 1000 km	Marsilea Pan, Turkey Claypan
Triops sp. I	Creek pools	within 250 km	Lower Crescent pool
Triops sp. L	Freshwater lake	Australia wide	Lower Lake Eliza
Triops sp. N	Black Box swamps, Poplar Box flats	within 1000 km	Carols Poplar Box flat
Triops sp. O	Poplar Box flats, Creek pools, Samphires	Within 500 km	Carols Poplar Box flat Lower Crescent pool Roszkos Samphire

*Data from Meusel and Schwentner, 2017 using their notation.

Table 4. List of clam shrimps (Laevicaudata, Spinicaudata, Cyclestherida) recorded in the central Paroo, northwestern New South Wales

Species	Spread in central Paroo	Distribution beyond central Paroo	Regularity of appearance	Habitat range
Lynceus macleayanus (King 1855)	< 5 sites	Australia wide	Some fillings	Clear fresh waters, 3–12 mth hydroperiod
Australimnadia grobbeni Daday, 1925	1 site only	Northern Australia	Rare	Clear fresh waters, 3–12 mth hydroperiod
Eulimnadia australiensis Timms, 2016	< 5 sites	Qld and NSW	Some fillings	Fresh waters of < 3 mth hydroperiod
Eulimnadia beverleyae Timms, 2016	< 5 sites	Endemic?	Some fillings	Clear fresh waters, 1–2 mth hydroperiod
Eulimnadia canalis Timms, 2016	< 10 sites	Endemic?	Some fillings	Fresh waters of < 3 mth hydroperiod
Eulimnadia hansoni Timms, 2016	< 10 sites	Within 250 km	Most fillings	Fresh waters of < 3 mth hydroperiod
Limnadopsis birchii (Baird, 1860)	> 100 sites	Inland Australia	All fillings	All types of fresh waters
Limnadopsis bloodwoodensis Schwentner, Timms and Richter, 2012	3 sites only	Endemic?	Some fillings	Samphire swamps, fresh to hyposaline
Limnadopsis paratatei Schwentner, Timms and Richter, 2012	< 5 sites	Within 250 km	Some fillings	Variety of fresh waters
Limnadopsis parvispinus Henry, 1924	> 50 sites	Inland Qld and NSW	Most fillings	Many fresh waters, esp. Black Box Swamps
Limnadopsis tatei Spencer and Hall, 1896	> 50 sites	Inland Australia	Most fillings	All types of fresh waters
Paralimnadia queenslandicus Timms, 2016	> 20 sites	Inland Qld and NSW	Most fillings	Fresh waters of < 3 mth hydroperiod
Eocyzicus argillaquus Timms and Richter, 2009	< 10 sites	Inland Qld, NSW, adj. SA	Most fillings	Mainly turbid clay pans
Eocyzicus armatus Tippelt and Schwentner, 2018	< 5 sites	Northern and central Australia	Many fillings	Clear fresh and hyposaline waters
Eocyzicus parooensis Richter and Timms, 2005	< 10 sites	Endemic?	All fillings	Hyposaline stages of salt lakes
Eocyzicus phytophillus Tippelt and Schwentner, 2018	< 5 sites	Within 500 km	Most fillings	Vegetated fresh waters, 3–12 mth hydroperiod
Eocyzicus richteri Tippelt and Schwentner, 2018	< 10 sites	Within 1000 km	Most fillings	Turbid waters, inc. claypans and cane grass swamps
Eocyzicus ubiguus Tippelt and Schwentner, 2018	< 10 sites	Widespread	Most fillings	Any freshwater site, but rarely turbid waters
Ozestheria lutraria (Brady, 1886)	< 10 sites	Within 1000 km	Some fillings	Many wetland types
Ozestheria rubra (Henry, 1924)	1 site only	within 1000 km	Freq. unkown	Creek pool
Ozestheria sp. A[2]	< 5 sites	within 1000 km	Freq unknown	Many wetland types
Ozestheria sp. B[2]	1 site only	within 1000 km	rare	Black Box swamp
Ozestheria sp. I[2]	< 5 sites	endemic in Paroo	Freq. unknown	Mainly Black Box swamps, also turbid wetlands
Ozestheria sp. K[2]	1 site only	within 500 km	Rare	Back Box swamp
Ozestheria sp. M[1]	> 10 sites	within 1000 km	Freq. unknown	Many wetland types
Ozestheria sp. N[1]	< 5 sites	within 1000 km	Freq. unknown	Many wetland types
Ozestheria sp. Q[2]	< 10 sites	Australia wide	Freq	Many wetland types
Ozestheria sp. S[2]	< 10 sites	within a 1000 km	unknown	Poplar Box flats
Eoleptestheria nr. *ticinensis* Balsamo-Crivelli, 1859	1 site only		rare	Black Box swamp
Cyclestheria nr. *hislopii*, Baird, 1859	1 site only	Northern Australia	rare	Poplar Box flat

[1]Summarized previously under name *O. berneyi* (Gurney, 1927); [2]summarized previously under the name *O. packardi* (Brady, 1886).

Table 5. Comparison of diversity of branchiopods in the wetlands of central Paroo, northwestern NSW

Wetland Type	No. of sites	No of samp-les	Years of study	No. of fairy shrimp sp.	Dominant species	No. of clam shrimp sp.	Dominant species	Average no. of sp. per sample
Black Box swamps	22	117	Mainly 2010–2021	6	*B. arborea* *B. australiensis*	8	*L. birchii* *L. parvispinus* *O. packardi*	6.41
Poplar Box flats	6	15	Mainly 2010–2021	6	*B. arborea* *B. campbelli*	7	*L. parvispinus* *L. queenslandicus* *O. packardi*	5.86
Claypans	15	55	1998; 2010–2021	7	*B. affinis* *B. lyrifera* *B. occidentalis*	4	*E. argillaquus* *O. lutraria* *O. packardi*	6.27
Lakes	3	33	mainly 2010–2021	5	*B. australiensis* *B. arborea*	5	*O. lutraria* *O. packardi*	3.75
Creek Pools	2	20	1998; 2010–2021	8	*B. australiensis*	8	*L. birchii* *O. packardi*	4.05
Grassy Pools	3	12	1987–2012	4	none	8	*Eulimnadia* spp. *Limnadopsis* spp.	4.58
Salt Lakes	5	33	1987– 2021	3	*P. minuta*	3	*E. parooensis*	1.09

(Timms, in press). The remaining four wetland types are based on few sites, though generally at least 20 samples were taken over the years per site. They are less speciose, certainly the salt lakes, though the situation in creek pools and grassy pools is not as clear. The two creek pools included in this study are the most speciose of the eight initially studied (Timms, 2001) but it is hard to characterize them by a standard aggregation of species as composition is variable as indicated by a total species list of eight species each for both fairy and clam shrimps. These two sites are regularly flushed and though they may have some resident species, many are probably introduced from overflow from other habitat types depending on rainfall distribution. It is possible the data for grassy pools are incomplete as few sites were available for study and they filled so few times. However, their lower number of anostracans then elsewhere may be valid due to the apparent adverse influence of thick vegetation on anostracan life styles.

Some species are habitat specialists, others more catholic. While *Parartemia minuta* is recorded as a salt lake specialist, it is found in only two of the five salt lakes studied, but there in large numbers. The clam shrimp *Eocyzicus parooensis* is more widely distributed in the salt lakes (four sites out of five), but it appears only in the initial brief freshwater and

Table 6. Number of co-occurences of branchiopods in different types of wetlands

No. of species	Black Box Swamps	Poplar Box Flats	Claypans	Freshwater Lakes	Creek pools	Grassy Pools	Salt Lakes
0	0	0	0	0	0	0	9
1	0	0	0	0	0	0	14
2	1	0	0	6	3	2	8
3	2	1	0	8	3	4	2
4	6	1	3	10	6	3	
5	21	4	8	6	6	3	
6	48	4	21	3	2	2	
7	20	3	17				
8	12	2	6				
9	5						
10	2						

subsaline stages. *Limnadopsis bloodwoodensis* is found only in the freshwater and subsaline early stages of samphire swamps. *Eocyzicus argillaquus* is characteristically found only in quite turbid waters, hence its dominance in many claypans. *Eulimnadia* spp occurs in sites with short hydroperiods and is rarely found beyond the grassy pools and Poplar Box flats. *Paralimnadia* is more common and widespread, but this may be an artifact due to its wider habitat preferences and longer life cycle. Among the anostracans, *Branchinella lyrifera* and *B. occidentalis* arecharacteristic of the turbid claypans, but occasionally are found also in other moderately turbid sites. *Branchinella campbelli* is usually restricted to the clear waters of Poplar Box flats and *B. wellardi* to all clear waters.

Limnadopsis birchii is also catholic, appearing in almost all sites in major fills, including briefly in the freshwater and subsaline stages of some salt lakes! Normally it is a characteristic of Black Box swamps. *Limnadopsis parvispinus* is characteristic of the two types of treed swamps, so given the abundance of treed swamps, it too was common. The most common anostracans are *Branchinella australiensis* and *B. arborea.* Both are associated with mildly turbid waters, a common condition in Black Box swamps, freshwater lakes, creek pools, and claypans at least on initial filling.

Discussion

Fifty-six species — of which thirty-eight are formally described — are known from Bloodwood, Tredega and Muella Stations and were all found in an area of nearly 500 km^2. If the southwestern half of Bloodwood Station (ca 280 km^2) with by far the most wetlands is considered alone the list is still 34 described species (including all 16 anostracans). Timms and Sanders (2002) and Timms and Richter (2002) originally studied an area of 2000 km^2 and counted 29 species of large branchiopods at that time. Many species were overlooked due to limited taxonomic understanding at that time. If the whole of Queensland and the adjacent northern quarter of NSW from 32° N (area 2.02 x 10^6 km^2) which includes the Paroo study area are included, the list increases to 83 species of which 52 are formally described (table 7) with the proviso there are areas within this vast domain not yet sampled.

Variations in diversity between continents (Brendonck et al., 2008; Rogers, 2009, 2014 a, b, 2015; Rogers and Timms, 2014) usually have complex contributing factors including biogeographical bases and are beyond detailed contemplation here. It is those for local

Table 7. Large branchiopods in the central Paroo (Bloodwood, Tredega, Muella Stations) and also in Queensland and far northern New South Wales

Taxonomic group	Paroo species	+ undescribed	All Qld + Nth NSW (N of 32°S)	+ undescribed
Branchinella	13	–	17	–
Australobranchipus	1	–	2	–
Streptocephalus	1	–	1	–
Parartemia	1	–	1	–
Lynceus	1	–	2	1
Eulimnadia	4	4	5	9
Paralimnadia	1	–	5	–
Limnadopsis	5	–	6	–
Australimnadia	1	–	1	–
Eoleptestheria	1	–	1	–
Eocyzicus	6	–	8	–
Ozestheria	2	8	2	10
Cyclestheria	1	–	1	1
Triops	0	6	0	10
Total	38	18	52	31

Note. Based on Meusel and Schwentner, 2016; Schwentner, 2020; Schwentner et al., 2009, 2012 a, b, 2013, 2014, 2015; Timms, 2009, 2015; Timms & Schwentner, 2012.

Table 8. Large Branchiopod species richness in areas about the same size as the central Paroo

Studied area	Area km^2	No. of samples	No. of sp. Anostraca	No. of sp. Notostraca	No. of sp. clam shrimps	Maximum syntopy	Reference
Greater Bloodwood Australia	440	117	16	8	40	10	This study
Save Conservancy Zimbabwe	150	36	8	1	7	12	Nhiwatiwa et al., 2014.
Chaouia Plain Morocco	550	59	7	2	2	10	Thiéry, 1991
Kiskunság NP Hungary	500	89	6	2	3	5	Boven et al., 2008
Morava Floodplain Austria and Slovakia	500	–	3	2	5	–	Schernhammer, 2020 and pers. com.
Part of KwaZulu-Natal, South Africa	1100	10	7	1	6	10	Hamer and Appleton, 1991
Doñona NP Spain	1200	–	6	1	2	4	Diaz-Paniagua et al., 2010
Melenic, Banat prov. Serbia	0.003	–	5	2	3	7	Petrov and Cvetković, 1997

areas (say less than about 1000 km^2) where marked discrepancies in diversity can occur and which often can at least be partly explained by various ecological factors, including climate, habitat characteristics and biotic factors (Hamer and Appleton, 1991; Rogers, 2014 a, b; Rogers and Timms, 2014; Petrov and Cvetković, 1997). Some of the more speciose examples are listed in table 8. Of these about 14 species in 500 to 1000 km^2 seems close to a maximum diversity and generally contributed to by 50 % anostracans, 7 or 14 % notostracans and the remainder spinicaudatans (table 8) and sometimes a laevicaudatan (Roessler, 1995). Instantaneous coexistences (syntopy) for individual pools average less than five (table 7 and table 4 in Nhiwatiwa et al., 2014) but can reach 10, and rarely, 12 species. While sites with these numbers could be considered hotspots, it is mainly Nhiwatiwa et al. (2014) who consider their data from Save Conservancy, Zimbabwe indicate a hotspot of diversity with its list of 16 species and maximum syntopy of 12 species. However, all these implied and outspoken claims fade into insignificance compared with the diversity in the central Paroo, Australia (tables 2, 3, 4, 7) with its 56 species or ~10 % of the globally known diversity of large Branchiopoda in this comparably small region. Surely this is a "super" hotspot of large branchiopod diversity. Interestingly the maximum instantaneous syntopy of species is still in the same order of magnitude as other hotspot contenders, i. e. about 10 to 12 species. This figure may be the maximum possible for syntopic species given their various separable niches (Thiery, 1991; Nhiwatiwa et al., 2014).

The high species diversity in the middle Paroo is based on its high habitat diversity, with at last seven distinct types of wetlands all within close proximity (tables 1, 5; figs. 1, 2). These have different ranges of hydroperiod, turbidity, salinity, and habitat complexity which influence diversity of the large branchiopod inhabitants (Timms and Sanders, 2002; Timms and Richter, 2002). Most other speciose groups of sites explain their diversity on differences in areas, depths, and hydroperiod (e. g. Hamer and Appleton, 1991; Petrov and Cvetković, 1997). Changes during a seasonal filling (e. g. Melanic ponds in Serbia, Petrov and Cvetković, 1997) are of little importance in the Paroo, though two instances occur regularly there. In the saline lakes there is early colonization by *Eocyzicus parooensis* followed by *Parartemia minuta* in the hypersaline lakes and by *Branchinella buchananensis* in the mesosaline Gidgee Lake. Also in the claypans, predation by *Branchinella occidentalis* on other anostracans could influence the proportions of species present during a filling, though this has not been specifically detailed (Rogers and Timms, 2017; Hancock and Timms, 2002).

Sometimes diversity is enriched by the area being the junction of biogeographic provinces as it may be in the Zimbabwe example (Nhiwatiwa et al., 2014). This is not the case in the Paroo, but the rich branchiopod fauna across Australia provides a larger than normal pool of species that contributes to Paroo's elevated diversity (Rogers and Timms, 2014; Schwentner et al., 2015 a). Four species are apparently endemic to the central Paroo, *Eulimnadia beverleyae*, *E. canalis*, *Eocyzicus parooensis* and *Limnadopsis bloodwoodensis* while a few more like *Branchinella angelica, Eulimnadia hansoni* and *Limnadopsis paratatei* and have limited distributions beyond the Paroo (tables 2, 4). By far the majority of species have a wide distribution, sometimes extending to central or even Western Australia. It is likely that the extensive diversity we observed in the central Paroo has not necessarily evolved in this small area, but that it is an amalgam of species that colonized this area over a long period of time (Rogers and Timms, 2014). Their ability to successfully colonize the central Paroo catchment was probably facilitated by its rich diversity of habitat types.

It remains to consider just what constitutes a hotspot in large Branchiopod diversity. The situation in the Paroo is exceptional and to consider it as the only hotspot worldwide in large branchiopod diversity detracts from other diverse places. In many countries the number of branchiopod species may exceed the figures dealt with here, but their area is much, much larger. Two examples will suffice: India has about 22 species of anostracans found over 3.3 million km^2 (Padhye et al., 2017) and southern Africa (i. e. the area south of the Kunene, Okavango and Zambezi rivers) has 46 species of large branchiopods over an area of 3.8 million km^2 (Hamer and Brendonck, 1997). Whole biogeographic regions not surprisingly have many species of all branchiopod groups, e. g. about 200 in the Nearctic (Brendonck et al., 2008; Rogers, 2009). There has been no suggestion that these large areas are termed hotspots, no matter what their diversity or specific area. Instead the focus is on smaller areas or individual sites, more or less about the size considered here, i. e. up to about 1000 km^2. For these, a fauna of more than about 14 species and a maximum instantaneous coexistence of 8–10 or more species, as listed in table 7 and also in table 4 in Nhiwatiwa et al., 2014 is unusual and herewith is considered a hotspot for diversity. Such an acceptance would make the Paroo situation a super hotspot!

Conclusions

A 35 year study of 56 sites of seven types of wetlands (table 1) within a 500 km^2 part of the central Paroo in northwestern NSW yielded 38 described species and a further 18 undescribed (but molecularly defined) species of large branchiopods (table 7). These figures are unprecedented elsewhere in areas of similar size. Many species occur characteristically in each hydroperiod but some appeared only rarely. Instantaneous species per wetland type averaged from 6.41 in Black Box swamps to 1.09 in salt lakes (table 5). Maximal syntopic species ranged from 10 in Black Box swamps, eight in Polar Box flats and claypans, six in freshwater lakes, creek pools and grassy pools and just three in salt lakes (table 6).

While a rich continental fauna contributed to these figures, the main reason is the variable seven distinct wetland types differentiated by salinity, turbidity, hydroperiod and habitat complexity so that the component species select distinctive habitats most suited to their ecological needs.

Elsewhere in the world it is common to record up to about six syntopic species per wetland and about twice that number in the wider district (defined here at about 500 km^2). Some wetland districts record eight-12 syntopic species, and < 20 species district wise (table 8), this apparently being the upper limit imposed by non-overlapping niche requirements. Such situations are unusual and perhaps termed hotspots. If so, then the Paroo with its extreme alpha diversity is a super hotspot.

BVT is indebted to the Hansons of Bloodwood and the Batys of Muella and Tredega for access to their properties and for various other kind logistic help over the years. MS and DCR also visited the area and were most appreciative of this hospitality.

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Received 21 September 2021
Accepted 3 November 2021