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Aquatic invertebrate communities of perennial pans in Mpumalanga, South Africa: a diversity and functional approach

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ABSTRACT

Perennial pans are a common feature of the Mpumalanga Highveld in South Africa and are increasingly under threat from mining and agricultural activities. Pans are endorheic wetlands that can be perennial or ephemeral in nature. They are widespread in arid and semi-arid regions throughout the world. Although phyllopod crustaceans dominate pan communities in arid regions, the invertebrate communities of perennial pans have not been well studied. The aim of the current research was to characterise the invertebrate communities of several pans (both natural and impaired). A combination of taxonomic and functional approaches was followed to study these communities. The macroinvertebrate species diversity of the pans was comparable to similar ecosystems in southern Africa and other parts of the world. Results indicate large spatial and temporal variations in diversity. This variation became less obvious when the analysis was based on biological traits. It was also evident that both coal mining and agricultural activities had an impact on the aquatic invertebrate community structures. These changes were apparent in both the diversity and the biological traits of the invertebrate communities of adjacent pans.

KEY WORDS: Biological traits, branchiopods, diversity, functional feeding groups, succession.

INTRODUCTION

Wetlands in South Africa have been neglected both in terms of research and monitoring, despite their importance in the hydrological cycle (Malan & Day 2005). This is especially true when one considers endorheic wetlands, which are better known as pans. A 'pan' is a South African vernacular term for closed basins that accumulate rainwater only after sufficient rain has fallen. They are usually isolated systems with no outlet (Geldenhuys 1982), normally circular or oval in shape, and are shallow (less than 3 m deep). These ecosystems can be ephemeral or perennial depending on the rainfall pattern in the area concerned. Pans are common features throughout arid regions (Hutchinson *et al.* 1932). Because of this, the majority of studies have concentrated on ephemeral pans in the arid central and western regions of South Africa (Hutchinson *et al.* 1932; Seaman *et al.* 1991; Meintjies *et al.* 1994; Meintjies 1996; De Roeck *et al.* 2007).

The aquatic invertebrate communities of pans are probably the most prominent feature of these ecosystems. In arid regions, temporary water communities consist largely of crustacean orders collectively known as phyllopods. Some taxa that are commonly sampled in these temporary environments include Anostraca, Notostraca, Conchostraca, Cladocera, Ostracoda, Corixidae, Notonectidae, Dytiscidae, and Hydrophilidae (Hutchinson 1932; Rzóska 1961; Weir 1969; Williams 1985; Seaman *et al.* 1991; Meintjies 1996). There is, however, a general lack of literature on the invertebrate communities of perennial pans. These communities are very important as they have been identified as possible indicators of ecological integrity for wetlands (Bird & Day 2009). The use of macroinvertebrates in aquatic ecosystems as such indicators, including the community structure and species composition, began over a century ago (Haase & Nolte 2008) and is now well established in many countries around the world (e.g., Dickens & Graham

http://www.africaninvertebrates.org.za
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2002; Hawkins 2006; Ollis *et al.* 2006). There are two main approaches to using invertebrates as indicators. Firstly, there is the taxonomic approach, with the focus on diversity or taxa richness. If the application of the indicator is to assess biodiversity or the response of a community to a specific contaminant, then this approach is usually the most successful (Cummins *et al*. 2005). The taxonomic approach requires considerable effort to separate organisms into the correct taxonomic groups (Cummins *et al.* 2005). The second approach is focused on the ecological functions (traits) of the taxa that make up a given community and is more useful in determining the ecological condition of a system (Cummins *et al*. 2005). Although it has been suggested that identification of invertebrates to species level has many benefits (Schmidt-Kloiber & Nijboer 2004), the functional approach is more rapid. A functional approach is also relatively independent of factors like natural variation in diversity due to seasonal and geographical patterns (Beketov *et al.* 2009).

The aim of the present study was to characterise the invertebrate communities of perennial pans using both a taxonomic and a functional approach and to determine which of these would be most suitable for identifying the environmental factors responsible for differences in the aquatic invertebrate community structures of pans.

MATERIAL AND METHODS

Study area

Nine perennial pans were selected for the study, of which seven were sampled on a seasonal basis between July 2007 and July 2009 (eight surveys of each of the seven pans were carried out) and an additional two pans in the autumn (May) of 2009. All the pans were located in the Mpumalanga Province of South Africa. Since the land-use activities in the catchment areas of the pans were diverse, we noted the perceived influence of human activities (or the lack thereof) as this may be relevant to interpretation of the results. The primary human activities of concern in this region are coal mining and agriculture (Emery *et al.* 2002). Three pans were situated adjacent to coal mines (pans 1, 2 & 8) and one next to where farming takes place (pan 3). The remaining five pans were relatively unaffected by human activities (pans 4, 5, 6, 7 & 9). These five pans were all located in the Mpumalanga Lake District (MLD), also known as the Lake Chrissie area. The positions of the selected pans are indicated in Fig. 1. Based on the classification of Cowan and van Riet (1998), all the pans (apart from pan 6) were considered to be open pans. These pans are usually devoid of vegetation except around their shorelines. Pan 6 was designated as a reed pan, having dense growth of *Phragmites australis* on a mat of floating peat. Even though the physical structure of the reed pan is very different from that of the other pans, it was included in the current study to determine whether there are also differences in the aquatic invertebrate communities.

Aquatic invertebrate diversity

Aquatic invertebrate communities were sampled from a variety of biotopes in each pan. These biotopes included stones, gravel, sand and mud, and vegetation. Samples were collected by using a sweep net (500 µm netting mesh size), with the number of sweeps dependent on the extent of a particular biotope. The stone biotope was sampled for an average of 180 seconds, while gravel, sand and mud were each sampled for 60 seconds. When vegetation was present, sampling covered a total of two metres. Zooplankton

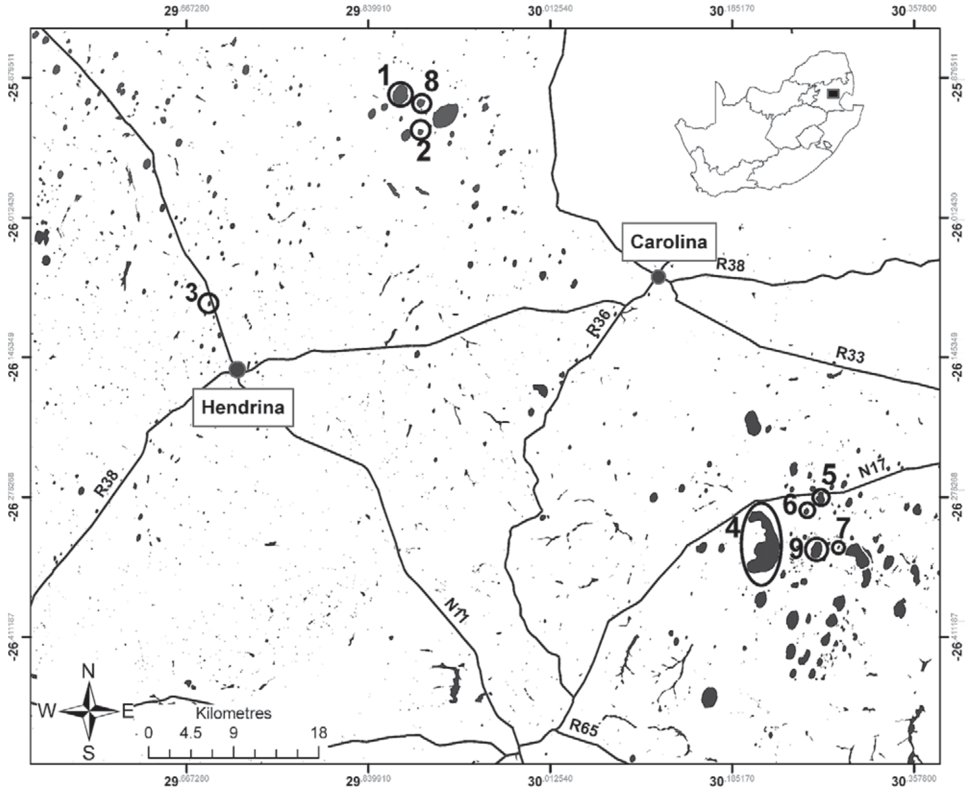

Fig. 1. Location of the various pans included in the study. Pans 1, 2 and 8 are influenced by mining activities, pan 3 by agricultural activities, and pans 4–7 and 9 are located in an area with few anthropogenic activities.

communities were sampled as well, using a plankton net of 60×60 cm with a 63 µm mesh size. In most cases, the pans were not deep enough to submerge the entire net and then the maximum depth to which the net could be submerged was noted. The plankton net was swept once through the water for a distance of 10–15 m, depending on the size of the pan. Benthic communities were sampled using a Petit Ponar grab (12.5×12.5×12.5 cm). The content of each grab was emptied into a bucket and a small amount of 10 % formalin was added to force invertebrates present to release their hold on any particulate matter. The bucket was filled with water and the mixture thoroughly stirred. The suspended matter was then decanted through a 63 µm mesh and the process repeated 5 times. The remainder of the sample was then transferred into a polyethylene (honey) jar. Additionally, submerged light traps (illuminated with a 6-inch cyalume dive stick) were left in the pans overnight (Jones & Grutter 2007). One sample from each biotope was fixed in 5 % neutrally buffered formalin in a polyethylene jar and stained by Rose Bengal. In the laboratory, invertebrates were removed and placed in 70 % ethanol. They were then identified to species level when possible (Day *et al.* 1999, 2001, 2002; Day & de Moor 2002; de Moor & Day 2002; de Moor *et al.* 2003*a*, *b*; Stals & de Moor 2007) and counted.

TABLE 1

List of aquatic invertebrate taxa recorded in the pans.

Crustacea: Anostraca

Branchinella sp.

Streptocephalus cafer (Loven, 1847)

Streptocephalus sp.

Crustacea: Cladocera

Alona sp.

Ceriodaphnia dubia Richard, 1895

Ceriodaphnia quandrangula (O.F. Müller, 1785)

Ceriodaphnia reticulata (Jurine, 1820)

Ceriodaphnia riguadi Richard, 1895

Daphnia barbata Weltner, 1897

Daphnia carinata King, 1853

Daphnia leavis Birge, 1874

Daphnia longispina O.F. Müller, 1785

Daphnia obtusta Kurz, 1874

Diaphanosoma excisum Sars, 1886

Eurycercus lamellatus (O.F. Müller, 1776)

Moina micrura Kurz, 1874

Simocephalus expinosus (Koch, 1842)

Crustacea: Conchostraca

Cyzicus sp.

Lepthestheria rubidgei (Baird, 1962)

Lynceus pachydactylus Barnard, 1929

Crustacea: Copepoda

Eucyclops sp.

Lovenula excellens Kiefer, 1929

Lovenula falcifera (Lovén, 1845)

Macrocyclops albidus (Jurine, 1820)

Metadiaptomus meridianus (van Douwe, 1912)

Metadiaptomus transvaalensis Methuen, 1919

Microcyclops sp.

Crustacea: Notostraca

Triops granarius (Lucas, 1864)

Crustacea: Ostracoda

Cyprideis sp.

Darwinula sp.

Gomphocythere obtusata Sars, 1910

Limnocythere sp.

Oncocypris sp.

Vestalenula sp.

Mollusca: Gastropoda

Afrogyrus sp.

Bulinus africanus (Krauss, 1848)

Bulinus natalensis (Küster, 1841)

Gyraulus connollyi Brown & van Eeden, 1969

Lymnea natalensis Krauss, 1848

Insecta: Coleoptera

Curculionidae

Cyrtobagous sp.

Dytiscidae

Dytiscidae larvae

Agabus sp.

Copelatus sp.

Cybister sp.

Hydrovatus sp.

Laccobius sp.

Methles sp.

Peschetius sp.

Philaccolus sp.

Philodytes sp.

Rhantus sp.

Gyrinidae

Aulonogyrus sp.

Haliplidae

Haliplus sp.

Hydrophilidae

Hydrophilidae larvae

Berosus sp.

Laccophilus sp.

TABLE 1 *(continued)*

List of aquatic invertebrate taxa recorded in the pans.

Hydrophilidae (continued)	**Insecta: Diptera (all larvae)**
Paracymus sp.	**Culicidae**
Noteridae	*Anopheles* sp.
Synchortus sp.	*Malaya* sp.
	Muscidae
Insecta: Ephemeroptera	**Chironomidae**
Baetidae	Chironominae
Cloeon sp.	
Caenidae	**Insecta: Trichoptera**
Caenis sp.	*Ecnomus thomasseti* Mosley, 1932
	Oecetis sp.
Insecta: Hemiptera	*Oxyethira* sp.
Belostomatidae	
Appasus sp.	**Insecta: Odonata**
Limnogeton sp.	*Aeshna* sp.
Corixidae	*Anax* sp.
Agraptocorixa sp.	*Ceragrion* sp.
Micronecta sp.	*Pantala* sp.
Sigara sp.	
Mesoveliidae	**Annelida: Oligochaeta**
Microvelia sp.	Oligochaeta
Naucoridae	**Annelida: Hirudinea**
Macrocoris sp.	*Batracobdelloides tricarinata* (Blanchard, 1987)
Nepidae	*Helobdella conifer* (Moore, 1933)
Ranatra sp.	*Helobdella stagnalis* (Linnaeus, 1758)
Notonectidae	
Anisops sp.	**Arachnida: Acari**
Notonecta sp.	**Pontarachnidae**
Nychia sp.	
Pleidae	
Plea piccanina Hutchinson, 1925	
Plea pullula Stål, 1855	

Biological traits

The traits of each of the identified taxa were determined by using relevant literature (Merritt & Cummins 1984; Barbour *et al.* 1995; Merritt *et al.* 2002). Pollution tolerance traits (Klemm *et al*. 2002) were calculated by taking into account the number of sensitive taxa (number of Ephemeroptera, Odonata and Trichoptera taxa). Traits based on taxon habit (Barbour *et al.* 1995) and Functional Feeding Groups (FFGs) (Merritt *et al.* 2002) were expressed both as richness of a given habit or FFGs (i.e. total number of taxa in a given habit or FFGs) and as richness of a given habit or FFGs relative to total assemblage richness (i.e. the proportion of total richness of a given habit or FFGs relative to overall taxa richness of the pan).

Spatial and temporal analysis

Similarities in the invertebrate communities and biological traits of each of the pans were assessed using a non-metric multidimensional scaling (NMDS) ordination in PRIMER version 6 (Clarke & Gorley 2006). Numerical counts of data were first log-transformed (log10(x+1)) to take account of the influence of large differences in abundances (Clarke & Gorley 2006). The data were used to calculate Bray-Curtis similarity coefficients for invertebrate diversity and abundances as well as biological traits of the pans. The data were then ordinated using NMDS analysis, employing 50 random restarts and a minimum stress of 0.01. Agglomerative cluster analysis based on the Bray-Curtis similarity coefficients was also calculated and the similarities at 40 % and 75 % were overlain on the ordination. Significant differences between pans were identified using the one-way ANOSIM procedure in PRIMER version 6. To determine which environmental variables were possibly responsible for the various groupings based on diversity and biological traits, a Redundancy Analysis (RDA) was completed using Canoco version 4.5. The RDA is a derivative of a Principle Component Analysis (PCA), with one additional feature. The values entered into the analysis are not the original data but the best-fit values estimated from a multiple linear regression between each variable in turn and a second matrix of environmental data. Thus, the PCA is constrained to optimize a fit to the environmental data so that this technique is the canonical version of PCA. The detailed water and sediment quality data that were used to construct the environmental matrix are not included but are provided in Ferreira (2010). Interpretation of RDA is through tri-plots (Shaw 2003). These tri-plots produce a map of the samples analysed on a 2-dimensional basis, where the placements of the samples reflect the (dis) similarities between the samples; in this case the sampling sites. Indices of diversity and evenness were also applied to describe the species abundance relationships among the invertebrate communities. These included the Shannon-Wiener diversity index (Shannon & Weaver 1963), Simpson's index (Simpson 1949), Margalef's species richness index (Margalef 1968) and Pielou's evenness index (Pielou 1971).

RESULTS

Invertebrate diversity

A total of 93 taxa belonging to 14 orders and 44 families were collected from the various pans during the two-year survey period (Table 1). The number of taxa is possibly even higher as many invertebrates could not be identified to species level. Pans 1 and 2 dried out completely during the first winter survey and pan 7 during the second winter survey. Pan 1 became dry for the first time in more than a decade (according to the local community). After the first subsequent rains, the invertebrate fauna in these particular pans consisted of many "typical" temporary pan invertebrates, including various large branchiopods like: Anostraca (Fairy shrimp), Conchostraca (Clam shrimp), and Notostraca (Tadpole shrimp). During the following survey, each of the same pans displayed typical succession patterns, with various predatory organisms dominating the community structure. Some of the other crustaceans that were abundant in all of the pans included the copepods *Lovenula falcifera*, *Metadiaptomus meridianus* and the cladoceran *Daphnia carinata*. The most common of the planktonic crustaceans that were encountered belonged to the order Cladocera. This included more than 13 taxa from four families. The most dominant groups of organisms sampled at all study sites were Hemiptera and Coleoptera. A total of 15 genera from the order Hemiptera were collected. Ten genera from the family Dytiscidae (order Coleoptera) were also recorded. Many of these genera were from pans 3 and 6. The genus *Cloeon* was the only representative of the mayfly families that occurred on a regular basis and the damselfly *Ceragrion*, also a member of the order Odonata, was often present as well.

Biological traits

A total of 32 traits were selected and compared between the various pans and seasons (Table 2). All the traits were expressed both as the number of taxa that display a specific trait and the percentage contribution of a trait to the overall assemblage. From the results, it became evident that during all the seasons most of the pans were dominated by crustaceans and insect taxa. Crustaceans made up 38 % (± 14) of the total assemblage in certain pans, with 18–47 % of these crustacean communities considered as zooplankton species. Insects comprised 51 % (± 13) of the overall assemblage. As mentioned above, most of these insects belonged to the orders Hemiptera and Coleoptera. As a result of the percentage contribution of these insects, the FFGs were dominated by predators (66 % ± 8). Because many of the crustaceans were zooplankton, filter feeders were the other dominant FFG observed in the pans. The majority of the taxa found were air breathers. Most of the invertebrates that were present in the pans were also free-swimming, with swimmers making up 68 % (± 13) of the community. In addition, clingers (18 % ± 9) made up a large proportion.

Spatial and temporal analysis

Results of the NMDS analysis indicate considerable variability between the different pans and sites in respect of taxon diversity. The ordination (Fig. 2) shows that at a similarity of 40 % (based on agglomerative cluster analysis), few pans have similar invertebrate community structures. When the similarity is set at 75 %, nearly every pan has a unique faunal composition with one way ANOSIM analysis revealing that the differences in assemblages are significant ($p<0.05$) for pans 1, 2, 5 and 7 (Global $R=0.263$). Results of the NMDS analysis based on the traits also show (Fig. 3) that the pans have significantly different assemblages (Global $R=0.227$). However, when the agglomerative cluster analysis is overlain, all the pans are similar at 40 % similarity. Even when the similarity is increased to 75 %, nearly all the pans are still similar, apart from pans 6 and 7 during the winter and autumn surveys of 2008. One way ANOSIM indicated that there were no differences in traits between the pans with the exception of pans 1 and 2, 1 and 5, 2 and 7, and 2 and 9, all of which were all significantly different ($p<0.05$).

Results of the of the Shannon diversity index (Fig. 4) indicate a loss in diversity at pan 1 when compared to pan 5, which was similar in physical habitat and trophic state. Results for Simpson's index were also lower at pan 1 as compared to the other pans. Results of Margalef's species richness index show higher species richness at pans 3, 4 and 6 in comparison with the other pans. Pielou's evenness index reflected a lack in

TABLE 2

List of biological traits that were included during the study (adapted from Blocksom *et al.* 2002; Solomini *et al.* 2008). Traits were expressed both as total number within the community and the percentage contribution to the overall community structure.

Abundances	**Functional Feeding Groups**
Number of taxa (families/orders included)	Collectors
Number of individuals	Scrapers
Mean number of individuals	Shredders
Crustacea	Predators
Mollusca	**Habits**
ETO (Ephemeroptera, Trichoptera, Odonata)	Burrowers
Ephemeroptera	Skaters
Trichoptera	Clingers
Odonata	Climbers
Non-insects (excluding crustaceans and molluscs)	Sprawlers
Non-insects	Swimmers
Insects	Swimmers (excluding zooplankton)
Oligochaeta	Flyers
Coleoptera (larvae and adults)	**Breathing Mechanisms**
Diptera (excluding Chironomidae)	Air breathers
Diptera (including Chironimidae)	Gills
Zooplankton	Other

evenness at pans 1–3 and 8. The RDA tri-plot based on diversity (Fig. 5) indicates that pan 3 appears to separate from the other pans in the study area because of a different community structure. Whereas the community structures of most of the pans consist mainly of crustaceans, the invertebrate fauna at pan 3 is made up of aquatic insects (including many Hemiptera, Ephemeroptera and Odonata). From the RDA, it appears that conductivity at pan 3 is one of the main physico-chemical variables responsible for the different community structures. The taxa that are responsible for the grouping include *Plea piccanina*, *Plea pullula*, and *Gomphocythere obtusata*. Many of the mayfly *Cloeon* sp. and the damselfly *Ceragrion* sp. were sampled in high abundances at this pan on a regular basis along with Diptera like *Anopheles* sp., *Malaya* sp., and individuals from the family Chironomidae. Pan 6 appeared to be different from the other pans in the study area as many of the taxa that were sampled occurred only in this pan and are invertebrates that are typically found in fresh water (with low salinity). These included various molluscs (*Afrogyrus* sp., *Bulinus africanus*, *Bulinus natalensis*, *Gyraulus connollyi*, and *Lymnaea natalensis*), the Trichoptera (*Oxyethira*) and larvae of Hydrophilidae. In the tri-plot based on the various biological traits (Fig. 6), it can be seen that on the first axis there is a separation of pan 3 and pan 6 from some of the study sites during some of the surveys. These sites include all the sampling sites apart from pans 8 and 9. The dissimilarity between pan 3 and pan 6 is brought about by the higher percentage of

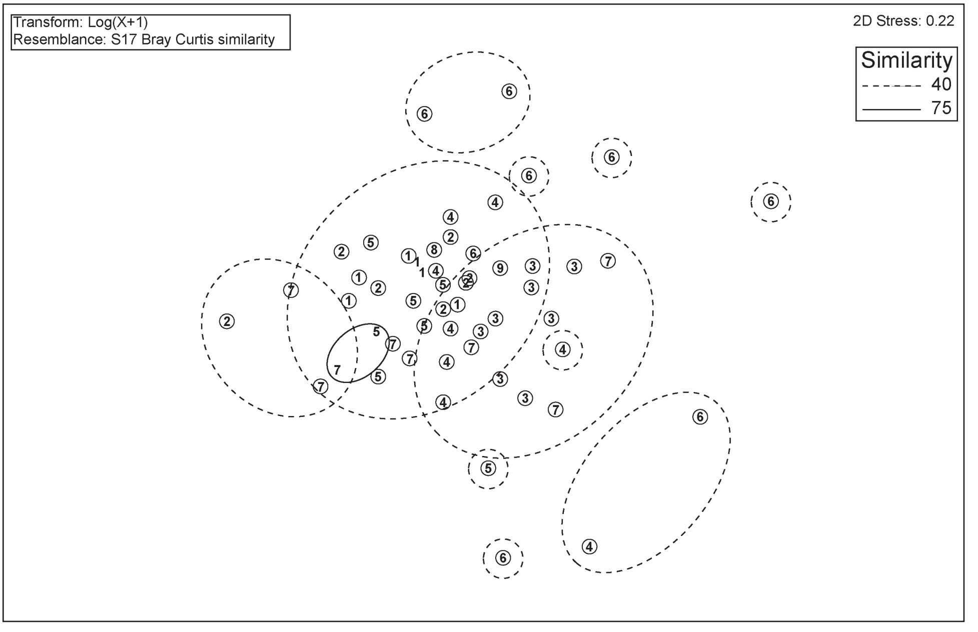

Fig. 2. MDS ordination of the invertebrate communities (diversity) of the selected pans with similarities based on agglomerative cluster analysis overlain. Numbers 1–9 represent the different pans, while repeated numbers represent the various sampling occasions.

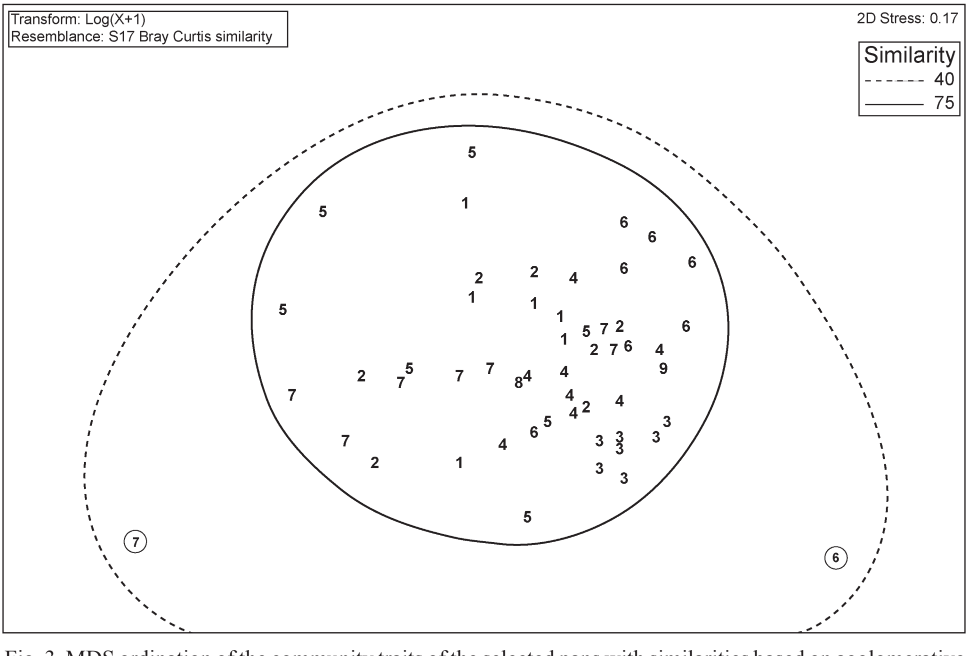

Fig. 3. MDS ordination of the community traits of the selected pans with similarities based on agglomerative cluster analysis overlain. Numbers 1–9 represent the different pans, while repeated numbers represent the various sampling occasions.

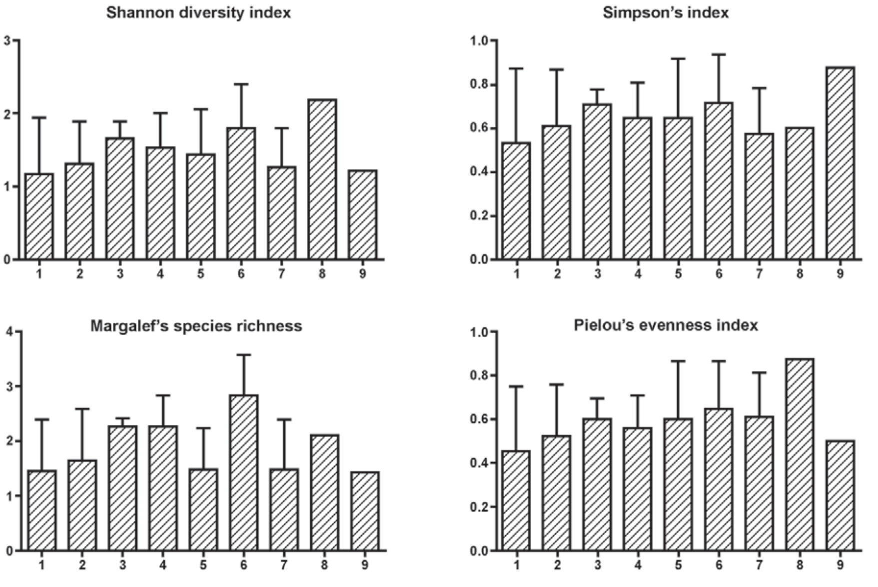

Fig. 4. Mean and standard deviation of the Shannon diversity index, Simpson's index, Margalef's species richness index, and Pielou's evenness index for each of the pans. The mean was obtained from the results of the various sampling surveys and as a result, the standard deviation indicates seasonal variation.

molluscs and clingers and a higher number of scrapers at pan 6. The dissimilarity of pan 3 is largely a result of a higher percentage of Diptera (including Chironomidae) at this site. There is marked similarity between the various sampling surveys of pan 3, indicating limited seasonal variation in the invertebrate community at this site.

DISCUSSION

Invertebrate diversity

Many of the taxa collected during the current study are comparable at a generic level with those in the results of Meintjies (1996). There are also similarities in respect of branchiopods between the Mpumalanga pans and turbid clay pans in Australia (Hancock & Timms 2002), ponds in Oxfordshire (UK) (Collinson *et al.* 1995), and saline lakes in Africa (Hutchinson *et al.* 1932; Rzóska 1961; Weir 1969; Williams 1985; Seaman *et al.* 1991; Meintjies 1996). Studies on clay pans in arid Australia, ponds in the UK, and African saline lakes likewise revealed many Coleoptera, Diptera, Trichoptera and Crustacea that are represented in the perennial pans of Mpumalanga at a generic and even species level (Seaman *et al.* 1991; Collinson *et al.* 1995; Hancock & Timms 2002). The invertebrate communities of the perennial pans of Mpumalanga can be regarded as containing typical ephemeral and/or perennial fauna depending on the levels and duration of desiccation or inundation (hydroperiod). These drying out and rainfall patterns are also major drivers of succession. In pans 1, 2 and 7, succession was in the form of a 'typical' pattern also observed by Hancock and Timms (2002). After the first seasonal inundation, characteristic ephemeral pan invertebrates such as branchiopods became dominant (Ferreira *et al.* 2011). These taxa were later replaced by

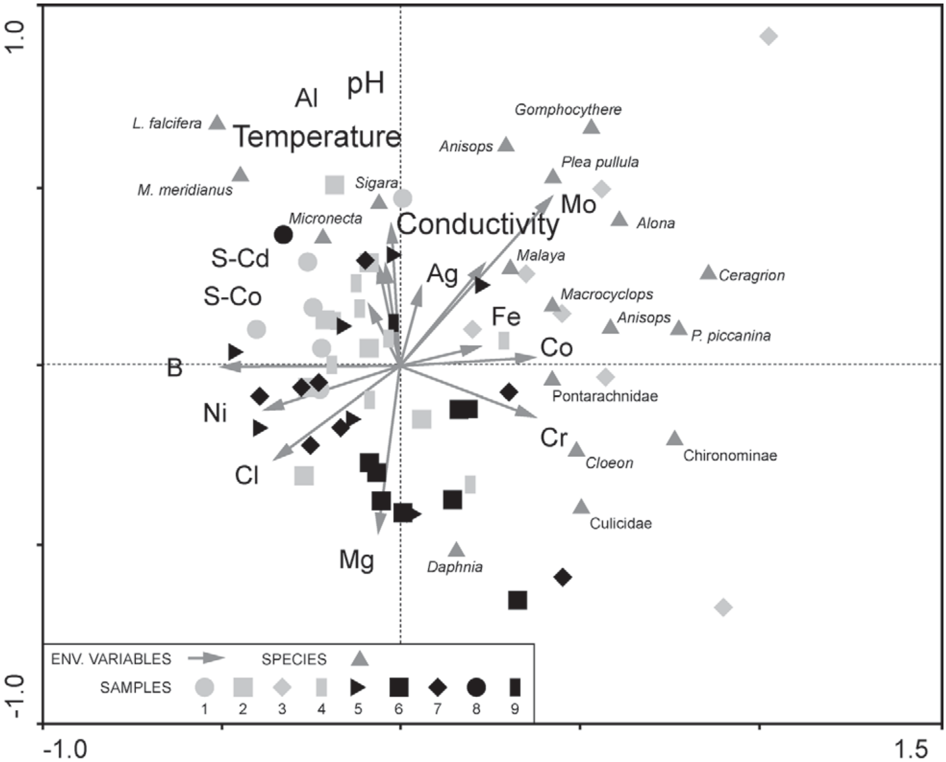

Fig. 5. RDA tri-plot illustrating the similarities between the various sites (and surveys) and the physico-chemical variables. The tri-plot describes 45.3 % of the variation, with 22.3 % being described on the first axis and 23 % on the second axis. Only the taxa of which more than 10 % is explained by the model and the 15 most significant environmental variables are visualised.

stable zooplankton communities and many predators from the families Corixidae and Notonectidae. The branchiopod taxa that were found during the study (Table 1) have become suited to temporary environments through various physiological, behavioural, life-history and structural adaptations (De Roeck *et al.* 2007). These organisms survive periods of desiccation by producing resting eggs (Brendonck *et al.* 1998). The eggs then hatch in response to environmental cues such as rain after prolonged desiccation. Due to the ephemeral nature of most pans, development to adult stages is usually rapid and mortality, because of insufficient nutrition, is high (Williams 1985; Hamer & Appleton 1991). Most of the branchiopod taxa sampled during the study are usually allopatric (i.e. do not normally occur together). The reason is that their eggs are dependent on different environmental conditions for hatching (Thiery 1991). However, Thiery (1991) found that when conditions are favourable, not only will different taxa from one order co-occur, but taxa from different orders may be found in the same system. Studies have shown that these conditions are often present in the deeper ephemeral ecosystems (Thiery 1991), of which perennial pans in Mpumalanga are an excellent example. In these systems, the rainy period is long enough to allow all the various groups to complete their life-cycles, not only those taxa with a rapid life-cycle. Apart from the branchiopod crustaceans, many of the crustaceans were free-swimming zooplankton taxa. The pre-

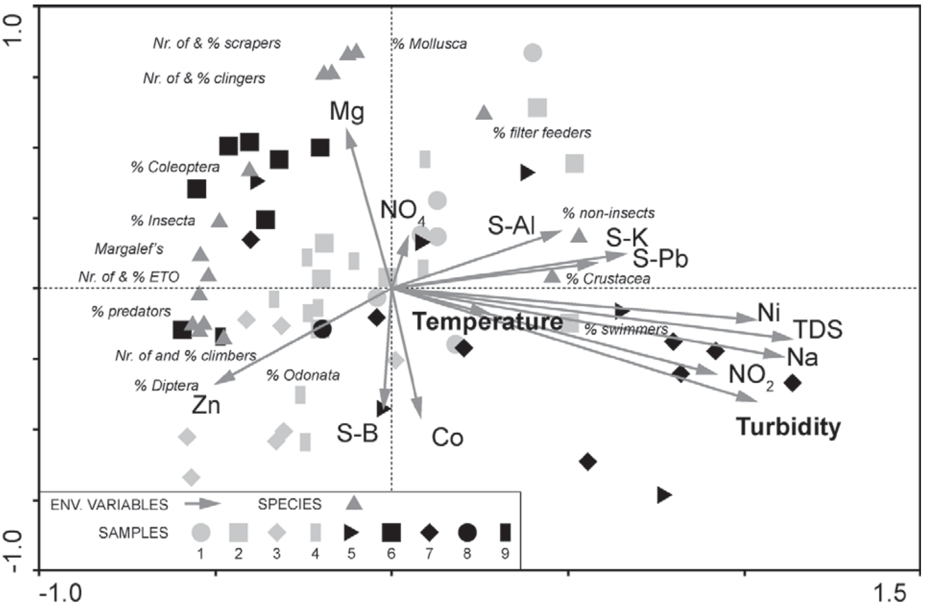

Fig. 6. RDA plot showing the similarity among sites during the different seasons, based on the various community traits (metrics) with physico-chemical variables superimposed. This tri-plot describes 56.2 % of the variation in the data, where 38.6 % is displayed on the first axis and 17.6 % on the second axis. Only metrics of which more than 31 % is explained by the model and the 14 most significant variables are visualised.

sence of *Lovenula falcifera* and *Metadiaptomus meridianus* was expected as they are known to co-occur; and together with *Daphnia carinata*. Both the former taxa have a cosmopolitan distribution (Seaman *et al*. 1999; Rayner 2001). Apart from the many crustaceans, the community structure was often dominated by Hemiptera. Individuals from the genus *Anisops*, *Micronecta*, *Sigara*, *Agraptocorixa* and *Notonecta* were all encountered during the two-year period and have often been found in similar aquatic environments around the world (Seaman *et al.* 1991; Collinson *et al.* 1995; Meintjies 1996; Hancock & Timms 2002; Wissinger *et al*. 2009). The occurrence of the recorded mayfly genus in pan environments is also not unusual. *Cloeon* species are known to be tolerant to salinity changes and are able to survive anoxic conditions (Forbes & Allanson 1970; Nagell 1977; Nagell & Fagerstrom 1978; Hassel *et al.* 2006).

There were large differences in assemblages on a spatial and temporal level. Pan ecosystems are dynamic, with a variety of factors contributing to the invertebrate community structure. Apart from physical variations (habitat, temperature, hydroperiod, etc.) it appears that chemical variations in the form of different trophic states also have a major influence on the community structure within perennial pans. Most of the pans in Mpumalanga province can be separated as being alkaline dystrophic or saline eutrophic. According to Hutchinson *et al.* (1932) alkaline dystrophic waters are shallow and are formed by wind erosion; are often dark (grey or brown) with very little light penetration; the pH is usually above 8; they are rich in suspended organic material from allochthonous origin; and support very few organisms. Saline eutrophic waters are also shallow and occupy basins close to estuaries or those that have been formed by wind erosion. The water is turbid, with little light penetration and the pH is above 7. The water is rich in organic material of both allochthonous and autochthonous origin. These lakes often support a variety of plants and animals in large numbers (Hutchinson *et al.* 1932). Based on the physico-chemical characteristics (Ferreira 2010), pans 1–3, 5, and 7–9 can all be classified as being alkaline dystrophic. Pan 4 is regarded as being saline eutrophic, while pan 6 is considered to be a normal eutrophic system.

It is difficult to distinguish between variations in diversity caused by human impacts or natural changes.

Biological traits

Based on the diversity observed, the dominance of predatory insects and crustaceans within the species assemblages was expected. Although many of the traits used in the current study have also been included in similar studies (Blocksom *et al.* 2002; Solomini *et al.* 2008), the most commonly used of the biological traits still remains the different FFGs. The reason for this is that FFGs emphasise the various linkages between food source and the ability of a specific invertebrate group to use this resource. The FFG approach is thus more directly related to ecosystem processes than the taxonomic approach (Statzner *et al*. 2001, 2007; Yoshimura *et al*. 2006). Functional Feeding Groups refer to different feeding mechanisms and not specifically to the food being eaten (Cummins & Klug 1979). Therefore, changes in food sources can lead to a change in the feeding strategy that is being applied. Changes in food sources are often brought about by human activities and the FFG approach can thus be used to assess impacts on a given ecosystem (Solomini *et al.* 2008). The numerically dominant FFG throughout this study was the predators. In a system where predators dominate, the system is known as a top down control system (Merrit *et al.* 2002). Predators can be expected to dominate in pans in which there are normal successional patterns (Meintjies 1996; Hancock & Timms 2002). Filter feeders were also abundant at all of the sampling sites. This is perhaps to be expected because of the abundance of zooplankton taxa in these ecosystems.

A change in community composition caused by a loss of predators may thus be a good indicator of health in pans, although the phase in succession should also be considered. This is because many predators, which occur in the pans, are able to fly and should conditions become unfavourable for a specific organism, it can simply avoid the adverse environment by flying away (Hutchinson 1981). It is important to note that in most ecosystems, predators are usually less abundant than their prey (Stazner *et al.* 2007), yet in pans they appear to be the dominant FFG. The fact that there were so few representatives of the other FFGs in the pans is not unusual. Shredders, for example, may occur in different abundances in a system depending on the diversity and quality of vegetation sources (Zilli *et al.* 2008). Furthermore, the presence of inorganic nutrients and sunlight can stimulate the growth of periphyton, which serves as a food source for shredders and scrapers (Rezanka & Hershey 2003). Although the reduction in the number of scrapers and shredders can in most ecosystems be a sign of environmental stress, these groups simply do not occur in high numbers in perennial pans due to a lack of suitable habitat and food sources. Only in those pans where suitable conditions were present did representatives of these groups occur. Because individual FFGs react differently to human impacts (Yoshimura *et al*. 2006), ratios between various FFGs have been suggested as possible indicators of ecological integrity (Merrit *et al*. 2002).

Very few of the other FFGs (like scrapers and shredders) were present during the different sampling surveys. It is clear that the presence of certain FFGs is driven by the availability of food sources and quality of the biotope, and more research needs to be completed if FFGs and the ratios between the different FFGs are to be successfully used in assessing the quality and status of perennial pan ecosystems. This complicates the use of FFGs in determining, in the present study, the impacts of the mining and agricultural activities. Moreover, it became apparent that the biological traits reflected the available biotopes and not necessarily the impacts of human activities. The habitat available to the various invertebrates can thus be seen as one of the most important driving variables of biological traits displayed by the community (Lamouroux *et al*. 2004). This explains the occurrence of so many free-swimming and air-breathing taxa, with a lack of aquatic macrophytes in these systems also contributing to the absence of certain traits (Brainwood & Burgin 2006).

Spatial and temporal analysis

A functional approach is relatively independent of factors like natural variation in diversity due to seasonal and geographical patterns (Beketov *et al.* 2009), and often smaller variations are observed when studies are based on a functional approach (Brainwood & Burgin 2006). This was the case in the current study as well. It is evident from Figs 2 and 3 that the diversity within these systems varies naturally, with less variation being apparent when analysis is based on biological traits. The reason for this is that a biological trait can be expressed within a community by more than one taxon. These biological traits are thus not dependent on a single taxon. Several studies found that the use of a large variety of biological traits is more reliable than community structure in detecting pollution (Varandas & Cortes 2010). Biological traits have often been used to determine the ecological integrity of aquatic ecosystems, especially because, unlike taxonomic composition, traits are relatively stable across large environmental gradients (Varandas & Cortes 2010). With there being less variation in respect of these biological traits, this approach may be considered a better tool to use in ecological integrity assessments of perennial pans than diversity of the invertebrate communities. Taxonomic and functional approaches are often seen as being complementary (Brucet *et al.* 2005; Ruhi *et al.* 2009), but the taxonomic approach appears to be unreliable when studying the invertebrate communities of perennial pans and the changes in these communities caused by anthropogenic impacts. During the present study, no separation could be made between natural and impaired pans on the basis of all the biological traits. The application of traits as a monitoring tool may only be possible if a specific set of traits is compared between systems. These traits will have to be empirically proven and theoretically responsive (Jessup *et al.* 2005; Solomini *et al.* 2008) and further research is necessary.

The Shannon diversity index (Shannon & Weaver 1963) incorporates both the species richness and equitability components and has long been used as an index of diversity together with the Simpson index (Simpson 1949), which is an index of concentration or dominance. Simpson's index measures the probability that two individuals selected at random from a sample will belong to the same species. The results for both these indices show that there have been definite changes in the invertebrate community at pan 1. As pan 1 is situated next to where coal mining takes place, it is clear that these activities are influencing the diversity within the pan. Pan 8 is also situated adjacent to these mining activities, yet the Shannon diversity index and Simpson's index did not indicate a change in diversity. It should be noted that a very low number of taxa was sampled at this site and as diversity indices take into account species richness (number of taxa) and evenness (number of individuals per taxa) (Hill 1973), the lower abundances clearly had an influence on the results for this site. Margalef's species richness index (Margalef 1968) measures the number of individuals present for a given number of species, incorporating both the total number of species and the total number of individuals. Results for this index indicate that pans near mining activities (pans 1, 2 and 8) and pans considered as relative reference pans (pans 5, 7 and 9) had a similar species richness. Pielou's evenness index (Pielou 1971) is an indication of how the individuals in a sample are distributed over the various species that make up a community and gives an indication of dominance. It became evident that the invertebrate community structure might become altered as a result of the mining and agricultural activities at the representative sites (Fig. 4). A lack of evenness is often considered a sign of dominance within a given biotic community. The community at pan 1 was dominated by zooplankton and oligochaetes, while zooplankton (*Lovenula falcifera*, *Metadiaptomus meridianus* and *Daphnia carinata*) dominated at pans 2 and 9. The invertebrate community at pan 3 (in the vicinity of agricultural activity) showed several alterations, with *Gomphocythere obtusata*, *Lovenula falcifera* and *Plea piccanina* dominating the community structure. Dominance is often seen as a sign of pollution, although zooplankton communities are expected to dominate in a perennial pan environment.

The results of the RDA based on both the diversity and the biological traits indicate that there is little difference in the community structure between the pans that are located next to mining activities and the reference pans. It is evident, however, that pans 3 and 6 differ from the other pans. It was expected that the community structure at pan 6 would be different as this is a reed pan. The reed pans are more perennial compared to other pans surveyed in the study and consequently the conductivity is generally lower. The habitat is dominated by *Phragmites australis* and various submerged macrophytes. The changes in the diversity and biological traits displayed by the taxa in pan 3 appeared to be the result of a change in habitat. Apart from pans 3 and 6, vegetation was confined to the margins of the pans. At pan 3, there was a large abundance of clingers and shredders, brought about by the presence of a suitable substrate and food source in the form of the fennel-leaved pondweed (*Potamogeton pectinatus*). This weed often covered large sections of the pan. The occurrence of many of these taxa (*Cloeon* sp. and *Plea* sp.) may thus be related to the presence of aquatic macrophytes as a habitat in an ecosystem where vegetation is usually restricted. The change in habitat may be a direct result of anthropogenic inputs from the agricultural activities. This includes eutrophication and a change in substrate caused by siltation.

CONCLUSION

The study revealed a large degree of variation when the invertebrate communities of different pans were compared taxonomically (regardless of the land use surrounding the pan). The variation is so large that the faunal composition of each pan can be considered unique on a spatial and temporal scale. This can make distinguishing between natural and impaired pans extremely difficult. Comparison of the communities based on biological traits showed small variations, with more than a 75 % similarity in the assemblages of the pans. The biological traits of the invertebrate communities of perennial pans could thus potentially be considered a better means of assessing land use-related impacts and in the future should receive consideration as a tool for the management of these ecosystems.

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