

Diversity patterns of subterranean invertebrate fauna in calcretes of the Yilgarn Region, Western Australia

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Abstract. Calcrete aquifers are unique groundwater habitats containing stygobiontic species endemic to each calcrete. The evolutionary history of stygofauna suggests the calcretes in Western Australia contain multiple ancient lineages, yet populations experience episodic variation in rainfall patterns, with little-known ecological consequences. The aim of the present study was to document stygofaunal diversity patterns and determine whether they are influenced by rainfall events. The average taxon richness in boreholes peaked shortly after periods of high rainfall, and when dominant taxa were excluded, evenness decreased after periods of both high and low rainfall, indicating that dominant taxa are an important factor in driving the system. Strong abundance–distribution relationships reflected the commonality of taxon groups; common taxon groups had broad distributions and high abundance levels, whereas rare taxon groups had small distributions and low abundance. After periods of intermediate and low rainfall, taxon groups had narrower distributions and the maximum number of individuals per borehole was lower. Finally, the majority of boreholes did not show changes in evenness over the 11-year study period, suggesting a reasonably stable ecosystem with episodic fluctuations that can be attributed to rainfall events. The results of the present study indicate that diversity patterns within boreholes are driven episodically by both external and internal factors, such as rainfall and rapid borehole dominance respectively.

Received 10 January 2017, accepted 16 June 2017, published online 30 August 2017

Introduction

Spatiotemporal patterns of diversity are highly dependent on both habitat and species traits (Chase and Leibold 2003). In general, species diversity increases with increasing habitat heterogeneity (MacArthur and MacArthur 1961) because species can occupy and exploit different niches. However, in fragmented habitats, diversity tends to decrease as dispersal and resource availability becomes limiting for new colonisation events, and competition limits population growth (Mouquet and Loreau 2003; Munguia *et al.* 2011; Munguia 2015). Patchiness in small fragmented landscapes can facilitate specialisation that may otherwise not occur and can result in the evolution of endemic species (MacArthur and MacArthur 1961). Fragmentation can also lead to some species being more abundant than others in particular environments and potentially lead to the formation of areas with only one taxon group present (MacArthur and MacArthur 1961; Davies and Margules 1998).

A unique fragmented habitat comprising groundwater calcretes in the Yilgarn region of central Western Australia was recently shown to contain a diverse ecosystem of groundwater subterranean animals known as stygofauna. These groundwater calcretes formed in the arid Yilgarn region where the mean annual rainfall is below 200 mm and potential evapotranspiration exceeds 3 m (Mann and Horwitz 1979). Such groundwater habitats are generally entirely enclosed, having been deposited from the groundwater as it approaches base level close to playas (salt lakes) in palaeodrainage systems (Humphreys 2001). The Yilgarn region contains over 200 large isolated calcretes, with several phylogeographic studies having demonstrated that species are each restricted in their distribution to a single calcrete (Cooper *et al.* 2002, 2007, 2008; Leys *et al.* 2003), an endemism that can be attributed to the insular form of the calcretes and the nature of the intervening regolith (Anand and Paine 2002) likely preventing dispersal between calcretes (Guzik *et al.* 2010).

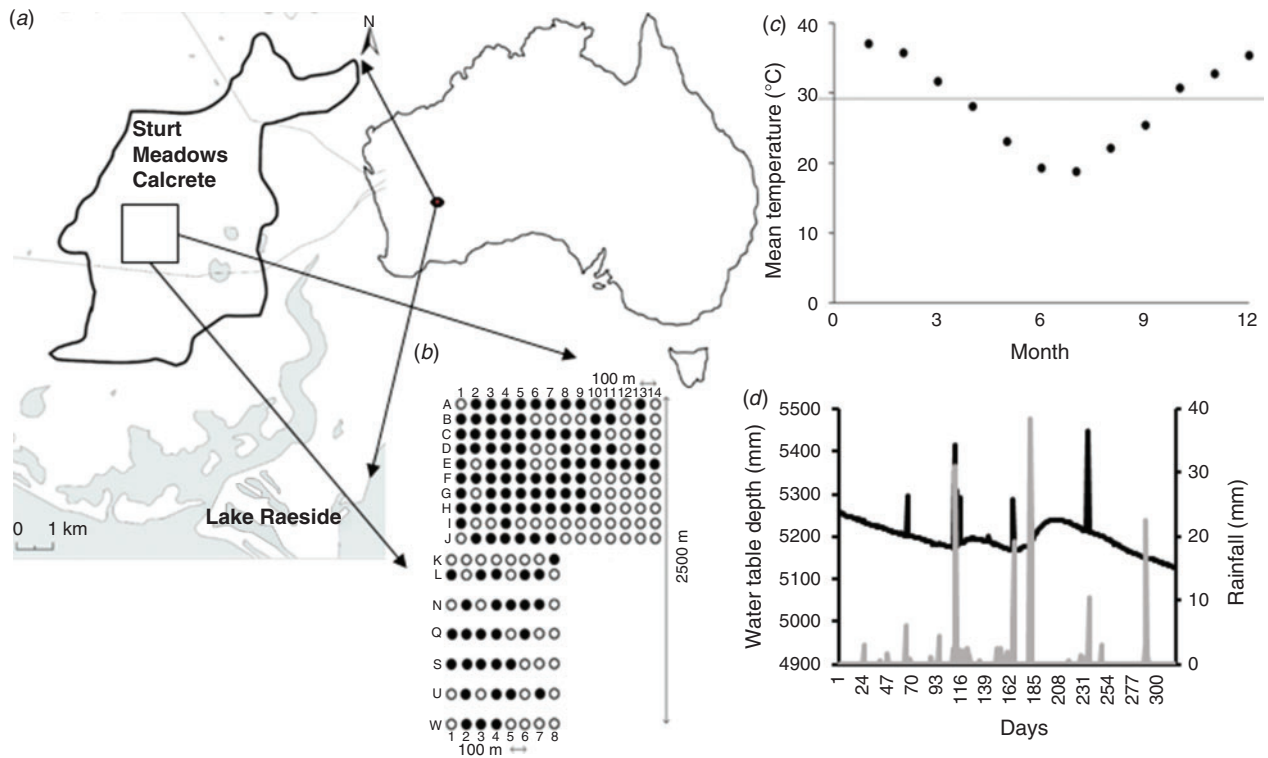


Fig. 1. (a) Location of Sturt Meadows within Australia and (b) the study area with sampled boreholes (black circles). (c) Climatological data showing mean temperature. The horizontal line indicates mean temperature for the year. (d) Borehole monitoring for recharge over a 12-month period at one borehole location, showing water depth (black line) and rainfall events (grey line).

In subterranean habitats, the trophic structure is simplified relative to epigeal habitats owing to the absence of primary producers, save in rare systems that have chemoautotrophic primary producers and parasites (Gibert and Deharveng 2002), and sparse energy resources (Huppopp 2000; Culver and White 2005). Because subterranean ecosystems are continuously dark, micro-organisms (bacteria and fungi) are usually dependent on organic carbon for energy capture. The energy that does enter the system is primarily mediated by the movement of water, and the exogenic organic matter carried in by water is, in turn, thought to be affected by both rainfall and plant growth (Deharveng and Bedos 2000; Humphreys 2012). Rainfall in the Australian arid zone is episodic both within and between years (Mann and Horwitz 1979), and amounts equivalent of mean annual rainfall may occur in a single event or, in contrast, drought can span several years. As such, carbon inputs into the calcrete aquifers are also likely to be highly variable, but the ecological effect of this variability on stygofaunal communities is unknown.

Herein we document stygofauna diversity patterns within a calcrete located at the Sturt Meadows pastoral property in central Western Australia, which contains a suite (~100) of boreholes that enable assessment of spatial and temporal ecological changes across part of the aquifer (Fig. 1). Because the system experiences episodic rainfall events followed by long periods of no precipitation, we focused on how rainfall may affect diversity sampled within boreholes. We calculated the number of taxon groups and faunal evenness occurring within

individual boreholes and estimated changes in common and rare taxon groups driven by rainfall patterns. Given the boom-and-bust population dynamics observed in other arid zone aquatic systems (e.g. Lake Eyre aquatic invertebrates; Davis *et al.* 2013), we explored whether sampled boreholes were dominated by a single taxon group. Given the periodic changes in the water table and the heterogeneous structure of the calcrete (Guzik *et al.* 2009; Bradford *et al.* 2013), we hypothesised that specific taxon groups may become the dominant group within a borehole because of reduced connectivity during low water table periods. We discuss two potential mechanisms arising from the observed rainfall patterns that could affect the dynamics of this unique subterranean ecosystem: (1) changes in connectivity within the calcrete due to fluctuations in the water table affecting dispersal; and (2) nutrient replenishment driven by rainfall. Ultimately, these proximate, episodic mechanisms could be the drivers behind the high levels of endemism.

Materials and methods

The study site was at a calcrete located on the Sturt Meadows pastoral station in the Yilgarn region, Western Australia (Fig. 1), with an area of ~43 km². The surface vegetation is an open *Acacia* woodland with lowland shrubs. In a few places, the calcrete is exposed on the surface, whereas for the most part the top of the calcrete is up to 2 m below the surface (Allford *et al.* 2008; Bradford *et al.* 2013). Bores were originally drilled for mineral exploration to a depth of 10.3 m and a diameter of

Table 1. Sampling data information from 2004 to 2015 including month, period, rainfall and number of boreholes sampled

Month	Year	Period	Number of boreholes sampled	Rainfall in the 30 days before sampling (mm)
March	2004	High rainfall	14	68.4
September	2004	Low rainfall	66	3.6
March	2005	Low rainfall	26	2.6
April	2005	Low rainfall	64	1.4
March	2006	High rainfall	54	57.6
July	2006	Low rainfall	52	0
November	2006	Intermediate rainfall	52	10.4
February	2007	High rainfall	53	59
May	2007	Intermediate rainfall	54	27
May	2011	Intermediate rainfall	23	11.2
April	2015	Intermediate rainfall	53	12

100 mm. Two bore grids were drilled, a northern and a southern grid. The northern grid has bores spaced at 100 m in each direction and is 1.4×0.9 km; the southern grid has bores spaced at 100 m east–west and 200 m north–south and is 1.2×0.9 km (Fig. 1). The present study site covered both grids and an area of ~ 2.34 km². The current condition of the bores allows access to the water table from ~ 1.9 to 4.0 m below the surface, with water depth varying between 0.4 and 8 m among each of the 116 bores that have been accessed to date across the bore grid (Allford *et al.* 2008).

The Sturt Meadows calcrete stygofauna consists of 18 known macroinvertebrate taxa. There is a sister species triplet of dytiscid diving beetles *Paroster macrosturtensis*, *P. mesosturtensis*, and *P. microsturtensis* (Watts and Humphreys 2006), three species of chiltoniid amphipods, namely *Yilgarniella sturtensis*, *Scutachil-tonia axfordi* and *Stygochil-tonia bradfordae* (Bradford *et al.* 2010; King *et al.* 2012), at least four divergent lineages of oligochaete worms (Bradford *et al.* 2010) and eight copepod species (T. Karanovic, pers. comm.). There are also trogllobiont species present above the water table, including two oniscidean isopod species (*Troglarmadillo* sp. and *Paraplatyarthus occidentonicus*; Javidkar *et al.* 2015, 2017), at least one mite species (Acari), one centipede species (Chilopoda), one palpi-grade species (*Eukoenia guzikae*; Barranco and Harvey 2008) and one springtail species (Collembola; Bradford *et al.* 2010).

The study comprised 11 sampling events at the Sturt Meadows calcrete: 2 in 2004 (March and September), 2 in 2005 (March and April), 3 in 2006 (March, July and November), 2 in 2007 (February and May) and 1 each in 2011 and 2015 (May and April respectively). All samplings from 2004 to 2015 were undertaken using a small weighted plankton net (250 μ m) hauled through the water column. In addition, sampling between 2005 and 2007 used a pump to retrieve samples. Previous research has shown that these two methods do not differ in their sampling intensity (Allford *et al.* 2008). The sampling effort from 2004 to 2015 resulted in the collection of 9118 stygobitic macroinvertebrate specimens from 512 sampling events from 116 boreholes (with 78% of boreholes sampled at least twice). Identification to family level for the amphipods, copepods and oligochaetes and species level for the beetles was performed in the field, and samples were stored in liquid nitrogen, or in 75 or 100% ethanol. Copepods and oligochaetes could not be identified to species level in the field because of a lack of taxonomic

information for these groups. Morphological descriptions of three amphipod species were recently published by King *et al.* (2012), but these were not available for the early collections, where specimens had been discarded, so we were unable to identify the amphipods to species level. Therefore, our analyses clustered copepod, amphipod and oligochaete species each into distinct functional groups because these species usually share similar trophic levels (Gibert and Deharveng 2002; Bradford *et al.* 2014).

Environmental data as specified in Watts and Humphreys (2006) were collected in March 2006 and April 2015 and obtained while invertebrate samples were being collected. The nearest pertinent meteorological data were sourced from the Australian Bureau of Meteorology, namely rainfall events at Sturt Meadows from 2004 to 2015 and average temperature data from two different stations located 1.4 km apart in Leonora (~ 42 km from the Sturt Meadows calcrete) because neither station had complete records for the 2004–15 period. The average pan evaporation is 2400 mm year⁻¹, which far exceeds the average yearly rainfall of just over 200 mm.

Data analysis

Monitoring water table levels in the aquifer from July 2006 to May 2007 indicated that recharge occurred shortly after a major rainfall event, with low rainfall events (<10 mm) having little or no effect on groundwater levels, rainfall events between 10–30 mm resulting in a moderate increase in groundwater levels and rainfall events >30 mm leading to a major recharge of the aquifer (Fig. 1). Therefore, we defined low-, intermediate- and high-rainfall periods based on total rainfall in the 30 days before sampling (Table 1). Low rainfall was defined as <10 mm of rain in the previous 30 days, intermediate rainfall was defined as <30 mm of rainfall in the previous 30 days and high rainfall was defined as ≥ 30 mm of rainfall in the previous 30 days.

We first compared taxon richness and evenness among the three rainfall periods (high, intermediate and low rainfall) using mixed models (e.g. Darnell *et al.* 2015). Rainfall period was used as a fixed factor and sampling year was used as a random effect to account for year-to-year variability. Borehole occupancy, including unoccupied sites, was compared among rainfall periods for each taxon group using a contingency test to contrast periods and a Cochran–Mantel–Haenszel test to assess among-year differences in the number of sites occupied.

To determine the effects that the different rainfall events had on the various taxon groups, site occupancy was calculated for all taxon groups. The average number of individuals present was calculated for each rainfall period. The taxon groups were ordered in the graph by their rank site occupancy in the high-rainfall period.

Taxon group abundance–distribution patterns were compared for each of the three rainfall periods. An analysis of covariance (ANCOVA) tested differences in the relationship between maximum abundance within boreholes against the number of boreholes occupied by each taxon group. A positive relationship between borehole abundance and distribution was expected because it is a common pattern across systems and taxa (Magurran 1988; Munguia 2014). Therefore, we followed the ANCOVA with individual regressions to test whether the slope of abundance to distribution was different from zero in each of the three rainfall periods. Data were log transformed to meet parametric assumptions.

Given the hypothesis that dominant taxa were driving the system, we further investigated the observed sites where a single taxon group was exclusively found (henceforth referred to as ‘dominant taxon sites’). To determine whether all taxon groups were equally likely to become dominant, the proportion of sites with dominant taxon groups from the total number of sites in a given sampling period averaged across each rainfall period was calculated and a Chi-Square test was used to compare their frequency across the three rainfall periods.

To test changes in long-term diversity patterns, the 18 boreholes that were repeatedly sampled most often over the 11 sampling events were selected and evenness was compared in both 2006 and 2015 using a paired *t*-test. Finally, a principle component analysis (PCA) was used to associate environmental parameters of each individual borehole (depth, O₂, temperature, pH and salinity) from each of the 2006 and 2015 surveys. Principal components were rotated using varimax and Factor 1 was used to represent the environmental gradient present in boreholes. Next, a mixed model tested the effect of environment (as PCA Factor 1) on richness, total abundance and evenness using year as a random effect. All analyses were performed in JMP (SAS Institute, Cary, NC, USA).

Results

Stygofaunal diversity in boreholes differed among the three rainfall periods. Diversity was lowest during the low-rainfall period (Fig. 2a) and greatest during the high-rainfall period ($F = 8.057$, $P = 0.0004$), with year-to-year variation accounting for 13% of the variance. Evenness also differed among rainfall periods, with boreholes showing lowest evenness during the high-rainfall period (Fig. 2b) and highest evenness during the intermediate- and low-rainfall periods ($F = 7.316$, $P = 0.001$), with year-to-year variation accounting for 7.6% of the variance. When removing sites with a single dominant taxon group, both the high- and low-rainfall periods had the lowest evenness (Fig. 2b) and the intermediate-rainfall period maintained the highest evenness ($F = 10.029$, $P < 0.001$), with year-to-year variation accounting for 6.7% of the variance.

The effect of rainfall on the distribution of different taxon groups varied (Fig. 3). For example, copepods occupied a large

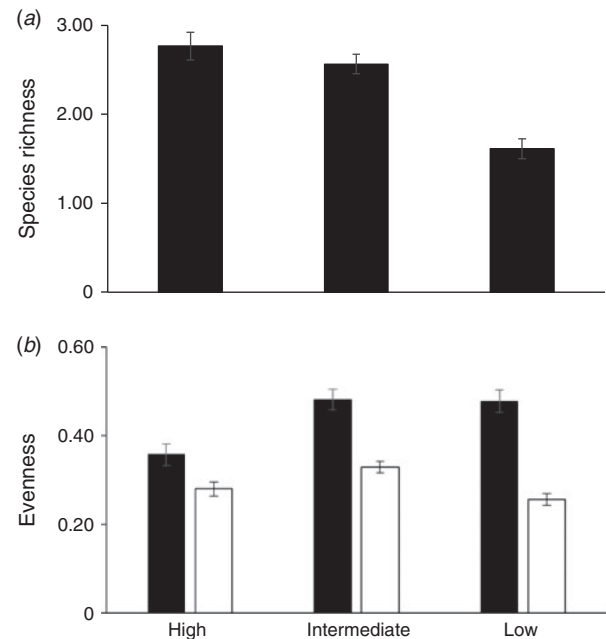


Fig. 2. (a) Species richness and (b) evenness for the three different episodic phases in Sturt Meadows calcrete. In (b), black columns represent total evenness, whereas open columns represent evenness with dominant taxa removed. Data are the mean \pm s.e.m.

proportion of sites during high- and intermediate-rainfall periods (57 and 51% respectively), but few sites (16%) during low-rainfall periods. In contrast, the dytiscid beetle *P. microsturtensis* did not significantly change proportional occupation of sites with changes in rainfall period (0, 2 and 1.5% for high, intermediate and low respectively, Table 2).

The more boreholes a taxon group occupied, the greater its abundance (ANCOVA, $F = 4.46$, $P = 0.011$; Fig. 4), yet this pattern varied within each rainfall period. A positive relationship between rainfall events and maximum abundance was observed in each rainfall period (Fig. 4). During high-rainfall events, a species' maximum abundance was independent of its distribution among boreholes (Fig. 4a; $F = 3.04$, d.f. = 1, $P = 0.11$, $R^2 = 0.43$). In the intermediate-rainfall season, although there was a tendency for a relationship between maximum abundance and distribution in the intermediate-rainfall season, it did not reach statistical significance (Fig. 4b; $F = 6.22$, d.f. = 1, $P = 0.054$, $R^2 = 0.55$), whereas during the period of low rainfall a significant relationship was found between maximum abundance and distribution (Fig. 4c; $F = 11.21$, d.f. = 1, $P = 0.02$, $R^2 = 0.69$). Copepods had the greatest abundance levels during high- and intermediate-rainfall periods, yet they did not affect the overall results of the regressions.

The proportion of sites that had dominant taxon groups varied among rainfall periods ($\chi^2 = 30$, $P < 0.05$; 10.7% during high rainfall, 37.6% during intermediate rainfall and 30% during low rainfall; Fig. 5). For sites that had dominant taxon groups, these groups were mainly either amphipods or copepods. However, dominance shifted; during intermediate- and high-rainfall periods, copepods dominated; during low-rainfall periods amphipods dominated.

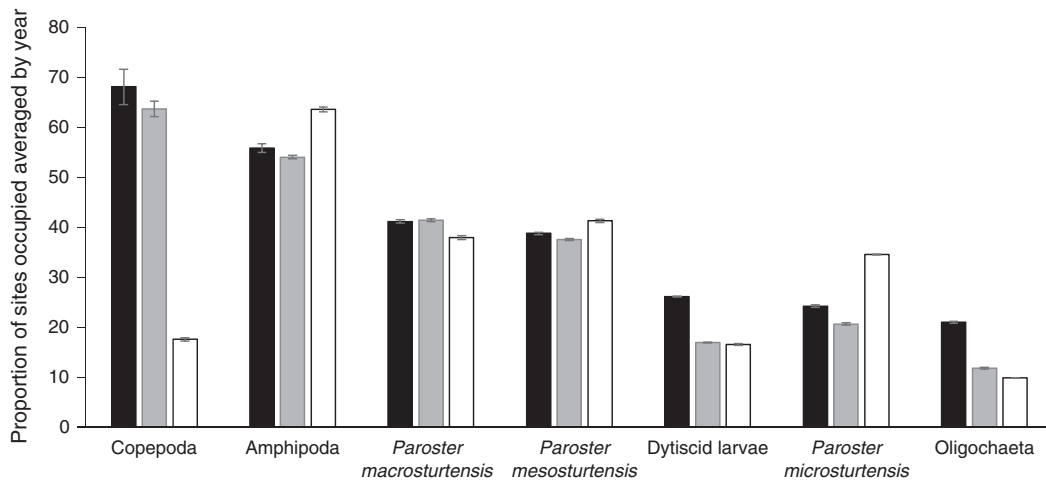


Fig. 3. Relative abundance calculated by the average number of individuals by year by high rainfall (black columns), intermediate rainfall (grey columns) and low rainfall (white columns) by the seven different species groups in Sturt Meadows calcrete. Data are the mean \pm s.e.m.

Table 2. Chi-Square distribution tables calculated for the relative abundances of each taxon group from each rainfall period. A Cochran–Mantel–Haenszel (CMH) test was used to assess among-year differences in the number of sites occupied (Fig. 3)

Taxon group				CMH test		
	d.f.	χ^2	<i>P</i> -value	χ^2	d.f.	<i>P</i> -value
Copepoda	2	137.697	<0.0001	48.152	2	<0.0001
Amphipoda	2	4.804	0.091	4.295	2	0.117
<i>Paroster mesosturtensis</i>	2	4.605	0.100	3.393	2	0.183
<i>Paroster microsturtensis</i>	2	1.962	0.374	7.387	2	0.024
Dytiscidae	2	6.259	0.0437	12.413	2	0.002
<i>Paroster macrosturtensis</i>	2	8.675	0.0131	0.279	2	0.869
Oligochaeta	2	19.213	<0.0001	10.733	2	0.005

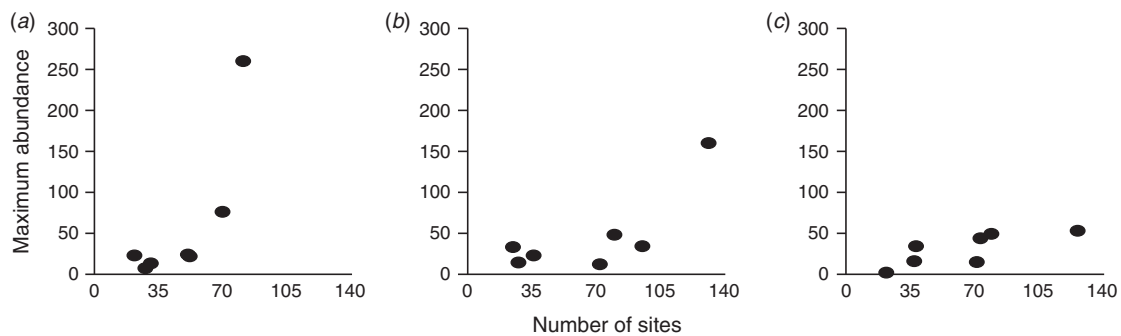


Fig. 4. Maximum abundance for the total number of individuals over the entire sampling period by borehole, for periods with (a) high, (b) intermediate and (c) low rainfall.

Borehole diversity remained stable between 2006 and 2015 (Fig. 6), with evenness not differing between these 2 years (paired *t*-test, $t = 0.77$, $P = 0.45$), and remaining reasonably low (J' (evenness) = 0.32 and 0.39 in 2006 and 2015 respectively). There were four sites that showed increases in evenness, and this pattern was driven by the dominant taxon groups in 2015.

Boreholes showed consistency in environmental gradients between the 2 years of 2006 and 2015 (Table 3). In both years, an environmental gradient was produced in PC Factor 1 (PC1) from high temperature and pH to high salinity and greater depth (Table 3). Oxygen did not contribute greatly to this gradient; instead, it was influential on an orthogonal gradient (PC2; Table 3). Taxon richness increased with the environmental

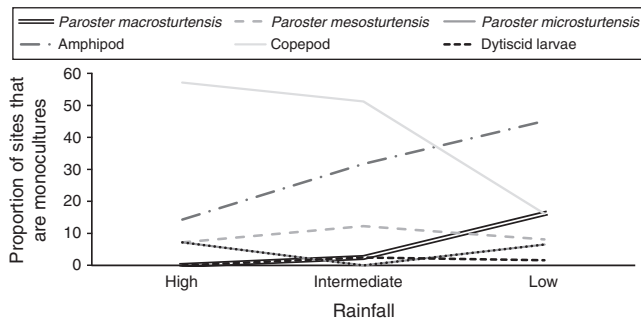


Fig. 5. Proportion of sites by taxon group that were present as dominant taxa (only one taxon group present in an individual borehole).

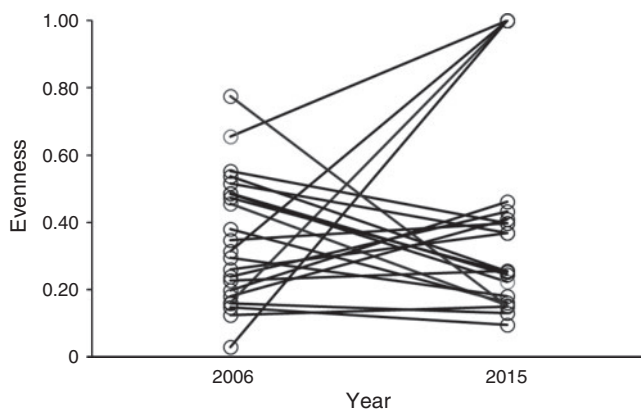


Fig. 6. Species evenness (J') of the 20 most sampled boreholes of the total sampling period in 2006 and 2015.

gradient ($F = 4.11$, $P = 0.046$) where year explained only 0.8%, of the total variance (Fig. 7a, b). Similarly, evenness dropped as the scores on PC1 increased ($F = 5.65$, $P = 0.02$) and year did not explain any of the variance in the model (Fig. 7c, d). However, these relationships were weak because environment only explained a small proportion of the variation in either taxonomic richness or evenness (Fig. 7).

Discussion

At Sturt Meadows, the subterranean invertebrate community sampled within boreholes exhibited shifts in composition with an increase in taxon richness during periods of high and intermediate rainfall. It also showed periods of high taxon evenness during times of intermediate and low rainfall after sites with a single dominant taxon group were excluded from the analyses. Variation in community composition appears to be driven to a large extent by the dominant taxon groups and, in particular, copepods. The proportion of sites that had dominant taxon groups decreased during high-rainfall periods, whereas the composition of dominant taxon sites also changed with rainfall period. This system has dynamic variation that is determined by rainfall. However, evidence from long-term temporal patterns suggests that over long periods of time the system is also stable.

Significant precipitation events and subsequent aquifer recharge increased borehole occupancy. After moderate to large

precipitation events, the water table in the calcrete increased (Fig. 1), possibly leading to easier movement between different areas of the calcrete. After these rainfall events, the proportion of sites that contained dominant taxon groups decreased, suggesting that precipitation events affect taxon group composition of individual boreholes. Because the timing and amount of rainfall vary, we suggest that the connectivity of the calcrete changes and stochastic dispersal events are likely to play a role in the frequency and abundance of taxon groups within individual boreholes. When the water table decreases, taxa may become isolated at specific locations and concentrated into a smaller volume of water. Habitat heterogeneity, possibly resulting from porosity and water chemistry changes, is also likely to affect species composition in these subterranean systems.

Water chemistry can be important in structuring invertebrates in fresh water, with studies detailing a decrease in taxon richness where water chemistry is extreme (Heino 2000), for example when the pH is below 5 or salinity is >1.5 (calculated from Reeves *et al.* 2007). Conversely, except for salinity, water chemistry seems to have remarkably little effect on the distribution of ostracods in groundwater systems of the Pilbara Region of Western Australia, including in calcretes (Reeves *et al.* 2007), suggesting that individual taxonomic groups may show idiosyncratic responses to water chemistry. High pH and low oxygen concentrations create thresholds that can cause local extinctions by changing prey abundance or nutrients in the water column (Adlassnig *et al.* 2012). Although the distribution of species in calcretes is affected by rainfall, it is also possible that other factors, such as the spatial heterogeneity of the calcrete due to a fluctuating water table, provide niche space availability and the potential for refugia in deep calcrete deposits, as well as extinction of populations in shallow calcrete areas (Bradford *et al.* 2013). Potentially, this could result in temporary or long-term isolation of species, thus affecting their distribution and abundance.

The Western Australian calcretes have provided habitat for stygofauna for millions of years. The isolation of these calcretes following post-Miocene aridification of the Australian continent has been inferred from the distribution of multiple obligate stygobiotic lineages and molecular phylogeographic studies (Cooper *et al.* 2002; Leijts *et al.* 2012). Owing to the long-term stability and isolation of the calcretes, and the long evolutionary history of their resident communities, we would expect localised borehole extinctions and year-to-year variation. However, rainfall events cause rapid and extreme changes to the environment and a platform for environmental variation.

The chemocline of the water table within calcretes is expected to support a complex microbiological community, based on studies of similarly complex anchialine systems (Humphreys *et al.* 2009). Salinity in groundwater calcretes increases towards groundwater base level, typically as it moves towards a salt lake. At the Sturt Meadows study site, salinity increases across the calcrete towards Lake Raeside (Humphreys *et al.* 2009). Infiltration of rainfall carrying particulate organic carbon and dissolved organic carbon into the calcrete would affect the microbiological community, which is likely to be the lowest trophic level in the food chain. Changes to the composition and abundance of the microbial community would potentially cascade up the system, affecting the invertebrates and their location and abundance.

Table 3. Principal component analysis loadings of the environmental parameters for Factors 1 and 2 in 2006 and 2015
Numbers in parentheses are the percentage variance explained by each factor. Salinity was measured on the practical salinity scale (PSS)

	2006		2015	
	Factor 1 (37.77%)	Factor 2 (29.95%)	Factor 1 (47.16%)	Factor 2 (25.34%)
Temperature (°C)	-0.562	-0.741	0.927	-0.026
pH	-0.502	0.384	0.663	0.329
Salinity (PSS)	0.753	-0.055	-0.465	-0.629
O ₂ (mg L ⁻¹)	-0.202	0.890	-0.101	0.872
Depth (m)	0.845	0.079	-0.912	-0.015

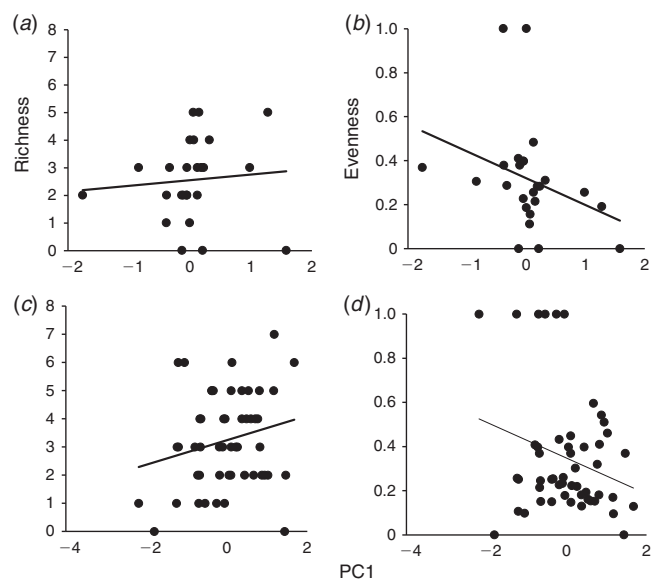


Fig. 7. (a, b) Species richness in 2006 (a) and 2015 (b) by the environmental factors calculated into principal component (PC) 1 and then rotated and depth excluded. (c, d) Species evenness in 2006 (c) and 2015 (d) by the environmental factors calculated into PC1 and then rotated and depth excluded. However, the R^2 values for the models were low: (a) $R^2 = 0.01$, (b) $R^2 = 0.05$, (c) $R^2 = 0.10$ and (d) $R^2 = 0.06$.

The present study has revealed a highly dynamic and episodically rainfall-dependent subterranean system that has ancient lineages of taxa inhabiting groundwater calcretes. Although one of the most significant factors in driving diversity patterns within the boreholes is periodic recharge from rainfall, this does not explain all the changes within the system. It is possible that changes in the water table, the introduction of nutrients, or a combination of factors are also affecting changes in species composition and abundance, and further research will be necessary to determine whether this is the case.

Conflict of interest

The authors declare that they have no conflicts of interest.

Acknowledgements

The authors thank Adam Allford for the sampling data he provided to this study, and Michelle Guzik and Tessa Bradford for assistance with collections. The authors also thank Flora, Peter and Paul Axford of the Sturt

Meadows Station for providing both accommodation and access to their property. In addition, the authors thank Ron Smernik for comments that greatly improved the manuscript. This research was funded by Australian Research Council linkage grants (LP0348753, LP100200494 and LP140100555) to Steven J. B. Cooper, William F. Humphreys, Andrew D. Austin and Pablo Munguia, with industry partners Newmont Australia, Placer Dome Asia Pacific, Minara Resources Limited, the Western Australian Museum, the South Australian Museum, Biota Environmental Sciences, Bennelongia Environmental Consultants and the Department of Parks and Wildlife (WA).

References

- Adlassnig, W., Koller-Peroutka, M., Bauer, S., Koshkin, E., Lendl, T., and Lichtscheidl, I. K. (2012). Endocytotic uptake of nutrients in carnivorous plants. *The Plant Journal* **71**, 303–313. doi:10.1111/J.1365-313X.2012.04997.X
- Allford, A., Cooper, S. J. B., Humphreys, W. F., and Austin, A. D. (2008). Diversity and distribution of groundwater fauna in a calcrete aquifer: does sampling method influence the story? *Invertebrate Systematics* **22**, 127–138. doi:10.1071/IS07058
- Anand, R. R., and Paine, M. (2002). Regolith geology of the Yilgarn Craton, Western Australia: implications for exploration. *Australian Journal of Earth Sciences* **49**, 3–162. doi:10.1046/J.1440-0952.2002.00912.X
- Barranco, P., and Harvey, M. S. (2008). The first indigenous palpigrae from Australia: a new species of *Eukoena* (Palpigrae: Eukoenaeniidae). *Invertebrate Systematics* **22**, 227–233. doi:10.1071/IS07031
- Bradford, T., Adams, M., Humphreys, W. F., Austin, A. D., and Cooper, S. J. B. (2010). DNA barcoding of stygofauna uncovers cryptic amphipod diversity in a calcrete aquifer in Western Australia's arid zone. *Molecular Ecology Resources* **10**, 41–50. doi:10.1111/J.1755-0998.2009.02706.X
- Bradford, T., Adams, M., Guzik, M. T., Humphreys, W. F., Austin, A. D., and Cooper, S. J. B. (2013). Patterns of population genetic variation in sympatric chiltoniid amphipods within a calcrete aquifer reveal a dynamic subterranean environment. *Heredity* **111**, 77–85. doi:10.1038/HDY.2013.22
- Bradford, T., Humphreys, W. F., Austin, A. D., and Cooper, S. J. B. (2014). Identification of trophic niches of subterranean diving beetles in a calcrete aquifer by DNA and stable isotope analyses. *Marine and Freshwater Research* **65**, 95–104. doi:10.1071/MF12356
- Chase, J. M., and Leibold, M. A. (2003). 'Ecological Niches: Linking Classical and Contemporary Approaches.' (University of Chicago Press: Chicago, IL, USA.)
- Cooper, S. J. B., Hinze, S., Leys, R., Watts, C. H. S., and Humphreys, W. F. (2002). Islands under the desert: molecular systematics and evolutionary origins of stygobitic water beetles (Coleoptera: Dytiscidae) from central Western Australia. *Invertebrate Systematics* **16**, 589–590. doi:10.1071/IT01039
- Cooper, S. J. B., Bradbury, J. H., Saint, K. M., Leys, R., Austin, A. D., and Humphreys, W. F. (2007). Subterranean archipelago in the Australian arid zone: mitochondrial DNA phylogeography of amphipods from

- central Western Australia. *Molecular Ecology* **16**, 1533–1544. doi:10.1111/J.1365-294X.2007.03261.X
- Cooper, S. J. B., Saint, K. M., Taiti, S., Austin, A. D., and Humphreys, W. F. (2008). Subterranean archipelago: mitochondrial DNA phylogeography of stygobitic isopods (Oniscidea: Haloniscus) from the Yilgarn region of Western Australia. *Invertebrate Systematics* **22**, 195–203. doi:10.1071/IS07039
- Culver, D. C., and White, W. B. (2005). 'Encyclopedia of Caves.' (Elsevier: Amsterdam, Netherlands.)
- Darnell, M. Z., Nicholson, H. S., and Munguia, P. (2015). Thermal ecology of the fiddler crab *Uca panacea*: thermal constraints and organismal responses. *Journal of Thermal Biology* **52**, 157–165. doi:10.1016/J.JTHERBIO.2015.06.004
- Davies, K. F., and Margules, C. R. (1998). Effects of habitat fragmentation on carabid beetles: experimental evidence. *Journal of Animal Ecology* **67**, 460–471. doi:10.1046/J.1365-2656.1998.00210.X
- Davis, J., Pavlova, A., Thompson, R., and Sunnucks, P. (2013). Evolutionary refugia and ecological refuges: key concepts for conserving Australian arid zone freshwater biodiversity under climate change. *Global Change Biology* **19**, 1970–1984. doi:10.1111/GCB.12203
- Deharveng, L., and Bedos, A. (2000). The cave fauna of Southeast Asia. Origin, evolution and ecology. In 'Subterranean Ecosystems, Ecosystems of the World, Vol. 30'. (Eds H. Wilkins, D. C. Culver, and W. F. Humphreys.) pp. 603–632. (Elsevier: Amsterdam, Netherlands.)
- Gibert, J., and Deharveng, L. (2002). Subterranean ecosystems: a truncated functional biodiversity. *Bioscience* **52**, 473–481. doi:10.1641/0006-3568(2002)052[0473:SEATFB]2.0.CO;2
- Guzik, M., Cooper, S. J. B., Humphreys, W. F., and Austin, A. D. (2009). Fine-scale comparative phylogeography of a sympatric sister species triplet of subterranean diving beetles from a single calcrete aquifer in Western Australia. *Molecular Ecology* **18**, 3683–3698. doi:10.1111/J.1365-294X.2009.04296.X
- Guzik, M. T., Austin, A. D., Cooper, S. J. B., Harvey, M. S., Humphreys, W. F., Bradford, T., Eberhard, S. M., King, R. A., Leys, R., and Muirhead, K. A. (2010). Is the Australian subterranean fauna uniquely diverse? *Invertebrate Systematics* **24**, 407–418. doi:10.1071/IS10038
- Heino, J. (2000). Lentic macroinvertebrate assemblage structure along gradients in spatial heterogeneity, habitat size and water chemistry. *Hydrobiologia* **418**, 229–242. doi:10.1023/A:1003969217686
- Humphreys, W. F. (2001). Groundwater calcrete aquifers in the Australian arid zone: the context to an unfolding plethora of stygal biodiversity. *Records of the Western Australian Museum* **64**(Suppl.), 63–83. doi:10.18195/ISSN.0313-122X.64.2001.063-083
- Humphreys, W. F. (2012). Diversity patterns in Australia. In 'Encyclopedia of Caves', 2nd edn. (Eds W. B. White and D. C. Culver.) pp. 203–219. (Elsevier: Amsterdam, Netherlands.)
- Humphreys, W. F., Watts, C. H. S., Cooper, S. J. B., and Leijts, R. (2009). Groundwater estuaries of salt lakes: buried pools of endemic biodiversity on the western plateau, Australia. *Hydrobiologia* **626**, 79–95. doi:10.1007/S10750-009-9738-4
- Huppog, K. (2000). How do cave animals cope with the food scarcity in caves? In 'Subterranean Ecosystems, Ecosystems of the World, Vol. 30'. (Eds H. Wilkins, D. C. Culver, and W. F. Humphreys.) pp. 159–188. (Elsevier: Amsterdam, Netherlands.)
- Javidkar, M., Cooper, S. J. B., King, R. A., Humphreys, W. F., and Austin, A. D. (2015). Molecular phylogenetic analyses reveal a new southern hemisphere oniscidean family (Crustacea: Isopoda) with a unique water transport system. *Invertebrate Systematics* **29**, 554–577. doi:10.1071/IS15010
- Javidkar, M., King, R. A., Cooper, S. J. B., Humphreys, W. F., and Austin, A. D. (2017). Taxonomy of *Paraplatyarthrus* Javidkar and King (Isopoda: Oniscidea: *Paraplatyarthridae*) with description of five new species from Western Australia, and comments on Australian *Trichorhina* Budde-Lunde, 1908 (Platyarthridae). *Zootaxa* **4243**, 401–431. doi:10.11646/ZOOTAXA.4243.3.1
- King, R. A., Bradford, T., Austin, A. D., Humphreys, W. F., and Cooper, S. J. B. (2012). Divergent molecular lineages and not-so-cryptic species: the first descriptions of stygobitic chiltoniid amphipods (Talitroidea: Chiltoniidae) from Western Australia. *Journal of Crustacean Biology* **32**, 465–488. doi:10.1163/193724012X626566
- Leijts, R., van Nes, E. H., Watts, C. H., Cooper, S. J. B., Humphreys, W. F., and Hogendoorn, K. (2012). Evolution of blind beetles in isolated aquifers: a test of alternative modes of speciation. *PLoS One* **7**(3), e34260. doi:10.1371/JOURNAL.PONE.0034260
- Leys, R., Watts, C. H. S., Cooper, S. J. B., and Humphreys, W. F. (2003). Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. *Evolution* **57**, 2819–2834.
- MacArthur, R. H., and MacArthur, J. W. (1961). On bird species diversity. *Ecology* **42**, 594–598. doi:10.2307/1932254
- Magurran, A. E. (1988). Why diversity? In 'Ecological Diversity and its Measurement'. (Ed. A. E. Magurran.) pp. 1–5. (Springer: Amsterdam, Netherlands.)
- Mann, A., and Horwitz, R. (1979). Groundwater calcrete deposits in Australia some observations from Western Australia. *Journal of the Geological Society of Australia* **26**, 293–303. doi:10.1080/00167617908729092
- Mouquet, N., and Loreau, M. (2003). Community patterns in source–sink metacommunities. *American Naturalist* **162**, 544–557. doi:10.1086/378857
- Munguia, P. (2014). Life history affects how species experience succession in pen shell metacommunities. *Oecologia* **174**, 1335–1344. doi:10.1007/S00442-013-2849-7
- Munguia, P. (2015). Role of sources and temporal sinks in a marine amphipod. *Biology Letters* **11**, 20140864. doi:10.1098/RSBL.2014.0864
- Munguia, P., Osman, R. W., Hamilton, J., Whitlatch, R., and Zajac, R. (2011). Changes in habitat heterogeneity alter marine sessile benthic communities. *Ecological Applications* **21**, 925–935. doi:10.1890/09-2398.1
- Reeves, J. M., De Deckker, P., and Halse, S. A. (2007). Groundwater ostracods from the arid Pilbara region of northwestern Australia: distribution and water chemistry. *Hydrobiologia* **585**, 99–118. doi:10.1007/S10750-007-0632-7
- Watts, C. H. S., and Humphreys, W. F. (2006). Twenty-six new dytiscidae (Coleoptera) of the genera *Limbodessus* Guignot and *Nirripiriti* Watts & Humphreys, from underground waters in Australia. *Transactions of the Royal Society of South Australia* **130**, 123–185. doi:10.1080/3721426.2006.10887055