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A preliminary survey of the abundance, diversity and distribution of terrestrial macroinvertebrates of Gcwihaba cave, northwest Botswana

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Abstract
Inventories of cave species and in-depth understanding of cave ecosystems are essential for informing conservation approaches for the unique and vulnerable cave fauna. Gcwihaba cave is the largest cave in Botswana but its ecology is poorly understood. This study set out to provide the first quantitative survey of the cave's terrestrial macroinvertebrates. Macroinvertebrates were collected from sample sites at 10 m intervals into the cave from the cave entrance. At each site, macroinvertebrates on the cave floor were collected by quadrat sampling while macroinvertebrate from cave walls were collected by visual opportunistic searches. Moisture content, pH and electrical conductivity of the cave floor substrate were measured at each site to examine the influence of the floor properties on the distribution of macroinvertebrates on the cave floor. Twelve species in 10 families and 8 orders of terrestrial macroinvertebrates were collected. The occurrence of taxa varied across the sites, with most taxa occurring in the light and twilight sectors of the cave (within 30 m), whereas the dark sector (beyond 30 m) was dominated by cave cockroaches (*Gyna* sp.). The abundance of the cave cockroaches, darkling beetles (Tenebrionidae, *Tenebrio* sp.) and cave wasps (Sphecidae) positively correlated with floor substrate of high moisture content and high electrical conductivity, which became increasingly common with distance into the cave. The abundance of other taxa from the cave floor positively correlated with a floor substrate of high pH and low moisture, which was common near the cave entrance.

Keywords
Bat guano cave, beetles, crickets, cockroaches, environmental variables, quadrat sampling, spiders, visual survey

Introduction

Ecological studies of cave ecosystems are essential for understanding, conserving and managing subterranean ecosystems (Schneider and Culver 2004). Conservation of cave ecosystems is crucial not only because they support unique and vulnerable biodiversity Mammola 2019), but also because their stable environments (Culver and Pipan 2013) serve as natural laboratories to study evolutionary processes such as adaptation and speciation. Nonetheless the importance of having a standardised data to be compared in the long term is crucial for species conservation assessment (Lunghi et al. 2020).

Macroinvertebrates are an important component of the cave biota because of their relatively high diversity compared to the vertebrate biota, and because of their significant roles in cave ecosystem functions (Moseley 2009). They are crucial for nutrient cycling in the cave. For example, carbon inputs into caves from bat guano, and organic matter from surface floods, are preliminarily broken into smaller pieces by macroinvertebrates facilitating further break down by microbes. Some macroinvertebrates, such as cave crickets, serve as key trophic links between the surface ecosystems and the cave as they forage on the surface during the night and return to the cave at daytime (Lavoie et al 2007). The diversity of cave invertebrates is therefore important for maintaining cave ecosystem functions, necessitating an inventory of cave invertebrate species and an understanding of their niche separation.

Gcwihaba cave, in the remote area of northern Botswana, is the largest in the country but ecologically poorly understood. Few studies at the caves include a non-comprehensive survey of its bat species (Seamark and Pretorius 2018). There is no published literature on macroinvertebrate assemblages of the cave despite their crucial role in cave ecosystem functions (Cooke and Baillieul 1974; Dandurand et al. 2019). A quantitative survey of the cave's macroinvertebrates is necessary for inventory of the cave's macroinvertebrates taxa and for improving the ecological understanding of the caves, and hence inform conservation priorities (Wynne et al 2019).

The current study surveyed terrestrial macroinvertebrates of Gcwihaba cave and examined their distribution against distance into the cave to identify environmental drivers of their community structure and dynamics. The distance from cave entrance into the cave is associated with gradients of environmental variables such as light, temperature and humidity, which can potentially influence the distribution of macroinvertebrates within the cave (Lungi et al. 2015; Mayer et al. 2016). This study presents the first quantitative survey of the cave's terrestrial macroinvertebrates.

Methods

Study area

Gcwihaba cave (also known as Drotsky's cave) is in the north west part (Ngamiland district) of Botswana, along the border with Namibia. It is located under one of the five low-lying dolomite hills in the Gcwihaba Valley, the Gcwihaba hills (20°01'30.2"S,

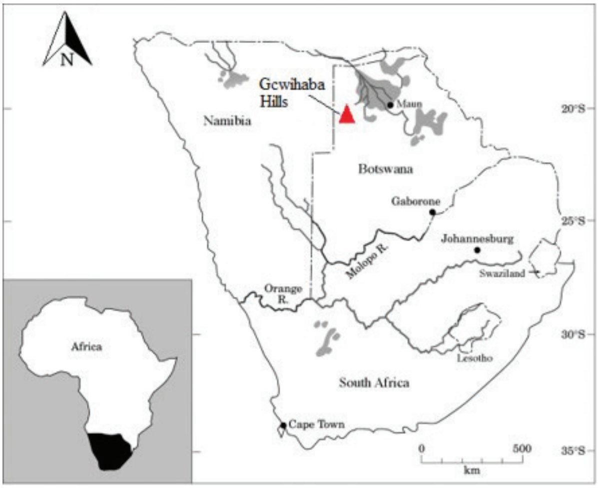

Figure 1. Location of Gcwihaba hills in Botswana indicated by a red triangle (Reprinted from Robbins et al. 1996 with permission from Lawrence Robbins).

21°21'27.5"E and 20°1'26.4"S, 21°21'14.4"E) (Figure 1). The habitat surrounding the hills is a semi-arid, dense, shrub savanna, referred to as the Kalahari Thirstland (Pickford and Mein 1990). The climate of the arid Kalahari is characterised by hot summers with warm nights, and warm winters with cold nights. The fieldwork trip to the cave for this study was undertaken in July 2019 when night temperatures were about 6 °C and daytime temperatures were about 25 °C.

The cave is mainly horizontal and has two entrances in the steep and rocky western slope of the Gcwihaba hills (Figure 2). The Gcwihaba cave is an underground maze of chambers with secondary flowstone and dripstone formations including stalactites, stalagmites and pillars. Some of the cave chambers are about 10 meters high while others range between 3 to 5 m in height.

Sampling

Terrestrial macroinvertebrates were collected from the cave between 10am and 3pm, from the 6th to the 10th of July 2019 (4 days), by a team comprising two cave guides, the principal investigator and a research assistant. The samples were collected from the cave floor and walls at approximately 10 m distance intervals (sample sites) into the north east chamber, starting from the South entrance (Figure 2). The sample sites were numbered 1 to 6 from the entrance (Figure 2), with site 1 at the cave entrance, sample sites 2 and 3 in the twilight sector and sites 4 to 6 in the dark sector. At each survey site, macroinvertebrates on the cave floor were collected from three positions (sampling points): at the base of each wall and in the middle of the chamber. Samples were collected by placing a 1 m^2 wooden quadrat of height 0.2 m and then visually collecting macroinvertebrates from the surface within the quadrat

Figure 2. The plan view of Gcwihaba cave (also known as Drotsky's cave) showing its chambers, the approximate position of cave sites surveyed for this study and other internal features (Modified from Dandurand et al. 2019, with permission from Gregory Dandurand).

for 20 minutes using tweezers. Where there were guano piles, macroinvertebrates were searched in the guano within a depth of 5cm. Macroinvertebrates on the cave walls were collected by opportunistic visual searches concurrently with each quadrat collection, thus making a total duration of one-hour wall survey time at each survey site. To ensure a consistent sampling effort the same collectors were maintained throughout the survey. All collected specimens of macroinvertebrates were put into a labelled vial containing 70% ethanol. The collected macroinvertebrates were then identified using the morphospecies approach (Derraik et al. 2002).

To measure cave floor cave properties, namely pH, electrical conductivity (EC) and moisture content, triplicate 20g samples of cave floor substrate were collected into labelled plastic bags at each survey site. Each sample was collected from where the quadrat was placed for macroinvertebrate collections. All the substrate samples were kept in a cool dark container prior to analyses.The cave floor substrate was mainly soil at the cave entrance but at other sample sites, it was mixture of soil and bat guano with the proportion of bat guano generally increasing with distance into the cave. The cave floor properties were measured as described in Ferreira et al. (2007) within a week of collection. Based on the procedure, the parameters were measured from 2.5 g subsamples from each sample. The subsamples were homogenised in 20ml distilled water and then measured for pH and EC. Moisture content was determined as weight loss of sample after drying 10g of each subsample at 100 °C for 24 h.

Statistical methods

Abundance frequencies of each taxa at the sample sites were compared using Chi Square (χ^2) tests. Simpson diversity index was computed for samples from each survey site and used to compare macroinvertebrate diversity across the sample sites. Relationships between the measured substrate variables were examined using the Pearson Correlation test. Canonical correspondence analysis (CCA) was used to examine the associations between the measured variables and macroinvertebrate taxa collected from the cave floor. CCA requires that species data should be unimodal and there was evidence from preliminary detrended correspondence analyses (DCA) that the macroinvertebrate data exhibited unimodal responses (length of first axis was 4.46; Lepš and Šmilauer 2003). All statistical tests were performed in SPSS version 25 (IBM Corp. 2017) and R software, version 3.6.1(R Core Team 2019) using a significance level of 5%.

Results

Terrestrial macroinvertebrates of Gcwihaba cave and their distribution within the cave

A total of 12 macroinvertebrate taxa including 8 orders and 10 families were collected, amongst which 10 taxa were identified to genus level. The common macroinvertebrate taxa in Gcwihaba cave (those collected from four sample sites or more) were cave cockroaches (*Gyna* sp.), cave crickets (likely *Spelaeiacris* sp.), darkling beetles (*Eurychora* sp.) and violin spiders (*Loxosceles* sp.) (Figure 3).

All the cockroaches (Blaberidae) were collected from the cave floor. Other taxa mostly found on the cave floor include pseudoscorpions (Withiidae), darkling beetles (*Tenebrionidae*.), assassin bugs and sphechid wasps (likely *Sphex* sp.). Violin spiders (Sicariidae), thread-legged bugs (Emesinae), moth larvae (Actiidae), flat spiders (Selenopidae.) and cellar spiders (Pholcidae.) were found more on the cave wall than on the cave floor. The number of cave crickets (Rhaphidophoridae) and darkling beetles (Tenebrionidae) collected from the cave floor was similar to that collected from the cave wall (Table 1).

Sample sites differed significantly in terms of the overall number of macroinvertebrate specimens collected (χ^2 (5), = 638.4, p < 0.001), the overall number of specimens collected from the cave floor and walls generally increased with distance into the cave, although the site at 40 m had a lower number of specimens than the site at 30 m and the site a 50 m (Figure 4). The increase in the number of collected macroinvertebrates with distance into the cave did not correspond with an increase in the diversity of the macroinvertebrates as there was an overall general decrease in macroinvertebrate diversity corresponding with increasing distance into the cave (Figure 4). Abundance and diversity of macroinvertebrates collected from the cave floor also showed this general trend (Figure 4). The diversity of cave floor macroinvertebrates sharply decreased at 30 m and then remained almost constant across sample sites at 40 and 50 m meters into the cave. Unlike macroinvertebrates collected from the cave floor, the number of macroinvertebrates from cave walls were greater at sample sites close the cave entrance, with a progressive increase from 30 specimens at the cave entrance to 54 specimens at 20m, whereas at sample sites beyond 20m the number of specimens fluctuated between 6 and 26 (Figure 4). For both macroinvertebrates collected from the cave floor and from cave walls, the number of specimens collected at sample sites further than

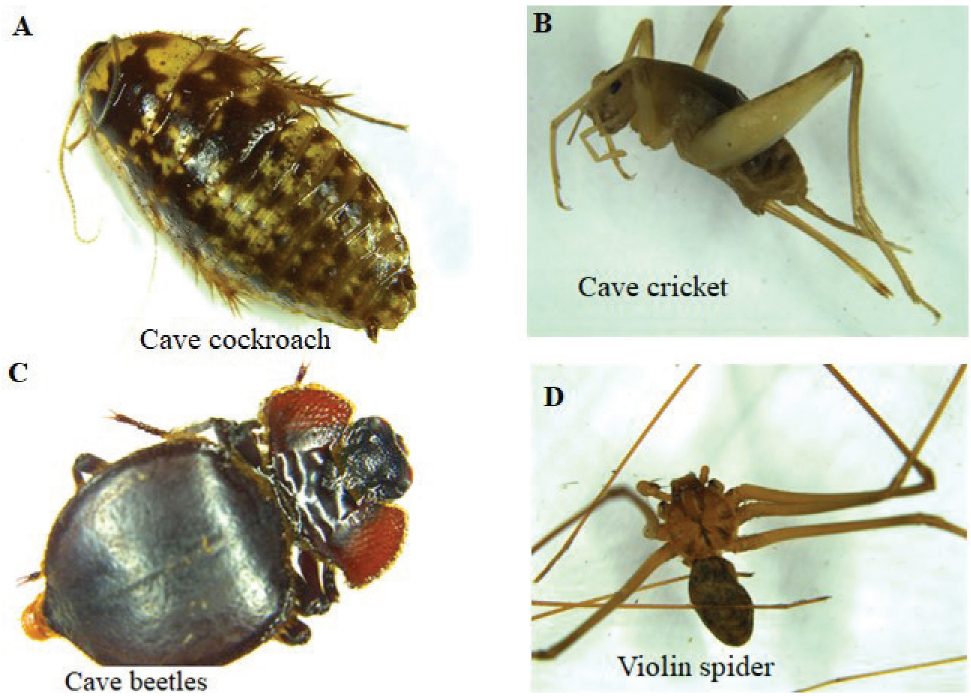

Figure 3. Common macroinvertebrate taxa found in Gcwihaba cave (photos by R. Mazebedi). **A** Cave cockroach (Gyna sp.) in family Blaberidae **B** cave cricket (likely *Spelaeiacris* sp.) in the family Rhaphidophoridae **C** darkling beetle (*Eurychora* sp.) in the family Tenebrionidae **D** violin spider (*Loxosceles* sp.) in the family Sicariidae.

Table 1. Taxa collected from Gcwihaba cave, Botswana. For each taxon, the overall number of individuals collected (Total count), the number of individuals collected from the cave floor (Floor count) and the number of individuals collected from cave walls (Wall count), are shown.

Order	Family/Subfamily (common name)	Genus/Species	Total count	Floor count	Wall count
Blattodea	Blaberidae (Cave cockroaches)	*Gyna* sp.	444	444	0
Orthoptera	Rhaphidophoridae (Cave crickets)	*Spelaeiacris* sp.	55	25	30
Coleoptera	Tenebrionidae (Darkling beetles)	*Eurychora* sp.	34	14	20
Araneae	Sicariidae (Violin spiders)	*Loxosceles* sp.	33	4	21
Hemiptera	Reduviidae/Emesinae (thread legged bugs)		14	2	12
Coleoptera	Tenebrionidae (Darkling beetles)	*Tenebrio* sp.	14	11	3
Pseudoscorpiones	Withiidae (Pseudoscorpion)		11	11	0
Hemiptera	Reduviidae (Assassin bugs)		6	**5**	1
Lepidoptera	Arctiinae		5	0	5
Hymenoptera	Sphecidae (wasps)	Likely *Sphex* sp.	4	4	0
Araneae	Pholcidae (Cellar Spiders)	*Smeringopus* sp.	4	1	3
Araneae	Selenopidae (Flat spiders)	*Selenops* sp.	3	0	3

20 m into the cave was lowest at 40m. As for macroinvertebrates collected from the cave floor, the diversity of macroinvertebrates from the cave walls generally decreased with distance into the cave.

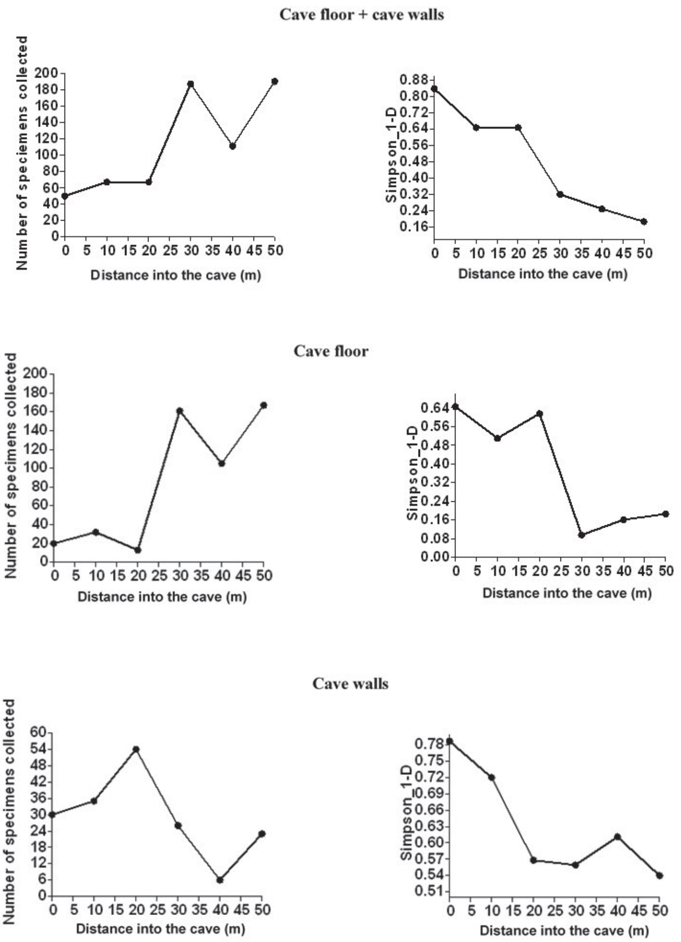

Figure 4. Variation of the abundance and diversity of terrestrial macroinvertebrate samples with respect to distance into Gcwihaba cave, including all samples collected at each site, samples collected only from the floor at each site and samples collected only from the cave walls at each site.

The four most abundant macroinvertebrate taxa; cave cockroaches, cave crickets, darkling beetles and violin spiders were not evenly distributed along the 50m transect. The cave cockroach abundance increased with distance into the cave (χ^2 (5), = 72.7, $p < 0.001$) (Figure. 5). The number of cave crickets, cave beetles and violin spiders collected also varied across sample sites along the 50m transect into the cave, (χ^2 (5), = 46.9, $p < 0.001$, χ^2 (5), = 46, $p < 0.001$, and χ^2 (5), = 15.5, $p < 0.001$ respectively). The relative abundance of macroinvertebrate taxa was greater near the cave entrance but decreased with distance into the cave. The proportion of the three taxa decreased strongly after the 20m distance into the cave, with the relative abundance of cave crickets and violin spiders reducing from over 20% each to less than 10%. Among the four most abundant taxa, darkling beetles were the most collected at the cave entrance (37%) but were not collected at sample sites past 30 m into the cave (Figure 5).

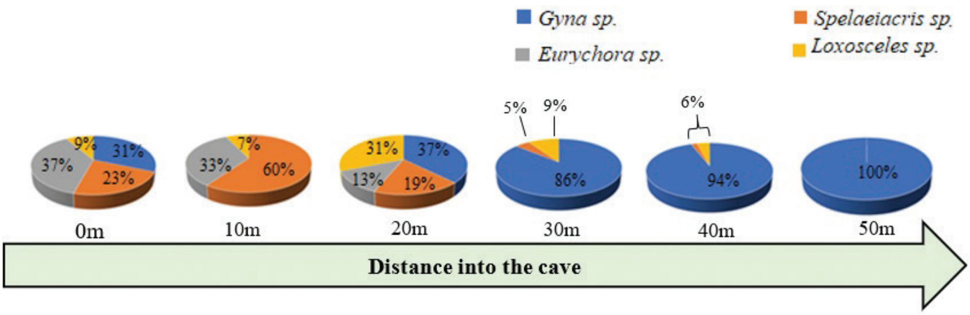

Figure 5. Proportion of the four most abundant macroinvertebrate taxa along a 50 m transact into Gcwihaba cave.

Environmental variables

Among the measured variables in the cave, pH ranged between 4.9 and 7.0, with a mean of 6.2. Electrical conductivity (EC) of the cave floor substrate ranged from 1179 to 12180 μS/cm with a mean of 6075 μS/cm. Moisture content of the cave floor substrate ranged from 15% to 35% with a mean of 12%. Moisture content of the floor substrate increased with distance into the cave (Figure 6) and was positively correlated with its EC levels ($t = 7.07$, $df = 19$, $p < 0.001$). Substrate pH decreased progressively with distance into the cave until it reached a minimum of 4.9 at 40m before slightly rising to 6.15 pH at 50m (Figure 6). The pH was negatively correlated with levels of substrate moisture ($t = -4.39$, $df = 19$, $p < 0.001$) and EC ($t = -2.87$, $df = 19$, $p = 0.01$).

Relationships between environmental variables and cave floor macroinvertebrate taxa in Gcwihaba cave

The total variation explained by the measured variables was 46% of which 36.8% was explained by canonical axis 1 (CCA) (Table 2). Distance into the cave had the greatest loading on axis 1 (0.83), followed by moisture content of the cave floor substrate (moisture) (0.63) and electrical conductivity (EC) of the floor substrate (0.56) (Table 2).

Based on CCA analysis, the abundance of cave cockroaches (Blaberidae), darkling beetles (Tenebrionidae, *Tenebrio* sp.) and cave wasps (Sphecidae) was positively associated with axis 1, with cave cockroaches showing the strongest association with the axis. The adult cave cockroaches were strongly associated with floor substrate with high moisture levels whereas the abundance of the cockroach nymphs showed strong association with distance into the cave and EC levels of the floor substrate. (Figure 7). The abundance of other macroinvertebrate taxa from the cave floor was negatively associated with axis 1 (Figure 7). The abundance of the taxa thus showed negative correlations with distance into the cave, moisture and EC levels of the cave floor substrate, but showed a positive correlation with the pH level of the cave floor substrate. The taxa that showed the greatest negative correlation with the first axis were the moths (Arctiinae) and spiders (Selenopidae and Pholcidae) (Figure 7).

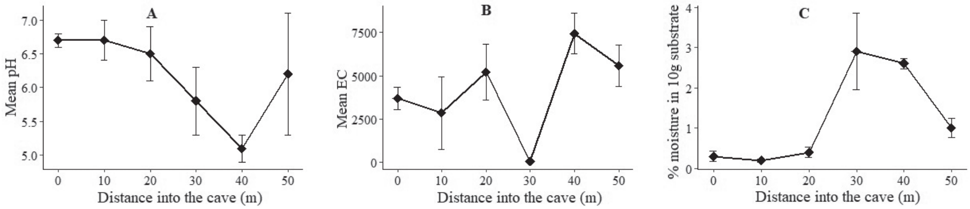

Figure 6. Changes in the measured environmental cave substrate variables relative to distance from cave entrance, the error bars indicate standard deviation of the measurements at each sampling point. **A** Acidity (pH) **B** electrical conductivity (µS/cm) **C** percentage soil moisture.

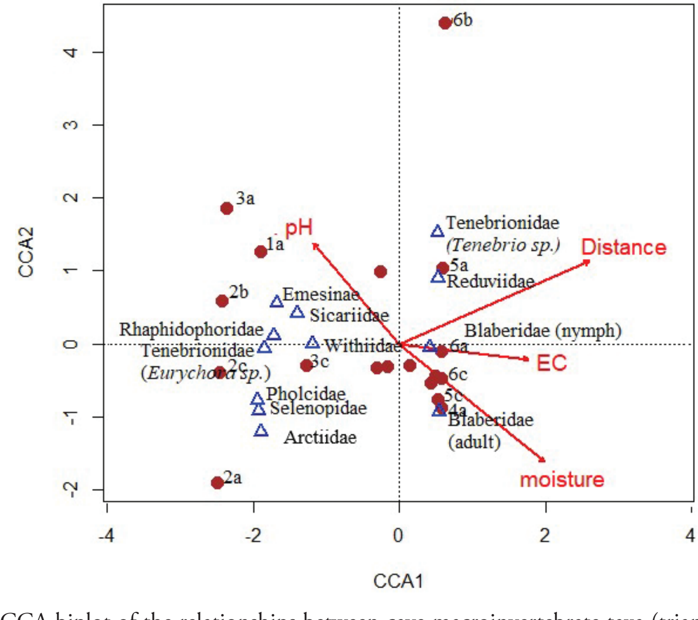

Figure 7. A CCA biplot of the relationships between cave macroinvertebrate taxa (triangles), sampling points (filled circles) and the measured environmental (variables lines with arrows). Environmental variables are presented as vectors, with arrow heads indicating their direction of increase. A positive correlation between the environmental variables and macroinvertebrate taxa and sampling points is indicated by their proximity to the arrowhead. Taxa and sampling points with a negative correlation with the variable axis plot on the opposite side of the arrowhead relative to the centroid, with the correlation strength increasing with distance of the symbols from the centroid.

Table 2. Proportion of variation in the distribution of cave floor macroinvertebrate explained by measured variables and the loadings of the variables to CCA axes 1–4.

	Total	CCA1	CCA2	CCA3	CCA4
Variance explained	**46%**	36.8%	5.3%	3.9%	0.06%
pH loading		-0.38	-0.44	-0.60	0.55
EC (µS/cm) loading		0.56	-0.065	0.50	0.66
Moisture (% in 10g)		0.63	-0.51	0.43	0.38
Distance (m)		0.83	0.36	-0.17	-0.39

Discussion

The macroinvertebrate fauna that was collected from Gcwihaba cave during the current study include taxa which were previously collected from other caves in northwest Botswana. Macroinvertebrate groups such as cave cockroaches (Blaberidae) and assassin bugs (Reduviidae) were also collected by Du Preez et al. (2013) in Bone cave, which is about 19 km from Gcwihaba cave. The total number of families from each cave sampled in that study varied, but was always less than the total number (10) found in the current study; Bone cave (6 families), Diviner's cave (5 families) and Blue cave (3 families all from Areneae). Factors that can explain the greater number of macroinvertebrate taxa in Gcwihaba cave compared to Bone cave is bat presence and cave size.

Despite the collected samples indicating greater diversity of terrestrial macroinvertebrates for the cave compared to other caves in Botswana's north west region, the macroinvertebrate diversity observed in our study is likely an underestimate of the total macroinvertebrate diversity that exist Gcwihaba cave. There is evidence that some macroinvertebrate species that occur in the cave were missed, for example a cave beetle (*Ptinus peringueyi*) previously reported by Philips and Smith (2016) in the dark zone of the cave was not collected during our survey. Our preliminary survey collected macroinvertebrates from only the northeast chamber of the cave, a more comprehensive survey will likely reveal a greater number of taxa. Other macroinvertebrates that may potentially be present in the cave include those collected in other caves within the north west region of Botswana. These inculde groups which were collected by Du Preez et al. (2013) such as ants (Formicidae), true crickets (Gryllidae) soft ticks (Argasidae) at Bone cave and centipedes (Cryptopidae), woodlice (Platyarthridae), japynids (Diplurans) and termites (Termitidae) at Diviner's cave.

In general, the collected macroinvertebrates taxa are those which can be expected from a cave in southern Africa. According to Sharratt et al. (2000), macroinvertebrate faunas of most caves in southern Africa consist of cave cockroaches, crickets, tenebroid beetles, reduviids and ants; these are among the groups which were collected in this study except for ants. Generally, there are few recorded troglobitic species for African caves, likely because of relatively high fluctuations of weather conditions in the caves (Sharratt et al. 2000). Another factor that may be contributing to the low records of troglobitic species in African caves is the low sampling efforts. A recent discovery of a new species of troglobiont pseudoscorpion (*Botswanancus ellisi*) in Diviner's caves (Harvey and Du Preez 2014) was the first troglobitic species recorded in Botswana. In our collections, no troglobiont species have been confirmed yet but troglomorphic features (Christiansen 2005) were observed in the collected pseudoscorpions (Withiidae), which had slightly elongated legs and pedipalps and possibly, albeit perhaps less likely, cave crickets (*Spelaeiacris* sp.) which had pale coloration.

Generally, cave systems have low macroinvertebrate diversity because of the limited variety of food sources at the base of their food webs (Venarsky and Huntsman 2018). Therefore, the low number of macroinvertebrate taxa (10 families) was to be expected especially in an arid landscape of Botswana which may limit the quantity and variety of allochthonous food sources into the cave. Compared to other caves in Africa and beyond, the number of collected taxa is comparable to caves with similar climatic and environmental settings. For example, the number of macroinvertebrate taxa reported for caves of Ghana, the majority of which are formed under hills, similar to the Gcwihaba cave, range from 3 to 16 morphospecies with an average of 9 morphospecies (Philips et al. 2016). Some macroinvertebrate taxa which were found to be abundant in Gcwihaba such as *Gyna* sp. (cave cockroaches) and Tenebrionidae (darkling beetles) were also found to be abundant is some of the caves studied by Philips et al. (2016). Three spider species were found in this survey, which given the low species richness is as expected. Spiders are prevalent in caves with more than a 1000 troglobionts and many more troglophile and trogloxenes (Mammola and Isaia 2017). However, while web-building spiders in general, and orb spiders in particular, are common in the entrance and twilight zones of temperate caves (Rector 2009; Mammola et al. 2017; Hesselberg et al. 2019), none of the three species found in Gcwihaba cave build complex webs. A similar lack of orb web-building spiders is reported from other African caves (Sharratt et al. 2000; Dippenaar-Schoeman and Myburgh 1997). While the reason for this difference is not known, it could be related to lower proportions of smaller flying prey and the general drier environment in these caves. Gcwihaba cave for example have a humidity between 60% and 70% rH (Dandurand et al. 2019), while spider-rich European caves have relative humidities above 80% rH (Manenti et al. 2015; Hesselberg and Simonsen 2019).

The diversity of macroinvertebrates collected from the cave floor decreased with distance into the cave likely responding to environmental variables associated with proximity to the cave entrance. The measured abiotic variables, including pH, EC and moisture content of the cave floor, showed distinct trends that were associated with distance from the cave entrance (Figure 5). Cave floor pH deceased (became more acidic) with distance into the cave likely due to greater quantities of bat guano in deeper sites since bat guano has acidic pH (Sikazwe and De Waele 2004). Greater diversity of macroinvertebrates has been shown to occur in higher soil pH closer to cave entrance (Kurniawan et al. 2018). Decomposition of bat guano releases ions (Sikazwe and De Waele 2004) into the cave floor which can explain greater EC at deeper sites where bat guano is more abundant. Moisture content of the cave floor substrate increased with distance into the cave likely because of lower rates of air circulation in deeper sites. The sample sites located further into the cave generally support fewer species because of minimal air circulation, high humidity, limited or no light and minimal fluctuation of environmental conditions (Culver et al. 2013).

Cave macroinvertebrate communities are generally food limited; their diversity can therefore be expected to be greater near the cave entrance where food resources are likely more diverse (Prous et al. 2015) as was generally the case in this study. Cave cockroaches (Blattodea) notably dominated the deeper sites of the cave, where there are fewer taxa, likely because they exploited the greater quantities of guano at sites as food and habitat resources (Bell et al. 2007). In addition, the cave entrance zone provides intermediate climatic conditions between the epigean environment and the subterranean environment, enabling taxa from both environments to thrive in the cave zone

(Prous et al. 2015). Surface dwelling macroinvertebrates are likely to accidentally enter the cave when they crawl near the cave entrance. Some of the less abundant species found near the entrance in this study could have entered the cave accidentally or to temporally find shelter.

Conclusions

This study is the first quantitative survey of Gcwihaba cave macroinvertebrates and has identified 12 species in 10 families and 8 orders of terrestrial macroinvertebrates. The macroinvertebrate diversity of the cave was found to decrease with distance into the cave with the deeper sites being dominated by cave cockroaches. Properties of the cave floor soil showed trends corresponding with distance into the cave; pH progressively decreased with distance into the cave whereas soil moisture content and electrical conductivity progressively increased. The environmental gradients may have played a role in the observed patterns of macroinvertebrate distributions in the cave. While the number of collected macroinvertebrates is comparable to that collected in other southern African caves, the number of macroinvertebrate taxa collected may be an underestimate of Gcwihaba macroinvertebrate diversity since they were collected from the cave's north east chamber only. The preliminary survey is, however, an important contribution to our knowledge about cave biodiversity in arid regions, as it provides a baseline on which to build a future programme. Surveying further into the cave and conducting a more comprehensive macroinvertebrate survey is therefore recommended especially examining seasonal variability of the invertebrate fauna as the strong seasonality of the surrounding desert landscape is likely to influence seasonality in cave biodiversity.

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