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ORIGINAL PAPER

Egg banks in dryland wetlands provide information on the diversity and vulnerability of branchiopod communities along a longitudinal aridity gradient

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Abstract Continued degradation of temporary wetlands and rapidly declining freshwater biodiversity call for identification of vulnerable species as targets for conservation and management efforts. Branchiopod crustaceans are endemic to temporary waters and rely on banks of drought-resistant eggs in the sediment for survival across dry seasons. These egg banks are like archives to biologists and allow them to estimate population status and resilience, without the need to sample active communities. Such an approach has, however, not yet been fully explored. Here, we investigate egg bank abundance and morpho-species richness to assess the vulnerability of branchiopod communities in dryland landscapes. For study systems, we use 98 temporary wetlands across the Northern Cape Province, South Africa, which contained eggs of Notostraca, Anostraca, Spinicaudata and Cladocera. We invoked the insurance hypothesis to investigate community resilience and studied egg bank abundance to reveal population status. Our results indicate that branchiopod communities become more vulnerable along an aridity gradient, from the semi-arid eastern regions to the arid western parts of the province. Apart from longitude, we also considered a suite of other environmental descriptors to explain variability in egg bank abundance and richness patterns and found that egg bank abundance decreased with alkalinity.

Keywords Morpho-species richness · Egg bank abundance · Insurance hypothesis · More-individuals hypothesis · pH

Introduction

Branchiopods (Crustacea, Branchiopoda) rely on the production of resistant eggs that accumulate in egg banks for their continued persistence through unfavourable dry periods in temporary waters (Ripley et al. 2004). These egg banks comprise an amalgamation of

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dormant progeny from past wet phases, primarily in the top few centimetres of the sediment, indicated as the 'active' egg bank (Brendonck and de Meester 2003; Brendonck et al. 2017). The egg banks typically comprise large quantities of eggs from different species and can survive for decades and even centuries under harsh conditions, including drought, extreme temperatures, and high salinity levels (Ripley et al. 2004; Schwentner and Richter 2015; Brendonck et al. 2017). Therefore, egg banks stabilise populations and act as buffers against catastrophes (De Roeck et al. 2007; Graham and Wirth 2008; Henri et al. 2014).

Natural events such as wind erosion, predation, extended length and frequencies of droughts, abortive hatching due to early drying, disease, and burial in deep sediment layers due to sediment mixing, may cause loss from egg banks or obstruct recruitment of a new generation (Brendonck et al. 1998, 2017; Brendonck and de Meester 2003; Gleason et al. 2003; Pinceel et al. 2020). In addition to these natural stressors, anthropogenic disturbance may also severely affect the egg bank's buffering capacity and threaten species survival. Common activities like mining, agriculture and urban development have led to destruction and fragmentation of temporary wetlands at a rapid pace across the globe (Belk 1998; Ripley et al. 2004; Brendonck et al. 2008). A recent review by Tickner et al. (2020) revealed an alarming decline in freshwater biodiversity globally and urged for the implementation of a recovery plan to prevent additional species loss. Only through protecting the egg banks of temporary wetlands will their permanent residents be conserved (Belk 1998). Therefore, in order to plan for conservation and management strategies of temporary wetlands it is vital to characterise egg banks and improve our understanding of processes that contribute to egg bank dynamics (Maffei et al. 2002; Brendonck and de Meester 2003).

Since branchiopod egg morphology is often species specific (Martin 1992; Brendonck and Coomans 1994a, b; Yan-bin and Di-ying 2008; Padhye et al. 2016), studying egg banks may serve as a convenient way to reconstruct branchiopod communities, especially in arid regions where sporadic rainfall limits the opportunity for sampling active populations (Bohonak and Jenkins 2003; Brendonck and de Meester 2003; Brendonck et al. 2008). Regarding 'total biodiversity' of the permanent inhabitants of temporary waters, egg banks even offer a more complete picture than the active community (Boero et al. 1996). At any one moment of sampling, the active community generally only represents a portion of the entire community (Brendonck and de Meester 2003). This partly relates to the fact that hatching is conditional with extensive intra- and interspecific variation in cues including salinity, pH and temperature required to stimulate hatching (Brendonck 1996). Therefore, during some inundations, conditions may simply be unsuitable for hatching of some species while others do hatch (Brendonck et al. 2017). In addition, all branchiopod eggs require light for hatching which means that only eggs from the top layer will ever hatch since eggs in deeper layers are deprived of light due to a thick cover (Pinceel et al. 2013). Finally, not all branchiopods hatch at the same time during an inundation or remain present throughout the entire inundation. While fairy shrimps (Branchiopoda, Anostraca) for instance typically hatch within the first days of inundation and dominate the early stages, water fleas (Branchiopoda, Cladocera) typically hatch later with some species only emerging after 7–14 days. Also, due to variation in predation sensitivity, some groups such as fairy shrimps which are prone to predation by actively dispersing insects may disappear from the community in later stages of the hydroperiod, while less sensitive groups such as clam shrimps (Branchiopoda, Laevicaudata and Spinicaudata) remain present (Jocqué et al. 2007). Combined, this means that the moment of sampling during an inundation may impact the species that are encountered as well. Studying egg banks, however, largely avoids these effects of temporal variability (Vagle and McCain 2020) and affords a more reliable way of estimating species richness (Gyllström et al. 2007).

In addition to being an archive to reconstruct species composition, the egg banks also provide information on the vulnerability of the populations present (Downing and Leibold 2010; Sada et al. 2013; Henri et al. 2014). Yet, very few studies have demonstrated such links since it requires quantification of egg bank size, which is labour intensive (Sada et al. 2013). Most studies that have measured egg banks, included only those eggs within the top few centimetres of the soil, i.e.; the active egg bank (Cáceres and Hairston 1998; Mura 2004; Wang et al. 2014). However, vertical sediment mixing may result in viable egg banks that easily reach between 10–30 cm deep (Hairston et al. 2001; Mura 2004;

Rogers 2014b). Although only eggs in the top layers will be immediately exposed to hatching triggers (Herzig 1985), churning over time can bring eggs back to the surface (Hairston et al. 2001; Gyllström et al. 2007; Rogers 2014b). Ultimately, the presence of egg banks in both top- and sub layers provides a supplementary egg bank reserve and may enhance its long-term buffering capacity (Brendonck and de Meester 2003).

Species richness has generally been accepted as an indicator of community resilience, i.e. a community's ability to recover to a pre-disturbance condition of stability (Downing and Leibold 2010). This can be explained through the insurance hypothesis, which stipulates that higher species richness provides a stronger buffering capacity by offering a wider array of responses to disturbances (Yachi and Loreau 1999). Species richness usually correlates well with productivity (Srivastava and Lawton 1998; Romanuk and Kolasa 2002; Šímová et al. 2013). This productivity—species richness relationship has been best explained by the more-individuals hypothesis (McGlynn et al. 2010; Storch et al. 2018; Vagle and McCain 2020), which states that increased energy availability supports a higher total number of individuals (abundance) and species in a community (Wright 1983). Even though these hypotheses have been widely accepted in ecology, the dynamics driving their constituents are still unclear and seem to be habitat- and community specific as well as scale-dependent (Downing and Leibold 2010; Storch et al. 2018; Vagle and McCain 2020). Branchiopod distribution patterns are usually influenced by climate and the physiochemical characteristics associated with each habitat (Maeda-Martínez et al. 1997; Boven et al. 2008; Sada et al. 2013; Rogers 2014a; Rogers and Timms 2014). However, to fully comprehend the ecological processes that drive the occurrence of branchiopods across habitats in a specific region, it is important to understand how community abundance and species richness are linked (Storch et al. 2018), and what the drivers behind this relationship are (Rombouts et al. 2009; Gillman et al. 2015; Nhiwatiwa et al. 2017).

In this study, we investigate the potential buffering capacity of branchiopod communities in light of ongoing wetland pressures in dryland landscapes. For this, we use a set of 98 temporary wetlands across the Northern Cape, South Africa, which contained eggs of Notostraca, Anostraca, Spinicaudata, and Cladocera. South Africa has a rich branchiopod fauna (De Roeck et al. 2007; Bird et al. 2019) and the Northern Cape is the largest, most arid (MAP < 350 mm) province with temporary wetlands across four geomorphic regions (Partridge et al. 2010; Meyer-Milne et al. 2020). This makes it an ideal study system to first of all test the insurance hypothesis and explore resilience and population status between distinct dryland regions. Next, we assess if local and regional egg bank characteristics are linked to community abundance and species richness and if more species-rich communities also have more individuals, to test the more-individuals hypothesis.

Materials and methods

Study area

The study was performed in the Northern Cape Province of South Africa, in four distinct geomorphic regions where temporary wetlands are abundant (Fig. 1), i.e.; Kalahari, Bushmanland, Ghaap Plateau and Upper Karoo. These wetlands, similar to playas and dry lakes, are natural, small (< 10 ha) to large (> 10,000 ha) depressions with bare or semi-vegetated, clayey soil surfaces. They occur in low lying areas of the landscape and are only filled occasionally for a couple of weeks from surface runoff after substantial summer rains. An aridity gradient spans our study region (Fig. 1) with annual rainfall of 120 mm (Bushmanland) and 156 mm (Kalahari) in the west, to 276 mm (Ghaap Plateau) and 296 mm (Upper Karoo) in the east. Annual evaporation rates exceed 2 400 mm in the Bushmanland and Kalahari regions, but range between 2 001 and 2400 mm in Ghaap Plateau and Upper Karoo.

Data collection

A total of 98 dry wetlands were sampled from August to November 2017, across the four study regions; i.e.; Kalahari (n = 23), Bushmanland (n = 25), Ghaap Plateau (n = 25) and Upper Karoo (n = 25). In each wetland, sediment holding the egg bank was sampled at a minimum of three plots, but more (up to six) plots were added for larger wetlands to roughly maintain the same sampling effort to surface ratio. A hand spade was used to remove at least 1L of the top 5 cm of

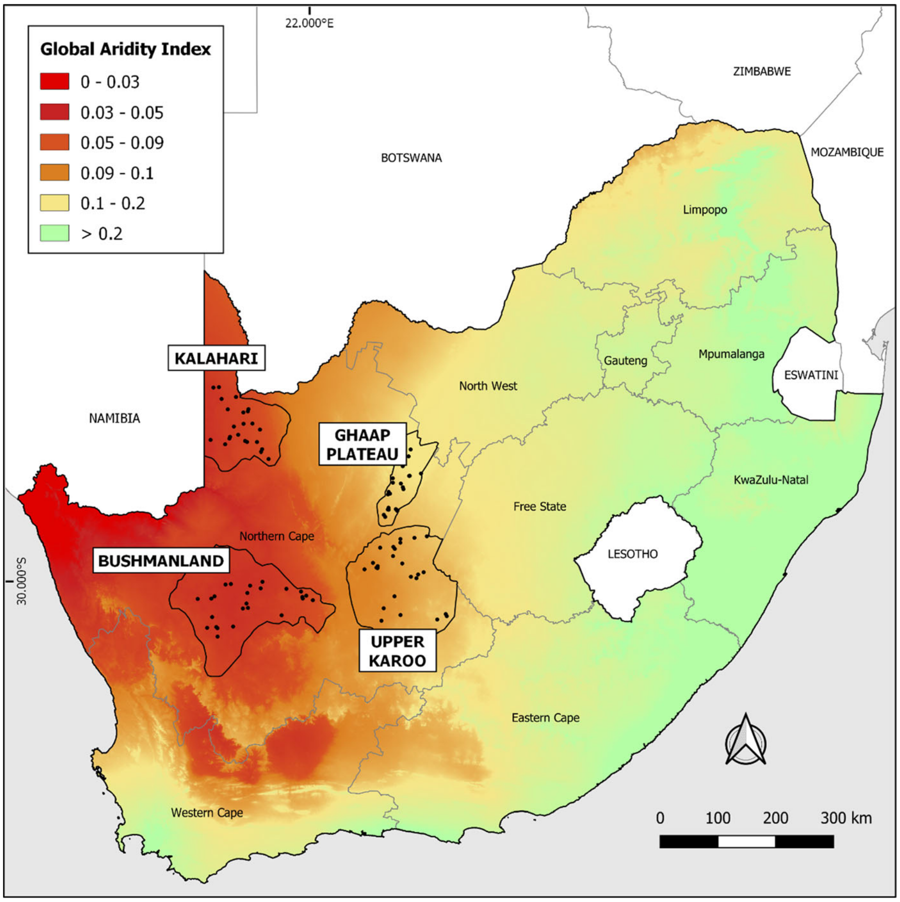


Fig. 1 Map of the study area in the Northern Cape Province of South Africa, indicating the locations of 98 study sites (circles) across four regions in which branchiopod egg banks were sampled, as well as the Global Aridity Index according to Trabucco and Zomer (2018). Green colours represent more humid conditions, with red colours representing higher aridity

solidified crust at each ± 30 cm × 30 cm plot, while a soil auger was used to sample 1L of subsoil directly below the crust up to bed rock or the first 20 cm. A total of 616 (308 crust and 308 subsoil) samples were collected for this study (Kalahari (n = 144), Bushmanland (n = 152), Ghaap Plateau (n = 152) and Upper Karoo (n = 168)). We then followed a standardised sugar flotation method developed by Onbé (1978) and modified by Marcus (1990) to extract branchiopod eggs from the crust samples using 20 mL of soil in 50 mL centrifuge tubes. After extraction, eggs were allowed to air dry on petri dishes. We then sorted the eggs according to unique morphology under a dissecting microscope, using methodology adapted from Meyer-Milne (2021). Egg bank abundance was defined as the sum of egg counts from each sample, and egg morpho-species richness as the total number of different egg morphotypes per sample.

Seven environmental descriptors were selected for this study, i.e.; latitude, longitude, wetland size, electrical conductivity, pH, turbidity and chlorophyll *a*. Latitude and longitude represent the absolute locations (in degrees) of the centre of each wetland and wetland size denotes the surface area (ha) calculated for each wetland. These three variables, along with the study map were generated in QGIS (QGIS Essen 2.14.5, http://www.qgis.org). Water quality variables were measured during inundation experiments in the lab using handheld multimeters. For each wetland, two replicates of 35 g pooled crust sediment were inundated with 1.5 L of type II RO water in 2-L plastic aquaria and then aerated for three days before measuring chlorophyll *a* and Turbidity (Turner Aquafluor Handheld Fluorometer/Turbidimeter), Electrical Conductivity (WTW Multiline P4 Universal Meter) and pH (Hanna HI-98190 Professional Waterproof pH/ORP Meter). The trials were run under strictly controlled conditions using specialised incubators to allow for consistent light cycles, light intensity, aeration, and temperature. Three readings of each parameter were taken randomly in each sample and then averaged to obtain the final measurements.

Data analyses

We compared egg morpho-species richness (as a proxy for community species richness) and egg bank abundance (as a proxy for community abundance) between the four study regions with nonparametric Kruskal–Wallis and Dunn's multiple comparison rank sum test. For this, we separated the crust and subsoil samples and transformed egg abundance and morpho-species richness data with $\log(x + 1)$. We used linear regression to test the more-individuals hypothesis and to investigate the relationship between egg bank abundance and morpho-species richness across regions. We performed multiple regression analysis in order to identify the independent environmental descriptors (latitude, longitude, wetland size, electrical conductivity, pH, turbidity and chlorophyll *a*) that best account for variation in branchiopod egg abundance and morpho-species richness. The matrix of correlation coefficients, variance inflation factor, and tolerance statistics were observed to assess collinearity in models. For all regression analyses we only used data from crust samples and transformed egg abundance and morpho-species richness data with $\log(x)$. All statistical analyses were performed using RStudio, R version 4.0.2; RCommander package version 2.6–2, accompanied by the 'dunn.test' package v 1.3.5 (Dinno 2015) and 'olsrr' package v 0.5.3 (Hebbali 2020). Data was visualised with the 'ggplot2' package v 3.3.2 (Wickham 2016). All sites, for which both the crust and subsoil rendered no eggs, were removed for statistical analyses.

Results

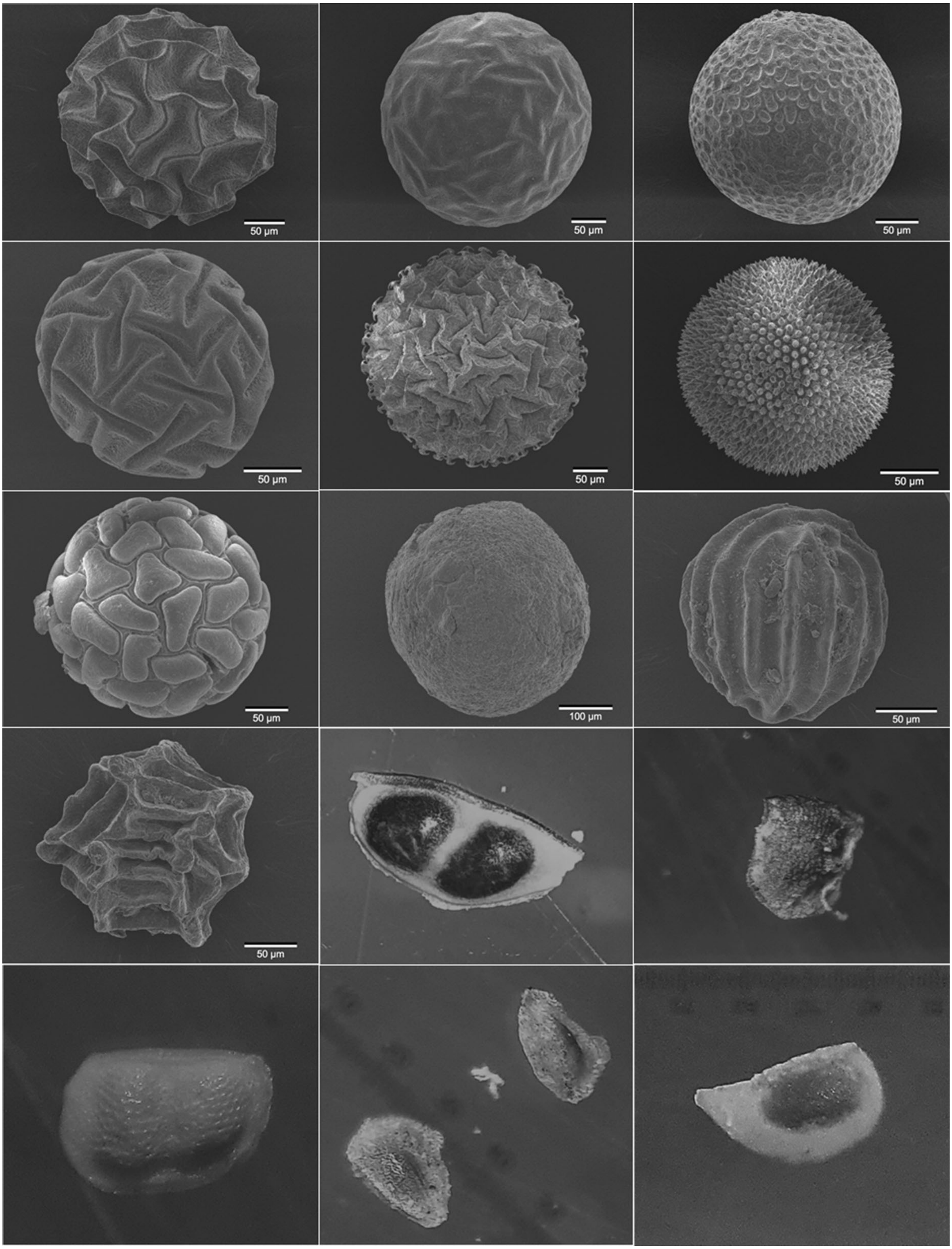
Overall, a total of 3 546 eggs were extracted from 82 sites and processed for this study. A total of 2 826 eggs were uncovered from the crust and 720 from the subsoil. Egg abundance ranged from one to a maximum of 320, with an average of 43 eggs per pooled wetland sample. Thirty-six morphotypes were identified (Fig. 2). Egg morpho-species richness ranged from one to 11, with an average of four morpho-species per wetland. These included notostracan, anostracan, and spinicaudatan eggs, as well as cladoceran ephippia.

Egg abundance

Egg abundance differed significantly between regions for egg banks located in the crust ($H = 16.40$, $p < 0.001$) and subsoil ($H = 13.33$, $p = 0.004$) (Fig. 3). Egg abundance in the crust of the Ghaap Plateau wetlands were significantly higher than in any other region (Dunn's post-hoc, $p_{K,BL} < 0.001$, $p_{UK} < 0.014$). There was no difference in the egg abundance of crusts between the Kalahari, Bushmanland or Upper Karoo wetlands (Dunn's post-hoc, $p_{all} > 0.05$). The egg banks located in the subsoil substrates of the Kalahari wetlands had the lowest egg abundance, and were also significantly lower than the subsoils of all other regions (Dunn's post-hoc, $p_{BL} = 0.02$, $p_{GP} = 0.003$, $p_{UK} < 0.001$). There was no difference in the egg abundance of subsoils between the Bushmanland, Ghaap Plateau or Upper Karoo wetlands (Dunn's post-hoc, $p_{all} > 0.05$).

Egg morpho-species richness

There was a significant difference in egg morpho-species richness between regions for egg banks located in the crust ($H = 30.20$, $p < 0.001$) and subsoil ($H = 18.49$, $p < 0.001$) (Fig. 3). Egg bank morpho-species richness in the crust of Ghaap Plateau wetlands was highest (Dunn's post-hoc, $p_{K,BL} < 0.001$, $p_{UK} < 0.007$). The Upper Karoo crusts also had higher morpho-species richness than the Kalahari (Dunn's post-hoc, $p = 0.006$), but there was no difference in egg bank morpho-species richness of crusts between the Upper Karoo and Bushmanland (Dunn's post-hoc, $p = 0.03$), or between the Bushmanland and Kalahari wetlands (Dunn's post-hoc, $p = 0.20$). The egg banks in the subsoils of the Ghaap Plateau and Upper Karoo wetlands had higher egg morpho-species richness than those of the Bushmanland (Dunn's post-hoc, $p_{GP} = 0.015$, $p_{UK} = 0.003$) and Kalahari (Dunn's post-hoc, $p_{GP,UK} < 0.001$). There was however no difference in morpho-species richness between egg banks in the subsoils of Ghaap Plateau and Upper Karoo wetlands (Dunn's post-hoc, $p = 0.233$), or between the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◀**Fig. 2** Examples of branchiopod egg morphotypes identified from the wetlands in the Northern Cape

Kalahari and Bushmanland wetlands (Dunn's post-hoc, p = 0.120).

The more-individuals hypothesis

A significant morpho-species richness–abundance relationship existed in the egg banks of the Upper Karoo ($R^2 = 0.903$, $p < 0.001$), Ghaap Plateau ($R^2 = 0.703$, $p < 0.001$) and Bushmanland ($R^2 = 0.345$, $p = 0.005$) wetlands, with the strength of this relationship decreasing in that order (Table 1, Fig. 4). There was however no significant relationship between egg bank abundance and morpho-species richness in the Kalahari wetlands ($R^2 = 0.132$, $p = 0.183$).

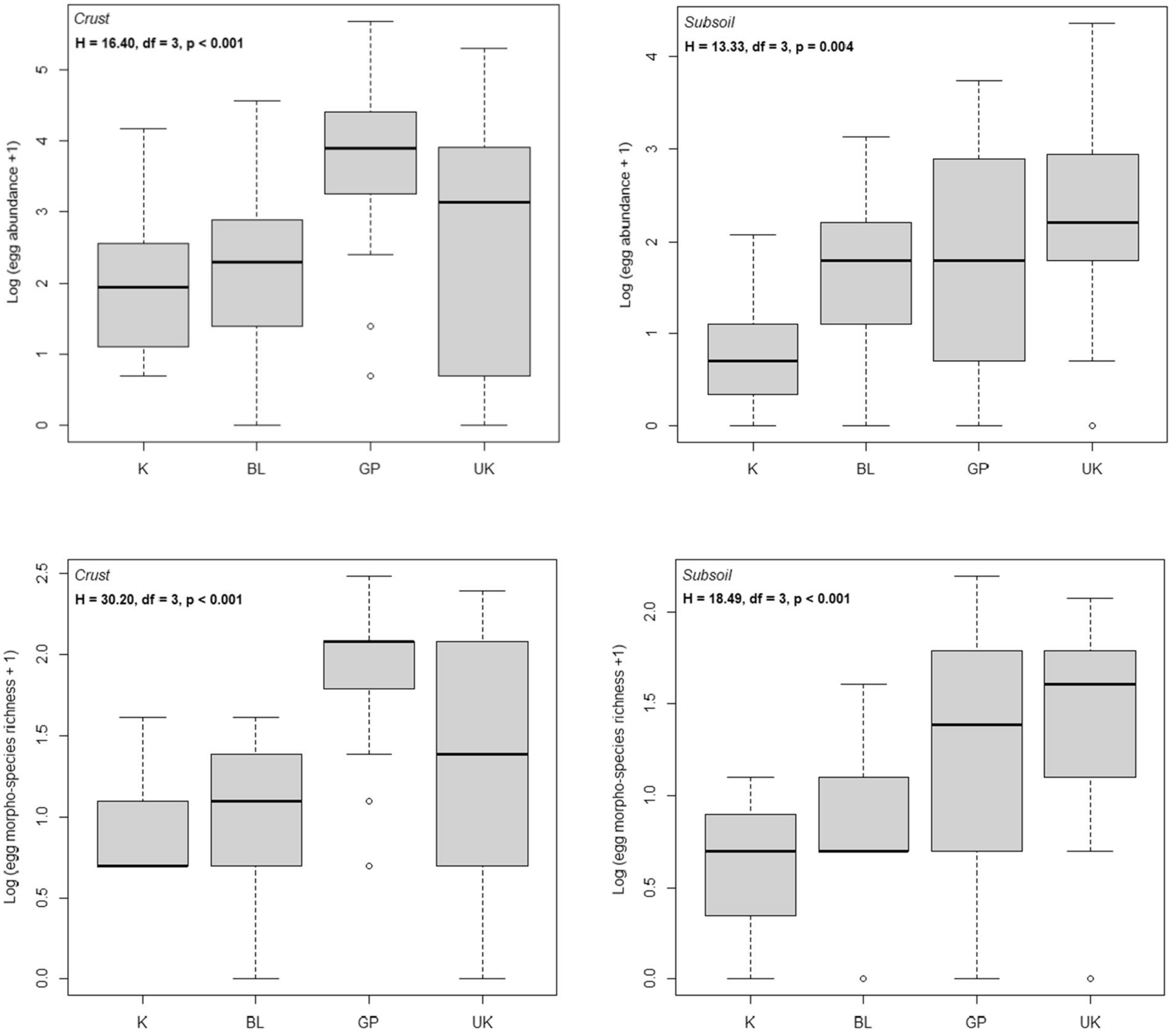

Fig. 3 Boxplots comparing egg bank abundance and egg bank morpho-species richness from the crust and subsoil between the study regions in the Northern Cape, South Africa. Outliers are depicted by circles. The results of the Kruskal–Wallis tests are indicated in the top left corner of each graph

Table1 Summary of linear regression statistics showing the relationship between egg abundance and egg morpho-species richness in the egg banks of wetlands across four regions of the Northern Cape

Region	*B*	SE	*t*	R^2	df	*F*	*p*
Kalahari	0.145	0.103	1.406	0.132	13	1.975	0.183
Bushmanland	0.242	0.076	3.164	0.345	19	10.01	**0.005***
Ghaap Plateau	0.376	0.051	7.374	0.703	23	54.38	**< 0.001***
Upper Karoo	0.454	0.034	13.270	0.903	19	176.1	**< 0.001***

Significant relationships are indicated with*

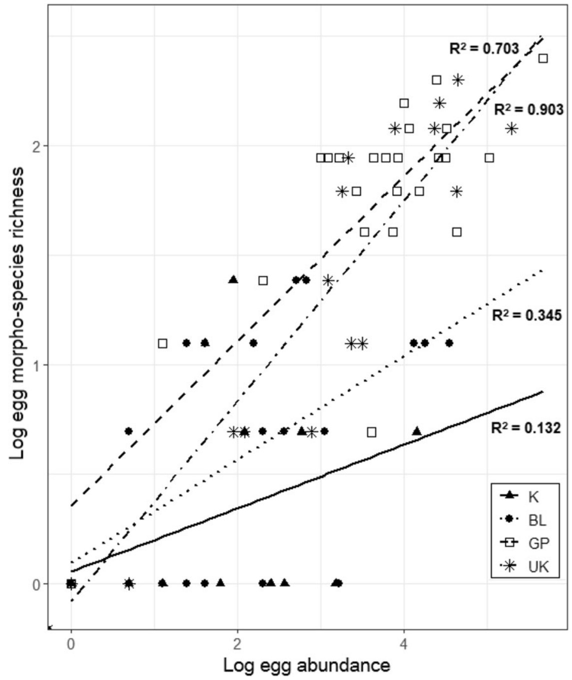

Fig. 4 Simple linear regression indicating the relationship between egg morpho-species richness and egg abundance in wetlands across the four study regions of the Northern Cape, South Africa

Association between egg banks and environmental conditions

No collinearity existed between the seven independent environmental descriptors (Table 2) that were included in the multiple regression analysis. The results of the regression indicated that the seven predictors explained 28% of the variance ($R^2 = 0.278$, $F(7,74) = 4.078$, $p < 0.001$) in egg bank abundance and 40% of the variance ($R^2 = 0.404$, $F(7,74) = 7.172$, $p < 0.001$) in egg morpho-species richness. pH significantly predicted egg bank abundance (β = -— 0.85, p = 0.02), with egg abundance decreasing with increased alkalinity (Fig. 5). It however had no direct effect on variability in egg morpho-species richness. Longitude was also a significant predictor of egg bank abundance (β = 0.31, p = 0.02) and morpho-species richness (β = 0.22, $p < 0.001$) with both egg abundance and morpho-species richness increasing significantly towards the east (Fig. 5). Latitude, wetland size, electrical conductivity, turbidity and chlorophyll *a* had no effect on the variability in egg bank abundance or morpho-species richness (Table 2).

Discussion

The buffering capacity of branchiopod communities

We studied dormant egg banks to improve our understanding of the buffering capacity of branchiopod communities in the temporary wetlands of drylands along an aridity gradient. Our results revealed that branchiopod communities become more vulnerable along an aridity gradient, from the semi-arid eastern regions to the arid western parts of the Northern Cape. Most wetlands in the province comprised high-abundance branchiopod egg banks in the crust with on average around 100 000 eggs per m^2 and some additional egg reserves in the sublayer. Consistent with our expectations, 80% of all eggs were uncovered from the crust. The top few centimetres of sediment typically have the highest egg abundance since most recently produced eggs end up in this layer (Cáceres and Hairston 1998; Brendonck and de Meester 2003). While most studies ignore egg reserves in the sublayers, such reserves could be highly relevant

Table 2 Summary of multiple regression statistics showing effects of latitude (LAT), longitude (LONG), wetland size, electrical conductivity (EC), pH, turbidity and chlorophyll *a* on egg abundance and egg morpho-species richness in the egg banks of wetlands from the Northern Cape

		Egg abundance				Egg morpho-species richness			
	VIF	*B*	SE	*t*	*p*	*β*	SE	*t*	*p*
LAT	1.274	0.152	0.154	0.989	0.326	0.050	0.073	0.693	0.491
LONG	1.549	0.315	0.131	2.409	**0.019***	0.219	0.062	3.555	**< 0.001***
Wetland size	1.128	< −0.001	< 0.001	−1.673	0.099	< -0.001	< 0.001	−1.236	0.221
EC	1.302	< 0.001	< 0.001	1.438	0.155	< -0.001	< 0.001	−1.436	0.155
pH	1.714	−0.846	0.350	−2.421	**0.018***	−0.323	0.165	−1.957	0.054
Turbidity	1.644	< −0.001	< 0.001	−0.407	0.685	< 0.001	< 0.001	0.673	0.503
Chlorophyll *a*	1.479	0.001	0.002	0.501	0.618	−0.002	0.001	−1.550	0.126

The variance inflation factor (VIF) values are reported to indicate no collinearity

Significant effects are indicated with*

for long term community dynamics and resilience to catastrophic conditions (Hairston et al. 2001; Mura 2004). Therefore, the relatively high morpho-species richness in the crust and subsoil of the Ghaap Plateau and Upper Karoo wetlands suggest that branchiopod communities from these regions could be most resilient to disturbances (Yachi and Loreau 1999). In contrast, the more arid Kalahari and Bushmanland wetlands appear to be less buffered, with particularly poor subsoil reserves.

Likely, the ability of any temporary wetland community to buffer against catastrophes would still depend on the scale and extent of disturbance events (Brendonck and de Meester 2003; Sada et al. 2013). While branchiopod communities across dryland regions are typically well buffered against natural disturbance, including prolonged droughts, early drying events and wind (Fryer 1996; Brendonck et al. 1998, 2017), the opposite is expected with regard to physical disturbances caused by anthropogenic activities. Extreme alterations such as total habitat destruction or deliberate transformation of the hydrological regime typically result in complete species losses (Martens and De Moor 1995; Eder and Hödl 2002). Although branchiopod communities are not able to cope with such catastrophic events, communities in the semi-arid regions would be better buffered against moderate impacts. Gleason et al. (2004) attested that natural recolonization of invertebrates in restored wetlands is possible. Therefore, the onus of branchiopod communities persisting in the more arid regions amidst increasing anthropogenic pressures falls on effective land use management and conservation policies.

The more-individuals hypothesis

In most regions of the Northern Cape there was a distinct positive relationship between dormant egg abundance and morpho-species richness, with these associations being strongest in the Ghaap Plateau and Upper Karoo wetlands. Typically, the 'more-individuals hypothesis' is invoked to explain such associations (McGlynn et al. 2010; Storch et al. 2018; Vagle and McCain 2020). This hypothesis proposes that increased energy, and thereby resource availability, supports a higher number of individuals in a community (Drever et al. 2009), which, in turn, sustains more species by lowering the risk of local extinction (Wright 1983). Therefore, it seems likely that the wetlands of the semi-arid regions have higher resource availability to sustain higher branchiopod abundance and more species, compared to the arid regions. We could postulate that energy availability is compromised in the most arid wetlands of the Kalahari region through reduced vegetation cover, frequent wind scouring, lower precipitation- and increased evaporation rates, but ecosystems are dynamic and therefore this assumption should be accepted with caution. After all, various processes such as climate change, food web feedback loops, interaction strengths, and competition can obscure the species richness–productivity

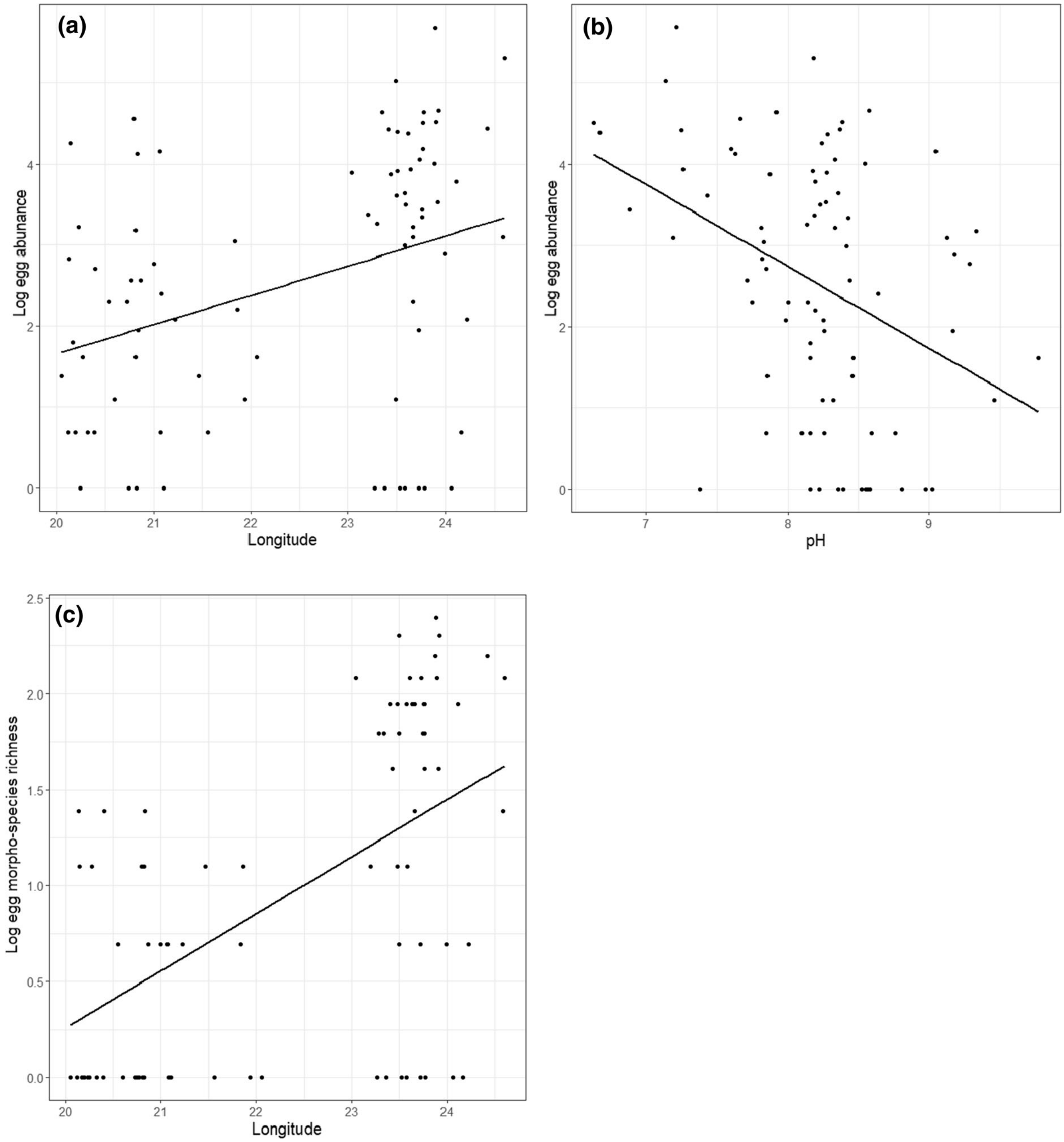

Fig. 5 Scatterplots indicating significant effects of **a** longitude and **b** pH on egg abundance, and **c** longitude on egg morpho-species richness, in the wetlands of the Northern Cape, South Africa

relationship (Rombouts et al. 2009; Downing and Leibold 2010; Gillman et al. 2015). Surprisingly, there was no effect of chlorophyll *a* on egg bank abundance or morpho-species richness. Algae are indeed, as primary producers, the main food source for filter feeding branchiopods (Brostoff et al. 2010). It is therefore reasonable to expect that chlorophyll *a*, as a proxy for energy availability, would be associated with dormant community characteristics (Rombouts et al. 2009; McGlynn et al. 2010; Gillman et al. 2015). The lack of association in our study could be due to our artificial setup in the laboratory, starting from dried sediments. The energy flux during the wet phase of a natural setting is probably more extensive. Nevertheless, the solid association between the total number of individuals and morpho-species richness of the studied communities implies that egg abundance counts could serve as proxies to infer community resilience.

Drivers behind egg bank community characteristics

Studying the relationship between dormant morpho-species richness and abundance alone is not sufficient to understand biodiversity patterns and buffering capacities across landscapes. Distinguishing the mechanisms behind these patterns is pivotal (Drever et al. 2009; Rombouts et al. 2009). We tested a suite of environmental descriptors to explain variability in egg bank abundance and morpho-species richness patterns across our study region and identified longitude and pH as significant contributors. Egg bank abundance and morpho-species richness were indeed higher in wetlands of the Ghaap Plateau and Upper Karoo regions compared to the more arid regions. This indicates an increased egg bank buffering capacity from the arid western regions to the semi-arid eastern parts of the province. Natural aridity gradients are notorious for their effect on species richness and abundance as a result of changes in temperature and rainfall (Hawkins et al. 2003; Pérez-Sánchez et al. 2013). The longitudinal aridity gradient in our study is likely associated with more consistent hydroperiods and reproductive success of populations in the east. This reiterates the vulnerability of temporary wetlands in the more arid regions to land use changes. Our results further indicate that egg bank abundance decreased proportionately with alkalinity (i.e.; pH increase). This effect of pH is not surprising, as it is known to influence branchiopod reproductive strategies, even at very small variations (Korhola and Rautio 2001; Schönbrunner and Eder 2006; Naceur et al. 2012). Although more research is needed to understand the processes behind the variation in pH values it seems to be an important variable to consider when monitoring temporary wetland communities.

Conclusion

Through a depth integrated egg bank analysis, we reconstructed abundance and richness of dormant freshwater communities in Northern Cape temporary wetlands. Our results suggest that branchiopod egg banks in the studied systems are mainly structured by variation in pH and level of aridity. If morpho-species richness and egg bank size are indeed good proxies for branchiopod resilience, our results suggest that the buffering capacity of branchiopod egg banks decreases with increasing aridity. Consequently, branchiopod communities in the more arid areas should be prioritized for conservation efforts and stringent land use management. Future monitoring protocols should include egg abundance counts and pH measurements to deduce changes in egg bank buffering capacities. These findings are especially insightful, because extensive live sampling across dryland landscapes is nearly impossible due to sporadic rainfall patterns. We recommend that also egg banks in deeper sublayers of the sediment are considered along with soil properties and physical processes that may drive sediment mixing and recruitment of dormant individuals from these layers.

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Data availability The data support our published claims and comply with field standards. All raw data used in this study belongs to SAEON. Please contact the corresponding author for data sharing options.

Code availability All data analyses were performed using packages in the R Statistical Environment, as discussed in the methodology section. Please contact the corresponding author for script sharing options.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Belk D (1998) Global status and trends in ephemeral pool invertebrate conservation: implications for Californian fairy shrimp. In: Witham CW (ed) Ecology, conservation, and management of vernal pool ecosystems. California Native Plant Society, Sacramento, pp 147–150

Bird MS, Mlambo MC, Wasserman RJ, Dalu T, Holland AJ, Day JA, Villet MH, Bilton DT, Barber-James H, Brendonck L (2019) Deeper knowledge of shallow waters: reviewing the invertebrate fauna of southern African temporary wetlands. Hydrobiologia 827(1):89–121

Boero F, Belmonte G, Fanelli G, Piraino S, Rubino F (1996) The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? Trends Ecol Evol 11(4):177–180

Bohonak AJ, Jenkins DG (2003) Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecol Lett 6:783–796

Boven L, Vanschoenwinkel B, De Roeck E, Hulsmans A, Brendonck L (2008) Diversity and distribution of large branchiopods in Kiskunság (Hungary) in relation to local habitat and spatial factors: implications for their conservation. Mar Freshw Res 59:940–950

Brendonck L (1996) Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). Hydrobiologia 320:85–97

Brendonck L, De Meester L (2003) Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. Hydrobiologia 491:65–84

Brendonck L, Riddoch BJ, Van de Weghe V, Van Dooren T (1998) The maintenance of egg banks in very short-lived pools - a case study with anostracans (Branchiopoda). Arch Hydrobiol Special Issues Advanced Limnology 52:141–161

Brendonck L, Rogers DC, Olesen J, Weeks S, Hoeh WR (2008) Global diversity of large branchiopods (Crustacea: Branchiopoda) in freshwater. Hydrobiologia 595:167–176

Brendonck L, Pinceel T, Ortells R (2017) Dormancy and dispersal as mediators of zooplankton population and community dynamics along a hydrological disturbance gradient in inland temporary pools. Hydrobiologia 796:201–222

Brendonck L, Coomans A (1994) Egg morphology in African Streptocephalidae (Crustacea: Branchiopoda: Anostraca) Part 1: south of Zambezi and Kunene rivers. Arch Hydrobiol 3:313–334

Brendonck L, Coomans A (1994) Egg morphology in African Streptocephalidae (Crustacea: Branchiopoda: Anostraca) Part 2: North of Zambezi and Kunene rivers, and Madagascar. Arch Hydrobiol 3:335–356

Brostoff WN, Holmquist JG, Schmidt-Gengenbach J, Zimba PV (2010) Fairy, tadpole, and clam shrimps (Branchiopoda) in seasonally inundated clay pans in the western Mojave Desert and effect on primary producers. Saline Syst 6:11

Cáceres CE, Hairston NG (1998) Benthic-pelagic coupling in planktonic crustaceans: the role of the benthos. Arch Hydrobiol 52:163–174

De Roeck E, Vanschoenwinkel B, Day J, Xu Y, Raitt L, Brendonck L (2007) Conservation status of large Branchiopods in the Western Cape. South Africa Wetlands 27(1):162–173

Dinno, A. 2015. Dunn's test of multiple comparisons using rank sums. CRAN R-Project

Downing AL, Leibold MA (2010) Species richness facilitates ecosystem resilience in aquatic food webs. Freshw Biol 55:2123–2137

Drever MC, Goheen JR, Martin K (2009) Species–energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. Ecology 90(4):1095–1105

Eder E, Hödl W (2002) Large Freshwater Branchiopods in Austria: Diversity, Threats and Conservational Status. In: Escobar-Briones E, Alvarez F (eds) Modern Approaches to the Study of Crustacea. Springer, Boston, MA, pp 281–289

Fryer G (1996) Diapause, a potent force in the evolution of freshwater crustaceans. Hydrobiologia 320:1–14

Gillman LN, Wright SD, Cusens J, McBride PD, Malhi Y, Whittaker RJ (2015) Latitude, productivity and species richness. Glob Ecol Biogeogr 24:107–117

Gleason RA, Euliss NH, Hubbard DE, Duffy WG (2003) Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. Wetlands 23(1):26–34

Gleason RA, Euliss NH, Hubbard DE, Duffy WG (2004) Invertebrate egg banks of restored, natural, and drained wetlands in the prairie pothole region of the Unite States. Wetlands 24(3):562–572

Graham TB, Wirth D (2008) Dispersal of large branchiopod cysts: potential movement by wind from potholes on the Colorado Plateau. Hydrobiologia 600:17–27

Gyllström M, Lakowitz T, Brönmark C, Hansson L (2007) Bioturbation as driver of zooplankton recruitment, biodiversity and community composition in aquatic ecosystems. Ecosystems 11:1120–1132

Hairston NG, Hansen A, Schaffner WR (2001) The effect of diapause emergence on the seasonal dynamics of a zooplankton assemblage. Freshw Biol 45(2):133–145

Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'brien, E.M., Porter, E.E., and Turner, J.R.G. (2003) Energy, water and broad-scale geographic patterns of species richness. Ecology 84(12):3105–3117

Hebbali, A. 2020. Olsrr: Tools for Building OLS Regression Models. CRAN R-Project

Henri AJ, Wepener V, Ferreira M, Malherbe W, Van Vuren JHJ (2014) The effect of acid mine drainage on the hatching success of branchiopod egg banks from endorheic wetlands in South Africa. Hydrobiologia 738:35–48

Herzig A (1985) A quantitative study of the life history of a fairy shrimp (Branchiopoda: Anostraca) in relation to the temporary nature of its habitat, a Kenyan rainpool. J Anim Ecol 54:99–110

Jocqué M, Riddoch BJ, Brendonck L (2007) Successional phases and species replacements in freshwater rock pools: towards a biological definition of ephemeral systems. Freshw Biol 52(9):1734–1744

Korhola A, Rautio M (2001) Cladocera and other branchiopod crustaceans. In: Smol JP, Birks HJB, Last WM (eds) Tracking Environmental Change Using Lake Sediments: Zoological Indicators, Kluwer Academic Publishers. The Netherlands, Dordrecht

Maeda-Martínez AM, Belk D, Obregón-Barboza H, Dumont HJ (1997) Large branchiopod assemblages common to Mexico and the United States. Hydrobiologia 359:45–62

Maffei C, Mura G, Zarattini P (2002) Assessing anostracan (Crustacea: Branchiopoda) cyst bank size: an attempt at a standardized method. Hydrobiologia 486:255–261

Marcus NH (1990) Calanoid copepod, cladoceran, and rotifer eggs in sea bottom sediments of northern Californian coastal waters: identification, occurrence and hatching. Mar Biol 105:413–418

Martens K, De Moor F (1995) The fate of the rhino ridge pool at Thomas Baines nature reserve: a cautionary tale for conservationists. S Afr J Sci 91:385–387

Martin JW (1992) Branchiopoda. In: Harrison FW (ed) Microscopic Anatomy of Invertebrates, vol 9. Wiley-Liss, New York, pp 25–224

McGlynn TP, Weiser MD, Dunn RR (2010) More individuals but fewer species: testing the 'more individuals hypothesis' in a diverse tropical fauna. Biol Lett 6:490–493

Meyer-Milne E, Mlambo MC, Rogers DC (2020) Distribution of clam shrimps (Crustacea: Laevicaudata and Spinicaudata) in South Africa, with new records from the Northern Cape Province. Zool Stud. https://doi.org/10.6620/ZS.2020.6659-6639

Meyer-Milne E, Brendonck L, Pinceel T (2021) Egg morphology may underpin the successful distribution of large branchiopods in temporary waters. Aquat Ecol 55(1):237–251 https://doi.org/10.1007/s10452-020-09826-1

Mura G (2004) Structure and functioning of the "egg bank" of a fairy shrimp in a temporary pool: Chirocephalus ruffoi from Pollino National Park (Southern Italy) as a case study. Int Rev Hydrobiol 89(1):35–50

Naceur HB, Jenhani ABR, Romdhane MS (2012) Impacts of salinity, temperature, and ph on the morphology of Artemia salina (Branchiopoda: Anostraca) from Tunisia. Zool Stud 51(4):453–462

Nhiwatiwa T, Brendonck L, Dalu MTB (2017) Understanding factors structuring zooplankton and macroinvertebrate assemblages in ephemeral pans. Limnologica 64:11–19

Onbé T (1978) Sugar flotation method for sorting the resting eggs of marine cladocerans and copepods from sea-bottom sediments of Ise Bay and Uragami Inlet, Central Japan. Bull Jpn Soc Sci Fish 44:1411

Padhye S, Timms BV, Ghate HV (2016) Large branchiopod (Crustacea: Branchiopoda) egg morphology of Western Ghats, Maharashtra. India Zootaxa 4079(2):246–254

Partridge TC, Dollar ESJ, Moolman J, Dollar LH (2010) The geomorphic provinces of South Africa, Lesotho and Swaziland: a physiographic subdivision for earth and environmental scientists. Trans R Soc South Africa 65(1):1–47

Pérez-Sánchez AJ, Lattke JE, Viloria AL (2013) Patterns of ant (Hymenoptera: Formicidae) richness and relative abundance along an aridity gradient in Western Venezuela. Neotrop Entomol 42:128–136

Pinceel T, Vanschoenwinkel B, Brendonck L (2013) Flexible dispersal dimorphism in zooplankton resting eggs: an example of repeated phenotypic coin flipping? Biol J Linn Soc 110(4):749–756

Pinceel T, Vanschoenwinkel B, Weckx M, Brendonck L (2020) An empirical test of the impact of drying events and physical disturbance on wind erosion of zooplankton egg banks in temporary ponds. Aquat Ecol 54:137–144

Ripley BJ, Holtz J, Simovich MA (2004) Cyst bank life-history model for a fairy shrimp from ephemeral ponds. Freshw Biol 49:221–231

Rogers DC (2014b) Larger hatching fractions in avian dispersed anostracan eggs (Branchiopoda). J Crustac Biol 34(2):135–143

Rogers DC, Timms BV (2014) Anostracan (Crustacea: Branchiopoda) zoogeography III. Australian Bioregions Zootaxa 3881(5):453–487

Rogers DC (2014) Anostracan (Crustacea: Branchiopoda) zoogeography II. Relating distribution to geochemical substrate properties in the USA. Zootaxa 3856(1):1–49

Romanuk TN, Kolasa J (2002) Abundance and species richness in natural aquatic microcosms: a test and refinement of the Niche-Limitation Hypothesis. Community Ecol 3(1):87–94

Rombouts I, Beaugrand G, Ibaňez F, Gasparini S, Chiba S, Legendre L (2009) Global latitudinal variations in marine copepod diversity and environmental factors. Proc Royal Soc B 276:3053–3062

Sada DW, Rosamond C, Adams KD (2013) Effects of recreational use on Branchiopod egg and ephippia density, black rock desert-high rock canyon emigrant trails national conservation area, Nevada, USA. J Crustac Biol 33(2):286–292

Schönbrunner IM, Eder E (2006) pH-related hatching success of Triops cancriformis (Crustacea: Branchiopoda: Notostraca). Hydrobiologia 563:515–520

Schwentner M, Richter S (2015) Stochastic effects associated with resting egg banks lead to genetically differentiated active populations in large branchiopods from temporary water bodies. Hydrobiologia 760:239–253

Šímová I, LI, Y.M., and Storch, D. (2013) Relationship between species richness and productivity in plants: the role of sampling effect, heterogeneity and species pool. J Ecol 101:161–170

Srivastava DS, Lawton JH (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. Am Nat 152(4):510–529

Storch D, Bohdalková E, Okie J (2018) The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity–diversity relationship. Ecol Lett 21(6):920–937

Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E., Cooke, S.J., Dalton, J., Darwall, W., Edwards, G., Harrison, I., Hughes, K., Jones, T., Leclère, D., Lynch, A.J., Leonard, P., McClain, M.E., Muruven, D., Olden, J.D., Ormerod, S.J., Robinson, J., Tharme, R.E., Thieme, M., Tockner, K., Wright, M., and Young, L. 2020. Bending the Curve of Global Freshwater Biodiversity Loss: An Emergency Recovery Plan. BioScience biaa002 Doi: https://doi.org/10.1093/biosci/biaa1002

Trabucco, A. and Zomer, R.J. 2018. Global Aridity Index and Potential Evapo-Transpiration (ET0) Climate Database v2. CGIAR Consortium for Spatial Information. https://cgiarcsi.community. Accessed 26 October 2021

Vagle GL, McCain CM (2020) Natural population variability may be masking the more-individuals hypothesis. Ecology 101(5):e03035

Wang C, Liu J, Chou L (2014) Egg bank spatial structure and functional size of three sympatric branchiopods (Branchiopoda) in Siangtian pond. Taiwan J Crustac Biol 34(4):412–421

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York

Wright DH (1983) Species-energy theory: an extension of species-area theory. Oikos 41:496–506

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Ecology 96:1463–1468

Yan-Bin S, Di-Ying H (2008) Extant clam shrimp egg morphology: taxonomy and comparison with other fossil branchiopod eggs. J Crustac Biol 28(2):352–360